

A Comparison of the Particulate Feeding Abilities of Three Species of Gorgonian Soft Coral

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ABSTRACT: Particulate feeding abilities of *Briarium abestimum*, *Pseudoplexaura porosa* and *Pseudopterogorgia americana* were measured from *in situ* and flow tank experiments. Although these species do not readily capture naturally occurring zooplankton they can capture and ingest particulate matter (*Artemia* cysts). Suspension feeding capabilities of the three are ranked *P. porosa* > *P. americana* > *B. abestimum*. Variance in feeding between polyps, branches, and even colonies of the same species is high. In flow tank experiments polyps on the downstream side of *B. abestimum* colonies had greater capture rates than upstream polyps. The inability to capture zooplankton and the effect of polyp position on particle capture is believed to be a consequence of low densities of nematocysts among these three species.

INTRODUCTION

Most anthozoans may be characterized as carnivores which capture prey using specialized cells, the nematocysts. In fact, many anthozoans, particularly reef dwellers, are capable of utilizing additional food sources. The most notable of these is the use of photosynthate from symbiotic zooxanthellae (Muscatine and Hand, 1958). Bacteria (Disalvo, 1971), dissolved organic matter (Stephens, 1962), and particulate matter (Lewis and Price, 1976) have also been implicated as potential food sources. It is likely that any single species utilizes a number of these food sources. Therefore, attempts to characterize anthozoan energy budgets, particularly those comparing the use of photosynthate to other sources, must consider many different modes of feeding. In this study I report on the potential importance of particulate feeding by three species of gorgonian soft coral.

Among corals the large contribution of the zooxanthellae and readily observable zooplankton captured by polyps has overshadowed the significance of suspension feeding. However, corals do form mucus nets which can capture particulate matter (Lewis and Price, 1976) and both Roushdy and Hansen (1961) and Lewis

(1976) have demonstrated that corals are capable of removing suspended particulate matter from the water column.

The available data suggest that feeding on suspended particulates may be especially important among gorgonians. Although capture of zooplankton like *Artemia* nauplii has been observed in laboratory experiments (Leversee, 1976), field observations (Lasker, unpubl.) indicate that in most instances zooplankters striking gorgonian tentacles swim away unaffected. Furthermore, Mariscal and Bigger (1977) report that ingested *Artemia* nauplii are frequently regurgitated whole. Mariscal and Bigger also point out that the cnidom of both *Leptogorgia virgulata* and *Renilla mulleri* has fewer numbers and types of nematocysts than the scleractinian *Balanophyllia elegans*.

Despite their low nematocyst densities and relative inability to utilize zooplankton, gorgonians are capable of capturing and assimilating particulate matter. Roushdy and Hansen (1961) showed that *Alcyonium digitatum* is able to filter diatoms (*Skeletonema costatum*) from the water and to ingest them, and Murdock (1978) has demonstrated ingestion, digestion and assimilation of animal tissue (rat livers) placed on polyps' tentacles.

Among hermatypic species, which contain zooxanthellae, reduced zooplankton feeding may imply increased reliance on the zooxanthellae and may not

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be indicative of an increased role for suspension feeding. However, Mariscal and Bigger (1977) worked with ahermatypic species. Reduced zooplankton feeding by these species necessitates some other form of feeding like suspension feeding (or, as they suggest, uptake of dissolved organic matter).

Particulate feeding enables gorgonians to utilise non-motile suspended particulate matter. Plant and animal detritus make up a large fraction of suspended particulate matter on reefs (Johannes et al., 1970; Glynn, 1972), and this material may be an excellent food source due to microbial populations inhabiting the particles (Fenchel, 1973). Additionally, mucus flocs, which are also of high nutritional quality (Ducklow, 1979a, b) are common in reef waters (Johannes, 1967; Marshall, 1967; Rublee et al. 1980). The capture of non-motile particulate matter is, therefore, a feeding mechanism of potential value to gorgonians.

MATERIAL AND METHODS

The feeding capabilities of 3 gorgonian species were determined. *Briarium abestinum* (Pallas), a common gorgonian of all reef habitats, forms short (< 50 cm) branches, joined at a common base. The polyps have long (> 5 mm) pinate tentacles which are continuously expanded. Colonies of *B. abestinum* were studied *in situ* at Crawl Cay near Bocas del Toro, Panama and at Churchill Beach, Grand Bahama Island.

Pseudopterogorgia americana (Gmelia) is a common gorgonian of shallow water patch reef environments. The species grows as large arborescent colonies up to 1 m in height. Polyps are small with short (\approx 2 mm), stubby tentacles. Polyps are characteristically contracted at night. Experiments on *P. americana* were conducted at Churchill Beach, Grand Bahama Is.

Pseudoplexaura porosa (Houttuyn) is a large (> 2 m) arborescent gorgonian found in shallow water back reef environments. Its polyps are large with long (\approx 5 mm), pinate tentacles. Polyps are expanded day and night. Two colonies of *P. porosa* were examined on a small patch reef off Nalu Nega in the San Blas Is., Panama. These colonies will be referred to as *P. porosa* A and *P. porosa* B.

The ability of these species to feed on naturally occurring zooplankton was determined by exposing colonies to dense swarms of zooplankton attracted to dive lights at night. Carefully holding a dive light about 15 cm from a colony exposed polyps on the near branches to exceptionally high concentrations of zooplankton. After a 5 min exposure to the plankton swarm, the light was removed and several 10 cm branch tips cut from the colony. These were immediately sealed in plastic bags and preserved by injecting

formalin into the bag. Removal of the branch tip and preservation required less than 1 min and branch tips were frequently preserved with their polyps still expanded. A control sample was collected prior to illumination.

Feeding was detected by determining numbers of prey in the guts of 20 randomly selected polyps. Polyps were carefully dissected and the gut examined at 40 X.

Particulate feeding was evaluated by measuring ingestion of *Artemia* cysts presented to branch tips in an *in situ* chamber. The chamber (Fig. 1) is modified from the design of Gust (1977), and consists of a polyethylene bag held open at the base by a Plexiglas frame. The base is placed over branch tips attached to PVC piping and is held flush against the sand bottom with lead weights. The top of the bag is held in position by a Plexiglas disc and styrofoam float. The chamber is 30 cm in diameter, 35 cm high and when placed over the bottom traps approximately 25 l of water. There are no rigid components connecting the base to the top of the chamber and both the top and sidewalls oscillate as a function of water movement. Gust (1977) reports that water movement within such a chamber closely approximates natural conditions.

Two series of particulate feeding experiments were conducted on the colonies of *Pseudoplexaura porosa* at Nalu Nega. In the first, 18 branch tips from a single colony (*P. porosa* A) were attached to PVC piping with cable ties. The branches were arranged into 3 groups of 6 branch tips each and were allowed to acclimate for 24 h. After the acclimation period chambers were carefully placed over each of the 3 groups. Polyps of all the branches were fully expanded both prior to and immediately after the chambers were emplaced. *Artemia* cysts (2 cm^3) were then injected into each chamber and the colonies allowed to feed for 15 min. At the end of the experiment the branches were removed and preserved as described above. The number of ingested cysts in 20 polyps per branch were determined by dissection.

The second set of experiments compared branch tips from the two colonies of *Pseudoplexaura porosa*. On each of 3 d, 3 branch tips from each of the colonies were removed and attached to PVC pipes with cable ties. One branch from each colony was attached to the same pipe. After 24 h a chamber was lowered over each of the paired branch tips and 2 cm^3 of cysts injected. The colonies were allowed to feed for 15 min. Nine paired samples were collected in this manner.

At Churchill Beach pairwise experiments of *Briarium abestinum* and *Pseudopterogorgia americana* were conducted following the procedure described above. In these experiments the acclimation period was reduced to 4 h, with no visible effect on behavior of the branch tips. Analysis of the *Briarium-Pseudop-*



Fig. 1. Feeding chamber with branch tips of *Briarium abestinum* enclosed within

terogorgia comparison is based on examination of 40 polyps from each branch tip.

The chambers used in the *in situ* experiments cannot be used in areas of strong currents or wave action. Two of the species examined in this report, *Briarium abestinum* and *Pseudopterogorgia americana*, are commonly found in areas of rapid water movement. In order to examine feeding in high-current environments, colonies of *B. abestinum* were fed *Artemia* cysts in a flow tank at current speeds of 3.5 and 7.3 cm s⁻¹.

The flow tank used is elliptical, holds 30 l, and is similar in design to that described by Leversee (1977). A Plexiglas partition was used instead of straws to reduce turbulence. Colonies used in the experiments were collected from Triumph Reef in the Florida Keys and were maintained in flowing sea water at the Rosenstiel School of Marine and Atmospheric Sciences.

Colonies were placed in the flow chamber 2–4 h prior to the start of the experiment. Two colonies were

usually tested simultaneously. After polyps on the branches were expanded 0.15 g (approximately 0.35 cm³) of *Artemia* cysts were added and the colonies allowed to feed for either 15 or 60 min. At the end of the experiment the upstream side of the branch was notched and the colony preserved. Twenty polyps were dissected from the midline of both the up and downstream side and the number of ingested *Artemia* cysts determined.

RESULTS

Pseudopterogorgia americana colonies were contracted at night. Therefore, night illumination experiments were only conducted on *Briarium abestinum* and *Pseudoplexaura porosa*. Polyps of both species reacted rapidly to the dense zooplankton swarms attracted by the dive lights. Zooplankters frequently came into contact with polyps invoking a rapid contraction of the polyp. This reaction is similar to that

observed when polyps capture prey, but careful examination of these events indicated that the zooplankter involved invariably escaped from the contracting polyp. Twenty polyps from each of 2 *B. abestinum* and 3 *P. porosa* colonies were examined and in all cases, their guts were empty. A single copepod exoskeleton was found in 1 of the *P. porosa* control samples. No prey were found in the *B. abestinum* controls.

Polyps of all 3 species actively fed on *Artemia* cysts. Reaction to the cysts was rapid and frequently resulted in polyp contraction as described above. However, in this case particles were regularly found in the gut.

Results of the first series of Nalu Nega experiments are presented in Table 1. In these experiments 18

Table 1. *Pseudoplexaura porosa*. Mean number of ingested *Artemia* cyst/polyp in branches from 3 replicate experiments. Twenty polyps were sampled from each branch

Chamber A	Chamber B	Chamber C
7.25	7.25	7.15
5.15	5.60	3.65
4.95	6.40	2.90
7.65	2.75	4.70
3.25	9.55	1.60
4.50	12.40	1.90

Analysis of variance*				
	df	Mean square	F	% of variance
Chamber	2	91.84	3.88**	10.7
Branches	15	23.70	6.34***	18.8
Polyps	342	3.74		70.4

* Nested ANOVA (random effects model) on $\sqrt{X + 0.5}$ transformed data
 ** $P < 0.05$
 *** $P < 0.001$

branches from the same colony were simultaneously tested in 3 experimental chambers. The number of cysts ingested by any single polyp proved to be highly variable and accounted for the largest portion of the total variance. Variance in number of ingested cysts among polyps from the same branch was closely correlated to the mean number ingested for the branch ($r = 0.74$, $P < 0.001$), but the distribution of numbers of cyst/polyp does not fit Poisson expectations among any of the 18 branches (χ^2 - test of S^2/\bar{X}). Despite the large among polyp variance significant differences between branches and between chambers were found. These effects are evident in the means presented in Table 1. Significant differences are found despite the fact that the branches were all from the same colony and were tested simultaneously in identical chambers.

Variation between polyps and failure of the number of captured cysts to fit a Poisson function indicates

either differential supply over the length of the branch or differential feeding ability. Similarly, differences between branches may be attributed to either supply effects or actual differences in feeding ability. Although the question of supply cannot be ignored, every attempt was made to insure a uniform distribution of the cysts. They were injected from the base of the chamber and directed up and away from the branches. The cloud of cysts which formed dispersed within 60 s. It is likely that the dispersion accounts for much of the between branch variance. However, the proximity of polyps on the same branch makes such an explanation less likely when examining among polyp variation. Variation between chambers is interpreted as an experimental artifact due perhaps to small differences in cyst density and dispersion.

Variance among polyps and between chambers is again evident in the pairwise comparison of colonies *Pseudoplexaura porosa* A and *P. porosa* B (Table 2). Among polyp and between chamber effects account for over 60 % of the total variance in these experiments. Only a single branch from each colony was used in a chamber and it is impossible therefore to partition a branch effect, but much of the branch effect should be present in the interaction term, which is significant. Despite the similarities in form between these two colonies there is a significant colony effect, *P. porosa* A ingesting more cysts than *P. porosa* B. Once again this difference is discerned against a background of enormous lower level variation. In this case, the pairwise experimental procedure allows for a 2-way analysis of variance. If the colonies had not been paired a nested analysis of variance would have been used and in this

Table 2. *Pseudoplexaura porosa*. Mean numbers of ingested *Artemia* cysts/polyp in branches from 2 colonies. Nine replicate pairwise experiments are presented

Species	Chamber								
	1	2	3	4	5	6	7	8	9
<i>P. porosa</i> A	13.75	10.20	1.80	6.15	1.60	1.65	6.90	12.65	4.0
<i>P. porosa</i> B	10.30	8.60	1.45	4.45	2.60	2.45	0.85	2.70	1.5

Analysis of variance*				
	df	Mean square	F	% of variance
Groups	17	15.42		
Colony	1	30.96	4.51**	12.6
Chamber	8	22.04	20.80***	20.7
Interaction	8	6.86	6.48***	32.2
Polyps	342	1.06		41.8

* 2-way ANOVA (mixed model) of $\sqrt{X + 0.5}$ transformed data
 ** $P < 0.005$
 *** $P < 0.001$

case the species difference would not be recognized as being significant.

Results of the *Pseudopterogorgia americana* and *Briarium abestinum* comparisons are presented in Table 3. The results are quite similar to those of the

Table 3. *Briarium abestinum* and *Pseudopterogorgia americana*. Mean numbers of ingested *Artemia* cysts/polyp for colonies tested simultaneously

Species	Chamber					
	1	2	3	4	5	6
<i>B. abestinum</i>	0.55	0	2.90	0.45	1.20	0.25
<i>P. americana</i>	1.75	2.05	2.50	0.95	3.43	2.90
Analysis of variance*						
	df	Mean square	F	% of variance		
Groups	11	4.15				
Species	1	14.06	8.34**	16.2		
Chamber	5	4.63	13.07***	16.8		
Interaction	5	1.69	4.76***	10.5		
Polyps	228	0.36		56.6		

* 2-way ANOVA (mixed model) of $\sqrt{X + 0.5}$ transformed data
 ** P < .005
 *** P < .001

previous experiments. Between polyp and chamber effects account for most of the total variance. However, a significant species effect is also evident, *P. americana* ingesting more cysts than *B. abestinum*. The *in situ* experiments using *Artemia* cysts demonstrate the ability of these gorgonian species to capture and ingest suspended particulate matter. Furthermore, differences in feeding capabilities – even among colonies of the same species – are evident in pairwise comparisons. In an effort to compare the results from both sets of experiments the results were analysed in a stepwise test procedure using the Mann-Whitney U statistic (Sokal and Rohlf, 1969). Those results in combination with the ANOVAs of Tables 2 and 3 indicate the feeding abilities of these 4 species may be ranked as *P. porosa* A > *P. porosa* B ≈ *P. americana* > *B. abestinum*.

Mean numbers of ingested cysts from the flow tank experiments are presented in Table 4. The density of cysts in these experiments was approximately 20 % lower than in the *in situ* chamber experiments and not surprisingly the number of ingested cysts is also reduced. As in the previous cases among polyp effects make the greatest contribution to total variance. In the ANOVA neither the effects of current speed nor up/downstream positioning are significant. There is, however, a significant time effect – mean numbers of ingested cysts increasing with time. Increases in mean

Table 4. *Briarium abestinum*. Number of *Artemia* cysts ingested per polyp in flow tank experiments

Current speed	Length of experiment				
	15 min		60 min		
	Upstream	Downstream	Upstream	Downstream	
3.5 cm s ⁻¹	0.0	0.0			
	0.0	0.0	0.10	0.05	
	0.0	0.0	0.35	0.65	
	0.05	0.05	0.35	0.50	
	0.05	0.0	0.10	0.30	
	0.40	0.60	0.70	0.05	
	0.15	0.45	0.05	0.0	
	\bar{X}	0.09	0.16	0.28	0.26
7.3 cm s ⁻¹	0.10	0.45	0.0	0.10	
	0.0	0.0	0.55	1.50	
	0.05	0.03	0.05	0.05	
	0.0	0.05	0.30	1.30	
	0.05	0.0	0.10	0.30	
		\bar{X}	0.04	0.11	0.18

numbers of ingested cysts with time can be attributed to either an increase in the number of particles ingested by polyps which feed or to the proportion of polyps which capture cysts. No significant differences were observed in the number of cysts in polyps which fed. However, the proportion of polyps capturing prey in the 3.5 cms⁻¹ – 60 min treatment is greater than that in either of the 15 min treatments (P < 0.05, STP test with Mann Whitney U test; Sokal and Rohlf, 1969). A pairwise comparison of ingestion rates on upstream and downstream sides of branches indicates that ingestion is greater on the downstream side of the branch (Wilcoxon matched pairs test, P < 0.05).

DISCUSSION

Polyp behavior during night-illumination experiments is best described as a feeding response. However, samples collected at the completion of these experiments were uniformly devoid of ingested prey. The technique of preserving specimens *in situ* at the finish of the experiment precludes the possibility of prey regurgitation and immediate preservation precludes digestion and/or internal redistribution of prey. The conclusion therefore is that the species tested were incapable of capturing zooplankton attracted to the dive lights.

Some gorgonians are capable of capturing zooplankton in experimental situations (Leversee, 1977). However, *Artemia* nauplii – used in these experiments – are small, slow-moving prey. The zooplankters attracted to

dive lights are usually larger and faster. Microscopic examination of sections from specimens collected in this study (E. Peters, pers. comm.) indicate that these species, like those studied by Mariscal and Bigger (1977), have reduced nematocyst densities. Given the dramatically reduced nematocyst densities of these gorgonians, it is not surprising that large zooplankters readily escape. In similar experiments with scleractinian corals like *Moptastrea cavernosa* and *Colpophyllia natans* zooplankters attracted by dive lights are frequently captured. The gorgonians inability to capture large zooplankters is best explained by their reduced cnidom. The effect of this on feeding in nature is to limit their prey to only a small fraction of the total zooplankton population. It is also probable that gorgonians capture fewer of the smaller prey than scleractinians even though these prey are more easily captured.

Although the species examined in this study do not readily capture zooplankton, these gorgonians are capable of capturing and ingesting non-motile prey (*Artemia* cysts). All 3 species readily ingested cysts, but not all exhibited equivalent abilities to do so. Even 2 colonies of the same species were found to differ in their feeding capacity.

Several authors have discussed models of feeding in organisms like gorgonians (Porter, 1976; Koehl, 1977; Leversee, 1976; Rubenstein and Koehl, 1977; Sebens, 1979). These models employ as variables size of the tentacle, current speed, particle size, size of the polyp, number of polyps, and orientation of feeding structure. Changes in any of these parameters will change the efficiency with which a given prey particle is utilized. Similarly, differences in a coelenterates cnidom will also affect capture efficiency. Many of these factors vary among the species examined in this study and it is of interest to compare the results of this study with those predicted by other authors.

Porter (1976) and Sebens (1979) both predict a positive correlation between size of polyps and zooplankton capture. This relationship is based on a simple interception model in which the number of captured prey is proportional to the surface area of the capture organ. Size of the capture surface may also effect the size range of particles which may be captured (Sebens, 1979) and similar limitations will be exerted by differences in the cnidom. Among organisms with a similar cnidom and for a particle of set size (i.e. an *Artemia* cyst) the relationship of capture surface to capture rate should hold. The true capture area of a gorgonian polyp is not characterized by the polyp diameter but rather by the diameter of the polyp plus its expanded tentacles. Using this as an index, the capture surfaces of polyps of the four specimens in this study can be ranked *Briarium abestinum* > *Pseudoplexaura porosa* A \approx *P. porosa* B \gg *Pseudopterogorgia americana*. This

ranking bears little resemblance to the ranking based upon cyst ingestion rates. *B. abestinum*, the species with the largest capture area per polyp, has the lowest ingestion rate and its polyps even ingest fewer cysts than the much smaller *P. americana* polyps. Even more striking is the significant feeding difference observed between the two *P. porosa* colonies which have virtually identical polyps.

This lack of correspondence between observed and predicted ingestion rates most likely reflects the complexity of the feeding process. The capture surface model relies on a simple impact-capture sequence in which the probability of a particle striking a polyp is a function of the capture surface area and capture is a constant proportion of all intercepted prey. As has already been noted, differences in the cnidom affect the proportion of prey which are actually subdued and ingested. Given inter-specific differences in the cnidom, this model still predicts that captures among polyps of the same colony will follow a Poisson distribution. In the experiments reported here captures did not follow a Poisson distribution. All polyps apparently do not have an equal chance at capturing prey.

Differences among polyps on the same branch may relate to modes of particle capture not directly related to tentacular size. Some gorgonians, like *Pseudopterogorgia americana*, produce copious quantities of mucus. This mucus may be involved in capture via mucus nets (Lewis and Price, 1976). In such a case ingestion of prey would not be random. Furthermore, the presence of this mucus may increase the proportion of intercepted particles ingested. This effect would explain the surprisingly high cyst-ingestion rates of *P. americana*.

Additional mechanisms for non-random distributions of capture events are illustrated by the flow tank experiments. In these experiments polyps on the downstream side of branches captured greater numbers of prey than on the upstream side. *Briarium abestinum* has relatively few nematocysts. Consequently, adhesion of a captured particle to the tentacle is most probably related to the 'stickiness' of the mucus. In the higher flow regime of the upstream side, intercepted particles may be stripped from the tentacles before they can be ingested. Instances of such 'escapes' were frequently observed in the flow tank experiments. Additionally polyps on the upstream surface of the branch are deformed by the current. Leversee (1976) hypothesized that in strong current, polyps of *Lep- togorgia* colonies were 'bent over' and fed primarily on the downstream side of the colony. In *Briarium* the branch is thick and forward facing; polyps may simply be deformed so that they are unable to feed. Finally, eddies on the downstream side may result in reduced currents allowing more efficient capture and also may

result in small localized concentrations of prey. Porter (1979), for instance, observed increased feeding on the downstream sides of *Montastrea cavernosa* colonies.

When compared to other reef anthozoans, the range of morphologies exhibited by these 3 gorgonian species is small, and their zooplankton-feeding abilities were indeed predictable from their cnidom. However, differences among these species are not easily explained by morphology alone. Detailed studies may explain some of the variance. However, as evidenced by the differences among *Pseudoplexaura porosa* colonies, factors not included in many existing models may account for much of the variance in gorgonian feeding rates.

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