EFFECTS OF NITROGEN EXCRETION BY THE DAMSELFISH *Dascyllus aruanus* ON THE GROWTH RATE OF THE CORAL *Acropora aspera*

by

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Approved: _____

Stephen G. Nelson, Chairman, Thesis Committee

The effects of nitrogen excretion by the humbug damselfish Dascyllus aruanus on the growth of the coral Acropora aspera were studied. Growth experiments were conducted by the placement of coral colonies in tanks with and without resident fish. Experiments were also conducted to find the effects of nitrogen, at the levels excreted by the damselfish, on the rates of respiration and photosynthesis.

It was found that the presence of resident fish increased the growth of the coral Acropora aspera. It was also shown that corals in seawater enriched to 10 μM NH_4^+-N exhibited higher rates of gross photosynthesis and respiration than those in unenriched seawater. These results support the hypothesis that resident fishes stimulate coral growth by increasing the amount of regenerated nitrogen available to the coral.

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INTRODUCTION

It has been suggested that the nitrogenous excretions of resident coral reef fishes stimulate the rate of coral productivity. This hypothesis was tested by Meyer et al. (1983) and Meyer and Schultz (1985a, 1985b) in field studies in the Caribbean. They examined the effects of resident grunts, Haemulon flavolineatum and H. plumieri, on the growth of the corals, Porites furcata and Acropora palmata. These grunts are migratory fishes which feed in the seagrass beds during the night and aggregate over the coral heads during the day. In the studies by Meyer and colleagues, no significant differences were found between growth rates of corals with and without resident fish. However, when they measured the growth of coral colonies with resident fish present and again after the removal of the resident fish, they found that the coral growth was significantly reduced in the absence of the fish. Meyer et al. (1983) also noted that the concentrations of dissolved ammonia among the coral branches were higher within coral colonies which housed resident fishes. Thus, the effect of the fishes on coral growth was attributed to the increased availability of regenerated nitrogen which resulted from the excretions of the resident fishes. Further verification of the proposed effect of fish on coral productivity would be desirable before it is accepted as a significant phenomenon in coral reef ecology.

Although the Pacific does not have the large schools of grunts (Haemulidae) which reside near coral heads, as does the Caribbean,

there are a variety of other fishes which live within corals for protection. One such species, common on the reefs of Guam, is the humbug damselfish Dascyllus aruanus (Linnaeus). These damselfish are territorial and stay within a small area for prolonged periods (Sale, 1971). Groups of Dascyllus aruanus are closely associated with branching corals, such as Acropora aspera (Dana) and Porites spp., and feed on benthic algae and plankton (Sano et al., 1984; Sale, 1972a).

Since D. auranus feed in the water column, rarely range more than one meter away from their "home" coral (Sale, 1971), and withdraw between the coral branches at night or when in the presence of danger, they could conceivably stimulate coral growth in a manner similar to that proposed for the migratory grunts in the Caribbean.

The hypothesis of a stimulatory effect on the corals of ammonia excreted by resident fishes is reasonable since rapid uptake of ammonia by corals has been demonstrated (Muscatine and D'Elia, 1978). Also, ammonia increases both photosynthesis and photosynthate release by single-celled algae (Byerrum and Benson, 1975), and this has been proposed as a possible mechanism operating in coral-zooxanthellae relationships.

The purpose of this work was to test the hypotheses that resident fish, Dascyllus aruanus, stimulate the growth of the coral Acropora aspera, and that exposure of coral branches to low concentrations of dissolved ammonia, the major nitrogenous excretory product of fishes, increases the rate of coral productivity.

METHODS AND MATERIALS

COLLECTION OF CORALS AND FISH

Twenty colonies of the coral *Acropora aspera*, between 15 cm and 30 cm in diameter, and their associated damselfish, *Dascyllus aruanus*, were collected from Agana Bay on the western coast of Guam. They were transported in 63 x 45 x 34 cm polyethelene tubs, partially filled with seawater from the collection site, to the University of Guam Marine Laboratory. Both the *Acropora* and the *Dascyllus* were maintained at the laboratory in flowing seawater (28°C) in 119 cm x 204 cm cement tanks filled to a depth of 28 cm and exposed to the natural photoperiod. The organisms were maintained in the tanks for an acclimation period of two to four days prior to their use in the experiments. The *Dascyllus* were fed dried euphausids and freeze-dried brine shrimp once daily throughout all experiments.

FISH EXCRETION

Thirty-two *Dascyllus* were used to determine the relation between the fish size and their rate of ammonia excretion. This relation was then used to calculate the rate of ammonia production by the fish in each of the experimental trials. The fish ranged from 1.7 cm to 5.9 cm with a mean fork length of 3.93 cm (n=32, S.D.=1.395) and were held individually in 350-ml glass jars during the 2-hr monitoring period. These jars were filled with 300 ml of 0.45-μm filtered seawater aerated though glass

tubing. The jars were then placed in a thermoregulated water bath and maintained at 28°C±0.5°C. To determine the rate of ammonia excretion for individual fish, 10-ml water samples were taken every 30 minutes for two hours from each jar. Each 10-ml sample was then divided into two 4-ml subsamples. The phenolhypochlorite method (Amer. Pub. Health Assoc., 1976) was used to determine the NH_4^+-N concentration in each of the samples. The absorbance of these subsamples was measured with a Bausch and Lomb Spectronic 710 at 632 nm. The relation between fish size, expressed as length, and rate of excretion was calculated by the regression of the natural log (ln) of the excretion rate on the natural log of size.

CORAL GROWTH

Fourteen-day growth trials were conducted in the flow-through cement tanks described above. The flow rates of each of the cement tanks varied between 8 and 18 l min^{-1} during the trials (the variation resulted from the condition of the seawater pump during the experiment). The tanks were divided into two equal compartments with a 0.8-cm mesh screen overlayed with a 0.2-cm nylon screen and tied to a frame made of 1.9-cm diameter PVC pipe. This divider, used to restrict the movement of the fish, did not restrict the water flow. Two such divided tanks were used for each of the two sets of trials.

Twenty-five D. aruanus were used per tank for each trial. This is consistent with the density of resident fish of this species in corals in natural situations (Sale, 1972a). The fish

were placed only in one side of the divided tank; the other side was left without fish. Tank 1 had fish placed on the right side of the screen while tank 2 had fish placed on the left side of the screen. The wet weight and fork length of each fish was taken after each trial. The fish were weighed on a Mettler PN163 balance to the nearest 0.001 g and their fork lengths determined to the nearest 0.1 cm. The fish ranged from 2.0 to 6.2 cm with a mean fork length of 4.3 cm (n=100, S.D.=1.1). The weights of the fish ranged from 0.129 g to 8.050 g with a mean of 2.948 g (n=100, S.D.= 2.007). The fish were maintained in the tanks for several days prior to the addition of the corals.

The corals were dyed so that their growth rates could be later determined. To accomplish this, the corals were placed individually in plastic bags containing a 0.02 ppm solution of aliziran red. Aliziran red dye was used because it has relatively little effect on the corals (Lamberts, 1978). This dye stains the coral skeleton red with all subsequent growth remaining white. The bags were tied closed and placed for eight hours in one of the tanks.

When they were removed from the dye, the corals were broken into equal parts with a hammer and chisel. Two equal sections of each coral were placed in the tank, one section was placed on the side with fish while the other was placed on the side without fish. The relative locations of the coral halves within the tank halves were identical. Five corals were used per tank half, four paired corals being 20 cm from each corner and one in the center

of each side (Figure 1). These procedures were replicated with two tanks used per replicate (a total of 20 corals). The mean diameters of all corals were measured and their volumes calculated as if they were spheres.

At the termination of the growth trials, the corals were placed in fresh water for 72 hours. A high pressure stream of water was then used to remove all the dead tissue from the carbonate skeletons. The skeletons were then air dried at room temperature. The length and diameter of the new growth were determined by the discrete junction of the dye on the coral skeleton. Measurements of new growth were made to the nearest 0.05 mm with a Mitutoyo caliper. The new growth was sectioned off the branch and its weight determined to the nearest 0.1 mg on a Mettler H10 balance.

PHOTOSYNTHESIS AND RESPIRATION

Rates of apparent (net) photosynthesis (P) and respiration (R) of ten Acropora aspera axial tips were determined in a 122-ml, thermostated ($28^{0}C \pm 0.5^{0}C$), plexiglass respiration chamber equipped with a Radiometer oxygen electrode attached to a Strahkelvin dissolved oxygen meter. The oxygen meter was attached to an OmniScribe strip chart recorder. This system was designed by, and is similar to the one used by, P. S. Davies (1984) in a study of photosynthesis and respiration of the coral Pocillopora eydouxi. The chamber was illuminated with a Kodak slide projector to produce a photon flux density of 410 $\mu E\ m^{-2} sec^{-1}$ at the surface of the

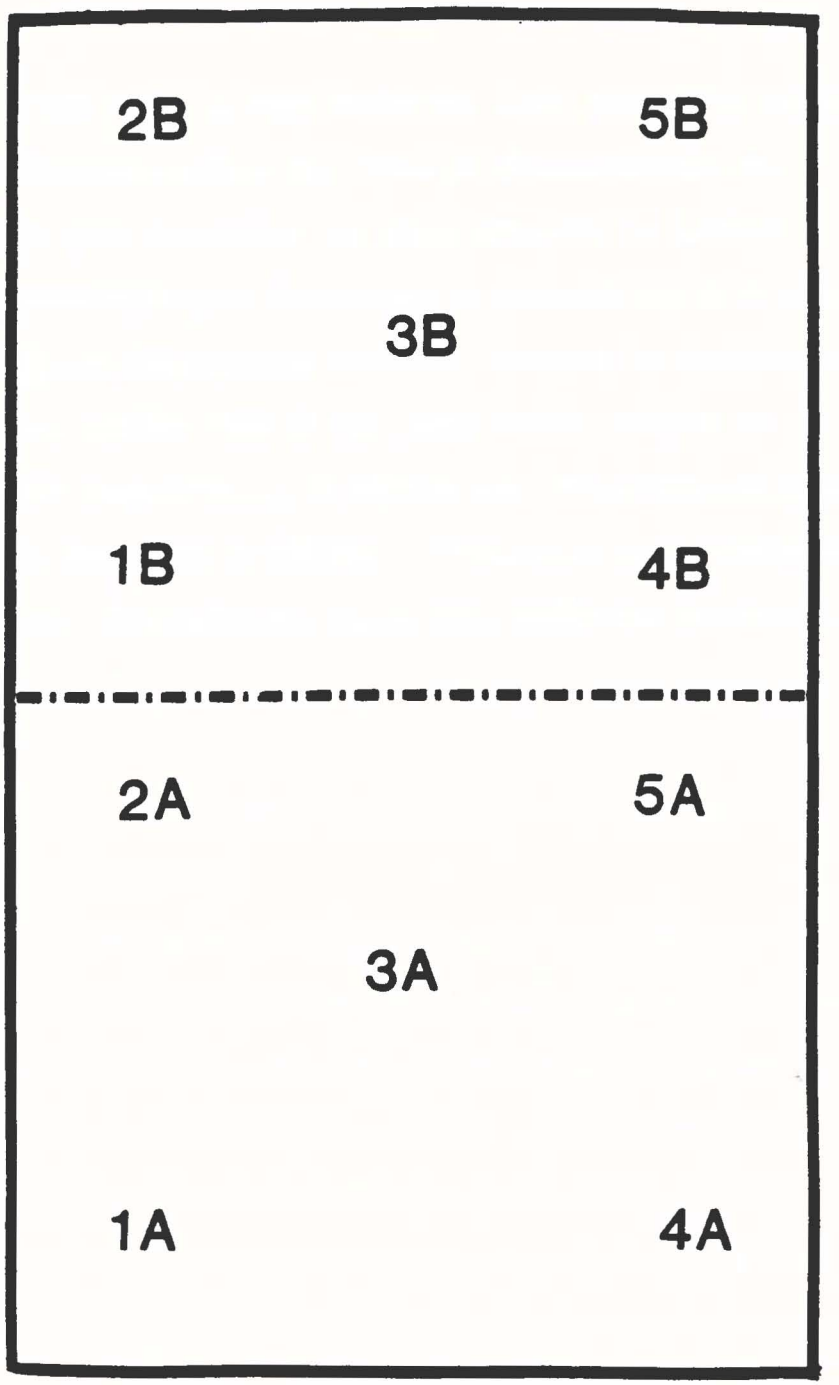

Figure 1: Illustration of the placement of corals in each tank. Dotted line is the screen dividing the tank. The numbers represent individual coral colonies. A and B represent corresponding halves of individual coral colonies 1 through 5.

chamber. This value is well above the light saturation point for Acropora (Chalker, 1981). The rates of photosynthesis and respiration were determined for coral branches in 0.45-µm filtered seawater either unenriched or enriched to 10 µM of NH_4^+ (with NH_4Cl as the nitrogen source). Changes in dissolved O_2 were plotted against time on the strip chart recorder as percentage of dissolved O_2 at saturation. The slopes of these regressions were used to estimate the rates of photosynthesis and respiration. Two replicate trials were conducted with each coral tip.

RESULTS

FISH EXCRETION

There was a linear relation between the ln of fish size and the ln of excretion rates; however, there was considerable variance in this relationship. The r^2 value of the $\log_n$ length vs. $\log_n$ excretion rate was found to be 0.4925. This indicates that slightly less than half of the variance in excretion rates resulted from the differences in size of the fish. Figure 2 shows the data and the line of best fit, which was determined by the least-squares method. This line is described by the equation $\ln(y) = 1.566 \times \ln(x) - 3.747$ where y is the excretion rate (μg-atm NH_4^+-N hr^{-1}) and x is the fork length (cm) of the fish.

The total estimated excretion rates of the combined fish in each of the coral-fish interaction experiments were calculated from the above equation. The fork length of each fish was used to estimate its rate of nitrogen excretion. The estimated amounts of nitrogen excreted by each individual were summed to provide an estimate of the total amount of nitrogen produced by the fish in each trial. Estimated total excretion values were 11.4 μg-atm NH_4^+-N hr^{-1} for trial 1 and 12.3 μg-atm NH_4^+-N hr^{-1} for trial 2 (Table 1). These values were then divided by the total volume of the corals housing resident fish to obtain mean excretion rates per coral volume. These rates were determined to be 5.46×10^{-4} μg-atm NH_4^+-N hr^{-1} cm^{-3} for trial 1 and 8.66×10^{-4} μg-atm NH_4^+-N hr^{-1} cm^{-3} for trial 2.

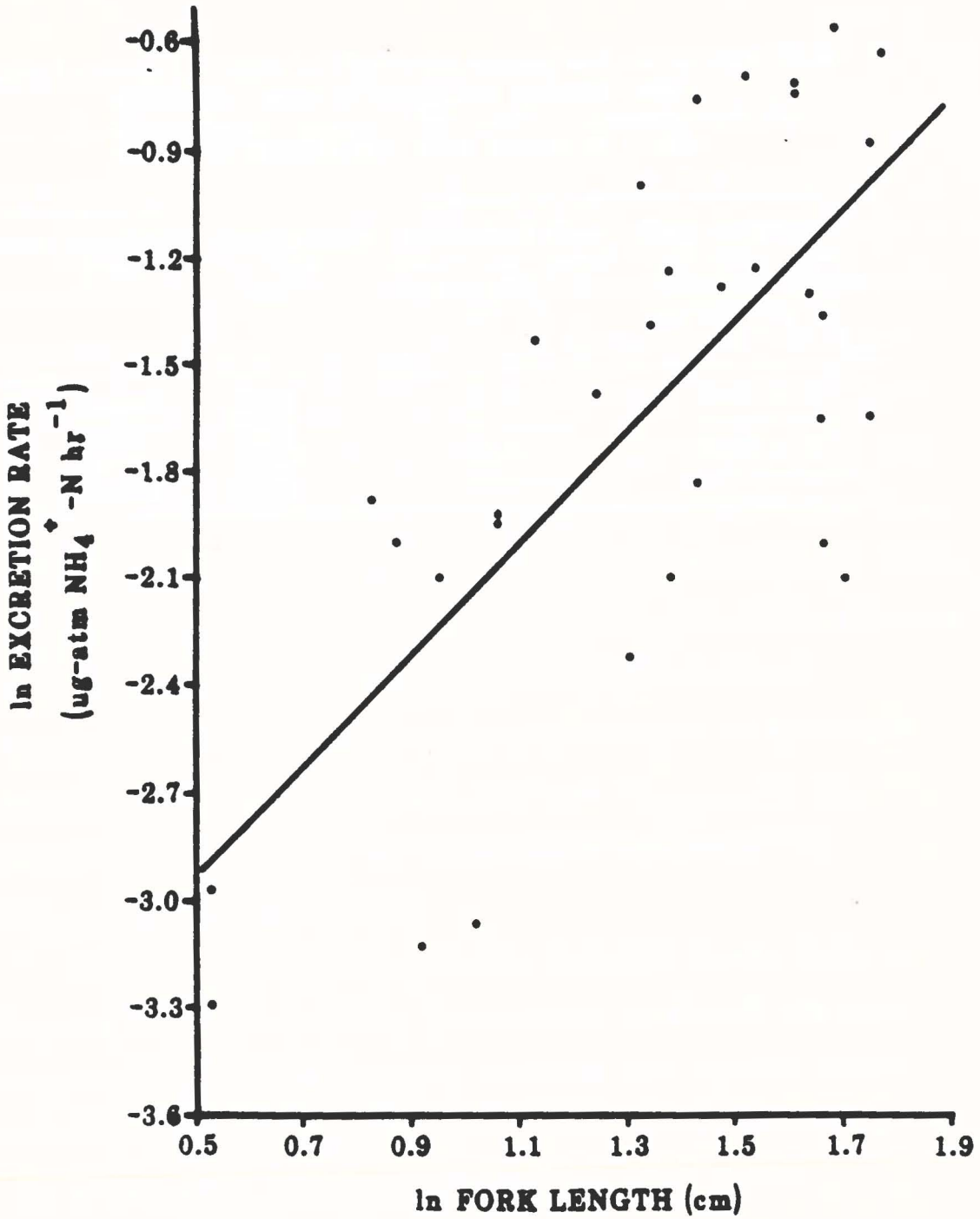

Figure 2: Plot of ln fish excretion (µg-atm NH_4^+-N hr^{-1}) and ln length (cm). The best fit line is described by the equation ln(y) = 1.566xln(x)-3.747 with an r^2 value of 0.4925. The confidence limits of the slope are ±0.5937.

Table 1. Total volumes of Acropora aspera and calculated fish excretion rates of Dascyllus aruanus used in experimental trials. See text for description of method of calculating fish excretion rates.

Trial	Resident Fish	Total coral volume (cm^3)	Estimated fish excretion rates ($\mu g\text{-}atm\ NH_4^+\text{-}N\ hr^{-1}$)	Mean estimated fish excretion rates per volume ($\mu g\text{-}atm\ NH_4^+\text{-}N\ hr^{-1}\ cm^{-3}$)
1	Present	20849	11.4	5.46×10^{-4}
1	Absent	24756		
2	Present	14165	12.3	8.66×10^{-4}
2	Absent	10389		

CORAL GROWTH

The growth rates of 1821 Acropora aspera calices were measured. These measurements were made on 934 calices from corals with fish present and 887 calices from corals without fish. An analysis of variance (ANOVA) was used to compare the growth rates of corals with and without resident fish, and to detect differences in the growth rates between coral pairs. The results are shown in Tables 2 and 3. Table 2 demonstrates that there is a significant effect of the fish on the growth of coral (expressed as total length (mm) for the trial period) ($F_{[1,1817]}=3.874$, $P<0.05$). The mean length of the new growth for the colonies with fish was 2.178 mm (N=934, S.D.=1.725) while the mean length of new growth without fish was 1.819 mm (N=887, S.D.=1.709). Also, the differences in growth rates of the paired coral colonies were significantly different ($F_{[1,1817]}=20.103$, $P<0.001$). As well, there was a significant interaction term ($F_{[1,1817]}=18.543$, $P<0.001$).

The results of an ANOVA comparing the coral growth rates, in terms of weight, were similar and are shown in Table 3. The mean weight of the new coral growth in the tanks with fish was 0.007 g while the weight for the new growth without fish was 0.005 g, for the 14-day period. This indicates that for coral growth, expressed in mg, there were significant differences ($F_{[1,1817]}=6.525$, $P<0.05$) in the rates of growth of corals between those tanks with fish and those without and in the rates of growth

Table 2. Analysis of variance comparing lengths of new growth of *Acropora aspera* in the laboratory with and without resident damselfish *Dascyllus aruanus*

	Source	DF	Mean-Square	F-Ratio	P
1	FISH	1	11.316	3.874	0.046
2	CORAL	1	58.717	20.103	<0.001
	1*2	1	54.160	18.543	<0.001
	ERROR	1817	2.921		

Table 3. Analysis of variance comparing weights of new growth of *Acropora aspera* in the laboratory with and without resident damselfish *Dascyllus aruanus*

Source	DF	Mean-Square	F-Ratio	P
1 FISH	1	0.000261	6.525	0.010
2 CORAL	1	0.001143	28.575	<0.001
1*2	1	0.001000	25.000	<0.001
ERROR	1817	0.000035		

between paired coral colonies ($F_{[1,1817]}=28.575$, $P<0.001$). There was also a significant coral-fish interaction factor ($F_{[1,1817]}=25.000$, $P<0.001$).

PHOTOSYNTHESIS AND RESPIRATION

The mean rates of photosynthesis and respiration of 10 Acropora branches are presented in Table 4. The mean respiration rate of the coral branches was 0.498 ml O_2 hr^{-1} in unenriched seawater and 0.650 ml O_2 hr^{-1} in enriched seawater. These mean rates were were found to be significantly different ($t=5.554$, $P<0.05$). The mean rates for apparent photosynthesis were 0.453 ml O_2 hr^{-1} in the unenriched seawater and 0.468 ml O_2 hr^{-1} in enriched seawater; there was no significant difference between these two groups ($t=0.504$, $P>0.05$).

Table 4. Mean rates of apparent photosynthesis and respiration of Acropora aspera branches in unenriched and enriched seawater. All numbers in the parentheses are standard deviations (N=2).

Coral	Apparent Photosynthesis		Respiration	
	unenriched	enriched	unenriched	enriched
1	0.617 (0.080)	0.675 (0.000)	0.437 (0.221)	0.676 (0.064)
2	0.421 (0.000)	0.421 (0.000)	0.412 (0.012)	0.521 (0.057)
3	0.505 (0.000)	0.463 (0.059)	0.452 (0.111)	0.563 (0.044)
4	0.463 (0.050)	0.397 (0.011)	0.477 (0.078)	0.389 (0.000)
5	0.398 (0.086)	0.449 (0.014)	0.459 (0.000)	0.674 (0.000)
6	0.360 (0.062)	0.589 (0.120)	0.343 (0.065)	0.582 (0.071)
7	0.463 (0.059)	0.430 (0.013)	0.399 (0.115)	0.577 (0.023)
8	0.433 (0.102)	0.510 (0.072)	0.658 (0.091)	0.749 (0.039)
9	0.368 (0.029)	0.317 (0.028)	0.658 (0.091)	0.807 (0.049)
10	0.505 (0.000)	0.430 (0.013)	0.687 (0.219)	0.964 (0.064)

DISCUSSION

Tropical oceans near coral reefs are characteristically low in nutrients, and nutrients, particularly nitrogen, may be one of the major factors limiting coral production. Meyer et al. (1983) and Meyer and Schultz (1985a, 1985b) proposed that fish schools residing around corals could reduce the nitrogen limitation through their excretion of ammonia. This hypothesis is supported by the results of this study.

The mechanism for the uptake of ammonia by corals is not fully understood, but it has been shown by several investigators that the uptake and utilization of ammonia by corals is mediated by their zooxanthellae (Burris,1983; Szmant-Froelich and Pilson, 1984). Burris (1983) conducted studies of various corals, including species of Acropora, and concluded that zooxanthellae assimilate NH_4^+ from the surrounding enviroment. Burris (1983) observed that this nitrogen is then transferred to coral tissue and provides energy for coral growth. Thus, the increase in NH_4^+ caused by fish excretion could allow increased coral growth as was observed in this study.

I found significantly greater respiration rates of corals (Acropora aspera) in ammonia-enriched seawater than in unenriched seawater. Although gross photosynthesis was stimulated by NH_4^+, there was no significant difference in the rates of apparent photosynthesis between corals in enriched and unenriched seawater. Similarly, Szmant-Froelich and Pilson (1984) reported that corals fed

with a high-nitrogen diet three times a week had higher respiration rates than those fed only once per week; they also noted that there was no significant difference in apparent photosynthetic rates between these two groups. In addition, Woo and Canvin (1980) reported that the effect of ammonia on isolated spinach cells was to stimulate total photosynthetic CO_2 fixation. It is also known that an increase in photosynthesis causes an increase in the rate of skeletal deposition of coral tissue (Vandermeulen et al., 1972; Goreau and Goreau, 1959). Also, Byerrum and Benson (1975) have shown that, for single-celled algae, ammonia causes increases both in photosynthesis and in the release of photosynthate products. The extra energy available to the coral, in the form of photosynthate products, could result in increased growth rate.

The excretion rate calculated for the mean weight of the Dascyllus (2.948 g, S. D.= 2.007) was 6.14 μg-atm NH_4^+ day^{-1} and is similar to nitrogen excretion rates reported for other species of fish. For example, Savitz (1969) found the excretion rates of Lepomis macrochirus to be 10.43 μg-atm NH_4^+ day^{-1} for similarly sized fish at 29-32^{0}C.

It is possible that Dascyllus have a greater effect on coral growth than that of the grunts that were studied by Meyer et al. (1983) and by Meyer and Schultz (1985a, 1985b). The Dascyllus actively feed in the vicinity of the corals during the day (Sale, 1971); however, the grunts feed in seagrass beds during the night and then migrate to the corals where they stay during the day (Randall, 1967). It has been shown that the excretion rates of fish and

invertebrates increase, in some cases up to a factor of seven, during and immediately after feeding (McCarthy and Whitledge, 1971; Nelson et al., 1979; Meyer and Schultz, 1985a). Therefore, fish that feed in the immediate vicinity of the corals should provide greater amounts of regenerated nitrogen than fish which feed elsewhere.

The significant interaction between the fish and coral colonies in their effect on coral growth (Tables 2 and 3) could have resulted from the behavior of the fish, the larger of which defended territories during the experiments. The territoral behavior of D. aruanus has been previously documented by Sale (1972b). The territorial behavior of the larger fish caused the smaller individuals to be grouped together in a few corals. Uneven distributions of fish per coral could have resulted in some disparity in the regime of regenerated nitrogen to which the corals were exposed. Since the fish stimulate coral growth, the uneven distribution of fish among the coral colonies could conceivably result in a differential response of the colonies to the presence of the fish and, thus, in a significant coral-fish interaction.

Oliver (1984) noted that morphologically distinct coral tips within a colony differ in growth rate; therefore it is not particularly surprising that a significant difference was found between the growth rates of the different colonies within treatments in this experiment.

The results of this study support the hypothesis that coral-associated reef fishes benefit their "home" coral colonies by stimulation of coral growth. This effect can be attributed, in part,

to the nitrogen provided by the fish which are in close proximity to the coral. This study also shows that corals respond to brief exposures to dissolved ammonia with an immediate increase in the rate of gross photosynthesis. Presumably this would translate into increased growth of the coral. Nitrogen regeneration by coral-residing fishes may thus be a significant factor favoring the growth of branching corals in tropical coral reef habitats.

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