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Energetics of a Predator-Prey Interaction: Corals and Coral-feeding Fishes[1]

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ABSTRACT: Various hypotheses have been proposed to account for defense of a feeding territory by coral-feeding fishes. However, before the adaptive significance of feeding territories can be fully understood, energetics of the predator/prey relationship must be quantified. Energetics of the interaction between the coral *Pocillopora meandrina* and the territorial coral-feeding damselfish *Plectroglyphidodon johnstonianus* were examined to determine the minimum energetic requirement of the predator and the effect of predation on productivity of the prey. Coral productivity for colonies exposed (experimental) and not exposed (control) to predation, and metabolic rates of the fish were determined. Fish required 240 cal/day, while corals produced 0.21 cal/cm^2/day. A typical colony of *P. meandrina* did not produce enough energy to sustain a fish. Data presented here indicate that territories of two or more colonies should provide sufficient energy. Predation by an individual *P. johnstonianus* did not have a measurable effect on coral primary productivity.

TERRITORIALITY IS COMMON IN a wide range of taxa. Food, nest sites, shelter, and mates may be defended against members of the same species and of other species (Hixon 1980). Of these resources, food supply is particularly important since it is used to meet the energetic requirements for maintenance, growth, and reproduction (Tricas 1986). Therefore, food abundance is a major factor affecting territory size, and territory size should vary with food supply (Ebersole 1980, Tricas 1986). One hypothesis relating to optimal territory size states that animals defend territories that contain enough food to satisfy their short-term energy requirements; any aditional area defended would yield no additional benefit at an increased cost of defense (Myers et al. 1979, Tricas 1986). This hypothesis predicts that territory size should vary as an inverse function of local food quality, quantity, and distribution. An alternative hypothesis states that animals defend as large an area as possible, but food competitors constrain the size of the defensible area. An area containing high-quality food resources would attract more competitors; therefore, territory size would be adjusted as an inverse function of competitor density rather than food supply directly (Myers et al. 1979, Tricas 1986). Evidence in support of both of these hypotheses has been cited in many studies (see references in Myers et al. 1979, Hixon 1980, and Tricas 1986). Although these two hypotheses are not mutually exclusive and may both play a role in determining territory size in coral-feeding fishes (Tricas 1986), only the first hypothesis was examined in this study.

Hermatypic corals represent an economically defendable resource since they are immobile, predictable in space and time, and continuously renewing (Brown 1964, Hixon 1980). For animals defending such a resource, selection should favor a territory occupant that maintains a maximum sustainable yield, since this would permit maximal long-term energy gain from the defended area (Hixon 1980).

Territory size varies greatly among coral-feeding fish: from one to several hundred square meters (Reese 1981, Sutton 1985,

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Tricas 1986, Hourigan 1987). Some coral-feeding chaetodontids have been shown to change the size of their defended territory in response to variations in the abundance and distribution of living coral (Sutton 1985, Tricas 1985, 1986, 1989*a*, Hourigan 1987, Hourigan et al. 1988). Fish appear to adjust their territory boundaries in response to variations in the quantity and quality of available corals to include enough coral to sustain themselves without making the territory so large that the cost of defense renders metabolic demands on the fish too great to be met by the defended resource (Tricas 1985, 1986, 1989*a*, Hourigan 1987, Hourigan et al. 1988).

To better understand the relationship between food supply and territory size, it is necessary to evaluate the energy requirements of the territory occupant and the productivity of its food supply. I chose the coral-feeding damselfish *Plectroglyphidodon johnstonianus* as a model system. This species occurs throughout the Indo-West Pacific and occupies a variety of habitats off Oahu, Hawaii. These habitats vary greatly in coral abundance and species composition, and there is a corresponding variability in territory size of the fish. In this study, I compare the productivity of the coral *Pocillopora meandrina* with the metabolic requirements of *P. johnstonianus* to answer two questions: (1) how much *P. meandrina* surface area is sufficient to meet the metabolic requirements of an individual *P. johnstonianus*?, and (2) is coral productivity negatively affected by predation by *P. johnstonianus*?

MATERIALS AND METHODS

Field Observations and Collection of Corals

I observed individual *P. johnstonianus* in three types of habitats off Oahu, using SCUBA. One habitat was a large patch reef (110 × 130 m) in northern Kaneohe Bay, with nearly 100% live coral cover, predominantly *Porites compressa* and *Montipora verrucosa* (MacDonald 1981, Cox 1986). The second habitat was a smaller (8 × 20 m) patch reef in southern Kaneohe Bay, which consisted of a small *P. compressa* reef (4 × 7 m) and 20–50 separate colonies (each 30–80 cm diam.) of *Pocillopora eydouxi*. The third habitat type occurred at certain deeper sites off the outer coast of Oahu, at which the coral community consisted of small (25 cm diam.) colonies of *P. meandrina* (1–3 m apart) on bare rock substratum.

Pocillopora meandrina was used for this experiment because *P. johnstonianus* prefers this species to *P. compressa* and *M. verrucosa* for feeding (Dieckhaus, pers. comm.). Six colonies of *P. meandrina* were collected from 2 m depth on the barrier reef flat in northern Kaneohe Bay. The corals were transported to the Hawaii Institute of Marine Biology in buckets of seawater. Colonies were approximately equal in size, each about 25 cm in diameter. Each coral head was cut approximately in half using a rock saw, to produce genetically identical control and experimental colonies. Each half colony was affixed to a plastic screen using color-coded wire so that the two halves of each colony could be distinguished. The screens minimized handling when transferring coral heads between aquaria. All visible infauna were removed manually from each coral head. Before each set of respirometry experiments, the screens and nonliving portions of the coral heads were scrubbed with a wire brush to remove macroalgae.

Photosynthesis

Initial photosynthesis-irradiance (P-I) curves were produced for each half colony based on measurements made over a 24-hr period. The respirometry chamber used for the corals consisted of a 34 × 20 × 25 cm (17- liter) glass aquarium. The aquarium was uncovered between measurements, with unfiltered seawater flushed through. Just before each trial, water inflow was stopped and a Plexiglas cover was set on the surface of the water. The cover fit snugly but did not form a tight seal around the rim of the aquarium. A polarographic oxygen probe (YSI 5739) with a vibrator was placed in the tank through a hole in a corner of the cover, at a distance

of 15 cm from the coral head. A propeller was placed in the tank next to the oxygen probe vibrator. The motor for the propeller was mounted on a wood platform next to the aquarium, with the propeller's shaft protruding into the tank through a hole in the cover. Mixing provided by the propeller and vibrator was sufficient to create a flow of water over the oxygen probe membrane but did not approximate the water motion of the natural habitat of *P. meandrina*. The chamber was placed in a water table containing running seawater to a height of 17 cm on the chamber, to maintain a constant temperature.

Five chambers were run simultaneously, with each half of two coral colonies in a separate chamber, while a fifth chamber contained only a screen and served as a control. The cover was placed on each chamber for 15 min and then moved to the next chamber, so that oxygen in each chamber was measured every 75 min. A YSI 51B oxygen meter was used to measure oxygen concentration when the cover was first placed on the chamber and after 15 min, and the difference was calculated. Ambient light in the photosynthetically active radiation (PAR) range of 400–700 nm was recorded simultaneously with each oxygen measurement using a cosine light probe on a ringstand in air, 30 cm above the corals in the chambers. Maximum irradiance at the probe was 2400 $\mu E/m^2/s$, while light in the chambers was reduced 33.2% because of water and the Plexiglas cover.

Predation Treatment

Fish were collected using hand nets from a small reef in the Sampan Channel in Kaneohe Bay and were kept in aquaria at HIMB for at least 1 week before use in experiments. After the pretreatment P-I curves were determined, each half colony was transferred to a separate glass aquarium (51 × 26.5 × 20.3 cm; 27.4-liter), with running seawater. Because mucus produced during transfer could stimulate fish feeding, corals were allowed to acclimate to the aquaria for several hours before an individual *P. johnstonianus* was placed in the aquarium containing one-half of each colony. The other half of each colony remained in a predator-free aquarium. Predation on experimental colonies occurred for 6 days. During the second and third days, observations on the number and location of bites on corals by four of the fish were recorded for 10-min intervals, at various times of day, to provide a measure of feeding rate.

At the end of the 6-day period, P-I curves were again produced for each half colony using the method described previously. Because there is no effective method for measuring coral respiration in the light (Marsh and Smith 1978), I used the average nighttime respiration rate to calculate P-I curve parameters.

Coral Surface Areas

After respiration was measured, the surface area of each half colony was determined and the photosynthetic rate was normalized to surface area. Each half colony was immersed in a bucket of bleach, dried, and weighed. Paraffin was heated to ca. 62°C, just above its melting point, and the half colonies were quickly dipped into it, so that the wax coated the once-living portions of the colony, while the screen and dead basal portions remained uncoated. The half colonies were then reweighed, and the difference between the weights was compared to a standard curve obtained by dipping blocks of coral of known surface area into paraffin. Colony halves averaged 12.5 cm in diam., with a mean surface area of 594 cm^2 (range 239–1212 cm^2). This wide range in surface areas is due to the difficulty in cutting a colony into two equal pieces given the branch morphology.

Fish Metabolism

Oxygen consumption of *P. johnstonianus* was determined using respirometry chambers consisting of 2.8-liter plastic containers with tight-fitting lids. The sides of the chambers were covered with aluminum foil so that the fish would not be disturbed by external activity. Inflow and outflow valves were located in the lid of the chamber, and seawater was flushed through the chamber except during measurement periods, when the inflow and

outflow valves were shut. Another stoppered hole in the lid held the oxygen probe during measurement periods. The chamber was placed in a water table with running seawater to maintain constant temperature. A water-powered magnetic stirrer was placed under each chamber, and a stir bar in the bottom of the chamber provided water flow over the membrane of the oxygen probe.

A fish was removed from a holding tank and transferred to the chamber where it was allowed to acclimate for 12 hr before measurements began. A chamber with a fish and a control chamber without a fish were run simultaneously. The measurement periods were 30 min long at 30-min intervals. After the experiment, each fish was weighed in a beaker of seawater, and its standard length was measured. The four fish used in this experiment ranged from 5.1 g to 16.1 g in weight and from 4.6 cm to 6.8 cm in standard length. These individuals were all small members of the population.

Data Analysis

P-I curves were produced from the oxygen flux data for each half colony for the initial and final testing periods. Data were fitted by a hyperbolic tangent function of the form:

$$P = P_{\max}\tanh(I/I_k) + R$$

(Chalker et al. 1983, Kinzie and Hunter 1987), using PROC NLIN (SAS Institute, Inc. 1985). In this equation, P is the net photosynthetic rate (rate of oxygen production in μmol $O_2/cm^2/hr$), $P_{\max}$ is the asymptotic maximum rate of light-saturated photosynthesis (μmol $O_2/cm^2/hr$), I is the irradiance ($\mu E/m^2/s$), I_k is the irradiance at which the initial slope of the curve intersects $P_{\max}$, and R is the respiration rate (rate of oxygen consumption in μmol $O_2/cm^2/hr$). These parameters are graphically illustrated in Chalker et al. (1983) and Kinzie and Hunter (1987). For each half colony, the $P_{\max}/R$ ratio was calculated from these parameters.

Paired t tests were used to compare $P_{\max}$, I_k, R, and $P_{\max}/R$, and measured values of productivity and respiration between control and experimental colonies both initially and after predation treatment. I also compared initial and final values within treatments.

RESULTS

Field Observations

On the large patch reef with nearly 100% live coral cover, *P. johnstonianus* aggressively defended feeding territories up to ca. 16 m^2 against conspecifics and other species of coral-feeding fish (Dieckhaus, pers. comm.; pers. obs.). Large territories on this reef and the diets of *P. johnstonianus* occupying them were composed predominantly of *Porites compressa* and *Montipora verrucosa*. On the smaller patch reef with separate *P. eydouxi* colonies, each colony sheltered up to nine individuals of *P. johnstonianus* at a given time. In the deeper habitat, I frequently saw individual *P. johnstonianus* defend a territory of two or three *P. meandrina* colonies.

P-I Curve Parameters

Control and experimental colonies did not differ in $P_{\max}$, I_k, R, or $P_{\max}/R$ either initially or at final measurement (Table 1). Comparisons within treatments showed a significant decrease in R between initial and final measurement in both control and experimental colonies ($t = 3.12$, $df = 5$, $P < .05$, control; $t = 3.85$, $df = 5$, $P < .05$, experimental). $P_{\max}/R$ increased in control colonies (Wilcoxon signed-rank test, $T = 0$, $n = 6$, $P < .05$).

Measured Productivity

An estimate of the mean daily net productivity of the 12 half colonies was calculated based on 13 hr of daylight (Table 2). Values were converted to mg $C/cm^2/day$ for comparison, based on calculations provided in McCloskey et al. (1978). Mean values for daily net productivity for all colonies were 0.12 mg $C/cm^2/day$ (SD = 0.068) initially, and 0.13 mg $C/cm^2/day$ (SD = 0.070) finally. Mean nightly respiration rates of all colonies were 0.13 mg $C/cm^2/day$ (SD = 0.055) ini-

TABLE 1

Pocillopora meandrina P-I CURVE PARAMETERS [mean (SD)]

PARAMETER	INITIAL			FINAL		
	CONTROL	EXPERIMENTAL	COMPARISON	CONTROL	EXPERIMENTAL	COMPARISON
P_{max} μmol $O_2/cm^2/hr$	1.1 (0.46)	1.5 (1.3)	NS	1.2 (0.47)	1.1 (0.58)	NS
I_k $\mu E/m^2/s$	343 (266)	475 (333)	NS	570 (146)	463 (139)	NS
R μmol $O_2/cm^2/hr$	−0.41 (0.18)	−0.45 (0.21)	NS	−0.31 (0.17)	−0.30 (0.13)	NS
P_{max}/R	2.7 (0.38)	3.0 (1.3)	NS	4.0 (1.2)	3.5 (0.66)	NS

NOTE: Paired t tests (df = 5) were used to make comparisons between control and experimental colonies.

TABLE 2

MEASURED NET PRODUCTIVITY AND RESPIRATION FOR *Pocillopora meandrina* [mean (SD)]

PARAMETER	INITIAL			FINAL		
	CONTROL	EXPERIMENTAL	COMPARISON	CONTROL	EXPERIMENTAL	COMPARISON
Daily net productivity mg $C/cm^2/day$	0.12 (0.022)	0.13 (0.10)	NS	0.11 (0.032)	0.15 (0.10)	NS
Total nightly respiration mg $C/cm^2/day$	−0.10 (0.041)	−0.12 (0.058)	NS	−0.081 (0.045)	−0.080 (0.031)	NS

NOTE: Paired t tests (df = 5) were used to make comparisons between control and experimental colonies.

tially and 0.094 mg $C/cm^2/day$ (SD = 0.040) finally. There was a decrease in respiration in the experimental colonies between initial and final readings ($t = 2.73$, df = 5, $P < .05$, Figure 1). The initial and final 24-hr net productivity curves for one experimental colony are seen in Figure 2.

Fish Metabolism

Mean oxygen consumption rate of *P. johnstonianus* at rest was 13 mg O_2/g fish/day for a 5.1-g fish and 5.1 mg O_2/g fish/day for a 16.1-g fish. There was a significant linear regression of mean oxygen consumption rate on log fish weight (Figure 3; $P < .05$). There was no clear trend in oxygen consumption at different times of day.

Fish Feeding Rates

Feeding rate on experimental corals was 240 bites per hour (SD = 73, $n = 18$). Most bites (88.4%) were on live coral tissue. Bites were also directed at algae growing on the glass walls of the aquarium, on the screen, or on the nonliving base of the coral colony. Of bites directed at live coral tissue, 91% were on the tips and sides of branches, while 9% were toward the base of the branches. Feeding rate varied during the day but not in a discernible pattern.

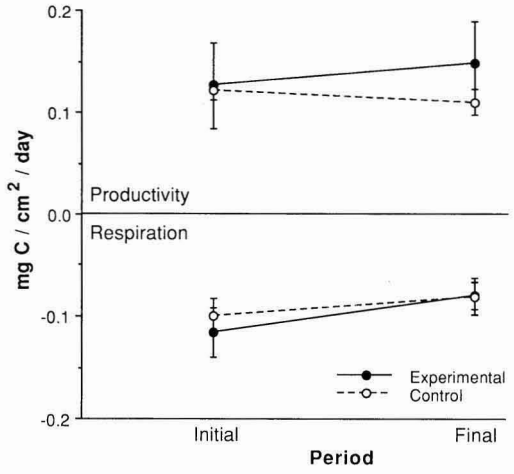

FIGURE 1. Comparison of *Pocillopora meandrina* productivity (*top*) and respiration (*bottom*) initially and after 6 days of exposure to fish predation. Vertical bars indicate standard errors of the mean. See text for discussion of significant differences.

DISCUSSION

Net productivity values for *P. meandrina* obtained in this experiment compare well with those reported for other species of coral (Franzisket 1969, Davies 1980, Lasker 1981, Dubinsky et al. 1984, Muscatine et al. 1984, Porter et al. 1984, Jokiel and Morissey 1986, Kinzie and Hunter 1987). Davies (1984) and Edmunds and Davies (1989) obtained much greater values for productivity of *P. eydouxi* and *Porites porites*. However, those studies used small nubbins of corals instead of entire colonies. Nubbins should have higher productivity per unit surface area than whole colonies because there are no parts of a nubbin that are shaded or subjected to reduced water flow by neighboring branches (Jokiel and Morrissey 1986).

Metabolic rates of *P. johnstonianus* in this study are higher than those reported for tem-

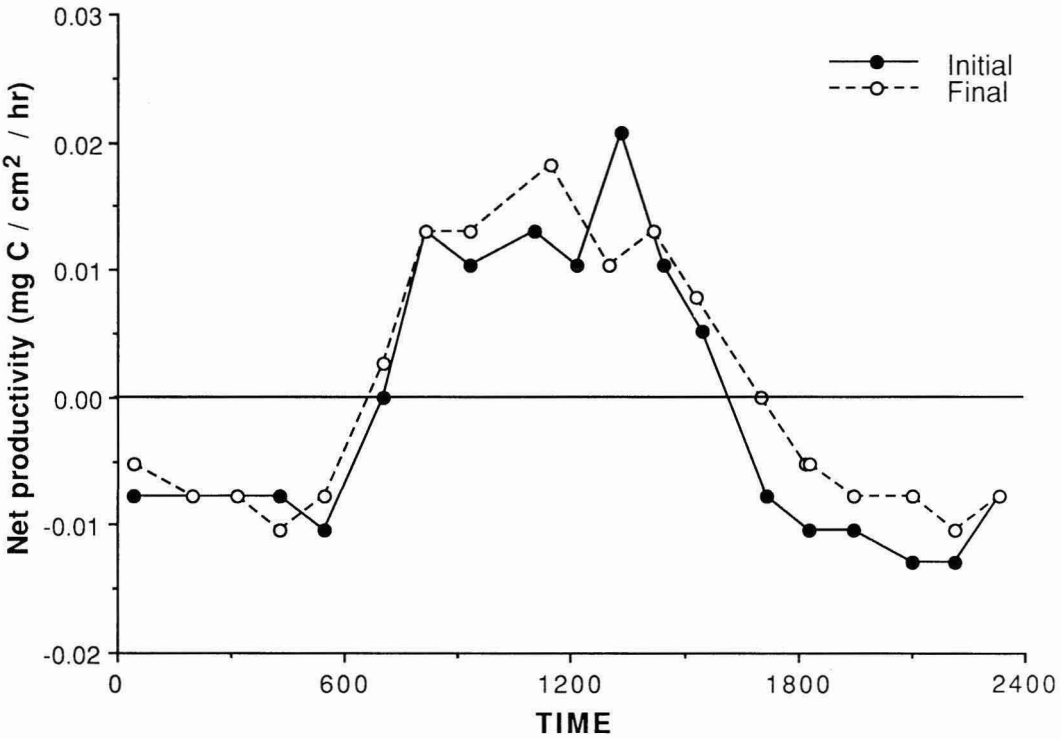

FIGURE 2. Sample daily net productivity curves for an experimental colony of *Pocillopora meandrina* initially and after 6 days of exposure to fish predation.

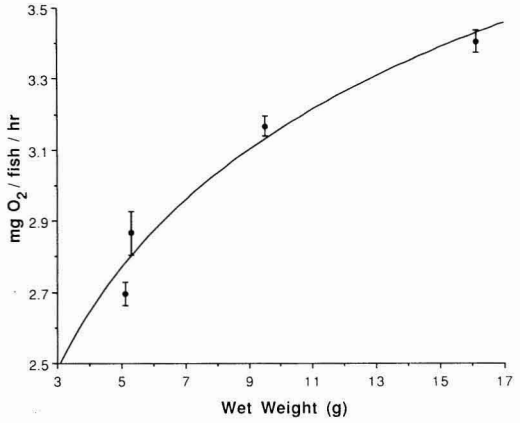

FIGURE 3. Oxygen consumption of *Plectroglyphidodon johnstonianus* at rest. Mean oxygen consumption is regressed on log wet weight ($y = 1.86 + 1.30$ (log x), $R^2 = 0.956$). Vertical bars indicate standard errors of the mean.

perate species (Brett 1973, Brett and Groves 1979, James and Probyn 1989) but compare favorably to those reported for the congeneric territorial herbivore *P. lacrymatus* (Polunin and Klumpp 1989). Tropical fish are predicted to have higher metabolic rates than temperate fish (Brett and Groves 1979), but few published estimates of metabolism are available for tropical reef fishes.

Daily net productivity of corals was converted into mean calories produced with the assumption that photosynthetically fixed carbon is reduced to glycerol, which is translocated from the symbiotic algae to the coral animal (Falkowski et al. 1984). The caloric value of glycerol is 1.684 kcal/g C. Using this conversion factor, the net productivity of *P. meandrina* was 2.1×10^{-4} kcal/cm^2/day. A typical colony with 1188 cm^2 of surface area would produce 0.25 kcal/colony/day. Mean daily oxygen consumption of *P. johnstonianus* was converted into calories using an oxycalorific equivalent of 3.25 cal/mg O_2 (Corbin 1977, Brett and Groves 1979). Therefore, the mean daily energetic requirement of a 5.1-g fish at rest is 0.041 kcal/g/day, and 0.017 kcal/g/day for a 16.1-g fish. On average, 0.237 kcal/fish/day would be required.

A complete energy budget has not been constructed for *P. meandrina*. An energy budget is, however, available for *P. eydouxi* (Davies 1984). Using small nubbins, Davies (1984) presumed that 48% of the net photosynthesis was lost from a coral colony. As stated above, values obtained using nubbins instead of colonies may not be representative of entire colonies. Jokiel and Morrissey (1986) found that production efficiency of a coral colony increased as canopy size increased. Net primary production of the colony increased with canopy size while respiration remained approximately the same (Jokiel and Morrissey 1986), which would result in more energy being available to feeding fish. My measurements indicate oxygen production above what the coral needed for its own maintenance. Using Davies's (1984) values and assuming, based on the congeneric relationship of these corals, that these values are similar for *P. meandrina*, then a minimum of 1.0×10^{-4} kcal/cm^2 was lost over a 24-hr period. Most of this loss in *P. eydouxi* was assumed to be in the form of mucus (Davies 1984), which may also be available for fish consumption (Benson and Muscatine 1974, Richman et al. 1975). Thus, for *P. meandrina*, an estimated 0.25 kcal/colony/day was produced, an amount similar to that required by a fish at rest (0.24 kcal/fish/day). If these values are correct, then an average-size *P. johnstonianus* territory would need at least 1200 cm^2 (equivalent to one large colony or two typical colonies) of *P. meandrina* to support a fish. This was generally the case in territories of *P. johnstonianus* including *P. meandrina* (pers. obs.).

The metabolic rate of *P. johnstonianus* measured in this experiment was a resting metabolic rate. However, under natural conditions, territorial coral-feeding fish, such as *P. johnstonianus*, spend most of the day actively foraging and chasing other fish (Tricas 1986, Hourigan 1987), and consequently they should require more energy to sustain themselves. Studies on other fishes have shown that active metabolic rate is 1.5 to 15 times greater than resting metabolic rate (Muir and Niimi 1972, Brett 1973, James and Probyn 1989). Thus, a minimum of 1700 cm^2 and as much as 17,000 cm^2 of *P. meandrina* tissue would be required to sustain a single *P. johnstonianus*.

In addition, not all of the living tissue on

the coral colony surface is accessible to coral-feeding fishes, so not all of the colony's daily productivity is available. *Pocillopora meandrina* has high-energy lipid bodies deep in its polyps (Stimson 1987) that presumably are not accessible to fish that only graze on polyps without removing skeletal material. Only the outer edges and tips of branching corals are accessible to some coral-feeding fish (Neudecker 1977). These are probably the sites of new tissue production (Gladfelter et al. 1989) and may have a lower concentration of nematocysts or toxins or the polyps may be unable to retract as rapidly as elsewhere on the colony. Gladfelter et al. (1989) found that tips of *Acropora palmata* branches had higher respiration rates and lower photosynthetic rates than more proximal regions. If this is true for other corals as well, feeding on the tips and sides of branches may reduce the standing stock of high-respiration-rate tissue, and this could contribute to the observed reduction in respiration rate for the experimental corals after predation by *P. johnstonianus* (Table 1, Figure 1, *bottom*).

Plectroglyphidodon johnstonianus is a daytime feeder (MacDonald 1981, Dieckhaus, pers. comm.; pers. obs.). Assuming that daytime feeding rate is relatively constant, which appears to be the case for other coral-feeding fishes (Cox 1986, Tricas 1986, 1989*a*, Hourigan 1987, Dieckhaus, pers. comm.), and estimating 13 hr of daylight, then an individual *P. johnstonianus* may be expected to take about 3100 bites per day. Under natural conditions, feeding rates might be lower because other activities, such as searching for food, watching for predators, defending a territory, and mating, would detract from time spent feeding. However, the feeding rate observed in this experiment (240 bites/hr) is lower than that observed for *P. johnstonianus* in the field (353 bites/hr; Dieckhaus, pers. comm.) and for two species of coral-feeding butterflyfish (584 and 710 bites/hr; Hourigan 1987). This may be explained by the fact that the experimental fish could only feed on a single colony, and that after a few bites, the polyps might be retracted and not available for further feeding until recovery.

The productivity of a coral colony under natural conditions may be higher than that measured in this experiment. *P. meandrina* generally grows in an environment characterized by very high water motion, which the experimental setup could not approximate. Jokiel (1978) found that *P. meandrina* colonies kept in the laboratory under conditions of low water motion did not grow and experienced much greater tissue mortality than colonies in conditions of higher water motion. In his low-water-motion environments, the verrucae that characterize the surface of *P. meandrina* reduced water flow at the surface of the colony and reduced diffusion of metabolic materials from the surrounding water (Jokiel 1978). This would be expected to dramatically reduce productivity measurements, and may also explain low productivity in the experiment reported here. Any effect of handling colonies might also reduce productivity. Productivity measurements reported here therefore represent minimum values.

The lack of measurable effect of *P. johnstonianus* on the productivity of *P. meandrina* in this experiment is surprising. The data predict that the fish should require more energy than the coral produces on a daily basis; if the fish were to get its entire supply of nutrients from the coral, it would have to consume some existing tissue in addition to mucus or new growth. Fish predation could prevent coral growth, as has been observed in butterflyfish (R. Kosaki, pers. comm.; Cox 1986), and could ultimately lead to substantial tissue mortality and colony death. That predation did not reduce coral productivity in the present experiment may be due to its short duration. Also, the presence of only one colony meant that polyps would be retracted for much of the time, which would reduce feeding intensity and efficiency.

In most habitats off Oahu, individual *P. johnstonianus* defend a territory composed of more than one coral colony, and frequently more than one coral species. Thus, bites taken by a fish in such a territory are distributed among the corals available. In fact, most *P. johnstonianus* observed in multicolony territories appear to make rounds of their territories, taking only a few bites from one colony before moving on to the next (pers. obs.).

This type of behavior has been observed in other coral-feeding fishes (Neudecker 1985, Hourigan 1987) and is probably due in part to polyp retraction. A single coral colony is rarely the subject of many consecutive bites, as were the colonies in my experiments. Therefore, *P. johnstonianus* would be predicted to have reduced effects on corals in the field than on the experimental colonies.

An exception to the multicolony territories is a small *P. eydouxi* reef in Kaneohe Bay, on which several *P. johnstonianus* of various sizes shelter in and feed on a single coral head. On that reef, feeding intensity on a colony would be predicted to be more intense than in the present experiment. However, colonies on that reef are much larger than the *P. meandrina* colonies used in this experiment, and productivity or regeneration rates may be greater for *P. eydouxi* than for *P. meandrina*, so that any effect of fish predation may be compensated by rapid regrowth. Alternatively, the caloric value of *P. eydouxi* may be greater, and fish may require less tissue for equal energetic gain.

In general, feeding territories were smaller in habitats consisting of *Pocillopora* spp. despite the much lower coral cover. *Pocillopora meandrina* has a higher caloric value than *P. compressa* (Tricas 1986, 1989*b*) and *M. verrucosa* (Glynn and Krupp 1986), giving more available energy per unit area. An alternative explanation for these observations in the present study may be higher productivity by *Pocillopora* spp. (Yonge et al. 1931). In addition, experiments involving *P. johnstonianus* (Dieckhaus, pers. comm.) and a variety of coral-feeding chaetodontids (Tricas 1986, 1989*b*, Hourigan 1987, Hourigan et al. 1988) have related feeding preference to caloric value, and pocilloporids rank high in both caloric value and preference rating.

The productivity and metabolism values reported in this paper are perhaps low estimates for *Pocillopora meandrina* and for *Plectroglyphidodon johnstonianus*, respectively, because of the unnatural laboratory conditions. However, based on my calculations, it appears that *P. johnstonianus* defends territories that contain sufficient coral to meet its short-term metabolic needs. The variability in territory size in different habitats may relate to the nutritional values and productivity of other coral components in those habitats or to the presence of competitors. Before we can fully understand the intricate relationships of organisms to their environments, we must evaluate the energetics of the system.

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