The Feeding Ecology of *Cyphoma gibbosum* on *Gorgonia ventalina*: Farmer or Predator?

Tiana Melquist
Peter Holt
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Discovery Bay, Jamaica
Dr. J. Gilbert
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Abstract

This study examines the feeding ecology of *Cyphoma gibbosum* (the Flamingo Tongue) and its relation to its primary prey, *Gorgonia ventalina*. Grazing rates for *Cyphoma* were approximately twice as great as the rates of regeneration of this damage for *G. ventalina*. Observational lab studies revealed that *C. gibbosum* is surprisingly mobile - moving up to 6 cm./min. ~~We found that~~ Although *Cyphoma* has not necessarily evolved a feeding rate that matches *G. ventalina's* regeneration rates, ~~but that *Cyphoma* is a predator on *G. ventalina*, and is probably~~ it may be prevented from destroying the colonies by high levels of toxic compounds in the Gorgonian.

Introduction:

Compared to tropical seas world-wide, gorgonians are much more prevalent in the Caribbean. "The gorgonians, remarkably adapted to the reef system and its inhabitants, are truly the hallmark of the Caribbean reefs," (Kaplan, 1982). Gorgonia ventalina, the common sea fan is commonly found in shallow or turbulent water, undulating with the current. The sea fans tend to grow in planes perpendicular to the water current (Griggs, 1972), having polyps on both sides which, unlike the Scleractinians, are extended during the day as well as at night. The Gorgonia species are comprised of a flexible axial skeleton made of gorgonin - a proteinaceous material. Spicule ($CaCO_3$) embedded living tissue covers the gorgonin skeleton into which the polyps retract for protection. The polyps are connected by a primitive (slow) nervous system and a common digestive system, (Kaplan, 1982).
Many gorgonians contain large amounts of chemical compounds which have no obvious function. Plexaura homomalla (common bushy soft coral) contains PGA_2 which is toxic to mammals and fish and thus may deter predation, (Gerhart, 1984). Toxic compounds in soft corals have also been shown to have a role in interspecific competitive interactions, (Sammarco, et al, 1983).

There are several known predators on gorgonians: Cyphoma gibbosum (Flamingo Tongues), Coralliophila abbreviata (short coral snail), and the polychaete fireworm Hermodice carunculata, (Preston & Preston, 1975). The Flamingo Tongue is the only predator frequently found on sea fans and therefore can be assumed to have evolved adaptations to overcome these toxic compounds or to utilize these compounds for their own defense. K. Hoy, (Dartmouth 1983) demonstrates that the brightly colored mantle of the Flamingo Tongue may be an aposymatic display of its own toxicity.

Destruction of an entire colony is unlikely to result from predation by any of the common gorgonian predators although predation can affect the course of competition, (Preston & Preston, 1975). However, grazing by Flamingo Tongues leaves a visible trail of damage where the axial skeleton is exposed and susceptible to settlement and overgrowth by Millepora or algae. Therefore, the ability of sea fans to regenerate lost tissue affects their very existence.

This study measures rates of regeneration under normal levels of natural injury caused by Flamingo Tongues. Our aim is to determine how closely matched Flamingo Tongue feeding rates are with sea fan regeneration rates. Kaplan, (1982) suggests that the Flamingo Tongue may be a 'farmer' rather than a predator although this balance is sometimes upset by multiple attacks on a colony. Our data does not reflect the ability of gorgonians to regenerate after natural disasters such as storms and hurricanes, nor is it indicative of the damage-regeneration relationship for other gorgonian predators.

METHODS:

Field and laboratory studies were conducted February 28 - March 8 at Discovery Bay Marine Laboratory, Jamaica, West Indies. Field data were collected from Glynton's Mine, 20 meters northwest of the mooring at Mooring 1, West Fore Reef. This segment of reef was chosen because it supports a large and representative population of sea fans distributed over a 100m x 30m area. Thirteen gorgonians of the species G. ventalina were studied at the site and one additional sea fan was collected for laboratory experiments. Each fan chosen for study had no evidence of previous damage or predators which might affect Flamingo Tongue grazing or fan regeneration. Because regeneration rates have been shown to vary over depth for particular gorgonian species, (Wahle, 1983), all sea fans chosen for study were at an intermediate depth; 40-60 feet. Environmental conditions were observedly similar throughout the study site. Flamingo Tongues were transplanted to 8 intact sea fans, 2 systems already in progress were located & labeled, and 3 fans were artificially damaged to generate our grazing and regeneration data. Grazing data ~~was~~ were obtained by allowing Flamingo Tongues to graze for up to 8 days and recording movement and feeding rates. Grazing data were also monitored on fans with Flamingo Tongues where grazing trails were already apparent, and on our laboratory specimen. Each fan was given a 1-5 damage rating; 1 being the least damaged.

For regeneration rates, we allowed Flamingo Tongues to graze and create natural damage trails that we could watch regenerate. We removed 3 Flamingo Tongues after 3 days so that no further damage was induced while we measured regeneration on these fans. Five snails were left on sea fans so that we could monitor regeneration capabilities of more extensively damaged sea fans. Three fans were artificially damaged, using a scalpel to scrape a trail of known length and width. Injury regeneration rates for these various sized scrapes were recorded over several days. For purposes of this study, the regeneration process was deemed complete when the gorgonin skeleton was again tissue covered, accompanied by a change in color from black or dark purple to light purple. Wahle, (1983), considered a gorgonian regenerated when the internal axis was completely covered by tissue and no longer susceptible to fouling. To measure precisely Flamingo Tongue movements and G. ventalina regeneration, thread markers were tied onto the fan at critical boundary points from which daily measurements could be made. Mann-Whitney "U" tests were used to compare grazing and regeneration rates and degrees of damage with regeneration rates.

RESULTS:

The data are summarized in Tables 1 & 2. The mean grazing rate is 2.4 cm²/day, while the mean regeneration rate is 1.3 cm²/day. These two rates differ significantly (Mann-Whitney U $\alpha = .001$). Sea fans assigned a damage rating of 3 or 4 were found to have significantly slower regeneration rates than those assigned 1 or 2 (Mann-Whitney U $\alpha = .05$). Grazing damage was observed to occur on all areas of sea fans - web, skeleton, base, and tip. The maximum amount of damage observed over a one-day period was 6.4 cm²; the maximum distance moved on a fan was 8 cm in one day. The mean movement rate per day is 5 cm² and the maximum amount of regeneration seen in one day was 2 cm². The average regeneration time for each damage trail is 4 days. Most nonexperimental sea fans observed in and around our site had one or two Flamingo Tongues, although a few were seen with as many as four, and there are reports of up to a dozen.

The laboratory studies yielded an interesting accumulation of data on feeding behavior, feeding mechanisms and dispersion and search patterns. Four Flamingo Tongues were released in a seawater tank 70 cm from a small (diameter = 20 cm) sea fan. After 2 hrs, 1 of the Flamingo Tongues had located and climbed up the sea fan. Another found the fan after about 12 hours, the remaining 2 snails required 4 days. In the lab movement rates of 6 cm/minute were recorded. The 70 cm to the sea fan was traversed in 1 hour by 1 Flamingo Tongue, although it missed the sea fan by a few centimeters and eventually looped back. The other Flamingo Tongues, each of which dispersed in a different direction, climbed up any vertical surface they encountered. When the Flamingo Tongues climbed up the walls of the tank, they stalled at the waterline, in some cases for several days. When we removed them to the bottom of the tank they resumed travel and eventually found the sea fan. Grazing rates in the laboratory were 5cm²/day with 2 snails on the fan - almost identical to the field rates on a per-Flamingo Tongue basis.

Examination under a dissecting microscope revealed that Flamingo Tongues protract their radula against the sea fan surface removing tissue and polyps from one side of a fan at a time, leaving the black gorgonin skeleton exposed, (Fig. 1). The polyps were never observed to be extended in the lab; this sea fan never seemed to recover from the shock of transplantation. The movement of this radula was rather like a human tongue removing the chocolate chips from chocolate chips cookies, while the pockmarked end result resembled a cookie with all the chips removed.

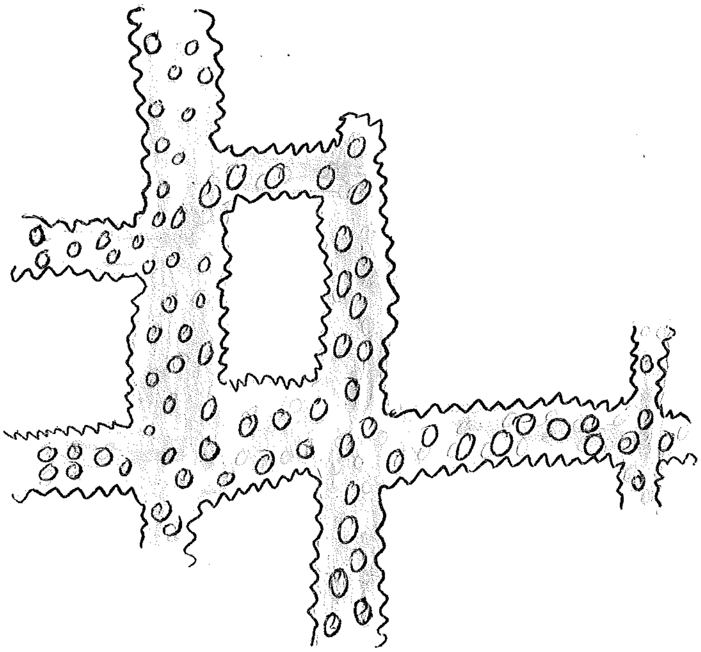
DATA

TABLE 1: GRAZING DATA

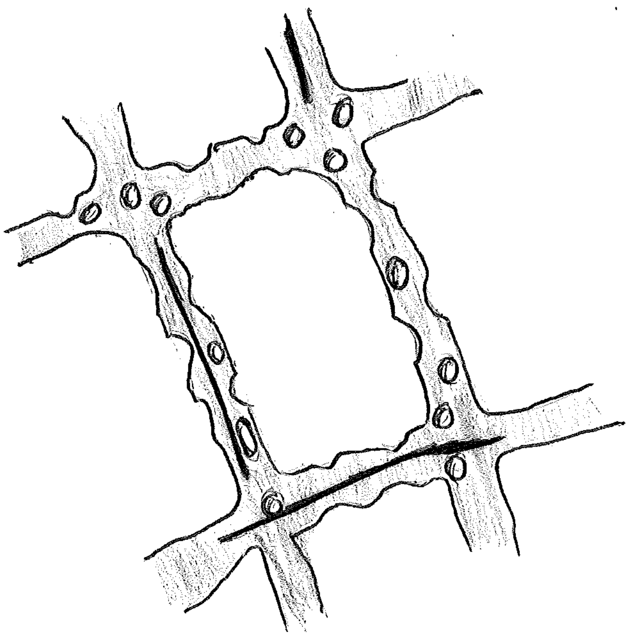
COLONY LABEL	MEAN MOVEMENT/DAY	MEAN GRAZING DAMAGE/DAY	Location of Damage
15	5 cm	6.4 cm x 1 cm	skeleton and web
ASW	2.4 cm	0.5 cm x 1 cm	skeleton
D	8 cm	1.5 cm x 1 cm	web near base
B	2.4 cm	2.5 cm x 1 cm	skeleton and web
C	7 cm	1.0 cm x 1 cm	web
B^2	—	2.5 cm x 1 cm	skeleton
	$\bar{x}$ = 5.0 cm	$\bar{x}$ = 2.4 cm	
	σ = 2.6 cm	σ = 2.1 cm	

TABLE 2: REGENERATION DATA

COLONY	MEAN REGENERATION/DAY	DAMAGE RANKING 1-5	TIME TO TOTAL REGENERATION
9	1.7 cm	2	4 days
E	0.67 cm	4	4 days
F	0.50 cm	4	> 4 days
D	0.75 cm	4	> 4 days
B	2.0 cm	2	> 4 days
B^2	1.7 cm	2	> 2 days
K_1	1.8 cm	3	4 days
K_2	1.6 cm	3	5 days
Ø	—	1	4 days
A	—	2	< 3 days
	$\bar{x}$ = 1.34 cm	$\bar{x}$ = 3.2	$\bar{x}$ = 4
	σ = .60 cm	σ = 2	σ = .6



Intact Sea Fan Section
light purple tissue covers all surfaces
many bumps visible, into which polyps retract



Cyphoma-Damaged Sea Fan Section
All tissue + polyps gone
Heavy, deep scoring in gorgonin Skeleton
Craters left from removed polyps

Figure 1

Discussion:

The results indicate that the mean grazing rate (i.e. rate of damage generation) of an individual Flamingo Tongue is approximately twice as great as the mean regeneration rate of that same damage. This result alone neither falsifies nor supports Kaplan's suggestion that the Flamingo Tongue is a 'farmer,' not a predator. However, auxiliary data enable us to infer that the nature of this relationship is indeed predatory, in the usual sense.

The regeneration rate must be regarded in terms of how quickly a ~~stuck~~ section of exposed gorgonin skeleton must be covered by tissue in order to minimize the chances that algae or _Millepora_ larvae will begin colonization there, with subsequent overgrowth of the colony. Sea fans overgrown by both _Millepora_ and algae were seen - the latter were often damselfish territories. Our experimental sea fans did suffer slight algal colonization on the exposed skeletons after several days - however, in all cases the fans seemed to regenerate in spite of the algae, and avoided algal overgrowth. By the end of the study, the algae was deteriorating. From our observations and data, we conclude that the damage caused by one _Cyphoma_ can be withstood by most sea fans. The same holds for pairs of _Cyphomas_. - pairs occur fairly often, due to a tendency to aggregate in male-female pairs (Ghiselin & Wilson, 1966). These fans had greater ~~damage~~ amounts of damage, but seemed to be healing throughout our study. As noted previously, severely over-grazed sea fans were observed; some were found with five Flamingo Tongues present, and the literature reports up to a dozen.

These observations, coupled with our finding that ~~xxxx~~ fans bearing heavy damage regenerate significantly more slowly than intact or slightly-damaged fans, lead us to conclude that in general an individual sea fan is able to tolerate grazing by one or two Flamingo Tongues, but as the number of Flamingo Tongues increases, the ability of the sea fan to withstand this grazing steadily declines. The total amount of damage increases relatively quickly while the regenerative ability of the sea fan decreases. As a greater area of skeleton is exposed to potential algal + larval colonizers, the probability of successful colonization increases.

Another unexpected observation which has some bearing on the feeding ecology of the Flamingo Tongue is the abandonment of sea fans by Cyphoma. This occurred at four of our sites, within a two day period. The disappearances could be the result of predation - however, such a predator would presumably be large and mobile (to cover the distances between fans) and so it is somewhat inexplicable that so many Flamingo Tongues remained on fans, if indeed a predator was responsible. Turbulence during these days was not appreciably greater than throughout our study, ~~xxxxx~~ so it seems unlikely that turbulence is responsible for the disappearances. For these reasons, we attribute these disappearances to 'voluntary' abandonment rather than 'involuntary' removal. Each of these fans was the recipient of a transplanted Cyphoma, at virtually the same time. Similarly, all the Flamingo Tongues that disappeared did so at approximately the same time.

None of the abandoned sea fans bore heavy damage, eliminating the possibility that the Flamingo Tongues had grazed as much as possible. The damage sustained was generally so minimal that the sea fan could almost definitely have endured further grazing and still regenerated quickly. The most likely explanation for these disappearances seems to be that the sea fan itself orchestrated the departure of the Flamingo Tongue. Gorgonians are known to contain a variety of toxic compounds, which decrease their desirability to potential predators. Gorgonians in general have very low rates of predation. These chemicals may have played any of several possible roles in the _Cyphoma_ disappearances. Several days may have been required for the Flamingo Tongues to have determined that these particular sea fans contained intolerably high levels of these chemicals. Each of these fans did suffer some grazing during this period, however. The effect of these chemicals might manifest itself at the digestive level rather than through "taste" or initial palatability.

An alternative explanation parallels recent findings in a variety of terrestrial plants. In such plants, herbivore grazing triggers the polymerization of secondary compounds in the leaf under attack and also in neighboring leaves. In this marine system, the grazing of the Flamingo Tongue could trigger just such a reaction in the sea fan. As grazing progresses, damage-induced toxicity might steadily decrease the palatability, digestibility and/or overall nutritional value of a sea fan;

good argument

until finally the Flamingo Tongue is forced to move on. This does not account for the susceptibility of the sea fans to mass predation by many Flamingo Tongues - one possibility is that the polymerization/manufacture of these chemicals ~~may~~ requires several days, a time period in excess of that required for a group of Flamingo Tongues to severely damage - perhaps beyond repair - a sea fan. Different individuals would be expected to vary in their rates of toxin formation and that toxins' potency - this may explain why all the Cyphomae didn't desert their ~~fan~~ sea fans.

The abandonment of sea fans by Flamingo Tongues indicates that Flamingo Tongues are able to disperse and find new food resources. This is consistent with lab observations, in which Flamingo Tongues were seen to travel at rates equivalent to 3.6 meters per hour, on flat, horizontal surfaces. This rate is a maximum, but it indicates that the Flamingo Tongues are capable of enough movement to disperse to other Gorgonians. Two of our lab specimen Cyphomae did not reach the only Gorgonian available for four days, and presumably did not feed during that time. The majority of these four days were spent immobile, stalled at the waterline of the tanks. After being removed to the base of the tank, both proceeded to the fan, and displayed no ill effects. Assuming that these Flamingo Tongues could travel for six hours per day at their maximum rate, for four days, they could cover a linear distance of over eighty meters. Clearly, they have the ability to disperse. Their observed behavior of climbing anything vertical is also adaptive – Gorgonians are often found surmounting patch reefs or on other high points, due to their dependency on having currents reach them. The Flamingo Tongues clearly display a variety of behaviors which seem to augment their ability to disperse to Gorgonians.

This ability to disperse to and find Gorgonians relates to the role _Cyphoma_ plays in predation on sea fans. If Flamingo Tongues were restricted to individual sea fans for life (or sizeable portions of their lifespans), there would be much greater incentive for Flamingo Tongues to evolve and therefore display grazing rates easily tolerated by the sea fan, in order to minimize the chances of ~~w~~ inflicting fatal damage on the host organism. However, since the Flamingo Tongues are definitely not confined to individual sea fans, their evolutionary 'incentive' not to overgraze is substantially weakened. Since large portions of abandoned sea fans remained ungrazed, it seems likely that _Cyphoma_ grazing rate is limited by compounds present in the sea fan. (and dispersal)

In summary, the slow grazing rate of _Cyphoma_ has led to speculation that this rate is an 'attempt' by Flamingo Tongues to conserve their resources. Such a concept assumes that Flamingo Tongues are limited in their resources – i.e., in the number of grazable sea fans accessible to them. However, their dispersal abilities indicate that they can indeed travel from one Gorgonian to another. Therefore, it is to an individual's advantage to graze as much as possible on each sea fan before leaving it for another. Since one or even two Flamingo Tongues do not generally inflict serious damage on a sea fan, we conclude that Flamingo Tongues are in fact predators but are limited by the presence of toxic compounds in the Gorgonians - the effectiveness of these is evidenced in the overall low rates of predation on Gorgonians. The abandonment of several relatively undamaged sea fans also implies a degree of damage-induced toxicity. An interesting follow-up would be to test the palatability of Flamingo Tongue damaged sea fan versus intact, undamaged sea fan. Ground extracts could be fed to fish, or preference tests could be done with Flamingo Tongues.

good

A study of the time needed to pick each polyp from its hole might reveal that the Flamingo Tongues' primary constraint on grazing rate is morphological - evolution is in general more ingenious than that, though. The grazing is most likely limited by problems in digesting the compounds present in the Gorgonian. The proposal that the sea fan becomes more toxic when under attack explains our ~~[illegible]~~ observed abandonments, and the presence of toxins at all times explains the generally slow grazing rates.

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A very good, creative project on a new subject. Results are clearly presented and discussed.

It would have been interesting to compare grazing rates on successive days to see if these decreased with time, perhaps in response to production of defensive compounds by sea fan.