ON THE FEEDING OF SOME SCLERACTINIAN CORALS WITH BACTERIA AND DISSOLVED ORGANIC MATTER

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ABSTRACT

Feeding experiments were carried out with 6 species of common scleractinian reef-building corals from reefs of the Bismarck Archipelago. Their ability to utilize planktonic bacteria and dissolved organic matter (protein hydrolyzate) as food was demonstrated by using radiocarbon. The amount of organic carbon assimilated per day by animals given labeled food at concentrations approaching those found in situ was equivalent to 10–20% of the carbon content of the polyp's body. The rate of consumption and assimilation of some planktonic algae by corals was much lower. Corals could consume organic phosphorus bound in the cells of planktonic bacteria more actively than inorganic phosphate at the same concentration (several μg liter^{-1}). The rate of consumption of phosphorus was 3 μg g^{-1} day^{-1}.

According to the experimental data of Yonge and Nicholls (1931) zooplankton provides a principal food source for polyps of scleractinian corals. However, recent field observations have shown that zooplankton is usually very scarce in tropical oceanic waters passing over coral reefs (Johannes et al. 1970). Coral polyps certainly utilize organic matter produced by symbiotic zooxanthellae (Muscatine 1967; Franzisket 1969) but active photosynthesis by zooxanthellae requires an extensive inflow of nutrients which are very scarce in tropical waters. Polyps are believed to have additional sources of food, both particulate and dissolved. Stephens (1962) showed that polyps can consume glucose from solution at concentrations ranging from 2–20 mg liter^{-1}. The polyps of corals usually have well-developed cilia which can separate planktonic organisms such as algae and bacteria (Abe 1937; Roushdy and Hansen 1960). The ability of corals to consume and digest planktonic bacteria has been shown by Di Salvo (1969) and Sorokin (1971*a*).

Quantitative studies of possible feeding mechanisms of the polyps of reef-building corals are required for calculation of the energy budget of coral reef ecosystems, which are among the richest in the ocean (Odum and Odum 1955). During cruise 50 of RV *Vitjaz* in the western tropical Pacific I had an opportunity to measure the assimilation of dissolved organic matter and phosphorus by coral polyps.

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MATERIAL AND METHODS

Specimens of some of the common species of reef-building corals, including species of *Montipora*, *Pocillopora*, *Porites*, *Pavona*, and *Acropora* were used in experiments carried out at field laboratories set up on islands in the St. Andrew reefs and at Ninigo atoll (Bismarck Archipelago). Branches of corals were cut off under water with scissors and the cut was sealed with soft plastic to prevent the secretion of mucus. The branches so prepared were maintained in an aquarium submerged near shore. Experiments were carried out at night to exclude the possible assimilation of labeled CO_2 by symbiotic zooxanthellae. It is possible that evolution of small amounts of CO_2 can take place during metabolism of food organisms.

The intensity of feeding by corals was studied by the radiocarbon method (Sorokin 1968, 1971*a*,*b*). Natural bacterioplank-

ton, planktonic algae maintained in culture, and dissolved organic matter (DOM) were labeled and used as food.

Bacterioplankton was labeled with ^{14}C by the addition of a portion (0.2–0.5 mg C liter^{-1}) of labeled hydrolyzate of algal protein (Sorokin 1971*b*) to the surface seawater sample taken in the open ocean and prefiltered through a fine plankton net. After 25–40 hr of exposure in the dark at 30°C the labeled hydrolyzate was almost completely (95–97%) consumed by the bacteria. The water was then acidified with HCl and the labeled CO_2 formed during microbial metabolism was removed by bubbling air through the water. The water, containing the labeled bacterioplankton, was then brought to pH 8.0 by adding an alkaline solution. The practically complete absence in this water of small nannoplanktonic forms was shown by direct microscopy of the membrane filters.

The planktonic algae were labeled in growing cultures by introducing labeled ^{14}C-CO_3^{2-} during photosynthesis. Cultures of *Amphidinium klebsii* and of a mixture of several species of green flagellates (isolated and maintained by L. Lanskaya) were used. The labeled phytoplankton and bacterioplankton were used at the optimal concentration for filter feeding by most marine filterers (0.5–0.7 mg of the wet biomass per liter).

Labeled acid hydrolyzate of algal protein was used as the labeled DOM (Sorokin 1971*b*). The neutralized solution of the hydrolyzate was preserved in sterilized ampoules. Before use it was dissolved in seawater in the proportion 1:10 and filtered under sterile conditions through a membrane filter (pore size, 0.3μ). The concentration of hydrolyzate in the expermental vessels was 0.3 mg C liter^{-1}. To prevent microbial growth in the vessels, and consequently the formation of particulate labeled organic matter in the vessels during experiments with DOM as food, streptomycin was added at a concentration of 50 mg liter^{-1}. Control experiments showed that at this concentration the streptomycin almost completely stopped microbial assimilation of labeled organic matter by the microflora of seawater for up to 10 hr. At the same time the presence of streptomycin enhanced the survival of corals and other benthic animals, as well as of planktonic animals.

As a criterion of the intensity and efficiency of feeding of corals the index of assimilation values C_a/C was used. This index is the per cent ratio of carbon in assimilated labeled food (calculated per 24 hr) to the carbon content in the body of the consumer (Sorokin 1968). To measure it, 8–12 g of coral branches, prepared as described above, were placed in aquaria filled with 1–2 liters of prefiltered seawater. A portion of labeled food was added to each aquarium. After 6–7 hr exposure, the corals were washed clean of adhering labeled food material by actively rinsing them for 1 min in seawater. The washed corals were placed in beakers with 200 ml of seawater previously boiled with HCl and then adjusted to pH 8.2 to remove HCO_3^- ions. At the end of the experiment radioactivity was measured in the tissues of coral (R) and in CO_2 evolved by the coral during the second stage of the experiment (r_o).

The value of R was measured in preparations of the alkaline hydrolyzate of coral tissues. These were prepared by boiling the corals in a small portion (3–5 ml) of 0.1 N KOH solution. After the tissues were dissolved the residual material was washed from the skeleton by a jet of water. The hydrolyzate was neutralized with HCl, its volume adjusted to 20 ml, and 0.5-ml aliquots were poured into planchets and dried. Self-absorption in the preparations was measured by estimating the decrease of count of the standard portions of labeled algae introduced into similar preparations of the coral's nonlabeled tissues. The value of r_o was estimated after distillation of CO_2 from the water and precipitation as $BaCO_3$.

Simultaneously, control experiments were performed with corals previously fixed with

Table 1. Consumption of labeled planktonic algae and bacteria by corals. Inverse specific activity of food (10^{-3} $\mu g \cdot cpm^{-1}$): bacterioplankton (Bac)—0.75; Amphidinium *(Amp)—1.12; mixture of flagellates* Platymonas *sp. (Pla)—0.58; dissolved organic matter (DOM)—0.25. (For definitions of other symbols* see materials and methods*)*

	Kinds of food	Wet wt of coral colony (g)	R (10^3 cpm colony^{-1})	r_c (10^3 cpm colony^{-1})	A (μg C colony^{-1})	C_a/C (%)	r_a/R (%)
Montipora sp.	Bac	5.0	20.2	6.3	19.7	13.7*	31
	Amp	11.2	8.15	0.61	9.8	3.0*	8
	Pla	8.8	4.4	0.46	2.86	1.10*	11
	DOM	9.7	161.3	31.4	48.2	16.8*	19
Pocillopora damicornis	Bac	6.8	36.1	11.2	35.7	17.9	31
	Amp	7.4	7.8	1.1	9.9	4.5	14
P. caespitosa	Pla	5.8	4.1	0.56	2.68	1.58	14
	DOM	8.0	150.0	30.5	46.1	19.6	20
Pocillopora damicornis	Bac	8.2	49.6	16.8	49.7	20.4	34
	Amp	8.4	3.8	0.7	5.0	2.0	18
P. bulbosa	Pla	10.1	1.8	0.2	1.16	0.4	11
	DOM	12.6	362.8	109.0	107.0	29.0	30
Pavona sp.	Bac	6.0	21.0	8.4	21.8	12.4*	40
	Amp	8.0	6.7	1.4	9.0	3.8*	21
	Pla	12.1	2.1	0.35	1.47	0.4*	16
	DOM	5.9	61.9	30.3	23.1	13.3*	49
Acropora pulchra	Bac	4.8	27.6	12.0	25.0	21.0*	43
	Amp	7.2	1.39	0.24	1.6	0.89*	17
	Pla	6.4	1.6	0.19	1.03	0.60*	12
	DOM	7.5	83.0	26.1	27.3	14.6*	31
Porites compressa	Bac	7.0	14.6	5.5	12.7	7.3*	38
	Amp	7.4	0.03	0.005	0.04	0.02*	17
	Pla	10.6	0.58	0.1	0.4	0.16*	17
	DOM	8.5	126.0	69.2	48.6	22.8*	55

* Calculated as described on p. 382.

10% formaldehyde. The values R and r_c obtained for the controls were subtracted from the corresponding experimental data.

The quantity of labeled food assimilated by coral during the experiment, A, was calculated using the following equation: $A = C_r\ (R + r_c)$ mg C colony^{-1}, where C_r = inverse specific radioactivity of food carbon, mg C$\cdot$cpm^{-1}. The value of the index of assimilation (C_a/C) was calculated by the equation: $C_a/C = A(100)24\%(Wt)^{-1}Wt^{-1}$ where W = organic carbon content in the bodies of polyps of the colony used in the experiment and t = time of feeding of coral with the labeled food in hours. The approximate values of W were calculated on the assumption that the average carbon content in the bodies of polyps was equal to 0.01% of the wet weight of coral. This ratio was chosen on the basis of data in the literature (Odum and Odum 1955) and in my measurements of its value in the polyps of *Pocillopora*. The polyps were hardened by fixation in strong formaldehyde solution and then isolated from the crushed coral. Their carbon content was determined by wet combustion and calculated per colony according to the number of polyps in it.

The consumption of phosphate by corals was studied by using ^{32}P. The intensities of consumption of inorganic phosphate and of particulate organic phosphate were compared. Two parallel series of experiments were made. In one of them the corals were kept for 6 hr in water containing streptomycin (500 meq ml^{-1}) and labeled inorganic phosphate having the actual radioactivity 7×10^5 cpm and the inverse specific

Table 2. Consumption of inorganic phosphate (P_i) and organic phosphorus in cells of bacteria (P_o) by corals. R = *radioactivity in coral tissue* (see materials and methods)

	Kind of P	Wet wt of colony (g)	R (10^3 cpm colony^{-1})	P consumed (μg P g^{-1} day^{-1})	P consumed by corals (as % of initial)
Pocillopora damicornis	P_o	9.5	368	3.1	32
	P_i	9.9	120	0.9	10
P. bulbosa	control P_i	8.6	5	—	—
	control P_o	5.8	3	—	—
Porites compressa	P_o	10.3	320	2.5	26
	P_i	8.0	91	0.8	9
	control P_i	8.4	4	—	—
	control P_o	9.3	6	—	—

radioactivity (P_r) 2×10^{-5} mg P·cpm^{-1}. In the second series the same amount of labeled phosphate was added in the form of organic phosphate contained in cells of planktonic bacteria. To obtain the bacterioplankton the portion of inorganic phosphate and 3 mg of glucose were added to 1 liter of seawater filtered through a fine plankton net. After 2 days in the darkness the labeled inorganic phosphate was almost completely consumed by the bacterioplankton. This water containing ^{32}P-labeled bacterioplankton was diluted with seawater in the proportion 1:3 and used in the experiments. In the controls corals fixed with Formalin were again used.

At the end of the experiment the corals were carefully washed and the radioactivity of ^{32}P consumed was measured in their tissues as described above. The amount of ^{32}P consumed (D) was calculated by the equation $D = R\,P_r\,\mu$g P·colony^{-1}.

RESULTS AND DISCUSSION

The data on the intensity of feeding by corals on the different kinds of food (Table 1) show that all of the species studied were capable of selective filter feeding. The corals actively assimilate the substance of planktonic bacteria at a concentration of 1.2–1.6 $\times$ 10^6 cells ml^{-1} (wet biomass 0.4–0.6 g m^{-3}). The index of assimilation of bacterioplankton by polyps (C_a/C) reaches values of 10–20%, which are of the same level as those found for the feeding of small crustaceans with labeled food (Sorokin 1968). The index of assimilation of planktonic algae by corals was 10–20 times less than that for their feeding on bacterioplankton. Of the two kinds of algae tested, the mixture of flagellates (*Platymonas*) was utilized to a lesser extent than the *Amphidinium* samples. Some of the corals (e.g. *Porites* and *Acropora*) were virtually unable to feed on the algae tested. *Montipora* and *Pocillopora* can consume and digest algae to a limited extent ($C_a/C = 0.5$–4%).

The mechanism of selective filtration by corals is based on their ability to change the direction of movement of their cilia under the influence of the type of particles present in the water (Yonge and Nicholls 1931; Abe 1937). In the presence of edible particles ciliary movement is directed to the mouth. In the presence of nonedible material (e.g. carmine), the movement reverses under the influence of chemoreception so that this material is removed from the surface of the polyp's body.

The relative amount of labeled metabolic CO_2 evolved by corals during the relatively short second stage of the experiment was much higher when they were fed bacteria than when they were fed algae, showing that the assimilation of bacteria consumed is greater than that of algae. The ratio "$r_c : R$" by the feeding of corals with bacteria was 30–40%, indicating the intensive metabolism of coral polyps.

The experiments involving the feeding of corals with labeled dissolved organic matter revealed their ability to utilize it at

a very low concentration, 0.2–0.5 mg C liter^{-1}, close to natural concentrations of low molecular weight organic matter in neritic waters. Their intensity of feeding on DOM was even higher than on the equivalent amount of labeled bacterioplankton. The DOM consumed was quickly assimilated and incorporated, shown by the intensive evolution of labeled CO_2 during the respiration of corals previously fed with DOM. The consumption of labeled DOM by corals was so high that a colony of 10–12 g wet weight consumed up to 50% of its initial amount (0.3 mg C liter^{-1}) from 1 liter of water. These data indicate that under certain conditions low molecular weight DOM can serve as one of the sources of food for corals, and possibly for other coelenterates having ciliary epithelium increasing the contact surface. The concentration of DOM in coastal waters approximates 3–6 mg C liter^{-1}, and a significant part of the organic matter is represented by low molecular weight fractions (Chailow 1971). Little is known about the mechanism of consumption of DOM by coral polyps, but it may be analogous to the mechanism of assimilation of organic molecules by ciliated epithelium in the intestines of animals (Ugolev 1967).

The results of experiments on the utilization of labeled inorganic and organic phosphorus (Table 2) show that the common corals *Pocillopora* and *Porites* consume particulate organic phosphorus present in the substance of cells of bacterioplankton much more intensively than inorganic phosphate in solution at the same concentration. It is apparent that as well as phosphorus the polyps and their symbiotic zooxanthellae can also receive other important nutrients, e.g. nitrogen, iron, or vitamin B_{12}, as a result of feeding on bacteria. Therefore the ability of corals to filter feed, as well as their capacity for preying on planktonic organisms and for utilizing DOM provides not only energy and organic matter for biosynthesis by the polyps but also provides the nutrient supply for photosynthesis of their symbiotic algae. With regard to chlorophyll content and intensity of photosynthesis, corals do not differ from true plants such as coralline algae or macrophytes. But their autotrophic metabolism is basically different from the metabolism of plants, for it is not dependent on the inflow of mineral nutrients from the surrounding water. These nutrients can be supplied by the consumption of organically bound nutrients prevailing in tropical waters and partially (Pomeroy and Kuenzler 1969) by nutrient recycling inside the colony. This peculiarity of coral physiology perhaps explains the extremely intensive photosynthesis of corals which provides the high productivity of coral reef communities surrounded by surface tropical waters poor in nutrient salts.

Only the assimilation of labeled organic matter retained as a body carbon was measured. Since this is actually only one side of a balance and does not account for the possible simultaneous excretion of organic matter by corals, the experiments do not measure the net uptake. According to Pomeroy and Kuenzler (1969), under experimental conditions the net excretion of phosphorus can take place. Therefore the balance experiments are necessary for the complete quantitative description of the feeding of corals.

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