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# GEOGRAPHIC PATTERNS OF CORAL BIOEROSION: A PRODUCTIVITY HYPOTHESIS

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**Abstract:** The numbers of boring bivalves in corals in large museum collections were used to indicate relative bioerosional damage to the corals. The proportion of corals from different locations that contain boring bivalves is highly correlated with global patterns of plankton primary productivity. The densities of five other, non-boring, groups of planktivores associated with the same corals are similarly correlated with productivity.

The proportion of corals containing boring bivalves and the number of boring bivalves per coral head can be ranked by region as follows: eastern Pacific > western Atlantic > Indian Ocean > western Pacific. This ranking also corresponds to primary productivity differences.

Measurements of the basal, margin of live tissue, and maximum circumferences of the coral heads indicate that western Atlantic massive corals have more of their skeletal surface exposed to borers, i.e. not covered by live tissue, than do Indo-Pacific corals. Consequently, the former also have weaker basal attachments which suggests that they are more likely to be dislodged during storms. The reason why massive corals in the western Atlantic tend to have less of their skeleton covered by live tissue than corals in the rest of the world is unknown.

## INTRODUCTION AND HYPOTHESIS

Recently, X-radiographic techniques have been developed that make it possible to quantify accurately damage to coral skeletons by boring organisms. The mean amount of skeletal material excavated from massive corals in Florida (Hein & Risk, 1975) and Barbados (MacGeachy & Stearn, 1976) is 28% and 15%, respectively. In the Pacific, massive corals at Enewetak average less than 4% excavation (Highsmith, 1979). Boring sponges were responsible for the most skeletal damage in all three studies. Boring bivalves accounted for ≈15% of the excavation in Florida corals and the mean number of bivalves per head at Barbados was 3.1 At Enewetak, only three bivalves were found in 102 heads.

These regional differences, i.e. larger boring sponges and higher boring bivalve densities in the western Atlantic than in the Pacific, raise the possibility of a fundamental difference between Caribbean and Indo-west Pacific coral reefs additional to those listed by Milliman (1973). Bertram (1936), however, estimated that boring bivalves were responsible for colony detachment in 20% of cases at Al-Ghardaqa, Red Sea. Relatively high densities of boring bivalves also occur in corals at Phuket, Thailand (Nielsen, 1976) and Heron Island, Australia (Connell, 1973; Kleemann,

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1977). Conversely, corals at Curacao, in the western Atlantic, are only 1–2% excavated (Bak, 1976). Thus, it is apparent that a simple inter-ocean explanation for bioerosional differences is inadequate. Because sponges and bivalves are primarily filter-feeders, I hypothesize a direct relationship between the abundance of these boring organisms and plankton primary productivity in different geographic regions. This paper reports a test of this hypothesis based on examination of several hundred corals from a variety of geographic locations.

## METHODS

Massive corals were examined at the Smithsonian Institution, the Museum of Comparative Zoology at Harvard University, and at the Peabody Museum of Natural History at Yale. Since I was not at liberty to section the corals and measure the actual volume excavated, I counted boring bivalve siphonal openings present in each head. These openings are sufficiently characteristic to permit easy recognition of the genus of bivalve responsible (MacGeachy & Stearn, 1976). From analysis of the results of Hein & Risk (1975), MacGeachy & Stearn (1976), and my observations at Enewetak, I showed that the abundance of boring bivalves tends to fluctuate directly with overall bioerosional damage to corals (Highsmith, 1979). Therefore, abundances of boring bivalves are useful estimates of relative bioerosional damage to corals from different geographic locations. I also recorded abundances of non-boring bivalves, ahermatypic corals, serpulid polychaetes, and barnacles attached to the coral skeletons.

Most boring organisms settle on and bore into dead surface areas around the base of corals (Bak, 1976; MacGeachy & Stearn, 1976; Highsmith, 1979). The ratio of the basal attachment circumference to the live tissue margin circumference is a convenient estimate of the extent to which basal surfaces of massive corals are protected from attack by borers, i.e. covered by live tissue (Highsmith, 1979). A ratio of one indicates the base is covered with live tissue down to the substratum; lower ratios reflect increasing amounts of dead surface exposed to attack. Similarly, the ratio of the circumference of the basal attachment to maximum head circumference indicates relative strength of attachment to the substratum (Highsmith, 1979); the smaller the ratio of base to maximum circumference, the lower the strength of attachment.

Plankton primary productivity at different geographic locations was determined by reference to the Koblentz-Mishke *et al.* (1970) map of primary production in the world ocean (Fig. 1).

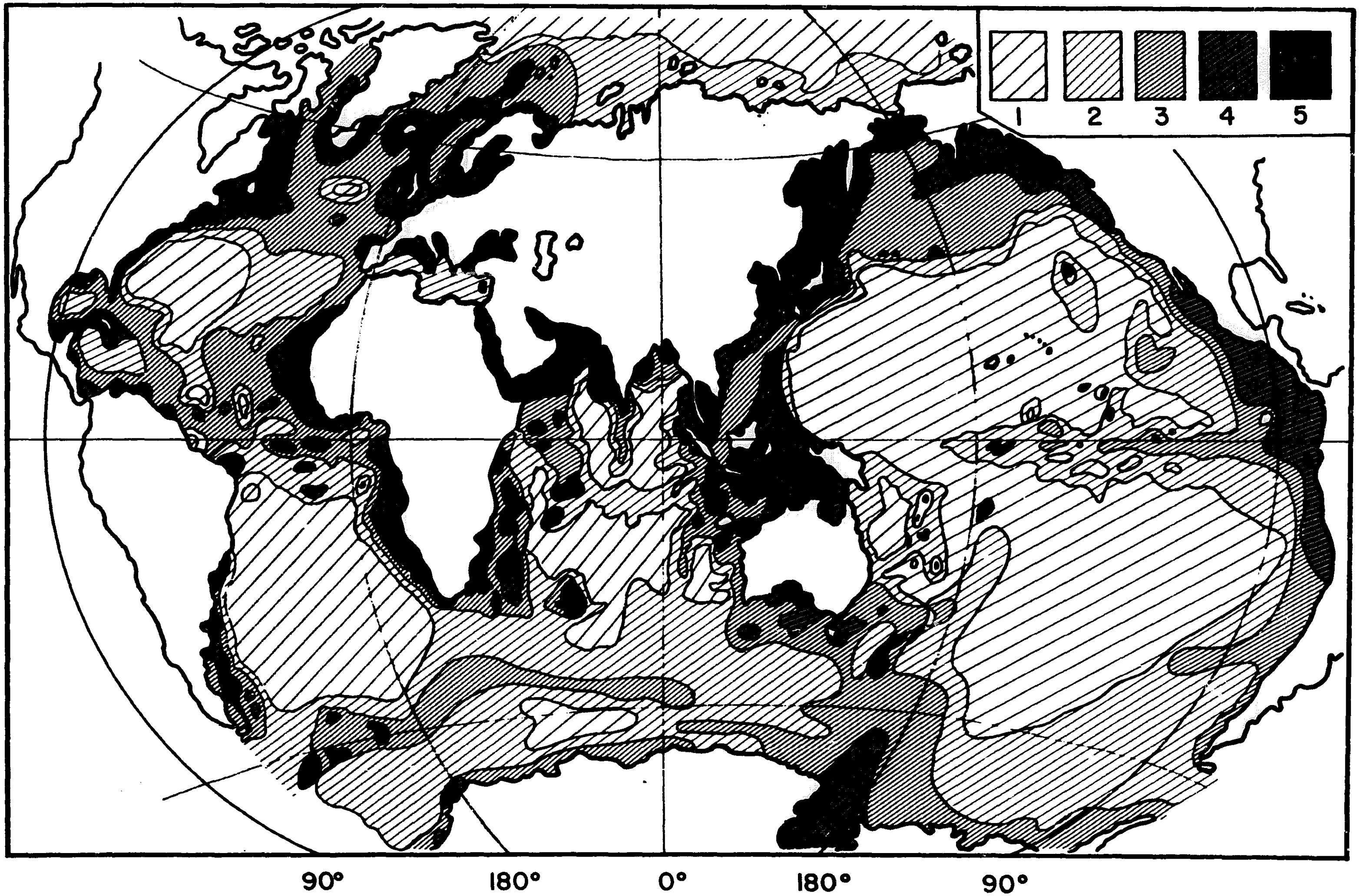

Fig. 1. Distribution of gross primary production in the world ocean: units are in mg C · m$^{-2}$ · day$^{-1}$; 1, <100; 2, 100–150; 3, 150–250; 4, 250–500; 5, >500; reproduced from Koblentz-Mishke *et al.* (1970), p. 185, with permission of the National Academy of Sciences, Washington, D.C.

## RESULTS

### GEOGRAPHIC DATA AND SKELETAL FACTORS

The proportions of heads with boring bivalves and mean number of boring bivalves per coral head (Table I) differ in the four oceanic areas considered. For percentage of massive corals containing boring bivalves, the areas rank as follows: eastern Pacific > western Atlantic > Indian Ocean > western Pacific (Fig. 2). All differences are significant at $P < 0.0005$ (2 × 2 chi-square tests). Considering only corals with one or more boring bivalves, the number of bivalves per head is significantly different in each area and in the same rank order as above (Fig. 2; Jonckheere's test for ordered alternatives, $Z = 3.17$, $P = 0.0008$). In all four areas the mean number of boring bivalves and percentage of heads with boring bivalves are usually relatively high at locations near continents (Table I).

|  |  | Indian Ocean (35) | Western Atlantic (128) | Eastern Pacific (33) |  |
|---|---|---|---|---|---|
|  | ▨ | 369 | 1822 | 719 | Western Pacific (28) |
| Indian Ocean | 20 | ▨ | 2224 | 954 | Indian Ocean (35) |
| Western Atlantic | 83 | 12 | ▨ | 3180 | Western Atlantic (128) |
| Eastern Pacific | 163 | 56 | 34 | ▨ |  |
|  | Western Pacific | Indian Ocean | Western Atlantic |  |  |

Fig. 2. Lower left, $\chi^2$ values for 2 × 2 contingency tests on data in Table I; ocean regions in rows have a higher proportion of corals with boring bivalves than regions in the corresponding column; all values are significant at $P < 0.0005$. Upper right, $J$ values for Jonckheere's test for ordered alternatives (Hollander & Wolfe, 1973) for coral heads containing one or more bivalves; ocean regions in columns have more bivalves per head than regions in corresponding rows; number of coral heads with boring bivalves is indicated in parentheses.

Most boring bivalves occur in dead surface areas on coral heads (Table I). After adjustment for individuals that initially penetrated a dead surface and were sub-

TABLE I

Mean number of boring bivalves per coral head and percentage of coral heads with boring bivalves: figures in parentheses are adjusted to show numbers of bivalves apparently encircled by coral growth after settlement which were removed from the live surface category and added to the dead surface column; live surface is that part of the skeleton covered by live coral tissue; the balance of the skeletal surface is counted as dead surface.

| | | Mean no. bivalves/head | | | | | |
|---|---|---|---|---|---|---|---|
| Location | Genus | Total | Live surface | Dead surface | No. of heads | % Heads with bivalves | Coral diameter range (cm) |
| Indian Ocean | | | | | | | |
| Red Sea | *Porites* | 0.6 | 0 | 0.6 | 16 | 31 | 4–32 |
| | *Favia* | 0.3 | 0 | 0.3 | 10 | 30 | 7–26 |
| | *Goniastrea* | 4.4 | 0 | 4.4 | 9 | 67 | 11–26 |
| Ceylon | *Porites* | 0 | 0 | 0 | 2 | 0 | 5–7 |
| | *Favites* | 1.0 | 0 | 1.0 | 1 | 100 | 8 |
| | *Goniastrea* | 0 | 0 | 0 | 1 | 0 | 9 |
| Singapore | *Favia* | 1.4 | 0.6 | 0.8 | 10 | 60 | 7–13 |
| | *Goniastrea* | 1.7 | 0 | 1.7 | 3 | 67 | 7–8 |
| | *Platygyra* | 2.0 | 0.3<br>(0) | 1.7<br>(2.0) | 3 | 100 | 9–15 |
| Maldive Islands | *Porites* | 0.1 | 0 | 0.1 | 13 | 8 | 7–20 |
| | *Favia* and *Favites (4)* | 0.14 | 0.14<br>(0.07) | 0<br>(0.07) | 14 | 14 | 5–18 |
| | *Goniastrea* | 0 | 0 | 0 | 4 | 0 | 9–16 |
| Seychelles Islands | *Porites* | 0 | 0 | 0 | 2 | 0 | 8–9 |
| | *Favia* | 0 | 0 | 0 | 1 | 0 | 14 |
| | *Goniastrea* | 0 | 0 | 0 | 7 | 0 | 8–13 |
| Chagos Islands | *Porites* | 0 | 0 | 0 | 8 | 0 | 5–17 |
| Zanzibar | *Porites* | 0 | 0 | 0 | 2 | 0 | 3–5 |
| Aldabra | *Porites* | 6.6 | 5.6<br>(0.2) | 1.0<br>(6.4) | 5 | 80 | 11–14 |
| | *Goniastrea* | 0.5 | 0 | 0.5 | 2 | 50 | 12–17 |
| Cosmoledo | *Porites* | 0 | 0 | 0 | 1 | 0 | 6 |
| | *Goniastrea* | 0 | 0 | 0 | 2 | 0 | 11–12 |
| Farquhar | *Favia* | 0 | 0 | 0 | 2 | 0 | 5–7 |
| Mauritius | *Porites* | 0 | 0 | 0 | 8 | 0 | 9–21 |
| | *Favia* | 0 | 0 | 0 | 2 | 0 | 6 |
| Totals | | | | | 128 | 26 | |
| Western Pacific | | | | | | | |
| Philippine Is. | *Porites* | 0.6 | 0.13<br>(0) | 0.5<br>(0.6) | 8 | 50 | 9–15 |
| | *Favia* | 0 | 0 | 0 | 9 | 0 | 8–18 |
| | *Goniastrea* | 1.0 | 0.5 | 0.5 | 2 | 50 | 12–15 |
| Saipan | *Porites* | 0 | 0 | 0 | 14 | 0 | 5–17 |
| | *Favia* | 0 | 0 | 0 | 5 | 0 | 4–11 |
| | *Goniastrea* | 0 | 0 | 0 | 26 | 0 | 8–22 |
| Enewetak* | *Porites* | 0.02 | 0 | 0.02 | 63 | 1.6 | 6–32 |
| | *Favia* | 0 | 0 | 0 | 17 | 0 | 8–30 |
| | *Goniastrea* | 0.09 | 0 | 0.09 | 22 | 9 | 6–26 |
| Gilbert Islands | *Porites* | 0.5 | 0.2<br>(0) | 0.3<br>(0.5) | 32 | 9 | 4–41 |
| | *Favia* | 0 | 0 | 0 | 12 | 0 | 12–27 |
| | *Goniastrea* | 0 | 0 | 0 | 4 | 0 | 7–12 |

TABLE I *(continued)*

| Location | Genus | Mean no. bivalves/head<br>Total | Live surface | Dead surface | No. of heads | % Heads with bivalves | Coral diameter range (cm) |
|---|---|---|---|---|---|---|---|
| Australia | *Porites* | 0.1 | 0 | 0.1 | 13 | 8 | 9-41 |
| | *Favia* | 1.2 | 0 | 1.2 | 19 | 32 | 7-37 |
| | *Goniastrea* | 0.4 | 0.1 | 0.3 | 12 | 25 | 6-31 |
| Samoa | *Porites* | 0 | 0 | 0 | 10 | 0 | 8-15 |
| Tonga | *Porites* | 3.2 | 2.7<br>(0.6) | 0.5<br>(2.6) | 13 | 62 | 8-13 |
| Tuamotu Islands | *Porites* | 0.14 | 0.07<br>(0) | 0.07<br>(0.14) | 14 | 7 | 5-16 |
| | *Favia* | 0.09 | 0 | 0.04 | 11 | 9 | 5-16 |
| Totals | | | | | 306 | 10 | |
| Eastern Pacific | | | | | | | |
| Gulf of Panama | *Porites* | 33.7 | 18.7<br>(14.0) | 16.5<br>(21.2) | 11 | 100 | 6-19 |
| | *Pavona* | 20.9 | 5.1<br>(4.4) | 15.8<br>(16.5) | 11 | 91 | 5-18 |
| Galapagos Is. | *Porites* | 13.8 | 12.3 | 1.5 | 4 | 100 | 6-12 |
| | *Pavona* | 31.0 | 4.9<br>(4.6) | 26.1<br>(26.4) | 8 | 100 | 6-13 |
| Totals | | | | | 34 | 97 | |
| Western Atlantic | | | | | | | |
| Florida | *Porites* | 1.2 | 0.17 | 1.04 | 23 | 39 | 10-30 |
| | *Dichocoenia* | 1.8 | 0 | 1.8 | 5 | 60 | 8-36 |
| | *Colpophyllia* | 0 | 0 | 0 | 3 | 0 | 13-24 |
| | *Diploria* | 5.1 | 0.2<br>(0) | 4.9<br>(5.1) | 9 | 100 | 19-46 |
| | *Montastrea* | 3.2 | 0.1<br>(0) | 3.1<br>(3.2) | 10 | 50 | 11-31 |
| Bahama Islands | *Porites* | 1.3 | 0.3<br>(0) | 1.0<br>(1.3) | 15 | 40 | 11-27 |
| | *Dichocoenia* | 7.1 | 0.4<br>(0) | 6.7<br>(7.1) | 14 | 93 | 5-19 |
| | *Colpophyllia* | 1.0 | 0 | 1.0 | 2 | 100 | 9-18 |
| | *Montastrea* | 1.3 | 0.05<br>(0) | 1.24<br>(1.3) | 17 | 65 | 8-19 |
| Puerto Rico | *Porites* | 0.06 | 0 | 0.06 | 15 | 6 | 11-23 |
| | *Diploria* | 0.17 | 0 | 0.17 | 6 | 17 | 15-32 |
| | *Montastrea* | 1.0 | 0.17 | 0.83 | 6 | 33 | 6-43 |
| Jamaica | *Porites* | 0.09 | 0 | 0.09 | 11 | 9 | 7-18 |
| | *Diploria* | 0.3 | 0 | 0.3 | 3 | 33 | 8-18 |
| | *Montastrea* | 0 | 0 | 0 | 3 | 0 | 8-19 |
| Haiti | *Porites* | 0.14 | 0 | 0.14 | 7 | 14 | 7-15 |
| | *Diploria* | 0 | 0 | 0 | 1 | 0 | 18 |
| St. Thomas | *Porites* | 0.6 | 0.33 | 0.25 | 12 | 25 | 9-22 |
| | *Colpophyllia* | 0 | 0 | 0 | 2 | 0 | 9-25 |
| | *Montastrea* | 0 | 0 | 0 | 6 | 0 | 6-19 |
| Belize | *Colpophyllia* | 0 | 0 | 0 | 2 | 0 | 11-26 |
| | *Siderastrea* | 0 | 0 | 0 | 2 | 0 | 9-17 |
| Guadaloupe | *Porites* | 2.0 | 0 | 2.0 | 2 | 50 | 11-29 |

TABLE I *(continued)*

| | | Mean no. bivalves/head | | | | | |
|---|---|---|---|---|---|---|---|
| Location | Genus | Total | Live surface | Dead surface | No. of heads | % Heads with bivalves | Coral diameter range (cm) |
| Barbados | *Porites* | 0.1 | 0 | 0.1 | 10 | 10 | 7–20 |
| | *Dichocoenia* | 4 | 0 | 4 | 1 | 100 | 8 |
| Curacao | *Porites* | 1.5 | 1.0 | 0.5 | 9 | 40 | 6–13 |
| | | | (0.6) | (0.9) | | | |
| | *Colpophyllia* | 0 | 0 | 0 | 7 | 0 | 10–21 |
| Colombia | *Porites* | 0 | 0 | 0 | 4 | 0 | 6–15 |
| Panama | *Colpophyllia* | 1.75 | 0.75 | 1.0 | 4 | 50 | 13–22 |
| Venzuela | *Porites* | 2.0 | 0.4 | 1.6 | 8 | 50 | 7–16 |
| | | | (0.2) | (1.8) | | | |
| | *Dichocoenia* | 20.0 | 0.3 | 19.7 | 3 | 67 | 9–24 |
| | | | (0) | (20) | | | |
| | *Diploria* | 3.4 | 0.4 | 3.0 | 7 | 57 | 8–22 |
| | | | (0) | (3.4) | | | |
| | *Montastrea* | 4.0 | 0.3 | 3.7 | 10 | 70 | 7–22 |
| | | | (0) | (4.0) | | | |
| | *Siderastrea* | 4.9 | 3.0 | 1.9 | 7 | 100 | 4–16 |
| | | | (1.1) | (3.8) | | | |
| | *Meandrina* | 5.3 | 0 | 5.3 | 3 | 100 | 21–25 |
| | *Stephanocoenia* | 3.9 | 2.7 | 1.2 | 11 | 91 | 6–17 |
| | | | (1.1) | (2.8) | | | |
| Brazil | *Porites* sp. | 0.9 | 0.5 | 0.4 | 12 | 42 | 7–25 |
| | | | (0.2) | (0.7) | | | |
| | *Favia* sp. | 1.2 | 0.4 | 0.8 | 10 | 70 | 5–11 |
| | | | (0.1) | (1.1) | | | |
| Totals | | | | | 282 | 45 | |

* Data are from a study of bioerosion at Enewetak (Highsmith, 1979).

sequently surrounded by coral growth, 79% of the bivalves were in dead surface zones. In all geographic areas excepting the eastern Pacific, 92% of bivalves occurred in dead zones. Some or all of the remainder may have been encircled by later coral growth but this could not be determined with certainty. Few boring bivalves are known to settle on live coral tissue (Highsmith, 1979).

Ratios of the circumference of the basal attachment to the circumference of live coral tissue were determined for locations in which five or more coral heads were measured (Table II). Ratios for western Atlantic locations are significantly lower than those for western Pacific ($P < 0.001$) or Indian Ocean locations ($P < 0.01$; Mann–Whitney $U$-tests). Western Pacific and Indian Ocean ratios are not significantly different. Data from the two eastern Pacific locations are not sufficient for statistical comparisons, but the values are closer to those for the Indian Ocean and western Pacific than those for the western Atlantic.

One consequence of failing to maintain tissue over the lower part of the skeleton is that corals cannot enlarge their bases as they grow. As expected from the base/live ratios, the base to maximum circumference ratios (Table II) for the western Atlantic are lower than those for western Pacific ($P < 0.001$) or Indian Ocean sites ($P < 0.01$; Mann–Whitney *U*-tests). Western Pacific and Indian Ocean ratios are not significantly different.

TABLE II

Mean ratios of basal circumference to live tissue circumference and maximum circumference: *N*, number of coral heads measured; ratios were not calculated for samples of $N < 5$.

| | | Circumference ratios | |
|---|---|---|---|
| Location | *N* | Base/live | Base/max. |
| Indian Ocean | | | |
| Red Sea | 34 | 0.61 | 0.65 |
| Singapore | 8 | 0.62 | 0.58 |
| Maldive Is. | 30 | 0.58 | 0.54 |
| Seychelles Is. | 9 | 0.45 | 0.40 |
| Chagos Is. | 8 | 0.85 | 0.78 |
| Aldabra | 5 | 0.65 | 0.52 |
| Cosmol. & Farquhar | 5 | 0.41 | 0.34 |
| Mauritius | 8 | 0.66 | 0.45 |
| $\bar{X}$ | | 0.60 | 0.53 |
| Western Pacific | | | |
| Philippine Is. | 17 | 0.76 | 0.65 |
| Saipan | 26 | 0.62 | 0.57 |
| Enewetak | 47 | 0.70 | 0.69 |
| Gilbert Is. | 29 | 0.63 | 0.55 |
| Australia | 34 | 0.45 | 0.40 |
| Samoa | 6 | 0.78 | 0.43 |
| Tonga | 12 | 0.72 | 0.55 |
| Tuamotu Is. | 24 | 0.72 | 0.59 |
| $\bar{X}$ | | 0.67 | 0.55 |
| Eastern Pacific | | | |
| Gulf of Panama | 12 | 0.62 | 0.61 |
| Galapagos Is. | 5 | 0.72 | 0.72 |
| $\bar{X}$ | | 0.67 | 0.67 |
| Western Atlantic | | | |
| Florida | 45 | 0.39 | 0.36 |
| Bahama Is. | 47 | 0.49 | 0.43 |
| Puerto Rico | 24 | 0.35 | 0.32 |
| Jamaica | 16 | 0.39 | 0.35 |
| Haiti | 7 | 0.40 | 0.39 |
| St. Thomas | 20 | 0.45 | 0.39 |
| Barbados | 6 | 0.52 | 0.48 |
| Curacao | 16 | 0.43 | 0.35 |
| Venezuela | 48 | 0.39 | 0.35 |
| Brazil | 22 | 0.35 | 0.33 |
| $\bar{X}$ | | 0.42 | 0.38 |

Although some of the mean ratios for geographic areas are not statistically different, they are in the same rank order, except for the eastern Pacific, as the percentage of corals with boring bivalves and mean number of boring bivalves per head. The eastern Pacific appears to be unique in that many bivalves occur in the live part of corals (Table I). Thus, eastern Pacific corals contain more boring bivalves than expected from the relatively high base/live circumference ratios (Table II).

Most western Atlantic massive coral genera do not occur in the Indo-Pacific. Members of the genus *Favia*, however, are closely related to *Montastrea* species (J. W. Wells, pers. comm.) and *Porites* is circumtropical. Therefore, I have compared western Atlantic and Indo-Pacific attachment/live ratios within *Porites* and between *Montastrea* and *Favia* (Table III). *Porites* attachment/live circumference ratios are significantly larger in the Western Pacific ($P < 0.001$) and Indian Ocean ($P < 0.001$) than in the western Atlantic (Mann–Whitney *U*-tests). There is no difference between

TABLE III

Mean ratios of basal circumference to live tissue circumference for massive *Porites* spp. and *Montastrea–Favia* spp. from different geographic locations: *N*, in parentheses, number of coral heads measured; ratios were not calculated for $N < 5$.

| Location | *Porites* sp. (*N*) | *Montastrea–Favia* sp. (*N*) |
|---|---|---|
| Indian Ocean | | |
| Red Sea | 0.91 (16) | 0.55 (9) |
| Maldive Is. | 0.75 (13) | 0.65 (10) |
| Chagos Is. | 0.85 (8) | |
| Mauritius | 0.68 (6) | |
| $\bar{X}$ | 0.81 | |
| Western Pacific | | |
| Philippine Is. | 0.93 (6) | 0.68 (9) |
| Saipan | 0.76 (12) | 0.94 (5) |
| Enewetak | 0.70 (14) | 0.78 (16) |
| Gilbert Is. | 0.75 (17) | 0.47 (9) |
| Australia | 0.56 (9) | 0.55 (16) |
| Samoa | 0.78 (6) | |
| Tonga | 0.72 (12) | |
| Tuamotu Is. | 0.68 (13) | 0.78 (11) |
| $\bar{X}$ | 0.71 | 0.68 |
| Western Atlantic | | |
| Florida | 0.30 (20) | 0.44 (9) |
| Bahama Is. | 0.38 (14) | 0.53 (17) |
| Puerto Rico | 0.27 (15) | 0.59 (6) |
| Jamaica | 0.35 (10) | |
| Haiti | 0.38 (6) | |
| St. Thomas | 0.41 (12) | 0.72 (6) |
| Barbados | 0.49 (5) | |
| Curacao | 0.54 (9) | |
| Venezuela | 0.37 (9) | 0.46 (10) |
| Brazil | 0.27 (11) | 0.47 (10) |
| $\bar{X}$ | 0.36 | 0.52 |

Western Pacific and Indian Ocean *Porites* ratios. For *Montastrea-Favia*, attachment/live ratios are also greater in the western Pacific than the western Atlantic ($P < 0.05$). Thus, the tendency for the basal area of western Atlantic massive coral skeletons to lack living tissues does not appear to be a growth characteristic of coral genera that happen to be restricted to that region.

## BIOEROSION AND PRODUCTIVITY

Table IV gives the locations where corals were collected and the percentages of coral heads containing boring bivalves, arranged by productivity class (from Fig. 1). I used intermediate categories (100, 150, and 250 mg C · m$^{-2}$ · day$^{-1}$) for locations on borders between productivity classes. The overall percentage of corals with boring bivalves for each class is strongly correlated with productivity (Fig. 3; Spearman rank correlation coefficient, $r_s = 0.86$, $P < 0.01$). The regression $Y = 0.15\,X - 6.17$, where $Y$ = percentage of corals with boring bivalves and $X$ = gross primary productivity in mg C · m$^{-2}$ · day$^{-1}$, accounts for 80% of the variance, and the regression coefficient is significant at the 0.005 level.

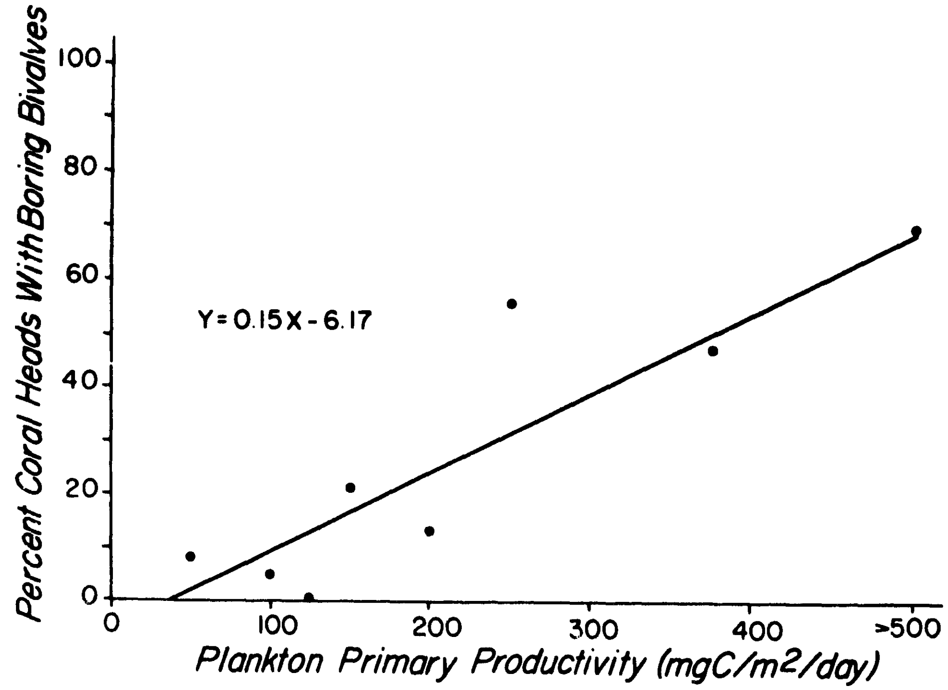

Fig. 3. Percentage of massive corals with boring bivalves as a function of plankton primary productivity: see Table IV for number of observations.

Abundances of non-boring bivalves ($r_s = 0.83$, $P < 0.01$), ahermatypic corals ($r_s = 0.87$, $P < 0.01$), and serpulid polychaetes ($r_s = 0.76$, $P < 0.05$) associated with the same coral heads are also all significantly correlated with phytoplankton productivity (Fig. 4A). Further, numbers of pyrgomatine (Balanidae: Pyrgomatinae) barnacles

TABLE IV

ocation and percentage of coral heads with boring bivalves arranged according to phytoplankton productivity at the location (data from Fig. 1): *N*, in parentheses, number of heads.

| Plankton primary productivity (mg C · $m^{-2}$ · $day^{-1}$) | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| < 100 | | ≈ 100 | | 100–150 | | ≈ 150 | | 150–250 | | ≈ 250 | | 250–500 | | < 500 | |
| ocation (*N*) | % | Location (*N*) | % | Location (*N*) | % | Location (*N*) | % | Location (*N*) | % | Location (*N*) | % | Location (*N*) | % | Location (*N*) | % |
| hagos Is. (8) | 0 | Gilbert Is. (48) | 6 | Seychelle Is. (10) | 0 | Maldive Is. (31) | 10 | Ceylon (4) | 25 | Bahama Is. (48) | 67 | Red Sea (35) | 40 | Aldabra (7) | 71 |
| auritius (10) | 0 | Samoa (10) | 0 | Farquhar (2) | 0 | Australia (44) | 23 | Zanzibar (2) | 0 | Curacao (16) | 25 | Philippine Is. (19) | 26 | Singapore (16) | 69 |
| aipan (45) | 0 | | | | | Tonga Is. (13) | 62 | Cosmoledo (3) | 0 | | | Galapagos Is. (12) | 100 | Gulf of Panama (22) | 95 |
| newetak (102) | 3 | | | | | Jamaica (17) | 12 | Puerto Rico (27) | 15 | | | Panama (4) | 50 | Florida (50) | 52 |
| uamotu Is. (25) | 8 | | | | | Haiti (8) | 12 | Belize (4) | 0 | | | | | Venezuela (49) | 76 |
| razil (22) | 55 | | | | | St. Thomas (20) | 15 | Barbados (11) | 18 | | | | | | |
| | | | | | | Guadaloupe (2) | 50 | Colombia (4) | 0 | | | | | | |
| $\Sigma N = 212$ | | $\Sigma N = 58$ | | $\Sigma N = 12$ | | $\Sigma N = 135$ | | $\Sigma N = 55$ | | $\Sigma N = 64$ | | $\Sigma N = 70$ | | $\Sigma N = 144$ | |

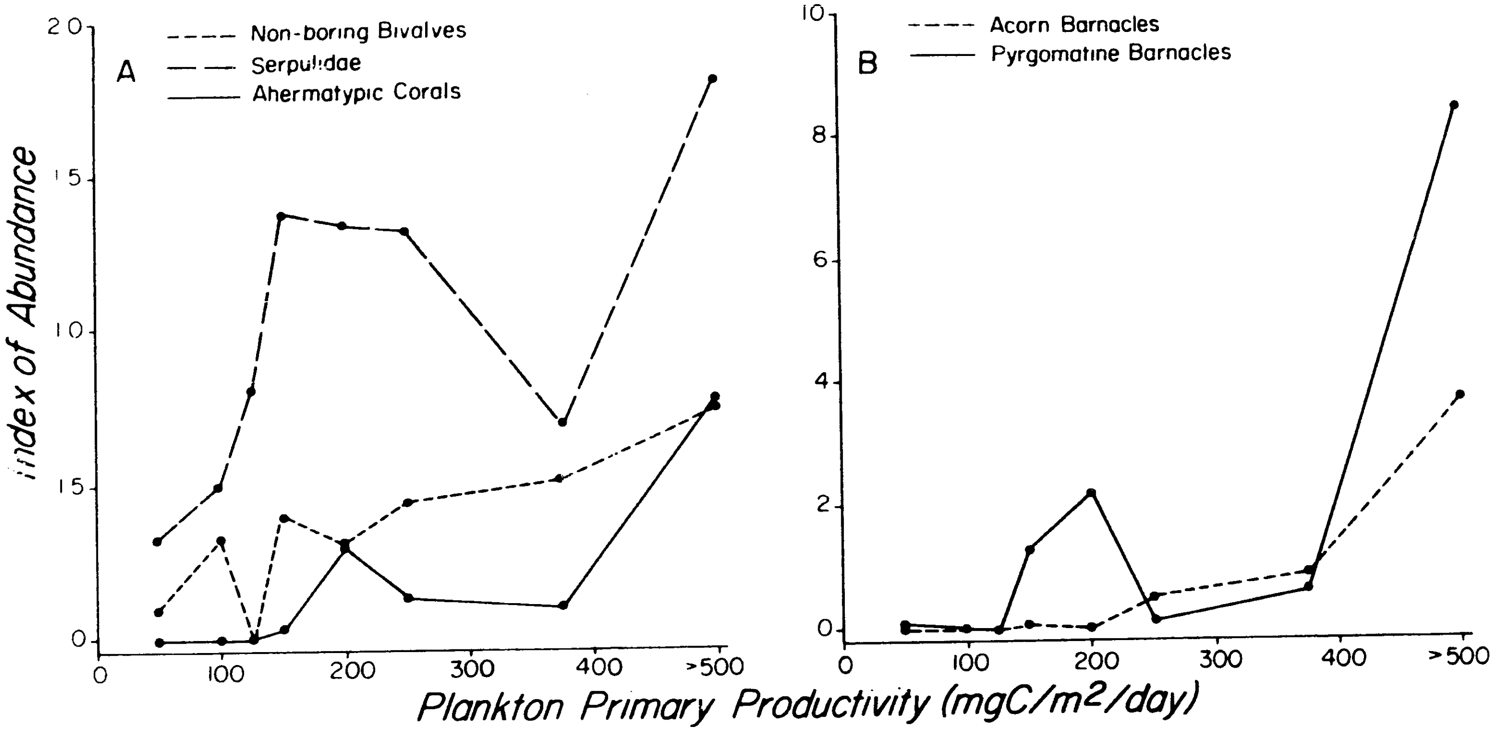

Fig. 4. A, abundance of serpulid polychaetes, non-boring bivalves, and ahermatypic corals attached to massive corals: index = mean number of individuals per head for non-boring bivalves and ahermatypic corals; for serpulids, index = mean rank where 1 = 1–4, 2 = few, 3 = several, 4 = many, 5 = numerous; B, mean number of pyrgomatine barnacles per coral head on live (at time of collection) surfaces and mean number of acorn barnacles per coral head on dead skeletal surfaces; see Table IV for number of observations.

($r_s = 0.73$, $P < 0.05$) in the live (at time of collection) portion of coral heads and acorn (Balanidae: Balaninae) barnacles ($r_s = 0.73$, $P < 0.05$) on dead surfaces are also significantly correlated with productivity (Fig. 4B). Data for Brazilian corals are excluded from the pyrgomatine curve in Fig. 4B. The 22 heads contained 2965 of these barnacles. The corals were collected near Porto Seguro, which according to Fig. 1 is in the lowest productivity category. This low ranking is probably due to a lack of data rather than low productivity (K. Sebens, pers. comm.). All other coastal zones in Fig. 1 are in higher productivity classes.

## DISCUSSION

### BIOEROSION AND PRODUCTIVITY

The productivity map of Koblentz-Mishke *et al.* (1970) is based on data from over 7000 stations. These stations were spread over an enormous area and most were undoubtedly in open water. There have been very few studies of plankton primary productivity on coral reefs. Furthermore, most reef data were collected by different methods in different seasons and years, making valid comparisons difficult. The data available suggest that plankton productivity may, however, be seasonal in the western Atlantic (Curl, 1960; Richards, 1960; Jones, 1963, Margalef, 1968; Milliman, 1969; Reiswig, 1971; Glynn, 1973; Sander & Steven, 1973; Kidd & Sander, 1979) and Indian Ocean (Kabanova, 1968; Qasim & Sankaranarayanan, 1970; Qasim *et al.*, 1972; Krey & Babenerd, 1976), that plankton productivity on western Atlantic reefs is generally higher than that on western Pacific reefs (Doty & Oguri, 1956; Marshall, 1965; Jeffrey, 1968; Gordon *et al.*, 1971; Marshall *et al.*, 1975; Sournia & Ricard, 1975, 1976; Sournia, 1976a, b; Ricard, 1976, 1977), and that productivity of water passing over reefs generally increases 2- to 5-fold. Bacterial biomass increases similarly (Sorokin, 1973; Moriarity, 1979). Plankton productivity on and behind coral reefs is a small multiple of productivity in the surrounding ocean waters. Thus, Fig. 1 is suitable for estimating relative plankton primary productivity for coral reefs in different geographic regions.

The highest densities of boring bivalves occur in corals from eastern Pacific locations where waters are enriched by upwelling (Forsbergh, 1963; Smayda, 1966; Wooster & Guillen, 1974; Glynn, 1977; Glynn & Macintyre, 1977). Significantly more western Atlantic corals contained boring bivalves than did Indo-west Pacific corals and a larger proportion of western Atlantic reefs are in areas of high productivity (Fig. 1). Similarly, more Indian Ocean reefs are in regions of high productivity than are western Pacific reefs (Fig. 1).

The significant relationship between abundance of boring bivalves and plankton productivity (Fig. 3) supports the hypothesis that bioerosional damage to coral skeletons by boring organisms is a function of plankton primary productivity. The correlations of non-boring bivalve, ahermatypic coral, serpulid, pyrgomatine and acorn barnacle abundances with plankton productivity (Fig. 4) serve as independent tests of the hypothesis. These are not boring organisms but, like boring bivalves and sponges, are planktivorous.

The large-scale correlation of borer abundance with productivity suggests that a similar correlation should obtain on a local scale. As water crosses reefs and productivity increases (see above), the abundance of boring sponges and bivalves, with concomitant damage to coral skeletons, should also increase, especially if productivity is raised above 150–200 mg C · m$^{-2}$ · day$^{-1}$.

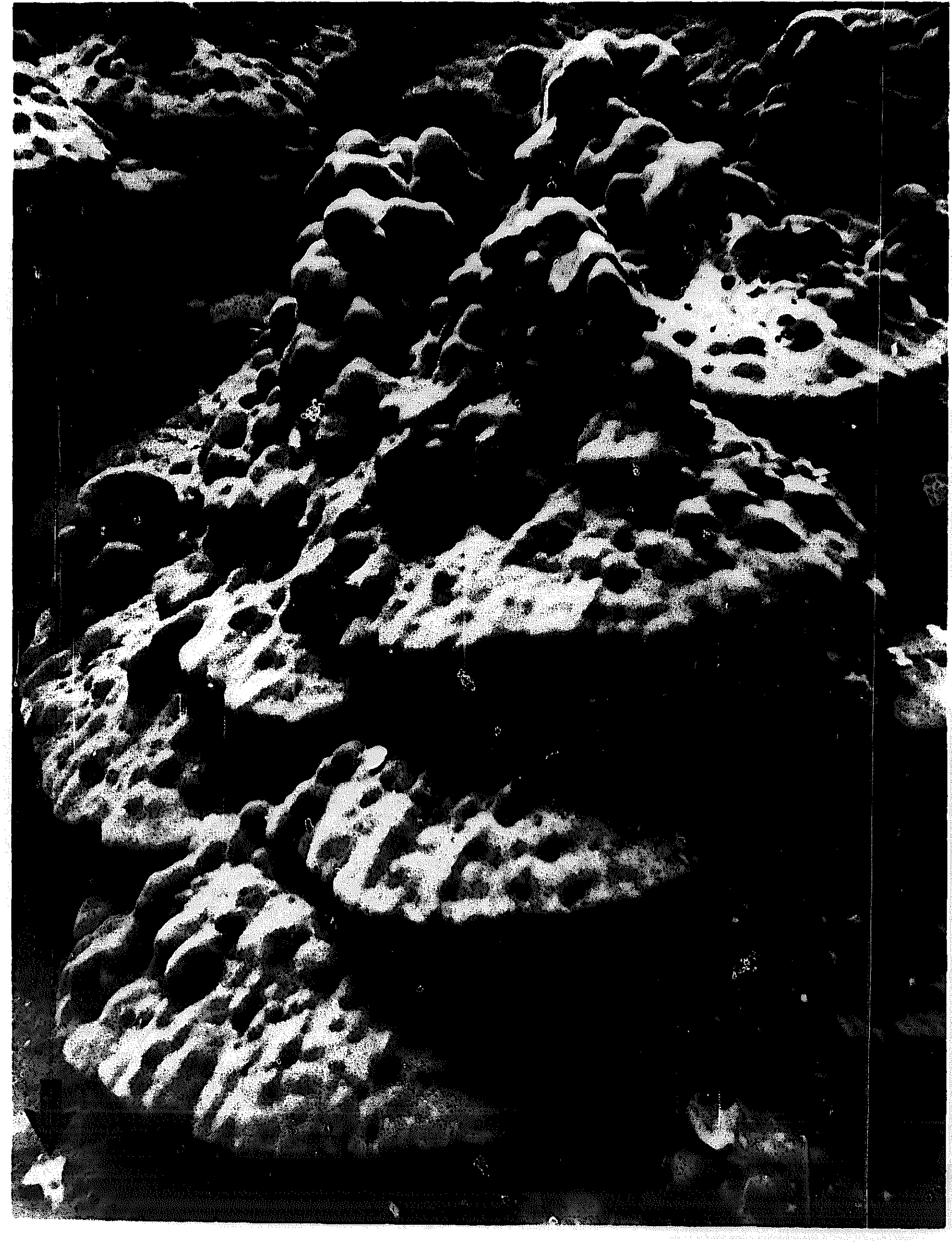

Fig. 5. *Porites lobata* Dana colony damaged (arrows) by the triggerfish *Pseudobalistes naufragium* (Jordan & Starks, 1895) in order to feed on lithophagine bivalves: note empty *Lithophaga* burrows; photograph by Mark Stouder, Saboga, Pearl Islands, Panama.

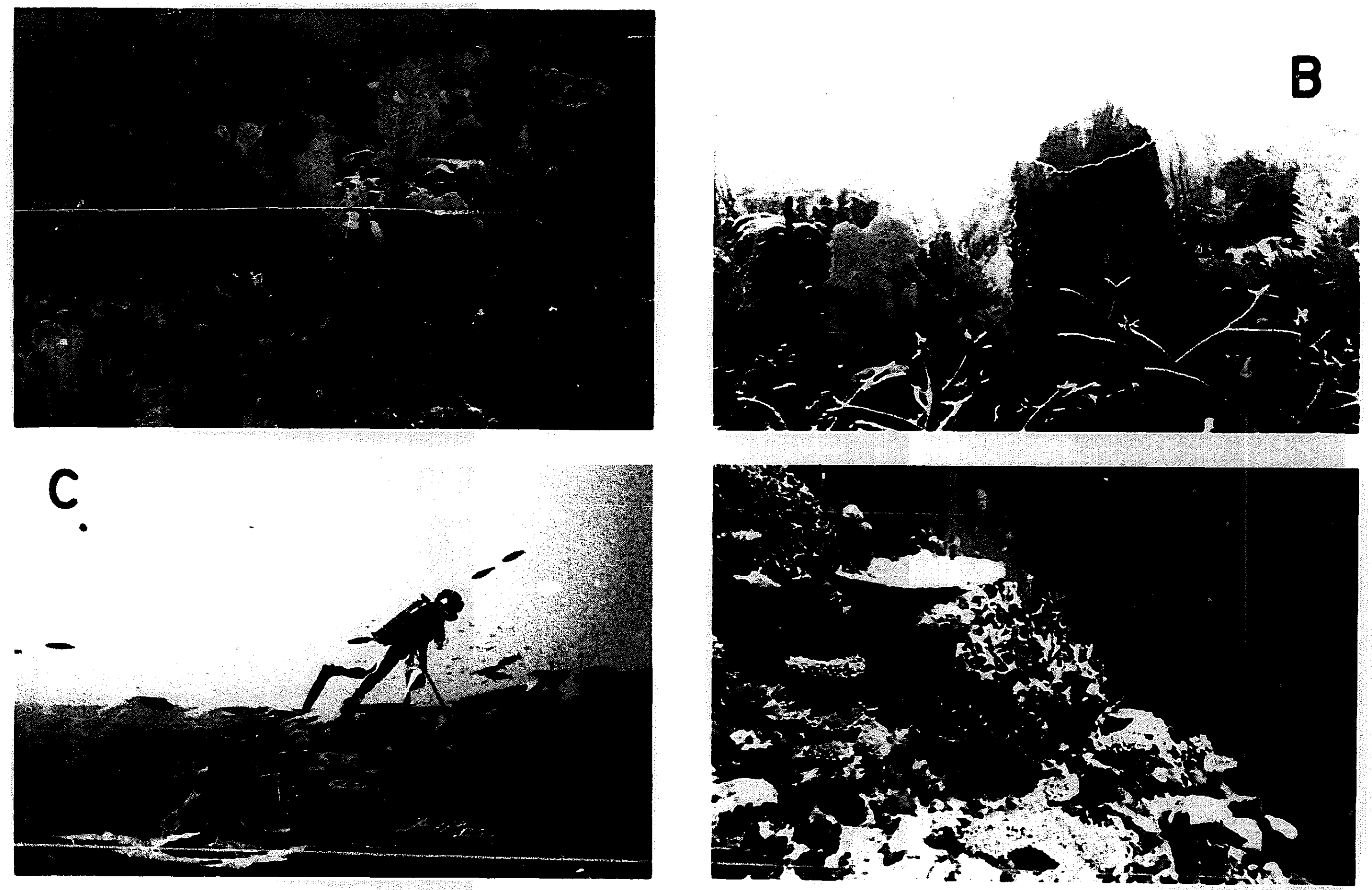

Fig. 6. A and B, reef scenes on Belize barrier reef where plankton primary productivity is relatively high (Fig. 1); note presence of gorgonians and sponges, depth ≈ 15 m; C, windward reef terrace at Enewetak Atoll, Marshall Islands, where plankton productivity is low (Fig. 1); note dominance of corals and lack of other large, sessile organisms; depth ≈ 20 m; D, lagoon pinnacle at Enewetak Atoll, Marshall Islands; depth ≈ 10 m.

Margalef (1968) suggested that hermatypic corals are indicators of infertile waters and that corals are restricted to low latitudes by increased productivity at higher latitudes, rather than temperature. The correlations discussed above suggest the mechanism by which high productivity may restrict coral distribution. They indicate that planktivores will be more abundant on coral reefs where plankton primary productivity is relatively high, and lead to the hypothesis that corals will be progressively less dominant members of the reef community over a gradient of increasing phytoplankton productivity. This increased productivity provides an energy source for a variety of new food chains containing members that (1) burrow into and weaken coral skeletons (Highsmith, 1979), (2) damage corals in order to prey on the planktivorous infauna (Fig. 5; Glynn *et al.*, 1972) and (3) compete with corals for food or space (Fig. 6; Birkeland, 1977). Hence, waters with high phytoplankton productivity should be less favorable locations for hermatypic corals as, for example, found in the Marquesas Islands (Sournia, 1976b) or along the Pacific coast of Panama (Glynn *et al.*, 1972) where reef development is poor.

Conditions favoring high phytoplankton productivity such as elevated nitrogen and phosphate concentrations also favor high productivity by benthic algae (Kinsey & Domm, 1974; Birkeland, 1977). Rapid recruitment and growth of benthic algae reduces the area of hard substratum available for coral larval settlement and may also result in overgrowth of juvenile corals (Adey *et al.*, 1976; Birkeland, 1977; Rogers, 1979). As with phytoplankton, food chains originating with benthic algae may contain members that kill or damage corals. Pomacentrid fish, for example, kill portions of coral colonies within their territories in order to "farm" algae (Kaufman, 1977). In the highly productive area of the Pearl Islands, Panama, pomacentrids are an extremely important source of coral mortality (G. Wellington, P. Glynn, pers. comm.).

Thus, high primary productivity, both planktonic and benthic, appears to affect the distribution of corals by inhibiting coral recruitment and enhancing establishment of food chains containing members that damage or compete with corals. Furthermore, the high phosphate concentrations at locations with high productivity may directly reduce coral growth rates by inhibiting calcium carbonate crystal formation (Kinsey & Davies, 1979). Lower growth rates would impair the ability of corals to compete with benthic algae and filter feeders.

## WESTERN ATLANTIC AND INDO-PACIFIC CORALS

While bioerosion is a dynamic process correlated with productivity, there may indeed be a substantial difference between Indo-Pacific and western Atlantic coral species' ability to maintain live tissue over the lower part of their skeletons (Table II). Western Atlantic corals have less of the basal area on their skeleton covered by live tissue, resulting in greater exposure of the base to colonization by boring organisms and weaker basal attachments because the base cannot be enlarged as the upper part of the head continues to grow. On the average, western Atlantic massive corals have ≈45% less skeletal material in their bases than do western Pacific corals having the same maximum circumference and similar bulk densities. Since this is not simply a characteristic of western Atlantic coral genera (Table III), the causes remain unclear. Some western Atlantic corals exhibit periodic growth (Fig. 7), suggesting there may be unfavorable periods (seasons?) when tissue on the periphery of the colony does not survive. Many colonies of the important reef-building coral *Montastrea annularis*, however, simply maintain live tissue only on the very top of the skeleton, resulting in a columnar growth form (Fig. 4B in Macintyre & Smith, 1974; Fig. 7 in Scatterday, 1974).

Fig. 7. *Siderastrea siderea* (Ellis & Solander) from −20 m, Morro Grande, Colombia, showing intermittent skeletal deposition: collection by A. Antonius, Jan. 1971; scale bars = 1 cm.

What effect does the generally higher level of bioerosion and weaker basal attachment of massive, western Atlantic corals have on reef development? On the average, more western Atlantic corals should be dislodged by storms than Indo-Pacific corals in storms of equal intensity. At least some Caribbean reefs have, however, grown as fast or faster than Indo-Pacific reefs during the Holocene (Adey, 1978). Apparently, corals and coral reefs recover rather quickly from all but the most intense storms (Stoddart, 1974; Shinn, 1976). Since the drag force per unit area required to detach massive corals is very high for small heads (Highsmith, 1979), western Atlantic corals may become large enough to reproduce and/or survive detachment before they reach a size likely to be broken off by storms. Corals, particularly larger heads and fragments, often survive detachment and continue to grow in new locations (Glynn *et al.*, 1965; Dollar, 1975; Randall & Eldredge, 1977; Highsmith, 1978, 1979; Birkland *et al.*, 1979). At Carrie Bow Cay, Belize, over 40% of coral colonies and fragments >10 cm in greatest dimension survived detachment during Hurricane Gerta in 1978 (Highsmith *et al.*, in prep.).

The evolutionary reasons for and ecological consequences of Western Atlantic corals retaining live tissue over less of their skeleton than do massive corals elsewhere in the world provide an interesting challenge for future work.

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