

EFFECTS OF DEPTH ON THE FEEDING CAPABILITIES OF TWO OCTOCORALS

H. R. Lasker

Department of Biological Sciences,
State University of New York,
Buffalo, NY 14260 USA

M. D. Gottfried

M. A. Coffroth

Rosenstiel School of Marine and
Atmospheric Science, University of Miami,
4600 Rickenbacker Causeway, Miami, FL 33149 USA

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H. R. Lasker¹, M. D. Gottfried² and M. A. Coffroth²

¹ Department of Biological Sciences, State University of New York; Buffalo, New York 14260, USA

² Rosenstiel School of Marine and Atmospheric Science, University of Miami; 4600 Rickenbacker Causeway, Miami, Florida 33149, USA

Abstract

Feeding abilities of *Plexaura homomalla* and *P. nina* were measured during a saturation dive in the underwater habitat Hydrolab at Salt River Canyon, St. Croix, US Virgin Islands. Feeding rates were measured as the number of Sphadex beads ingested by polyps exposed to a known density of beads for 15 min. At Salt River, *P. homomalla* is found above 20 m and *P. nina* below 20 m. Feeding abilities were measured in each species' own habitat. At both 17 and 29 m *P. nina* had greater feeding rates than *P. homomalla*. These differences can be attributed to *P. nina*'s larger polyps. Feeding rates of both species tend to be lower at 29 m than at 17 m, but feeding rates of *P. homomalla* at 17 m are equal to those of *P. nina* at 29 m. Habitat related differences in feeding rates correlate with light availability, but the distribution pattern of *P. nina* and *P. homomalla* at Salt River cannot be explained by their heterotrophic and photoautotrophic abilities.

Introduction

The feeding biology of organisms has always been one of the central concerns of ecologists, and for many species feeding is the interaction with the environment that most limits population growth. It is not surprising therefore that the feeding biology of reef anthozoans has long attracted the attention of researchers (c.f. Yonge, 1931), and to this day remains a subject of intense interest. Continued research on the feeding of reef anthozoans is attributable in part to the great diversity and complexity of their feeding biology. Much attention has been given to the symbiosis between anthozoans and zooxanthellae, which makes many reef anthozoans at least partially photoautotrophic (Trench, 1971; Taylor, 1973; Muscatine and Porter, 1977; Muscatine, 1980). Reef anthozoans also

utilize a variety of mechanisms of heterotrophic feeding which include the capture of zooplankton (Yonge, 1931; Porter, 1974; Lasker, 1976; Sebens, 1977), phytoplankton (Roushdy and Hansen, 1961), detritus (Lewis and Price, 1975; Sebens, 1977; Lasker, 1976, 1978; Russell, 1981) and the uptake of dissolved organic matter (Stephens 1962).

Like most other reef anthozoans many octocorals contain zooxanthellae, enabling them to utilize photosynthetic products as well as particulate matter captured by the polyps. The ability of octocorals to utilize photoautotrophic and heterotrophic food sources has been examined by a number of authors in a variety of octocorals (Gohar, 1940; Roushdy and Hansen, 1961; Kinzie, 1970; Lewis and Smith, 1971; Murdock, 1978; Lasker, 1981a). Wainwright (1967), using behavioral data, attempted to relate photoautotrophic and heterotrophic feeding among octocorals. However, there have been no attempts to measure directly both heterotrophic and autotrophic ability, and there has been only one attempt to compare the relative feeding abilities of different species (Lasker, 1981a).

In this paper we compare the particle feeding abilities of two closely related Caribbean gorgonians *Plexaura homomalla* and *P. nina*. These species form arborescent colonies up to 1 m in height. *P. nina*, which is characteristically found in deeper waters, forms less bushy colonies with fewer branches than *P. homomalla*. As *P. homomalla* and *P. nina* inhabit different depth ranges (Kinzie, 1970), a comparison of their feeding abilities also provides data on the effect of inhabiting locations with different light levels.

Material and Methods

Experiments were carried out *in situ* in April 1980, utilizing the N.O.A.A. underwater habitat Hydrolab. The feeding abilities of *Plexaura homomalla* and *P. nina* were compared at 17- and 29-m sites in Salt River Canyon, St.

Croix, US Virgin Islands. 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 using 10-cm branch tips cut from colonies adjacent to the experimental sites. *Plexaura 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. Branch tips attached to rods in this fashion expand their polyps within several hours of attachment and appear to behave normally. Branch tips of many species, including *P. homomalla*, will often overgrow glass rods when left attached to the rod for a week or more.

Experiments were conducted at both sites on each of 5 consecutive days between 1030 and 1200 hrs. Experiments at the 29-m site were conducted first, followed by those at the 17-m site approximately 45 min later. Nighttime measurements at the 17-m site were made on 4 nights between 2100 and 2200 hrs. 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 Plexiglas base and top (25×25 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 (1977) and Lasker (1981a) and transmit oscillatory movement to water within the chamber (Gust, 1977). 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 for 24 h prior to the experiment. The hydrated Sephadex beads ranged from 25 μm to greater than 100 μm . The modal size class was 50–75 μm in diameter and 29, 37 and 25% of the particles fell in the 25–50, 50–75 and 75–100 μm size classes respectively. The beads are denser than sea water and settled out during the course of the experiment. Almost all of the beads reached the base of the chamber after 15 min. Although Sephadex beads are not a natural prey item, gorgonians reacted to the beads much as they do to other non-motile particles in the water column (Lasker, personal observation). Capture of these particles does not, of course, mimic that of motile prey. However, all gorgonians, which have been examined, have proved to be ineffective zooplankton feeders (Lasker, 1981a). During the experiment polyps could be observed capturing the particles. None were observed to regurgitate beads in this time period. After 15 min 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 80 \times for the presence of Sephadex beads.

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. Duplicate water samples were collected in Niskin bottles at each site on each day. These 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 analyzer (Beckman 215A). Chlorophyll *a* was measured fluorometrically according to the method of Yentsch and Menzel (1963). Suspended particulates were measured by filtering 1 000-ml samples through precombusted, pre-weighed GF-C filters, rinsing with ammonium formate and drying. Dry weights were determined and ash free dry weight measured following 12 h combustion at 400 °C. Bacterioplankton density was determined by the acridine orange direct counting method (Hobbie *et al.*, 1977). Bacteria were divided into two classes: those found on particles > 3 μm and free living.

Results

Results of the daytime feeding experiments are presented in Fig. 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. 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. Feeding data were transformed by \sqrt{x} prior to analysis. Per cent polyps feeding were analyzed as the number of polyps (out of 20 sampled) which had ingested particles and were also square root transformed. Regardless of the index used, significant differences were found in the feeding of *Plexaura nina* and *P. homomalla* ($P=0.001$, 0.001 and 0.01 for the three indices respectively). At both depths *P. nina* ingested more particles than *P. homomalla*. Significant differences were also found in feeding between the five days of experiments (ANOVA, $P\leq 0.001$, all three indices of feeding). Differences in feeding among days can be attributed to the reduced feeding on April 22 and 23, which both differ from the previous 3 d (least significant difference test, $P<0.05$, Sokal and Rohlf, 1969). Branch tips used in the experiments were less fully expanded on April 22, but no obvious differences in expansion were observed on April 23 (Table 1). As will be discussed, water conditions on April 22 and 23 differed from the previous days. All interaction effects between day, species and/or depth were not significant.

Significant differences between 17 and 29 m 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

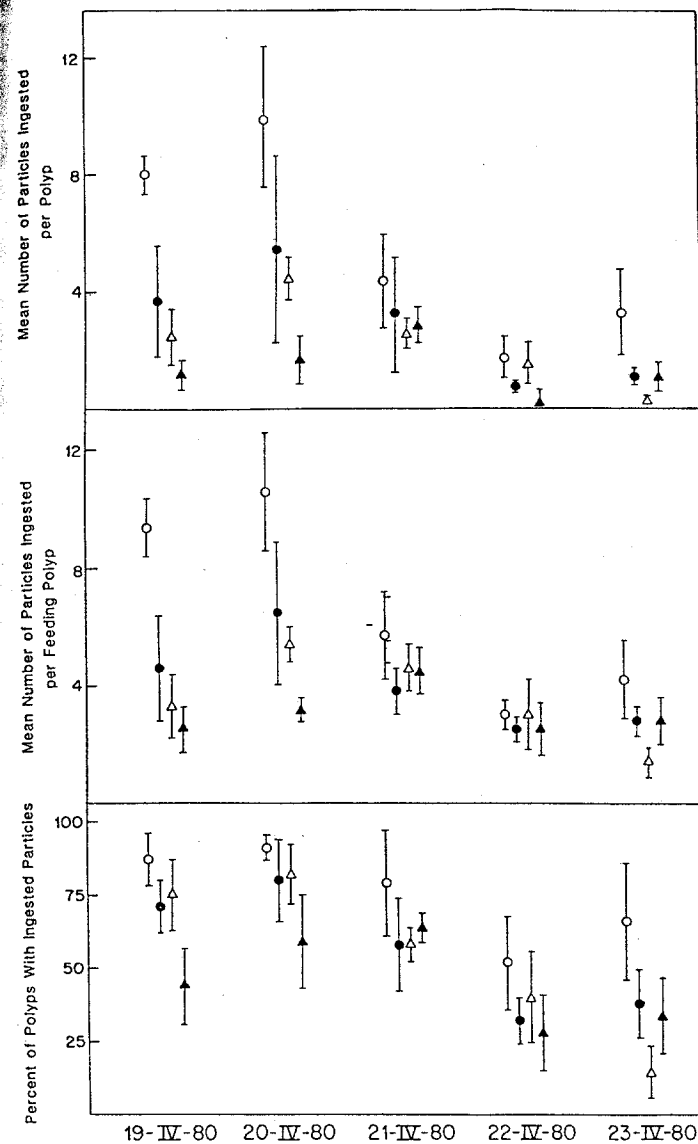


Fig. 1. *Plexaura homomalla* and *P. nina*. Results of feeding experiments. Three different indices of feeding, which portray feeding rates of *P. homomalla* (triangles) and *P. nina* (circles), are presented. Feeding rates at 17 m are presented as open symbols and feeding rates at 29 m are presented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

Table 1. *Plexaura homomalla* and *P. nina*. Proportion of experimental colonies fully expanded during the feeding experiments

	<i>P. homomalla</i>		<i>P. nina</i>	
	17 m	29 m	17 m	29 m
19 April 1980	1/4	2/4	4/4	4/4
20 April 1980	4/4	4/4	4/4	2/4
21 April 1980	2/4	3/4	4/4	1/4
22 April 1980	1/4	1/4	2/4	3/4
23 April 1980	3/4	3/4	4/4	2/4

between species and depth, indicating that both species responded to depth similarly. However, *a posteriori* analysis indicates that only *Plexaura nina* had greater feeding rates at the 17-m site (least significant difference test, $P < 0.05$). *P. homomalla* on the average had greater feeding rates at 17 m but the differences were not significant when compared independently of the *P. nina* data.

Nighttime feeding rates are presented in Table 2. As in the daytime experiments there were significant differences in feeding rates between *Plexaura homomalla* and *P. nina* and among days (3 way ANOVA, $P < 0.001$, all 3 measures of feeding). There were no significant differences in feeding rates between day and night (3 way ANOVA, $P = 0.513, 0.305, 0.863$, for the 3 measures in Table 2). *P. homomalla's* nighttime feeding rates closely paralleled the pattern of daily variation observed in the daytime feeding rates. However, *P. nina* feeding rates were more homogeneous over the 4 nights than during those 4 days.

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). With the exception of chlorophyll *a*, no differences were observed between depths. Chlorophyll *a* concentrations were greater at the shallow site (ANOVA, $P < 0.05$) but 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 among all parameters, and a

Table 2. *Plexaura homomalla* and *P. nina*. Nighttime feeding rates of branch tips (\pm standard error, $n = 4$) measured at 17 m depth

	<i>P. homomalla</i>				<i>P. nina</i>			
	4/19	4/20	4/21	4/22	4/19	4/20	4/21	4/22
Average number of particles ingested per polyp	2.6 (0.6)	4.4 (1.2)	3.7 (2.3)	0.8 (0.2)	6.3 (1.0)	6.7 (1.6)	6.2 (0.9)	7.5 (2.4)
Average number of particles per feeding polyp	4.1 (0.5)	5.2 (1.0)	5.2 (1.9)	2.6 (0.7)	7.2 (0.9)	7.2 (2.4)	7.3 (0.9)	8.5 (2.5)
Percent of polyps with ingested particles	61.3 (12.8)	80.0 (11.8)	40.0 (5.4)	32.5 (3.3)	87.5 (4.8)	72.5 (12.7)	83.8 (5.2)	88.8 (6.6)

Table 3. Particulate matter and dissolved organic content (mean \pm standard deviation) at the 17- and 29-m sites during the 5 d of feeding experiments

	17 m day	17 m night	29 m day
Bacteria (free-living; $\times 10^5$ cells ml ⁻¹)	6.95 \pm 1.20	4.81 \pm 0.94	7.03 \pm 2.26
Bacteria (on particles $> 3 \mu\text{m}$ $\times 10^5$ cells ml ⁻¹)	0.46 \pm 0.09	0.47 \pm 0.09	0.46 \pm 0.06
Chlorophyll <i>a</i> (mg chl <i>a</i> m ⁻³)	1.83 \pm 1.31	1.23 \pm 0.32	0.95 \pm 0.22
Particulate matter (dry wts; mg l ⁻¹)	2.59 \pm 0.77	3.19 \pm 2.32	2.20 \pm 0.66
Particulate organic matter (POM; mg l ⁻¹)	0.92 \pm 0.26	1.01 \pm 0.33	0.84 \pm 0.17
Dissolved organic carbon (DOC; mg C ml ⁻¹)	3.39 \pm 1.85	3.48 \pm 1.99	3.10 \pm 1.41

significant difference between days in particulate organic matter was observed (2 way ANOVA, $P < 0.025$). Free living bacterial density was the only parameter which differed significantly between day and night (2 way ANOVA, $P < 0.05$). The values reported here are at the upper range of those reported for other reefs (Westrum and Meyers, 1978; Ducklow and Mitchell, 1979; Marshall *et al.*, 1975; Simmons, 1979).

Discussion

The feeding experiments indicate that polyps of *Plexaura nina* had higher feeding rates than *P. homomalla* polyps, regardless of the depth at which they were tested. There is some indication in Table 1 that *P. homomalla* colonies were less fully expanded during the experiments. However, if non-feeding polyps are excluded from the analysis (Fig. 1, middle), *P. nina* still has higher feeding rates than *P. homomalla*. Thus, expansion behavior alone cannot account for feeding rate differences between these two species. Furthermore, those polyps, which were expanded, behaved in much the same fashion as polyps on whole colonies do when exposed to prey.

Much, if not all, of the differences in feeding rates can be attributed to differences in morphology of the polyps. In order to estimate polyp dimensions, measurements of ten polyps/species were taken from photographs of branch tips with expanded polyps. *Plexaura nina* polyps had significantly larger tentacle tip to tentacle tip diameters ($\bar{x} = 2.35 \pm 0.3$ mm (standard deviation) vs 1.7 ± 0.3 , $t = 4.54$, $P < 0.001$). The diameter across the tentacles was used to calculate the surface area over which a polyp captured particles. *P. nina* polyps sampled a larger area than *P. homomalla* polyps (4.4 ± 1.3 mm² vs 2.3 ± 0.8 mm², $t = 4.40$, $P < 0.001$). The importance of a polyp's feeding area is suggested by the observation that the distribution of particles among polyps followed Poisson expectations for each branch tip tested (χ^2 -test of S^2/\bar{x} , all 112 values $P > 0.05$). Particle feeding by these two species can, therefore, be modeled as an essentially random process in which rates are monotonically related to the area which a polyp samples. The importance of feeding area in the differences observed in these experiments is probably a consequence of the species' taxonomic similarity. Comparisons of less similar gorgonian species (Lasker, 1981a)

indicate that polyp feeding area alone cannot account for the variance in observed feeding rates.

Differences in the feeding rates of *Plexaura homomalla* and *P. nina* were measured and are reported here as per polyp feeding rates. Gorgonians are colonial, and feeding rates must also be analyzed with respect to a measure of total colony feeding rate. Feeding rates can be corrected for the number of polyps per colony or branch. However, such indices ignore differences in the biomass of individual polyps and also in the biomass of non-polyp tissue. Since maintenance costs of a colony are proportional to both the number of polyps and their biomass (Lasker, 1981b; Sebens, 1981), a feeding index, which reflects feeding per unit biomass, is probably the best indicator of net colony gain. *P. nina* has significantly fewer polyps per unit branch than *P. homomalla* (41.3 polyps \cdot cm⁻¹ ± 6.8 vs 50.9 ± 8.8 , $t = 3.88$, $P < 0.001$, $n = 20$ branches). However, *P. nina* also has significantly lighter branches (5.49 mg ash free dry weight \cdot cm⁻¹ ± 1.08 vs 9.22 ± 2.47 , $t = 4.77$, $P < 0.001$), and in aggregate *P. nina* has more polyps per unit biomass than *P. homomalla* (7.72 polyps \cdot mg ash free dry weight⁻¹ ± 1.32 vs 5.44 ± 1.53 , $t = 5.06$, $P < 0.001$). Therefore, if corrected to common biomass, the feeding differences between the species are even greater than when reported on a per polyp basis.

The feeding experiments were conducted at both 17 and 29 m so that each species could be compared in its natural habitat and when transferred to the other species' habitat. This procedure tests not only for difference among species, but also for habitat induced differences in feeding rates. As indicated above and in Fig. 1, habitat related effects were evident. *Plexaura nina* transferred up to 17 m had higher feeding rates than at its own depth, whereas *P. homomalla* transferred down to 29 m tended to have lower feeding rates than at its own depth. The stress of the transfer does not appear to be the dominant factor in the altered feeding rates since the two species had opposite responses to the act of transfer to a new habitat. Both species, however, showed the same response to the two habitats, greater feeding rates at 17 than 29 m.

As noted in the water analysis, the water column at Salt River appeared homogeneous between 17 and 29 m. With only one exception was water quality similar at both sites. There was no noticeable difference in temperature between the two depths, and temperatures measured on March 24, 1982 were 26 °C at 17 m and 26.5 °C at 29 m

(C. Wahle, personal communication). Chlorophyll *a* concentrations were greater at 17 m, the site with higher feeding rates. Thus, it is possible that feeding rates by the two species were responding to a greater phytoplankton density at the shallow water site. However, the fluctuations in feeding rates observed between days (Fig. 1) do not match the pattern observed in the chlorophyll *a* data.

The parameter which does correlate well with feeding rate is light availability. On April 22, a day on which light measurements were taken, the 17-m site received a midday light intensity of $58 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ while the 29-m site received an intensity of only $17 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Similarly April 22 and 23, the days with the lowest feeding rates, were days of cloud cover (April 22) or turbidity (April 23).

The possible correlation between light level and feeding rates could be a consequence of differences in photosynthetic rates at the two sites. Photoadaptation is, of course, common among corals (Wetthey and Porter 1976; Davies, 1977; Dustan, 1982). However, in the described cases of photoadaptation, colonies usually have lower net photosynthesis rates at depth than in shallow water (see Erez, 1977 for a possible exception). This also appears to be the case for *Plexaura nina* and *P. homomalla*. Crude estimates of net productivity of these species were determined by measuring O_2 fluxes of branches of each species at each site on April 20, 21 and 22. The branches were enclosed in smaller 1-l volume versions of the feeding chambers. These chambers had Saran instead of polyethylene walls to retard oxygen diffusion. Oxygen content of water samples drawn from the chambers was measured at the start and finish of ≈ 3 - to 5-h incubations, and the observed O_2 flux corrected for the length of the incubation and the ash free dry weight of the branches. The means of the observed fluxes are presented in Table 4. These data are presented only in support of the argument that photosynthetic rates are greater at 17 m than at 29 m. A stronger statement cannot be made since the chambers were probably not fully resistant to diffusion of oxygen, and since incubation times at 17 and 29 m were not equal. (See McCloskey *et al.*, 1978 for a critique of coral respirometry measurements.)

Feeding capabilities of *Plexaura homomalla* and *P. nina* reflected differences in both their morphologies and the habitats they occupy. *P. nina* with its larger polyps was capable of capturing greater numbers of particles than *P. homomalla* both per polyp and per unit biomass. However, there also appeared to be a habitat related difference in feeding rates in which rates at the 17-m site

were greater than at the 29-m site. The difference correlates with light levels and presumably rates of photosynthesis. Although the nature of the correlation is unknown, the data suggest a correlation between feeding and photosynthetic rates. It is also of interest to note that, when compared in their respective habitats, *P. nina* and *P. homomalla* had very similar per polyp feeding rates. Whether these trends can be generalized must await the examination of additional species and a more thorough understanding of the factors controlling feeding.

Feeding is unquestionably essential to an organism's survival. However, the distribution pattern of these two species is independent of their relative feeding abilities. *Plexaura nina* at 17 m has both higher feeding rates and photosynthetic rates than *P. homomalla*, yet *P. nina* does not naturally occur at these depths. *P. nina*'s absence from shallow water does not correlate with its feeding abilities, and explanations for partitioning of the reef habitat by these species must examine factors other than heterotrophy and photoautotrophy.

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Table 4. *Plexaura homomalla* and *P. nina*. Daytime rates of oxygen production (mean of 3 observations \pm standard error) of colonies at 17 m and 29 m sites. Values are in $\text{mg O}_2 \times \text{hr}^{-1} \times \text{g ash free dry weight}^{-1}$

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

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