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Heterotrophic feeding by gorgonian corals with symbiotic zooxanthella

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Abstract

Gorgonians are one of the most characteristic groups in Caribbean coral reef communities. In this study, we measured in situ rates of grazing on pico-, nano-, and microplankton, zooxanthellae release, and respiration for the ubiquitous symbiotic gorgonian coral *Plexaura flexuosa*. Zooplankton capture by *P. flexuosa* and *Pseudoplexaura porosa* was quantified by examination of stomach contents. In nature, both species captured zooplankton prey ranging from 100 to 700 μm, at a grazing rate of 0.09 and 0.23 prey polyp^{-1} d^{-1}, respectively. Because of the greater mean size of the prey and the higher mean prey capture per polyp, *P. porosa* obtained 3.4×10^{-5} mg C polyp^{-1} d^{-1} from zooplankton, about four times the grazing rate of *P. flexuosa*. On average, *P. flexuosa* captured 7.2 ± 1.9 microorganisms polyp^{-1} d^{-1} including ciliates, dinoflagellates, and diatoms, but they did not appear to graze significantly on organisms <5 μm (heterotrophic bacteria, *Prochlorococcus* sp., *Synechococcus* sp., or picoeukaryotes). Zooplankton and microbial prey accounted for only 0.4% of respiratory requirements in *P. flexuosa*, but they contributed 17% of nitrogen required annually for new production (growth and reproduction). Although the contribution of microbial prey to gorgonian energetics was low, dense gorgonian populations found on many Caribbean reefs may be important grazers of plankton communities.

The role of food as a constraining factor in population and community ecology has been widely debated (Hairston et al. 1960; Schoener 1974; Olson and Olson 1989). Depletion of planktonic microbial (Linley and Koop 1986; Ayukai 1995), phytoplankton, and zooplankton communities (Glynn 1973; Buss and Jackson 1981) has been observed on coral reefs, suggesting an important role for nutrient limitation in the distribution and abundance of suspension feeders (Schoener 1974). However, the natural diets of most suspension feeders are poorly known, and our lack of knowledge about their feeding habits has become a limiting step in understanding the factors that constrain populations.

The coral–zooxanthella symbiosis makes feeding biology in reef anthozoans particularly complex. Reef anthozoans obtain high energy compounds (mainly carbohydrates) from the symbiotic algae through translocation (Johannes et al. 1970; McCloskey and Muscatine 1984; Muscatine et al. 1984). The translocated products are used mostly for respiration, and only a small proportion is destined for new production (growth and reproduction) of the colony (Davies 1984; Falkowski et al. 1984), probably because the photosynthetic products are deficient in nutrients such as nitrogen and phosphorous (Muscatine 1967; Battey and Patton 1986). Therefore, heterotrophic feeding might be required to provide indispensable elements for growth and reproduction of the coral (Muscatine 1973; Muscatine and Porter 1977; Sebens 1987).

In corals (Hexacorallia), zooplankton capture seems to be the main source of heterotrophic feeding (Muscatine and Porter 1977; Sebens 1987), although it has been quantified for only a small number of hard corals (Porter 1974; Johnson and Sebens 1993; Sebens et al. 1996) and zoanthids (Koehl 1977; Sebens 1977). Among the soft corals (Alcyonacea), zooplankton capture has been quantified for several species (Lewis 1982; Sebens and Koehl 1984), and recently, phytoplankton has been documented also to be an important component of the diets of some asymbiotic species (Fabricius et al. 1995*a,b*). However, although gorgonians are one of the most characteristic components of tropical seas (Bayer 1961; Tursch and Tursch 1982), their natural diets are still poorly understood.

Although it has been shown that gorgonians are able to ingest particulate matter (Leversee 1976; Lasker et al. 1983; Sponaugle and LaBarbera 1991), field studies have rarely observed grazing on natural prey (Kinzie 1973; Lasker 1981; Lasker et al. 1983). This apparent lack of grazing might be an artifact due to the methodology, gut content analysis, used by previous studies. This method is useful in the study of prey organisms with hard parts, but it potentially underestimates small soft-bodied prey because they leave no recognizable remains. Therefore, the role of these small and soft-bodied organisms in the diet of benthic suspension feeders appears to be largely unknown (*see* Pile et al. 1996, 1997; Pile 1997), although it could be relevant due to the fact that pico- and nanoplankton are major contributors to biomass and productivity of the water column (Platt et al. 1983).

In this study, we examine the natural diets of the ubiquitous symbiotic gorgonian corals *P. flexuosa* and *P. porosa*.

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We focused on three main goals: (1) to determine which planktonic taxa were grazed on by gorgonians; (2) to estimate grazing rates on these taxa; and (3) to examine the role of heterotrophic feeding in symbiotic gorgonians. We found that gorgonians could graze on some microorganisms, which may have a substantial impact on the plankton community over coral reefs.

Materials and methods

Study site—This study was mainly conducted in House and Korbiski reefs, San Blas Islands (Panamá), close to the field station of the Smithsonian Tropical Research Institute (*see* map in Brazeau and Lasker 1992). Additional samples for the stomach contents study were collected also in the Florida Keys (Pickles reef: 24°59′N, 80°24′W and Conch reefs: 24°57′N, 80°27′W). *P. flexuosa* is among the most common and widely distributed anthozoans of the shallow Caribbean reefs (Kinzie 1973; Opresko 1973).

Feeding on zooplankton—Gut content analyses were used to quantify predation on zooplankton prey >50 μm that left recognizable remains. *P. porosa* samples were collected at Korbiski reef every 3 h from 0800 on 13 August to 0800 h on 14 August 1993. For each sampling, one terminal branch from each of five different colonies was collected and immediately fixed in 10% formalin. Samples were rinsed thoroughly to remove any plankton remaining on the colony surface. The gut contents of 20 randomly chosen polyps from each sample were examined under a microscope at ×400. Thus, for each sample, 100 polyps were examined, yielding a total of 900 polyps of *P. porosa* for the entire 24-h cycle. For *P. flexuosa,* terminal branches from 40 colonies were collected on various dates in 1994 and 1995 in the Florida Keys (Pickles and Conch reefs) and Panamá (Korbiski reef). Ten polyps were dissected per branch, giving a total of 400 *P. flexuosa* polyps. The other procedures were the same as used for *P. porosa.* In both cases, prey were identified to the level of major taxonomic group; length and width of all prey were measured under the microscope.

Grazing rate, expressed as the number of prey items captured per polyp and hour, was calculated using the following equation (Coma et al. 1994):

$$C = N\left[\sum_{t=0}^{D} 1 - (t/D)\right]^{-1} \quad (1)$$

where C = number of prey captured polyp^{-1} h^{-1}; N = prey items per polyp; t = time (in hours); and D = digestion time (in hours). Gut contents were extrapolated to daily rates of intake by assuming a digestion time of 6 h (Lewis 1982).

Prey biomass was estimated from biovolumes (Sebens and Koehl 1984), using conversion factors to wet weight (1.025; Hall et al. 1970), dry weight (13% of wet weight; Beers 1966; Murphy 1971), and carbon content (45% of dry weight; Biswas and Biswas 1979). The nitrogen content was estimated from the carbon : nitrogen ratio of each group (Gorsky et al. 1988).

Plankton feeding experiments—Predation on pico-, nano-, and microplankton was assessed only for *P. flexuosa.* We used continuous flow incubation chambers placed on the reef at a depth of 3 m. The incubation chambers (one with gorgonian and one control) were made from hemispherical pieces of ultraviolet (UV)-transparent Plexiglas approximately 3 liters in volume. Seawater was recirculated through the chamber with a pump at a speed of 1.2 cm s^{-1}; this flow becomes turbulent inside the chambers. Small colonies (8–10 cm in colony height) of *P. flexuosa* were removed from their natural substratum and attached to polyvinyl chloride posts (1 cm in diameter, 1.5 cm tall) embedded in small cement flats (9 cm in diameter, 1 cm tall, as in Kim and Lasker [1997]). These colonies were kept in their natural environment with conspecifics until used in incubation experiments. A total of seven incubation experiments were carried out: four during daylight hours (between 0800 h and 1700 h) and three during the night (between 1900 h and 2400 h) on seven different days. At the beginning of each experiment, a *P. flexuosa* colony on a cement flat was placed on the gorgonian chamber. Colonies were allowed to expand fully before the experiment started. Colonies that did not expand within a few minutes were eliminated from the experiment. After this acclimation time, both incubation chambers were closed and three replicate water samples of 200 ml were collected from both chambers and preserved for further analysis (*see below*). After 3 h, three replicate water samples were collected again. Predation was calculated from decreases in prey concentration in the gorgonian chamber relative to the control chamber. The potential prey items in this fraction included: heterotrophic bacteria, *Synechococcus* sp., *Prochlorococcus* sp., eukaryotic picoplankton, ciliates, and phytoplankton (diatoms and dinoflagellates).

To quantify heterotrophic bacteria, *Prochlorococcus* sp., *Synechococcus* sp., and picoeukaryotes, we used flow cytometry. Two-milliliter water samples from the incubation chambers were preserved for flow cytometry by standard protocols (Campbell et al. 1994) and were frozen in liquid nitrogen; afterward, they were stored in dry ice or at −80°C. Samples were analyzed using a Coulter EPICS 753 flow cytometer (Coulter Electronics) equipped with two 5-W argon lasers and a Micro-Sampler-Delivery-System. The flow cytometer was set up for UV (220 mW) and 488 nm (1 W) colinear analysis. Hoechst 33342 was used to stain DNA (Monger and Landry 1993). Five parameters were collected in list mode and analyzed with custom-designed software (CYTOPC by Daniel Vaulot): red fluorescence (from chlorophyll *a* [Chl *a*]), orange fluorescence (from phycoerythrin), blue fluorescence (from DNA stained with Hoechst 33342), and forward- and right-angle light scatter signals (FALS and RALS). The sizes of each picoplankton group were determined under epifluorescence microscopy by measuring between 200 and 400 cells of each group, except *Prochlorococcus* sp., for which a mean size of 0.7 μm was assumed (Chisholm et al. 1988).

To quantify phytoplankton, ciliates, and zooxanthellae, 350-ml water samples were preserved with Lugol's acid (1% final concentration). Subsamples of 100 ml were placed in settling chambers, and major groups of nano- and microplankton were quantified under an inverted microscope. The

microscope was equipped with a color CCD video camera connected to a video recorder. Images of the organisms were recorded and digitized, and sizes were measured using an image analysis software (National Institute of Health (NIH) image). For each subsample, 20 individuals of the most common groups were measured. The volumes were estimated from the length and width measurements assuming ellipsoidal or cylindrical shapes (Edler 1979).

Depletion rates of plankton were calculated assuming exponential growth and clearance of prey (Frost 1972; Saiz 1993). Thus, the prey growth rate is computed k (h^{-1})

$$k = \frac{\ln(C_1/C_0)}{t_1 - t_0} \quad (2)$$

where C_0 and C_1 are the prey concentrations in the chamber at the initial time t_0 and at the final time t_1. The clearance rate F (volume swept clear colony^{-1} time^{-1}) is computed:

$$F = V(g/n) \quad (3)$$

where V is the volume of the chamber, n is the number of individuals (colonies or polyps) and g is the grazing coefficient (h^{-1}), computed as:

$$g = k_c - k_g \quad (4)$$

where k_c is the prey growth rate in the control chamber, and k_g is the apparent growth in the grazing chambers. Finally, the ingestion rate I (prey ingested individual^{-1} time^{-1}) is:

$$I = FC \quad (5)$$

where C is the average prey concentration during the experiment, calculated as follows:

$$C = \frac{C_0[e^{(k-g)(t_1-t_0)} - 1]}{(k - g)(t_1 - t_0)} \quad (6)$$

The significance of predation on each kind of prey was tested by comparing k_c and k_g with a two-tailed Wilcoxon test (Sokal and Rohlf 1981).

Carbon and nitrogen content of prey items were estimated using literature conversion factors. For phytoplankton, biovolume (V, μm^3) was converted to carbon (C) and nitrogen (N) weight using the equations: pg C cell^{-1} = 0.109 $V^{0.991}$, and pg N cell^{-1} = 0.0172 $V^{1.023}$ (Montagnes et al. 1994). For ciliates, volume was converted to carbon weight using the factor 0.19 pg C μm^{-3} (Putt and Stoecker 1989), and volume was converted to nitrogen weight using the factor 0.026 pg N μm^{-3} (DeBiase et al. 1990).

Respiration rates—Respiration by *P. flexuosa* was determined from oxygen uptake in nighttime incubations to avoid oxygen production by zooxanthellae. We used the same *P. flexuosa* colonies used for the feeding experiments. The experimental setup was the same as the one previously described for the feeding experiments. In both chambers, oxygen concentration was recorded continuously using Wissenschaftlich-Technische Werkstäten (WTW) oxygen electrodes model EOT 196. Respiration was estimated from two different series of experiments: (1) dark feeding incubations (three experiments), where oxygen concentration was measured at the start and end of the experiments, and (2) 7-h dark incubations (from 2300 to 0600 h), during which oxygen concentration was recorded in both chambers every 2 min by a data logger. During the 7-h dark period experiments, the water inside both chambers was totally renewed when the oxygen concentration changed 20% from its initial level (Crisp 1984). Respiration rates were estimated from the decrease in oxygen concentration in the gorgonian chamber during each experimental period. The control chamber was used to detect possible oxygen variations not due to the gorgonian colony. Metabolic rate (mg O_2 polyp^{-1} d^{-1}) of whole colonies (animal + algal) was determined from mean nighttime hourly oxygen respiration rates extrapolated to 24 h and divided by the number of polyps. Oxygen units were converted to carbon equivalents using the carbon to oxygen conversion factor of 0.375 (McCloskey et al. 1994).

P. flexuosa dry weight was determined by drying at 60°C, and ash-free dry weight was determined by combustion at 450°C for 5 h. The number of polyps per colony (N) was estimated from colony height (H, cm) using the regression equation: $N = 0.934\ H^{3.062}$ (Beiring 1997). For the determination of nitrogen content, 10 terminal branches ca. 10 mm in length were ground and dried at 60°C. The samples were assayed on a Perkin-Elmer model 240 carbon, hydrogen, and nitrogen analyzer.

The gastrovascular cavity was examined with a scanning electron microscope (Hitachi S-570). Ten polyps of *P. flexuosa* from five different colonies were dissected (a total of 50 polyps) and dehydrated in graded ethanol. Afterward, the polyps were dried by the critical point method (using CO_2 as transition fluid), mounted on aluminum stubs, and coated with gold in a sputter coater.

Results

Feeding on zooplankton—Gut contents of *P. flexuosa* and *P. porosa* were dominated by zooplankton prey, particularly gastropod larvae; only on a few occasions were other groups observed (protozoan and diatoms; Table 1). Both species grazed zooplankton prey items ranging in size from 100 to 700 μm. The number of prey per polyp grazed by *P. porosa* over the daily cycle ranged from 0 to 0.10 prey polyp^{-1}. Mean *P. porosa* daily zooplankton grazing rate was 0.23 prey polyp^{-1} (Table 2). *P. flexuosa* exhibited lower zooplankton grazing rates (0.09 prey polyp^{-1} d^{-1}) than *P. porosa*. Because of the greater mean size of the prey items and the higher mean prey capture per polyp, *P. porosa* obtained 0.034 μg C polyp^{-1} d^{-1} from zooplankton, almost four times the grazing rate of *P. flexuosa* (Table 2).

Feeding on small plankton—Figure 1 shows net growth rates calculated for each plankton taxa (not including zooplankton >100 μm) in the control chamber and in the gorgonian chamber, together with the mean size of each taxa. Growth rates of *Thalassionema* sp., pennate diatoms, dinoflagellates, and ciliates were significantly lower in the gorgonian chamber than in the control chamber (Fig. 1). Ingestion rates for these organisms are presented in Table 3. The highest ingestion rate was for dinoflagellates (3.7 prey items polyp^{-1} d^{-1}), followed by pennate diatoms (1.9), ciliates (1),

Table 1. Number and type of prey items captured by *Pseudoplexaura porosa* over the diel sampling period (13–14 August 1993; 900 dissected polyps) and *Plexaura flexuosa,* from 40 colonies collected between 1994 and 1995 (400 polyps dissected).

	Number of prey at each time										Mean prey size	
	0800 h	1100 h	1400 h	1700 h	2000 h	2300 h	0200 h	0500 h	0800 h	Total	Length	Width
Pseudoplexaura porosa												
Gasteropod larvae	6	1	1	—	—	—	—	3	—	11	245	150
Copepod egg	1	3	1	1	—	—	—	—	—	6	158	—
Harpacticoid	2	1	—	—	1	1	1	1	—	6	311	110
Calanoid	—	—	1	—	—	—	1	—	—	2	518	163
Copepod fragment	—	—	—	—	—	—	—	1	—	1	173	134
Nauplii	—	—	—	—	—	—	—	—	—	1	250	115
Cladocera	—	—	—	—	—	—	—	1	—	1	461	192
Protozoa	1	—	—	—	—	—	—	—	—	1	240	150
Centric diatom	—	—	—	1	—	—	—	—	—	1	115	—
Total	10	5	3	2	1	1	2	6	—	30		
Plexaura flexuosa												
Gasteropod larvae										4	150	138
Protozoa (Foraminifera)										1	300	300

and *Thalassionema* sp. (0.4). Within the range of pennate diatom, dinoflagellate, and ciliate concentrations (1–3.5 × 10^6 μm^3 $liter^{-1}$) present during the experiments, grazing rates of *P. flexuosa* on these groups were similar and did not vary with concentrations (Fig. 2). Therefore, these groups appear to be close to the maximum grazing rate. Grazing on *Thalassionema* sp. was lower than on the previously mentioned groups. This could be due to the low concentration of this group or, although unlikely, to a selection against it (Fig. 2). On average, *P. flexuosa* polyps ingested 4.0 ± 1.4 × 10^{-9} g C $polyp^{-1}$ d^{-1} (Table 3). Therefore, the contribution of nanoplankton and microplankton as carbon source was about half of the zooplankton captured (Tables 2, 3).

The mean size of the picoeucaryotes was 1.47 ± 0.30 μm (n = 307). Net growth rates of picoeucaryotes were not significantly different between the gorgonian chamber and the control chamber (Fig. 1). Growth rates of heterotrophic and autotrophic bacteria (*Prochlorococcus* and *Synecoccocus* sp.) were also not significantly different between the gorgonian chamber and the control chamber (Fig. 1). Therefore, *P. flexuosa* did not appear to graze significantly on organisms <5 μm in our study.

The number of round cells (7–9 μm) increased during the incubations from initially <0.1 cell ml^{-1} to final densities of $10–10^2$ cells ml^{-1}. These round cells were identified as zooxanthellae by comparison with a culture of isolated zooxanthellae (T. Goulet unpubl. data). To determine the origin of these zooxanthella, we examined by scanning electron microscopy (SEM) the gastrovascular walls of the polyps from incubated colonies. Apparently healthy and viable zooxanthellae were pinched off and released by host cells as described by Gates and Muscatine (1992). Examination of *P. flexuosa* polyps from freshly collected colonies showed that expulsion of zooxanthellae seems to occur regularly under natural conditions. Zooxanthella release by *P. flexuosa* was greater during the daytime (mean = 878 ± 658 cells cm^{-2} h^{-1}) than at night (mean = 289 ± 216 cells cm^{-2} h^{-1}). The estimate of the expelletion rate for natural colonies was based only on our nighttime estimate, because it has been suggested that an increase in oxygen level could be a physiological stress leading to the expulsion of zooxanthellae (Lesser and Shick 1989), and we observed that oxygen concentrations increased during daytime incubations (due to light-dependent photosynthesis). Our estimate is that a total of 6,840 zooxanthellae cells cm^{-2} d^{-1} were released.

Table 2. Zooplankton prey capture rate (prey $polyp^{-1}$), prey size, prey biomass, daily prey capture, and daily biomass capture in carbon (C) and nitrogen (N) units. Mean ± SD.

	P. porosa	*P. flexuosa*
Number of polyps	900	400
Prey $polyp^{-1}$	0.03±0.03	0.01±0.005
Prey size (μm)	261±100	180±68
Prey biomass (μg C)	0.150	0.104
Prey $polyp^{-1}$ d^{-1}*	0.227	0.086
μg C $polyp^{-1}$ d^{-1}	0.034	0.009
μg N $polyp^{-1}$ d^{-1}	0.006	0.002

* Daily prey capture based on a digestion time of 6 h (Lewis 1982).

Respiration rates—Oxygen concentration in the control chamber did not change significantly over time for both dark feeding experiments and the monitoring through the 7-h dark incubation (*see Methods; Fig. 3*). The computed respiration rates for *P. flexuosa* were similar: 1.31 ± 0.05 mg O_2 h^{-1} g^{-1} ash-free dry weight (AFDW) for the dark feeding experiments and 1.48 ± 0.25 mg O_2 h^{-1} g^{-1} AFDW for the 7-h dark incubation experiment. This oxygen consumption represents a daily requirement of 12.77 ± 1.88 mg C g AFDW $^{-1}$ d^{-1} or 3.72 × 10^{-6} ± 5.46 × 10^{-7} g C $polyp^{-1}$ d^{-1}.

Based on data on prey size and ingestion rates, we estimated the contribution of various prey items to total carbon and nitrogen needs of the gorgonian. *P. flexuosa* obtained about 8.9 × 10^{-3} μg C and 1.6 × 10^{-3} μg N $polyp^{-1}$ d^{-1} from zooplankton (Table 2), and 4.0 × 10^{-3} μg C and 0.6

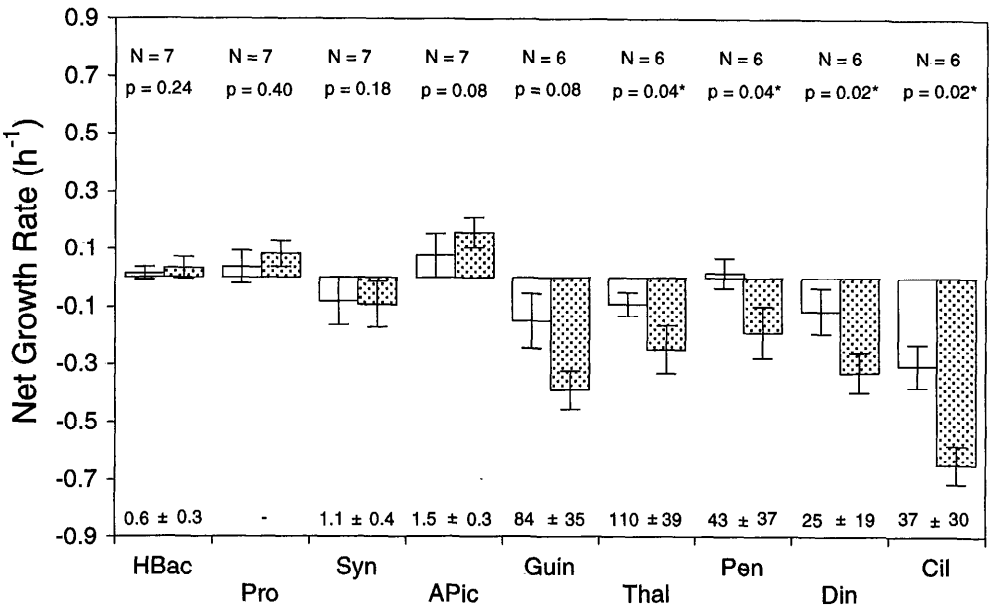

Fig. 1. Net growth rates of prey (mean ± SE) at the gorgonian chamber (k_g in dotted bars) and in the control chamber (k_c in empty bars) for each plankton group. Maximum length (μm) of each group (mean ± SE) at the figure bottom. HBac, heterotrophic bacteria; Pro, *Prochlorococcus* sp.; Syn, *Synechococcus* sp.; APic, autotrophic picoeucaryotes; Guin, *Guinardia* sp.; Thal, *Thalassionema* sp.; Pen, pennate diatoms; Din, dinoflagellates; Cil, ciliates. N = number of experiments, and p = significance degree from two-tailed Wilcoxon test.

$\times 10^{-3}$ μg N polyp^{-1} d^{-1} from feeding on other plankton (Table 3). Ciliates contributed the most to C and N requirements (51%), followed by diatoms (30%) and dinoflagellates (18%). Together, zooplankton and other plankton prey accounted for only 0.4% of the estimated respiratory requirement in carbon units.

Discussion

To our knowledge, this study is the first attempt to study gorgonian feeding in situ utilizing the entire natural range of potential prey. Previous studies have already shown the ability of octocorals to feed on particulate matter (Leversee 1976), dissolved organic matter (Schlichter 1982), mucus (Coffroth 1984), and microzooplankton (Sorokin 1991), but these studies were conducted either in the laboratory (Leversee 1976; Sorokin 1991; Dai and Lin 1993) or in situ, but with simplified diets (Lasker et al. 1983; Coma et al. 1994).

What planktonic taxa do gorgonians feed on?—Gut content examinations showed that *P. flexuosa* and *P. porosa* captured small zooplankton, similar to the types of prey documented for other gorgonians (Coma et al. 1994) and octocorals (Lewis 1982; Sebens and Koehl 1984; Fabricius et al. 1995*b*). That gorgonians prey only on small zooplankton has been attributed to the low density of nematocysts in octocorals (Mariscal and Bigger 1977). Gorgonians potentially can capture this type of plankton, in part because these small organisms cannot outswim most water currents bearing them to the corals.

P. flexuosa also captured an important number of microplankton prey such as ciliates, dinoflagellates, and diatoms.

Table 3. *Plexaura flexuosa* daily capture rates (mean ± SE) of diatoms, dinoflagellates, and ciliates expressed as cell number, carbon (C) and nitrogen (N) per polyp, per dry weight (DW), and per ash-free dry weight (AFDW). Total mean was estimated from averaging all experiments. All values but cell number are $\times 10^{-9}$.

Ingestion	Diatoms		Dinoflagellates	Ciliates	Total
	Thalassionema	Pennate			
Cells polyp^{-1} d^{-1}	0.39±0.20	1.88±0.63	3.67±2.12	1.05±0.31	7.20±1.95
g C polyp^{-1} d^{-1}	0.02±0.01	0.43±0.19	0.93±0.32	2.37±1.30	4.00±1.39
g C g DW^{-1} d^{-1}	12.80±6.69	247±106	531±185	1,350±743	2,280±793
g C g AFDW^{-1} d^{-1}	76.70±41.90	1,480±639	3,190±1,110	8,140±4,470	13,700±4,770
g N polyp^{-1} d^{-1}	0.004±0.002	0.09±0.04	0.13±0.05	0.31±0.17	0.58±0.18
g N g DW^{-1} d^{-1}	2.49±1.38	50.1±21.8	74.90±26.0	176±96.6	332±104
g N g AFDW^{-1} d^{-1}	15.0±8.30	301±131	450±157	1,060±581	2,000±625

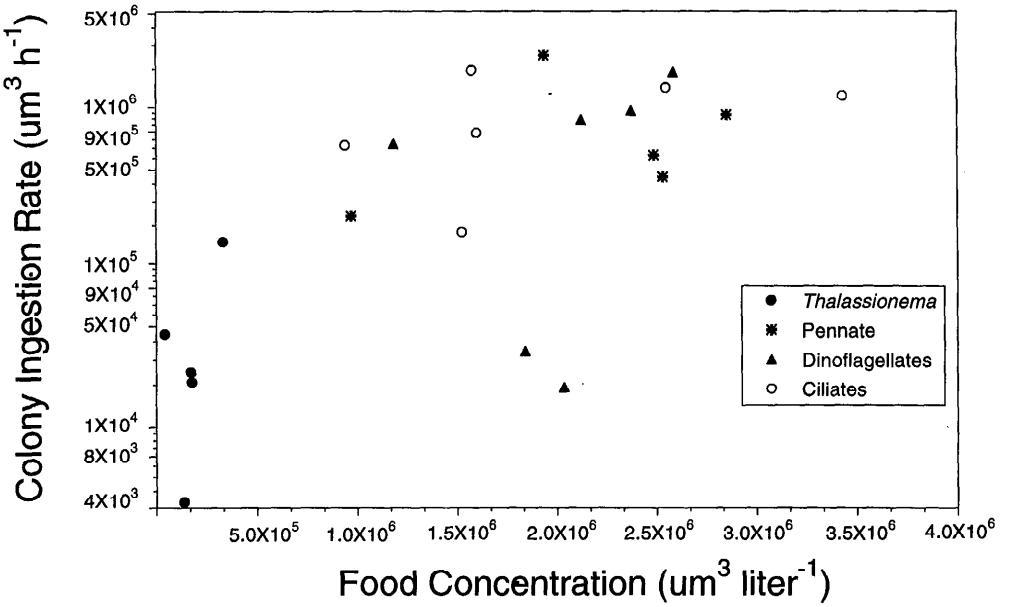

Fig. 2. Relationship between food concentration (μm^3 liter^{-1}) and ingestion rates (μm^3 h^{-1}, in log scale).

Although cnidarians traditionally have been considered strictly carnivorous (Hyman 1940), more recent studies have found evidence of herbivory (Roushdy and Hansen 1961; Fabricius et al. 1995*a,b*), which is supported by the presence of plant-digesting carbohydrases in certain soft coral species (Elyakova et al. 1981). It was surprising that *P. flexuosa* did not significantly decrease heterotrophic and autotrophic picoplankton concentration, because it has been documented that many hard corals are able to feed upon particles in this size range (Sorokin 1973). As pointed out by Sorokin (1991), there seems to be substantial variability in the feeding spectrum of different soft corals (Octocorallia) species.

What is the capture rate by gorgonians?—Our estimated capture rates of *P. flexuosa* and *P. porosa* on zooplankton agree with previous observations on tropical gorgonian feed-

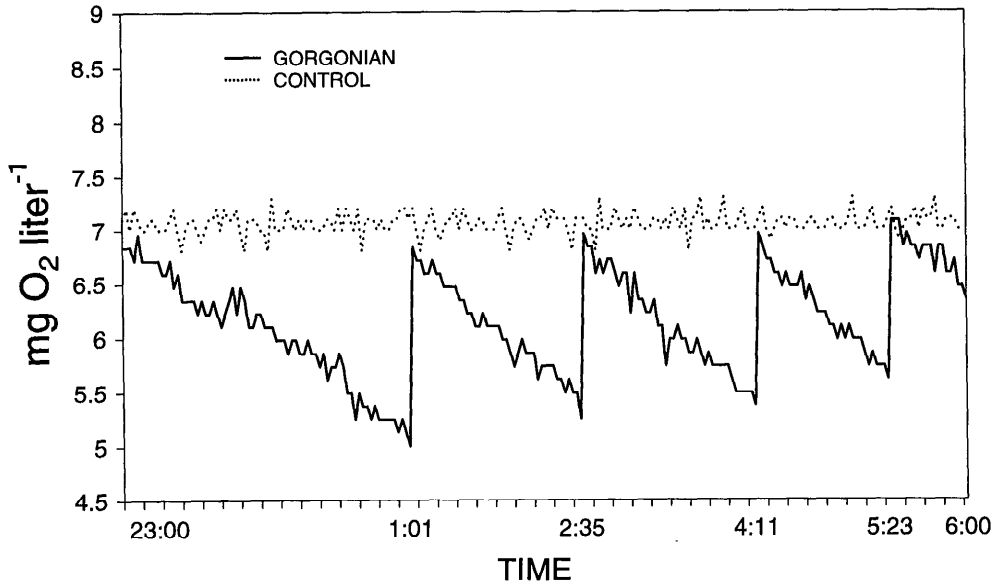

Fig. 3. Oxygen concentration (mg O_2 liter^{-1}) inside the chambers during the 7-h dark period (from 2300 to 0600 h). Oxygen was recorded every 2 min in both chambers; when oxygen concentration changed 20% from its initial level, water inside both chambers was renewed. Gorgonian: chamber with gorgonian colony. Control: chamber without gorgonian colony. Respiration by *P. flexuosa* was determined from decrease in oxygen concentrations over time.

Table 4. Prey capture rates for various hexacorallian and octocorallian species.

	Prey polyp^{-1}	Reference
Octocorallia		
Gorgonacea		
Pseudoplexaura porosa	0.03	This study
Plexaura flexuosa	0.01	This study
Paramuricea clavata	0.6	Coma et al. 1994
Alcyonacea		
Xenia elongata	0.3	Lewis 1982
Sacrophyton trocheliophorum	0.7	Lewis 1982
Lemnalia sp.	<0.1	Lewis 1982
Lobophytum cristagalli	0.1	Lewis 1982
Sinularia densa	<0.1	Lewis 1982
Sinularia capillosa	0.2	Lewis 1982
Sinularia microclavata	0.2	Lewis 1982
Dendronephthya hemprichi	0.02	Fabricius et al. 1995*b*
Hexacorallia		
Madreporaria		
Monastrea cavernosa	0.1–0.7	Porter 1974
Meandrina meandrites	1.8	Johnson and Sebens 1993
Monastrea cavernosa	0.23	Sebens et al. 1996
Madracis mirabilis	0.11	Sebens et al. 1996
Zoanthidea		
Palythoa variabilis	0.11–0.12	Sebens 1977
Palythoa caribaeorum	0.03–0.04	Sebens 1977
Zoanthus solandri	0.04	Sebens 1977
Zoanthus sociathus	0.02–0.05	Sebens 1977

ing for other species (Kinzie 1973; Lasker 1981; Lasker et al. 1983). These low capture rates contrast with those of *Paramuricea clavata,* the only gorgonian species in which significant in situ capture of naturally occurring prey has been demonstrated to date (Coma et al. 1994) (Table 4). This is probably because *P. clavata* is exclusively heterotrophic, while *P. porosa* and *P. flexuosa* have symbiotic zooxanthellae, as do most tropical shallow-water gorgonians. The zooplankton capture rates estimated for both species in our study were within the lower range of values observed on corals (Table 4); some of the higher values reported in the literature could be overestimates because they were quantified after a period of starvation and with zooplankton concentrations up to 10–30 times higher than natural zooplankton concentration (Sebens et al. 1996).

The percent of respiration supported by heterotrophic feeding (in carbon units) was used to compare *P. flexuosa* feeding rates on plankton to those obtained for other gorgonian species by Sorokin (1991). In *P. flexuosa,* mean compensation for respiratory losses by heterotrophic feeding was 0.035% (with a maximum of 0.07%) on algae and 0.037% (with a maximum of 0.09%) on ciliates. Sorokin (1991) estimated feeding rates on algae and ciliates for three symbiotic gorgonians in the laboratory using radioactively labeled prey. In his work, algae accounted for 0.1–3% of respiratory losses and ciliates for 1.7–3.6%. The higher values observed by Sorokin (1991) may have been due to the high prey concentrations used in his experiments, although it may also be due to variability in feeding rates among different species.

What is the role of heterotrophic feeding in symbiotic gorgonians?—The respiration rate estimated for *P. flexuosa* was similar to those obtained for other octocoral species by Megner and Svoboda (1977; 2.5–3 mg O_2 g AFDW^{-1} h^{-1}) and Svoboda (1978; 1.3–2.9 mg O_2 g AFDW^{-1} h^{-1}), working with whole colonies and similar temperatures. Our respiration rates are also similar to the respiration values reported by Fabricius and Klumpp (1995) for soft coral species in expanded state and in shallow waters (0.54–1.21 mg O_2 g AFDW^{-1} h^{-1}). However, the respiration rate we found is higher than that reported by Lewis and Post (1982); their low respiration rates might be an artifact due to incubation without continuous flow, which induces the contraction of colonies (unpubl. data) and consequently lowers respiration rates (Sebens 1987; Fabricius and Klumpp 1995).

The estimated respiration rate allowed us to evaluate the quantitative importance of zooplankton and other plankton in the energy budget of the gorgonian. Zooplankton and other plankton did not appear to be important sources of energy for *P. flexuosa,* accounting for <1% of the carbon required by basal metabolism. This result contrasts with the importance of zooplankton in heterotrophic gorgonians, which has been estimated to account for 50% of the energy demand (Coma et al. 1998). Other external carbon sources, such as dissolved organic matter, have been shown to be quantitatively unimportant for gorgonians (Sorokin 1991; Lasker unpubl. data). Therefore, our results suggest that carbon for *P. flexuosa* comes mainly from their symbiotic zooxanthellae.

To determine the importance of zooplankton and micro-

organisms as N sources for gorgonians, we estimated the relative contribution of these prey to the N needs of *P. flexuosa.* The nitrogen requirement for new production was estimated as the requirement for annual growth. New production usually includes growth and reproduction, but in small colonies (<20 cm), all new production is invested in growth (Beiring 1997). The average growth rate per branch of small *P. flexuosa* colonies was 2 cm yr^{-1} (Coma unpubl. data), and nitrogen content of the colony tissue was 0.045 ± 0.011 mg N mm^{-1} of terminal branch (n = 10) or 0.6 ± 0.09% of dry weight. Therefore, a *P. flexuosa* colony of 11-cm height (total length = 57.4 cm) with 18 primary branches would require a minimum of 16.2 mg N yr^{-1}. A colony of this size derives 2.0 mg N yr^{-1} from the zooplankton (Table 2) and 0.7 mg N yr^{-1} from other plankton (estimate based on 50 polyp cm^{-2} [Beiring 1997] and grazing rates in Table 3), which together represent 17% of the minimum annual nitrogen needs for new production.

Our data indicate that feeding on zooplankton and other plankton had a relatively low contribution to the overall nutrient requirement of *P. flexuosa.* Plankton patchiness could produce sporadic episodes of high prey capture rates, as has been documented in another gorgonian (Coma et al. 1994). However, these sporadic events probably do not account for all the remaining N requirement. This small role of zooplankton and other plankton as food source for symbiotic gorgonians suggests that not only C but also N might come from the symbiotic zooxanthellae.

P. flexuosa colonies continuously expelled significant numbers of apparently healthy and viable symbiotic zooxanthellae. This observation supports the hypothesis that the expulsion of zooxanthellae by the host is a natural mechanism for regulating the concentration of algae in the tissues and maintaining the efficiency of the symbiosis (Steele 1976; Hoegh-Guldberg et al. 1987; Trench 1987). We examined the importance of this zooxanthellae release for the C and N budget of the coral by taking into account that the density of zooxanthellae per unit area of coral tissue seems to remain quite constant (1–2 × 10^6 cells cm^{-2}; Drew 1972; Muscatine et al. 1985). Our observed release rate of 6.8 × 10^3 cells cm^{-2} d^{-1}, which is on the same order of magnitude as that observed in *P. damicornis* by Stimson and Kinzie (1991), was <0.5% of the total standing stock. Therefore, zooxanthellae release was not a significant loss of fixed carbon. No significant loss of fixed carbon due to zooxanthellae release has been observed for several taxa (Hoegh-Guldberg et al. 1987; Stimson and Kinzie 1991). At the estimated rate of zooxanthellae release, the annual loss of nitrogen through expelled zooxanthellae would account for 0.84 mg N. Since this amount represents only about 5% of the previously estimated nitrogen requirement for new production, it appears that the expelled zooxanthellae were not a very important loss of nitrogen for the coral.

Effect of gorgonian predation on plankton communities— Density of *P. flexuosa* in the studied area was 0.45 colonies m^{-2}, with a mean height of 44 cm in a study area of 100 m^2 with 45 colonies. This density would give a total of 9.5 × 10^4 polyps m^{-2} for this gorgonian, based on the relationship between colony height and polyp number found by Beiring (1997). At the estimated capture rates (Table 3), *P. flexuosa* polyps can ingest about 1.7 × 10^5 diatoms, 2.3 × 10^5 flagellates, and 6.8 × 10^4 ciliates m^{-2} d^{-1}. Overall, this capture is equivalent to removing 0.15 mg C m^{-2} d^{-1} from the plankton. Ambient concentrations of these prey items during the experimental period (25 August–1 September 1995) were 1.97 ± 0.46 diatoms ml^{-1} (including only *Thalassionema* sp. and pennate species [N = 12]), 2.27 ± 2.00 dinoflagellates ml^{-1} (N = 12), and 0.62 ± 0.29 ciliates ml^{-1} (N = 12). This implies a daily removal of 9% of the diatoms, 10% of the dinoflagellates, and 11% of the ciliates of the water mass within 1 m of the reef.

The estimated impact of *P. flexuosa* on the microbial assemblages is not negligible. *P. flexuosa* is a ubiquitous Caribbean gorgonian, and similar densities of this species have been documented on other reefs in Panama (Lasker et al. 1988) and Florida (Beiring 1997). It has also been shown that other gorgonian species can prey on microorganisms (Sorokin 1991). The high density of gorgonians species and populations in the Caribbean reefs suggests that gorgonians could be important predators on plankton communities. Furthermore, it seems that predation impact by sponges on microorganisms can be much greater than in gorgonians (Pile et al. 1996, 1997; Pile 1997). Therefore, in shallow-water ecosystems, the effect of grazing by macroinvertebrates on water column microorganisms might be much greater than previously thought and might need further study.

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