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Original Article

Supplementation of probiotics in Nile tilapia fingerling cultivation subjected to microbial challenge

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Abstract

The intensification of aquaculture has brought about the need to find alternative feed supplement sources to reduce production costs. One of the alternative sources of feed in fish farming is animal manure. However, the use of animal manure may cause health problems in fish cultures. The objective of this study was to determine the effects of probiotics on *Nile tilapia* fingerlings subjected to microbial challenge using swine manure. Three hundred (300) fingerlings weighing 2±0.05g and measuring 5±0.06 cm, were distributed among four treatments with three replications each. Swine manure was inoculated in water in the proportion of 10 % of fingerlings live weight. Probiotics *Saccharomyces cerevisiae* and *Lactobacillus plantarum* were used as ration supplements in the proportions of 0.5 % per 100 g of ration. The results showed no significant differences (P>0.05) in terms of growth between treatments. The inclusion of *S. cerevisiae* reduced the number of pathogenic bacteria in the intestine of fingerlings and resulted in better production performance. Feed supplementation with *L. plantarum* had no effect, neither on production, nor on intestinal microbial population. The fingerlings under study showed typical signs of yersiniosis, edwardiellosis and mycobacteriosis. From the experiment it was concluded that the supplementation of the probiotic *S. cerevisiae* on the Nile tilapia fingerlings treated with swine manure showed a positive effect in the sense that this probiotic avoided the intestinal colonization of fingerlings by pathogenic bacteria. Additionally, the presence of the probiotic seems to promote better grow performance and hence reinforce the results of previous studies on the role of probiotics in aquaculture. More experimental studies are required, particularly *in situ* experiments, with the addition of other performance analyses linked to the immune response of the fingerlings.

Keywords: aquaculture, fish farming diseases, *Oreochromis niloticus*, probiotics

Introduction

Aquaculture is an agricultural system for the production of aquatic organisms, which has been expanding globally with the increase of human populations and urbanization. It is estimated that aquaculture production will double by 2030 in order to meet the demand for fish (Subasinghe, 2015). In Mozambique fish farming began in the 1950s, with the goal of producing food rich in animal protein to help improve diets and the quality of life for rural communities (INAQUA, 2012). Nationally, fish farming has developed at an industrial and small scale. Aquaculture production of 5,517 tons was expected in 2019, of which 3,770 were reached, against 3,245 tons produced in 2018 (Ministério do Mar, Águas Interiores e Pesca, 2020).

The expansion of fish farming resulted in increasing demands for fish ration and its main ingredient, fish meal, which is seldom available and expensive. Fish meal limitations in turn leads to the need for alternative sources of good nutritional quality feed, which would enable fish farmers to improve production, and maintain the integrity of the ecosystems (Boscolo *et al.*, 2005; Castellani and Abimorad, 2012).

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Integrated fish farming encompasses a combination of fish culture with agricultural systems (Mishra, 2010), an excellent alternative for overcoming ration deficits in fish farming (Castellani and Abimorad, 2012). In such integrated systems, swine manure is used as fertilizer in fish tanks to promote the growth of photosynthetic microorganisms, or it can be fed directly to fish (Dang *et al.*, 2011). The use of swine manure as fertilizer involves some risks due to the accumulation of organic matter in fish tanks, which stimulates the growth of pathogenic bacteria which can cause illnesses in cultivated organisms (Hilbrands and Yzerman, 2004).

A viable alternative for preventing the occurrence of illnesses in fish farming could be the use of probiotics, which when administered in the proper amounts, provide health benefits for the host organisms by improving the balance of their intestinal flora (Azevedo and Braga, 2012). Although evidence already exists that probiotics play an important role in aquaculture, the present study sought to further explore the subject to obtain a better understanding, using Nile tilapia (*Oreochromis niloticus*) fingerlings grown in closed systems in Mozambique. Specifically, the objective of the study was to assess the effects of probiotic supplements on Nile Tilapia fingerlings subjected to microbial challenge using swine manure.

Material and methods

Nile tilapia fingerlings

Sex reversed Nile tilapia fingerlings were obtained from Aquacultura Chibaha Ltd, a company located in the district of Vilankulo, Inhambane Province, Mozambique, weighing an average 2 ±0.05 g and measuring 5 ±0.06 cm. The fingerlings were transported in 50-liter transparent plastic bags with approximately 5 L of water and 15 L of dissolved oxygen, at a density of 250 g of fish per 5 L of water. Once in the laboratory, the fingerlings were placed inside aquaria for 15 minutes, while still in plastic bags, to equilibrate the temperatures before their release.

Analysis of the microbial composition in swine manure

Swine manure was collected weekly at the Agrarian Institute of Umbeluzi, located in the district of Boane, Maputo Province, Mozambique. A sterilized spatula was used for collection, and the collected manure was placed in a tightly closed container and transported in 4 °C temperature. The manure was kept in the laboratory for one week, after which the remaining manure was discarded and substituted with fresh manure to avoid reduction of quality during storage (Hilbrands and Yzerman, 2004).

The presence of pathogenic bacteria in swine manure was determined from 10^{-1} to 10^{-6} dilutions of 1 g swine manure in 0.1 % peptone water. From each of the dilutions, 1 ml was drawn and double inoculated in Agar Lowenstein-Jensen and Agar MacConkey. One-half of each dilution was incubated at 37°C by 48 hours in the Agar Lowenstein-Jensen culture and the other half for 24 hours in Agar MacConkey culture. Following the incubation period, the presence of pathogenic enterobacteria in samples of swine manure was determined, using the Gram method. In order to determine the presence of Mycobacteria in the manure, 12 samples were sent to the microbiology laboratory at the Central Hospital of Maputo for analysis, based on the Ziehl-Neelsen test.

Experimental design

The experiment was carried out for a period of 90 days, from May to July, at the Ecology Laboratory in the Department of Biological Sciences, Faculty of Sciences of the Eduardo Mondlane University in Maputo. The climate in Maputo is humid subtropical, with a cool dry (winter) season from April to October, and a warm wet (summer) season for the rest of the year (Gomes *et al.*, 2014; Macamo *et al.*, 2015). During summer the average temperature is around 30-31 °C in January and in the winter season the average temperature is about 25-26 °C during the months of July and August (Gomes *et al.*, 2014). Agriculture and fisheries are two of the most important economic activities in Maputo and its satellite cities (Macamo *et al.*, 2015).

The experimental design was a complete randomized design with four treatments with three replicates. The fingerlings were distributed among 12 aquaria of 50 litres each at 25 fingerlings per aquarium. In aquaria designated for the control treatments (C), fingerlings were fed commercial fish rations without probiotics and swine manure. Treatment (T1) consisted of treating the fingerlings with swine manure and feed ration without probiotic supplements. For treatment (T2) the fingerlings were treated with swine manure and a ration supplemented with the probiotic *Saccharomyces cerevisiae,* while treatment (T3) consisted of treating fingerlings with a combination of swine manure and a ration supplemented with the probiotic *Lactobacillus plantarum.*

The aquaria were equipped with an aeration system composed of micropores linked by silicone hoses connected to an air pump. Water replacement was carried out daily at a rate of 50 % in the mornings by means of a siphon to remove faeces and the remainder of rations. Water quality was assessed through daily measurements of temperature and the dissolved oxygen in the mornings (8:00 hrs) and in the afternoons (16:00 hrs), with a PCE-PHD 1 measurement device. The pH was measured once a day (at 16:00 hours) using a pH meter (HI 9025 Microcomputer, HANNA Instruments) and the electric conductivity was determined weekly, in the mornings before siphoning, with a conductivity measuring device (524 S/N 4289 CRISON). Sodium thiosulfate was applied to the aquaria in the proportion of one drop for every litre of water, immediately after water was replaced (Meurer *et al.*, 2006) to neutralize the effect of chlorine present in the water.

The application of swine manure to treatments 1, 2 and 3 was done in the morning soon after syphoning in the proportion of 10 % of the live weight of the fingerlings adjusted biweekly in accordance with the determined weights of the fingerlings. Swine manure was diluted in 100 ml of distilled water and then sterilized to inoculate the aquaria (Meurer *et al.*, 2006).

The probiotic *S. cerevisiae* containing about $3.2*10^{10}$ live microorganisms for each gram of the product was obtained from the Mozambican brewery (2M), located in the city of Maputo, Mozambique. This probiotic was added to treatment 2 at the proportion of 0.5 g per 100 g of ration. The number of yeasts per gram of the product as well as of ration were analysed by counting in plates with 1 ml of the dilutions from 10^{-1} to 10^{-3}. The selective culture medium *Yeast Growth Cloramphenicol* (YGC) was used for yeast.

The probiotic *L. plantarum*, containing about $1.8*10^{10}$ live microorganisms per gram of the product was obtained from the ProLab laboratories. This probiotic was added in the proportion of 0.5 g per 100 g of ration. Dilutions 10^{-1} to 10^{-3} in peptone water 0.1 % solution were made for the quantification of acid-lactic bacterium per gram of the product and of the ration. One (1) ml of each dilution was incubated in anaerobic conditions in *Man Rugoso and Sharp* (MRS) culture medium in the microbiology laboratory of the Central Hospital in Maputo.

Determination of the microbial composition in fingerlings supplemented with probiotics following microbial challenge

In order to determine the presence of pathogenic bacteria in the water of the experimental aquaria, three (3) ml of aquarium water was sampled in the morning, at the beginning of the experiment before siphoning and inoculated in duplicate samples of Agar MacConkey, Agar Lowenstein-Jensen and YGC e MRS medium. To determine the extent of intestinal colonization by the swine manure bacteria as well as the ration supplemented with probiotics, six fingerlings were collected from each treatment after a 24-hour fast and sacrificed by decapitation. After local disinfection with a sterile gauze soaked in 70 % alcohol, the intestine was removed and transferred to sterilized Petri dishes. The intestine was then triturated while still fresh and placed in previously sterilized test tubes, diluted in 2 ml of distilled water and then homogenized in a vortex for 1 min. Following the homogenization, decimal dilutions were made from 10^{-1} to 10^{-3} in sterile distilled water. One (1) ml of each dilution was drawn and inoculated in duplicate, in plates containing the above-mentioned culture media for counting of the colony-building units.

Determination of growth and survival

Growth was determined by measuring the length of 300 fingerlings under study at the beginning and at the end of the experiment, using the formulae of Pooramini *et al.*, (2009, 2014):

Weight gain = average final fish weight – average initial fish weight (1)

% Weight gain = [(average final weight – average initial weight)]/average initial weight (2)

Specific growth rate = [(lnWf – lnWi)]/(t2-t) (3)
Where: lnWf = ln for the average final fish weight;
lnWi= ln for the average initial fish weight;
(t2-t1) = duration of the experiment in days.

Condition Factor (CF) = [(W/L)*100] (4)
Where W = fresh fish weight;
L = length of fish (cm).

Apparent Feed Conversion Rate (AFC) = [F/ (Wf–Wi) (5)
Where F= Feed provided (g);
Wf = average final fish weight;
Wi = average initial fish weight.

Furthermore, the determination of survival was carried out using the formula of Koch *et al.*, (2015):

Survival = [(Nf/Ni)]*100 (6)
Where: Nf – number of fish at the end of the experiment;
Ni = number of fish at the start of the experiment.

Observation of clinical signs of the *O. niloticus* fingerlings

In order to determine the clinical signs in fish, 15 fingerlings from each treatment were captured every 15 days and observed for possible signs of illnesses (Ostrensky and Boeger, 1998). Essentially, the fingerlings were assessed for the presence or absence of typical signs of yersinioses, edwardsioloses and of micobacterioses, including mutilated fins, absence of scales, dark pigmentation of the skin, reddish-coloured gills, puffy and opaque eyes, with signs of haemorrhages around the eye and/or on the body skin. At the end of the experiment six fingerlings were sacrificed in each treatment for observation of internal signs including dark gall bladders and empty intestine (Kubitza, 2005).

Data analysis

Collected data were subjected to the Shapiro-Wilk test for normality, and the Leven test for the homogeneity of variances. Mean comparisons were based on one-way ANOVA, for the variables with normal distribution and homogeneous variances (weight gain, % weight gain, specific growth rate, and apparent feed conversion rate). For the variables which did not show normal distribution (condition factor and survival), the Kruskal-Wallis test was used. As for data on colony-building units from which significant differences were observed, the Tukey and Newman-Keuls tests were used for variables with normal distribution and those without normal distribution, respectively.

Results and discussion

Water quality

The results of the analyses of water quality parameters observed in the aquaria used in this experiment were as follows: water temperature in the morning and in the afternoon 21.5 ±0.01 °C, and 22.3 ±0.01 °C respectively; dissolved oxygen in the morning and in the afternoon 7.1 ±0.05 mg/l, and 6.8 ± 0.04 mg/l respectively; pH 8 ± 0.01; and conductivity 99.9 ±0.23µS/cm. Statistical analyses showed no significant differences among the treatments ($P>0.05$). The results from this study were in line with the observations of Meurer *et al.* (2006) and Hortmam *et al.* (2014). The experiments were carried out within the established guidelines for good species performance, except for the variable temperature, which was a few degrees below the recommended level. Previous studies with *O. niloticus* culture reported ideal parameters to range between 6.5 to 9 for pH; 25 to 35 °C for water temperature; dissolved oxygen concentration above 5.0 mg/L and water conductivity of 96µS/cm (Hilbrands and Yzerman, 2004; Meurer *et al.*, 2008; Dias *et al.*, 2011). The low temperatures observed in the present study are reflective of seasonal weather patterns in the city of Maputo in May to July which corresponds to the cold season with temperatures averaging 20.0±1.0 °C.

Microbial population in swine manure

Non-lactose fermented enterobacteria to the value of $7.1*10^6$ UFC and *Mycobacteria* spp to the value of $1.2*10^5$ UFC were identified as microbial challenges from the swine manure utilised for the present study. The values obtained correspond to those by Bona *et al.* (2013) when they isolated the microbial flora of anaerobic treatment systems of swine manure inoculants and found a $8.0*10^6$ UFC enterobacteria composition. These values confirm the findings of Ziemer *et al.* (2008), which from his studies with swine manure observed that the fresh swine manure usually contains 10^{10} bacterial cells per gram. The pathogenic bacterium found in swine manure in the present study were also reported by Ziemer *et al.* (2008), from a study which showed that swine manure contains pathogenic bacterium which include *Mycobacterium spp, Yersinia spp, Eschericia coli, Brucella spp, Listeria monocytogenes, Bacillus anthracis, Leptospira spp, Clamydia spp and Campylobacter spp.*

Amount of probiotics

The microorganisms used as probiotics in this study accounted for 100 g of ration, $1.6*10^5$ UFC of *S. cerevisiae* and $9*10^4$ UFC of *L. plantarum*. These values were lower compared to those recommended by Martins *et al.* (2006). However, the values for *S. cerevisiae* were similar to the values of 10^5 live cells per gram of ration obtained by Meurer *et al.* (2008). The values for the *L. plantarum* probiotic found in this research contradicted the values observed by Leandro *et al.* (2010) in studies where they found that feed supplemented with *L. plantarum* contained about 10^6 UFC/g of the food.

Microbial composition of pathogenic bacteria in water and in the Nile tilapia fingerlings

Enterobacteriasis non-lactose fermentors and mycobacteria were isolated in aquarium water and in the intestine of fingerlings used in this experiment. The latter were not observed in the intestine of the fingerlings subjected to Treatment (T2). Similar results were obtained by Pupo (2006) in studies where he isolated several species belonging to the Enterobacteriaceae and which have been known for their

Table 1. Microorganism colony-building units in aquarium water and in the intestine of *O. niloticus* fingerlings, by treatment (with or without probiotics).

		Treatments			
		C(1)	**T1(2)**	**T2(3)**	**T3(4)**
Non-lactose fermenting Enterobacteria	In the Water	$5*10^{3}$ (a)	$7.7*10^{4(b)}$	$2.3*10^{4(a)}$	$4.7*10^{4(a)}$
	In the Intestine	$6.7*10^{4(b)}$	$1.5*10^{5(c)}$	$8*10^{3(a)}$	$1.7*10^{5(c)}$
Mycobacteria	In the Water	$5*10^{4}$	$6.2*10^{4}$	$3.3*10^{4}$	$4.5*10^{4}$
	In the Intestine	$5.7*10^{4(f)}$	$6.6*10^{4(df)}$	0(e)	$1*10^{5(f)}$
Yeast	In the Water	$5*10^{3(c)}$	$2.8*10^{4(d)}$	$7*10^{3(c)}$	$2.7*10^{4(d)}$
	In the Intestine	$1.5*10^{5}$	$2.5*10^{4}$	$3*10^{4}$	$1.4*10^{5}$
Acid-Lactic Bacteria	In the Water	$2*10^{4(c)}$	$4.8*10^{4(c)}$	$1*10^{4(c)}$	$8.2*10^{4(c)}$
	In the Intestine	$1.5*10^{5(b)}$	$1.7*10^{5(b)}$	$4.5*10^{4(b)}$	$2.1*10^{5(b)}$

Mean comparisons showed significant differences among treatments (P<0.05). Different letters (a,b), (c,d) in the data for microbes in water indicate significant differences based on Tukey's and Newman Keuls tests, respectively. Different letters (a,b,c), (e,f) in the intestinal microbiology data also indicate significant differences based on Tukey's and Newman Keuls tests, respectively.

pathogenic potential. Eissa *et al.* (2008) isolated the pathogenic bacterium *Yersinia ruckeri* in 100 cultivated fish. Ahmed and Refaey (2013) isolated 5 % of enterobacteriacea non-lactose fermentors in *Rhamdia quelen* (*Edwardsiella delays and Y. ruckery*) in the kidneys and external lesions of the same species.

In relation to mycobacteria, the results of this study are similar to the results of work carried out with ornamental fish and other freshwater species (*Cichlasoma bimaculatum, Carassis auratus* and *Cichlasoma meeki*), where five mycobacteria species were isolated including *Mycobacterium fortuitum, Mycobacterium marinum*, among others (Ishikawa *et al.*, 2001). In a study with *O. niloticus*, the inclusion of 10^9 UFC of *M. marinum* did not induce fish death during the experiment, but indicative signs of the presence of Micobacteriasis were observed in fish (Ishikawa *et al.*, 2001). However, in *Carassius auratus*, mycobacterial inoculations at the concentrations of 10^9 and 10^8 UFC per animal provoked diseases followed by the death of organisms after 17 days of its inoculation.

Colony-building units (CBU)

The average number of colony-forming units in aquarium water and in the intestines of fingerlings are presented in Table 1. Significant differences were observed among treatments (P <0.05). Supplementation of *S. cerevisiae* under treatment T2 resulted in a significantly lower number of CBU of pathogenic enterobacteriaceae and average number of colony-forming units of acid-lactic bacteria, compared with other experimental treatments. Results published by Meurer *et al.* (2006) showed that the number of CBU of pathogenic bacteria were significantly less in fish fed a ration containing these probiotics, as compared with the control treatment, which is corroborated by the present study.

Supplementation of *L. plantarum* in treatment T3 resulted in a higher number of CBU of acid-lactic bacteria in the intestines of fingerlings. However, it did not reduce the intestinal colonies of pathogenic bacteria in fingerlings, when compared with the control treatment. Similar results were observed by Jotobá

Table 2. Growth parameters of *O. niloticus* fingerlings evaluated in treatments with and without probiotics.

Growth Parameters	**Treatments**			
	C(1)	**T1(2)**	**T2(3)**	**T3(4)**
Final Weight	3.3	3.2	3.5	3.2
Final Length	5.8	5.6	5.6	5.6
Weight Gain	1.0	0.9	1.3	0.9
% Weight Gain	30.3	28.1	36.1	28.1
Specific Growth Rate	1.2	1.2	1.3	1.2
Condition Factor	1.7	1.8	2.0	1.8
Apparent Feed Conversion Rate	0.45	0.5	0.3	0.5
Survival	100	96	100	100

(1) Control, (2) Treatment with swine manure without probiotics, (3) Treatment with swine manure with *S. cerevisiae*, (4) Treatment with swine manure and *L. plantarum*. There were no significant differences amongst treatments. (P> 0.05).

and Mouriño (2015), whereby supplementation with acid-lactic bacteria resulted in a large population of these bacteria (about $5*10^4$ CBU per gram of the intestine) in fish. Hortmam *et al.* (2014) also reported similar results which showed that the intestines of tilapia fingerlings fed with probiotics had a larger number of lactic acid and a lower number of pathogenic bacteria, compared with fish fed with the control diet.

Effects of probiotics on the growth and survival of the *O. niloticus* fingerlings

Results of the fingerling growth parameters and survival under each treatment are presented in Table 2. Fish weight changes during the experiment are illustrated in Figure 1. Statistical analyses showed no significant differences in terms of growth parameters and survival among the treatments (P>0.05). However, the death of one fish was recorded in Treatment 1 (T1) during the experiment and the fish in question had lost the scales on its skin.

Treatment 2, together with *S. cerevisiae* resulted in better performance in the Nile tilapia fingerlings for all of the growth parameters, except for the fish length which showed higher average values in the control treatment. Similar results were observed by Pooramin *et al.* (2009; 2014) and Jotobá and Mouriño (2015) who worked with probiotics, using fish as the indicator organism. The longest final length observed in the control treatment without probiotic supplements corroborates with the findings of Pooramini *et al.* (2009; 2014) who also found longer final lengths for fish artificially fed control diets without the inclusion of probiotics.

Supplementation of *L. plantarum* in Treatment 3 did not have any effect on the performance of fingerlings as compared with the control treatment, but resulted in better performance than Treatment 1 (T1). Similar results were found by Suzer *et al.* (2008) from studies where the use of *Lactobacillus sp* as a probiotic in *Sparus aurata* had no effect on weight gain. The main disadvantage of the use of some probiotics resides in the absence of spores, which hinders their inclusion and durability in commercial diets (Leandro *et al.*, 2010; Vieira, 2010).

Effect of swine manure on *O. niloticus* fingerlings

Internal and external clinical signs were observed to determine the effects of swine manure on *O. niloticus* fingerlings. Results from the observations revealed the following signs: dark gall bladders and empty intestine, an indication that the fingerlings did not feed for several days; bleeding around the eye and the skin; absence of scales; opaque eyes; mutilated fins; reddish-coloured gills (sign of anaemia); lack of appetite, and the death of one fingerling. The clinical signs illustrated in Figure 2 were observed under Treatment 1 which included swine manure without probiotic supplements. However, they were not observed either in the control or in Treatments 2 and 3, which included *S. cerevisiae* and *L. plantarum* supplements, respectively.

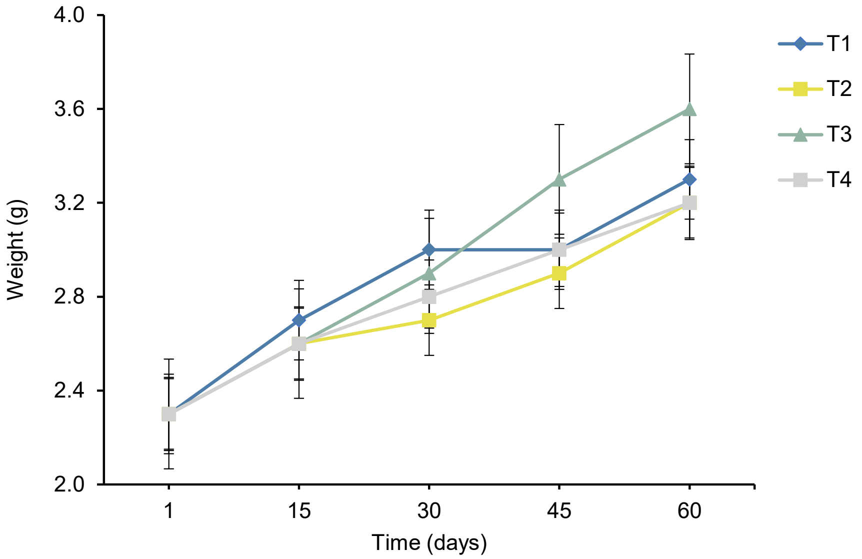

Figure 1. Differences in weight during the experimental period (starting from date of swine manure inoculation in aquariums) in treatments with and without probiotics. (T1) Control treatment, (T2) Treatment with swine manure without probiotics supplements, (T3) Treatment with swine manure with the probiotic *S. cerevisiae*, (T4) Treatment with swine manure with the probiotic *L. plantarum*.

Figure 2. Signs observed on fish under Treatment 1 (Swine manure without probiotics supplement). A. Dark-green gall bladder; B. Empty stomach; C. Haemorrhage (bleeding) around the eye; D. Dead tilapia fingerling showing no scales, opaque eyes and mutilated fins; E. Mutilated fins; F. Haemorrhages on the skin; G. Pale-red to rose coloured gills.

The presence of these signs suggest that the microbial challenge had an effect on *O. niloticus* fingerlings, from contact with pathogenic microorganisms contained in the swine manure. These are typical signs of yersiniosis, edwardsiellosis and mycobacteriosis in fish (Ostrensky and Boeger, 1998; Carson and Wilson, 2009).

The signs described above were also observed by Meurer *et al.* (2009). According to Kubitza (2005) the emergence of these signs is associated with high concentrations of faecal material in the cultivation tanks. These signs where fish were infected with enterobacteriacea *Y. ruckery*, showed clinical signs including lack of appetite, dark pigmentation of the skin, haemorrhages around of the mouth, the eye and the fins and swollen abdomen were associated with faecal material in cultivation tanks (Carson and Wilson, 2009; Ahmed and Refaey, 2013).

Swine manure inoculated in the experimental aquariums contained bacteria that are pathogenic for fish. Pathogenic microorganisms present in cultured fish have the potential to colonize the intestine of fingerlings. Pathogenic bacteria contained in swine manure had no effect on growth, but affect survival of fingerlings due to the inclusion of probiotics in the commercial ration used.

The supplementation of the probiotic *S. cerevisiae* in the feed of *O. niloticus* fingerlings treated with swine manure showed a positive effect in the sense that the probiotic prevented the intestinal colonization of fingerlings by pathogenic bacteria. The application of manure in fish farming to increase food production seems to be a good alternative, but supplementation with probiotics to reduce contamination by pathogenic bacteria as observed in the present experiment provides an added advantage.

The circular economy approach, which focuses on “reducing, reusing and recycling” resources including animal waste such as swine manure, can be used due to the presence of proteins and other valuable compounds for cultivated organisms in the manure. In the present experiment, swine manure was added directly to the fish cultivation system similarly to the practice used by farmers. Instead of applying manure directly to the fishponds that can lead to contamination from pathogenic bacteria, an alternative approach could be to add manure to separate food production systems to stimulate the growth of protei-rich phytoplankton and zooplankton that are the basis of the food web and can then be fed to omnivorous fish.

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Original Article

Retained fish catches of artisanal fishers is dependent on fishing area, season and fishing gear type: A case study from the south coast of Kenya

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Abstract

The artisanal fishery is one of the sources of livelihood along the Kenya coast. Catches of retained fish of artisanal fishers between two fishing areas on the south coast of Kenya were compared. Artisanal fishers usually retain a portion of their daily catch which is reserved for family consumption while the rest is traded for cash to meet other family needs. This study hypothesized that retained fish catches were influenced by fishing area, fishing gear type and season. Daily fish landings and retained fish catches among artisanal fishers were monitored between August 2020 to July 2021 covering the South East Monsoon (SEM) and North East Monsoon (NEM) in Msambweni and Vanga fishing areas. A total of 60 fishers (30 for each area) were randomly selected and their retained catch monitored on a daily basis. The overall total fish landings were 23.3 tons and 210 tons in Msambweni and Vanga, respectively. The mean catch rate at Msambweni was 3.3 ± 0.12 $kg.fisher^{-1}day^{-1}$ in the NEM season and 2.2 ± 0.09 $kg.fisher^{-1}day^{-1}$ in the SEM season. Fish catch rates in Vanga was 8.5 ± 0.28 $kg.fisher^{-1}day^{-1}$ in the NEM season and 7.9 ± 0.29 $kg.fisher^{-1}day^{-1}$ in the SEM season. A total of 0.98 tons (only 4.2 %) of fish was retained *versus* 22.32 tons (95.8 %) not retained by the artisanal fishers in Msambweni, while in Vanga a total of 1.64 tons (only 0.78 %) was retained *versus* 208.36 tons (99.22 %) not retained. Retained fish catch varied significantly with season and type of fishing gear used ($p < 0.05$). Among the retained species in Msambweni, *Siganus sutor* made the highest contribution (53 %), followed by *Lethrinus mahsena*, (5.08 %). The species *Euthynnus affinis* and *Sphyraena obtusata* were mostly retained in Vanga with a contribution of 10.4 % and 10.2 %, respectively. The same retained fish species represented the most abundant species in the overall fish landings, however sizes were significantly smaller than those not retained by fishers ($p < 0.05$). Results of non-Metric Multidimensional Scaling (nMDS) ordination showed differences in species composition between fishing areas, seasons and fishing gear types with implication on fishers' retained catches.

Keywords: artisanal fisheries, food security, south coast of Kenya

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Introduction

Studies by Fraval *et al.* (2019) indicate that one out of four people in sub-Saharan Africa is estimated to be undernourished as a result of food insecurity. Fish has been singled out to play a distinct important role in global food and nutrition security accounting for the most consumed source of animal protein and other nutrients in many low and middle-income countries (Reksten *et al.*, 2020). According to FAO (2020), approximately 3.3 billion people across the world rely on fish for an integral part of their animal protein. Further, FAO (2020) indicated that fish is a fundamental source of animal protein for several African and Asian countries.

Coastal and marine artisanal fisheries play a significant role in supporting human wellbeing as well as maintaining food security (Schuhbauer and Sumaila, 2016). The sub-sector forms a critical source of food and income for many regions, especially developing nations (Lancker *et al.*, 2019). Globally, artisanal fisheries contribute to nearly 50 % of the total capture fisheries production which provide the world's rapidly expanding population with a vital food source (Bennet *et al.*, 2018). In Africa, coastal and marine artisanal fisheries provide about 19 % of the essential animal protein to local households and provide up to 80 % of household income which makes it a potential reducer of food insecurity and starvation (Samoilys *et al.*, 2017; Chan *et al.*, 2019). The marine fishery in Kenya is primarily artisanal (Kamau *et al.*, 2021) characterized by low capital investment, the use of low technology, making short near shore fishing trips, and is normally undertaken by local individual household fishers (Monaco *et al.*, 2017). Artisanal fisheries can be subsistence providing for local consumption of fisher households or commercial when it involves selling of fish for money (Batista *et al.*, 2014). About 90 % of the small-scale fish landings along the coast is traded and consumed locally (FAO, 2020).

In Kenya where increasing population has increased the demand for food (Ogello and Munguti, 2016), about 1.3 million people face food insecurity and poor nutrition (USAID, 2020). Fish contributes to more than half of the total animal protein intake in Kenya (Aloo *et al.,* 2014). Along the Kenyan coast, more than 200,000 people meet their livelihoods through fishing and trading in fish and fish products (Matsue *et al.*, 2014). On the south coast of Kenya, in particular, artisanal fisheries make a vital contribution to local community livelihoods. Fish is considered as the most readily available and affordable source of animal protein for the local communities (Aloo *et al.*, 2014) but the contribution of small-scale fisheries towards food provision and improvement of livelihoods has been rarely considered (Obiero *et al.*, 2019). Additionally, fishing households arguably consume more fish compared to non-fishing households (Bruyn *et al.*, 2021). This study therefore, aimed to assess the composition of retained fish catches in selected fishing areas on the south coast of Kenya. The study hypothesized that retained catches of artisanal fishers is dependent on fishing areas, fishing gear types and seasons.

Materials and methods

Study area

This study was conducted in Msambweni and Vanga fishing areas on the south coast of Kenya. Msambweni is located more than 50 km from the city of Mombasa, situated at S 04046'53", E 039048'13" and Vanga further south at the border with Tanzania situated at S 04039'37", E 039013'11" (Ogongo *et al.*, 2015; Fig. 1). Both sites started as small fishing villages but have been developing rapidly over time, characterized by improved infrastructure and increasing population. The sites are among the most active fishing areas in Kenya where the artisanal fishery is considered a major source of livelihood (Agembe *et al.*, 2010). Fishing grounds in these areas have been reported to be rich in biological diversity and provide vital a food source and boosts the economy and wellbeing of the local fishing communities (KCDP, 2016). Fishing activities mainly occur within nearshore reef lagoons characterised by artisanal multi-gear and multi-fleet operators targeting and landing multiple species (Agembe *et al.*, 2010), and are highly influenced by the warm north east monsoon (NEM) and cool south east monsoon (SEM) seasons.

Data Collection

Shore-based catch assessment for retained catches

A total of 60 fishers representing 60 fisher households (30 from each fishing area) were randomly selected through the assistance of respective beach management unit (BMU) representatives. Fishers were selected using a stratified sampling technique to represent the key fishing gears used at each fishing area. A total of four and six different fishing gear types were selected for this study in Msambweni and Vanga, respectively (Table 1). The details of each fisher household recorded included household size, age of the fisher and fishing experience.

Daily fish landings by weight and taxa were recorded for Msambweni and Vanga during the entire study period covering the SEM and NEM seasons. Shore-based catch assessment from the selected fishers were conducted by resident trained field assistants at the fish landing sites between August 2020 to July 2021. Recorded data included total weight of catch per fisher per day and catch retained, species composition and individual fish weight (g), and total length (TL, cm) measured using a graduated fish measuring board. Retained catches were entirely sampled for species composition since these represented smaller portions of the total catch per fisher.

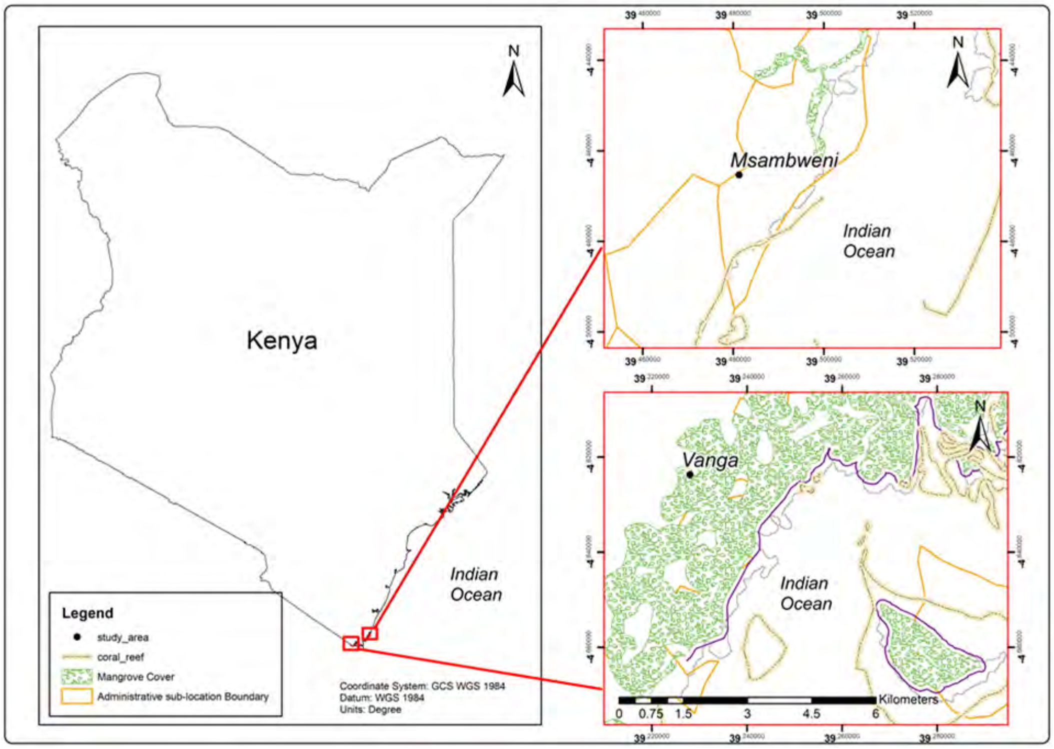

Figure 1. Location of Msambweni and Vanga fishing areas, south coast of Kenya, where retained fish for household consumption was monitored over the study period.

Data and statistical analyses

Overall artisanal fish landings and fishing effort

The overall total fish landings were analysed for trends in relative abundance by taxa over time. The daily catch from the selected fishers was analysed for catch rate (kg.fisher^{-1}day^{-1}) by gear type, fishing area and season. Catch rate was calculated using the following formula (Samoilys *et al.*, 2017):

$$\text{Catch Rate} = \frac{\text{Mean total catch (kg) per day}}{\text{Mean fisher crew per day}} \quad \text{..................} \ (i)$$

To meet the requirements for the parametric ANOVA test, homoscedasticity of variance of means of the actual catch rate data was first confirmed using the Levene's test at $p > 0.05$. When this requirement was not fulfilled, data was log-transformed. If data still did not meet the ANOVA requirements even after transformation, the alternate non-parametric Kruskal-Wallis test was used. All tests were conducted using STATISTICA statistical software version 7 and significant differences were set at $p < 0.05$.

Fish species composition

Data from overall fish landings and retained fish catches from the 60 fishers was analysed for species composition. The multivariate non-Metric Multidimensional Scaling (nMDS) technique was used to identify if there was distinct species composition across fishing areas with seasons combined based on Bray-Curtis similarity using Primer statistical software version 6 (Clark *et al.*, 2014). The spatio-temporal differences in species composition were further analysed by 1-way Analysis of Similarity (ANOSIM) with combined fishing area-season as a factor where when *R* statistic approached 1, the differences in species composition was significant at $p < 0.05$.

Table 1. Number of fishers and household sizes surveyed by fishing area and gear type over the study period.

Fishing area	Gear type	Number of fishers	Mean household size	Total dependants
Msambweni	Basket traps	13	7	96
	Hand lines	13	6	79
	Gill nets	2	7	13
	Spear guns	2	6	12
Vanga	Ring nets	10	7	72
	Reef seines	11	7	80
	Spear guns	5	10	50
	Hand lines	2	7	13
	Gill nets	1	7	7
	Beach seines	1	13	13

One-way Similarity Percentage (SIMPER) analysis identified which fish species were most influential to the dissimilarity.

Results

Monthly total fish landings by fishing area and fishing gear

Basket trap and hand line fishers were the majority in Msambweni while ring net and reef seine fishers were the majority in Vanga. Despite being illegal, spear guns and beach seines were still in use with spear gun observed in both areas and beach seine in Vanga. Mean household size of selected fishers ranged between six and 13 members. The largest mean household size was 13 recorded for beach seine fishers in Vanga closely followed by an average household of 10 for spear gun fishers recorded in the same area (Table 1).

Total catch by fishing area, season and fishing gear type varied over the study period. In Msambweni, overall total landing was 23.3 tons and only 0.98 tons (4.2 %) was retained by the artisanal fishers. The NEM season recorded higher fish landings of 15 tons compared to 8.3 tons in the SEM season. Basket trap fishers recorded the highest catch while spear gun fishers recorded the lowest catch (Fig. 2a). Highest monthly total catch in basket traps was in the months of November (3.9 tons) and January (2.5 tons). Hand line was the second most productive gear in the area with highest catch observed in September (0.471 tons) and March (0.417 tons). For gill nets, September recorded the highest total catch with 0.383 tons, followed by February (0.332 tons). For spear guns, the highest monthly catch was recorded for September with 0.021 tons, with no catch recorded in the months of February, March and April (Fig. 2a).

The overall total fish landings in Vanga was 210 tons and 1.64 tons (0.78 %) was retained by the artisanal fishers. Seasonal fish landings in the area was higher for the NEM (112 tons) than the SEM (98 tons). In this area, ring net fishers recorded the highest catch while spear gun fishers recorded the lowest (Fig. 2b). For ring nets, highest monthly total catch was recorded in

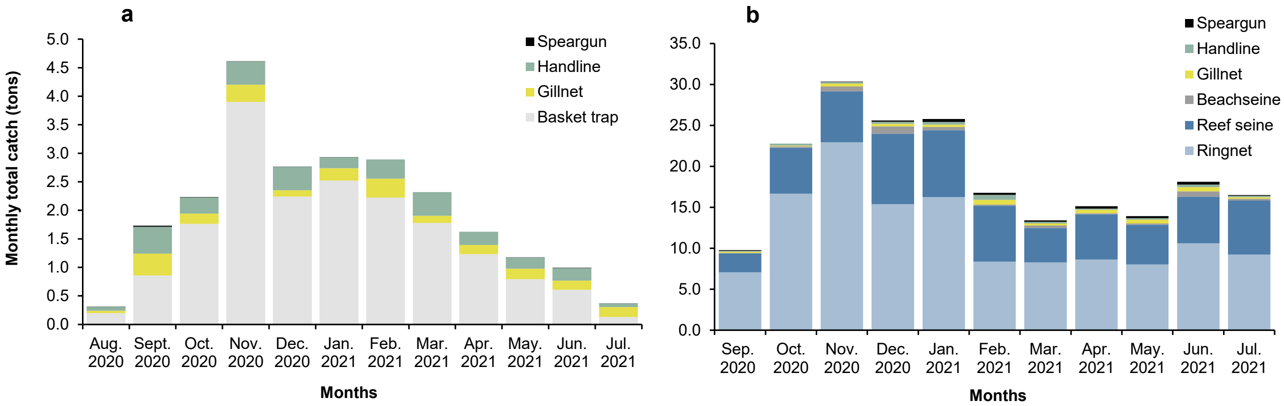

Figure 2. Monthly total fish landings sampled from the selected artisanal fishers by fishing gear type for a) Msambweni, and b) Vanga, south coast of Kenya.

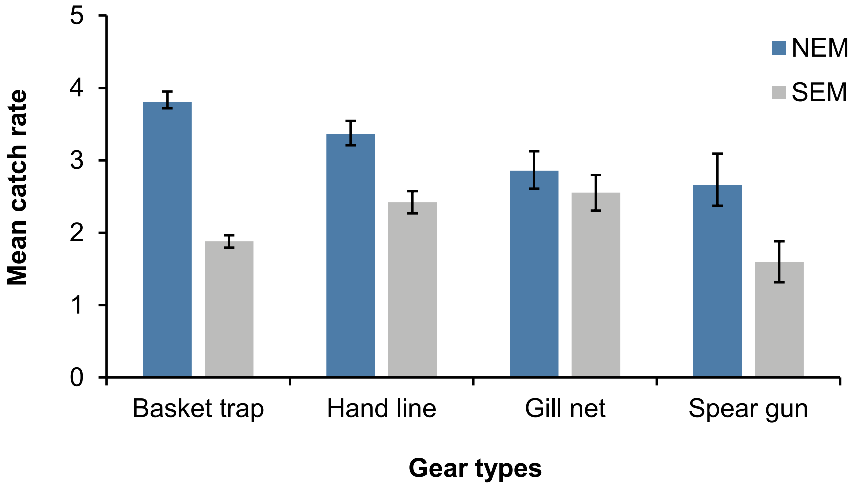

Figure 3. Fish catch rate (mean ± SE) by gear type and seasons in Msambweni, south coast of Kenya.

November with 22.94 tons. Reef seine nets followed with the highest catch in December with 8.62 tons, followed by January (8.15 tons). For gill nets, highest monthly total catch was recoded in February with 0.57 tons. Beach seine nets, among the least productive gear followed and highest total landings for this gear was recorded in December at 0.90 tons. For hand lines, February recorded the highest total catch with 0.61 tons followed by January (0.34 tons). For spear guns, the highest monthly catch was recorded for January with 0.36 tons with no catch recorded in the month of October.

Fish catch rates

Catch rate (kg. fisher^{-1}day^{-1}) varied by fishing area, season and fishing gear. In Msambweni, mean catch rate was 3.3 ± 0.12 kg.fisher^{-1}day^{-1} in the NEM season and 2.2 ± 0.09 kg.fisher^{-1}day^{-1} in the SEM season. In this area, catch rate was highest for basket trap in the NEM season (3.8 ± 0.15 kg) and least for spear gun fishers in the SEM season (1.6 ± 0.28 kg). Catch rate for basket traps was significantly higher in the NEM season than the SEM season (Kruskal-Wallis: p = 0.00, H =108.67) (Fig. 3). For hand lines, Kruskal-Wallis test indicated significant differences in catch rate across study sites and between seasons ($p < 0.05$; Fig. 3 & 4). The same test showed highly significant gill net catch rates in Vanga compared to Msambweni (p = 0.000) with higher catch rate recorded in the NEM than the SEM season but not statistically different (p = 0.915) (Fig. 3 & 4). For spear guns, results of Kruskal-Wallis test confirmed significantly higher catch rates in Vanga than Msambweni (p = 0.009) but they were statistically similar between seasons (p = 0.486) (Fig. 3 & 4).

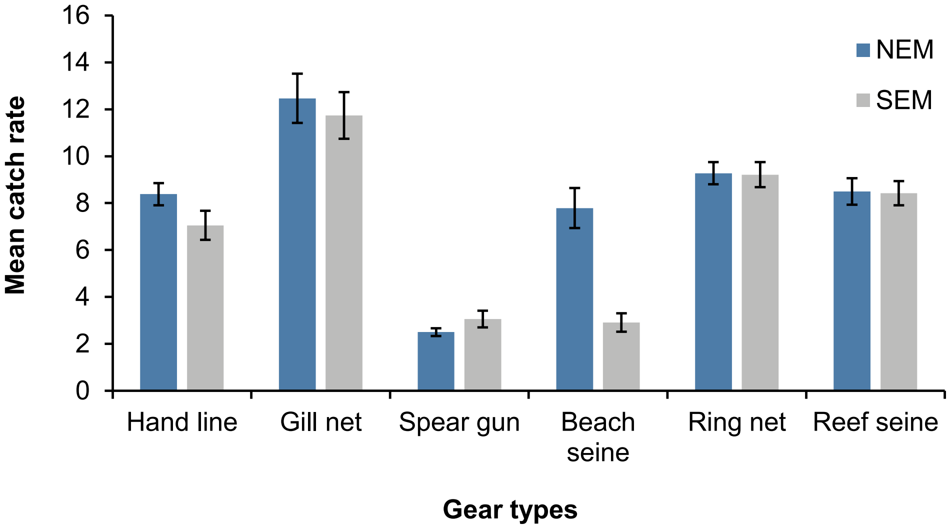

Figure 4. Fish catch rate (mean ± SE) by gear type and seasons in Vanga, south coast of Kenya.

In Vanga, overall mean catch rate was 8.5 ± 0.28 kg. fisher-^{1}day-1 in the NEM season and 7.9 ± 0.29 kg.fisher^{-1}day^{-1} in the SEM season. Fish catch rate in this area was highest for gillnet fishers (12.46 ± 1.05 kg), followed by ring nets (9.27 ± 0.48 kg) and lowest for spear guns (2.50 ± 0.16 kg). For beach seinse, catch rates were significantly higher in the NEM than the SEM season (1-way ANOVA: p = 0.00, df =1, f = 42.23) (Fig. 4). For ring nets and reef seines, results of 1-way ANOVA showed no significant differences in catch rates between seasons (p > 0.05 in all cases) (Fig. 4).

Overall fish species composition

An overall total of 372 fish species were sampled over the study period representing a total of 297 fish species recorded in Msambweni and a total of 172 species recorded in Vanga. Among the top 10 most abundant species in Msambweni, *Siganus sutor* made the highest contribution (58.4 %), followed by *Lethrinus mahsena* (7.8 %). *Siganus sutor* recorded a mean total length of 25.33 ± 0.04 cm with a range of 11.7 to 45.5 cm. The same species recorded a minimum weight of 34 g, maximum weight of 1,515 g and a mean weight of 235 ± 0.76 g. *Lethrinus mahsena* recorded a mean length of 25.16 ± 0.04 cm and mean weight of 313.92 ± 4.84 g. The species *Lethrinus variegatus* and *Calotomus carolinus* made the lowest contribution among the top ten abundant species (Table 2). In Msambweni, the overall mean size of fish not retained by fishers was significantly larger (25.78 ± 0.05 cm) than those retained (22.77 ± 0.08 cm; 1-way ANOVA: p = 0.000).

Among the top ten most abundant species in Vanga, *Sphyraena forsteri* made the highest contribution (23.9 %), followed by *Sphyraena obtusata* (13.7 %). *Sphyraena forsteri* recorded a mean total length of 18.68 ± 0.06 and a mean individual weight of 36.10 ± 0.24 while *Sphyraena forsteri* had a mean total length of 21.10 ± 0.19 cm and a mean individual weight of 58.82 ± 1.24 cm. The species *Hemiramphus far* and *Lethrinus lentjan* made the lowest contribution among the top ten most abundant species in the area (Table 2). In Vanga, fish sizes also varied where fish not retained by fishers were significantly larger (24.11 ± 0.19 cm) than those retained (20.98 ± 0.07 cm; p = 0.000).

Results of non-Metric Multidimensional Scaling (nMDS) ordination showed separation of species by fishing area with season combined (Fig. 5). Results of the 1-way ANOSIM test indicate a significant difference in species composition by fishing area with season combined (R = 0.224; p = 0.001). The pair-wise comparison test confirmed a significant difference existed between all fishing area-season combinations (p = 0.001 in all cases). One-way SIMPER analysis confirmed seasonal differences in species composition in Msambweni was

Table 2. Overall species composition and mean sizes of most abundant fish species.

Site	Species	Common name	Proportional abundance (%)	Mean length (cm)	Mean weight (g)
Msambweni	*Siganus sutor*	Shoemaker spinefoot rabbitfish	58.35	25.33 ± 0.04	234.89 ± 0.76
	Lethrinus mahsena	Sky emperor	7.84	25.16 ± 0.12	313.92 ± 4.84
	Lethrinus rubriopeculatus	Spotcheek emperor	3.70	20.22 ± 0.22	127.96 ± 2.57
	Lethrinus borbonicus	Snubnose emperor	3.28	21.33 ± 0.13	185.30 ± 3.56
	Lethrinus lentjan	Pink ear emperor	2.56	26.60 ± 0.17	304.26 ± 6.83
	Lethrinus harak	Thumbprint emperor	1.89	25.35 ± 0.33	244.17 ± 4.77
	Lutjanus fulviflamma	Black-spot snapper	1.73	21.03 ± 0.15	157.34 ± 3.79
	Parupeneus barberinus	Dash-and-dot goatfish	1.45	29.60 ± 0.25	351.43 ± 8.22
	Calotomus carolinus	Carolines parrotfish	1.34	26.12 ± 0.74	324.02 ± 5.86
	Lethrinus variegatus	Slender emperor	1.01	15.53 ± 0.11	55.27 ± 1.61
Vanga	*Sphyraena forsteri*	Bigeye barracuda	23.94	18.68 ± 0.06	36.10 ± 0.24
	Sphyraena obtusata	Obtuse barracuda	13.74	21.10 ± 0.19	58.82 ± 1.24
	Rastrelliger kanagurta	Indian mackerel	9.34	19.16 ± 0.15	76.0 ±1.60
	Gerres oyena	Common silver-biddy	5.75	17.65 ± 0.17	63.39 ± 1.20
	Pterocaesio tile	Dark-banded fusilier	5.14	20.40 ± 0.21	89.95 ± 2.0
	Decapterus macarellus	Mackerel scad	4.46	22.31 ± 0.21	121.65 ± 3.78
	Hemiramphus lutkei	Lutke's halfbeak	3.93	26.31 ± 0.08	81.50 ± 0.78
	Lethrinus lentjan	Pink ear emperor	3.69	18.54 ± 0.19	91.81 ±3.01
	Hemiramphus far	Black-barred halfbeak	3.20	26.86 ± 0.20	112.24 ± 3.49
	Decapterus macrosoma	Shortfin scad	2.43	19.27 ± 0.32	86.67 ± 4.55

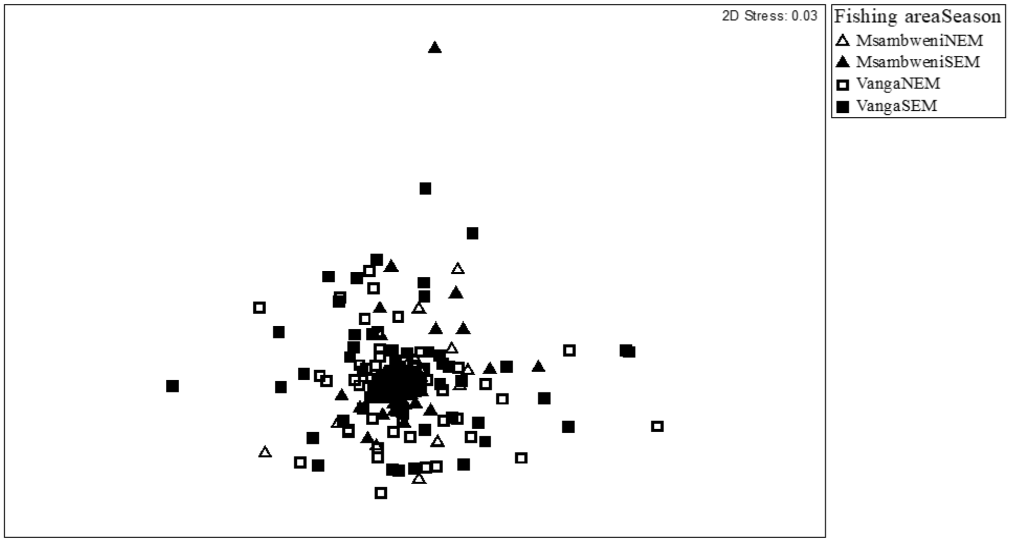

Figure 5. Non-metric MDS plots showing distinct catch composition of all fish species by fishing area with season combination based on species abundance from catch monitoring data over the study period.

attributed to more abundant *Siganus sutor* and *Lethrinus mahsena* in the NEM than the SEM season. In Vanga, seasonal differences in species composition was attributed to more abundant *Sphyraena forsteri* and *Sphyraena obtusata* in the NEM than the SEM and more abundant *Euthynnus affinis* in the SEM than the NEM season. The seasonal dissimilarity in species composition was 75.96 % in Msambweni (Table 3) and 95.55 % in Vanga (Table 4).

Species composition of retained fish

Overall, a total of 18,864 individuals weighing 2.63 tons (1.13%) from 284 species were retained by fishers in both study sites with 4,807 individuals weighing 0.98 tons of 174 species retained in Msambweni and 14,507 individuals weighing 1.67 tons of 170 species retained in Vanga. Among the top ten most retained species in Msambweni, *Siganus sutor* made the highest contribution (53 %), followed by *Lethrinus mahsena*, (5.08 %) and *Calotomus carolinus* (5.06 %). The species *Scarus rubroviolaceus* and *Acanthurus xanthopterus* made the least contribution among the top ten most retained species in the area (Table 5). Among the top ten retained fish species in Vanga, *Euthynnus affinis* made the highest contribution (10.4 %), followed by *Sphyraena obtusata* (10.2 %), *Sphyraena forsteri* (8.9 %) and *Decapterus macarellus* (8.2 %). The species *Lethrinus lentjan*, and *Caesio xanthonota* made the least contribution of retained species in the area (Table 5).

Table 3. SIMPER results showing seasonal differences and species contributing to dissimilarity in Msambweni with an average seasonal dissimilarity of 75.96 %.

	Msambweni NEM	Msambweni SEM		
Species	Average abundance	Average abundance	Average Dissimilarity	Contribution (%)
Siganus sutor	**44.08**	41.85	22.56	29.70
Lethrinus mahsena	**11.86**	6.43	7.31	9.63
Lethrinus rubriopeculatus	4.13	5.19	4.27	5.62
Lethrinus borbonicus	3.60	5.03	3.84	5.06
Lethrinus lentjan	3.49	4.00	3.44	4.53
Lethrinus harak	0.49	4.22	2.31	3.05
Lutjanus fulviflamma	1.04	3.53	2.19	2.89
Uroteuthis duvaucelii	2.99	1.34	2.11	2.78
Coryphaena hippurus	2.73	0.00	1.36	1.80
Parupeneus barberinus	1.31	1.27	1.20	1.58
Lutjanus gibbus	1.23	0.99	1.07	1.40
Calotomus carolinus	1.72	0.41	1.03	1.36
Lethrinus olivaceus	0.73	1.37	0.99	1.31

Table 4. SIMPER results showing seasonal differences and species contributing to dissimilarity in Vanga with an average seasonal dissimilarity of 95.55 %.

	Vanga NEM	**Vanga SEM**		
Species	**Average Abundance**	**Average Abundance**	**Average Dissimilarity**	**Contribution (%)**
Sphyraena forsteri	**15.81**	8.94	10.89	11.39
Sphyraena obtusata	**11.01**	5.48	7.60	7.96
Euthynnus affinis	4.36	**11.44**	7.40	7.75
Rastrelliger Kanagurta	9.07	3.88	6.04	6.32
Gerres oyena	2.64	6.53	4.37	4.57
Lethrinus lentjan	3.31	5.35	4.10	4.29
Pterocaesio tile	5.79	2.54	4.01	4.19
Chirocentrus nudus	2.65	5.37	3.87	4.05
Decapterus macarellus	3.36	4.43	3.74	3.91
Siganus sutor	3.28	3.94	3.46	3.63
Hemiramphus far	4.47	1.93	3.11	3.25
Hemiramphus lutkei	6.11	0.04	3.07	3.21
Lutjanus fulviflamma	2.26	2.09	2.11	2.21
Sphyraena putnamae	1.90	2.34	2.08	2.17
Carangoides orthogrammus	0.08	3.95	2.01	2.10

Results of non-Metric Multidimensional Scaling (nMDS) ordination combining fishing area with season showed distinct separation of catch samples of retained fish species by fishing area and to some extent by season (Fig. 6). Results of the 1-way ANOSIM test indicated a significant difference in catch composition across fishing area with season combination (R = 0.105; p = 0.001). Results of the pair-wise comparison test indicated significant difference in catch composition of retained catch across all fishing area with season combinations ($p < 0.05$ for all cases). One-way SIMPER analysis confirmed a significant difference in seasonal overall catch composition of retained species between Msambweni and Vanga. The overall seasonal dissimilarity in catch composition across Msambweni and Vanga was 96.75 %.

Table 5. Species composition and mean sizes of retained fish by fishing area on the south coast of Kenya over the study period.

Site	**Species**	**Common name**	**Proportional abundance (%)**	**Mean length (cm)**	**Mean weight (g)**
Msambweni	*Siganus sutor*	Shoemaker spinefoot rabbitfish	52.91	23.04 ± 0.07	177.96 ± 1.63
	Lethrinus mahsena	Sky emperor	6.52	20.45 ± 0.27	174.19 ± 8.73
	Calotomus carolinus	Carolines parrotfish	5.34	25.17 ± 0.26	317.40 ± 7.32
	Lethrinus borbonicus	Snubnose emperor	3.30	18.56 ± 0.17	119.04 ± 3.41
	Scarus ghobban	Blue-barred parrotfish	2.34	28.10 ± 0.88	450.48 ± 44.02
	Lutjanus fulviflamma	Black-spot snapper	2.16	22.34 ± 0.32	192.17 ± 10.69
	Acanthurus xanthopterus	Yellowfin sergeonfish	1.63	27.05 ± 1.21	4.2.21 ± 47.70
	Leptoscarus vaigiensis	Marbled parrotfish	1.61	23.06 ± 0.23	199.03 ± 5.26
	Lethrinus rubriopeculatus	Spotcheek emperor	1.53	20.36 ± 0.29	130.53 ± 7.32
	Scarus rubroviolaceus	Redlip parrotfish	1.30	28.98 ± 0.77	480.35 ± 39.63
Vanga	*Euthynnus affinis*	Mackerel tuna	13.34	49.08 ± 0.98	1596.99 ± 85.34
	Sphyraena forsteri	Bigeye barracuda	8.34	18.51 ± 0.04	35.34 ± 0.25
	Sphyraena obtusata	Obtuse barracuda	8.23	19.85 ± 0.12	51.05 ± 1.18
	Rastrelliger kanagurta	Indian mackerel	7.53	18.78 ± 0.11	72.08 ± 1.79
	Decapterus macarellus	Mackerel scad	5.23	21.61 ± 0.35	118.14 ± 4.66
	Pterocaesio tile	Dark-banded fusilier	4.52	19.99 ± 0.25	83.01 ± 1.93
	Hemiramphus lutkei	Lutke's halfbeak	4.32	26.31 ± 0.08	81.38 ± 0.77
	Hemiramphus far	Black-barred halfbeak	4.12	26.94 ± 0.22	113.68 ± 4.04
	Lethrinus lentjan	Pink ear emperor	2.85	18.26 ± 0.26	92.59 ± 4.27
	Chirocentrus nudus	Whitefin wolfherring	2.63	46.12 ± 1.21	336.90 ± 19.46

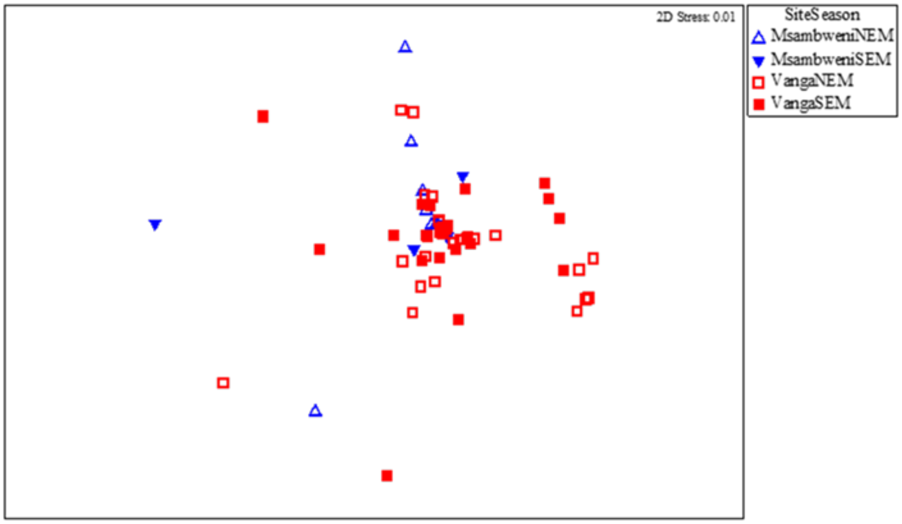

Figure 6. Non-metric MDS plots showing distinct catch composition of retained fish species by fishing area with season combination based on species abundance from catch monitoring data over the study period.

Results of non-Metric Multidimensional Scaling (nMDS) ordination showed to some extent distinct separation of catch samples of retained fish species by gear types (Fig. 7). The one-way ANOSIM test indicated a significant difference in species composition between fishing gear types (R = 0.263; p = 0.001). Results of the pair-wise comparison test confirmed significant differences in species composition between all fishing gear type comparisons (p = 0.001 in all cases) except for gillnet *versus* hand line, and spear gun *versus* beach seine (p > 0.05)

The most abundant fish species in the overall landings corresponded with the species that were retained by the artisanal fishers. One way SIMPER results confirmed that *Sphyraena forsteri* and *Sphyraena Obtusata* contributed highest to species seasonal dissimilarity among both landed and retained fish species in Vanga. In Msambweni, seasonal differences in species composition of both landed and retained catch were attributed to more abundant *Siganus sutor* and *Lethrinus mahsena*. The most common abundant species that were landed were in turn mostly retained by the fishers. These included *Sphyraena forsteri* and *Sphyraena obtusata* in Vanga and *Siganus sutor* and *Lethrinus mahsena* in Msambweni.

Discussion

The overall total fish landings during the NEM season was higher than the SEM season. Usually, artisanal

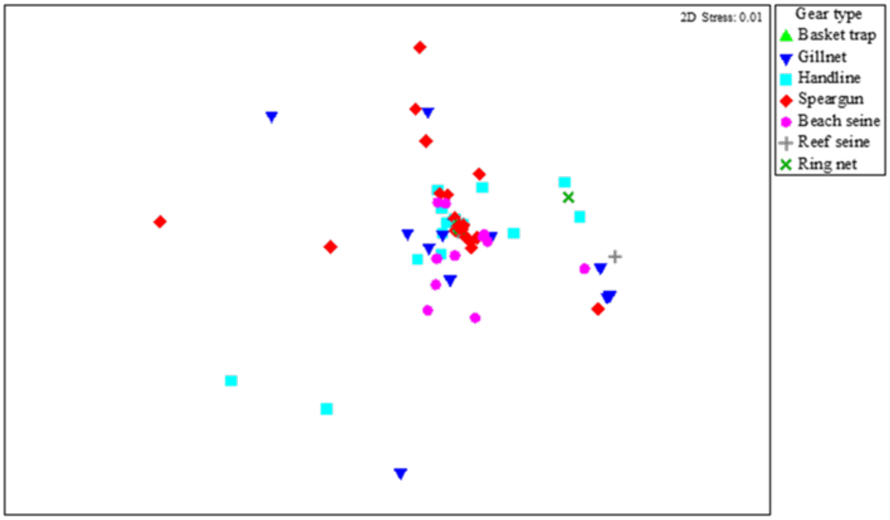

Figure 7. Non-metric MDS plots showing differences in the species composition of retained fish by fishing gears based on species abundance from catch monitoring data over the study period.

fish landings are affected by change of season where higher landings have been associated with the NEM season. This disparity of seasonal change in artisanal landings have previously been reported by other works (Munga *et al.*, 2011; Okemwa *et al.*, 2017). For both fishing areas of Msambweni and Vanga, higher fish landings were recorded during the NEM season especially in the months of November, December and January over the study period. Calm seas prevail in the warm NEM season favouring navigation enabling fishers to access offshore fishing grounds using small fishing boats that are mostly manually or wind-propelled (McClanahan, 1988). The warm NEM season also triggers spawning in many tropical fish species. As such, some fish species become an easy target for capture while in spawning aggregations (Robinson *et al.*, 2008; Woesik, 2010; Maina *et al.*, 2011). Lower fish landings in the SEM season, notable in September, May and June as observed in this study is likely due to limited access to offshore fishing grounds, and in this season, artisanal fishing activity is restricted to shallow and protected fishing grounds due to strong currents (Munga *et al.*, 2011; Okemwa *et al.*, 2017). Migration of fishers to other fishing grounds at the onset of the cool and rough SEM season also contributed to lower landings and reduced fishing activity especially in Vanga (Fulanda *et al.*, 2009; Okemwa *et al.*, 2017).

Catch rates for basket trap and hand line fishers recorded in this study were similar to those recorded by Musembi *et al.*, (2019) in Gazi on the south coast of Kenya, while ring net catch rates were within the range of those presented by Maina *et al.*, (2008) at Diani-Chale on the south coast. This study however, recorded slightly higher catch rate for reef seine net fishers compared to that recorded by Maina *et al.*, (2008). Musembi *et al.*, (2019) recorded higher catch rate for spear gun fishers compared to findings of this study. This study recorded higher catch rate for gill net and beach seine fishers than those reported by Maina *et al.*, (2008). The variations in fish catch rates by fishing gear types could be as a result of differences in fish abundance, fishing technique, geographical location, fishing ground characteristics, fishing effort and other determinant factors of fish catchability (Maina *et al.*, 2008; Purcell *et al.*, 2020).

Fish catch rates are notably influenced by seasonal dissimilitude (Niella *et al.*, 2017). In this study mean catch rates were higher during the NEM than the SEM season. This observation is in agreement with previous studies along the Kenyan coast (Munga *et al.*, 2014; Kiilu *et al.*, 2019; Dzoga *et al.*, 2020). These findings have also been supported by Kamau *et al.* (2021) who reported higher fish catch rates from October to March for coastal and marine fisheries on the north coast of Kenya coinciding the NEM season. Vanga and Msambweni fisheries are largely artisanal, dependent on small non-mechanized fishing crafts. The lower fish catch rates during the SEM season were attributed to adverse rough sea conditions (Munga *et al.*, 2014) while higher catch rates during the NEM season were driven by calmer waters which favoured fishing activities (McClanahan *et al.*, 1988; Kiilu *et al.*, 2019). However, the variation in mean catch rates for ring net and reef seine fishers was not significantly affected by the seasons. Ring nets and reef seines are relatively large nets which are used with larger outboard engine powered wooden boats (dhows) which ease navigation to offshore richer waters even in the cool and rough seas during the SEM season (Munga *et al.*, 2014; Dzoga *et al.*, 2020).

Artisanal fisheries of Vanga and Msambweni exhibited contrasts in terms of the catch composition of total sampled landings across seasons. In Msambweni, the species *Siganus sutor* and *Lethrinus mahsena* contributed to the dissimilarity between the NEM and SEM seasons. Overall species composition dissimilarity across seasons in Vanga was attributed to *Sphyraena forsteri* and *Sphyraena obtusata* which were more abundant in the NEM season and *Euthynnus affinnis* which was more abundant in the SEM season. Distinct separation in composition of retained species across fishing areas and seasons was to some extent evident. The overall dissimilarity in catch composition of retained fish species in Msambweni and Vanga was ascribed to more abundant *Siganus sutor*, *Lethrinus mahsena* and *Lethrinus borbonicus* in Msambweni during the NEM season, and more abundant *Euthynnus affinnis*, *Sphyraena forsteri*, *Gerres oyena*, *Lethrinus lentjan* and *Sphyraena obtusata* in Vanga during the SEM season. Additionally, retained fish species were to a larger extent influenced by catch composition of overall landings. The species *Siganus sutor* and *Lethrinus mahsena* which were mostly landed in Msambweni were also mostly retained by fishers. In Vanga, *Sphyraena forsteri*, *Sphyraena obtusata* and *Rastrelliger kanagurta* which were more abundant among the total sampled catch in Vanga were also mostly retained.

The variation in fish catch composition across fishing areas could have been exacerbated by factors such as existing critical habitats, sea conditions, gear types used, fishing pressure, fish recruitment, fishing effort and depth (Agembe *et al.*, 2010; Munga *et al.*, 2014; Dzoga *et al.*, 2020). In this study, a significant difference in catch composition of fish species across seasons was evident. The NEM season recorded the highest species diversity due to easy accessibility to better fishing grounds in the calm waters unlike the non-tranquil conditions of the SEM season (Munga *et al.*, 2011). Fluctuating sea conditions influence fish species distribution and the ability of fishers to access offshore fishing grounds (Locham *et al.*, 2010). In Msambweni, a shift in fishing technique of some basket trap fishers to the use of gill nets and some speargun fishers to the use of basket traps in the SEM season could have also contributed to the seasonal dissimilarity in catch composition (pers. obs.).

Dissimilarity in seasonal species composition between Vanga and Msambweni could have been caused by different fishing gear types and fishing locations. In Vanga, bigger wooden fishing boats capable of navigating to offshore fishing grounds using large fishing nets was associated mainly with pelagic fish species. On the contrary, the Msambweni fishery which involved the use of traditional canoes restricted to the nearshore was associated with demersal coral reef fish species. Additionally, Msambweni is dominated by basket trap fishers who target inshore fish families such as Siganidae, Lethrinidae and Scaridae while Vanga is dominated by ring net fishers who target pelagic species including Sphyraenidae, Scombridae, Carangidae and Lutjanidae (Samoilys *et al.*, 2011). Choice of gear type depends on the experience of fishers, for example Msambweni fishers who were older by age compared to Vanga fishers mostly used basket traps, being traditionally experienced in using basket traps (Mangi *et al.*, 2007). In contrast to Msambweni fishers who use traditional sail dhows which confined them in inshore waters within the reef areas, Vanga fishers have bigger wooden boats fitted with outboard engines which enable them to access different offshore fishing grounds with higher species diversity.

Conclusions

The findings of this study have revealed that overall fish landings to a large extent determine the composition of retained catches by artisanal fishers. This study also concludes that species composition and catch rates of retained fish catches, just like overall fish landings, are also affected by gear type, season and fishing area. Ocean tranquillity is a favourable driver of successful and productive artisanal fishing. Both overall fish landings and retained catches were higher during the NEM season than the SEM season. Total fish catch in Msambweni where basket traps and small canoes were dominant, were mostly composed of demersal coral reef species. In Vanga where large nets and wooden boats fitted with outboard engines were used, more pelagic fish species were landed. The most abundant species in the overall landings in the respective fishing areas made the highest composition of retained catches. Retained fish was less in the SEM season which was characterized by lower landings and fish catch rates compared to higher catch rates in the NEM season. Sizes of retained fish were significantly smaller than fish that was not retained by the fishers.

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Original Article

Zoonotic helminths and protozoa infesting commercially important marine crustaceans along the Kenyan coast

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Abstract

Marine crustaceans support important small-scale fisheries along the Kenyan coast. Annual catches have been declining, with climate change, pollution, overfishing and parasites proposed as causes. It is unknown whether parasite intensity and diversity change between locations, seasons and host species. The current study aimed to address this by analysing gastro-intestinal (GIT) parasites of two prawn species, *Penaeus indicus* and *Metapenaeus monoceros*, and two lobster species, *Panulirus ornatus* and *P. homarus*. A total of 240 prawns and 240 lobsters were collected from Malindi, Kilifi and Gazi, and intestinal contents microscopically examined for the presence of parasites. Observed parasites included *Schistosoma mansoni* (mean egg per gram (EPG) of 112.33), *Strongyloides* spp. (mean EPG of 94.80), *Hymenolepis diminuta* (mean EPG of 104.55), and *Hymenolepis nana* (mean EPG of 104.85). The Protozoa *Entamoeba coli* (mean EPG of 75.76) was observed. There was a significant difference in parasite intensity among host species ($p<0.00$) as well as intensity between seasons. There was no significant difference in intensity among landing sites, except in *E. coli* ($p=0.05$). Parasite diversity was not dependent on sites or seasons but varied with host species. The current study found that all the GIT parasites identified are zoonotic and could present a human health threat.

Keywords: crustaceans, Kenyan coast, gastro-intestinal parasites, zoonotic parasites, parasite intensity

Introduction

Parasites are organisms that live on the outside or inside of another organism (host) and depend on the host for food and shelter (Brazenor *et al.*, 2018). The parasites that live on the outer body of the host are referred to as ectoparasites. On the other hand, endoparasites are parasites that live inside the host's body. This contact weakens the host by generating diseases, leading to death in severe cases.

Coastal and marine waters contain parasites that have severe implications for population dynamics, management and conservation of fisheries resources (Aloo *et al.*, 2004). Kenya is one of the developing nations in the western Indian Ocean region whose coastal people rely on marine fisheries for food and employment (Kimani *et al.*, 2018). Economically important organisms targeted on the Kenyan coast range from fish, lobsters, molluscs and crabs. However, the sustainability of these resources remains uncertain since annual catches from most of these fisheries have indicated declining trends over the past decades (Fulanda *et al.*, 2011).

A decline in catch landings can be attributed to overfishing, recruitment failure or population bottlenecks

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through parasite infestations and diseases (Overstreet *et al.*, 2017). In most cases, fisheries managers have used management options such as fishing gear restrictions to prevent the entry of illegal gear among fishers who may want to boost their dwindling catches (Cinner *et al.*, 2008). The sustainability of food production, either originating from capture fisheries or aquaculture ponds, could be greatly hampered by altering the biological, chemical and physical environments either under anthropogenic or climate change perturbations (Petriki *et al.*, 2021). An alteration of the external environment in which these organisms live could easily compromise the organism's immune system, thus leading to disease outbreaks, which might result in heavy mortalities, recruitment failure or population collapse, among which parasites and protozoa play an important role.

Several species of parasites are zoonotic (transmissible between animals and humans), being able to cause health problems in humans (Chaiaa *et al.*, 2005). Adequate knowledge on disease-causing parasites infesting crustaceans in the Kenyan marine waters is generally lacking. The aim of this study was to conduct a comparative assessment of the parasites infesting prawns and lobsters in Kenyan marine waters. The specific objective was to determine whether parasite intensity significantly differed among sampling sites, host species, and seasons.

It is intended that the findings from this study on parasite species composition, temporal and geographic distribution trends, intensity and diversity will provide insight into parasite dispersal patterns, which is crucial for managing and preserving exploitable fisheries resources.

Methodology

Study Area

Kenya has a coastline of about 640 km stretching from 1°30′S at the Somali border to 5°25′S at the Tanzanian border. The marine waters of Kenya are warm – a characteristic of the tropical climate in the region. Two main rivers, Sabaki and Tana drain their waters into the Indian Ocean, thus creating estuarine habitats suitable for the existence of a diverse fisheries resource. The coastal region is influenced by the South East (SE) monsoon winds between April and October and the North East (NE) monsoon winds between November and March (McClanahan, 1988). Other than the monsoonal winds, the region is also influenced by the northerly flowing East Africa Coastal Current (EACC) and the southerly flowing Somali Current (SC). The Somali current reverses its flow direction

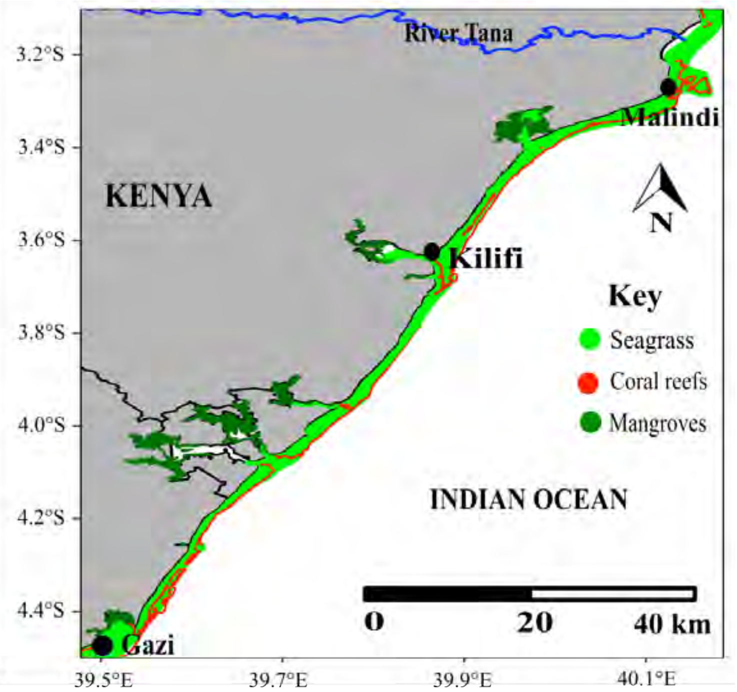

Figure 1. Map of the Kenyan coast showing sampling sites.

between April and October to align itself with the SE monsoonal wind direction (McClanahan, 1988). The area where the SC and EACC converge marks the beginning of an offshore South Equatorial Counter Current (SECC). These oceanographic features of the Kenyan coast presumably facilitate host and parasite larval dispersal and mixing, with implications for distribution patterns and genetic population structure for both parasites and hosts. Samples were collected at Mijikenda landing site in Malindi, Kilifi Central landing site in Kilifi and Gazi landing site (Fig. 1).

Sample collection and preparation

Two hundred and forty whole prawn and 240 lobster samples (total 480 samples) were collected from the three study sites, namely Gazi, Kilifi and Malindi (i.e., 20 individuals ×4 species ×3 sites × 2 seasons=480) between September 2020 and May 2021. Sampling was conducted during the NE and SE monsoon seasons. Each sampling station was sampled once per season, making two temporal sampling events at each site. Fresh prawns and lobsters were bought from 15 artisanal fishers at random, depending on who fished in the sampling area and had the species of lobsters and prawns needed. The samples were stored on ice in cooler boxes for four hours while in the field and frozen at -80 °C in the laboratory prior to parasitological examinations.

Laboratory procedure

During the parasitological examination, each sample specimen was defrosted at room temperature. The eyes, skin, carapace, nostrils and mouth cavity of each specimen was investigated using a hand lens for lesions or any symptoms of disease manifestation. The body cavity was opened using sterilised scissors to examine the liver, stomach, pyloric caeca, intestines and gonads for endoparasites. Stool samples were collected from the intestines and parasites were microscopically observed using the wet mount technique (CDC, 2021a), where a drop of faecal matter was placed on a slide, stained with 10 % Lugol's iodine, covered with a coverslip and observed under a compound microscope at a magnification of 40×10. Parasites were identified up to the species level morphologically by using guides available for faecal parasites (CDC, 2021a). McMaster concentration technique, according to WHO (2019), was used to quantify the parasites, where the number of parasites and eggs found in that portion of stool was be multiplied by 50 for estimation of eggs per gram (EPG).

Data analysis

Data was recorded in Microsoft Excel and imported into the IBM SPSS Statistics software (IBM Corp, Armonk, NY, USA) for analysis. A statistical test was considered significant when the p-value was ≤0.05. Analysis of Variance (ANOVA), which is used to compare means between more than two groups (Hae-Young, 2014), was used to test for any significance difference in the parasite intensity among the three landing sites. ANOVA was also used to determine if there was any significant difference in the parasite intensities among the hosts (two species of

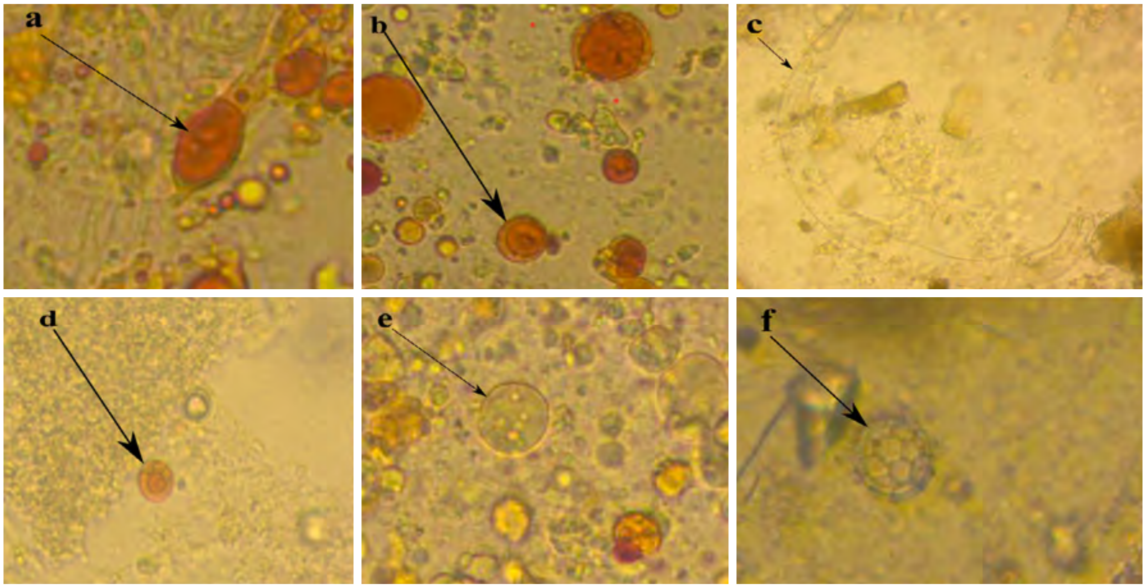

Figure 2. Helminth eggs (a) *Schistosoma mansoni*, (b) *Hymenolepis diminuta*, (c) *Strongyloides spp*, (d) *Hymenolepis nana*, (e) *Entamoeba coli* found in both prawns and lobsters, and (f) an unidentified cyst found in lobsters under x400 magnification.

Table 1. Mean egg per gram (EPG) ± standard deviation (SD) and analysis of variance test results conducted to compare means in parasite load among host species.

Parasite	Mean EPG ± SD *P. indicus* (n=120)	Mean EPG ± SD *M. Monoceros* (n=120)	Mean EPG ± SD *P. homarus* (n=120)	Mean EPG ± SD *P. ornatus* (n=120)	df	F	*p*-value
Strongyloides spp	101.22 ± 54.19	106.06 ± 49.62	78.85 ± 42.83	86.00 ± 33.91	3	12.43	<**0.00**
Schistosoma mansoni	118.97 ± 57.60	104.65 ± 48.57	110.53 ± 42.75	111.67 ± 61.14	3	8.50	<**0.00**
Hymenolepis nana	115.63 ± 57.41	112.50 ± 49.82	97.06 ± 51.45	77.78 ± 30.78	3	19.70	<**0.00**
Entamoeba coli	103.85 ± 55.76	70.00 ± 38.19	76.67 ± 37.16	57.69 ± 18.78	3	2.15	0.09
Hymenolepis diminuta	110.34 ± 52.41	113.79 ± 47.99	89.13 ± 52.13	100.00 ± 51.45	3	3.64	<**0.00**

prawns and two species of lobsters). A student's t-test, used to compare means between two groups (Hae-Young, 2014), was used to determine if there was any significant difference in parasite intensity between the two monsoon seasons. R programming environment (R Core Team, 2021) was used to generate diversity box plots. Mean EPGs were generated using Microsoft Excel.

Results

A total of 240 specimens of prawns (i.e., 120 *Penaeus indicus* and 120 *Metapenaeus monoceros*) and 240 lobsters (i.e., 120 *Panulirus ornatus* and 120 *Panulirus homarus*) were collected and observed for parasites. The specimens were healthy externally showing no lesions or any symptoms of disease manifestation. Five species of intestinal parasites were found to infest prawns and lobsters in the study sites. These included both helminth and intestinal protozoa. Helminth eggs identified include *Schistosoma mansoni*, *Hymenolepis diminuta*, *Strongyloides spp, Hymenolepis nana* and one protozoan cyst *Entamoeba coli* (Fig. 2). These parasites were observed under the magnification of ×400. One cyst found in lobsters under the magnification of ×400 was unidentified (Fig. 2).

Parasite intensity and diversity between prawn and lobster host species

There was no significant difference in *E. coli* intensity among the different host species analysed (p=0.09), but there were significant differences in the other parasite intensities (p<0.001) (Table 1). Parasite diversity also varied in prawns and lobsters, with a diversity index of 0.75 and 0.00 respectively (Fig. 3). Mean EPGs indicated that prawns were more parasitized than lobsters.

Parasite intensity and diversity among landing sites

There was no significant difference in parasite intensities among landing sites (p>0.05) (Table 2). A significant difference in means among the landing sites was noted in *E. coli* (p =0.05). The diversity of parasites was not dependent on landing sites, since all sites had a diversity index of 0.00 (Fig. 4).

Parasite intensity and diversity between seasons

The student t-test showed a significant difference in parasite intensity between the two seasons in all the parasites (p<0.05) and no significance in the protozoa *E. coli* (p=0.59) (Table 3). The diversity of parasites does not depend on the seasons since both seasons had a diversity index of 0.00 (Fig. 5).

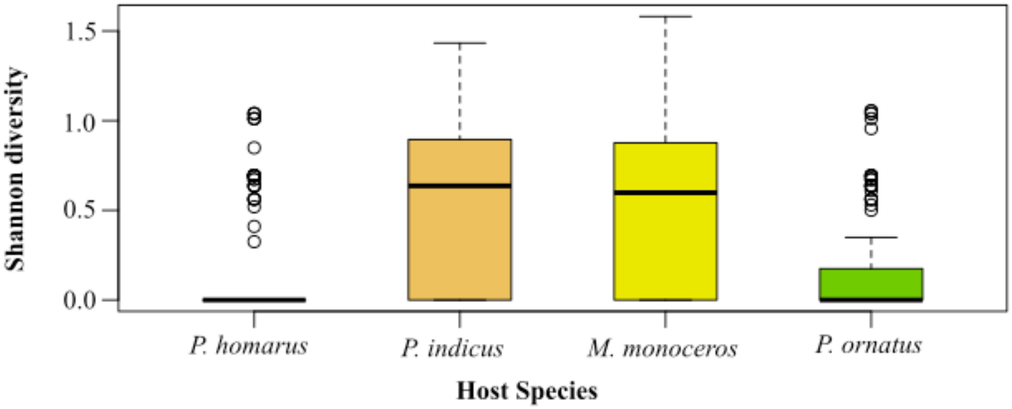

Figure 3. A boxplot showing parasite diversity among the host species of prawns and lobsters.

Table 2. Mean egg per gram (EPG) ± standard deviation (SD) results and analysis of variance results for a test conducted to compare means in parasite intensity among landing sites.

Parasite	Mean EPG ± SD in Mijikenda (n=160)	Mean EPG ± SD Kilifi Central (n=160)	Mean EPG ± SD in Gazi (n=160)	df	F	*p*-value
Strongyloides spp	93.33 ± 50.68	103.57 ± 48.63	86.84 ± 43.00	2	1.31	0.27
Schistosoma mansoni	113.33 ± 54.77	107.41 ± 50.85	116.67 ± 57.15	2	2.01	0.14
Hymenolepis nana	97.06 ± 53.57	108.11 ± 52.06	109.38 ± 48.26	2	0.35	0.70
Entamoeba coli	79.55 ± 49.96	75.00 ± 41.00	71.43 ± 32.31	2	3.13	**0.05**
Hymenolepis diminuta	113.46 ± 52.07	100.00 ± 50.00	102.63 ± 51.92	2	1.30	0.27

Discussion

Gastro-intestinal parasites found were zoonotic helminths, which cause diseases in humans and animals. An increase in helminth burden causes manifestation of the disease, leading to abdominal pain, nausea, weight loss, general body weakness, diarrhoea, blood in stool, loss of appetite and sometimes lymphedema, in extreme cases in humans (Bogitsh *et al.,* 2013). Presence of these parasites in prawns and lobsters could indicate their possible roles as reservoir hosts and faecal contamination of Kenyan marine waters.

Hymenolepis nana and *H. diminuta* are species of rodent tapeworms that cause Hymenolepiasis, using grain eating arthropods as intermediate hosts (CDC, 2021b). Human infections occur on ingestion of infected arthropod or insects (Panti-May *et al.,* 2020). Cysticercoids develop in intermediate hosts upon ingestion of mature eggs in faeces, passed by infected rodents or humans, and infect humans and rodents when the intermediate host is eaten, then develop into adults in the small intestines (CDC, 2021b). Eggs are released by gravid proglottids when they disintegrate in the ileum. In *H. nana*, autoinfection occurs when the eggs release their oncosphere embryo that penetrate the villus (Muehlenbachs, 2015). Infected insects could be eaten by amphibians, reptiles and humans, who then release eggs through faecal matter that finds its way into the ocean, infecting the prawns and lobsters.

Schistosoma mansoni is a parasitic flatworm that causes *Schistosomiasis*, also known as Bilharzia in humans, which has been categorised as a neglected tropical disease. More than 250 million people are infected, with 85 % occurring in Sub-Saharan Africa (Rinaldo *et al.,* 2021). Their presence in lobsters and prawns could also be a contributing factor for the highly prevalent parasitic infection. When eggs are released in faecal matter, they hatch into miracidia which penetrate snail tissues. In the snail, multiple generations of sporocysts and cercariae are produced, and upon release, the free swimming cercariae penetrates the skin of the human, shedding their tail to become schistosomulae and migrate to the lungs (CDC, 2021c). Adult worms migrate to blood vessels where females lay eggs that are released in stool or urine (WHO, 2021), depending on the parasite species. Infestation in prawns and lobsters could be by penetration of free swimming cercariae through the skin as observed in humans or when snails, which miracidia develops in, are eaten by prawns (Sokolow *et al.,* 2017). Symptoms of Schistosomiasis in humans include abdominal pain, blood in stool, hepatomegaly and splenomegaly (Rinaldo *et al.,* 2021). Lobsters infested with microsporidian parasites

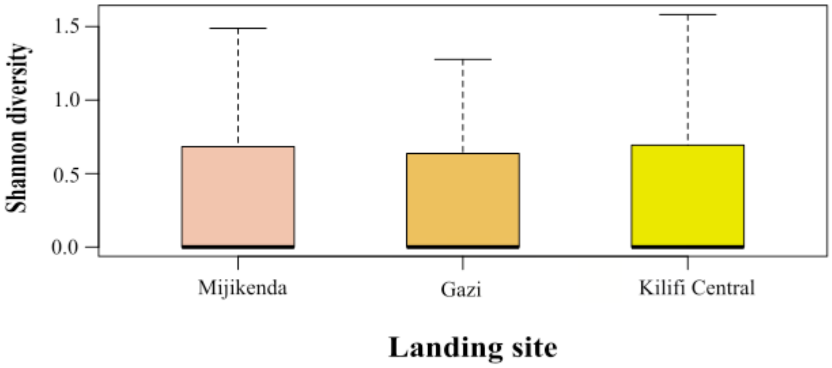

Figure 4. A boxplot showing the diversity of parasites among the landing sites.

Table 3. Mean egg per gram (EPG) ± standard deviation (SD) results and Student t-test results for a test conducted to compare means in parasite intensity between North East (NE) monsoon season and South East (SE) monsoon seasons.

Parasite	Mean EPG ± SD NE monsoon (n=240)	Mean EPG ± SD SE monsoon (n=240)	df	F	*p*-value
Strongyloides spp	96.58 ± 52.92	92.31 ± 40.08	478	7.28	**0.01**
Schistosoma mansoni	114.38 ± 55.58	110.39 ± 52.78	478	6.54	**0.01**
Hymenolepis nana	100.00 ± 51.51	109.43 ± 51.01	478	15.90	<**0.00**
Entamoeba coli	72.73 ± 39.71	78.79 ± 43.36	478	0.29	0.59
Hymenolepis diminuta	111.00 ± 52.77	97.94 ± 48.90	478	30.64	<**0.00**

have been found to be lethargic, with atypical external appearances like altered coloration and increased carapace opacity (Stentiford *et al.*, 2010). Gregarine parasites have been found in the prawn *Macrobrachium rosenbergii* (Zakariah *et al.*, 2022).

Strongyloides spp are parasitic nematodes that can be found in animals, insects, water, soil, fruits and vegetables (White *et al.*, 2019). There are over 50 species of these parasites affecting millions of people worldwide (Viney and Lok, 2015). These parasites live in the host's gut, where the females lay eggs that are passed through stool, where the eggs are eaten or larvae penetrate the skin to infect a new host (Viney and Lok, 2015). Presence of *Strongyloised spp* in prawns and lobsters indicate fecal contamination in this part of the Indian Ocean. The nematode *Strongyloides strercoralis* is the main source of infection in humans while *S. fuellerboni*, found in African primates, can also be transmitted to human hosts (Viney and Lok, 2015). Autoinfection also occurs in some species of *Strongyloides,* where eggs hatch in the host's gut, releasing larvae. The presence of a large number of primates living in mangroves along the Kenyan coast may explain the presence of *Strongyloides spp* in prawns and lobsters.

Entamoeba coli is a non-pathogenic protozoa transmitted though faecal exposure (Fotedar *et al.*, 2007), indicating that the Kenyan Indian Ocean contains human faecal contamination. Encystation occurs in the small intestine and the cystic eggs are passed through the large intestine into the environment, where transmission occurs by consumption of contaminated food or water (Haidar and De Jesus, 2021). Although non-pathogenic and asymptomatic in humans (Haidar and De Jesus, 2021), the effect of the protozoa on prawns and lobsters is yet to be studied. Most of the microscopic parasites found are zoonotic faecal parasites, suggesting faecal contamination in these coastal waters. Polyparasitism observed is likely to accelerate the decline in host health, reproductive ability and lifespan.

Parasite diversity and means in prawn species were higher than those in lobsters. This may be due to the ability of prawns to feed on some intermediate hosts of like snails that are known to carry numerous parasites like *Schistosoma* spp (Sokolow *et al,* 2017). This phenomenon has led to the introduction of prawns and crayfish in water bodies to reduce the prevalence of bilharzia (Swartz *et al,* 2015). The prawn's softer exoskeleton, compared to the lobster's, could also be

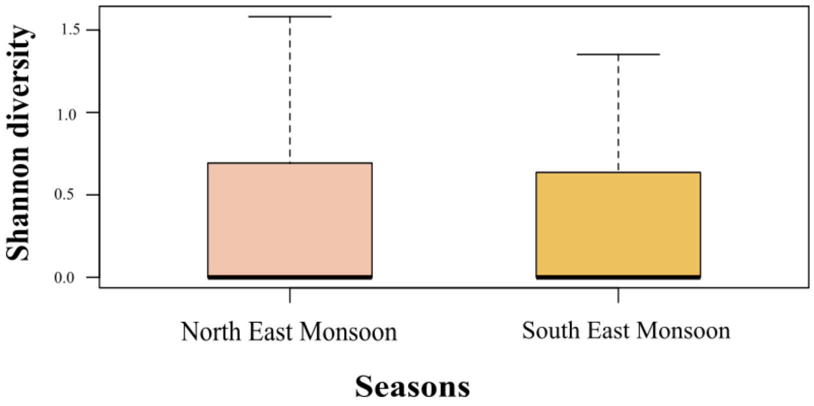

Figure 5. A boxplot showing the diversity of parasites between seasons.

a factor, making it easier for the cercariae to penetrate their bodies in the same way they penetrate the skin of a human host.

While Malindi is a densely populated town in the north coast of Kenya and Kilifi is moderately populated, Gazi is a small, sparsely populated fishing village on the south coast of Kenya. Sewage and garbage from the more populated towns of Malindi and Kilifi easily gets into the ocean, causing introduction of human parasites, like *H. nana, E. coli* and *H. diminuta.* Presence of the same parasites in the fishing village of Gazi could be due to the tendencies of the locals, who use mangroves as lavatories during low tides, and during high tides, the faecal matter is washed into the ocean and parasites introduced into the benthic prawns and lobsters. Monkeys and other primates, which have been recorded to be hosts to several parasites (Teklemariam *et al.,* 2018), are present in abundance, especially in mangroves along the coast of Kenya, increasing the chances of faecal contamination of the ocean.

Parasites found in the prawns and lobsters of Kenya marine waters are zoonotic, causing infections in humans. Early infections in humans are asymptomatic, making it hard to diagnose infected individuals while allowing the parasites to multiply. Measures taken to control these parasites include public health awareness campaigns, where individuals are educated on the risks they face and roles they play in the spread of schistosomiasis. Avoiding contact with contaminated water (CDC, 2021c) is also recommended but impractical for some populations like fishermen. Therefore, preventive chemotherapy using repeated mass drug administrations of antihelminths like praziquantel, administered at a dosage of 40 mg per kg of body weight, for at-risk individuals like fishermen, children and women, who may get infected when carrying out domestic chores (Inobaya *et al.*, 2014), has been introduced. Praziquantel, however, only targets the adult worm and does not protect against reinfection (Li *et al.,* 2019), and therefore drinking boiled water in endemic areas and proper washing and cooking of food (CDC, 2021c) is recommended alongside the other control strategies.

Significant differences in parasite intensity between seasons, with more parasite mean EPGs in samples collected during the NE monsoon than those collected during the SE monsoon, could be due to the high productivity associated with the high chlorophyll content of the water during the NE monsoon season due to river runoff after the long rains (Heip *et al.,*1995). High productivity may also lead to increased parasite populations in other marine organisms.

Conclusions

All parasites infesting the prawns and lobsters in this study are zoonotic and this is likely to impact on their commercial value as well as causing infection to human consumers. The parasites are also likely to affect the growth rate of the crustaceans hence also reduce the commercial value. This situation calls for the Ministry of Health to put in place control measures to reduce transmission from these hosts, especially during NE monsoon season since this is when the parasite abundance is highest in the most affected sites. Since very few studies have been done on prawn and lobster parasites, especially the intestinal ones, parasites found were identified using guides available. Metabarcoding should done to check for species integrity and to find out if there are new parasites in prawn and lobster faecal samples collected during this study and preserved at -80 °C for future analysis.

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Original Article

Free-living marine nematode communities in a *Rhizophora mucronata* Lam. (Rhizophoraceae) forest at Mida Creek, Kenya

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Abstract

Nematodes are among the most abundant organisms in marine ecosystems where they play a critical role in nutrient cycling, provision of nourishment to the higher organisms in the food web, pest control, and act as disease-causing vectors. This study determined the abundance and community structure of nematodes in three plots of *Rhizophora mucronata* forest stand at Kirepwe Macho and Dabaso sites at Mida Creek, Kenya. Replicated sediment samples were randomly collected from one forest plot in Kirepwe Macho and two plots in Dabaso during the months of January and April 2011. Total organic matter, sand and silt proportions were not significantly different across the study sites and between January and April. A total of 90 and 81 nematode genera were encountered in the month of January and April, respectively. At both sampling times, the nematode community was dominated by *Terschellingia* (20.5 %-15.3 %) and *Paracomesoma* (10.6 %-6.6 %). The Shannon-Weiner diversity index was relatively high in the three forest plots both in January and April ranging from 2.76 to 3.40. There was no significant difference in nematode community assemblage within sites (p>0.05, 0.901) but there were differences between sampling time (p>0.05, 0.001). The results showed that the three sites had similar nematode community structure suggesting that the three *Rhizophora mucronata* mangrove forest plots did not differ in terms of nematode generic composition even though the plots were not all close to each other.

Keywords: mangroves, *Rhizophora mucronata*, free living nematodes, diversity, nematodes community structure, Mida Creek

Introduction

Mangroves are woody halophytic plant communities which are found in tropical and sub-tropical regions worldwide (Giri *et al.*, 2011). They offer a wide variety of goods and services including food, timber, dyes, medicine, carbon sequestration, land accretion, pollution control, animal habitat and coastal protection from tsunamis, cyclones, floods and tidal inundations (Hogarth, 2015). Initially, three quarters of all tropical and sub-tropical coastal regions were occupied by mangroves, but currently more than half of the mangrove forests are degraded (Shapiro-ilan *et al.*, 2012). These forests are globally threatened, and it is estimated that 1-2 % of global cover is lost every year (Duke *et al.*, 2007; Giri *et al.*, 2011). This trend varies from region to region and differences might be caused by proximity to urban areas which leads to deforestation to create room for a growing population (Lee *et al.*, 2014). However, forest cover increase has recently also been documented in some areas across the globe

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(Saintilan *et al.*, 2014; Giri *et al.*, 2015). Kenyan mangrove ecosystems have declined at a rate of 0.7% per year between 1985 and 2010 leaving the current acreage to be 45,590ha (Kirui *et al.*, 2013). The decline was accelerated by overharvesting of mangrove products, change of land use and weak policies (Kirui *et al.*, 2013; Ashton, 2022). However, recent efforts to rehabilitate mangroves has received attention and placed Kenya in the lime light as hosting the world's first conservation project to link mangrove forests to the global carbon market (Cameron *et al.*, 2019).

Muddy sediments associated with mangroves provide an important habitat for benthic communities, especially the meiofauna (< 1mm and > 38 µm) which is well represented by nematodes making up > 80% of the total meiofauna community (Portnova, *et al.*, 2017). Meiofauna, and especially nematodes, represent the most abundant benthic metazoan organisms (Venekey *et al.*, 2010) in organically enriched sediments with low oxygen levels such as mangrove sediments. Nematoda, usually referred to as roundworms, are a diverse animal phylum inhabiting a broad range of ecosystems from polar regions to the tropics, marine to fresh water, mountain tops to ocean trenches (Gaston *et al.*, 1997; Ramirez-Llodra *et al.*, 2010). They are ubiquitous in freshwater, marine, and terrestrial environments, where they often outnumber other animals in both numbers and species count (Abebe *et al.*, 2008). They represent 90 % of all animals on the ocean floor (Jairajpuri and Ahmad, 1992; Hourston *et al.*, 2009) and numerically often exceed a million individuals per square meter (Blome and Faubel, 1996; Bongers and Bongers, 1998). They play crucial ecological role as a food source for higher trophic levels (Alves *et al.*, 2013) while they are important in the decomposition of organic matter and soil bioturbation (Hourston *et al.*, 2009; Schratzberger and Ingels, 2018).

Nematodes are classified in three broad groups depending on their source of food. Plant parasitic nematodes feed on plants, entomopathogenic nematodes feed on insects' larvae and free-living nematodes feed on bacteria, fungi, and some are predators. The free living nematode community structure and composition varies depending on sediment composition, water depth, oxygen levels (direct or indirect), hydrodynamic disturbances (Ingels *et al.*, 2009) and food availability (Muthumbi *et al.*, 2004; Leduc *et al.*, 2014). Within marine environments, free-living nematodes are recognized as the most abundant invertebrate group in sediments and the dominant taxon in heavily polluted habitats (Coull and Chandler, 1992). Despite their similar basic morphology, they perform different roles and occupy distinctive trophic levels in the sediments where many species feed on bacteria, algae, detritus and dissolved organic matter (Alongi *et al.*, 1993; Schmid-Araya and Schmid, 2000). Nematodes also are used for fishing bait, control of pests and can be disease-causing vectors, while a considerable number form prey for larger animals (Schmid-Araya *et al.*, 2002). Thus, the high functional and structural diversity of nematodes makes them very versatile and able to survive in diverse environments, including in polluted areas. They have thus been proposed within the Water Framework Directive (Lepper, 2005) as tools for evaluating the ecological quality status of vulnerable marine ecosystems (Baan, *et al.*, 2013).

Researchers have focused on topics relating to mainstream ecology such as latitudinal patterns of biodiversity (Mokievsky and Azovsky, 2002; Gobin and Warwick, 2006), links between taxonomic diversity, functional traits (Schratzberger *et al.*, 2006) and ecological factors driving the structure of assemblages of nematodes (Hua *et al.*, 2009). Changes in structure and composition of nematode communities are mainly correlated to sediment composition, but especially food, oxygen and salinity determine the species composition of these communities (Ingels *et al.*, 2009). According to Abebe *et al.*, (2008) and Pinto *et al.*, (2012), diversity of marine nematodes has been proven to be high in mangrove ecosystems compared to other benthic taxa. However, the patchy distribution patterns of nematodes in different microhabitats are yet to be explored. Knowledge on nematodes distribution in different microhabitats will provide a baseline for mangrove conservation measures using the meiofauna community as a proxy for the sediment conditions representing a major component of marine biodiversity. Little is known about free living nematode distribution in specific mangrove forest areas related to specific tree species.

This study focused on the spatial and seasonal variability in the nematode communities of the *Rhizophora mucronata* Lam. single species mangrove forest in Mida Creek on the north coast of Kenya.

Materials and methods

Description of the study area

The study was conducted in Mida Creek (3°23' S 39°56' E) located east of Arabuko Sokoke forest, 20 km southwest of Malindi town and 15 km from Watamu town (Fig. 1). It is an extensive area of 31.6 km^2 consisting of a tidal inlet, sand and mud flats, located near Dabaso village (Kairo *et al*., 2002). This is one of the most productive mangrove regions and has been recognized as an international bird area where waders, kingfishers, waterfowls, crab plovers and migrating birds from Europe and Eurasia overwinter (Frank *et al*., 2017). Together with Arabuko Sokoke forest, Mida Creek forms a UNESCO Biosphere Reserve. Mida Creek is characterized by two rainy seasons; a short rainy season from October till December and a long rainy season from April to June with temperatures ranging from 22°C to 31°C (Kenya Meteorological Department). The mangrove area in the creek is estimated to cover 1757.8 ha (Cohen *et al*., 2013) comprising seven species of mangroves with *Ceriops tagal*, *Rhizophora mucronata* and *Avicennia marina* as the dominant species (Gang and Agatsiva, 1992). Mida Creek forest mangrove coverage consists of mixed species zones. *Avicennia marina - Lumnitzera racemose - Xylocarpus granatum species tend to* occupy the landward side, *Rhizophora mucronata - Bruguiera gymnorhiza - Ceriops tagal species* occurs mainly in the middle zone, while *Sonneratia alba - Rhizophora mucronate - Avicennia marina* occurs on the seaward side (Ruwa, 1993).

Figure 1. Map of the Mida Creek study site, showing the location of the sampling stations (Kir Mac-Kirepwe Macho, Dab For 1-Dabaso 1 and Dab For 2-Dabaso 2).

Sampling

Sampling was conducted in the months of January and April 2011 during the spring low tide. Two study sites, Kirepwe Macho and Dabaso, were selected in Mida Creek since they had monospecific stands of *Rhizophora mucronata*. Dabaso forest was composed of mature *R. mucronata* trees with no undergrowth of young trees. Two adjacent stations (20 m apart) separated by a small channel were selected (Dabaso 1 and Dabaso 2). The third station was situated in Kirepwe Macho and had mature *R. mucronata* trees with an undergrowth of young trees. Three sediment cores were collected randomly at each sampling station using transparent Perspex tubing of 3.6 cm diameter, pushed 10 cm deep in the sediment during low tide and preserved with 5 % buffered formaldehyde solution.

Nematode extraction

The meiofauna samples were rinsed and sieved through a 1 mm sieve and collected on a 38 µm mesh size sieve. The samples were then centrifuged twice at 6000 rpm using magnesium sulphate of 1.25 specific density and once using specific density of 1.28. The supernatant was rinsed and preserved with 5 % buffered formaldehyde solution and stained with three drops of Rose Bengal overnight. Using a dissecting microscope, a minimum of 200 nematodes were picked from each

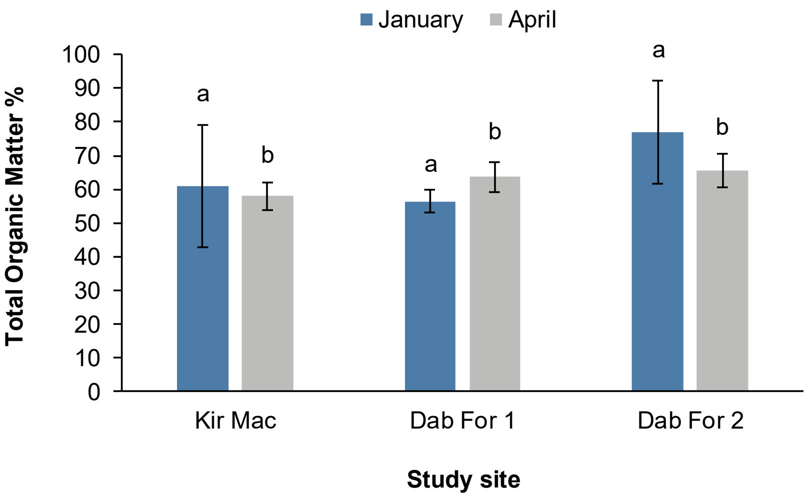

Figure 2. Total organic matter percentage from Mida Creek sampling stations (Kir Mac-Kirepwe Macho, Dab For 1-Dabaso 1 and Dab For 2-Dabaso 2) for the two sampling months (January and April). Values represent mean ± standard error for three replicates. For each sampling site, means with the same letter have no significant difference (P>0.05, Turkey test).

sample, processed and mounted onto permanent glass slides (Somerfield and Warwick, 1996).

Nematode identification

Identification of nematodes to genera was carried out with a compound microscope equipped with a X 100 oil immersion lens, and identification keys of Platt and Warwick (1988).

Statistical analysis

The Shannon-Wiener diversity index (H), Evenness_ e^H/S and species richness was calculated using PAST software (Hammer *et al.*, 2001). Two-way Analysis of Variance (ANOVA) was used to determine the difference in the total organic matter, grain size, nematodes diversity, evenness and sampling time differences among the three sites. Community assemblage was analyzed using Multidimensional scaling on Plymouth Routines in Multivariate Ecological Research (PRIMER) software (Clarke and Warwick, 2001).

Results

Abiotic parameters

Total Organic Matter (TOM)

In January, Dabaso 2 recorded the highest TOM (77 %) followed by Kirepwe Macho (61 %) and Dabaso 1 had the least organic matter (56 %). Similarly, in April, Dabaso 2 recorded the highest TOM (66 %), followed by Dabaso 1 (64 %) and Kirepwe Macho (58 %) (Fig. 2). The mean TOM content was not significantly different during the month of January (P value=0.242) and April (P value=0.194) in Kirepwe Macho, Dabaso 1 and Dabaso 2.

Grain size

January samples had the highest sand percentage recorded in Kirepwe Macho (74 %) followed by Dabaso 2 (66 %) and finally Dabaso 1 (65 %). Silt proportion was highest in Dabaso 1 (35 %) followed by Dabaso 2 (34 %) and Kirepwe Macho recorded the lowest silt proportion (26 %) (Fig. 3). There was no significant difference between sand and silt proportion in all study sites (P value=0.132).

April samples recorded the highest sand percentage in Kirepwe Macho (67 %), followed by Dabaso 1 (62 %) and Dabaso 2 (59 %). Silt proportion was highest in Dabaso 1 (41 %) followed by Dabaso 2 (38 %) and finally Kirepwe Macho (33%) (Fig. 3). There was no significant difference between sand and silt proportion in all study sites (P value=0.073).

Biotic parameters

Nematode composition and abundance

A total of 121 nematode genera from 31 families were encountered in the *R. mucronata* forest in the two study sites during the sampling period in Mida Creek. For the month of January, 90 nematode genera belonging to 25 families were encountered (Fig. 4 and Table 1). The family Linhomoidea recorded the highest relative abundance ranging between 27.1-31.5 % in the three stations followed by Desmodoridae (10.4-18.4 %) and Comesomatidae (10.3-17.1%). The three families cumulatively accounted for 56.1 % while the other 22 families accounted for 43.9 % (Table 1). The 14 most abundant genera accounted for 80 % of the nematode community in

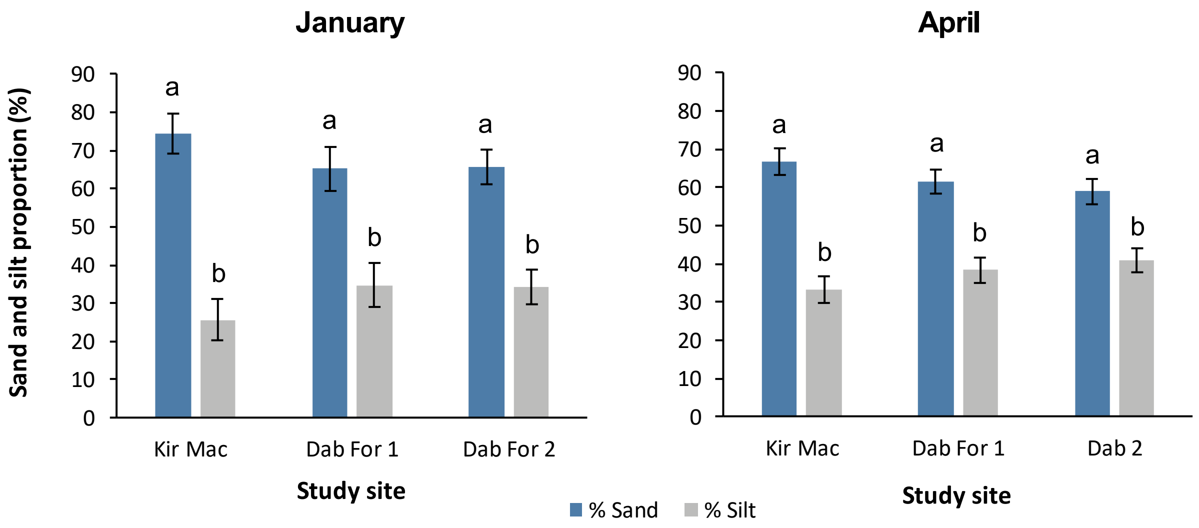

Figure 3. Sand and silt percentage proportion from Mida Creek sampling stations (Kir Mac-Kirepwe Macho, Dab For 1-Dabaso 1 and Dab For 2-Dabaso 2) for the two sampling months (January and April). Values represent mean ± standard error for three replicates. For each sampling site, means with the same letter have no significance different (P>0.05, Turkey test).

Kirepwe Macho, 70 % in Dabaso 1 and 60 % in Dabaso 2 (Fig. 4). The most abundant genera were *Terschellingia* with the highest relative abundance of all genera (between 18 % to 25 %) in the three forest plots (Fig. 4) followed by *Paracomesoma* (5%-8%) and *Spirinia* (1 %-5 %). The rest of the genera had less than 3 % abundance in each station.

In the month of April, a total of 81 genera belonging to 28 families were encountered. Desmodoridae was

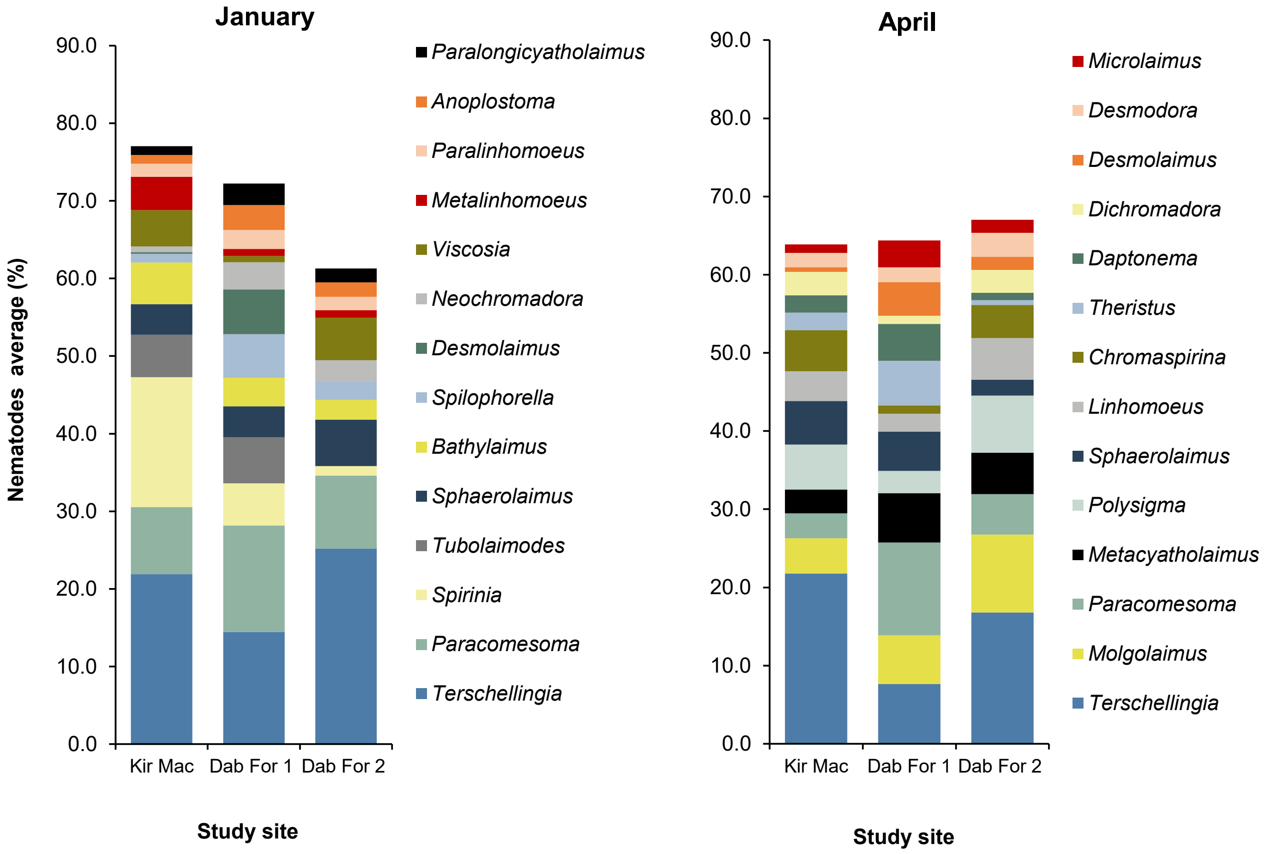

Figure 4. Percentage average of nematode genera from Mida Creek sampling stations (Kir Mac-Kirepwe Macho, Dab For 1-Dabaso 1 and Dab For 2-Dabaso 2) for the two sampling months (January and April).

Table 1. Percentage averages of nematode families in three sampling stations in the month of January and April. Kir Mac-Kirepwe Macho, Dab For 1-Dabaso 1 and Dab For 2-Dabaso 2.

	Sampling stations					
	January			April		
Nematode Families	**Kir Mac**	**Dabaso For 1**	**Dabaso For 2**	**Kir Mac**	**Dabaso For 1**	**Dabaso For 2**
Linhomoeidae	31.5	27.1	30.0	30.0	16.1	25.8
Desmodoridae	18.4	12.0	10.4	18.7	14.8	30.9
Comesomatidae	10.3	17.1	11.6	4.3	16.3	10.8
Chromadoridae	10.8	8.0	9.6	4.6	6.0	6.5
Spaerolaimidae	3.9	4.0	6.0	5.6	5.0	2.0
Oncholaimidae	4.9	1.0	6.5	0.3	0.8	0.4
Tripuloididae	5.4	3.7	2.6	1.3	1.3	1.4
Tubolaimoididae	5.5	5.9	0.0	0.0	0.0	0.0
Xyalidae	2.2	3.6	5.3	5.2	12.6	2.6
Hypodontolaiminae	1.1	5.6	2.3	1.2	3.0	1.0
Cyatholaimidae	2.0	3.6	2.9	10.5	8.6	10.4
Anoplostomatidae	1.1	3.2	1.9	2.8	1.3	0.9
Selachinematidae	0.4	0.6	3.4	3.1	1.3	1.4
Oxystominidae	0.4	0.4	1.8	0.7	0.2	0.7
Anticomidae	0.0	0.0	1.7	0.6	0.0	0.0
Axonolaimidae	1.5	0.4	0.0	0.0	0.2	0.0
Microlaimidae	0.0	0.4	1.4	1.3	3.4	1.7
Ironidae	0.2	0.2	1.1	2.0	0.5	0.6
Leptolaimidae	0.0	1.5	0.0	0.0	3.6	0.0
Enchelidiidae	0.0	0.6	0.6	1.1	0.0	0.5
Monhysteridae	0.0	0.2	0.5	0.3	0.5	0.0
Neotonchidae	0.2	0.0	0.2	0.8	2.6	0.2
Paramicrolaimidae	0.0	0.4	0.0	0.0	0.0	0.0
Rhadinematidae	0.0	0.2	0.0	0.0	0.0	0.0
Camacolaimidae	0.0	0.2	0.0	0.0	0.0	0.7
Haliplectidae	0.0	0.0	0.0	1.8	0.0	0.0
Trefusiidae	0.0	0.0	0.0	1.8	0.0	0.0
Aponchiidae	0.0	0.0	0.0	0.0	0.5	0.9
Monoposthiidae	0.0	0.0	0.0	0.0	0.8	0.0
Phanodermatidae	0.0	0.0	0.0	0.4	0.2	0.0
Desmoscolecidae	0.0	0.0	0.0	0.0	0.0	0.4

the most abundant family ranging between 14.8-30.9 % in the three forest plots followed by Linhomoidae (16.1-30 %) and Comesomatidae (4.3-16.3%). The three families accounted for 54.9 % cumulatively while the other 25 families accounted for a total of 45.1 % (Table 1). *Terschellingia* was the most abundant genus with relative abundance between 5 % and 15.3 % in the three forest plots (Fig. 4) followed by *Molgolaimus* at 4 % to 10 % and *Paracomesoma* at 2 % -12 %. Other genera had less than 4 % of the total relative abundance each.

Nematode community assemblages (based on Multidimensional scaling-MDS plots) from the three forest plots did not show differences between sampling sites (R = 0.5; P = 0.901), however, there was a significant difference (R = 1; P =0.001) between the nematode community encountered in January and in April (Fig. 5). Analysis of Similarities (ANOSIM) results illustrated no statistical differences among sites (R = -0.5; P value=1) while there were statistical differences between sampling times (R = 1; P value=0.001).

Nematode diversity and evenness

The Shannon-Wiener diversity index (Fig. 6) showed that both Dabaso plots had a similar diversity index of between 3.3 and 3.4 in both sampling times (January and April). Kirepwe Macho Forest recorded a diversity of 2.8 in January and 3.3 in April. Analysis of variance showed no significant difference between forest stands in terms of diversity indices indicating that the three study sites and sampling times had very similar diversities (P value = 1.00, 0.99) respectively. The nematode community was relatively even with the January evenness ranging from 0.38 to 0.50 while that in April ranged from 0.48 to 0.56 (Fig. 6).

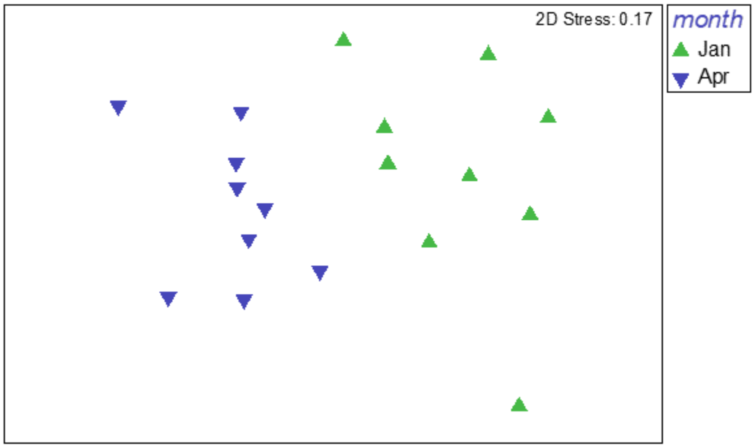

Figure 5. Non-Metric Multidimensional scaling plot of nematode community assemblage in January and April based on square root transformed data.

Discussion

In general, the factors that play a significant role in nematode community distribution include organic litter (Rahman *et al.*, 2014), sediment depth, oxygen levels (Muthumbi *et al.*, 2011), sediment composition (Adão *et al.*, 2009), macro- and meiobenthos interactions (Schrijvers *et al.*, 1995; Carlén and Ólafsson, 2002) and mangrove species (Torres-Pratts and Schizas, 2007). This study recorded similar TOM, sand and silt proportions in all sites, and this could be attributed to sites having the same species and being in the same general location with minimum interference by human activities. Kyalo (2016) recorded higher TOM in Mida sediments compared to Gazi Bay in Kenya, and a higher productivity in Mida Creek leading to a high diversity of nematodes. Additionally, Mida Creek sediments were mainly sandy, and these results aligned with *R. mucronata* sediments studied by Kyalo (2016).

The sediments of *R. mucronata* mangrove plots in Mida Creek were characterized by taxonomically rich nematode communities similar to other mangrove areas worldwide (Table 2). Vietnam, Brazil and some parts of India recorded slightly lower numbers of nematode families and genera compared to Mida Creek (Mokievsky *et al.*, 2011; Pinto *et al.*, 2012).

The most abundant families in Mida Creek were Linhomoidea, Desmodoridae and Comesomatidae, in that order in all study sites and during the two sampling times (January and April). These results differed from those by Mokievsky *et al.* (2011) who encountered more Chromadoridae, Oncholaimidae and Zylidae families in Vietnam. India recorded Comesomatidae and Xyalidae as the most abundant families (Chinnadurai and Fernando, 2007). Itamara Island in Brazil recorded some similarities where Chromadoridae,

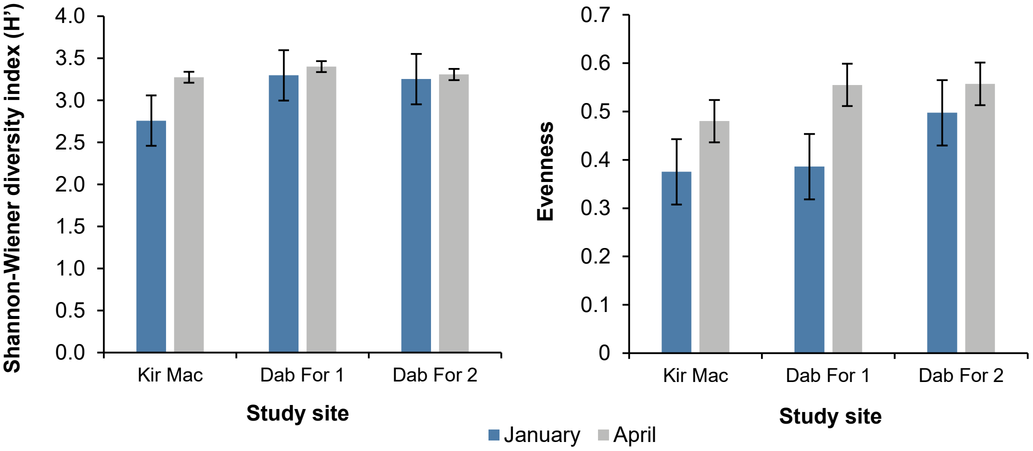

Figure 6. Nematode genus Shannon-Wiener diversity index (H') (on the left) and Evenness (on the right) in January and April sampling months at Mida Creek sampling stations (Kir Mac-Kirepwe Macho, Dab For 1-Dabaso 1 and Dab For 2-Dabaso 2). Values represent mean ± standard error for three replicates. For each sampling site, means with the same letter have no significance different (P>0.05, Turkey test).

Table 2. Nematodes distribution in mangrove forest sediments (Rhizophora spp.) from different locations in the world.

Mangrove species (ecosystem)	Country	Families	Genera	Author	GPS Co-ordinates
Aegiceras corniculatum, *Avicennia marina,* *Bruguiera gymnorrhiza,* *Kandelia obovata,* *Rhizophora stylosa,* and *Sterculia apetala.*	South China	-	67		Lat. 20°15´-21°55´N; Long. 109°40´-110°55´E
Sterculia apetala and *Kandelia obovata*	South China	-	50		Lat. 24°38´-24°39´N; Long. 118°11´-118°12´E
Sediments dominated by *Avicennia marina* and *Rhizophora apiculate*	India	28	36	(Chinnadurai *et al.*, 2007)	Lat. 11°27´N; Long. 79°47´E
Avicennia aff. alba and *Rhizophora mucronata*	Vietnam	24	48	(Mokievsky *et al.*, 2011)	Lat. 12°12´N; Long. 109°11´E
Rhizophora mangle	Brazil	25	73	(Pinto *et al.*, 2012)	Lat. 7°46´S; Long. 34°52´W
Avicennia marina	India	18	27	(Ansari *et al.*, 2014)	Lat. 11°29´N; Long. 79°46´E
Rhizophora mucronata	India	18	25	(Ansari *et al.*, 2014)	Lat. 11°29´N; Long. 79°46´E
Rhizophora mucronata	Kenya	25	90	Present study	Lat. 3˚23´ S; Long. 39˚56´ E

Cyatholaimidae, Desmodoridae, Xyalidae, and Linhomoeidae were the dominant families (Pinto *et al.*, 2012). Other parts of Brazil recorded Chromadoridae and Linhomoeidae as the most dominant families. This results from this study showed some similarities with South Asia data where Linhomoidea, Comesomatidae and Desmodoridae were the most abundant families (Fu *et al.*, 2021).

Nematode diversity as indicated by the Shannon-Wiener diversity index were in a similar range as observed by Mokievsky *et al.* (2011) who found a value of 2.99 in *Rhizophora stylosa* sediments in Be River, central Vietnam. Forest stands of similar mangrove species had high benthic diversity dominated by nematodes which were the most abundant infauna organisms. Pinto *et al.* (2012) found a significant difference in nematode assemblage structure in different microhabitats (sandy mud, mud flat, cyanobacteria mat, *Rhizophora* mangle and pneumatophores). Nematodes are adapted to a vast range of ecosystems, but specific genera colonize suitable habitats with adequate resources. Regional variations of nematode distribution in mixed species mangrove forests were also noted in Zanzibar (Ndaro and Olafsson, 1999), India (Ansari *et al.*, 2014) and southern Vietnam (Xuan *et al.*, 2007). However, according to Ansari *et al.* (2014), there was no significant difference in nematode diversity between *Avicennia marina* and *R. mucronata* mangrove stands/forests.

In addition to only small taxonomical differences observed in terms of dominant nematode families and genera composition, the high abundance of Terschellingia is a common observation in many areas. Terschellingia was the most abundant genus in the three sampling stations and in both the month of January and April, while previous research has also shown that Terschellingia species survive well in hypoxic environments (Soetaert and Heip, 1995; Kotwicki et al., 2016), such as the organically enriched soft sediments in mangrove biotopes. The dominance of Terschellingia suggested that all stations sampled in this study had limited oxygen and that the present nematode communities had the ability to adapt and colonize hypoxic environments (Armenteros et al., 2009). The results from this study were only partly in accordance with observations in Rhizophora mangle sediments in Brazil (Pinto et al., 2012) and a R. stylosa habitat in Vietnam (Mokievsky et al., 2011) which recorded Terschellingia as the second most abundant genus after the genus Haliplectus, despite having the same mangrove genus of Rhizophora.

Seasonal changes in the ecosystem resulted in differences in recorded taxa which could be explained by abiotic and biotic variability (Venekey *et al.*, 2019; Ólafsson and Elmgren, 1997). The differences in nematode composition between the month of January and April as encountered in Mida Creek could be attributed to different factors such as temperature, food availability and salinity differences. The dry season recorded different nematode communities compared to the wet season which was contrary to the findings by Kyalo (2016) who found no seasonal differences, while Beier and Traunspurger (2003) did observe seasonal differences such as higher nematode densities in summer and low density during autumn and winter. Additionally, favorable hydrological conditions in the dry season like low water depth, slow water discharge to the ocean, sediment stability, high salinity and favorable temperatures for nematode metabolism are likely vital factors for nematode community stability in marine sediments compared to storm water disturbances, lower temperatures, reduced salinity and reduced water evaporation due to cloud cover during the wet season.

This study confirmed that similar mangrove habitats are likely to have similar nematode communities and diversity when the habitats are within the same location. Hence, it is possible to extrapolate the diversity and composition of nematodes, which are proxy for other ecosystem components, to larger forest areas in Mida Creek, particularly for *R. mucronata*, without the need for intensive sampling. However, it remains to be established how far apart similar habitats can be and still harbour similar nematode communities (genera distribution and diversity).

Most of the previous studies focused on mixed forest stands. There is a need to accumulate more data with pure forest stands in different mangrove regions to certify whether results vary with region. Similar experiments should be conducted in the remaining pure stands of mangrove species worldwide to determine whether the nematode community structure is affected by the mangrove tree species. This information will assist in conservation practices and governance of mangrove ecosystems in tropical and sub-tropical regions.

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Original Article

Seasonality of juvenile fish community structure and diversity in a tropical seagrass meadow at Watamu, Kenya

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Abstract

Seagrass are important marine habitats that function as nursery grounds for juvenile fish. Human activities and other natural factors have contributed to their decline, and this has compromised their role as nurseries, specifically in non-continuous patchy seagrass beds. In this study, juvenile fish abundance from tropical seagrass beds of Watamu were examined, while testing the hypothesis that seagrass cover and seasonality influenced juvenile fish abundance and diversity. Two sampling stations were identified, Watamu Blue Lagoon (WBL) and Watamu Beach (WB), based on seagrass cover, and were sampled for a period of 10 months that included two south-east monsoon (SEM) and two north-east monsoon (NEM) seasons. Monthly samples were collected by seining within the shallow seagrass habitats of WBL and WB. A total of 31 juvenile fish families were obtained, the dominant taxa being Lutjanidae and Siganidae. Seasonal and interannual variability in juvenile abundance was observed over the two years ($p<0.05$); year 1 recorded higher abundance than year 2, specifically during the SEM. In year 2 a higher mean abundance was recorded during the NEM when compared to the SEM. Chlorophyll *a* ($p<0.05$) and salinity ($p<0.05$) were found to significantly influence juvenile fish abundance.

Keywords: juvenile fish, seasonality, seagrass beds, abundance, diversity, Watamu, Kenya

Introduction

A nursery is a habitat that enhances growth and survival of juveniles and contributes to the recruitment of the adult population. A nursery also contributes to growth and maturity of juveniles before they are able to move to other habitats as sub-adults as well (Beck *et al.*, 2001; Parsons *et al.*, 2014). A suitable nursery allows connectivity between habitats enabling colonization by juveniles or larvae, migration of subadults to adult habitats, and adequate interaction within the community (Whitfield and Pattrick 2015; Berkström *et al.*, 2013; Irisson *et al.*, 2015). The proximity of seagrass beds to other habitats like coral reefs facilitates trophic transfers and cross-habitat utilization by fishes (Barnes *et al.*, 2012; Berkström *et al.*, 2013).

Shallow coastal habitats such as mangroves, seagrass beds and patch reefs, are important nursery habitats for fishes of economic and biodiversity importance (Igulu *et al.*, 2014; McDevitt-Irwin *et al.*, 2017;

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de Andrade-Tubino *et al.*, 2020). Seagrass beds in particular provide a structural complex of intertwined seagrass shoots that serve as nursery, providing shelter and protection of juveniles from predation (McCloskey and Unsworth, 2015). Dense seagrass cover also influences zooplankton and phytoplankton abundance, the major food source of ichthyoplankton, and plant detritus, thus attracting a greater assemblage of fauna (Gross *et al.,* 2017; Mateo and Tobias, 2008; Mwaluma, 2010; Parsons *et al.*, 2014). The shelter provided by shoot structure provide hiding spaces for larvae and juveniles because it limits movement and vision of larger predators (Gross *et al.,* 2019). This allows enough time for the development of larvae and juveniles, until they are able to migrate to a suitable adult habitat (Brown *et al.*, 2004; Berkström *et al.,* 2013; Igulu *et al.,* 2014). Seagrass beds are connected to other habitats, and thus create supportive conditions for marine organisms and fisheries in general (Cullen-Unsworth *et al.*, 2014). Seagrass therefore influence fish abundance, distribution, and their recruitment, supporting fish growth and survival through the pelagic larval phase (Berkström *et al.*, 2013).

It is hypothesized that dense seagrass meadows attract higher abundance of juvenile fish (Cullen-Unsworth *et al.*, 2014; McCloskey and Unsworth, 2015). However, due to both natural and anthropogenic disturbances, the distribution of seagrass has decreased by about 60 % globally since the 1980s (Copertino *et al.*, 2016; Soe-Htun, 2017). The same has been reported along the Kenyan coast where nearly half of the seagrass of Diani Chale lagoon was destroyed by sea urchin herbivory between 2001 and 2006 (Daudi *et al.,* 2013). Both natural and human activities are associated with decreasing seagrass cover, which subsequently compromise their nursery roles by limiting habitation of juveniles (McCloskey and Unsworth 2015; Moussa *et al.,* 2019).

Studies along the East African coast have concentrated on adult fishes in the seagrass habitats and mangroves (Kimirei *et al.,* 2011; Kimirei, 2012; Lugendo, 2007; Wainaina *et al.*, 2010; Kimani *et al.*, 1996; Huxham *et al.,* 2004, 2008). A few studies have identified the role that seagrass beds and mangroves can play in replenishing coral reef fish populations (Wanjiru *et al.,* 2021; Alonso *et al.*, 2014; Kimirei *et al.*, 2011; Lugendo, 2007). In most cases, the studies involving juvenile abundance have applied Underwater Visual Census including one that studied the distribution of juveniles in the rocky intertidal shallow habitats of Watamu Marine National Park (Igulu *et al.,* 2014; Kimirei *et al.*, 2011; Okemwa *et al.*, 2019; Sindorf *et al.* 2015). In the coastal Kenya, a study by Kimani *et al.*, (1996) was conducted at Gazi Bay, investigating fish communities using beach seines while another by Wanjiru *et al.* (2021) investigated the community structure of fishes and crustaceans in the Vanga mangrove ecosystem, Kenya, using fyke nets.

Higher fish catches and juvenile abundance have been reported during the NEM season in some studies (Okemwa *et al.*, 2019). Other studies have recorded high abundances of fish in the month of June, which falls in the SEM season (Kimani *et al.*, 1996). Environmental factors such as Chlorophyll-*a* and zooplankton abundance have been associated with fish abundance (Kamau *et al.*, 2021; Osore *et al.*, 2004; Kimani *et al.*, 1996).

In this study, a comparison of juvenile fish abundance and diversity was made between two sites in Watamu, with a null hypothesis that seasonality and abiotic factors do not influence fish juvenile abundance and diversity. A second objective was comparing juvenile abundance between the two sites at WBL and WB.

Methodology

Study area

The research was conducted in the Watamu Marine Reserve on the north coast of Kenya, which is adjacent to the Watamu Marine National Park. Both sites were enclosed lagoons with low uniform topography dominated by a mosaic of seagrass beds interspersed with varying seagrass cover. Two sites were identified as Site 1: Watamu Blue Lagoon coded WBL, which was composed of seagrass that was relatively continuous and with seagrass cover of 65 % and above. The dominant seagrass species were *Thalassodendron ciliatum* (Forsskål) which has average cover of 34 %. A second site was located at Watamu Beach coded WB, selected for comparison and termed as Site 2, was composed of seagrass cover of at least 62 %. The dominant seagrass species at this site were *T. ciliatum, Cymodocea rotundata* and *Halodule uninervis* which covered an average of 18 %, 17 % and 11 % respectively. The second site consisted of mixed meadows comprising of pioneer species that may have been as a result of previous reported urchin herbivory that had severely affected the region as evidenced by seagrass stumps seen during this study. The tidal cycle in both sites was mixed semidiurnal with two maxima and two minima per day with a tidal range of about 2.0 at the neap tide and 2.9 during spring tide (Mwaluma *et al.,* 2011).

Field procedures and laboratory analysis

In this study a beach seine was used for sampling as it is considered effective in sampling relatively shallow water, and effective in estimation of relative abundance (Hahn *et al.*, 2007). At both sites, juveniles were sampled using a seine net measuring 4 m in length, 2.5 m in height, and 1.5 cm mesh size. The sampled area was approximately 250 m^2. The area was determined by measuring length (50 m) and width (50 m), using a tape and marked with buoys. At each station, eight replicate samplings were randomly conducted within the measured perimeter. Sampling was done during spring low tide in the SEM months of July and August 2019/2020, and June, July, and August 2020/2021, and the NEM months (November, December, January) of 2019/2020 and 2020/2021. The net was laid perpendicular to the shore by two fishermen wading in the water on foot. The net was hauled towards the shore through a 90-degree arc against the current. Two more persons assisted the fishermen by lifting the net and collecting the fish after hauling. The same fishermen conducted the seining throughout the study period. The operation ranged between 20-30 minutes for a single haul. The total length of fish and the species name were taken before preservation in absolute alcohol. The fish species was recorded and the total length for each specimen was measured to the nearest 0.1 cm on a standard fish length measuring board before being preserved in absolute alcohol. The fish that were not identified at the site were coded and preserved for identification in the laboratory using Anam and Mostrada (2012), Heemstra and Smith (1986) and Lieske and Myers (2004).

The length at maturity for each fish species was checked before classifying it as a juvenile. The fish sampled were classified as juveniles only if (i) their length was less or equal to the minimum age at maturity, as reported in Fish Base (Froese and Pauly, 2016), and (ii) if their sizes were <25 % of maximum adult total length (Nagelkerken and Velde, 2002; Okemwa *et al.,* 2019).

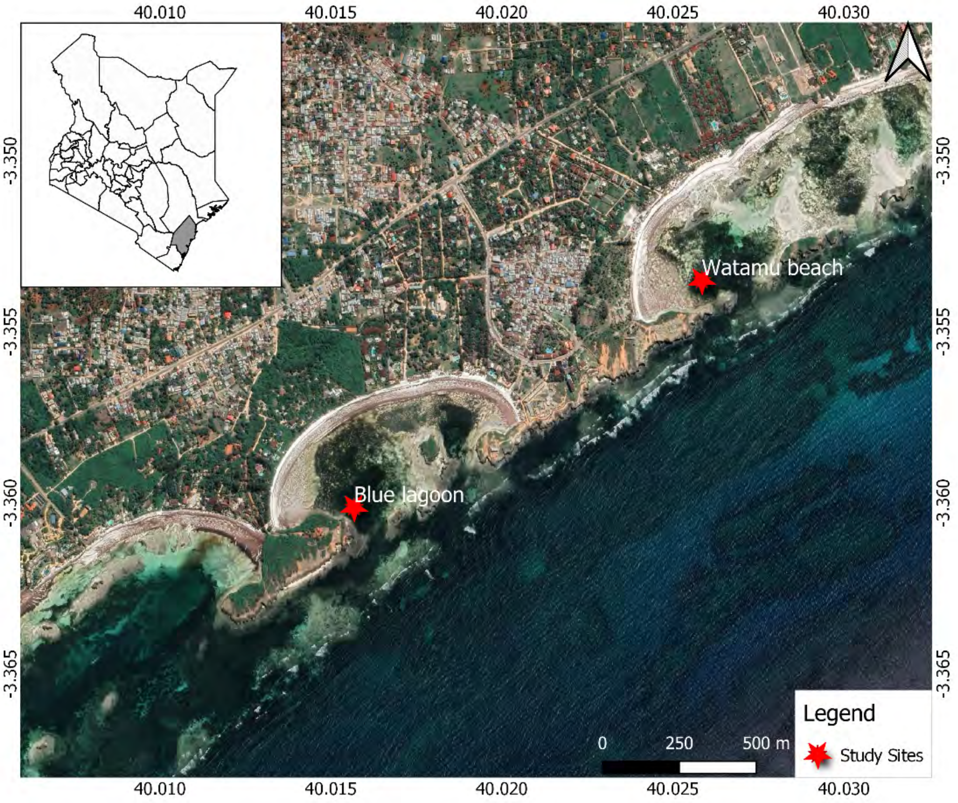

Figure 1. Map with the location of the study sites: Watamu Blue Lagoon (Site 1) and Watamu Beach (Site 2).

Water quality analysis

At each site, monthly water quality parameters (temperature, Chlorophyll-*a* and salinity) were measured. Water temperature and salinity were measured using a YSI multi-parameter probe, while for Chlorophyll-*a*, 5 L of seawater was filtered through 47 nm GFF filters.

In the laboratory, 10 mL of acetone was added to the filtrate and left overnight for the extraction process to take place. The contents were then centrifuged at 4000 rpm for 10 minutes. The absorbance was measured using a spectrophotometer (UV-S) at a wavelength 750 nm, with 90 % acetone used as a blank.

Data analysis

Shannon-Weiner diversity (H), Pielou's index of evenness (J), and Margalef's index of richness (d) were applied in the assessment of community biodiversity, calculated on the R studio package Vegan (version 2.5-6) (Oksanen *et al.*, 2013). Juvenile fish abundance was compared using PERMANOVA to test for differences between sites, months, and years. Community analysis was assessed using nMDS clusters. To ascertain the effect of biophysical factors on juvenile fish, stepwise generalized linear regression models (GLM) were used to obtain the significance and correlation coefficients of the interaction between juvenile abundance against temperature, salinity, and Chlorophyll-*a* (Martinez, 2016).

Results

Environmental variables

The environmental variables showed a significant variation between seasons and months. Temperature and salinity were highest during the NEM season months of November/December compared to the SEM months of June /July for both years (2019 and 2020) (Fig. 2).

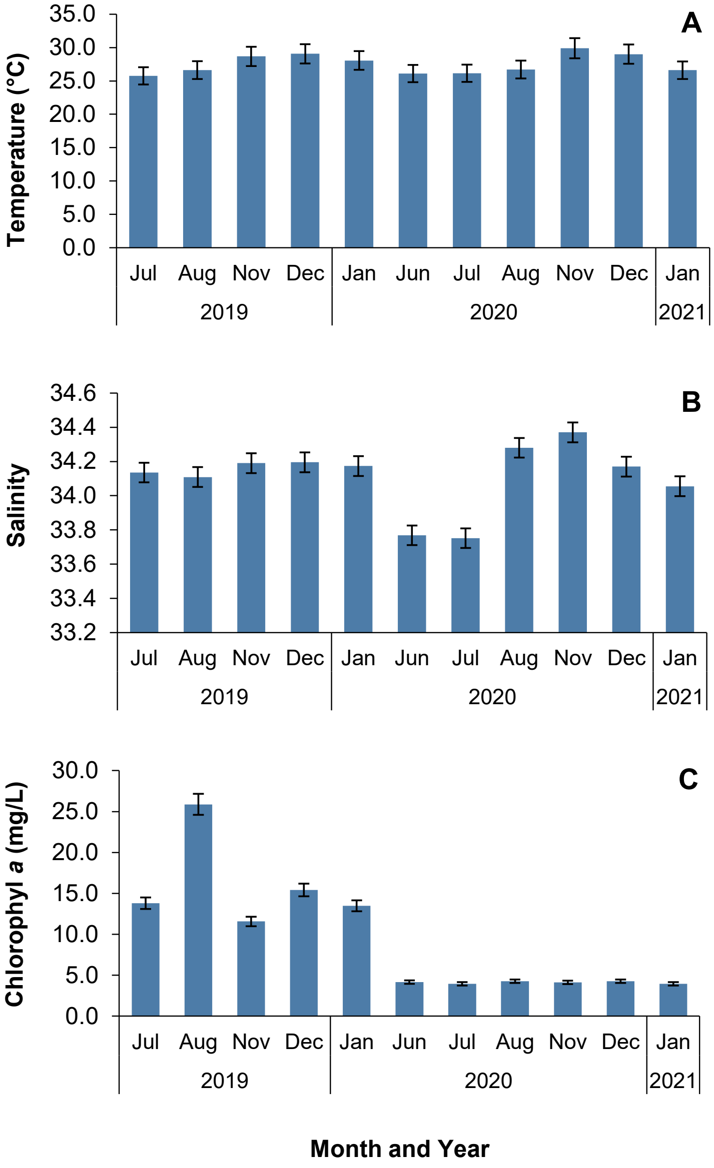

Figure 2. Mean monthly and seasonal variation in temperature (A), salinity (B), and Chlorophyll-a (C) measured between July 2019 and January 2021.

Table 1. The composition and abundance of juvenile fish found in Watamu Blue Lagoon (Site 1) and Watamu Beach (Site 2) sampled between July 2019 and January 2021.

		Blue Lagoon (Site1)		**Watamu Beach (Site 2)**	
Family	**Taxa**	**Abundance (n)**	**Size range (cm)**	**Abundance (n)**	**Size range (cm)**
Acanthuridae	*Acanthurus auranticavus* (Randall, 1956)	1	6.3	0	
	Acanthurus triostegus (Linnaeus,1758)	0	0	2	4.9-5.2
	Zebrasoma desjardinii (Bennett, 1836)	1	5.0	0	
Apogonidae	Apogonidae n.d.	1	4.8	0	
Belonidae	*Tylosurus crocodilus* (Péron & Lesueur, 1821)	7	15.0-30.0	0	
Diodontidae	*Diodon liturosus* (Shaw, 1804)	1	27.0	0	
Ephippidae	*Platax teira* (Forsskål, 1775)	2	8.9-11.8	11	4.0-13.0
Fistulariidae	*Fistularia commersonii* (Rüppell, 1838)	2	42.0 -52.0	0	
	Fistularia petimba (Lacepède, 1803)	4	18.0 -39.0	2	14.0-16.0
Gerreidae	*Gerres oyena* (Forsskål, 1775)	0		2	
Haemulidae	*Plectorhinchus schotaf* (Forsskål, 1775)	2	11.8-13.5	0	
Labridae	*Cheilinus oxycephalus* (Bleeker, 1853)	4	3.7-5.0	0	
	Cheilio inermis (Forsskål, 1775)	1	13.3	1	10.0
	Thalassoma hardwicke (Bennett, 1830)	0		1	7.0
Lethrinidae	*Lethrinus harak* (Forsskål, 1775)	13	4.9-13.0	6	5.0-15.5
	Lethrinus lentjan (Lacepède, 1802)	5	5.4-7.9	2	5.0-9.0
	Lethrinus mahsena (Forsskål, 1775)	1	8.0	2	7.0-8.9
	Lethrinus nebulosus (Forsskål, 1775)	1	10.0	2	7.0 -7.1
Lutjanidae	Lutjanidae n.d.	0		2	5.5-8.4
	Lutjanus fulviflamma (Forsskål, 1775)	26	5.2-10.6	60	4.0-11.5
Monacanthidae	*Amanses scopas* (Cuvier,1829)	1	5.3	3	3.0-4.0
	Monacanthidae n.d.	1	4.0	1	5.9
Mugilidae	*Crenimugil seheli* (Forsskål, 1775)	2	10.1-11.1	0	
Mullidae	*Mulloidichthys vanicolensis* (Valenciennes, 1831)	9	6.0-12.0	1	5.0
	Parupeneus macronemus (Lacepède, 1801)	1	9.0	0	
Ostraciidae	*Lactoria cornuta* (Linnaeus, 1758)	2	8.9-9.5	1	5.0
	Lactoria diaphana (Bloch & Schneider, 1801)	0		9	2.0-6.5
	Lactoria fornasini (Bianconi, 1846)	0		2	4.5-6.3
	Ostraciidae n.d	0		1	1.2
Plotosidae	*Plotosus lineatus* (Thunberg, 1787)	0		5	
Pomacentridae	*Abudefduf septemfasciatus* (Cuvier, 1830)	0		4	6.0 -6.5
	Abudefduf sexfasciatus (Lacepède, 1801)	0		2	6.0-7.0
	Abudefduf vaigiensis (Quoy & Gaimard, 1825)	3	5.0-5.7	1	5.0
	Dascyllus trimaculatus (Rüppell,1829)	2	2.0-3.8	0	
	Pomacentridae n.d.	3	9.2-10.0	0	
	Pomacentrus sp.	0		1	5.0
Scaridae	*Leptoscarus vaigiensis* (Quoy & Gaimard, 1824)	7	7.0-11.0	8	5.0 -9.5
Scorpaenidae	*Scorpaenopsis oxycephala* (Bleeker, 1849)	0		5	4.2-6.2
	Scorpaenopsis venosa (Cuvier, 1829)	0		1	5.0
Siganidae	*Siganus luridus* (Rüppell, 1829)	0		1	4.0
	Siganus sutor (Valenciennes, 1835)	38	3.4-12.2	30	4.1-10.6
Soleidae	*Pardachirus marmoratus* (Lacepède, 1802)	0		1	5.6
Sphyraenidae	*Sphyraena jello* (Cuvier,1829)	1	13.5	0	
Syngnathidae	*Syngnathus acus* (Linnaeus, 1758)	0		3	11.8-13.5
Tetraodontidae	*Canthigaster valentine* (Bleeker, 1853)	1	6.0	1	4.0
	Tetraodon lineatus (Linnaeus, 1758)	0		1	8.0
Tetrarogidae	*Ablabys macracanthus* (Bleeker,1852)	0		1	4.2

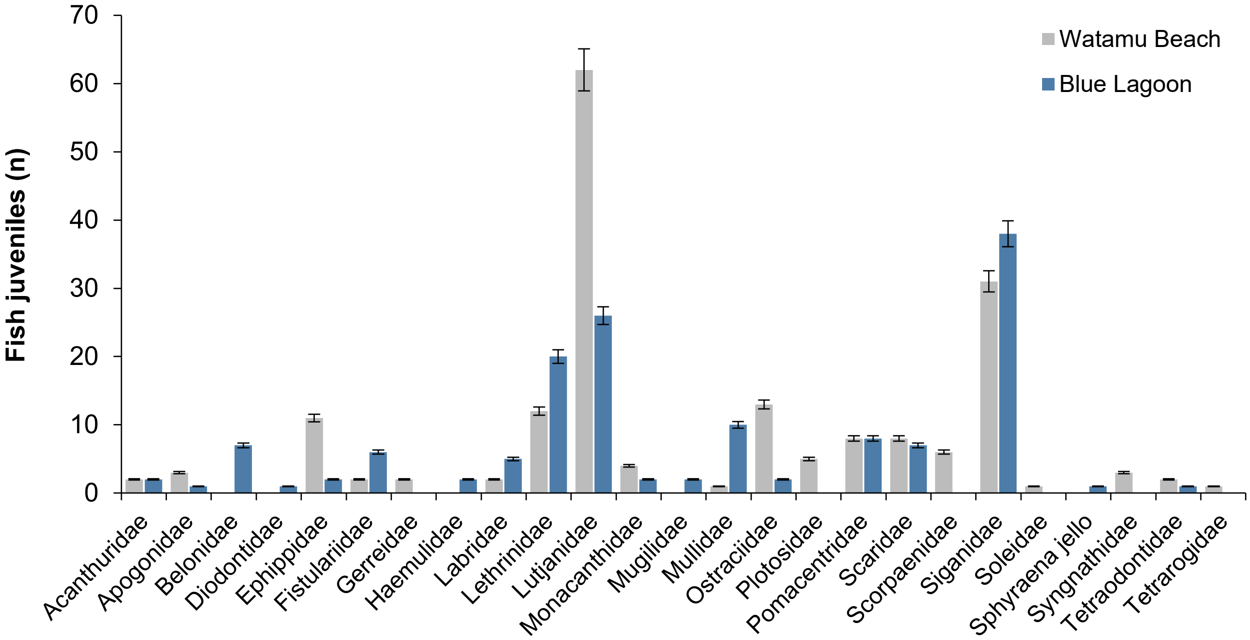

Figure 3. Distribution of juvenile fish families in Watamu Blue Lagoon (Site 1) and Watamu Beach (Site 2).

Chlorophyll-*a* on the contrary was highest during the SEM month of June 2019, but lower during the subsequent years indicating interannual variability.

Species composition and abundance

A total of 192 hauls were performed and 659 fish were collected over the 11-month study period at both sites. Of these 319 were considered juveniles after sorting using length at minimum maturity. The identified juveniles were from 41 species and 25 families (Table 1). Dominant families were Lutjanidae, Siganidae and Lethrinidae which contributed about 27.59 %, 21.63 %, and 10.03 % of total fish juveniles sampled, respectively (Fig.3). In the monthly samples, numbers ranged between 2-32 for Lutjaniids, and 1-23 for Siganids. Dominant species in order of abundance were

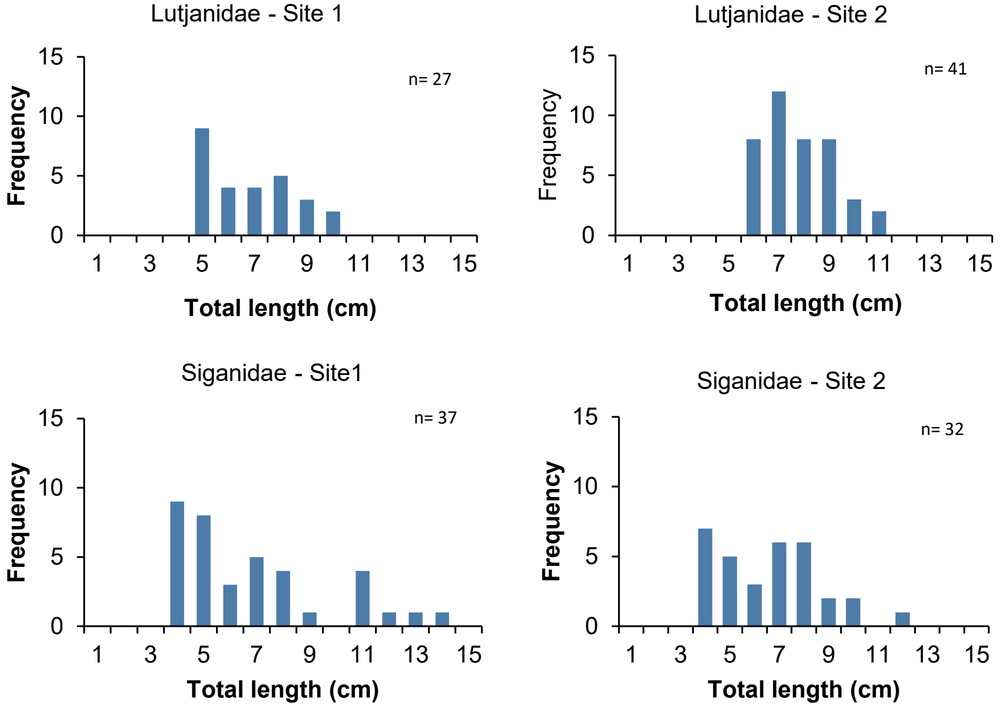

Figure 4. Length frequencies (%) of Lutjanidae, and Siganidae in Watamu Blue Lagoon (Site 1) and Watamu Beach (Site 2).

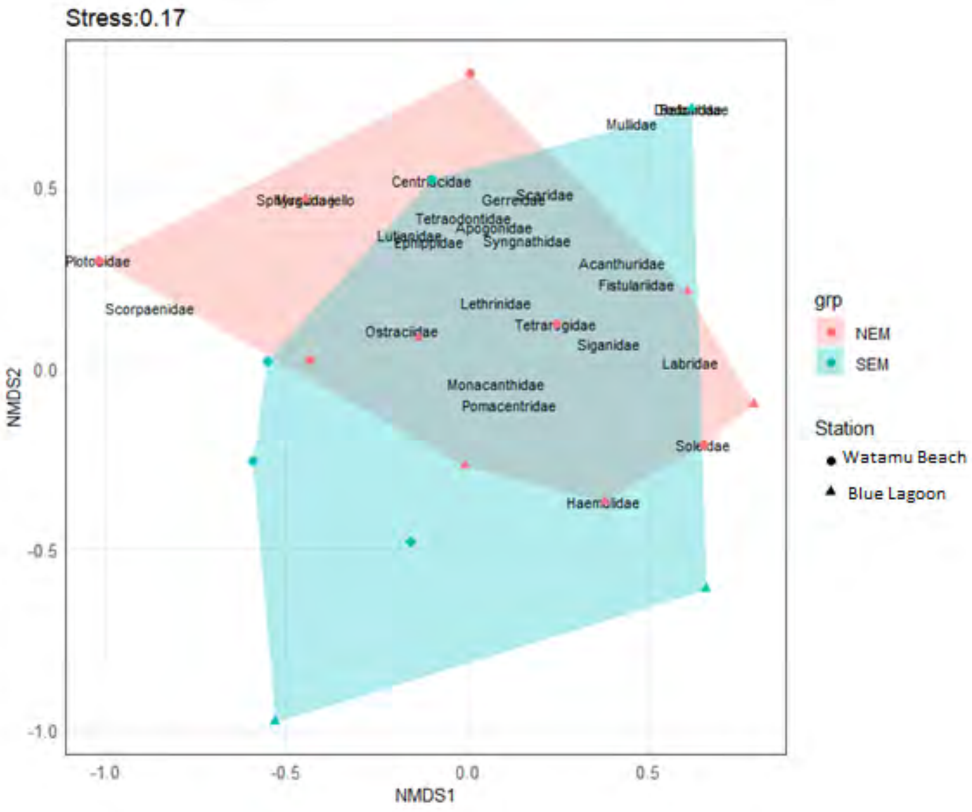

Figure 5. Ordination chart showing the distribution of juveniles in the two sites during the two seasons. Ordination is based on abundance, using Bray-Curtis distance matrix (Labri- Labridae, Scarid- Scaridae, Watamu Blue Lagoon (Site 1) and Watamu Beach (Site 2).

Lutjanus fulviflamma, *Siganus sutor*, *Lethrinus harak* and *Leptoscarus vaigiensis* (Table 1). No significant difference in abundance was observed between the two sites.

Overall, a higher number of juvenile fish were found distributed at WB (Site 2) as compared to WBL (Site 1) (Fig. 3). The dominant families were Lutjanids (*Lutjanus fulviflamma*) and Siganids (*Siganus sutor*). Lutjanids which were found to be more abundant at Site 2, along with Lethrinidae (*Lethrinus harak*) and Scaridae (*Leptoscarus vaigiensis*).

Size range distribution of dominant species

Modal lengths of Lutjanidae and Siganidae indicated no difference between the two sites (Fig. 4). The dominant size range for Siganidae was 4 cm at both sites. Lutjaniids were dominated by a size range of between 5-7 cm.

Species diversity

Overall species diversity (H') during the study period was higher at WB (H'=3.03) as compared to WBL (H'= 2.83). There was no significant difference in species richness between the two sites, although it was slightly higher at WB (d = 5.5) compared to WBL (d = 4.6). Evenness (J) was significantly lower in WB (J = 0.94) compared to WBL (J=0.95)

Juvenile communities showed an overlap as is evident from the ellipses representing the two sites. However, a few families showed distinct associations with specific stations. For instance, Lutjanidae, Centriscidae, Labridae, Scaridae, and Siganidae were closely associated with WHS, while Lethrinidae and Pomacentridae were associated with both sites.

Seasonal variation

Juvenile fish varied immensely between months and between seasons with interannual variability (Fig. 6). The highest abundance of juveniles was recorded in July 2019 at both Site 1 and 2. The abundance of juveniles was almost constant between the months of August 2019 to June 2020, with minimum variation. Peaks were observed in the year 2 NEM season.

The GLM results showed that salinity and Chlorophyll-*a* had a significant positive correlation with juvenile abundance, while the temperature was significantly inversely correlated ($p< 0.05$; Table 1).

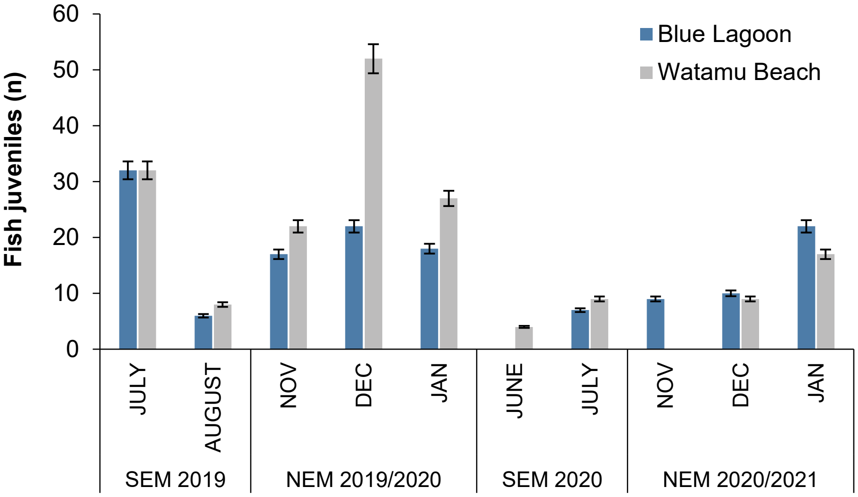

Figure 6. Monthly and seasonal variation in fish juvenile abundance at Watamu Blue Lagoon (Site 1) and Watamu Beach (Site 2) between July 2019 and January 2021.

Discussion

Species composition

Watamu Beach and Watamu Blue Lagoon registered a total of 25 families and 41 species. The dominant families were Lutjanidae, Siganidae and Lethrinidae for both sites . However, there was no significant difference in the abundance of juveniles between WB and WBL indicating that the sites were similar. Other studies have reported a similar community in seagrass beds within the tropics (Ambo-Rappe *et al.*, 2013; Kopp *et al.*, 2010; Lugendo, 2007). Other studies carried out nearby in the intertidal shallow lagoons of Watamu Marine National Park, however reported a dominance of Gobiidae, Blenniidae, Pomacentridae, and Labridae was reported (Sindorf *et al.,* 2015). The differences in species may be attributed to differences in habitat composition, the current study having sampled fish in seagrass beds while the other sampled in a rocky intertidal site.

The count of families sampled is lower than in other studies carried out in Kenya, possibly due to differences in physical characteristics such depth, effort and other operational details and the length of the sampling period. Although commonly used in shallow water studies beach seining is not suitable for catching faster-swimming fish and larger pelagic fish (Kimani *et a1.*, 1996). In another study by Okemwa *et al.* (2019) using underwater visual census (UVC) 190 species were found at five shallow fringing-lagoon reef sites in Kenya with the dominant families being Pomacentridae and Labridae. Even so, it is important to note that there have been very few studies on seasonal juvenile fish recruitment patterns within seagrass beds of the western Indian Ocean region that applied similar sampling methods. While most studies on recruitment have applied UVC, the current study sampled juveniles using a beach seine net. Because there have been few studies for comparison with the current study, it would be important to carry out similar studies using UVC in future to compare the methodologies.

Fish families such as Lutjanidae *(Lutjanus argentimaculatus, L. fulviflamma*), and Mullidae (*Parupeneus barberinus*, *P. rubescens*) that were found during this study inhabit the reef as adults, associating with seagrass beds that are adjacent to reefs as juveniles (Dorenbosch *et al.*, 2006). The presence of these families suggest that the seagrass beds at Watamu function as nurseries for fish that inhabit the neighbouring reefs. These families can therefore be classified as transient, spending part of their life in the seagrass habitats but will migrate to the reef due to a shift in ontogeny, using shallow habitats during the juvenile stages before moving to adult habitats. Similarly, while looking at juvenile abundance associated with both seagrass and reefs, Kimirei *et al.* (2011) found a high abundance of reef-associated species (*Lethrinus harak*, *L. lentjan*, *Siganus sutor,* and *Lutjanus fulviflamma*) in the seagrass beds of Mbegani, Tanzania, while the same adults were found in the adjacent reef habitats, a clear indication of ontogenetic habitat shift that occurs to meet changing dietary and physiological requirements such as spawning and competition (Kimirei *et al.*, 2013; Sheaves, 1995). In this study, *Lutjanus fulviflamma* was found abundantly in both stations, suggesting utilization of the seagrass beds obligately, because there are no mangroves within the proximity of the site, as it has been shown to prefer mangrove nurseries to seagrass beds in its juvenile stage (Kimirei *et al.*, 2011). It is also suggested that seagrass beds are capable of retaining fish larvae for several months before moving to other habitats. Therefore, most of the individuals sampled in these beds may have been retained after dispersal, before moving to the subadult habitats (Bell *et al.*, 1987; Jelbart *et al.*, 2007; McNeill and Fairweather, 1993).

From the ordination charts, it was evident that specific families were associated with specific stations. Labridae and Siganidae which were closely associated with WBL, are known to be seagrass-associated while Lethrinidae and Apogonidae are reef fish that use the seagrass beds as nurseries. Scaridae and Labridae are typically seagrass dwellers (Lugendo *et al.,* 2005; Kopp *et al.,* 2010).

Seasonal distribution

Environmental variables such as salinity and temperature are influenced by season and in turn may influence fish community structures (Wanjiru *et al.,* 2021). The overall juvenile fish abundance during the SEM was higher as was evenness, richness, and diversity. This observation concurs with results of Kimani *et al.* (1996) and Wanjiru *et al.* (2021) who studied juvenile fish from Gazi and Vanga on the south coast of Kenya, respectively. Even though reproductive activity of East African fish is not restricted to particular seasons (Nzioka *et al.,* 1979; Okemwa, 2019), it is possible that fishes spawned offshore in the NEM season move into the mangrove and seagrass nursery habitats during the rougher SEM seasons (Wanjiru *et al.,* 2021) because during this season seagrass beds offer refuge and shelter between the reefs and the inshore habitats with reduced wave action (Parsons *et al.*, 2014; Björk *et al.,* 2008).

The interannual variability observed in this study may be due to several factors such as recruitment of temporary residents, the timing of adult spawning, the timing of settlement, count of individuals settling at a given time, and fishes shifting to adult habitats (Middleton *et al.*, 1984). One study for instance showed that some of the common seagrass fishes in the Caribbean appeared to show seasonal variation with major recruitment pulses from late summer to late fall (Mateo and Tobias, 2008). Okemwa *et al.* (2019), working in shallow lagoons of Kuruwitu, found that recruitment occurred year-round with a consistent unimodal peak in recruit densities occurring between December and April.

Effect of biophysical factors

Many studies in tropical systems report seasonal influences on recruitment patterns. Increasing sea temperatures during the NEM season have been found to trigger spawning events when biological cues such as food availability become more suitable (Okemwa *et al.,* 2019). In this study Chlorophyll *a*, salinity and zooplankton abundance positively influenced juvenile abundance. These were found to vary annually and seasonally. The variation is possibly influenced by the interannual variability in juvenile abundance. The variation is caused by the occurrence of monsoon cycles that result in two seasons. The higher abundance of juveniles during a particular season may be associated with abundant food supply.

Conclusion

The results of this study indicate that coral reef-associated fish use seagrass habitats as nursery grounds; with the most common families being Lutjanidae, Siganidae and Lethrinidae. The presence of these families suggests that the seagrass beds at Watamu function as nurseries for fish that inhabit the neighbouring reefs. The higher abundance of juveniles associated with reefs found in the degraded sites suggests the transient nature of the juveniles and the interconnectedness of the two habitats studied, making it difficult to confidently identify why this preference exists. In this study, no significant difference in the abundance of juvenile fish was found between the two habitats. Seasonality is seen to play an important role with higher numbers of juveniles recorded during the SEM season. A higher abundance in the seagrass beds during this season could be due to the calm weather, with reduced currents, making the beds suitable for feeding and shelter. Biophysical factors are influenced by the monsoon cycle which consequently causes the interannual variability in juvenile abundance. Chlorophyll-*a* significantly affected the presence of juveniles, as higher juvenile abundance during SEM coincided with higher Chlorophyll-*a* in the samples.

This study confirmed that both continuous and patchy seagrass beds are critical nursery habitats for fish. Both types had similar juvenile abundance, suggesting they play similar roles in enhancing the survival and recruitment of juveniles. Sustainability in the provision of fishery services is dependent on sustainable exploitation and management of seagrass habitats. As a management measure, conservation of seagrass meadows is key to enhancing the nursery habitat function for juvenile fish and is key for replenishment of fish populations in coastal lagoons in East Africa.

Acknowledgments

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Original Article

Simulation of spatiotemporal interannual variability of oceanic subsurface temperature off East Africa

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Abstract

The oceanic subsurface variability off East Africa in the tropical western Indian Ocean plays a crucial role in ocean dynamics and living resources as well as weather and climate variability. A regional ocean model is applied to understand the oceanic subsurface interannual variability off East Africa. The region with the highest sea surface temperature (SST) variability in the offshore region lies adjacent to strong subsurface temperature variations located between 30 and 130 m corresponding with strong variations in the thermocline depth. The weakest SST variations in the Tanzanian shelf waters lie over the subsurface waters with the smallest temperature variations in the upper 200 m with weak variations in the thermocline depth. Such signals are associated with induced forcings from the Indian Ocean Dipole (IOD) and El Niño-Southern Oscillation (ENSO) in both regions with different intensity and peaking times. The IOD-induced forcings are weaker, evolving in October and November-December in the region with the weakest and strongest SST variations, respectively. Relatively stronger ENSO induced forcings occur in both regions. Stronger signals occur in the region with the stongest SST variations throughout the year, except in August, with a peak in January. The ENSO-induced forcings occur in January to May peaking in March and April in the region with the weakest SST. Consequently, anomalous Rossby waves as well as local Ekman downwelling and upwelling associated with both large-scale modes occur in the region leading to the subsurface temperature variations.

Keywords: oceanic subsurface temperature, thermocline, Indian Ocean Dipole, El Niño-Southern Oscillation, downwelling, upwelling.

Introduction

The tropical Indian Ocean experiences strong interannual variability of sea surface temperature (SST) associated with internal dynamics and remote forcing resulting in significant influences towards both regional and global climate activities. Several studies have been conducted on the SST variability in the tropical Indian Ocean (e.g., Behera *et al.*, 1999; Behera *et al.*, 2000; Collins *et al.*, 2012; Schott *et al.*, 2009; Manyilizu *et al.*, 2014) and a smaller number on the subsurface temperature and its relation to SST (e.g., Rao *et al.*, 2002; Sun *et al.*, 2021; Kakatkar *et al.*, 2019, 2020; Sayantani and Gnanaseelan, 2015). The subsurface temperature in the tropical western Indian Ocean determines the vertical temperature stratification that affects upper ocean circulation, marine ecosystems and mesoscale activities in the region (Brill, 1994; Feng and Wijffels, 2002; Schott and McCreary, 2001). Furthermore, the region is part of the tropical Indian Ocean that forms the largest warm pool on Earth which shapes both regional and global warming (Schott *et al.*, 2009). The recently reported break in global warming in the decadal variability in the early 21st century is associated with heat rearrangement between the surface and subsurface of the tropical Indian Ocean (Lee *et al.*, 2015; Liu *et al.*, 2016;

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Meehl *et al.*, 2011; Nieves *et al.*, 2015). In the late 20th century, the tropical Indian Ocean experienced rapid surface warming aligned with the significant subsurface cooling (Han *et al.*, 2006; Trenary and Han, 2008). However, such surface warming stopped in early 21st century when there was a rapid increase in subsurface warming and upper ocean heat content (Lee *et al.*, 2015; Nieves *et al.*, 2015). Thus, the subsurface temperature variability in the tropical Indian Ocean has peculiar features in comparison with its corresponding surface temperature.

Uniquely for the tropical Indian Ocean only, there is no co-variability between surface and subsurface spatially and temporally (Barnett *et al.*, 2005; Du and Xie, 2008; Han *et al.*, 2006; Nieves *et al.*, 2015; Pierce *et al.*, 2006; Trenary and Han, 2008) with the highest differences even opposite signatures between the trends in surface and subsurface temperatures among all oceans (Alory *et al.*, 2007; Han *et al.*, 2006; Nieves *et al.*, 2015; Trenary and Han, 2008). For instance, the decadal variability in the subsurface temperature of the tropical Indian Ocean shows a strong seasonality with a prominent east–west dipole structure (Sun *et al.*, 2021). At interannual variability scales with onsideration of the Indian Ocean Dipole (IOD) and El Niño-Southern Oscillation (ENSO) co-occurrence years, Sayantani and Gnanaseelan (2015) reported the existence of a north-south subsurface dipole in the tropical Indian Ocean. Such dipole evolves from September to November under forcing of the IOD and peaks from December through February (DJF) being reinforced by ENSO. Such patterns are maintained through March to May (MAM) of the following year. Moreover, the signals are associated with positive and negative wind stress curl anomalies in the south and north of 5°S which force downwelling and upwelling waves accordingly during the December to February period. Consequently, there is strong subsurface-surface feedback in this region which determines different surface dipole patterns apart from the commonly known of the large-scale modes; ENSO and IOD (Shinoda *et al.*, 2004).

The southwestern Indian Ocean region, for example, is associated with a thermocline dome named the Seychelles Dome by Yokoi *et al.* (2008) or the Seychelles-Chagos thermocline ridge by Hermes and Reason (2008) and the shallow thermocline as reported by Manola *et al.* (2015). The variations associated with the thermocline north and south of 10°S are associated with IOD and ENSO induced forcings, respectively (e.g., Saji *et al.*, 1999; Rao and Behera 2005; Yu *et al.*, 2005; Tozuka *et al.*, 2010; Yokoi *et al.*, 2012). The SST over this region is very sensitive to thermocline variability, and hence, it can influence the regional climate variability (Chowdary *et al.*, 2009; Izumo *et al.*, 2008; Jayakumar *et al.*, 2011; Jayakumar and Gnanaseelan, 2012; Manola *et al.*, 2015; Vecchi and Harrison, 2013; Yokoi *et al.*, 2008; 2012). The positive SST anomalies in this region retard the Inter-tropical convergence zone towards the Indian Subcontinent, and thus, it delays the beginning of rainfall there. Moreover, the strong SST anomalies over this region lead to strong devastating rainfall and cyclone activities over the southern Africa (Xie *et al.*, 2002). Therefore, the subsurface temperature in the tropical western Indian Ocean plays a vital role in surface variability as well as shaping both regional and global climate activities; a topic of great interest recently.

The coastal waters of East Africa, as part of the tropical western Indian Ocean, indicate spatiotemporal variability of SST which greatly affects social-economic activities (such as fisheries, tourism, recreation as well as marine and coastal shipping), and ultimately, the regional economy. It mainly determines regional rainfall distribution and sea levels as well as the distribution and abundance of marine living resources (e.g., Schott *et al.*, 2009; Obura *et al.*, 2002). In this region, the weakest interannual SST variations which are only significant at about a five-year period, occur in the Tanzanian shelf region to the south of 6°S extending to the north and west of Madagascar. Such SST variations are predominantly influenced by the surface heat fluxes related to shortwave radiation in conjunction with a contribution from advection of the North-East Madagascar Current (NEMC) as reported by Manyilizu *et al.* (2014). The strongest interannual SST variations in the zonally elliptical band occur between 2°S and 2°N extending offshore with two significant periods of about 2.7 and 5 years (Manyilizu *et al.*, 2014). These periods reflect the large-scale climate variability modes, namely ENSO (Reason *et al.*, 2000; Annamalai and Murtugudde, 2004; Schott *et al.*, 2009) and IOD (Behera *et al.*, 2000; Yamagata *et al.*, 2004), and hence suggesting their influences to such SST signals being lagged behind for two to four months (Klein *et al.*, 1999; Reason *et al.*, 2000; Manyilizu *et al.*, 2014).

However, the subsurface temperature variability as well as its relationship with the SST in the region off East Africa are not well documented. This is due to the fact that the tropical Indian Ocean experiences the highest differences spatially and temporally between the trends in surface and subsurface temperatures (Alory *et al.*, 2007; Han *et al.*, 2006; Nieves *et al.*, 2015; Trenary and Han, 2008). Therefore, filling in the gaps of understanding of the subsurface temperature variability particularly the region with the weakest and strongest SST variations using numerical studies is the subject for this study. The study also explores the mechanisms behind the subsurface-surface feedbacks for the upper ocean temperature in these regions.

Datasets and methodology

The Regional Ocean Model Systems (ROMS) is used to simulate subsurface variability in the ocean off East Africa from 1980-2007. The details of the model and its configuration, datasets as well as data analysis techniques used in the study are provided below.

Model description

This study applies the ROMS which is currently improved to the Coastal and Regional Ocean Community (CROCO) model (www.croco-ocean. org) to simulate the ocean off East Africa in the tropical western Indian Ocean. Previously, this model has realistically simulated the upper ocean physical features in this region (e.g., Hermes and Reason, 2008; Penven *et al.*, 2006; Manyilizu *et al.*, 2014; 2016; Collins *et al.*, 2014). The model is a free-surface, terrain-following ocean model which solves the three-dimensional hydrostatic primitive equations (Shchepetkin and McWilliams, 2003, 2005). It solves the equations using a split-explicit time-stepping scheme and a free-surface. Stretched, terrain-following coordinates are used in the vertical, and orthogonal curvilinear coordinates are applied in the horizontal on a staggered Arakawa C-grid. The surface heat flux is based on a bulk parameterization at the air-sea interface (Fairall *et al.*, 1996). Vertical mixing occurs through the K-Profile Parameterization (KPP; Large *et al.*, 1994).

The model domain setup in Manyilizu *et al.* (2014) was adapted for this study covering the region for 37.5-60°E and 4.85°N-18°S in the East African coastal waters. The study was conducted for interannual simulation forced from 1978 to 2007 with the National Center for Environmental Prediction (NCEP) reanalysis-2 of winds and heat fluxes with a two-year spin-up time. This model simulation was named as Model_NCEP. The monthly mean values were used to force the lateral open boundaries by means of a linear temporal interpolation. The lateral boundary conditions were based on a combination of active adaptive radiation conditions added to nudging (reaching a nudging time scale of 360 days) and sponge (reaching a viscosity/diffusivity value of 1000 m^2s^{-1}) layers 150 km wide (Marchesiello *et al.*, 2001). With this model, the 2' spatial resolution global dataset processed by Smith and Sandwell (1997) have been configured. The model simulation has 40 vertical levels, 1/6 ° horizontal resolution and time steps of 1800s. The model outputs were averaged every two model days which in turn were processed to calculate monthly and climatological data. The monthly anomalies of the interannual model output were extracted by subtracting the monthly climatological mean calculated for 28 years (i.e., 1980-2007) of the model interpretation.

For model validation, another simulation was forced with the monthly mean Comprehensive Ocean and Atmosphere Data Sets (COADS) winds and heat fluxes (da Silva *et al.*, 1994) for 10 years with a three-year spin-up time over the same domain. This model simulation was named as Model_COADS. The initial and lateral boundary conditions for this simulation were extracted from World Ocean Atlas 2001 global dataset with monthly climatology 1 ° resolution, WOA2001 (Conkright *et al.*, 2002).

Datasets

Further validation of the subsurface temperature in the study region was performed using data from the observational/hydrographical World Ocean Atlas 2009 data (WOA2009). The WOA2009 consists of the global monthly climatology at 1° grid resolution and interpolated to standard depth levels on both 1° and 5° grids (Antonov *et al.*, 2010; see www.nodc.noaa.gov). Thus, the model validation was conducted between the two simulations as well as data from WOA2009. Furthermore, the model configuration was validated through the SST variability using satellite and *in situ* data as shown in Figure 2 and 4 in Manyilizu *et al.* (2014).

The influences of the ENSO and the IOD on the variability of the region was assessed through correlation analysis using the Niño3.4 index and the Dipole Mode Index (DMI). The ENSO and the IOD are prominent climate modes in the tropical Indian Ocean. The DMI is provided by the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) represents the difference of the monthly SST (HadISST dataset from 1958 to 2010) between two boxes in the west (50-70°E, 10°S-10°N) and the east (90-110°E, 10°S-0) of the tropical Indian Ocean (see www.jamstec.go.jp). The Niño3.4 index is extracted from the National Ocean and Atmosphere Agency (NOAA) and is the monthly SST anomaly averaged over 5°N-5°S and 120-170°W (see gcmd.nasa.gov). It is commonly used to represent the SST variability associated with ENSO events.

Data analysis techniques

Analyses of the model results were performed using composites, correlation and Empirical Orthogonal Function (EOF) decomposition. All these techniques were applied to the monthly anomalies of the subsurface temperature and forcing variables. The correlation and standard deviations of the monthly SST anomalies were computed from the ROMS model. The possible linkage between the interannual variations of the subsurface temperature in the regions with the weakest and strongest SST was examined through correlation analysis. The EOF analysis was used to identify the leading modes of the spatiotemporal variability of the subsurface temperature in the region. The leading modes that explained more than 10% of the total variance of the subsurface temperature variability from the EOF analysis were retained.

In order to understand the subsurface temperature variations in the regions with the weakest and strongest SST variations in the ocean waters off East Africa, two transects were extracted. The first transect averaged between 1 and 1.5°S was extracted crossing the zonally elliptical band between 2°S and 2°N extending offshore. This transect represented the region with the strongest interannual SST variations that peaks at its center and it was named as the offshore region. The second transect averaged between 9 and 9.5°S. It was extracted crossing the weakest interannual SST variations which are in the Tanzanian shelf region to south of 6°S that extends to the north and west of Madagascar peaking at its center and it named as the inshore region. The selection of both transects aimed at studying the vertical subsurface temperature variations in these respectively regions. Furthermore, the transect for validation was considered around 10°S, the latitude which divides the interannual variations in two patterns as well as forcings to its north and south. The variations associated with the thermocline north and south of 10°S are associated with IOD and ENSO induced forcings, respectively (e.g., Saji *et al.*, 1999; Rao and Behera 2005; Yokoi *et al.*, 2005; Tozuka *et al.*, 2010; Yokoi *et al.*, 2012). Therefore, the vertical structure of the annual mean temperature across the domain from 38 to 60°E averaged over 10-10.5°S in the upper 250 m was used to evaluate the ability of the model to reproduce subsurface variability. This transect indicates that the ROMS model realistically simulated the subsurface temperature in the region.

Results and discussion

The tropical western Indian Ocean experiences spatial and temporal variability of subsurface temperature which does not show co-variabity with its corresponding sea surface temperture. This study focused on simulating the spatiotemporal interannual varibility of the oceanic subsurface temperature in this region off East Africa. The model validation and results of this study are provided below.

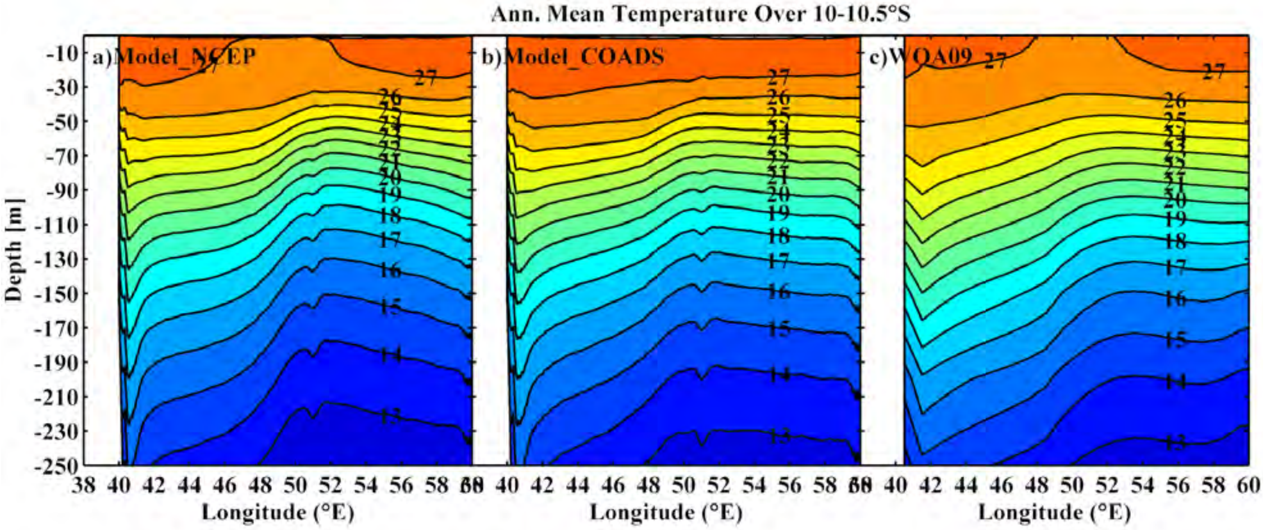

Figure 1. Annual mean of the vertical temperature in °C for Model_NCEP (1st column) and Model_COADS (2nd column), and from WOA2009 (3rd column) averaged over 10-10.5°S from 38 to 60°E with contour intervals of 1°C.

Annual subsurface temperature

The annual subsurface temperature off East Africa in the tropical western Indian Ocean is shown through a vertical transect in Figure 1. Since the 10°S latitude appears to divide north-south patterns of the interannual variability and its respective possible forcings in this region, the vertical transect around 10°S was extracted from both simulation configurations (Model_NCEP and Model_COADS) as well as from observational/ hydrographical WOA2009 data for validation.

The vertical structure of the annual mean temperature across the domain from 38 to 60°E averaged over 10-10.5°S in the upper 250 m is evaluated to understand the ability of the model to reproduce subsurface variability (Fig. 1). Relatively warm temperature (>26°C) appears in the upper 50 m in Model_NCEP and Model_COADS as well as in the WOA2009 data (Fig. 1a-c). Similar temperature patterns occur below 50 m with about 14°C isotherm laying around 250 m near the coast in both model simulations and the WOA2009 data. In short, the model seems to reproduce the annual mean of the subsurface temperature in the ocean waters off East Africa in the tropical western Indian Ocean fairly well. However, the COADS simulation shows slightly different patterns in the upper 30 m towards the sea surface. These discrepancies could be due to differences in the spatial and temporal resolutions as well as the initial and lateral boundary conditions for Model_NCEP and Model_COADS. However, the subsurface temperature variability is similarly represented in both simulations as well as in the WOA2009 data.

Therefore, the ROMS model simulated the annual mean state in the oceanic subsurface waters in this region reasonably well. This is shown by a good agreement of the mean state of the upper ocean properties from both model configurations and that from observational/ hydrographical data. Furthermore, the interannual validation of the sea surface temperature is shown in Figure 4 from Manyilizu *et al.* (2014). Thus, the next section focuses on the subsurface temperature variability in the region with the strongest SST variations.

Subsurface temperature variations off East Africa

The subsurface temperature variations in this region off East Africa were studied through the regions with the weakest and strongest SST interannual variations. The aim was to investigate the subsurface temperature signals in these regions. Thus, two transects were extracted; the first one averaged between 1 and 1.5°S crossing the zonally elliptical band between 2°S and 2°N extending offshore with the strongest interannual SST variations, and with the peak center named the offshore region. The second transect averaged between 9 and 9.5°S was extracted crossing the weakest interannual SST variations which are in the Tanzanian shelf region to the south of 6°S that extends to

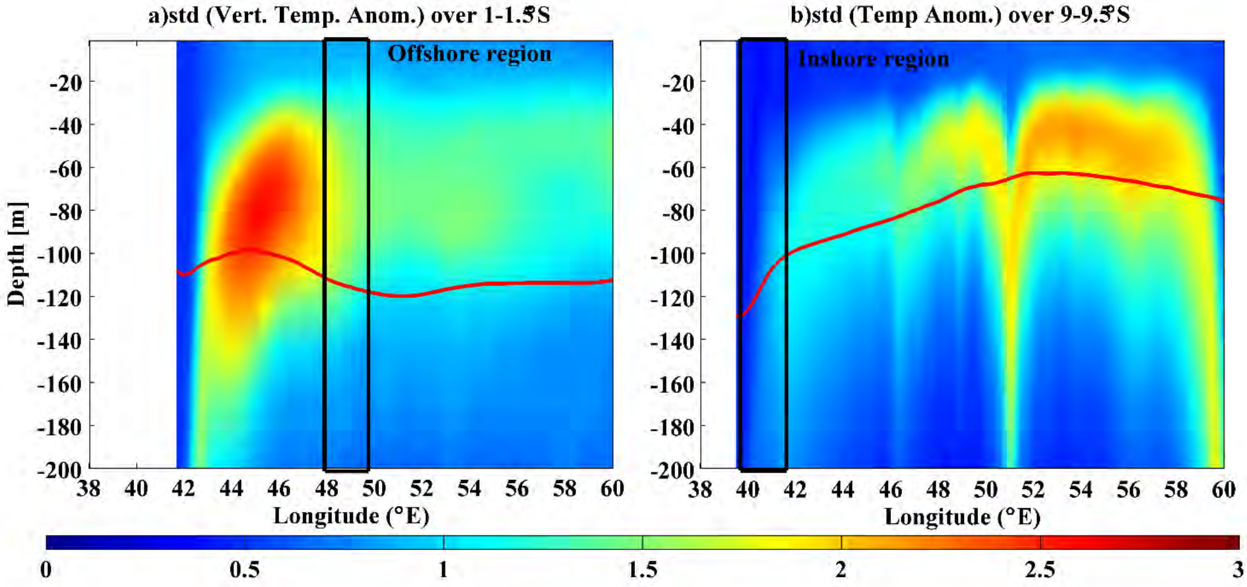

Figure 2. Standard deviation of the vertical temperature anomaly and the annual thermocline depth (red line) from 38 to 60°E averaged over (a) 1-1.5°S and (b) 9-9.5°S from 1980 to 2007 in the upper 200 m depth.

the north and west of Madagascar, with its peak center named the inshore region.

Figure 2 displays standard deviation of vertical temperature anomalies and the annual mean thermocline depth (red line) in the regions which experience the strongest and weakest interannual SST variations. The vertical transect of the standard temperature anomalies were extracted from the coast at 38 to 60°E, and averaged between 1 and 1.5°S for Figure 2a and between 9 and 9.5°S for Figure 2b from 1980 to 2007. The former transect crosses through the offshore region, and the latter one goes through the inshore region as shown in Figure 2; the regions with the strongest and weakest interannual variability of the SST, respectively.

The vertical temperature transect that crosses through the offshore region shows strong interannual temperature variations (standard deviation of about 2-3°C) in the subsurface waters between 30 and 130 m (Fig. 2a). Such patterns of subsurface temperature which show strong variations around 100 m depth were reported by Sun *et al.* (2021) and Kakatkar *et al.* (2020, 2019) as well as Sayantani and Gnanaseelan (2015). The transect displays very deep thermocline depth at the annual mean ranging from 100 to 130 m (Fig. 2a). The highest interannual variations of the vertical temperature are confined to the subsurface waters near the offshore region where the annual thermocline depth is relatively elevated. Relatively weak interannual variations of the upper ocean temperature (standard deviation <1°C) occur in the upper 30 m and below 130 m. The 130 m depth is the annual mean thermocline depth in the offshore region.

The variations of the temperature in the upper 30 m depth in the transect seems to be mainly explained by seasonality, and they are confined to the coast, where they reach below 200 m depth. The offshore region corresponds to strong interannual variations in the thermocline depth with a standard deviation which ranges from 18 m at 50°E to 24 m at 48°E (Fig. 3). Consequently, variations in the thermocline depth are associated with strong variations in the upper temperature in the offshore region.

The vertical temperature transect through the coastal waters in the Tanzanian shelf region shows weak interannual variations (standard deviation <0.5°C) in the upper 200 m depth (Fig. 2b). The annual mean of the thermocline depth ranges from 70-80 m in the Seychelles-Chagos thermocline ridge as reported by Hermes and Reason (2008) and Yokoi *et al.* (2008) to the deepest value (130 m) in the Tanzanian shelf region. In this transect, strong seasonality is present in the upper 40 m (explained variance >80% not shown), and it is confined to the coast where it reaches below 200 m. High subsurface temperature variations (standard deviations of about 1.5-2.0°C) occur between 30 and 80 m to the east of the transect which seems to advect towards the Tanzanian shelf region. These high subsurface temperature variations are located between 48 and 60°E. The region corresponds with relatively high standard deviation of the thermocline depth (>13 m) which becomes higher than that in the offshore region

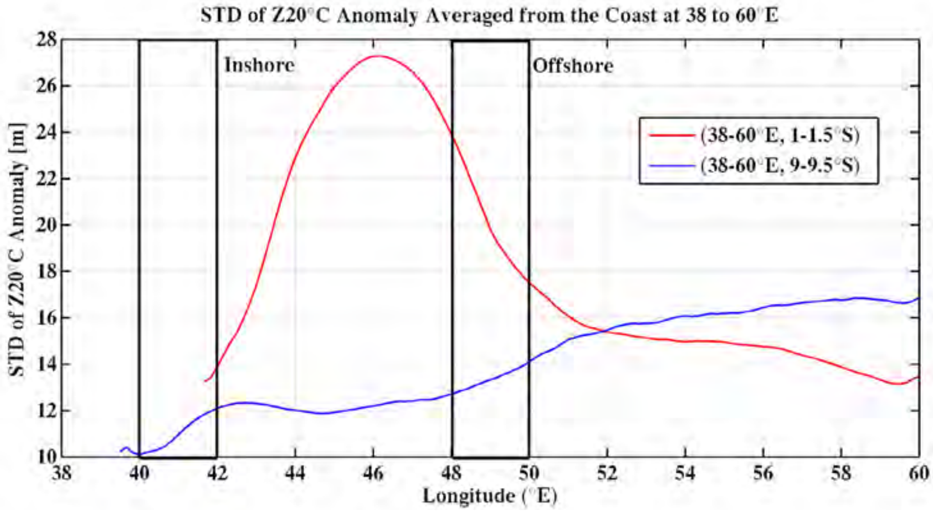

Figure 3. Standard deviation of the thermocline anomalies from the ROMS model in the tropical western Indian Ocean averaged from the coast at 38 to 60°E over 1-1.5°S (red) and 9-9.5°S (blue).

towards the east of 52°E (>15 m). This region reflects the thermocline dome named the Seychelles Dome by Yokoi *et al.* (2008) or Seychelles-Chagos thermocline ridge by Hermes and Reason (2008); the shallow thermocline also reported by Manola *et al.* (2015). Thus, uniformly weak variations of the temperature in the upper 200 m occur in the Tanzanian shelf region which is mainly dominated by seasonality and some contribution from advection from the region with high variations to the east in the subsurface waters.

In general, the region with the highest SST variability in the offshore region lies adjacent to strong subsurface temperature variations located between 30 and 130 m. Moreover, the region corresponds with strong variations in the thermocline depth. The weakest SST variations in the Tanzanian shelf waters lie over the subsurface waters with the smallest temperature variations in the upper 200 m. It matches with weak variations in the thermocline depth. The highest regional variability of the subsurface temperature is further explained by interannual variability. Thus, the next section deals with subsurface temperature in the region in association with large-scale climate variability modes.

Subsurface temperature with large-scale climate variability modes

An Empirical Orthogonal Function (EOF) analysis was applied to the upper ocean temperature (0-200 m depth) in the vertical transects through the Tanzanian shelf region and offshore in the tropical western Indian Ocean off East Africa. The analysis was performed on the monthly vertical temperature anomalies to determine the dominant modes of variability.

Vertical interannual temperature variability through the region with the weakest SST variations

The EOF analysis in the transect through the region with the weakest SST variations in the Tanzanian shelf waters was performed on the monthly vertical temperature anomalies from 38 to 60°E averaged between 9 and 9.5°S from 1980 to 2007 (Fig. 4). The first two leading modes of the vertical temperature anomalies in the upper 200 m of the EOF, which collectively explain about 64% of the total variance, were retained.

The first mode explains about 51% of the total variance with the same sign everywhere in the transect (Fig. 4a). The weakest loadings are in the Tanzanian shelf region reflecting the weakest temperature

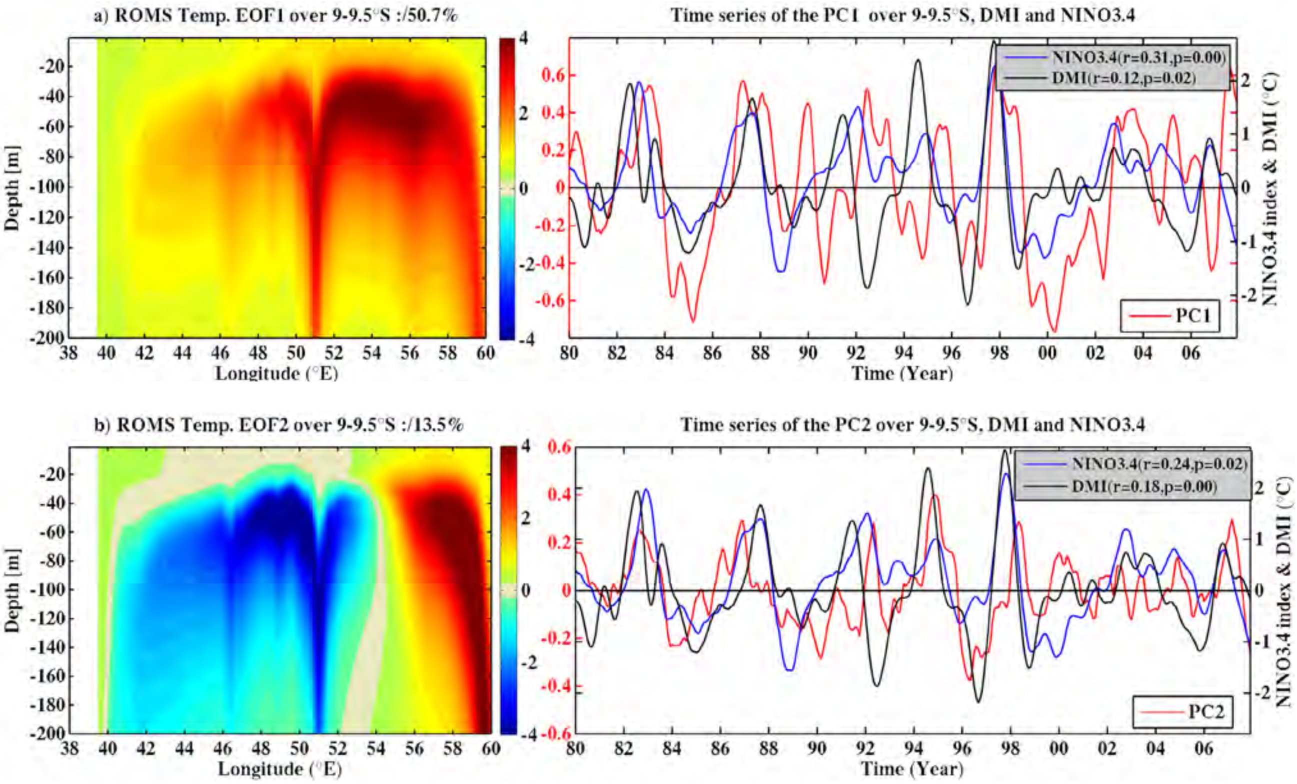

Figure 4. The first two EOF modes for the upper ocean temperature (0-200 m) from 38 to 60°E averaged over 9-9.5°S and their corresponding principal component time series (in red). The DMI (in black) and the Niño3.4 index (in blue) are added. The time series is smoothed by a seven-month running mean. (a) 1st EOF, (b) 2nd EOF.

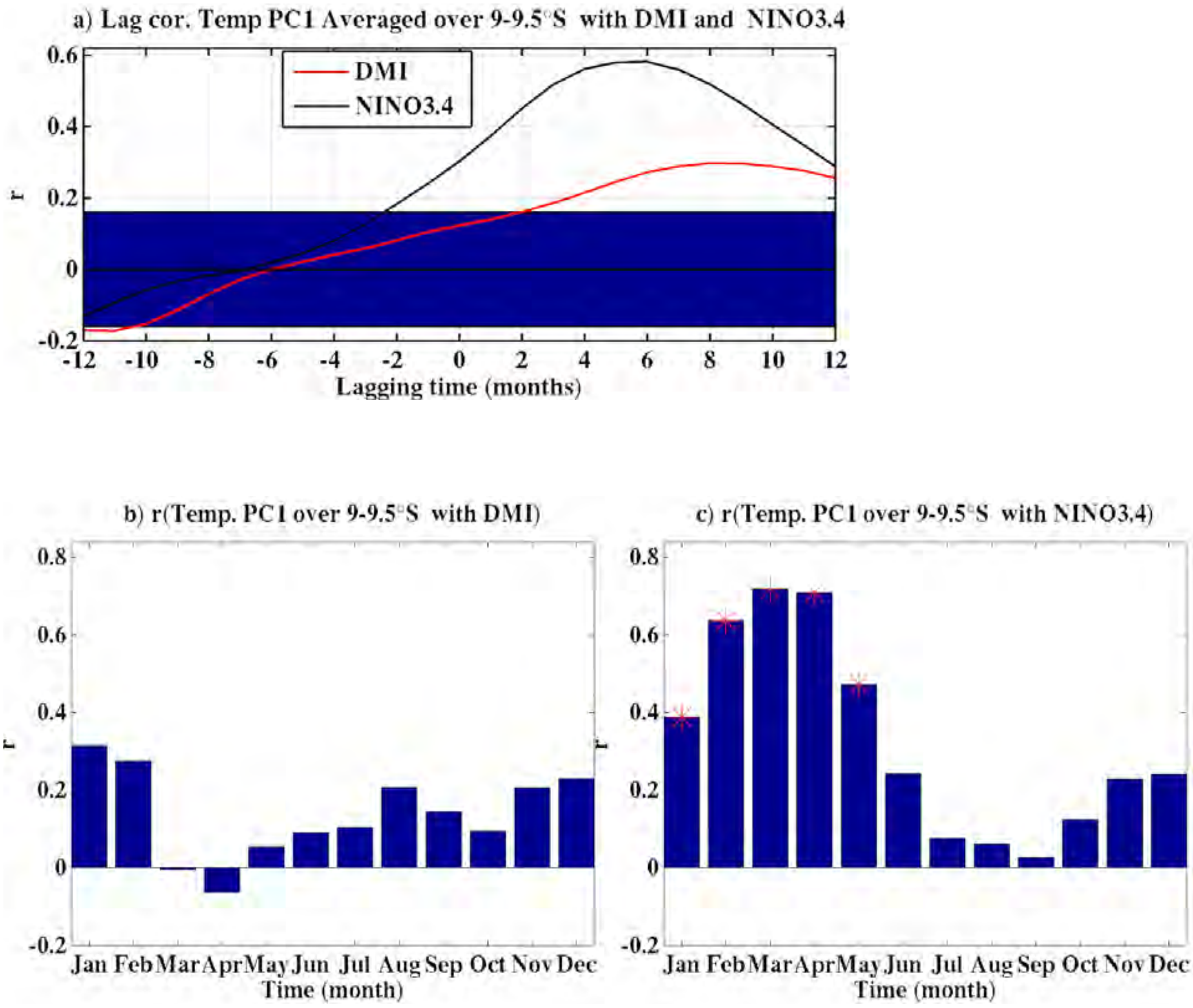

Figure 5. (a) Lag correlation of the Niño3.4 index (black) and the DMI (red) with the PC1 of the vertical temperature EOF from 38 to 60°E averaged over 9-9.5°S in the upper 200 m. Bar diagrams of the monthly correlation coefficients between the PC1 with (b) the DMI (left) and (c) the Niño3.4 index (right). The unshaded region in (a) and the red stars in (b) and (c) indicate statistically significant correlation at 95% significant levels (p<=0.05).

variations. However, strong spatial loading patterns occur to the east between 48 and 60°E in the subsurface waters between 20 to 140 m where they match with strong standard deviation in the vertical temperature anomalies. Such loadings reflect those of the Seychelles Dome (Yokoi *et al.*, 2008) or Seychelles-Chagos ridge (Hermes and Reason, 2008), the shallow thermocline also reported by Manola *et al.* (2015). The principal component time series of the first EOF (PC1) of the anomalies in the upper temperature correlates with the Niño3.4 index and the DMI with values of 0.31 and 0.12 at 95% significant level, respectively. Such findings suggest a relatively stronger influence of the ENSO than the IOD with the IOD and ENSO-induced Rossby waves dominating to the north and south of 10°S, respectively (Rao *et al.*, 2005; Yu *et al.*, 2005).

The second mode of the EOF analysis explains about 14% of the total variance with an east-west dipole spatial pattern in the subsurface waters (Fig. 4b). The lowest values close to zero occur in the upper 30 m being confined to the Tanzanian shelf region. The PC2 shows correlation with the Niño3.4 index and the DMI with values of about 0.24 and 0.18 at 95% significant levels, respectively. The first two modes of the monthly vertical temperature anomalies through the Tanzanian shelf waters show correlation with ENSO and IOD signals. Very low and relatively high values of correlation between the large-scale indices (Niño3.4 index and DMI) occur with the upper temperature in the Tanzanian shelf region and offshore, respectively. However, significantly small values of correlation of the PC1 and PC2 with the Niño3.4 index and the DMI

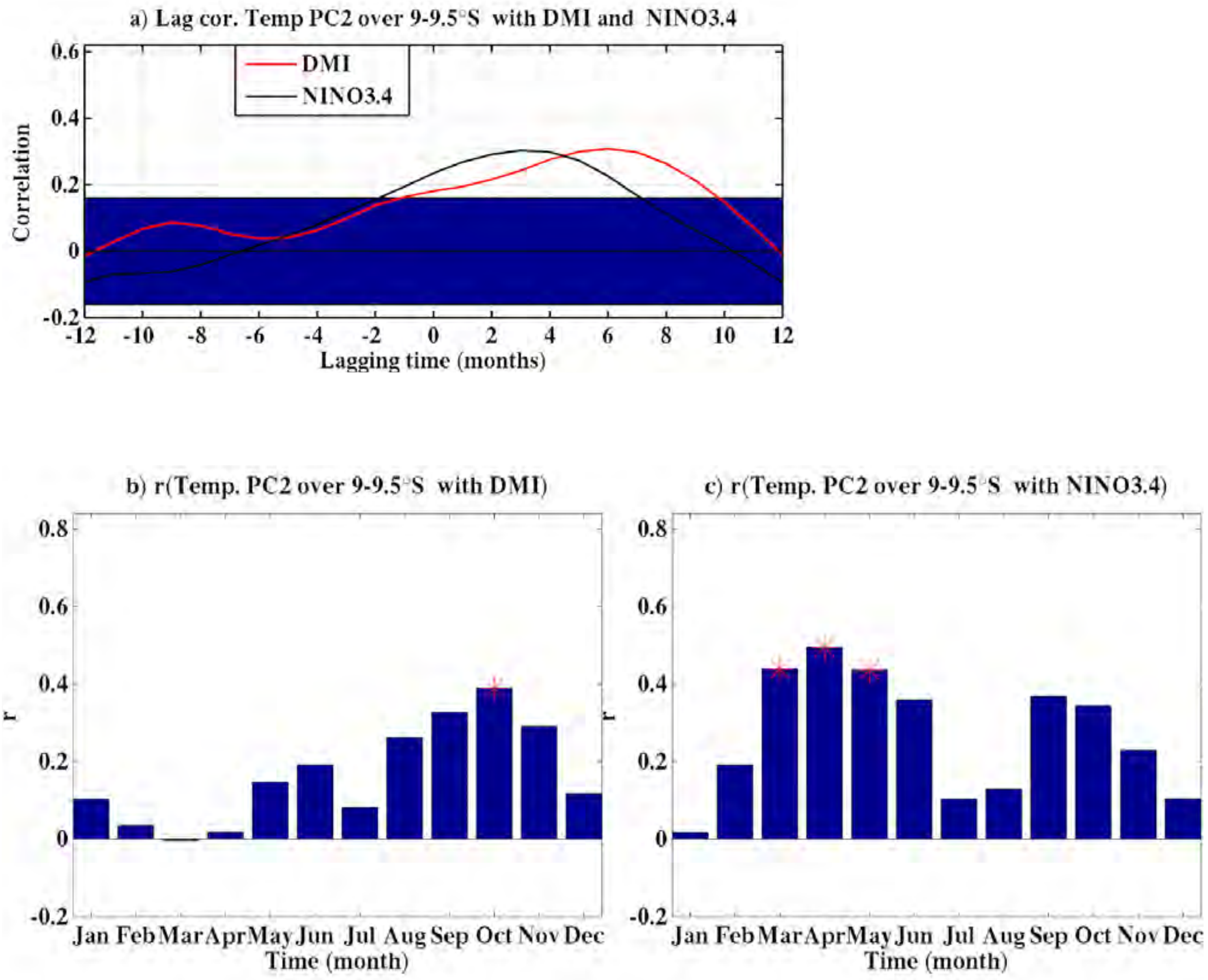

Figure 6. (a) Lag correlation of the Niño3.4 index (black) and the DMI (red) with the PC2 of the vertical temperature EOF from 38 to 60°E averaged over 9-9.5°S in the upper 200 m. Bar diagrams of the monthly correlation coefficients between the PC2 with (b) the DMI (left) and (c) the Niño3.4 index (right). The unshaded region in (a) and the red stars in (b) and (c) indicate statistically significant correlation at 95% significant levels ($p<=0.05$).

could be associated with strong seasonality of the indices. Thus, stratification of the PC1 and PC2 as well as their correlation with the Niño3.4 index and the DMI in calendar months can provide strong correlation in seasonal variations.

To understand the seasonal variations of the vertical temperature anomalies in the Tanzanian shelf region and their relation to the ENSO and IOD signals, the principal component time series of the first two leading modes and their correlation with the Niño3.4 index and the DMI were stratified by calendar months. The PC1 of the vertical temperature anomalies in the region mostly correlated with the Niño3.4 index ($r>0.6$) at a 95% significant level when the Niño3.4 index lags behind the PC1 by 3-7 months (Fig. 5a). However, the correlation between the PC1 of the vertical temperature anomalies with the DMI is very weak. Furthermore, no significant monthly correlation exists between PC1 of the vertical temperature anomalies and the DMI (Fig. 5b). On the other hand, the Niño3.4 index and the PC1 of the vertical temperature anomalies show a strong correlation from January to April, peaking in March-April at about 0.7 (Fig. 5c). Such findings appear to capture the influence of the ENSO in the subsurface temperature in the region reported to be in December-February which might be maintained to the following March-May season (Shidona *et al*., 2004; Sayantani and Gnanaseelan, 2015). Weak signals of the ENSO and IOD appear in the PC2 of the vertical temperature anomalies which are relatively weakly correlated ($r\sim=0.3$) when the Niño3.4

index and the DMI lags behind the PC2 by 2-3 and 5 months, respectively (Fig. 6a). No significant monthly correlation of the PC2 with the DMI exists except in October (r~=0.4; Fig. 6b). The combination of the seasonal influences of the ENSO and IOD signals reflects the analysis of Sayantani and Gnanaseelan (2015) that the IOD influences the subsurface variations in the September-November (SON) season being intensified by the ENSO from December to February and retained through March to May. These results suggest strong variations of the interannual vertical temperature anomalies around 9-9.5°S in the tropical western Indian Ocean are more associated with ENSO signals than IOD signals as was previously reported by Rao *et al.* (2005) and Yu *et al.* (2005).

Vertical interannual temperature variability in the region with the strongest SST variations

The monthly temperature anomalies of the vertical transect through the offshore region are used to compute the EOFs in the region from 38 to 60°E averaged between 1 and 1.5°S. The first leading mode of the vertical temperature of the EOF which explains about 52% of the total variance with a homogeneous signal of the spatial pattern is retained (Fig. 7). Strong spatial loading patterns occur between 20 and 160 m depth matching the strong variations in temperature. The offshore region appears to the east of the strongest loadings in this EOF with upward advection toward the surface waters. The PC1 of the upper temperature anomalies correlate with the Niño3.4 index and the DMI with values of 0.58 and 0.21 at 95% significant level, respectively. Therefore, the vertical temperature anomalies in the offshore region between 48 and 50° E and the nearby are associated with the ENSO and the IOD signals. Moreover, significant correlation of the PC1 with the Niño3.4 index and DMI could be obtained if they are stratified in calendar months due to the fact that the ENSO and IOD signals in the tropical Indian Ocean are annually phase-locked.

Figure 8 displays the standard deviation of the monthly PC1 through the offshore region from 38 to 60°E averaged between 1 and 1.5°S for the vertical temperature anomalies stratified in calendar months. The PC1 shows relatively strong standard deviation from August to December which peaks in December at about 0.4°C. The vertical temperature anomalies in this region mostly correlate with the Niño3.4 index (r=~0.6) at 95% significant level when the Niño3.4 index lags behind the PC1 by 1-3 months. Moreover, the correlation between the PC1 of the vertical temperature anomalies in the region with the DMI peaks at 2-4 lag months. Monthly correlation of about 0.42 appears between the PC1 of the vertical temperature anomalies and the DMI in only December at the 95% significant level (Fig. 8b). However, the Niño3.4 index and the PC1 of the vertical temperature anomalies show significantly strong correlation throughout the year, except in August, and the correlation peaks in January at about 0.8 (Fig. 8c). Such patterns could be explained by the analysis of Sayantani and Gnanaseelan (2015) who showed that the subsurface temperature in the tropical Indian Ocean evolves from September to November forced with the IOD, intensifying and peaking in the following season in December–February (DJF), being reinforced by ENSO. Such patterns are maintained through March–May (MAM) of the following year.

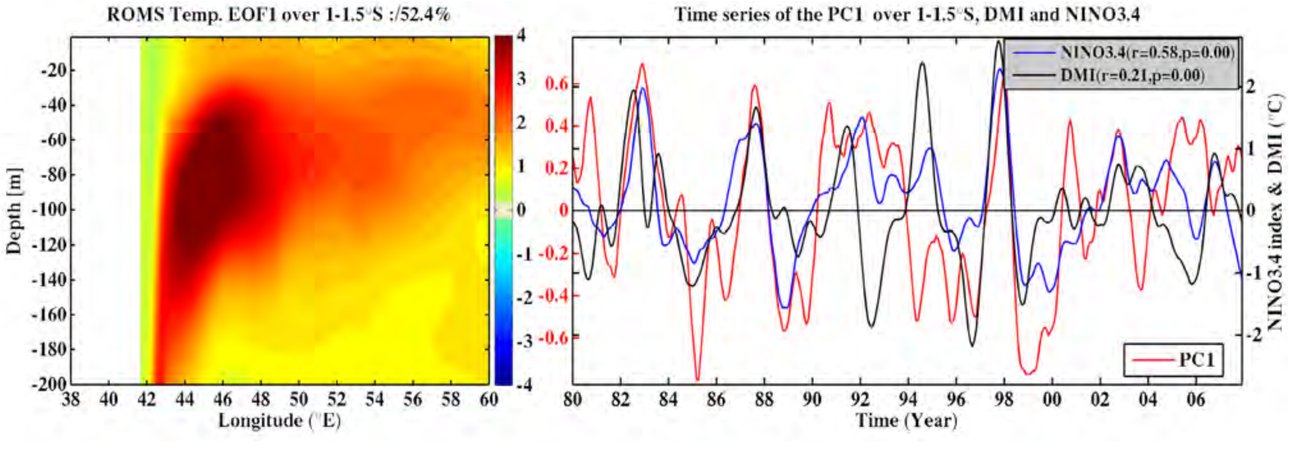

Figure 7. The first EOF mode for the upper ocean temperature (in 200 m depth) from 38 to 60°E averaged over 1-1.5°S in tropical western Indian Ocean and their corresponding principal component time series (in red). The DMI (in black) and the Niño3.4 index (in blue) are added. The time series is smoothed by a seven-month running mean.

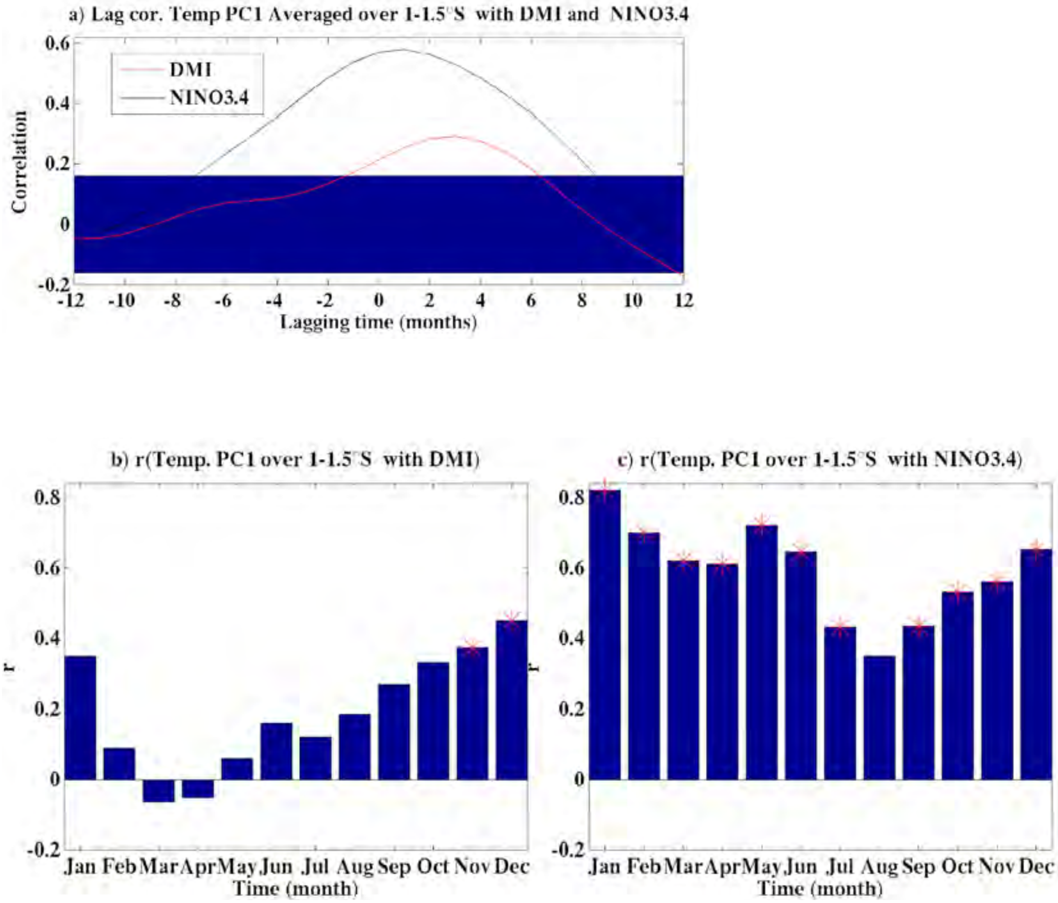

Figure 8. (a) Lag correlation of the Niño3.4 index (black) and the DMI (red) with the PC1 of the vertical temperature EOF from 38 to 60°E averaged over 1-1.5°S in the upper 200 m. Bar diagrams of the monthly correlation coefficients between the PC1 with (b) the DMI (left) and (c) the Niño3.4 index (right). The unshaded region in (a) and the red stars in (b) and (c) indicate statistically significant correlation at 95% significant levels (p<=0.05).

In the Sayantani and Gnanaseelan (2015) study, the patterns were linked with positive and negative wind stress curl anomalies in the south and north of 5°S which force downwelling and upwelling waves respectively during the December-February period. Therefore, there is strong subsurface-surface feedback in the tropical Indian Ocean which determines different surface dipole patterns apart from the commonly known large scale modes of ENSO and IOD (Shinoda *et al.*, 2004). It is apparent that strong variations of the interannual temperature in the upper 200 m which are related to the thermocline variations in the offshore region are associated mainly with the ENSO and IOD signals.

Summary and conclusion

The ROMS which has been improved into the CROCO model was used to simulate the oceanic subsurface temperature off East Africa in the tropical western Indian Ocean. The study focused on understanding the subsurface variations in the regions with the strongest and weakest SST variations in the region from 1980 to 2007. The ability of the model to reproduce the variability in this region is reasonable as the model outputs are in good agreement with observations and hydrographical data.

The upper ocean temperature in the tropical western Indian Ocean showed spatial and temporal variability. The offshore region around 48-50°E averaged between 1 and 1.5°S showed high interannual temperature variability in the upper 200 m. Weak inter-annual variations of the vertical temperature anomalies occur in the Tanzanian shelf region in the upper 200 m. The region experiences weak inter-annual variations in the thermocline suggesting that local forcing is responsible for the variability. However, strong variability in the thermocline to the east of the Tanzanian shelf waters leads to strong subsurface inter-annual variability which could influence the Tanzanian shelf region at that depth through advection. The offshore region experiences strong inter-annual variability in the vertical temperature with the highest variability between 30 and 130 m depth. The regional variability of the subsurface temperature cannot be explained by seasonality, and thus, it is related to modes of inter-annual variability. Strong inter-annual variability in the thermocline depth associated with the local surface forcing and the remote forcing from ENSO and the IOD is responsible for the strong inter-annual variability in the region. The strongest inter-annual variability in the mid depth between 40 and 130 m seems to be upwelled towards the surface. Therefore, surface and subsurface temperatures in the Tanzanian shelf region vary in the same way with weak inter-annual variability. However, stronger inter-annual variability of the temperature occurs in the subsurface waters than in the SST in the offshore region. The strong variability in the offshore region is related to strong inter-annual variability in the thermocline associated with the ENSO and the IOD.

This study provides an understanding of the subsurface temperature variability in relation to the SST in the tropical western Indian Ocean; factors that are very important for climate and marine living resources. Such understanding improves planning and management of climate sensitive activities in the East African marine ecosystem region and marine shipping activities in the Tanzanian shelf region.

To summarize, the upper ocean temperature in the tropical western Indian Ocean shows spatial and temporal variability. The offshore region around 48-50°E averaged between 1 and 1.5°S shows high interannual temperature variability in the upper 200 m. The highest temperature variations are confined to the subsurface, and they match with anomalous thermocline depths. Moreover, the subsurface temperature variations in the offshore region strongly relate to the ENSO and IOD. The Tanzanian shelf region indicates weak temperature variations in the upper 200 m with weak influences of ENSO and the IOD.

Acknowledgments

The numerical model data for this study can be obtained by contacting the corresponding author, Majuto Manyilizu (via email address: majuto.manyilizu@udom.ac.tz or majuto.manyilizu@gmail.com). The WOA2009 data are accessed through www.nodc.noaa.gov. The DMI is provided by the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) on www.jamstec.go.jp and the Niño3.4 index is extracted from National Ocean and Atmosphere Agency (NOAA) through gcmd.nasa.gov. Special thanks to the Carnegie-IAS Regional Initiative in Science and Education (RISE) through the western Indian Ocean Regional Initiative in Marine Science and Education (WIO-RISE) network for funding this research.

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Original Article

Caudal fin as a proxy for dorsal muscle for nutrient enrichment monitoring using stable isotope analysis: the case of *Gerres filamentosus* and *G. oyena* from mangrove creeks of Tanzania

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Abstract

The use of fish dorsal muscles in stable isotope studies, which is an invasive method that results in fish deaths, limits their applicability for rare and endangered fish species, as well as when large sample sizes and replicates are required, prompting research into feasible non-lethal sampling methods. The possibility of employing fin clippings (a non-invasive approach) was investigated as a proxy for dorsal muscle in nutrient pollution monitoring studies using two common mangrove fish species, namely *Gerres filamentosus* and *G. oyena*, which are known to spend their early life stages primarily within mangroves. The dorsal muscles and caudal fin tissues of fish from the mangrove creeks of Kunduchi and Mbegani, Tanzania, were examined for ^{13}C and ^{15}N signatures. Dorsal muscles from Kunduchi (mean SD: ^{13}C = -16.8 ± 2.86, ^{15}N = 9.34 ± 1.15) were more enriched than from Mbegani (mean SD: ^{13}C = -18.60 ± 2.11, ^{15}N = 7.27 ± 1.09), and this enrichment was consistent across the two studied species. Caudal fins indicated similar enrichment trends. Fin tissue stable isotope values explained between 62% and 87% of dorsal muscle ^{13}C and between 89% and 98% of dorsal muscle ^{15}N variability. These findings support the use of fin-clipping as a non-lethal proxy for stable isotope analysis of the studied species for nutrient enrichment, and additional research into non-lethal sampling methods is recommended.

Keywords: mangrove fish, coastal pollution, western Indian Ocean, fin clipping, stable isotopes, non-lethal sampling.

Introduction

Mangroves provide critical habitats for a diverse range of fish species, the majority of which are commercially valuable. They are also important as nurseries for many coral reef fishes (Bradley *et al.*, 2019; Igulu *et al.*, 2014; Kimirei *et al.*, 2016; Lugendo *et al.*, 2006; Lugendo *et al.*, 2007; Nagelkerken *et al.*, 2008), contributing significantly to artisanal coral reef fisheries when assessed at the species level (Kimirei *et al.*, 2013; Nakamura *et al.*, 2008). Nonetheless, mangroves are disappearing globally owing to both natural and human causes (Alongi, 2014; Duke *et al.*, 2007; FAO, 2007), threatening their ability to provide ecosystem goods and services (Abrantes *et al.*, 2019; Guannel *et al.*, 2016; Kimirei *et al.*, 2016).

Most Indo-Pacific mangrove habitats have large tidal ranges, which affect tidal movement of large amounts

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of seawater and fish between neighbouring habitats, reducing their value as nursery, shelter, and feeding habitats (Faunce and Layman, 2009; Nagelkerken, 2009; Nagelkerken and Velde, 2004) and fisheries (Blaber, 2009). Mangroves may potentially become functionally extinct as a result of degradation, with unexpected consequences for the viability of coastal artisanal fishing, which is a lifeline for many coastal inhabitants (Kimirei *et al.*, 2016; Staehr *et al.*, 2018).

Coastal pollution and eutrophication induced by land-based point and non-point sources are just two of the many threats to mangroves and associated habitats (seagrass beds and coral reefs), particularly on urbanised coasts (Boesch, 2019; Oczkowski *et al.*, 2014; Vikas and Dwarakish, 2015; Xiao *et al.*, 2017). Nutrient input into mangroves and estuaries, as well as other forms of chemical pollution are threatening the mangrove ecosystems and surrounding ecosystems (Asmala *et al.*, 2019; Staehr *et al.*, 2017; Staehr *et al.*, 2018). For example, coastal eutrophication can cause proliferation of harmful algal blooms (HAB) and deoxygenation of coastal waters (Breitburg *et al.*, 2018; Oczkowski *et al.*, 2014), which can lead to the deterioration of ecosystem integrity, loss of critical habitats (coral reefs and seagrasses), and changes in ecological structure (Howarth *et al.*, 2011). Domestic, industrial and agricultural effluents, as well as wastes from aquaculture operations, are example of anthropogenic nitrogen and phosphorus contamination (Lovelock *et al.*, 2009). While mangroves are known to filter nutrients and other forms of pollution, protecting adjacent ecosystems from pollution, excessive pumping of nutrients and pollutants into these wetlands may reach a tipping point, causing die-offs and a critical decimation of their protective and provisioning capacities/services (Selkoe *et al.*, 2015; Serrao-Neumann *et al.*, 2016; Watson *et al.*, 2018). As a result, monitoring nutrient pollution and accumulation, as well as other types of mangrove disturbances, is crucial.

Nutrient analysis and long-term monitoring programs can be used to monitor coastal pollution. Traditional approaches, particularly spectrophotometric analysis, have long been used to assess and monitor nutrient inputs into aquatic ecosystems (Parsons *et al.*, 1984). While this is feasible and can easily document long-term changes in nutrients inputs and accumulation in coastal waters and ecosystems, it may be costly and unsustainable, particularly for resource-poor countries (as it may require regular sample collection), where investment in monitoring programmes may not be a priority. In addition, this technique only reveals the present condition, with the possibility of missing nutrient input events that occurred weeks or months earlier (Gearing, 1991), thus needing regular monitoring. As an alternative, stable isotope analysis may be used in studying nutrient pollution to infer enrichment patterns from a few samples that are relatively easy and cheap to replicate over time (Carmichael *et al.*, 2004; Teichberg *et al.*, 2010).

Although other organisms such as plants, sediment and water samples are also used (Cole *et al.*, 2004; Costanzo *et al.*, 2001; Costanzo *et al.*, 2005; Gritcan *et al.*, 2016; Lugendo and Kimirei, 2021; Savage, 2005), fish and shellfish tissues have been routinely used to examine nitrogen enrichment in coastal waters. Carbon stable isotopes have also been investigated recently to serve the same purpose as nitrogen isotopes (Oczkowski *et al.*, 2020).

Despite the widespread use of fish in ecological studies using the stable isotopes approach, the use of dorsal muscles extracted from fish - an invasive method that results in the death of the specimens, limits their applicability in species of concern such as rare and endangered species, or when large sample sizes and replicates are required. This has prompted research into plausible non-lethal sampling methods that may be used as a proxy for dorsal muscle, with various studies selecting fish fins, fish scales, mucous, liver, plasma, and red blood cells as candidates (Boardman *et al.*, 2022; Church *et al.*, 2009; Hayden *et al.*, 2015; Hayden *et al.*, 2017; Matley *et al.*, 2016; McIntosh and Reid, 2021; Tronquart *et al.*, 2012).

The overarching objective of the current study was to investigate the possibility of using fin clippings as a non-invasive method and a proxy for dorsal muscle in nitrogen pollution monitoring studies in coastal habitats of Tanzania, and the western Indian Ocean (WIO) region in general. This was achieved by comparing the levels of nitrogen and carbon stable isotopes in dorsal muscle and caudal fin tissues of two common mangrove fish species (*Gerres filamentosus* and *G. oyena*). Furthermore, the purpose of this study was to compare the nitrogen enrichment levels of fishes collected from polluted (Kunduchi, Dar es Salaam) and relatively pristine (Mbegani, Bagamoyo) mangrove habitats in Tanzania, and to determine whether or not the nitrogen enrichment in the two species is consistent across the two mangrove areas. There is a dearth of such research in the WIO, but it is particularly lacking in Tanzania.

Materials and methods

Study area

This study was carried out in Tanzanian coastal waters in two mangrove-lined creeks, namely Kunduchi and Mbegani. Kunduchi is located along the coast of Dar es Salaam, about 20 km away from the Dar es Salaam City Centre, and prone to more pollution than Mbegani, which is located along the Bagamoyo coast, about 50 km away from the Dar es Salaam City (Fig. 1). Several species of mangroves occur at Kunduchi with *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata* dominating. On the other hand, Mbegani consists of a strip of mangroves (approximately 420 m wide) of mainly *Sonneratia alba*, mixed with *R. mucronata*, *A. marina*, and *Bruguiera gymnorhiza* (Kimirei *et al.*, 2011). Both sites are characterised by large tidal creeks, which never empty completely, even during low spring tides. At the landward side of Mbegani creek, there is a stream (Nyanza River), a potential source of freshwater leading into the mangrove forest during the rainy season. Data were collected here during the dry season.

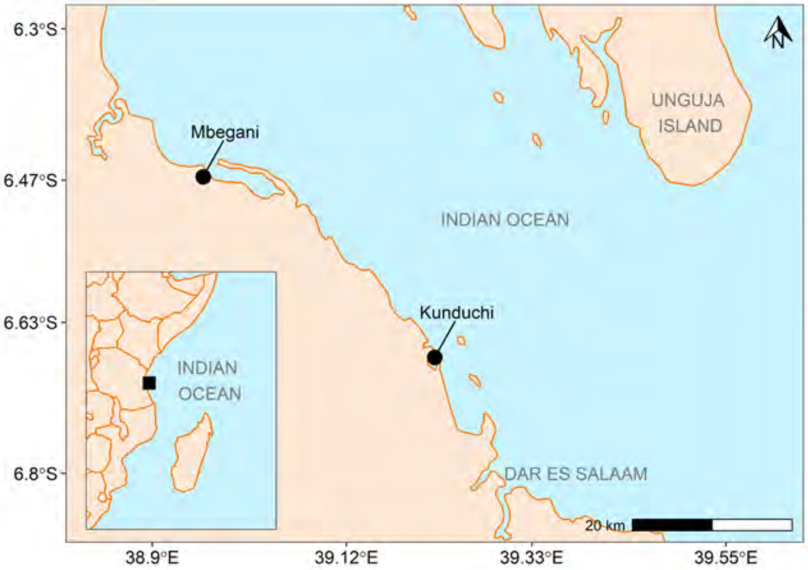

Figure 1. Map showing the study sites.

Sampling design

A total of 425 individual fish were collected using a seine net from the Kunduchi and Mbegani mangrove creeks, during low tide between January and December 2009. In the field, the fish samples were put in a cool box and later frozen at -20 °C pending sorting into species, preparation and analysis.

Sample preparation and stable isotope analysis

The collected fishes were sorted into species, and a total of 23 (6 *Gerres filamentosus* and 17 *G. oyena*) from Mbegani and 24 (4 *G. filamentosus* and 20 *G. oyena*) from Kunduchi were selected. The two species were selected primarily based on their life histories and their presence in the catches from both sites. The two species are known to spend their early lives primarily within mangroves (Mwandya *et al.*, 2009). The size (Total Length) of *G. filamentosus* and *G. oyena* from the two sites ranged between 4.6 and 10 cm, which represents juvenile stages of the two species, respectively, the stage in which they reside in mangroves (Mwandya *et al.*, 2009). A total of 94 tissue samples (47 dorsal muscle tissues and 47 caudal fin tissues) were collected from the two species. Samples were then dried at 70°C for 48 h and ground to a homogeneous powdery mixture. A pre-determined sample of known weight was placed in ultra-pure tin capsules and combusted in a CHN Elemental Analyser from Carlo Erba® (Thermo group), interfaced with a continuous flow isotope ratio mass-spectrometer, the DeltaPlus from Thermo Finnigan, Bremen, Germany, and the stable carbon and nitrogen isotopes of the selected fishes were measured. The reference gasses were calibrated with the International Atomic Energy Agency (IAEA) reference standards, IAEA-N-2 and IAEA-CH-6.

Data analysis

The data ($\delta^{13}C$ and $\delta^{15}N$ values) of fish tissues between sites, species and tissues were tested for normality

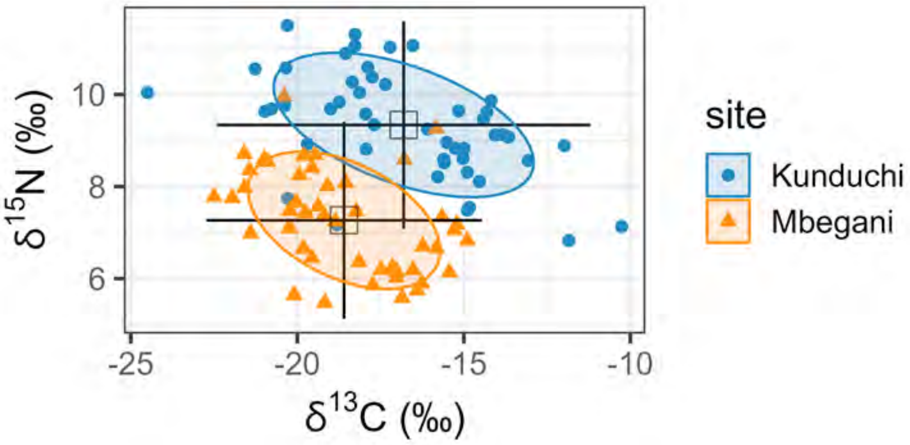

Figure 2. Stable carbon and nitrogen isotope enrichment signatures of fishes collected from Kunduchi (n=48) and Mbegani (n=46). The data for each site include both species and tissue types. Eclipses show the direction of mean values.

using the Shapiro – Wilk test. Measures of central tendencies and descriptive statistics (mean, media, standard deviations, and standard error of mean) were computed and compared across sites, species, and tissues. To test for differences between sites, the carbon and nitrogen stable isotopes data of muscle and fin tissues were pooled across fish species and sites. A non-parametric Wilcoxon Rank Sum test was used to test whether the median of the stable carbon and nitrogen isotope of the combined fish species differed between sites. A two-way ANOVA with interaction was used to test if the enrichment in stable carbon and nitrogen isotopes of *Gerres filamentosus* and *G. oyena* were consistent between the two sites. Comparisons of stable isotopes between tissues for species and sites were performed using the independent samples t-tests on robust location measures (Yuen t-test) for trimmed means (Yuen, 1974). The Yuen test was chosen rather than the student t-test because it is a robust parametric test for the data that violates normal distribution and equal variance rules. Finally, correlation analysis was used to compare stable isotope data of dorsal muscle and fin tissues to elucidate whether fin clips can be used as a proxy for dorsal muscle of the two species for monitoring nutrient pollution in coastal waters of Tanzania. All analyses and plotting were carried out in R programming language (R Core Team, 2020).

Results

Comparison of stable isotopes (δ15N and δ13C) of fishes between sites

The mean stable isotope signatures of the pooled data of both fish species from Kunduchi were more enriched with mean (±SD) δ^{13}C and δ^{15}N values of -16.81 ± -2.86‰ and 9.34 ± 1.15‰, respectively (Fig. 2), than those from Mbegani, which were appreciably depleted both for δ^{13}C (-18.60 ± 2.11) and δ^{15}N (7.27 ± 1.09) (Fig. 2). The stable isotope signatures formed

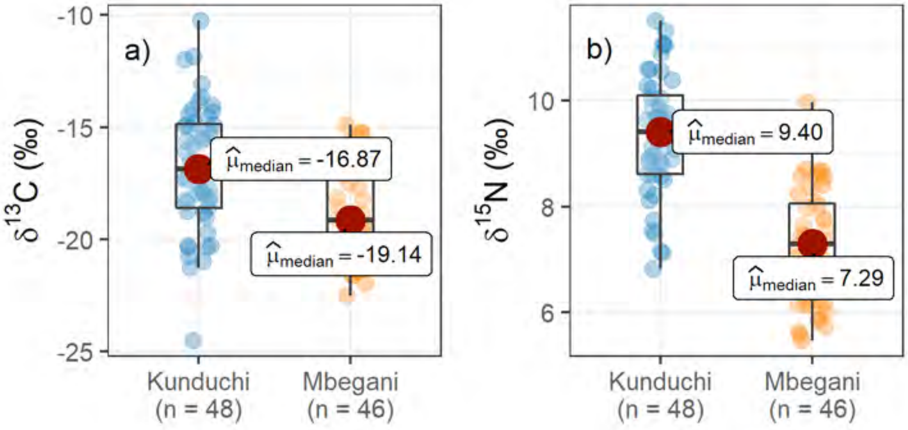

Figure 3. Comparison of a) δ^{13}C and b) δ^{15}N stable isotope signatures of fishes between Kunduchi and Mbegani mangroves.

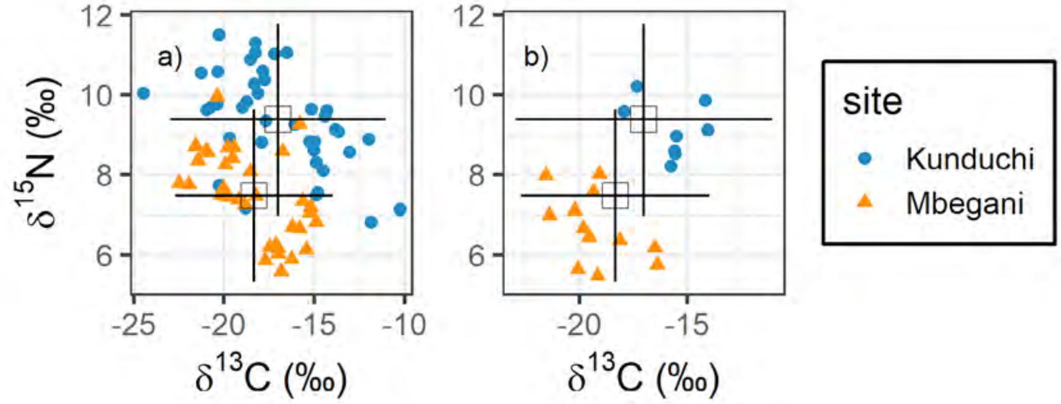

Figure 4. Comparison of stable isotope variation in tissues of a) *G. oyena* (n=74) and b) *G. filamentosus* (n=20) at Kunduchi and Mbegani.

distinct groups as an indication of enrichment status (Fig. 2). The median δ^{13}C signature was -16.87‰ at Kunduchi while it was -19.14‰ at Mbegani (Wilcoxon rank sum test, W = 1544, $p < 0.05$, Fig. 3a). Similarly, Kunduchi had more enriched δ^{15}N values than at Mbegani, where the median value of nitrogen isotope was 9.40‰ at Kunduchi and 9.29‰ at Mbegani (W = 1988.5, $p < 0.05$, Fig. 3b).

Comparison between species

The δ^{15}N and δ^{13}C signatures of *G. oyena* and *G. filamentosus* were compared to test for the stability of stable isotope enrichment pattern between species without taking tissue types into account. There were no significant differences in stable isotope enrichment between species ($F_{(1,183)}$ = 2.61; p = 0.108) indicating a consistent enrichment pattern between them. However, the δ^{15}N and δ^{13}C signatures of the two species were consistently more enriched at Kunduchi than at Mbegani ($F_{(1,183)}$ = 47.60; $p < 0.001$; Fig. 4), indicating that the observed pattern is stable across species and sites. The mean (±SD) of δ^{15}N and δ^{13}C signatures for *G. oyena* at Kunduchi were 9.38 ± 1.22 and -17.02 ± 3.04, respectively, while at Mbegani they were 7.47 ± 1.10 and -18.35 ± 2.23, respectively. For *G. filamentosus*, the mean (±SD) of δ^{15}N and δ^{13}C signatures for Kunduchi were 9.13 ± 0.70 and -15.75 ± 1.35, respectively, and 6.68 ± 0.87 and -19.29 ± 1.62, respectively, for Mbegani (Fig. 4).

Comparison between muscle and fin tissue

The carbon stable isotope values of muscle tissue (-16.2 ± 2.4‰) were significantly more enriched than those of fin tissue (-16.9 ± 2.1‰) (Yuen t-test, $t_{(65.82)}$ = 2.246, p = 0.028) when samples were pooled for species and sites. The nitrogen stable isotope values, although enriched in muscle tissue (9.56 ± 1.9‰), were barely different from the fin tissue values (8.8 ± 1.9‰) (Yuen t-test, $t_{(65.11)}$ = 1.946, p = 0.056). On an individual species level, the δ^{13}C and δ^{15}N values were generally more enriched in muscle than fin tissue for all species (Fig. 5). However, the difference were significant in carbon isotope (Yuen t-test, $t_{(43.23)}$ = 2.452, p = 0.018)

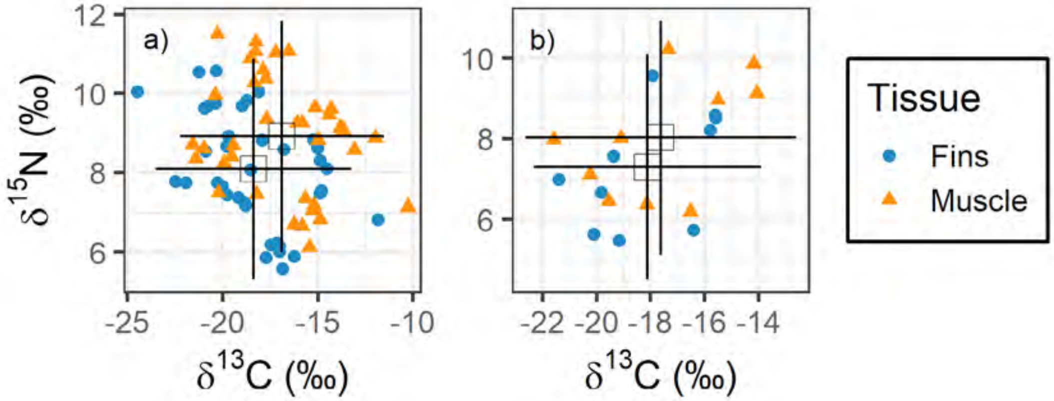

Figure 5. The δ^{13}C and δ^{15}N signatures in dorsal muscle and caudal fin tissues of fish species for a) *G. oyena* (n=37 for fin tissues and 37 for muscle tissues) and b) *G. filamentosus* (n=10 for fin tissues and 10 for muscle tissues).

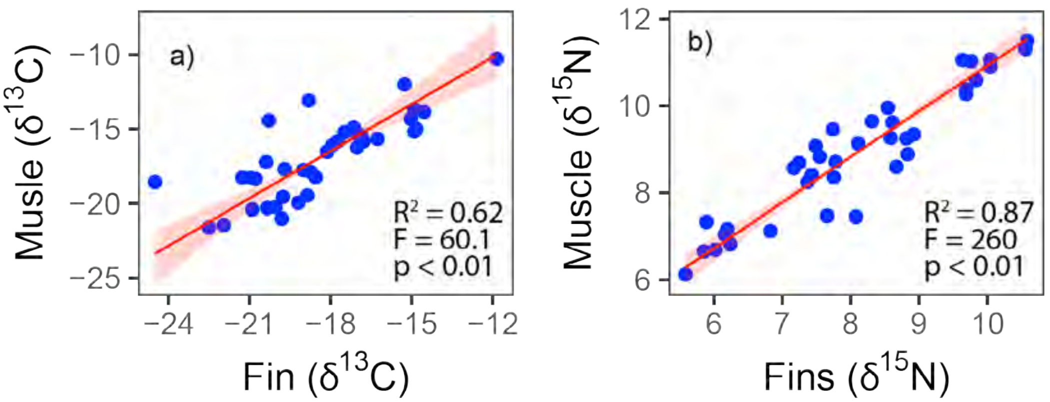

Figure 6. Correlation of a) $\delta^{13}C$ and b) $\delta^{15}N$ signatures between dorsal muscle and caudal fin tissues of *G. oyena* combined for all sites (n=37).

but not for nitrogen ($t_{(43.841)}$ = 1.880, p = 0.067; Fig. 5a). There was no significant difference in values of carbon ($t_{(17.46)}$ = -0.467, p = 0.646) and nitrogen ($t_{(17.97)}$ = -1.119, p = 0.278) stable isotopes between muscle and fin tissues for *G. filamentosus* (Fig. 5b).

Fin-clip as a proxy of muscle δ13C and δ15N

The stable carbon and nitrogen isotopes of *G. oyena* (Fig. 6) and *G. filamentosus* (Fig. 7), combined for both sites, were significantly correlated between dorsal muscle and caudal fin tissues. While $\delta^{13}C$ values of fin tissue explained 62% of stable isotope variations in dorsal muscle tissue of *G. oyena*, $\delta^{15}N$ values explained 87% of the variations (Fig. 6). For *G. filamentosus*, $\delta^{13}C$ values of fin tissue explained 89% of the variations and 98% of variation in $\delta^{15}N$ in the dorsal muscle values (Fig. 7).

Discussion

This study found that stable nitrogen isotope ($\delta^{15}N$) ratios were more enriched in fish samples caught in the Kunduchi mangroves as compared to those collected in Mbegani. While the nitrogen isotope ratio was 10‰ at Kunduchi, and 7‰ at Mbegani, the $\delta^{15}N$ value at Kunduchi was a magnitude higher than the value of 9‰ measured at the same location in 2005 (Kruitwagen *et al.*, 2006). The high $\delta^{15}N$ values at Kunduchi indicate signs of nutrients enrichment (Kruitwagen *et al.*, 2006; Lugendo *et al.*, 2007; McClelland *et al.*, 1997; Samper-Villarreal *et al.*, 2018). Similar $\delta^{15}N$ enrichment observations have been reported in the Mtoni Kijichi mangroves (Kruitwagen *et al.*, 2006; Kruitwagen *et al.*, 2008), where values as high as 13‰ were measured in mudskippers (Kruitwagen *et al.*, 2006), and mangrove snails (Kimirei *et al.*, unpublished data). Both Kunduchi and Mtoni Kijichi mangroves are located in areas with high population densities (NBS, 2013). Also, Mtoni Kijichi receives large quantities of industrial effluents (Kruitwagen *et al.*, 2006; Kruitwagen *et al.*, 2008; Machiwa, 1992; Machiwa, 2010). The Dar es Salaam City has poor waste disposal facilities, which further contributes to the coastal pollution problem (Kimirei *et al.*, 2016).

Like $\delta^{15}N$, the stable carbon isotope ($\delta^{13}C$) values for fish from Kunduchi were slightly enriched when compared to fish from Mbegani. Both *G. oyena* and

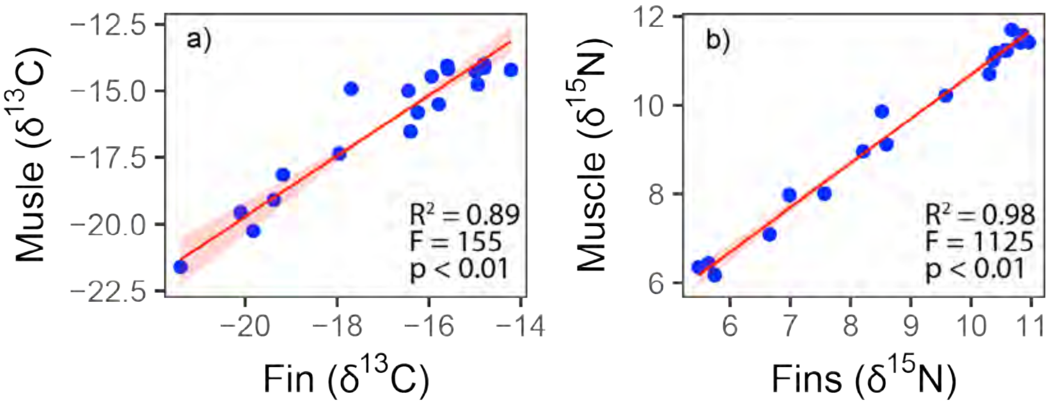

Figure 7. Corelation of a) $\delta^{13}C$ and b) $\delta^{15}N$ signatures between dorsal muscle and caudal fin tissues of *G. filamentosus* combined for all sites (n = 20).

G. filamentosus are generalists (Mavuti *et al.*, 2004), and share various carbon sources at Kunduchi, as indicated by the highly mixed $\delta^{13}C$ signatures (see Fig. 3a). However, the $\delta^{13}C$ signatures were different between *G. oyena* and *G. filamentosus* at Mbegani, with $\delta^{13}C$ isotopes enriched in *G. oyena* in both muscle and fin tissues (see Fig. 3b). These results may indicate that the two species have significantly different carbon sources at Mbegani, although they have been reported to feed in similar environments (Lugendo *et al.*, 2007).

When compared to Mbegani, the fishes collected from the Kunduchi mangrove creek appear to have a substantially higher level of nutrient enrichment, which is indicated by the high $\delta^{15}N$ ratio. While Kunduchi was considered relatively pristine in other studies (Kruitwagen *et al.*, 2008), this study indicates that during the sampling time, it was becoming increasingly polluted (Jiang *et al.*, 2019; McClelland and Valiela, 1998; McClelland *et al.*, 1997). The increased enrichment in Kunduchi may be due to increasing human population, industrial and domestic effluents, and urban agriculture, which utilize inorganic fertilizers to boost production. Mangroves are increasingly being polluted (Machiwa, 1992; Machiwa, 2010), perturbed and cleared (Ajai and Chauhan, 2017), which decimates the value they play in terms of ecosystem services (Kimirei *et al.*, 2016). While the data analysed in the current study are based on samples collected a decade ago, it has significance in assessing the role of population growth and anthropogenic pollution on nutrients pollution in mangroves (see Lugendo and Kimirei, 2021).

On an individual species-level, $\delta^{15}N$ values were always more enriched in muscle than in fin tissues while the opposite was true for the $\delta^{13}C$ values which were higher in fins than in muscles. Similar observations were made for *Oncorhynchus tshawytscha* and *O. mykiss* (Sanderson *et al.*, 2009). While it is beyond the scope of this study, the differences in isotopic enrichment between muscle and fin tissues may be explained by the abundance of both essential and non-essential amino acids for $\delta^{15}N$, and lipids for $\delta^{13}C$ (Pinnegar and Polunin, 1999; Sanderson *et al.*, 2009). Nonetheless, it was found that both carbon and nitrogen stable isotope signatures were highly correlated between muscle and fin tissues of the fish species examined. The nitrogen isotopes of fins explained >80% of the variations in stable isotope values of muscle tissue. These findings indicate that fin-clipping can be used as a reliable non-lethal method for stable isotope analysis (SIA) of nitrogen enrichment for the studied fish species. Fin-clipping has been found to be especially useful in monitoring endangered species (Jardine *et al.*, 2011; Kelly *et al.*, 2006; Sanderson *et al.*, 2009; Valladares and Planas, 2012), as well as in situations requiring large sample sizes and replications (Sanderson *et al.*, 2009). Stable isotope analysis as a tool for monitoring nitrogen enrichment in coastal waters should be especially useful in countries with minimal financial resources to run long-term monitoring campaigns.

The findings of this study support the use of fin-clipping as a non-lethal proxy for stable isotope analysis for the fish species under consideration. Furthermore, this study found that the stable nitrogen and carbon isotope signatures of fish collected from Kunduchi mangrove creeks were more enriched than those collected from Mbegani, and this enrichment was consistent across the two studied species. The results of this study, the first in the WIO region to examine the non-lethal collection of fish tissues for use in stable isotope studies, are positive, and should encourage the use of fin clipping as an alternative to the extraction of dorsal muscle tissues in stable isotope studies involving fishes. It is also recommended that more research is done on non-lethal sampling techniques to include more species and tissue types.

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Original Article

Artificial reef structures and coral transplantation as potential tools for enhancing locally-managed inshore reefs: a case study from Wasini Island, Kenya

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Abstract

Many severely degraded reefs in the western Indian Ocean region show no signs of natural recovery and have remained for decades as barren, unconsolidated coral rubble fields with depleted commercially important fish groups. Consequently, several restoration techniques have been designed and developed to mitigate the localized impacts on coral reefs. Evaluating the efficacy of combined use of artificial reef structures and coral transplantation in enhancing habitat and recovery of key functions in severely degraded reefs is key to improved conservation of coral reefs. In this study, the survival of corals transplanted on reef structures is assessed, and changes in coral and fish abundance on artificial reef units and nearby natural reefs over time are compared. Coral cover on artificial reef structures increased from a mean of 17 % one year after initial attachment of fragments to 41 % after two years, with *Acropora* corals providing the highest cover. The artificial reef structures were also rapidly colonized by reef fish, with fish densities of 18±13 indiv./100 m^2 showing a three-fold increase compared to natural reefs after two years. Greater numbers of commercially important fish groups (e.g., Lutjanids and Acanthurids) were observed on artificial reefs while natural reefs harboured more small sized fish (Pomacentrids and Labrids). These findings provide insights for artificial reef projects that are capable of restoring the regenerative capacity of the human-induced coral rubble beds.

Keywords: coral transplantation, artificial reefs, community conservation areas (CCAs), reef restoration, reef conservation

Introduction

Coral reefs are among the most productive and biologically diverse ecosystems in the world (Burke *et al.*, 2011). While the value of coral reefs is intrinsic for many, there are also tangible physical and economic benefits especially for coastal communities including coastal protection, artisanal fisheries production, and tourism revenues (Burke *et al.*, 2011). The estimated value of Kenya's marine ecosystems is around US$ 2.5 billion per year (some 4 % of its GDP), of which 70 % is from tourism and reef-based fisheries, which are highly dependent on healthy reef ecosystems (Obura *et al.*, 2017a). Coastal tourism and subsistence fisheries are the two primary sources of livelihoods for coastal populations.

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However, just like in many parts of the western Indian Ocean (WIO), Kenyan coral reefs have suffered from the severe impacts of human activities, resulting in long-term decline (Wilkinson, 2008; Obura *et al.*, 2017b). These anthropogenic impacts include local stressors such as overfishing, land-based pollution, and global stressors such as climate change (Hoegh-Guldberg *et al.,* 2017; Mwaura *et al.,* 2017). Climate change-associated stressors, such as elevated seawater temperature and ocean acidification, are some of the global disturbances representing the greatest threat to coral reefs, over and above the many local threats (McClanahan *et al.*, 2002; Hughes *et al.*, 2018). In Kenya, previous inshore reef monitoring has shown that over 70 % reefs are in a poor condition (0-15 % live coral cover) and less than 5 % are in good condition (30-60 %) (Obura *et al.,* 2017b). The low status of live coral cover on most reefs is due to unusually higher ocean temperatures that cause stress to corals resulting to massive death (bleaching) of susceptible corals such as *Acropora* and other thermally sensitive and branching corals (McClanahan and Mangi, 2000; McClanahan *et al.*, 2004). According to the Global Coral Reef Monitoring Network many coral reefs are in decline due to more frequent and severe bleaching events, forcing regime shifts to macroalgae dominated habitats (Shaver *et al.*, 2020). In Kenya, large-scale coral bleaching events have been recorded in 1997/98, 2010, 2012, and in 2016, with many reefs experiencing very little or no natural recovery over time (Gudka *et al.,* 2018). The loss of coral cover following mass bleaching events can have a considerable impact on habitat complexity and associated fish populations over longer timescales (Wilson *et al.*, 2006).

At the local level, loss of habitat caused by destructive fishing methods is one major threat to coral reefs (Burke *et al.*, 2011). One of the most notable is the beach seine net fishing method, which destroys the structural complexity of the reef by shattering corals into pieces (McManus and Nanola 1997; Mangi and Roberts, 2006). The widespread use of destructive gears is also unsustainable as it not only harvests target fish species (i.e., commercially-important fish) but also non-target species (McManus *et al.,* 1997).

Several reef lagoons in Kenya including the Wasini Island shallow reefs have been affected by degradation. As indicated by a recent scientific report, these areas used to be dominated by fast growing branching corals such as *Acropora* and *Pocillopora* spp. (Karisa *et al.*, 2020). But as a consequence of destructive fishing and large-scale bleaching of corals (*Acropora* spp.), most back-reefs are severely devastated and characterized by low hard coral cover and fish abundance (3 %, <10 individuals per 1000-m^2 area) , respectively (Mwaura and Murage, 2013). The absence of recovery is not due to a lack of larval availability; many reefs are generally well-connected and some outer reefs maintain a mixed coral community at over 40 % (Karisa *et al.*, 2020). Some fragments usually survive after destruction, but after several days or weeks most are known to eventually die (Fox *et al.*, 2003). Post-settlement mortality is usually high because of the mobility of loose rubbles that inhibits coral spat or juvenile attachment and growth (Fox, 2004). In such situations, the choice of restoration techniques and current state of the reef to be restored are fundamental considerations in reef conservation (De la Cruz *et al.*, 2014).

Artificial reefs structures can provide additional, albeit unnatural habitat, and are increasingly being used to mitigate impacts on coral reefs (Fadli *et al.*, 2012, Murage and Mwaura, 2015; Williams *et al.*, 2019). These artificial reefs which include man-made structures (e.g., shipwrecks, concrete structures, iron-rod structures), and sometimes with coral fragments attached, are intended to mimic natural reefs and enhance habitat availability for corals and reef-associated fish recovery (Abelson *et al.*, 2006; Thanner *et al.*, 2006). In severely degraded reefs, artificial reefs have been designed and developed to be used to rehabilitate their physical structure and function and consequently serve as a conservation tool (Williams *et al.*, 2019). Specific conservation goals of artificial reefs include: restoration of 3-dimensional structures on degraded reef (Rinkevich, 2005), enhancement of commercially important fish (Fadli *et al.*, 2012), and provision of firm substratum for coral transplantation and growth (De la Cruz, 2014). Successful reef rehabilitation using a combination of artificial reef structures and coral fragment transplantation have been undertaken with a view of enhancing coral and fish abundance on severely degraded reefs (Fadli *et al.*, 2012; Williams *et al.*, 2019). However, there is a paucity of information on their role as reef conservation or enhancement tools in severely degraded marine environments, especially in the WIO (Bostrom-Einarsson *et al.*, 2020). To assess the efficacy of both artificial reef structures and transplantation of coral fragments as conservation tools, it is important to compare the key ecological changes or patterns between artificial and adjacent natural reefs.

An ecological justification for deployment of artificial reef structures onto which coral fragments are transplanted is that the area and condition of rubble-reef may limit reef fish abundance and firm substratum for coral recruitment (Fadli *et al*., 2012; Williams *et al*., 2019). In this study, it was hypothesized that the deployment of artificial reef structures in addition to coral transplantation will have a significant effect on the abundance of coral cover and reef fish, especially those targeted in the reef fishery, surpassing those on adjacent natural reefs.

The study objectives were therefore to 1) describe the technique for building the artificial reef structures, 2) document survivorship rate of transplanted corals, and 3) compare changes in coral cover and reef fish abundance on the artificial reef with the adjacent natural reef over time.

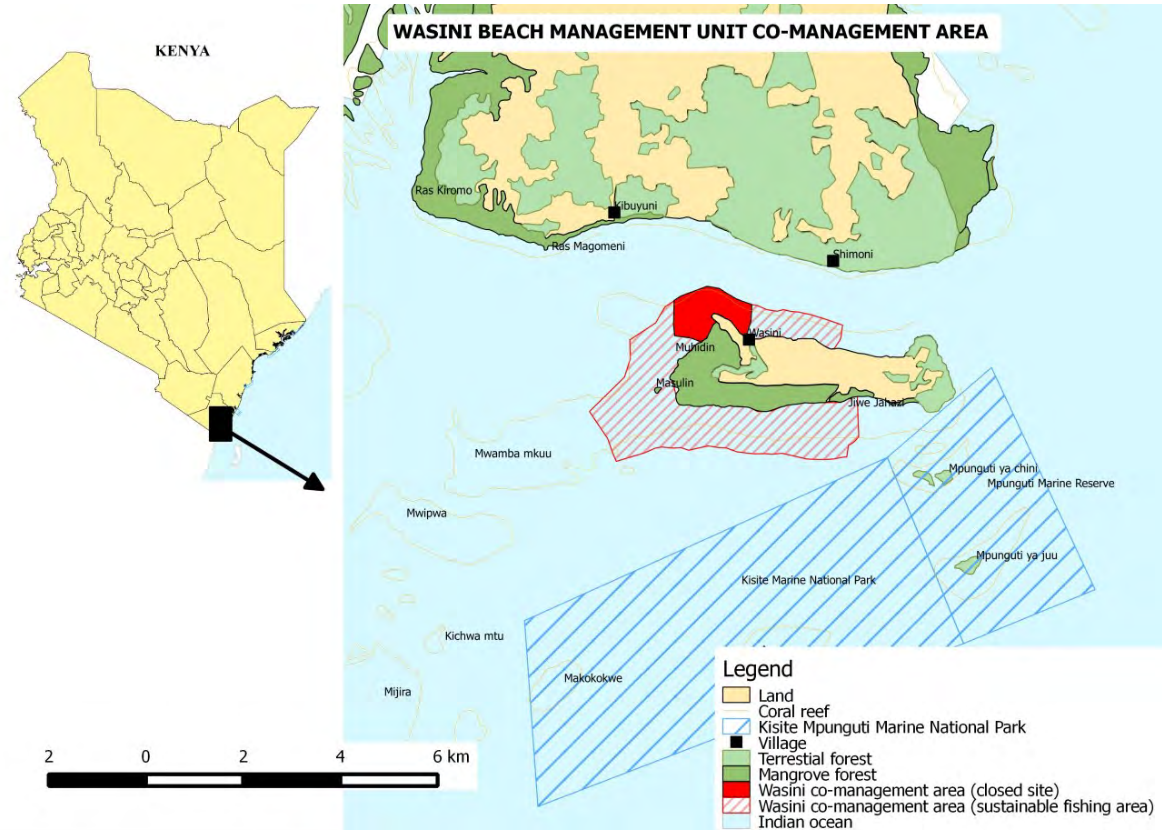

Figure 1. Map showing the location of the community conservation area at Wasini Island (no-take zone in red), southern coast of Kenya where the artificial reef project was undertaken in 2019 and 2021.

Materials and methods

Site description

The reef rehabilitation project was undertaken at Wasini Island, located on the southern coast of Kenya (Fig. 1). The rehabilitation work was initiated in response to funding by the GEF-Small-Grants Programme of United Nations Development Programme-Kenya, to support coral reef conservation in Wasini Island where a community-managed conservation area (CCA) had been set aside since 2010. The reefs around the Island support various tourism activities and are improtant artisanal fishing grounds.

Community engagement in artificial reef work

The initiation of the artificial reef project started with a two-day workshop with key stakeholders and identification of their individual role/tasks in project implementation. The meetings also entailed awareness raising and training of stakeholders on basic coral biology and reef ecology, concepts of coral reef restoration, the activity objectives, transplanting techniques and the need for active restoration.

With the help of 30 local participants, the construction of artificial reefs was initiated by the making of rectangular wooden moulds, each with a dimension of 20x20x150 cm. A concrete mix was then made from three parts aggregate (predominantly coral boulders

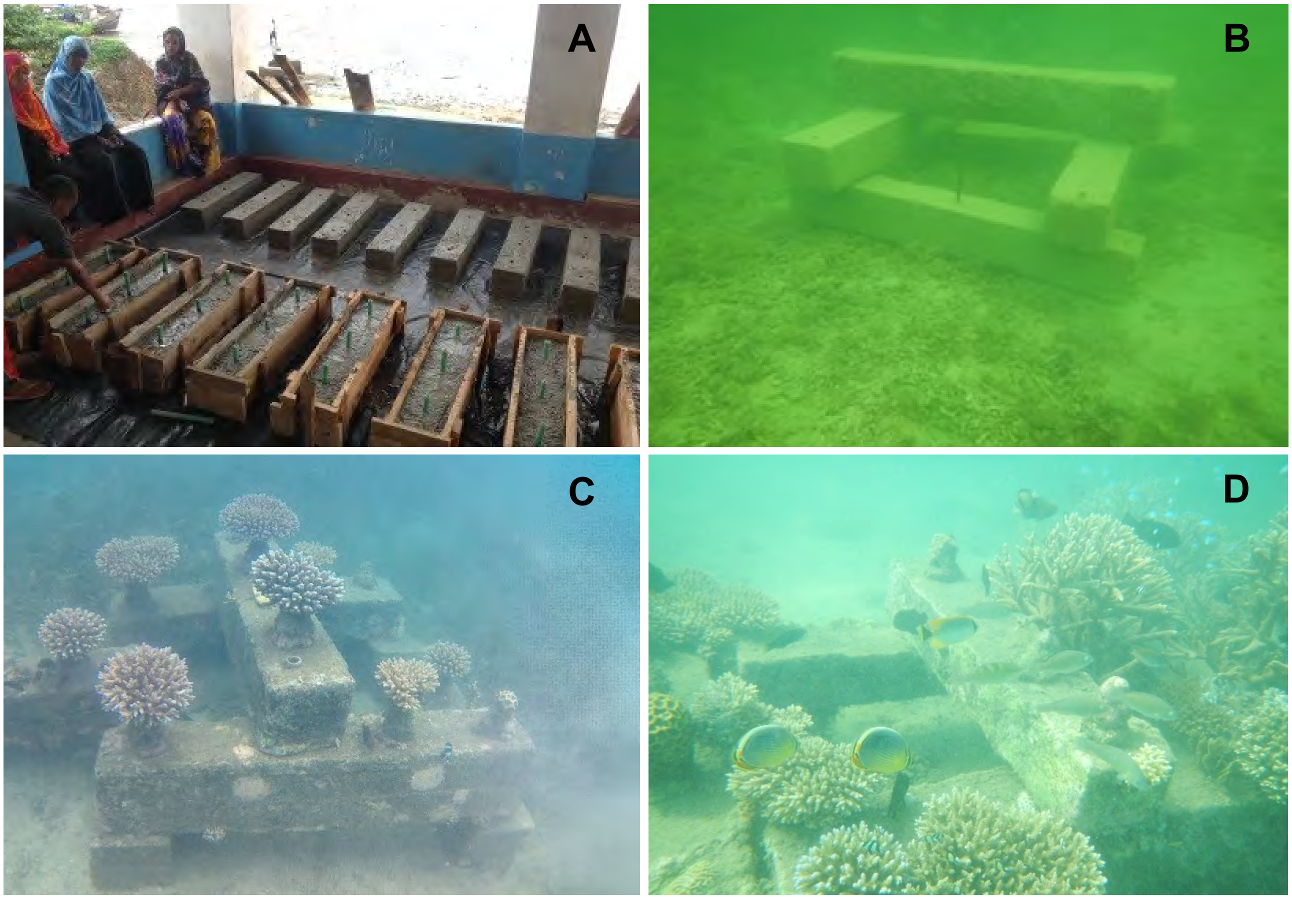

Figure 2. A - construction of artificial reef structures. B - deployed artificial reef structure units as replicates in the study. C- coral fragments attached to artificial structures after one year. D - abundant reef fish on artificial reef structures after two years.

crushed into particles, with a particle size of 2-20 cm) mixed with three buckets of sand and one bag of normal Portland cement. This concrete mix was then poured into the prepared wooden moulds to create a concrete block which was then reinforced using 8 mm steel bar (Fig. 2A). The constructed concrete blocks were then left on the beach to dry for 1-2 weeks. Divers then manoeuvred the blocks underwater and positioned them on bare-rubble habitat to form a pyramid-shaped reef structure (Fig. 2B). In this way, the artificial reef was made up of a network of over 20 groups of pyramid reefs deployed in similar depths within a no-take zone (Fig. 2B).

A few days prior to the transplantation activity, live coral fragments were collected by the authors assisted by about 20 trained community members. Fragments were sourced from a healthy reef on the northern side of Wasini Island (Fig. 1). The donor site was chosen on the basis that it had abundant and suitable branching coral species such as *Acropora* spp., *Porites*, and *Stylophora* which were targeted for use in this restoration, although other genera were also included. Fragments were augmented by loose coral fragments ("coral of opportunity") collected from the back reef at the rehabilitation site as they would otherwise perish from being buried in soft sediments or swept about by currents. Upon removal from the source reef, the harvested fragments were kept in plastic buckets filled with sea water and immediately transported by boat and laid down (≈2m deep) next to the artificial reef site. With the help of 20 local participants, more than 800 coral fragments were transplanted onto the concrete artificial reef surfaces. The transplantation was performed by attaching the coral fragment to the artificial reef surface using cement-sand mixed with seawater (i.e., cement balls). The fragments were placed 20-30 cm apart to avoid space competition among them as detailed by Omori and Iwao (2014). Periodic maintenance of transplanted corals was also carried out by local community participants for a period of 3 months, which involved cleaning/scrubbing of the concrete base of fragments, replacement of dead fragments and re-securing the dislodged ones.

Study design and data collection

This restoration project is a community-led project and the artificial reef was not intended as an experimental study. As such, this study design was superimposed onto the existing artificial reef to meet the objectives of this study.

The artificial reef network comprised over 10 groups of artificial reefs; only three of these artificial reef aggregations were selected as replicates for this study. To investigate the influence of artificial reefs, the changes in fish abundance and coral cover were monitored over time and compared to those in adjacent natural reefs. The monitoring also involved periodic observation on survivorship of transplanted corals which were tagged or labeled in order to track them. Survivorship of coral species was rated by number of corals that were alive compared to the total transplanted.

Changes in coral cover and fish abundance were assessed over three years, once before and twice after artificial reef structure deployment (i.e., before deployment, after 1 year, and after 2 years). As the artificial reef structures were deployed on sand-rubble habitat, the 'before' samples represented data prior to the deployment of the artificial reef structures. The percentage benthic cover within each of the three replicate artificial reef units was estimated using the 10 m line intercept method (PIT), following the protocol described in English *et al.* (1997). The observer recorded the benthic cover type under the tape at 0.5 m intervals.

The response of the fish community to the artificial reef treatment was assessed following modification of the line transect (Samoilys and Carlos, 2000). Each of the three artificial reef units was considered as a plot. The diver and transect layer swam along the three transects in one plot counting the fishes within a 5 m wide belt and 20 m long transect. The fish species counted at family level were later assigned into either "indicator" species (e.g. Chaetodontidae) and "target group" (e.g., Lutjanidae) and "other" families. The authors performed all the monitoring of the parameters. To compare the changes of benthic cover and fish abundance on the artificial reefs to those on adjacent natural reefs, three representative natural reefs were also monitored following the sampling protocol for the artificial reefs.

Statistical analysis

Statistical analyses were performed in R version 4.0.05 (R Core Team, 2021). One-way ANOVA was used to test for difference in mean coral cover and fish density before deployment, 1 year and 2 years after deployment, and on the natural reef substratum. Raw values of coral cover were used after examination of the residuals and revealed no major bias. Tukey's post-hoc tests were used to determine which treatments differed.

Fish family density was used to test the degree of change between the two reef types, i.e. natural and artificial reefs. Therefore, variations in fish family community structures was compared between natural and artificial reefs as treatment factors. A sample-family density matrix was developed with a sample size of six (6) for both natural and restored reefs. This was followed by a square root transformation to reduce species density variation within the dataset. Bray-Curtis similarity was used in the multivariate Permutation Analysis of Variance (PERMANOVA) to test for significance of differences between the two treatments. Permutation of Dispersion (PERMDISP) was used to test the degree of sample point variation in multivariate space, which were visualized in a non-metric Multi-Dimensional Scaling (nMDS) graph. Finally, Similarity Percentage (SIMPER) analysis was used to draw an understanding of the fish families responsible for the variation in community structure.

Results

Transplanted coral survival rate

After one year the overall survival rates of the coral transplants ranged between 30-100 % for the 15 genera with a high average survivorship of 76 % (Table 1). There was strong variation between genera, with higher mortalities being recorded in corals such as *Pocillopora*, *Goniopora*, and *Echinopora*. On the other hand *Acropora*, *Stylophora*, *Porites* massive and *Porites* branching exhibited higher survivorship (89-100 %). Generally, six months after transplantation, 86 % of the transplants survived well. One important observation was that it was critical to regularly clean the fragment base to avoid algal overgrowth on transplanted corals in the first three months after deployment. A few transplant mortalities were evident during the initial months and may be attributed to dislodgement from the concrete substrate due to poor cementing and accidental knocks/detachment by community members during cleaning, rather than natural mortality.

Coral cover

Mean percentage coral cover on artificial reef structures significantly increased from a mean of 3.3 %±SD 5.6 %, to 16.5 %±SD18.3 % one year after initial attachment of coral fragments to 41 %± SD20 % after 2 years

Table 1. Percentage survival rates of transplanted coral fragments.

Coral genus	Initial number of transplants	Live transplants observed	Survival rate (%)
Acropora	80	78	97.5
Favia	37	30	81.1
Favites	43	35	81.4
Hydnophora	25	18	72.0
Goniopora	5	2	40.0
Echinopora	34	17	50.0
Stylophora	7	7	100.0
Diploastrea	8	6	75.0
Platygyra	34	28	82.4
Pocillopora	50	15	30.0
Pavona	17	15	88.2
Lobophylia	10	8	80.0
Porites (massive)	46	43	93.5
Porites (branching)	38	34	89.5
Leptoria	19	14	73.7
Overall	453	350	75.6

(P<0.001; Fig. 3). In contrast, coral cover on the nearby natural reef remained low (4 % to 8 %), indicating no evidence of substantial change over the study period (Fig. 3). Coral cover of 41 %± SD20 % after two years of artificial reef deployment (Fig. 3) was almost entirely because of the increase in the cover of transplanted *Acropora* corals (Fig. 2C).

Fish abundance

The artificial reefs were quickly colonized by damsel and other small-bodied fish (see Fig. 2D). Pairwise differences revealed no evidence of differences in fish density both on artificial and natural reefs before deployment (Fig. 4). However, there were significant differences in fish density, with reef fish density increasing from a mean of 7± SD6.7 indiv./100 m^2 after 1 year and to 18± SD12.9 individuals/100 m^2 after 2 years on artificial reefs (Fig. 4). In contrast, there was no evidence of changes in fish abundance at the natural reefs over time.

Non-metric Multidimensional Dimensional Scaling (nMDS) showed a separation of sample points between natural and artificial reefs (Fig. 6). This was supported by PERMANOVA (Table 2) and PERMDISP, which both showed a significant difference between the two reef types (P<0.005). While the former demonstrated a variation in fish family community structure, the latter demonstrated a significant variation in the dispersal of sample points in multivariate space (Fig. 6). SIMPER results showed 57 % dissimilarity between natural and transformed reefs with Acanthurids (16 %),

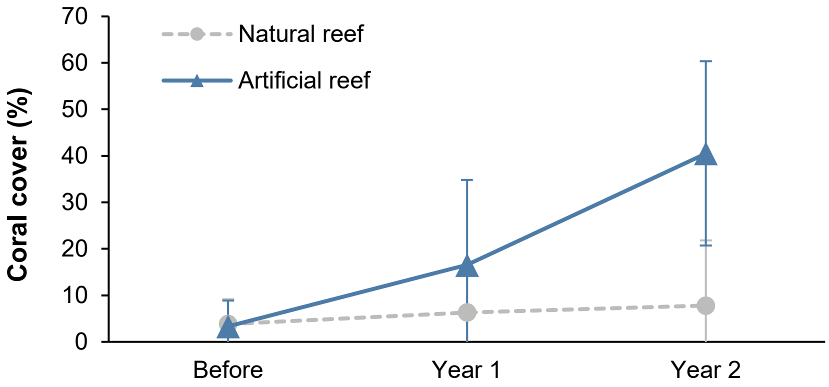

Figure 3. Percentage coral cover (m±stdev). Time steps are before artificial reef structure deployment, 1 year after and 2 years after artificial reef structure deployment. Dashed line with circles represent the natural reef and solid line with triangles represent the artificial reef.

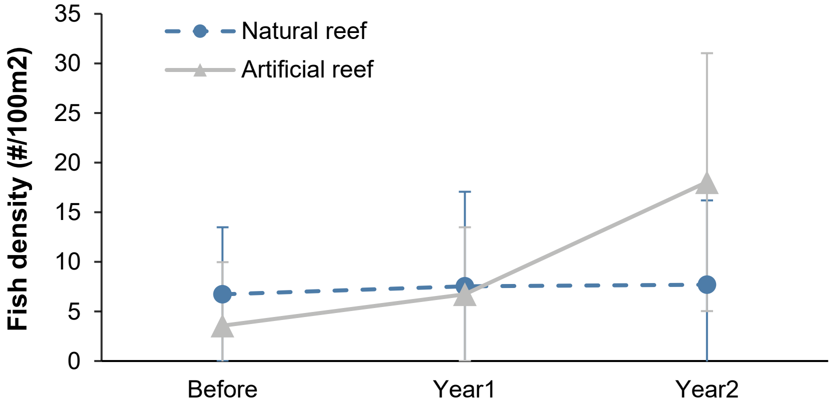

Figure 4. Average fish density (m+stdev). Time steps are before artificial reef structure deployment, 1 year and 2 years after artificial reef structure deployment. Dashed line with circles represent the natural reef, and solid line with trianges represent the artificial reef.

Pomacentrids (14 %) and Labrids (10 %) accounting for most of the variation; all three being more abundant on the natural reef (Table 3). However, commercially important families such as Scarids, Lutjanids, Serranids, Lethrinids, Haemulids, Siganids and Chaetodontids were all more prevalent on the artificial reef compared to the natural reef (Fig. 5).Two year-old artificial reefs had well-developed corals to the point where they had begun to attract reef health indicator fish species (i.e., Chaetodontids) (Fig. 5).

Discussion

This study reveals the potential of the combined application of artificial reef structures and coral transplantation as conservation tools in speeding up habitat restoration and recovery of key functions in a severely degraded reef system. It was found that before the deployment of artificial reef structures, the density of fish was similar to that at nearby natural reef. One year after the deployment and transplantation of coral fragments, fish abundance was significantly higher than those on natural reefs. Throughout the study, fish abundance on natural reef either slightly increased or showed no evidence of change over time. When viewed in conjunction with other research in the literature that showed higher fish density following the deployment of artificial reef structures (Fadli *et al.*, 2012), this study provides compelling evidence that artificial reef structures create new reef habitat, that provides a potential basis that favours foraging opportunities and increases shelter availability for fish, (Raymundo *et al.*, 2007; Charbonnel *et al.*, 2002). Besides the effect of new reef habitat, differences in reef heterogeneity and increased niche partitioning could also explain the higher density on artificial reefs compared to the natural reef. In fact, even if the habitat complexity has not been quantified in this study, it should be noted that natural reefs is

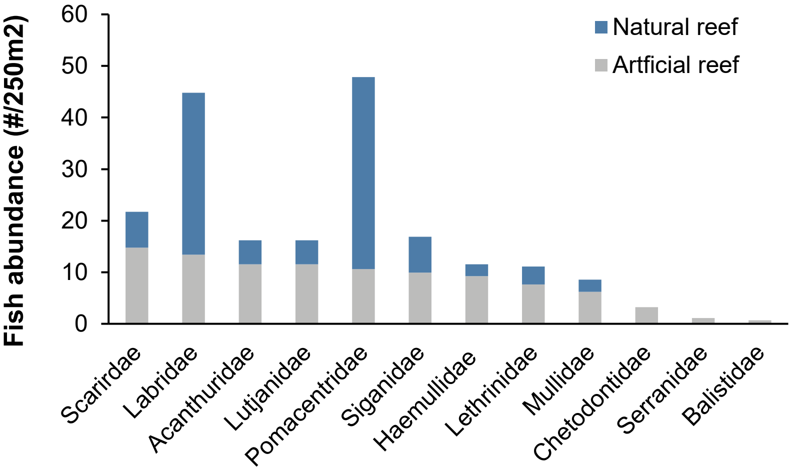

Figure 5. Proportion of fish abundance by Family two years after artificial reef deployment, and on natural reef.

Table 2. One-way PERMANOVA results comparing the community structure of fish families between natural and artificial reefs.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Treatment	1	2682.2	2682.2	3.6618	0.004	411
Residuals	10	7324.7	732.47			
Total	11	10007				

a extensively rubble-dominated field with some few rocky boulders, whereas rehabilitated area is small (i.e., 0.012 ha) and comprises several deployed discontinuous artificial reef subsets. Coral reefs are complex biogenic habitats, combining both physical (e.g., high structural heterogeneity) and biological (e.g., live coral cover) characteristics (Walter and Haynes, 2006; Feary *et al.*, 2007). Several fishes are dependent on live coral for food (Pratchett, 2005) and structural heterogeneity increases available habitat; providing refuge from predation and attracting fish recruits (Lindahl *et al.*, 2001). As the current study showed, this effect is especially important when both the structural and biological component potentially influence the abundance and composition of the associated fish community on artificial reefs. The difference is perhaps linked to the lower coral cover in natural reefs given that coral dependent fish such as Chaetodontids require higher coral cover (Boström-Einarsson *et al.,* 2018).

Few studies have investigated the effects of adding new habitat using before and after reef construction samples. In the current study before and after reef construction was used to investigate the effects of artificial reefs on fish abundance. The study hypothesis proposed that if the addition of new reef habitat on sandy-rubble reef serves to overcome habitat limitation, then addition of corals on constructed artificial reef structures would promote greater fish abundance. Indeed, the density of fish after one year on artificial reef was not considerably different to before the deployment, but was significantly higher after two years, and higher than on natural reefs. It should be noted that the carrying capacity of these artificial reefs may be is bottlenecked by the lack of large corals which are so crucial for habitat provision in natural reefs (Holbrook *et al.*, 2002). The artificial reefs were purposely deployed to optimize habitat complexity and rugosity but clearly cannot compare to healthy natural reefs in terms of habitat provision for fish. However, increased habitat area provided by artificial reef does show the effectiveness of these structures in their ability to facilitate survivorship and increased growth of transplanted corals. Where coral mortality is low, it would be expected that these corals would grow to larger sizes, increase habitat complexity and support larger fish populations (Halford *et al.*, 2004). In this study, the artificial reefs were rapidly colonized after one to two years by numerous reef fish including those important in the fishery such as the Lutjanids, Acanthurids as well as ecological indicators such as Chaeotodontids. The exceptional increases in abundance for both indicator and target fish groups on artificial reefs suggest that these might have important positive implications for the ecological status of coral reefs and the livelihoods of the coastal fishing communities (Cabaitan *et al.*, 2008; Spalding, 2016).

The probable key to success in rapidly creating new reef habitat in this study was the choice of a fast-growing coral species (*Acropora* spp.) that was resistant to handling, easy to transplant, survived well and grew

Table 3. SIMPER results showing the comparison in average abundance of fish families between the natural and artificial reefs.

Families	Natural Reef Av.Abund	Artificial Reef Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Acanthuridae	22.17	9.5	12.42	2.1	20.8	20.8
Pomacentridae	27.17	15	11.15	1.14	18.68	39.48
Labridae	10.67	17	7.13	1.6	11.94	51.42
Scaridae	9	14.17	5.45	1.28	9.12	60.54
Lutjanidae	7.83	10	5.11	1.8	8.57	69.11
Serranidae	0	6.17	4.25	0.73	7.12	76.23
Lethrinidae	2.5	11	4.07	0.87	6.82	83.05
Haemulidae	0	8.83	3.53	1.33	5.91	88.96
Siganidae	5.17	9.33	3.04	1.4	5.09	94.05

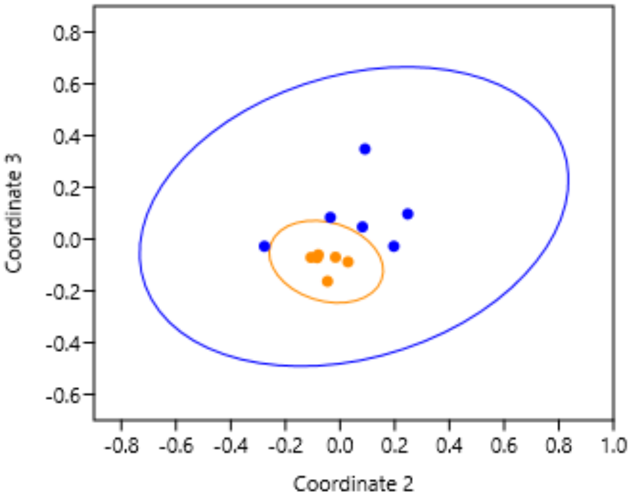

Figure 6. nMDS plot demonstrating variation in fish community structure among sample points where brown and blue dots represent natural and artificial reef samples, respectively.

rapidly. There was a clear pattern in terms of the coral cover of coral communities on the artificial reef over time. The cover of *Acropora* corals increased over time from deployment, perhaps due to the high survival of transplanted corals and also the artificial reef substratum being rapidly colonized by coral recruits (Rinkevich, 2000, pers obs.). One explanation for this is that *Acropora* corals have been identified as an opportunistic genus with life history traits that allow for the quick colonization of newer substrates (Jouval *et al.*, 2020). In this study, coral cover and habitat complexity may have improved to attract more reef fish within a relatively short time period as the project used mainly fast-growing *Acropora* coral species (Rinkevich, 2000).

The relatively high survival of transplanted corals could also be attributed to community participation in maintenance efforts (i.e., once a week for three months) on transplanted corals. Proper training and education of participating community members was important in order to maintain the structural integrity of artificial structures and transplanted corals to reduce impacts from potential competing taxa (i.e., macroalgae, sponges). A similar study has shown that higher survival of coral transplants is mostly related to the avoidance of adverse conditions, including algal overgrowth, by maintenance cleaning (Hernández-Delgado *et al.*, 2014).

Anecdotal reports suggest an immediate benefit of involving the local community in supporting artificial reef projects. The use of artificial reefs as a method to increase reef habitat as part of ecological restoration is a valid application, particularly in areas with tourists. Community members have increasingly been showcasing their restoration sites to tourists, thus providing an additional benefit that could develop into an alternative livelihood for local residents as indicated in another study (Cadiz and Calumpong, 2000). On average, there has been an 80-100 % increase in weekly income for the Wasini community members, from US 60 to US 220, during high tourism seasons (unpublished data).

In conclusion, the results from this study provide compelling evidence that the use of artificial reef structures in conjunction with coral transplantation represent viable restoration tools as they have the potential to restore habitat and enhance coral and fish abundance on severely degraded reefs. Additionally, this project demonstrates that local communities can be practically involved in restoration of their degraded reefs (e.g., regular cleaning of algal overgrowth on coral fragments) when provided with training on restoration skills, as it encourages their active participation and stewardship in reef restoration (as also observed in related studies, e.g., De la Cruz *et al.*, 2014). The deployment of artificial reef structures and subsequent transplantation of corals upon them has generally shown a positive trajectory of coral and fish recovery in a severely degraded reef area over a short timescale (2 years). Given the continued growth of transplanted corals and natural recruitment of corals on the artificial reef structures it would be expected that, in the long-term, the eventual development of large corals could support larger populations of fish (Halford *et al.*, 2004), and contribute to showcase the potential use of combined artificial reef structures and coral fragment transplantation as a conservation tool in severely degraded reefs.

The present study, being one of a few implemented in the WIO, raises many opportunities for reef researchers and local communities to continue partnering to develop this method further, as well as monitoring in order to understand fully the benefits and/or impacts of this reef restoration approach. If scaled-up with consideration of initial successes and lessons learnt, this combined use of artificial reef structures and coral transplantation can contribute towards the UN-proclaimed Decade of Ecosystem Restoration (2021-2030), which aligns with a wide range of Sustainable Development Goals (SDGs), including enhancing healthy of coastal ecosystems and biodiversity conservation (UNEP, 2019). In light of this global target, the ongoing assessment of this artificial reef can be used to gain insights into the effectiveness of artificial reefs as a conservation tool for habitat restoration and recovery in degraded coral reef ecosystems, and become an important focus for coastal communities.

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Original Article

Local perceptions, opportunities, and challenges of community-based ecotourism in Gazi Bay, Kenya

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Abstract

Community Based Ecotourism (CBET) has the potential to both improve the conservation status of mangrove ecosystems and stimulate local economies. However, these ecotourism initiatives often fail due to a lack of active local participation, poor management and a lack of an appropriate benefit sharing scheme. This paper explores perceptions, opportunities and challenges of community mangrove-based ecotourism in Gazi Bay, Kenya. Data collected from household surveys, key informant interviews and focus group discussions were used to examine local perceptions, challenges and opportunities with respect to their participation in ecotourism as a tool for mangrove conservation. The results obtained indicated that 81.4 % of the Gazi village community was aware of the ecotourism activities being undertaken in the area with 62.8 % acknowledging the socio-economic as well as the environmental impacts of the ecotourism activities. Also, 66.0 % of the local community identified cultural traditions and local skills possessed by the community as having the potential to promote sustainable ecotourism activities in the area. For the design and implementation of any ecotourism venture and the management of mangroves to be sustainable, including that undertaken by the Gazi community, this study recommends prioritising effective local participation and capacity building. In addition, private sector involvement is essential for the mobilisation of resources to further enhance the management and conservation of mangroves in the long-term. The results provide key insights needed not only to improve the design and management of community-led marine conservation initiatives but also for ensuring that optimal conservation benefits are achieved.

Keywords: community-based ecotourism, perception, community participation, mangrove conservation, Gazi Bay, Kenya

Introduction

Ecotourism is embraced as an alternative means to stimulate conservation of natural ecosystems (He *et al.*, 2008; Walter, 2013; Jamaliah and Powell, 2018; Ma *et al.*, 2019). However, in the general literature there is a lack of clear definition of what specifically constitutes ecotourism. Despite this lack of clarity, ecotourism ventures include those that protect the

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environment, create awareness, preserve people's culture and experience, while at the same time generating economic benefits (Cobbinah, 2015, 2017). Bluwstein (2017) defines ecotourism as responsible travel to natural areas with the intention to promote conservation of the environment and enhance the wellbeing of the local people. The ecotourism concept first gained global attention in the 1980s in response to the idea that traditional tourism had damaging impacts to the environment (Wondirad *et al.*, 2020). The first global outlook of a single environment facing similar threats emanated from the Brundtland report of 1987 – 'Our common future ', which recognized the fact that humans and the environment are inseparable from one another. It further suggested that the exploitation of resources, direction of investments, orientation of technological development, and institutional change be made consistent with the future as well as present needs (WCED, 1987). Therefore, when ecotourism promotes the wellbeing of the host communities (IES, 2018), Community-Based Eco-Tourism (CBET) is realized, which encompasses both environmental conservation and socio-economic impacts in its execution (Ma *et al.*, 2019). Other forms of tourism including sustainable tourism and nature tourism that captures the components of ecotourism have also been highlighted in literature.

Sustainable tourism encompasses all types of tourism that meet the needs of tourists and host places while accounting for its current and future social, economic and environmental impacts (Hall, 2019). This includes ecotourism, soft tourism, alternative tourism, green tourism, and rural tourism. Nature tourism on the other hand is a form of alternative tourism that focuses on bringing together conservation communities and sustainable development through travel (Andreea *et al.*, 2008). Sustainable tourism is anticipated to result in the management of all resources in a manner that satisfies economic, social and aesthetic requirements while preserving cultural integrity, vital ecological processes, biological diversity and life support systems (UNCTAD, 2011).

Target 8.9 of the 2030 Agenda for Sustainable Development Goals (SDGs), aims to "devise and implement policies to promote sustainable tourism that creates jobs and promotes local culture and products". The importance of sustainable tourism is also highlighted in SDG target 12.b which aims to "develop and apply tools to assess sustainable development impacts for sustainable tourism that creates jobs and, promotes local culture and products". Meanwhile, Chapter IV, paragraph 43 of the Johannesburg Plan of Implementation Page (UNCED, 2002), advocated for the promotion of sustainable tourism development, including non-consumptive use of the environment and ecotourism, during the 2002 World Summit on Sustainable Development in Johannesburg in 2002.

Ecotourism activities have generally promoted the conservation of fragile natural ecosystems and endangered species while boosting local economies (Bluwstein, 2017). Specifically, CBET has recorded tremendous benefits towards the conservation of wildlife and natural ecosystems worldwide. The practice promotes conservation of natural resources, management of tourism activities while promoting the protection of the natives' cultural heritage, training of members in the local tourism industry, as well as integration of public and private sector activities, among others (Ma *et al.*, 2019). The CBET approach underscores the importance of local communities and helps in enhancing their contribution to the tourism value chain by providing products and services such as village tours, homestays, gift items and cultural shows (Mondino and Beeny, 2018). These communities can benefit by incorporating their rich culture in ecotourism development to enhance conservation efforts (Bluwstein, 2017; Ma *et al.*, 2019). In response to the rising tourism demand, however, traditional cultural practices may be perverted by choreographing for touristic display and consumption. (Habinc, 2012).

CBET ventures have positively impacted on local perceptions towards the sustainable utilization and management of natural resources among communities (Hunt *et al.*, 2014). In developing countries such as Kenya, ecotourism activities have been implemented not only for the purpose of preserving the environment but also for poverty reduction (Manyara and Jones, 2007). However, most of the coastal-based community-managed ecotourism establishments and activities remain largely undocumented which is exacerbated by the domestic and international promotion of the charismatic "big five" wildlife tourism in national parks and reserves. This lack of documentation has far-reaching implications in terms of how the model of these initiatives can be improved to achieve optimal environmental and local benefits (Ma *et al.*, 2019). To date, striking a balance between economic benefits from ecotourism activities and maintaining ecological sustainability and preserving indigenous socio-cultural practices remains the major challenge in developing countries including

Kenya (Wondirad *et al.*, 2019, 2020). There is still a lack of consensus on whether ecotourism has managed to live up to its expectations or not (Wall, 1997; Gossling, 1999; Cater, 2006; Manyara and Jones, 2007; Bluwstein, 2017; Ma *et al.*, 2019).

The fall and underperformance of some CBET projects is linked to poor governance structures, lack of effective stakeholder involvement and competing interests among stakeholders, weak institutional arrangement, lack of social accountability and lack of local participation (Towner, 2018). Effective local support and participation has been identified as a key pillar for sustaining ecotourism-based conservation ventures (Wondirad *et al.*, 2020). A high level of local participation in CBET implementation is associated with the existence of good governance structures, socio-economic impacts and ecological effectiveness (Bennett *et al.*, 2019). Mostly, these ventures are established within communities that live adjacent to natural resources (e.g., mangrove ecosystems) as applied in this case study of Gazi Bay, on the south coast of Kenya (Kairo *et al.*, 2009). Due to varying perceptions of how these resources are utilized or managed, it is necessary to closely examine the local context and performance of community-led ecotourism initiatives. Several factors, including social norms, demographic demographics, place connection, values, rewards, and governance structures, have been identified as drivers of local attitudes towards CBET conservation programmes. (Christie, 2005; Bennett *et al.*, 2019).

To generate a better understanding of CBET, this study examines local perceptions as well as challenges and opportunities of mangrove-based ecotourism activities in Gazi Bay, Kenya. Specifically, the study objectives were to (i) identify the perceptions regarding local participation and performance of a mangrove-based ecotourism initiative, (ii) identify perceived challenges impeding its success, and lastly (iii) identify the perceived opportunities in the area that could be tapped to promote the sustainable development of ecotourism.

Case study: Mangrove-based ecotourism initiative in Gazi Bay, Kenya

Mangroves are salt-tolerant intertidal ecosystems that provide various goods and services ranging from climate regulation through carbon sequestration (Donato *et al.*, 2011; Githaiga *et al.*, 2017), to provisional services such as exploitation for firewood and construction materials (Kairo *et al.*, 2001). Similarly, the complex structure of the mangrove root system provides ideal nursery grounds for juvenile fish thus directly supporting local artisanal fisheries (Huxham *et al.*, 2004, 2015). However, the sustenance of these ecosystem goods and services from mangroves in Gazi Bay is threatened mainly by anthropogenic stressors such as poaching

Figure 1. A section of the ~500 m Gazi women boardwalk providing visitors with a beautiful walk in a serene mangrove forest.

and overharvesting, among other related stressors from the surrounding communities (Aboudha and Kairo, 2001; Kirui *et al.*, 2013). The overreliance of the Gazi village population on mangroves for construction materials and fuel wood has left a highly disturbed forest structure (Aboudha and Kairo, 2001; Huxham *et al.*, 2004). It is estimated that mangroves provide approximately 70 % of the local community's wood requirements. (Government of Kenya, 2017). This need for wood and population growth poses a significant threat to the mangroves in Gazi Bay.

Policy documents integrating community participation in forest management (Kenya's Forest Act and Forest Conservation and Management Act 2016), establish a legal framework for Nature-Based Enterprises (NBE) as a sustainable compromise between generating economic incentives and nature conservation. As a result, many strategies have been developed to leverage on the advantages and opportunities presented by the current regulations and policy framework.

The Gazi community's interest in addressing the negative human impacts on mangroves attracted donor support which led to the establishment of the 'Gazi Women Boardwalk Group' in 2006. The project started through the support from the city of Overijse in Belgium and the International Ocean Institute (IOI) through coordination by Kenya Marine and Fisheries Research Institute (KMFRI). The KMFRI-affiliated project partners have a long history of cooperation with the local communities in Gazi Bay, with the Mikoko Pamoja carbon offset project (https://www.planvivo.org/mikoko-pamoja) and the Gazi ecotourism project being products of that contact. A team of Belgian scientists presented the mangrove ecotourism boardwalk to the Gazi Community as a reward after their successful mangrove research in Gazi Bay. When asked what they would prefer as a show of appreciation, the residents of Gazi sought assistance in launching an ecotourism venture. The objective of the project was to empower women and establish alternative livelihood activities for the benefit of the entire community as incentives to mangrove conservation.

This venture is run by 28 female members, including a chairperson, treasurer, and secretary who serve as the project's executive members, and a member who acts as a field tour guide. This group that currently serves as the project custodian on behalf of the Gazi community, used the start-up funding from Overijse Municipality of Belgium to construct an initial 300 m long nature boardwalk (which at present stands at ~500 m long; Fig. 1) adjacent to the seaward fringe mangroves. The strategic location of the boardwalk enables visitors to experience the view of all the 9 mangrove species occurring in Kenya, the most dominant in the area being *Rhizophora mucronata* (mkoko) and *Ceriops tagal* (mchu). The other species found along the boardwalk include *Avicennia marina*, *Sonneratia alba*, *Bruguiera gymnorrhiza Xylocarpus granatum*, *Heritiera littoralis*, *Lumnitzera racemosa* and *Xylocarpus moluccensis* (Kairo *et al.*, 2001).

The model of this ecotourism initiative offers field-guided excursions and cultural experiences through learning about the history of the village and enjoying coastal cuisines. Revenue generated from entrance, commodity and service fees is ploughed back to maintain the structural component of the boardwalk from wear and tear, support community development projects and mangrove conservation activities. In 2018, unpredictable revenue streams, poor management, internal conflicts amongst group members and high maintenance costs caused the enterprise to almost collapse. The consequence of this type of failure will be intensified mangrove resource-use pressure, thus re-exposing and exacerbating degradation and over-exploitation of the already fragile mangroves of Gazi.

Materials and methods

Study area

The study was conducted in Gazi Bay on the south coast of Kenya (4°25'S and 39° 30'E) located 55 km south of Mombasa Island along Lunga-Lunga road which comprises the two villages of Gazi and Makongeni. Gazi village was chosen for this study because it hosts the Gazi Women Boardwalk ecotourism venture (Fig. 2). The bay comprises a total of 650 ha of mangrove forests by area and is home to all the 9 species of mangroves found in Kenya as well as marine fauna and migratory seabirds (Kairo *et al.*, 2001; Kirui *et al.*, 2013). The bay lies within the Diani-Chale peninsula – a tourism hotspot with one of the best sandy beaches in the world, yet the initiative has not capitalized on its strategic position. Nevertheless, Gazi receives a significant number of local and international students linked to the KMFRI-Gazi station and its networks that are interested in mangrove conservation and research.

Gazi has a total human population of ~5,000 living within 500 households (KNBS, 2020). The Digo, part of the Mijikenda ethnic community, is the dominant population in the village. This ethnic group is organized around matriarchy, a social system that defines unique dynamics in resource use, value or perceptions and governance (Mugaju, 1980). An itinerant fisher community (Pemba), originally from the neighbouring country of Tanzania, forms a small and significant demography in the village. The Pemba people offer affordable and highly skilled fishing services while Digo people provide the capital for fishing operations, serve as middlemen and coordinate fish sales (Wanyonyi, 2016).

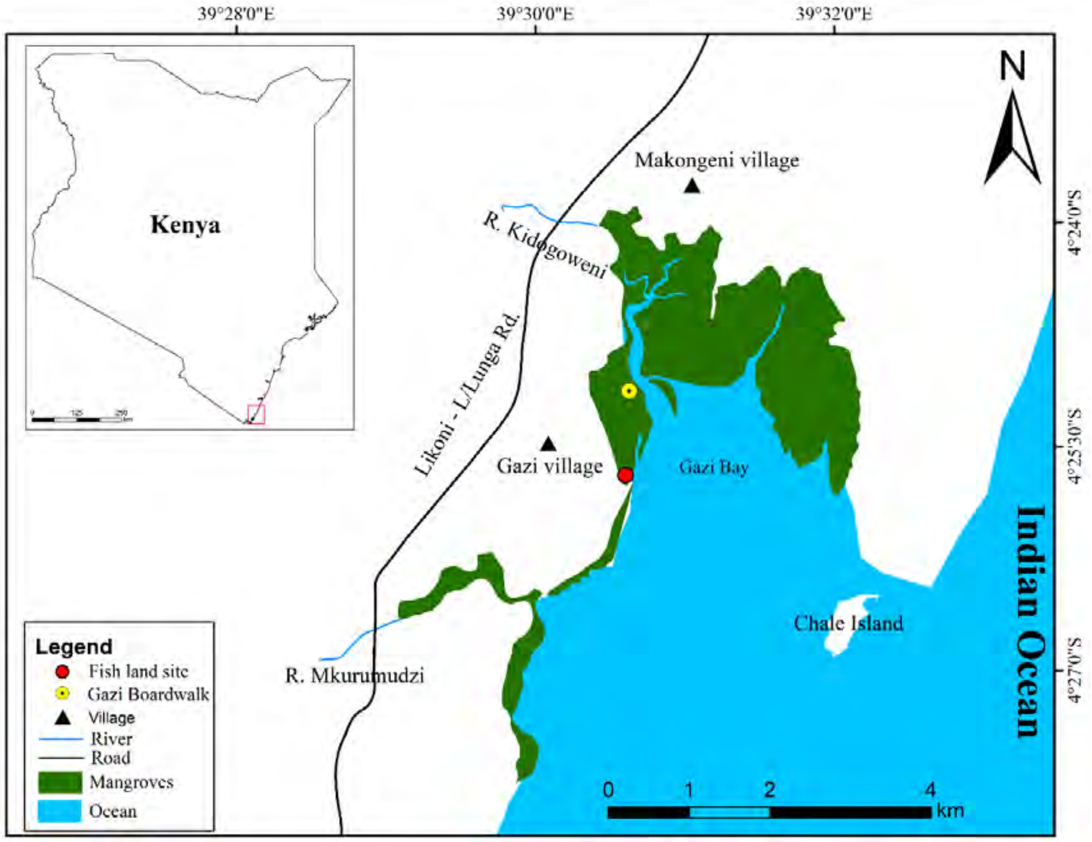

Figure 2. Map of study site showing the two adjacent villages of Gazi and Makongeni and the extent of mangroves in Gazi Bay, south coast of Kenya. Inset - map of Kenya locating the Bay.

Sampling design and data collection

A total of 102 households were systematically selected and surveyed based on a list provided by the village head (each fifth household was picked from the list). A semi-structured questionnaire was used, and this covered local perceptions on performance (impact and challenges) of the ecotourism venture and opportunities that can enable sustainable ecotourism development as well as promote sustainable use and mangrove conservation. The household head was the primary target for the survey. Prior to the main data collection exercise, a reconnaissance survey was conducted in five randomly selected households to test the questionnaire. The questionnaire was subjected to a thorough revision ensuring that all the redundant questions were removed. The team made final changes on the questionnaire and a Swahili language translation was provided for each question since this is the commonly spoken language in the area. Six key informants from KMFRI, Worldwide Fund for Nature (WWF-Kenya), Kwale County Government, local tour operator, Gazi Women Boardwalk Group and the local Beach Management Unit (BMU) were selected for the interview based on their prior working knowledge of the subject matter. Two Focus Group Discussions (FGDs) were undertaken with participants drawn from Gazi Women Boardwalk Group and Gazi BMU (Table 1). Each group was made up of 15 members and a series of open-ended questions on mangrove conservation and ecotourism were discussed and recorded.

Data analysis

Data analysis was carried out with Microsoft Excel (v.2010) and SPSS (v.22.0) software. Descriptive statistics were mostly applied, which helped to transform

Table 1. Participants in key informant interviews and actors in ecotourism and mangrove conservation in Gazi Bay.

Key Informants/Actors	Role
Gazi Women Boardwalk Group	They are the project administration and custodian of the ecotourism venture in Gazi village in charge of day-day operations.
Gazi Beach Management Unit	Comprises members drawn from Gazi (such as fishermen, fish traders, transporters) that ensure sustainable use of fishery resources including mangrove breeding grounds.
Kenya Marine and Fisheries Research Institute	A government institution that conducts research on aquatic resources and mangroves. They provide technical support, and a link between the community and international funders/institutions.
Kenya Forest Services	A government agency that oversees conservation, protection and management of all state-owned forests including mangroves.
Kwale County government (Tourism department)	A devolved unit of the national government in charge of administration. Through the tourism department, they formulate policies aimed at promoting sustainable tourism practice.
Worldwide Fund for Nature-Kenya	A non-governmental organization that supports local communities to conserve, protect and restore natural resources including mangroves.
Local tour operators	These include private tour and travel agencies that are responsible for organising and preparing holiday and travel packages to tourists which include ecotourism sites.

raw data into a form that summarized a set of factors in a way that it was easy to understand and interpret. The Chi-squared test was used to statistically test relationships between categorical variables. Yate's Correlation for Continuity (Yate's Chi-square) was used as it compensated for overestimates of Chi-square values while the association among various categorical variables was tested using the Pearson Chi-square test. The p-value of < 0.05 was assigned to each statistically significant relationship.

Results

Socio-demographic characteristics of Gazi village

By gender, 78.4 % and 21.6 % of the respondents were female and male, respectively. Ethnic diversity was observed with 70.6 % Digo as the majority, and the communities of Pemba, Gunya, Fundi, Duruma, Bajun, Arabs, Kamba and Luo as the minority comprising the remaining 29.4 % (Table 2). The study depicted low literacy levels where approximately 4 % of the respondents confirming to have gone through tertiary education while ~10 % completed 12 years of formal education (Table 2). The study established that men (95 %) were the household heads, providing support towards subsistence through small-scale business and fishing (25.5 %).

The average household size was 7 members, with each household having an average of 3 individuals above 18 years. Fishing and small-scale business were identified as the main livelihoods sources. Farming, food vending and dealership in wood fuel provide alternative and significant sources of livelihood (Table 2).

Perceptions of the local community towards the mangrove-ecotourism initiative

Ecotourism venture in Gazi

The majority (81.4 %) of the respondents acknowledged having knowledge of ecotourism activities in Gazi village. Cross tabulation of educational level against knowledge of ecotourism activities revealed no significant association between the two variables (χ^2 (7, N = 102) = 9.00, $p > 0.05$). Respondents identified visiting the Gazi women mangrove boardwalk as the main tourist activity in the area (Fig. 3). Other activities identified to promote ecotourism in Gazi included educational and research activities by the KMFRI Gazi station, sharing of Swahili culture and traditions between locals and visitors, artisanal fishing, boat riding and visiting the sandy beach.

A relatively small number of respondents (19.6 %) reported to be directly involved in ecotourism activities in Gazi either as active members of the Gazi women mangrove boardwalk group, tour guides or as cooks to facilitate the picnics for those visiting the ecotourism initiative. Results of Chi-square test between gender and involvement in ecotourism activities

Table 2. Socio demographic characteristics of respondents in Gazi village.

Demographic Characteristics			
		Number	**Percentage**
Gender	Male	22	21.6%
	Female	80	78.4%
Ethnicity	Digo	72	70.6%
	Pemba	17	16.7%
	Gunya	7	6.9%
	Other (Fundi, Duruma, Bajun, Arabs, Luo, Kamba)	6	5.9%
Age	Range	18 – 80	
	Mean	38.89 ±13.9	
	Mode	30	
Marital status	Single	17	16.7%
	Monogamous Married	75	73.5%
	Polygamous Married	4	3.9%
	Living together without marriage	5	4.9%
	Widowed	1	1.0%
Literacy Levels	No Education	14	13.7%
	Incomplete Primary	15	14.7%
	Complete Primary	25	24.5%
	Incomplete Secondary	10	9.8%
	Complete Secondary	10	9.8%
	Higher Education	4	3.9%
	Madrassa	23	22.5%
	Adult Education (*Ngumbaru*)	1	1.0%
Livelihood Activities	Fishing	26	25.5%
	Farming	6	5.9%
	Small Scale Business	40	39.2%
	Food Vending	4	3.9%
	Transport Business	1	1.0%
	Fish Dealer	2	2.0%
	Others	23	22.5%

(χ^2 (1, N = 102) = .013, $p > 0.05$); and ethnicity and involvement in ecotourism activities (χ^2 (7, N = 102) = 4.85, $p > 0.05$), showed no significant association. The majority of the people (69.5 %) reported to have an interest in being involved in ecotourism activities in Gazi while 27.6 % of the respondents reported that their family members were already involved in the ecotourism initiative through the Gazi women mangrove boardwalk group and as tour guides.

Socio-economic impact of ecotourism in Gazi

Cross tabulation of respondents' involvement in ecotourism activities against impact of ecotourism on respondents' wellbeing revealed a significant association between the two (χ^2 (1, N = 102) = 40.29, $p < 0.05$); the majority (60 %) of individuals involved in the ecotourism initiative said they had benefited either directly or indirectly from ecotourism. Benefits realized by the community included the creation of business and employment opportunities for locals in Gazi, supporting educational activities in the local school and madrassa (e.g., salary for madrassa teacher), and ploughing back the revenue obtained from ecotourism into the renovation of the mangrove boardwalk which forms the major source of income (in form of tourist fees) for the ecotourism initiative. In addition, earnings from mangrove-ecotourism were used to support portable water projects for the community, to buy school equipment, and sponsor school-going children. Generally, the respondents agreed that ecotourism in Gazi village made a positive contribution towards access to education, access to better health, boosting small enterprises, access to credit, expansion of employment opportunities, environmental conservation, as well as enhanced entrepreneurial skills for the locals in the village, either directly or indirectly (Table 3).

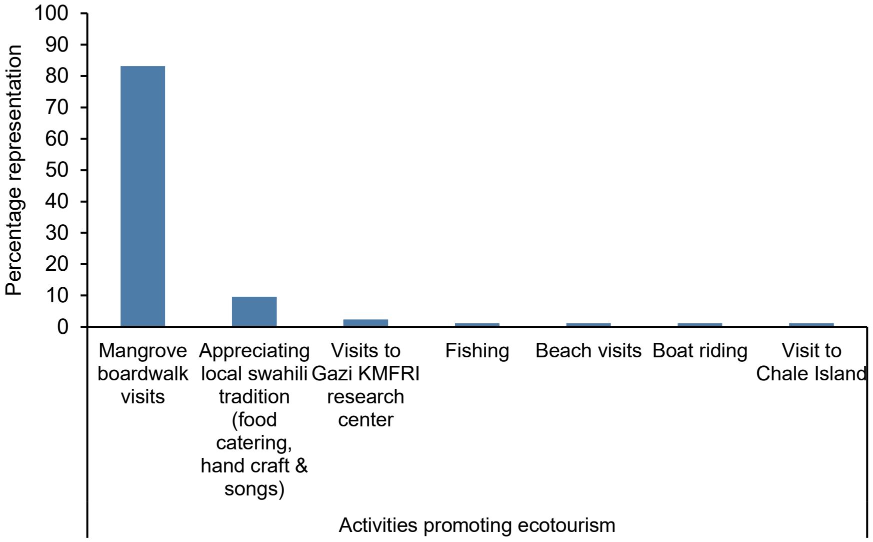

Figure 3. Activities promoting ecotourism in Gazi village, south coast of Kenya as perceived by the local community.

Impact of ecotourism to mangroves in Gazi

From the survey, 82 % of the respondents reported that there were frequent visits to the mangrove forest in Gazi by the locals and tourists. The highest frequency of visits observed included monthly visits (27 %), daily visits (21 %), weekly visits (18 %) and annual visits (16 %) (Fig. 4). Results of Chi-square test between gender and visit to mangrove areas (χ^2 (1, N = 102) = .058, p > 0.05) showed no significant association, meaning gender had no influence on the frequency of visits to the mangrove forest.

In order of preference, the place within the mangrove forest that had the highest frequency of visits was the Gazi women mangrove boardwalk for recreational purposes followed by the mangrove forest (mostly by women to collect fuelwood) and lastly the beach area (by fishermen accessing the landing site, and swimming for villagers and visitors; Fig. 5).

On the question of whether ecotourism activities had an impact on mangrove conservation the majority (64.4 %) of the respondents agreed that ecotourism had reinforced ongoing efforts to conserve mangroves in Gazi Bay (Fig. 6). Association between the level of knowledge of ecotourism activities and impact on mangrove conservation was not significant (χ^2 (2, N = 102) = 15.63, p > 0.05). Also, the level of education of respondents had no association with the knowledge of ecotourism activities and mangrove conservation (p > 0.05). In Gazi, participation in ecotourism activities and mangrove conservation is not contingent on formal education level. However, they acknowledged receiving informal education on ecotourism activities and mangrove conservation from state (e.g. KMFRI) and non-state (e.g. WWF-Kenya) actors as well as active members of the Gazi Women Boardwalk Group. These interactions between state, non-state and community actors are considered to

Table 3. Socio-economic impact of ecotourism in Gazi village, south coast of Kenya.

Ecotourism contribution	Level of Agreement	
	Yes	No
Access to education	59.8% (n = 61)	40.2% (n = 41)
Access to health facilities	85.3% (n = 87)	14.7% (n = 15)
Increased small enterprise opportunities	77.5% (n = 79)	22.5% (n = 23)
Access to credit	95.0% (n = 96)	5.0% (n = 6)
Expansion of employment opportunities	69.6% (n = 71)	30.4% (n = 31)
Environmental conservation	54.9% (n = 56)	45.1% (n = 46)
Sale of goods and services locally	87.3% (n = 89)	12.7% (n = 13)
Training on entrepreneurial skills	88.2% (n = 90)	11.8% (n = 12)

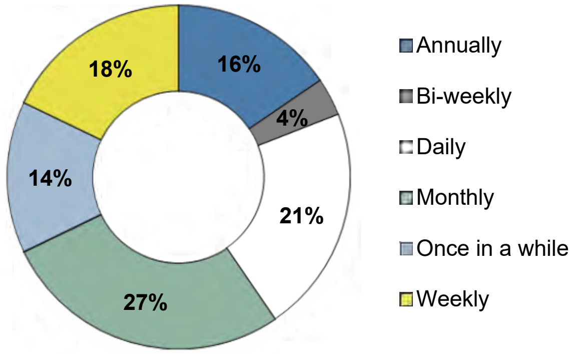

Figure 4. Frequency of visits to the mangrove forest in Gazi village, south coast of Kenya.

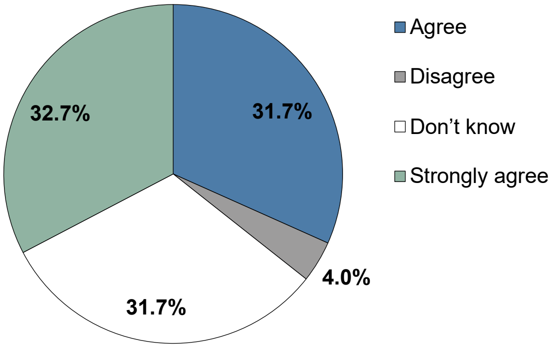

Figure 6. Respondents' level of concurrence on the positive impact of ecotourism on mangrove in Gazi, south coast of Kenya.

influence local perceptions and participation in mangrove conservation activities, including ecotourism.

Challenges of local participation in mangrove-based ecotourism

About 66 % of respondents believed the local community had no control over the existing ecotourism initiative in Gazi and that they do not draw financial benefits from the initiative (71 %). Moreover, 87 % of the respondents did not belong to any conservation group. Of the remaining 13 % who belonged to different community groups, the majority (72.7 %) were from the Gazi Women Boardwalk Group, 18.2 % from Mikoko Pamoja community organization (carbon-offset project) while 9.2 % were members of the local BMU.

The major challenges identified by the respondents that hinder ecotourism development and participation in Gazi village included poor condition and maintenance of the boardwalk due to theft and vandalism (22.4 %), poor management (no transparency) and marketing skills of ecotourism activities (17.2 %), and low tourist visits (13.8 %). Also, a low level of local participation, lack of measurable social economic impacts, inadequate accommodation facilities for visitors coming to Gazi village, lack of formal knowledge on ecotourism by the locals, the language barrier, moral decadency and discrimination were identified as challenges impeding long-term development of ecotourism. Moreover, a significant proportion of the respondents (28 %) felt they were dissatisfied with the way the operations and activities of the ecotourism initiative were conducted by the Gazi Women Boardwalk Group (project custodian).

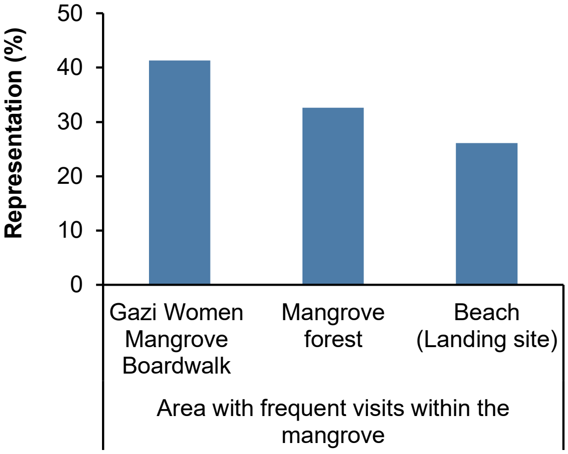

Figure 5. Most frequently visited areas within the mangrove forest of Gazi, south coast of Kenya.

Opportunities for promoting sustainable mangrove ecotourism development

Usage was used as an indicator for examining the value placed by the local community on the mangrove ecosystem. Both use value and non-use value of mangroves were identified by respondents. Use value (92.1 %) dominated mangrove usage and it comprised direct use value (70.1 %) and indirect use value (22 %). The direct use value of the mangrove ecosystem in Gazi included extraction of construction material (36.3 %), collection of firewood (30.3 %), use of mangroves for medicinal purposes (treatment of stomach ailments) (1.5%), use of mangrove poles for sailing boats (1 %) and use of mangrove areas for human waste disposal (0.5 %) (Fig. 7). The indirect benefits of the mangroves as identified by respondents included tourist attraction (7.5 %), carbon credit through carbon sequestration to mitigating global warming (7 %), breeding grounds and habitat for fish and other faunal communities (4.5 %), shoreline protection (2.5 %), and use of mangroves for scientific research (0.5 %). The non-use value of mangroves as identified by respondents were freshening of air (6.5 %), aesthetic value (1.5 %), and attraction of rainfall (0.5 %).

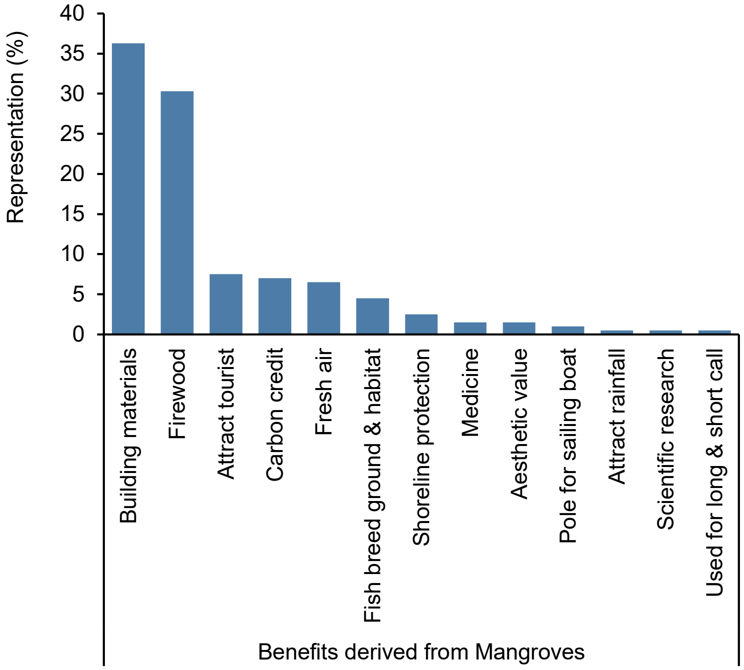

Figure 7. Perceived benefits derived from mangroves in Gazi Bay, south coast of Kenya.

Local talent such as handcrafting, music and photography (66 %) were identified as an enabler that could be tapped and marketed together with ecotourism activities in Gazi village to generate more conservation incentives. Of the remaining 34 %, internet accessibility and social media usage were recognized as factors that have the potential of promoting ecotourism and conservation activities. On internet accessibility, only 32.4 % of the respondents had access to the internet. Of these, 29.4 % said they were able to access social media platforms. The most utilized social media platforms were WhatsApp (59.6 %), followed by Facebook at 25.5 %, Twitter (2.1 %), Messenger (2.1 % and others (10.7 %). A cross tabulation of access to the internet against use of social media revealed significant association between the two (χ^2 (1, N = 102) = 76.21, $p < 0.05$); access to the internet influenced respondents' use of social media platforms. Most respondents (77 %) reported using social media daily.

Discussion

Socio-demography of Gazi village community

Demographic variables such as gender, ethnicity and marital status describe the population structure, especially gender-specific roles, and interest and participation in socio-economic activities (Wang and Yamamoto, 2009; Bennett *et al.*, 2019). With reference to gender, the study recorded a higher number of females than males. Gazi is a fishing village and fishing is a male-dominated activity. The observed high involvement of females in the survey was due to absence of majority of men being involved in fishing at sea and in fish distribution, while women dominated value addition and subsistence fish mongering within the village (Huxham *et al.*, 2015), and active participation in Gazi Women Boardwalk ecotourism initiative. Most of the study's respondents were in their economically productive age (< 60 years), indicating that the success of any conservation or economic interventions would require careful consideration targeting this group as a priority (Ochiewo *et al.,* 2020).

The study further revealed that most adults in Gazi village are characterised by a relatively high illiteracy level. This could either mean that education was either previously inaccessible or its relevance in the community was ignored. A study by Kenya Demographic and Health Survey (2014) identified education as a key determinant of lifestyle and social status. Besides, previous studies by Richard (2013) and the European Association for the Education of Adults (2010) pointed out that education increases prospects of gainful employment resulting in a decrease in poverty and an increase in innovations among a population. The effort by the ecotourism venture in Gazi village to promote education among youths will greatly enhance employability and expand livelihood options among locals in the future.

Perceptions of the local community towards the ecotourism initiative

The perceptions of the community were not based on gender, ethnicity and education level, especially regarding the knowledge of ecotourism activities in Gazi village. The respondents acknowledge that the Gazi women boardwalk was the main active tourists attraction site in Gazi. Other activities perceived by the community as forms of ecotourism were the field research tours by KMFRI, sharing of the Swahili culture and traditions, fishing activities and walks along the sandy beach of Gazi. Specifically, the presence of the KMFRI research station in Gazi has attracted visitors coming for educational excursions and research (local and international) and has promoted sustainable utilization of mangroves through their research and conservation activities (Kirui *et al.*, 2008; Kairo *et al.*, 2009; Huxham *et al.*, 2015; Huff and Tonui, 2017).

From this study, it is evident that many of the locals in Gazi were aware of the existing ecotourism activities and attractions, and mangrove conservation, yet many were not actively involved in them. The results showed that awareness of ecotourism activities had a low impact on local participation. The informal interaction between state (e.g. KMFRI, KFS) and non-state (e.g. WWF-Kenya) actors facilitated the improved awareness of ecotourism and mangrove conservation activities. However, the weight of active local participation is placed upon availability of good governance by the project custodian, social inclusion, measurable social impacts and ecological effectiveness (Bluwstein, 2017; Bennett *et al.*, 2019; Hunt *et al*; 2019); traits which the community feels are missing in the management of the ecotourism initiative. Inconsistent and insufficient revenues from the ecotourism initiative and poor management discourage locals from participating in ecotourism.

The results showed a strong relationship between ecotourism-derived benefits and enhanced local participation in ecotourism. Though a precise measure of the impacts as recommended by Bennett *et al.* (2019) and Cobbinah (2015) could not be provided, the ecotourism venture carried out by the Gazi Women Boardwalk Group generates direct income via tourist fees and indirect income to local businesses (e.g., sale of handicrafts and food). This revenue goes a long way in supporting education activities in the village and boosts the local economy of the people. Again, direct employment is created when participants in the ecotourism project are paid during the mangrove planting exercises either from funds generated from ecotourism or financed by NGOs, private companies or other government institutions like KMFRI and the Kenya Fisheries Service (KeFS). Besides this, other community-based organizations such as the Mikoko Pamoja project engage locals in mangrove nursery establishment and planting and subsequently create employment for youths and women (https://www.planvivo.org/mikoko-pamoja). Sustainable ecotourism can improve the living standards of the local community and can enhance environmental protection, thereby reducing the pressure on the area's already vulnerable mangrove resources (Ma *et al.*, 2019).

Ecotourism activities were perceived by most of the respondents to have an impact on mangrove conservation in Gazi. The number of visits to the mangrove forest is used as an indicator of place attachment and value put on mangroves by the locals (Ma *et al.*, 2019). The frequency of visits to the mangroves as captured in the study indicated a weak link with gender and education levels. However, the number of visits to the Gazi women boardwalk facility enhanced the place attachment of the locals and how they valued the mangrove forest. According to the findings, the locals derive both use and non-use value from mangroves. These direct and indirect uses of mangroves in Gazi include extraction of building materials, firewood collection, carbon sequestration, shoreline protection, breeding grounds for fish and use for scientific research. Meanwhile, the non-use value of mangroves as identified include the exploitation for their aesthetic purposes, use for their clean air and precipitation attraction. A functional ecotourism initiative has the potential to elevate the conservation status of natural systems and especially of ecosystems and species under human threats (Hunt *et al.*, 2014). Ecotourism in Gazi has enhanced the value and conservation of mangroves via awareness creation campaigns, restoration of degraded areas and enhanced surveillance of the mangrove forest.

Challenges of local participation in mangrove-based ecotourism

The study identified several challenges that are considered a hindrance to local participation and sustainable development of ecotourism activities in Gazi village that include poor management and lack of marketing skills. Also, the high cost of maintaining the boardwalk was considered as a bottleneck to ecotourism development. In this instance, the boardwalk serves as an anchor for ecotourism activities, and its dilapidated condition means that there will be no incentive for tourists to visit certain mangrove areas, resulting in diminished incentives for mangrove conservation. These findings are in line with Bennett *et al.* (2019) and Hunt *et al.* (2015) which links the poor performance of CBET initiatives to poor governance and conflicts, lack of active local participation and lack of measurable social economic impacts (Towner, 2018; Bennett *et al.,* 2019). Due to these obstacles, the success and capacity of ecotourism as a sustainable tool to generate incentives for mangrove conservation in Gazi is limited.

Opportunities for promoting sustainable mangrove ecotourism development

The study confirms the existing reliance on mangrove resources by the community mainly as construction materials, firewood and supporting local fisheries (Kimani *et al*., 1996; Huxham *et al*., 2004, 2015). The value placed by the local community on mangrove resources is seen as an opportunity to rally the community to support mangrove-related ecotourism and conservation activities. Various specific opportunities were identified as potential enablers for promoting sustainable development of ecotourism and mangrove conservation in Gazi Bay. First, the availability and use of local talent if included in ecotourism marketing, could enhance the initiative's visibility and attract visitors and subsequently generate more revenue. For instance, this might include the use of a professional photographer and a local brand ambassador to both serve as promoters of Gazi bay as an ecotourism hub. Also, talented members of the community (e.g., fishing, weaving, folk songs, Swahili cuisines etc.) can also be incorporated into the ecotourism initiative. Lastly, the local community can take advantage of the existing low-cost internet services and access to market ecotourism and mangrove conservation activities via social media platforms. The majority of the locals were found to be conversant with various social media platforms which can be used to reach a wider audience at a relatively low cost.

Conclusions

Poor governance, lack of transparency in benefit sharing and high operational costs are directly linked to low participation of the community in mangrove-based ecotourism. However, these results are context-specific and might vary with location hence cannot be generalised. Future research will benefit from taking sampling bias into account by ensuring that all groups, especially the marginalised, are well represented in the sample. Again, expanding this survey to the larger Gazi Bay communities (Gazi and Makongeni) will provide a comprehensive understanding of local perception towards ecotourism and mangrove conservation. Still, this case study in Gazi offers an opportunity to assess and compare the impact of ecotourism on local communities *vis-à-vis* mangrove conservation efforts. Lessons and experiences derived from this study can be used as a benchmark to inform how strategies and policies to conserve and manage mangroves are formulated.

For a community-based ecotourism initiative to be successful, the study recommends full participation of the locals from initial project design to full implementation. Specifically, capacity building is seen as one of the key elements recommended to sustain ecotourism activities. Also, a full refurbishment of the boardwalk with new durable materials would go a long way in minimizing the maintenance cost and thus unlocking funds available for nursery establishment and mangrove planting. On the other hand, the involvement of marginalized members of the community such as youths will ensure social inclusion is realized which will improve the general performance of these initiatives in the future. With the project solely depending on tourists earnings, it is suggested that private sector involvement be made a priority which will not only uplift the face value of the project but also provide additional resources to enhance the management of ecotourism activities in the area.

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Original Article

A checklist of the southwestern Madagascar sponge fauna with taxonomic updates based on the current systematics

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Abstract

Sponges are important components of coral reefs with diverse ecological roles. They can be dominant in certain ecosystems of the western Indian Ocean (WIO) region, but their biodiversity remains poorly studied. Most of the knowledge from this region originates from studies conducted 50 years ago in the South Western (SW) region of Madagascar, near Toliara, prior to the degradation of coral reefs and associated ecosystems caused by large environmental disturbances. Here, a reference list is presented including all sponge species that were recorded at that time in different marine habitats of Toliara. This state-of-the-art work includes taxonomic updates. So far, the sponge fauna of Toliara accounts for 267 species, belonging to 3 classes, 23 orders and 68 families, a remarkable diversity when compared to other tropical locations. More than 50 % of the past taxonomic names needed to be updated and with this new baseline it will be possible to allow assessment of long-term changes in sponge biodiversity in relation to environmental stressor changes that have occurred in the SW of Madagascar during the last 50 years.

Keywords: Porifera, inventory, Toliara, Indian Ocean, biodiversity

Introduction

Sponges, phylum Porifera, are the oldest metazoans, inhabiting all aquatic ecosystems on the planet. In the ocean, these animals are distributed from the intertidal to the abyssal depths at all latitudes (for a review see Rützler, 2004). Sponges can dominate benthic communities, both in terms of diversity and biomass, and shape structural complexity of a habitat or seascape (Vacelet, 1980; Maldonado *et al.*, 2015). Sponges are keystone components of numerous benthic ecosystems, providing a number of key ecological functions. Filter feeding on a large variety of nano-pico- and microplanktonic particles and recycling dissolved and particulate organic matter contained

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in the water column (de Goeij *et al.* 2013), they contribute to bioconstruction and bioerosion processes, and offer refuge for numerous reef species (Díaz and Rützler, 2001). They also count among the diet of various predators (e.g., hawksbill turtle, angelfishes, nudibranchs, sea stars) (Wulff, 2012).

The World Porifera Database (WPD) currently accounts more than 9 000 valid sponge species from around the world (de Voogd *et al.*, 2023). However, it is widely understood that this figure is vastly understated, owing in part to challenges in accessing remote environments (e.g., deep-sea and marine cave ecosystems) and understudied biogeographic regions such as the western Indian Ocean (WIO). The WIO region is home to a potentially rich sponge fauna that has mostly gone unstudied, owing to a lack of local taxonomic competence and of regional research programmes (Barnes and Bell, 2002; Van Soest *et al.*, 2012). Nonetheless, this sponge fauna of the WIO has been subjected to local inventories (e.g., Rützler, 2004; de Voogd *et al.*, 2023), resulting to the description of new taxa (e.g., Samaai *et al.*, 2020; Klautau *et al.*, 2021).

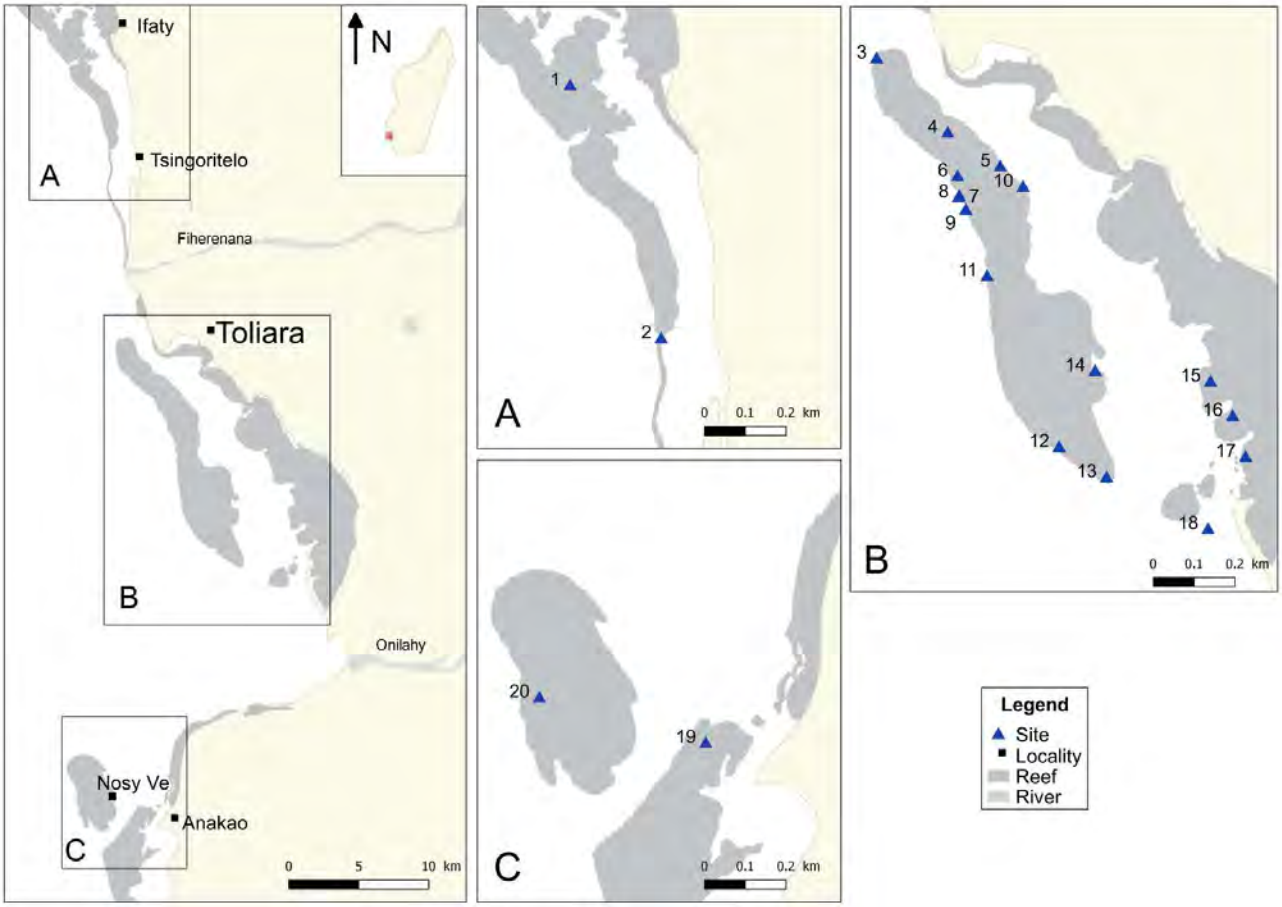

Figure 1. Detailed map of the region of Toliara (southwest of Madagascar) with enlargement of the three zones (A, B and C rectangles) where the studied sites are indicated by blue triangles.

Toliara's reefs were once known as the WIO's most biodiverse reefs in South Western Madagascar (Bruggemann *et al.*, 2012). French scientists made significant efforts to investigate sponge biodiversity in the 1960s and the 1970s (Lévi, 1956; Vacelet and Vasseur, 1971; Hooper, 1996; Rützler, 2004). However, because the reef has deteriorated significantly, sponge communities in the Toliara region may have evolved substantially since these pioneering observations. Indeed, over the last 50 years, this region's marine ecosystems have faced major environmental stressors (Walker and Fanning, 2003; Fencl, 2005; Harris *et al.*, 2010; Bruggemann *et al.*, 2012; Andréfouët *et al.*, 2013). The main drivers are linked to population growth (notably explained by migrations towards coastal cities), followed by a large number of additive anthropogenic disturbances (overfishing, pollution, habitat destruction), as well as human-induced global climate change (Harris *et al.*, 2010; Bruggemann *et al.*, 2012).

Before investigating the potential changes in sponge communities as a result of the increasing threats to marine ecosystems in this region, a proper reference list of historical records of sponge species is needed. In this context, the aim of this study was to establish a reference list of this fauna per habitat type, updated following current systematics, but based on historical inventories of the sponge fauna of the Toliara area.

Material and methods

Data compilation and taxonomy updating

Sponge species from Toliara marine environments were inventoried and compiled in a database, mainly from the publications of Vasseur (1964), Vacelet and Vasseur (1965, 1971, 1977), Vacelet (1967a, b, 1977), and Vacelet *et al.* (1976). These pioneering studies were carried out between 1961 and 1977 as part of international research initiatives such as the "Expédition Internationale de l'Océan Indien" and the "Programme de Biologie International" (Vacelet *et al.*, 1976). Some data were also gathered from the ecological works of Barnes and Bell (2002). The World Porifera Database was used to verify the species names (de Voogd *et al.*, 2023). The taxonomic status of each recorded species was checked and updated according to the most recent sponge classification (Cárdenas *et al.*, 2012; Morrow and Cárdenas, 2015) and up-to-date species records in the WPD (de Voogd *et al.*, 2023).

Study sites

In these past studies, sponges were collected and recorded from a wide range of marine habitats from the Toliara region, including the outer reef slope (outer slope, coral flagstone, creek, pass), the reef flat (outer reef flat, residual pool, detrital ridge, inner flat), reef tunnels and galleries, lagoons (lagoon, inner slope, enclosed lagoon, reef pool, reef lagoon), phanerogam meadows, and mangroves. In these studies, scuba diving and dredging devices were used to explore these habitats from the sea surface to 60 m depth.

Here, the past study area is devided into three main zones: (A) a septentrional zone located in the north of Fiherenana river, which includes the barrier reef of Ifaty and the fringing reef of Tsingoritelo; (B) a central zone located in the bay of Toliara, which includes the barrier reef of Toliara (GRT), some patch reef of Toliara lagoon (Belaza, Dimadimatsy, and Norinkazo), and the fringing reef of Anakao and the reef cay of Nosy Ve. Overall, twenty studied sites were recognized across these three zones, each site including one to seven sampling stations (Fig. 1; Table 1).

Table 1. Location of the studied sites and sampled habitats (C = Cave, F = Flat-reef, L = Lagoon, M = Mangrove, P = Phanerogam meadow, R = Reef).

Zone	Site id.	Site Name	Latitude	Longitude	Habitat
A	1	Ifaty	-23.162778	43.581944	R, L, F
A	2	Tsingoritelo	-23.234444	43.607778	R, C, L, M
B	3	Corne Nord	-23.357222	43.6125	R, C, F, L, P
B	4	Grande Vasque	-23.3825	43.636667	L, F, P
B	5	Balise Nord	-23.393889	43.654444	F
B	6	Grande Crique	-23.403889	43.640556	R, C
B	7	Tunnel C	-23.404444	43.640278	C
B	8	Crique en V	-23.408611	43.642778	C
B	9	Trois Vasques	-23.397222	43.64	F
B	10	Pointe Angèle	-23.400833	43.662222	F, P
B	11	Antseteky	-23.431111	43.65	R, F
B	12	Crique Sud	-23.489167	43.674444	F
B	13	Corne Sud	-23.499444	43.690556	R, F, P
B	14	Ankarandava	-23.463333	43.686667	L
B	15	Norinkazo	-23.466944	43.725833	L
B	16	Dimadimatsy	-23.478611	43.733333	L
B	17	Belaza	-23.4925	43.737778	L
B	18	Sarodrano	-23.516944	43.725	F
C	19	Anakao	-23.509444	43.628056	
C	20	Nosy Ve	-23.649444	43.59	R

Reef habitats

Generally, the outer slopes of Toliara reefs comprise two main zones: (i) the coral flagstone situated between 20 m and 50 m depth, dominated by fleshy algae, sponges, hydroids, gorgonians and anthipatharians (Pichon, 1978); and (ii) the upper zone, characterized by an alternation of spurs and grooves which give to the reef front a toothed edge aspect, characteristic of Toliara reefs (Vasseur, 1964). These shallow water habitats are dominated by scleractinians, coralline algae and alcyonacea, but conspicuous sciaphilic organisms can also be present on overhangs and subvertical walls (Vasseur, 1964; Pichon, 1978). Spurs can be 50 to 100 m long and 5 to 10 m wide, whereas grooves can be up to 3 m wide and up to 5 m deep (Vasseur, 1964). In these outer reef parts, the presence of large creeks, up to 100 m long, 50 m wide and 10 m deep, is another main characteristic trait of Toliara reefs (Vasseur, 1964; Clausade *et al.*, 1971; Battistini *et al.*, 1975). Toliara reef flats are generally composed of: (i) an outer reef flat, which is exposed to the wave action and dominated by scleractinians and macrophytes; (ii) a boulder tract made of detrital elements that pursues the outer flat (Clausade *et al.*, 1971) and that generally hosts a rich fauna (Vasseur, 1964; Pichon, 1978); and (ii) an inner reef flat that may host seagrass patches and diverse types of coral formations such as lagoon reef (Belaza, Dimadimatsy, Norinkazo) (Pichon, 1978). The presence of enclosed lagoon and reef pools on the reef flat is also a particular feature of Toliara reefs (Vasseur, 1964).

Reef tunnels and galleries

Reef tunnels are large cavities, usually up to 50 m long and 5 m large, resulting from the junction of two consecutive spurs thanks to bio-construction. These formations can extend from the back of a groove to below the outer reef flat, and communicate through surge openings, blowholes and fissures. The irradiance is diffuse into these reef tunnels and backwash can be high, depending on the exposure of the reef to the open ocean. These cavities are sometimes followed by galleries, which are true dark cavities (up to 10 m long and 1.5 m large) in the Toliara area and more generally on the reefs of Western Madagascar (Vasseur, 1964).

Mangroves

Mangroves are diverse along the littoral of the study area. Here, only the mangrove located in the vicinity of Tsigonritelo fringing reef was explored by past works, but no mention of the covered surface and the bathymetric range was reported.

Results

Toliara sponge inventory

Based on the available historical data, the sponge fauna of the Toliara region would be nowadays composed of at least 267 species. In this inventory, 39 sponges were identified only at the genus level and might thus include several species (e.g., *Oceanapia* spp., *Mycale* spp., *Halichondria* spp.) (Table 2). Following the World Porifera Database (WPD), 166 sponges classified at the genus and species levels have been given new valid names. For 135 of the 166 species, these updates are due to changes in taxonomic status. For example, *Acanthella carteri* is nowadays accepted as *Stylissa carteri*, after a genus transfer. *Acanthella aurantiaca* has also been transferred to the genus *Stylissa*, but is considered a junior synonym of *Stylissa carteri*. The updates also include names offered as a result of incorrect use of the Zoological code of Nomenclature. This pertains to eight sponge species, including the former *Bubaris conulosus*, now known as *B. conulosa*, and the former *Gellius cymiformis*, now known as *Haliclona (Gellius) cymaeformis*. The updates also include 28 obviously incorrect identifications. Because their original distributions (type localities) are in the Mediterranean Sea or the Atlantic Ocean, their names were amended by identifying their affinities (ex. *Cliona* aff. *schmidtii* or *Oscarella* aff. *lobularis*). However, three of these were true misidentifications, such as *Axinosia incrustans*, which is actually *Scopalina rubra*. Finally, *Clathria pulcherrima* is currently deemed nomen nudum, which implies that it has not been published with a sufficient description and hence remains an invalid name. It is assumed that this record by Barnes and Bell (2002) refers to a spelling error of *Clathrina pulcherrima* that was documented prior to Vacelet and Vasseur (1977), hence it was removed from the inventory.

The sponge fauna of Toliara is distributed among three classes, 23 orders, and 68 families. The class Demospongiae is the most abundant, accounting for 92 % of the reported species (247 species), whereas Calcarea and Homoscleromorpha are underrepresented, accounting for 5 % (13 species) and 3 % (7 species) of the recorded species, respectively (Fig. 2a). Poecilosclerida, with 53 species (of which eight species identified only at the genus level), Haplosclerida, with 44 species (of which eight species identified only at the genus level), and Tetractinellida, with 42 species (of which seven species identified only at the genus level), are the most numerous orders in the Demospongiae.

Table 2. Sponge inventory of Toliara, southwest Madagascar and their distribution among habitats. C = cave and galleries, F = reef flats, L = lagoon, M = mangrove, P = phanerogam meadows, R = reef; * species whose taxonomic status has been changed according to the most recent sponge classification (Morrow and Cárdenas, 2015). Sources: **1** Vasseur (1964); **2** Vacelet and Vasseur (1965); **3** Vacelet (1967a); **4** Vacelet (1967b); **5** Vacelet and Vasseur (1971); **6** Vacelet *et al* (1976); **7** Vacelet (1977); **8** Vacelet and Vasseur (1977); **9** Barnes and Bell (2002). All given names have been checked in WPD.

Class	Order	Family	Species	Site id.	Habitat	Source
Calcarea						
(Calcaronea) Baerida						
		Lepidoleuconidae	*Lepidoleucon inflatum* Vacelet, 1967	2, 7	C	**4, 7, 8**
(Calcaronea) Lithonida						
		Minchinellidae	*Plectroninia hindei* Kirkpatrick, 1900	1, 11	R	**6, 7, 8**
			Plectroninia minima Vacelet, 1967	1, 2, 7, 11	R, C	**4, 6, 8**
			Plectroninia pulchella Vacelet, 1967	1, 7, 11	R, C	**4, 5, 6, 8**
			Plectroninia radiata Vacelet, 1967	1, 2, 7, 11	R, C	**4, 5, 6, 7, 8**
			Plectroninia tecta Vacelet, 1967	2, 7	C	**3, 4, 5**
			Plectroninia sp.	19		**9**
			Tulearinia stylifera Vacelet, 1977	7	C	**7, 8**
(Calcinea) Clathrinida						
		Clathrinidae	*Arturia darwinii* (Haeckel, 1870)*	19		**9**
			Clathrina pulcherrima (Dendy, 1891)	1, 4	L	**8**
		Leucettidae	*Leucetta* aff. *primigenia* Haeckel, 1872*	2	C, L	**1, 2**
		Lelapiellidae	*Lelapiella incrustans* Vacelet, 1977	7	R, C	**7, 8**
		Paramurrayonidae	*Paramurrayona corticata* Vacelet, 1967	7	C	**4, 5, 8**
Demospongiae						
(Heteroscleromorpha)						
Agelasida						
		Agelasidae	*Acanthostylotella cornuta* (Topsent, 1897)	3, 6	R, F	**5, 8**
			Agelas bispiculata Vacelet, Vasseur & Lévi, 1976	11	R	**6**
			Agelas marmarica Lévi, 1958	2, 7, 9	C, F, L	**1, 2, 5**
			Agelas mauritiana (Carter, 1883)	1, 2, 7, 11	R, C	**2, 5, 6**
		Astroscleridae	*Astrosclera willeyana* Lister, 1900	1- 3, 11	R, C	**1, 2, 3, 5, 6, 7, 8**
Axinellida						
		Axinellidae	*Axinella arborescens* Ridley and Dendy, 1886*	3, 13, 14	R, L	**6, 8**
			Axinella donnani (Bowerbank, 1873)*	3, 6, 13, 14	R, L	**6, 8**
		Heteroxyidae	*Myrmekioderma granulatum* (Esper, 1829)*	1, 2, 4, 5, 11	F, L, P	**1, 2, 5, 8**
			Myrmekioderma dendyi (Burton, 1959)*	2, 7	C, L	**5**
		Raspailiidae	*Aulospongus gardineri* (Dendy, 1922)*	3	R	**5**
			Aulospongus involutus (Kirkpatrick, 1903)*	3, 13	R	**6**
			Didiscus aceratus (Ridley & Dendy, 1886)*	7	C	**5, 8**
			Didiscus aff. *stylifer* Tsurnamal, 1969*	3	R	**5, 6**
			Didiscus placospongioides Dendy, 1922	3, 7	R, C	**5, 6**
			Echinodictyum conulosum Kieschnick, 1900	3	R	**5, 6, 8**
			Echinodictyum jousseaumi Topsent, 1892	3	R	**5, 8**
			Echinodictyum sp.	19		**9**
			Eurypon calypsoi Lévi, 1958	3	R	**6**
			Eurypon sp.	3, 11	R	**6**
		Stelligeridae	*Higginsia petrosioides* Dendy, 1922	2, 3, 7, 9, 13	R, F, C, L	**1, 2, 5, 6, 8**
Biemnida						
		Biemnidae	*Biemna anisotoxa* Lévi, 1963	1	L	**5**
			Biemna bihamigera (Dendy, 1922)	20	R	**5**
			Biemna fortis (Topsent, 1897)	2, 3	F	**8, 9**
			Biemna sp.	19		**9**
		Rhabderemiidae	*Rhabderemia mammillata* (Whitelegge, 1907)*	2, 7, 8	C	**8**
			Rhabderemia aff. *toxigera* Topsent, 1892*	2, 7, 8	C	**8**

Class	Order	Family	Species	Site id.	Habitat	Source
Bubarida						
		Bubaridae	*Bubaris conulosa* Vacelet & Vasseur, 1971*	3	R	**5, 8**
			Cerbaris topsenti (Hentschel, 1912)*	4	L	**2**
		Desmanthidae	*Desmanthus* aff. *incrustans* (Topsent, 1889)*	11	R	**6**
		Dictyonellidae	*Acanthella klethra* Pulitzer-Finali, 1982	19		**9**
			Acanthella sp.	19		**9**
Clionaida						
		Clionaidae	*Cliona* aff. *lobata* Hancock, 1849*	3	R	**6**
			Cliona aff. *schmidtii* (Ridley, 1881)*	7, 8	C	**6**
			Cliona celata Grant, 1826	3	F	**5**
			Cliona ensifera Sollas, 1878	3, 13	R	**6**
			Cliona sp.	2, 4	F, L	**1, 9**
			Cliona jullieni Topsent, 1891	3	R, F	**6**
			Cliona mucronata Sollas, 1878	3, 7, 9, 11, 13	R, F, C	**5, 6**
			Cliothosa aff. *hancocki* (Topsent, 1888)*	3	R, F	**6**
			Pione margaritiferae (Dendy, 1905)*	3	F	**5**
			Spheciospongia excentrica (Burton, 1931)*	1, 3, 11, 14	R, L	**6, 8**
			Spheciospongia inconstans (Dendy, 1887)*	3, 13	R	**2, 5, 6, 8**
			Spheciospongia inconstans var. *digitata* (Dendy, 1887)*	2, 4	F, C	**1, 2, 5**
			Spheciospongia poterionides (Vacelet & Vasseur, 1971)*	10, 15, 16	F, L	**5, 8**
			Spheciospongia solida (Ridley & Dendy, 1886)	19		**9**
			Spheciospongia vagabunda (Ridley, 1884)*	2	P	**8, 9**
		Placospongiidae	*Placospongia carinata* (Bowerbank, 1858)	1, 2, 7, 11	R, F, C, L	**1, 2, 5, 6, 8, 9**
			Placospongia melobesioides Gray, 1867	19		**9**
		Spirastrellidae	*Diplastrella gardineri* Topsent, 1918	3	R	**6**
			Spirastrella aff. *cunctatrix* Schmidt, 1868*	3, 9	R, F	**5, 6**
			Spirastrella curvistellifera (Dendy, 1905)*	2, 6, 7, 11, 20	R, C, L	**1, 2, 5, 6, 8**
			Spirastrella pachyspira Lévi, 1958	2, 3, 7, 11, 20	R, F, C, L	**1, 2, 5, 6, 8**
			Spirastrella sp.	19		**8, 9**
Haplosclerida						
		Callyspongiidae	*Callyspongia (Callyspongia)* sp.	4	L	**1, 2**
			Callyspongia (Cladochalina) subarmigera (Ridley, 1884)*	4	L	**6**
			Callyspongia (Toxochalina) dendyi (Burton, 1931)*	3, 13	R	**6**
			Callyspongia (Toxochalina) robusta (Ridley, 1884)*	3, 6, 13	R	**5, 6, 8**
			Callyspongia (Toxochalina) sp.	19		**9**
			Callyspongia confoederata (sensu Ridley, 1884)	3, 11, 13, 15	R, L	**6**
			Callyspongia reticutis var. *salomonensis* (Dendy, 1922)	3	R	**6**
		Chalinidae	*Haliclona (Flagellia) amirantensis* Van Soest, 2017*	3	R	**6**
			Haliclona (Gellius) cymaeformis (Esper, 1806)*	10	P	**5, 8, 9**
			Haliclona (Gellius) laubenfelsi Van Soest & Hooper, 2020*	2	F, P	**5, 8**
			Haliclona (Gellius) ridleyi (Hentschel, 1912)*	7	C	**5**
			Haliclona (Halichoclona) centrangulata (Sollas, 1902)*	3	R	**6**
			Haliclona (Reniera) sp.	2	C	**1**
			Haliclona fragilis (Vacelet, Vasseur & Lévi, 1976)*	11, 14	R, L	**6**
			Haliclona sp.	19		**9**
			Haliclona madagascarensis Vacelet, Vasseur & Lévi, 1976	3	R	**6**
			Haliclona polypoides (Vacelet, Vasseur & Lévi, 1976)*	3, 6, 13	R	**6 ,8**
			Haliclona striata Vacelet, Vasseur & Lévi, 1976	3, 13	R	**6**
			Haliclona tulearensis Vacelet, Vasseur & Lévi, 1976	3, 11	R	**6**

Class	Order	Family	Species	Site id.	Habitat	Source
		Niphatidae	*Gelliodes incrustans* Dendy, 1905	2, 19	F	**8, 9**
			Gelliodes petrosioides Dendy, 1905*	11	R	**6**
			Gelliodes sp.	2	R, C, L	**1, 2**
		Petrosiidae	*Neopetrosia chaliniformis* (Thiele, 1899)*	19		**9**
			Neopetrosia seriata (Hentschel, 1912)*	3	R, F	**5, 6**
			Petrosia (Petrosia) densissima Dendy, 1905*	3	R	**6**
			Petrosia (Petrosia) microxea (Vacelet, Vasseur & Lévi, 1976)*	11	R	**6**
			Petrosia (Petrosia) nigricans Lindgren, 1897*	11, 13, 14, 19	R, L	**6, 9**
			Petrosia (Petrosia) spheroida Tanita, 1967*	1, 3, 4, 11	R, L	**6, 8**
			Petrosia (Strongylophora) durissima (Dendy, 1905)*	2, 7	C	**1, 2, 5, 8**
			Petrosia sp.	19		**9**
			Xestospongia testudinaria (Lamarck, 1815)*	1, 3-4	R, F, L	**1, 2, 5, 6, 8**
			Xestospongia viridenigra (Vacelet, Vasseur & Lévi, 1976)*	1, 3	R, F, L	**2, 5, 6**
			Xestospongia sp.	19		**9**
		Phloeodictyidae	*Oceanapia amboinensis* Topsent, 1897	1, 7, 11	R, C	**5, 6**
			Oceanapia cribrirhina (Vacelet & Vasseur, 1971)*	3, 7	R, C	**5, 6**
			Oceanapia dura (Vacelet & Vasseur, 1971)*	3	R	**5**
			Oceanapia fistulosa (Bowerbank, 1873)*	3, 4, 13	R, L	**6, 8**
			Oceanapia incrustata (Dendy, 1922)*	1, 3, 4, 13, 14, 19	R, L	**5, 6, 8, 9**
			Oceanapia minuta (Vacelet, Vasseur & Lévi, 1976)*	3, 11	R	**6**
			Oceanapia mucronata (Vacelet, Vasseur & Lévi, 1976)*	1, 3, 13, 14	R, L	**6**
			Oceanapia sp.	1, 3, 11, 19	R, L	**6, 8, 9**
			Oceanapia polysiphonia (Dendy, 1922)*	1, 3	R	**6**
			Oceanapia sagittaria (Sollas, 1902)*	3	F	**5, 8**
			Oceanapia toxophila Dendy, 1922	3	R	**6, 8**
Merliida						
		Merliidae	*Merlia normani* Kirkpatrick, 1908	3	R	**5**
Poecilosclerida						
		Acarnidae	*Acarnus bergquistae* Van Soest, Hooper & Hiemstra, 1991*	3	R	**6**
			Cornulella minima (Vacelet, Vasseur & Lévi, 1976)*	1, 3, 11 ,13	R	**6**
			Paracornulum strepsichela (Dendy, 1922)*	3	R	**6**
			Zyzzya fuliginosa (Carter, 1879)*	1	R	**6**
		Chondropsidae	*Batzella aurantiaca* (Lévi, 1958)*	1, 3, 11	R, F, L	**5, 6**
			Chondropsis lamella (Lendenfeld, 1888)*	1	R	**6**
		Coelosphaeridae	*Coelosphaera (Coelosphaera) fucoides* (Topsent, 1897)*	13	R	**6**
			Coelosphaera sp.	19		**9**
			Lissodendoryx (Ectyodoryx) arenaria Burton, 1936*	3, 19	R	**6, 8, 9**
		Crambeidae	*Crambe acuata* (Lévi, 1958)	3, 11, 13	R	**6, 8**
			Crambe aff. *crambe* (Schmidt, 1862)*	19		**9**
			Monanchora dianchora de Laubenfels, 1935*	3, 4	R, L	**5, 6**
			Monanchora unguiculata (Dendy, 1922)*	3	R	**5, 6**
		Crellidae	*Crella (Pytheas) ula* (de Laubenfels, 1950)*	3, 17	R, L	**6**
			Spirorhabdia alata Vacelet, Vasseur & Lévi, 1976	11	R	**6, 8**
		Esperiopsidae	*Ulosa aff. incrustans* (Burton, 1930)*	9	F	**5**
		Guitarridae	*Coelodischela diatomorpha* Vacelet, Vasseur & Lévi, 1976	11	R	**6**
		Hymedesmiidae	*Acanthancora stylifera* Burton, 1959	4	F, L, P	**2, 5**
			Hymedesmia (Hymedesmia) mertoni Hentschel, 1912*	3	R	**6, 8**
			Hymedesmia sp.	2, 7, 8, 19	C	**8**
			Phorbas clathrodes (Dendy, 1922)*	3	R	**6**
			Phorbas scabida (sensu Vacelet, Vasseur & Lévi, 1976)*	3	R	**6**
		Iotrochotidae	*Iotrochota baculifera* Ridley, 1884	1-3	R, F, L, P	**1, 2, 5, 6**
			Iotrochota purpurea (Bowerbank, 1875)	1-4, 13	R, F, L, P	**1, 2, 5, 6, 8**

Class	Order	Family	Species	Site id.	Habitat	Source
		Microcionidae	*Clathria (Clathria) foliascens* Vacelet & Vasseur, 1971*	3	R	5, 6, 8
			Clathria (Clathria) spongodes Dendy, 1922*	1	R	6
			Clathria (Microciona) microxea (Vacelet & Vasseur, 1971)*	3	F	5
			Clathria (Microciona) vacelettia Hooper, 1996*	2	L	1, 2
			Clathria (Microciona) sp.	1- 3, 6, 8, 9, 19	R, F, C, L, P	5, 6, 9
			Clathria (Thalysias) abietina (Lamarck, 1814)*	3	R	6, 8
			Clathria (Thalysias) cactiformis (Lamarck, 1814)*	2, 3	R, F, P	5, 6, 8
			Clathria (Thalysias) cervicornis (Thiele, 1903)*		R	5
			Clathria (Thalysias) sp.	1, 3	R, F, L	5, 6
			Clathria (Thalysias) toxifera (Hentschel, 1912)*	2	P	8
			Clathria (Thalysias) vulpina (Lamarck, 1814)*	3, 14	R, F, L	6, 8
			Clathria (Wilsonella) cercidochela (Vacelet & Vasseur, 1971)*	1, 3	R, L	5, 6, 8
			Clathria sp.	19		9
		Mycalidae	*Mycale (Aegogropila) crassissima* (Dendy, 1905)*	3	F	5
			Mycale (Aegogropila) sulevoidea (Sollas, 1902)*	1, 4, 7, 19	C, L, P	1, 2, 5
			Mycale (Arenochalina) imperfecta Baer, 1906*	1, 19	L	5, 8
			Mycale (Grapelia) vaceleti Hajdu, 1995*	11	R	6
			Mycale (Mycale) grandis Gray, 1867*	1, 4, 9	F, L	1, 2, 5, 8
			Mycale (Mycale) gravelyi Burton, 1937*	2, 4	R, L	1, 2, 5
			Mycale (Naviculina) cleistochela Vacelet & Vasseur, 1971*	9	F	5, 8
			Mycale (Naviculina) microxea Vacelet, Vasseur & Lévi, 1976*	3	R	6
			Mycale sp.	3, 4, 19	F, L	5, 9
		Podospongiidae	*Diacarnus globosus* (Vacelet, Vasseur & Lévi, 1976)*	3	R	6, 8
			Sigmosceptrella quadrilobata Dendy, 1922	2, 6	R, C	6, 8
		Tedaniidae	*Strongylamma arenosa* (Vacelet & Vasseur, 1971)*	3, 19	R	5, 8
			Strongylamma sp.			8
			Strongylamma wilsoni (Dendy, 1922)*	3	R	5
			Tedania (Tedania) assabensis Keller, 1891*	1, 3, 11	R, L	5
			Tedania (Tedania) sp.	6, 7, 9	R,F, C	5
Polymastiida						
		Polymastiidae	*Polymastia megasclera* Burton, 1934	3	R	6, 8
Scopalinida						
		Scopalinidae	*Scopalina* aff. *lophyropoda* Schmidt, 1862*	3	R	5, 6, 8
			Scopalina rubra (Vacelet & Vasseur, 1971)*	2-4, 9, 19	R, F, C, L, P	5, 6, 8, 9
			Stylissa carteri (Dendy, 1889)*	2-4, 7, 11, 13-14, 19	R, C, L	1, 2, 5, 6, 8, 9
			Stylissa conulosa (Dendy, 1922)*	19		9
Suberitida						
		Halichondriidae	*Amorphinopsis fistulosa* (Vacelet, Vasseur & Lévi, 1976)*	3, 13	R, F, P	6
			Amorphinopsis foetida (Dendy, 1889)*	2, 19	M	2, 8, 9
			Axinyssa aplysinoides (Dendy, 1922)	3, 7, 20	R, C, P	5, 6
			Ciocalypta sp.	19		9
			Ciocalypta microstrongylata Vacelet, Vasseur & Lévi, 1976	3, 19	R	6, 8, 9
			Halichondria sp.	2- 4, 19	R, F, L	1, 6, 8
			Hymeniacidon aff. *perlevis* (Montagu, 1814)*	2, 4	F	1, 2
			Spongosorites indicus Hentschel, 1912*	2, 4	F	1, 2
			Topsentia halichondrioides (Dendy, 1905)*	3	R	6
			Topsentia stellettoides (Lévi, 1961)*		R	6
		Suberitidae	*Aaptos* aff. *aaptos* (Schmidt, 1864)*	2, 4, 11	R, F	2, 5, 6
			Terpios cruciatus (Dendy, 1905)*	3	R, F	6
			Terpios granulosus Bergquist, 1967*	3, 9	R, F, P	5, 6, 8
			Terpios sp.	19		9

Class	Order	Family	Species	Site id.	Habitat	Source
Tethyida						
		Hemiasterellidae	*Hemiasterella complicata* Topsent, 1919	3	R	6
			Liosina arenosa (Vacelet & Vasseur, 1971)*	1, 19	L	5, 8, 9
		Tethyidae	*Tethya seychellensis* (Wright, 1881)	7, 11, 19	R, F, C	1, 2, 5, 6, 8, 9
		Timeidae	*Timea aff. unistellata* (Topsent, 1892)*	2, 7, 11	F, C, L	1, 2, 5,, 8
			Timea sp.	19		9
Tetractinellida						
		Ancorinidae	*Ancorina* aff. *radix* Marenzeller, 1889*	3, 7	F, C	5
			Ancorina nanosclera Lévi, 1967*	1, 3, 11, 14	R, L	6
			Asteropus simplex (Carter, 1879)	3	R	5, 8
			Dercitus (Stoeba) extensus (Dendy, 1905)*	3	F	5, 8
			Dercitus (Stoeba) sp.	3	F	5, 8
			Ecionemia acervus Bowerbank, 1862*	2, 3, 11, 14, 18, 19	R, F, L	8, 9
			Jaspis aff. *johnstonii* (Schmidt, 1862)*	4, 19	L	8, 9
			Jaspis diastra (Vacelet & Vasseur, 1965)*	2	L	1, 2
			Jaspis sp.	19		9
			Stelletta osculifera (Lévi, 1964)*	7	C	8
			Stelletta tulearensis Vacelet, Vasseur & Lévi, 1976	3, 11	R	5
			Stellettinopsis laviniensis (Dendy, 1905)*	11	R	6
		Geodiidae	*Caminus* aff. *sphaeroconia* Sollas, 1886*	3	R	6
			Erylus lendenfeldi Sollas, 1888	2, 3, 9, 13, 19	R, F, C	5, 6, 8, 9
			Geodia carcinophila (Lendenfeld, 1897)*	3	R	6
			Geodia littoralis Stephens, 1915	2	L	5
			Geodia peruncinata Dendy, 1905	8	C	5, 8
			Geodia sollasi (Lendenfeld, 1888)*	7, 9, 11	R, F, C	5, 6
			Geodia sphaerulifer (Vacelet & Vasseur, 1965)*	7, 2	R, C	2, 5
		Neopeltidae	*Homophymia lamellosa* Vacelet & Vasseur, 1971	2, 6-8, 11	R, C	5, 6, 8
			Macandrewia sp.	2, 7, 8	C	1, 2, 8
			Sollasipelta cavernicola (Vacelet & Vasseur, 1965)*	1, 2, 7, 11	R, C	5, 6, 8
			Sollasipelta mixta (Vacelet, Vasseur & Lévi, 1976)*	2, 3, 7, 8	R, C	6, 8
			Sollasipelta ornata (Sollas, 1888)	2-4, 7, 11	R, C, L	5, 6, 8
			Sollasipelta sp.	19		9
		Pachastrellidae	*Acanthotriaena crypta* Vacelet, Vasseur & Lévi, 1976	3	R	6, 8
		Phymaraphiniidae	*Kaliapsis incrustans* (Vacelet & Vasseur, 1971)*	1-3, 7, 8, 11	R, C	1, 2, 5
		Scleritodermidae	*Aciculites spinosa* Vacelet & Vasseur, 1971	8	C	5, 8
			Aciculites tulearensis Vacelet & Vasseur, 1965	2-3, 7	C	2, 5, 6, 8
			Scleritoderma nodosum Thiele, 1900	13	R	5, 8
		Tetillidae	*Cinachyrella australiensis* Carter, 1886*	2	L	1, 2, 5, 6, 8
			Craniella aff. *cranium* (Müller, 1776)*		R	6, 8
			Paratetilla bacca Dendy, 1905	1-4, 7	R, C, L	2, 5
			Paratetilla sp.	19		9
		Theonellidae	*Discodermia discifera* (Lendenfeld, 1907)*	2	L	2, 5
			Discodermia sp.	19		9
			Discodermia dubia Vacelet & Vasseur, 1971	7	C	6, 8
			Discodermia japonica Döderlein, 1884	1, 7, 11	C, R	5, 8
			Discodermia panoplia Sollas, 1888	2, 3, 7, 8, 11	C, R	5, 6, 8
			Theonella conica (Kieschnick, 1896)	1-3, 13	R, F, L	5, 6, 8
			Theonella swinhoei Gray, 1868	1, 13, 14	R, L	1, 2, 5, 6
		Thoosidae	*Alectona primitiva* Topsent, 1932	7	C	6

Class	Order	Family	Species	Site id.	Habitat	Source
(Keratosa)						
	Dendroceratida					
		Darwinellidae	*Aplysilla* aff. *sulfurea* Schulze, 1878*	3, 4, 19	R, L	**1, 2, 5, 6, 8**
			Chelonaplysilla aff. *noevus* (Carter, 1876)*	3, 5	R, F	**5**
			Darwinella australiensis Carter, 1885	4	L	**5, 6, 8**
		Dictyodendrillidae	*Igernella mirabilis* Lévi, 1961		F	**5, 6**
			Spongionella nigra Dendy, 1889*	11	R	**6**
			Spongionella retiara (Dendy, 1916)*	3	R	**5**
	Dictyoceratida					
		Dysideidae	*Dysidea cinerea* Keller, 1889	13	R	**6**
			Dysidea sp.	19		9
		Irciniidae	*Ircinia* aff. *dendroides* (Schmidt, 1862)*	1, 3	R, L	**1, 2, 5**
			Ircinia aff. *strobilina* (Lamarck, 1816)*	1, 3	R, L	**6**
			Ircinia cylindracea Vacelet, Vasseur & Lévi, 1976	3	R	**6, 8**
			Ircinia irregularis (Poléjaeff, 1884)	3, 2	R, L	**6, 8**
			Ircinia sp.	1, 4	L	**6**
			Ircinia ramosa (Keller, 1889)*	1, 4	L	**6**
		Spongiidae	*Spongia* sp.	3	R	**6**
		Thorectidae	*Phyllospongia papyracea* (Esper, 1806)*	3, 4, 11, 12, 19	R, F, L	**5, 6, 8, 9**
			Phyllospongia foliascens (Pallas, 1766)*	3	R, F	**5, 6, 8**
			Lendenfeldia dendyi (Lendenfeld, 1889)*	1, 4, 10	F, L, P	**6, 8**
			Hyrtios cavernosus (Vacelet, Vasseur & Lévi, 1976)*	13	R	**6**
(Verongimorpha)						
	Verongiida					
		Ianthellidae	*Hexadella* aff. *racovitzai* Topsent, 1896*	3, 11, 13	R, F	**6, 8**
			Hexadella sp.	1, 2, 4, 7, 19	F, C, L	**9**
			Ianthella sp.	19		**9**
		Pseudoceratinidae	*Pseudoceratina purpurea* (Carter, 1880)*	3, 14, 17	R, L	**6, 8**
	Chondrillida					
		Chondrillidae	*Chondrilla* aff. *nucula* Schmidt, 1862	3, 13, 19	F	**5, 8, 9**
			Chondrilla australiensis Carter, 1873*	3, 4	L, F	**1, 2, 5**
			Chondrilla mixta Schulze, 1876*	3	R, F	**5, 6**
			Chondrilla sacciformis Carter, 1879	2	C	**1, 2, 5**
		Halisarcidae	*Halisarca ectofibrosa* Vacelet, Vasseur & Lévi, 1976	2, 3	R, C	**6, 8**
			Halisarca sp.	1, 4, 5	L, F	
	Chondrosiida					
		Chondrosiidae	*Chondrosia debilis* Thiele, 1900	3, 5, 9	F	
Homoscleromorpha						
	Homosclerophorida					
		Oscarellidae	*Oscarella* aff. *lobularis* (Schmidt, 1862)*	3, 7	C, P	**6**
		Plakinidae	*Plakina* aff. *monolopha* Schulze, 1880*	7	C	**5**
			Plakina aff. *trilopha* Schulze, 1880*	3	R	**6**
			Plakina corticioides Vacelet, Vasseur & Lévi, 1976	3	R	**6**
			Plakinastrella ceylonica (Dendy, 1905)	11	R	**5, 6**
			Plakinastrella sp.		R	**8**
			Plakortis aff. *simplex* Schulze, 1880*	3, 14	R, L	**6**

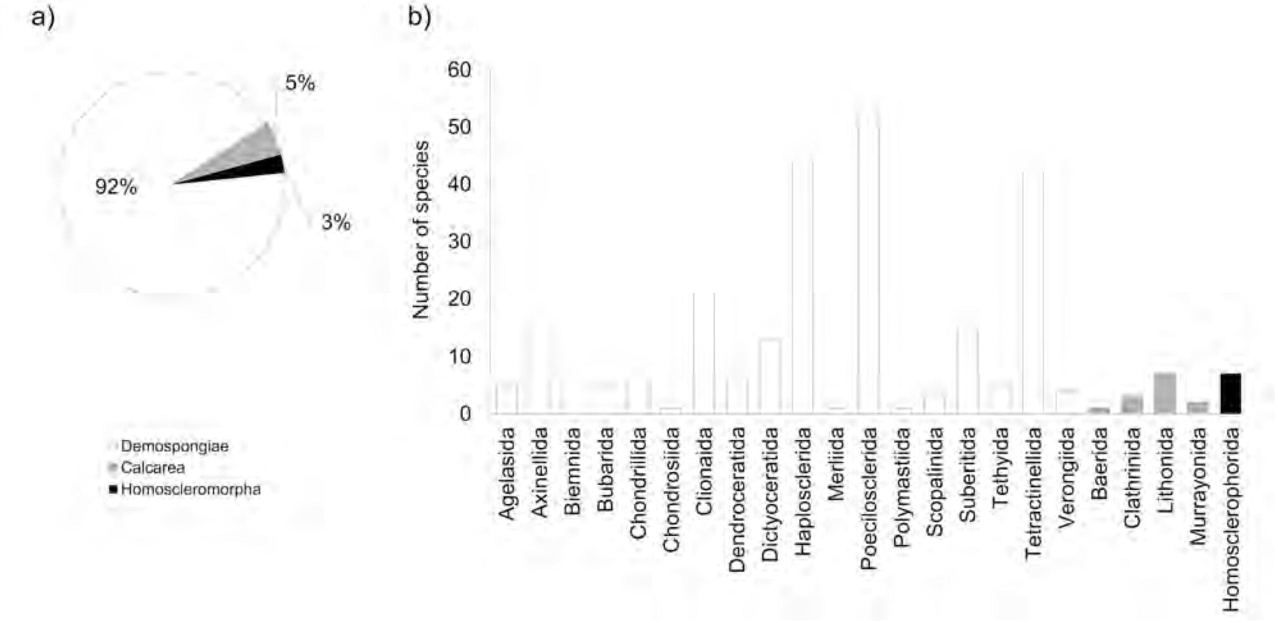

Figure 2. Taxonomic distribution of the sponge species recorded in the region of Toliara. a) pie representing the proportion of sponges per class; b) histogram representing the proportion of sponges per order.

Chondrosiida, Merliida, and Polymastiida are the three Demospongiae orders with the fewest species each. Among the four Calcarea orders now accepted, Lithonida has the most species with seven, while Baerida has only one (Fig. 2b). Toliara sponge fauna presents only seven species of the Homoscleromorpha class, which currently includes only one order, Homosclerophorida.

Ecological distribution of Toliara sponge species

Of the 267 species, 257 species were found on hard bottoms (238 Demospongiae, 12 Calcarea, and seven Homoscleromorpha) and 39 on soft bottoms (37 Demospongiae, one Calcarea, and one Homoscleromorpha) (Fig. 3a). Thus, 236 species were restricted to one type of substratum and 30 species were found in both types of substratum.

According to the rather precise indications given by Vasseur and his co-workers (Vasseur, 1964; Vacelet and Vasseur, 1965, 1971, 1977; Vacelet 1967a, b, 1977; Vacelet *et al.*, 1976), 239 species could be assigned to a habitat type.

The outer reef slope had the highest number of species (163). There were 76, 67, and 64 species in lagoons, reef flats, and caves, respectively. There were 17 species found in phanerogam meadows and only one species in mangroves (Fig. 3b). The sponge fauna of the outer slope was composed of about 94 % of Demospongiae (53 families), 3 % of Calcarea (2 families) and 3 % Homoscleromorpha (1 family). In the lagoon, 96 % of the species were Demospongiae (38 families), 3 % Calcarea (2 families) and only 1 % was Homoscleromorpha (one family). In the reef caves and tunnels, the reported species were composed by 83 % of Demospongiae (33 families), 14 % of Calcarea (5 families) and 3 % of Homoscleromorpha (2 families). In the phanerogam meadows, 94 % of the species were Demospongiae (11 families) and the remaining 6 % were Homoscleromorpha (1 family). On reef flats and in the mangrove, the only species recorded was Demospongiae.

Among all sponges recorded, 102 species (95 Demospongiae, 5 Calcarea and 2 Homoscleromorpha) had a broad distribution, recorded in at least two different habitats. However, only two sponges were recorded in all five habitat categories; *Scopalina rubra*, and an undetermined *Clathria (Microciona)* which may actually correspond to a different species. On the other hand, 137 species (126 Demospongiae, six Calcarea and five Homoscleromorpha) seem to be restricted to only one habitat category. For instance, *Plectroninia hindei*, *Plakina corticoides* or *Petrosia* (*Petrosia*) *microxea* are among the species which were recorded only on the outer reef slope. *Cliona celata*, *Clathria* (*Microciona*) *microxea* or *Igernella mirabilis* were only recorded on reef flats. *Lepidoleucon inflatum, Aciculites spinosa* or *Plakina* aff. *monolopha* are typical cave-dwelling sponge species, whereas *Clathrina pulcherrima*, *Jaspis diastra* or *Liosina arenosa* are exclusive to reef lagoons.

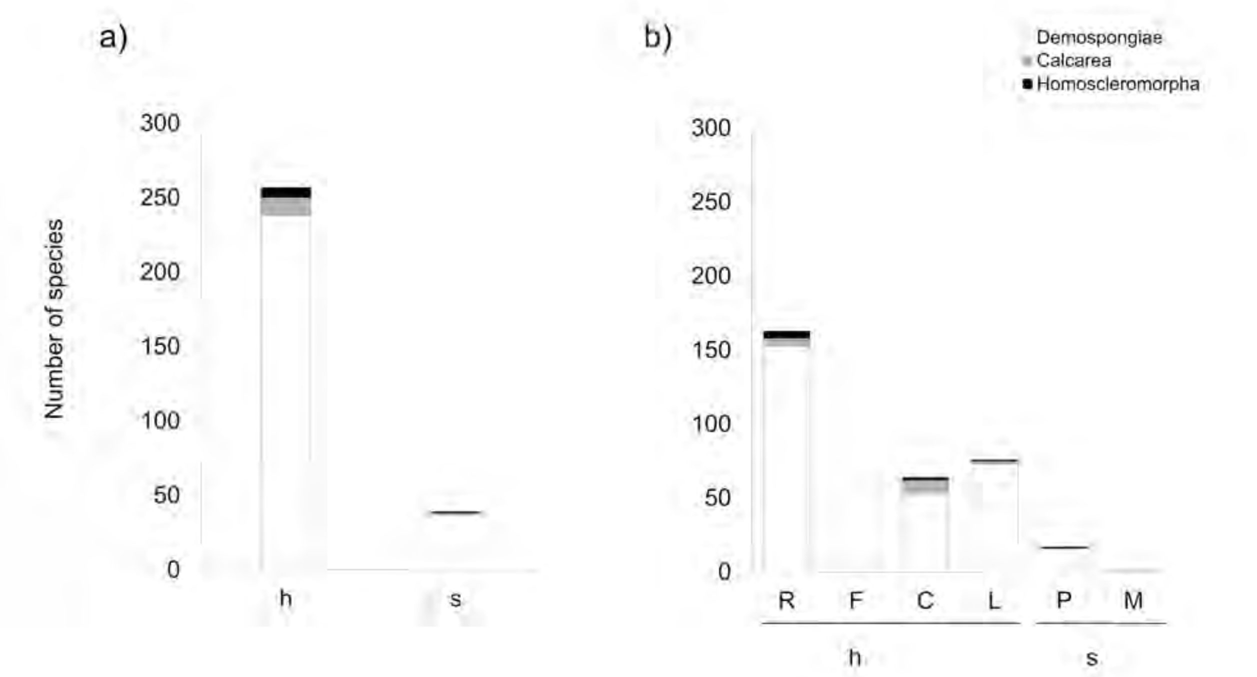

Figure 3. Ecological distribution of Toliara sponge species. a) species distribution per type of substratum according to Barnes and Bell (2002) and later references references. h = hard bottoms, s = soft bottoms. b) species distribution per habitat category according to Vasseur (1964), Vacelet and Vasseur (1965, 1977), Vacelet (1967a, 1967b, 1977), Vacelet *et al.* (1976). C = cave and galleries, F = reef flats, L = lagoon, M = mangrove, P = phanerogam meadows, R = reef.

Discussion

The marine sponge fauna in the Toliara region has at least 267 species, however this inventory is likely underestimated and is it is believed that this will increase in the near future. This check-list was obtained by updating almost 62 % of the species referenced in the WPD in our database (de Voogd *et al.*, 2023). This update allows the presentation of a reliable repository that can be used by scientists from different disciplinary fields (e.g., ecology, biodiversity, conservation, chemistry) and managers of the marine environment. This revision rate illustrates the great changes in the taxonomy and systematics of sponges (Porifera) that has occurred over the last two decades (Cárdenas *et al.*, 2012; Morrow and Cárdenas, 2015). However, this inventory also includes species to which affinities have been assigned and for which new descriptions will have to be made. In addition, this list could also be enriched if genus-level identifications of some sponges were completed. Therefore, more than 10 % of the fauna known today should be re-examined to provide more precise identifications.

Toliara's sponge biodiversity alone accounts for 67 % of all known valid species in the WIO (401 species) (de Voogd *et al.*, 2023). However, this part of the world ocean is still largely unexplored (Barnes and Bell, 2002), which explains why its sponge biodiversity now accounts for only 4 % of all valid species recorded worldwide (de Voogd *et al.,* 2023). Ten years after the state of the art by Van Soest *et al.* (2012), the highly fragmented nature of the knowledge related to sponge diversity has not changed, and a special effort should be made in the Indian Ocean. Given the extent of Madagascar and the latitudes covered, the inventory undertaken in Toliara suggests a high potential for new discoveries. Indeed, the Toliara region alone has 2.5 times the number of species of the Indian Peninsula (George *et al.*, 2020). However, when compared to other regions where extensive sampling has been undertaken, sponge diversity in the Toliara region appears to be quite low, accounting for only a fifth of North Western Australia's sponge biodiversity (Fromont *et al.*, 2016), for example. Despite the fact that the Calcarea and Homoscleromorpha classes in these two later regions display comparable number of species, the greater diversity of Demospongiae and the presence of Hexactinellida in the NW Australia inventory compared to the present inventory may be explained in part by the larger bathymetric range explored (0 to 5000 m) in the NW Australia (Fromont *et al.*, 2016). Finally, in comparison with other tropical regions that have been studied extensively, such as the Caribbean region for example (Van Soest, 1981; Díaz *et al.*, 2004;

Díaz and Rützler, 2009; Valderrama and Zea, 2013; Rützler *et al.*, 2014; Pérez *et al.*, 2017), Toliara region harbours about half the specific richness, which confirms a little more the potential for new sponges to be inventoried and described in Madagascar and in the western Indian Ocean.

In this Toliara sponge inventory, the class Demospongiae, which contains 82 % of the species recognized today, is naturally the best represented (247 species), with 18 orders out of the 36 recognized (de Voogd *et al.*, 2023). Quite classically as in tropical, subtropical and temperate areas well studied so far (*e.g.* Fromont *et al.*, 2016; Pérez *et al.*, 2017; Grenier *et al.*, 2018; Castellanos-Pérez *et al.*, 2020), Poecilosclerida and Haplosclerida are the two dominant orders displaying the largest number of inventoried species. In contrast, the Calcarea and Homoscleromorpha are the two least represented classes in this inventory. Although these two sponge classes also include the lower numbers of sponge species worldwide, it is believed by these authors that their diversities may be largely underestimated in the Toliara region. Indeed, a better exploration of cryptic habitats, such as underwater caves and reef tunnels, may reveal a greater number of new species, as found in other regions (Pérez *et al.*, 2017; Klautau *et al.*, 2021). In Reunion Island for example, very few explorations of underwater caves resulted in 11 new records of Calcarea, seven of which being new to science (Klautau *et al.*, 2021).

In addition, further investigation of some habitats could significantly increase Toliara's sponge inventory. Indeed, the great variability in species richness observed among habitat types also illustrates a great variability in sampling efforts. In the mangrove, for example, only one species has been recorded, but this environment has been mostly unexplored (Vacelet and Vasseur, 1977). Sponges, on the other hand, are good colonisers of mangrove roots in many places of the world, such as in the Caribbean, where species richness can range from 3 to 147 species (Díaz *et al.*, 2004). The number of sponge species in Toliara's mangrove may thus be greatly underestimated, even if this habitat has recently been significantly reduced in this region, due to the exploitation of mangrove trees for fuel wood and livestock feed (Vasseur, 1997), and because of the Ambondrolava sand spit extending to the north, at an average of 50 m per year (Onjanamboa 2018). Furthermore, even in habitats where sampling efforts have been important, such as the outer slopes or reef tunnels of Toliara, Vasseur (1964) did not rule out the possibility that many sponges have been missed during these past surveys because they were not very visible or were difficult to collect.

After 50 years of increasing environmental pressures, it is likely that significant modifications may be observed in the coastal ecosystems of the Toliara region. Since sponges are excellent bio-indicators (Carballo *et al.*, 1996; Pérez, 2000), several trends could be expected: (i) an increase in sponge biomass related to the coral decline, with a dominance of excavating sponges (Carballo *et al.*, 1996); or (ii) a decrease in sponge biomass and species richness related to pronounced competition between sponges and fleshy algae in degraded shallow habitats (Rützler, 2004); and/or (iii) a decrease in sponge biomass and species richness due to mass mortality events related to sponge diseases (Webster, 2007). In particular, heavy coastal urbanization and increased untreated wastewater discharges may have benefited Clionaidae, a family known for its ability to proliferate by boring calcareous bioconstructions of algae and corals (Rützler, 2012; Schönberg and Wisshak, 2014). Coral reef degradation in Toliara (Bruggemann *et al*, 2012; Andréfouët *et al.*, 2013) could be another factor favoring Clionaidae development, particularly in shallow areas (lagoon or reef flat). On the other hand, underwater caves are ecosystems that are generally much better preserved from nearshore disturbances (Harmelin *et al.*, 1985). They could therefore be used as "reference ecosystems", being little impacted by the changing pressure regime. Thus, a good characterization of these pressure regimes, from the past to the present, will allow Toliara to become an observatory of anthropic disturbances on marine benthic ecosystems using sponges as bioindicators, thanks to the present updated inventory.

Aknowledgements

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Appendix

Supplementary material S1. Revision of species names in the World Porifera Database.

N°	Species	Status	Accepted name
1	*Aaptos aaptos* (Schmidt, 1864)	inaccurate distribution	*Aaptos* aff. *aaptos* (Schmidt, 1864)
2	*Acanthella aurantiaca* Keller, 1889	genus transfer & junior synonym	*Stylissa carteri* (Dendy, 1889)
3	*Acanthella carteri* Dendy, 1889	genus transfer	*Stylissa carteri* (Dendy, 1889)
4	*Acarnus tortilis* Topsent, 1892	misapplication	*Acarnus bergquistae* van Soest, Hooper & Hiemstra, 1991
5	*Adocia fragilis* Vacelet, Vasseur & Lévi, 1976	genus transfer	*Haliclona fragilis* (Vacelet, Vasseur & Lévi, 1976)
6	*Anchinoe clathrodes (Dendy, 1922)*	genus transfer	*Phorbas clathrodes* (Dendy, 1922)
7	*Ancorina radix* Marenzeller, 1889	inaccurate distribution	*Ancorina* aff. *radix* Marenzeller, 1889
8	*Ancorina radix* var. *nanosclera* Lévi, 1967	status change	*Ancorina nanosclera* Lévi, 1967
9	*Aplysilla sulfurea* Schulze, 1878	inaccurate distribution	*Aplysilla* aff. *sulfurea* Schulze, 1878
10	*Axinella (Homaxinella) arborescens* Ridley & Dendy, 1886	unaccepted	*Axinella arborescens* Ridley & Dendy, 1886
11	*Axinella (Stylissa) donnani* (Bowerbank, 1873)	unaccepted	*Axinella donnani* (Bowerbank, 1873)
12	*Axinella carteri* (Dendy, 1889)	genus transfer	*Stylissa carteri* (Dendy, 1889)
13	*Axinosia incrustans* Burton, 1930	misapplication	*Scopalina rubra* (Vacelet & Vasseur, 1971)
		genus transfer & inaccurate distribution	*Ulosa* aff. *incrustans* (Burton, 1930)
14	*Bajalus* Lendenfeld, 1885 sp. (undetermined)	junior synonym	*Halisarca* Johnston, 1842 sp. (undetermined)
15	*Bubaris conulosus* Vacelet & Vasseur, 1971	agreement in gender	*Bubaris conulosa* Vacelet & Vasseur, 1971
16	*Cacospongia lamellosa* (Esper, 1794)	unaccepted	*Phyllospongia foliascens* (Pallas, 1766)
17	*Callipelta cavernicola* (Vacelet & Vasseur, 1965)	genus transfer	*Sollasipelta cavernicola* (Vacelet & Vasseur, 1965)
18	*Callipelta mixta* Vacelet, Vasseur & Lévi, 1976	genus transfer	*Sollasipelta mixta* (Vacelet, Vasseur & Lévi, 1976)
19	*Callipelta ornata* Sollas, 1888	genus transfer	*Sollasipelta ornata* (Sollas, 1888)
20	*Callipelta* Sollas, 1888 sp. (undetermined)	preoccupied	*Sollasipelta* Van Soest & Hooper, 2020 sp. (undetermined)
21	*Callyspongia subarmigera* (Ridley, 1884)	alternate representation (subgenus assignment)	*Callyspongia (Cladochalina) subarmigera* (Ridley, 1884)
22	*Caminus sphaeroconia* Sollas, 1886	inaccurate distribution	*Caminus* aff. *sphaeroconia* Sollas, 1886
23	*Ceraochalina* Lendenfeld, 1887 sp. (undetermined)	junior synonym	*Callyspongia (Callyspongia)* Duchassaing & Michelotti, 1864 sp. (undetermined)
24	*Chelonaplysilla noevus* (Carter, 1876)	inaccurate distribution	*Chelonaplysilla* aff. *noevus* (Carter, 1876)
25	*Chondrilla nucula* Schmidt, 1862	inaccurate distribution	*Chondrilla* aff. *nucula* Schmidt, 1862
26	*Chondrillastra australiensis* (Carter, 1873)	reverted genus transfer	*Chondrilla australiensis* Carter, 1873
27	*Chondrillastra mixta* (Schulze, 1877)	reverted genus transfer	*Chondrilla mixta* Schulze, 1876
28	*Clathria dichela* Hentschel, 1912	junior synonym	*Clathria (Thalysias) vulpina* (Lamarck, 1814)
29	*Clathria foliascens* Vacelet & Vasseur, 1971	alternate representation (subgenus assignment)	*Clathria (Clathria) foliascens* Vacelet & Vasseur, 1971
30	*Clathria spongodes* Dendy, 1922	alternate representation (subgenus assignment)	*Clathria (Clathria) spongodes* Dendy, 1922
31	*Clathria typica* (Carter, 1881)	junior synonym	*Clathria (Thalysias) cactiformis* (Lamarck, 1814)

32	*Clathrina darwinii* (Haeckel, 1870)	genus transfer	*Arturia darwinii* (Haeckel, 1870)
33	*Clathriopsamma cercidochela* Vacelet & Vasseur, 1971	genus transfer	*Clathria (Wilsonella) cercidochela* (Vacelet & Vasseur, 1971)
34	*Cliona lobata* Hancock, 1849	inaccurate distribution	*Cliona* aff. *lobata* Hancock, 1849
35	*Cliona margaritiferae* Dendy, 1905	genus transfer	*Pione margaritiferae* (Dendy, 1905)
36	*Cliona schmidtii* (Ridley, 1881)	inaccurate distribution	*Cliona* aff. *schmidtii* (Ridley, 1881)
37	*Cliothosa hancocki* (Topsent, 1888)	inaccurate distribution	*Cliothosa* aff. *hancocki* (Topsent, 1888)
38	*Coelosphaera fucoides* (Topsent, 1897)	alternate representation (subgenus assignment)	*Coelosphaera (Coelosphaera) fucoides* (Topsent, 1897)
39	*Cornulum strepsichela* Dendy, 1922	genus transfer	*Paracornulum strepsichela* (Dendy, 1922)
40	*Crambe crambe* (Schmidt, 1862)	inaccurate distribution	Crambe aff. crambe (Schmidt, 1862)
41	*Craniella australiensis* (Carter, 1886)	genus transfer	*Cinachyrella australiensis* Carter, 1886
42	*Craniella cranium* (Müller, 1776)	inaccurate distribution	*Craniella* aff. *cranium* (Müller, 1776)
43	*Desmanthus incrustans* (Topsent, 1889)	inaccurate distribution	*Desmanthus* aff. *incrustans* (Topsent, 1889)
44	*Didiscus clavigerus* (Kirkpatrick, 1900)	junior synonym	*Didiscus aceratus* (Ridley & Dendy, 1886)
45	*Didiscus styliferus* Tsurnamal, 1969	adaptation of species name & inaccurate distribution	*Didiscus* aff. *stylifer* Tsurnamal, 1969
46	*Ecionema rotundum*	misspelling of species name & junior synonym	*Ecionemia acervus* Bowerbank, 1862
47	*Ecionemia laviniensis* Dendy, 1905	genus transfer	*Stellettinopsis laviniensis* (Dendy, 1905)
48	*Gelliodes flagellifera* (Ridley & Dendy, 1886)	genus transfer	*Haliclona (Flagellia) amirantensis* Van Soest, 2017
49	*Gellius centrangulatus Sollas, 1902*	genus transfer	*Haliclona (Halichoclona) centrangulata* (Sollas, 1902)
50	*Gellius cymiformis*	genus transfer & misspelling of species name	*Haliclona (Gellius) cymaeformis* (Esper, 1806)
51	*Gellius petrosioides* (Dendy, 1905)	genus transfer	*Gelliodes petrosioides* Dendy, 1905
52	*Gellius ridleyi* Hentschel, 1912	genus transfer	*Haliclona (Gellius) ridleyi* (Hentschel, 1912)
53	*Gellius sagittarius* Sollas, 1902	genus transfer	*Oceanapia sagittaria* (Sollas, 1902)
54	*Hemectyonilla involuta* (Kirkpatrick, 1903)	genus transfer	*Aulospongus involutus* (Kirkpatrick, 1903)
55	*Hexadella racovitzai* Topsent, 1896	inaccurate distribution	*Hexadella* aff. *racovitzai* Topsent, 1896
56	*Hymedesmia mertoni* Hentschel, 1912	alternate representation (subgenus assignment)	*Hymedesmia (Hymedesmia) mertoni* Hentschel, 1912
57	Hymeniacidon conulosa (Dendy, 1922)	genus transfer	Stylissa conulosa (Dendy, 1922)
58	*Hymeniacidon sanguinea* (Grant, 1826)	junior synonym & inaccurate distribution	*Hymeniacidon* aff. *perlevis* (Montagu, 1814)
59	*Inflatella dura* Vacelet & Vasseur, 1971	genus transfer	*Oceanapia dura* (Vacelet & Vasseur, 1971)
60	*Ircinia (Sarcotragus) ramosa* (Keller, 1889)	unaccepted	*Ircinia ramosa* (Keller, 1889)
61	*Ircinia fasciculata* var. *dendroides* (Schmidt, 1862)	status change & inaccurate distribution	*Ircinia* aff. *dendroides* (Schmidt, 1862)
62	*Ircinia strobilina* (Lamarck, 1816)	inaccurate distribution	*Ircinia* aff. *strobilina* (Lamarck, 1816)
63	*Isops carcinophila* Lendenfeld, 1897	unaccepted	*Geodia carcinophila* (Lendenfeld, 1897)
64	*Isops sollasi* Lendenfeld, 1888	unaccepted	*Geodia sollasi* (Lendenfeld, 1888)
65	*Isops sphaerulifer* Vacelet & Vasseur, 1965	unaccepted	*Geodia sphaerulifer* (Vacelet & Vasseur, 1965)
66	*Jaspis johnstonii* (Schmidt, 1862)	inaccurate distribution	*Jaspis* aff. *johnstonii* (Schmidt, 1862)
67	*Latrunculia globosa* Vacelet, V asseur & Lévi, 1976	genus transfer	*Diacarnus globosus* (Vacelet, Vasseur & Lévi, 1976)
68	*Laxosuberites arenosus* Vacelet & Vasseur, 1971	genus transfer	*Liosina arenosa* (Vacelet & Vasseur, 1971)

69	*Laxosuberites cruciatus* (Dendy, 1905)	genus transfer	*Terpios cruciatus* (Dendy, 1905)
70	*Leucetta primigenia* Haeckel, 1872	inaccurate distribution	*Leucetta* aff. *primigenia* Haeckel, 1872
71	*Lissodendoryx arenaria* Burton, 1936	alternate representation (subgenus assignment)	*Lissodendoryx (Ectyodoryx) arenaria* Burton, 1936
72	*Macandrewia cavernicola* Vacelet & Vasseur, 1965	genus transfer	*Sollasipelta cavernicola* (Vacelet & Vasseur, 1965)
73	*Macandrewia ornata* (Sollas, 1888)	unaccepted	*Sollasipelta ornata* (Sollas, 1888)
74	*Megalopastas nigra* (Dendy, 1889)	unaccepted	*Spongionella nigra* Dendy, 1889
75	*Megalopastas retiara* Dendy, 1916	genus transfer	*Spongionella retiara* (Dendy, 1916)
76	*Microciona curvichela* Vacelet & Vasseur, 1965	genus transfer & subsequent preoccupation	*Clathria (Microciona) vacelettia* Hooper, 1996
77	*Microciona toxifera* (Hentschel, 1912)	unaccepted	*Clathria (Thalysias) toxifera* (Hentschel, 1912)
78	*Microciona* Bowerbank, 1862 sp. (undetermined)	genus transfer	*Clathria (Microciona)* Bowerbank, 1862 sp. (undetermined)
79	*Mycale (Grapelia) parasitica* (Carter, 1885)	misapplication	*Mycale (Grapelia) vaceleti* Hajdu, 1995
80	*Mycale cleistochela* Vacelet & Vasseur, 1971	alternate representation (subgenus assignment)	*Mycale (Naviculina) cleistochela* Vacelet & Vasseur, 1971
81	*Mycale crassissima* (Dendy, 1905)	alternate representation (subgenus assignment)	*Mycale (Aegogropila) crassissima* (Dendy, 1905)
82	*Mycale grandis* Gray, 1867	alternate representation (subgenus transfer)	*Mycale (Mycale) grandis* Gray, 1867
83	*Mycale gravely*i Burton, 1937	alternate representation (subgenus transfer)	*Mycale (Mycale) gravelyi* Burton, 1937
84	*Mycale imperfecta* Baer, 1906	alternate representation (subgenus assignment)	*Mycale (Arenochalina) imperfecta* Baer, 1906
85	*Mycale microxea* Vacelet, Vasseur & Lévi, 1976	alternate representation (subgenus transfer)	*Mycale (Naviculina) microxea* Vacelet, Vasseur & Lévi, 1976
86	*Mycale sulevoidea* (Sollas, 1902)	alternate representation (subgenus assignment)	*Mycale (Aegogropila) sulevoidea* (Sollas, 1902)
87	*Myriastra osculifera* Lévi, 1964	unaccepted	*Stelletta osculifera* (Lévi, 1964)
88	*Myrmekioderma granulata* (Esper, 1829)	agreement in gender	*Myrmekioderma granulatum* (Esper, 1829)
89	*Neofolitispa dianchora* (de Laubenfels, 1935)	genus transfer	*Monanchora dianchora* de Laubenfels, 1935
90	*Neofolitispa unguiculata* (Dendy, 1922)	genus transfer	*Monanchora unguiculata (Dendy, 1922)*
91	*Oligoceras cavernosa* Vacelet, Vasseur & Lévi, 1976	genus transfer	*Hyrtios cavernosus* (Vacelet, Vasseur & Lévi, 1976)
92	*Oscarella lobularis* (Schmidt, 1862)	inaccurate distribution	*Oscarella* aff. *lobularis* (Schmidt, 1862)
93	*Paracornulum atoxa* Vacelet, Vasseur & Lévi, 1976	genus transfer & junior synonym	*Zyzzya fuliginosa* (Carter, 1879)
94	*Paracornulum minimum* Vacelet, Vasseur & Lévi, 1976	genus transfer	*Cornulella minima* (Vacelet, Vasseur & Lévi, 1976)
95	*Paratenaciella microxea* Vacelet & Vasseur, 1971	genus transfer	*Clathria (Microciona) microxea* (Vacelet & Vasseur, 1971)
96	*Pellina* Schmidt, 1870 sp. (undetermined)	junior synonym	*Halichondria (Halichondria)* Fleming, 1828 sp. (undetermined)
97	*Petrosia densissima* Dendy, 1905	alternate representation (subgenus assignment)	*Petrosia (Petrosia) densissima* Dendy, 1905
98	*Petrosia imperforata* Thiele, 1899	junior synonym	*Petrosia (Petrosia) nigricans* Lindgren, 1897
99	*Petrosia nigricans* Lindgren, 1897	alternate representation (subgenus assignment)	*Petrosia (Petrosia) nigricans* Lindgren, 1897
100	*Petrosia seriata* Hentschel, 1912	genus transfer	*Neopetrosia seriata* (Hentschel, 1912)
101	*Petrosia spheroida* Tanita, 1967	alternate representation (subgenus assignment)	*Petrosia (Petrosia) spheroida* Tanita, 1967
102	*Petrosia testudinaria* (Lamarck, 1815)	genus transfer	*Xestospongia testudinaria* (Lamarck, 1815)

103	*Phyllospongia dendyi* Lendenfeld, 1889	genus transfer	*Lendenfeldia dendyi* (Lendenfeld, 1889)
104	*Phyllospongia madagascarensis*	misspelling of species name & junior synonym	*Phyllospongia papyracea* (Esper, 1806)
105	*Plakina monolopha* Schulze, 1880	inaccurate distribution	*Plakina* aff. *monolopha* Schulze, 1880
106	*Plakina trilopha* Schulze, 1880	inaccurate distribution	*Plakina* aff. *trilopha* Schulze, 1880
107	*Plakortis simplex* Schulze, 1880	inaccurate distribution	*Plakortis* aff. *simplex* Schulze, 1880
108	*Plumohalichondria gardineri* Dendy, 1922	genus transfer	*Aulospongus gardineri* (Dendy, 1922)
109	*Prianos aurantiaca* Lévi, 1958	genus transfer	*Batzella aurantiaca* (Lévi, 1958)
110	*Pronax scabida* sensu Vacelet, Vasseur & Lévi, 1976	genus transfer	*Phorbas scabida* (sensu Vacelet, Vasseur & Lévi, 1976)
111	*Prostylissa fistulosa* Vacelet, Vasseur & Lévi, 1976	genus transfer	*Amorphinopsis fistulosa* (Vacelet, Vasseur & Lévi, 1976)
112	*Prostylissa foetida* (Dendy, 1889)	genus transfer	*Amorphinopsis foetida* (Dendy, 1889)
113	*Psammaplysilla purpurea* (Carter, 1880)	genus transfer	*Pseudoceratina purpurea* (Carter, 1880)
114	*Psammascus lamella* (Lendenfeld, 1888)	genus transfer	*Chondropsis lamella* (Lendenfeld, 1888)
115	*Pytheas ula* (de Laubenfels, 1950)	unaccepted	*Crella (Pytheas) ula* (de Laubenfels, 1950)
116	*Racodiscula incrustans* Vacelet & Vasseur, 1971	genus transfer	*Kaliapsis incrustans* (Vacelet & Vasseur, 1971)
117	*Raspaigella tulearensis* Vacelet & Vasseur, 1971	genus transfer & junior synonym	*Myrmekioderma dendyi* (Burton, 1959)
118	*Reniera polypoides* Vacelet, Vasseur & Lévi, 1976	genus transfer	*Haliclona polypoides* (Vacelet, Vasseur & Lévi, 1976)
119	*Reniera viridenigra* Vacelet, Vasseur & Lévi, 1976	genus transfer	*Xestospongia viridenigra* (Vacelet, Vasseur & Lévi, 1976)
120	*Reniera* Schmidt, 1862 sp. (undetermined)	genus transfer	*Haliclona (Reniera)* Schmidt, 1862 sp. (undetermined)
121	*Rhabderemia toxigera* Topsent, 1892	inaccurate distribution	*Rhabderemia* aff. *toxigera* Topsent, 1892
122	*Rhabdoploca topsenti* Hentschel, 1912	genus transfer	*Cerbaris topsenti* (Hentschel, 1912)
123	*Rhabdosigma mammillata* (Whitelegge, 1907)	genus transfer & inaccurate distribution	*Rhabderemia* aff. *mammillata* (Whitelegge, 1907)
124	*Rhaphidophlus aculeatus* (Ridley, 1884)	unaccepted	*Clathria (Thalysias) abietina* (Lamarck, 1814)
125	*Rhaphidophlus cervicornis* Thiele, 1903	genus transfer	*Clathria (Thalysias) cervicornis* (Thiele, 1903)
126	*Rhaphidophlus* Ehlers, 1870 sp. (undetermined)	junior synonym	*Clathria (Thalysias)* Duchassaing & Michelotti, 1864 sp. (undetermined)
127	*Rhaphidophlus typica* (Lendenfeld, 1888)	genus transfer & junior synonym	*Clathria (Thalysias) cactiformis* (Lamarck, 1814)
128	*Rhizochalina cribrirhina* Vacelet & Vasseur, 1971	genus transfer	*Oceanapia cribrirhina* (Vacelet & Vasseur, 1971)
129	*Rhizochalina fistulosa* (Bowerbank, 1873)	genus transfer	*Oceanapia fistulosa* (Bowerbank, 1873)
130	*Rhizochalina incrustans* Barnes & Bell, 2002	misspelling of species name	*Oceanapia incrustata* (Dendy, 1922)
131	*Rhizochalina incrustata* (Dendy, 1922)	genus transfer	*Oceanapia incrustata* (Dendy, 1922)
132	*Rhizochalina minuta* Vacelet, Vasseur & Lévi, 1976	genus transfer	*Oceanapia minuta* (Vacelet, Vasseur & Lévi, 1976)
133	*Rhizochalina mucronata* Vacelet, Vasseur & Lévi, 1976	genus transfer	*Oceanapia mucronata* (Vacelet, Vasseur & Lévi, 1976)
134	*Rhizochalina polysiphonia* (Dendy, 1922)	unaccepted	*Oceanapia polysiphonia* (Dendy, 1922)
135	*Rhizochalina* Schmidt, 1870 sp. (undetermined)	junior synonym	*Oceanapia* Norman, 1869 sp. (undetermined)
136	*Scopalina lophyropoda* Schmidt, 1862	inaccurate distribution	*Scopalina* aff. *lophyropoda* Schmidt, 1862
137	*Spirastrella cunctatrix* Schmidt, 1868	inaccurate distribution	*Spirastrella* aff. *cunctatrix* Schmidt, 1868
138	*Spirastrella excentrica* Burton, 1931	genus transfer	*Spheciospongia excentrica* (Burton, 1931)
139	*Spirastrella inconstans* (Dendy, 1887)	genus transfer	*Spheciospongia inconstans* (Dendy, 1887)

140	*Spirastrella inconstans* var. *digitata* (Dendy, 1887)	genus transfer	*Spheciospongia inconstans* var. *digitata* (Dendy, 1887)
141	*Spirastrella poterionides* Vacelet & Vasseur, 1971	genus transfer	*Spheciospongia poterionides* (Vacelet & Vasseur, 1971)
142	*Spirastrella solida* Ridley & Dendy, 1886	genus transfer	*Spheciospongia solida* (Ridley & Dendy, 1886)
143	*Spirastrella vagabunda* Ridley, 1884	genus transfer	*Spheciospongia vagabunda* (Ridley, 1884)
144	*Spongosorites indica* Hentschel, 1912	unaccepted	*Spongosorites indicus* Hentschel, 1912
145	*Stoeba extensa* Dendy, 1905	genus transfer	*Dercitus (Stoeba) extensus* (Dendy, 1905)
146	*Stoeba* Sollas, 1888 sp. (undetermined)	status change	*Dercitus (Stoeba)* Sollas, 1888 (undetermined)
147	*Strongylophora durissima* Dendy, 1905	genus transfer	*Petrosia (Strongylophora) durissima* (Dendy, 1905)
148	*Tedania anhelans var. assabensis* Keller, 1891	unaccepted	*Tedania (Tedania) assabensis* Keller, 1891
149	*Tedania* Gray, 1867 sp. (undetermined)	alternate representation	*Tedania (Tedania)* Gray, 1867 sp. (undetermined)
150	*Tedanione wilsoni* Dendy, 1922	genus transfer	*Strongylamma wilsoni* (Dendy, 1922)
151	*Tedaniopsamma arenosa* Vacelet & Vasseur, 1971	unaccepted	*Strongylamma arenosa* (Vacelet & Vasseur, 1971)
152	*Terpios granulosa* Bergquist, 1967	correction of species name to match gender of genus name	*Terpios granulosus* Bergquist, 1967
153	*Theonella discifera* Lendenfeld, 1907	genus transfer	*Discodermia discifera* (Lendenfeld, 1907)
154	*Timea curvistellifera* (Dendy, 1905)	genus transfer	*Spirastrella curvistellifera* (Dendy, 1905)
155	*Timea unistellata* (Topsent, 1892)	inaccurate distribution	*Timea* aff. *unistellata* (Topsent, 1892)
156	*Toxadocia microxea* Vacelet, Vasseur & Lévi, 1976	genus transfer	*Petrosia (Petrosia) microxea* (Vacelet, Vasseur & Lévi, 1976)
157	*Toxadocia violacea* de Laubenfels, 1950	genus transfer & preoccupied	*Haliclona (Gellius) laubenfelsi* Van Soest & Hooper, 2020
158	*Toxochalina robusta* Ridley, 1884	genus transfer	*Callyspongia (Toxochalina) robusta* (Ridley, 1884)
159	*Toxochalina robusta var. dendyi* Burton, 1931	unaccepted	*Callyspongia (Toxochalina) dendyi* (Burton, 1931)
160	*Toxochalina* Ridley, 1884 sp. (undetermined)	genus transfer	*Callyspongia (Toxochalina)* Ridley, 1884
161	*Trachyopsis aplysinoides* (Dendy, 1922)	genus transfer	*Axinyssa aplysinoides* (Dendy, 1922)
162	*Trachyopsis halichondrioides* Dendy, 1905	genus transfer	*Topsentia halichondrioides* (Dendy, 1905)
163	*Trachyopsis stellettoides* Lévi, 1961	genus transfer	*Topsentia stellettoides* (Lévi, 1961)
164	*Ulosa rubra* Vacelet & Vasseur, 1971	genus transfer	*Scopalina rubra* (Vacelet & Vasseur, 1971)
165	*Xestospongia exigua* (Kirkpatrick, 1900)	genus transfer	*Neopetrosia chaliniformis* (Thiele, 1899)
166	*Zaplethea digonoxea diastra* Vacelet & Vasseur, 1965	genus transfer & upgrade to species	*Jaspis diastra* (Vacelet & Vasseur, 1965)

Original Article

Comparative assessment of the impacts of artisanal trolling and industrial longlining on yellowfin tuna exploited off the Kenyan coast

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Abstract

The Indian Ocean yellowfin tuna stock has been classified as overfished and remains subject to overfishing by industrial and artisanal fleets despite the implementation of catch reduction measures to rebuild the stocks. This study assessed the impacts of artisanal trolling and industrial pelagic longlining on the population structure of yellowfin tuna exploited in Kenyan waters. Catch data including fork length, sex and gonad maturity were examined for the two fisheries between April 2019 and April 2021. Selection patterns were then compared using eight length-based indicators and a suite of indicator ratios. Results showed that artisanal trolling caught individuals with smaller fork length, ranging from 32–177 cm with a mean of 76 ± 0.5 cm and a mode of 71 cm. The industrial fishery caught significantly larger individuals ($p > 0.05$) ranging from 52 – 204 cm with a mean of 137 ± 0.7 cm and a mode of 160 cm. Length at first capture (L_c) for artisanal trolling was estimated at 36 cm and 80 cm for the industrial fishery. Statistical tests further revealed significant differences in length distribution and selectivity curves. It was clear that the fisheries consistently captured distinct components of the yellowfin tuna population structure. The industrial fishery was dominated by mature individuals above length at 50 % maturity (>100 cm, L_{50}) constituting 90 % of the sampled catch of which 56 % were large mega-spawners above the optimum length ($> L_{opt} + 10\%$). On the other hand, 92 % the artisanal trolling fishery constituted small individuals below L_{50} and no mega-spawners. Overall, the average monthly sex ratio was skewed to males (F:M ratio = 1: 1.14). Deviations from the expected 1:1 sex-ratio were not significant; however, industrial longline catches were skewed towards large males, and artisanal trolling catches towards small females. The study illustrates application of widely used length-based approaches to derive insights on fishery interactions in data limited scenarios.

Keywords: tuna fisheries, selectivity, length-based indicators, western Indian Ocean

Introduction

Yellowfin tuna support numerous small-scale and highly valuable industrial fisheries worldwide and is ranked among the most valued and sought-after commercial species (Miyake *et al.*, 2010). Yellowfin tuna rank as the second most important commercial tuna species harvested worldwide after Skipjack (Galland *et al.*, 2016). The species is highly migratory, inhabiting the tropical and subtropical seas. Due to adaptation to subsurface feeding they occur in waters of up to 250 meters depth within coastal, neritic and oceanic waters (Schaefer and Fuller, 2002). The most recent regional assessment has classified the Indian Ocean (IO) yellowfin tuna stock as overfished (Fu *et al.*, 2021). Despite the overfished state, the stock remains subject to overfishing due to increasing fishing effort by industrial and artisanal fleets (Fu *et al.*, 2021). Catches of yellowfin tuna in the region have consequently continued to increase from 402,913 mt in 2015 to 432,623 mt in 2019, averaging at 434,568 mt annually (Fu *et al.*, 2021). Industrial longline catches of yellowfin tuna in the IO region average 73,240 mt, annually representing about 17 % of the total annual catch (ISSF, 2019). The proportion of yellowfin tuna caught by artisanal

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fleets has also increased from 30 % in the 2000s to 50 % in more recent years (Lecomte *et al.*, 2017).

Kenya lies within the rich tuna belt in the western Indian Ocean (WIO), which is mainly exploited by foreign industrial fishing vessels. Kenya's artisanal tuna fleet consists of an estimated 600 fishers using 414 vessels and diverse gear types including longlines, trolling lines, handlines, multifilament and monofilament nets (Ndegwa *et al.*, 2020). The fleet landed an estimated to 2,740 tons of tuna in 2019 (Ndegwa *et al.* 2020). Handlines, longlines and trolling lines are selective passive gears which consist of a mainline that is attached with baited hooks. Deployment strategies for these gear types are adjusted by changing the fishing depth, bait type and even construction materials to target specific species (Watson and Kerstetter, 2006). Artisanal trolling in Kenya involves use of monofilament lines which are hooked with artificial lures or natural baits. The lines are towed and hauled using a pole along the water surface. The fishers use mechanized fibreglass vessels which enable them to travel far distances in search of tuna. Reliable estimates of yellowfin tuna catches by the artisanal fishery are however lacking due to the strong seasonality and migratory nature of the fishery. Kenya's industrial longline fishery operates within the Exclusive Economic Zone (EEZ) (Ontomwa *et al.*, 2021). Industrial longline fishing uses multiple branch lines which are deployed at varying depths. In 2020, three industrial longline vessels were licensed to fish in Kenya's EEZ landing approximately 670 metric tonnes of assorted species of which approximately 132 mt (20 %) constituted yellowfin tuna (Government of Kenya, 2021).

Interactions between artisanal and industrial fisheries can arise when the same species are targeted, and such overlaps can cumulatively influence overall fishery performance (Powelle and Leslie, 2020). Studies on fishery interactions are important in understanding sources of fishing mortality and impacts of fished populations to inform the development of sustainable management strategies. There are some assessments characterizing interactions in tuna fisheries (Hampton *et al.*, 1996; Leroy *et al.*, 2016). Information on tuna fishery interactions is limited in the WIO region, and particularly Kenya. Use of length-based indicators to assess data-poor fisheries has become popular, as they are reported to perform as well as catch-based models (Kell *et al.*, 2022). This is more so because length composition data is easy to obtain and hence the most frequently collected data parameter among data-poor fisheries. Thus, this study applies a suite of length-based methods to derive insights on the impacts of artisanal trolling and industrial longlining on yellowfin tuna exploited off the Kenya coast

Materials and methods

Study Area

Monitoring of artisanal trolling catches was conducted at three selected fish landing sites along the Kenyan coast: Watamu, Amu and Kiwayu Island (Fig. 1). The fishing grounds within these sites are characterized by patchy and fringing reefs with high coral diversity, seagrass beds and extensive mangrove forests (Fulanda *et al.*, 2009). The continental shelf extends 15 - 60 km and covers an estimated area of 35,300 km^2. Kiwayu Island is located north-east of Amu town and borders the 250 km^2 Kiunga Marine National Reserve (KMNR).

Catch characterization

Publicly available data on yellowfin tuna landings across the WIO region for the years 1979 to 2020 was obtained from the IOTC website (www.iotc.org) to assess regional trends in annual yellowfin tuna catches by sector (industrial vs artisanal). For the more localized comparative assessment, yellowfin tuna caught off the Kenya coast by artisanal trolling lines were monitored monthly for four days at the three study sites between July 2020 and April 2021 for a duration of 10 months. Timing of sampling dates was informed by alerts sent by representatives of the beach management units on the presence of yellowfin tuna in landings at each site. All landed yellowfin tuna caught by artisanal trolling were sampled. Yellowfin tuna data collected by scientific observers from the Kenya Marine and Fisheries Research Institute deployed onboard industrial longline vessels between April 2019 and June 2020 was extracted. The observers collected catch data following the observer sampling protocol for longline fishing (Groeneveld and Heinecken, 2010). A simple random sampling protocol was employed in which fish were randomly sampled after an entire line hauling period. A total of 56 hauls (representing one haul per day) were sampled, and each haul contained between 1,950 and 2,720 hooks. Biometric measurements recorded included fork length (FL), measured to the nearest 0.1 cm on a measuring board and individual fish weight measured to the nearest 0.1 kg using an electronic weighing scale. Gonads from a sample of the measured fish were then visually examined to determine the sex of each fish.

Data processing and analysis

Length distribution and sex ratio

Length frequency histograms for the two fisheries were compared using a length interval of 10 cm. The Kolmogorov–Smirnov two-sample test was then applied to determine whether the length frequency distribution significantly differed between the fisheries. Sex ratio was calculated as the proportion of females to males (F:M), and the differences in sex ratio between the two fisheries was assessed using Chi-square test ($\chi 2$).

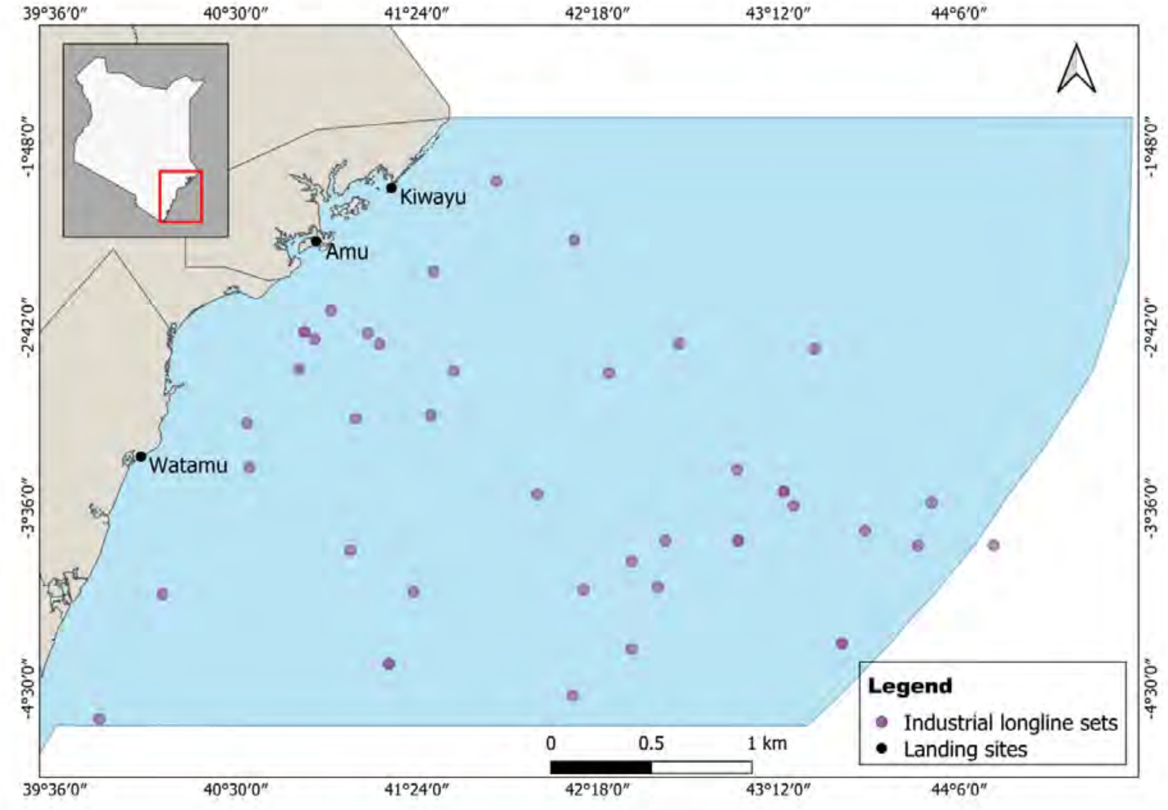

Figure 1. Map showing the artisanal fishery landing sites at Watamu, Amu and Kiwayu along the Kenyan coast, and industrial longline sets where yellowfin tuna were caught off Kenya's EEZ between April 2019 and April 2021.

Length indicators and indicator ratios

Length at first capture was estimated as the length of 50 % (SL_{50}) and 95 % (SL_{95}) of the fish retained by the two fisheries (trolling and pelagic longlining). The analysis was conducted on the online platform available at http://barefootecologist.com.au/. Each measured individual was classified as immature, maturing, mature or as a mega-spawner as defined by Froese (2004). Immature fish were classified as those below the reported size at first maturity (L_m), maturing as those between L_m and the length at which 50 % of fish were sexually mature (L_{50}), mature fish as those above L_{50}, and mega-spawners as fish larger than the optimum length (L_{opt}) plus 10 %. Optimal length is defined by Froese and Binohlan (2000) as the length when total biomass of a year-class reaches a maximum value. Classification of maturity status was based on length thresholds reported by Creech and Gunasekera (2020) as follows: immature (<76 cm), maturing (76-100cm), mature (>100 cm) and mega-spawners (≥143 cm). Length-based indicators by Froese (2004), and Cope and Punt (2009) were calculated for the two fisheries as: (i) percentage of mature fish in catch, with 100 % as target; (ii) percent of specimens with optimum length in catch, with 100 % as target; and (iii) percentage of 'mega-spawners' in catch, with target of 30-40 %. Life history parameters and length thresholds for life stages of yellowfin tuna are shown in Table 1. Length ratios defined in ICES (2015) were then calculated for each fishery and then for the pooled data and the derived ratios were compared against expected values as shown in Table 2. A traffic lights table was then generated assigning a colour code of either red or green to the derived ratios, with red reflecting a dangerous condition and green reflecting satisfactory conditions.

Table 1. Life history parameters and length thresholds for life stages of yellowfin tuna.

Parameter	Value	Source
L_∞	195 cm	Kimakwa *et al.* (2021)
L_{max}	165 cm	Creech and Gunasekra (2020)
L_{50}	100 cm	IOTC (2017)
L_{95}	121 cm	Creech and Gunasekra (2020)
L_{mat}	76 cm	Binohlan and Froese (2009)
K	0.44	Kimakwa *et al.* (2021)
M	0.59	Kimakwa *et al.* (2021)
M/K	1.37	calculated
L_{opt}	130	Froese and Binohlan (2000)

Results

Long-term temporal trends of yellowfin tuna landings catch estimates reported by IOTC indicated a general increasing trend in yellowfin tuna landings from the 1980s, peaking in 2004 followed by a decline until 2009 and a subsequent increase (Fig. 2). Over the last five years (up to 2020), industrial fleets accounted for 59 % of the yellowfin tuna landings in the region. Industrial longlines and artisanal trolling lines in the region altogether contributed about 32,000 mt (9 %) of yellowfin tuna landings annually.

Length distribution, sex ratio and maturity composition

Length distribution - Overall, a total of 3,138 yellowfin tuna individuals were sampled over the study period. A total of 916 and 1,076 tuna individuals were visually examined for sex ratio and maturity in the artisanal trolling and industrial longline fishery, respectively. Analysis of the length composition showed that the overall fork length distribution ranged from 32 - 204 cm (Fig. 3). Yellowfin tuna caught by the industrial longline fishery ranged from 52 - 204 cm with modal fork length of 160 cm, while that for the artisanal trolling fishery ranged from 32 - 177 cm with modal fork length of 71 cm. The Kolmogorov-Smirnov test revealed significant differences in length distributions and selectivity curves between the two fisheries (D = 0.821 > 0.05, at 0.05 CI).

The average monthly sex ratio was skewed to males (F:M ratio = 1: 1.14). Monthly variations in the sex ratio were observed in both fisheries; however, results of the Chi-square test showed no significant differences

Table 2. Comparison of monthly sex ratios (F: M) of *Thunnus albacares* catches in the artisanal trolling and industrial longline fishery occurring in Kenyan waters during March 2020 to April 2021.

Fishery	Month	Female	Male	F : M ratio		Chi-square	p-value
	August	78	76	1	0.97	0.504	*p*=0.478
Artisanal trolling line	September	73	71	1	0.97	0.462	*p*=0.497
	October	22	9	1	0.41	2.084	*p*=0.149
	November	59	32	1	0.54	1.890	*p*=0.169
	December	36	27	1	0.75	0.044	*p*=0.834
	January	73	70	1	0.96	0.392	*p*=0.531
	February	58	32	1	0.55	1.699	*p*=0.192
	March	64	57	1	0.89	0.106	*p*=0.745
	April	35	29	1	0.83	0.0028	*p*=0.958
	July	18	16	1	0.89	0.0286	*p*=0.867
	April	63	76	1	1.21	2.412	*p*=0.1204
Industrial longline	May	80	214	1	2.68	3.351	*p*=0.067
	June	38	69	1	1.82	0.0037	*p*=0.952
	August	63	59	1	0.94	6.712	*P*=0.500
	September	63	140	1	2.22	0.775	*p*=0.379
	October	80	139	1	1.74	0.120	*p*=0.913
	December	13	13	1	1.00	1.11	*p*=0.292

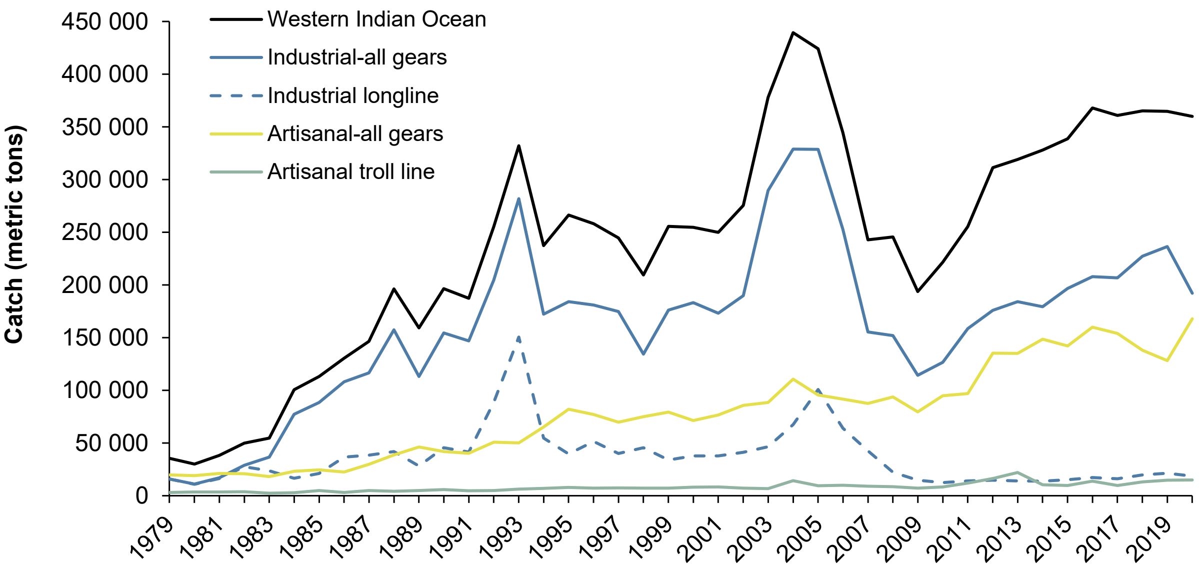

Figure 2. Annual time series of yellowfin tuna catches (mt) caught by the industrial and artisanal fleets within the western Indian Ocean region from 1979 to 2020 (Source: IOTC).

(Table 3). By fishery, the average monthly sex ratio was 1: 0.78 for the artisanal trolling fishery and 1: 1.66 for the industrial longline fishery. This indicates that yellowfin catches by the artisanal trolling fishery are skewed to females, while industrial pelagic longline fishery catches are skewed to males. Mature individuals (>100 cm) of yellowfin tuna constituted 90 % of the industrial longline, of which 56 % were mega-spawners, while 92 % of the yellowfin tuna targeted by artisanal trolling was immature with no mega-spawners (Fig. 3). The selectivity curves revealed the catch of fish was below the size at maturity for artisanal trolling while the industrial longline selected fish above size at maturity (Fig. 4). It was also apparent that both fisheries consistently caught a higher proportion of the dominant life phases across months demonstrating high selectivity as the proportions did not vary significantly between months (Fig. 5).

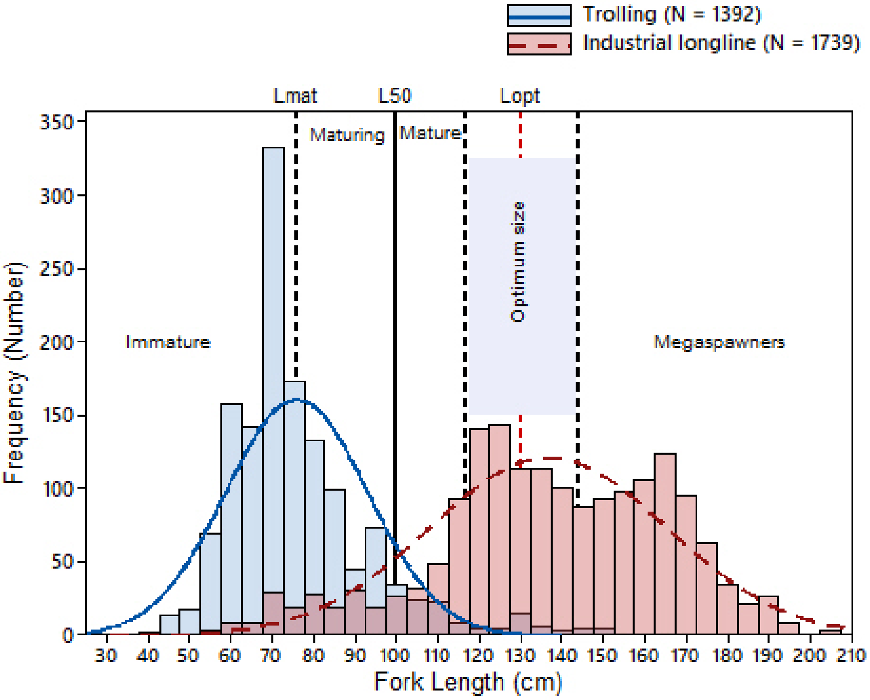

Figure 3. Length frequency distribution for yellowfin tuna caught by the artisanal trolling and industrial longline fishery off the Kenyan coast between April 2019 and April 2021.

Table 3. Summary of length-based indicators used in the assessment and the derived estimates.

Source	Indicators	Calculation	Reference point	Artisanal trolling	Industrial longline
ICES (2015)	L_c	Length at first capture (50% of the overall mode)	L_{mat}	36 cm	80 cm
	$L_{25\%}$	25th percentile of length distribution	L_{mat}	65 cm	114 cm
	L_{maxy}	Length class with maximum biomass in catch	$L_{opt} = \frac{3}{3+\frac{M}{k}} \times L_{inf}$	71 cm	165 cm
	$L_{95\%}$	95th percentile of length distribution	L_{inf}	73 cm	187 cm
	L_{mean}	Mean length of individuals > Lc	$L_{opt} = \frac{3}{3+\frac{M}{k}} \times L_{inf}$	93 cm	140 cm
	$L_{max5\%}$	Mean length of largest 5%	L_{inf}	127 cm	187 cm
Froese (2004)	P_{mat}	Percentage of mature fish above L_{50}	L_{50}	0.07	0.90
	P_{opt}	Percentage of fish at optimum length	L_{opt}	0.03	0.38
	P_{mega}	Percentage of mega-spawners	0.3 – 0.4	0.01	0.43

Length indicators and indicator ratios

Length at first capture of 50 % (SL_{50}) and 95% (SL_{95}) was estimated to be 63 cm (95 % CI, 61 – 64 cm) and 69 cm (95 % CI, 67 – 71 cm) respectively for artisanal trolling. For the industrial longline SL_{50} and SL_{95} was 138 cm (95 % CI, 127 – 148 cm) and 191 cm (95 % CI, 176 – 204 cm), respectively. The findings showed that the two fisheries predominantly captured different life phases of yellowfin tuna (Table 4). The summary of the generated length indicator ratios for the two fisheries shows that ratios for artisanal trolling were all below expected values indicating poor conservation outcomes due to the high proportion of immature sizes (Fig. 5). On the other hand, the ratios for the industrial longline fishery were all above expected values. Ratios for the pooled dataset showed an overall poor conservation outcome with immature and mega-spawners remaining below expected values.

Discussion

This study applied length-based metrics to compare the impacts of artisanal trolling and industrial longlining on yellowfin tuna exploited off the Kenya coast. The study derived insights on interactions between

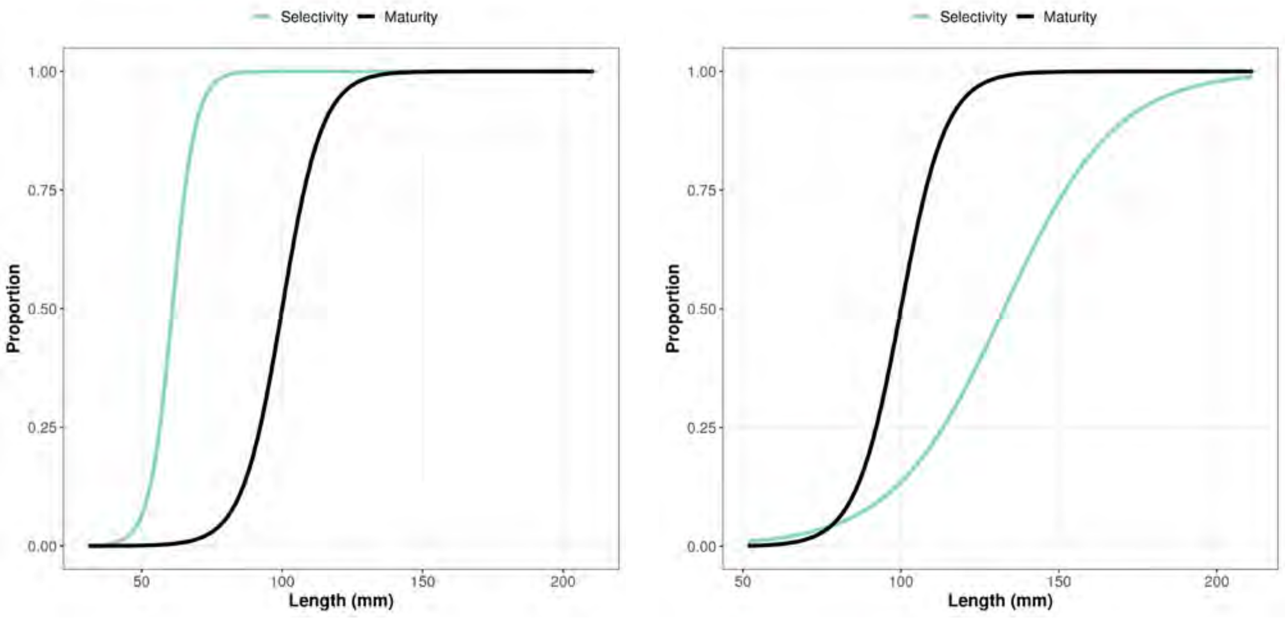

Figure 4. Selectivity and maturity curves for yellowfin tuna caught by a) artisanal trolling and b) industrial longline off the Kenyan coast between April 2019 and April 2021.

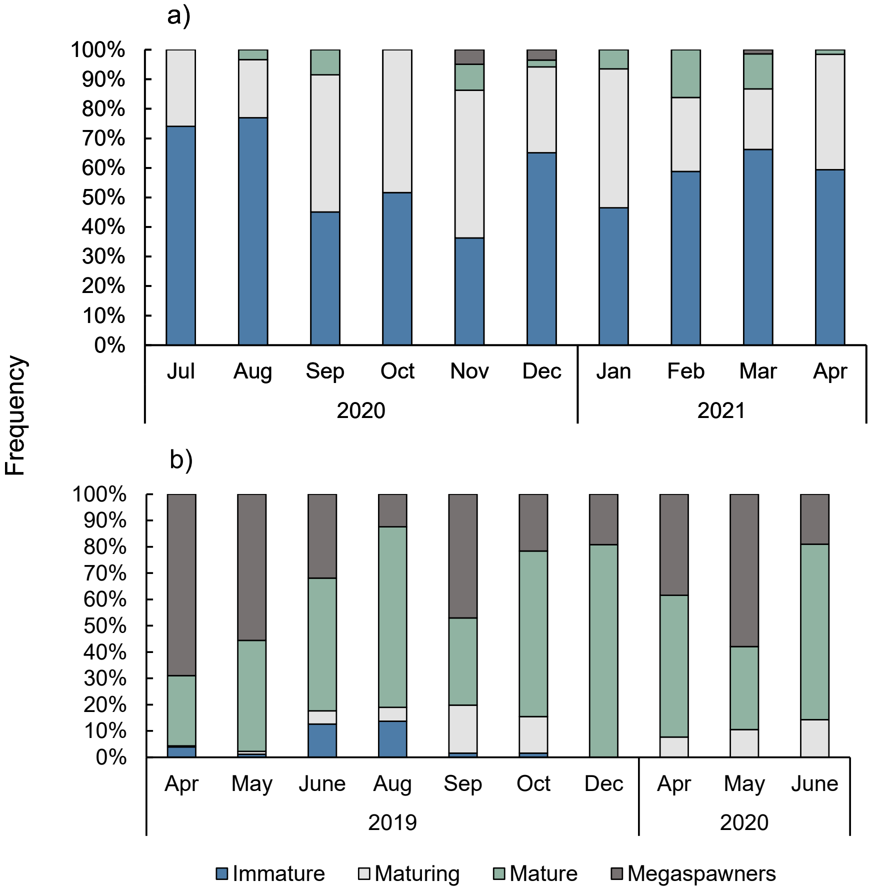

Figure 5. Monthly variation in the proportion of immature and mature yellowfin in the sampled catches caught by a) artisanal trolling and b) industrial pelagic longline off the Kenyan coast. Maturity length thresholds used: immature (<76 cm), maturing (76-100cm), mature (>100 cm) and mega-spawners (≥143 cm).

industrial and artisanal tuna fisheries in the WIO region. The observed fork length ranges for artisanal trolling (32 cm – 177 cm) were within reported ranges for the Indian Ocean region of 30 – 180 cm (IOTC, 2017). A maximum length of 204 cm recorded for the industrial longline fishery was much higher than the reported range for the region, but falls within the maximum reported length of 239 cm (Froese and Pauly, 2022).

Artisanal trolling mainly caught immature and maturing fish below the size at 50 % maturity (100 cm) while the industrial longline mainly caught mature fish. The high capture of juvenile yellowfin tuna in artisanal fishing gears has been reported within the Indian Ocean region (GTA, 2021). Juveniles mainly occur in surface waters and migrate to deeper depths as they mature. Thus, juvenile and immature sizes of yellow fin tuna will more likely be caught in artisanal fishing

Table 4. Summary of the indicator ratios for the traffic lights system. Cells shaded green are above the expected value and those shaded in red are below expected values.

Management outcome	Indicator ratio	Expected value	Artisanal trolling	Industrial longline
Conservation of immature fish	L_c / L_{mat}	> 1	0.47	1.05
	$L_{25\%} / L_{mat}$	> 1	0.86	1.50
Conservation of mature individuals	$L_{max5\%} / L_{inf}$	> 0.8	0.65	0.95
	P_{mega}	≥ 0.3	0.01	0.43
Optimal yield	L_{mean} / L_{opt}	≈ 1	0.48	0.72
MSY	$L_{mean} / L_{F=M}$	≥ 1	0.87	1.10

gears. In contrast, industrial longline fishery preferentially targets larger individuals of yellowfin tuna which are found in deeper offshore waters indicating more of a logistic curve. Therefore, the selection curve for the artisanal fishery is more likely to be dome shaped while that of the industrial fishery will approach a logistic curve.

The spatial distribution of immature and mature phases of yellowfin tuna is reported to be influenced by various environmental conditions that affect the horizontal distribution and vertical partitioning of yellowfin tuna life stages by size or sex. These environmental conditions include depth of deployment and type of bait used (Løkkeborg and Bjordal, 1992, Ingólfsson *et al.*, 2017 Eighani *et al.*, 2019). Juvenile yellowfin tuna are also known to be attracted to floating objects which act as fish aggregating devices (FADs) (Girard *et al.*, 2004; Dagorn *et al.*, 2013; Scutt Phillips *et al.*, 2017). Artisanal fishers are known to fish around natural floating objects to enhance fishing efficiency. Thus, the strong association of yellowfin tuna juveniles with FADs makes them highly vulnerable to capture by trolling lines and other surface associated fishing gears.

The observed skew in sex ratio to males for the industrial longline fishery corresponds with Zhu *et al.* (2008) who reported an increasing abundance of males with size. The observed skew to males could also be a general reflection of the population dynamics of yellowfin tuna, as older females have been reported to have a higher natural mortality than males (Fu *et al.*, 2018). The skew to females observed in the artisanal trolling catches could be an artefact of spawning patterns, as a high abundance of yellowfin tuna females have been reported to aggregate in coastal areas to spawn during the northeast monsoon season (Zudaire, 2013), which coincides with the peak in artisanal fishing effort. However, a more intense sampling regime may further ascertain this hypothesis.

The study reveals that the two fisheries impact on different but critical life phases of the yellowfin tuna population. The observed differences in length distributions and selectivity curves may be influenced by the availability and catchability in the two regions and the gears. This however remains to be tested. Selective removal of these life phases can result in truncation of the affected size classes (Berkeley *et al.*, 2004; Hsieh *et al.*, 2010), and alter related demographic processes such as maturation and sex ratios (Kendall *et al.*, 2012). Extrapolation of the findings to the yellowfin tuna stock will require some weighting of the two fisheries based the fishing mortality contributed by each fishery across the region. However, the available catch estimates reported to IOTC for both the industrial and artisanal sectors are known to be under-estimated due to under-reporting and illegal fishing (Le Manach *et al.* 2012, 2015). It is important to note that the length-based assessment methods utilized in this study are most appropriate when applied in the context of a full stock. This study has applied the methods in a novel manner to derive insights on interactions between industrial and artisanal tuna fisheries and impacts on yellowfin tuna population structure. These findings highlight issues of conservation concern with regards to overharvesting of immature yellowfin tuna by artisanal fleets, and the need for localized measures within national jurisdictions to control high fishing mortality of immature fish and mega-spawners. Future assessments should integrate stock-wide data as well as the full spectrum of fishing gear types for a more comprehensive understanding of fishery interactions on the yellowfin tuna stock within the WIO region.

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Original Article

Tidal cycle and time of day control pH levels in coastal habitats of the western Indian Ocean: the case of Mnazi and Chwaka Bays in Tanzania

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Abstract

Ocean acidification, a progressive decrease in the pH and change in the carbonate chemistry of seawater caused by the uptake of carbon dioxide (CO_2) from the atmosphere, is a growing crisis that threatens marine species. pH data relevant to a species' natural habitat in the coastal waters of the western Indian Ocean (WIO) is still sparse, limiting the capacity to undertake manipulative studies to better understand the impacts of ocean acidification on marine species. This study investigated tidal and day-night pH variations in mangrove, seagrass, and coral reef habitats of the WIO by using Tanzania as a case study. The mean pH of the studied coastal habitats was highest in seagrass (8.49 ± 0.29), followed by coral reef (8.33 ± 0.06), and lowest in mangrove (8.20 ± 0.17). Seagrass habitats had the highest pH (9.06) during the day at low spring tides, mangrove habitats had the highest pH (8.45) during the day at high spring tides, and coral reef habitats had the highest pH (8.47) during the day at low tides. Seagrass habitats had the widest pH range (1.03), followed by mangrove habitats (0.54), while coral reef habitats had the narrowest range (0.23). The water with the highest pH during the day was transported to nearby mangrove habitats during incoming tides and to coral reef habitats during outgoing tides, resulting in the highest mean pH in mangrove and coral reef habitats during spring high and low tides, respectively. pH within the seagrass habitats correlated strongly and positively with changes in temperature (r=0.80), dissolved oxygen (r=0.84), and salinity (r=0.72), while pH in mangrove habitats correlated moderately and positively with dissolved oxygen (r=0.59). This study provides in-situ evidence on the pH fluctuations in the WIO's coastal habitats over time and space, with water from seagrass habitats capable of raising the pH of water in nearby mangrove and coral reef habitats during the day, thereby potentially helping in the mitigation of the effects of ocean acidification on these habitats.

Keywords: pH, ocean acidification, western Indian Ocean, mangroves, coral reefs, seagrasses

Introduction

Ocean acidification (OA) is a progressive decrease in the pH and change in carbonate chemistry of seawater caused by carbon dioxide (CO_2) absorption from the atmosphere (Doney *et al.*, 2009; Gattuso *et al.*, 2015). As a result, the pH of the open oceans has decreased from a previously stable value of 8.2 over the past century to a current value of 8.1, signifying a 30 % increase in acidity on average (Feely *et al.*, 2009; Orr, 2011). Based on the Intergovernmental Panel on Climate Change (IPCC) worst-case business-as-usual CO_2 emissions scenario, biogeochemical models predict a further decrease in the pH of the open oceans, leading to an acidity increase of up to 150% by 2100 (Doney *et al.*, 2009; Feely *et al.*, 2009). Prediction of pH in coastal waters containing mangrove, seagrass, and coral reef

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habitats is, however, challenging because it is influenced by a complex set of factors such as community metabolism (a balance between primary productivity of vegetation cover and community respiration), eutrophication, inputs from the open ocean, underground freshwater discharge and rivers, and climatic factors (temperature and dissolved oxygen), some of which may be localized in nature (Hofmann *et al.*, 2011; Pacella *et al.*, 2018; Pauline *et al.*, 2011; Proum *et al.*, 2017; Unsworth *et al.*, 2012). As a result, natural pH variability may occur at much higher rates than the rate at which CO_2 decreases ocean pH.

Mangrove, seagrass, and coral reef habitats of the WIO are also subject to semi-diurnal tidal variability, with two high tides and two low tides during each day-night cycle, resulting in fluctuations in physicochemical variables such as salinity, temperature, and dissolved oxygen (George *et al.*, 2018; Mahongo, 2014; Shaghude *et al.*, 2012). These changes affect the pH of the water column by modulating community metabolism (photosynthesis and respiration) within habitats (Semesi *et al.*, 2009a; Semesi *et al.*, 2009b), allowing for a high degree of pH variability (day-night cycling) in the water column of these habitats. A study by Hofmann *et al.* (2011), which examined temporal changes in different coastal habitats, does not adequately represent pH variability in coastal habitats of the WIO. This is because the effect of tidal cycles on pH variability in mangrove, seagrass, and coral reef habitats was not considered. pH variations in such habitats could have a significant impact on the development of resistance in resident marine species, or they could combine with the persistent effects of OA to produce severe occurrences with significant consequences on resident marine species. In either case, understanding pH variations in mangrove, seagrass, and coral reef habitats as well as their underlying drivers is crucial for a better understanding of the effects of future OA on marine species. Therefore, the aim of this study was to characterise the pH variability in Tanzanian coastal habitats over space and time as well as their underlying drivers. In this study, we tested four hypotheses: (1) mangrove, seagrass, and coral reef habitats have different pH levels; (2) pH levels within mangrove, seagrass and coral reef habitats vary with tidal cycles; (3) pH levels within mangrove, seagrass, and coral reef habitats are higher during the day than at night, regardless of tidal cycle; and (4) water with a higher pH from seagrass habitats is flushed to nearby mangrove and coral reef habitats during the day at high tides, raising their pH and helping to mitigate the effects of OA in these habitats.

Materials and methods

Study area

This study was carried out in spatially isolated mangrove, seagrass, and coral reef habitats located in non-estuarine bays: Chwaka Bay in Unguja Island, Zanzibar, and in Mnazi Bay in Mtwara, Mainland Tanzania (Fig. 1). The climate along the Tanzanian coast is influenced by the northeast (NE) monsoon winds (which are present from November to April) characterized by heavy rainfalls, weak winds and high stable average air temperatures, and the southeast (SE) monsoon winds (which are present from June to September) characterized by weak rainfalls, strong winds and low stable average air temperatures (Mahongo, 2014). The inter-monsoon months (May and October) are comparatively calm. The monsoon season also creates two rainy seasons: heavy or long rains between March and May, and short rains, which occur irregularly between September and December (Francis and Mahongo, 2012; McClanahan, 1988). The coast is also characterised by semi-diurnal tides, consisting of two high tides and two low tides of approximately equal magnitude each day-night cycle, resulting in fluctuations in the physicochemical conditions of the water column that modulate biogeochemical processes and community metabolism within habitats, affecting pH of the water column (Cederlof *et al.*, 1995; George, 2019; Shaghude *et al.*, 2012). This study was conducted between September (2018) and July (2019), covering periods of both the NE and SE monsoons.

Study design

In each bay, large permanent plots (50 m x 50 m) in mangrove, seagrass, and coral reef habitats and their adjacent open ocean were marked using a Global Positioning System (GPS) and monitored during low and high spring tides during the NE and SE monsoons. Within each habitat at low spring tides, three 30 m transects were established using measuring tapes parallel to the shoreline to minimize the impact of depth gradient, as it has been demonstrated that water motion determines how much the local pH is influenced by vegetation metabolism (James *et al.*, 2020). A 0.25 m x 0.25 m quadrat was randomly selected along each transect at a distance of approximately 10 m during low spring tides. In each quadrat, six measurements of pH, temperature, salinity and dissolved oxygen were taken for both the day (between 10:00 am and 3:00 pm) and night (between 10:00 pm and 3:00 am). Because the properties of the water column in shallow water habitats are similar, data (pH, temperature, salinity, and dissolved oxygen) were collected at the surface of the water in a specific coastal habitat during high spring tides. *In-situ* measurements of pH, dissolved oxygen, salinity, and temperature were performed once during spring tides of each season over a 24-hour period covering high and low tides for each habitat within bays in order to capture the effect of the tidal cycle and time of day on pH levels.

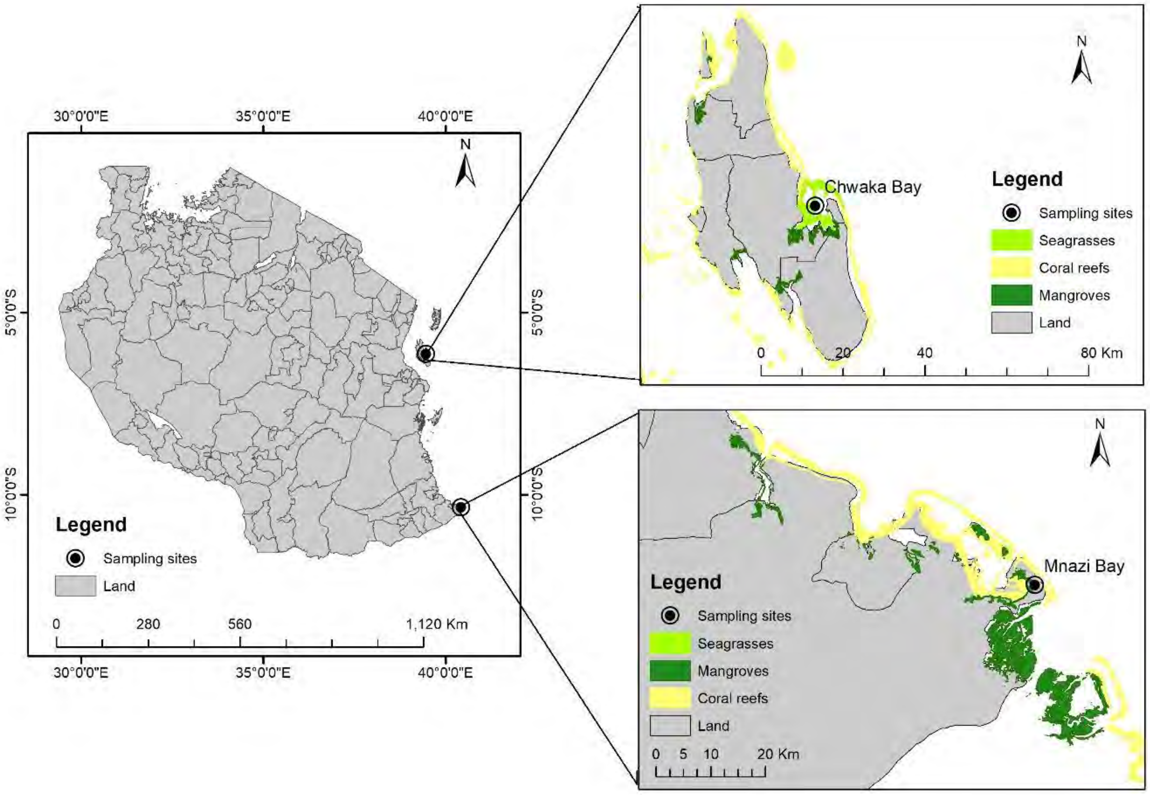

Figure 1. Map of Tanzania showing locations of study sites (Mnazi and Chwaka Bays).

Measurements of dissolved oxygen, salinity, pH and temperature

Dissolved oxygen, salinity and pH were manually measured by using an O_2 electrode (FDO 925, WTW), salinity electrode (TetraCon 925, WTW) and a pH electrode (SenTix 940, WTW), respectively, connected to a multimeter (Multi 3430 WTW, Germany) one at a time. Prior to measurement, the pH meter was calibrated (three-point calibration; pH 4.10, 7.01, and 10.00) using a buffer that was purchased together with the instrument. This procedure allowed for the acquisition of reliable data. Electrodes also measured the temperature of water.

Statistical analyses

Mean and standard deviation for pH, temperature, salinity and dissolved oxygen values were computed and compared between sites, time of the day, and tides. Prior to statistical analysis, the data were subjected to a Shapiro-Wilk test to determine their normality. The differences in mean pH levels between habitats were tested using a One-way Analysis of Variance (ANOVA), followed by the Tukey's test post-hoc for pairwise habitat comparisons. Furthermore, the differences in mean pH within habitats were tested using the T-test. The differences in dissolved oxygen, salinity and temperature between day-night time and between high-low tides within habitats were tested using a Two - way Analysis of Variance (ANOVA). Moreover, a spearman rank correlation analysis was performed to test the relationship between dissolved oxygen, salinity, temperature (predictors) and pH. The significance level was established at <0.05. All statistical analyses were performed using Python version 3.2.

Results

pH variability in the mangrove, seagrass and coral reef habitats

The mean pH levels between mangrove, seagrass, and coral reef habitats varied significantly (Fig. 2). However, while the difference in mean pH levels between

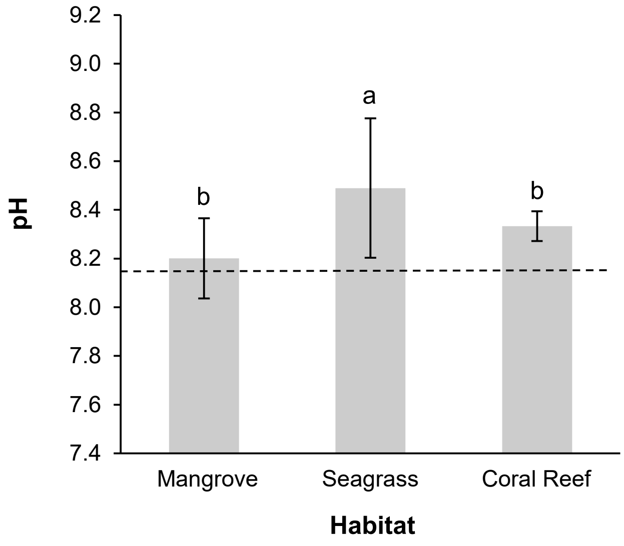

Figure 2. Mean pH levels in seagrass, mangrove, and coral reef habitats. The dotted line indicates the mean pH of the adjacent open ocean. Error bars indicate standard deviations. The letters above the bars indicate significant differences in pH levels between mangrove, seagrass, and coral reef habitats (based on one-way ANOVA tests) at $p \leq 0.05$. N = 16.

seagrass and mangrove habitats, and between seagrass and coral reef habitats was significant, the difference between mangrove and coral reef habitats was not (Fig. 2). Seagrass habitats had the highest mean pH of 8.49 ± 0.29, followed by coral reef habitats with a mean pH of 8.33 ± 0.06 and mangrove habitats with the lowest mean pH of 8.20 ± 0.17. The adjacent open ocean had a mean pH of 8.16 ± 0.05, which was 0.04 pH units lower than that of mangrove habitats, 0.33 pH units lower than that of seagrass habitats, and 0.17 pH units lower than that of coral reef habitats (Fig. 2).

Tidal and day-night variability in pH levels in the mangrove, seagrass and coral reef habitats

Significant tide-dependent variations in mean pH levels were observed in mangrove and seagrass habitats, but not in coral reef habitats (Fig. 3; Table 1). The mean pH level in mangrove habitats was highest during the day at high spring tides (8.38 ± 0.06) and lowest during the night at low spring tides (8.01 ± 0.08). The mangrove habitats had a pH range of 0.54, with the highest pH (8.45) occurring in the day at high spring tides and the lowest pH (7.91) occurring during the night at low spring tides. In seagrass habitats, the mean pH was highest during the day at low spring tides (8.862 ± 0.21) and lowest during the night at low spring tides (8.16 ± 0.11). The pH range of the seagrass habitats was 1.03, with the highest pH (9.06) occurring in the day at low spring tides and the lowest pH (8.03) occurring during the night at low spring tides. The mean pH values for day high spring tides, day low spring tides, night high spring tides, and night low spring tides in coral reef habitats were 8.34 ± 0.01, 8.35 ± 0.09, 8.30 ± 0.06, and 8.33 ± 0.06, respectively, and did not significantly differ from one another. The highest pH for the coral reef habitats was 8.47 and the lowest was 8.24, with a range of 0.23. Interestingly, the mean pH levels in seagrass,

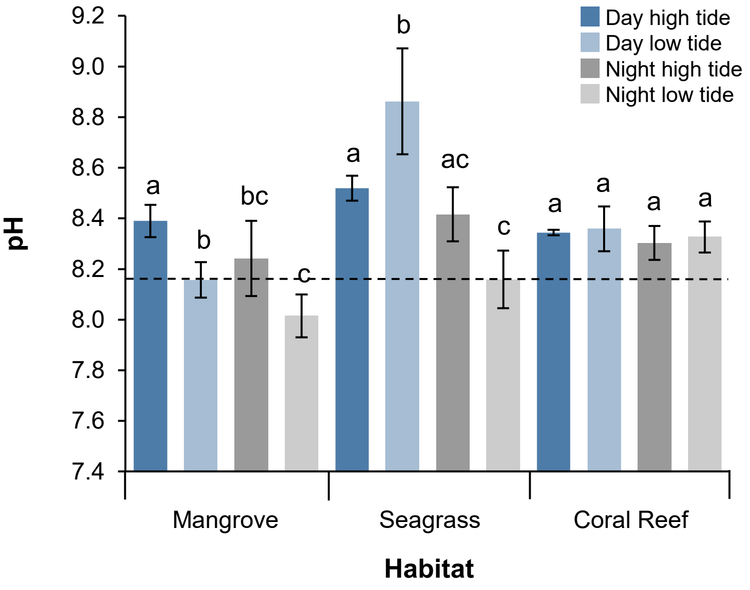

Figure 3. Tidal variability in mean pH levels in mangrove, seagrass and coral reef habitats. The dotted line shows the mean of pH value of the adjacent open waters. Error bars indicate standard deviations. The letters above the bars indicate significant differences in pH levels between mangrove, seagrass, and coral reef habitats (based on one-way ANOVA tests) at $p \leq 0.05$. N = 4.

Table 1. The mean, standard deviation (SD), minimum and maximum pH values recorded in mangrove, seagrass, and coral reef habitats (n=4).

Habitat	Tidal cycle	Mean	SD	Minimum	Maximum
Mangroves	Day high tide	8.34	0.06	8.34	8.45
	Day low tide	8.16	0.07	8.06	8.20
	Night high tide	8.24	0.15	8.11	8.37
	Night low tide	8.01	0.08	7.91	8.08
Seagrasses	Day high tide	8.52	0.05	8.45	8.55
	Day low tide	8.86	0.21	8.68	9.06
	Night high tide	8.42	0.11	8.33	8.55
	Night low tide	8.16	0.11	8.03	8.25
Coral reefs	Day high tide	8.34	0.01	8.33	8.35
	Day low tide	8.36	0.09	8.25	8.47
	Night high tide	8.30	0.06	8.24	8.36
	Night low tide	8.33	0.06	8.24	8.37

mangrove, and coral reef habitats were higher during the day than at night, and were lower than that of adjacent open water in the mangrove habitats at night by 0.02 pH units (Fig. 4).

Day-night variability in water temperature, dissolved oxygen and salinity

The mean temperature in mangrove habitats did not vary significantly between day-night cycles (F=2.82, p>0.05) or tides (F=0.96, p>0.05), with both the highest (35.79 °C) and the lowest (25.29 °C) values recorded during the daytime low spring tide (Table 2). Similarly, the mean salinity in mangrove habitats did not vary significantly between day and night (F=0.37, p<0.05) or between tides (F=169, p>0.05), with both the highest (39.70‰) and the lowest (17.10‰) values recorded during low spring tide during the day. The mean dissolved oxygen value in the mangrove habitats, on the other hand, varied significantly between tides (F=14.58, p<0.05), but not between day and night (F=1.25, p>0.05), with the highest value (14.65 ml/L) recorded during high spring tide during the day, and lowest value (7.66 ml/L) recorded during low spring tide during the day (Table 2).

The mean temperature in seagrass ecosystems fluctuated significantly between tides (F=4.48, p<0.05) and between day and night (F=15.50, p<0.05). The highest value (35.08 °C) was recorded during daytime low spring tide, and the lowest (26.33 °C) during

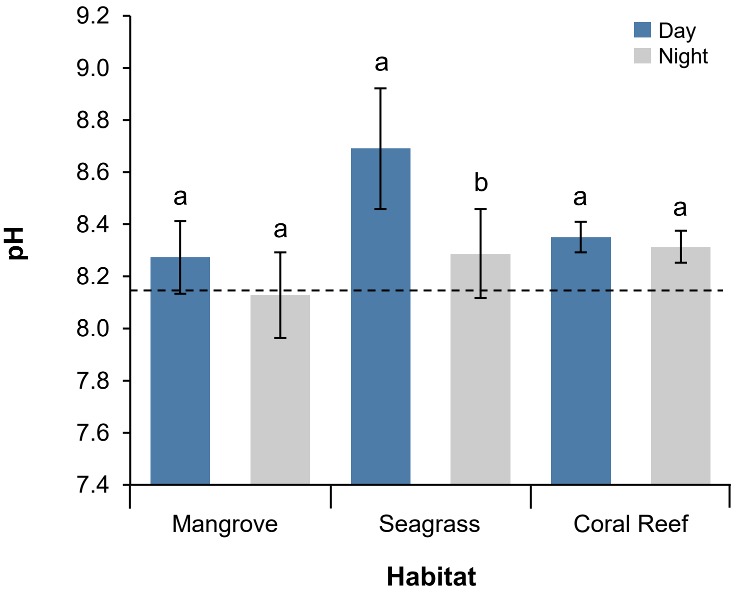

Figure 4. Day-night variability in mean pH in the mangrove, coral reef and seagrass habitats. The dotted line shows the mean of pH of the adjacent open waters. Error bars indicate standard deviations. The letters above the bars indicate significant differences in pH levels between mangrove, seagrass, and coral reef habitats (based on one-way ANOVA tests) at *p*≤0.05. N = 8.

Table 2. The mean, standard deviation (SD), minimum, and maximum values of water temperature (°C), salinity (‰) and dissolved oxygen recorded (ml/L) in mangrove, seagrass and coral reef habitats (n=4).

Habitat	Variable	Tidal cycle	Mean	SD	Minimum	Maximum
Mangrove	Temperature	Day high tide	28.90	1.50	27.01	30.55
		Day low tide	32.65	4.95	25.29	35.79
		Night high tide	28.84	1.04	27.45	29.66
		Night low tide	27.90	0.61	27.33	28.76
	Salinity	Day high tide	37.75	0.50	37.00	38.00
		Day low tide	32.72	10.6	17.10	39.70
		Night high tide	37.75	0.50	37.00	38.00
		Night low tide	35.92	1.87	34.30	38.00
	Dissolved oxygen	Day high tide	14.23	0.56	13.56	14.65
		Day low tide	9.86	1.98	7.66	11.54
		Night high tide	14.19	0.48	13.65	14.61
		Night low tide	11.76	2.79	9.31	14.64
Seagrass	Temperature	Day high tide	29.11	0.62	28.65	30.02
		Day low tide	34.14	1.13	32.73	35.08
		Night high tide	28.45	0.74	27.64	29.38
		Night low tide	27.45	0.85	26.33	28.33
	Salinity	Day high tide	37.75	0.50	37.00	38.00
		Day low tide	38.57	1.29	37.37	40.00
		Night high tide	37.75	0.96	37.00	39.00
		Night low tide	37.00	1.15	36.00	38.00
	Dissolved oxygen	Day high tide	14.02	0.50	13.68	14.69
		Day low tide	15.29	0.79	14.49	15.99
		Night high tide	14.13	0.59	13.54	14.72
		Night low tide	11.45	0.58	10.91	12.02
Coral reef	Temperature	Day high tide	29.12	0.62	28.65	30.02
		Day low tide	28.62	1.19	27.47	29.69
		Night high tide	28.43	0.62	27.72	29.11
		Night low tide	28.73	0.49	28.16	29.36
	Salinity	Day high tide	37.75	0.50	37.00	38.00
		Day low tide	38.25	0.96	37.00	39.00
		Night high tide	37.75	0.50	37.00	38.00
		Night low tide	37.75	0.50	37.00	38.00
	Dissolved oxygen	Day high tide	14.11	0.59	13.50	14.72
		Day low tide	14.55	0.28	14.12	14.72
		Night high tide	14.06	0.56	13.58	14.59
		Night low tide	13.99	0.56	13.46	14.52

night-time low spring tide. Salinity within seagrass beds, on the other hand, did not vary significantly with tides or between day-night cycles ($p>0.05$). The highest salinity value (40.00‰) was, however, recorded during low spring tide during the day while the lowest value (36.00‰) was recorded during low spring tide at night. The mean dissolved oxygen in seagrass ecosystems varied significantly between day-night samplings ($F=10.55$, $p<0.05$), but not with tides ($F=1.76$, $p>0.05$), with the highest value (15.99 ml/L) recorded during daytime low spring tide and the lowest value (10.91 ml/L) reported during low spring tide at night (Table 2).

The mean temperature, salinity and dissolved oxygen in the coral reef habitats did not vary significantly between tides and day-night cycles ($p>0.05$). The highest temperature (30.02 °C) was recorded during daytime high spring tide and the lowest (27.47 °C) during daytime low spring tide. The highest salinity (39.00‰) was recorded during low spring tide in the daytime, while the lowest value (37.00‰) stayed constant independent of time of day or tide status. The highest dissolved oxygen value (14.72 ml/L) was recorded during high and low spring tides during the day, and lowest value (13.46 ml/L) recorded during low spring tide at night (Table 2).

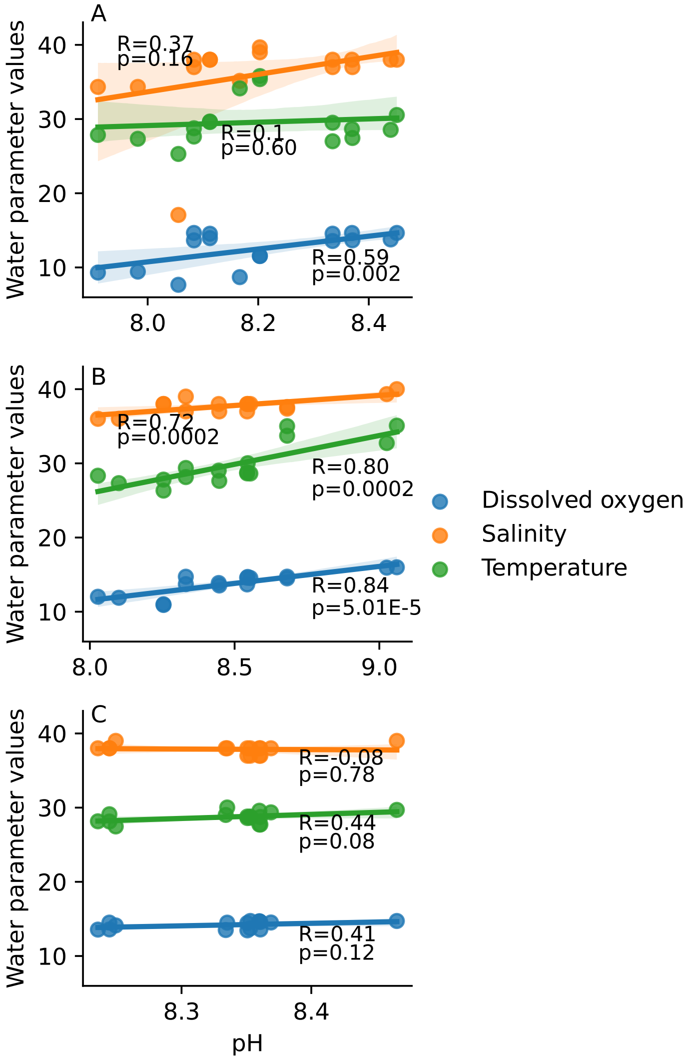

Figure 5. Relationship between pH and temperature, salinity and dissolved oxygen in A) mangrove, B) seagrass and C) coral reef habitats.

Correlation between pH and other environmental variables

pH in mangrove habitats associated only modestly and positively with dissolved oxygen (r=0.59), whereas pH in seagrass habitats significantly and positively linked with variations in temperature (r=0.80), dissolved oxygen (r=0.84), and salinity (r=0.72). pH in the coral reef habitats was found to be weakly and negatively related to salinity (r=-0.08) but moderately and positively related to temperature (r=0.44) and dissolved oxygen (r=0.41).

Discussion

This study found that the tidal cycle and time of day (day or night) controls pH levels in mangrove, seagrass, and coral reef habitats of Tanzania and the WIO. As a result, mangrove, seagrass, and coral reef habitats experience large pH fluctuations, indicating that resident marine species are subject to wide pH ranges, which should be considered in future experimental studies evaluating the effects of OA on marine species. Water with the highest pH from seagrass habitats is transported to nearby mangroves during incoming daytime high tides as well as to nearby coral reefs during outgoing daytime low tides, raising their pH levels and helping to mitigate OA on these habitats. These results will guide management strategies to safeguard healthy seagrass meadows that maintain high primary productivity and act as refugia against OA.

Seagrass habitats had the greatest mean pH levels, which, when compared to nearby mangrove and coral reef habitats, show that seagrass productivity (the balance between photosynthesis and respiration) affects the pH of its surrounding waters (Hendriks *et al.*, 2014; Pacella *et al.*, 2018). The observed differences in pH levels and dissolved oxygen (DO) between day and night also suggested that the effect of seagrasses was related to their productivity (Pacella *et al.*, 2018). Daytime photosynthesis and nighttime community respiration have different effects on pH levels in coastal habitats (Semesi *et al.*, 2009b). Seagrasses remove carbon from the water column during photosynthesis (Borum et al., 2007; Brodersen et al., 2018; Larkum et al., 2007), lowering the partial pressure of CO_2 and thus the amount of dissolved inorganic carbon in the water column. As a result, the pH of the water column rises (Brodersen *et al.*, 2018; Olsen *et al.*, 2018). During the nighttime, however, seagrass photosynthesis is inactive, and community respiration is high, resulting in an increased partial pressure of CO_2 and, thus, dissolved inorganic carbon in the water column (Brodersen *et al.*, 2018; Olsen *et al.*, 2018; Pedersen *et al.*, 2016). As a result, the pH of the water column decreases (Hofmann *et al.*, 2011). These could explain why the highest and lowest pH values in seagrass habitats were observed during low spring tides in the day and night, respectively, resulting in the observed highest pH range. In light of these findings, it is important to take into account the day-night pH variations in coastal habitats when designing new experimental studies aimed at better understanding the effects of OA on resident marine species. Despite the fact that this study focused on pH, future studies should include assessments of total alkalinity, partial pressure of CO_2, and dissolved inorganic carbon as indicators of OA to better understand the changing seawater carbonate chemistry in the WIO.

Lowest pH levels in mangrove habitats compared to seagrass and coral reef habitats have been linked to river inflow and underground discharge (Pauline *et al.*, 2011). Because Chwaka and Mnazi Bays are non-estuarine, the lowest pH levels observed during low spring tides were primarily caused by groundwater discharge. During incoming daytime high tides, water with the highest pH from nearby seagrass habitats is transported to mangrove habitats, helping to raise the pH of water in these habitats. Similarly, during outgoing day low tides, seagrass habitats raise the pH of water coming from mangrove habitats, preventing the water with the lower pH from reaching coral reefs. Low pH water inhibits coral calcification processes and, in extreme conditions, may cause reef dissolution (Kroeker *et al.*, 2013). The ability of seagrass habitats to mitigate the effects of OA on nearby mangrove and coral reef habitats is dependent on their health and has been shown to decline with disturbances (Carstensen and Duarte, 2019).

Climate change-related stressors such as freshwater flooding, anoxia, and ocean warming are threatening seagrass survival (García *et al.*, 2013; George, 2019; Rasmusson *et al.*, 2020). Positive correlations between pH and salinity, dissolved oxygen, and temperature were found in this study, and these relationships are discussed separately. A positive correlation between pH and O_2 shows the influence of primary productivity and community respiration on pH. Healthy seagrass habitats have been shown to support high primary productivity, producing water with high pH and O_2 levels that will be transported to adjacent coastal habitats (Hendriks *et al.*, 2014; Semesi *et al.*, 2009a; Semesi *et al.*, 2009b; Unsworth *et al.*, 2012). On the other hand, degraded habitats with low primary productivity, have been shown to compromise the ability of seagrass habitats to mitigate OA (Van Dam *et al.*, 2021). Eutrophication-induced hypoxia has become a major threat to seagrass survival because it reduces plant primary productivity, reducing the ability of seagrass habitats to mitigate the effects of OA in coastal areas (Che *et al.*, 2022). Increased water temperatures have been linked to increased primary productivity of tropical seagrasses, and, as a result, rising pH in their water column during the day (George *et al.*, 2018; George *et al.*, 2020). On the other hand, temperatures over optimal ranges of tropical seagrasses can impair primary productivity, and, consequently, lower the pH of the water column (Carstensen and Duarte, 2019). Increased flood occurrences in coastal areas are predicted to lower pH in mangrove, nearby seagrass, and coral reef habitats, increasing the effects of OA on these ecosystems (Orr, 2011). Therefore, these findings suggest that minimizing disturbances in coastal habitats will improve the capacity of seagrass habitats to absorb CO_2 from the water column and, in turn, increase their capacity to elevate the pH of surrounding mangrove and coral reef habitats.

Similar studies are generally lacking in the WIO region. However, a study by Camp *et al.* (2016) in three locations in the Atlantic, Indian, and Pacific Oceans found similar trends, with seagrass habitats consistently having a higher mean pH (8.15 ± 0.01) than the nearby outer-reef habitats (8.12 ± 0.03), and mangrove habitats having a lower mean pH (8.04 ± 0.01). Camp *et al.* (2016) reported day-night pH variations that were similar to the current findings, with high pH during the day time associated with CO_2 uptake during photosynthesis and low pH at night associated with CO_2 release during respiration in the absence of photosynthesis. This study concentrated on non-estuarine bays, therefore it is suggested that future research should concentrate on estuarine coastal habitats in order to obtain a complete picture of pH dynamics in WIO coastal habitats.

Conclusions

The tidal cycle and time of day control pH levels in mangrove, seagrass, and coral reef habitats of the WIO, resulting in large pH fluctuations in these coastal habitats. As a result, resident marine species in mangrove, seagrass, and coral reef habitats face wide pH ranges, which should be considered in future manipulative studies evaluating the effects of OA on marine species from coastal habitats. Water with the highest pH from seagrass habitats is transported to nearby mangroves during incoming daytime high tides and to nearby coral reefs during outgoing daytime low tides, raising their pH levels and helping to mitigate OA on these habitats. To better understand the changing seawater carbonate chemistry in costal habitats of the WIO, future studies should include assessments of total alkalinity, pCO_2, and dissolved inorganic carbon as indicators of OA not covered in this study.

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

k. Tables and Figures: each table and figure should be numbered consecutively, accompanied by a complete caption, and must be cited in the text. Please follow the **Guidelines for illustrations** for details.

l. Supplementary material: in case it is found relevant, authors may submit appendices with relevant information of major interest for the interpretation of the manuscript results. This is not applicable for the raw data of normal research. The editors will decide its eventual inclusion as appendices.

12. A complete **Review Article** manuscript must include the following: title page, abstract, keywords, introduction, main body text (the central sections vary with specific divisions according to the theme), acknowledgements, references, tables and figures (with figure legends) in that order.
13. A complete **Short Communication** manuscript must include the same structure as an Original Article in a shorter format.

Failure to follow any point of these guideline may delay or compromise the editorial process. Unless there are communication problems, all communications and exchange of documents shall be made strictly via the AJOL editorial interface. Authors must comply with timing for processing manuscripts, either requested revisions or proof check, or otherwise inform the editors of any delays.

Guidelines for illustrations

Figures

To maintain a graphic consistency throughout all articles and issues of the journal, we advise the use of these guidelines.

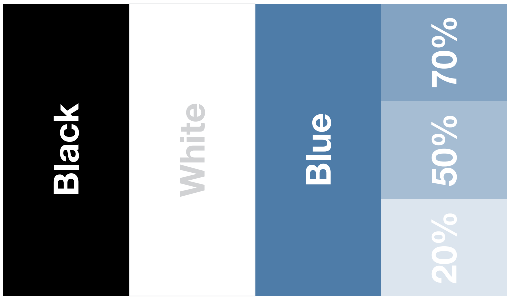
The original figures files should be sent separately from the text file to ensure the good quality of the figure reproduction.

Color palette

To maintain visual harmony in the illustrations, we recommend using mainly a monochromatic palette with the introduction of the Western Indian Ocean Journal's identity blue color.

When necessary to allow greater contrast between patterns and colors, the use of the secondary palette is considered.

main



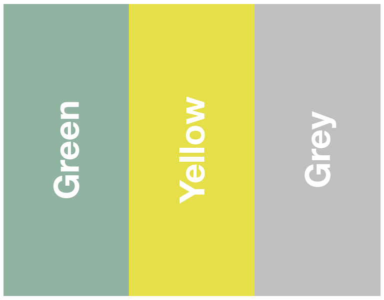
R 0
G 0
B 0

R 255
G 255
B 255

R 77
G 124
B 168

Shades of blue

secondary



R 144
G 179
B 162

R 229
G 223
B 73

R 191
G 191
B 191

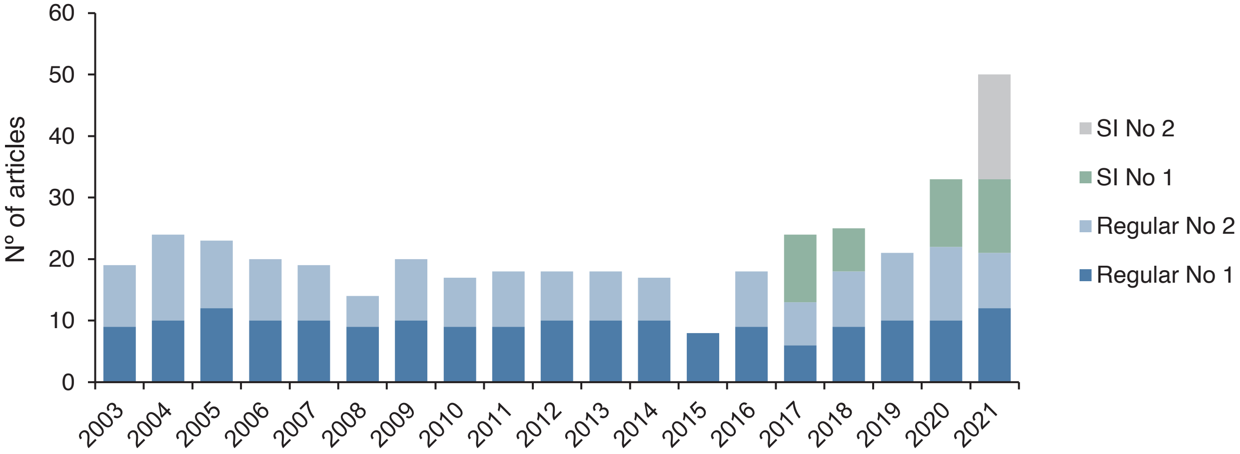
Graphs

Graphs should be clear and appealing figures.

The lettering should be of a size readable after reduction for the final layout.

We recommend using the Helvetica font in its various styles (Regular, Medium, Italic, Bold) for the axes and captions of graphs and other figures, as it is a classic, simple and easy reading font.

Preferably exported to pdf files to maintain viewing quality. They must be also sent separately in an editable format in the program in which they were made, for possible edits if necessary.



Example of formatted graph according to WIOJMS graphical guidelines

Published articles per year on WIOJMS.

Photographs

Photographs should have good quality/resolution to maximise contrast and detail during printing (15cm longest edge @300 dpi), be focused and well composed.

Example of low resolution

not enough for printing

Example of high resolution

good for printing

Maps

Maps must have good resolution for efficient viewing and good reading

Example of low resolution

not enough for printing

Example of high resolution

good for printing

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