

LIFE HISTORIES AND POPULATION DYNAMICS
OF EARLY SUCCESSIONAL CORALS

LES CYCLES BIOLOGIQUES ET LA DYNAMIQUE
DES POPULATIONS DE CORAUX PENDANT LES JEUNES STADES
DE LA SUCCESSION

T.P. HUGHES

Dep't. Biol. Sci.'s, University of California, Santa Barbara
Santa Barbara, CALIFORNIA 93106, U.S.A.

ABSTRACT

The sequence and progression of early colonization by Jamaican reef corals was followed for up to six years. Replicate m^2 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 control areas was almost 4 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 cucullata 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. cucullata 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.

RESUME

La succession et la progression du début de la colonisation par les coraux à la Jamaïque, ont été suivis sur des périodes allant jusqu'à 6 ans. Plusieurs mètres carrés, par 10 à 20 m. de fond, ont été initialement dénudés, puis photographiés chaque année. On a observé un recrutement asexué et un recrutement par larves. Le taux de recrutement des larves dans les quadrats dénudés est égal, en moyenne, à 18 larves/ m^2 /an à 10 m et 7 larves/ m^2 /an à 20 m. Par contre, le recrutement larvaire dans les aires non touchées est presque 4 fois moins important. Cela revient à dire que la colonisation par les coraux et/ou la survivance des jeunes, dépendent directement de la densité de la population en place. Le recrutement asexué est, en revanche, indépendant de la couverture corallienne. Presque 90% des larves sont des larves de Leptoseris cucullata et de Agaricia agaricites, espèces qui sont caractérisées par un taux de croissance rapide, un squelette lamellaire et fragile, une colonie de petite taille, et un taux de mortalité élevé. Les propagules asexuées des coraux sont virtuellement absentes à 20m, mais quelques fragments branchus de Madracis mirabilis, Porites porites, Acropora cervicornis sont responsables d'un tiers du total des recrues à 10m. Ces espèces ont peu de larves, un taux de croissance rapide, et forment de grandes colonies branchues. Bien que les recrues asexuées soient plus grandes que les jeunes larves, leur survie est généralement bien moins importante. Les taux de recrutement et de mortalité ont varié de façon significative d'une année à l'autre. Le nombre de larves a varié du simple au quadruple, tandis que le nombre des recrues asexuées variait de 1 à 12. La mortalité, en particulier chez les jeunes coraux a été très élevée en 1983/84, à la suite d'une explosion d'algues résultant de la disparition totale des populations d'oursin, Diadema antillarum. Le nombre de colonies d'A. agaricites et de L. cucullata dans les quadrats dénudés a atteint puis dépassé celui des zones témoins après seulement 4 ans. Pourtant, après 6 ans, très peu de colonies avaient atteint la taille des colonies voisines. Les populations de ces 2 espèces ont été reconstituées presque complètement dans les sites perturbés, tandis que les autres espèces en étaient virtuellement absentes.

INTRODUCTION

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 1973; Bak and Luckhurst 1980; Pearson 1981; Davis 1982; Potts 1984; Hughes 1984; 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 (Dustan 1977; Woodley et al., 1981).

(2) Other, more delicate corals are damaged or broken up by routine disturbances, such as winter storms, but are usually not killed outright. Many of these species, such as Acropora palmata and A. cervicornis, grow quickly to form loosely branched clones, which may be a morphological adaptation promoting asexual reproduction by fragmentation (Highsmith 1982).

(3) The last major category comprises corals that are often killed outright by disturbances (i.e. genet death occurs). In the Caribbean, the most common examples, Leptoseris cucullata and Agaricia agaricites, usually form weak foliaceous skeletons, which rarely grow 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 morphology also result in a predictable sequence of colonization and succession following a disturbance, an experiment was designed to imitate 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.

METHODS

Twelve 1 m² quadrats made of plastic tubing were tied permanently with nylon rope to the reef at Rio Bueno, Jamaica in 1977. The quadrats were positioned on a steep wall, six each at 10 m and 20 m. Each quadrat was subdivided by monofilament into 4 equal sections (a total of 48 1/4 m² areas) which were photographed individually from a distance of about 1 m. The resolution of the projected color slides was less than 1 cm, so that surviving larval recruits were detected within a year of settlement (Bak and Engel 1979; Rylaarsdam 1983). Asexually generated fragments were readily distinguished from larval recruits by their larger size, irregular shape, and mode of attachment to the substrate. In 1978, immediately after the second photographic census, three of the quadrats at 10 m and 20 m were chosen randomly, and all macroorganisms (mainly corals, sponges, and fleshy algae) were removed with a hammer and by hand, to expose bare rock. These cleared quadrats were monitored photographically every summer for a further six years, until 1984. The remaining undisturbed quadrats were also monitored annually, 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 dots (100/m²). Quantitative 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 10m are on the edge of an underwater cliff, that slopes initially at about 60 degrees. Scleractinians include branching (primarily Madracis mirabilis, Porites furcata, Acropora cervicornis), massive (Colpophyllia natans, Montastrea annularis), and foliaceous species (Agaricia agaricites, Leptoseris cucullata, Porites astreoides). At the deeper site at 20 m, the wall is closer to vertical than at 10 m (the slope of each site will become important later). Branching colonies are much less common, and the most abundant massive or encrusting corals are Montastrea cavernosa and Siderastrea siderea. Foliaceous corals at 20 m are relatively more abundant and diverse (with the addition of Agaricia lamarcki and A. grahamae) compared to the shallower site.

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 1cm diameter) of about 20/m²/year (Figure 1). Almost eighty percent of the recruitment was larval, primarily by Leptoseris cucullata and Agaricia agaricites, and by the small ahermatype Tubastraea aurea (Table 1). Recruitment by broken fragments of Madracis mirabilis, Porites furcata and Acropora cervicornis accounted for the remaining twenty percent. Single larval recruits of Madracis and Acropora (species unknown) were also detected. Several

long-lived species which are common at Rio Bueno, 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 4/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, r_s = 1.0, P<0.01 for both 10 m and 20 m). Surprisingly, the number of larval recruits declined even at relatively low total cover (Figure 1). In contrast, there was no significant difference in mean rates of recruitment by fragments into cleared and uncleared quadrats (Mann-Whitney U-test, U = 7, n.s.), nor was there any significant correlation between mean rates of asexual recruitment and the amount of cover by resident

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.

Larval recruitment	10m	20m	Total	No. Alive in 1984(%)
<i>Leptoseris cucullata</i>	165	66	231	84 (36)
<i>Agaricia agaricites</i>	154	36	190	56 (29)
<i>Tubastraea aurea</i>	98	0	98	18 (18)
Other larval recruits	14	29	43	17 (40)
Asexual recruitment				
<i>Madracis mirabilis</i>	71	5	76	13 (17)
<i>Porites furcata</i>	57	0	57	12 (21)
<i>Acropora cervicornis</i>	15	0	15	0 (0)
Total	574	135	709	200 (28)

macroorganisms (Spearman rank order correlation coefficient, r_s = -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

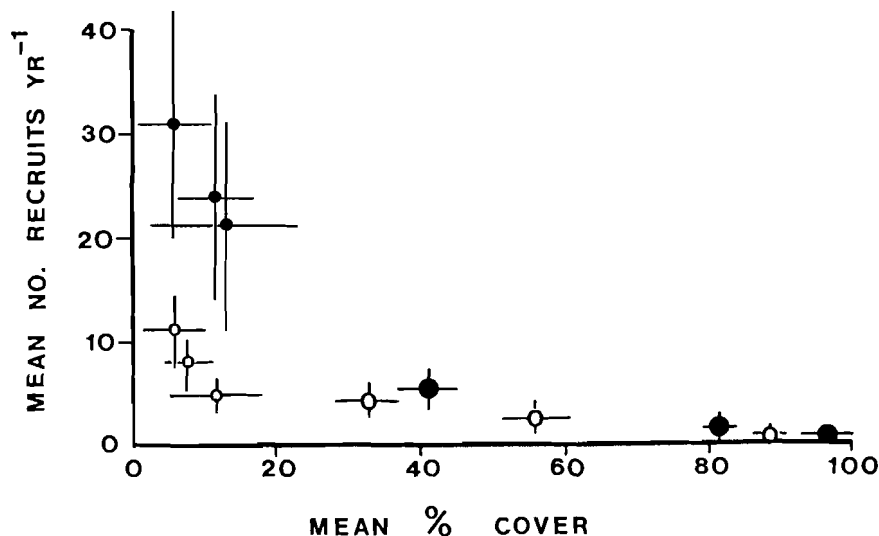


Fig. 1. Mean annual coral recruitment rate \pm S.D. (1977-1984) versus mean total living cover within 12 1m² quadrats. Big symbols are crowded, unmanipulated quadrats, small symbols are quadrats initially cleared. Filled symbols are quadrats at 10m, open symbols are at 20m.

departure from unity. For the most abundant species (L. cucullata, A. agaricites, T. aurea, M. mirabilis, P. furcata and A. cervicornis), ratios varied from 3.8 to 21.6, indicating episodic (clumped in time) patterns of recruitment (X^2 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 asexual recruits detected during the six years. At Rio Bueno, the storm substantially reduced populations of Acropora cervicornis, to less than 20% of their 1977 cover (pers. obs.), and no subsequent recruitment was detected into any of the monitored areas. Madracis mirabilis and Porites furcata suffered only moderate damage, and continued to recruit asexually in smaller numbers every year.

Juvenile Mortality

Survivorship was low among both larval and asexual recruits (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 age and size. The largest sample sizes are for Leptoseris and Agaricia, which show some of the complexities 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 15/45), 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 recruited, from 0.44 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 bared 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 sizes 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 asexual fragments (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.

Leptoseris cucullata

Interval	No. of colonies alive					
	1979	1980	1981	1982	1983	1984
Recruited						
1978-1979	24	8	5	5	3	2
1979-1980		18	14	11	11	6
1980-1981			52	35	29	14
1981-1982				25	10	4
1982-1983					78	30
1983-1984						28
Total present	24	26	71	76	131	84
Deaths/year	-	16	7	20	23	76
Mortality rate	-	.67	.27	.28	.30	.58

Agaricia agaricites

Interval	No. of colonies alive					
	1979	1980	1981	1982	1983	1984
Recruited						
1978-1979	14	11	8	6	5	2
1979-1980		10	5	4	3	1
1980-1981			61	46	32	18
1981-1982				33	16	6
1982-1983					53	18
1983-1984						11
Total present	14	21	74	89	109	56
Deaths/year	-	3	8	18	33	64
Mortality rate	-	.21	.38	.24	.37	.59

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 ramose Porites or Madracis.

The population structures in 1984 (e.g. Table 2) illustrate the high rate of mortality and turnover of colonies, with fewer than 5% 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

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

SPECIES	Mean size at 1st year (cm)	S.D	N
<u>T. aurea</u>	1.6	0.9	98
<u>A. agaricites</u>	2.5	1.0	190
<u>L. cucullata</u>	2.6	1.2	231
<u>M. mirabilis</u>	3.7	2.8	76
<u>P. furcata</u>	4.4	3.1	57
<u>A. cervicornis</u>	18.4	9.2	15

remarkably constant (Hughes and Jackson 1980, 1985).

DISCUSSION

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 Colpophyllia 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 slowly increase in abundance over time and replace early colonists remains to be seen.

The species producing the most juveniles, A. agaricites and L. cucullata, also share a suite of life history characteristics. Several studies throughout the Caribbean indicate that both settle throughout the year, and typically produce more larval recruits 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; Jackson and Hughes 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 1974; 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 overgrowth can still be high even when a substantial amount of bare space is available. However, whether the mechanisms involved here include adult-juvenile competition for space or some other interaction, is unknown. Because A. agaricites and L. cucullata 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; Jackson and 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 (Hughes 1984). Fragments are often dispersed to unfavourable habitats, such as sand patches and over steep cliffs, and their survivorship is low (Highsmith et al., 1980; Knowlton et al., 1980; Bak and Criens 1981; Table 1). During more severe disturbances, such as major hurricanes, these species run the further risk of local extinction, and recovery through larval recruitment alone may be very slow (Knowlton et al., 1981; Woodley et al., 1981). The rapid growth and low rates of larval recruitment of corals such as A. palmata and A. cervicornis in contrast to the slower 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 acroporids, grow fast, produce large numbers of fragments, but in contrast to congeners in the Caribbean also have high rates of larval recruitment (e.g. Connell 1973; Birkeland et al. 1981; Bothwell 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 intertidal scleractinians are found only in the Indo-Pacific.

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