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APPENDIX 1. GROWTH FORM MODIFICATION OF *PAVONA CACTUS* BY *SINULARIA FLEXIBILIS*

Observations of stunted and abnormal forms of *Pavona cactus* growing adjacent to the alcyonacean *Sinularia flexibilis* prompted the following study. Ten interactions involving the two species were photographed and followed for two years. Colonies were tagged with numbered perspex labels and stakes were positioned so that interactions could be rephotographed from the same reference position. After one year, three colonies of *S. flexibilis* were removed and subsequent growth of *P. cactus* was monitored. At the same time a further ten colonies of *S. flexibilis* were placed next to healthy colonies of *P. cactus*, having typical convoluted and columnar morphologies.

Colonies of *P. cactus* in naturally occurring interactions deteriorated over the two year period. Within distances of approximately 30cm of *S. flexibilis*, vertical growth of fronds appeared to cease and frond tips were often necrotic (Figure 1A). The bases of fronds enlarged, suggesting that although vertical growth was inhibited, radial growth was still occurring. Consequently, fronds appeared stunted and knarled. *S. flexibilis* overgrew *P. cactus* by up to 15cm in 5 of the 7 natural interactions followed for the 2 year period. As the soft corals advanced, new fronds within a 30cm radius were affected. When the soft corals were removed, fronds of *P. cactus* resumed vertical growth, and within 6 months regained their normal appearance (cf. Figure 1B and 1C). Conversely, frond tips of colonies next to transplanted soft corals became necrotic within 2 months of establishing the interaction. Affected fronds were generally within contact distance of the soft corals. It is possible that terpenes leached from the soft coral mediated an allelochemical interaction (Sammarco *et al.*, 1983). It is also possible that direct physical contact between tentacles of *S. flexibilis* and fronds of *P. cactus* modified the growth of the latter species, through contact transfer of terpenes or other chemicals in mucus, nematocyst discharge, and/or physical abrasion.

FIGURE 1

Growth form modification of *Pavona cactus* by *Sinularia flexibilis*

The interaction was photographed *in situ* at Eclipse Island, Palm Island Group. The sequence of photographs shows the effect of a naturally-occurring interaction on *P. cactus*, and recovery of fronds following removal of the soft coral. The perspex label was 15cm in length, and is visible in all three photographs for reference. Arrows on photographs B and C point to the same frond.

Top photograph (A): Naturally occurring interaction photographed on 28 February 1981. Fronds of *P. cactus* closest to *S. flexibilis* are stunted, while those on the opposite periphery of the colony are normal in appearance.

Middle photograph (B): Close-up of a portion of *P. cactus* affected by *S. flexibilis*. Photographed 28 February 1981.

Bottom photograph (C): Close-up of the same portion of *P. cactus* photographed 19 June 1981, seventeen weeks after the removal of *S. flexibilis*. Fronds have resumed vertical growth and are approaching an appearance typical of convoluted colonies.

APPENDIX 2. PUBLICATIONS
FROM RESEARCH ASSOCIATED WITH THIS THESIS

PHENOTYPIC PLASTICITY VERSUS PHENOTYPIC STABILITY IN THE REEF CORALS *TURBINARIA MESENTERINA* AND *PAVONA CACTUS*

PLASTICITE PHENOTIPYQUE CONTRE STABILITE PHENOTYPIQUE CHEZ LES SCLERACTINIAIRES RECIFAUX *TURBINARIA MESENTERINA* ET *PAVONA CACTUS*

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ABSTRACT

Reciprocal transplant studies were used to test for the presence of phenotypic plasticity in Turbinaria mesenterina and Pavona cactus, two morphologically variable species of Scleractinia. The extremes of the morphological range were identified in each species, and the distribution of morphs correlated with depth (both species) and reef slope (P. cactus).

In one species, Turbinaria mesenterina, reciprocal transplantation of morphs between two depths resulted in significant changes in colony morphology over a 3.5 year period (phenotypic plasticity). Morphometric analysis of colonies before and after transplantation indicated that colonies modified their growth forms through changes in the angle of corallite addition during linear extension. Growth became more horizontally-directed in "convoluted" colonies transplanted from a shallow to a deep site. Conversely, growth became more vertically-directed in "plate" colonies transplanted from a deep site to a shallow site.

In contrast, reciprocal transplantation of two morphs of Pavona cactus, between 4 sites of differing depth and reef slope, resulted in no apparent change in colony morphology over a 2.5 year period (phenotypic stability). This result is consistent with an electrophoretic study of P. cactus (WILLIS & AYRE, 1985), which indicated that morphological variation is genetically-determined in this species. Therefore morphological variation in 2 coral species, found in similar habitats on shallow fringing reefs, has evolved through two distinct pathways.

RESUME

Pour vérifier si la plasticité phénotypique existe chez Turbinaria mesenterina et Pavona cactus, deux espèces de Scléractiniaires qui sont morphologiquement variables, nous avons fait des études de greffes réciproques. Pour chaque espèce, nous avons identifié les limites extrêmes de la gamme morphologique et nous avons mis en corrélation la distribution des morphes avec la profondeur de l'eau (pour les deux espèces) et avec la pente récifale (pour P. cactus).

Dans une des deux espèces, Turbinaria mesenterina, la greffe réciproque de morphes d'une profondeur à une autre, a entraîné d'importants changements morphologiques de la colonie, observés au cours d'une période de trois ans et demi (plasticité phénotypique). L'analyse morphométrique de certaines colonies avant et après les greffes indique que la forme des branches de croissance récente a subi une modification due à des changements de direction des additions coralliennes au cours de leur extension linéaire. Dans les colonies convolutées greffées d'une station assez près de la surface à une autre en eau profonde, les nouvelles branches croissaient dans une direction plus horizontale. Réciproquement, les nouvelles branches croissaient dans une direction plus proche de la verticale dans les colonies aplaties transplantées d'une station profonde à une autre station située plus près de la surface.

Par contre, aucun changement évident ne s'était manifesté dans la morphologie de la colonie pendant deux ans et demi d'observations à la suite de greffes réciproques de deux morphes de Pavona cactus, faites dans quatre stations de profondeurs différentes et de différentes pentes récifales (stabilité phénotypique). Ce résultat s'accorde avec une étude électrophorétique de Pavona cactus (Willis et Ayre, 1985) qui indique que, dans cette espèce, les modifications morphologiques sont déterminées génétiquement. La variabilité morphologique de deux espèces de coraux vivant dans des habitats similaires de récifs frangeants peu profonds a donc évolué de deux façons fort différentes.

INTRODUCTION

Much has been written about the high levels of morphological variation exhibited by many species of corals, both in studies of overall colony form (recently: Veron, 1981; Potts, 1983, 1984), and in studies of corallite structure (Wijsman-Best, 1974; Brakel, 1977; Foster, 1980; Veron, 1981). Although it is often speculated that variability of growth form reflects phenotypic plasticity, experimental evidence of phenotypic plasticity is sparse. Reciprocal transplantation techniques have been used extensively to illustrate phenotypic plasticity in plants (e.g. Clausen *et al.*, 1940). Such studies are necessary to distinguish this type of variation from genetically-determined variation, and from phenotypic instability (i.e. variation that is neither genetic nor apparently environmental in origin, but seemingly random in direction (*sensu* Bradshaw, 1965)).

A major problem in applying transplant techniques to corals has been the length of the experimental period required to produce sufficient growth to allow detection of changes in colony morphology. With the exception of studies by Potts (1978) and Graus and Macintyre (1982), past experimental studies of growth form variation in corals have involved the transplantation of colonies to different habitats for periods less than one year (Stephenson and Stephenson, 1933; Roos, 1967; Maragos, 1972), or for periods that have resulted in inadequate growth to test for the presence of phenotypic plasticity of growth form (Dustan 1979). In many non-manipulative studies, colonies of the same species from different habitats have been compared, and correlations between morphological variation and environmental gradients suggested, particularly with respect to light and hydrodynamic energy (Stephenson and Stephenson, 1933; Goreau, 1963; Veron, 1981). However, such studies cannot conclusively differentiate between habitat related selection for specific genotypes, and environmentally-induced phenotypic plasticity.

In the present study two inshore species of corals, *Turbinaria mesenterina* and *Pavona cactus*, were tested for the presence of phenotypic plasticity of growth form. Both species have similar depth distributions on shallow fringing reefs. Similarly, both species exhibit variation in the degree of convolution of colonies throughout their geographic distributions (Veron and Pichon, 1983), and have moderate growth rates (2-4 cm/yr, unpubl.). Colonies of the convoluted form of *T. mesenterina* (Figure 1c, 1d) have highly-folded, vertical lamina in shallow water (1-2m). Lamina become progressively more horizontal and less folded as depth increases, culminating in the plate form (Figure 1a, 1b) at depths greater than 5m in turbid biotopes. In contrast, the morphological extremes of *P. cactus* overlap in their depth distributions, but are restricted to different reef slopes at Eclipse Island (central Great Barrier Reef region). The convoluted form (Figure 2A) and columnar form (Figure 2B) of *P. cactus* have been described elsewhere (Willis and Ayre, 1985). The convoluted form is found at depths ranging from 2 to 4 metres on the northern reef slope at Eclipse Island, whereas the columnar form is found between 4 and 6 metres on the steeper western reef slope.

Reciprocal transplantation of colonies between depths (both species) and between reef slopes (*P. cactus*) was used to test for the presence of phenotypic plasticity of growth form in the two species. Preliminary analyses of changes in growth form following transplantation are presented for both species.

MATERIALS AND METHODS

Study sites were established on shallow fringing reefs at Nelly Bay, Magnetic Island (19°10'S, 146°51'E), and at the northern end of Eclipse Island in the Palm Island group (18°46'S, 146°33'E). Both are inshore continental islands in the central Great Barrier Reef region.

At Nelly Bay, colonies of *T. mesenterina* were reciprocally transplanted between the top (2m) and bottom (6m) of the reef slope. These depths corresponded to peaks in the distributions of the convoluted and plate forms respectively. Colonies of each morph ($n \geq 10$) were placed at the transplant site located beyond that morph's naturally-occurring depth range. A further ten or more colonies of each morph were placed at the control site which corresponded to the depth of origin for that form. Pairs of transplant and control colonies of the convoluted morph were collected from the same source colonies. Plate colonies could only be matched for general size and shape, due to the lack of suitably large colonies. All ranged between 20 and 30 cm in diameter. Colonies were attached to large steel mesh grids secured to cement blocks at each site. All transplants and controls were photographed initially, and then yearly through-out the 3.5 year study (May 1981 to November 1984).

At Eclipse Island, study sites were established at 2 depths (3.0 and 6.0 m) on each of two reef slopes (northern and western). The 3.0 m site on the northern slope was located within the region where the convoluted form of *P. cactus* was most abundant ('convoluted' control site), and the 6m site on the western slope corresponded to the region of maximum abundance of the columnar form ('columnar' control site). Between 3 and 5 colonies of each morph, approximately 10 cm in mean radius, were collected from localized patches adjacent to each form's respective control site, and transplanted to the deep and shallow sites on each of the 2 reef slopes. Plastic cable-ties were used to fasten the lower dead portions of each colony to the vertical sides of plastic-covered metal racks, which were anchored to the substratum. Colonies were transplanted in January 1980 and collected approximately 2.5 years later in May 1982.

In order to distinguish between skeletal growth before and after transplantation, all colonies of both species were stained with alizarin red S by releasing a solution of the stain into plastic bags enclosing each colony. Colonies were exposed to a solution of approximately 15 ppm for 6 hours. To minimize trauma, colonies were stained and allowed to recover for 2 weeks before transplantation. Throughout the study periods of the 2 species, racks were cleared of algal growth on bimonthly visits to each site. Following collection, colonies were bleached in dilute calcium hypochlorite solution, and where necessary, the alizarin stain line was exposed by grinding away surface skeletal layers.

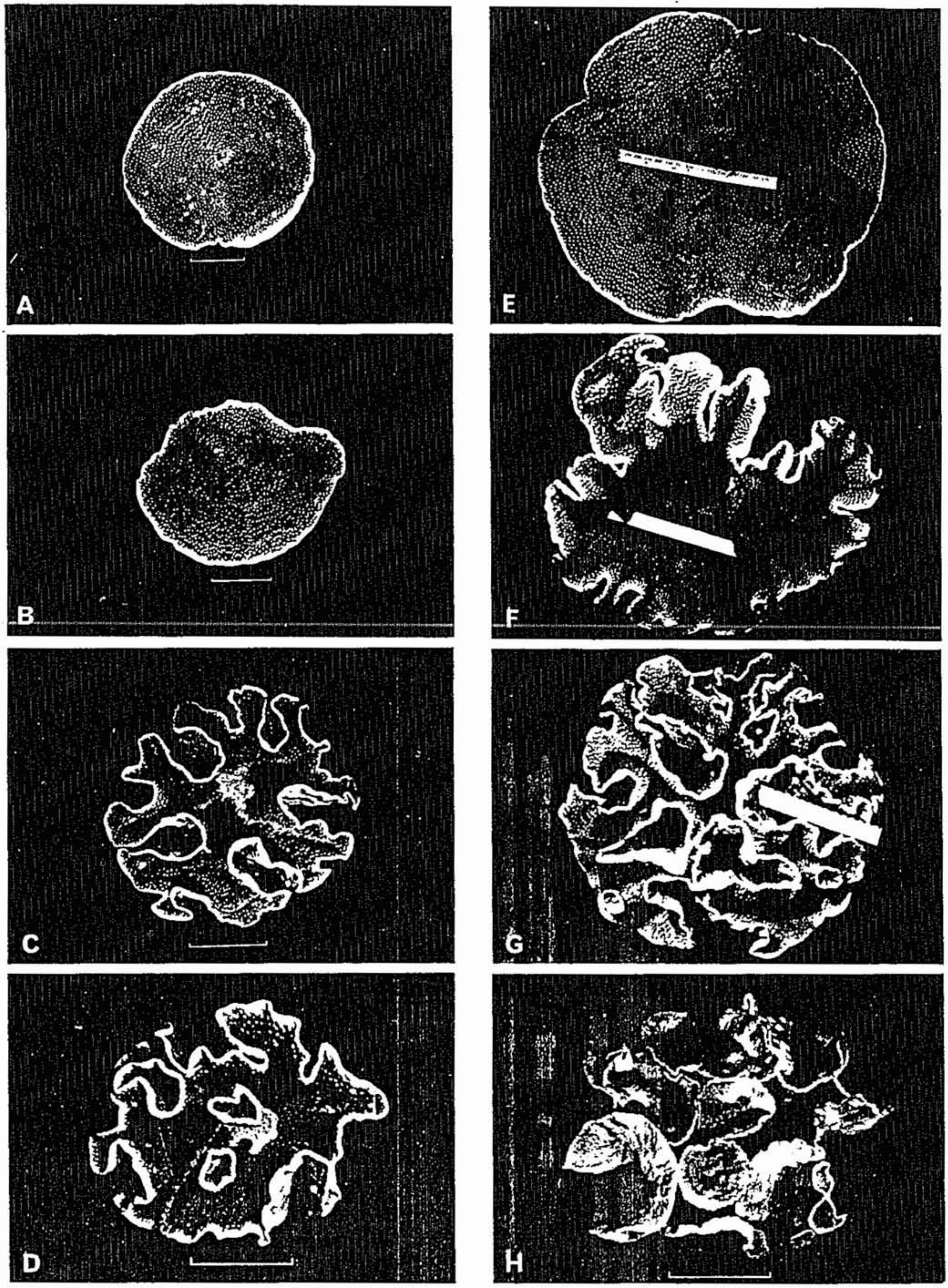

Figure 1. Photo mosaics of 4 colonies of *Turbinaria mesenterina* taken before (A to D) and after transplantation (E to H). A and B, plate colonies; C and D, convoluted colonies; E, plate control colony after 3.5 years at the deep site; F, plate transplant colony 3.5 years after transplantion to the shallow site; G, convoluted control colony after 2.5 years at the shallow site; H, convoluted transplant colony 2.5 years after transplantation to the deep site. Scale bars represent 5 cm, and are the same for each pair of photographs.

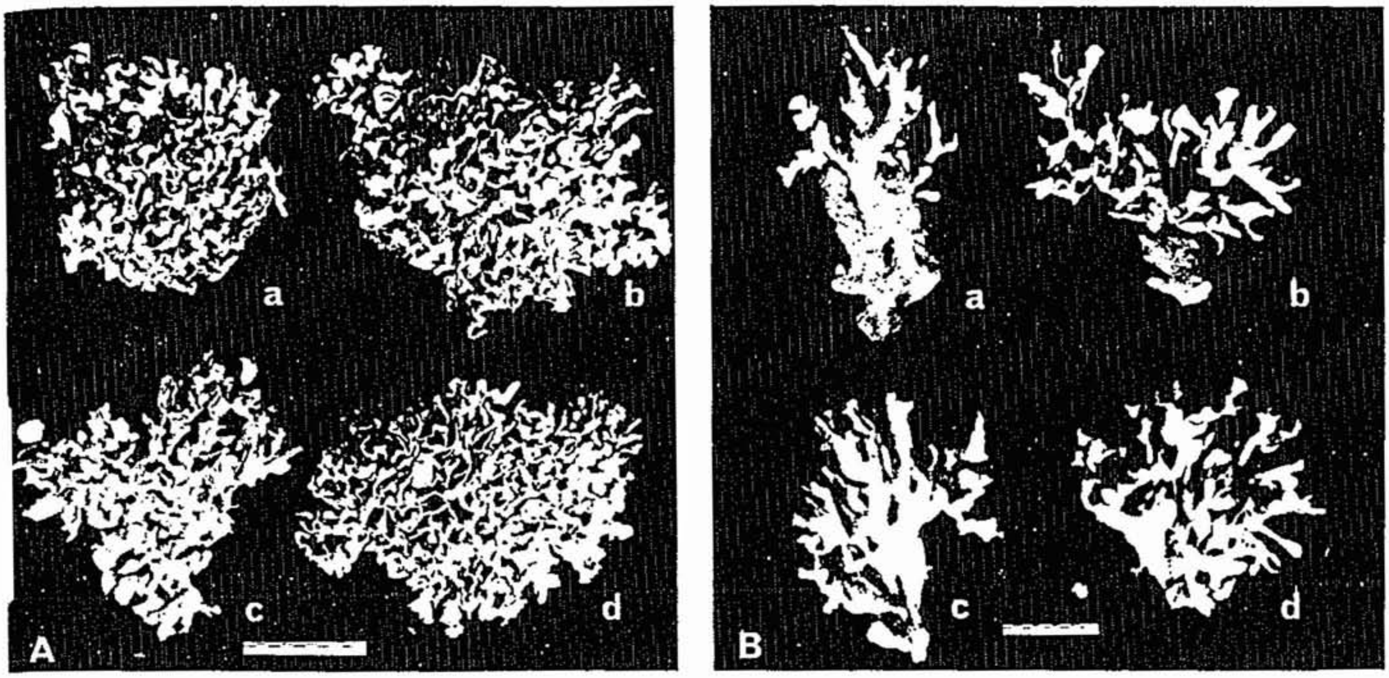

Figure 2. Colonies of Pavona cactus photographed 2.5 years after transplantation. A, convoluted colonies; B, columnar colonies; a, colonies transplanted to the shallow site on the northern slope; b, colonies. transplanted to the shallow site on the western slope; c, colonies transplanted to the deep site on the northern slope; d, colonies transplanted to the deep site on the western slope. Control colonies: Aa (convoluted form), Bd (columnar form). Scale bars represent 10 cm.

For P. cactus 'distance between fronds' was selected as an indicator of colony morphology (i.e. degree of convolution). Thirty points were randomly located within squares defined by a quadrat having 5 by 6 adjustable rows. The distance from these 30 points to the nearest neighbouring frond, was recorded in each case. The effect of growth form, reef slope, depth, and colony on this measure of frond spacing was assessed in a 4-way analysis of variance performed using the MANOVA routine of SPSS (Hull and Nie 1981).

RESULTS

Colonies of T. mesenterina grew between 50 and 85 mm in radius in the 3.5 year period, which approximately doubled the original size of some colonies. Of the initial 46 colonies, 6 were found dislodged and were therefore collected prematurely. Five of the 6 dislodged colonies were located at the shallow site where wave energy was generally greater. Only 1 of the control colonies (a plate colony) suffered mortality over a significant proportion (>10%) of its surface area. None of the plate colonies transplanted to the shallow site suffered significant mortality. However 2 of 13 convoluted colonies transplanted to the deep site degenerated and eventually died. In both cases the colonies appeared healthy for at least 1 year, but regions of localized mortality (possibly resulting from sediment accumulation) subsequently spread to the rest of the colony. This left a minimum of 9 colonies in each of the 4 categories for comparisons of growth form.

Photographs of a control and a transplanted colony of each morph, taken before and after transplantation (Figure 1), show typical effects of the 2 depth treatments on each growth form. All control colonies of the plate form (n=9) continued to extend linearly at approximately the same angle of growth so that after 3.5 years, colonies were simply enlarged versions of their original growth forms (Figure 1a, 1e). In contrast, the axis of growth of transplanted plate colonies became more vertically-directed following transplantation to the shallow site, as determined in comparisons of the growth angle above and below the alizarin stain line. In some cases the angle of growth changed sharply, approximately 5 to 10 mm beyond the stain line, whereas in others the transition to the new angle of growth was gradual. Given that asexual budding along the edge of the colony continued to increase the circumference of the plate, but that the radius of the plate did not continue to increase at a commensurate rate (because the colony was growing predominantly upwards rather than outwards), the edges of the transplanted colonies were forced to fold to accommodate this change in the radius to circumference ratio (Figure 1b, 1f). Hence a change in growth form, from horizontal flat laminae to more upright folded laminae, was observed for all transplanted plate colonies (n=10).

Growth of all control colonies of the convoluted morph of T. mesenterina (n=11), continued to have a strong vertical component throughout the experimental period, which resulted in increased folding of the laminae (Figure 1c,1g). In contrast, growth of convoluted colonies transplanted to the deep site became more horizontally-directed following transplantation. This initially led to the formation of horizontal lips throughout the colony, as previously upright surface features changed their direction of growth. Figures 1d and 1h demonstrate the flattening exhibited by all transplanted convoluted colonies (n=11) in the first 2 years of the study. Many of these lips subsequently grew together because of pre-existing morphological constraints. Following contact laminae either fused or reverted to vertically-directed growth. Abnormal forms were sometimes produced because of geometric constraints imposed by morphological features existing at the time of transplantation. For example, the flattening of funnel-like formations caused all polyps to ultimately face downwards. Curiously, this occurred in many cases where it would have seemed possible to avoid the inversion of polyps by preferentially extending those sections of the colony which were initially more horizontally-directed (compare Figures 1d and 1h).

All transplanted and control colonies of *P. cactus* survived, with minimal evidence of ill-effect, at the 2 depths (deep and shallow), and on the 2 reef slopes (northern and western). All colonies had mean linear extensions of at least 70 mm in the 2.5 year period. Therefore substantial growth occurred while colonies were exposed to the 4 different depth and reef slope environments. In fact, almost all of the living portions of the convoluted colonies at the end of the study, represented growth which had occurred during the 2.5 years (due to dense frond packing, only the top 50-80mm of the colony is alive).

Final growth forms of representative colonies of the 2 morphs, at the 4 sites, are shown in Figure 2. All transplanted colonies from the western slope sites were used in the frond spacing analysis (n=3 colonies per morph per depth treatment). However on the northern slope where 5 colonies of each morph were transplanted to each depth, 3 of the 5 colonies were randomly selected for analysis. The effects of 2 growth forms, 2 reef slopes, 2 depths, and 3 colonies per treatment on frond spacing were analysed in a 4-way analysis of variance, where the first 3 factors were orthogonal, and colony was nested within each combination of the 3 other factors. The appropriate F statistics were determined according to procedures in Zar (1984-Appendix A). The variances of the untransformed data were found to be heterogeneous when Cochran's test was performed. When the data were transformed using the square-root transformation, Cochran's test gave a non-significant result (p=.124).

TABLE 1. 4-WAY ANALYSIS OF VARIANCE OF FROND SPACING IN *P.CACTUS*.

Source of Variation	DF	Mean Square	F	Sign. of F
Within cells	696	0.671	-	-
Colony (nested)	4	9.684	14.433	0.000**
Morph^{+}	1	774.840	80.016	0.001**
Slope^{+}	1	1.424	0.147	0.721
Depth^{+}	1	1.707	0.176	0.696
Morph by slope^{+}	1	2.790	0.288	0.852
Morph by depth^{+}	1	0.385	0.040	0.852
Slope by depth^{+}	1	1.429	0.148	0.720
Morph by slope by depth^{+}	1	0.019	0.002	0.967

$^{+}$ Mean square tested against mean square of colony (nested).

** Highly significant.

Columnar and convoluted colonies of *P. cactus* differed in the spacing of their fronds, but their respective growth forms did not change significantly when transplanted reciprocally between 2 reef slopes, nor when transplanted between 2 depths. Significant differences in frond spacing were found between individual colonies within the different treatments (P<.001, Table 1). However, there were still highly significant differences in frond spacing between the two growth forms over and above this variation (p<.001). The treatments, reef slope and depth, did not significantly affect frond spacing (p>.69). Similarly, the second and third order interaction effects were not significant.

DISCUSSION

The ability of a sessile organism with a planktonic larval stage to vary its growth form, has obvious advantages for survival in a heterogeneous environment. This has been shown to be so for plant species (Bradshaw, 1965), but is largely assumed to be true for sessile animals (Jackson, 1979). Selection for morphological variability within a species may lead to the development of one of at least 2 distinctive strategies. Individual genotypes may become capable of varying their phenotypic expression in response to environmental differences (phenotypic plasticity), so that each genotype is able to exist in a greater range of habitats. Alternatively, individual genotypes may become morphologically specialized for different habitats, and retain little or no ability to change in response to environmental variation (phenotypic stability) (Bradshaw, 1965). In the latter case, the distribution of specialized morphs is largely determined at the recruitment stage in corals, and the species distributional range is dependent on the number of morphs maintained within the population.

The present study has shown that in one species, *T. mesenterina*, individual genotypes were clearly plastic in their phenotypic response to depth-related environmental changes. It is not possible to separate the effects of light and water motion on the basis of this transplant study. However, the occurrence of the plate form in shaded, shallow habitats, and the total absence of the convoluted form in deep water at Nelly Bay, suggest that light may be the controlling factor. The mechanism by which colonies of *T. mesenterina* vary their phenotypic response is related to the angle of corallite addition. The plane of corallite addition clearly changed and became more vertical in plate colonies transplanted to the shallow site, and conversely became more horizontal in convoluted colonies transplanted to the deep site. A similar decrease in maximum corallite angle with increasing depth was found to contribute significantly to the flattening of hemispherical colonies of *Montastrea annularis* in computer simulations (Graus and Macintyre, 1982).

In contrast, colonies of *P. cactus* were found to be phenotypically stable over a 2.5 year period when transplanted reciprocally between 2 depths and 2 reef slopes. In this species depth distributions of the 2 morphs overlapped. Although the morphs were restricted to different reef slopes, environmental differences between the 2 slopes were unclear. These results are consistent with an electrophoretic study of *P. cactus* (Willis and Ayre, 1985), which indicated that morphological variation in this species is primarily genetically based. Differences in the recorded distributions of the 2 morphs may be due to chance recruitment patterns, historical events, or differential responses at the microhabitat level. The highly asymmetric competitive abilities of the 2 morphs in intra-specific interactions (Willis and Ayre, 1985) would also contribute to their spatial separation.

Although many species of corals are known to have growth forms which vary in a consistent way with depth or hydrodynamic energy, attempts to demonstrate phenotypic plasticity for non-branching forms (cf. Oliver et al., 1983) have produced conflicting results. The flattening of colonies of Montastrea annularis has been an oft-quoted example of morphological change in response to decreasing light intensity (eg. Goreau, 1963). When Dustan (1979) tested M. annularis for phenotypic plasticity in a 2-year transplant experiment, he reported that colonies of this species had a small capacity to change their form. Moreover, he distinguished 2 ecotypic races of zooxanthellae in the depth range of the species. Conversely, in a 3-year study of the same species, Graus and Macintyre (1982) reported that 8 colonies transplanted to varying depths consistently resembled resident colonies from the same depth. The only other long-term test of phenotypic plasticity involved reciprocal transplantation of morphological variants of Acropora palifera and A. cuneata between 5 different reef habitats (Potts, 1978). Potts (1984) found minor evidence of phenotypic plasticity and suggested that complex regimes of disruptive selection operated in the early life history stages to select for specialized genotypes, thus maintaining high levels of genetic variation in these 2 species.

Given the extreme heterogeneity of the reef environment, morphological variablitiy should be an important life history character for coral species. Disruptive selection in space may lead to the evolution of either genetic polymorphism or phenotypic plasticity in populations which are not reproductively isolated (Bradshaw, 1965). The present study demonstrates that selection for both strategies has occurred in corals living at similar depths on inshore fringing reefs.

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PATTERNS IN THE MASS SPAWNING OF CORALS ON THE GREAT BARRIER REEF FROM 1981 TO 1984

CARACTERISTIQUES DE LA PONTE EN MASSE DE CERTAINS CORAUX DE LA GRANDE BARRIERE DE 1981 A 1984

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ABSTRACT

The mass spawning of corals, at an "inshore" reef in the central Great Barrier Reef Province, has consistently occurred during the week following the October full moon, in the past 4 years. One annual mass spawning period was observed when the full moon fell in the second half of October. In contrast, the mass spawning period was split, in 2 years when the full moon fell in the first half of October (two spawning periods separated by 1 lunar month). Three years of data, at an "offshore" reef at approximately the same latitude, confirm that the offshore mass spawning period occurs exactly one lunar month later than the "inshore" spawning period.

In 1984, spawning during a mass spawning period was documented for 25 scleractinian species which had not been studied during previous spawning periods. The cumulative number of mass spawning species on the Great Barrier Reef now totals 133 (total number of species = 356). In comparison, other studies have found 14 species on the Great Barrier Reef which planulate or spawn only at other times of the year. The mode of release of reproductive products has been documented for 12 of the 15 Great Barrier Reef families. The Faviidae, Oculinidae, Mussidae, and Pectiniidae so far contain only mass spawning species. The Acroporidae is by far the largest family, and of species studied to date, 88% spawn during a mass spawning period. It is therefore likely that the majority of corals on the Great Barrier Reef participate in the annual mass spawning phenomenon.

A preliminary analysis of reproductive rhythms of mass spawning corals is presented. Lunar and diel light cycles have been identified as zeitgebers for spawning synchrony. Variation in the number of synodic months between annual mass spawning periods indicates that an endogenous rhythm, if present, must interact with the lunar cycle. Such an interaction would maintain annual mass spawning periods within relatively constrained environmental limits, and result in reasonably precise seasonality of spawning.

RESUME

Chaque année depuis 1981, la ponte en masse des coraux d'un récif qui fait face à la côte dans la province centrale de la Grande Barrière s'est produit régulièrement pendant la semaine suivant la pleine lune. Quand la pleine lune avait lieu dans la seconde partie du mois d'octobre, nous n'avons observé qu'une seule période annuelle de ponte en masse ; par contre, les deux années où la pleine lune est tombée pendant la première moitié du mois d'octobre, il y a eu deux périodes de ponte en masse, à un intervalle d'un mois lunaire. Les observations faites pendant trois ans sur un récif de latitude similaire, mais plus au large, confirment que la période de ponte en masse dans les régions qui font face à la côte précède exactement d'un mois lunaire celle des régions situées face au large.

En 1984, des recherches détaillées ont été faites sur 25 espèces de scléractiniaires qui n'avaient pas encore été étudiées. Le nombre cumulatif des espèces qui pondent en masse sur la Grande Barrière est à présent de 133 (nombre total d'espèces = 356). En comparaison, on a trouvé 14 espèces qui libèrent des planula ou qui pondent seulement à d'autres époques de l'année. On a décrit la façon dont les produits génitaux sont expulsés pour 12 des 15 grandes familles de la Grande Barrière. Pour les Faviidae, les Oculinidae, les Mussidae et les Pectiniidae, on n'a trouvé jusqu'ici que des espèces qui pondent en masse. La plus grande famille, et de beaucoup, est celle des Acroporidae et 88% de toutes les espèces étudiées jusqu'ici pondent en masse pendant une période commune. Il est donc probable que la plupart des coraux de la Grande Barrière participent au phénomène annuel de ponte en masse.

Notre étude présente une analyse préliminaire des rythmes reproductifs des coraux qui pondent en masse. Il a été possible d'identifier des cycles lunaires et solaires comme déclencheurs synchronisants de la ponte. La variation du nombre de périodes synodiques prouve que tout rythme endogène, pour autant qu'il existe, doit aussi aller de pair avec les cycles lunaires. Une telle réciprocité maintiendrait les périodes annuelles de ponte dans un environnement relativement restreint et assurerait des saisons de ponte assez précises.

INTRODUCTION

The mass spawning phenomenon of corals has only recently been reported (Harrison et al., 1984; Babcock et al., in press). There are clear reasons why individuals within a species would synchronize the release of gametes (in particular, to promote cross fertilization), but the reasons for synchrony of spawning between species are less clear. Possibly predators are satiated during a mass spawning period, so that more eggs escape predation than if species partitioned their gamete release in time. Alternatively, populations of different species may reach a state of reproductive maturity concurrently, to take advantage of favourable environmental conditions for larval development. Synchrony of spawning between species may then occur if the release of gametes is timed by the same zeitgeber(s) in all species (eg. moonlight/diel light cycles) (Babcock et al., in press).

In this paper, mass spawning is defined as the synchronous release of gametes by many species of corals, in one evening between dusk and midnight. The annual mass spawning period refers to the 8 nights following a full moon in spring, during which spawning has been observed over the past 4 years (Harrison et al., 1984; Babcock et al., in press; this paper). The calendar month of mass spawning varies between 'inshore' and 'offshore' reefs, and appears to depend on whether the full moon falls early or late in the month. Years during which species are observed to spawn in two successive months, on one reef, will be referred to as years of 'split spawning'.

Olive and Garwood (1983) have suggested that all gametogenic cycles have an element of endogenously-maintained, long-term timing, and that it is unlikely that any reproductive rhythms are driven solely through exogenous events. Examination of yearly records of the timing of the mass spawning, might permit endogenous and exogenous factors to be identified, since any variation in the calendar date of mass spawning could be correlated with the timing of exogenous events.

In 1981, mass spawning was observed in two separate months on a fringing reef at Magnetic Island, an 'inshore' reef in the central Great Barrier Reef Province (Harrison et al., 1984). This split spawning coincided with an early full moon in the month of October. Conversely, a single spawning period in both 1982 and 1983, coincided with a late October full moon in these two years (Harrison et al., 1984; Babcock et al., in press). The objective of the present research was to document the spawning period(s) at Magnetic Island during 1984, when the full moon again fell early in the month (October 10th). The spawning periods at two 'offshore' reefs were also documented, in order to build up long term records of mass spawning dates at a number of reef locations. 1981 to 1984 records are compared to identify patterns in the number of spawning periods at 'inshore' versus 'offshore' reefs, and to test the observed correlation between lunar night and night of mass spawning.

METHODS

Mass spawning periods at Magnetic Island, Orpheus Island, and on Yonge Reef were predicted for the spring of 1984 from records of mass spawning at the former two sites and at Lizard Island in the previous 1 to 3 years (Harrison et al., 1984; Babcock et al., in press). Fringing reefs at Magnetic Island ($19^{\circ}10'$S, $146^{\circ}51'$E) and Orpheus Island ($118^{\circ}46'$S, $146^{\circ}33'$E) are located in the central Great Barrier Reef region, and are distinguished as 'inshore' and 'offshore' reefs, on the basis of differences in local bathymetry and concomitant sea temperature patterns (Babcock et al., in press). Yonge reef (14°,41'S,$145^{\circ}28'$E) is an outer-shelf reef due east of Lizard Island, in the northern Great Barrier Reef region.

In previous years, mass spawning periods occurred between mid October and early November on the 'inshore' reef, and between mid November and early December on 'offshore' reefs. Spawning has occurred on the first night following the full moon through to the eighth lunar night, during all mass spawning periods previously observed. It was predicted that the same would be true in 1984. Field and lab observations of gonad maturation, as described in Harrison et al. (1984) and Babcock et al. (in press), were made in the weeks prior to the predicted spawning periods. Thus, the progress of egg maturation was monitored, and the period during which nightly observations were required to record spawning, was delimited.

Spawning records during the mass spawning period were based on direct field and aquaria observations for all species recorded to spawn at Orpheus Island and on Yonge Reef, and for most species at Magnetic Island. Some records at the latter site are based on sequential sampling of tagged colonies, to detect the disappearance of gonads between sampling dates (Table 1).

RESULTS

Twenty-five previously unstudied scleractinian species spawned during the October or November spawning periods in 1984. This brings the cumulative number of species recorded to spawn during a mass spawning period on the Great Barrier Reef to 133 (Harrison et al., 1984; Babcock et al., in press; this paper). The night of spawning and the manner in which spawning records were collected at Magnetic Island and Orpheus Island, are presented in Table 1. Eight species were also observed spawning on Yonge Reef between lunar nights 4 and 7.

Most species spawned on the fourth to the sixth nights following the full moon, during both the October 'inshore' and the November 'offshore' spawning periods (Figure 1). On these nights of major spawning, between 10 and 31 species were directly observed to spawn in the field or in aquaria. Minor spawning (i.e. of between 1 and 6 species) was observed at both sites on 2 nights immediately preceding and following the major period of spawning.

In 1984, the full moon occurred earlier in the month of October than it had in the previous 3 years (Figure 2). By the end of the 'inshore' spawning period, it was apparent that not all colonies had spawned in 16 of the species studied. Large eggs were visible in tagged colonies of these species when sampled on the eighth day following the full moon. However, eggs were only faintly coloured, indicating that the final stages of maturation had not been completed. Gamete maturation in these colonies was equivalent to that of colonies at Orpheus Island, which subsequently spawned in November.

SPECIES	NUMBER & TYPE OF SPAWNING RECORD	LUNAR NIGHT OF SPAWNING M.I. OCT.	M.I. NOV.	O.I. NOV.
ACROPORIDAE (H)				
Acropora cytherea	3a,1d	4		4
A. digitifera	3g	4		
A. divaricata	1a	4		
A. elseyi	5c	16		5
A. formosa	8a,2b,5c 9d,5g	4	1-8*	3-5
A. florida	2f			4
A. gemmifera	1f			4
A. grandis	3c			4,5
A. humilis	3a,2b,3d	4	1-8*	
A. hyacinthus	27a,5b,4c, 7d,3g	3-5	1-8*	4
A. latistella	2b,c,3c	17 Sept. 16 Oct.		
A. longicyathus	2d		1-8*	
A. microphthalma	4a,2g	4,6		
A. millepora	31a,2b,4c,4d	4	1-8*	3,4
A. nasuta	21a,1c			4,5
A. nobilis	6a,5d,4d	4	1-8*	
A. pulchra	2a,1b,2d,1g	4,8	1-8*	
A. samoensis	1a			4
A. sarmentosa	5a,1c			4,5
A. selago	1a			4
A. solitariensis	1a	5		
A. tenuis	6a,1b,9d,3g	4,6,7	1-8*	4
A. valenciennesi	1c			4
A. valida	10a,1b,2d, 3g,1f	4,8		4
A. cf. vaughani	1c			4
Montipora digitata	13a,4g,16c	1-3		2,3
M. aequituberculata	5a	5,6		
M. hispida	1a,1c	4		5
M. informis	1a	3		
AGARICIDAE (G)				
Pachyseris rugosa	2c			3,4
P. speciosa	1a,3c,3e	6-8		3,4
CARYOPHYLLIDAE (G)				
Catalaphyllia jardineri	1g	5		
Euphyllia ancora	1a,1c	5,6		
E. divisa	3c			4,5
Physogyra lichtensteini	1c			4
DENDROPHYLLIIDAE (G)				
Turbinaria frondens	1a	6		
T. reniformis	1c			7
FAVIIDAE (H)				
Australogyra zelli	1c			5
Caulastrea furcata	2c			3
Cyphastrea chalcidicum	3a	6		
C. microphthalma	1a	5		
C. serailia	1g	5		
Echinopora lamellosa	1c,1e,1g	5		1e
Favia matthai	1a			6
F. pallida	8a,6c,6d	4,5	1-8*	5-6
F. rotumana	1c			6
Favites abdita	1d,2c		1-8*	5,6
Favites chinensis	3a			5,6
F. complanata	1d		1-8*	
F. flexuosa	1f			6
F. halicora	1a,1c			5,6
F. pentagona	7a	5,6		
Goniastrea aspera	10a,14c 5e,3g	4-7		4,5
G. favulus	1a,11c,13d	4	1-8*	3-5
G. palauensis	2a	6		
G. pectinata	1c			5
G. retiformis	9a			5,6
Leptoria phrygia	7a			5
Montastrea curta	1c			5
M. magnistellata	1a			5
M. valenciennesi	3a,1f	6		
Moseleya latistellata	4g	4-6,8		
Oulophyllia crispa	2c			5,6
Platygyra daedalea	1a,2g	6,7	1-8?	
P. sinensis	2a,6c,42d	4,5	1-8*	4,5
FUNGIIDAE (G)				
Fungia concinna	6c			7-10
F. fungites	1a,1g	5,6		
F. paumotensis	1a			6
Heliofungia actiniformis	2c	5		5
Polyphyllia talpina	1c,1d	6	1-8?	
MERULINIDAE (H).				
Scapophyllia cylindrica	1c			5
MUSSIDAE (H)				
Acanthastrea echinata	1c			6
Lobophyllia corymbosa	1a,1c			5,6
L. hemprichii	4a,21c	6,7		5-7
Scolymia vitiensis	1c			6
Symphyllia recta	2d		1-8*	
OCULINIDAE (H)				
Galaxea astreata	1c,1g	5		5
G. fascicularis	15a,5c	4-6		4-6
PECTINIDAE (H)				
Echinophyllia aspera	2c,2g	7,8		
Mycedium elephantotus	3c,1g	6,7		6
Oxypora lacera	3c,1g	6		6
Pectinia alcicornis	3a,4c			4-6
P. lactuca	4a	6		
P. paeonia	2a,1c,2g	6,7		5,6
PORITIDAE (G)				
Goniopora columna	1a,1c,1d	6		6
G. dijboutiensis	1e			7
G. lobata	1g	6		
G. norfolkensis	3a,2g	5,6		
G. tenuidens	1c			6
Goniopora sp.	2c			5
Porites cylindrica	13c			4

Table 1. Records of species spawning during the 1984 October and November mass spawning periods at Magnetic Island (M.I.) and Orpheus Island (O.I.). The number of colonies studied for each type of spawning record is given, followed by the manner in which the record was obtained (listed in order of precision). a, field observation; b, daily field samples; c, aquaria observations (flow-through system); d, sequential field samples more than 2 days apart; e, eggs observed in aquaria; f, setting of egg-sperm bundles observed but no further observations; g, aquaria observations (static aquaria); *, colonies sampled Oct. 18 and Dec. 6 - spawning assumed to fall in mass spawning period; ?, colonies sampled on Oct. 18 but not thereafter. The lunar nights of spawning are based on direct field and aquaria observations (i.e. record types a-c). G, gonochoric; H, hermaphroditic.

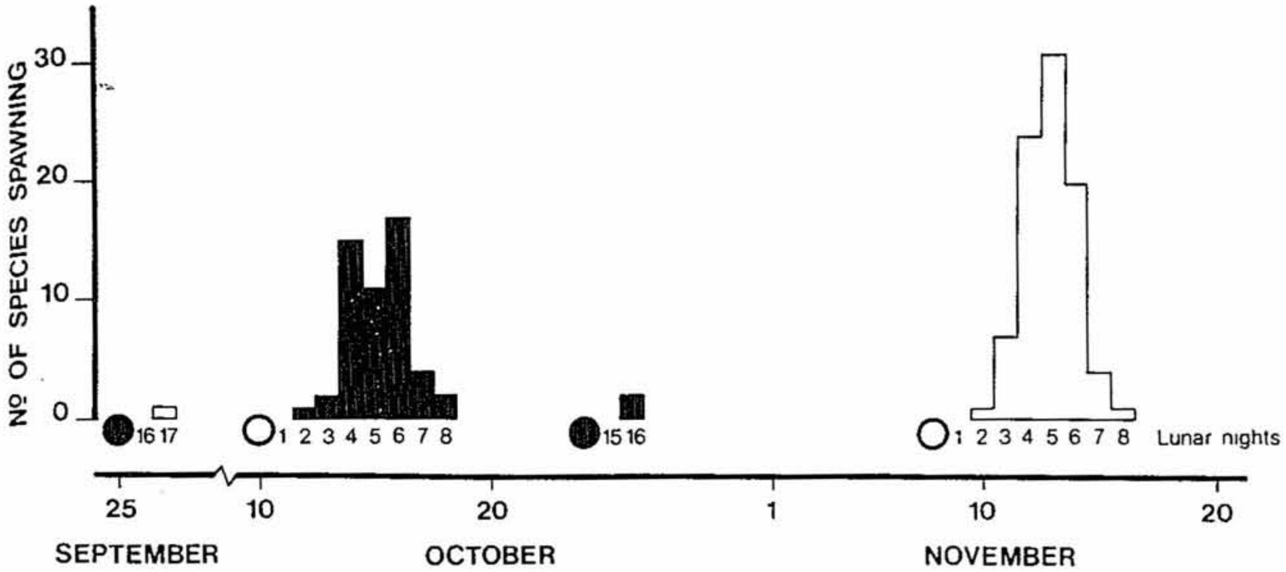

FIGURE 1. Summary of 1984 spawning records. All records are based on direct field or aquaria observations. Solid x-axis gives calendar date of spawning and intermittent x-axis gives the lunar nights (numbered from the full moon) on which colonies were observed. Field samples at other times indicated that colonies were not ready to spawn. ■ Magnetic Island records; □ Orpheus Island records; ○ Date of full moon; ● Date of new moon.

When 14 of these species were sampled on December 6th, gametes were absent. These colonies presumably spawned during the November spawning period.

The proportion of each Magnetic Island population delaying spawning, varied from species to species. Where split spawning was documented in the genus Acropora, most of the colonies studied spawned in October (Table 1). In contrast, where split spawning was found in faviid species, most colonies delayed spawning until November. Single colonies split their spawning period in 9 of the species studied. In these species individual colonies were observed to spawn in October, but still had large, faintly-coloured eggs at the end of the October spawning period. Four other species, appeared to spawn only in November.

DISCUSSION

At least 133 of 356 species recorded on the Great Barrier Reef (Veron, in press), are known to spawn during a mass spawning period in spring (Harrison et al., 1984;, Babcock et al., in press; this paper). Gametogenic cycles have been followed throughout the year in 33 of these species (Babcock et al., in press), and none show evidence of a semi-annual reproductive rhythm. It is likely that many of these species, have circa-annual spawning rhythms which culminate in a mass spawning event, with moonlight and diel light cycles acting as zeitgebers (Harrison et al., 1984;, Babcock et al., in press; this paper).

Mass spawning species have been documented in 11 of the 15 families of scleractinian corals recorded from the Great Barrier Reef (Figure 3) (Harrison et al., 1984; Babcock et al., in press; his paper). The Pocilloporidae is the only amily in which all Great Barrier Reef species ave been reported to planulate (Marshall & tephenson, 1933; Bothwell, 1981; Sammarco, 1982; arriott, 1983b; Loya, 1983). No records exist or the mode of reproduction on the Great Barrier Reef for the remaining three families.

The Acroporidae and the Faviidae are the two largest families. Of the species studied, all of the Faviidae and most of the Acroporidae spawn during a mass spawning period. Exceptions in the Acroporidae are the subgenus, Isopora (Bothwell, 1981; Kojis, 1984) and 3 species of Acropora which spawn at other times of the year (Harrison et al., 1984; Babcock et al., in press; Wallace, 1985; this paper). Furthermore, all species studied in the Agariciidae, Oculinidae, Mussidae and Pectiniidae are mass spawning species. The Dendrophylliidae is the only family in which no species appear to have spawning restricted to the mass spawning period (Fisk, 1981; Harrison et al. 1984; Willis, unpubl.). The majority of species remaining to be investigated for reproductive rhythms belong to predominantly mass spawning families. It is therefore likely that the majority of the species on the Great Barrier Reef participate in annual mass spawning phenomena.

Yearly variation in the calendar date of the full moon, means that spawning will occur 11 to 12 days earlier in the month in successive years (Figure 2). At some critical stage the spawning period must be delayed by one lunar month so that reproductive seasonality is maintained. Consequently, 13 synodic months will elapse between spawning periods involving 'adjustment' years (sensu Dan & Kubota, 1960). Patterns in the calendar dates of mass spawning periods, emerging after four years of study, permit a preliminary interpretation of annual spawning rhythms for corals in the central Great Barrier Reef Province.

Split spawning occurred on an inshore fringing reef at Magnetic Island in the first and fourth year of the study (Figure 2), (Harrison et al.; 1984 Babcock et al., in press; this paper). In these years the full moon occurred early in the month of October. Species differed in their response to the early full moon, some spawning predominantly in October and others in November

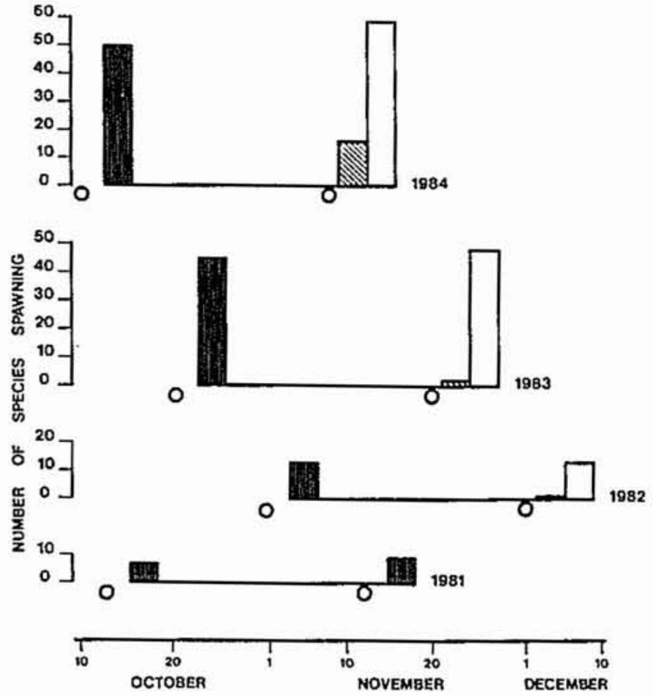

FIGURE 2. Relationship between spawning period and lunar phase, and incidence of split spawning at an 'inshore' and an 'offshore' reef in the Central Great Barrier Reef Region, between 1981 and 1984. X-axis gives date of full moon. Histograms of spawning records are positioned midway between lunar nights 1 and 8 and represent the total number of species recorded, or inferred to spawn, during that period.

■ Magnetic Island: 'inshore' reef records based on direct field or aquaria observations of spawning, or, based on the disappearance of gametes between sequential field samples collected between lunar nights 1 and 8, from tagged colonies.

□ Orpheus Island: 'offshore' reef records as above.

▧ Magnetic Island records inferred from: a) disappearance of gametes between field samples collected after the first spawning period and before the full moon following the second spawning period; or b) colouration of eggs in samples collected at the end of the first spawning period (6 species records). Species were assumed to spawn in the week following the next full moon.

○ Date of full moon.

(Table 1). Both colonies within a population, and individual polyps within a colony, were found to spawn asynchronously in some cases. In 'single spawning years' (1982, 1983), the full moon occurred later in the month of October. Even in these years 1 or 2 species provided a background level of split spawning (Figure 2). However, in general, years in which most species realigned their annual reproductive rhythms at Magnetic Is. were associated with early October full moons.

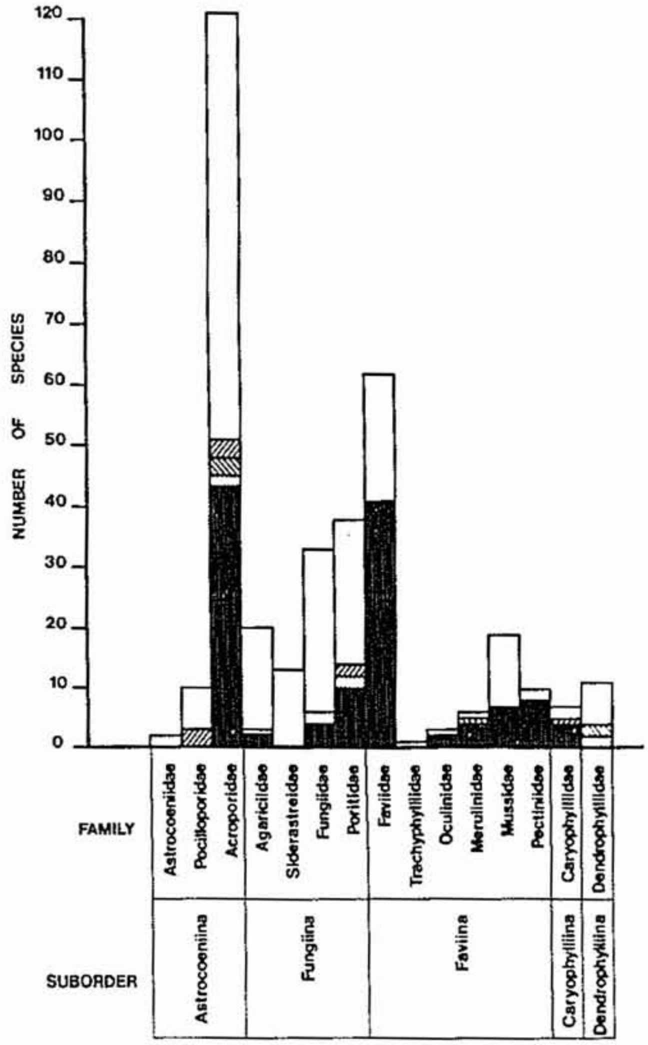

FIGURE 3. The distribution of spawning and planulating species within families of the Scleractinia on the Great Barrier Reef (nomenclature according to Veron, in press).

Mass spawning species: Species recorded to spawn only during a mass spawning period by this research group (Harrison *et al.*, 1984; Babcock *et al.*, in press; Wallace, 1985; this paper), and Marshall and Stephenson (1933). Species are divided into the following 2 categories:

■ 4 or more colonies studied (all spawned);

▩ Less than 4 colonies studied (all spawned).

▦ Mass spawning species: Species recorded to spawn during a mass spawning period and at other times of the year (Harrison *et al.* 1984; Babcock *et al.*, in press; Wallace, 1985; this paper; Kojis & Quinn, 1981; Harriott, 1983a; J.O., unpubl.; B.W., unpubl.).

▧ Spawning species: Species recorded to spawn only outside one of the spring mass spawning periods (Harrison *et al.*, 1984; Babcock *et al.*, in presss; Wallace, 1985; this paper; Fisk, 1981).

▨ Planulating species; (Haddon, 1892; Kojis & Quinn, 1981; Bothwell, 1981; Sammarco, 1982; Harriott, 1983b; Loya, 1983; Kojis, 1984).

□ No records exist on the Great Barrier Reef.

Patterns in the intervals between annual spawning periods are complicated by split spawning years, so that intervals vary between 12 and 13 synodic months. In general, intervals between 4 years of documented spawning periods follow a 12-12-12 pattern for acroporiid species. Split spawning species of *Acropora*, either at the within- or between-colony level, differ somewhat from this pattern. In contrast, a 13-12-12 cycle in the synodic month interval between spawning periods has been found for *G. aspera*, and a 13-12-13 cycle has been found for *G. favulus*. Only 3 spawning periods have been observed on the 'offshore' fringing reefs at Orpheus Island, and these have been separated by 2 intervals of 12 synodic months.

Spawning rhythms in single populations of marine invertebrates may be either lunar or semi-lunar (Korringa, 1957). Good long term spawning records (Dan & Kubota, 1960; Kubota, 1980; Caspers, 1984) exist for Comanthus japonica and for the palolo worm, Eunice viridis. Semi-lunar rhythms can be tuned more finely than lunar rhythms, as has been demonstrated in C. japonica. Spawning intervals for this species follow a 12.5-12.5-12.0 synodic month sequence (Dan & Kubota, 1960). This species has a single annual spawning period but spawning can occur on either the first or the third quarter moon. Therefore, the calendar dates of spawning from year to year are as consistent as possible, while still maintaining a lunar zeitgeber. In contrast, spawning of the Pacific palolo worm corresponds closely with the third quarter moon in either October or November. As described for corals, the annual spawning may be split between both months (Caspers, 1984). Collin (1897, cited in Dan & Kubota, 1960) reported that 12 synodic months separate spawning periods with an interval of 13 synodic months interposed every 3 years.

The rhythm described for Eunice viridis appears to be closest to the pattern emerging from preliminary analysis of coral mass spawning data. Variation in the number of synodic months separating mass spawning periods suggests that if endogenous timing mechanisms exist in corals, they must interact with exogenous factors to define periods which are appropriate for spawning (cf. Olive and Garwood, 1983). Differences in timing between species suggest either that adjustments operate at a coarse level, or different species respond to the same environmental cues in different manners. It is predicted that 13 synodic months will elapse between both the October 1984 (i.e. the major 'inshore' spawning period of acroporiid species) and the November 1984 ('offshore') mass spawning, and the equivalent 1985 mass spawning periods. Such a 'realignment' would keep the mass spawning periods within acceptable environmental limits.

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