

Resource Availability and Suspension Feeding by Gorgonian Soft Corals

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INTRODUCTION

Like reef corals, many octocorals contain symbiotic algae, zooxanthellae, which enable the host to feed on algal photosynthate as well as particulate matter captured by the polyps. The ability of octocorals to utilize both of these sources has been experimentally demonstrated (Kinzie, 1970; Lasker, 1981; Lewis and Smith, 1971; Murdock, 1978; Roushdy and Hansen, 1961). However, the relationship between these modes of nutrition is poorly understood for both octocorals and scleractinian corals.

Do species capable of obtaining large amounts of photosynthate rely on particulate feeding less than other species or are the two modes of nutrition largely independent of each other? Porter (1976) hypothesized that the photosynthetic and particulate feeding abilities of Caribbean reef corals are complementary. Sorokin (1978, 1979) working with Pacific corals presents data which do not show complementarity. Both Porter and Sorokin compared corals encompassing different families and with radically different morphologies. Morphological differences were a major component of Porter's (1976) hypothesis and were used by him as an index of photosynthetic activity.

In this paper we compare the feeding potential of two closely related Caribbean octocorals Plexaura homomalla and Plexaura nina. In addition to their taxonomic relatedness, both species have similar arborescent colony forms and similar polyp size. However, P. homomalla and P. nina exhibit different depth ranges (Kinzie, 1970), and resultantly they have different photosynthetic rates. In comparing the feeding capabilities of these two species, we can determine whether feeding and photosynthesis covary in a predictable fashion.

METHODS

Experiments were carried out in situ in April 1980 while working out of the N.O.A.A. underwater habitat Hydrolab. The feeding abilities of Plexaura homomalla and P. nina were compared at 17 m and 29 m sites in Salt River Canyon, St. Croix, U.S. Virgin Is. These two species occupy non-overlapping depth distributions in Salt River Canyon. P. homomalla is visually the most abundant gorgonian above 20 m and P. nina is one of the most abundant species below 20 m.

Feeding ability was measured from 10 cm branch tips cut from colonies adjacent to the experimental sites. P. homomalla colonies were collected from the shallow site and P. nina colonies collected from the deep site. Branch tips were collected the afternoon preceding each experiment and attached to glass rods with cable ties. Half of the branch tips of each species were left at the site of collection and the remaining half transferred to the other site.

At the start of the feeding experiment, one branch tip of each species was enclosed in a 7.5 l chamber made of a square plexiglass base and top (25 x 25 cm) and flexible polyethylene sidewalls 12 cm in height. The top of the chamber was supported by a small polystyrene float. The chambers were modified from those of Gust (1975) and Lasker (1981) and permit near normal water movement within the chamber (Gust, 1975.) After being enclosed in the chambers the branch tips were examined for polyp expansion and 0.5 g of Sephadex G-10 gel filtration beads in 15 ml of sea water were injected into the top of the chamber. The sephadex beads used in the experiments were presoaked in sea water 24 h prior to the experiment. After being injected into the chamber they sank, and almost all of the beads reached the base of the chamber after 15 minutes. During the experiment polyps could be observed capturing the particles. After 15 minutes the branch tips were removed from the chamber, placed in plastic bags and formalin immediately injected. The experiment was repeated 4 times at each depth on each of 5 consecutive days. Twenty polyps from each branch tip were later dissected and examined at 80x for the presence of Sephadex beads.

In addition to the feeding experiments, rates of photosynthesis were measured by determining oxygen fluxes of branch tips kept in 1.5 l chambers similar to those used in the feeding experiments. The side walls of these chambers were constructed of Saran which is impermeable to oxygen. Dissolved oxygen concentrations at the start and end of the incubations were determined by withdrawing replicate 50 ml samples. The samples were transferred to the surface and dissolved oxygen content measured with a YSI 57 oxygen meter. A control for oxygen flux of the sea water was made by simultaneously incubating 50 ml water samples in syringes next to the experimental chambers. Measurements were made on three successive days between 1030 and 1600 hr (29 m site and 1200 and 1500 hr (17 m site). Oxygen flux was adjusted for elapsed time and ash free dry weight of the branch tips.

Since feeding rates may be affected by stimuli from naturally present particulate matter, several measures of water and food particle quality were made at the time of the experiments. Replicate water samples were collected in Niskin bottles at each site on each day. They were analyzed for dissolved organic carbon, suspended particulates, chlorophyll *a*, and bacterioplankton. Samples for dissolved organic carbon analysis were preserved by acidification to pH 1-2. At the time of analysis 50 ml samples were purged of CO₂ with N₂, oxidized by UV photolysis and CO₂ determined with a non-dispersive IR analyser (Beckman 215 A). Chlorophyll *a* was measured fluorometrically according to the method of Yentsch and Menzel (1963). Suspended particulates were measured by filtering 1000 ml samples through precombusted, pre-weighted GF-C filters, rinsing with ammonium formate and drying. Dry weights were determined and ash free dry weight measured following 12 hours combustion at 400°C. Bacterioplankton were determined by the acridine orange direct counting method (Hobbie, Daley and Jasper, 1977). Bacteria were divided into two classes, those found on particles > 3µm and free living.

RESULTS

Results of the feeding experiments are presented in Figure 1. Three indices of feeding are presented, mean number of particles ingested per polyp, mean number of particles ingested per “feeding” polyp (i.e., only polyps capturing particles are considered) and percent of polyps capturing prey (Figs. 1A, 1B and 1C respectively). The data were analyzed using a 3-way analysis of variance (ANOVA) which compared effects of species, depth, day of the experiment and all interactions. Regardless of the index used, significant differences were found in the feeding of *P. nina* and *P. homomalla* ($p = 0.001, 0.001$ and 0.01 for 1A, 1B and 1C respectively). At each depth *P. nina* ingested more particles than *P. homomalla*. Similarly significant differences were found in feeding between the five days of experiments (ANOVA, $p < 0.001$, all three indices of feeding). Differences in feeding among days can be attributed to the reduced feeding on 22 and 23 April, which both differ from the previous 3 days (least significant difference test, $p < 0.05$, Sokal and Rohlf, 1969). Branch tips used in the experiments were less fully expanded on 22 April but no obvious differences in expansion was observed on 23 April, Table 1. As will be discussed, water conditions on 22 and 23 April differed from the previous days. All interaction effects between day, species and/or depth were not significant.

Significant differences between depths (i.e., the depth at which the experiment was conducted) were found in the mean number of particles ingested ($p = 0.018$) and in the mean number of particles ingested by feeding polyps ($p = 0.002$.) No significant interaction was observed between species and depth indicating that both species responded to depth similarly. However, *a posteriori* analysis indicates that only *P. nina* had greater feeding rates at the 17m site (least significant difference test, $p < 0.05$). *P. homomalla* on the average had greater feeding rates at 17m but the differences were not significant

when compared independent of the *P. nina* data.

Mean rates of photosynthesis during the three days of measurements are presented in Table 2.

Characterization of the water column through measurements of chl *a*, bacteria counts, particulate organic matter (POM) and dissolved organic carbon (DOC) reveal that the water column remained relatively homogeneous with depth (Table 3). Significant differences were observed in chl *a* values with depth, chl *a* values being greater (ANOVA, $p < 0.05$) at the shallow site. Measurements of POM, DOC and bacteria attached to particles did not show any significant differences with depth. More variability was found between days than between depths and a significant difference between days in particulate organic matter was observed (ANOVA $p < 0.05$). The values are at the upper range of those reported for reefs (Ducklow and Mitchell, 1979; Marshall et al., 1979; Simmons, 1979; Westrum and Meyers, 1978).

DISCUSSION

The feeding experiments indicate that *P. nina* had higher feeding rates than *P. homomalla* at both sites. Given the same conditions, *P. nina* is capable of greater rates of particle feeding than *P. homomalla*. However, *P. nina* and *P. homomalla* are not ordinarily exposed to the same conditions. *P. nina* is restricted to depths greater than 20 m and *P. homomalla* is usually found in shallower waters. Therefore, more correct indicators of the rate of particle feeding by these species are feeding rates within their natural depth ranges. When the feeding rates of *P. nina* at 29 m are compared to those of *P. homomalla* at 17 m there are no significant differences (least significant difference test). This suggests that these two species normally capture similar amounts of particulate matter despite *P. nina*'s greater particle feeding capability.

The feeding rates of *P. nina* and *P. homomalla* within their respective habitats are similar because *P. nina* has lower feeding rates at 29 m than at 17 m. The reduction in feeding rate at 29 m “cancels” *P. nina*'s greater feeding capability. Similarly, the trend in the *P. homomalla* experiments also indicates higher feeding rates at 17 m than at 29 m.

The difference between depths could be caused by responses to differences in particulate availability. However, as noted above, only chlorophyll *a* varied between the two sites. Furthermore, the only water quality parameter which changed on days with significantly reduced feeding (April 22 and 23) was the particulate organic content of the water. Particulate organic content did not, however, vary between depths.

The parameter which does correlate well with feeding rates is photosynthetic production. Both species have increased rates of photosynthesis at 17 m and both have higher feeding rates at that depth. Similarly, April 22 and 23, the days with the lowest feeding rates, were days of heavy cloud cover (April 22) or turbidity (April 23) which would reduce light and therefore photosynthesis.

This implies that feeding rates are in some way tied to photosynthetic rates. Davies (1978) has observed higher respiration rate in corals with high rates of photosynthesis, and Lasker (1979) reports that activity patterns in *Montastrea cavernosa* may also correlate with photosynthetic rate. The increased feeding rates observed in this study may reflect a similar increase in the colony's metabolic rate. Clayton and Lasker (submitted) have noted decreased feeding rates in *Pocillopora damicornis* maintained in darkness. The mechanism controlling the photosynthesis-feeding rate interaction is unknown at this time.

The differences in feeding rates reported here are indicative of the roles of phagotrophy and phototrophy among gorgonians. In comparing the two species and depths we argue that both species obtain fewer nutrients from photosynthesis at 29 m than at 17 m. The measured oxygen fluxes support

this conclusion, but in reaching the conclusion several important assumptions are made. First, we assume that extended incubations (several hours), and measurement made over less than 24 h do not bias measurements at one depth or for one species more than another (see McCloskey et al. [1978]). Second, our conclusion assumes both species have similar respiration rates and obtain similar percentages of photosynthate from their zooxanthellae. Due to these assumptions we do not suggest our measures of photosynthesis are absolute values of gorgonian primary production. Our measures are, however, indices of primary production and strongly suggest that *P. homomalla* has greater rates of primary production within its habitat (17 m) than *P. nina* in its habitat (the 29 m site). When measured in the same habitat *P. nina* appears to have greater rates of photosynthesis.

Porter (1976) suggested that Caribbean reef corals rely to differing degrees on either zooplankton feeding or phototrophy to meet their metabolic needs. Particulate feeding and phototrophy by *P. nina* and *P. homomalla* do not display such a complementary relationship. *P. nina*, the species normally receiving less energy from photosynthesis, does have greater feeding capabilities than *P. homomalla*, but the two species when examined within their own habitats do not have different feeding rates. Furthermore, *P. nina*, and possibly *P. homomalla*, exhibits its highest feeding rates when transferred into shallow water when photo-synthetic rates are also highest.

Phototrophy and phagotrophy in *P. nina* do not display the complementary relationships Porter suggested nor are the two independent. When the two species' feeding rates are compared at single depths or the feeding rates of either species compared over depth, it is the specimens with the greatest photosynthetic rates which have the greatest feeding rates. Among specimens of *P. nina* and *P. homomalla* phagotrophy and phototrophy are positively correlated.

Acknowledgements

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TABLE 1 - Proportion of Experimental Colonies Fully Expanded During the Feeding Experiments.

			<u>P. homomalla</u>		<u>P. nina</u>	
			<u>17m</u>	<u>29m</u>	<u>17m</u>	<u>29m</u>
19	April	1981	1/4	2/4	4/4	4/4
20	"	"	4/4	4/4	4/4	2/4
21	"	"	2/4	3/4	4/4	1/4
22	"	"	1/4	1/4	2/4	3/4
23	"	"	3/4	3/4	4/4	2/4

TABLE 2 - Daytime rates of oxygen production (mean of 3 observations \pm standard error) of *P. homomalla* and *P. nina* colonies at 17m and 29m sites. Values are in mg O₂ - hr⁻¹ - g ash free dry weight⁻¹.

	<u>17m</u>	<u>29m</u>
<u>Plexaura homomalla</u>	0.30 (0.16)	0.02 (0.02)
<u>P. nina</u>	1.26 (0.36)	0.07 (0.10)

TABLE 3 - Particulate matter and dissolved organic content of sea water samples (mean + standard deviation) during the five days of feeding experiments.

	<u>17m</u>	<u>29m</u>
Bacteria (free-living; $\times 10^5$ cells/ml)	6.95 \pm 1.20	7.03 \pm 2.26
Bacteria (on particles $>3\mu\text{m}$ $\times 10^5$ cells/ml)	0.46 \pm 0.09	0.46 \pm 0.06
Chlorophyll <u>a</u> (mg chl <u>a</u> /m ³)	1.83 \pm 1.31	0.95 \pm 0.22
Particulate matter (dry wts; mg/l)	2.59 \pm 0.77	2.20 \pm 0.66
Particulate organic matter (POM; mg/l)	0.92 \pm 0.26	0.84 \pm 0.17
Dissolved organic carbon (DOC;mg C/ml)	3.39 \pm 1.85	3.10 \pm 1.41

Appendix A - Equipment and documentation

Personnel

Mission Team

Howard R. Lasker - Dept. of Biological Sciences, SUNY at Buffalo Principal Investigator and Team Leader

Mary Alice Russell - Rosenstiel School of Marine and Atmospheric Sciences - Assisted Lasker with particulate feeding experiments and conducted mucus feeding experiments.

Mark Gottfried

David Gordon - Rosenstiel School of Marine and Atmospheric Science, University of Miami - collected water samples, zooplankton samples and took current readings. Gottfried was responsible for subsequent analysis of water samples.

Support Divers

Douglas G. Capone - Marine Sciences Research Center, SUNY at Stony Brook.

Lawrence Lee - Dept of Biological Sciences, SUNY at Buffalo

Lynda Dugay -Capone - Marine Science Research Center, SUNY at Stony Brook - Responsible for surface cataloging and processing of samples.

Chronology

13 April, 1980 - Arrive St. Croix

14-16 April Training

17-24 April Mission

24 April Surface

26 April Leave St. Croix

Facilities See quick look report

Scientific Equipment See quick look report

Appendix C - Dissemination of results

The results of the mission have been submitted for publication to Marine Biology.

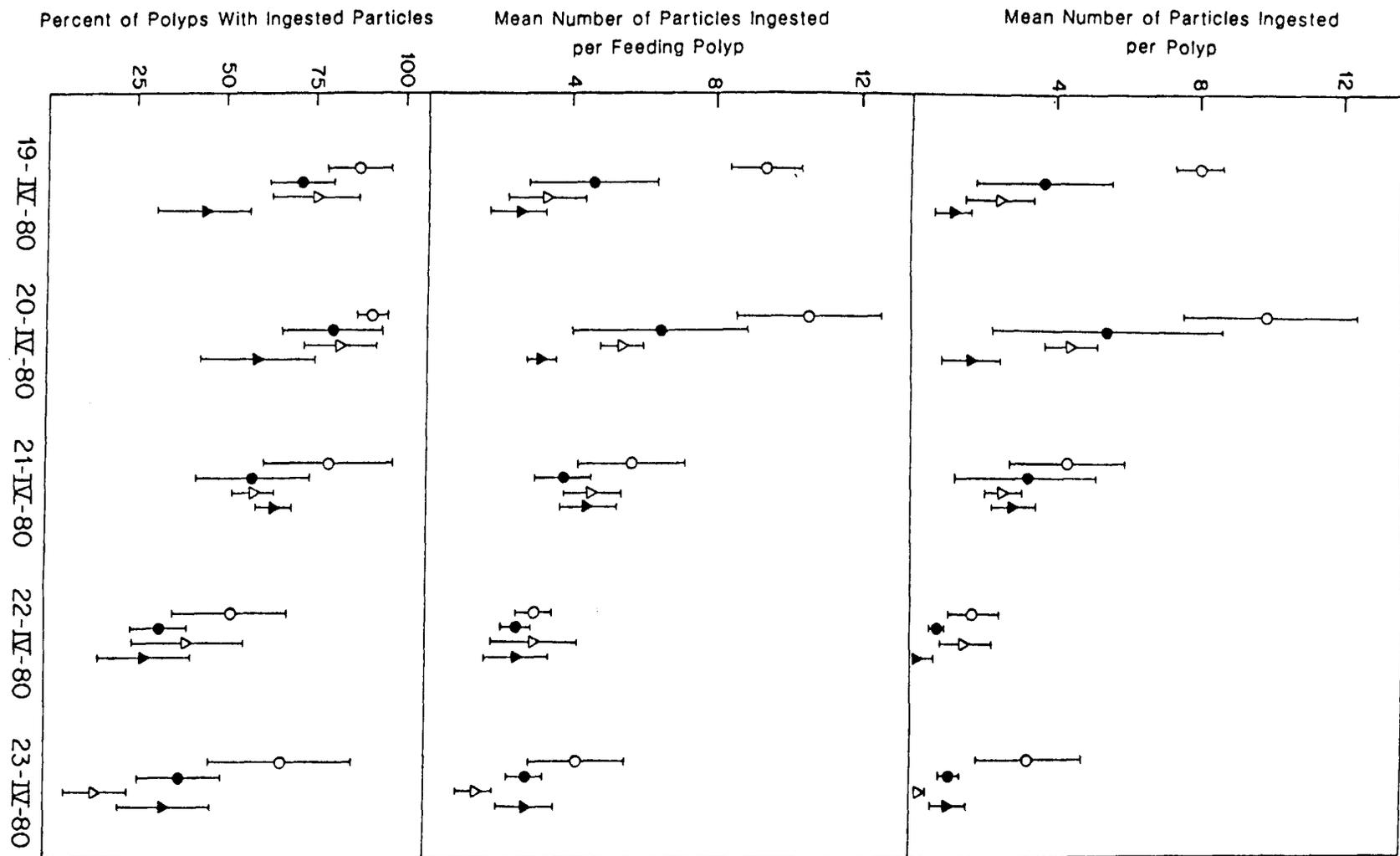


Figure Caption

Figure 1 - Results of feeding experiments. Three different indices of feeding are presented which portray feeding rates of *P. homomalla* (triangle) and *P. nina* (circles). Feeding rates at 17 m are presented as open symbols and feeding rates at 29 m are presented as closed symbols. Each value is the mean of four experiments. Error bars are one standard error in length.