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Density, diversity, and survival of juvenile corals on reefs of Zanzibar, Tanzania

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Abstract

The sustainability of coral populations depends on the steady supply of sexually produced offspring, especially as coral populations attempt to adjust to climate change. Therefore, information on the density, diversity, and survival of juvenile corals is vital for predicting recruitment success and determining the trajectories of coral populations. This study investigated the dynamics of juvenile corals in Zanzibar in three habitats (reef flat, reef crest, and reef slope) and at three sites (Chumbe, Chunguu, and Mnemba) from November 2010 to May 2012. In total, 10,932 juvenile corals were recorded, which belonged to 13 coral families and 38 coral genera. The mean density of juvenile colonies ranged from 10.3 ± 0.8 to 16.4 ± 1.3 colonies per m^2. Among the coral genera recorded, *Acropora* and *Porites* were the most prolific. Survival of juvenile corals was high at all three sites, between 60−78%, with the highest survival on the reef slopes of Chumbe. There were significant seasonal differences in juvenile coral survival rates, with the highest survival occurring during the northeastern monsoon. On the western coast, at Chumbe, the co-occurrence of juvenile and adult *Acropora* implies that self-seeding is occurring. In contrast, the lack of *Acropora* adults at Chunguu suggests that the site receives recruits from other reefs. On the eastern coast, Mnemba had the lowest survival rates of all three sites, supporting mainly faviids and massive *Porites*. The results suggest that the western reefs have a more significant potential to recover from disturbances than the eastern reefs.

Keywords: Juvenile corals, density, diversity, survival, Zanzibar, Tanzania.

1. Introduction

In the past three decades, coral reefs worldwide have experienced numerous stresses that have contributed to the coral loss and changes in reef composition (Loya *et al.,* 2001; Sweatman *et al.,* 2011). Many reefs in Tanzania have also experienced a considerable loss of corals because of severe predation by population outbreaks of *Acanthaster planci* (Muhando, 2003; Ussi, 2009; Muhando and Lanshammar, 2009), and by thermal-stress events (Nzali *et al.,* 1998; Wilkinson, 2000; Muhando, 2001). Both predation and thermal stress on the reefs of Tanzania have shifted the coral dominance away from the *Acropora* species (Muhando and Lanshammar, 2009). Reefs can recover from these stresses, although several processes prevent recovery, including (i) low densities of adult stocks (Hughes *et al.* 2000), (ii) the interruption of the coral's reproductive cycle that reduces the density of recruits (Glynn and De Weerdt, 1991; Muhando, 2003), and (iii) low survival of recruits (Gilmour, 1999; Bassim and Sammarco, 2003; Obura *et al.,* 2004; Fabricius, 2005; van Woesik *et al.* 2014). Therefore, information on juvenile dynamics is crucial in predicting coral recovery and determining population trajectories.

Different approaches have been used to study reef-community dynamics using the early life stages of corals. The approaches include studies on larval settlement (recruitment), post-settlement survival, growth of recruits, and the dynamics of juvenile corals (Edmunds, 2007; Ritson-Williams *et al.,* 2009). These studies show that the early life stages of corals strongly influence the coral populations (Ritson-Williams *et al.,* 2009) and can be used to study the dynamics of reef systems. In this study, we investigated the density, diversity, and survival of juvenile corals on the reefs of Zanzibar to provide information on some critical processes that influence the dynamics of coral populations.

Physical and biological factors directly influence juvenile coral dynamics and survival. Physical factors that are highly influential on juvenile survival include water-flow rates (Amar *et al.,* 2007), water temperature (Nozawa and Harrison, 2007), irradiance (Mundy and Babcock, 1996), eutrophication (Tomascik, 1991), and sedimentation (Babcock and Davies, 1991). Biological factors that are influential on juvenile survival include the density of macroalgae, corallimorphs, and soft corals, all of which can inhibit the settlement and growth of juvenile corals (McCook *et al.,* 2001; Harrington *et al.,* 2004). Other biological factors that influence juvenile corals settlement and growth include herbivory (Sammarco, 1980; Tomascik, 1991; Baird and Hughes, 2000) and predation pressure (Penin *et al.,* 2011; O'Leary *et al,* 2013).

Although several studies have described the diversity of adult coral populations in Zanzibar (Bergman and Öhman 2001; Mbije *et al.* 2002), little information is available on the diversity and survival of scleractinian corals at early life stages in different habitats. Such information is crucial for long-term predictions of the recovery of reef communities (Adjeroud *et al.,* 2009), which in turn determines the structure and complexity of reef systems and their overall function.

Seasonal weather conditions have a strong influence on reproductive cycles of scleractinian corals (van Woesik, 2010). Understanding these seasonal influences on the reproduction can have important management implications, especially if management options can be seasonally optimized to protect reef fauna. Currently, limited information is available on the influence of local weather conditions on the ecological processes of the early life stages of scleractinian corals. In this study, we investigated the density, diversity, and survival dynamics of juvenile corals as well as benthic reef cover to provide information that may help explain the dynamics of reef systems on Unguja Island, Zanzibar.

2. Materials and methods

2.1 Study sites

The density, diversity and survival rates of juvenile scleractinian corals were studied at three reef sites in Unguja Island, Zanzibar: (i) Chumbe (06°16.3′S; 039°10.2′E), (ii) Changuu (06°06.8′S; 039°09.8′E), and (iii) Mnemba (05°48.5′S; 039°21.3′E) reefs (Fig. 1). Chumbe and Changuu reefs are located on the western side of Unguja Island, facing the Zanzibar channel. Mnemba reef is located on the eastern side of Unguja Island (Fig. 1). Weather condition of Unguja Island, as in most of the East African coast, is highly subjected to the Inter-Tropical Convergence Zone winds, commonly known as monsoon winds. There are two main monsoons, the northeast monsoon (NEM) and the southeast monsoon (SEM) (UNEP, 1998). The NEM occurs from October to March and peaks between December and January, and the SEM occurs from April to September, with peaks between June and July. Chumbe experiences relatively rough weather during the SEM and calm weather during the NEM. Mnemba reef experiences rough weather during NEM and is relatively calm during SEM. Chumbe and Mnemba reefs are in marine protected areas, whereas the Changuu reef is not. All reef sites experience reversing north-south tidal currents, which are stronger in Mnemba than in Chumbe and Changuu (Mwaipopo, 1990). Chumbe and Changuu reefs are in close proximity to other patch reefs, whereas Mnemba reef is isolated by deep 100 m channels.

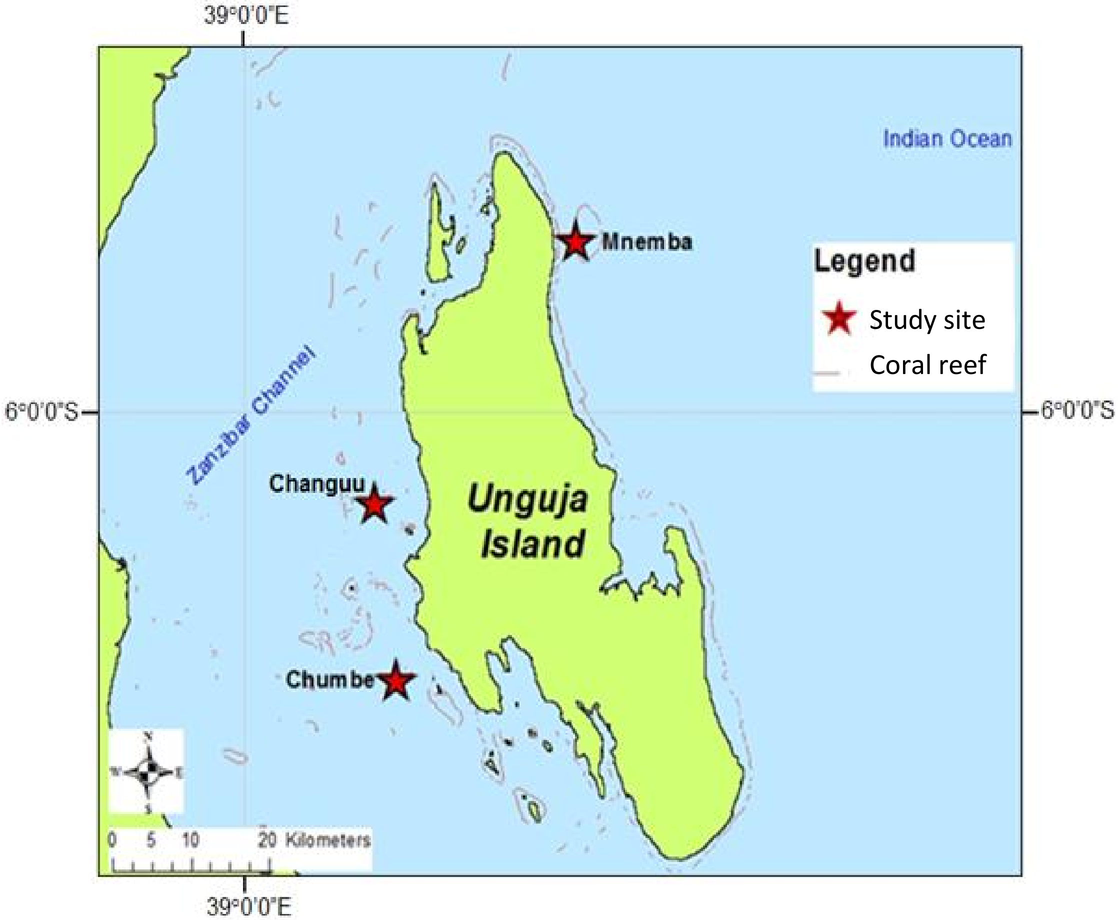

Figure 1. Map showing the study sites at Chumbe, Changuu and Mnemba reefs.

2.2 Sampling design

Two randomly selected stations were marked at each study site. Each station was approximately 50 m x 75 m, covering all reef habitats (i.e., reef flat, reef slope and reef crest). The stations were approximately 300 m apart. Six 2 m x 2 m permanent plots were established in each station; two in each reef habitat. The plots had carbonate substrate, which was suitable for coral recruitment. The plots were demarcated with five markers (i.e., iron bars), nailed into the reef substrate at each corner, and one at the center. A 1-m^2 PVC quadrat, partitioned into 16 equal-sized sections by nylon string, was used to map the localities of all juvenile coral colonies within each plot. Sampling was conducted in November 2010, May 2011, November 2011, and May 2012; the November and May observations were intended to capture SEM and NEM seasons, respectively.

2.3 Data collection

Reef composition within each plot was assessed using the line-intercept transect method (English *et al.,* 1994). Three 20 m transects were randomly placed within each reef habitat. A total of 63 benthic categories were monitored, summarized into 8 major groups: hard corals (49 categories), soft corals, sponges, algae (5 categories), corallimorpharians, hard substrates (4 categories), soft substrate and others (Muhando, 2009).

A coral was considered a juvenile coral if visible underwater (~ 1 mm) and was less than or equal to 10 cm in diameter (Bak and Engel, 1979). All juvenile corals found in the plots were identified to genus level and their locations were mapped for easy relocation during the subsequent monitoring. A juvenile coral mapped in a previous sampling period but not observed in the subsequent sampling, was considered dead. All juvenile corals that were completely overgrown with algae were also considered dead. The survival rate was calculated as the ratio of juvenile corals that survived from the previous sampling. Two additional quadrats were randomly sampled per station to increase the sample size of juvenile corals. The density of juvenile corals was expressed as a number of coral colonies per square meter. The Shannon-Wiener Diversity Index (H') was used to express the diversity of juvenile coral genera within sites and within reef zones. A Strauss Linear Selectivity index (L) was used for comparison of proportions of juvenile to adult colonies, to determine whether there were mismatches, which may indicate an external or a local larval supply.

2.4 Data analysis

A Generalized Linear Model repeated measures was used to compare juvenile coral density among sites, habitats, seasons, and plots. A one way-ANOVA test was used to compare juvenile colony survival among sites, habitats, seasons, and plots. A Bartlett test was used to test for the validity of using parametric analyses. Heterogeneous data were log-transformed to meet parametric requirements. Student-Newman Keuls test (SNK-test) was used to determine the differences among the means. Kruskal-Wallis test was used to compare the mean cover among benthic categories when the data did not meet the assumptions of parametric tests, and t-tests were used to compare diversity indices among groups.

3. Results

3.1 Juvenile densities and diversity

A total of 10,932 juvenile corals, belonging to 13 families and 38 genera, were recorded in this study. The average density of juveniles was 12.7 m^{-2}. The juvenile coral densities did not significantly differ between plots in all sites; and therefore plots data were pooled. Changuu reef recorded significantly ($p<0.0001$) higher mean juvenile coral densities (16.4 ± 1.3 m^{-2}) than Chumbe (11.2 ± 0.6 m^{-2}) and Mnemba (10.3 ± 0.8 m^{-2}) (Table 1). Acroporidae, Poritidae and Pocilloporidae were the most frequently recorded coral families. Acroporidae dominated Chumbe reef, Poritidae dominated Changuu reef, and Pocilloporidae dominated Mnemba reef. Mussidae, Pectiniidae and Merulinidae were among the rarest families, with a frequency of less than 1% in all sites. There was no significant difference ($p> 0.05$) in juvenile coral density among reef habitats in Chumbe, but significantly fewer colonies on the reef flats than on the reef slopes at the other two sites (Fig. 2).

Table 1. The mean density of juvenile (± SE) corals and their recovery-potential indexes for Chumbe (Chu), Changuu (Cha) and Mnemba (Mn). The index is a product of density and survival rate of a genus. The indexes indicate that genera with higher values are likely to recover faster from a disturbance than those with lower values.

Family	Genus	Genus's density in site			Recovery possibility index		
		Chu	Cha	Mn	Chu	Cha	Mn
Acroporidae	Acropora	5.22±0.50	1.63±0.25	1.81±0.26	4.216	1.2914	0.8833
	Astreopora	0.09±0.03	0.00±0.00	0.07±0.03	0.0038		0.0096
	Montipora	0.23±0.05	0.31±0.06	0.20±0.04	0.126	0.1597	0.0524
Agariciidae	Gardineroseris	0.00±0.00	0.01±0.01	0.03±0.01			0.0026
	Pachyseris	0.01±0.01	0.07±0.03	0.00±0.00		0.0082	
	Pavona	0.05±0.02	0.12±0.02	0.22±0.05	0.0033	0.0456	0.0516
Astrocoeniidae	Stylocoeniella	0.06±0.03	1.23±0.37	0.02±0.02	0.0043	0.4446	
Euphyllidae	Physogyra	0.00±0.00	0.02±0.01	0.00±0.00		0.0013	
Faviidae	Caulastrea	0.00±0.00	0.00±0.00	0.00±0.00			
	Cyphastrea	0.05±0.02	0.02±0.01	0.07±0.03			0.003
	Diploastrea	0.00±0.00	0.00±0.00	0.01±0.02			
	Echinopora	0.25±0.05	0.37±0.07	0.10±0.03	0.1038	0.1842	0.0065
	Favia	0.19±0.03	0.09±0.01	0.31±0.02	0.0277		0.0095
	Favites	0.10±0.02	0.06±0.02	0.31±0.04	0.0336	0.0061	0.206
	Goniastrea	0.04±0.02	0.11±0.04	0.09±0.04		0.0162	0.0075
	Leptastrea	0.12±0.03	0.06±0.02	0.23±0.04	0.0304	0.013	0.0582

	Leptoria	0.00±0.00	0.03±0.01	0.01±0.01		0.0043	0.0004
	Platygyra	0.20±0.04	0.16±0.03	0.05±0.02	0.0887	0.0612	0.0061
Fungiidae	Fungia	0.18±0.05	2.22±0.47	0.11±0.03	0.0454	1.2483	0.0046
	Herpolitha	0.01±0.01	0.00±0.00	0.00±0.00			
Merulinidae	Hydnophora	0.10±0.03	0.05±0.01	0.05±0.02	0.0344	0.0094	0.0075
	Merulina	0.01±0.01	0.01±0.01	0.00±0.00		0.0004	
Mussidae	Acanthastrea	0.00±0.00	0.01±0.01	0.06±0.02			0.0023
	Lobophyllia	0.04±0.02	0.08±0.03	0.00±0.00	0.0017	0.0155	0.0001
Oculinidae	Galaxea	0.08±0.02	0.56±0.10	0.05±0.02	0.01	0.3356	0.0019
Pectiniidae	Echinophyllia	0.01±0.01	0.01±0.01	0.00±0.00	0.0003	0.0004	
	Mycedium	0.05±0.02	0.02±0.01	0.00±0.00	0.0056	0.0017	
	Oxypora	0.01±0.01	0.04±0.01	0.00±0.00	0.0012	0.0064	
	Pectinia	0.00±0.00	0.00±0.00	0.00±0.00			
Pocilloporidae	Pocillopora	1.31±0.12	1.88±0.28	2.75±0.49	0.9407	1.2591	1.2537
	Seriatopora	0.28±0.06	0.02±0.01	0.00±0.00	0.1542	0.0026	
	Stylophora	0.01±0.01	0.35±0.09	0.86±0.12		0.0658	0.3379
Poritidae	Alveopora	0.00±0.00	0.00±0.00	0.00±0.00			
	Goniopora	0.30±0.06	0.01±0.01	0.03±0.01	0.1435		0.0035
	Porites	1.86±0.16	6.10±0.72	1.83±0.18	1.3357	3.089	1.129
Siderastreidae	Coscinarea	0.33±0.05	0.98±0.10	0.79±0.10	0.1551	0.7121	0.369
	Psammocora	0.02±0.01	0.09±0.02	0.08±0.02	0.0014	0.0144	0.0074
All juvenile corals		11.2 ± 0.6	16.4 ± 1.3	10.3 ± 0.8			

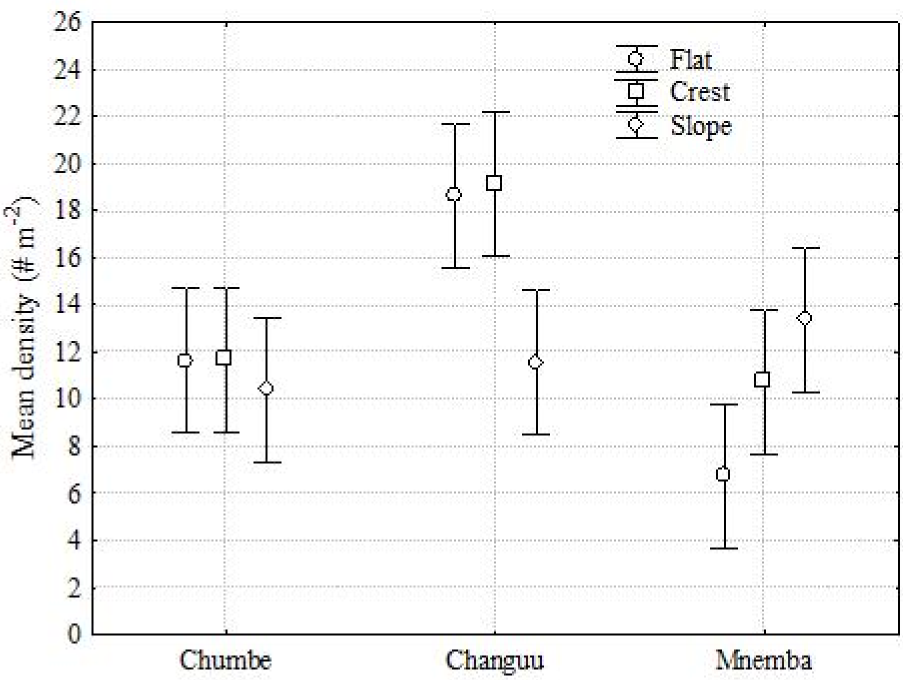

Figure 2. Mean juvenile coral density (# m-2) among reef habitats in Chumbe, Changuu and Mnemba reefs (vertical bars denote 0.95 confidence intervals).

Juvenile coral genera diversity was highest at Changuu (H'= 1.01) and was lowest at Chumbe (H'= 0.87). Juvenile coral genera diversity differed significantly across reef habitats ($p < 0.05$). Generally, the highest diversity was in Chumbe and Changuu reef slopes. By contrast, the highest diversity at Mnemba was on the reef flat. Juvenile coral genera richness was highest on the reef slopes, which ranged from 26 genera at Mnemba to 31 genera at Changuu, whereas the reef flats recorded the lowest richness to as low as 21 genera at Changuu and Mnemba.

3.2 Juvenile Survival

Juvenile coral survival rates were significantly ($p<0.0001$) higher at Chumbe (78%) than at Changuu (70%) and Mnemba (60%). In general, *Porites* had the highest survival rate, followed by *Acropora* and *Pocillopora* on the western reefs (Fig. 3). *Favites* and *Porites* had the highest survival rates on the eastern reefs. At Chumbe, the genera *Astreopora*, *Echinophyllia*, *Lobophyllia*, *Pavona* and *Stylocoeniella* showed the lowest survival rates (<10%). At Changuu, *Echinophyllia*, *Merulina*, *Mycedium* and *Physogyra* showed the lowest survival rates. At Mnemba, *Acanthastrea*, *Cyphastrea*, *Fungia*, *Galaxea*, *Leptoria*, *Lobophyllia* and *Psammocora* showed the lowest survival rates.

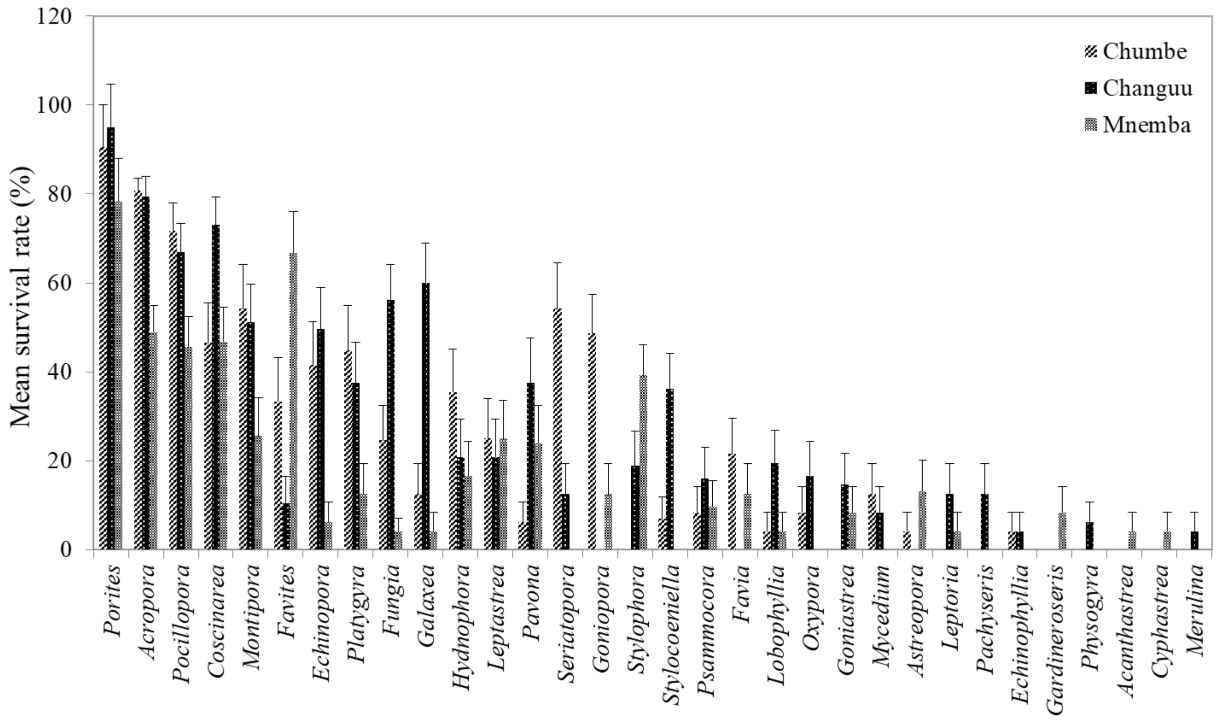

Figure 3. Mean survival rates of juvenile corals (± SE) in three reef sites; Chumbe, Changuu and Mnemba in Unguja, Zanzibar.

The survival rate of juvenile corals on reef slopes was over 10% higher at Chumbe than at Mnemba and Changuu. By contrast, Changuu and Mnemba reefs showed the lowest juvenile survival on reef flats (Figs. 4−6). There was no significant ($p>0.05$) habitat variability in juvenile coral survival at the genus level. Likewise, the trend in the dominance of survival rates of juvenile corals, within genera and among reef habitats, was not consistent across all sites (Figures 4 and 5). However, the genus *Pocillopora* was the dominant survivor on reef slopes at Chumbe and Mnemba, whereas the genus *Echinopora* was the dominant survivor at Changuu on the reef crest (Fig. 6).

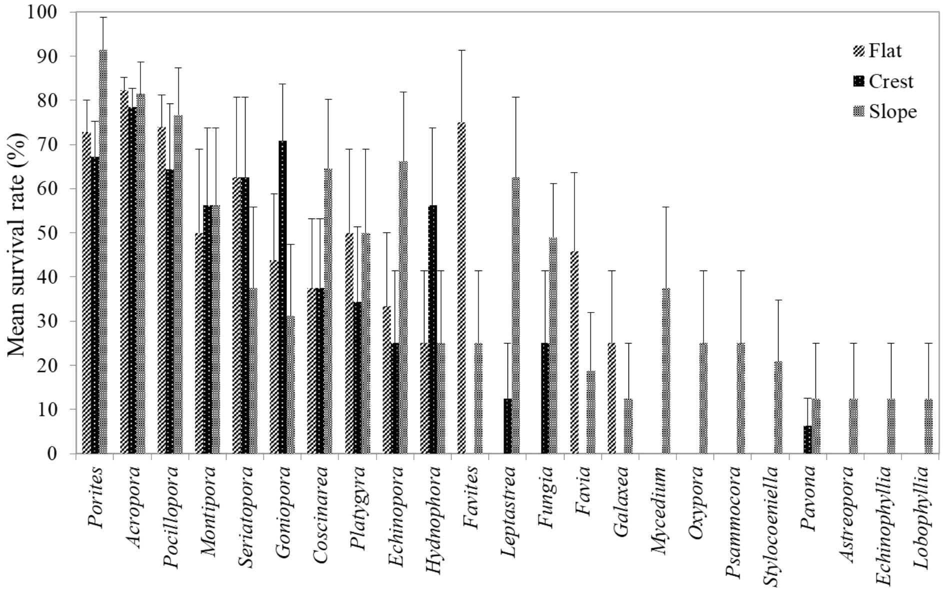

Figure 4. Comparison of juvenile coral genera survival rates (± SE) across habitats at Chumbe reef.

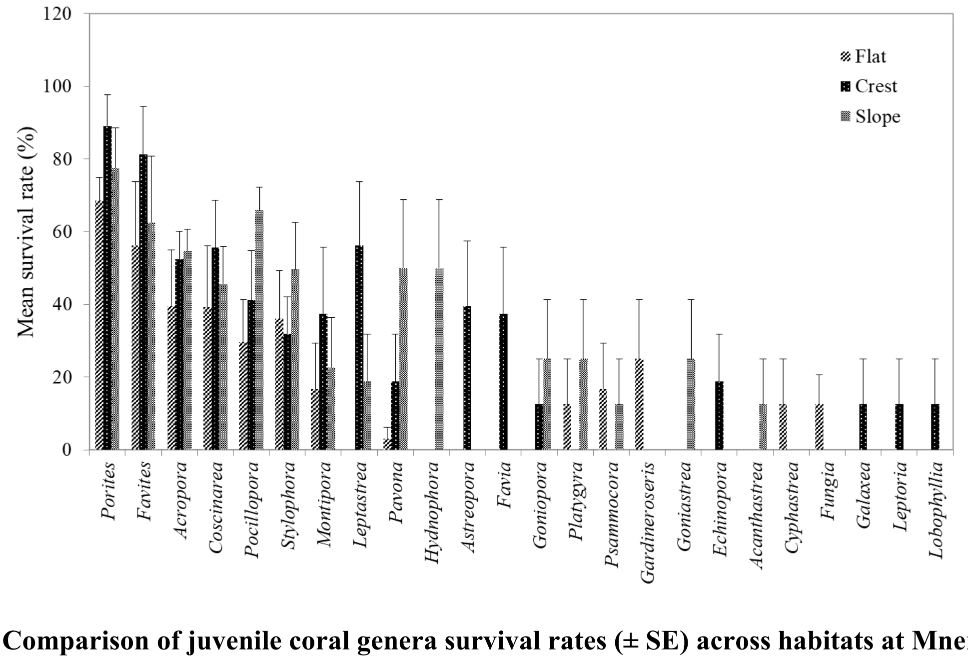

Figure 5. Comparison of juvenile coral genera survival rates (± SE) across habitats at Mnemba reef.

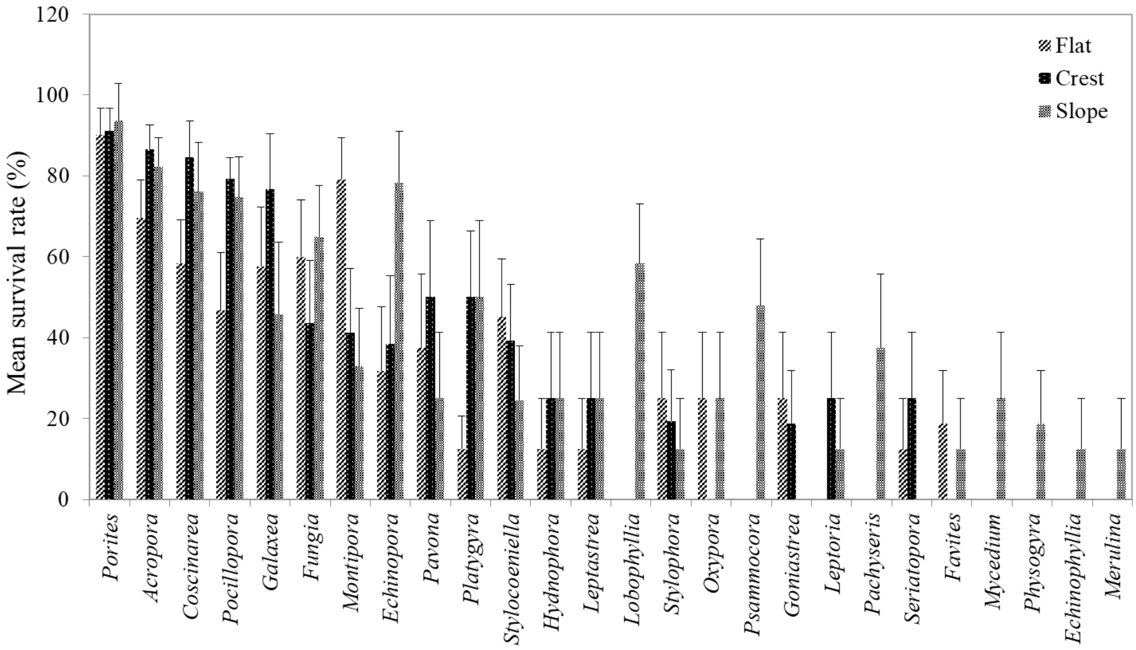

Figure 6. Comparison of juvenile coral genera survival rates (± SE) across habitats at Changuu reef.

There was no significant seasonal variability of juvenile corals' densities within sites and reef habitats (Table 3). However, the study found a significant seasonal variability ($p<0.05$) in survival at Chumbe reef, with over 10% more survival during NEM than during SEM (72%). The higher survival rates were mainly observed for the genera *Acropora*, *Porites, Pocillopora*, *Seriatopora*, *Goniopora*, *Platygyra*, *Echinopora*, *Leptastrea, Galaxea Pavona, Astreopora, Echinophyllia* and *Lobophyllia* (Fig. 7).

Table 3. Seasonal variability of juvenile coral density at genus level within sites; NEM = northeast monsoon and SEM = southeast monsoon.

	Chumbe		Changuu		Mnemba	
Genus	SEM	NEM	SEM	NEM	SEM	NEM
Acropora	5.02±0.73	5.37±0.69	1.47±0.38	1.74±0.34	1.93±0.51	1.72±0.27
Porites	1.80±0.28	1.91±0.31	6.64±1.33	4.13±1.59	2.05±0.38	1.61±0.23
Pocillopora	1.44±0.19	1.22±0.16	2.06±0.51	1.76±0.33	2.13±0.53	3.2±0.73
Coscinarea	0.37±0.09	0.31±0.06	1.03±0.16	0.93±0.13	0.84±0.17	0.75±0.13
Goniopora	**0.18±0.06**	**0.38±0.08**	0.01±0.01	0.02±0.01	0.03±0.02	0.02±0.01
Seriatopora	0.23±0.08	0.32±0.08	0.02±0.01	0.02±0.01	0.00±0.00	0.00±0.00
Echinopora	0.26±0.07	0.24±0.07	0.44±0.13	0.32±0.09	0.1±0.05	0.11±0.04
Montipora	0.23±0.07	0.23±0.06	**0.36±0.09**	**0.28±0.07**	0.28±0.09	0.15±0.04
Platygyra	0.18±0.05	0.21±0.05	0.17±0.05	0.16±0.04	0.04±0.02	0.05±0.02
Fungia	0.12±0.06	0.23±0.08	2.43±0.81	2.07±0.56	0.11±0.06	0.11±0.04
Favia	0.16±0.06	0.11±0.03	0.03±0.02	0.01±0.01	0.08±0.04	0.08±0.02
Leptastrea	0.12±0.05	0.13±0.04	0.06±0.03	0.07±0.03	0.28±0.08	0.2±0.04
Favites	0.11±0.04	0.10±0.03	0.06±0.03	0.06±0.03	0.37±0.07	0.27±0.06
Hydnophora	0.12±0.05	0.08±0.03	0.04±0.02	0.05±0.02	0.03±0.02	0.05±0.02
Astreopora	0.09±0.05	0.09±0.04	0.00±0.00	0.01±0.01	0.1±0.07	0.05±0.02

Galaxea	0.07±0.03	0.09±0.03	0.57±0.11	0.55±0.15	0.07±0.04	0.03±0.02
Stylocoeniella	0.08±0.04	0.05±0.03	1.36±0.43	1.13±0.54	0.00±0.00	0.03±0.03
Cyphastrea	0.09±0.05	0.02±0.01	0.02±0.02	0.02±0.02	**0.13±0.07**	**0.04±0.02**
Pavona	0.03±0.03	0.07±0.03	0.11±0.04	0.13±0.03	0.24±0.06	0.2±0.07
Mycedium	0.07±0.05	0.03±0.02	0.02±0.01	0.02±0.01	0.00±0.00	0.00±0.00
Goniastrea	0.03±0.03	0.05±0.03	0.10±0.05	0.12±0.06	0.06±0.05	0.11±0.06
Lobophyllia	0.02±0.01	0.06±0.03	0.11±0.06	0.06±0.03	0.00±0.00	0.01±0.01
Psammocora	0.02±0.01	0.02±0.01	0.09±0.04	0.09±0.03	0.07±0.04	0.08±0.03
Herpolitha	0.01±0.01	0.02±0.01	0.01±0.01	0.00±0.00	0.00±0.00	0.00±0.00
Oxypora	0.01±0.01	0.02±0.01	0.05±0.02	0.03±0.02	0.00±0.00	0.00±0.00
Merulina	0.02±0.01	0.01±0.01	0.02±0.01	0.01±0.01	0.00±0.00	0.00±0.00
Stylophora	0.00±0.00	0.02±0.02	0.21±0.11	0.45±0.13	1.06±0.19	0.72±0.14
Echinophyllia	0.01±0.01	0.01±0.01	0.00±0.00	0.02±0.02	0.00±0.00	0.00±0.00
Pachyseris	0.00±0.00	0.01±0.01	0.08±0.06	0.06±0.04	0.00±0.00	0.00±0.00
Alveopora	0.00±0.00	0.01±0.01	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Caulastrea	0.00±0.00	0.01±0.01	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Physogyra	0.00±0.00	0.01±0.01	0.02±0.02	0.02±0.02	0.00±0.00	0.01±0.01
Acanthastrea	0.00±0.00	0.00±0.00	0.00±0.00	0.01±0.01	0.03±0.03	0.07±0.03
Diploastrea	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.03±0.04	0.00±0.00
Gardineroseris	0.00±0.00	0.00±0.00	0.01±0.01	0.01±0.01	0.04±0.03	0.02±0.01
Leptoria	0.00±0.00	0.00±0.00	0.03±0.02	0.04±0.02	0.01±0.01	0.01±0.01
Pectinia	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.01±0.01	0.00±0.00

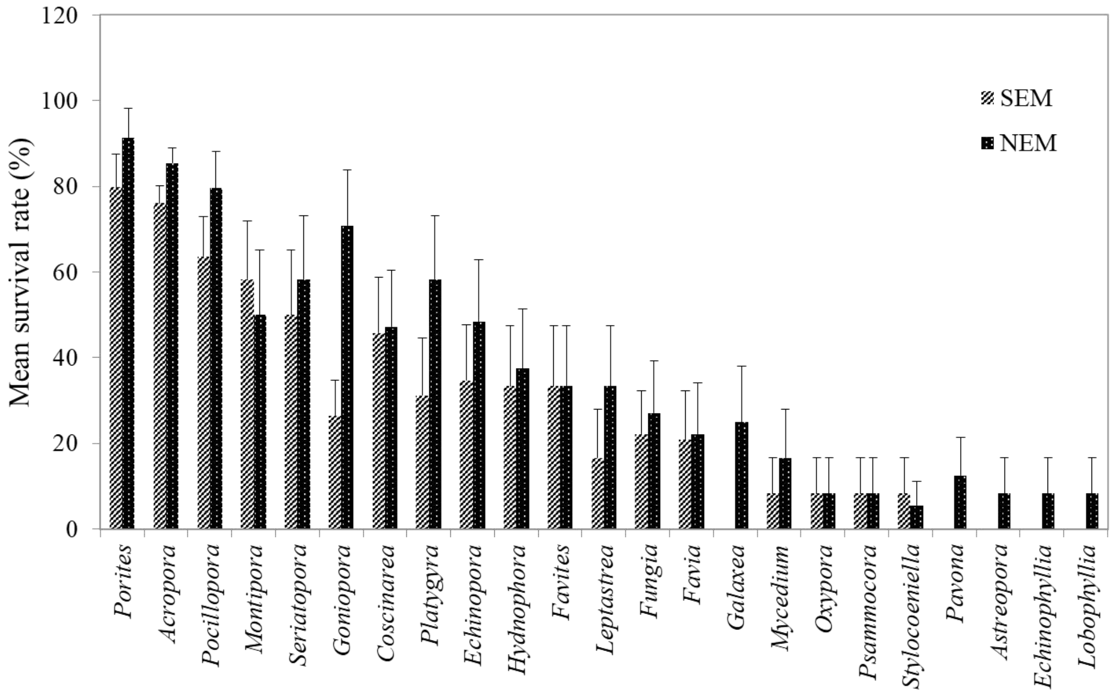

Figure 7. Seasonal variability in mean survival rates (± SE) of juvenile coral genera at Chumbe reef.

3.3 Juvenile to adult ratios

The proportion of corals with high juvenile to adult ratios was highest in Changuu at 35% (Table 2). The genera *Coscinarea*, *Fungia, Leptastrea, Stylophora, Psammocora*, *Pocillopora* and *Pavona* had consistently high juvenile to adult ratios across all reef sites. The genera *Acropora*, *Favites, Goniopora, Montipora, Mycedium,* and *Seriatopora* had high juvenile to ratios of juveniles at Chumbe and Changuu. At Mnemba the genera Pocillopora, *Leptastrea*, *Stylophora* and *Fungia* had the highest juvenile to adult ratios. Based on the genera recovery possibility index, the genera that were likely to contribute to rapid recovery were *Acropora*, *Porites and Pocillopora,* which collectively contributed over 55% across all sites (Table 1). The genus *Acropora* was the most important for Chumbe, as it was *Porites* for Changuu, and *Pocillopora* for Mnemba. Other genera that were important in contributing towards recovery were *Coscinarea*, *Echinopora*, *Galaxea*, *Montipora* and *Favites*.

Table 2: Proportions of benthic cover of adult coral populations (A), the corresponding proportions of juvenile corals (J) and the Linear Selectivity Index (L) for Chumbe, Changuu and Mnemba reefs. "L" values range from -1 to 1, with positive values indicating higher proportions of juveniles relative to its adult population and negative values indicating low proportions of juveniles relative to its adult population. High L also implies both external source of larvae and/or higher survival after settlement.

Site	Chumbe			Changuu			Mnemba		
Genus	A	J	L	A	J	L	A	J	L
Acanthastrea	0.0014	0.0000	-0.0014	0.0000	0.0002	**0.0002**	0.0007	0.0048	**0.0041**
Acropora	0.4254	0.4674	**0.0420**	0.0452	0.0876	**0.0424**	**0.2096**	**0.1847**	-0.0249
Alveopora	0.0000	0.0003	**0.0003**	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Astreopora	0.0995	0.0081	-0.0914	0.0000	0.0000	0.0000	0.0428	0.0073	-0.0356
Caulastrea	0.0002	0.0003	0.0002	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Coscinarea	0.0016	0.0298	**0.0283**	0.0029	0.0554	**0.0525**	0.0051	**0.0806**	**0.0755**
Cyphastrea	0.0066	0.0044	-0.0022	0.0022	0.0013	-0.0009	0.0087	0.0073	-0.0014
Diploastrea	0.0011	0.0000	-0.0011	0.0000	0.0000	0.0000	0.0032	0.0014	-0.0018
Echinophyllia	0.0080	0.0006	-0.0074	0.0001	0.0006	**0.0005**	0.0000	0.0000	0.0000
Echinopora	0.0380	0.0224	-0.0156	0.0273	0.0231	-0.0042	**0.1431**	0.0100	-0.1331
Favia	0.0156	0.0115	-0.0041	0.0006	0.0011	**0.0005**	0.0174	0.0073	-0.0101
Favites	0.0064	0.0090	**0.0026**	0.0002	0.0036	**0.0034**	0.0290	0.0287	-0.0003
Fungia	0.0055	0.0165	**0.0110**	0.0186	**0.1474**	**0.1288**	0.0002	0.0135	**0.0133**
Galaxea	0.0208	0.0071	-0.0137	**0.1304**	0.0348	-0.0956	0.0022	0.0045	**0.0023**
Gardineroseris	0.0003	0.0000	-0.0003	0.0002	0.0004	**0.0003**	0.0073	0.0031	-0.0042
Goniastrea	0.0137	0.0037	-0.0100	0.0004	0.0070	**0.0066**	0.0338	0.0080	-0.0259
Goniopora	0.0101	0.0264	**0.0163**	0.0000	0.0006	**0.0006**	0.0086	0.0028	-0.0059
Herpolitha	0.0007	0.0012	**0.0006**	0.0006	0.0004	-0.0001	0.0000	0.0000	0.0000
Hydnophora	0.0184	0.0087	-0.0097	0.0014	0.0021	**0.0008**	0.0020	0.0048	**0.0028**
Leptastrea	0.0010	0.0109	**0.0099**	0.0002	0.0030	**0.0028**	0.0079	0.0221	**0.0142**
Leptoria	0.0001	0.0000	-0.0001	0.0002	0.0021	**0.0019**	0.0082	0.0010	-0.0072
Lobophyllia	0.0059	0.0037	-0.0022	0.0023	0.0057	**0.0034**	0.0018	0.0003	-0.0015

Merulina	0.0095	0.0009	-0.0086	0.0005	0.0006	**0.0001**	0.0000	0.0000	0.0000
Montipora	0.0132	0.0208	**0.0077**	0.0004	0.0187	**0.0183**	**0.0613**	0.0211	-0.0402
Montastrea	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0020	0.0000	-0.0020
Mycedium	0.0016	0.0040	**0.0025**	0.0007	0.0013	**0.0006**	0.0000	0.0000	0.0000
Oxypora	0.0048	0.0012	-0.0035	0.0000	0.0023	**0.0023**	0.0000	0.0000	0.0000
Pachyseris	0.0027	0.0006	-0.0021	0.0000	0.0040	**0.0040**	0.0000	0.0000	0.0000
Pavona	0.0038	0.0047	**0.0008**	0.0023	0.0085	**0.0062**	0.0191	0.0208	**0.0017**
Pectinia	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0003	**0.0003**
Physogyra	0.0011	0.0003	-0.0008	0.0035	0.0013	-0.0023	0.0008	0.0003	-0.0004
Platygyra	0.0240	0.0177	-0.0063	0.0009	0.0091	**0.0082**	0.0148	0.0055	-0.0092
Plerogyra	0.0001	0.0000	-0.0001	0.0003	0.0000	-0.0003	0.0006	0.0000	-0.0006
Pleiastrea	0.0016	0.0000	-0.0016	0.0000	0.0000	0.0000	0.0031	0.0000	-0.0031
Pocillopora	0.0257	**0.1175**	**0.0918**	0.0143	**0.1069**	**0.0926**	**0.0850**	**0.2774**	**0.1924**
Podabacia	0.0004	0.0000	-0.0004	0.0002	0.0000	-0.0002	0.0000	0.0000	0.0000
Porites	**0.1811**	**0.1532**	-0.0279	**0.0648**	**0.2899**	**0.2252**	**0.2446**	**0.1750**	-0.0695
Psammocora	0.0002	0.0016	**0.0014**	0.0002	0.0049	**0.0047**	0.0005	0.0073	**0.0068**
Seriatopora	0.0093	0.0255	**0.0162**	0.0002	0.0013	**0.0010**	0.0000	0.0000	0.0000
Stylocoeniella	0.0004	0.0056	**0.0052**	0.0000	0.0778	**0.0778**	0.0037	0.0017	-0.0020
Stylophora	0.0000	0.0009	**0.0009**	0.0043	0.0142	**0.0099**	0.0257	**0.0913**	**0.0656**
Symphyllia	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0002	0.0000	-0.0002

4. Discussion

Coral recruitment is an important indicator of the potential for population recovery after disturbances (Fox, 2004). Therefore, understanding the dynamics of juvenile corals is vital for effective reef management (Hughes *et al.,* 2010). The present study describes the patterns of juvenile corals (< 10 cm) across reef sites in Unguja, Zanzibar. The observed juvenile densities and diversities reflect the successful passage of recruits through various vicissitudes.

Compared with the eastern reefs, the higher density of juvenile colonies on the western reefs could be explained by differences in larval supply, the coral community structure, and/or the extent of macroalgal cover. The density of juveniles was highest on the western reefs, where reefs are in close proximity, and lowest on Mnemba reef, on the eastern coast, which is isolated by a deep channel (Muhando, 2003; Ussi, 2014). Cowen and Sponaugle (2009) explained the supportive role of hydrodynamic connectivity to larval supply and population sustainability across reef systems. It is, therefore, plausible that the higher juvenile coral densities in Changuu and Chumbe reefs were attributed to a high larval supply, which in turn supports a high settlement rate and recruitment.

Mnemba reef is exposed to more severe tidal flow and currents (Mwaipopo, 1990), which may lead to larvae settlement failure (Richmond and Hunter, 1990). Large waves and strong flow also cause sand abrasion, which is detrimental to newly settled corals (Sammarco and

Andrews, 1989; Pineda *et al.,* 2007; Ruiz-Zárate *et al.,* 2000; Sale *et al.,* 2010). The lowest juvenile survival rate was also observed in Mnemba reef. This further suggests that the carbonate substrate at Mnemba reef may not provide enough shelter for juvenile corals, compared with the structurally more complex habitat and less physically disturbed Changuu reef. The benthic cover of macroalgal was also highest in shallow habitats of Mnemba reef, which is also well known to be detrimental to coral settlement success and survival (Wells, 1957). Therefore, despite having ample available carbonate for coral settlement on Mnemba, juvenile density was comparatively low because of both unsuccessful settlement and high post-settlement mortality.

Reef slopes generally support the highest diversities (Done 1982) and experience the most optimal physical conditions, including low fluctuations in temperature, salinity, and water-flow rates, and lower sedimentation (Larcombe *et al.,* 1995). Therefore, we expected to find relatively higher densities of juvenile coral colonies on reef slopes than on the reef flats and crests. This was not always the case however. The low densities of juvenile coral colonies recorded on the reef slope of Changuu could be related to the impact of excessive grazing by high densities of the sea urchin, *Diadema setosum* and *Diadema savignyi* recorded during surveys. These urchins had average densities of 5 urchins m^{-2} (Ussi, 2014). These urchins can damage coral colonies, particularly juvenile coral colonies, by incidental grazing of algal-covered substrate (Sammarco, 1982). The low juvenile coral density in Mnemba reef, could also be related to the grazing impact of *Echinothrix diadema* (~ 3 urchins m^{-2}) (Ussi, 2014) and the high cover of macroalgae (Fig. 2), which dominated the reef flats from May to October. Macroalgae are known to reduce coral recruitment by (i) releasing allelochemicals that prevent coral settlement (Gross, 2003; Paul and Puglisi, 2004; Miller *et al.,* 2009), (ii) providing an unstable and ephemeral substrate for coral settle, uprooted in rough weather (Harriott and Fisk, 1988; Birrell *et al.,* 2005, Kuffner *et al.,* 2006, Vermeij *et al.,* 2009), and (iii) competing with coral recruits for space and light (McCook *et al.,* 2001; Box and Mumby, 2007). It is plausible that macroalgae in Mnemba were responsible for low coral recruitment success.

Because the Chumbe and Mnemba reefs are protected marine parks, we expected higher juvenile coral diversity than on the unprotected reefs of Changuu (Hughes *et al.,* 2003). Likewise, juvenile coral diversity was anticipated to agree with adult coral populations, with the eastern reefs supporting relatively higher diversity than the western reefs, as explained by Bergman and Öhman, (2001) and Mbije *et al.,* (2002). However, reef protection and adult coral diversity were not good predictor of the diversity of juvenile corals in the present study. The highest juvenile coral diversity was recorded on the unprotected, western Changuu reef. We suspect that Changuu reef might receive larval from various sources. Larval dispersal, along the western reefs of Zanzibar, is primarily northward throughout most of the year (Muzuka et *al.,* 2010), therefore because of its geographic position, the Changuu reef may be an active larval-sink reef.

Branching *Porites* and *Acropora* were found to survive better than other coral genera at Changuu and Chumbe. This high survival could explain why the genus *Acropora* maintains dominance at Chumbe. By contrast, the high survival of *Favites* and *Porites* at Mnemba suggests that these genera are resistant to high wave energy. This study also found that the lowest survival of juvenile corals occurred during the southeastern monsoon, which exposes corals to large waves and strong currents between May and September. The southeastern monsoon is known to also cause high sedimentation rates (Muhando, 2003; Muzuka *et al.,* 2010). Together, large waves and high sedimentation could be responsible for juvenile coral mortality during the southeastern monsoon. These results suggest that the best time to establish coral nurseries or undertake restoration or transplantation onto reefs is between October and January.

The generally high densities of juveniles and high survival of *Porites* and *Acropora* indicate that the reefs are potentially recovering from severe degradation in the late 1990s and early 2000s. Studies have shown that most Acroporidae and Poritidae are broadcast spawners (Richmond and Hunter, 1990; Harrison, 2011; Bronstein and Loya, 2014). Broadcast spawners can have a significant influence on the recovery of neighboring reefs, facilitating regional recovery once they reach a critical mass (Harrison, 2011). Changuu and Chumbe reefs, on the western coast, generally had more *Acropora* and *Porites* juvenile and adult colonies than Mnemba reef, on the eastern coast, which was also reflected in the high Strauss Linear Selectivity index (Table 6). These results suggest that the western reefs are potentially self-seeding, especially for *Acropora* and *Porites.*

The results revealed a lack of co-occurrence between juvenile and adult corals at Changuu and Mnemba reefs. These findings reflect a high probability of high post-settlement mortality and a reliance on an external larval source. These findings also highlight the importance of connectivity in supporting reef recovery and reshaping of the diversity of the adult coral communities following disturbances by *Acanthaster planci* and thermal stress. The mismatch between juvenile and adult corals has been reported in a several other coral recruitment studies (e.g., Banks and Harriott, 1996; Hughes *et al.,* 1999; Muhando, 2003; Karisa *et al.,* 2008). The co-occurrence of juvenile and adult of the genus *Acropora* implies that self-seeding is occurring at Chumbe but not at Changuu and Mnemba reef and recovery is likely rapid at locations where such co-occurrence is high.

5. Conclusions

The density of juvenile corals was highest on the western reefs, specifically at Changuu, and was lowest on the eastern Mnemba reef. At Changuu, Poritidae was the most dominant juvenile coral, at Chumbe, Acroporidae was the dominant juvenile coral, and at Mnemba, Pocilloporidae was the dominant juvenile coral. Similarly, juvenile coral diversity was highest at Changuu, followed by Mnemba, and was lowest at Chumbe. The highest diversity was observed on reef slopes at Changuu and Chumbe, and on the reef flat at Mnemba. The survival of juvenile corals was highest at Chumbe, with the reef slope recording the highest survival rates. *Acropora*, *Porites* and *Pocillopora* had higher survival on Chumbe and Changuu, with Chumbe having higher survival during the northeastern monsoon. Unlike western reefs, Mnemba had higher survival of *Porites* and *Favites.* Based on the genera recovery-potential index, the most important genera that were likely to contribute to recovery were *Acropora*, *Porites and Pocillopora.* The genus *Acropora* was most important for Chumbe, *Porites* was most important for Changuu, and *Pocillopora* was most important for Mnemba. The results of this study imply that the recovery potential of disturbed reefs in Zanzibar relies primarily on the performance of *Acropora* and *Porites.*

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Appendix 1. Benthic categories used in the assessment of reefs benthic characteristics; HC = Hard Corals, S-Coral = Soft Corals, HS = Hard Substrate and SS = Soft Substrate

Major group	Count	Benthic category	Acronym

HC	1	*Acropora*	*Acro*
	2	*Acanthastrea*	*Acan*
	3	*Alveopora*	*Alve*
	4	*Astreopora*	*Astr*
	5	*Blastomussa*	*Blas*
	6	*Caulastrea*	*Caul*
	7	*Coscinarea*	*Cosc*
	8	*Cyphastrea*	*Cyph*
	9	*Diploastrea*	*Dipl*
	10	*Echinophyllia*	*Echph*
	11	*Echinopora*	*Echpo*
	12	*Euphyllia*	*Euph*
	13	*Favia*	*Favia*
	14	*Favites*	*Favit*
	15	*Fungia*	*Fung*
	16	*Galaxea*	*Gala*
	17	*Gardinoseris*	*Gard*
	18	*Goniastrea*	*Gonia*
	19	*Goniopora*	*Gonio*
	20	*Halomitra*	*Halo*
	21	*Herpolitha*	*Herp*
	22	*Hydnophora*	*Hydn*
	23	*Leptastrea*	*Lepta*
	24	*Leptoria*	*Lepto*
	25	*Lobophyllia*	*Lobo*
	26	*Merulina*	*Meru*
	27	*Montipora*	*Monti*
	28	*Montastrea*	*Monta*
	29	*Mycedium*	*Myce*
	30	*Oulastrea*	*Oula*
	31	*Oulophyllia*	*Oulo*
	32	*Oxypora*	*Oxyp*
	33	*Pachyseris*	*Pachy*

Major group	Count	Benthic category	Acronym
HC	34	*Pavona*	*Pavo*
	35	*Pectinia*	*Pecti*
	36	*Physogyra*	*Physo*
	37	*Platygyra*	*Platy*
	38	*Plerogyra*	*Plero*
	39	*Plesiastrea*	*Plei*
	40	*Pocillopora*	*Poci*
	41	*Podabacia*	*Poda*
	42	*Porites*	*Por*
	43	*Psammacora*	*Psam*
	44	*Seriatopora*	*Seri*

	45	*Stylocoeniella*	*Styloco*
	46	*Stylophora*	*Styl*
	47	*Symphyllia*	*Symp*
	48	*Turbinaria*	*Turb*
S-CORAL	1	Soft corals	SC
SPONGES	1	Sponges	SP
ALGAE	1	Algal Assemblage	AA
	2	Halimeda	HA
	3	Macroalgae	MA
	4	Turf algae	TA
	5	Coralline algae	CA
OTHERS	1	Others	OT
CO-MORPH	1	Corallimorpharia	RH
HS	1	Dead coral	DC
	2	Rock	RCK
	3	Dead coral with algae	DCA
	4	Rubble	R
SS	1	Sand	S

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