

# Specialist predation on the Caribbean gorgonian *Plexaurella* spp. by *Cyphoma signatum* (Gastropoda)

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**ABSTRACT:** The rare marine snail *Cyphoma signatum* is a trophic specialist on gorgonians *Plexaurella* spp. A comparative study of this snail species with its generalist congener *C. gibbosum* showed that feeding behavior differs between the 2 species. Feeding by the specialist often damages the polyps and scleratinized matrix of *Plexaurella* or bares its proteinaceous axis, while the generalist tends to feed primarily on the polyps of *Plexaurella*. As a result, *C. signatum* ingests more total *Plexaurella* tissue (including sclerites) and more organic material, though fewer polyps per time, than does *C. gibbosum*. Differences in radular morphology are implicated as the proximal cause of species-specific feeding behavior. The lateral teeth of *C. signatum* are wider and their median teeth have a long central point not present in *C. gibbosum*, which may enable more extensive wounding of colonies. The feeding behavior of the specialist results in a higher amount of damage to *Plexaurella*, from which the coral recovers more slowly, as gorgonian regeneration times are inversely proportional to wound depths. Permanent damage to *Plexaurella* may result when bared proteinaceous axes are fouled by algae or other encrusting organisms. Although the shallow wounds of *C. gibbosum* are common on *Plexaurella*, they regenerate within 6 d. Gorgonian censuses at 4 sites showed that high proportions of permanently damaged *Plexaurella* ( $\geq 50\%$  permanent damage per colony) were correlated with areas of high *C. signatum* density. In the short term, predation by *C. signatum* appears to increase permanent damage and mortality of *Plexaurella*. The specialist snail may therefore impose greater selection on the gorgonian than does the generalist.

## INTRODUCTION

In coral reef ecosystems, predators often contribute a substantial amount of the injury sustained by coral colonies (Reese 1977, Lasker 1985, Wahle 1985, Harvell & Suchanek 1987, Lasker et al. 1988). Destruction of individual modules diminishes a colony's feeding ability and reproductive output, and thus reduces fitness without necessarily causing complete mortality (Jackson 1977, Palumbi & Jackson 1982). The severity of damage from different partial predators depends on the rates at which modules are destroyed and subsequently regenerate.

The upright, branching gorgonians *Plexaurella* spp. are prey for 2 closely-related species of tropical marine ovulid. *Cyphoma signatum* specializes on gorgonians of this genus as its sole food source, while *Cyphoma gibbosum* feeds on most of the gorgonian genera found

in the Caribbean (Birkeland & Gregory 1975, Harvell & Suchanek 1987, Lasker et al. 1988). This study examined predator-prey interactions, concentrating on differences in feeding behavior and prey wounding patterns for the specialist and generalist predators. We examined the specific hypotheses that: (1) *C. signatum* feeds faster and makes deeper wounds on *Plexaurella* than its generalist congener; (2) *C. signatum* has morphological specializations which allow it to ingest the matrix of *Plexaurella* despite its high sclerite content; (3) predation by *C. signatum* causes higher rates of permanent damage and colony mortality relative to predation by the generalist.

## METHODS

Research was conducted primarily at the West Indies Laboratory, St. Croix, US Virgin Islands. We collected *Cyphoma gibbosum* and *C. signatum* from 4 shallow

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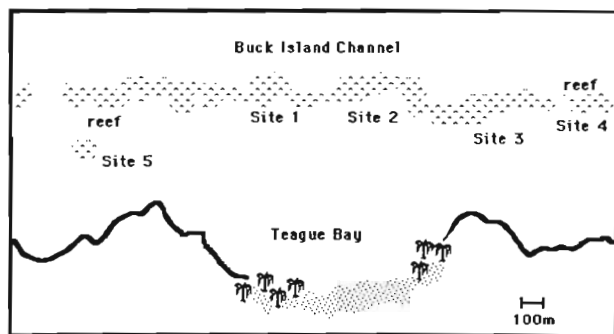


Fig. 1. Census Sites 1 to 4 along Teague Bay back reef and the Site 5 patch reef off the island of St. Croix, US Virgin Islands

(< 5 m) sites haphazardly chosen along Teague Bay back reef (TBRR) and from a nearby patch reef (Fig. 1), spending ca 1 h at each location. We found *C. signatum* only on colonies of *Plexaurella* spp., while *C. gibbosum* was present on several gorgonian genera, including *Briareum*, *Pseudopterogorgia*, *Plexaura*, *Pseudoplexaura*, *Muricea*, *Gorgonia*, and *Plexaurella*. For each

snail collected from *Plexaurella*, we noted (1) its location on the colony relative to total colony height, and (2) the depth of the wound it had made while feeding. Wound depth was categorized as (1) surface damage involving removal of polyps only, (2) damage to the cortex showing loss of matrix material and sclerites, as well as polyps, and (3) damage barring the proteinaceous axis (Harvell & Suchanek 1987) (Fig. 2a, b).

We marked individual *Cyphoma signatum* ( $n = 18$ ) and *C. gibbosum* ( $n = 18$ ) by etching a series of grooves into their shells, and subsequently released them at the patch reef (Site 5) in early August 1988. Snails on the patch reef were recensused in January 1989.

**Feeding behavior.** Data from the snail collections were used to establish average location and feeding depth of the 2 species on *Plexaurella* spp. To examine feeding rates, we used monofilament line to tether *Cyphoma gibbosum* ( $n = 7$ ) and *C. signatum* ( $n = 10$ ) to separate, undamaged, haphazardly-chosen *Plexaurella* colonies in 10 m of water at Salt River Canyon, St. Croix. After 6 d, the length (L), width (W), and depth (surface, cortex, axis) of all feeding wounds on the

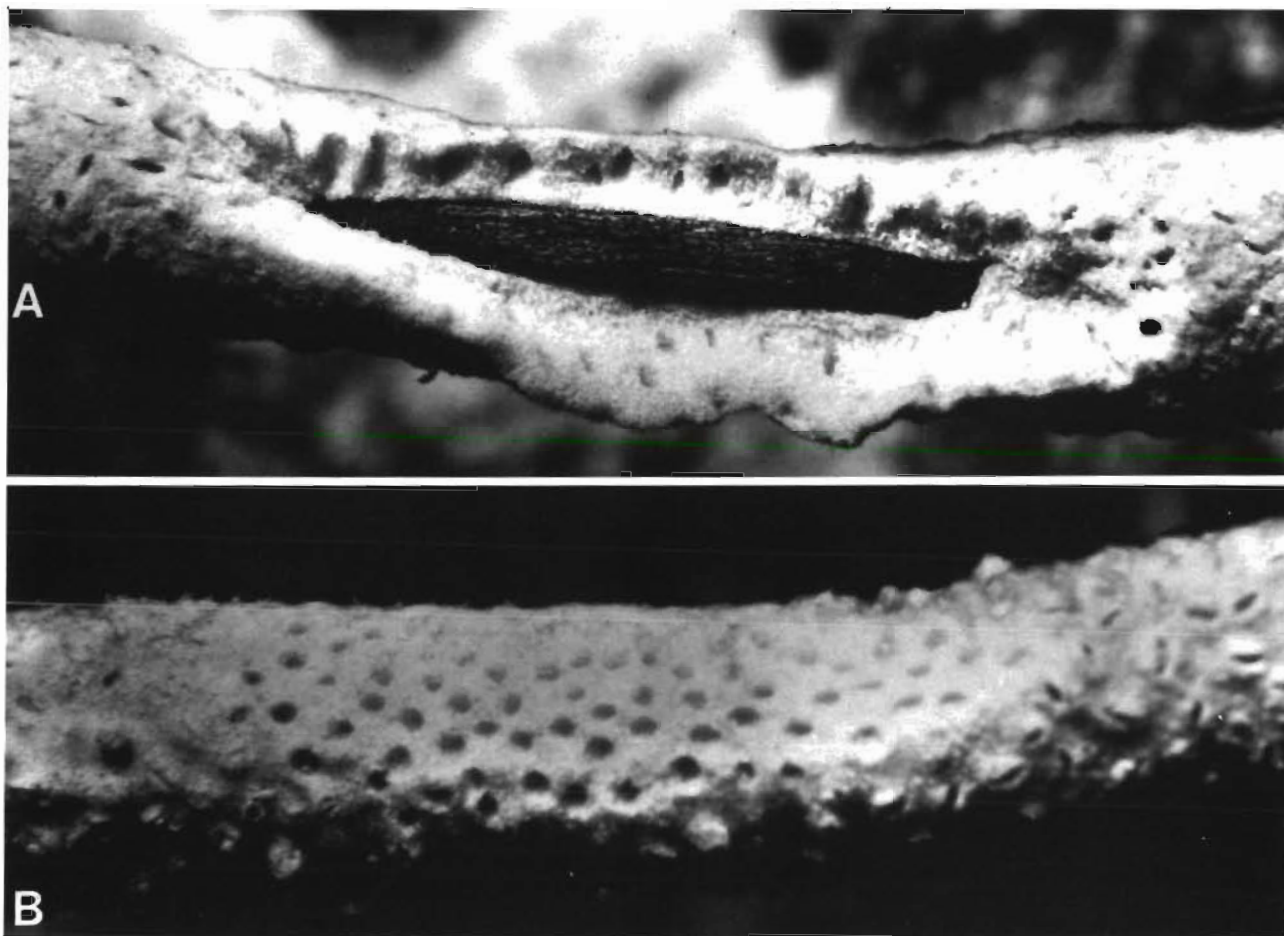


Fig. 2. *Plexaurella* spp. (a) Wounding by *Cyphoma signatum*; the scleratinized matrix has been removed, and the proteinaceous axis is visible. (b) Wounding by *C. gibbosum*, showing removal of polyps only

colonies were recorded. Area ( $A$ ) of each surface wound was estimated by the formula:  $A=LW$ . We found the volume ( $V$ ) of tissue removed during damage to the cortex using the formula:  $V=3\pi W^2L/32$  (one-quarter of the volume of a thick-walled cylinder); for damage to the axis, the formula used was:  $V=\pi W^2L/8$  (one-half the volume of a solid cylinder) (Fig. 3).

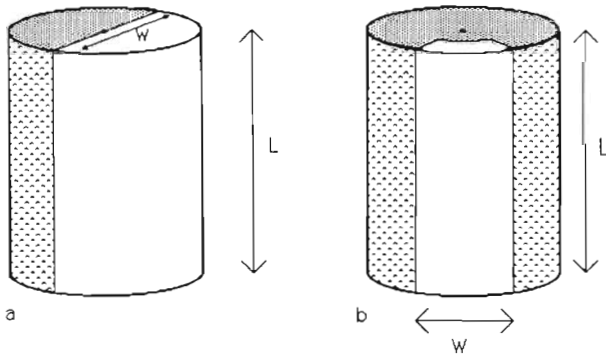


Fig. 3. *Plexaurella* spp. Diagrammatic representation of a segment of a colony branch showing: (a) how length and width measurements of feeding wounds to the axis were transformed into volume estimates; (b) how length and width measurements of cortex wounds were transformed into volume estimates. (Volume corresponds to the unshaded region)

We were most interested, however, in the weight, not volume, of tissue removed. Dry weight should correspond to the total amount of ingested material, including sclerites, and organic weight should indicate the amount of nutritive tissue available for metabolism. Area or volume of tissue removed during feeding was converted to dry and organic weight using conversion factors established for standard *Plexaurella* samples. We dried known volumes of *Plexaurella* from 3 colonies at 60°C for 48 h to establish standard dry weight; organic content was the difference between the dry weight and the weight of the sample after ashing in a muffle furnace at 450°C for 2 h (Harvell & Suchanek 1987). Standard dry and organic weights were also determined for polyps dissected from a known area of 3 *Plexaurella* colonies. Standard polyp densities were found from counts of the number of polyps per area of *Plexaurella* ( $n = 3$  colonies).

Tissue damage to colonies is likely to be influenced not only by the predator's feeding rate, but also by the length of time a partial predator spends on the colony. We assessed residence time using 7 *Cyphoma signatum* and 11 *C. gibbosum*, which we found naturally on *Plexaurella* in July 1988; we observed them for 10 d and recorded their movements among colonies.

***Cyphoma* morphology.** Shell and radula morphology in some gastropods have been found to be related to feeding behavior. Kemp & Bertness (1984) showed that shell allometry and thickness varied with food availability in individuals of a single gastropod species,

indicating that snail feeding and growth rates helped determine shell dimensions. Feeding rates in turn are likely to be influenced by the form of the radula. Radulae dissected from a specialist and a generalist limpet species were morphologically distinct when viewed by Scanning Electron Microscopy (SEM), and differed in the amount of normal force required to scrape various food substrates (Padilla 1985).

Using Vernier calipers (nearest 0.05 mm), we measured (1) maximum shell length, (2) maximum shell width at the dorsal transverse ridge, and (3) the thickness of the horizontal ridge at the lip of the shell (*Cyphoma signatum*:  $n = 42$ ; *C. gibbosum*:  $n = 58$ ). The thickened shell lips present on all specimens indicated that these were adult snails. Because we had no a priori basis for assigning a dependent variable, we calculated allometric relations among these measurements using functional regression (Jensen 1986).

Radulae from 2 specimens of each snail species were viewed using a SEM. They were prepared by dissection from snails preserved in 70 % ethanol and boiled in water for 5 to 10 min. Residual organic tissue was cleared by soaking in bleach. Radulae were rinsed in water and dehydrated by submersion in 2,2-dimethoxypropane for about 30 s (D. K. Padilla pers. comm.). A gold-palladium coating was applied to all specimens to reduce charging. Specimens were viewed with an AMR-1000A SEM (Cornell University).

**Damage to *Plexaurella*.** Permanent damage to *Plexaurella* spp. depends both on the feeding behavior of its predator and the colony's ability to regenerate. To assess recovery ability, we artificially wounded 6 previously undamaged *Plexaurella* colonies and observed regeneration over 10 d. Each colony received three 1×5 cm wounds, on separate branches, corresponding to surface, cortex, and axis damage.

In gorgonians, incomplete regeneration can result in a bare or algal-covered proteinaceous axis. We examined between 100 and 170 gorgonians for permanent damage at Sites 1 to 4 along TBRR, where we had previously collected snails and thus had an estimate of *Cyphoma* spp. density. We assessed the percentage of tissue missing from each gorgonian colony in 5 % increments from 0 to 10 % and from 90 to 100 %, and in 10 % increments otherwise. A 3-way William's G-test was used to test whether increased damage to *Plexaurella* was associated with sites of high *C. signatum* density (Sokal & Rohlf 1981).

## RESULTS

All of the 47 *Cyphoma signatum* found during this study were collected from gorgonians of the genus *Plexaurella*. Though the *Plexaurella* genus is easily

identifiable in the field, species are difficult to separate. Bayer (1961) recognizes 6 species of *Plexaurella*, based on differences in colony and sclerite morphology. At least 2 of these species, *Plexaurella grisea* and *P. dichotoma*, were present on TBBR; *C. signatum* was observed to feed on both under natural conditions. *C. signatum* comprised ca 15% of the total number of *Cyphoma* of both species; their densities, however, ranged from quite low ( $\leq 3$  per 1 h collecting dive) at Sites 1 and 2, to high ( $\geq 12$  per 1 h collecting dive) at Sites 4 and 5.

### Feeding behavior

Damage from predation by *Cyphoma gibbosum* consisted primarily of shallow, surface wounds, while *C. signatum* often wounded the cortex or bared the proteinaceous axis of *Plexaurella*. *C. signatum* was significantly more likely to inflict deep wounds, damaging the matrix of *Plexaurella* (sub-surface damage), than was *C. gibbosum* ( $\chi^2$  test:  $p < 0.01$ ) (Table 1).

Table 1. *Plexaurella* spp. Number of surface and subsurface (cortex and axis) wounds made by *Cyphoma gibbosum* and *C. signatum*

Wound type	Snail species	
	<i>C. gibbosum</i>	<i>C. signatum</i>
Surface	30	10
Sub-surface	4	37

Snails of both species were found on average in the central region of *Plexaurella* colony branches, though the variance was high (Fig. 4). Arc-sine transformed data showed no significant difference in the location

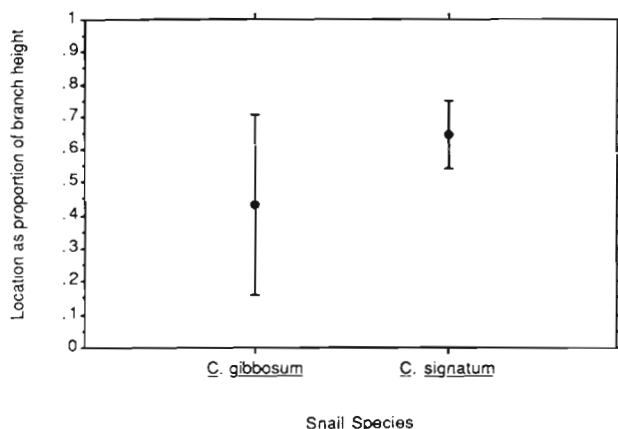


Fig. 4. *Cyphoma gibbosum* and *C. signatum*. Location on *Plexaurella* as a proportion of total colony height. Error bars show 95% confidence intervals. *C. gibbosum*:  $n = 9$ ; *C. signatum*:  $n = 20$

preferred by the 2 snail species (unpaired t-test:  $p > 0.05$ ).

In field trials with tethered snails, the 2 species fed at different rates. All *Cyphoma gibbosum* used in the trials made only surface wounds, while 9 of 10 *C. signatum* inflicted damage to the cortex. Table 2 shows the standard conversion factors used to convert volume

Table 2. Conversion factors for transforming wound volume to dry weight and organic weight of the material ingested. Results are given as  $\text{mg cm}^{-3}$  for the whole colony ( $n = 3$ ), and as  $\text{mg cm}^{-2}$  for the polyps ( $n = 3$ ). 95% confidence intervals are in parentheses

	Standard dry wt (mg)	Standard organic wt (mg)
Polyps	5.6 ( $\pm 10.0$ )	1.5 ( $\pm 0.3$ )
Whole colony	718 ( $\pm 37$ )	69 ( $\pm 2.5$ )

to mass of tissue ingested. Organic content of the whole colony was low relative to that of the polyps due to the presence of  $\text{CaCO}_3$  sclerites embedded in the matrix. Mean polyp density was  $22.3 \text{ polyps cm}^{-2}$  ( $\pm 2.1$ ). *C. signatum* ate significantly more than *C. gibbosum* in terms of total tissue (dry wt) and organic material (dry wt – ash wt) during the 6 d of the experiment (unpaired t-test:  $p < 0.01$ ). *C. gibbosum*, however, ate significantly more polyps (unpaired t-test:  $p < 0.01$ ) (Fig. 5).

Both *Cyphoma* species fed for extended periods of time on a single colony and were often found in aggregations. Residence times on *Plexaurella* spp. for snails observed over 10 d averaged about 1 wk for both species, though these are likely to be underestimates due to the short observational period. Four of 7 *C. signatum* and 5 of 11 *C. gibbosum* remained on a single colony during the entire 10 d. Twelve of the 24 *C. signatum* collected in January were found on *Plexaurella* with one or more other snails.

### *Cyphoma* morphology

Functional regression (Jensen 1986) of measurements of shell dimensions showed a significant slope for the relation between maximum shell length and maximum shell width in both snail species (Fig. 6). These slopes were also significantly different from each other, indicating that allometric relations differ between the 2 species. Average shell length of *C. signatum* was significantly greater than that of *Cyphoma gibbosum* (unpaired t-test:  $p < 0.01$ ). The dorsal transverse ridge, however, as measured by shell thickness at the lip, was significantly more pronounced in *C. gibbosum* (unpaired t-test:  $p < 0.01$ ). The recap-

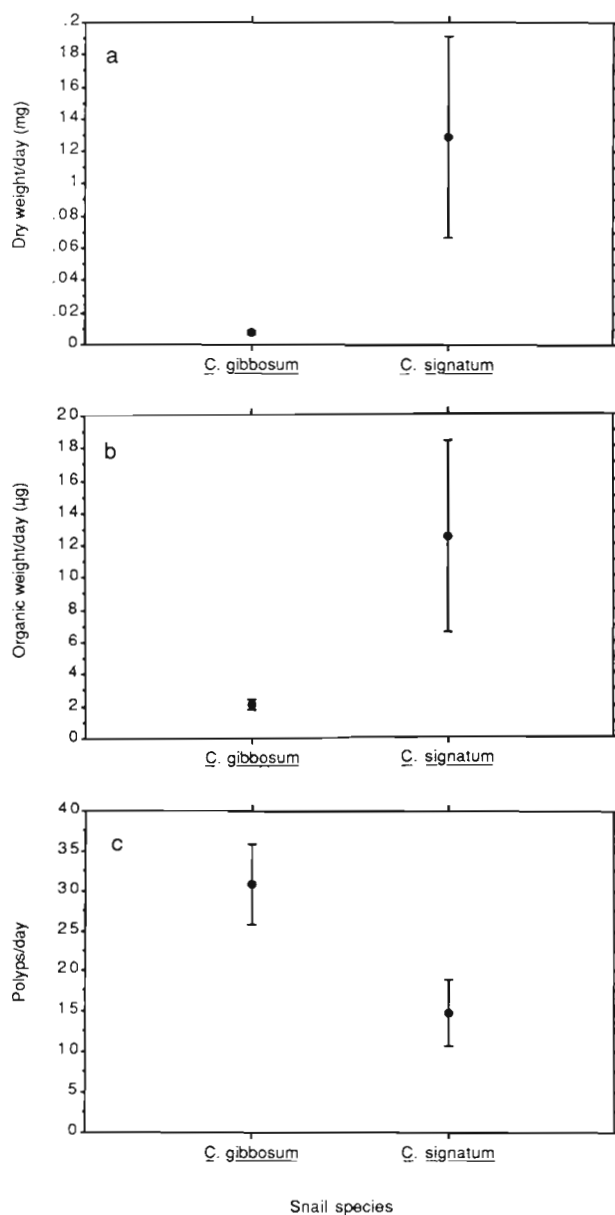


Fig. 5. *Cyphoma gibbosum* and *C. signatum*. Mean dry weight, organic weight, and polyp number ingested over 6 d while tethered to *Plexaurella*. Error bars show 95% confidence intervals. (a) Dry weight of ingested tissue; (b) organic content weight of ingested tissue; (c) polyp number ingested. *C. gibbosum*:  $n = 7$ ; *C. signatum*:  $n = 10$

ture rate of marked snails left at Site 5 for 6 mo was 38.9% for *C. signatum* and 33.3% for *C. gibbosum*. It is unlikely that the missing snails migrated away from the patch reef, but, as we found no empty shells, we cannot separate mortality from our inability to find them. No measurable shell growth was recorded in either species after 6 mo, giving further evidence that these were adult snails of full shell size.

Fig. 7 shows scanning electron micrographs of radulae dissected from a 3.2 cm specimen of each

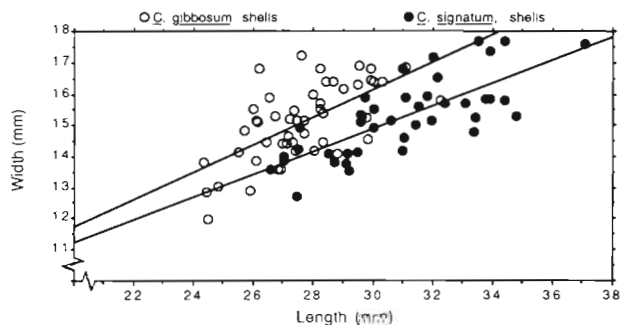


Fig. 6. *Cyphoma gibbosum* and *C. signatum*. Functional regression between maximum shell length and maximum shell width. *C. gibbosum*:  $y = 0.4103x + 0.3732$ ,  $n = 58$ ; *C. signatum*:  $y = 0.3670x + 0.3870$ ,  $n = 42$ . One *C. signatum* specimen was discarded from the analysis due to an extremely unusual width measurement, probably a measuring error

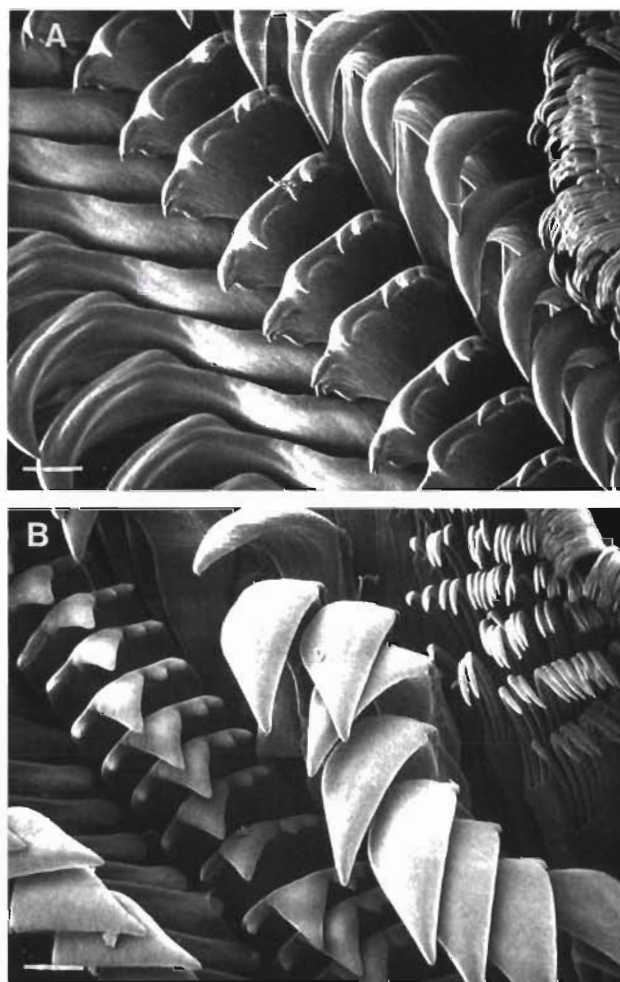


Fig. 7. Scanning electron micrographs of mature teeth of (a) *Cyphoma gibbosum* radula, (b) *C. signatum* radula (150 $\times$ ). Scale bars = 0.05 mm

species. Other radulae viewed under a dissecting microscope showed similar species-specific morphology; however, only one SEM was taken of each species. The rachidian tooth, which, along with the flanking lateral

teeth, is responsible for much of the rasping action of the radula (Hickman 1980, Hughes 1986), is slightly wider in *Cyphoma gibbosum*, but the central point of the tooth is half as long as that of its congener. Relative to *C. gibbosum*, *C. signatum* has wider lateral teeth and more rows of teeth per length of radula (Table 3).

Table 3. *Cyphoma gibbosum* and *C. signatum*. Measurements of radulae of single 3.2 cm specimens, from SEMs at 210× and 550× magnification

	<i>C. gibbosum</i>	<i>C. signatum</i>
Rows/length	14.7/ mm	23.1/ mm
Width		
Rachidian	0.15 mm	0.13 mm
Lateral	0.04 mm	0.07 mm
Rachidian point	0.03 mm	0.06 mm

### Damage to *Plexaurella*

Regeneration of artificial damage to *Plexaurella* spp. occurred more quickly for shallow than for deep wounds. In all 6 cases, polyps were feeding from regenerated surface wounds within 3 d, although the scars remained visible for at least 10 d. Proteinaceous axes were covered by new matrix material only after 4 d. Regenerating cortex and axis wounds took more than twice as long to produce new feeding polyps as did surface wounds (Table 4).

Table 4. *Plexaurella* spp. Regeneration from artificial wounds (1 × 5 cm) of various depths. 95 % confidence intervals are in parentheses. n = 6 colonies per wound type

Depth of wound	Regeneration (d)		
	Axis recovered	Polyps feeding	Scar visible
Surface	–	2.5 (0.6)	> 10
Cortex	–	8.7 (1.4)	> 10
Axis	4.2 (0.4)	9.5 (1.7)	> 10

*Plexaurella* spp. ranged from 11.0 to 27.5 % of the total gorgonian fauna at the 4 census sites. High proportions of permanently damaged colonies (judged as ≥ 50 % damage/colony) were found at sites with high *Cyphoma signatum* density (Wilson's G-test:  $p < 0.05$ ) (Fig. 8). If this correlation indicates a causal link between *C. signatum* and *Plexaurella* damage, it is a striking departure from the relatively small amount of damage usually caused by *C. gibbosum* (Wahle 1983, Harvell & Suchanek 1987). At Site 4, where snail density was greatest, 4 of 11 *Plexaurella* colonies were completely

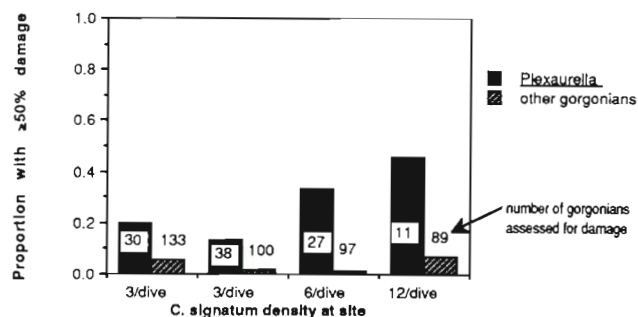


Fig. 8. Proportion of gorgonians (*Plexaurella* spp. and others) with more than 50 % damage per colony at 4 sites along TBBR. Sites 1 and 2 had approximately equal densities of *Cyphoma signatum*, while Sites 3 and 4 had higher densities

killed. This site also had the lowest proportion of *Plexaurella* relative to total gorgonian presence.

## DISCUSSION

### Specialization and rarity

*Cyphoma gibbosum* is ubiquitous throughout the Caribbean and can be found on most gorgonian genera (Birkeland & Gregory 1975, Gerhart 1986, Harvell & Suchanek 1987, Lasker & Coffroth 1988, Lasker et al. 1988). Though the biology and behavior of *C. gibbosum* have been well studied (Ghiselin & Wilson 1966, Bandel 1973, Birkeland & Gregory 1975, Gerhart 1986, Harvell & Suchanek 1987, Lasker & Coffroth 1988), *C. signatum* has received relatively little attention, in large part because it has been found too rarely for in-depth study.

Small numbers of *Cyphoma signatum* have been found near Union Island in the Grenadines (C. D. Harvell pers. obs.), San Blas, Panama (Lasker & Coffroth 1988), Puerto Rico (Ghiselin & Wilson 1966), Jamaica (Wahle 1985), and the Bahamas (J. L. Ruesink & C. D. Harvell pers. obs.), indicating that the species as a whole is widespread throughout the Caribbean. Rarity of *C. signatum* is likely to be a result, primarily, of habitat specificity (Rabinowitz 1981), as the snail appears to be a trophic specialist on *Plexaurella* spp. and the frequency and location of that gorgonian genus must to some extent determine its predator's distribution. Along TBBR, where *Plexaurella* comprises between 11 and 29 % of the total gorgonian fauna, *C. signatum* made up some 15 % of all *Cyphoma*, so that the specialist was found in proportion to the abundance of its food source. However, at Salt River Canyon, a site off St. Croix with similar proportions of *Plexaurella*, there were no *C. signatum*. Thus, as not all suitable habitats are colonized, the snail also appears to be rare because of restricted local population sizes (Rabinowitz

1981). At this point, there is insufficient information on the biology of *C. signatum* to know whether these patterns might be due to recruitment or to post-recruitment mortality; neither do we know what may prevent the specialist's utilization of other gorgonian genera.

### Differential partial predation

We assessed feeding behavior in terms of feeding rate, wound depth, residence time, and gregariousness. Although not all specialists are measurably more efficient than generalists at ingesting and metabolizing their food source (Scriber 1983), *Cyphoma signatum* feeds at a significantly faster rate than its congener by ingesting both more total tissue and more organic material, and by making deeper wounds. While this could be interpreted as a feeding advantage for the specialist, we have been unable to confirm that the intake of more organic material results in any measurable advantage in growth, survival, or reproduction. Although direct growth rate comparisons were impossible, as the collected snails had reached full shell size, differences were detected in the greater length and less pronounced transverse ridge of *C. signatum*. Within a species, relatively thinner, more globose shells indicate a faster growth rate (Kemp & Bertness 1984, Hughes 1986), but the allometric differences between *C. signatum* and *C. gibbosum* may be of genetic origin, rather than an example of phenotypic plasticity due to growth rate.

It is likely that gorgonian sclerites act as a defence against predation by *Cyphoma gibbosum*. Harvell & Suchanek (1987) found that a snail's residence time on a colony was inversely proportional to the percentage of non-organic material in that species, suggesting that high sclerite content deterred feeding (but see Lasker et al. 1988). Feeding experiments using artificial food of carageenan embedded with gorgonian sclerites have shown that sclerite content and size affect food choice in *C. gibbosum*; in particular, higher proportions of sclerites tend to decrease snail feeding (C. D. Harvell & J. L. Ruesink unpubl.).

*Cyphoma signatum* may be able to ingest more tissue and wound more deeply than its congener because of its specialized radula morphology. The relatively wider lateral teeth and the long central point on the rachidian tooth of *C. signatum* may allow the snail to feed despite the presence of densely packed, small (0.1 to 0.3 mm) sclerites embedded in the matrix of *Plexaurella* spp. The nutritional content of this matrix material is not high, as sclerites make up over 90 % of the matrix dry weight (as compared to < 50 % in the polyps). However, despite the higher proportion of sclerites in its diet, the specialist ingests more organic

material, as well as more total material, than the generalist when feeding on *Plexaurella*. The ability to feed on all the tissue of this gorgonian would be adaptive if prey were limiting, as it could be for a fairly non-motile, specialist predator such as *C. signatum* with a patchy food source.

The residence times we recorded for both snail species (> 1 wk) were considerably longer than those reported by Harvell & Suchanek (1987) for *Cyphoma gibbosum* (< 2 d); however, in that study *C. gibbosum* were placed on colonies, while we monitored the location of snails already on *Plexaurella*. Our results are almost certainly underestimated because of the short observational period, but it is uncertain whether they would match the extended periods recorded by Lasker et al. (1988) for *C. gibbosum* on *Pseudoplexaura*. Aggregation tendencies in *Cyphoma* have been reported by several other researchers (Birkeland & Gregory 1975, Hazlett & Bush 1982, Gerhart 1986, Lasker & Coffroth 1988).

### The question of coevolution

Partial predation on colonial organisms decreases feeding and reproductive potential, disrupts colony integration, and may allow overgrowth and death (Jackson & Palumbi 1979, Palumbi & Jackson 1982, Wahle 1983, Harvell & Suchanek 1987). Wahle (1985) established that the main sources of injury to gorgonians were abrasion and predation by *Hermodice carunculata* and *Cyphoma* spp., the last of which contributed little to colony damage. *C. gibbosum* may account for just 4 % of colony mortality in all gorgonians, as colony tissue is generally regenerated more quickly than it is consumed by *Cyphoma* (Kinzie 1970 in Lang da Silveira & van't Hof 1977, Birkeland & Gregory 1975). Although regeneration rates of most gorgonians are rapid (Wahle 1983), deeper wounds recover more slowly (Table 4), longer wounds and repeatedly damaged areas recover more slowly (Lang da Silveira & van't Hof 1977), and algal settlement on bared axes may completely prevent regrowth (Wahle 1980, Harvell & Suchanek 1987). The feeding behavior of *C. signatum*, including a high rate of tissue ingestion, deep wounding, long residence time, and a tendency to aggregate, results in extensive damage to *Plexaurella* colonies. High densities of *C. signatum* are correlated with high levels of permanently damaged *Plexaurella* colonies.

Closely-associated species have the greatest potential for showing evidence of coevolution (Reese 1977, Rausher 1988); however, a strict coevolutionary definition requires both specificity and reciprocity of adaptation (Janzen 1980, Futuyma & Slatkin 1983). While a

specialized radular morphology may be an adaptation allowing faster feeding by *Cyphoma signatum* on *Plexaurella* spp., any coevolutionary response by *Plexaurella* to this augmented predator ability remains less clear. Selection on *Plexaurella*, at least under some circumstances, must be intense, as damaged colonies not only would be at a size and reproductive disadvantage, but could, like many of the Site 4 colonies, be completely overgrown by algae and killed. We might expect, then, increases over time in *Plexaurella*'s toxicity to *C. signatum*, sclerite content, and regenerative abilities. The specialist's relative rarity, however, may relegate its effects to local disturbances of *Plexaurella* populations, preventing *C. signatum* from ever having much effect as a selective agent.

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#### LITERATURE CITED

- Bandel, K. (1973). Notes on *Cypraea cinerea* Gmelin and *Cyphoma gibbosum* (Linnaeus) from the Caribbean Sea and description of their spawn. *Veliger* 15: 335–337
- Bayer, F. M. (1961). The shallow-water Octocorallia of the West Indian region. Martinus Nijhoff, The Hague
- Birkeland, C., Gregory, B. (1975). Foraging behavior and rates of feeding of the gastropod, *Cyphoma gibbosum* (Linnaeus). *Bull. nat. Hist. Mus. Los Ang. Cnty* 20: 57–67
- Futuyma, D. J., Slatkin, M. (1983). Introduction. In: Futuyma, D. J., Slatkin, M. (eds.) *Coevolution*. Sinauer Associates, Sunderland, p. 1–13
- Gerhart, D. J. (1986). Gregariousness in the gorgonian-eating gastropod *Cyphoma gibbosum*: tests of several possible causes. *Mar. Ecol. Prog. Ser.* 35: 255–263
- Ghiselin, M. T., Wilson, B. R. (1966). On the anatomy, natural history, and reproduction of *Cyphoma*, a marine prosobranch gastropod. *Bull. mar. Sci.* 16: 132–141
- Harvell, C. D., Suchanek, T. H. (1987). Partial predation on tropical gorgonians by *Cyphoma gibbosum* (Gastropoda). *Mar. Ecol. Prog. Ser.* 38: 37–44
- Hazlett, B. A., Bush, C. E. (1982). Distribution pattern of the Flamingo Tongue Shell (*Cyphoma gibbosum*) on its gorgonian prey (*Briareum asbestinum*). *Mar. Behav. Physiol.* 8: 305–309
- Hickman, C. S. (1980). Gastropod radulae and the assessment of form in evolutionary paleontology. *Paleobiol.* 6: 276–294
- Hughes, R. N. (1986). A functional biology of marine gastropods. JHU Press, Baltimore
- Jackson, J. B. C. (1977). Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *Am. Nat.* 111: 743–767
- Jackson, J. B. C., Palumbi, S. R. (1979). Regeneration and partial predation in cryptic coral reef environments: preliminary experiments on sponges and ectoprocts. In: Levi, C., Bourg-Esnault, N. (eds.) *Biologie des spongiaires*. Centre Nationale de la Recherche, Paris, p. 303–309
- Janzen, D. H. (1980). When is it coevolution? *Evolution* 34: 611–612
- Jensen, A. L. (1986). Functional regression and correlation analysis. *Can. J. Fish. Aquat. Sci.* 43: 1742–1745
- Kemp, P., Bertness, M. D. (1984). Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. *Proc. natn. Acad. Sci. U.S.A.* 81: 811–813
- Lang da Silveira, F., van't Hof, T. (1977). Regeneration in *Plexaura flexuosa*. *Bijdr. Dierk.* 47: 98–108
- Lasker, H. R. (1985). Prey preferences and browsing pressure of the butterflyfish *Chaetodon capistratus* on Caribbean gorgonians. *Mar. Ecol. Prog. Ser.* 21: 213–220
- Lasker, H. R., Coffroth, M. A. (1988). Temporal and spatial variability among grazers: variability in the distribution of the gastropod *Cyphoma gibbosum* on octocorals. *Mar. Ecol. Prog. Ser.* 43: 285–295
- Lasker, H. R., Coffroth, M. A., Fitzgerald, L. M. (1988). Foraging patterns of *Cyphoma gibbosum* on octocorals: the roles of host choice and feeding preference. *Biol. Bull. mar. biol. Lab., Woods Hole* 174: 254–266
- Padilla, D. K. (1985). Structural resistance of algae to herbivores: a biomechanical approach. *Mar. Biol.* 90: 103–109
- Palumbi, S. R., Jackson, J. B. C. (1982). Ecology of cryptic coral reef communities. II. Recovery from small disturbance events by encrusting bryozoa: the influence of 'host' species and lesion size. *J. exp. mar. Biol. Ecol.* 64: 103–115
- Rabinowitz, D. (1981). Seven forms of rarity. In: Synge, H. (ed.) *The biological aspects of rare plant conservation*. John Wiley and Sons, Chichester, p. 205–217
- Rausher, M. D. (1988). Is coevolution dead? *Ecology* 69: 898–901
- Reese, E. S. (1977). Coevolution of corals and coral feeding fishes of the family Chaetodontidae. *Proc. Third Intl. Coral Reef Symp.* 1: 267–274. Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Florida
- Scriber, J. M. (1983). Evolution of feeding specialization, physiological efficiency, and host races in selected Papilionidae and Saturniidae. In: Denno, R. F., McClure, M. S. (eds.) *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, p. 373–426
- Sokal, R. R., Rohlf, F. J. (1981). *Biometry*. Freeman, San Francisco
- Wahle, C. M. (1980). Detection, pursuit, and overgrowth of tropical gorgonians by milleporid hydrocorals: *Perseus* and *Medusa* revisited. *Science* 209: 689–691
- Wahle, C. M. (1983). Regeneration of injuries among Jamaican gorgonians: the roles of colony physiology and environment. *Biol. Bull. mar. biol. Lab., Woods Hole* 165: 778–790
- Wahle, C. M. (1985). Habitat-related patterns of injury and mortality among Jamaican gorgonians. *Bull. mar. Sci.* 37: 905–927

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