Spatial and Temporal Variation in Coral Recruitment and Mortality in Coastal Kenya

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ABSTRACT

Measuring recruitment patterns and mortality of corals is important for understanding mechanisms that regulate their populations and mediate species coexistence. However, there is limited data on coral recruitment dynamics in Eastern Africa and much of the WIO. We studied spatial and temporal patterns of coral recruitment and mortality in four lagoonal reefs in Kenya. The objectives of the study were to compare coral recruit densities and juvenile mortality between sites, months, seasons and years. Twelve 1m² permanent quadrats were sampled for the variables at each site on a monthly basis from February 2006 to June 2007. Recruit density in the protected Mombasa Marine Park was significantly higher (7.45 recruits/m²) than the other sites that are not protected. Recruit density was higher in SEM (Southeast Monsoon) than in NEM (Northeast Monsoon) seasons in both years with 2006 having higher recruitment than 2007. A total of 16 genera were recorded with Mombasa Marine Park having the highest number of genera (13) while a non protected site Kanamai had a significantly lower density (3.52 recruits/m²) with a low genera number (8). Other non-protected sites (Nyali and Vipingo) had intermediate recruit densities. Dominating genera were Favia, Porites, Favites, Pocillopora and Pavona in their order of overall abundance. Coral genera exhibited site specific abundance and mortality rates with Pocillopora having high abundance in Nyali (3.46 recruits/m²) and high mortality rate in Vipingo (85%). Benthic cover was dominated by Hard coral, turf algae, sand and rubble in all the sites. There was significant variation in seawater temperature levels with Kanamai recording the highest mean temperature (27.83°C), temperature range (12.27) and also recorded the highest maximum temperature (36.23°C). These findings suggest that there is spatial and temporal variation in recruit density, genera richness and survival of coral genera. Results also indicate that area protection and seawater temperature influence recruitment between habitats but benthic substrate characteristics influence recruitment within a habitat.

INTRODUCTION

Coral recruitment can operationally be defined as the initial sighting of recently settled juveniles in the adult habitat (Caley et al., 1996). Successful recruitment is...
critical for the survival of a coral population. Measuring recruitment patterns and mortality of corals is of fundamental importance for understanding the mechanisms that regulate their populations and mediate species coexistence (Underwood and Fairweather 1989).

Recruitment in corals has been extensively studied, usually within the first weeks or months after initial settlement from the plankton (reviewed by Harrison and Wallace 1990), demonstrating considerable temporal variation between seasons and years, and spatial variation between sites (e.g., Birkeland 1977, Rogers et al., 1984, Wallace 1985a, b; Babcock 1988, Harriott and Fisk 1988). Spatial and temporal variation in recruitment has been shown to be an important component in the population dynamics of corals (Warner and Chesson, 1985). Differences in coral recruitment rates between and within sites has been measured in several sites in Kenya; (Obura et al., 2005, Maghribai et al., in review) and Tanzania (Muhando 2002) and has shown that seasonal variation in recruitment rates differ among taxa of corals, though a variety of locations show the general pattern of highest recruitment in the warmest season. Seasonality in recruitment has also been reported in the U.S Virgin Islands (Dustan 1998), Great Barrier Reef (Wallace and Bull 1982, Harriot 1992, Harriot and Fisk 1988) Okinawa (Sakai and Yamazato 1984) the northern Gulf of Mexico (Bagget and Bright 1985) and Hawaii (Fitzhardinge 1985). In all cases, most recruitment occurred in the spring and summer months, following the major spawning season. However, the interaction between recruitment and management regimes is little understood.

Settlement rates and taxonomic composition may be expected to vary spatially due to variations in geographic availability of larvae, prevailing hydrographic conditions and physical characteristics of sites. Most studies examining more than one site show significant differences in recruitment between sites, but replicated time-series show that many of these patterns are complicated by temporal variations (Baggett and Bright 1985, Wallace 1985). Taxonomic differences in recruitment patterns have also been found at the scale of individual reefs (Harriott and Fisk 1988). Some corals respond to specific settlement cues (Morse et al. 1988), which is likely to contribute to spatial variation in abundance. Similarly, preemption or overgrowth by established corals and algae is an important mechanism that can cause spatial variation in recruitment (e.g., Birkeland 1977, Sammarco 1980, and Hughes 1985). Studies of coral recruitment in the Caribbean have found variable rates of recruitment between species (Rogers et al., 1984 and Smith 1992, 1997) with large frame-building species showing low recruitment rates.

This study aimed at determining the spatial and temporal variation of genera recruitment and survival in the Kenyan coast. We asked 3 questions (1) whether there was site variability in coral recruitment and mortality rate (2) whether there was monthly,
seasonal and yearly variability in recruitment and mortality rate, and (3) whether area protection, temperature and coral cover area influenced coral recruitment and mortality rates.

MATERIALS AND METHODS

Study Area
The study area encompasses four reef sites; Mombasa Marine Park (MMP), Nyali, Vipingo and Kanamai on the North coast of Kenya (Fig. 1). MMP is characterized by water temperature range of 25-31°C throughout the year with stable salinity levels and moderately high nutrient level from terrestrial runoff and ground water. It has a reef height of 1.09m and the amplitude from neap tide to spring tide varies from 1.5 to 4m. This site experiences occasional water exchanges with the oceanic waters during high and low tides due to a small depression that forms a small channel through the reef crest. This site is protected from all extractive uses including fishing but is a primary site for glass bottom boat and snorkeling trips among tourists. Nyali resembles the MMP but traditional fishing is allowed. Kanamai and Vipingo are unprotected shallow sites characterized by extensive fishing and intensive exploitation of corals, shells and other marine organisms for commercial purposes. Their reef heights are 1.4 and 1.45m, respectively. All four sites are patch reefs within the shallow lagoon (0-7 m depth) that is formed by a 200 km fringing reef that extends from Shimoni (near the border with Tanzania) to Malindi.

Sampling Design
Two replicate stations were used at each site. The distance between stations ranged from 200m to 5m. A line transects of 25m long was used to permanently mark the area to be sampled at each station. Three 1m² permanent quadrats were sequentially located on each side of the line transect. The quadrats were randomly placed using a system of random numbers. Placement of the quadrats was such that they excluded at least 50% of coral cover, sand or other substrates that may inhibit settlement. Nails were driven into to the reef substrate at the corners of each square to delimit the quadrat area. A 1 m² PVC quadrat was used to help mark the quadrats for sampling (Fig. 2). Each station was then sampled once a month for a period of 16months.

Sampling for Recruits
Recruits were defined as corals that are less than 10cm in diameter. During the initial sampling, the number of recruits was recorded for each quadrat and recruits identified to genus level. The position of each recruit was recorded on an underwater paper for the purpose of sampling the same individual on subsequent sampling. The maximum diameter and the maximum perpendicular to that diameter of each recruit colony was measured to the nearest 1mm using a plastic caliper, from which the area of each coral was calculated. During subsequent sampling, new recruits (individuals not observed in the previous sampling) were recorded. Individuals observed in previous sampling period but not observed in immediate sampling period were considered to have died. Recruits that were overgrown with algae were also considered as dead.

The substrate characteristics at each station was described by characterizing the percentage intersection rate of the substrate type (e.g. hard coral, sand, rubble, algal turf, coralline algae, Halimeda, macroalgae, soft coral, sponge and zoanthids) along a 10m line transect. Seawater temperature was monitored throughout the study period using temperature loggers placed at each of the four sites.

Data Analysis
Monthly recruit density was derived from the number of recruits per 1m². Monthly mortality rate was derived from the number of dead recruits per 1m² per and was quantified as a percentage decrease. To determine site, monthly and yearly variations in recruit density and mortality rates t-tests were used.
RESULTS

Recruit Density
There was a significant difference in recruit density within MMP and Kanamai while stations within Nyali and Vipingo did not vary significantly. Mean recruit density varied from 3.51 ± 2.14 (Kanamai 1) to a maximum of 7.45 ± 4.09 (MMP 1) as shown in Table 1.

The highest number of recruits recorded in a single quadrat was 20 in MMP 1. Monthly recruit densities varied significantly in Kanamai 1, MMP 2 and Nyali whereas the other sites did not have any significant variation in monthly recruit densities. Highest monthly recruit density occurred in Nyali in March 2006 (6.00 ± 1.23) and the lowest in Kanamai 1 in Jun 2007 (2.3 ± 2.31, Fig. 2). Southeast Monsoon and Northeast Monsoon seasons varied in their recruit densities with SEM 2006 recording the highest density (6.14 ± 3.48) and lowest density was in NEM 2007 (3.51 ± 2.52, Fig. 3). Both NEM and SEM showed high recruit densities in the year 2006 and low densities in year 2007.
Genera Abundance and Mortality Rate

A total of 16 genera was recorded in all the sites. MMP recorded the highest number of genera (13, Table 2) while Vipingo showed the lowest number of genera (7) and the other sites showed intermediate numbers of genera. Recruitment was dominated by *Favia* (20%), *Porites* (19%) and *Favites* (19%) whereas *Pocillopora* and *Pavona* occurred in all sites but had very low abundance (13% and 8% respectively, Fig. 4). Abundance of other genera was very low with majority having ≤ 2% abundance and was grouped together as others.

<table>
<thead>
<tr>
<th>Genera</th>
<th>Mombasa</th>
<th>Nyali</th>
<th>Kanamai 1</th>
<th>Kanamai 2</th>
<th>MMP 1</th>
<th>MMP 2</th>
<th>Nyali</th>
<th>Vipingo</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Favia</em></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td>20%</td>
</tr>
<tr>
<td><em>Porites</em></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td>19%</td>
</tr>
<tr>
<td><em>Favites</em></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>19%</td>
</tr>
<tr>
<td><em>Pocillopora</em></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13%</td>
</tr>
<tr>
<td><em>Pavona</em></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8%</td>
</tr>
<tr>
<td><em>Platygyra</em></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6%</td>
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<tr>
<td><em>Galaxea</em></td>
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<td>x</td>
<td>x</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td><em>Acropora</em></td>
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<td>x</td>
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<td></td>
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<td></td>
<td>3%</td>
</tr>
<tr>
<td><em>Acanthastrea</em></td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2%</td>
</tr>
<tr>
<td><em>Montipora</em></td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1%</td>
</tr>
<tr>
<td><em>Astreopora</em></td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
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<td></td>
<td>1%</td>
</tr>
<tr>
<td><em>Cyphastrea</em></td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1%</td>
</tr>
<tr>
<td><em>Fungia</em></td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1%</td>
</tr>
<tr>
<td><em>Hydnophora</em></td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1%</td>
</tr>
<tr>
<td><em>Echinopora</em></td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><em>Alveopora</em></td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0%</td>
</tr>
</tbody>
</table>

Table 1. Mean, standard deviation, maximum and minimum of recruit density (no. per m$^2$) and the overall mortality rate of coral recruits in 2006 and 2007. There were no significant differences between replicate sites at Nyali and Vipingo, so data for each reef were pooled.

Table 2. Genus composition at each site and their overall abundance.
Figure 4. Composition of recruits population in the four sites from February 2006 to June 2007.

Table 3. Overall mean and standard deviation, maximum, minimum and range of sea-water temperature in four sites in Kenya in 2006 and 2007.

<table>
<thead>
<tr>
<th>Site</th>
<th>MMP</th>
<th>Nyali</th>
<th>Vipingo</th>
<th>Kanamai</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>27.57</td>
<td>27.50</td>
<td>27.47</td>
<td>27.83</td>
</tr>
<tr>
<td>StDev</td>
<td>1.40</td>
<td>1.41</td>
<td>1.45</td>
<td>1.92</td>
</tr>
<tr>
<td>Max</td>
<td>32.90</td>
<td>32.79</td>
<td>33.84</td>
<td>36.23</td>
</tr>
<tr>
<td>Min</td>
<td>24.03</td>
<td>24.65</td>
<td>23.74</td>
<td>23.95</td>
</tr>
<tr>
<td>Range</td>
<td>8.87</td>
<td>8.14</td>
<td>10.10</td>
<td>12.27</td>
</tr>
</tbody>
</table>

Favia was more abundant in Kanamai and MMP, Porites in Vipingo and Pocillopora in Nyali. There was monthly variation in the abundance of Favia and Favites with both having highest recruit densities in June 2006 (5.79 and 2.67 respectively), but Pocillopora and Porites did not have significant monthly variation in recruit densities. Genera also showed varying mortality rates between sites with Porites and Favites showing low mortality rates in Vipingo (38% and 50% respectively) and high mortality rates in Nyali (Fig. 5). Pocillopora recorded low mortality in Nyali (43%) and high mortality in Vipingo (85%).

Habitat Characteristics

Surveys on benthic cover reported high percentage cover of hard coral in Kanamai 1 (28%, Fig. 6), coralline algae and turf algae in MMP 2 (15%, 36% respectively) and macro algae in Nyali 2 (24%). Temperature varied significantly between sites with Kanamai having the highest mean temperature, 27.8 °C (Table 3).

Maximum temperature occurred in Kanamai (36.2 °C) and this site recorded the highest range in temperature over the entire study period (12.3 °C, Fig. 7), while the lowest range in temperature occurred in Nyali (8.1 °C).
Figure 5. Site specific mortality (%) of common genera in the four reefs. Mortality was calculated as the total number of recruits that died divided by the total number of recruits for each genus.

DISCUSSION

The pattern exhibited in this study was of significant variability across sites, seasons and years. Within this pattern, Mombasa Marine Park (MMP) showed higher abundances compared to the other sites. Recruitment was high in the SEM season and the year 2006 recorded the highest recruitment. In addition, MMP recorded the highest number of genera and generally, *Favia*, *Porites*, *Favites*, *Pocillopora* and *Pavona* were the dominating genera. Substrate characteristics showed site specific abundances with hard coral having a higher percentage cover in station 1 of MMP (28%, Table 2). Kanamai recorded the highest temperature...
Figure 6. Benthic cover at all the stations.

Figure 7. Hourly seawater temperature (°C) on coral reefs in MMP, Kanamai, Nyali and Vipingo from March 2006 to June 2007.
levels and the broadest range between maximum and minimum temperatures (Table 3).

A number of factors co-occurred at the site with the highest recruit density, in the MMP. This site had the highest coral cover, which has been shown to be correlated with production of larvae (Miller et al., 2000), though it is not known to what extent study sites may be self-seeding. Additionally the greater structural complexity provided by high cover of varying coral morphologies, as found in MMP, contributes to greater juvenile survival. MMP is also located near a channel which brings a strong current flow. This provides for greater exposure to coral larvae from the reef front, and the strong current flow makes the water more aerated and substrate surfaces cleaner hence more conductive to settlement and post-settlement survival (Obura et al., 2005). Temperature range was low in MMP compared to that in Kanamai and Vipingo which is favourable for recruit survival (Shepherd et al., 2002). Similar results of high recruitment in MMP were found in Obura et al., 2005 and Tamalander, 2002.

Variation in recruitment within the MMP can be associated with the differences in coral cover. However, the site in Kanamai with the highest coral cover area recorded the lowest recruitment. This implies that apart from coral cover area; there are other factors that influence recruit density and also recruitment is patchy. In this case, the high temperature variation between MMP and Kanamai could be a possible factor that contributed to the variations in recruitment. This shows that coral cover can determine recruit densities within habitats but other broader scale factors such as temperature variation may be strong determinants of recruit densities between different habitats.

Results on recruit density between Nyali and MMP contrast those recorded on settlement tiles where Nyali recorded high settlement density (Mangubhai et al., 2007). Spat abundance is linked to larval availability and dispersal whereas the density of juvenile corals within an area reflects post-settlement mortality (Clark, 2002). This shows that there are many larvae that settle in Nyali but only a few make it to the visible juvenile stage. The high mortality rates recorded in this site (Table 1) explain this variability. However, a synchronized study on settlement plates and artificial substrate is recommended to make strong conclusions. The influence of mortality rates on recruit density is also experienced within Kanamai and MMP whereby the stations with high mortality rate recorded low recruit densities (Table 1).

Monthly variability in recruit density was observed in some stations only, with Nyali recording the highest monthly recruit density in March 2006 and Kanamai recording the lowest density in June 2007. The month of March is associated with calm and clear conditions. The month of June is a rainy season with high sedimentation, macroalgal dominance due to input of nutrients from terrestrial runoff and physical disturbance from waves make the substrate conditions less favorable for recruitment and may cause increased mortality of recruits. At a broader scale, the SEM season had high recruit density compared to NEM season in both the year 2006 and 2007. Studies on settlement plates in the East African region have shown a general pattern of high recruitment during the warmest months and low recruitment in the cool months (Maghubhai et al., in press; Obura et al., 2005; Muhando, 2002 and Nzali et al., 1998). Results of this study recorded high recruitment during the cool months and this is explained by the fact that there is a time laps before visible juveniles are observed in the natural substratum.

MMP and Nyali had a higher number of genera compared to Kanamai and Vipingo (Table 2). This reflects differences in both temperature conditions and protection between the sites. MMP and Nyali experience lower absolute and range in temperature, which in general are more favorable for survival of coral recruits. In addition, MMP is protected and Nyali has limited protection while Vipingo and Kanamai are not protected, which may also result in higher coral diversity at the former. The abundance of coral genera varied with Porites being more abundant in Vipingo and MMP, while Pocillopora was more abundant in Nyali, similar to findings of McClanahan and Maina (2003) and (Mangubhai et al., 2007).
In conclusion, protection level and sea-water temperature may be influencing coral recruitment at these study sites. However, variation of recruitment within a habitat may be mainly influenced by substrate characteristics. Further studies on temporal variation of benthic substrate characteristics are recommended to determine how the seasonal dynamics in benthic cover affect seasonal variability in recruit densities.

ACKNOWLEDGEMENTS

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