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Coral Reefs

Seasonal and Depth Variation in Fecundity of *Acropora palifera* at Two Reefs in Papua New Guinea

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Abstract. Fecundity and abundance of *Acropora palifera* and the abundance of other scleractinians were compared at two reefs in the Huon Gulf, Papua New Guinea. While temperature and salinity were similar at both reefs, turbidity and sedimentation were higher on one of the reefs. A negative correlation was found between fecundity of *A. palifera* and three factors: depth, turbidity and sedimentation rate. There was also a negative correlation between coral cover and water transparency and sedimentation. The results suggest that high rates of sedimentation and low transparency depress fecundity of *A. palifera,* and limit the depth distribution and reduce the abundance of this species and other scleractinians. Lower fecundity in February and March was correlated with higher water temperatures. It is suggested that coral reproduction can be used as a biological indicator of stress on coral reefs.

Introduction

Studies of reproduction in hermatypic corals have largely provided information on the sexual biology (see Fadlallah 1983 for review) and life history of coral (see Connell 1973 for review; Harriott 1983a, 1983b; Moorsel 1983, Babcock 1984; Kojis 1984). A few researchers have studied deleterious environmental factors affecting coral reproduction (Loya 1975, 1976b; Loya and Rinkevich 1979), but none have examined the natural variability of coral fecundity.

The aim of this study was to utilize knowledge of reproduction in *Acropora palifera* on two reefs in the Huon Gulf, Papua New Guinea, to determine the fecundity of colonies on each reef throughout a year and at various depths on the same reef. One reef was in naturally turbid water and the other in clear water. Hydrological parameters were monitored and the possible factors affecting observed differences in fecundity are discussed. It is hypothesized that variability in the fecundity of *A. palifera* can be used to monitor the effects of environmental changes.

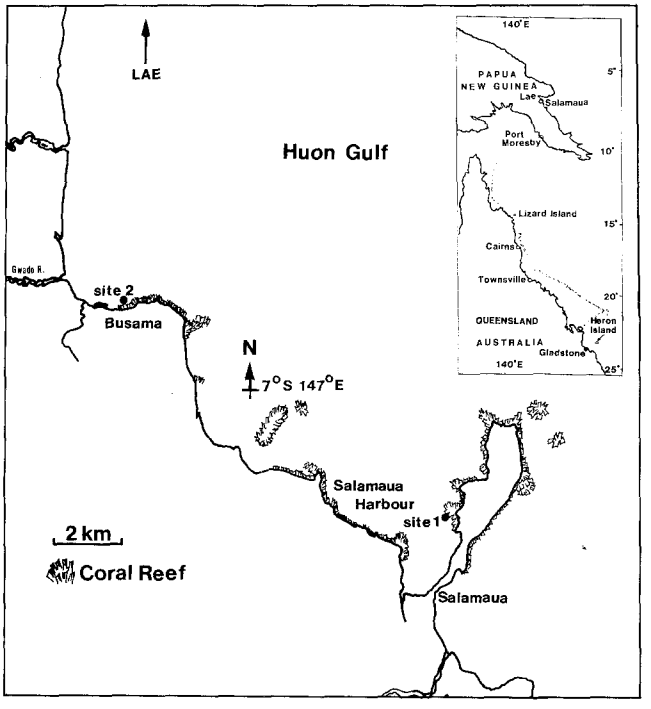

Fig. 1. Map of sites at Salamaua and Busama near Lae, Papua New Guinea

Materials and Methods

Sites

Acropora palifera was studied on reefs at Salamaua (Site 1), a clear water site and Busama (Site 2), a turbid water site (Fig. 1), in the Huon Gulf (7° S 147° E), Papua New Guinea. The sites are similar in that both are on fringing reefs protected from the southeast swells which occur from about June to September. These reefs are in the doldrums and outside the cyclone belt. The maximum spring tidal range at Lae is 1.1 m (Anon 1980) with only one notable tidal cycle each day. Salamaua (37 km south of Lae) and Busama (28 km south) have similar tidal regimes and water currents are generally slight.

The fringing reef at the Salamaua site drops off rapidly to about 40 m after which the slope diminishes and calcareous sand largely re-

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places the coral substrate. At Busama the reef drops off rapidly for only about 10–15 m before the slope diminishes and at depths > 15 m the substrate is primarily a fine silt with widely scattered coral boulders. The sediment at the Busama site is primarily derived from erosion in the watershed of several small streams which debouch into Busama Bay. The closest stream is about 1 km from Site 2. There are no major streams that affect the Salamaua site.

The region is mountainous and has a high rainfall, a combination that is conducive to landslides. This natural erosion is augmented by the local villagers in the area who cut and burn the rainforest on the mountain sides to create gardens. The population density is highest right along the coast where the original rainforest vegetation has been cut down and replaced largely by gardens or secondary growth. There are few villages inland within the watershed of the Busama streams.

Sedimentation

Sedimentation rates were measured by placing a pair of jars each with an opening 7.3 cm in diameter and depth of 17.5 cm at 3, 10, 20, 30, 40 m at Site 1 (Salamaua) and 3, 12 and 17 m at Site 2 (Busama). The jars were held in place by wedging them firmly in concrete blocks placed at each depth. They were collected and replaced approximately once every 3 months for over 2 years and the dry weight of accumulated sediment calculated.

On some occasions jars were turned on their side, probably the result of action by waves at the shallowest depth and fish and divers at all depths. Because of the number of missing replicate sediment samples, the data for each sampling time were averaged for each depth and time resulting in only one observation per cell. There was one empty cell in the Salamaua sediment data (5×9 matrix) and 3 empty cells in the Busama data (3×8 matrix). Values for these cells were estimated using the missing data formula and procedure suggested by Cochran and Cox (1957). For each site, two-way ANOVAs without interaction were used to compare sedimentation rates at depths and times. Tukey's test for non-additivity confirmed the assumption that there was no interaction between depth and time at either site ($P > 0.05$ for both sites).

Hydrological Measurements

Salinity and temperature at both sites were measured using a "Kahlisco" wheatstone bridge with thermistor. Water transparency was measured using a 20 cm diameter Secchi disc. At Salamaua a maximum/minimum thermometer was placed at 20 m. Measurements were taken at approximately monthly intervals. Time series analysis, as described in Quinn (1980), was performed on the data to delineate temporal patterns. By least squares regression, a combination of sinusoidal terms was fitted to the data. Only regressions which explained a significant amount of the variation ($P < 0.05$) were accepted and plotted.

Paired *t*-tests were used to compare hydrological parameters between the two sites. For the two depths, surface and 9 m, data were paired by months for each year. If more than one measurement was taken at one of the sites in a month, the data for that month were averaged.

Coral Transect

A 10 m transect line divided into 1 cm segments was laid at about 1.5 m depth intervals parallel with the reef crest. The reefs at Salamaua and Busama have a slope between 60–90° at depths of < 40 m and < 15 m respectively. Transect lines were stretched taut at each depth interval and placed on the reef. The total cover of live hermatypic coral and *Acropora palifera* underlying the line was recorded at both sites to the nearest centimetre. Within each 5 m interval, data were pooled from 3 or 4 10 m transects and expressed as percent coral cover. Data were recorded from 32 transects laid at Salamaua and 11 at Busama.

Colony Fecundity

Acropora palifera was chosen because it planulates year-round near Lae and because fecundity of samples can be determined without using histological procedures. Colonies of *A. palifera* were sampled by breaking a branch from each colony with a chisel and collecting a piece 4–6 cm in length. Samples were collected in May, July, August, and November 1982 and February and March 1983 at Salamaua and in all of the above months except November 1982 at Busama. Colonies chosen for sampling were minimally 40 cm in diameter and were assumed to be sexually mature. This seemed reasonable since all colonies of *A. palifera* on Heron Island, Great Barrier Reef, > 10–15 cm diameter were mature. At Salamaua, 26–34 colonies were sampled on each sampling date at depths < 21 m and depth was recorded for each sample. At Busama, 12–15 samples were collected on each sampling date at depths > 1 and < 5 m; few colonies exist below 5 m at this site. Only corals on the slope were sampled at Busama.

Samples were fixed in 10% formalin, decalcified in 2.5 M HCl and stored in 10% formalin. In preparation for analysis, each sample was cut lengthwise and spread out with forceps to expose the underside of the polyps and larvae. One of two techniques, both using a dissecting microscope, were used to determine the number of larvae cm^{-2}: (1) a form with a one centimetre square hole was placed on the tissue and the number of larvae in 4–10 squares was counted or (2) the number of larvae and polyps in a subsample of 50–80 polyps were counted and the results transformed to larvae cm^{-2} by determining the mean number of polyps $cm^{-2} \times$ tissue for representative colonies at each site and within each depth range. The former technique was preferred as it was quick.

Colonies of *Acropora palifera* release sperm every two months with some portion of the population releasing sperm one month and the remainder the next month. Maximum larval development time is about 2½ months. Thus, depending upon how many weeks earlier eggs had been fertilised in the sampled colony, one or two cycles of larvae, distinguishable by differences in size, could be expected. In samples with two cycles of larvae, only larvae from the most abundant cycle were counted. For each sampling date, results were pooled from all samples at each 5 m depth interval and mean fecundity determined for each site.

In this study, each colony is treated as an individual. This follows from evidence that there is integration among polyps within a colony. Connell (1973) pointed out that studies had shown that there was some integration between parts of a single colony with respect to coordination of colony growth, transfer of energy-rich material between adjacent parts of a colony and possibly the size at which a colony became sexually mature. Polyps within colonies of *Goniastrea favulus* delayed gamete production until the colonies had achieved a minimum number of polyps and the number of gametes produced by individual polyps increased as colony size increased (Kojis 1984). Thus it was felt that number of larvae cm^{-2} provided a better estimate of colony fecundity than number of larvae per polyp. However, the number of polyps cm^{-2} was determined for colonies at different depths at Salamaua and at < 5 m at Busama to determine if this would change the results significantly.

Differences in colony fecundity were compared over depth and time at the Salamaua site using a two-way ANOVA (SPSS MANOVA) (Hull and Nie 1981). Variations in fecundity between sites and over time were analysed in the same manner. Since the experimental design was unbalanced, different ANOVA solutions could be obtained depending upon which variable was added to the model first. This was taken into consideration by running the ANOVA twice for each experiment and changing the order variables were added. The results produced by doing this were nearly identical for both experiments, and thus only one ANOVA table is presented in the results. Change in fecundity over time at Busama was tested using a oneway ANOVA (SPSS ONEWAY) (Nie et al. 1975). Data used in each ANOVA were transformed ($\log N + 1$) and tested for homogeneity of variance using Bartlett-Box F and Cochran's C tests and normlacy using the Kolmogorov-Smirnov One-Sample Test (SPSS). For all sets of transformed data the null hypotheses of homogeneity of variance and normlacy were accepted ($P > 0.05$).

Results

Sedimentation

The water at Busama was highly sediment laden compared to Salamaua. Not only was the mean total of accu-

Table 1. Mean rate of sedimentation from June 1980 to February 1983 for various depths at Salamaua (Site 1) and Busama (Site 2). $\bar{x}$, mean sedimentation rate; SE, standard error; *N*, number of times sampled

Salamaua				Busama			
Depth (m)	$\bar{x}$ (mg $cm^{-2}d^{-1}$)	SE	*N*	Depth (m)	$\bar{x}$ (mg $cm^{-2}d^{-1}$)	SE	*N*
3	1.02	0.22	9	3	14.00	3.86	7
10	0.74	0.17	8	12	15.29	2.62	8
20	0.92	0.27	9	17	10.99	2.70	7
30	1.03	0.18	9				
40	1.27	0.28	9				
Total	1.00	0.10	44	Total	13.51	1.73	22

Tabelle 2. Two-way ANOVA without interaction[a] (SPSS MANOVA) for sediment collected at different depths and times of year at Salamaua (Site 1) and Busama (Site 2)

	SS	DF[b]	MS	F	*P*
Salamaua					
Residual	0.010	28	0.000		
Constant	0.078	1	0.078	238.86	<0.001
Depth	0.078	4	0.001	1.86	>0.05
Time of year	0.021	8	0.003	8.35	<0.001
Busama					
Residual	0.308	12	0.024		
Constant	9.294	1	9.294	392.15	<0.001
Depth	0.259	2	0.130	5.47	<0.025
Time of year	1.985	7	0.284	11.96	<0.001

[a] Tukey's test verified assumption of no significant interaction
[b] Degrees of freedom were adjusted for missing values

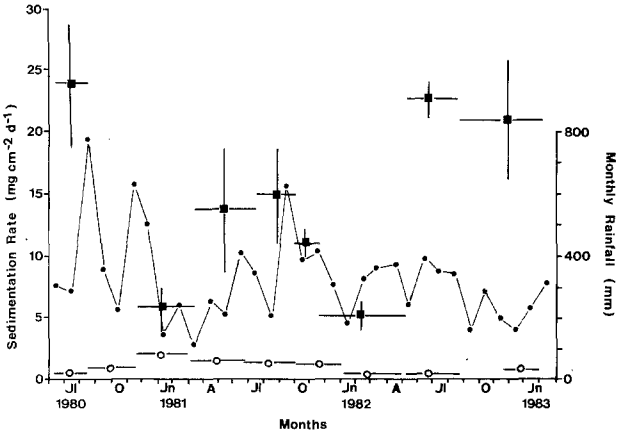

Fig. 2. The sedimentation rate between June 1980 and February 1983 at Salamaua (Site 1) (○) and Busama (Site 2) (■) averaged over depth, and the corresponding monthly rainfall pattern (●) recorded in Lae (Civil Engineering Department, Papua New Guinea University of Technology). *Horizontal bars* indicate the period of time over which sediment was trapped and *vertical bars* indicate the standard error. The standard error for the Salamaua sampling dates ranged from 0.037–0.253 and was too small to be distinguishable on the graph. The number of samples for each date was 4–5 for Salamaua and 2–3 for Busama

mulated sediment greater at Busama (> 10 times) but the rate of accumulation was higher for all times and depths sampled (Table 1, Fig. 2).

A significant difference in the rate of sedimentation existed between times at both sites (Table 2). While no annual pattern was apparent in the rate of sedimentation at Salamaua, the rate appeared to vary between years. The sedimentation rate was relatively high from November 1980 to December 1981 and low from at least January to August 1982. At Busama, the sedimentation rate was generally highest during the June to October wet season (Fig. 2). In spite of the generally low rainfall thoughout 1982 in Lae, the sedimentation rate at Busama was high during the usual rainy period. This lack of correlation with rainfall in 1982 may stem from differences in the amount of rain falling in the Lae area and in the watershed of the streams debouching near Busama.

There was a significant difference in the rate of sedimentation with depth at Busama but not at Salamaua (Table 2). The difference at Busama was not highly significant and appears to be due to the slightly lower sedimentation rate at 17 m compared to 3 m and 10 m (Table 1).

Hydrological Measurements

There was no significant difference in salinity at Salamaua and Busama either at the surface (*t*-test = 0.19, NS) or 9 m (*t*-test = 1.33 NS). The mean surface salinity at Salamaua was 31.3‰ ($N = 11$), while mean salinity at 9 m was 33.2‰ ($N = 11$). Surface salinity was highest during April/May, and at 9 m highest in August (Fig. 3A). At Busama the mean salinities at the surface and 9 m were 31.2‰($N = 11$) and 32.5‰ ($N = 11$) respectively. There was no annual pattern of surface salinity, but at 9 m an annual cycle existed with the highest values in September/October (Fig. 3B).

Similarly there was no significant difference in water temperature between sites (*t*-test surface temperature = 0.88, NS; *t*-test 9 m = 1.15, NS). The water temperature range at Salamaua was 27.5 °C to 31.8 °C (surface) and 27.5 °C to 31.0 °C (9 m) with a mean of 29.7 °C for sur-

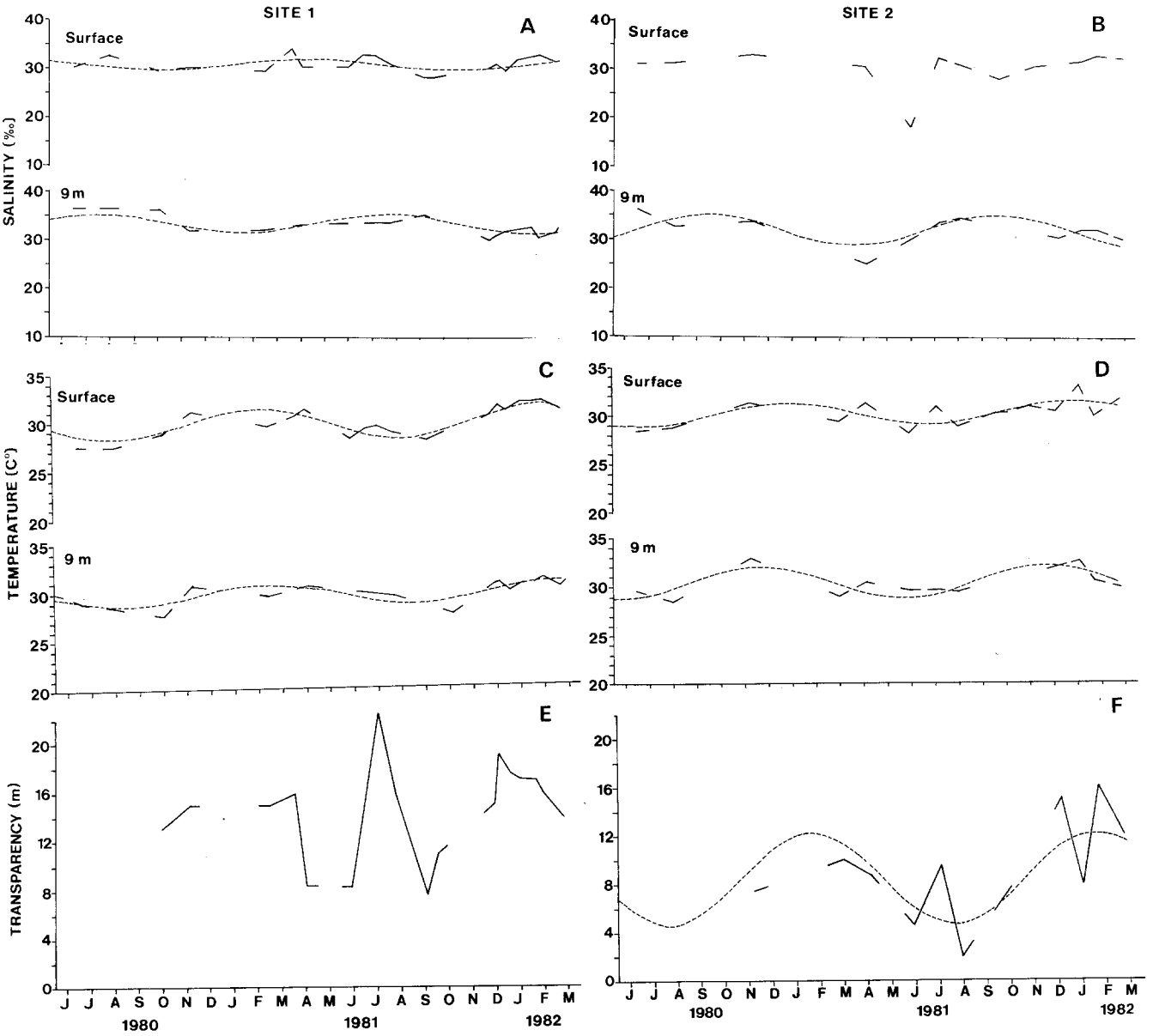

Fig. 3 A–F. Time series analysis of surface and 9 m salinity (**A, B**), temperature (**C, D**) and transparency (**E, F**) at Salamaua (Site 1) and Busama (Site 2). ——, observed values; – – –, predicted values

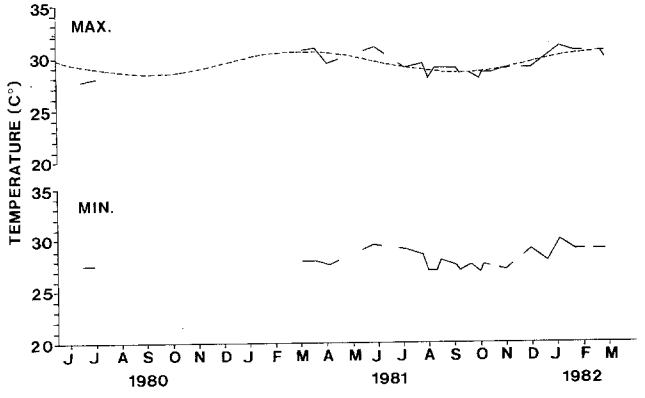

Fig. 4. Time series analysis of maximum and minimum water temperature at a depth of 20 m at Salamaua (Site 1). ——, observed values; – – –, predicted values

face temperature ($N=14$) and 30.0 °C for 9 m ($N=12$). The water at the surface and 9 m was warmest during February (Fig. 3C). At 20 m the maximum water temperature ranged from 27.5 °C to 31.0 °C – March being the warmest month. Minimum water temperatures had no apparent annual cycle but ranged from 26.5 °C to 30.0 °C (Fig. 4). Surface water temperatures at Busama ranged from 28.4 °C to 33.0 °C ($\bar{x}=29.9$ °C, $N=14$) (Fig. 3D). Warmest temperatures were most likely to occur in December/January. Water temperatures at 9 m also ranged from 28.3 °C to 32.9 °C ($\bar{x}=30.4$ °C, $N=12$) with December being the warmest month.

However, there was a significant difference in transparency (t-test $=3.46$, $P>0.01$). At Salamaua transparency ranged from 8 m to 22 m ($\bar{x}=14.1$ m, SD $=3.96$, $N=12$) (Fig. 3E). No significant annual pattern was de-

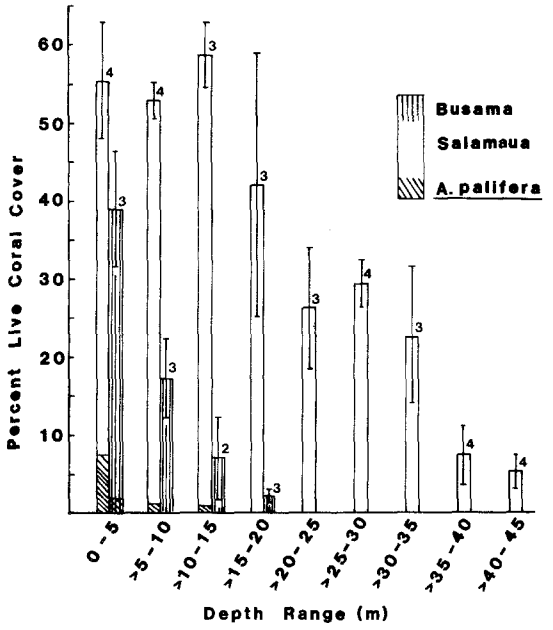

Fig. 5. Percent live coral cover for all species and *Acropora palifera* at both sites. The number of transects made at a particular depth range is indicated above the corresponding bar on the graph. *Vertical bars* indicate standard error

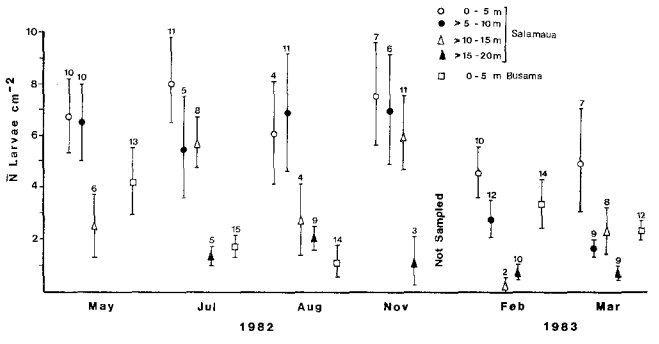

Fig. 6. Mean number ($\bar{N}$) of larvae cm^{-2} of tissue in colonies of *Acropora palifera* in 1982 and 1983 at Salamaua at different depth ranges and at Busama between 0–5 m. The *vertical bars* indicate the standard error and the *number above each bar* is the number of colonies sampled

tected in the time series analysis. Transparency at Busama was less than at Salamaua with a range from 2 m to 18 m ($\bar{x}=9.2$ m, SD = 3.83, $N=12$) (Fig. 3F). The greatest transparency is most likely to occur in January/February and lowest between July and September, the time of year designated the rainy season in Lae by the locals.

Coral Transect

In the relatively clear water of Salamaua, coral cover was high (43–58%) at depths <20 m, moderate (23–28%) between 20–35 m and diminished to <10% at depths >35 m (Fig. 5). At 45 m there was about 5% coral cover. In the turbid water at Busama, coral cover was lower than at Salamaua at all depths. Maximum cover was 38% at depths <5 m and declined rapidly to 18% at 5–10 m and <10% at 15–20 m. There were no corals at depths >20 m. *Acropora palifera* was most abundant in shallow water at both sites. It was not recorded below 5 m in transects at Busama and 15 m at Salamaua (Fig. 5).

Table 3. The mean fecundity of colonies of *Acropora palifera* for each depth range from May, July, August and November 1981 and February and March 1982. Mean fecundity ($\bar{x}$) is calculated from the unweighted average number of larvae cm^{-2} for each time. *N*, number of times colonies were sampled

Depth (m)	$\bar{x}$	*N*
0– 5	6.4	6
> 5–10	5.1	6
>10–15	3.3	6
>15–20	1.2	5[a]

[a] Colonies in this depth range were not sampled in May 1981

Table 4. Two-way ANOVA of fecundity of colonies of *Acropora palifera* at Salamaua (Site 1) at different depths and times

	SS	DF	MS	F	*P*
Within cells	16.256	154	0.106		
Constant	59.153	1	59.153	560.385	<0.001
Time of year	3.664	5	0.733	6.942	<0.001
Depth	4.059	3	1.353	12.817	<0.001
Interaction	1.254	14	0.090	0.848	0.616

Colony Fecundity

The fecundity of *Acopora palifera* at Salamaua was inversely related to depth (Table 3). Fecundity at 0–5 m was 5 times greater than at the limit of the depth distribution of this species (about 15–20 m).

Fecundity was also temporally variable. Colonies sampled in May, July, August and November 1982 were more fecund than those in February and March 1983 (Fig. 6, Table 4). The large variation in colony fecundity within depths, particularly at shallower depths (Fig. 6), is a function of the variability that exists within colonies in this population of *A. palifera*. Polyps within a branch had 0–7 larvae with most having 0–4 larvae. The number of larvae cm^{-2} varied from 0–10 both within a sample and among samples from different branches of the same colony.

There was also a significant difference in colony fecundity between sites at the same depth range (0–5 m) (Table 5). The mean fecundity of colonies at each site for the same months was calculated from the unweighted average fecundity for each sampling time and found to be more than twice as high at Salamaua ($\bar{x}=6.1$, $N=5$) as Busama ($\bar{x}=2.6$, $N=5$). The fecundity of colonies at Busama at depths <5 m was comparable to the fecundity of colonies at Salamaua between the depths of 10–15 m (Table 3). There was no significant difference in fecundity with time of year at Busama (Table 6) nor was there a significant difference when Busama and Salamaua data were analysed together (Table 5).

Table 5. Two-way ANOVA of fecundity of *Acropora palifera* colonies from 0–5 m depth between site and time of year

	SS	DF	MS	F	*P*
Residual	11.633	100	0.116		
Constant	31.720	1	31.720	272.67	<0.001
Site	3.204	1	3.204	27.55	<0.001
Time of year	0.656	4	0.164	1.41	>0.05
Interaction	0.632	4	0.158	1.37	>0.25

Table 6. One-way ANOVA of fecundity of *Acropora palifera* at Busama (Site 2) at different times of the year

	SS	DF	MS	F	*P*
Time of year	0.723	4	0.181	1.89	>0.12
Error	6.034	63	0.096		
Totoal	6.757	67			

Table 7. One-way ANOVA of number of polyps cm^{-2} for *Acropora palifera* at Salamaua (Site 1) at different depths

	SS	DF	MS	F	*P*
Depth	8.56	3	2.85	0.32	⩾0.05
Error	307.93	34	9.06		
Total	316.49	37			

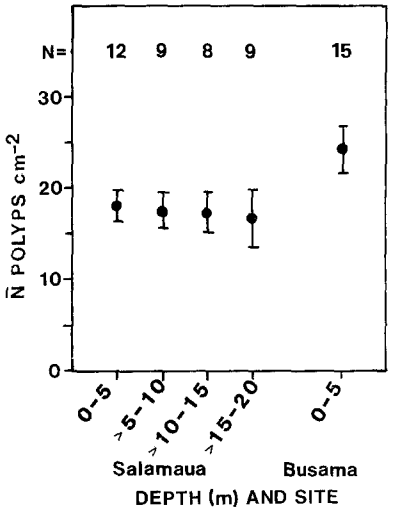

Fig. 7. Mean number of polyps ($\bar{N}$) cm^{-2} colonies of *Acropora palifera* at four different depth ranges at Salamaua and at one depth range at Busama. The *bars* indicate the standard deviation. *N* is the total number of cm^2 sampled. Three colonies were sampled at each depth range at each site

Number of Polyps cm^{-2}

The number of polyps cm^{-2} was compared in colonies of *A. palifera* among the four depth ranges at Salamaua and between sites. There was no significant differences in polyp number in colonies at different depths at Salamaua (Fig. 7, Table 7), but there was between the two sites. The number of polyps cm^{-2} for colonies at Salamaua ($\bar{x}$ = 17.3 (for colonies at all depths), N=38, SD=2.42) was significantly less than at Busama ($\bar{x}$=24.2, N=15, SD=4.61) (t-test=5.39, DF=18, P<0.001). This means that if fecundity differences between sites were based on the number of larvae per polyp, differences in fecundity between colonies at Salamaua and Busama would increase. Since there is no significant differnce in polyp number cm^{-2} between colonies at different depths at Salamaua, these results would not change.

Discussion

The differences in fecundity of *Acropora palifera* and total percent coral cover between the two sites were correlated with water clarity and sedimentation. The higher levels of sedimentation and lower transparency at Busama compared to Salamaua appear to have depressed the fecundity of *A. palifera* by more than half and severely limited the depth distribution and reduced the abundance of this species and scleractinian coral in general. High levels of sedimentation and turbidity have been shown to decrease coral growth (Dodge and Vaisnys 1977; Bak 1978; Lasker 1980), coral diversity and living cover (Loya 1976a), and to increase coral mortality (Mayer 1918; Marshall and Orr 1931). These two factors may act synergistically to decrease fecundity by lowering light levels and increasing the amount of energy colonies spend cleaning themselves at the expense of maintenance, growth and reproduction.

Fecundity at Salamaua was shown to vary naturally with depth and time of year. The fecundity of *A. palifera* at depths >15 m was only $^1/_5$ that of colonies at depths <5 m. It is hypothesized that this is the result of diminishing illumination with depth. Water movement associated with tides and waves may also contribute to the higher fecundity of colonies in shallow water at Salamaua (Site 1) and the survival of colonies at shallow depths at Busama (Site 2) by preventing the build-up of sediments on the coral surfaces (Johannes 1975). The low fecundity of colonies near the limits of the depth distribution of this species indicates that these colonies may contribute few recruits to the population. It also suggests that this species is physiologically restricted to shallow depths and thus will predominate only in shallow water habitats.

Fecundity of *A. palifera* was least in February and March when temperatures were highest. Larvae present in colonies during these months had begun developing 1–2 months earlier when water temperatures exceeded 31 °C. High water temperatures are known to be detrimental to corals. Thermal enrichment of 4–6 °C above ambient impeded coral growth and increased mortality of corals at Guam (Neudecker 1982). At Enewetak, where the annual temperature regime is similar to the Huon Gulf, prolonged exposure of reef flat corals (1–2 h) to water temperatures of 34 °C killed corals, while corals subjected to brief exposures at 34 °C lost zooxanthellar pigment indicating severe thermal stress (Coles et al. 1976). The maximum temperatures to which corals at Salamaua were exposed was between 31–32 °C which is

near the optimal temperature for primary production in *Pocillopora damicornis* and *Montipora verrucosa* on Enewetak (Coles and Jokiel 1977). However, the experiments were of short duration (<1 h) and cannot be extrapolated to long term effects.

Yap and Gomez (1982) found that the growth rate of *Acropora pulchra* decreased with increasing temperatures at Bolinao, northern Philippines, and that the mortality rate of coral transplants was positively correlated with temperature. The mean water temperature at their study site was similar to that at Salamaua and Busama reefs, ranging from 26.0–30.0 °C. They attributed the increased mortality of transplants during the warmer months to high water temperatures. Jokiel and Guinther (1978) found that the number of spat which settled on aquarium walls diminished by up to an order of magnitude with only a 1 °C temperature change from the optimum.

High light intensity also accurs at this time of the year and is thought to stress corals (Coles and Jokiel 1978; Delvoye 1982). However, it is considered a negligible factor here since fecundity of colonies was depressed at all depths and low light levels in deeper water were believed to be the primary factor depressing fecundity.

Reproduction usually has a narrower tolerance to stress than any other life function, while simultaneously having a pivotal role in the success or failure of the population (Kinne 1963; Gerking 1980). Over the past 15 years the sensitivity of reproduction in fishes has been recognized as an important parameter in assessing stress. Inhibition of reproduction occurs before deleterious effects can be detected by histopathological examination or measurements of growth (Gerking 1980). We suggest that the same is true of reproduction in tropical hermatypic corals, and that coral fecundity can be a sensitive indicator of sublethal reef stress.

To successfully use changes in coral fecundity to monitor reef stress, it is necessary to initially determine the fecundity of colonies within the depth range to be sampled and for time of year. The ideal species to use as a biological indicator is one that breeds year-round or at least most of the year so that assessment of pollution effects can be made whenever necessary. Since most corals reproduce seasonally and have very brief spawning periods (Kojis and Quinn 1980, 1981a, 1981b, 1982a, 1982b; Harriott 1983a; Harrison et al. 1984), the species must be chosen carefully. It also should be abundant and fecundity should be able to be determined easily. Species conforming to the above criteria will most likely be species that planulate. Analysis of fecundity in a number of planulating species, e.g. members of Pocilloporidae, may require elaborate histological techniques because of the small size of polyps and/or imperforate skeletal structure and, therefore, would not be suitable for rapid analysis. The perforate skeletal structure of the *Acropora* (*Isopora*) and the *Acropora* (*Acropora*), makes tissue from these groups better suited to analysis.

In conclusion, the marked differences in the fecundity of colonies of *A. palifera* associated with differences in water clarity and sedimentation, depth and season suggests coral reproduction can be used as a biological indicator of the sublethal effects of stress on coral reefs. Further quantitative experimental work is suggested to determine how rapidly stress depresses fecundity, whether it does so at all stages of the gametogenic cycle, and how long it takes colonies to recover after stress is terminated.

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