Coral recruitment patterns in the Florida Keys

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Abstract: This study examines scleractinian zooxanthellate coral recruitment patterns in the Florida Keys to determine if differences in density or community composition exist between regions. From July to September 2002, nine patch reefs, three in each of the upper, middle and lower Keys, were surveyed for coral recruits (colonies <5 cm in diameter) using randomly placed quadrats and transects. Coral recruits were enumerated, measured, and identified to genus. Fourteen genera of corals were observed across all sites and ranged from five to 13 per site. Densities ranged from 6.29 ± 1.92 (mean ± SE) to 39.08 ± 4.53 recruits m^{-2}, and there were significant site and regional differences in recruit densities. The density of recruits in the upper Keys was significantly lower than in the middle and lower Keys. In addition, the upper Keys were less diverse and had a different recruit size-frequency distribution. The majority of recruits were non-massive scleractinian species that contribute relatively little to overall reef-building processes, a finding that is similar to previous studies. Fewer recruits of massive species were found in the upper Keys compared to the middle and lower Keys. The recruitment patterns of the reefs in the upper Keys could potentially hinder their ability to recover from stress and disturbances.

Key words: coral, recruitment, Florida Keys, community composition, scleractinians.

Coral recruitment, defined as the settlement of larvae and growth discernible a size discernible with the naked eye, is an essential feature of population dynamics that underlies the perpetuation of coral reefs (Bak and Engel 1979, Dunstan and Johnson 1998, Edmunds 2000, Hughes and Tanner 2000). Many reefs worldwide are being degraded by both natural and anthropogenic causes. In general, coral reefs have been declining in Florida for the past two decades, shifting from dominance by coral to dominance by macro-algae (Dustan and Halas 1987, Porter and Meier 1992, Porter *et al.* 2002). Many factors contributing to this change have been implicated, including decreased water quality, *Diadema antillarum* die-off, increased fishing pressure, climate change, and disease outbreaks (Lessios 1988, Lapointe and Clark 1992, Smith and Buddemeier 1992, Lapointe 1997). In order for these reefs to recover and continue to grow, they must receive a supply of recruits that are able to establish themselves and reproduce.

Based on geographic criteria and environmental conditions, the Florida Keys can be partitioned into at least three regions: upper Keys, middle Keys, and lower Keys (Shinn *et al.* 1989, Ginsburg and Shinn 1994). The upper Keys extend from Soldier Key to Upper Matecumbe Key (Fig. 1). They are fairly continuous and are oriented in a north-east to south-west direction, parallel to the shelf break (Ginsburg and Shinn 1994). The middle Keys extend from Upper Matecumbe Key to Big Pine Key. The middle Keys are more discontinuous than the upper Keys and have many inter-island passes (Ginsburg and Shinn 1994). The lower Keys extend from Big Pine Key to Key West. These islands are composed of oolitic limestone and are oriented east to west (Ginsburg and Shinn 1994).

This study examined coral recruitment patterns in three regions of the Florida Keys to determine if local or regional differences in density or community composition exist. Most previous studies of recruitment in the Florida Keys have focused on the upper Keys, most likely due to ease of access. Therefore, little is known about recruitment in the middle and lower Keys regions.

MATERIALS AND METHODS

Between mid July and early September 2002, three patch reefs 3-8 m in depth were surveyed in each of the upper, middle, and lower Keys regions (Fig. 1). Reef sites were chosen based on ease of access. Upper Keys reefs included Alina's Reef, Turtle Rocks, and Watson Reef. Middle Keys included East Turtle Shoal, West Turtle Shoal, and Marker 48. Lower Keys included Lower 2, Lower 1, and West Washerwoman.

All reefs were surveyed for coral recruits, defined as visible colonies less than 5 cm in diameter. Assuming a 1-3 mm diameter monthly growth rate (Bak and Engel 1979, Van Moorsel 1988), corals 5 cm in size are approximately one to four years old. At each reef, four 25 m transects were laid parallel to each other and perpendicular to shore at random distances, but at least 5 m apart. Coral recruits were surveyed in 17 randomly placed 0.25 m^2 quadrats, totaling 4.25 m^2 per transect. This number of samples is sufficient to adequately characterize juvenile coral density on reefs in the Florida Keys (Edmunds *et al.* 1998). All recruits were enumerated, measured with calipers to the nearest mm, and identified to genus.

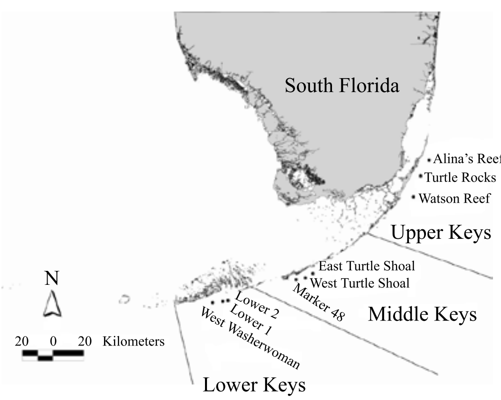

Fig. 1. Study sites. Upper Keys reefs include Alina's Reef, Turtle Rocks, and Watson Reef. Middle Keys include East Turtle Shoal, West Turtle Shoal, and Marker 48. Lower Keys include Lower 2, Lower 1, and West Washerwoman.

Density of recruits was calculated for each transect as the number of recruits m^{-2}. Before statistical analysis, density data were log transformed to meet assumptions of normality and equal variance (Shapiro-Wilk = 0.7498 and examination of residuals, respectively). To test the hypotheses of differences in recruit density among sites or regions, a block ANOVA was performed with region as the block.

For each transect, taxonomic composition of recruits was calculated as the percentage of recruits in each genus relative to all recruits present. An average percentage of taxonomic composition for each site was calculated for each genus by averaging across the four transects. A cluster analysis using Ward's minimum variance method was performed on the taxonomic composition data to determine if sites within regions were more similar to each other than to sites within other regions. A second cluster analysis using Ward's minimum variance method on the presence or absence of genera at each site was performed so that clustering of sites could be examined for all genera weighted equally.

The size frequency distribution of recruits was calculated for each site. A chi-squared contingency table analysis was used to test whether the size frequency distribution of recruits differed among sites.

RESULTS

The density of recruits ranged from 6.29 ± 1.92 (mean ± SE) to 39.08 ± 4.53 recruits m^{-2} (Fig. 2). Turtle Rocks in the upper Keys had the lowest recruit density, and Lower 1 in the lower Keys had the highest density. Recruit density for each region ranged from 8.18 ± 0.97

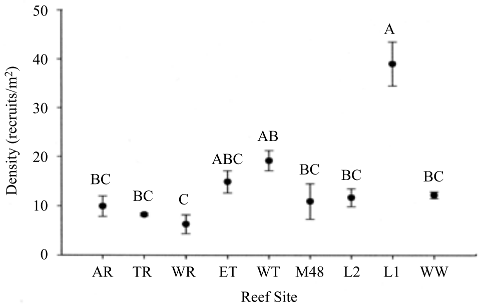

Fig. 2. Average density of coral recruits m^{-2} for nine sites. Sites are listed from north to southwest. AR=Alina's Reef, TR=Turtle Rocks, WR= Watson Reef, ET=East Turtle Shoal, WT=West Turtle Shoal, M48=Marker 48, L2=Lower 2, L1=Lower 1, and WW=West Washerwoman. Error bars represent one standard error of the mean. Sites with the same letters represent sites that are not significantly different.

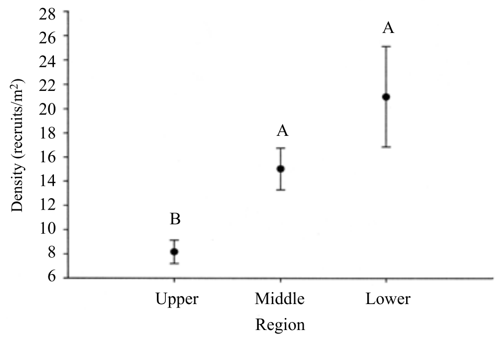

Fig. 3. Average density of coral recruits by region. Error bars represent one standard error of the mean. Regions with the same letter represent regions that are not significantly different.

to 21.01 ± 4.13 recruits m^{-2} (Fig. 3). The lower Keys region had the highest recruit density, followed by the middle, then upper Keys regions.

A block ANOVA with regions as blocks revealed significant differences in recruit density both among regions and among sites ($p=0.0001$ and $p=0.0012$, respectively). Tukey *a posteriori* pairwise comparisons showed that recruit density in the upper Keys was significantly lower ($p<0.05$) than in both the middle and lower Keys regions, but density in the lower and middle Keys was not significantly different. Tukey pairwise comparisons among sites revealed that recruit density at site Lower 1 in the lower Keys was significantly higher than all other sites except East Turtle and West Turtle and that West Turtle in the middle Keys had a significantly higher density than Watson Reef in the upper Keys ($p<0.05$). All other sites were not significantly different.

A total of 14 genera of coral were observed across all sites. The upper Keys had a lower taxonomic diversity, ranging from five to nine genera present per site (Table 1). The middle and lower Keys ranged from nine to 13 genera per site. *Porites* was the dominant genus in the upper Keys, and *Siderastrea* was the dominant genus in the middle and lower Keys (Table 1). These two genera comprised 62-94% of the total community composition of recruits at all sites. Species of *Agaricia* and *Dichocoenia* were present at all sites. The genus *Stephanocoenia* made up a large proportion of the recruit composition in the lower and middle Keys (6.9-18.2%) but contributed proportionately less in the upper Keys (0-1.4%). Recruits of the massive species *Colpophyllia natans* (Houttuyn, 1772) were only present in the middle and lower Keys. *Montastraea* spp. were present at all lower and middle Keys sites except one, but were absent from two of the three upper Keys sites. *Scolymia* and *Mycetophyllia* species were absent from all upper Keys sites but were present in the majority of middle and lower Keys sites (Table 1).

Cluster analysis, based on taxonomic composition of recruits, showed two main clusters of site locations (Fig. 4). One cluster consisted of all sites in the upper Keys plus one site from the middle Keys (Marker 48). The other consisted of sites from the lower Keys plus the remaining middle Keys sites. No clear regional clustering of the middle and lower Keys was apparent. Clustering based on the presence or absence of genera produced the same pattern with the upper Keys reef plus one middle Keys reef forming one cluster and the two remaining middle Keys plus the lower Keys forming another (Fig. 5).

Chi-squared contingency table analysis revealed that the size-frequency distribution

TABLE 1
Average taxonomic composition of recruits at each site

Genus	AR	TR	WR	ET	WT	M48	L2	L1	WW
Agaricia	3.1	0.7	5.0	5.2	6.6	0.4	6.3	8.1	9.0
Colpophyllia	0	0	0	0.8	1.4	0.3	0.6	0.3	0.6
Diploria	1.6	0	0.7	0.8	0. 9	0.4	2.1	0.3	0
Dichocoenia	0.4	3.6	1.8	1.6	3.5	1.0	2.9	1.0	1.9
Eusmilia	0.4	0	0	0	0	0.4	0	0	0
Favia	1.9	2.9	0	1.8	5.6	10.3	2.6	1.8	1.9
Montastraea	0.4	0	0	2.5	5.1	0	1.0	2.4	0.9
Mycetophyllia	0	0	0	0.4	0	0	0.6	0.6	2.0
Oculina	0	0	0	0	0	0	0	1.1	0
Porites	52.7	45.9	79.1	17.4	12.5	34.8	16.2	5.3	29.7
Solenastrea	0	0	0	0	0	0	0	2.1	0
Scolymia	0	0	0	1.3	1.3	0	0	1.8	3.1
Siderastrea	37.0	44.3	13.4	49.2	53.4	45.0	46.1	56.4	37.6
Stephanocoenia	0.6	1.4	0	18.0	8.2	6.9	18.2	15.1	10.4
Total Genera	9	6	5	11	10	9	10	13	10

Values represent the percent composition averaged over four transects. AR=Alina's Reef, TR=Turtle Rocks, WR= Watson Reef, ET=East Turtle Shoal, WT=West Turtle Shoal, M48=Marker 48, L2=Lower 2, L1=Lower 1, and WW=West Washerwoman.

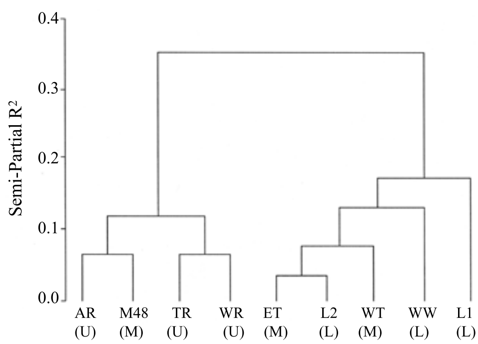

Fig. 4. Dendrogram of average taxonomic composition of recruits, using Ward's minimum variance cluster method. Sites clustering closer together are more similar. AR= Alina's Reef, TR=Turtle Rocks, WR= Watson Reef, ET=East Turtle Shoal, WT=West Turtle Shoal, M48=Marker 48, L2=Lower 2, L1=Lower 1, and WW=West Washerwoman. Letters in parentheses under the sites indicate the region of each site: U=upper Keys, M=middle Keys, L=lower Keys.

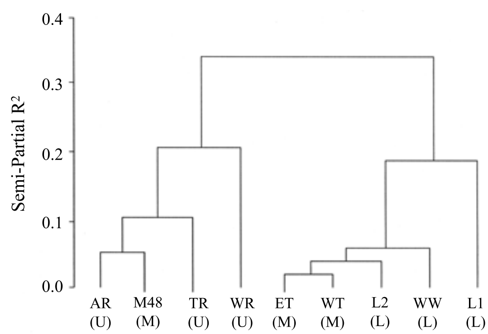

Fig. 5. Dendrogram of presence and absence data for genera of recruits at each site using Ward's minimum variance cluster method. Sites clustering closer together are more similar. AR= Alina's Reef, TR=Turtle Rocks, WR= Watson Reef, ET=East Turtle Shoal, WT=West Turtle Shoal, M48=Marker 48, L2=Lower 2, L1=Lower 1, and WW=West Washerwoman. Letters in parentheses under the sites indicate the region of each site: U=upper Keys, M=middle Keys, L=lower Keys.

of coral recruits varied significantly among sites ($p<0.0001$). The frequency of recruits decreased with increasing size class for most of the sites in the middle and lower Keys (Fig. 6). However, the upper Keys sites had a smaller proportion of the smallest size class (1-10 mm) compared to sites in the middle and lower Keys.

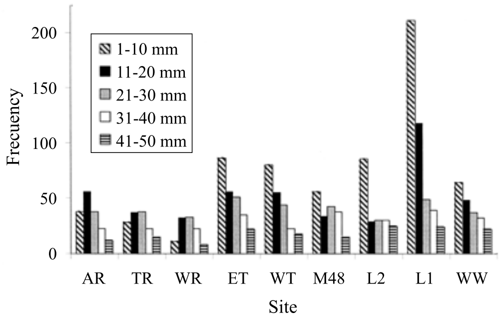

Fig. 6. Size-frequency distribution of coral recruits by site. Bars represent the number of recruits in each size class for each site. Sites are listed from north to southwest. AR=Alina's Reef, TR=Turtle Rocks, WR= Watson Reef, ET=East Turtle Shoal, WT=West Turtle Shoal, M48=Marker 48, L2=Lower 2, L1=Lower 1, and WW=West Washerwoman.

DISCUSSION

Density estimates of recruits in this study were higher than previously reported in the Florida Keys. Chiappone and Sullivan (1996) reported mean densities of 1.18 to 3.74 recruits m^{-2} on three different reef types in the upper Keys. Dustan (1977) reported densities of 9.6 to 11.8 recruits m^{-2} for reefs in the upper Keys, values closer to those found in this study for most of the reefs. However, both of these studies used different size classifications than the present study. Chiappone and Sullivan (1996) used colonies less than 4 cm in size and excluded all colonies of *Siderastrea radians* (Pallas, 1766) and *Favia fragum* (Esper, 1795) since colonies 2 cm in size are reproductively mature. Dustan (1977) included colonies less than 15 cm in size. The previous studies mentioned only sampled reefs in the upper Keys. However, the present study included sites from the middle and lower Keys, which were found to be significantly higher in recruit density than the upper Keys.

The upper Keys region seems to be distinct from the middle and lower Keys regions in several ways. Recruit density was significantly lower in the upper Keys than in the middle and lower Keys. The upper Keys region also had lower recruit diversity and a different taxonomic composition. The coral recruits in this region were predominately *Porites* compared to the middle and lower Keys which were dominated by *Siderastrea* recruits. *Stephanocoenia* recruits were common in the middle and lower Keys but were virtually absent in the upper Keys. In addition, fewer recruits of massive, reef-building genera, such as *Colpophyllia* and *Montastraea*, were found in the upper Keys. Lastly, the upper Keys had a different size-frequency distribution of recruits. The greatest proportion of recruits was from the smallest size class (1-10mm) in the middle and lower Keys, comprising 30-48% of all the coral recruits surveyed. However, only 10-23% of the recruits in the upper Keys were in the 1-10 mm size class.

Differences in recruitment can result from differences in larval production, larval mortality, dispersal, settlement, and benthic survival (Underwood and Keough 2001). Presumably, at least one of these processes is affecting the upper Keys differently than the middle and lower Keys. A possible reason for the differences in recruit density could be that the upper Keys simply experienced a poor recruitment year. This hypothesis is supported by the fact that a smaller proportion of the recruits in the upper Keys were in the smallest size class. If larval production were reduced or if larvae and/or newly settled recruits experienced greater mortality than in the middle and lower Keys, recruitment density would be reduced. Another possible explanation is that the upper Keys did not experience an anomalous recruitment year, but that they do indeed have less recruitment than the other two regions. Presumably, if this scenario is true, the reduced density of recruits would not be limited to the smallest size class. However, the density of recruits in the other size classes were sometimes, but not always, lower in the upper Keys compared to the other regions.

Although reasons for the differences in density and taxonomic composition in the upper Keys are not known, they can have important implications for the adult coral communities present in the region. The majority of recruits observed in this study were of non-massive species that contribute relatively little to overall reef-building processes, a finding similar to previous studies in the Caribbean (Bak and Engel 1979, Chiappone and Sullivan 1996, Smith 1997, Edmunds 2000). These differences in recruitment strength have been hypothesized to reflect different life history strategies (Bak and Engle 1979, Szmant 1986). Massive species such as *Montastraea* spp., *Diploria* spp., *C. natans*, and *Siderastrea siderea* (Ellis & Solander, 1786) are long-lived, strong competitors and tend to be spawners that reproduce only once a year (Szmant 1986). Thus, even though recruitment levels are low, they have high survival rates as adults and presumably as juveniles. The much higher recruitment rates of non-massive corals such as *Porites* spp., *Agaricia* spp., and *S. radians* reflect a different life history strategy. They are brooding species that reproduce many times a year and have high recruitment rates, but they are weaker competitors and do not live as long or grow as large as the massive species (Szmant 1986). Even though low recruitment of massive species is not unusual, most of the upper Keys sites had a lower percentage of these massive species than the middle and lower Keys.

The fact that the upper Keys region had both a lower density and lower taxonomic diversity of coral recruits could negatively affect the region's ability to recover from major stresses and disturbances. However, it is unknown which is the cause and which is the effect. The upper Keys may already be experiencing greater environmental stress, thus causing the region to have a lower diversity and density and have a different taxonomic composition of coral recruits. The upper Keys sites are closer to the northern limit of the extent of the Florida reef tract and are also closer to the city of Miami. Thus, the upper Keys may be experiencing more environmental stress that is affecting coral recruitment patterns.

In contrast to the idea of increased environmental stress in the upper Keys, Ginsburg *et al.* (2001) contend that the lower and middle Keys experience more environmental stress from the outflow of Florida Bay water through the numerous passages between the islands of the middle and lower Keys. Ginsburg *et al.* (2001) cite this phenomenon as the reason why patch reefs are more numerous in the upper Keys compared to the middle and lower Keys. However, the current study found that coral recruit density and richness were lower at the upper Keys, and that the taxonomic composition and size frequency distribution were different in the upper Keys compared to the middle and lower Keys. Because of the important implications of these different recruitment patterns, further studies of the causes are needed.

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RESUMEN

Se examina los patrones de reclutamiento de corales escleractinios zooxantelados en los Cayos de la Florida para determinar si existen diferencias en densidad o composición de la comunidad en diferentes regiones. Entre julio y setiembre del 2002, se inventariaron los reclutas (colonias de <5 cm de diámetro) usando cuadrantes y transectos al azar en nueve "parches" arrecifales: tres en los cayos del norte, tres en los del medio y tres en los del sur. Todos fueron numerados, medidos e identificados a nivel de género. Se observaron catorce géneros: entre cinco y 13 por sitio. Las densidades tuvieron un ámbito de 6.29 ± 1.92 (promedio ± DS) a 39.08 ± 4.53 reclutas m^{-2} , con diferencias estadísticamente significativas entre sitios y entre regiones. La densidad de reclutas en los cayos del norte fue significativamente menor que en los demás. Los cayos del norte tuvieron menor diversidad y diferente distribución de tamaños de reclutas. La mayoría de los reclutas eran de especies de escleractinios no masivas, las cuales contribuyen relativamente poco al proceso de crecimiento del arrecife, algo parecido a lo informado en otros estudios. Se encontraron menos reclutas de especies masivas en los cayos del norte. El patrón de reclutamiento en los arrecifes de los cayos del norte podría inhibir potencialmente la recuperación tras "impactos" y perturbaciones.

Key words: Coral, reclutamiento, Cayos de la Florida, composición comunitaria, escleractinios.

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