

# Partial predation on tropical gorgonians by *Cyphoma gibbosum* (Gastropoda)

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**ABSTRACT:** *Cyphoma gibbosum* (Gastropoda, Ovulidae), a generalized predator on tropical gorgonians, forages selectively among gorgonian species on shallow reefs at St. Croix, U.S. Virgin Islands. Mean residence times of marked snails on prey taxa ranged from 1.8 d on *Eunicea* spp. to 4.7 and 10 d on *Gorgonia ventalina* and *Plexaurella dichotoma* respectively. Juveniles were sedentary and remained on single hosts throughout the study period. An analysis of wounds caused by *C. gibbosum* on gorgonians revealed that colonies of some taxa were consistently stripped of tissue, baring the underlying proteinaceous axis, while others were only superficially grazed. Wounds baring the axial skeleton were considerably more severe than superficial wounds because the bared skeleton could be colonized by algae causing subsequent tissue regeneration to be inhibited. Within all species, wounds were not restricted to any single portion of the colony. However, most wounds occurred within the central regions of colonies and the lowest portions of colonies were seldom damaged. The short residence times and superficial grazing on some taxa such as *Eunicea* spp. and *Muricea* spp. may be a consequence of heavy spicular armor over polyps and over the proteinaceous axis in those taxa. Deep wounds to the axial skeleton occurred only on taxa with smaller spicules and a smaller proportion of spicules in the coenenchyme by dry weight. Residence time on a prey species was inversely proportional to both maximum spicule length and percent composition of spicules. Short residence times and shallow wounds on colonies of heavily spiculed species may be a response by *C. gibbosum* to foraging on suboptimal, heavily defended resources. Despite the short residence times, these potentially suboptimal prey taxa were regularly visited and preyed upon. This suggests that factors other than spicular architecture, such as gorgonian chemistry, may also play a role in the foraging of *C. gibbosum*.

## INTRODUCTION

Rather than killing their hosts and prey, many consumers such as herbivores, parasites, and grazers on colonies routinely remove only small quantities of tissue (Price 1980, Lubchenco & Gaines 1981, Thompson 1982, Harvell 1984a, 1986). Partial predation (*sensu* Jackson & Palumbi 1979, Harvell 1984a) is of particular theoretical interest because natural selection will operate differently on prey populations in which individuals typically survive encounters with predators. Attacks by non-lethal predators should favor inducible defenses and defenses that limit areal extent of damage (Harvell 1984a, b, 1986, Rhoades 1985). Colonial invertebrates are only rarely killed by their predators and, due to their modular body plan and capacity for regeneration, may be little impaired by consumer attacks (Jackson &

Palumbi 1979, Jackson 1983, Harvell 1984a, 1985). Understanding the interactions of partial predators with their prey is particularly important in tropical reef habitats where benthic communities are often dominated by reef-building colonial animals (Jackson 1983).

Although scleractinian and gorgonian corals (Cary 1918) dominate many benthic communities in the tropics, and gorgonian corals are known to be heavily invested with biologically active toxins (Coll et al. 1982, Fenical 1982, Gerhart 1983, 1984, Bakus et al. 1986), little is known of the patterns of attack by partial predators, or the consequences of attack and subsequent colony recovery. Types of attacks by corallivores are diverse and include tissue stripping (Birkeland & Gregory 1975, Brawley & Adey 1982, Glynn & Wellington 1983, Wahle 1985), nipping of branch tips (Glynn et

al. 1972, Neudecker 1979, Wellington 1982, Glynn & Wellington 1983, Wahle 1985), and removal of individual polyps (Birkeland & Neudecker 1981, Brawley & Adey 1982, Lasker 1985). Most corals appear to recover readily from removal of individual polyps and damage to branch tips (Neudecker 1979, Wellington 1982, Wahle 1983a), but even minor amounts of tissue stripping can be catastrophic because fast-growing algae or *Millepora* spp. (Wahle 1980) can permanently colonize bared skeleton and prevent subsequent tissue regeneration (Wahle 1983a, 1985, Harvell & Suchanek pers. obs.).

The effects of partial predation can be quantified as the proportion of an individual colony killed, but the functional role of lost units must also be considered since all parts of a colony do not function equivalently (Palumbi & Jackson 1983, Harvell 1984a). Most colonies have ontogenetically based functional gradients; thus the consequences of an attack depend on its location and magnitude. For example, in some bryozoans, the central, oldest regions of a colony often cannot regenerate as rapidly as the outer perimeter (Palumbi & Jackson 1983, Harvell 1984a). Attacks to the center of the colony may more often prevent colony recovery than attacks to the edge. Thus the consequences of damage to a colony are determined by both the location and scale of damage.

In this paper, we report on the interaction between a tissue-stripping tropical corallivore, *Cyphoma gibbosum* (Mollusca, Gastropoda) and its upright gorgonian prey. Although *C. gibbosum* feed exclusively on gorgonian corals, they can be considered trophic generalists because most available species in several gorgonian families are included in their diet (Birkeland & Gregory 1975). *C. gibbosum* are ubiquitous throughout the Caribbean on shallow gorgonian-dominated reefs (Kinzie 1971, 1974, Birkeland & Gregory 1975, Gerhart 1986). Two striking aspects of the interaction between *C. gibbosum* and its gorgonian prey are (1) the small amount of damage and low probability of mortality suffered by each attacked colony and (2) the great mobility of *C. gibbosum* while foraging among colonies (Birkeland & Gregory 1975, Gerhart 1986). This is a common pattern for many predators attacking colonial invertebrates (Harvell pers. obs.) and may be, in part, a consequence of colony defenses (Gerhart 1986). The *C. gibbosum*-gorgonian interaction is a tractable system for analyzing intra- and inter-colony patterns of predator attack and colony defenses. We address the following 3 questions: (1) What are the intra-colony patterns of damage inflicted by *C. gibbosum* on the most heavily attacked taxa of gorgonians; (2) Do patterns of damage reflect underlying variations in colony function or morphology; and (3) What are the interspecific patterns of attack?

## METHODS AND RESULTS

### Study sites

All experimental work was conducted in St. Croix, U.S. Virgin Islands, during NULS-1 HYDROLAB mission 82-12 from 26 August to 21 September 1982. (See Suchanek 1983 for location map.) A shallow (4 to 10 m) site was located on the gorgonian-dominated foreereef with western exposure. The study site adjoined the deeper HYDROLAB site at Salt River Canyon. Samples for spicule analysis were collected in the foreereef at Mama Rhoda Reef at Chub Cay in the northwestern Bahamas (25° 21' N, 77° 52' W).

### Feeding selectivity

**Methods.** Prey selection and residence times were quantified by marking all *Cyphoma gibbosum* and occupied gorgonians in the study area (100 m<sup>2</sup>) in St. Croix and recensusing the location of each snail daily. Each snail was uniquely marked by a system of 2 notches filed on the shell that coded for individuals from 1 to 80. This was a minimally disruptive technique for marking large numbers of snails *in situ*: specimens were handled only briefly, and their appearance was generally unchanged. The behavior of marked individuals did not differ noticeably from the behavior of 5 individuals with natural distinctive marks that we monitored for the duration of the study (12 d).

The proportion of prey available was determined by recording the identity of every colony within the study area. Because it was impossible to reliably identify all the gorgonian species in the field, we lumped species into taxonomic and functional groups where necessary. We combined *Plexaura flexuosa*, *P. homomalla*, and *Pseudoplexaura crucis* into a *Plexaura* group, and lumped *Muricea* spp., *Eunicea mammosa*, and *Eunicea* spp. into a *Eunicea* group. The remaining genera and some species could be reliably distinguished on the basis of field characters.

A predator is considered to feed selectively when it takes any prey item in disproportionate numbers relative to its availability. A number of 'electivity indices' exist to analyze the discrepancy between the proportion of prey available and the proportion of prey attacked. A critical problem in the interpretation of some of these analyses is the way relative abundance affects the magnitude of the electivity index. For example, the Ivlev index weights electivities for rare prey disproportionately by dividing the difference between available and selected prey by the sum of the two. Because there is considerable variation in the behavior of different electivity indices, we applied 3 of the most widely used indices to the data: Ivlev's  $\epsilon$  (1961),

Table 1. *Cyphoma gibbosum*. Comparison of different electivity indices calculated for snails foraging on gorgonians at St. Croix

Taxon	Proportion available (N = 365)	Proportion eaten (N = 149)	Chesson's $\alpha$	Ivlev's $\epsilon$	Jacobs' Log Q
<i>Plexaurella dichotoma</i>	0.05	0.07	0.27	0.22	0.15
<i>Eunicea</i> group	0.19	0.23	0.24 (0.01)*	0.09	0.10
<i>Plexaura</i> group	0.62	0.66	0.21 (0.01)*	0.03	0.07
<i>Briareum asbestinum</i>	0.01	0.01	0.19 (0.02)*	0	0
<i>Pseudopterogorgia americanum</i>	0.07	0.02	0.05 (0.15)*	-0.55	-0.57
<i>Gorgonia ventalina</i>	0.05	0.01	0.03 (0.81)*	-0.70	-0.87

\* Data recalculated from Birkeland & Gregory (1975)

Chesson's  $\alpha$  (1978), and Jacobs' log Q (1974). These were all developed for motile predators feeding on motile prey, but the extension to sessile prey does not violate any underlying assumptions. Electivity indices were calculated from the proportion of prey selected and the proportion of prey available. The proportion of prey selected was calculated by dividing the number of times a prey taxon was chosen by the total number of choices made.

To determine if *Cyphoma gibbosum* varied the duration of attacks on colonies of different species, we measured residence time: the number of days a snail remained on a prey colony. Residence times were only analyzed when the entire tenure of a snail on a colony was observed; individuals that stayed the entire study period on a single colony were assigned a residence time of 12 d for comparative analyses. Thus residence times in excess of 12 d will be underestimated by our observations. We monitored over 80 snails intensively to improve our estimates of residence time on the most abundant taxa.

**Results.** Table 1 summarizes the indices obtained using 3 different measures of electivity. There are 2 important features of this comparison to note: (1) the order (or 'preference' for the different prey items) does not change with different indices, giving us confidence in the relative ranking of preference for prey, (2) the range of values varies with the index used. Therefore, the rank order of preferences is relatively robust, while the absolute magnitude of scores for preferences is not. For our purposes, the ' $\alpha$ ' index (Chesson 1978) was most useful because (1) it varies continuously between 0 and 1 and is thus 'bounded' and (2) relative prey abundance affects the magnitude of the index so that selection of rare prey is detected, but the electivity for rare prey is not disproportionate. Our analysis failed to reject the null hypothesis that *Cyphoma gibbosum* attacked colonies in proportion to their relative abundance ( $\chi^2$ ,  $p > 0.05$ ) (Table 1); therefore, we conclude that there is no active selection of prey colonies during the initial encounter phase of interactions.

Another measure of selectivity for a colony is residence time, which can vary independently of electivity. Residence times of adult *Cyphoma gibbosum* (Table 2) varied significantly among different prey groups (*Plexaura*, *Eunicea*, and *Plexaurella*) (Kruskall Wallis Test,  $\chi^2 = 8.712$ ,  $p < 0.013$ ) where observations were numerous enough to permit analysis. A Median Test (Zar 1974) showed that residence time was significantly longer on the *Plexaura* group than on the *Eunicea* group ( $\chi^2 = 7.95$ ,  $p < 0.005$ ). Increased sample sizes for rarer taxa, such as *Pseudopterogorgia* spp. and *Gorgonia ventalina*, would probably yield significantly longer residence times than for other taxa. Juvenile *C. gibbosum* do not move frequently among prey species; all juveniles remained on single hosts for the entire sample period (Table 2).

### Scar length, depth, and position

**Methods.** For each of 6 taxa, *Plexaurella dichotoma*, the *Plexaura* group (*P. homomalla*, *Plexaura* spp., *P. flexuosa*, and *Pseudoplexaura crucis*), the *Eunicea* group, *Pseudopterogorgia americanum*, *Pseudopterogorgia* spp. (*P. rigida* and *P. acerosa*), *Gorgonia ventali-*

Table 2. *Cyphoma gibbosum*. Summary table of electivity and residence times (d) on different taxa of gorgonians

Taxon	Electivity (Chesson's $\alpha$ )	Residence time (d)		
		Mean	SD	(N)
<i>Plexaurella dichotoma</i>	0.27	1.8	1.2	(6)
<i>Eunicea</i> group	0.24	1.4	0.9	(29)
<i>Plexaura</i> group	0.21	2.9	2.4	(50)
<i>Briareum asbestinum</i>	0.19	1.0	0	(2)
<i>Pseudopterogorgia americanum</i>	0.05	4.7	4.1	(3)
<i>Gorgonia ventalina</i>	0.03	10.0	0	(2)
All adults		3.3	3.4	(92)
Juvenile <i>C. gibbosum</i>		12.0	0	(9)



Fig. 1. (a) *Cyphoma gibbosum* feeding on *Briareum asbestinum* and causing only superficial damage. (b) *C. gibbosum* feeding on the gorgonian *Plexaura* spp. The deep feeding scar has exposed the underlying gorgonin skeleton

*na*, and *Briareum asbestinum*, we measured the length of naturally occurring feeding scars (usually with a snail still present), the distance from the base of a colony to the base of a scar (here defined as the point of initiation), and the total height of each colony.

We scored the depth of naturally occurring feeding scars as either superficial or skeletal. Skeletal wounds completely bared the underlying gorgonin skeleton (Fig. 1). These categories were straightforward to distinguish and are functionally significant to the colony. For scars on *Briareum asbestinum*, a scleraxonian without a gorgonin skeleton, we classified skeletal wounds as those that exposed the innermost spicular layer. The frequency of individuals with skeletal scars in each taxon was compared over all taxa with a G-Test (Sokal & Rohlf 1981).

Intra-colony locations of scars were examined to detect consistent locations of preferred attack. The height from colony base to scar initiation was divided by the total height of a colony to provide a normalized measure for comparison among species.

**Results.** Feeding scars were distributed throughout the middle regions of colonies on all species. In Fig. 2 we have plotted the point of scar initiation normalized by colony height. The 95 % confidence intervals around the means are large. Scars were usually not initiated in the lower 20 % of colonies, suggesting that basal regions are avoided. With the exception of *Plexaurella dichotoma*, on which feeding scars were initiated in a narrow band in the midsection of colonies, scars appeared to be initiated broadly throughout central regions of colonies.

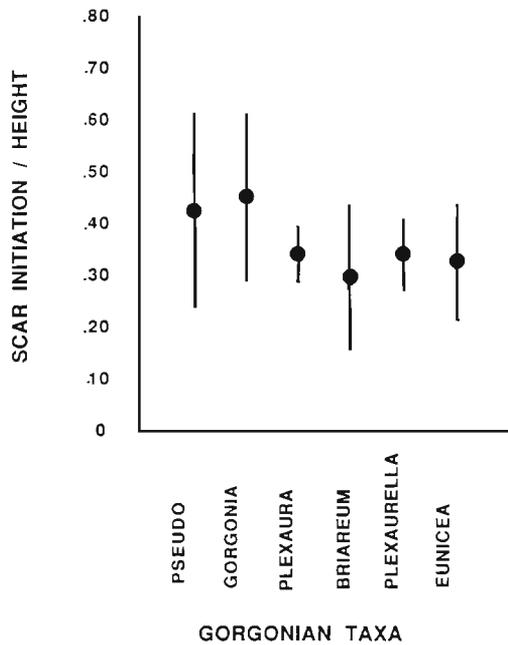


Fig. 2. Mean height of initiation of scars normalized by colony height (mean and 95 % confidence intervals) on 6 taxa of gorgonians. Abbreviations for taxa are as follows: Pseudo: *Pseudopterogorgia americanum*; Gorgonia: *Gorgonia ventalina*; Plexaura: *Plexaura* group; Briareum: *Briareum asbestinum*; Plexaurella: *Plexaurella dichotoma*; Eunicea: *Eunicea* group

Scar lengths did not vary significantly among prey species (Table 3) and were not correlated with colony height (Pearson Product Moment correlation coefficient  $p > 0.05$  for all taxa).

Scar depth varied significantly among prey taxa ( $G = 56.34$ ,  $p < 0.001$ ; Table 3). Gorgonian taxa could be divided into 3 groups based upon the depth of wounds: (1) those that were usually (>90%) wounded to the axis, including *Pseudopterogorgia* spp. and *P. americanum*; (2) those that were often (50 to 75%) wounded to the axis, including *Gorgonia ventalina*, the *Plexaura* group, and *Plexaura flexuosa*; and (3) those that were rarely or never (0 to 15%) wounded to the axis, includ-

ing *Plexaurella dichotoma*, *Briareum asbestinum*, and the *Eunicea* group. Frequencies of skeletal wounding are not significantly different within each of the groups (G-Test,  $p > 0.05$ ), but are significantly different among groups (G-Test,  $p < 0.001$ ).

### Spicule size and composition

**Methods.** Spicule size and percent composition in gorgonian colonies were analyzed to determine if maximum spicule size and percent composition of spicules were correlated with short residence times and superficial wounding. Spicule size was reported as the maximum spicule length given in Bayer (1961). The proportion of spicules was determined as the ash-free dry weight/total dry weight. Sections of gorgonian colonies, 3½ cm long, were collected at Chub Cay in the Bahamas and immediately preserved in 4 % buffered formalin. Samples were soaked for 1 h in distilled water, the central gorgonian core removed, and the outer tissue dried at 60°C in a drying oven. After colonies were completely dry (1 d after they stopped losing weight), they were weighed and placed in a muffle furnace at 450°C for 4 h. For this interval and temperature, only organic material should be combusted, and spicules should remain intact (Paine 1964). Above 500°C, water of hydration may be separated from the calcium carbonate causing a further, confounding loss of weight (Paine 1964, Harvell pers. obs.). To be certain that calcium carbonate did not lose weight during this procedure, inorganic reagent-grade calcium carbonate was also processed with the gorgonian samples; there was no significant weight loss in 5 replicate samples processed.

**Results.** The dry weight composition of spicules varied significantly among taxa, ranging from approximately 35 % for *Pseudopterogorgia americanum* to approximately 85 % for *Muricea* spp. (Fig. 3). Four taxa stand out as having the highest percent composition of spicules: the *Eunicea* group, *Plexaurella dichotoma*, *Plexaura flexuosa*, and *Muricea* spp.

Table 3. Length (cm) and depth of wounds caused by *Cyphoma gibbosum* on gorgonians. Wound depths were classified as skeletal or non-skeletal. Scar depth is reported as the percentage of skeletal wounds. —: no sample

Taxon	Scar length			Scar depth	
	Mean	SD	(N)	%	(N)
<i>Plexaurella dichotoma</i>	7.2	6.8	(5)	0	(9)
<i>Eunicea</i> group	15.0	8.8	(9)	6	(17)
<i>Briareum asbestinum</i>	13.4	7.7	(7)	14	(8)
<i>Plexaura flexuosa</i>	11.9	10.5	(9)	62	(8)
<i>Gorgonia ventalina</i>	—	—	—	50	(6)
<i>Plexaura</i> group	12.0	7.9	(21)	66	(7)
<i>Pseudopterogorgia americanum</i>	11.7	8.1	(10)	95	(20)
<i>Pseudopterogorgia</i> spp.	—	—	—	100	(10)

Maximum spicule length varied among taxa (Fig. 4) and with the exception of *Plexaurella dichotoma*, which has very small spicules, was generally proportional to percent composition of spicules (Pearson correlation coefficient 0.60,  $N = 7$ ) (Fig. 4).

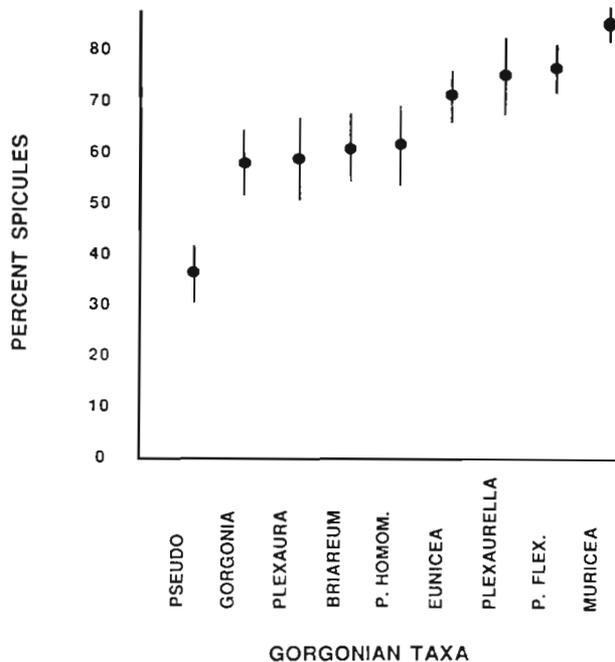


Fig. 3. Spicule composition of predominant prey taxa. Mean ( $N = 4$ ) and 95 % confidence intervals are plotted. Taxonomic abbreviations as in Fig. 2, plus P. homom.: *Plexaura homomalla*; P. flex.: *Plexaura flexuosa*; Muricea: *Muricea* spp.

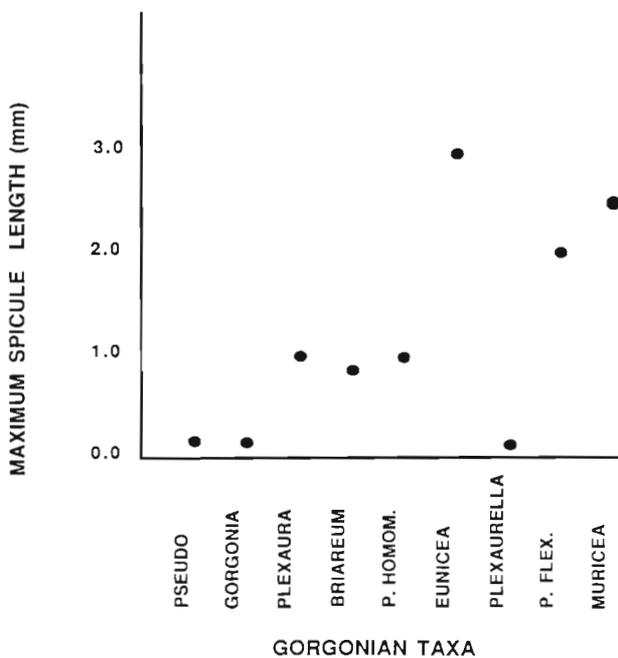


Fig. 4. Maximum spicule lengths of predominant prey taxa (lengths taken from Bayer 1961). Taxonomic abbreviations as in Fig. 2 & 3

## DISCUSSION

The extent of damage by *Cyphoma gibbosum* to gorgonian colonies varied among prey taxa. Only one species was consistently wounded to the skeleton (*Pseudopterogorgia americanum*), exposing it to invasion by colonizing algae. The depth of attack on gorgonian colonies appears to be determined by spicule size and architectural differences among prey taxa. Large spicules embedded in soft tissue or a high percent composition of spicules may act as a barrier to tissue-stripping predators such as *C. gibbosum*. Thus taxa with small or a low composition of spicules may routinely suffer attacks from which recovery is inhibited.

In addition to the depth of the wound, the configuration of tissue loss also has major consequences for colony function. For example, in bryozoans, Harvell (1985) has shown that grazing by molluscs can accelerate reproduction of the entire colony. Wahle (1983b) has demonstrated that 'girdling' a colony of *Plexaura homomalla* can isolate and desynchronize the reproductive function of upper branches. Most attacks of *Cyphoma gibbosum* leave vertical scars not exceeding 1 cm in width (pers. obs.) and not girdling branches; thus branch tips are only occasionally isolated by *C. gibbosum* attacks. Within colonies, attacks were initiated predominantly in the middle and thus were less frequent on the lower 20 % of colonies. The attack zone was broad enough on most taxa to suggest that there were no localized preferred sites within colonies.

Interspecific differences in prey quality appear to determine residence times of *Cyphoma gibbosum*, as well as the extent of damage to colonies. *C. gibbosum* spend significantly less time on heavily spiculed taxa such as *Muricea* spp., *Eunicea* spp., and *Plexaurella dichotoma* than on taxa from which they can extract more tissue ( $r = -0.49$  [residence time with % composition],  $r = -0.63$  [residence time with spicule length];  $N = 7$ ). Thus, in addition to playing a role in colony architecture and support, spicules may also function as a defense against predators.

The observed distribution of *Cyphoma gibbosum* on gorgonians results from the interaction of both initial electivity and residence time. For comparison, we have recalculated Birkeland & Gregory's data (1975) on electivity of foraging *C. gibbosum* for different gorgonian species (Table 1). They calculated electivity from censuses of *C. gibbosum* on marked gorgonians; thus their measure of electivity combines both the choices made by *C. gibbosum* among prey and the residence time on different prey. Their data show marked preference of *C. gibbosum* for *Gorgonia ventalina*, in complete contrast to our result of no significant electivity for any species. Because we followed the foraging choices of

marked individuals, we were able to separate electivity from residence time. We found that while electivity for *G. ventalina* was not greater than that for other species, residence times were longest on *G. ventalina*. Thus it appears that *C. gibbosum* can attack prey in proportion to their relative abundance, yet still exercise selection among prey species by varying residence time. We predict that the foraging behavior of any partial predator can be divided into these 2 components, and that residence time may often be the more important variable in determining the observed patterns of prey selection.

Diet mixing has been invoked as an explanation for the generalized foraging tendencies of several predatory and herbivorous partial predators. Birkeland & Gregory (1975), who also noted frequent movements of individual *Cyphoma gibbosum* among gorgonian prey species, concluded that *C. gibbosum* move often among prey to fulfill a diet-mixing requirement. Other corallivores also diet mix and maintain a wider diet breadth than expected from prey abundance alone. Birkeland & Neudecker (1981) demonstrated diet mixing in the butterfly fish *Chaetodon capistratus*, which feeds on a range of scleractinian and gorgonian corals. Some herbivorous insects are known to forage widely to detoxify an otherwise unpalatable diet (Scriber 1984). There are several mechanisms by which the detoxification hypothesis may act: (1) compounds may interact so that combining feeding deterrents from different species may nullify the negative effects of certain compounds; (2) consumers may have an absolute tolerance for particular compounds that limits residence time on any one species, but allows mixing of different compounds (Berenbaum 1986). While our observations suggest that residence time is in part limited by spicule composition or architecture, the initial choice of prey taxa could be influenced by nutritive requirements based on past foraging history. We did note that individual *C. gibbosum* appear to switch prey taxa in successive attacks.

Another hypothesis to explain the short residence times of *Cyphoma gibbosum* on individual colonies is the inducible defense hypothesis suggested by Harvell (1984a). Colonies may respond to attacks with elevated levels of chemical defenses, in which case residence times of *C. gibbosum* could be limited by declining colony quality. Gerhart (1986) showed that residence times of *C. gibbosum* on previously attacked colonies of *Plexaura homomalla* are shorter than on previously unattacked colonies, thus providing some support for the inducible defense hypothesis.

Partial predation is a common pattern among most corallivores and other predators on colonies (Jackson 1983, Harvell 1984a, Buss 1986) as it is with herbivores (Thompson 1982). Birkeland & Gregory (1975) calcu-

lated that while a population of *Cyphoma gibbosum* may account for 62 % of annual tissue loss to a population of gorgonians, they caused only 4 % of the mortality. However, partial consumers may have dramatic sublethal effects on morphology and patterns of allocation to growth, reproduction, and defense within attacked colonies (Kaufman 1981, Wahle 1983b, 1986, Harvell 1984a, b, 1985, 1986). For example; one species of temperate bryozoan produces defensive spines (Yoshioka 1982, Harvell 1984a) and initiates reproduction (Harvell 1985) in response to attacks by partial predators. These temporally varying responses to predation may in turn decrease the quality of the prey and encourage consumers to reduce the duration of attacks. The short duration of most attacks by *C. gibbosum* could be a consequence of inducible structural or chemical defenses (Harvell 1984a, Gerhart 1986). Thus as in plants (Rhoades 1985), many colonies may have complex combinations of constitutive and inducible defenses which govern the foraging behaviors of their consumers.

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