Asexual reproduction, fragmentation, and skeletal morphology of a plexaurid gorgonian

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ABSTRACT: The Caribbean gorgonian *Plexaura* A, a species of uncertain affinity, relies almost entirely on asexual reproduction for the formation of new colonies. At a site of the San Blas Islands, Panama, 94 % of the colonies < 10 cm in height had apparently developed from fragments of larger colonies. These fragments were formed when branches broke off from *Plexaura* A colonies. *In situ* tests of the force required to break off branches indicate that downward directed forces of as low as 0.1 Newton induced failure of *Plexaura* A branches. In contrast, branches of equivalent diameter of the sympatric congenor *P. homomalla* (Esper) frequently remained unbroken at forces up to 19.6 N. Most fragments broke off the colony at points exhibiting a constriction in the axial skeleton. Constrictions in the branch axis of *Plexaura* A were not distributed uniformly on the colony. Branch points distant from the branch tip were more likely to have axis constrictions than those close to the tip. Fragments are believed to be produced by wave action during squalls and loose fragments were regularly found at the study site. These data suggest the axis constrictions in *Plexaura* A may be an adaptation for enhanced asexual reproduction.

INTRODUCTION

The relative advantages and disadvantages of clonal and colonial growth forms have received increasing attention in the last few years (Harper, 1977; Jackson, 1977; Highsmith, 1982; Cook, 1983; Coates and Jackson, in press). An important characteristic of clonal organisms is their ability to 'regenerate' large populations from a small number of individuals. This regenerative ability is particularly great among physiologically integrated colonial forms, in which growth and survival are functions of colony size (Hughes and Jackson, 1980). Thus, colonial species probably can survive and recover from periods of high mortality more readily than aclonal, solitary organisms (Highsmith, 1982).

Among colonial forms the ability of a colony to regenerate itself from a small fragment of the colony provides not only a means of enhancing colony survival but also a means of further propagating and dispersing the clone. Propagation of this type occurs when fragments of colonies break off from a 'parent' colony and then continue to grow as independent colonies. In severe situations, like hurricanes, the forces responsible for fragmentation lead to the death of most of the colony (Knowlton et al., 1981; Woodley et al., 1981). In other cases, however, many of the fragments survive

and become separate colonies, each of which can grow to a size equal to or greater than that of the colony from which it was derived. Fragmentation occurs in a wide variety of taxa but has been most thoroughly documented in the corals (Glynn et al., 1972; Gilmore and Hall, 1976; Wilson, 1979; Highsmith, 1982; Highsmith et al., 1980; Bothwell, 1981; Knowlton et al., 1981; Tunnicliffe, 1981, 1982; Lasker, 1983). Among these species fragmentation can enhance the growth of the clone whenever growth of the newly formed colonies exceeds the mortality of unattached fragments. In such cases fragmentation is beneficial and should be selected for.

The presence of fragmentation in a group of species and their apparent success does not demonstrate an 'advantage' for this mode of propagation nor does it demonstrate selective processes. A more convincing, though circumstantial, argument can be made for those species which also exhibit unusual morphologies that facilitate fragmentation. Tunnicliffe (1981, 1982) examined *Acropora cervicornis* and concluded that *A. cervicornis,* 'is able to use an inherent weakness' to promote growth of the clone (Tunnicliffe, 1982). A more dramatic example of an apparent adaptation for fragmentation has been described in the Pacific gorgonian *Junceela fragilis* by Walker and Bull (1983). They

found that *J. fragilis* produces small fragments by resorbing tissue several centimeters below the branch tip. The end of the branch then breaks at the weakened point and reattaches, forming a new colony.

In this paper I report another case of a gorgonian which relies on fragmentation to generate new colonies and which exhibits unusual morphologic characteristics which facilitate fragmentation. The species, a *Plexaura* sp. of uncertain affinity, is similar to *Plexaura homomalla* forma *kukenthali*. The species is morphologically distinct from *P. homomalla* and may represent a new species or a hitherto synonomized species (F. M. Bayer, pers. comm.). For the purpose of identification I shall refer to this species as *Plexaura* A. *Plexaura* A can be distinguished from *P. homomalla* on the basis of the absence of a calicular lip, reduced polyp armature, straighter and simpler spindles and thicker, less foliate leaf clubs. The species is known from the San Blas Islands, Panama and the Florida Keys. *Plexaura* A differs from *P. homomalla* in one other important character. *P. homomalla* terminal branches are, as in most gorgonians, extremely flexible and considerable force is required to break off a branch. In contrast, *Plexaura* A branches are brittle and can be snapped off a colony with little effort. The brittleness of *Plexaura* A colonies is rare among Caribbean gorgonians and is unique among *Plexaura* species. In this study I show how the brittleness of *Plexaura* A branches greatly facilitates failure of the branches and thereby promotes the propagation of the species.

METHODS

Fragmentation was studied in a *Plexaura* A population located on Korbiski Reef near the Smithsonian Tropical Research Institute field station in the San Blas Islands, Panama. The gorgonian population was located at the northeastern end of the reef in water 0.5 to 4 m deep. The area features consolidated coral rock, coral heads (*Diploria* spp.) and pockets of sand. The study site, a 10 × 10 m area, was densely populated by the gorgonians *Plexaura* A, *Plexaura homomalla* (Esper), *Pseudopterogorgia americana* (Gmelin), *Pseudoplexaura porosa* (Houttuyn), *Plexaura flexuosa* (Lamouroux) as well as other species. *Plexaura* A densities within 1 × 1 m grids ranged from 0 to 34 colonies m^{-2}.

All *Plexaura* A colonies within the 100 m^2 area were included in the study. The height of each colony was measured and the base of the colony was carefully examined to determine whether the colony had developed from a reattached fragment. Colonies which originated from fragments were usually attached to the substrate at several points and often had several par-

allel branches growing up from a branch lying in the substrate (Fig. 1 A). These colonies were distinctly different in appearance from those developing from a larva. Larva-originated colonies had a single point of attachment and a single branch rising from the base (Fig. 1 B). The origin of colonies could most readily be determined among small colonies, since large colonies had enlarged holdfasts which obscured the origin of the colony. The holdfasts of large colonies also contained branches which probably had become reattached to the holdfast. Due to the difficulty of determining the origin of the larger colonies only those ≤ 10 cm height were considered in the analysis of colony origin.

In order to quantify the ability of *Plexaura* A to fragment, 2 simple mechanical tests were performed on branches of both *Plexaura* A and, for contrast, *P. homomalla.* The first of the experiments was conducted on colonies *in situ* at Korbiski Reef. In this experiment a branch was arbitrarily chosen and a spring scale attached with a cable tie to a point 5 cm above the branch's point of insertion. Force was then directed downward while the branch was held in place just below its point of insertion (Fig. 2). The force required to break the branch axis was recorded from the scale at the moment of failure. The maximum force applied to a branch was 19.6 Newtons (the maximum force the scale would record). Twenty branches on each of 3 *Plexaura* A and 2 *P. homomalla* colonies were tested in this fashion. At the time of the experiment the branch order (the maximum number of branch points between a point and the branch terminus; Fig. 3) was also recorded. Thickness of the axis 0.5 cm above the branch point was measured to the nearest 0.05 mm with vernier calipers at a later time.

The second experiment was conducted in sea water alongside a dock, using freshly collected *Plexaura* A and *P. homomalla* colonies. In these experiments a branch point was selected and the branch held above and below its point of insertion. Force was then applied normal to the branch. The force was kept normal to the bending branch by rotating the colony as the force was applied (Fig. 2). The branch was not allowed to bend beyond an angle of 180°. The force required to break the branch as well as the original and final branch angles were all noted. In 30 cases the branch which had been broken from the colony was itself tested to determine the force required to break the branch into 2 pieces.

Examination of the fragments generated in the experiments as well as those collected in the field indicated that branches frequently broke at thin points in the branch axis. In order to document the existence of these morphological features three colonies of *Plexaura* A and one of *P. homomalla* were collected, strip-
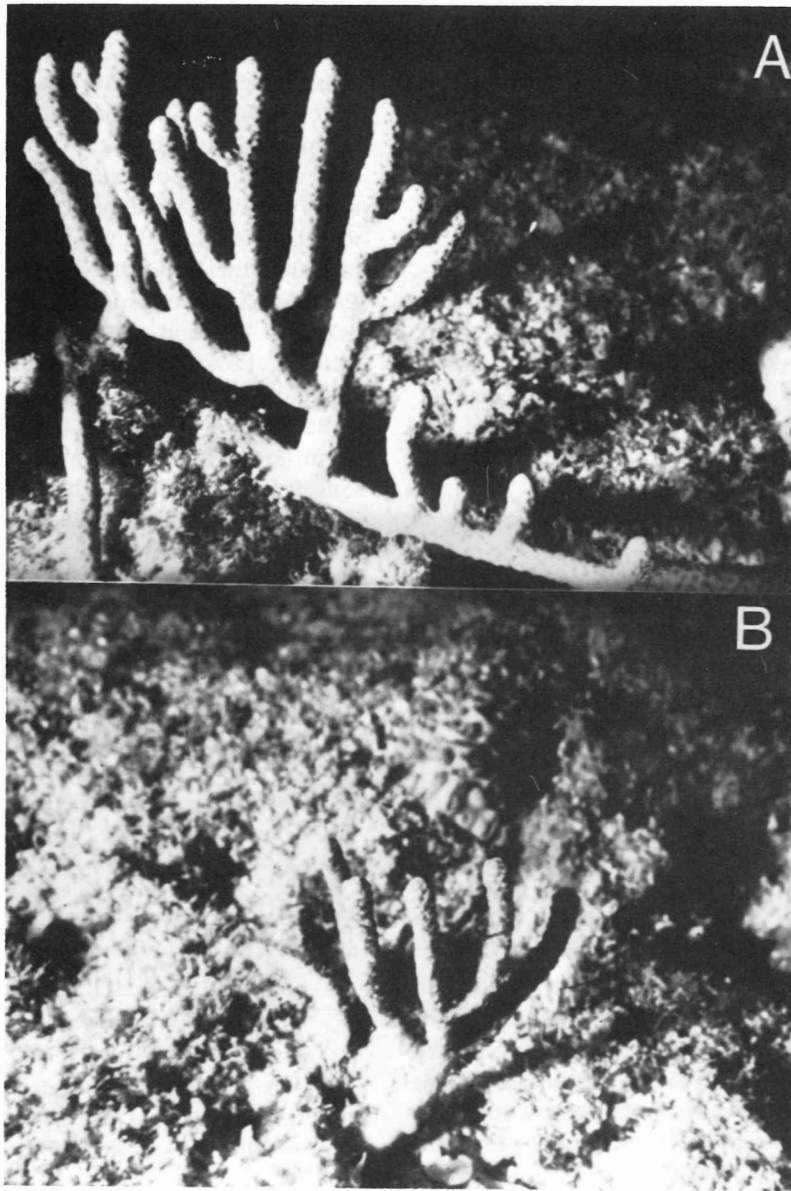
Fig. 1. *Plexaura* A. Colonies which developed from a fragment (A) and from a larva (B)

ped of coenenchyme and the axis of each branch examined for the presence of thin points. The colonies were subsequently broken apart at their branch points and the thickness of each branch measured at the break and 0.5 cm above the break. In 2 cases (1 colony of each species) minimum and maximum diameters were measured. Only minimum diameters of the remaining 2 *Plexaura* A colonies were measured.

The size and abundance of naturally occurring fragments were determined from a collection of all living unattached fragments. The length and number of all fragments were determined and axis diameters at the break point and 0.5 cm above the break point were measured with a vernier caliper.

RESULTS

Frequency of asexual reproduction

The size-frequency distribution of *Plexaura* A colonies is presented in Fig. 4. Although a number of colonies reached heights of 1 m or greater the majority of colonies were small and 25 % of the 212 colonies were less than 10 cm in height. Of the ≤ 10 cm tall colonies 94 % appeared to have developed from fragments. In contrast, only 19 *P. homomalla* colonies were found in the 100 m² area and all were greater than 10 cm in height. None appeared to have developed from fragments.
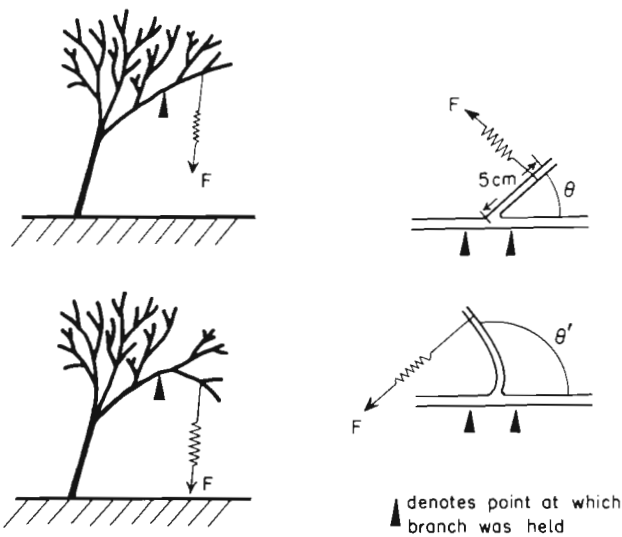
Fig. 2. Procedure used to test the breaking strength of gorgonian colonies. See text for explanation. *In situ* experiments depicted on the left, dockside experiments on the right
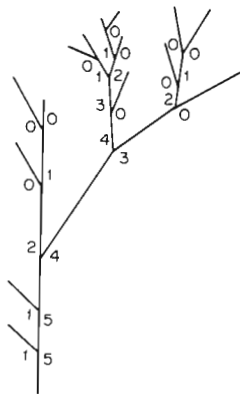

Fig. 3. Ranking of branches and branch points based on the number of junctions between a point and the farthest branch tip

Breaking experiments

The breaking experiments indicate that the large numbers of fragment-formed *Plexaura* A colonies can be related to the ease with which fragments can be produced. As is apparent in Fig. 5 *Plexaura* A branch points broke more easily than those of *P. homomalla* regardless of the branch axis diameter. The forces required to break off branches of the 2 species differed significantly (Mann-Whitney U test, p < 0.0001). Branch axis diameter was significantly correlated with breaking force among *Plexaura* A colonies (r = 0.43, p < 0.01), but was not correlated with breaking force among *P. homomalla* colonies. The weakness of *Plexaura* A branches is again evident in Fig. 6, which compares breaking force with respect to branch rank. *Plexaura* A branches broke off at lower forces than *P.*

homomalla branches regardless of rank (t-tests at each rank, all p < 0.001). The force required to break off branches correlated with branch rank (*Plexaura* A, r = 0.50, p < 0.001 – *P. homomalla*, r = 0.48, p < 0.005).

The dockside breaking experiments yielded data very similar to the *in situ* experiments. In the dockside experiments the maximum force applied to branches was 9.8 Newtons. Only 1 of the 20 *Plexaura homomalla* branch points broke at a force of 9.8 Newtons. All of the *Plexaura* A branch points fractured at lower forces. The angle of bending at which the branches failed also differed between the 2 species. The *Plexaura* A branches failed after they had been dislocated a mean of 85° (S.D. = 20°, n = 53), the maximum dislocation required to break off a branch was 120°. In contrast, the lone *P. homomalla* branch point which failed had been displaced 140° at the time of failure and in the other cases the branches were bent parallel to the branch they inserted into without inducing failure (a displacement of 150 to 160°, depending on the original branch angle).

The strength of branches at points other than the branch point was also tested in the dockside experiments. Repeated attempts to break *Plexaura ho-*
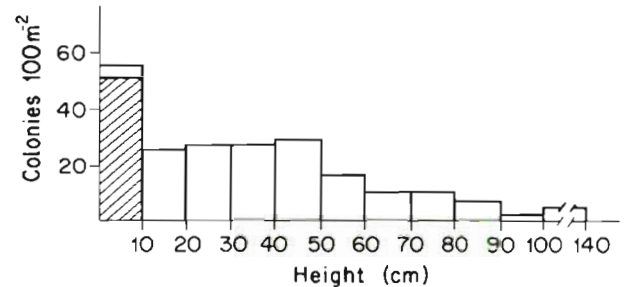

Fig. 4. *Plexaura* A. Size-frequency distribution of colonies on Korbiski Reef. Hatched area: colonies formed from fragments. Only colonies ≤ 10 cm are classified according to their origin
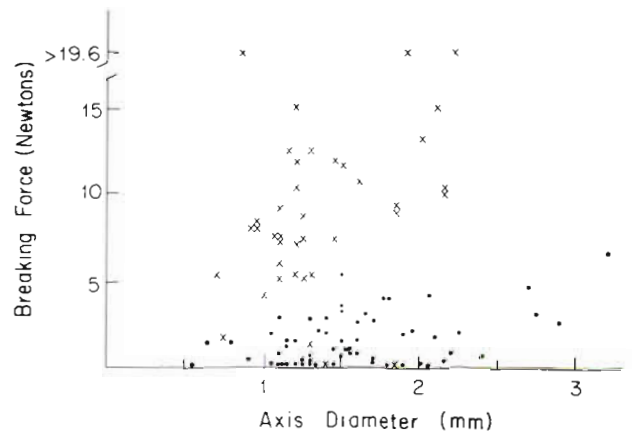

Fig. 5. Force required to break branches of *Plexaura* A (dots) and of *P. homomalla* (crosses) from the colony. Axis thickness was measured 0.5 cm above the break. The maximum force applied to the branch was 19.6 Newtons
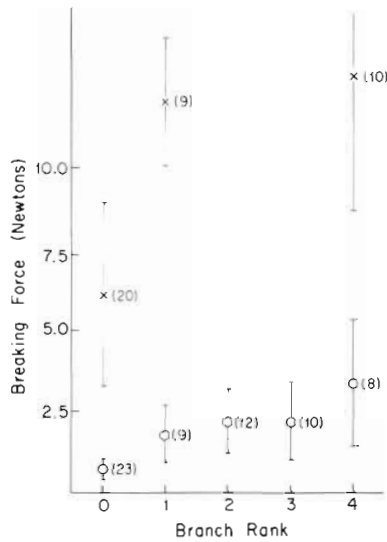
Fig. 6. Force (mean ± 95 % confidence interval) required to break *Plexaura* A (circles) and *P. homomalla* (crosses) as a function of branch rank. (See Fig. 3 for explanation of branch rank)
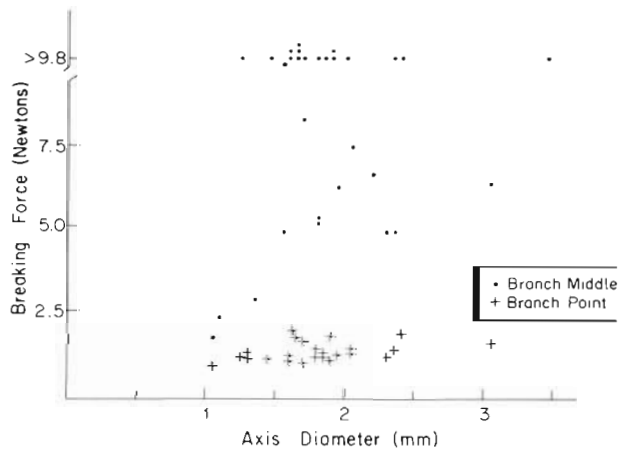

Fig. 7. *Plexaura* A. Force required to break branches from colonies at the branch point and force required to break those same branches in half
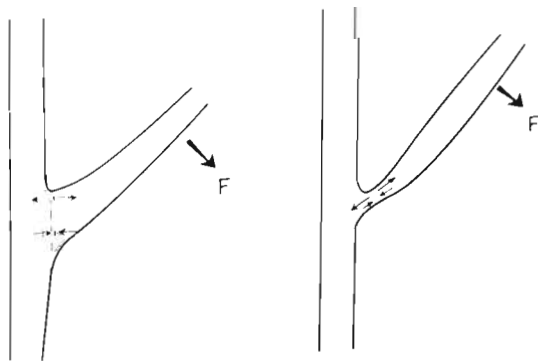

Fig. 8. Schematic representation of branch points with and without axis constrictions, and of the stresses encountered at the branch point

momalla branches failed. *Plexaura* A branches of similar diameter regularly broke at forces under 9.8 N, and in every case the force required to break branches was greater at the middle of the branch than at the branch point (Fig. 7).

Axis morphology

Analysis of the axial skeletons again revealed differences between the 2 species. *Plexaura homomalla* branch axes were round to elliptical in cross section and smoothly tapered from the base to the branch tips. An exception to this pattern occurred at the branch points, many of which were slightly compressed in the plane of branching (Fig. 8). As a consequence of the compression minimum diameter of the axis was lower at the branch point than above it, but maximum diameter was greater at the branch point. An estimator of cross-sectional area was calculated by multiplying minimum and maximum diameter. This index provides an estimator of the amount of gorgon laid down. Using that index 84 % of the 89 measured *P. homomalla* branches were thicker at the branch point than 0.5 cm higher. Analysis based on maximum and minimum diameters separately indicate that 92 and 46 % branches respectively were thicker at the branch point.

Plexaura A axes were notably different in appearance from those of *P. homomalla. Plexaura* A axes often had a sinuous appearance and tended to be elliptical or rectangular in cross section. Axis diameter thinned toward the branch tips but diameter fluctuated along the length of the branch. Constrictions in axis diameter were especially conspicuous at the branch points (Fig. 8). The constrictions were evident in analyses using cross-sectional area, minimum, and maximum diameter. The index of cross-sectional area (maximum × minimum diameter) of 133 branches, measured on one colony, revealed constrictions in 79 (55 %) of the branch points (*vs.* 16 % of the *P. homomalla* branch points). Estimates of the abundance of constrictions using maximum and minimum diameter were 41 and 55 %, respectively. Constrictions of the axis at the branch point were not distributed randomly among branch points (Fig. 9). The proportion of branch points with constrictions tended to increase with branch rank. The distribution was significantly different from random expectations ($x^2 = 16.74$, $p < 0.005$, df = 3). Although higher order branches had axis constrictions in disproportionate numbers, the greatest absolute number of constrictions occurred among the 1° and 2° branches (15 branches with constrictions in each class).

Minimum axis diameter was a good index of constrictions among *Plexaura* A colonies and minimum axis diameters of 2 additional colonies were also meas-
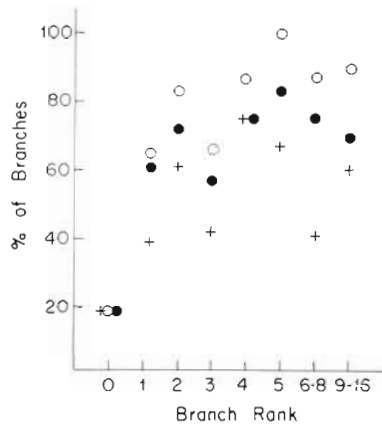
Fig. 9. Distribution of branch points with axis constrictions as a function of rank. Presence of axis constrictions was determined by measures of area (o) minimum diameter (●) and maximum diameter (+)

ured. These colonies, designated Colonies 2 and 3, also exhibited many branch points with constrictions (48 and 47 %, respectively). Constrictions in axis diameter were not randomly distributed among branches on Colony 2 ($x^2 = 11.47$, p < 0.025, df = 3). As in the previously described colony, constrictions were proportionately most abundant among higher rank branches and absolutely most abundant among 1° branches. Constrictions in axis diameter in Colony 2 were not randomly distributed with respect to axis diameter either ($x^2 = 8.11$, p 0.05, df = 3). Thicker branches were most likely to have branch points with constrictions among both colonies. Constrictions at the branch points of Colony 3 were randomly distributed with respect to both branch rank ($x^2 = 0.99$, p > 0.5, df = 3), and diameter on Colony 3 ($x^2 = 6.66$, 0.1 > p > 0.05, df = 3).

Fragmentation at Korbiski

Fragment size frequency distributions based on number of branches (Fig. 10) as well as length of the
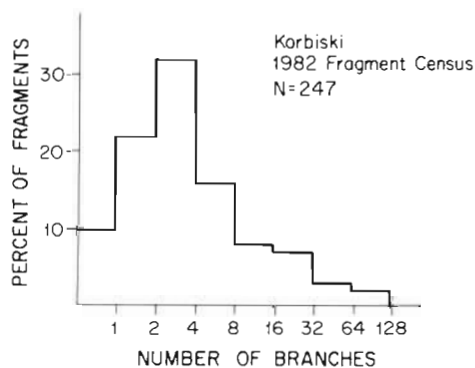

Fig. 10. *Plexaura* A. Size-frequency distribution of naturally occurring fragments collected on 100 m² in July, 1982

fragment indicate that intermediate sized fragments are most common. Comparison of the distribution of sizes with that of axis constrictions on intact colonies (Fig. 9) indicates that fragments produced by breaking 0° branches (1 branch) are underrepresented in the field collection. Naturally occurring fragments were also more likely to have axis constrictions at the point of fracture than are randomly chosen branch points on an intact colony. Using minimum diameter as an index of axis constriction the 3 measured, intact colonies had constrictions at 54 % of the branch points (N = 388, 95 % confidence interval = 50 to 58 %). Naturally occurring fragments had constrictions at their bases in 82 % of the cases (N = 138, 95 % confidence interval = 73 to 89 %). Fragments with constrictions at their bases were distributed uniformly with respect to branch rank ($x^2 = 0.66$, p > 0.9, df = 4).

DISCUSSION

Plexaura A unlike *P. homomalla*, and unlike most gorgonian species, produces most new colonies from fragments. The success of this mode of asexual propagation can be attributed to the ability of *Plexaura* A colonies to generate fragments, and the fragmentation of *Plexaura* A colonies can be attributed to both the morphology and brittleness of the branches. These traits are evident in the comparison of *Plexaura* A and *P. homomalla*.

Plexaura A branches are more brittle than those of *P. homomalla*. When 30 straight sections of *Plexaura* A were tested for strength only 53 % could be bent 180° and could resist an applied force of 9.8 N. In contrast tests of similar sized *P. homomalla* branches indicated that 100 % of the branches could be bent in such a fashion. In many cases *P. homomalla* branches could be tied in a knot and still did not fracture.

The branch morphology of the two species also differed and that further affected fragmentation. The effects of morphology on fragmentation can be recognized in an analysis of the process of failure of a branch. Wainwright et al. (1976), Koehl (1976, 1977) and Vosburgh (1977) have analysed stresses in forms like in gorgonians as cantilevers. Failure in such structures occurs when either the tensile or shear stress on a branch exceeds the strength of the structure. The experiment testing the strength of straight branches indicated that the 2 species differ in their inherent strengths. In addition the morphology of the 2 species suggests that equivalent forces applied to branches of each produces greater stresses in *Plexaura* A branches. In all of the experiments force was applied to a point 5 cm above the branch point thus the bending moment applied to the 2 species was equivalent for a given

force. However, the second moment of area of *Plexaura* A branch points is often less than that of *P. homomalla* because the area of many *Plexaura* A branch points is less than that of the branch axis above the branch point. Orientation of the branch further affects the second moment of area. *Plexaura* A again have smaller second moments of area than equal area equivalent *P. homomalla* branches, since cross sections of *Plexaura* A branch points are frequently compressed such that the long axis is horizontal and therefore normal to downward directed forces (Fig. 8). In contrast, *P. homomalla* branch points are compressed such that the long axis is parallel to downward directed forces. These features increase the second moment of area in *P. homomalla* axes and decrease it in *Plexaura* A axes. Tensile stress is inversely related to the second moment of area (Koehl, 1977) and as a consequence *Plexaura* A branches should experience greater tensile stresses than similar *P. homomalla* branches. Since the axes of both species fail on their upper surface it is believed that tensile stress leads to failure (as opposed to the shear stress exerted on the underside of the branch).

Plexaura A colonies had branches which were more brittle than *Plexaura homomalla* and had a morphology which further facilitated fragmentation. The question then arises whether *Plexaura* A morphology can be used to predict the pattern of breaking observed in nature. The pattern of branching in *Plexaura* A colonies is intermediate to both lateral and dichotomous branching patterns. Consequently, the number of branches increases geometrically as branch order decreases. This suggests that fragmentation should occur most commonly among the thinner lower order branches, which contain the greatest number of axis constrictions.

The manner in which forces are applied to colonies suggests, however, that larger, higher order branches should break more readily. The primary force responsible for breakage in *Plexaura* A colonies at Korbiski is probably drag on branches exerted by turbulent water movements during wet season squalls (maximum wind speeds of 55 to 95 km h^{-1}). During these squalls high rank branch points, which have more branches, are subject to greater forces and those forces are applied over greater lever arms (i.e. greater bending moment). Therefore, high rank branch points should be under greater stress than low rank branch points. Furthermore, the turbulence of the wave action is apt to apply forces in different directions to the same colony. The further apart the branches the more likely they are to receive forces from different directions. Therefore, high order branches are more apt to be 'pulled apart' than closely associated low rank branches. This latter point is important since forces applied uniformly to the entire colony primarily stress the colony holdfast and only create small stresses at the branch points.

The distribution of thin points on *Plexaura* A colonies suggests small fragments formed by breakage at low rank branch points should be most common. In contrast, the effects of turbulent currents on the colony suggests the colonies should fail at high rank branch points. The fragments collected in July, 1982 were most commonly of intermediate size and the small fragments expected from 0 and 1° branches were notably rare. This pattern may relate to the distribution of forces on the colonies or may relate to the greater probability of transport and burial which small fragments are subject to (unpubl. data).

The presence of large number of fragment formed colonies, the brittle axis of *Plexaura* A and the thin points on the axis demonstrate that *Plexaura* A morphology promotes asexual colony propagation. However, the brittle skeleton of *Plexaura* A may serve additional purposes. A common cause of mortality among gorgonian colonies is the toppling of the colony due to failure of the substrate which the holdfast is anchored to (Birkeland, 1974; Kinzie, 1974). Smaller colonies on which currents exert less drag are less likely to fail in this manner. The brittle skeleton of *Plexaura* A could effect a reduction in drag and thereby reduce whole colony mortality. This hypothesis is not mutally exclusive with the proposal that brittleness has been selected to further asexual reproduction, but it illustrates the difficulties of studying 'adaptations' using testable hypotheses as responses to any one selective force. The effects of fragmentation by *Plexaura* A suggest that asexual reproduction via fragmentation has been selected for in this species. However, a complete demonstration that asexual reproduction has been selected ultimately must include analysis of the success of genotypes which rely on fragmentation versus that of genotypes which produce fewer fragments.

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