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THE IMPORTANCE OF RATE OF BIOMASS ACCUMULATION IN EARLY SUCCESSIONAL STAGES OF
BENTHIC COMMUNITIES TO THE SURVIVAL OF CORAL RECRUITS

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ABSTRACT

Although hermatypic coral recruits grow faster on the upper surfaces of artificial substrata on coral reefs, survival is greater in the shade on vertical and under surfaces. Growth of recruits is faster in shallow waters but survival increases with depth, at least to 20 m, as the light decreases. Adult corals can survive and grow in cool nutrient-rich waters, but survival of recruits is more successful in nutrient-poor waters. Nutrients and light are beneficial to coral growth, but faster-growing fouling organisms respond more directly to a rich supply of nutrients and light. As levels of light and nutrient input decrease, the rate of biomass accumulation of the benthic community decreases, and hermatypic corals have a greater chance of reaching a refuge in size from being overgrown. Between geographic locations, the difference in rate of biomass accumulation at comparable depths is influenced by nutrient input. At a given locality, the rate of biomass accumulation of algae is related to light which decreases with shading and depth. K

Fish grazing on the benthic community is beneficial to the survival of coral recruits. Caribbean fish will avoid feeding on corals as small as 2.5 mm maximum diameter. ||

Species with r-selected characteristics are not just "opportunists" that depend on disturbance to release resources from tight competitive situations. Under conditions of high nutrient input from outside sources, r-selected species can be the perpetually superior competitors for space, preventing K-selected species from establishing themselves and gaining a refuge in size.

KEY WORDS: Biomass Accumulation, Coral Recruits, r-selected species, K-selected species.

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CHARLES BIRKELAND

Introduction

I will present data in this paper which indicate that coral recruitment is not likely to be most successful where conditions are optimal for rapid growth of corals. Factors such as light, and perhaps nutrients, may be favorable for coral growth but they are also favorable for the growth of benthic algae and indirectly, through increasing phytoplankton production, favorable for the growth of suspension feeders. Corals grow more slowly than short-lived organisms such as filamentous algae, leafy algae, bryozoans and barnacles, but they live longer and eventually obtain a refuge in size from competition for space with these faster-growing, short-lived species. However, with an increase in light or amount of nutrients in the water, the growth of short-lived species is more strongly affected and the recruitment of hermatypic corals is greatly endangered by competition for space.

The negative effects of increased nutrients in the water to the success of coral recruitment have not been recognized because the effects of cold water temperatures on corals have been confounding. The adverse effects of cold water on coral growth and survival have long been recognized from distributional observations (1-3) and these generalizations have been substantiated through experimental studies (4-6). Since both cold temperatures and nutrient richness are characteristic of upwelling waters, since both factors are detrimental to the success of coral recruitment, and since temperature is easier to measure than the indirect effects of nutrient input on the survival of coral recruits through competitive interactions, the effects of nutrient input have been masked.

Although cold upwelling waters reduce the rate of hermatypic coral growth (4-6), the corals still grow and survive. During five years of study in Panama, monthly trips were taken to a large submerged rock on the south side of Isla Taboguilla off the Pacific coast, an area exposed to upwelling waters during the dry (or windy) season from about mid-December through March or April. A coral community was on the rock. It was composed of about 35 colonies of Pocillopora and a few Pavona and Porites. The large, individually recognized colonies were present during the entire five year period. No successful recruitment was noticed. The individually recognized adult colonies of Pocillopora, the predominant coral, would grow and shrink, constantly changing shape over the five year period. A large

proportion of the rubble that washed around the base of the rock consisted of Pocillopora branches. The turbulent waters on this exposed side of the island often threw rubble and drifting objects around the corals and apparently broke branches off the living colonies which were added to the rubble. Although the Pocillopora colonies increased in size very slowly, their changes in shape indicated that production may not be as slow as it originally appeared. The Pocillopora lived for years and grew. The main problem corals had which was preventing them from becoming predominant in the area did not seem to be adult survival or growth.

Cement blocks were set among coral colonies in upwelling areas and other blocks were set on a solid cover of living Pocillopora on incipient reefs in the eastern Pacific. The cement blocks were never settled by hermatypic coral larvae. Their surfaces were quickly monopolized by barnacles, bryozoans, tunicates and algae. After two years, the Pocillopora on incipient reefs began to grow up and around the cement blocks which gave the illusion that the blocks were gradually sinking into the reef. Established colonies and coral stands were doing well, but there was no noticeable recruitment. Open space was invaded only by the growth of previously established colonies.

In contrast, cement blocks and terra cotta tiles at study sites in the Caribbean were almost invariably recruited by settling larvae of hermatypic corals. One block was settled by a total of 19 individual coral recruits of 4 species which together occupied 35% of the surface of the block within 4 years.

The major problems corals have in the eastern Pacific appear to be related to recruitment rather than to survival of adult colonies. To study interactions during early stages of succession on cleared patches, artificial substrata were set out in benthic communities of different levels of coral predominance on the Pacific and Caribbean coasts of Panama.

Recruitment of Corals to Artificial Substrata

Plexiglass Plates

A five-year study (1971-1975) of the recruitment of fouling organisms to plexiglass settling plates was made on the Caribbean and Pacific coasts of Panama. The methods, material and general results have been previously reported (7) but results specifically related to the recruitment of hermatypic corals will now be discussed.

Table 1. Rates of increase in dry weight of communities of fouling organisms on plexiglass plates from wet seasons and dry seasons on the Caribbean and Pacific coasts of Panama. Dry weights were taken for communities between 27 and 148 days old.

Location	Time of year	No. of plates	Regression of $Y(10^{-2} \text{ gms m}^{-2})$ on X (days)	S_b^*	r^2
Isla Taboguilla (Pacific)	Dry season		2.23		
	Dec. 16 to Apr. 15	113	$Y = 1.9 X$	0.165	0.62
	Wet season		2.15		
Galeta (Caribbean)	Apr. 16 to Dec. 15	138	$Y = 1.7 X$	0.136	0.65
	Dry season		1.83		
	Dec. 16 to Apr. 15	141	$Y = 1.2 X$	0.149	0.52
	Wet season		1.24		
	Apr. 16 to Dec. 15	154	$Y = 25.4 X$	0.117	0.42

*Standard error of the exponent.

Only two hermatypic corals, both Pocillopora sp., were found on a total of 251 plexiglass plates which were examined from the study site in a region subject to upwelling waters (south side of Isla Taboguilla, Bay of Panama). Both of these corals were on plates which had been in the ocean for less than two months. This coincides with the rate of settling and expansion of fouling animals on plexiglass plates because, in upwelling regions, all of the primary substratum is usually occupied by barnacles, bryozoans, tunicates, sponges and other animals after 60 days (8). The barnacles grow rapidly enough in upwelling regions to attain basal diameters of 15 mm within 56 days and are undoubtedly capable of pushing 2 mm coral recruits off the plates. Similarly, the bryozoans and tunicates can rapidly overgrow and smother the coral recruits. This might explain the inability of corals to settle and become established on the cement blocks placed on coral reefs in the eastern Pacific which were entirely occupied by barnacles and other organisms. The coral reef must have started by recruitment, but recruitment is nevertheless a rare event.

In contrast with results from the Pacific settling plates, a total of 262 hermatypic coral recruits were found on 262 plexiglass plates (a remarkable coincidence) at the Caribbean study site (Galeta). This is not surprising in view of the fact that only about 20 to 40% of the primary substratum was occupied after 60 to 70 days by organisms that would compete for space with corals (8). Thirty percent of the space on plates was still available for corals after 148 days (8).

The occupation of space is a difficult measure to interpret in terms of the problems for coral recruitment because space occupied by animals such as barnacles or tunicates is inaccessible to larval recruitment by corals while space occupied by crustose coralline algae or diatoms is sometimes settled by corals. The rate of increase in dry weight biomass in early stages of succession of the benthic community is a

better indication of the danger of the area for successful larval recruitment. The rates of biomass accumulation on artificial substrata at a depth of 8-9 m in wet and dry seasons for study sites on the Pacific and Caribbean coasts of Panama are given in Table 1. In the dry (windy) season when nutrient-rich upwelling waters come to the surface in certain areas along the Pacific coast, the amount of dry weight biomass that accumulates in the fouling communities on plexiglass plates in the Pacific is 8.7 times as great as the biomass on the plates in the Caribbean after 70 days and 11.7 times as great after 148 days. It is a rare event in areas of nutrient upwelling that a hermatypic coral recruit survives long enough to grow to a size at which it is safe from being overgrown or bulldozed. The ahermatypic coral Tubastraea sp. and the gorgonacean Lophogorgia alba survive on settling plates in the upwelling area. This is because they grow rapidly upward off the substratum so the bryozoans and tunicates encircle their bases and grow around them but not over them.

The inverse relationship between the development of the coral community and the rate of biomass accumulation of early successional stages in the benthic community was suggested on a finer scale when the dry weight biomasses of the fouling communities were measured from settling plates recovered after 77 days and compared from reefs of different degrees of coral predominance (Table 2). The Caribbean coral reefs in the San Blas Islands are truly impressive in terms of species richness and reef morphology (9); the reefs along the coast between Portobelo and Galeta are less well-developed (9). The rate of biomass accumulation on settling plates in the areas of luxuriant reefs is significantly less than in the areas of less well-developed reefs (Table 2). There is no upwelling of nutrients along the coast of Panama. The greater rate of biomass accumulation by fouling communities on the coast than on offshore islands is possibly because of nutrients provided by runoff from the land.

Table 2. The dry weight of fouling communities which grew on plexiglass plates during 77 day periods in August through October 1971. Each sample set consisted of 8 plates except the dry season value for Taboguilla which is a calculated estimate from the regression in Table 1. All plates were set at a depth of 9 m.

Location	Dry Weight $\bar{Y} \pm S$ (gms m ⁻²)
CARIBBEAN	
San Blas Islands	
Ucubsui--6.5 km off coast	27.3 $\pm$ 3.7
Ogogpuquid--13.5 km off coast	24.4 $\pm$ 3.5
Panama coast	
Drake's Island, Portobelo	51.9 $\pm$ 2.3
Punta Galeta	53.5 $\pm$ 3.8
PACIFIC	
Isla Taboguilla	
North--opposite side from upwelling	40.9 $\pm$ 4.2
South--exposed to upwelling	
wet season	188 $\pm$ 33
dry season	306

A similar comparison can be made between the coral dominance and rate of biomass accumulation in early successional stages on opposing sides of Isla Taboguilla in the Pacific. Scattered heads of *Pocillopora* and *Pavona* occur on the south side of the island exposed to upwelling waters. An extensive area of nearly solid cover of *Pocillopora* and large heads of *Porites* form an incipient reef on the north side, opposite the region of upwelling. The accumulation of dry weight biomass on settling plates in the area of incipient reef formation is only about 20% as great as that in the area of scattered colonies (Table 2) after 77 days in the wet season.

To aid in interpreting the distribution of coral recruitment on upper and lower surfaces of plexiglass plates and cement blocks, it will be helpful to be able to compare growth rates of settling corals on upper and lower surfaces. This is difficult because the recruitment of corals is sporadic in time and clumped in space. Since corals set on plexiglass plates at different intervals of time following the placement of the plates in the ocean, all regressions of size of coral on age of fouling communities will be underestimates of growth to differing degrees. In order to obtain an objective comparison of rates of growth on upper and lower surfaces, I measured only the largest diameters on both the upper and lower surfaces. To attempt to reduce the degree of underestimation of growth rate caused by later settling, I did not use diameter measurements from older plates that were smaller than those on younger plates. These qualifications greatly reduced the number of available data. However, the regression of maximum coral diameter on the length of time the settling plate

was in the water for the upper surfaces of plates has nearly twice the regression coefficient ($b = .73$ mm month⁻¹, $S_b = .15$) as does the regression for the lower surfaces ($b = .37$ mm month⁻¹, $S_b = .10$). The differences between regression coefficients is significant at only the 10% level by t-test. This is probably because of the small sample size and because of the variance in the relation between the age of the plate and the true age of the coral caused by the sporadic pattern of recruitment in time. Nevertheless, it appears that coral recruits grow faster on upper surfaces exposed to the light.

Although hermatypic corals appear to grow faster on upper surfaces of settling plates, there is a significant tendency for the largest corals to be found on the under surfaces of plates that have been in the ocean for 70 days or more (Table 3). The probability of survival may be greater on the under surface where the growth rate of algae is reduced and where sediment will not tend to accumulate.

Table 3. The location of the largest coral recruit on plexiglass settling plates with recruits on both upper and lower surfaces.

Period of time in the ocean	Surface of settling plate		Total
	UPPER	LOWER	
< 70 days	8	0	8
$\geq$ 70 days	7	12	19
Total	15	12	27

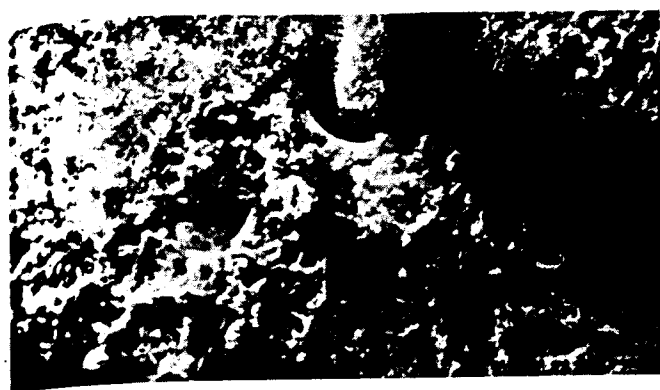
Fisher exact probability

$$= \frac{8! 19! 12! 15!}{27! 0! 8! 12! 7!}$$

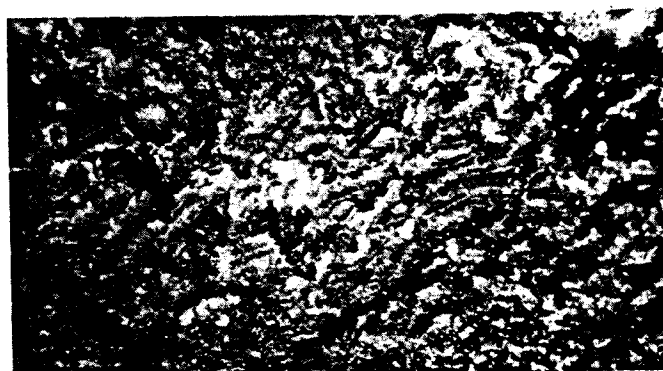
$$= 0.003$$

Cement Blocks

As was already mentioned in the Introduction, there was no recruitment of hermatypic corals to cement blocks on eastern Pacific incipient reefs, but corals settled and established themselves in abundance on cement blocks in the Caribbean. It was noticed, however, that most of the recruitment on blocks in the Caribbean was not on the exposed upper surfaces of the blocks but on the shaded vertical surfaces or on the undersides of the upper surfaces of the block. The upper surfaces were gradually invaded by the growth of coral colonies which had settled on the shaded surfaces. This observation seems at odds with the evidence that corals grow faster on upper surfaces of plexiglass plates in the light, but this may be explained by a greater chance of survival in the shade which is implied by the tendency of larger recruits to be found on under surfaces after 70 days. Corals may grow in the relative security of shade until they are large enough to grow out and face competition with



a



b

1 CM



c



d

Figure 1. Effects of fish grazing on the survival of coral recruits on settling plates. a. A coral being overgrown by algae on a plate not grazed by fish. b-d. Small coral recruits on intensely grazed settling plates are consistently avoided by herbivorous fishes.

Table 4. Abundance and size distributions of hermatypic coral colony recruitment to a series of 6 cement construction blocks at each of three depths along a Caribbean reef slope at Ucubsui, San Blas Islands, Panama. The blocks were set out 3 VIII 71 and the data in this table were taken 7 XI 74. The asterisks separating each pair of size distributions indicates the significance of their differences in ranks as computed by a Wilcoxon two-sample test: * = $p < .05$, ** = $p < .01$, ns = not significant.

	9 m (30 ft)		20 m (65 ft)		34 m (110 ft)
Number of recruiting corals	36		173		13
Number of identified genera	7		12		4
Proportion of corals recruiting to:					
UPPER SURFACES	14%		22.6%		100%
VERTICAL SURFACES	61%		64.7%		—
UNDER SURFACES	25%		12.7%		—
Diameters of recruiting corals (Quartiles of geometric means in mm)					
UPPER SURFACES	8-22-34	ns	6-10-20		5-7-10
	ns		**		
VERTICAL SIDES	9-29-43	*	6-13-24		—
	ns		*		
UNDER SURFACES	12-23-43	**	3- 8-13		—
Dry weight (gms m ⁻²) of fouling community on plexiglass plates after 77 days	27.3 ± 3.7		4.8 ± 0.8		2.3 ± 0.6

Table 5. Measurements of the effects of fish grazing on the accumulation of dry weight biomass by fouling communities on plexiglass plates over a period of 133 days. Each sample consists of 4 plexiglass plates, each 5 cm x 15 cm, with the dry weight taken of the communities on both the upper and lower surfaces. The asterisks separating each pair of values indicate the significance of their difference as computed by a t-test: ** = $p < .01$, *** = $p < .001$, ns = not significant.

Location	Dry Weight of Fouling Community (gms/150 cm ² ; $\bar{Y} \pm S$)	
	OPEN TO FISH GRAZING	CAGED
CARIBBEAN		
Isla Buenaventura (coral reef)	1.2 $\pm$.13 **	2.7 $\pm$.2 ***
Drake's Island (coral community)	2.6 $\pm$.5 **	3.6 $\pm$.6 ***
PACIFIC		
Isla Taboguilla		
north side (opposite upwelling)	3.7 $\pm$.3 **	7.0 $\pm$ 1.7 **
south side (exposed to upwelling)	36.8 $\pm$ 6.6	ns 27.5 $\pm$ 5.3

algae.

This pattern was also apparent in the recruitment of corals to three series of 6 cement blocks which were set at each of three depths on a well-developed reef in the San Blas Islands. After a period of 3.25 years (39 months) the distribution and sizes of 222 coral recruits to the cement blocks were observed (Table 4). As might be expected, the size distributions of corals decreased with depth and with the concomitant decrease in light. A slower growth rate with decreased light is implied. However, there was a tendency for the greatest numbers of corals and also for the largest corals to be on the shaded vertical sides of the blocks at intermediate depths and not on the upper surfaces, exposed more directly to the light.

Seventy-eight percent of the successful coral recruits were on the cement blocks at the depth of 20 m. The 16% of the corals that survived competition with algae at 9 m depth averaged larger in size than the recruits at 20 m, but these were probably the few that survived a greater risk of being killed in shallow well-lit waters. The 6% of the corals which were found on the 34 m blocks were relatively safe from competition with algae, but were apparently growing very slowly.

The proportion of corals settling and/or surviving on upper surfaces of blocks increased with depth. This was probably causally related to the decrease in rate of biomass accumulation with depth of early successional stages in the benthic community as indicated by dry weights of the fouling communities on plexiglass plates set beside the cement blocks (Table 4).

The success of coral recruitment is again found to be inversely related to the rate of biomass accumulation of early successional

stages in the benthic community. Between geographic locations, the difference in rate of biomass accumulation is probably strongly influenced by nutrient input. Within a given locality, the rate of biomass accumulation of algae is related to light which decreases with shading and depth.

Grazing of Settling Plates by Herbivorous Fish

The change in relative size distribution of corals with time on plexiglass plates (Table 3) might be interpreted as indicating a faster growth of corals on upper well-lit surfaces but a better chance of survival on shaded surfaces. The observed mortality on upper surfaces in the Caribbean was caused by the small corals being smothered in sediment. On ungrazed plates, the rapidly growing filamentous algae quickly surrounded the coral recruits and grew much taller. The filamentous algae did not directly overgrow or smother the coral but created a sediment trap between their bases (Fig. 1a). By grazing the algae, herbivorous fish enhance the survival of coral recruits. Many of the settling plates were very thoroughly grazed by acanthurids and *Scarus croicensis* (Fig. 1b-d). Four plates were observed during frequent visits over a year's time. The plates were frequently grazed. In no case was a coral recruit removed by fish grazing. Acanthurids and *Scarus croicensis* apparently avoid grazing corals as small as 3 mm in diameter.

Schools of acanthurids and small scarids were followed and observed during their feeding activities in the San Blas Islands. When the school converged on small patches and grazed them intensely, I examined the grazed areas after the school had moved on. There were often small coral recruits with tooth marks all around them, but the corals were never touched by the tooth marks.

To obtain a measure of how much greater the rate of biomass accumulation in early successional stages would be without grazing by fishes, settling plates were placed both inside and outside fish-exclusion cages on a coral reef and in a coral community about 3.2 km apart in the Caribbean and on an incipient coral reef and in a coral community on opposite sides of an island in the eastern Pacific (Table 5).

Discussion

r-selected species (such as filamentous algae, bryozoans and barnacles) and K-selected species (such as hermatypic corals) are both present in early stages of succession in benthic communities and on settling plates on both coasts of Panama. r-selected species (small, fast-growing, rapidly reaching reproductive maturity, short generation time) dominate the later stages of succession in the eastern Pacific while K-selected species (larger body or colony size, slower-growing, longer-lived, slower in reaching sexual maturity, and putting more resources into maintenance and defense and less into reproduction) dominate the later stages of succession in the Caribbean. The input of nutrients into the system by upwelling allows weedy fast-growing forms associated elsewhere with early stages of succession to perpetually outcompete the K-selected species, such as hermatypic corals, before the K-selected species can reach their refuge in size.

Evolutionary results of this process of succession leading to later stages predominated by r-selected species can be seen from comparisons on a geographic scale. When the Isthmus of Panama rose, the benthic communities on both coasts were from the same general species pool. The shallow waters of the Caribbean Sea and the eastern tropical Pacific Ocean were connected periodically for over 90 million years; the last period of separation has been for only 1 to 3 million years. This period of separation has been rather short in terms of evolutionary time and the long period of connection has provided similarities in the fauna that have led some zoogeographers to consider the Caribbean and eastern tropical Pacific as part of the same Atlanto-East Pacific Faunal Region (10-11). However, since the separation and the start of upwelling of nutrient-rich waters on the Pacific coast, there has tended to be more species in taxa with often large animals such as hermatypic corals, gorgonaceans, or fishes on the Caribbean side of the isthmus and more species of generally smaller animals such as bryozoans, polychaetes, and mollusks on the Pacific side.

Species with r-selected characteristics are not just "opportunists" that depend on disturbance to release resources from tight competitive situations. Under conditions of high nutrient input from outside sources, r-selected species can be the perpetually superior competi-

tors for space, preventing K-selected species from establishing themselves and gaining a refuge in size.

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