The sequence and progression of early colonization by Jamaican reef corals was followed for up to six years. Replicate m² areas at depths of 10m to 20m were initially cleared and monitored photographically at annual intervals. Both sexual (larval) and asexual (vegetative) recruitment occurred. Rates of larval recruitment into adjacent coral areas was almost 6 times lower, indicating that coral settlement and/or early survival is strongly density-dependent. Asexual recruitment was independent of coral cover.

Almost 90% of larval recruitment was by Leptoseris cucculata and Agaricia agaricites, which were characterized by rapid growth rates, fragile foliaceous skeletons, small colony size, and high mortality. Asexual propagules of corals were virtually absent at 20m, but ramose fragments of Madracis mirabilis, Porites porites, and Acropora cervicornis accounted for one-third of the total recruitment at 10m. These species had low rates of larval recruitment, fast growth rates, and formed large branching clones. Although asexual recruits were larger than newly settled larvae, their survivorship was generally much lower.

Recruitment and mortality rates varied significantly from year to year. Larval input varied four-fold, while asexual recruitment fluctuated over a 12-fold range. Mortality, especially of small corals, rose sharply in 1983/84 following an algal bloom caused by the mass mortality of the grazing echinoid Diadema antillarum.

The number of colonies of A. agaricites and L. cucculata in cleared quadrats reached and then exceeded control levels after only 4 years, although after 6 years few colonies had grown to the size of the largest colonies found nearby. Populations of these two species had almost fully recovered in the experimentally disturbed sites, while other locally abundant species were virtually absent.

**Resumen**

La sucesión y la progresión del debut de la colonización por los corales en Jamaica, han sido seguido durante los últimos 6 años. A lo largo de este período, la colonización fue muy desigual, con una densidad de colonias más alta en el primer año. En general, la colonización fue baja en comparación con las áreas controladas. Las especies de corales que colonizaron las áreas de la colonización, especialmente Leptoseris cucculata y Agaricia agaricites, que fueron las más abundantes, presentaron tasas de mortalidad alta. Las especies de corales asexuales, como Acropora cervicornis, fueron menos abundantes y tuvieron tasas de mortalidad más bajas.

Los resultados de este estudio indican que la colonización de corales en el mar de Jamaica es variable y depende de factores ambientales. Algunas especies de corales son más resistentes a la competencia de otras especies y pueden colonizar áreas en forma más rápida. Es importante continuar con el seguimiento de la colonización de corales en este área para entender mejor su dinámica y cómo se adaptan a los cambios en el ambiente marino. Se recomienda continuar con este tipo de investigación para mejorar nuestra comprensión de la colonización de corales en el mar de Jamaica.
Several recent studies have shown that local abundances and species compositions of scleractinians often shift significantly in relatively short periods of time, especially when rates of change are scaled in relation to the potential longevity of individual colonies (e.g., Connell 1977; Bak and Luckhurst 1980; Pearson 1981; Davis 1982; Potter 1984; Hughes 1986; Hughes and Jackson 1985). Intermittent disturbances, which may be due to a wide variety of physical and biological agents, usually cause the most dramatic alterations in the structure of a coral community (e.g., Connell 1978; Karlson 1980; Jackson and Hughes 1985). By clearing patches of substrate at various temporal and spatial scales, disturbance initiates local sequences of colonization and "recovery." In the present study, I investigate experimentally the progress of early colonization on a Jamaican reef.

Reef corals have evolved a wide diversity of life histories and morphologies, which often result in characteristic differences between species in their susceptibility to disturbances (Highsmith 1982; Hughes and Jackson 1985; Jackson and Hughes 1985). Three general patterns have been described so far for Caribbean corals:

1. Some species, such as Diploria strigosa and Montastrea annularis, have evolved slow growing, often massive or encrusting skeletons which are resistant to all but the most extreme events (e.g., Bak and Luckhurst 1980; Woodley et al., 1981). These cleared quadrats were monitored photo-

2. Other, more delicate corals are damaged or broken up by routine disturbances, such as wind storms, but are usually not killed outright. Many of these species, such as Acropora palmata, A. cervicornis, A. grahamae, and randomly form loosely branched clones, which may be a morpho-

3. The last major category comprises corals that are often killed outright by disturbances (i.e., high susceptibility). In the Caribbean, the most common examples are Leptoseris cucullata and Agaricia agaricites, usually form very large and are relatively short-lived (Bak and Engel 1979; Bak and Luckhurst 1980; Hughes and Jackson 1985).

To test if these differences in life histories and morphologies also result in a predictable sequence of colonization and succession following a disturbance, an experiment was designed to initiate the destruction and subsequent recolonization which commonly occurs on a reef following a storm or hurricane. This type of physical disturbance often results in patches of dead coral interspersed with undamaged areas, on a variety of spatial scales ranging from entire reefs to parts of colonies (e.g., Highsmith et al., 1980; Woodley et al., 1981). Replicate plots were cleared by hand, and along with unmanipulated areas, were monitored annually. I describe below the spatial and temporal patterns of recruitment and mortality, the development of population structure, and the influence of established communities on coral colonization.

INTRODUCTION

METHODS

RESULTS

Recruitment

Over 700 corals were detected within the six cleared square meters from 1978 to 1984, giving an average recruitment rate (for corals greater than 1 cm diameter) of about 20/cm²/year (Figure 1). Almost eighty percent of the recruitment was larval, primarily by Leptoseris cucullata and Agaricia agaricites, and by the small branching Madracis mirabilis. Asexually generated coral fragments were also monitored, serving as controls and extending the range of living cover from zero to close to 100%.

The photographs were projected at 0.5 magnification, and each coral was traced out, numbered and measured along its maximum length. Percent cover of all macroorganisms was estimated from each photograph using 25 randomly spaced (100/m²) circular descriptions of the faunal composition at Rio Bueno and of the population dynamics of corals within the unmanipulated quadrats are given in Hughes and Jackson (1985). The quadrats at 10 m are on the edge of an underwater cliff, that slopes initially at about 60 degrees. Scleractinians include branching (primarily Madracis mirabilis, Porites furcata, Agaricia grahamae), massive or encrusting corals such as Diploria strigosa, Montastrea annularis, and fimbriate species (Agaricia agaricites, Lespsotera cucullata). At the deeper site at 20 m, the wall is closer to vertical than at 10 m (the slope of each site will become less important given the greater depth at 20 m). Branching and massive corals in the deeper site are less common, and the more abundant corals are Agaricia lamarcki and Siderastrea siderea. The quadrats at 20 m were monitored annually, serving as controls and extending the range of living cover from zero to close to 100%.

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long-lived species which are common at Rio Rueno, such as Colpophyllia natans, Montastrea annularis, M. cavernosa, and Siderastrea siderea, failed to recruit into any of the monitored areas. The amounts and modes of recruitment into the bared quadrats differed significantly between the two depths (Table 1). The annual rate of larval recruitment was greater every year (on average three times more) at 10 m than at 20 m. In particular, there were over 200 fewer recruits of Leptoseris and Agaricia and no Tubastraea aurea at the deeper site. Furthermore, virtually all of the asexual recruitment occurred at 10 m, presumably because of the gentler slope and closer proximity to dense stands of branching corals in shallow water (3-12 m), which were the source of the fragments. In the adjacent unmanipulated areas larval recruitment was strikingly lower, averaging only 0.5/m²/year (Mann-Whitney U-test for difference between cleared and uncleared quadrats, U = 0, P<0.01). Combining data from all quadrats at each depth, there was a significant negative correlation between mean rates of larval recruitment and percent cover of previously established macroorganisms (primarily corals and algae) indicating that pre-emption of space had a marked inhibitory effect on net amounts of larval recruitment by the corals (Spearman rank order correlation coefficient, rs = -0.45, n.s.). Because recruitment by fragments was proportionately greater in the unmanipulated plots, the species compositions of new recruits were significantly different in the two treatments (Wilcoxon signed rank test, T = 6, P<0.05). However, Leptoseris and A. agaricites were also the most abundant species in the control quadrats, accounting for over 80% of larval recruitment (Hughes and Jackson 1985). Temporal variability in recruitment over the six years was examined by testing the ratio of variance to mean annual rates for significant macroorganisms (Spearman rank order correlation coefficient, rs = -0.45, n.s.). Because recruitment by fragments was proportionately greater in the unmanipulated plots, the species compositions of new recruits were significantly different in the two treatments (Wilcoxon signed rank test, T = 6, P<0.05). However, Leptoseris and A. agaricites were also the most abundant species in the control quadrats, accounting for over 80% of larval recruitment (Hughes and Jackson 1985). Temporal variability in recruitment over the six years was examined by testing the ratio of variance to mean annual rates for significant

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Table 1. Total numbers of larval and asexual recruits (fragments) measured annually from July 1978 to July 1984 within six 1m² quadrats, three each at 10m and 20m.

| Species                | 10m  | 20m  | Total in 1984(%)
|-----------------------|------|------|------------------
| Leptoseris cucculata  | 165  | 66   | 231 84 (36)      
| Agaricia agaricites   | 154  | 36   | 190 56 (29)      
| Tubastraea aurea      | 98   | 0    | 98 18 (18)       
| Other larval recruits | 14   | 29   | 43 17 (40)       
| Asexual recruits       |      |      |                 
| Madraca mirabilis     | 71   | 5    | 76 13 (17)       
| Pocilia furcata       | 57   | 0    | 57 12 (21)       
| Acropora cervicornis   | 15   | 0    | 15 0 (0)         
| Total                 | 574  | 135  | 709 200 (28)     

Fig. 1. Mean annual coral recruitment rate (SD, 1977-1984) versus mean total living cover within 12 1m² quadrats. Big symbols are crowded, unmanipulated quadrats, small symbols are quadrats initially cleared. Filled symbols are quadrats at 10m, open symbols are at 20m.
departure from unity. For the most abundant species (L. cucullata, A. agaricites, L. aurata, M. mirabilis, F. forcuta and A. cervicornis), ratios varied from 3.8 to 21.6, indicating episodic (clumped in time) patterns of recruitment (K² values ranged from 18.9 to 107.9, P<0.001 in all cases). The significant departure from random recruitment rates by fragments was due to a severe storm in 1978-1979. The storm caused extensive breakage and tumbling of corals in shallow water, generating over half of the annual recruits during one season. At Rio Bueno, the storm substantially reduced populations of Acropora cervicornis, to less than 50% of their 1977 cover, and no subsequent recruitment was detected into any of the monitored areas. Malacrina mirabilis and Portites forcuta suffered only moderate damage, and continued to recruit annually in smaller numbers every year.

Juvenile Mortality

Survivorship was low among both larval and annual recruitments (Table 1). Rates of mortality, like recruitment, varied over the six year period, although there was no consistent trend over time, even as the corals increased in average size and age. The largest sample sizes are for Leptoseris and Agaricia, which show some of the complications involved (Table 2). The mortality rate for colonies aged 1, 2 and 3 years (i.e., in the 1st to 3rd year after they were first detected) declined from 0.51 to 0.33 for L. cucullata (100/197, 18/67, and 15/65), but increased slightly to 0.44 for 4 year old colonies (7/16). Similarly, early mortality of Agaricia changed little in the first 3 years after they were recruited, from 0.46 to 0.39 (75/171, 28/78, 17/44), and in the fourth year declined to 0.33 (3/9). In their 5th year, half the colonies died (4/8, for both species combined). This curious increase in mortality amongst older colonies is largely the result of a single bad year, 1983-1984. Almost 60% of the Leptoseris and Agaricia populations in the cleared quadrats were killed during this period, reversing the steady increase in number of colonies for the previous 5 years. The apparent cause was a conspicuous algal bloom which followed unprecedented mass die-offs of the echinoid, Diadema antillarum in the summer of 1983 (Hughes et al., In Press). Nevertheless, the number of surviving colonies of Leptoseris and Agaricia in the cleared quadrats exceeded control densities after only 4 years, and after six years these two species had regained more than half the percent cover of the unmanipulated populations (Hughes and Jackson 1985).

The high mortality in 1983-1984 also disguised any clear correlation between colony size and survivorship among larval recruits in the cleared plots, although this relationship is known to be positive over a wider range of sites for A. agaricites and L. cucullata in the unmanipulated populations (Hughes 1984; Hughes and Jackson 1980, 1985). Furthermore, the proportion of new corals surviving at the end of six years was significantly higher among newly recruited larvae than aerial recruits (Table 1, \( x^2 = 11.75, P<0.005 \), even though the latter were on average more than twice the size of larval recruits at their first census (Table 3; Table 2. Larval recruitment and annual mortality rate (deaths/individual present) of L. cucullata and A. agaricites within six cleared \( m^2 \) quadrats.

<table>
<thead>
<tr>
<th>Interval</th>
<th>No. of colonies alive</th>
</tr>
</thead>
<tbody>
<tr>
<td>1978-1979</td>
<td>14</td>
</tr>
<tr>
<td>1979-1980</td>
<td>10</td>
</tr>
<tr>
<td>1980-1981</td>
<td>61</td>
</tr>
<tr>
<td>1981-1982</td>
<td>33</td>
</tr>
<tr>
<td>1982-1983</td>
<td>33</td>
</tr>
<tr>
<td>1983-1984</td>
<td>33</td>
</tr>
<tr>
<td>Total present</td>
<td>14</td>
</tr>
<tr>
<td>Deaths/year</td>
<td>3</td>
</tr>
<tr>
<td>Mortality rate</td>
<td>0.21</td>
</tr>
</tbody>
</table>

Mann-Whitney U-Test, (P<0.001). Sixty-four percent of the fragments died in place, while the remainder disappeared between censuses. The size of fragments among the three species that produced them reflected their colony morphology; Acropora cervicornis fragments were the largest, because its colonies have loosely-clumped, relatively spindly branches, which are much longer than those of Portites or Malacrina. The population structures in 1984 (e.g., Table 2) illustrate the high rate of mortality and turnover of colonies, with fewer than 50 of all corals surviving longer than 3 years. Even though the number of older colonies continued to increase slowly over time, their proportion of the population fluctuated in response to changes in recruitment. Thus, in 1983-1984 recruitment was generally low compared to the previous year, and the population structures changed accordingly. There is no indication that any of the corals in the cleared areas are approaching a stable-age or -size distribution. The age structure of corals in the unmanipulated quadrats is unknown because many settled before 1977, however, size frequencies there were...
The most striking result of the colonization experiment was the abundance of a handful of species, and the complete failure of recruitment by many locally abundant corals such as Colopophylla natans, Montastrea annularis, M. cavernosa, and Siderastrea siderea. Individuals of these species are characterized by slow growth, low rates of larval recruitment, good competitive ability and great longevity (Lang 1973; Dustan 1977; Bak and Engel 1979; Bak and Luckhurst 1980). Whether these long-lived corals will increase in abundance over time and replace early colonists remains to be seen.

The species producing the most juveniles, A. agaricites and L. cunicula, also share a suite of life history characteristics. Several studies throughout the Caribbean indicate that both settle throughout the year, and typically produce more larvae than all other corals combined (Bak and Engel 1979; Rylaarsdam 1983; Rogers et al., 1984; Hughes and Jackson 1985; Table 1). They grow faster than other foliaceous or massive corals, but are killed and injured more often and rarely grow very large (Bak and Luckhurst 1980; Hughes and Jackson 1985). In the Indo-Pacific, many tightly branched corals such as Pocillopora meandrina, P. damicornis and Stylophora pistillata share these same traits, and are also often among the first to colonize bare space (Grigg and Maragos 1976; Connell 1973; Loya 1976). Comparison of the rate of larval recruitment in the cleared and control plots indicates that crowding (density-dependence) is important even to these weedy corals, and increases in severity soon after recovery begins (Fig. 1). Birkeland et al., (1981) have argued that the risk of overgrowing can still be high even when a substantial amount of bare space is available. However, whatever the mechanisms involved here include adult-juvenile competition for space or some other interaction, is unknown. Because A. agaricites and L. cunicula depend on consistently high rates of recruitment to maintain numbers of colonies, I predict that if Diadema populations do not recover soon the reduction in recruitment will be much more damaging for them than more long-lived corals.

The corals recruiting in the bared areas by fragmentation also share a variety of common characteristics. They all produce large, rambling colonies that are frequently very long-lived (Highsmith 1980; Hughes 1985). Their primary mode of reproduction is by asexual fragmentation generated by moderate disturbances, as indicated by histocompatibility studies (Neigel and Avise 1983) and the paucity of larval recruits (Bak and Engel 1979; Rylaarsdam 1983; Rogers et al., 1984). If fragmentation is to be considered adaptive, the gains accrued when broken fragments survive and are passively dispersed would have to compensate for the considerable cost of chronic losses of parts of colonies (Birkeland et al., 1981).

Table 3. Sizes of colonies (maximum linear dimension) in the first year after they were detected.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>Mean size at 1st year</th>
</tr>
</thead>
<tbody>
<tr>
<td>T. aurea</td>
<td>1.6 0.9 98</td>
</tr>
<tr>
<td>A. agaricites</td>
<td>2.3 1.0 190</td>
</tr>
<tr>
<td>L. cunicula</td>
<td>2.4 1.2 233</td>
</tr>
<tr>
<td>M. micraster</td>
<td>3.7 2.8 76</td>
</tr>
<tr>
<td>P. furcata</td>
<td>3.1 2.4 57</td>
</tr>
<tr>
<td>A. cervicornis</td>
<td>18.4 9.2 15</td>
</tr>
</tbody>
</table>

Remarkably constant (Hughes and Jackson 1980, 1985).

**DISCUSSION**

The rapid growth and low rates of larval recruitment of corals such as A. palmata and A. cervicornis in contrast to the slow growth and high recruitment by weedy corals indicates that the relative energetic investment in growth, maintenance and sexual reproduction differs widely among corals. The colonization experiment described here suggests that different strategies of investment strongly influence patterns of distribution of corals between disturbed and more mature habitats. Interestingly, in the Indo-Pacific, shallow-water corals, particularly hermatypic, grow fast, produce large numbers of fragments, but in contrast to congeners in the Caribbean also have high rates of larval recruitment (Birkeland et al., 1973; Birkeland et al. 1981; Rothwell 1981). Having two well-developed modes of reproduction may enable colonization of highly disturbed habitats, and may be part of the reason why thriving assemblages of scleractinians are found only in the Indo-Pacific.

**ACKNOWLEDGEMENTS**

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