

RESEARCH ARTICLE

Where to fish in the forest? Tree characteristics and contiguous seagrass features predict mangrove forest quality for fishes and crustaceans

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Funding information

Derek and Maureen Moss; Earthwatch Institute; School of Applied Sciences, Edinburgh Napier University

Handling Editor: Bila-Isia Inogwabini

Abstract

1. Mangroves often support rich fish and crustacean communities, although faunal abundance and diversity show strong spatiotemporal variability. Consistent patterns in mangrove animal communities might be dictated by forest characteristics, by seascape context or by some combination of these factors. Predicting drivers of spatial heterogeneity in mangrove faunal communities can better support the zoning of forests for management purposes, for example by identifying sites important for fisheries nursery provision.
2. We sampled 14 sites within a large (4000 ha) mangrove forest in Kenya, quarterly over a period of 2 years. There were clear and consistent differences in the quality of sites for fish and crustacean abundance and diversity.
3. Forest characteristics (as summarised by the complexity index, CI) and seascape metrics (the presence, area and configuration of contiguous seagrass) were strong predictors of site differences. However, they showed opposite influences on dominant members of the fish and crustacean faunas, with CI correlated negatively with fishes and positively with crustaceans, and seagrass area correlated positively with fishes and negatively with crustaceans.
4. *Synthesis and applications.* Sites within the same mangrove forest exhibit consistent differences in fish and crustacean abundance. However, the fish and crustacean communities (and particularly dominant species within them) act differently in response to forest and seascape characteristics. Old growth, mature forest, set in a seascape of seagrass patches with bare sediment, was associated with highest crustacean abundance. In contrast, denser smaller trees and seascapes with larger, continuous areas of seagrass correlated better with fish abundance. Zoning for management, as mandated in new Kenyan policy, will need to consider these differences in seascape use between fish and crustaceans.

KEYWORDS

complexity, East Africa, ecosystem services, juveniles, mosaic, nursery habitat, seascape, shrimp

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1 | INTRODUCTION

Abundant evidence supports the notion that mangroves are usually important habitats for crustaceans and juvenile fishes (Faunce & Serafy, 2006). Meta-analysis demonstrate a positive relationship between mangrove presence or area and local fisheries catches at regional (10–100 km) scales (Carrasquilla-Henao & Juanes, 2016). Studies comparing areas with and without mangroves have provided convincing tests of nursery function (Mumby et al., 2004; Nagelkerken & Velde, 2002). Work at very local (1–100 m) scales has identified a range of plausible mechanisms that could underlie this effect. Dominant among these is the predator refuge hypothesis (Heck et al., 2003), which predicts that structurally complex habitats allow juveniles to hide from their larger predators. A large literature documents this in a range of habitats (e.g. Cocheret de la Morinière et al., 2004; Vance et al., 1996). Dense mangrove stands provide a striking example of structural complexity and experimental and comparative studies have shown how the density of mangrove roots and stems is positively related with fish abundance and diversity (MacDonald & Weis, 2013; Nagelkerken & Faunce, 2007; Sheridan & Hays, 2003).

Despite these insights, much remains uncertain about the roles of mangroves as habitat for mobile aquatic fauna. There is large, unexplained variability at the mesoscale (100 m–10 km). For example, research that samples fish beneath the mangrove canopy reports large temporal and spatial variability among sites (e.g. Crona & Rönnbäck, 2007; Huxham et al., 2004; Vance et al., 1996), which is not simply correlated with root density. Equally dense mangrove plots, in the same forest but separated by a few 100 m, may have very different fish communities. Some of this uncertainty may be related to other variables that change at local scales, such as turbidity, salinity, shade and temperature (Barletta et al., 2003; Macia, 2004; Verweij et al., 2006) but no one variable is consistently important. In general, it remains difficult or impossible to predict what areas of a forest are most valuable as fish habitats. Identifying whether some areas of mangroves are consistently better at providing nursery functions, and understanding why, would allow management to focus on conserving these areas.

An emerging perspective that can help to illuminate meso-scale variability comes from landscape ecology. For example, Bradley et al. (2019) describe how, at the small scale (1–10 m), habitat characteristics related to structure and complexity were important predictors of fish presence in their study of coastal fish communities in Australia. As expected, greater complexity correlated with higher numbers of fish. However, the identities of these fish differed between marine and estuarine sites separated by ~10 kms, as did the nature of the features that provided habitat complexity (such as mangrove roots, seagrass, and cobble). They concluded that faunal–habitat relationships are

context-dependent and stress the need to investigate the environmental context of habitats to understand their function, which links local scale variability with mesoscale characteristics. The seascape approach, adapted from landscape ecology, may shed light on what determines the quality of nearshore nursery habitats (Nagelkerken et al., 2015); in particular, it promises to help fill the knowledge-gap at the mesoscale. In the seascape, connectivity is determined by the extent to which patches allow or deter movement of resources and individuals between or across patches. Coastal ecosystems are not isolated, and their ecological status and resilience could be determined by their functional linkage with other habitats (Olds et al., 2016).

In the Caribbean and the Indo-Pacific, juvenile fishes have been recorded to use mangrove and seagrass habitats while adults utilise coral reefs (Dorenbosch et al., 2006; Mumby et al., 2004). In most forests, mangrove-dependent fish tend to move to adjacent seagrass habitats during low tides when the intertidal zone is not inundated (Jelbart et al., 2007; Sheaves, 2005). Fish may also seek refuge in mangroves during the day, when they are vulnerable to visually hunting predators, and later move to seagrass beds for nocturnal feeding (Nagelkerken et al., 2000; Verweij et al., 2006). In the Western Indian Ocean region, a diverse range of species from different trophic levels have been found to utilise nearshore habitats (including mangroves and seagrasses) as juvenile habitats (Berkström et al., 2012; Lugendo et al., 2005) but the ecological requirements and movements of individual species are often unknown.

In the current work, we test the prediction that mangrove forest structure and adjacent seascape composition, in particular, the presence and extent of seagrass, interact to shape the abundance and diversity of fishes and crustaceans. Our first objective was to use repeated sampling to search for predictable patterns among a range of sites within a single large mangrove forest in southern Kenya. Mangrove habitat variables, and the setting of the site in the seascape, may both be important in explaining habitat use by mobile aquatic fauna. Our second objective was to combine measures of habitat quality and seascape context, consisting of forest characteristics and data on extent and shape of contiguous seagrass coverage, to help explain variation among these sites and increase the predictability of mesoscale variation and hence the ability to identify sites of high fisheries importance.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is Vanga Bay on the south coast of Kenya (4° 39' 38.42" S, 39° 13' 9.71" E). Sea surface temperatures range between 24 and 29°C and salinity varies between 34.5 and 35.4, with lowest

salinities during the rainy southeast monsoon (SEM) and the highest during the dry northeast monsoon (NEM) season. The tidal regime is semidiurnal with amplitudes from 1.5m at neap to 4m at spring tides.

The Vanga mangrove forest covers an area of ~4000ha and six species of tree are found there: *Avicennia marina*, *Bruguiera gymnorhiza*, *Ceriops tagal*, *Rhizophora mucronata*, *Sonneratia alba* and *Xylocarpus granatum* (Figure 1; GoK, 2017). Fishing is the major economic activity with fishing grounds being a complex of mangroves, seagrass and coral reef ecosystems. The fishery in Vanga is mostly artisanal, multigear and multispecies (Fortnam et al., 2021).

2.2 | Sampling sites and methods

Fishes and crustaceans were sampled at 14 mangrove creek sites chosen using three criteria: First, to create a wide geographical coverage within the forest while still being accessible enough to allow regular sampling. Second, to sample creeks within the mangrove canopy of broadly similar size (3–4m width) and hydrology, so that any differences between sites were due to location rather than hydrology. Third, to sample across a range of forest characteristics (particularly using the complexity index (CI) as a summary variable; see below) that captured features of tree diversity, maturity and density. We used structural data collected by the Kenya Marine and Fisheries Research Institute (KMFRI) in 2015, which allowed us to see average CI for areas of the forest close to all the sites we selected; we subsequently directly measured and confirmed CI for each site during our own sampling (see below). Site locations were recorded with a Garmin GPS World Geodetic System (WGS) 1984

and projected onto the Universal Transverse Mercator (UTM) 37S. Sites were, on average, 0.7km from their nearest neighbouring site (with a maximum of 1.17 and minimum of 0.3km); this ensured that the sampling of forest characteristics surrounding each site did not include any overlapping areas (Figure 1). Faunal sampling was done using fyke nets, every 3 months during spring tides from September 2015 to September 2017 (excepting March 2017 for logistical reasons). Nets were deployed in the morning at low tide and collected 24 h later. Nets had two wings, each of length 9.55 m, height 1 m, and body frame length 3.6 m. The main frame measured 1×1m. There were three rings of diameter 0.9, 0.7 and 0.62m along the body frame and a net of mesh size 1.9cm when stretched.

Sampling all the sites typically took five consecutive days; the order in which sites were sampled was changed on each date. Eight replicate samples were taken from each of the 14 sites across the 2-year study period, resulting in a total of 112 samples. Samples were placed in a cool box and identified to the lowest taxon possible using Richmond (2011) and Anam and Mostarda (2012). Fish and crustacean abundance, biomass and number of species per net were obtained. Fish standard and total lengths and individual mass were recorded. Crustaceans were counted and weighed to the nearest 0.1g. The maximum length of each species was sourced from FishBase (Froese & Pauly, 2022). Fishes with total length $\leq 1/3$ maximum length were classified as small juveniles, between $>1/3$ to $\leq 2/3$ maximum length as large juveniles/sub adults and those $>2/3$ maximum length as adults (Nagelkerken & Velde, 2002). All samples were removed to the laboratory and used for additional data collection including for parasite fauna and stomach-content analysis (Wanjiru et al., 2022). Sampling and subsequent handling did not require formal ethical approval and

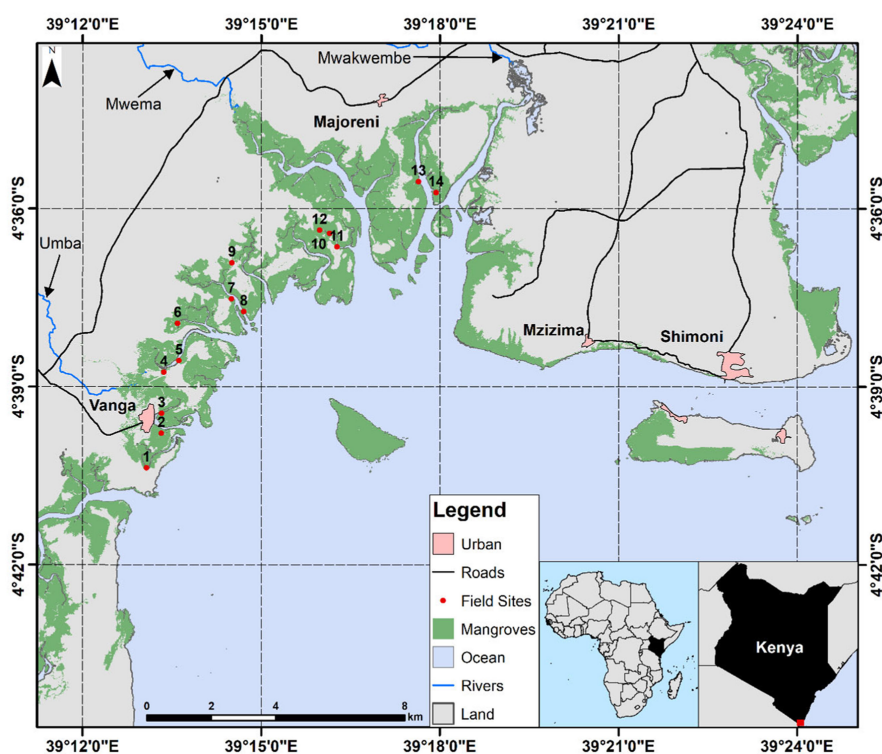


FIGURE 1 The Vanga mangrove forest (green) with sampling sites (red).

permission to work at the field site was obtained from KMFRI and Kenya Fisheries Service.

2.3 | Forest quality measurements

The floral and structural characteristics of the forest contiguous to each sampling site were captured using plots measuring 100 and 400 m². Plots were located within a semicircle of forest, centred on the sampling site with radius of maximum 100 m, and situated upstream or to the sides of the site. Following standard forestry protocols the plot size depended on the tree size and density; for large trees, 20×20 m was used but where trees were small and densely clustered, 10×10 m plots were used, giving more comparable numbers of trees between each plot. At each site, data from between 2–5 plots were used to summarise forest structure. Within each plot, the diameter at breast height (dbh, measured at around 1.3 m) (cm) and height (m) were measured for all trees with a dbh greater than 2.5 cm using a tree calliper and a graduated pole, respectively. Mean tree height, basal area, stem density and number of tree species were recorded, and used to calculate the CI, according to Holdridge (1964): $CI = 10^{-3} \times (d) \times (s) \times (h) \times (b)$ where d is the stand density, s is the number of tree species, h is the mean tree height and b is the basal area. The CI is often used to infer forest quality; degraded and younger stands tend to have lower CI compared to undisturbed ones (Roth, 1992).

2.4 | Spatial analysis of seascape features

A cloud-free Sentinel-2 image of the Vanga area at low tide was acquired from 27 March 2017. The spatial analysis was conducted in ArcGIS. A false colour composite was created using the near infrared (NIR), red and green bands. To differentiate land, sea and the intertidal, we calculated the Normalised Difference Water Index (NDWI) using the NIR and red bands and a threshold was set to detect the transition from land to water. Using a previously derived mask of the ocean at high tide (Harcourt et al., 2018), we differentiated the intertidal and subtidal regions. This was subsequently used to remove land from the analysis. Areas where seagrass was dominant were mapped by applying the technique of Harcourt et al. (2018) to the Sentinel-2 scene used in this study.

In the absence of any biological information on the movements of the main species, we used a simple empirical approach to obtain a maximum relevant distance from each site to be used in this analysis. For each of the 14 sampling sites, a set of buffers with intervals of 0.5 km were constructed, extending seawards to a maximum distance of 19 km from the sampling point (Figure 2). These buffers were used to calculate the distance between each mangrove field site to various seagrass points. To exclude land from these buffers, the ocean mask was used to extract only those regions covered by water. We calculated the direction from each field point at increments of 20° to isolate regions immediately in front of a sampling point (Figure 2b) and extracted the oceanic

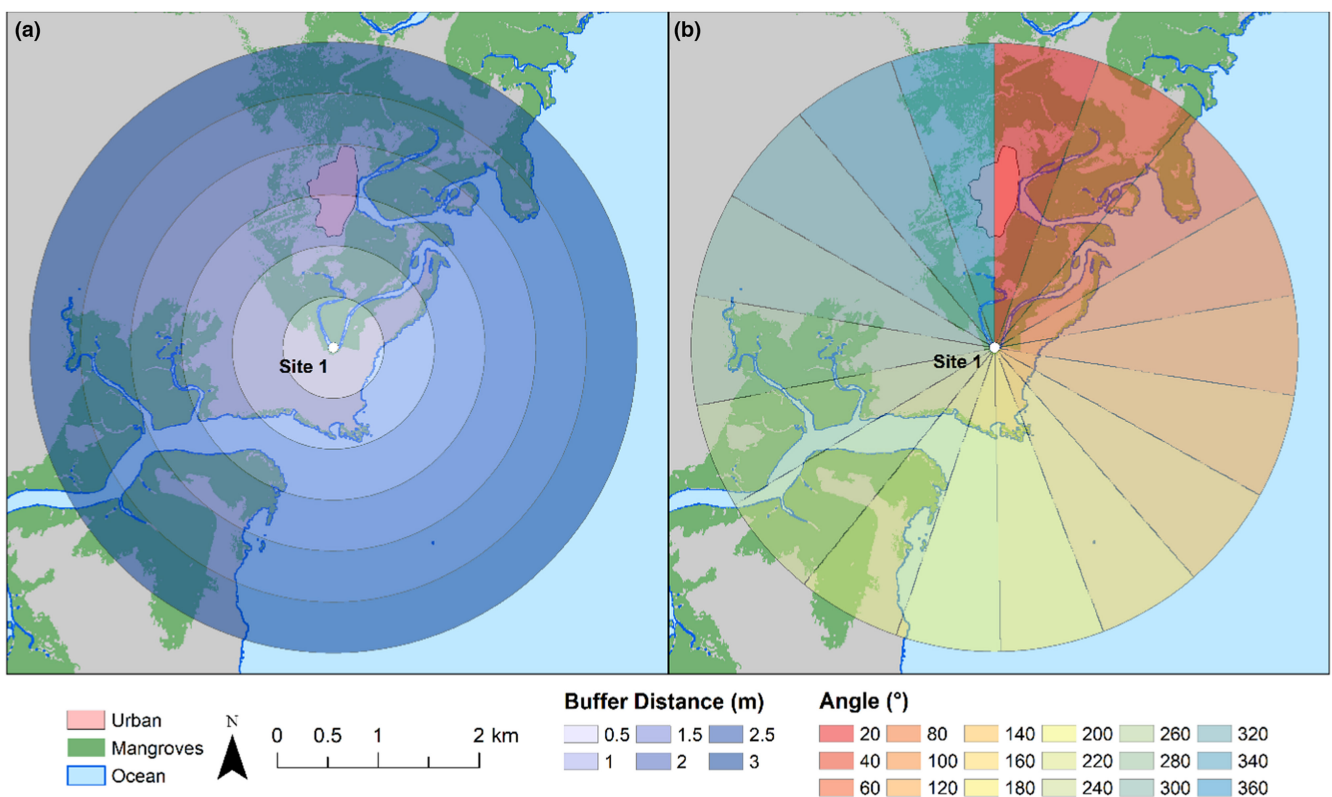


FIGURE 2 Example distance buffers at intervals of 0.5 km (a) and angular directions at 20-degree intervals (b) from Site 1.

section of these direction buffers. This was computed for each of the sites making 14 directional polygons. To extract the final datasets for statistical analysis, the intersection between seagrass presence and each of the directional and distance buffers was computed. The geometry of these patches was calculated to avoid including large seagrass patches that extend across multiple buffer boundaries and intersections. To establish the maximum distance to use in subsequent analyses, cumulative curves of the proportions of total seagrass habitat recorded in the bay allocated against each site were plotted. After 9 km there was only around 50% difference between sites in the proportions of cumulative area implying that beyond this distance more than half of the seagrass measured for any given site would be shared with another. Hence, 9 km was set as the maximum distance used from any given site for this study.

2.5 | Statistical analyses

Differences in fish and crustacean communities between sites were explored using analyses of ranked abundance (to remove variability between times and seasons) and univariate correlations. Means and total counts, for each site across all sampling dates, of abundance and biomass of fishes were correlated against total species count for each site, to explore whether large biomasses or abundances might be driven by high catches of just one or a few species. For crustaceans, which had low total species counts, the same approach was taken for abundance versus biomass.

The main relationships between predictor and response variables were explored and summarised with a principal components analysis (using the 'prcomp' command on R). Regression analyses were used to explore relationships between forest characteristics, seascape predictors, fish and crustacean variables, using a range of possible predictor and response variables (Table 1). The seagrass predictors were available for a range of total potential areas, up to and including 9 km distance. Stepwise regressions, with addition and subtraction approaches, were used to identify distances that consistently showed no or little evidence of effects; these were excluded from subsequent models. Best multiple regression models (on \log_{10} transformed data when necessary) were chosen by comparing R^2 values, p values, the strength of coefficients, and variance inflation factors (VIFs) for multicollinearity, with a VIF

of >5 deemed unacceptable. The strongest models incorporating forest and seagrass predictors were compared using the Akaike information criterion (AIC). Finally, simple linear regressions were performed between those predictors and response variables shown to have the strongest relationships through the multiple regressions and by visual inspection of the plots. Given the collinearity inherent in some of the predictor variables and the dangers of inflated Type 1 error following multiple tests, the results were examined for key signals rather than interpreted simply as significant or non-significant relationships.

Moran's 'I' was calculated using GeoDa software to test for spatial autocorrelation; there were no significant improvements after correction using spherical error terms, thus correction for autocorrelation was found unnecessary.

Statistical analyses were performed using Minitab 15 and R v 4.2.0 software.

3 | RESULTS

A total of 1879 fishes and 1132 crustaceans were sampled belonging to 59 and 16 species, respectively. The most abundant fish species were *Y. hyalosoma*, *A. japonicum*, *G. oyena* and *G. filamentosus* (62% of the total individuals caught) while the most abundant crustacean species were *P. semisulcatus*, *P. indicus* and *P. monodon* (88% of all crustacean individuals). 61.8% of all fish caught were juveniles, 38.1% were large juveniles/sub-adults, and only 0.2% were adults (from just two species, *Zenarchopterus dispar* and *Stolephorus commersonnii*). All dominant species are of direct importance for local fisheries, with the exception of *Y. hyalosoma*. Full information on fauna is given in Wanjiru et al. (2022).

3.1 | Differences among sites

There were large and consistent differences between sites, with some having predictably higher diversity and abundance than others. Species richness for fishes ranged from 7 (at site 14) to 24 (site 7). The strong positive correlation between mean fish biomass and total number of species per site ($R^2 = 0.93$, $df = 1, 12$, $p < 0.001$; Figure 3) demonstrates that sites with high fish biomass were not simply characterised by one or two dominant species,

TABLE 1 All predictor and response variables explored.

Predictor variables	Seagrass area, seagrass perimeter, cumulative seagrass area, cumulative seagrass perimeter, seagrass perimeter/area ratio, forest complexity index, mean tree height, number of tree species, tree basal area, stem density
Response variables (fish)	Total fish abundance, total fish biomass, species richness, ^a dominant fish species abundance: <i>Yarica hyalosoma</i> , <i>Acropoma japonicum</i> , <i>Gerres oyena</i> , <i>Gerres filamentosus</i>
Response variables (crustaceans)	Total abundance, total biomass, species richness, ^b dominant species abundance: <i>Penaeus semisulcatus</i> , <i>Penaeus monodon</i> , <i>Penaeus indicus</i>

^a62% of all individuals.

^b88% of all individuals.

FIGURE 3 Mean fish biomass caught at each site versus total number of fish species, showing sites with high biomass also tended to support many species.

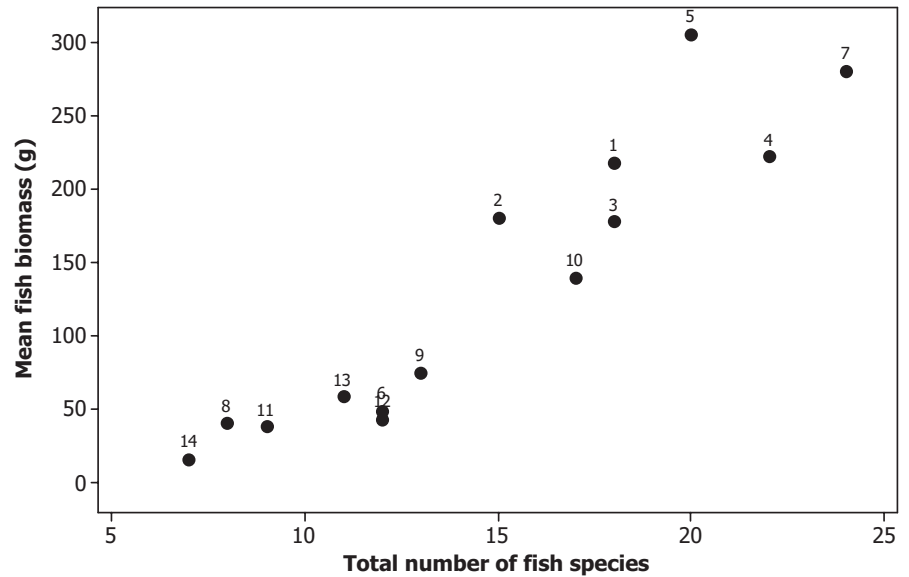
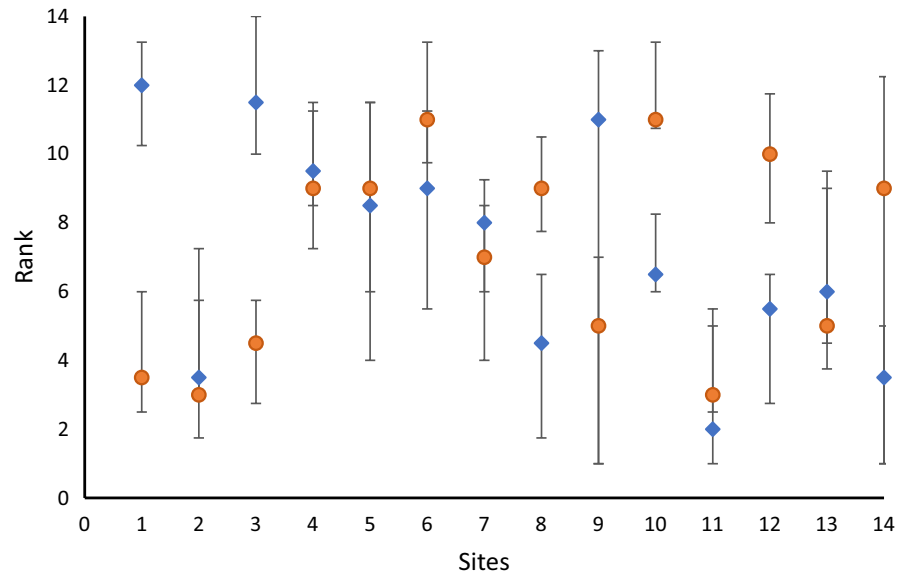


FIGURE 4 Median ranks of sites for fish (blue diamond) and crustacean (orange circle) abundance, with interquartile ranges, across 8 sampling times, ranked from highest to lowest on each sampling date.



but rather tended to be better for most species. Species richness counts for crustaceans ranged from 3 (site 7) to 9 (sites 4 and 10), however only three species (*P. semisulcatus*, *P. monodon* and *P. indicus*) dominated the catch with 88% of all individuals. Hence there was no relationship between abundance and species count for crustaceans. As expected, there were large differences between times, with catches during SEM around three times higher than NEM (Wanjiru et al., 2022). However, the rank order of sites remained broadly consistent, as shown by significant differences among median ranks across all eight dates for both fishes and crustaceans (Figure 4; Kruskal-Wallis tests for fishes, $\chi^2=31.9$, $df=13$, $p=0.0025$; for crustaceans, $\chi^2=40.8$, $df=13$, $p=0.0001$). Sites that supported high fish abundance did not necessarily support high crustacean abundances.

3.2 | Relationships between mangrove forest characteristics, seagrass coverage, fish and crustacean variables

3.2.1 | Summary PCA

A principal components analysis was used to visualise the main relationships between predictor and response variables (Figure 5). The first five principal components explained 80% of the variability, with PC1 contributing 29.9% and PC2, 25.7%. Principal component 1 aligns with seascape (seagrass) variables including SG1 and SG2 (seagrass area at 1 and 2 km) whilst PC2 aligns with the forest variables CI and basal area (which are themselves co-dependent). Key fish variables (total abundance, abundance of dominant

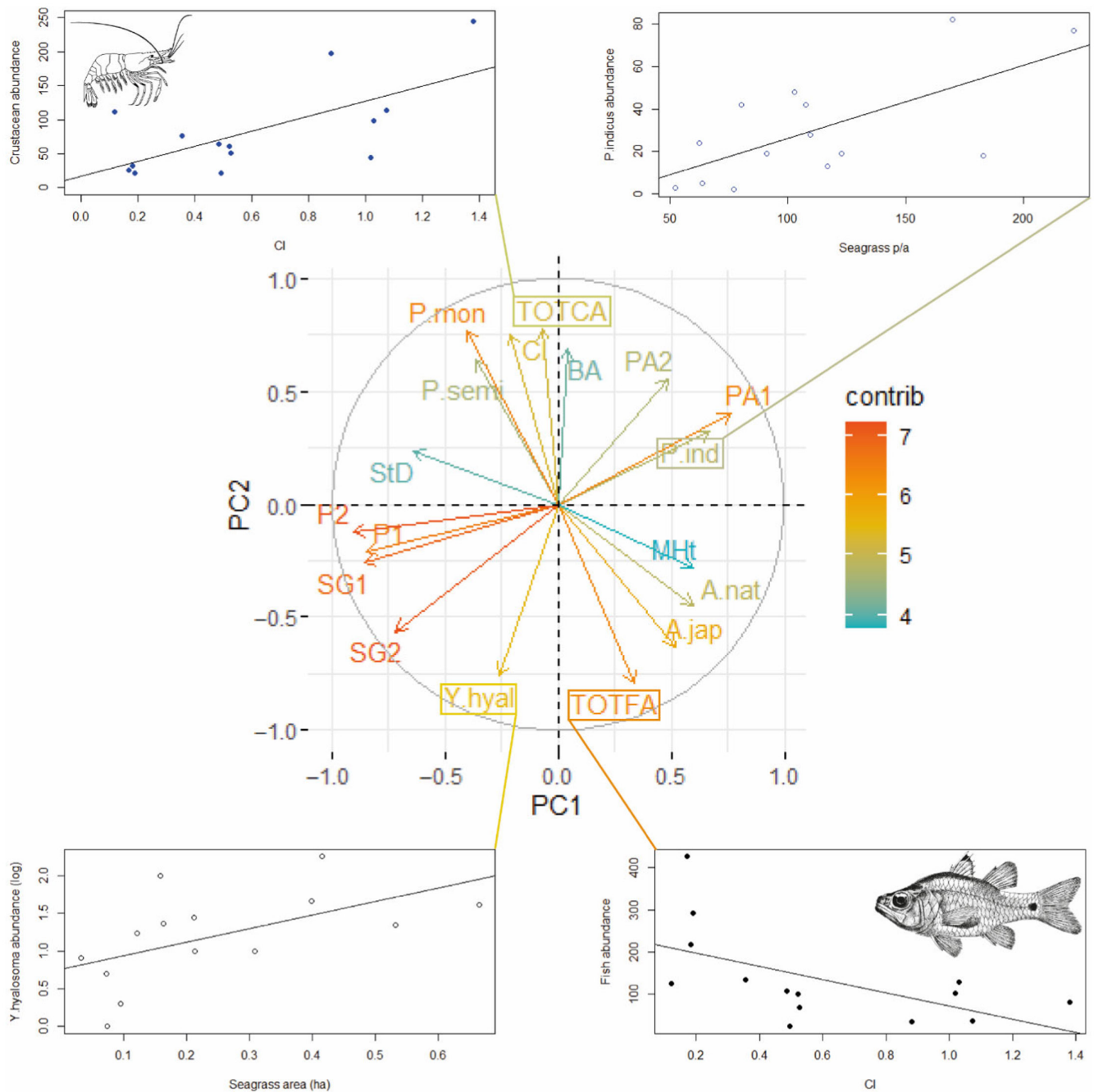


FIGURE 5 Principal Components Analysis showing the most important variables. Fauna: A.jap, *A. japonicum* abundance; A.nat, *Ambassis natalensis* abundance; BA, basal area; Mht, mean tree height; P.mon, *P. monodon* abundance; P.ind, *P. indicus* abundance. Forest variables: CI, complexity index; P.semi, *P. semisulcatus* abundance; StD, stand density; TOTCA, total crustacean abundance; TOTFA, total fish abundance; Y.hyal, *Y. hyalosoma* abundance. Seagrass variables: P1, perimeter at 1 km; P2, perimeter at 2 km; PA1, perimeter/area ratio at 1 km; PA2, perimeter/area ratio at 2 km; SG1, area at 1 km; SG2, area at 2 km. The four panels show key, significant univariate relationships. Table 2 gives model results for these regressions.

species *Y. hyalosoma* and *A. japonicum*) were negatively related to the CI and basal area of the forest while crustaceans (total abundance, *P. monodon* and *P. semisulcatus*) were positively correlated. By contrast, important fish variables were positively correlated

with seagrass area while crustaceans generally showed negative relationships with seagrass area (but positive ones with perimeter/area [P/A] and perimeter measures). Four of the univariate relationships informing these patterns are illustrated in Figure 5.

TABLE 2 Selected univariate regression results.

Predictor variable	Response variable	Coefficient	F	R ² (%)	p
CI	Total fish abundance	-160	5.71	32.22	0.034
	Total crustacean abundance	+110	9.66	44.60	0.009
	<i>Penaeus monodon</i> abundance	+6	8.51	41.50	0.013
	<i>P. semisulcatus</i> abundance	+96	8.21	40.63	0.014
Seagrass area 1.5 km	log (x + 1) <i>Yarica hyalosoma</i>	+23	23.44	66.11	<0.001
Seagrass P/A 1.5 km	<i>P. indicus</i> abundance	+13	13.03	52	0.004
Seagrass P/A 3.5 km	<i>Gerres filamentosus</i> abundance	-0.96	10.72	0.47	0.007

Abbreviations: CI, complexity index; P/A, perimeter/area ratio.

TABLE 3 Best fit multiple regression models.

Response variable	Predictor variable	Coefficient	Model F	Model R ² (%)	p
<i>Penaeus indicus</i>	Seagrass P/A 2.5 km	1.69	13.48	86	0.001
	Mean tree height	20.2			
	Tree species	12			
	Stem density	0.01			
<i>P. indicus</i>	Seagrass P/A 1.5 km	0.25	11.94	68	0.002
	No. tree species	9.74			
<i>Yarica hyalosoma</i>	Seagrass area 1 km	146	16.42	75	<0.001
	Stem density	-0.02			
<i>Y. hyalosoma</i>	Seagrass perimeter 1 km	3.81	11.28	80	0.001
	Seagrass area 1 km	-140.3			
	Basal area	-28.7			

Abbreviation: P/A, perimeter/area ratio.

3.2.2 | Univariate and multivariate regressions

CI was the most important floral variable in univariate analyses. Important seascape predictors were seagrass area and P/A ratio at 1.5 and 3.5 km distance (Table 2).

Combining variables in multiple regressions and using best subsets and AIC analyses to select the best fit models resulted in four final, highly significant models (Table 3). The exact combination of predictors and responses differed from those highlighted by the key univariate regressions but were consistent with the main trends they showed. For example, abundance of the dominant fish species *Y. hyalosoma* was positively correlated with the area of contiguous seagrass and negatively related with tree basal area (a key part of the CI). Abundance of the dominant shrimp species *P. indicus* correlated positively with P/A ratio of seagrass and with mean tree height (a positive contributor to CI).

4 | DISCUSSION

In this study, we addressed two research gaps: first, are there consistent differences in the fish and crustacean fauna found among

different sites within the same mangrove forest, sampled over 2 years? Second, can measures of forest structure, or context in the seascape, or combinations of both, be used to predict these differences?

4.1 | Consistency of mangrove forest sites as habitats for fishes and crustaceans

Our results revealed predictable patterns within the Vanga mangrove ecosystem. Some sites showed higher species richness, abundance and biomass than others, a pattern that persisted between years and seasons as shown by the significantly different rankings of the sites for these variables. This has important practical implications. Different services (such as carbon storage, fisheries habitat or nutrient filtration) may be associated with different locations in a habitat (Huxham et al., 2017). In principle, such patterning would allow differentiated use and protection of an ecosystem, for example through designating some parts of the forest for extractive use whilst protecting other areas as nursery sites or carbon stores. Indeed, zoning is already in place in the Vanga forest, which is home to Vanga Blue Forest, a mangrove carbon

project that uses 450 ha as protected areas for carbon benefits (ACES, 2022). The National Mangrove Ecosystem Management Plan, developed for application along the whole coast, mandates similar zoning for all Kenyan mangrove forests (GoK, 2017). Hence it would be useful if areas important as nursery sites could be clearly identified and there is a presumption in policy that this will be done. However, our results suggest that any simple classification of the forest into relatively 'good' and 'bad' areas for fisheries is not possible because of the contrasting responses of different species and faunal groups. There was a distinction between the main fish and crustacean species, with sites best for fish generally poor for crustacea, and vice versa.

4.2 | Fish, crustacea and mangrove structural variables

Enhanced biomass and diversity of coastal fish assemblages are often associated with more structurally complex habitats (Lefcheck et al., 2019) and a substantial literature explores what structural features of mangroves might attract fish at very local scales (Cocheret de la Morinière et al., 2004; Laegdsgaard & Johnson, 2001; Loneragan et al., 2005). For example, field studies and laboratory experiments have shown complex mangrove roots provide refuge for juvenile fish by deterring predators from attacking them (Laegdsgaard & Johnson, 2001; Macia, 2004; Sheridan & Hays, 2003). Here, total fish abundance, and the abundance of dominant fish species, were negatively associated with CI, while the opposite pattern was seen for crustaceans. On first impressions, this may seem to contradict the association between structural complexity and juvenile fish found at other sites and scales. However, the CI is positively related to basal area, which is positively related to the size of trees (Roth, 1992). Therefore, high CI implies older, less dense trees with a more diverse mangrove species mix, as found in mature, old-growth forests. In Kenya, the old growth forests with high CI values have the highest stocks of carbon and are thus the most important carbon sinks (Huxham et al., 2015). However, these results suggest that a lower CI is better for fish, and this is consistent with the idea that fish prefer very dense stands, which are often younger and less likely to be multispecies. Maintaining and enhancing the range of ecosystem services, including carbon storage and fisheries provision, that are provided by mangroves will require recognition of these spatial differences and caution about allowing single services, such as carbon sequestration, to dominate policy decisions.

In contrast, crustaceans (and specifically the dominant species of shrimp, *P. indicus*, *P. monodon* and *P. semisulcatus*) showed positive associations with CI suggesting that they are using the mangrove habitat in a different way than fishes. While most literature on shrimps in mangroves emphasises the importance of structural complexity, the type of complexity that matters may be different from that for fishes. For example, Rönnbäck et al. (1999) found fishes were more likely to associate with areas of dense pneumatophores rather than prop-roots, with shrimp preferring the latter.

Macia et al. (2003) showed an interaction between turbidity and habitat complexity for *P. indicus*; in turbid waters (such as those at Vanga) protection from predation decreased with increasing complexity. Hence, penaeid shrimp can use turbidity as a refuge from predators and are also able to burrow into suitable substrates to reduce their susceptibility to predation (Dall et al., 1990). This could imply a preference for more open habitats with substrates suitable for burrowing (Mohan & Siddeek, 1996; Rönnbäck et al., 2002; Vance et al., 1996).

4.3 | Fish, crustacea and seagrass seascape features

Context in the seascape may be more important in explaining tropical fish assemblages than habitat characteristics of specific patches (Goodridge Gaines et al., 2022; Green et al., 2012); indeed Bradley et al. (2019) conclude that the context-dependency of animal-habitat relationships in the coastal zone is of 'over-riding importance'. Most previous studies on how seascape context affects mangrove fauna have considered different scales and more fragmented mosaics than the current work, for example looking at patches of mangroves with varying degrees of isolation. Here, we looked at a single, continuous forest and considered how features of the seagrass growing next to it might influence vagile faunal communities. Some of the fish and crustacean variables were strongly associated with seagrass metrics. The P/A ratio of seagrass—which increases with increasing fragmentation and decreasing patch size of seagrass—proved the best predictor. Fish and crustacean variables were generally negatively and positively associated with this metric, respectively. The abundance of *P. indicus* gave the strongest association at 1.5 km ($R^2=0.52$) and *P. monodon* abundance was also significantly positively correlated to P/A ratio ($R^2=0.43$). Fish variables were mostly negatively correlated with P/A ratio and positively correlated with seagrass area. This generally positive influence of seagrass coverage on fish abundance was expected, as seagrass is well known as important habitat for many juvenile fish (Heck et al., 2003; Swadling et al., 2019). Here, we assume that fish found at the mangrove sites during high tide are conducting tidal migrations, to or through seagrass patches. Similar migrations, with site fidelity at high and low tide, have been demonstrated for juvenile Lutjanidae in Zanzibar (Dorenbosch et al., 2004) and Jelbart et al. (2007) demonstrated how patches of seagrass closer to mangroves in Australia supported higher densities of juvenile fish, including Ambassidae, at low tide.

The apparently negative relationship between shrimp and the area of contiguous seagrass may be linked to the use by shrimp of bare substrates, as discussed above. Even when seagrass has been shown to encourage higher invertebrate densities or diversities, the relationships are not always simple. For example, crustaceans sometimes have higher densities in smaller rather than large patches sizes of artificial seagrass (Eggleston et al., 1999). Different species are likely to interact with both the components and their spatial organisation of the seascape mosaic in different, and species-specific,

ways. This suggests that these relationships cannot be generalised but must be considered separately for each species.

The spatial area over which seascape features exert influence on the structures of communities caught at any site is in most cases unknown. Relevant information informing study design includes the home range and daily movement patterns of target species. For most taxa (including most of those in this study) such detail is missing, although information from tagging studies is slowly becoming available on the movements of some taxa such as *Haemulon* sp. (Appeldoorn & Bouwmeester, 2022) and Lutjanidae (Dorenbosch et al., 2004). The smallest ambit applied to seagrass metrics in the current study was 0.5 km from a catch site, and most of the faunal variables showed the strongest responses to seagrass metrics within 3 km.

4.4 | Combining seascape and habitat predictors

For one of the dominant fish species—*Y. hyalosoma*—and one of the shrimp—*P. indicus*—a combination of seascape and habitat factors produced very strong and highly significant regression models that explained up to 86% of the variance between sites. We recognise that correlative work like this can never demonstrate causality, and that there are other potentially relevant variables at the habitat (such as abiotic drivers like turbidity) and seascape (such as macroalgae coverage) levels that could in principle be included in analyses like these. However, the strength of these relationships and the corroboration of similar work in the literature suggests that these findings capture important features of the ecology of these species.

5 | CONCLUSIONS

We show that sites within the same large mangrove forest, with similar hydrological features, are significantly and predictably different in their faunal communities. However, there is no simple classification into 'good' and 'bad' places for fauna in general, since those with highest abundances for fishes often showed lower abundances of crustaceans. A combination of forest characteristics and measures of seagrass area and shape within 3 km of the catch sites were able to explain much of the variation between sites. Our results support the broad literature demonstrating the importance of mangroves as sites for juvenile fish and crustacean species, and the connectivity of mangroves with nearby seagrass. Sustaining rich faunal communities in mangrove and seagrass seascapes such as at Vanga requires not only the maintenance of the different habitat types but also the seascape diversity and connectivity that allows different species to flourish.

AUTHOR CONTRIBUTIONS

Caroline Wanjiru, Mark Huxham, Ivan Nagelkerken and Sonja Rueckert conceived the ideas and designed the main methodology. William Harcourt led on GIS design and analysis. Caroline Wanjiru collected data. Caroline Wanjiru and Mark Huxham led on

writing, but all authors contributed and gave final approval for the manuscript.

ACKNOWLEDGEMENTS

Our study was led by a Kenyan scientist and includes authors from Europe and Australia. It responds directly to a Kenyan, as well as international, policy agenda and contributed to training and capacity building for Kenyan students and citizen scientists. We thank the people of Vanga and the field team of Hamisi Kirauni, Derrick Omollo, Josphat Nguu, Sammy Kibor, Evans, Alfred Obinga, Boaz Orembo, Rashid Anam, Ben Onyango and Harith Mohamed. Derek and Maureen Moss, Earthwatch Institute and the School of Applied Sciences, Edinburgh Napier University, provided financial support for Caroline Wanjiru. Our lead author, Caroline Wanjiru, died in December 2022 and is sadly missed; this paper forms part of her legacy.

CONFLICT OF INTEREST STATEMENT

We declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Edinburgh Napier Repository <https://doi.org/10.17869/enu.2023.3069847> (Wanjiru et al., 2023).

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REFERENCES

- ACES. (2022). *The Association for Coastal Ecosystem Services*. <http://www.aces-org.co.uk>
- Anam, R., & Mostarda, E. (2012). *Field identification guide to the living marine resources of Kenya*. FAO.
- Appeldoorn, R. S., & Bouwmeester, B. L. K. (2022). Ontogenetic migration of juvenile grunts (*Haemulon*) across a coral reef seascape: Pathways and potential mechanisms. *Diversity*, 14(3), 168. <https://doi.org/10.3390/d14030168>
- Barletta, M., Barletta-Bergan, A., Saint-Paul, U., & Hubold, G. (2003). Seasonal changes in density, biomass, and diversity of estuarine fishes in tidal mangrove creeks of the lower Caeté Estuary (northern Brazilian coast, East Amazon). *Marine Ecology Progress Series*, 256, 217–228. <https://doi.org/10.3354/meps256217>
- Berkström, C., Gullström, M., Lindborg, R., Mwandya, A. W., Yahya, S. A. S., Kautsky, N., & Nyström, M. (2012). Exploring 'knowns' and 'unknowns' in tropical seascape connectivity with insights from east African coral reefs. *Estuarine, Coastal and Shelf Science*, 107, 1–21. <https://doi.org/10.1016/j.ecss.2012.03.020>
- Bradley, M., Baker, R., Nagelkerken, I., & Sheaves, M. (2019). Context is more important than habitat type in determining use by juvenile fish. *Landscape Ecology*, 34(2), 427–442. <https://doi.org/10.1007/s10980-019-00781-3>
- Carrasquilla-Henao, M., & Juanes, F. (2016). Mangroves enhance local fisheries catches: A global meta-analysis. *Fish and Fisheries*, 18, 79–93. <https://doi.org/10.1111/faf.12168>
- Cocheret de la Morinière, E., Nagelkerken, I., van der Meij, H., & van der Velde, G. (2004). What attracts juvenile coral reef fish to mangroves: Habitat complexity or shade? *Marine Biology*, 144(1), 139–145. <https://doi.org/10.1007/s00227-003-1167-8>

- Crona, B. I., & Rönnbäck, P. (2007). Community structure and temporal variability of juvenile fish assemblages in natural and replanted mangroves, *Sonneratia alba* Sm., of Gazi Bay, Kenya. *Estuarine, Coastal and Shelf Science*, 74(1–2), 44–52. <https://doi.org/10.1016/j.ecss.2007.03.023>
- Dall, W., Hill, B. J., Rothlisberg, P., & Sharples, D. J. (1990). *The biology of the Penaeidae*. Academic Press.
- Dorenbosch, M., Grol, M. G. G., Nagelkerken, I., & van der Velde, G. (2006). Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, *Cheilinus undulatus* and Caribbean rainbow parrotfish, *Scarus guacamaia*. *Biological Conservation*, 129(2), 277–282. <https://doi.org/10.1016/j.biocon.2005.10.032>
- Dorenbosch, M., Verweij, M. C., Nagelkerken, I., Jiddawi, N., & van der Velde, G. (2004). Homing and daytime tidal movements of juvenile snappers (Lutjanidae) between shallow-water nursery habitats in Zanzibar, western Indian Ocean. *Environmental Biology of Fishes*, 70(3), 203–209.
- Eggleston, D. B., Elis, W. E., Etherington, L. L., Dahlgren, C. P., & Posey, M. H. (1999). Organism responses to habitat fragmentation and diversity: Habitat colonization by estuarine macrofauna. *Journal of Experimental Marine Biology and Ecology*, 236(1), 107–132. [https://doi.org/10.1016/S0022-0981\(98\)00192-0](https://doi.org/10.1016/S0022-0981(98)00192-0)
- Faunce, C., & Serafy, J. (2006). Mangroves as fish habitat: 50 years of field studies. *Marine Ecology Progress Series*, 318, 1–18. <https://doi.org/10.3354/meps318001>
- Fortnam, M., Atkins, M., Brown, K., Chaigneau, T., Frouws, A., Gwaro, K., Huxham, M., Kairo, J., Kimeli, A., Kirui, B., & Sheen, K. (2021). Multiple impact pathways of the 2015–2016 El Niño in coastal Kenya. *Ambio*, 50(1), 174–189. <https://doi.org/10.1007/s13280-020-01321-z>
- Froese, R., & Pauly, D. (2022). FishBase. www.fishbase.org
- GoK. (2017). *National Mangrove Ecosystem Management Plan*. Kenya Forest Service.
- Goodridge Gaines, L. A., Henderson, C. J., Mosman, J. D., Olds, A. D., Borland, H. P., & Gilby, B. L. (2022). Seascape context matters more than habitat condition for fish assemblages in coastal ecosystems. *Oikos*, 2022(8). <https://doi.org/10.1111/oik.09337>
- Green, B., Smith, D., & Underwood, G. (2012). Habitat connectivity and spatial complexity differentially affect mangrove and salt marsh fish assemblages. *Marine Ecology Progress Series*, 466, 177–192. <https://doi.org/10.3354/meps09791>
- Harcourt, W. D., Briers, R. A., & Huxham, M. (2018). The thin (ning) green line? Investigating changes in Kenya's seagrass coverage. *Biology Letters*, 14, 28–31. <https://doi.org/10.1098/rsbl.2018.0227>
- Heck, K., Hays, G., & Orth, R. (2003). Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series*, 253, 123–136. <https://doi.org/10.3354/meps253123>
- Holdridge, L. R. (1964). *Life zone ecology*. Tropical Science Center. <https://books.google.co.uk/books?id=BIFgAAAAMAAJ>
- Huxham, M., Dencer-Brown, A., Diele, K., Kathiresan, K., Nagelkerken, I., & Wanjiru, C. (2017). Mangroves and people: Local ecosystem services in a changing climate. In V. H. Rivera-Monroy, S. Y. Lee, E. Kristensen, & R. R. Twilley (Eds.), *Mangrove ecosystems: A global biogeographic perspective* (pp. 245–274). Springer International Publishing. https://doi.org/10.1007/978-3-319-62206-4_8
- Huxham, M., Emerton, L., Kairo, J., Munyi, F., Abdurizak, H., Muriuki, T., Nunan, F., & Briers, R. A. (2015). Applying climate compatible development and economic valuation to coastal management: A case study of Kenya's mangrove forests. *Journal of Environmental Management*, 157, 168–181. <https://doi.org/10.1016/j.jenvman.2015.04.018>
- Huxham, M., Kimani, E., & Augley, J. (2004). Mangrove fish: A comparison of community structure between forested and cleared habitats. *Estuarine, Coastal and Shelf Science*, 60(4), 637–647.
- Jelbart, J. E., Ross, P. M., & Connolly, R. M. (2007). Fish assemblages in seagrass beds are influenced by the proximity of mangrove forests. *Marine Biology*, 150(5), 993–1002. <https://doi.org/10.1007/s00227-006-0419-9>
- Laegdsgaard, P., & Johnson, C. (2001). Why do juvenile fish utilise mangrove habitats. *Journal of Experimental Marine Biology and Ecology*, 257, 229–253.
- Lefcheck, J. S., Hughes, B. B., Johnson, A. J., Pfirman, B. W., Rasher, D. B., Smyth, A. R., Williams, B. L., Beck, M. W., & Orth, R. J. (2019). Are coastal habitats important nurseries? A meta-analysis. *Conservation Letters*, 12, e12645. <https://doi.org/10.1111/conl.12645>
- Loneragan, N. R., Ahmad Adnan, N., Connolly, R. M., & Manson, F. J. (2005). Prawn landings and their relationship with the extent of mangroves and shallow waters in western peninsular Malaysia. *Estuarine, Coastal and Shelf Science*, 63(1–2), 187–200. <https://doi.org/10.1016/j.ecss.2004.11.008>
- Lugendo, B. R., Pronker, A., Cornelissen, I., de Groene, A., Nagelkerken, I., Dorenbosch, M., van der Velde, G., & Mgaya, Y. D. (2005). Habitat utilisation by juveniles of commercially important fish species in a marine embayment in Zanzibar, Tanzania. *Aquatic Living Resources*, 18(2), 149–158. <https://doi.org/10.1051/alr:2005016>
- MacDonald, J. A., & Weis, J. S. (2013). Fish community features correlate with prop root epibionts in Caribbean mangroves. *Journal of Experimental Marine Biology and Ecology*, 441, 90–98. <https://doi.org/10.1016/j.jembe.2013.01.019>
- Macia, A. (2004). Juvenile penaeid shrimp density, spatial distribution and size composition in four adjacent habitats within a mangrove–Fringed bay on Unhanca Island, Mozambique. *Western Indian Ocean Journal of Marine Science*, 3(2), 163–178.
- Macia, A., Abrantes, K. G. S., & Paula, J. (2003). Thorn fish *Terapon jarbua* (Forskål) predation on juvenile white shrimp *Penaeus indicus* H. Milne Edwards and brown shrimp *Metapenaeus monoceros* (Fabricius): The effect of turbidity, prey density, substrate type and pneumatophore density. *Journal of Experimental Marine Biology and Ecology*, 291(1), 29–56. [https://doi.org/10.1016/S0022-0981\(03\)00097-2](https://doi.org/10.1016/S0022-0981(03)00097-2)
- Mohan, R., & Siddeek, M. S. M. (1996). Habitat preference, distribution and growth of postlarvae, juvenile and pre-adult Indian white shrimp, *Penaeus indicus* H. Milne Edwards, in Ghubat Hasish Bay, Gulf of Masirah, Sultanate of Oman. *Fisheries Management and Ecology*, 3(2), 165–174. <https://doi.org/10.1111/j.1365-2400.1996.tb00140.x>
- Mumby, P. J., Edwards, A. J., Arias-González, J. E., Lindeman, K. C., Blackwell, P. G., Gall, A., Gorczyńska, M. I., Harborne, A. R., Pescod, C. L., Renken, H., Wabnitz, C. C. C., & Llewellyn, G. (2004). Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, 427(6974), 533–536. <https://doi.org/10.1038/nature02286>
- Nagelkerken, I., Dorenbosch, M., Verberk, W., Cocheret de la Morinière, E., & van der Velde, G. (2000). Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecology Progress Series*, 194, 55–64. <https://doi.org/10.3354/meps194055>
- Nagelkerken, I., & Faunce, C. H. (2007). Colonisation of artificial mangroves by reef fishes in a marine seascape. *Estuarine, Coastal and Shelf Science*, 75(3), 417–422. <https://doi.org/10.1016/j.ecss.2007.05.030>
- Nagelkerken, I., Sheaves, M., Baker, R., & Connolly, R. M. (2015). The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries*, 16(2), 362–371. <https://doi.org/10.1111/faf.12057>
- Nagelkerken, I., & Velde, G. V. D. (2002). Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)? *Marine Ecology Progress Series*, 245, 191–204.

- Olds, A. D., Connolly, R. M., Pitt, K. A., Pittman, S. J., Maxwell, P. S., Huijbers, C. M., Moore, B. R., Albert, S., Rissik, D., Babcock, R. C., & Schlacher, T. A. (2016). Quantifying the conservation value of seascape connectivity: A global synthesis. *Global Ecology and Biogeography*, 25(1), 3–15. <https://doi.org/10.1111/geb.12388>
- Richmond, M. D. (Ed.). (2011). *A field guide to the seashores of Eastern Africa and the Western Indian Ocean Islands* (3rd ed., p. 464). Sida/WIOMSA.
- Rönnbäck, P., Macia, A., Almqvist, G., Schultz, L., & Troell, M. (2002). Do Penaeid shrimps have a preference for mangrove habitats? Distribution pattern analysis on Inhaca Island, Mozambique. *Estuarine, Coastal and Shelf Science*, 55(3), 427–436. <https://doi.org/10.1006/ecss.2001.0916>
- Rönnbäck, P., Troell, M., Kautsky, N., & Primavera, J. H. (1999). Distribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao Mangroves, Philippines. *Estuarine, Coastal and Shelf Science*, 48(2), 223–234. <https://doi.org/10.1006/ecss.1998.0415>
- Roth, L. C. (1992). Hurricanes and mangrove regeneration: Effects of Hurricane Joan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua. *Biotropica*, 24(3), 375. <https://doi.org/10.2307/2388607>
- Sheaves, M. (2005). Nature and consequences of biological connectivity in mangrove systems. *Marine Ecology Progress Series*, 302, 293–305. <https://doi.org/10.3354/meps302293>
- Sheridan, P., & Hays, C. (2003). Are mangroves nursery habitat for transient fishes and decapods? *Wetlands*, 23(2), 449–458. <https://doi.org/10.1672/19-20>
- Swadling, D. S., Knott, N. A., Rees, M. J., & Davis, A. R. (2019). Temperate zone coastal seascapes: Seascape patterning and adjacent seagrass habitat shape the distribution of rocky reef fish assemblages. *Landscape Ecology*, 34(10), 2337–2352. <https://doi.org/10.1007/s10980-019-00892-x>
- Vance, D. J., Haywood, M. D. E., Heales, D. S., Kenyon, R. A., Loneragan, N. R., & Pendrey, R. C. (1996). How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguensis* and fish in a tropical mangrove forest in northern Australia. *Marine Ecology Progress Series*, 131(1–3), 115–124. <https://doi.org/10.3354/meps131115>
- Verweij, M. C., Nagelkerken, I., Graaff, D. D., Peeters, M., Bakker, E. J., & Velde, G. V. D. (2006). Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: A field experiment. *Marine Ecology Progress Series*, 306, 257–268.
- Wanjiru, C., Nagelkerken, I., Rueckert, S., Harcourt, W., & Huxham, M. (2023). Data from: Where to fish in the forest? Tree characteristics and contiguous seagrass features predict mangrove forest quality for fishes and crustaceans. *Edinburgh Napier Digital Repository*. <https://doi.org/10.17869/enu.2023.3069847>
- Wanjiru, C., Rueckert, S., & Huxham, M. (2022). Composition and structure of the mangrove fish and crustacean communities of Vanga Bay, Kenya. *Western Indian Ocean Journal of Marine Science*, 20(2), 25–44. <https://doi.org/10.4314/wiojms.v20i2.3>

How to cite this article: Wanjiru, C., Nagelkerken, I., Rueckert, S., Harcourt, W., & Huxham, M. (2023). Where to fish in the forest? Tree characteristics and contiguous seagrass features predict mangrove forest quality for fishes and crustaceans. *Journal of Applied Ecology*, 60, 1340–1351. <https://doi.org/10.1111/1365-2664.14421>