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PHENOTYPIC VARIATION IN THE CORAL *MONTASTREA CAVERNOSA* AND ITS EFFECTS ON COLONY ENERGETICS

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Abstract

Variation in polyp expansion; zooxanthellae density; coloration; and polyp shape, size, and density can be used to divide shallow water (<20 m) colonies of *Montastrea cavernosa* into two morphs, diurnal and nocturnal. Respiration rates of the morphs are related to the number and size of polyps, an index of biomass. Small changes in the size or number of polyps, while not affecting the size of the whole colony, affect respiration rates. The diurnal morph has greater zooxanthellae densities than the nocturnal morph and correspondingly greater rates of gross primary production. Respiration and gross primary production are both increased by expansion of the polyps. Colonies with low rates of gross primary production are characterized by morphologies and behaviors that reduce maintenance costs. This suggests that limitations of primary production play a major role in the development (and/or evolution) of *M. cavernosa*.

Introduction

The role of zooxanthellae in reef corals has been debated extensively over the last 75 years. It has become increasingly clear that photosynthate from the zooxanthellae provide much or most of the energetic needs of many (if not all) reef corals (see Muscatine, 1973; Muscatine and Porter, 1977; McCloskey *et al.*, 1978). However, the role of zooxanthellae in shaping the behavior and morphology of reef corals remains unclear.

This study examines the effects of morphology and behavior upon the primary production of *Montastrea cavernosa* (Linnaeus). From such an analysis it is possible to determine the extent to which morphology and behavior in *M. cavernosa* colonies maximizes primary production. The study provides an understanding of the factors controlling productivity and also provides a first approximation of the selective importance of primary production in determining colony phenotype.

M. cavernosa is particularly suited for such an analysis. It is common in the fauna of most Caribbean reefs and exhibits a striking variety of phenotypes both within and between habitats. Thus the effects of phenotypic variation can be examined using colonies from both similar and dissimilar environments.

In Panama, differences among *M. cavernosa* colonies have led to the distinction of two morphs, referred to as the large and small polyp forms (Lehman and Porter, 1973) or the diurnal and nocturnal morphs (Lasker, 1976, 1977, 1979). The present study uses the diurnal-nocturnal classification of Lasker (1979), which distinguishes those colonies whose polyps are most commonly expanded during the day, the diurnal morph, from those colonies whose polyps are never expanded during the day, the nocturnal morph. The polyps of both morphs are fully expanded at night.

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METHODS

Laboratory experiments were conducted at the Galeta Marine Laboratory of the Smithsonian Tropical Research Institute in Panama. Field observations and collections of *M. cavernosa* were made in four areas along Panama's Caribbean coast: at Galeta Island (east of the Panama Canal), Buena Ventura Island (at the mouth of Portobelo Harbor), the San Blas Islands, and the Bocas del Toro region.

The morphologic and behavioral data presented here are based on observations of colonies encountered on "distribution dives" at each study site. During these dives all of the *M. cavernosa* colonies found within 3 m of the 2, 5, 10, and 15 m depth contours were examined and data collected concerning the colonies' expansion, polyp size, polyp height, colony shape, and color. At six sites closeup photographs were taken of every second coral. Equal areas were sampled at each depth, but area sampled differed between sites due to differences in the size of the reefs. At some localities, where the reef extended below 15 m, deeper depths were sampled.

Polyp size, in most cases, was scored as large or small depending on whether calice diameter was less than or greater than 6 mm. Polyp size was usually apparent at first observation, since most colonies with large polyps had mean diameters above the 6 mm cutoff (Fig. 1). In cases of uncertainty, 5–10 polyps were measured with a ruler and an average determined. If polyp size was still uncertain ($\bar{x} \simeq 6$ mm) the colony was classified indeterminent and excluded from the analysis. Only 7% of the 671 colonies examined were classified indeterminent.

Accuracy of the field observations was tested by comparing diameters of the 218 photographed colonies to their field classifications. Mean size was calculated from the diameters of 20 polyps measured (± 0.1 mm) from the projected negative of each photograph. Comparison of the two types of polyp size data indicates that 80% of the measured colonies were correctly classified. Closeup photographs were also analyzed for polyp density, by determining the number of polyps per 20 cm^2 of colony surface area.

Polyp height is the vertical distance from the coenosteum to the lip of the calice. Among *M. cavernosa* colonies three distinct states were observed: short, intermediate, and tall. Colonies with short polyps had almost flat surfaces (measured polyp height $\simeq$ 1mm) without distinct polyp walls. Colonies with intermediate polyps had irregular surfaces (polyp height, 2–4 mm) and displayed distinct polyp walls. Col-

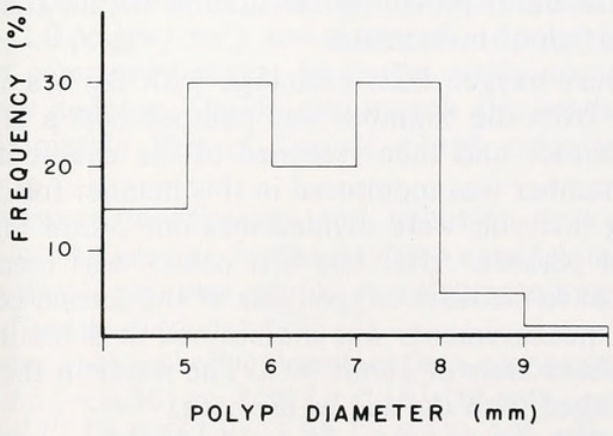

FIGURE. 1. Size frequency distribution of mean polyp diameter. The distribution is based on measurements of 218 colonies from Portobelo and the San Blas Islands. Nocturnal morph colonies usually had mean polyp diameters > 6 mm and diurnal morph colonies < 6 mm.

onies with tall polyps had corallites which distinctly stood out from the coenosteum (polyp height 3–7 mm).

Coenosarc color was scored by noting five apparently distinct colors: red, blue, green, brown, and a white ectodermal coloration. The brown color, which varied in intensity, was recorded as being absent, present, or abundant. The oral disc was usually the same color as the coenoosarc, but in some cases contained other colors. The presence or absence of both a white ectodermal coloring and a "fluorescent" green coloring on the oral disc was also noted.

Weights of polyp and coenosarc tissue were determined from preserved specimens decalcified in 5% HCl. Plugs of tissue then were removed with a cork borer, blotted dry, and weighed on an analytic balance.

Zooxanthellae densities were also determined from preserved specimens. Plugs of tissue from polyp and coenosarc were removed with a cork borer and homogenized in a tissue grinder. The number of zooxanthellae per milliliter of homengenate was then determined from replicate counts made with a hemocytometer. (See Lasker, 1977, for further details.)

Photosynthesis and respiration rates were determined by observing oxygen fluxes of 18 colonies in a closed chamber respirometry unit in light and darkness. Colonies were collected from virtually identical micro-habitats at 8–10 m depth on a fringing reef north of Buena Ventura Island. Colonies collected were small enough to fit in the 10 cm diameter respirometric chamber and were largely, but not wholly, free of encrusting and boring organisms. No adjustments were made for the respiratory activity of these forms.

Colonies were transported from the field to the laboratory in a darkened cooler and were always kept in sea water. The colonies were allowed to acclimate in shaded sea tables for 2–3 days and were checked for normal behavior and appearance before respirometric measurement. Colonies were classified nocturnal or diurnal on the basis of behavior at the time of collection and in the laboratory.

Respirometric measurements began within 5 days of collection. During the 5 to 6 days of measurement the colonies were kept in a constant temperature water bath at 28°C and were exposed to 12 h of 25 μEinsteins$\cdot m^{-2} \cdot s^{-1}$ illumination each day. Measurements were made as follows: Pairs of colonies, usually one of each morph, were measured in tandem. The colonies were placed in glass chambers between 0800 and 0900 h and were allowed to acclimate in the dark for several hours. During the acclimation, sea water was pumped into the chamber from the surrounding sea water bath, providing circulation within the chamber and preventing the accumulation of metabolites.

In order to measure oxygen flux, exchange with the sea water bath was discontinued; sea water from the chamber was pumped past a Hydrolab TDO-2 polarographic oxygen sensor and then returned to the chamber. Dissolved oxygen content within the chamber was monitored in this manner for 35 min. For analysis the 35 min sampling intervals were divided into one 5-min initialization and two 15-min measurement periods. After the first colony was measured the pumping system was rearranged to measure oxygen flux of the second colony. Flow through the chamber during measurements was maintained at 3 l/min, which resulted in a florescein dye residence time of about 90 s. The water in the chamber not being measured was exchanged with the sea water bath.

At the end of each day's measurements the colonies were removed and a measurement made of oxygen flux of the empty chamber. This value was then used to correct all of that day's measurements. The 190 l of sea water in the water bath

was replaced daily, and after several days of operation the entire system was drained, washed with 50% ethanol, and dried.

Photosynthesis of contracted colonies was measured at light intensities of 25, 93, and 1890 μEinsteins $\cdot m^{-2} \cdot s^{-1}$. Polyp expansion of the colony was noted at the start and finish of each 15 min period. In cases where polyp closure was desired the chamber was rocked until the polyps contracted. Colonies did not always expand fully during the experiment. Consequently, some were measured repeatedly to obtain large enough sample sizes. Two morning and two afternoon measurements (35 min each) were made at each light intensity. Dark-chamber measurements alternated with light measurements, and additional dark-chamber measurements were made at night. Measurements at 1890 μEinsteins $\cdot m^{-2} \cdot s^{-1}$ were always made the last day of the experiments in order to avoid non-reversible photoinhibition. Light at the two lower intensities was provided with cool white fluorescent bulbs, supplemented with incandescent flood lights for the high light intensity. Light measurements were made with a Lambda Instruments quantum flux sensor (LI-190).

Following the measurements, colonies were preserved in formalin. Surface area was measured by carefully wrapping aluminum foil over the colony and then determining the area of aluminum foil used from its weight. Volume of the corallum was determined by displacement in water, and then subtracted from the measurement chamber volume to determine the amount of sea water present during the experiment and thereby to calculate oxygen flux. The diameters of the calices of 20 polyps were measured to the nearest 0.05 mm with a vernier caliper and the means (reported here as polyp size) calculated. The number of polyps on each colony was also counted.

Results

Morphologic variation

M. cavernosa's morphs were defined on the basis of their expanison behavior, but they are also distinguishable on the basis of a number of morphological characters, most conspicuously polyp size. Mean polyp diameters of randomly selected colonies were bimodally distributed (Fig. 1) and large polyps were most commonly associated with nocturnal morph colonies (Table 1). Nocturnal morph colonies also had lower polyp densities (0.5–1.0 polyps/cm^2) and more frequently had tall polyps than the diurnal morph (Table I). The diurnal morph had small polyps, higher polyp densities (1.5–2.0 polyps/cm^2), and intermediate polyp height. Diurnal morph colonies were more commonly planar in shape, while nocturnal morph colonies were more commonly nodular. The diurnal morph also tended to have brown coloration, and approximately 50% of diurnal morph colonies had brilliant green oral discs.

Relationships between morphology and behavior were most pronounced at depths less than 15 m. At greater depths daytime expansion became less common (Fig. 2). Increasing depth also was related to a decrease in polyp density (polyps/cm^2) independent of polyp diameter (Fig. 3).

Polyps had greater zooxanthellae densities than coenosarc among both morphs (diurnal morph—6.65 [$\pm$0.36] vs. 3.39 [$\pm$0.16] 10^6 cells/cm^2 [$\pm$standard error]; nocturnal morph—4.72 [$\pm$0.56] vs. 2.93 [$\pm$0.17] 10^6 cells/cm^2). Polyps of the diurnal morph also had greater zooxanthellae densities than those of the nocturnal morph ($p < 0.05$, Mann-Whitney U test).

TABLE I

Contingency tables showing the relationship between daytime expansion and morphologic traits among colonies from reefs along Panama's Caribbean coast. See text for explanation of polyp size and polyp height.

		Daytime Polyp Expansion		Significance of χ^2-test
		contracted	expanded	
Polyp size	large	204	30	$P \ll 0.001$
	small	125	182	
Polyp height	tall	43	15	$P \ll 0.001$
	intermediate	117	173	
	short	207	37	
Colony shape	planar	122	131	$P \ll 0.001$
	nodular	229	85	
Brown coenosarc pigment	abundant	162	154	$P \ll 0.001$
	present	85	37	
	absent	111	29	
Green coenosarc pigment	present	133	49	$P < 0.005$
	absent	224	170	
White oral disc	present	23	36	$P < 0.002$
	absent	275	183	
Green oral disc	present	16	110	$P \ll 0.001$
	absent	283	106	

Respirometric measurements

Mean rates of respiration and gross primary production of each of the 18 colonies are presented in Table II. Variability among respiration rates of the colonies was great and no statistically significant differences between morphs were found. Respiration rates of colonies were significantly greater when polyps were expanded ($p = 0.01$, randomization test; Siegel, 1956). Unlike respiration rates, gross primary productivity of the diurnal morph was significantly greater than that of the nocturnal morph at all three light intensities ($p < 0.05$, Mann-Whitney U test). Gross primary production of diurnal morph colonies at 25 μEinsteins$\cdot m^{-2} \cdot s^{-1}$ was significantly greater when their polyps were expanded ($p = 0.027$, randomization test). The nocturnal morph could not be induced to expand in the light and consequently the effects of expansion on it could not be ascertained.

DISCUSSION

Effect of morphology and behavior on primary production

Colonies' and morphs' differing rates of respiration and photosynthesis (Table II) do not reflect different physiologies; rather, they are consequences of the colonies' differing morphologies. The effects of morphology are best illustrated by respiration rates. Respiration by any organism can be expected to vary with the organisms' biomass. Respiration rates presented in Table II are adjusted for the colonies' differing surface areas, an index of biomass. However, surface area alone is a poor estimator of colony biomass. Polyps were more massive than coenosarc (Fig. 4). Therefore, an accurate characterization of colony biomass must take the size and number of polyps into account. In Figure 5 respiration is plotted as a function of polyp area (the percent of the colony surface occupied by polyps). Polyp

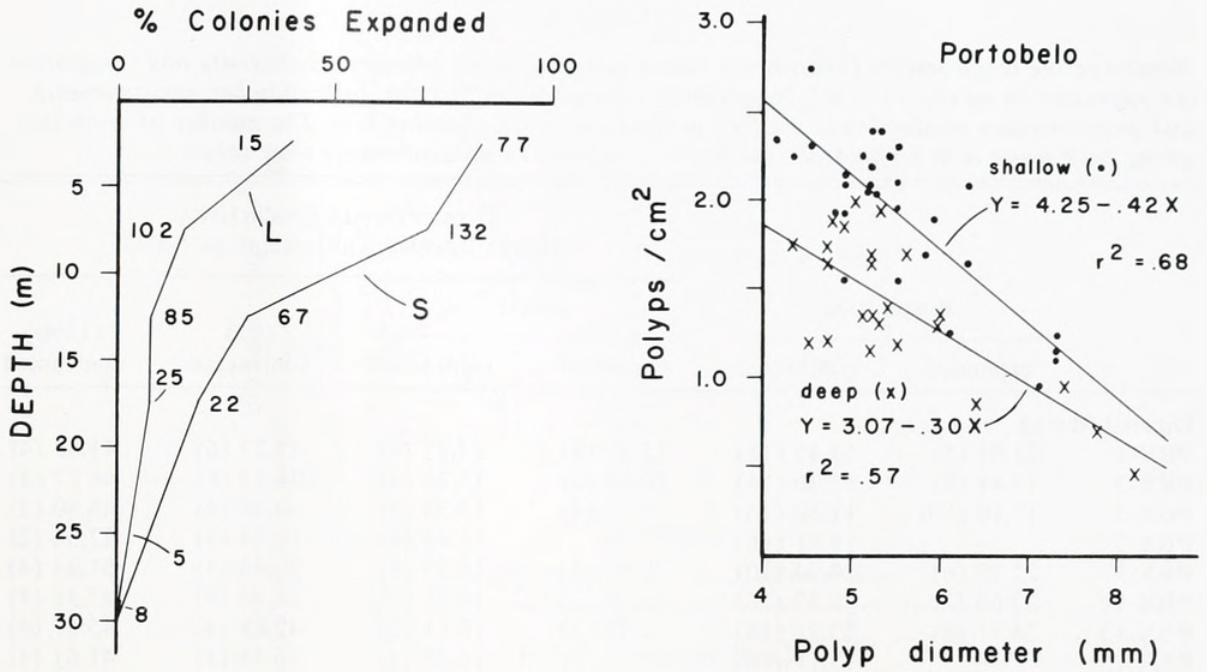

FIGURE 2. (Left) Proportion of colonies with large polyps (L) and with small polyps (S) found expanded in each of five different depth zones. Values based on transects from the San Blas Islands and Bocas del Toro regions of Panama. Values in parenthesis indicate numbers of colonies used to derive each data point, and roughly correspond to the colonies' relative abundances at the different depths.

FIGURE 3. (Right) Least squares regressions of polyp size on polyp density at 8 and 20 m depth from Portobelo. Mean diameter of polyps from the two populations do not differ, but polyp density of the deep population (20 m) is significantly lower than that of the shallow population (8 m) ($p < 0.05$, ANOVA).

area is an index of biomass per unit area and accounts for much of the variance in the respiration rates.

The importance of polyp size and number was again evident when data on whole colony respiration rates were analyzed. Linear regressions were determined between respiration and two measures of colony size:

$$R_T = 16.36A + 51.82, \qquad r^2 = 0.64 \tag{1}$$

$$R_T = 52.79A_p + 51.82, \qquad r^2 = 0.74, \tag{2}$$

where R_T is total respiration (μg O_2/h), A is total colony surface area (cm^2), and A_p is area of the polyps (cm^2). A greater portion of variance in respiration rates is explained by (2), which uses the area of the polyps as an estimator of biomass.

The solution of (2) was calculated in a stepwise linear regression procedure which considered, but rejected as insignificant, the effects of coenosarc area. This does not necessarily mean coensarc makes no contribution to respiration rate. Coenosarc and polyp areas among the 18 colonies were correlated ($r = 0.64$, $p < 0.01$), and the covariance between the areas of the two makes it difficult to discuss whether the two actually make an independent contribution to respiration. As a consequence of the correlation between polyp and coenosarc areas it is likely that the effect of coenosarc in (2) is already incorporated into the term for polyp area.

The contribution of coenosarc to the respiration rate can be tested in data sets

TABLE II

Results of the respirometry experiments. Mean values of gross primary productivity and respiration are expressed in μg $O_2 \cdot cm^{-2} \cdot h^{-1}$. Respiration values are net flux for dark chamber measurements, and gross primary production is net flux in light plus dark chamber loss. The number of replicates giving each mean is in parenthesis. Dashes (—) indicate no measurements were taken.

	Respiration		Gross Primary Productivity (Light Intensity (μEinsteins $\cdot m^{-2} \cdot s^{-1}$))			
			(25)		(93)	(1890)
	expanded	contracted	expanded	contracted	contracted	contracted
Diurnal Morph						
PBX-1	22.01 (5)	13.45 (18)	25.68 (4)	23.23 (4)	23.23 (6)	41.57 (4)
PBX-3	17.44 (8)	10.90 (16)	26.16 (6)	15.26 (4)	28.33 (6)	46.87 (4)
PBX-5	17.10 (10)	11.40 (16)	15.20 (4)	13.30 (8)	30.40 (4)	45.60 (2)
PBX-7	—	14.81 (16)	—	14.43 (4)	18.23 (4)	27.34 (2)
PBX-9	22.98 (6)	20.84 (20)	22.99 (4)	16.57 (8)	30.46 (4)	51.83 (4)
PBX-11	23.66 (2)	19.32 (20)	22.08 (2)	19.71 (6)	24.84 (4)	33.51 (4)
PBX-13	24.71 (2)	23.21 (18)	13.48 (2)	15.81 (2)	42.68 (4)	45.67 (4)
PBX-15	—	17.11 (16)	—	16.72 (4)	26.36 (4)	41.61 (4)
PBX-19	25.26 (2)	24.06 (6)	22.56 (2)	21.08 (6)	—	—
PBX-21	34.37 (4)	19.03 (4)	30.69 (5)	20.26 (3)	—	—
mean	23.10	17.41	22.36	17.64	28.06	41.75
Nocturnal morph						
PBX-2	17.63 (2)	13.4 (25)	—	12.34 (4)	24.33 (4)	22.57 (8)
PBX-4	16.59 (4)	15.72 (18)	—	15.28 (4)	19.21 (6)	27.07 (4)
PBX-6	—	9.39 (16)	—	8.54 (4)	16.50 (4)	37.84 (4)
PBX-8	11.65 (08)	12.76 (8)	—	7.21 (4)	26.63 (4)	40.50 (4)
PBX-10	29.95 (6)	21.54 (15)	—	11.02 (4)	19.54 (4)	26.5 (4)
PBX-12	—	23.21 (23)	—	2.36 (4)	21.20 (4)	29.11 (4)
PBX-14	—	18.78 (20)	—	6.4 (4)	27.32 (4)	41.83 (4)
PBX-16	—	15.59 (16)	—	15.05 (4)	18.28 (4)	26.34 (4)
mean	18.96	16.30		9.78	21.63	31.48

where polyp and coenosarc areas are not correlated. Respiration rates with expanded polyps could not be obtained for some colonies. Among this subset of colonies coenosarc and polyp areas were not correlated. The analogous solution of (2) among these colonies includes a term for coenosarc area (A_c).

$$R'_T = 44.69A_p + 18.21A_c - 285.56, \qquad r^2 = 0.78 \tag{3}$$

In the analysis presented above the best estimators of respiration are those which most accurately reflect differences in colony biomass. Among colonies of *M. cavernosa*, small morphologic differences that did not affect the size of the colony did affect biomass and respiration rates.

Like respiration, gross primary production is affected by morphology. But to explain variance in gross primary production one must also consider light level and the number of zooxanthellae in the colony.

Gross primary production data were fitted to a simple Michaelis-Menton model.

$$GPP(I) = 37.1I/(42.4 + I), \qquad r^2 = 0.64, \tag{4}$$

where GPP(I) is gross primary production (μg $O_2 \cdot cm^{-2} \cdot h^{-1}$) at light intensity

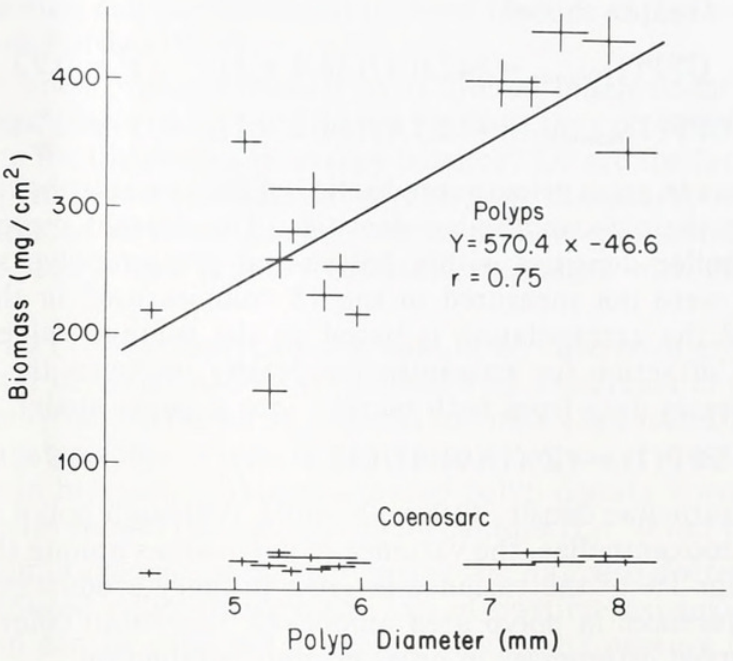

FIGURE 4. Biomass (preserved wet weight per cm^2) as a function of polyp diameter. The upper line presents the least squares linear regression of polyp diameter on polyp weight. The lower cluster of points are for coenosarc. Values are presented as means ± 1 standard error for each colony.

I (μEinsteins $\cdot m^{-2} \cdot s^{-1}$). Some of the remaining variance can be attributed to the significant differences between gross primary production of the diurnal and nocturnal morphs. Separate analysis of the two morphs improves the goodness of fit

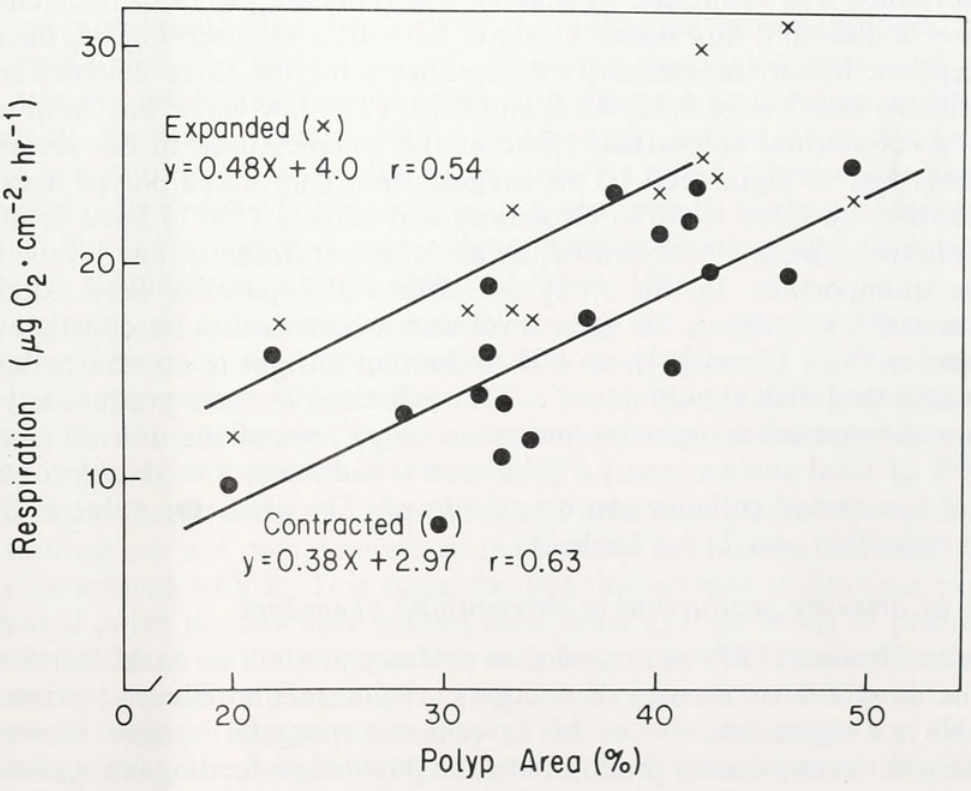

FIGURE 5. Relationship between respiration rate and polyp area of expanded (×) and contracted (dot) colonies of *M. cavernosa*.

of the Michaelis-Menton model,

$$GPP(I)_{Diurnal} = (42.0)I/(38.4 + I), \qquad r^2 = 0.73 \tag{5}$$

$$GPP(I)_{Nocturnal} = (32.5)I/(51.2 + I), \qquad r^2 = 0.74 \tag{6}$$

The differences in gross primary production of the two morphs can be attributed to differences in their zooxanthellae densities. The diurnal morph colonies had greater zooxanthellae densities within polyps and greater polyp areas. (Zooxanthellae densities were not measured in the 18 colonies used in the respirometry experiments, and the extrapolation is based on the average values derived from Lasker, 1977). Correction for zooxanthellae density improves the goodness of fit and also incorporates data from both morphs into a single model,

$$GPP(I) = (Z)(I)(91.4)/(42.4 + I), \qquad r^2 = 0.76, \tag{7}$$

where Z is zooxanthellae density (10^6 cells/cm^2). Although polyp area affects the total number of zooxanthellae, the variance in polyp areas among these 18 colonies only accounted for 1% of the variance in gross primary production. Unlike respiration rates, differences in polyp area among *M. cavernosa* colonies contributed little to the observed differences in gross primary production.

Equations (4)–(7) account for variation between colonies and morphs, but do not explain the increase in gross primary production with polyp expansion. Sebens and de Riemer (1978) suggested that this increase could result from a greater diffusive supply of limiting nutrients like ammonium. Lasker (1977), on the other hand, has suggested that contracted polyps shade their zooxanthellae, which reduces their photosynthetic activity. The coenosarc is comparable in zooxanthellae density and tissue thickness to the superficial layer of a contracted polyp. Absorbance of the coenosarc can, therefore, provide an estimate of shading in the polyp. Coenosarc light absorbance was estimated by placing five replicate pieces of decalcified coenosarc over a quantum flux sensor (Lamda LI-190) and observing the decrease in light reception. Mean transmissivity of coenosarc for the three colonies so tested (five replicates each) were 0.22, 0.22, and 0.12. (The low value was from a colony with white ectodermal coloration. None of the colonies used in the respirometry experiments was so pigmented.) This suggests that contracted polyps may reduce light reception by close to 80%. Crossland and Barnes (1977) have argued that because photosynthesis by zooxanthellae becomes saturated at low levels, shading should be unimportant. In this study the effects of expansion were tested at 25 μEinsteins $\cdot m^{-2} \cdot s^{-1}$. Given the light level and a half-saturation constant of 42.4 μEinsteins $\cdot m^{-2} \cdot s^{-1}$ (from [7]), an 80% reduction in light to zooxanthellae in the tentacles and oral disk should cause a 73% reduction in their productivity. Using the known zooxanthellae densities and mean polyp area of the diurnal morph colonies (39% of total surface area) a predicted reduction in the gross primary production of contracted colonies can be calculated. The predicted value is 20%; the observed reduction was 21% (Table II).

The role of primary production in determining phenotype

Spencer-Davies (1977) estimated that primary production in *M. cavernosa* accounts for 49–102% of a colony's energetic requirements. Clearly, primary production plays a significant role in *M. cavernosa's* energetic budget. However, the relationship between primary productivity and particulate feeding is not clear. Polyp size, density, and expansion affect a colony's ability to capture particulates as well as its primary production. Therefore, the presence of differing phenotypes among

M. cavernosa colonies can provide insights about the role of "autotrophy and heterotrophy," (sensu Porter, 1976).

What occurs when primary production is altered independent of morphology and behavior? Do changes occur in ontogeny (or have they occurred evolutionarily) which compensate for the change in energy balance? Or are the factors controlling phenotype in *M. cavernosa* independent of energetic considerations? These questions can be examined in two instances: where primary production changes with increasing depth, and where primary production changes with different zooxanthellae densities.

Spencer-Davies (1977) observed a decrease in *M. cavernosa* gross primary production with depth in Jamaica. This is paralleled by a decrease in respiration rate, some of which may be attributed to reduced biomass (Spencer-Davies, 1980). In Panama, one of the principal effects of depth was a reduction in polyp density (Fig. 2) and therefore in biomass. Although reduced polyp density lowers colony maintenance costs, it also should reduce particulate capture (*i.e.,* fewer capture organs).

The proportion of colonies expanded during the day also decreases with depth (Fig. 3). Like reduced polyp density, the loss of daytime expansion lowered respiration rates and can be expected to reduce particulate capture (less time spent feeding). But contraction of the polyps also reduced gross primary production. Therefore, the net energetic effect of contraction is dependent on changes to both respiration and gross primary production. At 25 μEinsteins $\cdot m^{-2} \cdot s^{-1}$ contraction effects a 24% reduction of respiration rate and a 21% reduction of gross primary production (Table II). At higher light levels, which occur through most of the day, the effect of contraction on gross primary production is reduced. Therefore, in most cases polyp contraction increases net primary production. Like decreased polyp density, daytime contraction conserves energy but should also reduce particulate feeding.

The lower zooxanthellae densities of the nocturnal morph reduces its gross primary production. As in the case of increasing depth, the nocturnal morphs' reduced primary production is correlated with daytime contraction and with low polyp density. Even after compensating for its larger polyps the nocturnal morph had lower polyp areas than the diurnal morph. As noted, these characters lower colony maintenance costs but should reduce particulate feeding. The nocturnal morph also has large polyps. Large polyps increase biomass and respiration but also increase zooplankton capture ability (Lasker, 1976).

Morphologic and behavioral variability among *M. cavernosa* colonies follows two patterns. The nocturnal morph, which has lower rates of gross primary production, has larger polyps, which will enhance zooplankton feeding. In this manner the morphs of *M. cavernosa* display complementarity between autotrophy and heterotrophy like that proposed by Porter (1976).

On the other hand, other morphologies and behaviors which also enhance particulate feeding are not complementary to primary production. Instead, they are positively correlated with it. This suggests that the benefits of daytime expansion and increased polyp density only exceed their costs at high levels of primary production. Dependence of these characters on primary production implies that their benefits are not energetic. Rather, the benefits may involve non-energetic aspects of particulate feeding (like nitrogen supply) or may involve aspects of *M. cavernosa's* ecology that are independent of feeding (sediment removal, for example; Lasker, 1980).

The level of gross primary production among *M. cavernosa* colonies correlates

strongly with trends in phenotypic variation. This indicates the important role that the zooxanthellae have played in the evolution and development of *M. cavernosa*. However, the complexity of the interactions between primary production and phenotype in this species suggests the relationship between "autotrophy and heterotrophy" among reef corals cannot be understood if colony energetics alone are examined.

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