Disturbance and growth of juvenile corals (*Agaricia humilis* and *Agaricia agaricites*, Scleractinia) in natural habitats on the reef of Curaçao

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ABSTRACT: Juvenile coral colonies (diameter <50 mm) of *Agaricia humilis* and *A. agaricites* (Scleractinia) were studied through time in their natural habitat between 5 and 23 m depth on the fringing reef of Curaçao (Netherlands Antilles, Caribbean). At 6 censuses (in 1 yr), data were collected on status, morphology and size of juveniles to investigate the following aspects of life histories: frequency of disturbance and mortality, nature of disturbing factors, frequency of fission and fusion processes, and growth during the 5 intervals, as well as annual growth. Absolute linear growth was not dependent on colony size. Maximum linear growth (diameter increase, $80 \mu\text{m d}^{-1}$, was potentially equal in both *Agaricia* species and independent of depth. However, different disturbance levels, related to depth, resulted in a significant difference in actual annual growth in relation to depth zones. A difference in species-specific coral morphology caused a different level of disturbance in the 2 species. In addition there was a negative relation between coral size and mortality in *A. humilis* juveniles. Dynamic aspects of the life histories of *A. humilis* and *A. agaricites* integrate well with depth-related differences in relative abundance and with differences in reproductive characteristics of the species.

INTRODUCTION

Early life histories of marine invertebrates constitute an important contribution to the development of community structure. On coral reefs this is especially true in the dominating inhabitants, the stony corals (Scleractinia). Species-specific susceptibility to disturbances may be related to morphological characteristics, and recovery after disturbance to growth rate. The importance of different reactions of juveniles in the development of coral population structure has been stressed by Bak & Engel (1979), Bak & Luckhurst (1980), Pearson (1981) and Rylaarsdam (1983). In view of this, it is remarkable how few data on growth and disturbance of juvenile corals (primary polyp or colony diameter <50 mm) exist.

Despite the paucity of quantitative data, there appears to be general subjective agreement that many corals calcify more rapidly during early stages of

growth immediately (possibly up to a few years) after planular settling, than at an older age (Connell 1973, Buddemeier & Kinzie 1976). Comparisons between juvenile and adult growth, however, have been interpreted variously because growth has been measured as different parameters: absolute or relative growth of length, surface area, volume or weight, or isotope uptake (Stephenson & Stephenson 1933, Goreau & Goreau 1960, Connell 1973). Moreover, in most coral species, colony morphology changes during their lifetime. Another problem is that maximum growth potential *in situ* is only found if coral growth is not hampered by environmental perturbation. Physical factors, spatial competition and biological depredation may disturb coral growth frequently but their importance is not well documented for juvenile corals. In ecological studies, biological interactions are often classified as either disturbance or competition (Dayton 1971, Karlson 1983). In this paper the term 'disturbance' is used to indicate all cases of physical and biological interference (including competition) of the growth process apart from cases resulting in mortality.

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In this investigation, juveniles of *Agaricia* species and their surrounding substratum were studied for 1 yr, by means of underwater photography. This retrospective approach yielded information, not anticipated at the beginning of the investigation, on the nature and importance of disturbance, fission and fusion processes, as well as on growth rates. In *Agaricia* it is especially attractive to study the relation between colony size and growth because large colonies frequently retain the 2-dimensional plate-like growth form which is characteristic for most hermatypic juveniles. *Agaricia* species constitute the majority of all juveniles on every Caribbean coral reef where juvenile abundance has been studied (Barbados: Lewis 1974; Curaçao and Bonaire: Bak & Engel 1979, Van Moorsel in prep.; Jamaica: Rylaarsdam 1983; St. Croix: Rogers et al. 1982, 1984; Panama: Wulff 1984).

I found significant differences in reproductive characteristics in 2 closely related *Agaricia* species, *A. humilis* Verrill and *A. agaricites* (Linnaeus) which could be explained in relation to the predictability of their habitats (Van Moorsel 1983). Unidentified agariciids are mentioned in several papers (e.g. Meyer & Birkeland 1974, Sammarco 1980, Rylaarsdam 1983), and others (e.g. Bak & Engel 1979) have not separated *A. humilis* and *A. agaricites* because at the time the former was considered to be only a growth form of the latter species. In the present paper qualitative and quantitative data on disturbance and growth rates of juveniles will be presented for both species in relation to size and depth.

MATERIALS AND METHODS

All data were collected using juvenile coral colonies of the species *Agaricia humilis* and *A. agaricites*. Mean diameter (see below) of the largest juvenile was

35.3 mm at the start of the year of investigation. Colonies were present in a transect between 5 and 23 m depth on the fringing reef of Curaçao, Netherlands Antilles (Fig. 1). For a description of this reef and its zonation see Bak (1977) and Van den Hoek et al. (1978).

Within the transect, I chose 20 substratum patches (often dead or partly dead *Montastrea cavernosa* (Linnaeus) colonies) which contained one or more *Agaricia* colonies. Each patch was marked with a small underwater float and nails painted fluorescent red. From these nails the position of all nearby juveniles was recorded by means of trilateration. The procedure resulted in a total sample of 166 corals. At the start of the investigation, I was unaware that 2 different species, *A. humilis* and *A. agaricites*, were involved. The difference was discovered during a concurrent study on reproductive strategies of these corals (Van Moorsel 1983). Consequently, no attempt was made to select equal numbers of each species at all depths. Characteristics used to identify the species are mentioned in Van Moorsel (1983).

I used a Nikonos III camera with strobe (Philips PUF 060) and 1:2 extension tube with focal frame to photograph each coral. Each 35 mm slide (Kodak Ektachrome 64) represented an area of 72 × 48 mm. Coral code and day number were included in the subject field. *In situ* photography has the advantage that it does not interfere with disturbance and growth by experimental manipulation. The photographic procedure was repeated 6 times during 1 yr on the following dates: in 1979, Sep 26–Oct 5, Dec 3–5; in 1980, Jan 22–31, Mar 26–Apr 14, Jul 3–4, Sep 24–25. Minimum time interval between censuses of individual corals was 49 d. During the year, 8 additional corals were included in the sample to supply more growth data.

For the analyses, slides were projected onto paper,

Fig. 1. Location of investigation transect (starred) near Caribbean Marine Biological Institute (Carmabi), Curaçao, Netherlands Antilles

Fig. 2. *Agaricia humilis*. Subsequent contours of corals. Top: juvenile colony which grew undisturbed during all time intervals. Bottom: large juvenile in which growth was severely disturbed during interval 4–5 by the sponge *Reniera carnabi*. Bar depicts 10 mm intervals. Tables list corresponding mean diameters ($\bar{D}$) and growth of $\bar{D}$

on which contours of the corals were drawn (scale $2.7 \times$ actual size). I projected successive slides of the same coral on 1 sheet in the same position and orientation, using information surrounding the coral (e.g. boring sponges or dead *Montastrea cavernosa* calices) or polyp configuration of the *Agaricia* juveniles. For an example see Fig. 2.

Using the 6 subsequent contours, other information on the slides, and additional field notes, I determined for each coral whether it grew with or without discernible disturbance, or died, during each of the 5 time intervals. The procedure did not distinguish undisturbed corals from corals which experienced a disturbance and regenerated before the end of the interval. However, considering the slow regeneration from even minor superficial lesions in *Agaricia agaricites* (Bak & Steward-Van Es 1980, Bak 1983), there must have been very few unrecorded disturbances between 2 successive censuses. If possible, the cause of disturbance or mortality was noted. Corals covered by only a few grains of sediment were listed as undisturbed.

All corals were placed in 1 of 3 categories according to the degree of disturbance: undisturbed (during all 5 successive intervals); disturbed (at least once); died in the course of the whole investigation period. Interac-

tions between species, size, depth and disturbance were analysed in two 3-way contingency tables. The analyses were based on log linear models and significance was compared with Freeman-Tukey deviates (Sokal & Rohlf 1981).

The slide sequences were also used to quantify the frequency of intracolony as well as intercolony fission and fusion.

As in all juvenile *Agaricia*, the corallum had a 2-dimensional structure: the surface area was easily determined using a digitizer (Hewlett Packard 9874A) and computer (HP 9835A) with morphometric program. From these areas a mean diameter of each coral surface was determined by

$$\bar{D} = \frac{2}{s} \sqrt{\frac{A}{\pi}}$$

where A = coral surface measured with digitizer and s = scale at which the coral was drawn. $\bar{D}$ can be defined as the diameter of a circle with the same surface area as the coral. This index of linear dimension converted from surface area is more reliable than direct measurement (Yamaguchi 1983). Daily absolute growth during an interval was calculated using

$$[\bar{D}_2 - \bar{D}_1] / [t_2 - t_1]$$

where $\bar{\varnothing}_1$ and $\bar{\varnothing}_2$ = mean diameters at day numbers t_1 and t_2 .

For statistical methods employed consult Sokal & Rohlf (1981) and/or Siegel (1956).

RESULTS

Between 5 and 10 m depth, 99 % of the 100 juvenile colonies found for this study belonged to *Agaricia humilis*. Between 12 and 23 m depth the sample contained 66 juveniles, 71 % belonging to *A. humilis* and 29 % to *A. agaricites*. The observed difference in relative abundance of the juveniles of the 2 species parallels an important reef characteristic: a depth of 10–12 m equals the location of the 'drop off', an abrupt increase in depth (Bak 1977). The extreme scarcity of juvenile *A. agaricites* on the shallow reef makes it feasible to compare *A. agaricites* and *A. humilis* juveniles from the deep reef (>11 m) only. In *A. humilis* an inter-depth (>11 m vs <11 m) comparison can be made.

The smallest size classes of *Agaricia humilis* were most common. This is reflected in a size distribution which is skewed to the left. This phenomenon was more pronounced in shallow juveniles than in deep juveniles (Fig. 3). Conceivably, coral size can show a relation to the degree of disturbance as well as to depth and species. Therefore, I decided to discriminate between 2 size classes. Small and large juveniles had mean diameters of <15 mm or >15 mm at the beginning of the investigation. This size distinction was chosen to obtain sufficient numbers in both size categories.

The factors disturbance, size, and depth in *Agaricia humilis* (Table 1) and disturbance, size, and species in deep (>11 m) corals (Table 2) showed non-significant 3-way interactions. Relatively large Freeman-Tukey deviates were only found for the mortality in large *A. humilis* at the deep reef. This was probably caused by the low values of observed (0 %) and expected mortality. It was not considered large enough to impede tests for 2-factor interactions.

Agaricia humilis: disturbance, size, and depth (Table 1)

(a) *test of independence of disturbance and size*. The significant decrease in fit of the model by deletion of a disturbance-size interaction term indicates that these 2 factors are not independent at each level of the factor depth. Small *Agaricia humilis* corals had a higher mortality than larger juveniles.

(b) *test of independence of disturbance and depth*. The increase of the G-value as a result of dropping the disturbance vs depth interaction term was very significant. Shallow *Agaricia humilis* corals had a high mortality and low rate of undisturbed growth, whereas for deep colonies the reverse was true.

(c) *test of independence of size and depth*. As suggested earlier, size and depth are not independent given the level of disturbance. In 'disturbed' *Agaricia humilis* at the shallow reef the number of small corals was higher than expected, and at the deep reef large corals were relatively abundant.

Fig. 3. *Agaricia humilis* and *A. agaricites*. Size distribution of juvenile colonies at different depths at the start of the investigation year. n: number of colonies; $\bar{\varnothing}$: mean diameter (5 mm categories)

Table 1. *Agaricia humilis*. 3-way contingency table, with depth, size, and disturbance, followed by 3-way analyses of frequencies. Interaction and independence expressed as G-values. Degrees of freedom in square brackets. Freeman-Tukey (F-T) deviates are listed if their absolute value is almost equal to or more than c (an approximate criterion for being large). * F-T deviates deduced from similarly marked value in contingency table; $\bar{\phi}$: mean colony diameter

Depth	< 11m		> 11m	
$\bar{\phi}$ (mm)	< 15	> 15	< 15	> 15
Disturbance				
undisturbed	0	0	2	1
disturbed	48	24	17	23
died	23	4	4	0*

Complete interaction	G-statistic	F-T deviate	c
	2.52 [2] p < 0.3	-1.16*	0.80

Conditional independence minus complete interaction	G-statistics	F-T deviates	c
		Depth	
		$\bar{\phi}$ (mm)	

Deep *Agaricia* (>11 m): disturbance, size, and species (Table 2)

(a) test of independence of disturbance and size. Deletion of this term caused a non-significant drop in the fit of the model. However, Freeman-Tukey deviates for *Agaricia humilis* (the same as in Table 1)

suggest that small corals have a higher mortality than larger juveniles.

(b) test of independence of disturbance and species. This test showed the strongest pairwise association. There was a lower number of undisturbed *Agaricia humilis* than expected, as opposed to a relative high number of undisturbed *A. agaricites* colonies.

Table 2. *Agaricia humilis* and *A. agaricites*. 3-way contingency table with species, size and disturbance at >11 m depth, followed by 3-way analysis of frequencies. For other information cf. Table 1.

Species	<i>A. humilis</i>		<i>A. agaricites</i>	
Ø (mm)	< 15	> 15	< 15	> 15
Disturbance				
undisturbed	2	1	3	4
disturbed	17	23	2	6
died	4	0*	2	2

Complete interaction					
	G-statistic		F-T deviate		c
	1.80 [2] p<0.5		-0.82*		0.80

Conditional independence minus complete interaction					
	G-statistics		F-T deviates		c
		Species	<i>A. humilis</i>	<i>A. agaricites</i>	
		Ø (mm)	< 15	> 15	
		Disturbance			
Disturbance/Ø	5.87 [2] p < 0.1	died	-1.27	-2.03*	1.13
Disturbance/species	14.89 [2] p < 0.001	undisturbed	-1.37	1.35	1.47
		disturbed		-1.18	-1.20
		died			1.23
Ø/species	3.03 [1] p < 0.1	died	-1.24*		0.98

Table 3. (a) Disturbance and mortality in *Agaricia humilis* at 5 to 10 m (<11 m) and at 12 to 23 m (>11 m), and in *A. agaricites* at 12 to 23 m (>11 m). Disturbing factors listed at left. %: relative frequency; n: actual frequency

	Disturbance						Mortality					
	<i>A. hum.</i> < 11 m		<i>A. hum.</i> > 11 m		<i>A. aga.</i> > 11 m		<i>A. hum.</i> < 11 m		<i>A. hum.</i> > 11 m		<i>A. aga.</i> > 11 m	
	%	n	%	n	%	n	%	n	%	n	%	n
Filamentous algae	53	38	20	8	13	1	22	6			25	1
Crustose coralline algae	22	16	10	4			7	2	50	2		
Endolithic algae	4	3	8	3	13	1	15	4				
<i>Gypsina</i>	6	4	10	4								
<i>Reniera carmabi</i>			10	4	13	1						
Bryozoa			3	1								
<i>Trididemnum solidum</i>	1	1	3	1								
<i>Millepora</i>			3	1					25	1		
<i>Lebrunia coralligena</i>							4	1				
<i>Madracis</i>			3	1							25	1
<i>Agaricia humilis</i>	1	1										
<i>Agaricia agaricites</i>	3	2			13	1						
<i>Montastrea cavernosa</i> *	3	2					11	3				
<i>Meandrina meandrites</i> *	1	1					4	1			25	1
<i>Isophyllastrea rigida</i> *	1	1					4	1				
<i>Cliona caribbaea</i> *							15	4			25	1
<i>Cliona laticavicola</i> *							4	1				
<i>Coralliophila abbreviata</i>			3	1								
Sediment	1	1	23	9	25	2						
Scar	1	1			25	2						
Part missing	1	1	8	3			7	2	25	1		
?							4	1				
?							4	1				
Total		72		40		8		27		4		4

* Factors causing abrupt mortality: disappearance between 2 successive censuses i.e. 50 to 98 d

Table 3. (b) Disturbance in *A. humilis* and *A. agaricites* expressed as n. (Includes 1 *A. agaricites* colony < 11 m (not in Table 3a) which contributes 1 to 'Others'.) G-statistics (G_{adj} : G-value adjusted with Williams' correction) are obtained from tests of independence, for factors in 2×2 tables, for 'Total' from $R \times C$ table

	Disturbance		G _{adj}
	<i>A. hum.</i> & <i>A. aga.</i>		
	< 11 m	> 11 m	
	n	n	
Filamentous algae	38	9	14.1 [1] p < 0.001
Crustose coralline algae	16	4	4.1 [1] p < 0.05
Encrusting animals	5	11	6.2 [1] p < 0.025
Sediment	1	11	15.3 [1] p < 0.001
Others	13	13	1.4 [1] ns
	—	—	
Total	73	48	32.7 [4] p < 0.001

ns = not significant

(c) test of independence of size and species. This resulted in a non-significant increase of the G-value. The only Freeman-Tukey deviate that indicated that size and species cannot be considered completely independent at each level of disturbance was based on

the above mentioned low mortality value of large *Agaricia humilis* > 11 m.

Conclusions: Small *Agaricia humilis* juveniles have a higher mortality than larger ones. Shallow *A. humilis* corals have a high mortality and the frequency of

Fig. 4 (a) *Agaricia agaricites* (left) with typical edge, elevated over the substratum, and *A. humilis* (right) in sediment covered by Cyanophyceae. (b) *A. humilis*. Overgrowth of colony by sponge *Reniera carmabi* (arrows). The lower part of the colony has been killed by the sponge in previous months. (c) *A. humilis*. Disturbance of upper part by endolithic algae. (d) *A. humilis*, partly killed by *Madracis* colony (right). (e) *A. humilis*. Intercolony fission; between colonies a distinct suture is visible. Scale bars = 10 mm

undisturbed corals is low in comparison with deep *A. humilis* corals. Large *A. humilis* juveniles are relatively uncommon at shallow locations compared to the deep reef. The largest difference in disturbance between *A. humilis* and *A. agaricites* (>11 m) is the higher number of undisturbed corals in the latter.

Causes of disturbance and mortality

For each juvenile colony, it was determined which factor contributed most to disturbance or mortality in the course of the whole investigation year (Table 3a). The effect of some of these factors on juveniles is depicted in Fig. 4a to d.

Within the corals listed as disturbed there was a significant difference in the relative importance of the disturbing factors in relation to depth ($p < 0.001$, $R \times C$ test of independence, see Table 3b). Overgrowth by filamentous and crustose coralline algae contributed 74 % to the total disturbance at shallow depth (<11 m), which is much more than in deeper juveniles (27 %, >11 m). In combination this difference is significant at the 0.1 % level. In the deeper group, especially sediment (Fig. 4a) was more important as a disturbing factor. The strong difference in disturbance by sediment resulted in the highest G-value (Table 3b). The overgrowth by non-coelenterate encrusting animals, *Gypsina* sp., *Reniera carmabi* Van Soest, Bryozoa and *Trididemnum solidum* (Van Name), was more important at the deep reef; the depth-related effect of *Reniera carmabi* (Fig. 4b) was especially significant ($p = 0.009$, Fisher's exact test of independence).

In Table 3a, a distinction has been made between cases of abrupt and gradual mortality. In the former cases, corals disappeared between 2 subsequent censuses (interval time 50 to 98 d), and in the latter cases, the living coral surface diminished over several intervals prior to death. The cause of mortality could not be traced in 2 of the total of 35 cases. Mortality was abrupt in 34 % of the cases. In 50 % of these cases substratum condition suggested weakening of the coral substratum attachment by boring sponges (5 times by *Cliona caribbaea* Carter and once by *C. laticavicola* Pang) sometimes in combination with endolithic (= boring) algae. In at least 3 cases where boring sponges were listed as the most important cause of mortality, the actual event (proximate cause) of disappearance was probably related to the activity of grazing organisms. The other 50 % were aggressive interactions with other corals: 3 with *Montastrea cavernosa*, 2 with *Meandrina meandrites* (Linnaeus) and 1 with *Isophyllastrea rigida* (Dana). In cases of gradual mortality (60 %), the most important causes were filamentous and endolithic algae, especially at

the shallow reef, where these factors were responsible for 40 and 27 % respectively of these mortality cases ($n = 15$).

The relative importance of endolithic algae (Fig. 4c) at the shallow reef, in non-lethal disturbance as well as in mortality, is somewhat underestimated. They often acted simultaneously or successively with factors which were considered to be more important. The gastropod coral predator *Coralliophila abbreviata* Lamarck and the sea anemone *Lebrunia coralligens* (Wilson) were encountered at the borders of 5 % and 14 % respectively, of all *Agaricia* colonies ($n = 166$) but in only 2 cases were they classified as most important factor contributing to disturbance or mortality.

Fission and fusion

Fission and fusion processes are considered separately as intracolony and intercolony phenomena (Fig. 5). In intracolony cases, 2 or more parts of 1 colony split up or reunify. Tissue fusion is complete. In intercolony cases, corals of different origin are involved and adjacent corals are characterized by the presence of a distinct suture at the common perimeters (Fig. 4e).

At the start of the investigation, 5 of the 166 colonies present showed intracolony fission (2 or 3 parts separated by dead skeleton). After 1 yr, 6 corals consisted of 2 or more parts (Fig. 5). However, these numbers underestimate the dynamics of intracolony fission and fusion. During the investigation year 15 corals were involved: 1 *Agaricia agaricites* and 14 *A. humilis* colonies, 50 % of which were found deeper than 11 m.

Of the original colonies, 18 showed intercolony fusion (as groups of 2 or 3 corals) at the start of the investigation period. 1 yr later, 20 juveniles participated in intercolony fusion, but only 55 % of these colonies were the same as the originally fused ones (Fig. 5). Corals involved in a change of their intercolony fission or fusion status during the investigation year numbered a total of 20. These were all *Agaricia humilis* colonies, 2 of which occurred deeper than 11 m.

In total, 21 % of the original corals ($n = 166$) were involved in a change of their intracolony or intercolony fusion or fission status.

Growth

Maximum growth

A frequency distribution of all data on growth interval⁻¹ is presented in Fig. 6. In *Agaricia humilis* maximum growth values interval⁻¹ of mean diameter were 66.7 $\mu\text{m d}^{-1}$ (<11 m) and 72.0 $\mu\text{m d}^{-1}$ (>11 m), in *A.*

Fig. 5. *Agaricia*. Overall picture of all of the original colonies involved in intracolony and intercolony fission and fusion. * *A. agaricites*, others *A. humilis*; S, E: situations at start and end of investigation year (situations between S and E only depicted if relevant); squares: colonies (black parts: died); points (in intracolony processes): number of parts separated by dead skeleton; n: number of observations; c: number of colonies per observation

agaricites (>11 m) it was $84.5 \mu\text{m d}^{-1}$. Based on the annual growth of real diameters (not depicted) the maximum growth of *A. humilis* was $79.9 \mu\text{m d}^{-1}$ and *A. agaricites* $78.3 \mu\text{m d}^{-1}$. Therefore, it seems safe to conclude that both coral species may show a diameter growth of $80 \mu\text{m d}^{-1}$ which is 29 mm on an annual basis.

In a few cases, radius growth (from a fixed point) was more than half of the maximum diameter growth. On a yearly basis, the maximum radius growth of *Agaricia humilis* and *A. agaricites* was $50.3 \mu\text{m d}^{-1}$ and $49.5 \mu\text{m d}^{-1}$ respectively. In these cases, growth in directions other than that of the maximum radius growth was

always much slower or even negative. It appears that slow growth along part of the coral's perimeter may be compensated for by 'supraoptimal' growth of another part.

Mean annual growth

Growth of mean diameter during the whole investigation year of all corals is presented in Fig. 7. Although both species have about the same maximum growth, actual annual growth is strongly influenced by the degree of disturbance. Therefore, occurrences of maximum growth ($80 \mu\text{m d}^{-1}$) during the whole year were

Fig. 6. *Agaricia humilis* and *A. agaricites*. Frequency distribution of all data on growth of mean diameter per interval. Depth indication (> or < 11 m), corresponds with Fig. 3. Length of bars depicts percentage of growth data exhibiting positive growth (pos.), expressed in different classes, or negative growth (neg.). Shading: white, undisturbed; hatched, disturbed. f: number of growth data

Fig. 7. *Agaricia humilis* and *A. agaricites*. Total annual growth separated for juvenile size (mean diameter) at the start of the investigation year: small (<15 mm) and large (>15 mm). Depth indication corresponds with Fig. 3. Length of bars depicts percentage of colonies exhibiting positive growth (pos.) expressed in different classes, negative growth (neg.) or death. Shading: white, undisturbed; hatched, disturbed; black, died. n: number of colonies

absent in shallow (<11 m) *Agaricia humilis*, infrequent in deep (>11 m) *A. humilis* and common in deep *A. agaricites*. A Mann-Whitney U-test on the positive annual growth values indicated a significant difference ($p < 0.01$) in *A. humilis* between the 2 depth ranges. Neither the difference between deep *A. humilis* and *A. agaricites*, nor the differences in annual growth between the 2 size classes, were significant.

Interval growth data (in Fig. 6) are not independent of coral sizes. For example, the fastest growing juveniles would prevail in the largest size classes more and more during the subsequent intervals as a result of their high growth rates. Fig. 7 supplies annual growth rates as function of size at the first census in the 3 species/depth categories.

Seasonal growth

Growth data obtained from intervals without disturbance are listed in Table 4. In all intervals mean and maximum growth values of deep (>11 m) *Agaricia humilis* are larger than at the shallow (<11 m) reef. The lower maximum growth in shallow *A. humilis* compared to the deep reef may be the result of mostly

smaller sample sizes (Table 4). A comparison of growth in the 5 intervals was made by comparing only those corals in Table 4 which had 2 or more intervals with undisturbed growth. Of 10 possible comparisons between time intervals per species, only 1 showed a significant difference ($p < 0.001$, Sign test) in growth: all *A. humilis* colonies which showed undisturbed growth in Dec/Jan as well as in Feb/Mar ($n = 12$), grew faster during the latter interval.

DISCUSSION

The depth-related difference in numerical abundance of *Agaricia humilis* and *A. agaricites* juveniles represents different recruitment patterns, which must be traced to settlement, fission and fusion, survival and growth. The importance of settlement will be treated elsewhere (Van Moorsel in prep.). The results in this paper have shown that the rates of disturbance and mortality of juvenile corals are related to colony size, depth, and species. I discuss first these variables (in this order), then fission and fusion, and finally growth.

Table 4. *Agaricia*. Mean and maximum growth per interval in colonies listed as undisturbed during intervals: in *A. humilis* at 5 to 10 m (>11 m), and at 12 to 23 m (>11 m) and in *A. agaricites* at 12 to 23 m (>11 m). Growth expressed as increase of mean diameter ($\mu\text{m d}^{-1}$)

		Interval month					Total
		Oct, Nov	Dec, Jan	Feb, Mar	Apr-Jun	Jul-Sep	
<i>A. humilis</i> < 11m	mean	36.5	21.1	33.5	27.4	34.7	32.1
	max	59.5	46.8	56.8	40.4	56.9	59.5
	n	19	6	11	12	9	57
<i>A. humilis</i> > 11m	mean	40.5	29.7	35.5	42.0	38.8	37.8
	max	72.0	55.6	61.2	70.1	67.6	72.0
	n	11	11	15	17	19	73
<i>A. agaricites</i> > 11m	mean	40.8	33.5	26.1	30.4	39.2	34.1
	max	65.4	59.2	55.2	62.7	84.5	84.5
	n	11	8	9	10	8	46

Size

Bak & Engel (1979) conducted a study on disturbance of growth and mortality of juvenile agariciids under natural circumstances on the same reef. Within the same depth range (zone I, II and III, their Table 4), 34 % (n = 195) were considered undisturbed in a 6 mo investigation period. If the chance of growing undisturbed is independent of coral identity and season, this value transfers to 11 % as a yearly estimate of undisturbed juveniles. This is somewhat higher than my annual total of 6 % (n = 166), but confirms the high risk agariciid juveniles face of being disturbed.

Bak & Engel (1979) found 25 % mortality in 6 mo, which is much higher than the annual 17 % (n = 166) in this study. This difference is largely the result of a size effect. In the former investigation, the range of initial maximum coral diameters was 2 to 20 mm. In the present study it was 3 to 46 mm. The higher survival of larger corals is related to the regeneration ability of corals: a certain level of disturbance which may kill a primary polyp gives a large coral (colony) an opportunity to recover. It is possible that smaller colonies have a relatively low regeneration capacity, as suggested by Connell (1973). Data on the absolute linear growth of damaged *Stylophora pistillata* (Esper) colonies (Loya 1976a, deduced from his Fig. 1) confirm this hypothesis.

The significant negative relation between size and mortality in *Agaricia humilis* in this study parallels the significant higher survival of large juveniles in Jamaica reported by Rylaarsdam (1983). The greatest diameters of her largest juveniles were <50 mm and are comparable to this study, but she found a relatively high (56 %) annual mortality in *Agaricia* juveniles. Hughes & Jackson (1980), working on *Agaricia* in Jamaica, found a lower yearly mortality (26 %, n = 216) in a size class with maximum diameters between 10 and 100 mm. At Heron Island, Great Barrier Reef, Connell (1973) also found a negative relation between size and mortality in a natural coral population. It appears that a careful description of size distribution is necessary in studies on juvenile scleractinian ecology.

Depth

The significant negative relation between depth and disturbance (Table 1) was not found in the study of juveniles by Bak & Engel (1979), but they suggested that the mortality of *Agaricia* juveniles on the shallow reef was influenced by catastrophic occurrences beyond their 6 mo investigation. In a 5 yr study of the Curaçaoan reef, Bak & Luckhurst (1980) demonstrated that the highest levels of abrupt (or catastrophic) mor-

tality (a process which starts and ends within an interval of 8 to 10 mo) of large corals (maximum diameter >30 cm) occurred at shallow depths. Table 3a seems to confirm this for juvenile *A. humilis*, but mortality was too low to demonstrate a significant difference ($p = 0.15$, Fishers's exact test of independence).

The difference in relative frequency of factors which caused disturbance and mortality at the 2 depth ranges (Table 3a, b) is partly the result of differences in light and water movement. The considerable overgrowth by filamentous and crustose coralline algae at the shallow reef is probably the result of relatively high irradiance. Endolithic algae were important factors in disturbance and mortality throughout the transect. In Curaçao, endolithic algae are present all over the limestone reef substratum and also under much of the living tissue of corals (Wanders 1977). Deep corals suffer relatively more from sediment, even though there is less sedimentation in this environment (Bak & Engel 1979, Van Moorsel in prep.). Due to reduced water movement, they can rely less on passive sediment clearing. Bak & Engel (1979) did not mention endolithic algae and in their Table 5, sediment seems to be most important at the shallow reef (3 to 9 m). However, in view of their large proportion of disturbance cases caused by unknown agents (> 50 %), it remains possible that these results are compatible with the present study. A high relative importance of overgrowth by the combination of encrusting forams, sponges, bryozoans and colonial ascidians on the deep reef was also found by Bak & Engel (1979). This reflects their higher bottom cover in that habitat. Ott & Lewis (1972) already observed *Coralliophila abbreviata* at the living margin of *Agaricia* and noted little damage in the field.

Species

The low mortality and high number of undisturbed colonies of *Agaricia agaricites* (Table 2) is to some degree the result of the growth form of this coral. All undisturbed *A. agaricites* colonies (n = 7) showed a typical colony edge which was at least partly elevated over the substratum (Fig. 4a; Van Moorsel 1983 Fig. 1a). This is effective in avoiding submergence in shifting sediments and overgrowth by spatial competitors such as filamentous algae and encrusting organisms. *A. humilis* is more encrusting, the colony edge following the contour of the substratum (Fig. 4a; Van Moorsel 1983 Fig. 1a). Consequently, this species is more susceptible to becoming engulfed by other bottom components.

The high mortality of *Agaricia humilis* caused by *Montastrea cavernosa* (Table 3) can be explained by the fact that *A. humilis* is often found in dead calices of

only partially dead colonies of this species. In such cases, re-growing *M. cavernosa* tissue constitutes a high risk. The abrupt nature of mortality near re-growing *M. cavernosa* tissue indicates that an aggressive interaction occurred, but the actual process was not observed. Since Chornesky (1983) did not observe tissue digestion in *A. agaricites* f. *purpurea* and f. *carinata* by *M. cavernosa*, this might indicate that *A. humilis* is less able to defend itself. I have not observed aggressive interactions between *A. agaricites* and *A. humilis*.

Fission and fusion

Fission and fusion have been investigated by Hughes & Jackson (1980) in colonies of *Agaricia agaricites*, *A. lamarcki* Milne Edwards & Haime and *Lep-toseris cucullata* (Ellis & Solander). They described only intracolony processes. In 1 yr, 6 % of all colonies ($n = 662$, largest diameter 500 mm) changed fission or fusion status. Their percentage is derived from a data set in which separate fragments of 1 original colony were given colony status. If this practice is used on intracolony fission and fusion data in the present study ($n = 166$ becomes 172), a similar figure (8 %) is found, but only if it is also solely derived from data at the start and end of the investigation year. The incorporation of data derived during the 1 yr investigation period as well as data on intercolony processes results in a significantly higher value of 21 %, which indicates a much more dynamic picture ($p < 0.001$, G-test of independence). In their study of the Curaçaoan reef, Bak & Luckhurst (1980) came to an analogous conclusion: coral cover was very constant over the 5 yr study period but spatial rearrangements, recorded at 8 to 10 mo intervals, outlined a community pattern that was surprisingly variegated through time.

Growth

The perimeter/surface area ratio of a unifacial plate-like coral will decrease with increasing size. If growth is restricted to the perimeter, and energy input into the growth process is proportional to surface area, absolute linear growth will be proportional to coral diameter. However, this study showed that absolute linear growth is independent of juvenile size. Maximum diameter growth of $80 \mu\text{m d}^{-1}$ in *Agaricia humilis* and *A. agaricites* agrees quite well with $76 \mu\text{m d}^{-1}$ in *Agaricia* juveniles as determined by Bak & Engel (1979). Large *A. agaricites* corals, with the same essentially 2-dimensional appearance of a juvenile have a maximum growth of $68 \mu\text{m d}^{-1}$ (Bak 1976). These are strong indicators of constant absolute linear growth. I

hypothesize that diameter growth drains energy only from a restricted zone, of a certain width, along the coral's perimeter. In this case, absolute linear coral growth of plate-like corals can be expected to be independent of size.

This hypothesis could be extended also to other species and growth forms. In his growth study of medium sized corals, Maragos (1972) found no size effect on growth rates when expressed as radius increase. The same result is obtained if data on maximum increase of surface area of smallest and largest corals (*Acropora*) in Connell (1973, Fig. 1a) are converted to diameter increase. If linear growth is constant, relative growth as a function of size or weight diminishes automatically. This was already found by Stephenson & Stephenson (1933), who used relative linear and area measurements, and by Goreau & Goreau (1960), who used relative calcification. Yamaguchi (1983) used a Gompertz growth curve to fit the data of the branching coral *Pocillopora damicornis* (Linnaeus) supplied by Stephenson & Stephenson (1933). Although the fit is good, the age/size relationship (his Fig. 2) strongly suggests constant linear growth within the size range for which the original growth data were collected. Loya (1976b) found the branching coral *Stylophora pistillata* to grow proportionally slower as it aged, but in absolute terms growth was constant. The increase of his smallest size group was even significantly less than the larger groups. This might be explained by the relatively more massive growth form of the smallest size group. Constancy of linear growth has also been found in large massive corals through sclerochronology, in which annual growth bands present in these corals are used as recorders of environmental history (Buddemeier & Kinzie 1976, Highsmith 1979, Shinn 1981). Constant absolute linear growth during all life phases appears to be the rule rather than the exception in Scleractinia.

In *Agaricia humilis*, annual growth is less in shallow (< 11 m) colonies than in deep colonies. However, growth measurements over short intervals clearly demonstrated that potential growth rates are not significantly different. More frequent disturbance in shallow juveniles was responsible for the difference in annual growth. To find constant growth with increasing depth (= decrease in irradiance) is not exceptional). The relation between growth and depth is negative in some species but positive in others (cf. review in Oliver et al. 1983). In large *A. agaricites*, Bak (1976) found a greater calcification per unit tissue area (mass increase) at 24 m than at 13 m depth. At 13 m, *A. agaricites* forms bifacial lobes, which have a relatively low ratio between length of growth perimeter and coral surface area, compared to the 24 m specimens which had unifacial surfaces. Assuming that, in both

forms, the perimeter is the main site of growth, relative calcification can vary with depth in spite of constant linear growth. Radial extension is only 1 parameter of calcification. Only when other parameters (cf. Oliver et al. 1983) are available can we better understand the growth of plate-like corals.

The high disturbance level of the shallow reef resulted in an effective low growth rate as well as a high mortality (often abrupt) of shallow juveniles. Therefore, a high proportion of these corals remain in the small size categories. *Agaricia humilis* is adapted to this situation by reaching sexual maturity at a small size (maximum diameter 28 mm) and by other characteristics which indicate a relatively high energy allocation to reproduction (Van Moorsel 1983). At the deep reef, spatial competition and sediment will become increasingly important. *A. agaricites* has the more advantageous growth form to face such adverse factors. Small *A. agaricites* probably put more energy into the maintenance of their growth form as they start reproducing at a much larger size (maximum diameter 108 mm) than *A. humilis* (Van Moorsel 1983).

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