sonably good inhibitor of the taste response. The suppression by DiCl-gal of the response to sweeteners of the gerbil's chorda tympani is consistent with the inhibitory mechanism proposed by Beidler for the following reasons: (i) DiCl-gal alone barely stimulates the gerbil's taste nerve and (ii) the kinetic plots of the taste to DiCl-gal mixed with sucrose or saccharin suggest that each sweetener and DiCl-gal are competing for the same receptor site.

The mechanism for the DiCl-gal suppression of sweet taste is puzzling despite the fact that kinetic plots indicate competitive inhibition. The reason is that, unless saccharin, sucrose, and DiCl-gal possess some common molecular feature, it is difficult to understand how DiCl-gal can be acting simultaneously as a competitive inhibitor with both sucrose and saccharin, especially since the two sweeteners are believed to bind to separate receptor sites (*3*). Because the molecular similarities are not evident, a possible explanation is that DiCl-gal is acting as an allosteric inhibitor which is diminishing only the rate constant (K_d) but not the maximum taste response (*13*). Its allosteric site could be independent, or it could be the sucrose site itself. The latter possibility, which takes into account the molecular similarities between DiCl-gal and sucrose, suggests that, when DiCl-gal binds to the sucrose site, not only is DiCl-gal a competitive inhibitor at that site, but also, at the same time it allosterically affects the saccharin binding site.

These results indicate that there are at least two reactions causing the sweet taste response. The first reaction is the binding of the sweetener to the receptor. The second reaction is activation of the receptor by the bound sweetener. The experimental results indicate that DiCl-gal was binding to the receptor but not activating it. On the other hand, sucrose was binding to the receptor as well as activating it. In these respects the mechanism of the sweetener taste response resembles the drug-receptor interaction mechanisms (*14*).

WILLIAM JAKINOVICH, JR.
Department of Biological Sciences, Herbert H. Lehman College, City University of New York, Bronx 10468

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15. I am indebted to V. Vlahopoulos for her contribution to both the electrophysiological experiments and the synthesis of DiCl-gal. I thank D. Sugarman for manuscript suggestions and E. Mallon for typing. This work was supported by grant RO1 NS16022-02 from the National Institutes of Health and PSC-CUNY.

18 June 1982; revised 9 August 1982

Net Primary Productivity in Coral Reef Sponges

Abstract. *Nine of the ten most common sponge species on the fore-reef slope of Davies Reef (Great Barrier Reef) contain symbiotic cyanobacteria. Six of the ten are net primary producers, with three times more oxygen produced by photosynthesis than is consumed during respiration. Light interception is enhanced by morphological flattening, thereby increasing the potential for phototrophic nutrition, a factor crucial in the ecology of most sessile coral reef invertebrates.*

Extensive tracts of coral reefs in nutrient-deficient tropical waters owe their existence to the symbiosis between corals and eukaryotic algae, the zooxanthellae (*1*). This symbiosis results in the translocation to the host of considerable amounts of fixed carbon (*2*) as well as nitrogen (*3*) and phosphorus (*4*).

Sponges are the second largest biomass component of the coral reef benthic fauna (*5, 6*), but the mechanisms by which these large sponge populations obtain sufficient nutrition from low-nutrient tropical waters has not been resolved (*7*). A symbiosis comparable to that in corals occurs between sponges and cyanobacteria (blue-green algae); these prokaryotic symbionts may be either uni- or multicellular (*8, 9*). This symbiosis is widespread in marine sponges in shallow tropical and warm temperate environments (*5, 6*). Speculation on the role of these cyanobacteria in sponge ecology has included light shielding, "farming," with subsequent intracellular digestion by the host, and translocation of glycogen (*8, 10*) or glycerol (*11*). I have found that these cyanobacterial symbioses are crucial in the nutrition and ecology of coral reef sponges.

Sponges with symbiotic cyanobacteria constitute approximately 80 percent of individuals and of the biomass to 20 m on the fore-reef slope of Davies Reef (Great Barrier Reef; latitude 18°15′S, longitude 147°38.5′E) (*6*). Nine of the ten most common sponge species contain symbiotic cyanobacteria morphologically similar to those in sponges from the southern Great Barrier Reef, Red Sea, and Mediterranean (*8, 9*). The proportion of cyanobacteria varies considerably from one species to the next, as is evidenced by the chlorophyll a content (Table 1). In *Pericharax heteroraphis* and *Jaspis stellifera*, the cyanobacteria are restricted to a thin layer of tissue exposed to light, whereas in *Neofibularia irata* and *Carteriospongia (Phyllospongia)* species, cyanobacteria are distributed throughout the tissue. Only one of these ten sponges, *Spongia* sp., had no photosynthetic symbionts.

The importance of the cyanobacteria was tested by examining the photosynthetic potential of the ten most common sponges. Seven of these showed ratios of instantaneous gross productivity to respiration (P/R) that were greater than 1 in the light (photon flux density of 200 microeinsteins (μE) per square meter per second, indicating net primary production under the experimental conditions (Table 1) (*12*). Indeed, six of these sponges showed P/R ratios in excess of 3 at the maximum light level at 20 m where the largest sponge population occurs (*6*).

Quantitatively similar results were obtained for parallel measurements of net $^{14}CO_2$ fixation and production of oxygen (Table 2) (*13*). In the seven sponges with large cyanobacterial populations, dark fixation rates were between 2.4 and 6.6 percent of light fixation, indicating that most of the incorporation occurs through photosynthetic pathways (Table 2). These sponges released between 1 and 5 percent of fixed ^{14}C as dissolved organic carbon during the first hour, indicating a small contribution to reef nutrition (Table 2).

The data summarized in Table 1 demonstrate that the majority of sponges on Davies Reef can obtain much of their nutrition from their symbiotic cyanobacteria. Extrapolation of instantaneous

Table 1. Gross production to respiration ratios (*P/R*) of the prominent sponge species on Davies Reef, Great Barrier Reef. *P/R* data have been extrapolated to yield potential proportion (expressed as percentage) of daily respiration requirements provided by cyanobacterial productivity at 10 m and 20 m during the daily period when light exceeds 200 (x) and 400 (y) $\mu E\ m^{-2}\ sec^{-1}$ (calculated from instantaneous oxygen values measured in an enclosed chamber) (*12*). Sponges are listed in order of quantitative (biomass) prevalence on the fore-reef slope of Davies Reef (*6*), and those marked with an asterisk are given provisional names subject to a reexamination of their taxonomy. P/R ratios are expressed as means ± standard deviation, with sample numbers in parentheses. P.N., photosynthesis negligible; +, most specimens were much thicker; a, summer (December); b, winter (June). Weights are expressed as live wet weight.

Sponge species	Shape and mean thickness (mm)	Ratio of surface area to weight ($cm^2\ g^{-1}$)	Chlorophyll a content ($\mu g\ g^{-1}$)	*P/R* at 200 (x) and 400 (y) $\mu E\ m^{-2}\ sec^{-1}$	Calculated 24-hour respiration ($\mu mole\ g^{-1}$)	Potential percentage of sponge respiration provided at	
						10 m	20 m
*Neofibularia irata**	Encrusting, 3.8	2.41	116.1	x: 3.00 ± 0.65 (6) y: 4.19 ± 0.37 (5)	34.1	162.9a 111.7b	97.8a 53.3b
Spongia sp.*	Hemisphere, > 30	1.33	P.N.	P.N.	23.8	P.N.	P.N.
Pericharax heteroraphis	Thick vase, 4.2+	1.23	1.9	x: P.N. y: 0.28 ± 0.04 (2)	22.8	8.8a 4.4b	P.N. P.N.
Carteriospongia foliascens	Thin dish, 2.3	7.38	75.8	x: 2.96 ± 1.18 (7) y: 3.42 ± 0.98 (7)	40.1	138.4a 99.1b	96.4a 52.6b
Pseudaxinyssa sp.*	Thick dish, 4.4	3.48	93.9	x: 3.07 ± 1.01 (6) y: 3.35 ± 0.85 (6)	22.6	137.1a 99.5b	99.8a 54.5b
Carteriospongia sp. code fp*	Dish/fan, 1.7	9.16	63.5	x: 2.73 ± 1.09 (6) y: 3.15 ± 0.67 (6)	56.6	127.6a 91.4b	89.0a 48.6b
Carteriospongia sp. code fr*	Dish/fan, 2.2	6.32	105.3	x: 2.81 ± 0.45 (4) y: 3.71 ± 0.74 (4)	56.2	145.8a 101.2b	91.5a 49.9b
Jaspis stellifera	Hemisphere, > 30	0.79	32.9	x: P.N. y: 0.39 ± 0.15 (4)	20.4	12.8a 6.1b	P.N. P.N.
*Phyllospongia papyracea**	Thin fan, 1.6	10.58	72.1	x: 3.86 ± 0.90 (4) y: 4.31 ± 1.70 (4)	57.8	175.9a 126.9b	125.8a 68.7b
Ircinia ramosa	Cylinder, 10.8	1.74	65.4	x: 1.75 ± 0.32 (3) y: 2.22 ± 0.48 (3)	18.5	87.9a 61.6b	56.9a 31.1b

measurements (*12*) shows that cyanobacterial photosynthesis could potentially provide much of the normal maintenance energy budget of these sponges (Table 1), if it is assumed that translocation of photosynthate occurs as demonstrated in Mediterranean, Red Sea, and Caribbean sponges (*11, 14*).

The highest *P/R* ratios occurred in thin, encrusting sponges or in dish or fan-shaped sponges with large surface areas and high ratios of chlorophyll a to weight (*N. irata*, the three *Carteriospongia* species, *Ph. papyracea*, and *Pseudaxinyssa* sp.) (Table 1). Their morphology is suited for the interception of light, probably augmenting phototrophy at the expense of heterotrophy. The estimated daily respiration rates (Table 1) are comparable to those reported by Jørgensen (*15*) (12.5 to 53.5 μmole of O_2 per gram) and Reiswig (*7*) (17.3 to 59.0 μmole of O_2 per gram) for Caribbean sponges. Reiswig (*7*) showed that heterotrophic filter feeding could account for the following percentages of sponge daily maintenance: *Mycale* sp., > 100 percent; *Tethya crypta*, 75 percent; and *Verongia gigantea*, 17 percent. He suggested that the 83 percent discrepancy in daily maintenance for *V. gigantea* could be accounted for by incorporation of dissolved organics from the water by the large population of symbiotic bacteria. By contrast, the present results suggest that symbiotic cyanobacteria can potentially contribute to the nutrition of both *T. crypta* and *V. gigantea* (*16*).

Table 2. Measurements of photosynthesis and dark respiration (*12*) on sponge species collected from the fore-reef slope of Davies Reef. Dark incorporation estimations in parentheses are derived from sponges with low rates of carbon incorporation indicative of little or no photosynthetic activity (P.N.)

Sponge species	Production of O_2 ($\mu mole\ g^{-1}\ hour^{-1}$)	Light incorporation (*L*) of $^{14}CO_2$ ($\mu mole\ g^{-1}\ hour^{-1}$)	Dark incorporation of $^{14}CO_2$ as percentage of *L*	Dissolved organic carbon released as percentage of *L*
Neofibularia irata	3.16	2.39	3.73	4.84
Spongia sp.	P.N.	0.03	(158.8)	4.39
Pericharax heteroraphis	P.N.	0.03	(44.99)	1.63
Carteriospongia foliascens	1.74	3.28	4.08	4.31
Pseudaxinyssa sp.	2.78	2.94	2.60	1.33
Carteriospongia sp. code fp	1.73	2.01	6.59	2.17
Carteriospongia sp. code fr	3.43	2.60	3.02	3.70
Jaspis stellifera	P.N.	0.63	(20.48)	0.50
Phyllospongia papyracea	4.55	3.58	2.36	2.74
Ircinia ramosa	0.22	1.68	3.71	1.16

Phototrophic symbiosis is the principal strategy employed by large sedentary benthic animals to augment nutrition in coral reef environments. Most species with photosynthetic symbionts are found in tropical regions—for example, hermatypic corals (*17*), sponges (*6, 8, 9*), ascidians (*18*), and tridacnid clams (*19*). Convergent evolution in sponges and corals (*20*) has increased surface areas to trap incident light, which results in efficient phototrophic symbioses, with *P/R* = 0.3 to 6.3 in sponges and 1.6 to 6.3 in corals (*21*). Therefore, these phototrophic symbioses are crucial to coral reef growth and maintenance. The relative significance of phototrophic versus heterotrophic nutrition is, however, unknown in sponges and corals (*22*) as are the reasons for preferential zonation of corals into shallow water (*23*) and sponges into deeper water (*6*).

CLIVE R. WILKINSON
Australian Institute of Marine Science, P.M.B. No. 3, Townsville M.S.O., Queensland 4810

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24. I thank L. Trott for assistance and J. S. Bunt, B. E. Chalker, E. A. Drew, N. D. Holland, R. E. Johannes, M. M. Mullin, J. R. Strickler, R. K. Trench for help during the preparation of this manuscript. B. E. Chalker generously supplied his data and equations concerning light measurement.

2 August 1982

Taste Flashes: Reaction Times, Intensity, and Quality

Abstract. *Human simple reaction times and magnitude estimates of taste intensity increased as the duration of 500-millimolar sodium chloride or 2-millimolar saccharin sodium pulses lengthened from 100 to 1000 milliseconds. Responses to "What was the taste?" ranged from 94 to 100 percent "sweet" for saccharin and 68 to 83 percent "salty" for salt across all pulse durations when both substances were randomized with water pulses.*

We can see much from the light provided during a flash of forked lightning (*1*), and we can hear an identifiable sound when a twig snaps or when someone gasps. These sensory stimuli, all of which are shorter than 1 second (*2*), end long before a human gross motor response to them occurs (*3*). We are thus generally able to detect and identify transient stimuli and unable to respond during or within a few hundred milliseconds of such transients.

What types of responses do humans make to taste stimuli that end before a motor response can be made? We have found that useful taste information is provided by 100-msec gustatory transients, that additional information is obtained during taste stimuli of longer duration, and that lengthy central nervous system processing of gustatory input precedes any behavioral response.

We measured, in volunteer participants (*4*), reaction times to simple tastes (Fig. 1) and judgments of taste quality (Table 1) and intensity (*5*) (Table 2) to single pulses of 500 m*M* NaCl (American Chemical Society) or 2 m*M* saccharin sodium (National Formulary) in distilled water (the experimental stimuli), or of distilled water alone (the control stimulus) (*6*). Pulse durations were 100, 200, 300, and 1000 msec, each presented four times per session in random order, with a 10-second distilled water flow before a pulse and a 5-second flow after (*7*). Each measurement session began with two practice identified stimulus and control trials. Three or more practice sessions preceded a series of data collection sessions for each type of measurement. Eight control stimuli and eight or more experimental stimuli were given during each session, with at least 60 seconds between stimuli. Both simple reaction times (Fig. 1) and judged stimulus intensity (Table 2) increased with pulse duration. In contrast, no statistically significant change in the taste quality of NaCl or saccharin occurred with change in stimulus duration (Table 1) (*8*).

Errors on experimental stimulus trials, that is, failure to notice a change in taste, did not exceed 4 percent across all par-

Table 1. Taste quality responses as percentages of total response.

Quality	Stimulus pulse duration (msec)							
	NaCl				Saccharin			
	100	200	300	1000	100	200	300	1000
Salty	68	70	70	83	3	0	0	0
Sweet	0	0	3	0	94	98	100	97
Bitter	13	17	7	7	0	0	0	0
Salty-sour	3	3	10	3	0	0	0	0
Sour	7	0	3	7	0	0	0	0
No change†	3	0	0	0	3	2	0	0
Cinnamon	0	0	0	0	0	0	0	3
Sweet-sour	0	3	0	0	0	0	0	0
Salty-bitter	3	3	7	0	0	0	0	0
Sour-bitter	0	4	0	0	0	0	0	0
Sweet-bitter	3	0	0	0	0	0	0	0

†Experimental stimulus trial error. Such trials were repeated immediately after the next scheduled control stimulus trial in the predetermined random order.