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Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panama

by Peter W. Glynn

ABSTRACT

The mean growth rate of the dominant reef-building coral *Pocillopora damicornis* was significantly different in upwelling (Gulf of Panama) and nonupwelling (Gulf of Chiriquí) environments on the Pacific coast of Panama. Mean annual growth was 3.1 cm/yr at Saboga Island, Gulf of Panama and 3.9 cm/yr at the Secas study site, Gulf of Chiriquí. Coral growth declined markedly in the dry season in the Gulf of Panama during upwelling and decreased gradually in both areas in the wet season with increasing cloud cover. Water temperature was significantly correlated with coral growth in the upwelling area, and cloud cover (determined from satellite imagery) was significantly correlated with coral growth at the nonupwelling study site year round and in the Gulf of Panama during the nonupwelling season. Zooplankton abundance also appeared to be a significant predictor of coral growth in the Gulf of Panama.

The growth rate of *P. damicornis* was significantly higher in Panama than in Hawaii and comparable to that reported in Samoa. Estimates of the gross production of CaCO₃ on Panamanian reefs, in the range $5.1 \times 10^8$ to $6.7 \times 10^8$ gm CaCO₃/m²/yr, rank among the highest known.

1. Introduction

While it is well known that reef corals "... flourish and breed best within the range 25-29°C." (Wells, 1957), little information is available on the growth rates of corals and extent of reef building in thermally marginal areas. It has generally been assumed that coral growth is greatly reduced and reef formations absent or poorly developed outside the optimum thermal range. However, some recent studies indicate that vigorous reef building does occur in certain marginal environments. For example, modern *Acropora* reefs are well developed along the Trucial coast in the Persian Gulf where water temperatures range seasonally from 16°C to over 40°C (Kinsman, 1964; Shinn, 1972). Rapid coral growth and reef development have also been reported in a well known upwelling area, the Pearl Islands, Gulf of Panama (Glynn and Stewart, 1973).

Pocilloporid corals are the chief reef builders on the Pacific coast of Panama and it was shown that while these corals can tolerate seasonally cool conditions,
most reef development occurs on island shores facing away from the full effects of upwelling (Glynn and Stewart, 1973). A short distance to the west of the Gulf of Panama, in the warm, nonupwelling waters of the Gulf of Chiriquí, coral growth and reef building appear to be more rapid than in the Gulf of Panama (Glynn et al., 1972). This situation provides an unusual opportunity to quantify the effects of upwelling on the growth of a single reef-building species at the same latitude. Comparative coral growth data spanning three years are presented here as part of a long-term study on coral reef development in the eastern Pacific region.

2. Study areas

The two study sites are located on small, low islands, one (the island of Saboga) in the northern sector of the Pearl Islands, Gulf of Panama and the other in the southeastern-most sector of the Secas Islands, Gulf of Chiriquí (Fig. 1). The nearest distance to the mainland from the Saboga and Secas study sites is 31 and 27 km.
respectively. Both islands are located just inside the 50 m isobath, have a relatively low relief (maximum elevations are 68 m on Saboga Island and 109 m on the Secas Island), and are drained by ephemeral creeks. Insufficient data are available to determine the relative influence of continental river drainage in the two areas. Several rivers empty into both gulfs and these could have an important effect on offshore islands during flooding (see Discussion). However, over the course of this study no excessive run-off effects were observed.

The locations of the study reefs are also indicated in Figure 1. Planar reef dimensions, determined by planimetry from vertical aerial photographs, are 13.2ha. and 7.6ha. for the Saboga and Secas reefs respectively. Both reefs are formed dominantly of pocilloporid corals and the most common species is \textit{Pocillopora damicornis} (Linnaeus). The latter species commonly covers 70-80% of the bottom in the seaward reef slope zone (Glynn, 1976). The maximum depth of reef framework construction along the transects is 6-7 m below mean low water spring datum (MLWS) on the Secas reef and 3-4 m below MLWS on the Saboga reef.

The major hydrographic difference between the two study sites is seasonal upwelling which occurs in the Gulf of Panama but not in the Gulf of Chiriquí. The upwelling system in the Gulf of Panama has been studied extensively (Forsbergh, 1969; Schaefer \textit{et al.}, 1958; Smayda, 1966). It is a local, wind-induced upwelling which has its origin in the NE Trade Wind system. During the dry season, from mid-December or January through mid-April, the Trades are positioned over Panama and wind movement is across the isthmus and over the Gulf toward the south. During this period the mean sea surface temperature commonly drops 3-4°C below a wet season mean of about 28°C; extreme low temperatures in the range 16-20°C also occur at this time (Glynn, 1972; Glynn and Stewart, 1973; Hildebrand, 1939). Temperatures only rarely drop below 16°C (15.6°C was recorded twice over a 69 year period at Balboa, Meteorological and Hydrographic Branch, Panama Canal Company). The duration of extreme cool conditions is also short-lived with temperatures of 18-19°C lasting no more than about 5 days. These seasonally cool conditions are confined to the Gulf of Panama and do not extend into the Gulf of Chiriquí (Glynn \textit{et al.}, 1972).

At Panama's latitudinal position (7-10°N), weather disturbances come predominantly from the E and NE. Because of the low relief across central Panama (Figure 1), these disturbances move into the Gulf of Panama with little modification. In the western highlands, however, air masses moving onto the mainland are intercepted, resulting in high cloud cover and heavy rainfall along the Caribbean side and relatively clear and dry conditions to the leeward on the Pacific side. At times, when atmospheric movements are from the S, SW or W (during the wet season), sky cover is greater in the Gulf of Chiriquí than in the Gulf of Panama. Uniformly overcast skies also occur over large parts of Panama in the wet season when the Intertropical Convergence Zone is stationary.
Figure 2. Growth rates of *Pocillopora damicornis* in reef slope zone (3.2 m) at Saboga Island reef, December, 1971, to October, 1974. Each sample comprised at least 2 colonies and 10 different measurements from each. The solid bars and lines show respectively ± one standard deviation, and the maximum and minimum values. Sampling time periods are indicated by lines along abscissa. The year of sample collection is noted by each sample (e.g. 72, 73, etc.). Curve computed from running averages of 3 sampling periods.

3. Methods

Coral growth was determined by staining live colonies of *Pocillopora damicornis* (L.) with Alizarin Red S bone stain (Barnes, 1971; Lamberts, 1974). The stained corals were allowed to grow over periods ranging from about 1 to 3 months at different stations on the study reefs, then collected, cleaned and measured as described below. Station depths at Saboga Island were 1.6 m and 3.2 m, representing reef flat and reef slope zones respectively. Because of the Secas reef's greater depth range, coral growth was measured at 5 depths, representing reef flat (1.5 m), upper (3.3 m and 3.8 m) and lower (4.6 m) reef slope and reef base (6.5 m) zones respectively. Three to 5 colonies were enclosed in plastic bags filled with about 25 liters of water and containing 0.25 gm of stain (i.e. ~ 10 ppm); these were anchored on the bottom for about 5 hours during midday. Colony size varied from 10 to 15 cm in diameter; all corals were collected from 2 m to 3 m depth. From 3 to 5 colonies were fastened (with polyolefin insulated hookup wire) to concrete supports in normal growth position at each station. Branches forming the upper portions of
colonies were measured; 10 branchtips per colony were measured (usually 3 to 5 colonies or 30-50 branchtips per station), and these were selected at random by marking branches blindly before measurement.

Bottom temperatures were recorded continuously in all reef zones with calibrated Peabody Ryan thermographs (model F), as reported in Glynn and Stewart (1973).

Cloud cover in the two study areas was determined from Defence Meteorological Satellite Program (DMSP) satellite imagery recorded on positive photographic transparencies (high resolution visual data, "low enhanced" i.e. with high contrast for low cloud cover). The mean elevation of the satellite was approximately 450 nautical miles and cloud cover was measured when the satellite passed over Panama between about 1130 and 1300 local time. A Transmission Densitometer (Model TD-102, Macbeth Instrument Corp.), calibrated for each transparency, was used to measure cloud cover. The densitometer yielded replicate data (on the same field) of within less than 1%. Further calibration was performed if gray shade variations were detected between the study areas. An aperture of 3 mm was used; this covered a surface area of 1600 km². Density differences between the islands and surrounding water in the two study areas were negligible.

Salinity was determined periodically with an AO Goldberg T/C refractometer (Model 10423, temperature compensated) and on four occasions a series of samples was analyzed by the Mohr titration (Strickland and Parsons, 1960).
Water clarity and visible light intensity were also determined periodically at various depths. Water clarity is based on estimates of the maximum lateral visibility determined between 3-5 m depth. Sekonic underwater exposure meters, calibrated in foot candles and converted to lux, were used simultaneously at the surface and at depth. Each value reported is the mean of 6 readings, 4 horizontally toward the N, S, E and W and 2 vertically up and down.

Rates of sediment deposition (largely due to resuspension of sediments) were measured with opaque bottle traps (1.4-2.0 cm aperture and 14 cm deep with an inside diameter of 6.5 cm) set vertically in concrete blocks; the bottle apertures were 20 cm (± 5 cm) above the bottom. The inorganic and organic fractions of sediments were determined by drying and then ashing. Further procedural details are given in Glynn and Stewart (1973). Four replicates were obtained on the Secas reef at 6 depths across the study transect at the climax of the wet season (September-November, 1972). Settling rates were similarly measured on the Secas reef (4 depths, upper and lower forereef slope zones) and the Saboga reef (1 depth, lower forereef slope) during the succeeding dry season (January-March, 1973).

4. Results

a. Coral growth. The long-term seasonal growth trends of *Pocillopora damicornis* are summarized for both study areas in Figures 2 and 3. Mean yearly growth at Saboga was 3.08 cm/yr versus 3.86 cm/yr on the Secas reef. In other words, coral growth in the Gulf of Panama was about 80% of that observed in the Gulf of Chiriquí. The greatest differences between localities occurred during the preupwelling and upwelling seasons (Figs. 2 and 3). During this period mean monthly growth rate centered around 2 mm at Saboga and between 3 and 4 mm on the Secas reef. From May to October, in the postupwelling and wet season periods, coral growth was more nearly comparable at the two study sites.

Conventional statistics are somewhat questionable in the present case because replicate measurements from the same colony are not independent. Therefore, to test the important question of whether these growth rates differ significantly, all the measurements (for a given depth) from a given reef in a given season are con-

2. Mean yearly growth calculated from the areas under the growth curves (by means of a digitizer used to integrate the respective areas) was 3.07 cm and 3.91 cm for the Saboga and Secas reefs respectively.
sidered as a single datum, and "replicate" measurements are those from different years. These figures were treated as a $2 \times 4$ factorial, Model I anova (cell frequencies unequal, computational procedures after Winer, 1962). Seasons were denoted as follows: upwelling (January–mid-April), postupwelling (mid-April–mid-June), wet season (mid-June–mid-November) and preupwelling (mid-November–December). The cumulative distribution of growth rates approximated a straight line on normal-probability paper, therefore, parametric statistics are justified. The variances between groups, however, were often unequal (as determined by the $F_{\text{max}}$ test, Sokal and Rohlf, 1969), so data were transformed into common logarithms. Anova demonstrated significant effects of sites and seasons on coral growth (Table 1). The interaction effect was not significant in this analysis.

Conventional 95% confidence intervals (using all measurements) were 2.55 to 3.61 cm/yr at Saboga versus 3.39 to 4.33 cm/yr on the Secas reef. The 95% confidence interval for the difference in yearly growth between sites is 0.07 to 1.49 cm/yr.

The data in Table 2 indicate significant differences between stations in the same reef over most periods. For example, growth was greatly reduced on the reef flat (station 1) at both study sites during the first three months in 1974. Peripheral branches and whole colonies were killed at this time due to extreme low water exposures (Glynn, 1976). The low rate of 1.44 mm on the Secas reef at 6.5 m (station 5) indicates a significant decline in growth along the reef base during the wet season. Therefore, the foregoing analysis was based only on observations at comparable depths at the two sites, namely 3.2 m at Saboga and 3.3 m to 4.6 m at Secas.

b. Sea water temperature. The coastal zone between the Azuero Peninsula, Panama north to the Gulf of Papagayo, Costa Rica comprises the southern-most sector of the warmest and thermally most stable water mass in the eastern Pacific (Renner, 1963; Wyrtki, 1964). Temperature transects obtained while under way between the study areas at the height of the dry season indicate that the thermal boundary in Panama is located off the Azuero Peninsula. For example, on March 7, 1973 a gradual warming trend, from 24.9°C to 30.6°C, was observed about 8 nautical miles offshore from 80° 03’ W to 81° 15’ W.

The continuous temperature records indicate the variations in temperature at different depths and seasons at the study sites (Fig. 4). The upper set of graphs, spanning 43 and 40-day periods, show a high and constant temperature on the Secas reef in the wet season. The mean temperatures at 1.5 m and 7.4 m were 29.03°C and 29.28°C respectively. A slight cooling effect from rains and surface runoff (small streams) is probably responsible for this inversion. In the dry season (Fig. 4, center) temperatures remained high on the Secas reef ($\bar{X} = 29.19^\circ\text{C}$, range 27.8°C-30.0°C) but declined and fluctuated markedly over the same period at
Table 2. Mean monthly growth (mm) of *Pocillopora damicornis* in relation to season and station depth. Number of colonies sampled are noted in parentheses. The *t*-test and Model I ANOVA were used for testing the Saboga and Secas data respectively. All data were transformed into common logarithms for statistical testing.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Period</th>
<th>Station and depth</th>
<th>Statistic</th>
<th><em>p</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(1.6m) (3.2m)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saboga</td>
<td>Jan.25-Apr.27'74</td>
<td>1.36(2) 2.65(6)</td>
<td><em>t</em>(79) =7.74</td>
<td>&lt;&lt;0.0005*</td>
</tr>
<tr>
<td></td>
<td>Apr.27-Jun.20'74</td>
<td>4.64(3) 4.53(3)</td>
<td><em>t</em>(58) =0.54</td>
<td>&gt;0.25</td>
</tr>
<tr>
<td></td>
<td>Jun.20-Aug.22'74</td>
<td>3.63(3) 3.58(5)</td>
<td><em>t</em>(78) =0.31</td>
<td>&gt;0.35</td>
</tr>
<tr>
<td>Secas</td>
<td>Sep.23-Nov.7'72</td>
<td>1.84(4) 2.18(6)</td>
<td><em>F</em>(4,245) =6.76</td>
<td>&lt;&lt;0.001**</td>
</tr>
<tr>
<td></td>
<td>Jan.22-Mar.8'73</td>
<td>2.89(4) —</td>
<td><em>F</em>(8,150) =12.72</td>
<td>&lt;&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Nov.8'73-Jan.20'74</td>
<td>1.31(4) 1.98(4) 2.53(3) 2.86(4) 2.31(3)</td>
<td><em>F</em>(4,175) =77.67</td>
<td>&lt;&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Jan.20-Apr.24'74</td>
<td>2.62(1) 3.77(3) 3.37(3) 3.39(3) 3.50(3)</td>
<td><em>F</em>(4,120) =8.68</td>
<td>&lt;&lt;0.001</td>
</tr>
</tbody>
</table>

* One-tailed test used for all Saboga samples.
** Two-tailed test used for all Secas samples.
† Underlined means are not significantly different from each other, α = 0.05, SNK a posteriori test (Sokal and Rohlf, 1969).
Figure 4. Continuous sea-water temperature traces from the Secas and Saboga Island study sites. Each panel represents a 24-hour period. Top set shows temperature differences at 1.5 m and 7.4 m (relative to MLLWS datum) at the Secas reef in wet season. Middle and bottom sets show temperatures at the study sites in the dry and transition wet-dry seasons respectively.
Saboga ($\bar{X} = 23.35^\circ C$, range $19.5^\circ C$-$27.3^\circ C$). Wet season temperatures at Saboga were relatively constant, as on the Secas reef (Fig. 4, bottom). For the wet season dates illustrated, the mean temperature at Saboga was $24.07^\circ C$ (range $22.9^\circ C$-$24.9^\circ C$) and on the Secas reef $27.44^\circ C$ (range $26.6^\circ C$-$28.9^\circ C$). Conditions were unusually cool at Saboga for that time of year. Mean temperatures are more often around $27^\circ C$ at the end of the wet season in the Pearl Islands (Wyrtki, 1964; Glynn and Stewart, 1973).

Table 3. Annual comparisons of median cloud cover over Saboga and the Secas study islands.

<table>
<thead>
<tr>
<th>Season</th>
<th>Study site</th>
<th>Year</th>
<th>Median</th>
<th>Number</th>
<th>$z^*$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Saboga</td>
<td>1973</td>
<td>9.2</td>
<td>157</td>
<td>-2.060</td>
<td>&lt;0.02</td>
</tr>
<tr>
<td>Dry</td>
<td>Saboga</td>
<td>1974</td>
<td>11.6</td>
<td>144</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Secas</td>
<td>1973</td>
<td>6.8</td>
<td>155</td>
<td>-2.221</td>
<td>&lt;0.02</td>
</tr>
<tr>
<td></td>
<td>Secas</td>
<td>1974</td>
<td>8.7</td>
<td>143</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Saboga</td>
<td>1973</td>
<td>58.4</td>
<td>149</td>
<td>-5.314</td>
<td>&lt;0.00003</td>
</tr>
<tr>
<td></td>
<td>Saboga</td>
<td>1974</td>
<td>39.0</td>
<td>170</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wet</td>
<td>Secas</td>
<td>1973</td>
<td>41.7</td>
<td>148</td>
<td>-3.935</td>
<td>&lt;0.00005</td>
</tr>
<tr>
<td></td>
<td>Secas</td>
<td>1974</td>
<td>32.3</td>
<td>170</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Standardized normal deviate, $\mu = 0$, $\sigma = 1$. 

Figure 5. Seasonal variations in cloud cover over the Secas (clear bars) and Saboga (solid bars) Island study sites (1973-74). Indicated for each monthly sample are the median, 95% confidence intervals of median (vertical bars) and range (vertical lines).
Table 4. Site comparisons of median cloud cover over Saboga and the Secas study islands.

<table>
<thead>
<tr>
<th>Year</th>
<th>Season</th>
<th>Study site</th>
<th>Median</th>
<th>N</th>
<th>z*</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Saboga</td>
<td>10.6</td>
<td>68</td>
<td>3.066</td>
<td>~0.001†</td>
</tr>
<tr>
<td>1972</td>
<td>Dry (Feb.-May)**</td>
<td>Secas</td>
<td>9.2</td>
<td>68</td>
<td>-1.169</td>
<td>~0.12 NS</td>
</tr>
<tr>
<td></td>
<td>Wet (June, Sept. &amp; Oct.)**</td>
<td>Saboga</td>
<td>30.9</td>
<td>41</td>
<td>-3.106</td>
<td>&lt;0.001†</td>
</tr>
<tr>
<td></td>
<td>Dry (Jan.-May, Dec.)</td>
<td>Secas</td>
<td>9.2</td>
<td>156</td>
<td>-2.814</td>
<td>&lt;0.003†</td>
</tr>
<tr>
<td></td>
<td>Wet (June-Nov.)</td>
<td>Saboga</td>
<td>58.4</td>
<td>152</td>
<td>-1.850</td>
<td>~0.03†</td>
</tr>
<tr>
<td>1973</td>
<td>Dry (Jan.-April, Dec.)</td>
<td>Secas</td>
<td>8.7</td>
<td>142</td>
<td>-1.514</td>
<td>0.066 NS</td>
</tr>
<tr>
<td></td>
<td>Wet (May-Nov.)</td>
<td>Saboga</td>
<td>39.0</td>
<td>199</td>
<td>-1.514</td>
<td>0.066 NS</td>
</tr>
</tbody>
</table>

* Standardized normal deviate, \(\mu = 0, \sigma = 1\).
** Data insufficient for complete seasonal analysis.
† Significant difference \((p < 0.05)\).

c. Cloud cover. Frequency distributions of cloud cover tended to be strongly positively skewed in the dry season, reflecting a preponderance of clear sky days. Wet season frequency distributions of cloud cover were more variable from year to year and ranged from positively skewed to platykurtic. Because of these deviations from normality, a distribution-free test (Mann-Whitney U-test) was used to compare yearly and study area differences.

The seasonal pattern of cloud cover was similar in the two study areas (Fig. 5). Median monthly cover was less than 20% from December through April or May. There was no indication that clouds or fog formed locally in the Pearl Islands through the influence of cool upwelled water. Cloud cover then increased abruptly in May or June with frequent overcast conditions prevailing until the end of November. Cloud cover in the wet season was significantly greater in 1973 than in 1974 at both study sites (Table 3). However, cloud cover in the dry season was significantly less in 1973 than in 1974.
Table 5. Surface salinities (‰) observed at the Saboga and Secas study sites, 1972-1975.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Season</th>
<th>Median</th>
<th>Range</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saboga</td>
<td>dry</td>
<td>33.5</td>
<td>27.0-34.8</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>wet</td>
<td>26.0</td>
<td>24.0-32.0</td>
<td>6</td>
</tr>
<tr>
<td>Secas</td>
<td>dry</td>
<td>34.0</td>
<td>28.0-36.0</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>wet</td>
<td>28.0</td>
<td>27.0-32.0</td>
<td>10</td>
</tr>
</tbody>
</table>

U-statistic and significance

* Significant difference ($p < 0.05$).

From 1972 to 1974 cloud cover was greater in all seasons over Saboga Island than over the Secas Islands (Table 4). In all cases cloud cover was 9 to 14% higher at Saboga Island. These differences were significant at $p < 0.05$ in 4 out of 6 comparisons (Table 4).

d. Salinity, light levels and sediment deposition. Surface salinities on the two reefs showed a significant seasonal difference (Table 5). Dana (1975) noted a similar but slightly lower seasonal difference in the Gulf of Chiriquí. Salinities between sites, within any given season, were not significantly different.

The few quantitative data available on water clarity failed to show any significant seasonal effect within the study sites (Table 6). Median visibility on the Secas reef ($\sim 12$ m) was about two times that observed at Saboga ($\sim 6$ m). This difference between the study sites was significant in both the dry and wet seasons. While water clarity is highly variable (depending in part on location on the reef and state of the tide), it does appear that in general it is greater at the Secas reef.

Table 6. Water clarity (m) at the Saboga and Secas study sites, 1972-1975.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Season</th>
<th>Median</th>
<th>Range</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saboga</td>
<td>dry</td>
<td>6.1</td>
<td>4.0-7.6</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>wet</td>
<td>6.4</td>
<td>4.6-7.6</td>
<td>5</td>
</tr>
<tr>
<td>Secas</td>
<td>dry</td>
<td>12.5</td>
<td>10.0-15.0</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>wet</td>
<td>12.2</td>
<td>4.0-18.3</td>
<td>9</td>
</tr>
</tbody>
</table>

U-statistic and significance

* Significant difference ($p < 0.05$).
Too few data are available to compare water transparency at the two study sites. Light intensity (% of surface) at 3-5 m depth was highest on the Secas reef toward the end of the wet season (75-81%, November) and in the dry season (58-66%, January). At the end of the dry season (April) and at the peak of the wet season (September and October), light intensity ranged between 43-48% and 14-32% of the surface, respectively. Measurements made two days apart in March, 1973, gave values of 36% at Saboga and 44% on the Secas reef. Median relative light intensities at 3-5 m over all seasons were 58% of surface values on reefs in the Pearl Islands (n = 7) and 74% on the Secas reef (n = 10). These data are not significantly different (p > 0.05, Mann-Whitney U-test).

Sediment settling rates on the Secas reef were not correlated with station depth in either the dry or wet season (p \geq 0.30, Kendall rank correlation test). Neither were significant differences observed between seasons within sites. Dry season settling rates, 5.9 mg/cm²/day at Saboga and 4.4 mg/cm²/day on the Secas reef (median values), were also similar between sites. Wet season data indicate that sediment deposition was somewhat higher (p \sim 0.008) at Saboga (5.2 mg/cm²/day) than on the Secas reef (3.2 mg/cm²/day). While these results are probably biased toward high settlement rates—because the body of the traps is much larger than the mouth—they should, nonetheless, provide a reasonable estimate of the amount of sediment settling on corals.

The organic matter content of sediments decreased significantly with station depth on the Secas reef. In the dry season the organic matter content of sediments on the reef flat at station 1 was 22.8%, decreasing to 14.4% on the lower reef slope at station 4 (p < 0.017). In the wet season station 1 sediments contained 19.4% organic matter and 13.0% in the reef base zone at station 5 (p < 0.0002). Within site seasonal differences were not evident. However, the organic matter content of sediments on the Secas reef (stations 1-3) was significantly higher than at Saboga (all stations). The median values for the Secas and Saboga sites were respectively 15.7% and 11.8% in the dry season (p < 0.001) and 19.4% and 11.1% in the wet season (p < 0.001).

5. Discussion

a. Correlates of coral growth. Sufficient data are available indicating that overall sea water temperature and water clarity were higher and cloud cover lower at the Secas reef compared with the Saboga reef. Coral growth and water temperature were significantly correlated (r = 0.833, p < 0.005, for 9 sampling periods) at Saboga Island (Fig. 6), but not so on the Secas reef (r = 0.036, p \gg 0.10, for 4 sampling periods). Glynn and Stewart (1973) also reported a significant relationship between coral growth and water temperature at several sites in the Pearl Islands.

3. Data on settling rates and the organic matter content of sediments are available from the Librarian, Smithsonian Tropical Research Institute.
The poor relationship between growth and temperature at the Secas reef is due to the nearly constant temperature conditions at that locality (27.4-29.0°C).

When coral growth and cloud cover are compared under relatively constant temperature conditions (i.e., year round at the Secas reef and during nonupwelling periods at Saboga), a significant inverse correlation ($r = -0.586$, $p < 0.025$ for 14 sampling periods) is evident (Fig. 7). The slope of the regression curve is significantly different from zero at $p < 0.05$.

Coral growth, water temperature and cloud cover were measured simultaneously over six periods on the Saboga reef and over four periods on the Secas reef. Coral growth at each site was regressed (forward stepwise inclusion) on temperature and cloud cover. The partial $F$-values of the second predictor variables, cloud cover for the Saboga regression and temperature for the Secas regression, were not significant ($\alpha = .05$), suggesting that the full model (coral growth as a function of temperature and cloud cover) is invalid. The simple bivariate models again demonstrated high and significant correlations between coral growth and temperature at Saboga ($r = 0.973$, $p < 0.005$) and between coral growth and cloud cover at the Secas reef ($r = -0.984$, $p < 0.01$).

Many of the annual differences in coral growth correspond with observed variations in temperature or cloud cover. For example, growth rates at Saboga during upwelling were significantly different, and showed an increasing trend, in 1972, 1973 and 1974 (Fig. 2). The corresponding mean water temperatures were 21.64°C, 23.35°C and 25.48°C respectively. The significant annual differences in coral growth during the wet season at both sites (Figs. 2 and 3, August-November), lowest in 1973, are in agreement with the more overcast skies in 1973 (Table 3).

While much of the variation in coral growth can be explained by temperature and cloud cover, other factors may also have an effect. Further study is required to determine the influence of salinity, water clarity and sediment settling rates.
Extreme turbidity in the Gulf of Chiriquí was noted by Dana (1975) during his wet season sampling in September, 1970; underwater visibility in the Secas Islands at that time was never greater than about 2.5 m. The minimum surface salinity was 29.2%. Water clarity was greater over the course of the present study, ranging between 4.6 and 18.3 m in the wet season. The year 1970 was unusually wet; sudden downpours in April and continuous heavy rainfall in September resulted in widespread flooding in Chiriquí Province. Total annual rainfall at Bambito (a southern slope station) was 3.3 m, 18.2% greater than the previous record over a 12-year period (Panama Canal Co., 1958-1970). Discharge rates of rivers draining into the Gulf of Chiriquí were 25.1% higher than the previous record in 1970 (C. Candanedo, pers. comm.). River discharge rates in 1973 were slightly higher than in 1970 (by 1.5%), but rainfall was more evenly distributed and no flooding resulted. Therefore, it appears that high turbidity on the offshore islands in the Gulf of Chiriquí occurs less frequently than suggested by Dana’s (1975) observations.

Generally, temperature has a positive effect on coral growth (e.g. Clausen and Roth, 1975; Glynn and Stewart, 1973, and this study; Lewis et al., 1968; Maragos, 1972; Shinn, 1966; Weber and White, 1974; Weber et al., 1975). As noted earlier, this was not the case on the Secas reef. Dodge and Vaisnys (1975) reported a negative temperature coefficient for long-term coral band width chronology. They interpreted the negative temperature relation as a positive response to nutrient supply, which increased during the annual cold water overturn at Bermuda. I regressed (forward step-wise inclusion) data from the synoptic growth curve of *Pocillopora* at Saboga Island on monthly means of sea surface temperature (18 yrs, 1951-68), cloud cover (2 yrs, 1973-74) and zooplankton standing crop (4½ yrs, 1954-59) in the Gulf of Panama. Temperature and zooplankton data (Z, ml/10³ m³) are from

![Figure 7. Relationship between growth rate of *Pocillopora* and median percent cloud cover. Data from Saboga obtained in wet season, data from Secas site in all seasons. Curve fitted by means of least squares, G = 3.90-0.028C. Broken lines indicate upper and lower 95% confidence limits.](image)
Forsbergh (1969), and cloud cover (C) from this study. While these records demonstrated similar annual cycles in temperature, cloud cover and zooplankton abundance (the latter highest following the upwelling period, from April through June), they do lack equivalency in time periods. In this analysis, zooplankton demonstrated the highest partial correlation coefficient ($r = 0.859, p < 0.001$) and the valid regression model was

$$G = -0.929 + 0.039Z + 0.018C.$$  

For the two predictor variables $Z$ and $C$, $r = 0.947$ ($p < 0.001$), in this case explaining 89.7% of the variance in coral growth. These results are suggestive and indicate the desirability of also assessing zooplankton abundance.

b. Regional differences in carbonate production. When the annual growth of *Pocillopora damicornis* in Panama is compared with that in Hawaii and Samoa it is seen that coral growth in the eastern Pacific, in both upwelling and thermally stable areas, is vigorous. Median annual growth in height, utilizing all published data, was 9.8 mm/yr in Hawaii (Edmondson, 1929) and 25.0 mm/yr in Samoa (Mayor, 1924). Comparable measurements in Panama, comprising all station data, were 29.0 mm/yr in the Pearl Islands, and 32.0 mm/yr in the Secas Islands. Anova indicates that these data are different ($p < 0.01$). Dunn’s multiple comparison test shows that the median growth of coral in Hawaii and the Secas Islands differs significantly ($\alpha = 0.05\%$). Maragos (1972) obtained growth rates in Hawaii that were 29.7% higher than Edmondson's (based on solid diameter growth). This higher rate is also significantly below ($p < 0.001$) that obtained in the Secas Islands.

The production rates of CaCO$_3$ on Panamanian reefs may now be related to the series of reefs compared by Chave et al. (1972). Following their method of calculation for potential production (m/yr $\times$ gm/m$^3$, assuming that corals have a density of 1 gm/cm$^3$ of organism), potential production for *Pocillopora* on the upper reef slopes at the Saboga and Secas reefs are $31 \times 10^3$ and $39 \times 10^3$ gm CaCO$_3$/m$^2$/yr respectively. Estimates of gross production (potential production $\times$ percent cover, assuming 52% live coral cover on both reefs, Glynn, 1976) are $16 \times 10^3$ and $20 \times 10^3$ gm CaCO$_3$/m$^2$/yr respectively. These values rank among the highest reported, including reefs at such western Pacific localities as Eniwetok, Rongelap and Samoa. However, Chave et al. (1972) concluded that rates in this range—25 $\times$ 10$^3$ gm CaCO$_3$/m$^2$/yr—probably best approximate potential production values in other reef areas, with gross production more typically in the range of 5 $\times$ 10$^3$ to 8 $\times$ 10$^3$ gm CaCO$_3$/m$^2$/yr. Chave et al. (1972) assumed 50% porosity for reef sediments in the conversion between gm CaCO$_3$/m$^2$/yr and mm/yr.

4. This comparison is based on medians and the nonparametric Kruskal-Wallis anova test because the variances of coral growth are heterogeneous. The observed variance ratio (F$_{max}$-test, Sokal and Rohlf, 1969) was significant ($p < 0.05$).
I have also calculated the mass of live coral produced annually by relating the total standing crop of *Pocillopora* (based exclusively on live branches) to that assumed produced by known growth increments. This was done by snipping the branchtips from colonies and then comparing their aggregate mass with that of the basal branches. In 5 quadrats (900 cm$^2$ each) of varying coverage (17.4-89.0%) branchtips of 3.9 cm length, equal to one year’s growth on the Secas reef, represented a mean value of 69.25% (66.3-74.7%) of the live, dry weight standing crop. Thus, nearly 70% of the live standing crop in the Gulf of Chiriquí is produced annually. Annual coral growth and coverage (cov., or standing crop density) were linearly related ($G = -2.1 + 0.695\text{cov.}$). The regression coefficient is significantly different from 0 at $p < 0.001$. Comparable data for Saboga Island indicate that 3.1 cm growth represents 52.92% (51.2-55.2%) of the standing crop. This relationship, $G = -12.1 + 0.552\text{cov.}$, was again linear and highly significant ($p < 0.001$). (Although the two regression equations were not significantly different at $\alpha = .05$, a 2-factor anova without replication did show a significant, $p < 0.025$, mass difference between the 3.1 and 3.9 cm annual growth increments.)

Production rates based on these calculations are $5.1 \times 10^3$ and $6.7 \times 10^3$ gm CaCO$_3$/m$^2$/yr for the Saboga and Secas reefs respectively. These lower values, about one-third of those calculated by the method of Chave *et al.* (1972), I believe are due in large part to the branching growth form of *Pocillopora* which results in a high proportion of free space ($>> 50\%$ of the reef frame). An undetermined mass also accrues through basal branch thickening, and this is not accounted for by the present method. Finally, since these production rates are based on incremental measurements, involving minimal losses from corallivores, they probably more closely approximate estimates of gross production. Gross production estimates (derived from the alkalinity method) for seaward reef flat environments in the western Pacific (Smith and Kinsey, 1976) ranged from $3.6 \times 10^3$ to $4.5 \times 10^3$ gm CaCO$_3$/m$^2$/yr. These values, which include all components of reef production—corals as well as coralline algae, etc.—are reasonably close to those reported here where *Pocillopora* is the dominant carbonate producer.

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