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Patterns of juvenile reef-fish recruitment in Kenya's shallow fringing-lagoon reefs

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Studies to understand local-scale patterns in the recruitment of juvenile coral-reef fishes within the western Indian Ocean (WIO) region are few, yet such knowledge is important in fisheries management. Underwater visual census surveys were conducted at five shallow fringing-lagoon reef sites along the Kenyan coast, between June 2012 and March 2016, to quantify patterns in the abundance of new recruits and juveniles. Recruitment was observed year-round, with a consistent pronounced seasonal peak in recruit densities and species richness during December to April of each year, which was strongly correlated with high sea temperatures. Annual variations in recruitment were also observed, with a higher recruitment peak in 2013 as compared with in other years. A total of 112 species belonging to 19 families were identified, dominated by species belonging to the Pomacentridae, Labridae and Apogonidae, which altogether represented 91% of the total number of recruits recorded. The species with the largest number of recruits (*Chromis viridis*, *Thalassoma hebraicum* and *Gomphosus caeruleus*) showed evidence of year-round recruitment, although the timing of recruitment peaks was not consistent. Multivariate analysis of the species composition separated mainland from offshore fringing-reef sites, and also revealed strong habitat associations, pointing towards increasing recruit abundance with increasing live hard-coral cover and rugosity. Live hard-coral cover, which constituted an average of 21%, was associated with 63% of the total number of recruits recorded. This study contributes new insight into local-scale patterns of juvenile reef-fish recruitment in Kenya and the WIO region, and demonstrates the important nursery function of shallow fringing-lagoon reefs.

Keywords: fish assemblage, habitat associations, nursery habitat, spatio-temporal variability, underwater visual census, western Indian Ocean

Introduction

Recruitment, broadly defined here as the addition of newly settled individuals from the pelagic larval phase, is among the most fundamental demographic processes responsible for the replenishment of reef-fish populations (Caley et al. 1996; Doherty 2002). Most coral-reef fishes have a life cycle that includes a planktonic larval phase that is driven by oceanographic processes linked to local topography and circulation at scales ranging from metres to thousands of kilometres (Leis 1991; Cowen and Castro 1994; Schmitt and Holbrook 1996), followed by a benthic phase. The two phases are coupled by a settlement phase, when larvae metamorphose into recruits and settle in suitable benthic habitats. Settling larvae detect suitable habitats by responding to various visual and chemical cues associated with the presence of adult conspecifics (e.g. Sweatman 1988; Lecchini et al. 2017), predators (e.g. Mitchell et al. 2011; Benkwitt 2017), and habitat characteristics (e.g. Igulu et al. 2013; Dixson et al. 2014; Brooker et al. 2016) and their associated auditory cues (e.g. Simpson et al. 2010; Parmentier et al. 2015; Gordon et al. 2018). Consequently, some sites may be preferred as recruitment hotspots, receiving a higher abundance of new recruits (Fowler et al. 1992; Sponaugle and Cowen 1996).

Nearshore shallow lagoon reefs contain a mosaic of substrate types, including hard corals, algal turf, seagrass

beds, seaweeds, sand, rubble and rocks, which provide important nursery habitats for juvenile reef fishes. The availability and structural complexity of these recruitment habitats play a major role in structuring the composition, abundance and distribution of reef-fish assemblages (Cowen and Castro 1994; Schmitt and Holbrook 1996; Graham and Nash 2013). However, the quality of these habitats continues to decline worldwide owing to human-induced stressors that include fishing, habitat degradation and the compounding effects of global warming (Rinkevich 2014; Macura et al. 2016).

Considerable research has been undertaken to understand the variable nature of reef-fish recruitment on a wide variety of spatial and temporal scales, especially in the Pacific region (see reviews by Sale et al. 1984; Caley et al. 1996; Doherty 2002; Hixon 2011; Sponaugle et al. 2012). In the western Indian Ocean (WIO) region, studies to quantify the distribution and abundance of reef-fish assemblages are well represented, but focus on either quantifying subadult/adult phases (e.g. Chabanet and Durville 2005; Tyler et al. 2009; Samoilyis et al. 2018) or larval phases (e.g. Mwaluma et al. 2010; Hedberg et al. 2018). Studies on the recruit and juvenile phases of coral-reef fishes in the WIO are few, with most investigations examining patterns of habitat use and connectivity in the mangrove–seagrass–coral-reef

continuum over narrow temporal scales (e.g. Bergman et al. 2000; Lugendo et al. 2005; Garpe and Öhman 2007). Knowledge of recruitment patterns is particularly important in the management of aquarium fisheries because they are highly dependent on the supply of juvenile fish (Barratt and Medley 1990). In Kenya, aquarium fishers are concentrated in shallow lagoon reefs (Okemwa et al. 2016), which also face other numerous anthropogenic pressures because of their proximity to land. This study investigated local-scale patterns of juvenile reef-fish recruitment in selected shallow fringing-lagoon reefs along the Kenyan coast over multiple temporal scales and examined the habitat associations of these fishes. The information generated provides an important baseline for future monitoring of environmental changes and for decision-making.

Materials and methods

General study area

The study was conducted on the Kenyan coast (Figure 1). Kenya's coastline is dominated by shallow fringing-lagoon reefs 100 m to 3 km in width, and extending to a depth of 20 to 25 m (Obura et al. 2000). The fringing-reef system is almost continuous along the southern coast from Msambweni to Malindi (approximately 200 km); patchy reefs are scattered northwards from Malindi to the Lamu Archipelago (approximately 100 km) and southwards from Msambweni to Shimoni (Obura et al. 2000). Water depth within the lagoon-reef systems is variable but reaches a maximum of ~12 m during spring low tide in some areas. Seasonality within the WIO is strongly influenced by cyclical climatic conditions driven by the Inter-Tropical Convergence Zone (ITCZ), which creates the northeast monsoon (NEM) season, from November to March, and the southeast monsoon (SEM) season, from April to October (Obura et al. 2000; Schott and McCreary 2001).

Recruitment surveys

Non-destructive underwater visual census (UVC) surveys were conducted between June 2012 and March 2016 at five study sites along the coast of Kenya: Kuruwitu, Kilifi, Sii, Mwipwa and Wasini (Figure 1). The surveys at Kuruwitu were conducted for six consecutive days monthly, over a period of 24 months, from June 2012 to June 2014, and thereafter every second month from August to December in 2014, in February and March in 2015, and a year later in March of 2016. The other four sites were surveyed for three consecutive days monthly, over a period of 10 months, from February 2013 to February 2015. Kuruwitu was selected for more-intense and longer-term monitoring due to year-round accessibility. The surveys were conducted in shallow depths of up to 2.5 m using the standard belt-transect method described by English et al. (1997). The first author (GMO) conducted the fish counts and size estimates by snorkelling slowly along a 50-m transect line laid parallel to the shoreline and recording all fish encountered within 1 m on either side (100 m²) on a white Perspex slate. This ensured that observer bias was consistent and hence comparable between sites (Samoilys and Carlos 2000). A T-shaped PVC pipe (1 m in width) was used to visually estimate the width of each transect. Individuals

were identified to species, as far as possible, based on morphological characteristics and colouration. Distinctive features of unidentified species were recorded and the species were later identified using fish identification guides. The total length (TL) of each fish was visually estimated with reference to a plastic 30-cm ruler attached to the slate. To minimise the error margin in size estimation, underwater trials were conducted prior to starting the surveys, using plastic cut-outs of known lengths until a margin of error of under 20% was achieved, following the methods of Pierre et al. (2002).

Each transect was surveyed twice, focusing on highly mobile fish during the first pass and on small (<10 cm TL) site-attached fish during the second pass. To enable repeated sampling within the same area, the location of each transect was georeferenced using GPS. Each survey took about 45 min to 1 h, depending on the site and season, and all surveys were carried out between 9 am and 3 pm, when light conditions were optimal. Prior to starting each survey, a waiting period of about 15 min was implemented to allow fish to resume normal behaviour. At each site, three to 12 transects were surveyed over time, with six transects at Kilifi, three each at Wasini, Sii and Mwipwa, and 12 at Kuruwitu. The smaller number of transects at some of the sites was due to issues of accessibility in terms of travel distance by boat, which limited survey time in relation to the tide as well as the spatial area. *In situ* sea temperature was measured using a HOBO Pro waterproof data logger (Onset Computer Corporation), attached to a sinker and buoy for easy retrieval.

Benthic habitat characterisation

Surveys to quantify the benthic cover at the study sites were conducted using the line intercept transect (LIT) method (English et al. 1997). The chain and tape method (Risk 1972) was used to measure structural complexity. A fibreglass measuring tape was placed along each transect parallel to a 50-m link chain (1.5 cm per link) which was carefully draped along the transect, following benthic contours and crevices as closely as possible, to measure the linear distance of the contours covered by the chain. As a measure of structural complexity, a rugosity index for each transect was calculated by dividing the contour length of the chain with the linear distance between the chain's endpoints (i.e. 50 m). An index of '1' indicated a flat substrate of low rugosity. The surveys of benthic cover were conducted once during the study period, with the assumption of minimal temporal variations in cover.

Habitat associations

Surveys to quantify the habitat associations of new reef-fish recruits and juveniles at the study sites were conducted in January 2014, except at Kilifi, where the survey was aborted because of poor visibility. New recruits and juvenile fish were identified to species level and quantified, and the microhabitat immediately beneath each individual at first observation was recorded, based on the methods of Wilson et al. (2010).

Data processing and analysis

The fish were classified by size, as either: (i) new recruits – very small and pale individuals (≤ 2 cm TL) with little or no pigmentation (except for Acanthuridae and Chaetodontidae

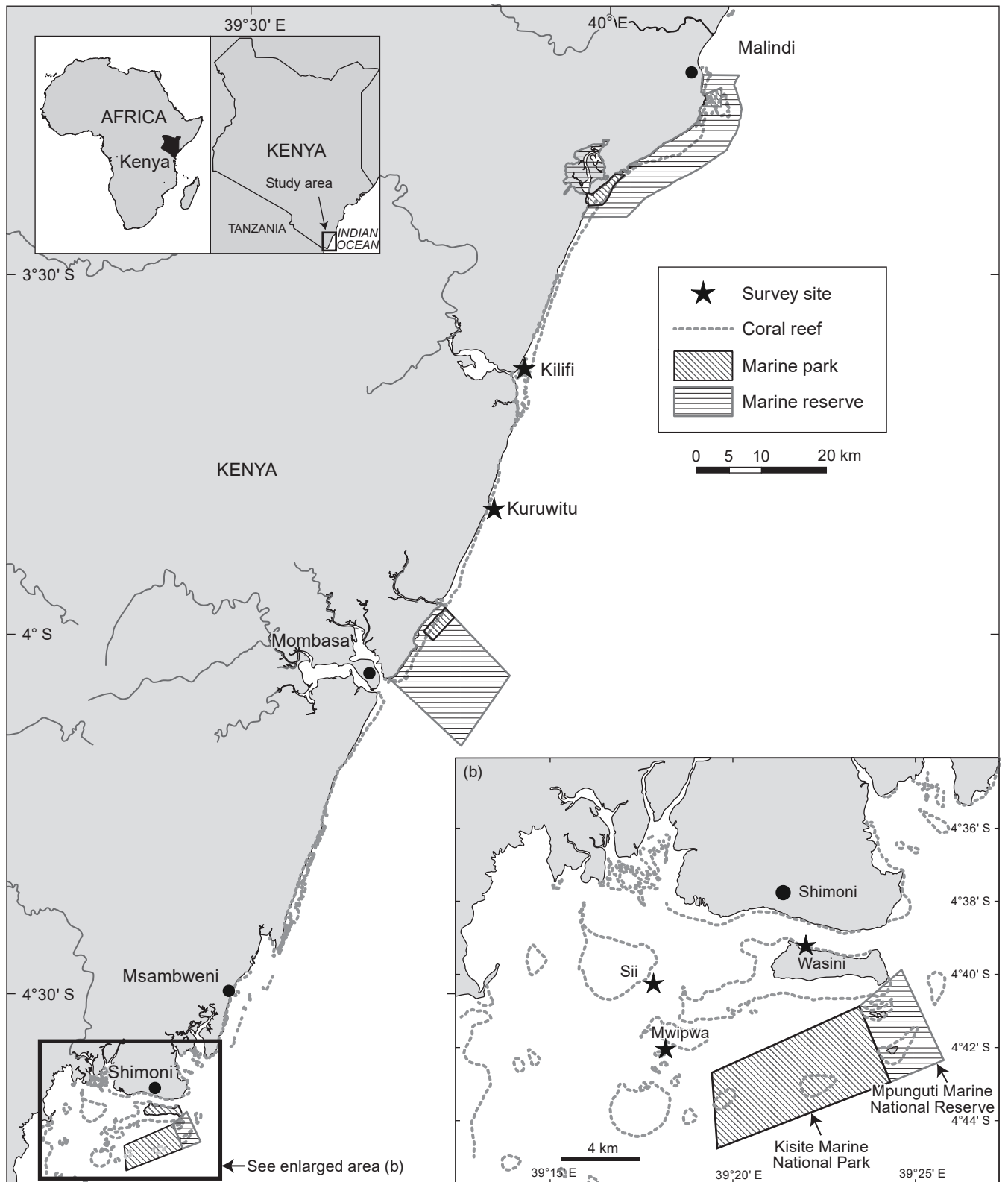


Figure 1: Maps showing the general location of the fringing-lagoon reef sites surveyed along the Kenyan coastline: Kilifi, Kuruwitu, Wasini, Sii and Mwipwa

species, which were observed at much bigger sizes of up to 4 cm TL; (ii) juveniles – distinctly coloured individuals <25% of the maximum adult TL, as reported in FishBase (Froese and Pauly 2016); or (iii) subadults/adults – individuals that were >25% of the maximum adult TL (adapted from Russell et al. 1977 and Walsh 1987). The species composition of the new recruits at each site was assessed at the family and species level by calculating relative abundance (%) and was described further using three community indices: Margalef's species richness D' , the Shannon–Wiener index H' , and Pielou's evenness index J' (Magurran 2004). The Kruskal–Wallis multiple *post hoc* pairwise test was used to test for significant differences between sites. A nonmetric multidimensional scaling (nMDS) ordination was applied to compare differences in the species composition of new recruits between sites. The data were square-root transformed prior to ordination to reduce weighting of abundant species, and a hierarchical group-average clustering based on a Bray–Curtis similarity matrix was overlaid to elucidate similarities between sites (Clark and Warwick 2001). The relative distance of the data points provides a measure of similarity. A posterior analysis of similarity (ANOSIM) test was further applied to check for significant differences in the species composition of recruits between sites, years and seasons, followed by a similarity of percentage (SIMPER) analysis, which was used to identify which species contributed most to dissimilarities between sites and their proportional contribution.

Recruit abundance was estimated as the mean number of new recruits per transect (\pm standard error). To elucidate temporal recruitment patterns at Kuruwitu, the mean recruit densities for each month sampled were presented graphically using bar graphs for some commonly occurring taxa (those having a high frequency of occurrence in the surveyed transects). Pearson's correlation coefficient was used to test for correlations with the mean monthly sea temperature. The Scaridae (parrotfishes) were assessed at family level only because it was difficult to distinguish the recruits of species that had very similar markings and colouration. The juvenile parrotfish were also highly mobile and moved in groups of mixed species, which made it difficult to reliably estimate numbers at the species level. The Gobiidae were also excluded from the analysis of density estimates because the species are very cryptic and hence difficult to count reliably.

To assess variations in fish densities between sites, the Kuruwitu data were filtered to include only the 10 months in which sampling was done at the other four sites. The nonparametric Mann–Whitney U -test was used to test for within-year seasonal differences among key families at Kuruwitu. Annual and seasonal differences in recruit densities for 10 abundant species at Kuruwitu were further tested using a two-way ANOVA on $\log_{10}(x + 1)$ transformed data to meet the model assumptions of homogeneity and normality (Zar 1999). Variations in the benthic substrate cover between sites were tested using a one-way ANOVA on arcsine-transformed data, and the habitat associations of the three life-cycle phases (new recruits, juveniles and subadults/adults) were visualised using a canonical correspondence analysis (CCA; Legendre and Legendre 1998) applied on the abundance data. Species-specific

habitat associations were further visualised using detrended correspondence analysis (DCA; Hill and Gauch 1980). The statistical analyses were conducted using STATISTICA (StatSoft, Inc.), PRIMER (Clarke and Gorley 2006) and PAST (Hammer et al. 2001). All tests for significance were performed at a confidence level of 95%.

Results and discussion

Spatial patterns in recruitment

Overall, a total of 24 946 new recruits were recorded, comprising 19 families and 112 species. New recruits and juveniles constituted 35% of the total number of individuals encountered at Kuruwitu, 45% at Kilifi, 49% at Sii, 67% at Wasini and 40% at Mwipwa. Families with the highest number of species recruiting included the Pomacentridae (23 species), Labridae (20 species), Chaetodontidae (10 species), Scaridae (7 species) and Acanthuridae (7 species). Kuruwitu had the highest number of species recruiting (67 species), and Mwipwa had the lowest (46 species). The Pomacentridae and Labridae were the most abundant taxa recruiting in all the study sites, which was similar to other tropical fringing-reef systems, such as in the Philippines (Abesamis and Russ 2010) and Tanzania (Garpe and Öhman 2007).

The average density of juvenile and subadult/adult phases among the common families of reef fishes was two- to four-fold higher than that of recruits at all the sites (Figure 2). Variability in recruit densities between the study sites was particularly evident among the common fish families. The recruit density of the Pomacentridae was highest at Sii and Wasini. The recruit density of the Labridae was highest at Kuruwitu, whereas the recruit and juvenile densities of the Scaridae and Acanthuridae were highest at Mwipwa. Although Kuruwitu had the highest abundance of subadult/adult phases of the Acanthuridae, the densities of recruit and juvenile phases were substantially lower. Juvenile and subadult/adult phases of the Apogonidae were most abundant at Sii.

The most-abundant species included the damselfishes *Chromis viridis* and *Neopomacentrus azysron*, the wrasses *Thalassoma hebraicum* and *Gomposus caeruleus*, and the cardinalfish *Ostorhinchus cookii*, which collectively comprised 60% of the total number of new recruits recorded (Table 1). *Chromis viridis* accounted for 25% of the total number of new recruits recorded at Kuruwitu, 27% at Kilifi, and 63% at Wasini. *Neopomacentrus azysron* and *N. cyanomos* recruits were recorded only at Sii, accounting for 59% and 13% of the total, respectively (Table 1). At Mwipwa, the dartfish *Ptereleotris evides*, the Scaridae and the surgeonfish *Zebrossoma scopas* were the most abundant. The high abundance of *N. azysron*, *C. viridis* and *P. evides* recruits at Sii and Mwipwa was most likely due to the high abundance of subadult/adult conspecifics and their aggregating behaviour.

The Kruskal–Wallis pairwise multiple comparison test revealed significant differences in the recruit community diversity between the sites, with Sii and Wasini being significantly different from the other sites ($H = 14.8$, $p = 0.005$). There was also a significant difference in the mean species evenness (J'), with Wasini being significantly

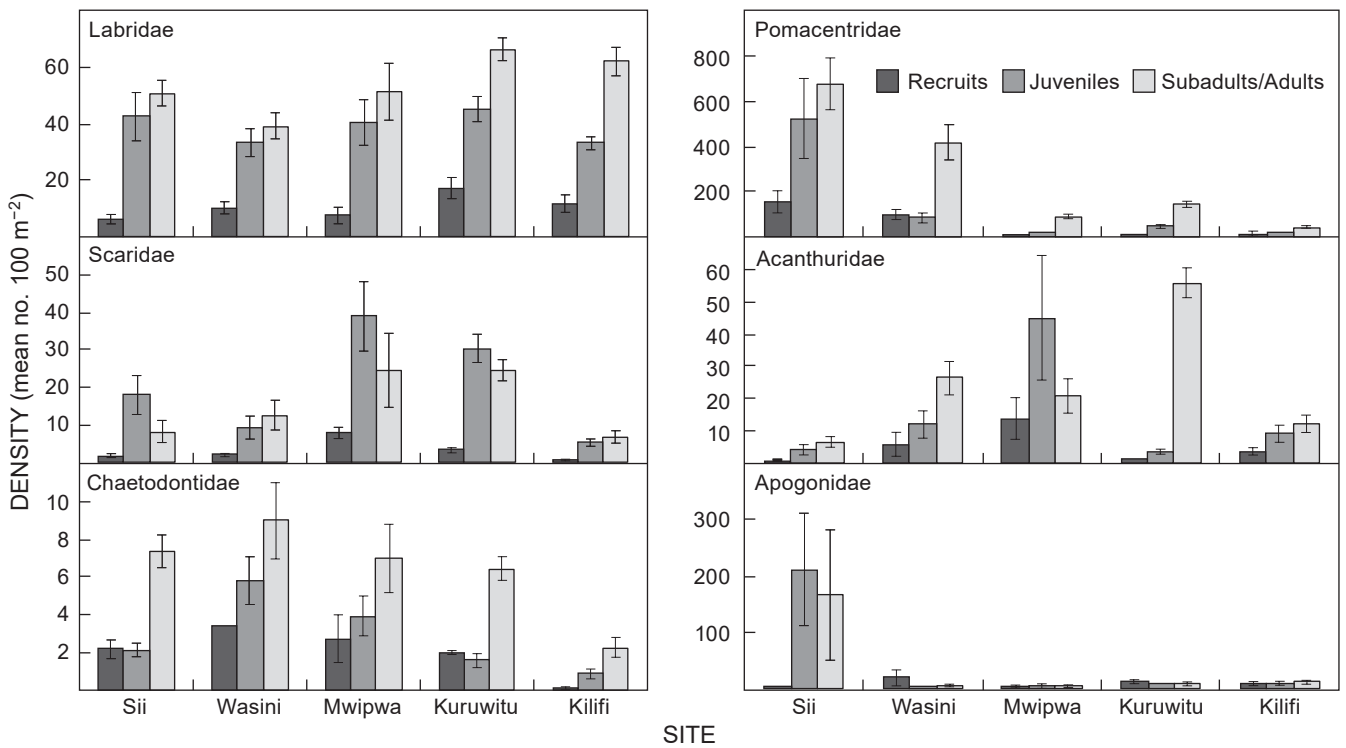


Figure 2: Mean density (±SE) of new recruits, juveniles and subadults/adults of six abundant reef-fish families at the sites surveyed on the Kenyan coast

Table 1: Relative abundance of the 25 most-abundant species of reef-fish recruits and the community assemblage characteristics at the five fringing-lagoon reef study sites on the Kenyan coast

Family	Species	Relative abundance (%)				
		Kilifi	Kuruwitu	Mwipwa	Sii	Wasini
Pomacentridae	<i>Chromis viridis</i>	27	25	0	7	63
Pomacentridae	<i>Neopomacentrus azyron</i>	0	0	0	59	0
Labridae	<i>Thalassoma hebraicum</i>	7	16	5	0	3
Apogonidae	<i>Ostorhinchus cookii</i>	2	12	0	0	0
Labridae	<i>Gomphosus caeruleus</i>	2	10	4	1	2
Scaridae	<i>Scarus</i> spp.	1	6	14	1	1
Pomacentridae	<i>Neopomacentrus cyanomos</i>	0	0	0	13	0
Microdesmidae	<i>Ptereleotris evides</i>	0	0	24	9	0
Pomacentridae	<i>Chrysiptera unimaculata</i>	1	5	0	0	0
Pomacentridae	<i>Dascyllus aruanus</i>	0	4	0	0	3
Labridae	<i>Thalassoma amblycephalus</i>	10	3	0	0	1
Apogonidae	<i>Cheilodipterus quinquilineatus</i>	6	0	2	0	9
Pomacentridae	<i>Abudefduf vaigiensis</i>	0	3	3	0	0
Siganidae	<i>Siganus sutor</i>	11	0	0	3	0
Labridae	<i>Halichoeres scapularis</i>	0	2	0	0	0
Acanthuridae	<i>Ctenochaetus striatus</i>	4	1	5	0	3
Labridae	<i>Stethojulis albobittata</i>	2	2	0	0	0
Labridae	<i>Thalassoma hardwicke</i>	0	2	2	0	0
Pomacentridae	<i>Stegastes nigricans</i>	0	1	3	0	1
Pomacentridae	<i>Plectroglyphidodon lacrymatus</i>	2	1	3	1	0
Acanthuridae	<i>Zebrassoma scopas</i>	0	0	12	0	0
Chaetodontidae	<i>Chaetodon trifasciatus</i>	0	0	1	1	2
Labridae	<i>Labroides dimidiatus</i>	2	1	0	0	0
Pomacentridae	<i>Dascyllus trimaculatus</i>	1	0	0	0	2
Community indices	Number of species	57	67	45	49	54
	Margalef's species richness <i>D'</i>	7.56	7.08	5.86	5.69	6.59
	Pielou's evenness <i>J'</i>	0.69	0.61	0.48	0.40	0.43
	Shannon–Wiener diversity <i>H'</i>	2.82	2.56	1.85	1.58	1.72

different from the other sites ($H = 13.1, p = 0.011$). However, the species richness (D') did not differ significantly ($H = 6.55; p = 0.16$). The results of nMDS with cluster analysis grouped the mainland fringing-reef sites (Kuruwitu and Kilifi) and Wasini as more similar in the species composition of new recruits when compared with the offshore island sites (Sii and Mwipwa) (Figure 3a). The species composition of subadult/adult life phases grouped as similar to that of new recruits at all the sites except for Mwipwa (Figure 3b). The results suggest that recruit assemblages in the mainland fringing-lagoon reefs may differ from offshore fringing reefs.

The SIMPER analysis identified *N. azysron* and *P. evides* as most responsible for discriminating the offshore sites from the mainland sites (Table 2). *Neopomacentrus azysron* also contributed most to the dissimilarity between Kilifi and Sii, Mwipwa and Sii, and Kuruwitu and Sii, and *C. viridis* contributed most to dissimilarities between Wasini and the other four sites. Dissimilarity between Kilifi and Sii was also influenced by the abundance of *T. hebraicum* and *C. viridis* recruits which, together with *N. azysron*, contributed about 20% to the dissimilarity, while the grouping of Kuruwitu with Kilifi was influenced by a high abundance of *C. viridis*, *T. hebraicum* and *O. cookii*, contributing about 19% to the dissimilarities. The observed patterns suggest that the species composition of new recruits at mainland fringing-reef sites might be distinct from that at offshore sites, and this could potentially be attributed to a multitude of factors that drive larval dispersal, settlement, and post-settlement survival, including the presence or abundance of conspecifics, the presence or abundance of predators, site-specific habitat and oceanographic features, as well as ontogenic shifts in movement by juveniles and older life phases as a result of changing food and habitat requirements (Beck et al. 2016; Lee et al. 2019).

Temporal patterns in recruitment

Recruitment at Kuruwitu was observed year-round with a consistent unimodal peak in recruit densities occurring between December and April during 2012/2013 and 2013/2014 (Figure 4). The seasonal peak correlated

positively with high mean monthly *in situ* temperatures ($r = 0.55, p = 0.002$), which peaked from November to March (NEM season) in 2012/2013 and 2013/2014. Collectively, recruitment of the four most-abundant families was approximately two-times higher during the NEM season compared with the SEM season ($U = -7.05, p < 0.01$; Table 3). A two-way ANOVA further detected significant effects of Year ($F = 12.06, p = 0.001$) and Season ($F = 79.29, p = 0.001$) on recruit densities, as well as significant interactions ($F = 143.9, p = 0.001$). The Labridae exhibited no significant seasonal differences in density (Table 3). *Thalassoma hebraicum* recruited year-round, with no consistency in the timing of the seasonal peak, although *G. caeruleus* showed some evidence of seasonality (Figure 5). In contrast, the pomacentrid species *C. unimaculata* and *D. aruanus* exhibited a more consistent seasonal peak (Figure 5). A significant interaction effect of Year and Season was observed for eight of the 10 most-abundant species (Table 4).

The increasing sea temperatures during the NEM season can trigger spawning events when biological cues such as food availability become more suitable, cascading into increased larval settlement rates (Lecchini et al. 2007; Okamoto et al. 2012). Despite a decline in recruit abundance during 2013/2014 as compared with 2012/2013, levels of species richness remained relatively strong, indicating that fewer individuals among species recruited rather than this being due to total recruitment failure (Figure 4).

Apart from sea temperatures, a number of other correlated factors might influence recruitment seasonality; for example, the timing of spawning is triggered by environmental variables such as the lunar and tidal cycles, wave action due to currents, wind stress and upwelling (Aburto-Oropeza and Balart 2001; Agostini and Bakun 2002; Nemeth and Appeldoorn 2009; Rankin and Sponaugle 2014). Several studies in tropical systems elsewhere report similar seasonal influences on recruitment patterns, for example in the Great Barrier Reef in Australia (Russell et al. 1977), Barbados (Tupper and Hunte 1994), the Mediterranean (Garcia-Rubies and Macpherson

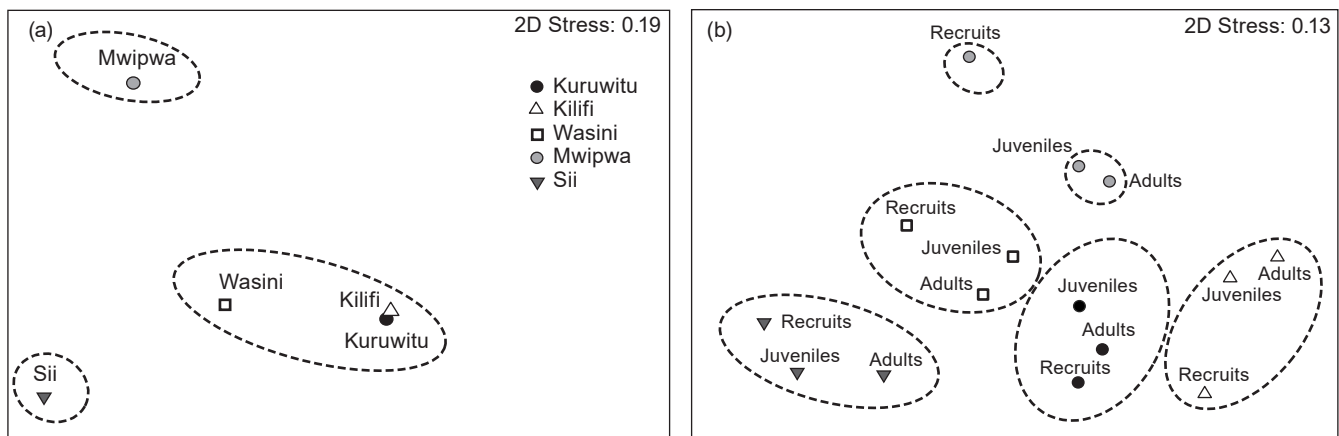


Figure 3: Non-metric multidimensional scaling ordination plots of the reef-fish assemblages at five study sites along the Kenyan coast, obtained using Bray–Curtis similarity contours on square-root-transformed data. (a) The composition of recruits compared at 40% similarity, and (b) the composition of recruits with juveniles and subadults/adults at 50% similarity

Table 2: Summary of SIMPER analysis showing the average dissimilarity in the species composition of new reef-fish recruits between study sites on the Kenyan coast, and the three species that contributed most to the overall dissimilarities

Species	Mean abundance (%)		Dissimilarity	Cumulative contribution (%)
	Kilifi	Sii		
			Av. diss. = 89.3	
<i>Neopomacentrus azysron</i>	0	4.77	8.88	9.95
<i>Thalassoma hebraicum</i>	3.61	0.56	5.87	16.53
<i>Chromis viridis</i>	0.82	2.57	5.02	22.15
			Av. diss. = 78.7	
<i>Chromis viridis</i>	0.82	7.64	12.16	15.42
<i>Cheilodipterus quinquilineatus</i>	1.85	1.56	4.73	21.42
<i>Thalassoma hebraicum</i>	3.61	1.41	4.26	26.83
			Av. diss. = 76.2	
<i>Chromis viridis</i>	2.57	7.64	11.16	14.64
<i>Neopomacentrus azysron</i>	4.77	0.13	9.68	27.34
<i>Neopomacentrus cyanomos</i>	2.69	0.24	5.28	34.26
			Av. diss. = 77.2	
<i>Ptereleotris evides</i>	0	4.5	7.35	9.53
<i>Cheilodipterus quinquilineatus</i>	1.85	1.01	3.93	14.63
<i>Thalassoma hebraicum</i>	3.61	1.56	3.82	19.59
			Av. diss. = 83.4	
<i>Neopomacentrus azysron</i>	4.77	0	8.76	10.51
<i>Ptereleotris evides</i>	1.23	4.50	7.8	19.87
<i>Neopomacentrus cyanomos</i>	2.69	0	4.71	25.52
			Av. diss. = 80.2	
<i>Chromis viridis</i>	7.64	0	13.08	16.3
<i>Ptereleotris evides</i>	0.11	4.5	7.92	26.17
<i>Cheilodipterus quinquilineatus</i>	1.56	1.01	2.99	29.89
			Av. diss. = 76.9	
<i>Ptereleotris evides</i>	4.5	0	7.4	9.62
<i>Chromis viridis</i>	0	3.07	4.76	15.81
<i>Thalassoma hebraicum</i>	1.56	4.24	4.72	21.94
			Av. diss. = 67.6	
<i>Chromis viridis</i>	0.82	3.07	4.96	7.35
<i>Thalassoma hebraicum</i>	3.61	4.24	3.83	13.02
<i>Ostorhinchus cookii</i>	1.69	2.21	3.83	18.68
			Av. diss. = 83.4	
<i>Neopomacentrus azysron</i>	4.77	0.21	8.73	10.46
<i>Thalassoma hebraicum</i>	0.56	4.24	7.10	18.98
<i>Chromis viridis</i>	2.57	3.07	5.73	25.85
			Av. diss. = 68.8	
<i>Chromis viridis</i>	7.64	3.07	8.58	12.47
<i>Thalassoma hebraicum</i>	1.41	4.24	5.27	20.14
<i>Gomphosus caeruleus</i>	1.07	3.17	4.23	26.29

1995), the US Virgin Islands (Miller et al. 2001), and the Philippines (Abesamis and Russ 2010). Although not assessed in this study, asynchrony in seasonal recruitment peaks can occur between sites, as reported by Planes et al. (1993) who observed more-stable recruitment patterns in inner nearshore reefs as compared with outer reefs in Moorea, French Polynesia.

Habitat characteristics

Benthic cover was recorded according to nine benthic categories: live coral, dead coral, coral rubble, rocky substrate, soft corals, sand, algal turf, macroalgae (mainly seaweeds) and sponges (Appendix). The main substrates constituted live hard corals, dead coral, rubble and rocky substrate. Results of the Kruskal–Wallis pairwise multiple

comparison test showed significant variations in benthic composition among the sites ($H = 19.8$, $p < 0.001$). Overall, the mean cover of live hard coral was 22.2%, ranging from 0.6% (SE 0.4) at Kilifi to 40.6% (SE 5.1) at Wasini. Live hard coral was the dominant cover at Kuruwitu and Wasini, and significantly differed between Kilifi and Kuruwitu ($p < 0.05$), and between Kilifi and Wasini ($p < 0.001$). No significant differences in mean live coral cover were observed among the other sites. Dead coral cover ranged from 0.3% (SE 0.2) at Kilifi to 19.2% (SE 16.8) at Mwipwa and did not differ significantly between sites. Coral-rubble cover ranged from 0.4% (SE 0.4) at Wasini to 43.7% (SE 7.2) at Kilifi, and was the dominant substrate at Kilifi, Mwipwa and Sii, whereas rocky substrate ranged from 1.2% (SE 0.7) at Kilifi to 23% (SE 2.2) at Mwipwa.

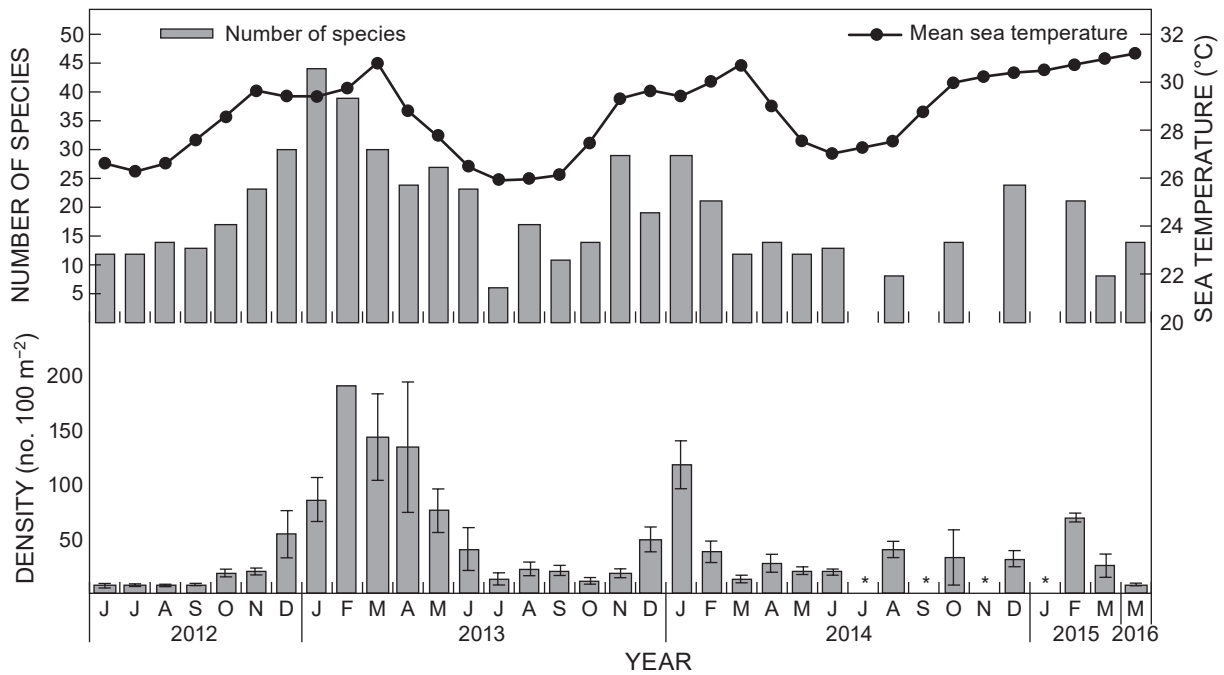


Figure 4: Monthly patterns in the abundance of new reef-fish recruits at Kuruwitu, Kenya, from June 2012 to March 2015 and in March 2016, presented as the total number of species and the mean density (\pm SE) per transect. Asterisks (*) indicate months when no data were collected

Table 3: Mann–Whitney *U*-test results comparing seasonal variations in densities (number of fish 100 m⁻²) of new recruits for the four most-abundant reef-fish families surveyed at Kuruwitu, Kenya, over the study period (June 2012 to December 2014, and February to March 2015). Seasons: NEM = northeast monsoon; SEM = southeast monsoon

Family	Year	Mean density (SE)		<i>U</i>	<i>p</i> -value
		NEM	SEM		
Labridae	2012	9.6 (1.5)	6.8 (1)	-1.69	0.09
	2013	23.0 (3)	15.4 (1.9)	-1.91	0.06
	2014	28.8 (7.8)	12.3 (1.8)	-0.93	0.35
	2015	3.9 (1.6)	–		
Pomacentridae	2012	27.3 (13.8)	2.5 (0.7)	-4.10	0.001*
	2013	44.0 (12.2)	22.4 (9.6)	-5.68	0.001*
	2014	10.7 (2.2)	9.8 (3.6)	-1.75	0.08
	2015	3.8 (2)	–		
Apogonidae	2012	0.4 (0.2)	0.2 (0.2)	-1.23	0.22
	2013	29.2 (12.4)	10.4 (5.7)	-1.36	0.18
	2014	13.4 (6.3)	7.5 (4.1)	-2.85	0.001*
	2015	12.4 (5.8)	–		
Scaridae	2012	1.9 (0.8)	0.1 (0.1)	-1.62	0.10
	2013	8.3 (1.9)	1.3 (0.5)	-3.22	0.001*
	2014	5.0 (1.3)	0.9 (0.3)	-3.28	0.001*
	2015	2.3 (0.8)	–		
Overall	–	60.2 (6.8)	31.3 (4.7)	-7.05	0.001*

*Significant effects

Habitat associations of new recruits and juveniles

Of the 3 268 recruits and juveniles recorded, 63% (2 059) were associated with live hard coral, compared with 45% estimated by Wilson et al. (2010) in Australia, and 11% (559) with dead coral. About 18% (945) were associated with seagrass, and the remaining 8% (432) with other substrates,

including rubble mixed with sand, rocky substrate, algal turf, macroalgae and sponges. Results of CCA ordination of benthic cover with the three life-history phases (recruits, juveniles and subadults/adults) indicated distinct habitat preferences (Figure 6). Live hard-coral cover and reef rugosity were the strongest predictors of recruit abundance, with

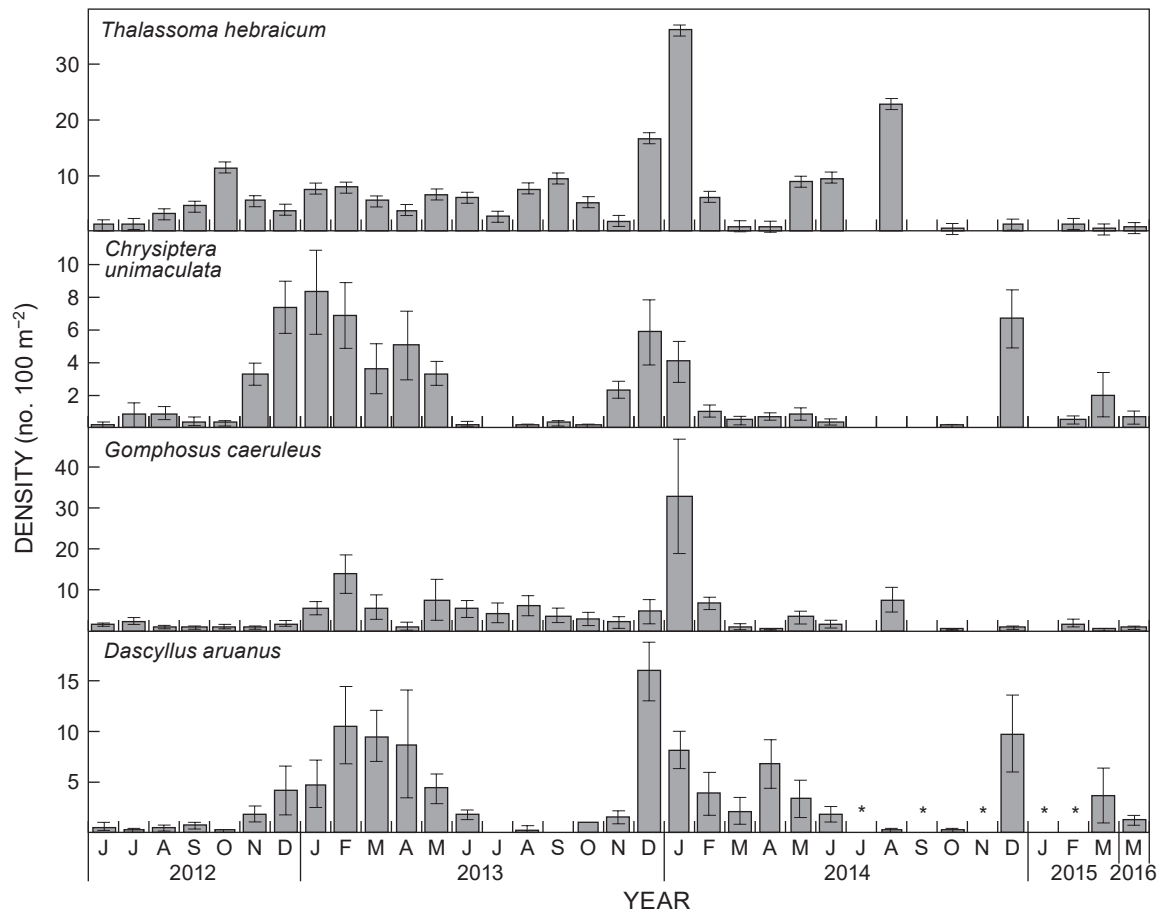


Figure 5: Monthly variation in the mean density (\pm SE) of new recruits for some abundant reef-fish species at Kuruwitu, Kenya

Table 4: Results of two-way ANOVA testing for effects of year (June 2012–December 2014) and season (northeast monsoon vs southeast monsoon) on new-recruit densities ($\log_{10}[x + 1]$ transformed data) for the 10 most-abundant reef-fish species at Kuruwitu, Kenya

Species	Year		Season		Year \times Season	
	F	p-value	F	p-value	F	p-value
<i>Thalassoma hebraicum</i>	8.15	0.001*	2.60	0.11	117.03	0.001*
<i>Gomphosus caeruleus</i>	4.35	0.001*	8.64	0.001*	56.64	0.001*
<i>Thalassoma hardwicke</i>	2.73	0.03*	25.40	0.001*	8.19	0.001*
<i>Ostorhinchus cookii</i>	4.02	0.001*	4.47	0.04*	6.31	0.001*
<i>Canthigaster valentini</i>	0.73	0.57	0.02	0.90	1.64	0.20
<i>Chromis viridis</i>	2.65	0.04*	0.25	0.62	15.84	0.001*
<i>Stegastes nigricans</i>	9.57	0.001*	80.97	0.001*	8.18	0.001*
<i>Chrysiptera unimaculata</i>	33.45	0.001*	142.66	0.001*	46.33	0.001*
<i>Dascyllus aruanus</i>	9.45	0.001*	19.15	0.001*	89.35	0.001*
<i>Zebrassoma scopas</i>	0.72	0.58	0.00	1.00	0.25	0.62

*Significant effect

abundance increasing with increasing cover and rugosity. The acute angle of the rugosity vector against Axis 1 reflected a stronger influence on recruit abundance. In contrast, the CCA revealed a decreasing pattern of recruit abundance with increasing seagrass, algal and dead-coral cover. The extended length of the rubble vector indicated a strong association among juvenile phases, whereas the seagrass

vector indicated a strong association with subadult/adult phases (Figure 6). Dixon et al. (2014) observed that some newly settled reef fish may selectively avoid certain habitats, such as macroalgae, using olfactory cues. The observed association of subadults/adults with seagrass was likely due to the high abundance of herbivorous species, notably members of the Labridae (*Thalassoma* species) and Acanthuridae.

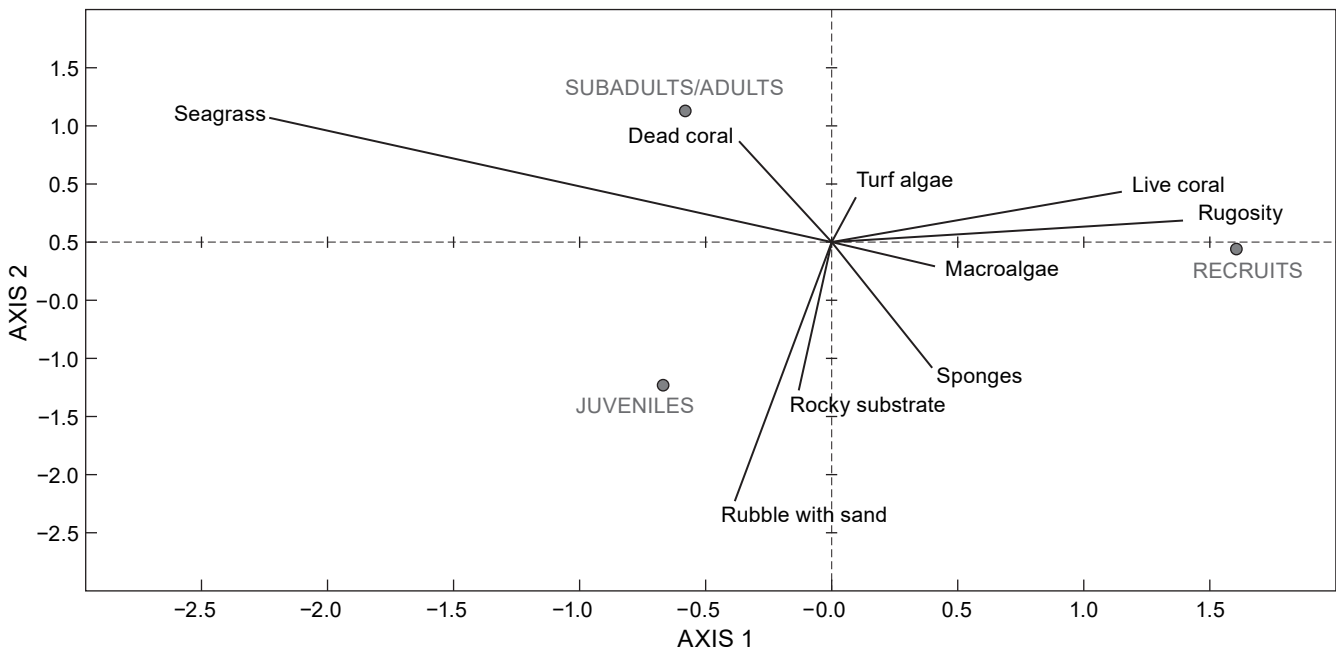


Figure 6: A canonical correspondence analysis biplot of the first two axes showing the general habitat associations (based on benthic cover) of the recruit, juvenile and subadult/adult phases of coral-reef fishes at the study sites on the Kenyan coast

Ordination of species-specific habitat associations using DCA revealed that species belonging to the Pomacentridae, Chaetodontidae, Microdesmidae and Apogonidae associated strongly with live hard coral, whereas members of the Acanthuridae associated with turf algae and macroalgae (Figure 7). Members of the Scaridae, Siganidae, Mullidae and Sphyraenidae associated strongly with seagrass. Species belonging to the Labridae associated with more-diverse substrates, including rocky substrate, dead coral with algae, and dead coral, whereas members of the Tetraodontidae, Gobiidae and Blennidae associated with rubble mixed with sandy habitats. Among the Pomacentridae, *C. viridis*, *D. aruanus* and *D. carneus* associated strongly with live hard coral, concurring with various studies (e.g. Öhman et al. 1998; Lecchini et al. 2007; Deocadez et al. 2008; Ticzon et al. 2012), whereas *Stegastes nigricans* and *Plectroglyphidodon lacrymatus* associated with dead coral and rocky substrates encrusted with algae. Among species of the Labridae, recruits and juveniles of *Halichoeres hortulanus* and *H. scapularis* associated strongly with sandy habitats mixed with rubble, especially under massive corals and rocks. However, *T. hebraicum*, *G. caeruleus*, *Thalassoma lunare* and the cleaner wrasse *Labroides dimidiatus* were associated with more-diverse habitats, indicating generalist behaviour and a larger niche breadth. Among the Acanthuridae, *Acanthurus nigrofuscus* associated strongly with seagrass and algal turf, whereas *Zebrassoma veliferum* and *Z. scopas* associated with live hard coral.

Some species of the Pomacentridae (e.g. *Stegastes nigricans*) are reported to exhibit site fidelity, foraging within a narrow home range, whereas others (e.g. *C. viridis* and *D. aruanus*) exhibit habitat specificity, associating strongly with specific growth forms of live coral (Wilson et al. 2008,

2010; DeMartini et al. 2010; Pratchett et al. 2012). Species with specialised preferences are highly susceptible to localised declines in live coral cover as they face intense density-dependent competition for space during settlement, leading to high post-settlement mortalities (Munday 2004; Bonin et al. 2009). Conversely, species exhibiting generalist behaviour are likely to be more resilient to environmental disturbances, particularly loss of coral cover and habitat complexity (Jones et al. 2004; Bonin et al. 2009).

Conclusions

This study reinforces the important role of shallow fringing-lagoon reefs as nursery grounds. The study suggests that mainland fringing-lagoon reef sites have a relatively distinct composition of juvenile reef-fish assemblages as compared with offshore sites, with recruit-habitat associations being best explained by the presence of hard-coral cover and increasing habitat complexity. The inherent limitations of UVC transect surveys are well documented (Samoilys and Carlos 2000; Emslie et al. 2018). However, the most critical in this study were: (i) the efficiency of searching for recruits, especially within structurally complex habitats; (ii) achieving accuracy in the estimation of fish lengths; and (iii) determining the cut-off size for recruit-phases of different species. Despite these limitations, the findings provide new insight into the recruitment patterns of juvenile reef fishes in Kenya and the WIO region, covering a number of temporal scales. Considering the impacts of climate change, including the projected consequences on reef-fish recruitment (Shoji et al. 2011; Hoey et al. 2016), future research should focus on establishing permanent sites for region-wide long-term recruitment monitoring, which can be undertaken during the identified peak season, to

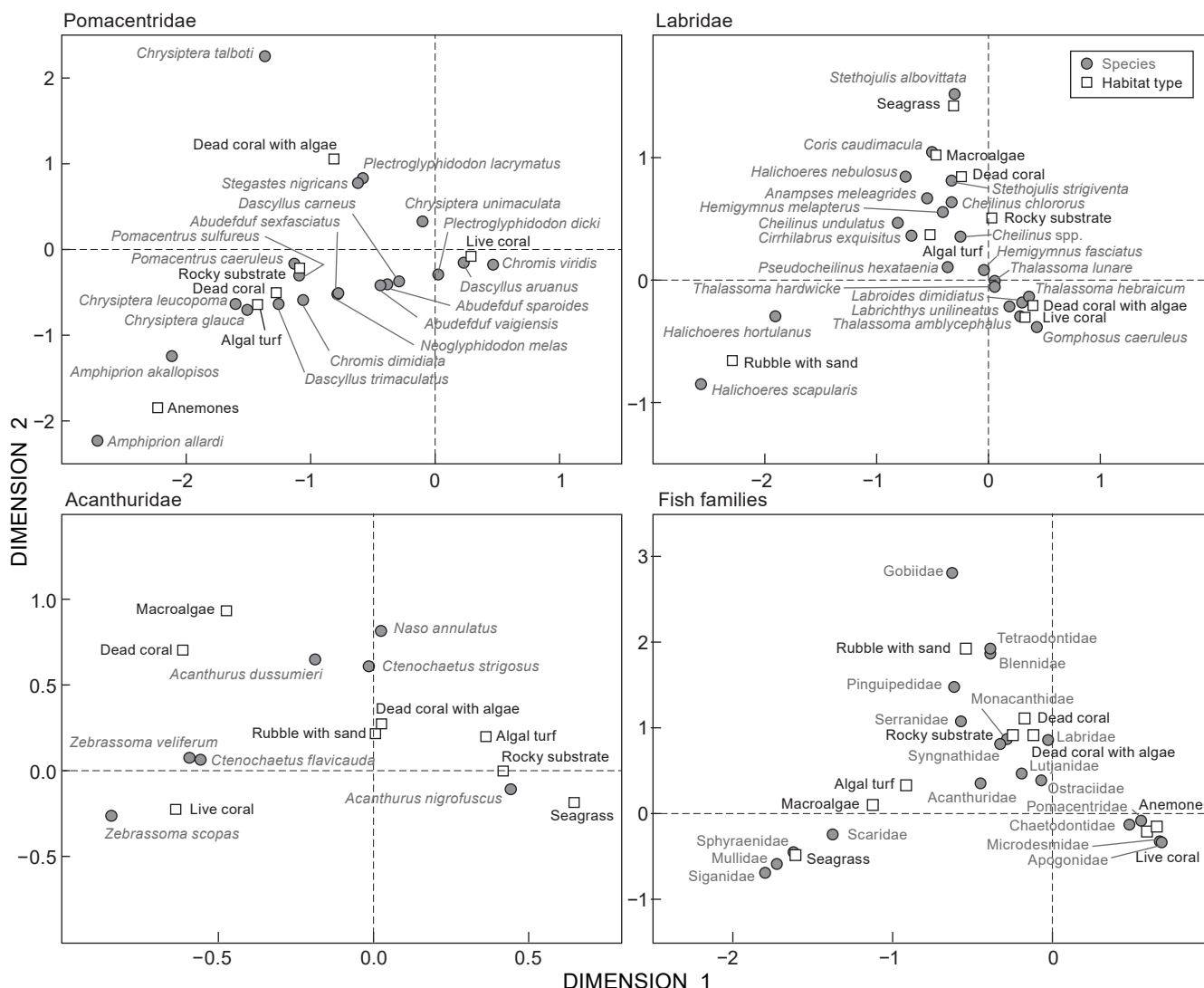





Figure 7: Detrended correspondence analysis plots of pooled data showing the habitat associations of new recruits and juveniles among the most commonly sighted reef-fish species and families at the Kenyan fringing-lagoon reef sites surveyed

track changes over time and to identify hotspots that might deserve conservation attention. Taking into consideration cost implications, it would also be ideal to combine UVC surveys with diver-operated stereo-video systems (stereo DOVs), which have been successful in providing comparable estimates (Wilson et al. 2018). This study represents a start in understanding local-scale patterns in the recruitment of post-settlement phases of reef fishes. Such knowledge has important implications for the design and placement of restorative measures aimed at enhancing reef-fish recruitment, such as closed seasons, spatial closures and artificial reefs.

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Appendix: Estimates of mean benthic cover (%) and the rugosity index (standard error) at the fringing-lagoon reef sites surveyed along the Kenyan coast

	Kilifi	Kuruwitu	Mwipwa	Sii	Wasini
Live coral	0.6 (0.4)	28.2 (3.7)	25.8 (15.4)	12.5 (0.9)	40.6 (5.1)
Dead coral	0.3 (0.2)	5.3 (1.8)	19.2 (16.8)	1.8 (0.9)	3.1 (0.9)
Rubble	43.7 (7.2)	4.3 (0.7)	30.4 (0.4)	26.6 (2.8)	0.4 (0.4)
Rocky substrate	1.2 (0.7)	17.2 (1.8)	23.0 (2.2)	19.3 (4.6)	6.3 (1.1)
Soft corals	0.1 (0.1)	2.4 (0.7)	1.4 (1.4)	14.4 (2.9)	0.9 (0.3)
Sand	5.5 (2.6)	2.8 (1.5)		2.9 (0.8)	33.8 (2.9)
Algal turf	17.3 (5.2)	3.1 (1)	0.2 (0.2)	4.4 (2.4)	6.9 (1.2)
Seaweeds	17.4 (5.6)	9.9 (2)		7.9 (5.7)	0.3 (0.1)
Sponges		0.4 (0.3)		3.3 (2)	0.3 (0.3)
Rugosity	1.49 (0.03)	1.88 (0.09)	2.16 (0.2)	2.60 (0.2)	2.21 (0.2)