

Mangrove dieback due to massive sedimentation and its impact on associated biodiversity

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Abstract

Emerging scientific evidence strongly suggests that the 1997/8 and 2000 rains in the Western Indian Ocean (WIO) region previously attributed to El-Niño were mainly caused by the Indian Ocean Dipole (IOD), a phenomenon whose frequency and intensity have increased over the years due to climate change. The abnormally high rainfall experienced during this time combined with poor land use management, caused intense sedimentation due to erosion of terrigenous sediments, leading to extensive mangrove die-back in several areas in the WIO region. The extent and impact of this die-back on mangrove-associated biodiversity has not been assessed to date. The objective of this study was to assess the impact of the die-back on mangrove associated biodiversity at Mwache Creek, Mombasa, Kenya, where about 200 ha of mangroves were decimated. Biodiversity in impacted sites was compared to reference sites (natural forests) in order to assess the impact of IOD-related massive sedimentation to mangrove-associated biodiversity namely crabs and molluscs. Transects (sea-landward transect) were laid 10 m apart to ensure independence of sampling units in both impacted and natural sites. Along each transect, 5 m² quadrats were made at 100 m intervals. Within the 5 m² quadrats, one 2 m × 2 m sub-quadrat was randomly placed for actual sampling where relevant physico-chemical variables were measured and mangrove biodiversity determined as an indicator of ecosystem change. Environmental factors showed a strong variability among transects whereas faunal assemblages significantly differed among the treatments (impacted and non-impacted). Salinity, temperature and total dissolved oxygen (TDSO) were the environmental factors that contributed to the changes in biotic composition among the treatments, whereas *Uca inversa*, *Uca annulipes*, *Cerithidea decollata* and *Perisesarma guttatum* contributed more to the differences in faunal composition between treatments. The degradation seems to have significantly reduced crab and mollusc species richness and densities and led to loss of other mangrove-associated faunal species in the impacted site. These results emphasize the effects of climate change-related impacts on mangrove-associated biodiversity and by implication, the ecosystem functions they support.

Key words: mangrove, sedimentation, fauna, molluscs, crabs, biotic

Introduction

Mangroves are important ecosystems, providing economic, cultural and ecological benefits where they occur (Bosire *et al.*, 2016; Carugati *et al.*, 2018; Rodriguez *et al.*, 2019). These forests provide a habitat to a unique and diverse set of associated fauna (Farnsworth and Ellison, 1996; Bosire *et al.*, 2008; Kairo *et al.*, 2008; Jenoh *et al.*, 2019; Barbanera *et al.*, 2022), with crabs and molluscs being the most abundant macrobenthic groups (Vanini *et al.*, 2006; Cannicci *et al.*, 2008). Crabs and molluscs play various important ecological roles in the mangrove ecosystem by influencing vegetation structure through selective predation of seedlings (Bosire *et al.*, 2005; Dahdouh-Guebas *et al.*, 1998; 2011), nutrient cycling (Lee, 1998; Cannicci *et al.*, 2008; Nagelkerken *et al.*, 2008; 2009; Carugati *et al.*, 2018), aerating and altering the mangrove sediments by the numerous burrows they dig (Bartolini *et al.*, 2011; Dahdouh-Guebas *et al.*, 2011) and reducing the pore water salinity by allowing flushing of the sediments via their burrows (Ridd, 1996). Despite the importance of mangroves, they have one of the highest rates of degradation (Mukherjee *et al.*, 2014; Bosire *et al.*, 2016; Brown *et al.*, 2020) due to varied causes (Farnsworth and Ellison, 1997; Alongi, 2002; Mohamed *et al.*, 2008; Jenoh *et al.*, 2019). Global environmental changes ranging from sea level rise, flooding, aridity and elevated salinities have added to the list of threats to the integrity of mangrove ecosystems (Kitheka *et al.*, 2002; Hansen *et al.*, 2003; McLeod, 2006; Bosire *et al.*, 2006; Case, 2006; IPCC, 2007; Mclanahan *et al.*, 1988; 2008; Di Nitto *et al.*, 2008; Huxham *et al.*, 2010).

In 1997/8 and 2000 the abnormally high rainfall experienced in the Western Indian Ocean (WIO) region, previously attributed to El-Niño (Kitheka *et al.*, 2002; Bosire *et al.*, 2016) and more later linked to Indian Ocean Dipole (IOD) (Saji *et al.*, 1999; Overpeck and Cole, 2007; Nakamura *et al.*, 2009; Bosire *et al.*, 2016), a phenomenon whose frequency and intensity has increased over the years due to climate change. The IOD causes either prolonged droughts or intense rainfall (during the short rain season), with diverse attendant consequences e.g. flooding,

sedimentation and crop failure among others (Bosire *et al.*, 2006; Overpeck and Cole, 2007; Hanley *et al.*, 2020; Krauss and Osland, 2020), with the potential to disrupt livelihoods of millions of dependent communities. In 1997/8 and 2000, the IOD-instigated heavy rains coupled with poor land use management systems upstream caused massive sedimentation due to erosion of terrigenous sediments, leading to extensive mangrove die-back in several areas in the WIO region. For instance, in Kenya, the peri-urban mangroves of Mwache Creek in Mombasa were severely affected, losing close to 200 ha of forest cover (Kitheka *et al.*, 2002; Bosire *et al.*, 2006). Other affected mangroves in Kenya were those in Tudor creek, Tana River and Lamu, but the extent of the die-back in these sites has not been determined.

While the response of coral reefs to these IOD events has been well documented in the region (Saji *et al.*, 1999; Wilkinson *et al.*, 1999; 2000; Obura, 2005; Overpeck and Cole, 2007), scanty information is available on the response of mangrove-associated biodiversity to the extensive sedimentation and the subsequent mangrove dieback. Mangrove-associated biodiversity has an intricate association with the mangroves and thus will indirectly suffer the impacts of mangrove ecosystem degradation, depending on their differential abilities to adapt to the resultant environmental changes (Hansen *et al.*, 2003; Brown *et al.*, 2020), which can greatly alter faunal composition, density and assemblages (Lovett *et al.*, 2005; Brown *et al.*, 2020). In some cases, this will cause reduction of biodiversity or even localized extinction (Erasmus *et al.*, 2002; Malcome *et al.*, 2002; Brown *et al.*, 2020; Barbanera *et al.*, 2022). Extensive mangrove dieback due to ecological degradation like extensive sedimentation is likely to affect species composition, constrict species range due to loss of habitats and eventually affect the population size of a species (Warren and Niering, 1993; Mumby *et al.*, 2004; Case, 2006; Brown *et al.*, 2020). The objective of this study was to assess the response of mangrove-associated biodiversity to the dieback following the 1997/8 and 2000 massive sedimentation.

Materials and methods

Description of study site

This study was conducted at Mwache Creek (Fig. 1), located in the upper Port Reitz area (Kitheka, 2003). Mwache Creek ($4^{\circ}3.01' S$, $39.06^{\circ}38.06'E$) is located 20 km Northwest of Mombasa city in Mombasa County, Kenya. The total area of the wetland is approximately 17 km² with about 70% of the surface area covered by mangroves. The creek has both basin and riverine mangroves and a distinct mangrove-fringed channel in the lower sections. The mangrove species found in Mwache Creek are: *Avicennia marina* (Forsk.) Vierh, *Rhizophora mucronata* (Lamk), *Ceriops tagal* (Perr.) C.B. Robinson, and *Sonneratia alba* Sm. (Kitheka, 2002). The creek receives freshwater from Mwache River, which is seasonal and thus there is usually no flow during the dry season, mainly between December and March, and July and September. The rate of sediment production within Mwache River basin reaches a maximum of 3,000 tons yr⁻¹ due to poor land-use activities e.g. overgrazing, shifting cultivation, cultivation on steep slopes without the application of soil conservation measures, high rainfall intensity during the rainy season and steep land gradient, among others (Kitheka, 2002).

These high erosion rates and sedimentation led to severe mangrove dieback due to smothering of mangrove roots as a result of excessive input of terrigenous sediments especially at the landward zone (Kitheka, 2002) during the IOD-related flooding of Mwache River. The most extensively affected species was *R. mucronata*, whereas *A. marina* was relatively less affected. The area affected is about 17% of the total mangrove forest acreage within the creek (Bosire, 2009).

Experimental design

The study was conducted during two spring tides of July and August 2008. To assess the impact of the mangrove dieback on associated biodiversity, two degraded sites (S1D and S2D) within Mwache Creek were used as the experimental units for this study. Each degraded area was sandwiched between natural forests (S1F1, S1F2 and S2F) which were either not impacted or relatively less impacted during the IOD event and were thus used as reference sites. The first degraded site had an additional reference forest (S1F2) at the landward side of the impacted site. Two transects perpendicular to the shoreline were made for both treatments (impacted and non-impacted) at the first site. Along each transect, 8 quadrats (5 m² each) per transect were made after every 100 m. whereas three transects were laid at the additional reference

forest of the first site. However, due to small size of the additional reference forest of the first degraded site (S1F2), only two quadrats per transect were made at this additional reference forest. In the second impacted site, the reference plot was wider than longer,

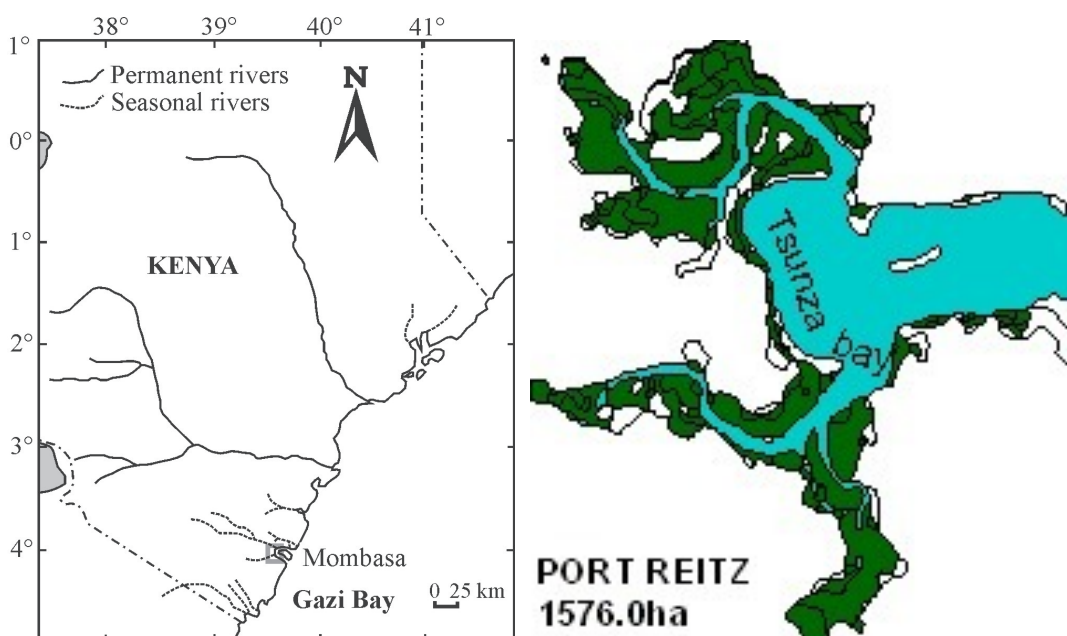


Figure 1. A map of the study area showing location of the two study sites. Each site had two sampling areas i.e. the reference forest and the degraded forest (Source: Authors).

hence only four quadrats per transect could fit, but three parallel transects were laid. Transects were laid 10 m apart to ensure independence of sampling units. Along each transect, 5 m² quadrats were made after every 100 m. Within the 5 m² quadrats, one 2 m × 2 m sub-quadrat was randomly placed for actual sampling.

Physico-chemical variables

In each sub-quadrat set-up as described above, a total of five sediment cores were randomly taken using a hand corer of diameter 6.4 cm to a depth of 15 cm during low spring tide. The samples were then sub sectioned (2 cm sections), immediately stored in cool boxes with ice and transported to the laboratory where they were frozen at -20 °C for various analyses. Three sediment cores were used for nutrients (NO₂⁻, NO₃⁻, NH₄⁺, and PO₄³⁻) and organic matter analysis, whereas the remaining two cores were used for grain size analysis. From one of the holes made by the removal of the sediment cores, interstitial salinity, temperature, dissolved oxygen and conductivity were determined using a universal multimeter (Hanna instruments). Before any analysis, corresponding segments from each core were pooled together and homogenized.

Pore water was extracted from 10 g of sediments in 40 mls 1M KCl, then flashed with white nitrogen gas (2 minutes) and mechanically shaken for 2 hours, to ensure adequate extraction. Each sample was then centrifuged using Van der Heyden, Heraeus Sepatech, Megafuge 1.0 R at a speed of 2000 × g.r.m. for 10 minutes. The supernatants were decanted then adequate amounts were put in volumetric flasks and diluted with distilled water. The resultant solutions were used for the determination of nutrients. Ammonium (NH₄⁺) and phosphate (PO₄³⁻) were determined according to methods described by Parsons *et al.* (1984), whereas nitrite (NO₂⁻) and nitrate (NO₃⁻) according to APHA (1995).

Sediment granulometry and organic content

Soil texture was assessed by sieving 100 g sub-samples of dry sediment through eight different sieves corresponding to as many grain size classes (>0.38 μm, >0.63 μm, >125 μm, >250 μm, >500 μm, >1 mm, >1.60 mm and >2.00 mm). The mass of the soil fractions in each class was then weighed and expressed as percentage of the original mass.

The organic content of the sediment was measured by baking 10 g of sediment for three days in a muffle furnace at 350°C. The organic fraction was estimated by calculating the weight lost of the sediment dry weight (24h, 80°C) and standardized as percentage.

Faunal colonization

For every 2 m × 2 m sub-quadrat above, all crab species were identified and counted using a binocular to assess the ratios among species and the sex ratios within the species (Skov *et al.*, 2002). In order to avoid underestimating those species not active during the direct binocular counts, three sub-quadrats (0.5 m × 0.5 m) were randomly placed in the 2 m × 2 m quadrat after the binocular counts in order to count the crab burrows (Skov *et al.*, 2002). Dichotomic identification keys by Cannicci *et al.* (1997) were used for species identification. Molluscan species were identified and counted within the 2 m × 2 m quadrat using keys in Richmond (1997). Molluscs species on trees falling within the sub-quadrat up to 1 m height from the ground were also identified and counted.

Statistical analyses

Multivariate methods were used to analyze changes in both abiotic and biotic assemblages in the treatments. Abiotic similarity matrix was computed using Euclidean distance on normalized data, while biotic similarity matrices were computed using Bray-Curtis distance on square root transformed data. A Principal Component Analysis (PCA) and Non-metric Multidimensional Scaling (NMDS) (Clarke, 1993; Field *et al.*, 1982) were used to visualize multivariate patterns on abiotic and biotic data respectively.

Two distinct distance-based permutational multivariate analysis of variance (PERMANOVA) designs (Anderson, 2005) were employed to test (at a significance level of $p = 0.05$), based on the null hypotheses of no differences in environmental factors and in faunal assemblages among treatments (impacted vs. primitively forested sites) and across sampling sites and treatments. Further, DistLM routine (using the "best fit" and "BIC" models) was employed to identify the abiotic factors able to explain the changes in biotic composition, whereas the Canonical Analysis of Principal coordinates (CAP) (Anderson and Robinson, 2003; Anderson and Willis, 2003) was used as a constrained ordination procedure to confirm the consistency in the variation in the biotic factors among treatments. In addition, a distance-based redundancy analysis (dbRDA) was employed for partial display on both the abiotic factors able to explain the changes in biotic composition. Multivariate analyses were performed using the PRIMER v.6.1 (Clarke and Gorley, 2006) and the PERMANOVA + for PRIMER routines v. 1.0 (Anderson *et al.*, 2008).

Results

Environmental factors

The environmental factors showed no defined trends between forested and impacted areas across the 2 sites as depicted by the PCA plot (Fig. 2). A 3-way PERMANOVA test with factors: treatment (orthogonal and fixed), site (orthogonal and fixed) and transect (nested in site and random), showed a strong variability among transects (Table 1). A DistLM analysis was used to search from all

sampled parameters the variables that contributed more to the changes in biotic composition among treatment. This test isolated salinity followed by temperature and TDSO in order of importance (Fig. 3).

Biotic factors

There were differences in faunal composition between treatments across the 2 study sites (Fig. 4). A 3-way PERMANOVA test with factors: treatment (orthogonal and fixed), site (orthogonal and fixed) and transect (nested in site and random); indicated significant differences in the biotic composition between treatments regardless of the sites and transects (Table 2). Canonical Analysis of Principal coordinates (CAP) analysis showed a significant effect between the treatments (Table 3). The test (CAP Leave-one-out test) was able to reallocate the samples to their original group with 94% and 100% of success, attesting to the strong difference in faunal composition between the treatments across the 2 sites (Table 3). A dbRDA test showed that *Uca inversa*

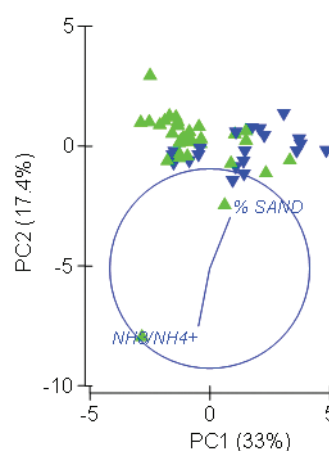


Figure 2. PCA ordination for environmental factors showing no visible differences between treatments regardless of sampling sites. Green symbols represent the forested sites, whereas blue symbols represent degraded sites.

Table 1. Results of the 3-way PERMANOVA testing the environmental factors between the treatments across the 2 study sites with transects (nested in site and random).

Source	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)
Site	1	32.809	32.809	2.1936	0.2005	29	0.0651
treat	1	44.57	44.57	2.2988	0.2326	8883	0.0873
TRANSECT(Site)	3	51.978	17.326	2.002	0.0356	9915	0.0087
Sitextreat	1	10.575	10.575	0.54543	0.6521	8935	0.7873
treatxTRANSECT(Site)	2	39.13	19.565	2.2607	0.0039	9910	0.0091
Res	45	389.45	8.6545				
Total	53	583					

(Hoffmann), *Cerithidea decollata* (Linnaeus), *Uca annulipes* (H. Milne Edwards) and *Perisesarma guttatum* (A. Milne Edwards) contributed more to the difference in faunal composition with *U. inversa* being typical of the impacted areas and *C. decollata*, *U. annulipes* and *P. guttatum* being more common in the forested areas (Fig.

Table 2. Results of the 3-way PERMANOVA testing the differences in the biotic composition between treatments, sites and transects.

Source	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)
Site	1	1675.4	1675.4	1.2692	0.3067	180	0.3025
treat	1	31548	31548	24.173	0.0186	9504	0.0008
TRANSECT(Site)	4	5545.7	1386.4	1.1677	0.2865	9918	0.3055
Sitextreat	1	764.32	764.32	0.58564	0.675	9506	0.696
treatxTRANSECT (Site)	2	2620	1310	1.1033	0.3629	9945	0.3612
Res	44	52241	1187.3				
Total	53	1.0094E5					

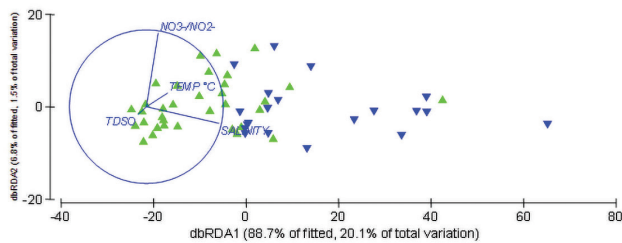


Figure 3. dbRDA showing the variation in the abiotic factors salinity, temperature and TDSO (in order of importance) as responsible for the changes in the biotic composition across the study sites.

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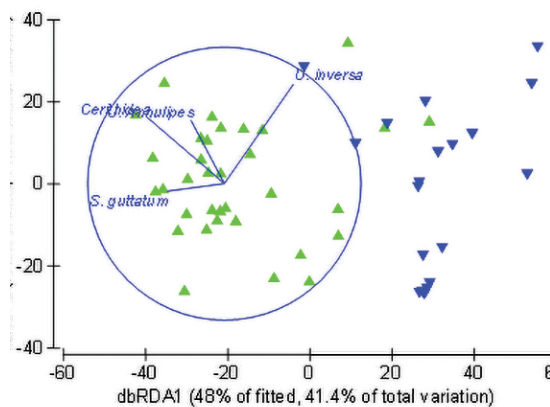


Figure 5. dbRDA plot of faunal assemblage showing that *U. inversa*, *C. decollata*, *U. annulipes* and *P. guttatum* contributed to the difference in faunal composition within the treatments. Green coloured triangles represent faunal samples drawn from reference sites whereas the blue triangles represent those from degraded sites.

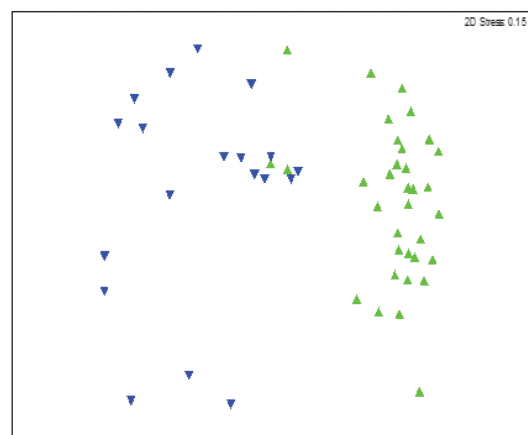


Figure 4. nMDS ordination of faunal assemblage showing visible differences among treatments regardless of the study sites. Green coloured triangles represent faunal samples drawn from reference sites whereas the blue triangles represent those from degraded sites.

Table 3. Results of a CAP Leave-one-out Allocation of observations to groups showing the consistency of the differences in faunal composition between the treatments across the study sites.

Orig. group	Classified		Total	%correct
	F	D		
F	32	2	34	94.118
D	0	20	20	100

Discussion

There was lack of variation in environmental parameters between the treatments (Table 1), suggesting that disturbance did cut across the entire study area. Previous studies have reported sedimentation levels of up to 3 m in the study sites (Kitheka, 2002) and since our coring depth was 15 cm, it is possible to find no variation in environmental variables between treatments as displayed in the PCA plot (Fig. 2). It may be useful in future to take deeper cores from the sites for both treatments and analyse for variations of selected physico-chemical parameters as a function of depth and treatment. However, for the purpose of this particular study, a 15 cm depth coring is sufficient to provide the information on environmental changes affecting most of the studied fauna since they are mostly epibenthic. Variability among transects depicts disturbance that was not uniform in local micro-areas, which may have led to different microenvironments within the sites. For instance, patchy sedimentation and shading level can affect the interstitial water temperature and salinity level due to evaporation differences in shaded and non shaded areas and even affecting total dissolved oxygen hence leading to great habitat modification thereby creating micro niches for different faunal groups. These factors i.e. salinity, temperature and TDSO could consequently impact the composition and density of mangrove-associated fauna as highlighted by the dbRDA plot (Fig. 3). Other studies on mangroves have found similar results and reported that sedimentation within mangrove habitats had resulted in negative functional and structural effects on benthic communities and was responsible for lower densities and biodiversity of macro-fauna (Ellis *et al.*, 2004; Alfaro, 2010).

Total crab densities recorded in this study (Fig. 6) were lower than those recorded in studies by Icely and Jones (1978); Skov and Hartnoll (2001) and Skov *et al.* (2002), who recorded crab densities ranging from 77–100 m^{-2} for fiddler crabs alone. However, these studies are not fully comparable since their studies were done in pristine mangroves whereas this particular study was conducted in a generally degraded mangrove area. The low crab density (Fig. 6) and significantly differing compo-

sition between the treatments (Table 2), attest to the negative impacts of sedimentation which triggered the mangrove dieback, once again emphasizing the intimate link between mangrove forest structure and species richness (Bosire *et al.*, 2004, 2008). The MDS plot (Fig. 4) indicates a clear difference in fauna composition between the treatments which had different characteristics, thus re-enforcing the role of habitat integrity in biodiversity conservation (Fondo and Marterns, 1998; Ellis *et al.*, 2004; Barbanera *et al.*, 2022). The reference sites supported more biodiversity and had certain species specifically occurring in these sites, probably due to the structural complexity they afford which made them functionally better (in terms of food, shelter, refuge from predators and shade from direct sunlight) than the impacted site (Ruwa, 1988; Fondo and Marterns, 1998; Ewel, *et al.*, 1998; Erasmus *et al.*, 2002; Bosire *et al.*, 2004; Barbanera *et al.*, 2022).

In this study, three molluscs species: *Cerithidea decollata* (Linnaeus), *Crassostrea cucullata* (Born) and *Littoraria Scabra* (Linnaeus) were recorded in both impacted and non-impacted sites. This similarity in composition in the treatments could be due to the mollusc's wide ecological amplitude (Plaziat, 1984) and thus higher tolerance to environmental perturbation (Powell, 1990). The densities of molluscs (Fig. 7) were low in the disturbed forest compared to the reference forest further attesting to the

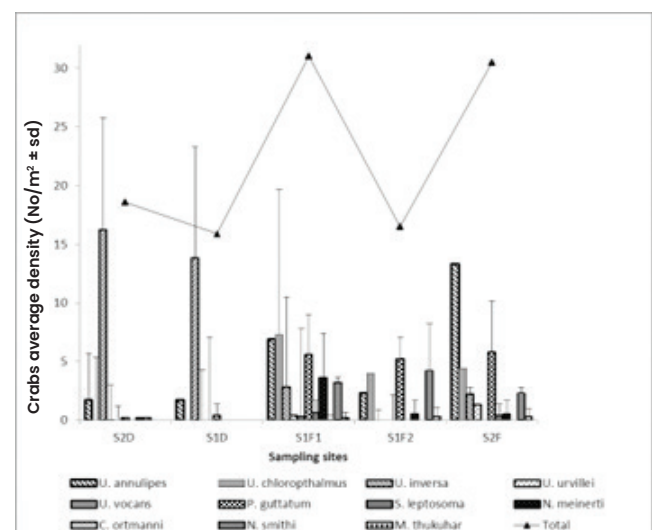


Figure 6. Average crab species density (number m^{-2}) and their corresponding standard deviation in the two study sites. (S1D, S1F1, S1F2, S2D, S2F).

importance of mangrove trees in supporting mangrove associated biodiversity. Even though this study did not record any *Terebralia palustris* (Linnaeus) which is the most important gastropod in terms of biomass in East African mangroves (Cannicci *et al.*, 2009), and is widely distributed in almost all Kenyan mangroves, there were visible traces of *T. palustris* shells on the mangrove floor across the sampling sites (*personal observation*). This suggested that this mollusc species had once existed in this mangrove before the massive sedimentation event that highly changed the sediment to sandy type, thereby leading to habitat modification, which resulted in its extinction in the local area. Studies conducted in the region on the impacts of sewage disposal on mangrove fauna found the gastropod nearly disappeared from impacted sites, suggesting a lower physiological tolerance of this gastropod to altered conditions (Cannicci *et al.*, 2009). The low density of the molluscs, especially *L. scabra* in the degraded area suggests the lack of optimal conditions for full recovery from the impacts of this event to the original densities or it could suggest a lower physiological tolerance of the molluscs to degradation. It is therefore likely that this species (*L. scabra*) may also disappear from the study site if the forest does not re-establish or in case of occurrence of another perturbation to the mangroves. The observed low tolerance to perturbation by some gastropod species suggests

the possibility of using them as bioindicators. Studies have found that extinction of species (at least on a local scale) is a real possibility in case of habitat degradation and mainly due to habitat loss (Thomas *et al.*, 2004). Abrupt sedimentation, like other environmental stressors which could lead to severe habitat degradation, precipitating a pronounced shift in environmental factors, have great potential to cause cascades of species loss including actual species extinctions (Erasmus *et al.*, 2002; Malcolm *et al.*, 2002; Lovett *et al.*, 2005). In South Africa, models done to predict the impacts of climate change predicted local extinction for some species and reduced species diversity of study areas as a result of habitat degradation (Erasmus *et al.*, 2002). Depending on the tolerance level of a species to change in local conditions, a species could either go extinct, reduce in density or even migrate to other areas where migration is possible (Erasmus *et al.*, 2002; Case, 2006).

Compared to the impacted sites, the relatively healthy mangrove forest attracted high species composition and densities of both crabs and molluscs. However, despite lack of shading, hence the high temperature, salinity and general absence of the *A. marina* leaves which is the preferred food source for *C. ortmanni* and *N. meinerti*, these crab species remained in the degraded sites, even though they have the ability to move to the less impacted sites. Their fidelity to the *A.*

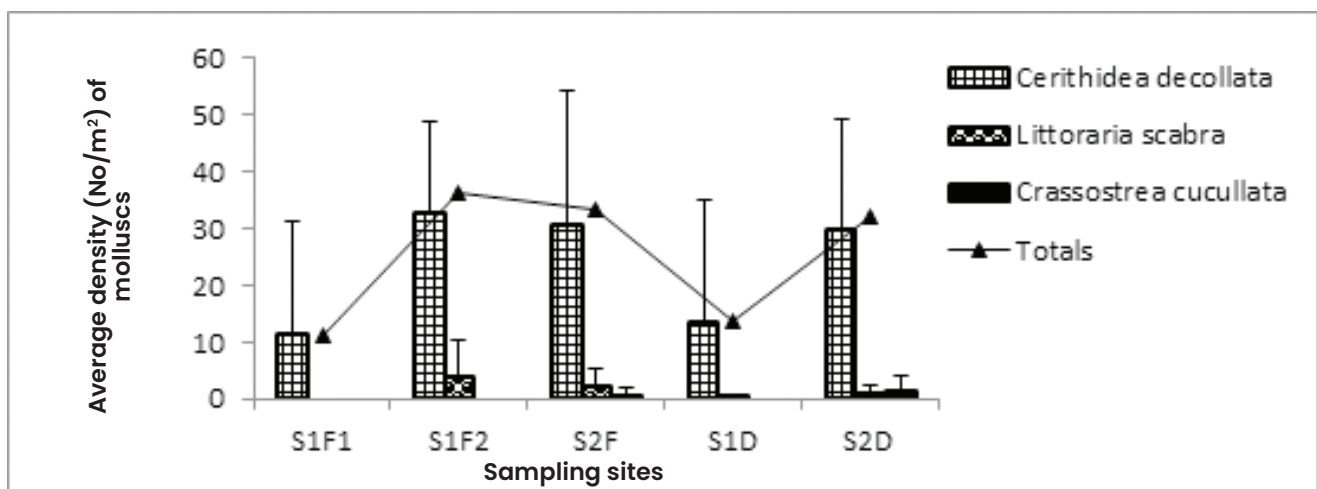


Figure 7. Average density (number/m²) and their corresponding standard deviation of Molluscs species at the different sampling sites.

marina zone despite the degradation could be explained by the fact that these crabs preferred *A. marina* leaves compared to *R. mucronata* leaves as their food (Ólafsson *et al.*, 2002) and the fact that sediments comprised higher percentage (70%) of their diet than leaves (Micheili, 1993; Ólafsson *et al.*, 2002; Skov and Hartnoll, 2002). It could therefore be thought to be energy wise non-profitable for these species to move to the less impacted sites where the leaves have the less desirable high tannin levels and the competition for the mangrove leaves from other crab species is higher. It seems that these crabs do not have much direct reliance to the mangrove tree. These crab species have been reported and observed to make burrows under terrestrial trees far from mangrove species. This suggests that in the case of pronounced mangrove die off (as in this case), the level of impact caused to mangrove associated fauna will depend on the degree of reliance of particular faunal group to the mangrove trees.

Some *Uca spp.* i.e., *U. inversa* and *U. annulipes* and molluscs were found to colonise the impacted site as well as the reference sites. In the reference sites, *Uca spp.* colonised mainly in areas which sedimentation type had changed to be sandy and with open canopy within the reference forest. The sandy sediment condition, combined with the open canopy in these reference forests resembles the conditions of the natural habitat for these *Uca* species i.e. the desert region of mangroves (the outer most side of mangroves which has either no mangrove or very sparse mangrove stands. The sediments are mainly sandy in this region). As for the molluscs, the function of shelter and attachment surface in the impacted sites was provided for by an invasive shrub *Suaeda maritima* (L. Dumort) which was colonizing the impacted site on places previously occupied by mangroves. On the other hand *Uca spp.* seemed not to strictly need the mangrove trees for either shelter or food, hence they were able to establish in both the impacted and reference forest. *U. inversa* which was responsible for the change in faunal composition, especially in the impacted area (Fig. 5) is known to thrive in generally high salinity (Gillikin, 2004) and the desert region of mangroves. This made *U. inver-*

sa to easily establish in the entire study area regardless of treatment, whereas *C. decollata*, *U. annulipes* and *P. guttatum* have been known to establish in forested areas of mangroves (McGuinness 1994; Richmond 1997; Vannini *et al.*, 2006), hence explaining their density in the reference sites, as opposed to the impacted sites. The above situation attests to the ability of degradation to influence either species range expansion or constriction.

Abrupt and massive sedimentation due to extreme weather events and consequently mangrove dieback, may lead to habitat modification which in turn may either constrict or expand faunal range. At Mwache site we observed an expansion of *Uca* species beyond their normal habitat range. A previous study (Fondo and Martens, 1998) observed that the absence of mangroves did not seem to affect all faunal groups, especially infauna. This is in harmony with the finding of this study. However, it is worth noting that compared to a healthy mangrove forest, the density of the crabs and molluscs were very low in this study, suggesting lack of optimal conditions for complete establishment. A study conducted by Bosire *et al.* (2004) also found that the number of sediment-infauna taxa in both the reforested and natural sites of all the mangrove species was similar and higher than in the comparable bare sites. Their results suggested that the reforested sites are supporting more faunal recolonisation, and therefore becoming more akin to the natural mangrove sites in terms of the investigated functional indicators.

At the degraded sites, there was high growth of grass and an opportunistic shrub (*Suaeda maritima*) with S2 having higher cover of this opportunistic shrub. Frequently molluscs; *C. ortmanni* and *N. meinerti* were encountered around the *A. marina* stumps or under the opportunistic shrub. This shrub provided attachment substrate for molluscs and shelter for the *C. ortmanni* and *N. meinerti*. It seems, therefore, that the opportunistic shrubs can maintain some mangrove-associated biodiversity though in much lower densities and diversities (Stevens *et al.*, 2006). However the limited mangrove biodiversity maintained by the invasive

species can act as an important precursor for quick recovery in case conditions change to support greater density and diversity. Therefore the opportunistic shrub acts as a reservoir of future colonization of species, even though such opportunistic shrubs don't provide the goods and services derived from mangroves to the ecosystem and the community. It seems, therefore that climate variability may trigger succession in degraded sites by inferior species without capacity to provide inherent ecosystem goods and services. This has ramifications on livelihoods of dependent communities e.g. in terms of wood provision, support to fisheries and coastal protection (Worm *et al.*, 2006; Semesi, 1998; Dahdouh-Guebas *et al.*, 2000; Kairo, *et al.*, 2001). Previous studies have indicated that an increased number of species invasions over time coincided with loss of biodiversity and that invasion does not compensate for loss of native biodiversity and services since they compromise other species groups, mostly microbial and small invertebrates which have an equally important role in the ecosystem functioning and stability (Barbier, 2007; Duke *et al.*, 2007; Alongi and Carvalho, 2008).

Conclusion and recommendations

Mangrove mortality seems to have significantly shifted crab and mollusc species composition and reduced their densities, besides leading to probable loss of other mangrove-associated faunal species. Although the invasive flora invading the impacted sites may support different fauna and bring some degree of ecosystem functioning besides acting as a precursor for future recovery, they do not provide all the goods and services provided by the mangroves like wood products, coastal protection, nutrient filtering, sediment trapping and high organic matter production among others. This could be an example of the concept of 'cryptic ecological degradation', where the loss of mangroves in the disturbed sites has been masked by the expansion of the less important (less functional) opportunistic semi-terrestrial species (*Suaeda maritima*). These results confirm that sedimentation-triggered degradation will have far reaching effects by compromising the composition, density and diversity of mangrove fauna

and associated biodiversity. In some cases, as was observed for *T. palustris*, there may be cascades which may trigger extinction of less tolerant species, with highly specialized niches and ecological compartmentalization. This study was conducted 10 yrs after impact and recovery of the mangroves was very limited. Human intervention by removal of physical impoundments to successive natural regeneration or actual restoration will be necessary (Bosire *et al.*, 2008). It will also be critical to link mangrove management downstream to land-use practices upstream and thus promote sustainable land-uses which minimize soil erosion, hence sedimentation downstream. This study should be conducted in other impacted areas to corroborate these findings and where possible different modeling scenarios undertaken to project future responses of mangrove associated biodiversity to such perturbations.

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