

Predator release of the gastropod *Cyphoma gibbosum* increases predation on gorgonian corals

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Abstract When large, predatory fishes and invertebrates were excluded from areas of a coral reef in the Florida Keys, USA, densities of the normally rare gastropod *Cyphoma gibbosum*, a principal predator of gorgonian corals, increased 19-fold. Gorgonians in predator enclosures were grazed more frequently and extensively by *C. gibbosum* than were gorgonians in uncaged areas. In enclosures, 14% of all gorgonians showed recent predation by *C. gibbosum*, with 62% of the entire colony surface being removed from these attacked individuals. In areas where predators of *C. gibbosum* were not excluded, only 5% of gorgonians exhibited recent damage, with only 26% of the colony surface being removed from these few damaged individuals. Thus, the increases in both frequency and extent of attack combined to produce an 8× increase in gorgonian damage following removal of large predators. These patterns suggest that predators typically suppress *C. gibbosum* populations, that overfishing of these predators could release *C. gibbosum* from top-down control, and that this release will allow increased damage to gorgonian corals.

Keywords Coral reef · Mesopredator release · Overfishing · Trophic cascade

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Introduction

Gorgonian corals are common in the Caribbean and are the dominant benthic invertebrates on some reefs (Yoshioka and Yoshioka 1989). Heavy predation on gorgonians appears rare, possibly because of their chemical and morphological defenses against consumers (Van Alsyne and Paul 1992; O'Neal and Pawlik 2002). Consequently, the role of predators in affecting gorgonians has rarely been assessed; instead, most investigations of how gorgonian populations are regulated have focused on reproduction (Lasker 1991), recruitment (Lasker et al. 1998), disturbance (Yoshioka and Yoshioka 1987), and disease (Kim and Harvell 2004).

The ovulid gastropod *Cyphoma gibbosum* is the primary consumer of gorgonians on Caribbean coral reefs (Birkeland and Gregory 1975; Gerhart 1986; Lasker et al. 1988). However, most studies of *C. gibbosum*–gorgonian interactions have focused on the distribution, movement, and host preference of *C. gibbosum* (Gerhart 1986; Lasker and Coffroth 1988) with less emphasis on the potential top-down effects of *C. gibbosum* grazing. As a result, the potential for *C. gibbosum* to impact gorgonian populations in the field has been considered modest, with most predation being only partial and producing minimal impact on gorgonian survivorship (Birkeland and Gregory 1975; Harvell and Suchanek 1987; Lasker et al. 1988).

Additionally, little is known about how predation influences populations of *C. gibbosum*. However, a large-scale survey of *C. gibbosum* abundance in the Florida Keys showed that *C. gibbosum* tended to be more abundant in areas where large predators were regularly harvested (Chiappone et al. 2003), suggesting that predators might control *C. gibbosum* populations. Removing top predators from ecosystems often results in the release of their prey

and can have cascading indirect effects on plants or animals two links away in the food chain (i.e., a trophic cascade or mesopredator release) (Hairston et al. 1960; Crooks and Soule 1999; Silliman and Bertness 2002). If predators suppress *C. gibbosum* populations, then removal of predators may allow increases in *C. gibbosum* abundance which may, in turn, increase predation on gorgonians. Here, we examine the role of large predators in regulating *C. gibbosum* densities and the cascading effects on gorgonian corals.

Materials and methods

In November 2003, we used NOAA's Aquarius, an undersea research laboratory on Conch Reef (24°57'N/80°27'W) in the Florida Keys, Florida, USA, to perform an experiment testing the effects of species richness of herbivorous fishes on the community structure of coral reefs. As part of the experiment we constructed 32 cages (2.5 cm mesh size) measuring 2 m × 2 m × 1 m tall (each covering 4 m² of the reef bottom) at depths of 16–18 m on a spur and groove reef formation. Cage frames were made of 0.6 cm steel bar and covered with PVC-coated, galvanized wire with zinc anodes attached to the wire and cage frame to prevent corrosion. We attached the cages to the reef by wiring the frames to 30-cm galvanized nails that had been hammered into the reef substrate. A 30-cm flange of mesh extended from the base of the cage and was conformed to the reef and affixed using galvanized fencing nails. This barrier prevented fishes within treatments from escaping and also prevented larger fishes and invertebrates from entering the cage, but the mesh size allowed small fishes and invertebrates to enter and exit at will, creating a potential refuge from predation for *C. gibbosum*.

The benthos inside the cages consisted of unmanipulated populations of macroalgae, corals, sponges, gorgonians, and other invertebrates. Different combinations of herbivorous fishes were maintained within these cages to test for the effects of herbivore species richness on coral reef community structure. The treatments consisted of: (1) two redband parrotfish, *Sparisoma aurofrenatum*, (2) two ocean surgeonfish, *Acanthurus bahianus*, (3) one redband parrotfish and one ocean surgeonfish, or (4) no large fish ($n = 8$ for each treatment and $n = 32$ total for the caged areas). We also monitored uncaged areas of equal size ($n = 8$). One replicate of each of the four fish treatments and an uncaged area were blocked in one general area. Treatments within blocks were generally 1–4 m apart whereas blocks of treatments were generally 10–15 m apart, and there were eight blocks of the five treatments. Cages were scrubbed inside and out every 4–6 weeks to remove fouling organisms and reduce shading. We did not

include cage controls (cages with tops, but some sides removed) because initial experiments showed that control cages at this large size attracted unnatural densities of large predators (e.g. grouper, jacks, sharks) that sheltered in or near the cages or that used them like barrier nets to chase prey against and increase prey capture (M. E. Hay, personal observation). These alterations in predator–prey behaviors appeared to produce larger artifacts on the benthic community than those associated with the mesh altering light or flow. Further, no effects of cage artifacts on benthic community development could be detected when mesh of this size was used to construct smaller cages on nearby reefs (Miller and Hay 1998).

In addition, we tested for the potential presence of caging artifacts on flow through the cages by measuring sediment accumulation on the top of two cinderblocks (~10 cm × 20 cm × 40 cm) present within each caged or uncaged area. At the end of the 10-month experiment, all cinderblocks were placed in individual garbage bags in situ and taken to the surface. The top of each cinderblock was lightly scraped with a paint scraper to remove all sediments and organisms. Organisms were removed and the remaining sediments were washed with seawater, filtered onto GF/C glass microfiber filters, and dried to a constant weight at ~60 °C. We averaged the data from the two cinderblocks within each treatment and used a *t*-test to test for differences in sedimentation between caged versus uncaged areas.

At the end of the ten-month experiment (August 2004), we assessed density of *C. gibbosum* in each caged and uncaged area. We also identified all gorgonians to genus or species as was practical under field conditions, and noted which gorgonians hosted *C. gibbosum*. Using these data, we assessed whether our different herbivorous fish enclosure treatments had affected either gorgonians or densities of *C. gibbosum*. Blocked, one-factor ANOVA showed no differences among fish treatments in gorgonian abundance (block $F_{(7,21)} = 0.87$, $P = 0.548$; treatment $F_{(3,21)} = 0.11$, $P = 0.935$) or in *C. gibbosum* abundance when scaled to either area (block $F_{(7,21)} = 1.16$, $P = 0.367$; treatment $F_{(3,21)} = 0.95$, $P = 0.434$) or gorgonian abundance (block $F_{(7,21)} = 0.85$, $P = 0.562$; treatment $F_{(3,21)} = 0.59$, $P = 0.629$). This lack of effect allowed us to pool data from all fish enclosure treatments into a “caged area” category. We tested for differences in the abundance of gorgonians between caged and uncaged areas using *t* tests. To assess differences in *C. gibbosum* abundance between caged and uncaged areas, we used a Mann–Whitney *U* test (due to the large number of zeros in the uncaged areas; Sokal and Rohlf 1995).

Due to bottom-time and weather constraints, we could not determine the extent of *C. gibbosum* feeding on every gorgonian in all 32 cages. Thus, we sampled gorgonian

Table 1 The abundance of *C. gibbosum* and their gorgonian hosts within the cages

Gorgonian	Individuals (no.)	% of total gorgonians	<i>C. gibbosum</i> (no.)	% of total <i>C. gibbosum</i>	<i>C. gibbosum</i> per gorgonian
<i>Pseudopterogorgia americana</i>	553	82.9	31	40.3	0.06
<i>Briareum asbestinum</i>	33	4.9	0	0	0
<i>Eunicea</i> spp.	32	4.8	30	38.9	0.93
<i>Pseudoplexaura</i> spp.	31	4.7	13	16.9	0.42
<i>Pseudopterogorgia acerosa</i>	10	1.5	3	3.9	0.3
<i>Gorgonia ventalina</i>	5	0.8	0	0	0
<i>Plexaurella</i> spp.	3	0.4	0	0	0
Total	667	100	77	100	0.12

The distribution of *C. gibbosum* on the gorgonians differed significantly from what would be expected given the gorgonian abundance data $P < 0.001$; $G = 84.6$; G test

damage in each uncaged area and then randomly selected a caged area in the same block of treatments to assess gorgonian damage with predator exclusion (i.e., $n = 8$ for both uncaged and caged areas). To quantify *C. gibbosum* damage to each gorgonian, we measured the total length of the live main axes of each gorgonian and then measured the total length of the main axes that had been stripped of its coenenchyme by *C. gibbosum* feeding. Grazing damage was scaled to the total length of the main axes. We did not include areas of exposed gorgonian skeleton that had been fouled by epiphytic algae or invertebrates, despite these being extensive on several gorgonians in the caged areas. Although this damage probably resulted from previous *C. gibbosum* grazing (Gerhart 1990), it could not be unambiguously attributed to predation by *C. gibbosum* and so was not included in our analyses. We also excluded gorgonians that were within 10 cm of the cage because these could have been damaged by wave action abrading them against the cage. We analyzed the frequency of grazed gorgonians in each treatment and the average grazing damage per gorgonian in each treatment using paired, one-tailed t tests that paired each caged and uncaged area from an experimental block. Data for average grazing damage per gorgonian were log-transformed to achieve homogeneity of variances as evaluated with Cochran’s test (Underwood 1997). We also analyzed the percent grazing damage per grazed gorgonian using a one-tailed, t test (a paired t test was not used here because some uncaged areas lacked gorgonians with any grazing damage while gorgonians suffered grazing damage in all caged areas). We used one-tailed t tests based on the hypothesis that caged areas that had more *C. gibbosum* would also have more damage to gorgonians.

Results

Pseudopterogorgia americana represented 83% of all gorgonians, with *Briareum asbestinum*, *Eunicea* spp., and

Pseudoplexaura spp. each comprising about 5% (Table 1; Fig. 1). Gorgonian densities did not differ between caged and uncaged areas (Fig. 1). *Cyphoma gibbosum* were 19× more abundant in caged than uncaged areas ($P = 0.008$, $W = 84.5$; Fig. 2). Seventy-seven *C. gibbosum* occurred in the 32 caged areas versus one in eight uncaged areas. *Cyphoma gibbosum* densities likely increased in the caged areas as a result of the aggregation of individuals to caged areas as well as recruitment of juveniles to these predator-free areas; several juvenile *C. gibbosum* occurred in the caged areas but none in the uncaged areas. Of the 77 *C. gibbosum* found in caged areas, 40% were found on the most abundant gorgonian, *P. americana*, 39% on *Eunicea* spp., 17% on *Pseudoplexaura* spp. and 4% on *Pseudopterogorgia acerosa* (Table 1). The distribution of *C. gibbosum* on gorgonian hosts differed significantly from

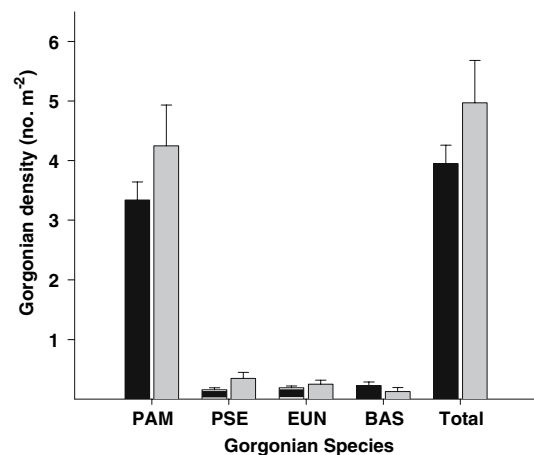


Fig. 1 Density of four species of gorgonians (mean + SE) for caged (black bars; $n = 32$) and uncaged areas (gray bars; $n = 8$). There were no differences in gorgonian densities between caged and uncaged areas for total gorgonians ($P = 0.223$) or for any gorgonian species or genus (*P. americana*, PAM ($P = 0.254$); *Pseudoplexaura* spp., PSE ($P = 0.124$); *Eunicea* spp., EUN ($P = 0.418$); *Briareum asbestinum*, BAS ($P = 0.265$)) as evaluated with t tests

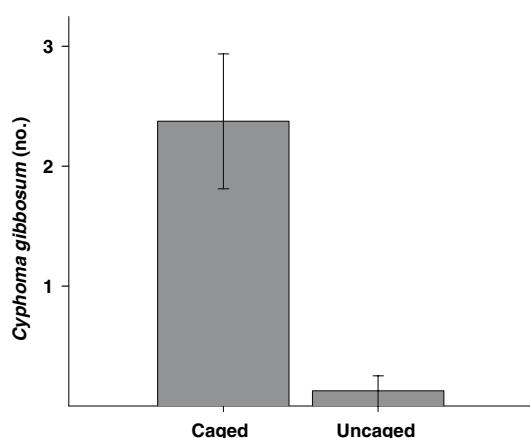


Fig. 2 *Cyphoma gibbosum* abundance (mean \pm SE) in caged ($n = 32$) versus uncaged ($n = 8$) areas. $P = 0.008$ via Mann–Whitney U test

what would have been expected given the abundances of the different gorgonians ($P < 0.001$, $G = 84.6$; Table 1) with density on *Eunicea* spp. 8 \times greater than expected given its abundance.

Cyphoma gibbosum could be observed feeding on gorgonians and were often at or near areas completely stripped of all tissue. The damage on gorgonians was consistent with previous descriptions of *C. gibbosum* feeding (Harvell and Suchanek 1987; Gerhart 1990) and inconsistent with damage done by *Hermodice carunculata* (Vreeland and Lasker 1989) which was infrequently observed inside the caged areas and rarely observed on gorgonians. Most grazing removed all soft tissue from the grazing scar and exposed the gorgonian skeleton, even for species that have thick coenenchyme such as *Eunicea* spp. or *Plexaurella* spp.

The percentage of gorgonians with grazing scars was greater in caged versus uncaged areas ($P = 0.043$, $t = 2.00$; Fig. 3a). The same trend was evident for the most abundant gorgonian *P. americana* ($P = 0.085$, $t = 1.53$; Fig. 3b). When averaged across all gorgonians, the extent of grazing damage per gorgonian was 8 \times higher in caged than in uncaged areas. On average, gorgonians had ~9% of the main axes damaged per individual in caged areas, but only 1% in uncaged areas ($P = 0.002$, $t = 4.14$; Fig. 3c). *Pseudopterogorgia americana* had ~12% of its main axes damaged per individual in caged areas versus ~1% in uncaged areas ($P = 0.001$, $t = 2.65$; Fig. 3d). When we considered only those gorgonians exhibiting damage from *C. gibbosum*, attacked individuals in caged areas lost $61 \pm 8\%$ of their length to *C. gibbosum* grazing, while attacked individuals in uncaged areas lost $25 \pm 8\%$ ($P = 0.016$, $t = 2.95$; Fig. 3e). Sediment that accumulated on top of cinderblocks showed no difference between caged versus uncaged areas (0.78 ± 0.10 vs.

0.69 ± 0.15 g/cinderblock for caged vs. uncaged areas, respectively, $P = 0.584$, $t = 0.56$; t test).

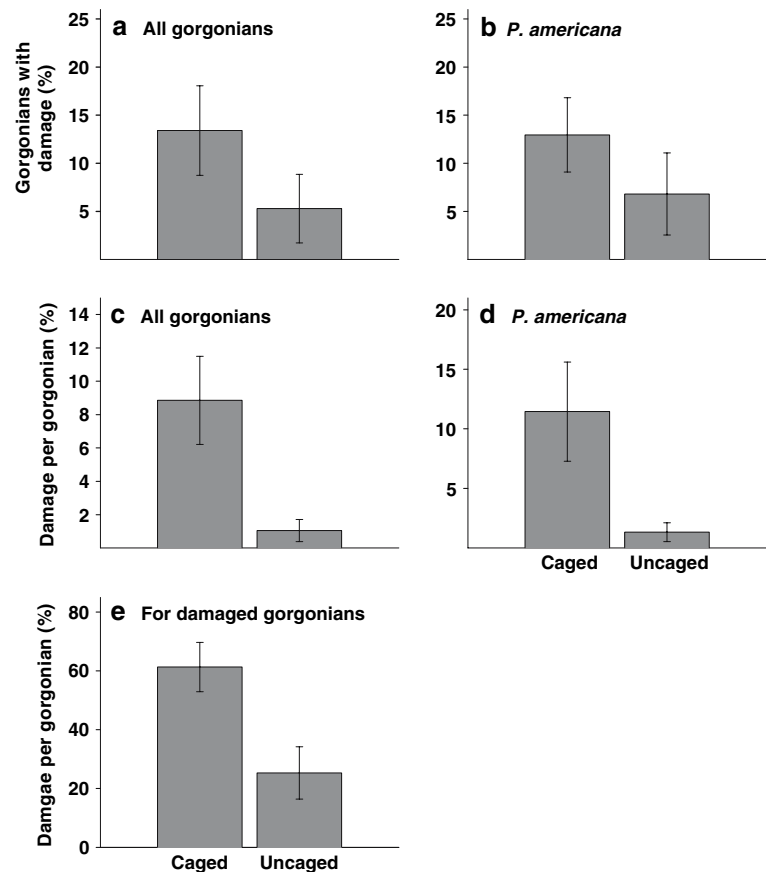
Discussion

Exclusion of large predators led to a 19 \times increase in the abundance of *C. gibbosum* (Fig. 2) and an 8 \times increase in recent damage to gorgonians (Fig. 3). Consistent with our findings, extensive surveys throughout the Florida Keys show that *C. gibbosum* densities are 4–5 \times greater on fished reefs than on reefs protected from fishing (Chiappone et al. 2003). Fishing is prohibited at our study site because it is in a special protection area within the Florida Keys National Marine Sanctuary, and predation on *C. gibbosum* is likely high relative to areas that are heavily fished. Hogfish, *Lachnolaimus maximus*, large pufferfishes (Tetraodontidae), and Caribbean spiny lobsters, *Panulirus argus*, were common at our study site, and these species prey on *C. gibbosum* and other gastropods (Randall and Warmke 1967; Turingan 1994; Cox et al. 1997). At the end of the experiment, the cages were removed and predators gained full access to the previously caged areas. When we surveyed the area eight weeks later, no *C. gibbosum* remained. This dramatic decline in *C. gibbosum* density could be due to predation, to *C. gibbosum* dispersing so widely that none remained in the survey areas, or to both predation and dispersal. However, regardless of the mechanism producing the decline, both our experiment and a large-scale survey of *C. gibbosum* abundance in fished and unfished areas (Chiappone et al. 2003) suggest that predators maintain *C. gibbosum* at low densities.

On many reefs, *C. gibbosum* grazing typically produces minimal damage to gorgonians, possibly due to physical defenses (i.e., spicules) or induced chemical defenses in the gorgonians (Gerhart 1986; Harvell and Suchanek 1987). However, in our predator exclusion cages, *C. gibbosum* removed most of the tissue from damaged areas and completely removed all the tissue from several *P. americana* (~0.2 m in height) and ~75% of the tissue from a 0.8-m-tall *Eunicea calyculata* in the caged areas (this individual was completely dead two months later). Thus, in our experiment, gorgonian defenses were ineffective against *C. gibbosum*. On unfished reefs, predators may commonly prevent *C. gibbosum* from intensively grazing gorgonians by keeping their densities low and possibly by causing them to move to safer refuge areas after only short bouts of feeding. Intense feeding from high densities of *C. gibbosum* following predator exclusion may also overwhelm the gorgonians' capacities to mount effective anti-predator defenses (Rhoades 1985).

Even though the increase in average grazing damage to gorgonians may appear modest (i.e., 9% damage in caged

Fig. 3a–e Percentage (mean \pm SE) of **a** all gorgonians ($P = 0.043$), or **b** *P. americana* ($P = 0.085$) with grazing scars or percent damage per gorgonian by *C. gibbosum* for **c** all gorgonians ($P = 0.002$), **d** *P. americana* ($P = 0.001$), or **e** only gorgonians that had been damaged ($P = 0.016$) in caged and uncaged areas. $n = 8$ for all bars except for the uncaged bar in **e** where $n = 3$. P values are from paired t tests (**a–d**) or t test (**e**)



areas vs. 1% in uncaged areas), the damage to those gorgonians that were grazed increased substantially from 26% tissue removal in uncaged areas to 62% tissue removal in caged areas (Fig. 3e). Further, our estimates of *C. gibbosum* damage to gorgonians are conservative in that we quantified only recent damage (i.e., feeding scars not yet overgrown with fouling organisms). Fouling of the exposed gorgonian skeleton following *C. gibbosum* predation is common, happens within only a few weeks (Gerhart 1990), and would have appreciably increased the estimates of *C. gibbosum* grazing had such damage been included. Although feeding by *C. gibbosum* did not change the density of gorgonians over the course of our ten-month experiment, further increases in the density of *C. gibbosum* and their cumulative grazing over longer periods might then lower gorgonian density.

Sublethal grazing from *C. gibbosum* may have both direct and indirect negative effects on gorgonians. For example, gorgonians that are fragmented by fouling or grazing have reduced fecundity (Wahle 1983). Additionally, colony breakage during storms is a significant source of mortality for gorgonians (Yoshioka and Yoshioka 1991), and grazing damage may increase gorgonian susceptibility to breakage, as in other marine organisms (Koehl and Wainwright 1977). Grazing by *C. gibbosum* might also

vector diseases such as aspergillosis among gorgonian colonies, as some coral predators are known to vector diseases as they feed on different colonies (Sussman et al. 2003; Williams and Miller 2005). If *C. gibbosum* vectors disease, or if damaged tissues are more susceptible to infection, then predator removal that leads to release of *C. gibbosum* populations could increase disease outbreaks, and such diseases are a major driver of gorgonian population dynamics (Kim and Harvell 2004).

One concern with using cages to examine the effects of predation is the potential for caging artifacts to confound the interpretation of the results (Connell 1997; Hindell et al. 2001). Thus, partial cages are often used to separate the effects of excluding predators and the effects of the cages themselves on prey densities. We did not use partial cages because, on these reefs, large control cages attract unnaturally high densities of large predatory fishes (M. E. Hay, personal observation) and because previous tests could find no effects of this large mesh size on benthic organisms due to shading or alterations of flow (Miller and Hay 1998). However, we assessed several possible cage artifacts that might have confounded our results; we could detect no such effects. First, caging did not affect the abundance of gorgonians (Fig. 1), the principal benthic organisms that would attract *C. gibbosum*. Second, total

macroalgal cover and algal species composition differed considerably among the different fish enclosure treatments inside the cages (D.E. Burkepile, unpublished data), but these differences did not affect *C. gibbosum* densities within the different cage treatments. Third, sediment accumulation on top of cinderblocks in caged versus uncaged areas did not differ, suggesting that hydrodynamic regimes were not strongly affected by the cages. Thus, differences in the abundance of *C. gibbosum* and their subsequent effects on gorgonians are likely due to differential predation pressure between caged and uncaged areas rather than to caging artifacts.

Increasing evidence suggests that overfishing of large, predatory fishes on coral reefs leads to a decline in reef health through population expansions of invertebrates such as coral-eating starfish and urchins, whose feeding decreases coral cover and increases erosion of the reef structure (McClanahan and Shafir 1990; Dulvy et al. 2004). We show that excluding large predators from areas of a coral reef released the normally rare gastropod *C. gibbosum* from top-down control and resulted in dramatic increases in their density and in their consumption of gorgonians. Our work further emphasizes the importance of large predators in maintaining the healthy function of coral reefs.

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