

NOTE

Observations of colony fission following ledge formation in massive reef corals of the genus *Porites*

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ABSTRACT: Massive colonies of the coral genus *Porites* (Scleractinia) are among the most important reef-builders of the Indo-West Pacific. Colony fission is an important means of asexual reproduction in these species, resulting in the production of genetic clones or ramets. Fission occurs either by disturbance, or during undisturbed growth, as a consequence of formation of ledges around lower portions of large colonies. Outward growth of ledges shades and kills the tissues directly beneath, causing tissues nearer the base of the colony to become isolated from the parent. Of 47 colonies >100 cm in diam. at North Brook Island Reef, Great Barrier Reef (GBR), 26 ledged colonies supported 148 ramets, of which 106 were established on 5 of the largest corals in the site (colony diam. >350 cm). Ramets episodically become separated from the parent colony, a process facilitated by the relatively light and weak skeleton of *Porites* and enhanced by bioerosion and wave action. Ledges form from the horizontal expansion of lobes, probably in response to reduction in illumination caused by the upward growth of colonies. While 6 species of *Porites* on the GBR are known to exhibit this morphology – *P. lutea*, *P. lobata*, *P. solida*, *P. australiensis*, *P. myrmidonensis* and *P. mayeri* – not all large colonies from similar biotopes develop ledges. Whether this morphological variation is attributable purely to environmental effects on the phenotype, or also to genotypic differences within the massive *Porites* species assemblage, is unknown at present.

Colony fission and fragmentation are regarded as important means of asexual reproduction in scleractinian reef corals, resulting in production of clones of daughter colonies or ramets (Hughes & Jackson 1980, Highsmith 1982). For some coral species, the production of ramets is genetically determined and forms an integral part of their life-histories. For example, the poritid *Goniopora stokesi* and the fungiids *Diaseris* spp., undergo fission in the normal course of growth (Highsmith 1982, Veron 1986). For other corals, particularly those of robust massive and branching form, fission and fragmentation occur only as a consequence

of external physical or biotic forces (Cameron & Endean 1985). Isolation of portions of colonies may occur from scouring by wave action, desiccation during extreme tides, bioerosion by boring organisms, or predation by corallivores (Highsmith 1980, 1982, DeVantier et al. 1986, Done 1987). Once isolated from the parent, ramets are prone to detachment by wave activity. Being of colonial form, they have a greater chance of survival than individual polyps (Jackson 1986, Hughes in press). Surviving ramets form a clone that may be widely dispersed over a section of reef, enhancing the reproductive potential of the genotype (Potts et al. 1985).

For most coral species, the propensity for fission or fragmentation lies between the purely intrinsic and extrinsic modes, a function of the complex interaction of environmental and genetic constraints on colony morphology. For example, the Caribbean coral *Montastrea annularis* exhibits great morphological variability, occurring in different biotopes as massive, columnar or plate-like colonies (Barnes 1973, Graus & Macintyre 1982). While fission and fragmentation have been reported for all 3 morphologies (Highsmith 1982), plate-like colonies appear particularly susceptible to breakage of outermost plates (Jones 1977).

Fission and fragmentation are considered to be significant modes of reproduction in massive colonies of *Porites* (Highsmith 1980, Kojis & Quinn 1981, Harriott 1983), facilitating perpetuation of genotypes over time periods well in excess of the ages of individual colonies (1 colony has been dated at 677 yr, Potts et al. 1985). Disturbance-induced damage has been considered to be the major mechanism of fission and fragmentation of these corals. This paper reports observations of *Porites* spp. from the Great Barrier Reef (GBR) which indicate that large corals also produce ramets in the course of undisturbed growth via the development of tiers of ledges or overhangs around the colony bases (Fig. 1).

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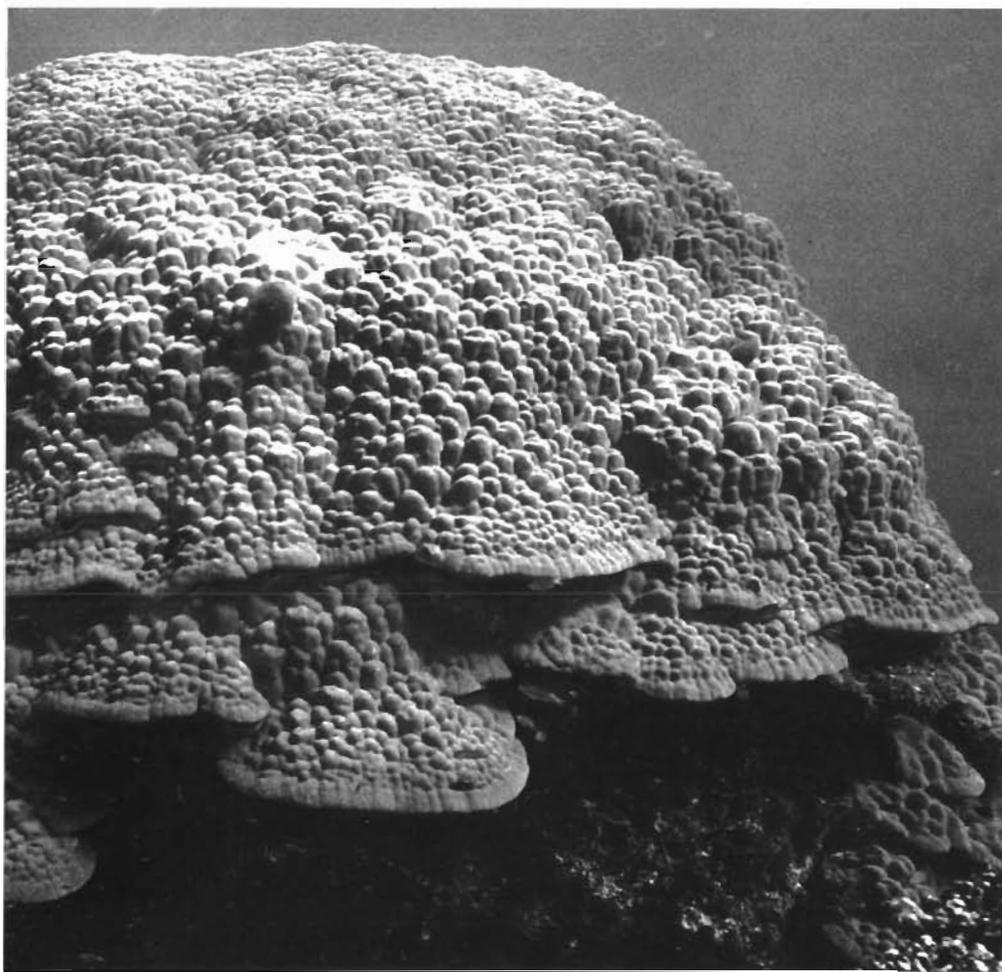


Fig. 1. *Porites* sp. A large massive colony (diam. ca 350 cm) exhibiting the developmental sequence of ledge formation from the horizontal expansion of lobes (midway down the colony, left side of photograph). The continued outward growth of the ledge shades underlying tissues (lower centre of colony). Death of the shaded polyps causes tissues on ledges further towards the colony base to become isolated from the parent (lower right). Continued outward growth of isolated tissues increases their susceptibility to detachment, as appears to have occurred at the colony base

Methods. To examine the mechanism of fission, censuses were conducted on the western lee slope of North Brook Island Reef, central GBR (lat. 18° 09' S, long. 146° 17' E) during January and September 1988. The survey area sloped evenly at ca 15° seawards from the reef crest and exhibited no obvious zonation. Both coral cover and species diversity were high. The great size and pristine condition of colonies of many coral species indicated that the area had not experienced any major disturbances for many years (Endean et al. unpubl. data).

The massive colonies of *Porites* spp. present at depths of 2 to 5 m within the study site (ca 1000 m²) were examined using SCUBA. The maximum diameter of each colony was measured using a plastic metric tape. For each colony, the presence/absence of ledges was recorded. Colony surfaces adjacent to ledges were inspected for evidence of damage, to assess whether ledges had formed in response to partial colony mortality. Disturbance-induced colony damage results in characteristic scarring and regeneration patterns in these species (DeVantier et al. 1986, Done 1987). The following recordings were then made: (1) the distance

of outward growth of ledges from the underlying colony side; (2) the number of instances where ledges shaded the underlying coral tissues; (3) the survival and distance of overlap of living tissues under ledges; (4) the steepness and heights of colonies above the uppermost ledges using a plumbline, protractor and metric tape; (5) the numbers and maximum diameters of all isolated regions of tissue (ramets still connected to the parent by skeletal material); (6) the distance of outward growth of ramets from the adjacent dead surface.

Results. Ledges were developed only on colonies greater than 100 cm diam. (Fig. 2). These corals are estimated to have a colony age of at least 50 yr, assuming a mean annual radial growth rate of 1 cm yr⁻¹ in the central GBR region (Isdale 1984). Of the 47 corals in the study site larger than 100 cm diam., 26 had developed ledges. Most of the remaining colonies had relatively smooth surfaces. Several colonies possessed both smooth and lobate regions of tissue. Ledge development was most common in the larger corals, with more than 2/3 of colonies greater than 250 cm diam. (ca 100 yr growth) exhibiting this morphology (Fig. 2). Most

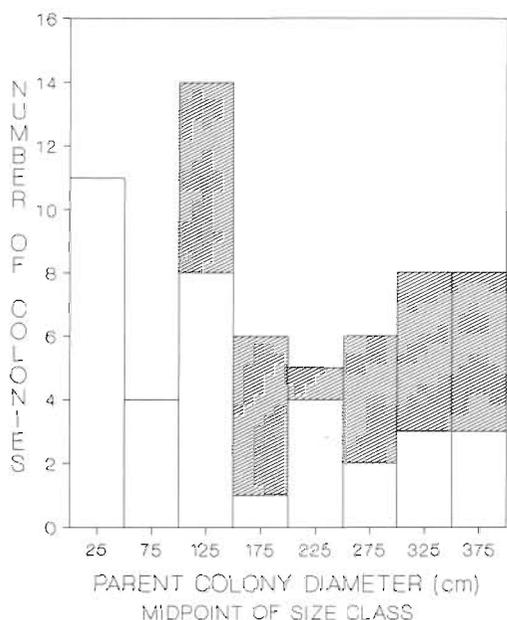


Fig. 2. *Porites* spp. Size structure of assemblage in an area of ca 1000 m², North Brook Island Reef, 1988. Relative proportion of ledged colonies in each size class indicated by cross-hatching

ledges were developed on the down-slope portions of colonies, at least 40 cm from the top of the colony and generally where the steepness of the colony wall was within 15° of vertical. On several corals, ledges also developed on other colony aspects, though in all cases, colony steepness was within 20° of vertical.

Ledges greater than 5 cm in outward extension from the colony side shaded the tissues underlying the ledge. Some overlap of living tissues under the lip of the ledge occurred. Generally this was limited to the outermost 2 to 3 cm under the ledge. The remaining lower surfaces of ledges were devoid of living tissues and covered by crustose coralline algae and other cryptic species (Fig. 3). The extent of underlying tissue death varied in relation to the size of the ledge and the extent of its horizontal projection. Tissue death resulted in either partial or complete isolation of living tissues near the colony base (Fig. 1).

The numbers of isolated regions of tissue increased markedly on largest corals (Fig. 4). Five of the largest colonies in the site supported 106 of the (total) 148 ramets. Ramets ranged in diameter from a minimum of 3 cm to a maximum of 103 cm (Table 1). Linear regression of ramet diameter against parent colony diameter was significant ($r^2 = 0.417$, $p = 0.001$). The heights of outward growth of ramets from the parent indicated periods of isolation ranging from 1 to 41 yr (assuming a growth rate of 1 cm yr⁻¹, Table 1).

Discussion. The production of ramets in massive colonies of *Porites* spp. occurs via the isolation of regions of tissue from the parent colony. This isolation results from partial colony mortality (areas of tissue death), caused by disturbance or by the sequential formation of tiers of ledges around the lower portions of large colonies. Over time periods of several years to decades, continued outward growth of isolated tissues results in



Fig. 3. *Porites* sp. A ramet (diam. 10 cm) after detachment from parent. Rim of unshaded living tissue and covering of crustose coralline algae and other cryptic species are clearly visible

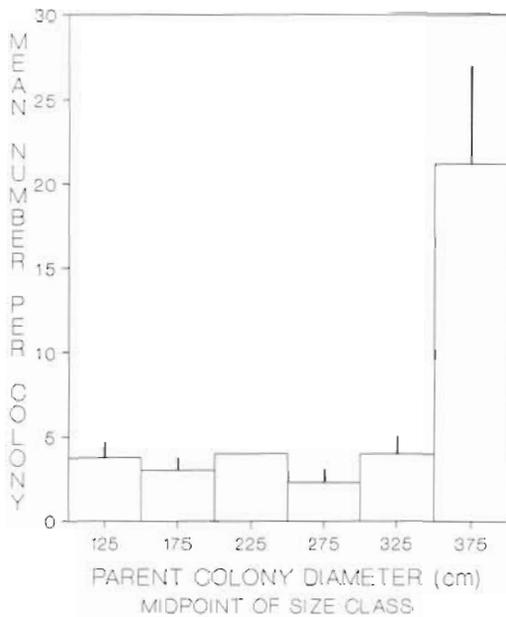


Fig. 4. *Porites* spp. Mean number (with SE) of ramets on parent colonies in each size class at North Brook Island Reef, 1988

an increase in weight and surface area relative to the area of skeletal attachment to the parent colony, thereby increasing ramets' susceptibility to detachment (Fig. 3). Detachment will be enhanced by the relatively light and weak skeleton of *Porites* (Hughes 1987, Scott & Risk 1988). Detachment and dispersal of ramets is further enhanced by strong wave activity and weakening of the connecting skeleton by bioeroding organisms (Highsmith 1982). Survival of ramets will depend upon several factors, particularly illumination, sediment load and competition with adjacent organisms.

Production of ramets will be most significant when opportunities for recruitment by sexually-produced propagules are limited. For example, dispersal of ramets by wave activity is important in enabling the colonization of sandy areas which are generally unsuitable for recruitment by planulae, and has been instru-

Table 1 *Porites* spp. Dimensions of ramets on parent colonies at North Brook Island Reef, central GBR, January 1988. Size class: parent diameter (cm); Diam., Height: ramet diameter and height above adjacent parent colony surface (cm). R: range; Med: median

Size class	Diam.		Height	
	R	Med.	R	Med.
101-150	4- 15	8	3-10	5
151-200	3- 8	6	4- 6	4
201-250	5- 61	14	2-13	8
251-300	4- 65	19	1-18	11
301-350	4- 35	11	4-25	10
351-400	5-103	41	3-41	12

mental in the leeward extension of many reefs throughout the Indo-West Pacific (Highsmith 1980). Over hundreds of years, ramets dispersed onto sandy reef margins have the potential to grow into large colonies which in turn develop ledged bases, initiating further fission and perpetuation of the parent genotype. By contrast, sexual reproduction provides novel genotypes in the form of planktonic larvae, facilitating dispersion over much greater distances (Oliver & Willis 1987).

The production of ramets via formation of ledges appears to represent a significant form of asexual reproduction for the 6 *Porites* species known to develop this type of morphology on the GBR (*P. lutea*, *P. australiensis*, *P. solida*, *P. mayeri*, *P. myrmidonensis* and *P. lobata*) (Veron & Pichon 1982, Veron 1986). These species exhibit many characters consistent with incorporation of fission into their life histories (Williams 1975, Highsmith 1982). These characters include a relatively light and weak skeleton (Scott & Risk 1988), relative longevity (Isdale 1984, Potts et al. 1985), large colony size and allocation of less energy to sexual reproduction than non-fragmenting species (dioecious spawners rather than larval brooders, Kojis & Quinn 1981, Harriott 1983). Ramets are of large size and almost certainly have relatively low mortality rates in comparison with sexual offspring (Hughes in press).

In the study area, ledges had developed only on colonies greater than 100 cm diam. However, smaller ledged corals have been observed in deeper and more turbid waters, which suggests that ledge formation is related to ambient light level. Changes in illumination have been proposed as one of the major factors responsible for growth form variability in scleractinians (Barnes 1973, Graus & Macintyre 1982, Veron 1986). Ledges form from the horizontal expansion of lobes on regions of the colony wall approaching the vertical. Growth of ledges probably is triggered by decreasing illumination caused by the colony's continued upward growth (Fig. 1). However, not all large colonies from similar biotopes develop ledges. Whether this morphological variation is attributable purely to specific environmental effects on the phenotype, or also to genotypic differences within the massive *Porites* species assemblage, is unknown at present.

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