Density and Gorgonian Host-occupation Patterns by Flamingo Tongue Snails (*Cyphoma gibbosum*) in the Florida Keys

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ABSTRACT.—A large-scale assessment of the density and gorgonian host-occupation patterns of the ovulid gastropod *Cyphoma gibbosum* L. was conducted at 63 shallow (< 7 m), low-relief hard-bottom and spur and groove sites in the Florida Keys. Mean densities of *C. gibbosum* were not significantly different between habitat types, among geographic regions, or between fished and protected areas. Based on sample allocation analyses, spur and groove sites open to fishing in the lower Keys region yielded more *C. gibbosum* than expected. Most *C. gibbosum* occurred individually (58 %) or in pairs (31 %) on gorgonians, indicating more gregariousness than expected based on random distribution. Snails were counted on 127 gorgonians representing 3 families and 12 species. Significant differences in gorgonian host-occupation were detected, with more Plexauridae and less Gorgoniidae occupied than expected. *Eunicea tourneforti, Plexaura flexuosa, P. homomalla,* and *Pseudoplexaura porosa* were occupied more than expected, while *Gorgonia ventalina* was occupied in proportion to its abundance. *Pseudopterogorgia americana* and other gorgonians were under-occupied, even when relatively abundant. Except for *P. homomalla, C. gibbosum* density was only weakly correlated with total gorgonian density and individual species densities. Spatial variations in *C. gibbosum* density are not readily explained by preferred gorgonian availability alone. While variable larval recruitment, post-settlement survival, and patchy gorgonian distribution may affect these patterns, differential predation pressure by fishes such as hogfish (*Lachnolaimus maximus*) could also partially explain the distribution patterns of *C. gibbosum* in the Florida Keys.

INTRODUCTION

Gorgonians occur at their greatest diversity and density in the wider Caribbean, often exceeding reef-building corals in species richness and colony density (Lasker and Coffroth, 1983; Yoshioka and Yoshioka, 1989). Most gorgonian predators, including ovulid gastropods such as the flamingo tongue *Cyphoma gibbosum* Linnaeus, cause only partial colony mortality, ranging from consumption of the polyps to rasping of the axial coenochyme, sometimes to the depth of the proteinaceous axis (Harvell and Fenical, 1989; Neudecker, 1985).

Usually found in male and female pairs, *C. gibbosum* is a generalist browser and has been the subject of numerous studies concerned with distribution and gorgonian occupancy patterns in the Caribbean (e.g., Birkeland and Gregory, 1975; Hazlett and Bach, 1982; Harvell and Suchanek, 1987).

Several hypotheses have been proposed to explain the factors that control *C. gibbosum* populations in typically prey-rich environments: recruitment limitation (which has yet to be adequately studied), predation by hogfish (*Lachnolaimus maximus*) and other predators (Randall and Warmke, 1967; Shoup, 1968), gorgonian structural defenses (Lewis and Von Wallis, 1991; Van Alstyne and Paul, 1992; West, 1997), and chemical defenses (Pawlik et al., 1987; Sammarco and Coll, 1992; Pawlik and Fenical, 1989; Van Alstyne and Paul, 1992). Although food abundance may be expected to lead to significant prey preference, considerable variability exists in observed patterns of gorgonian host occupancy by *C. gibbosum*. These patterns range from preference of several species (Birkeland and Gregory, 1975; Lasker et al., 1988) to occupancy of gorgonian species in proportion to their availability (Kinzie, 1970; Harvell and Suchanek, 1987). The variability in experi-

mental results may reflect temporal or geographic differences in preferences or variability in prey quality (Lasker et al., 1988). Gorgonian defenses such as sclerite content (Harvell and Suchanek, 1987; Van Alstyne and Paul, 1992; West, 1997) and secondary metabolites (Hazlett and Bach, 1982; Pawlik et al., 1987; Sammarco and Coll, 1992) do not clearly explain prey utilization patterns. *Cyphoma gibbosum* apparently tolerates high levels of gorgonian terpenes (Vrolijk and Targett, 1992) and may sequester these compounds in its mantle, like other ovulid gastropods do (Coll et al., 1983).

This paper presents a large-scale assessment of the density and gorgonian host-occupation patterns of *C. gibbosum* in the Florida Keys. While limited in temporal scope, the study is the first that considers multiple spatial scales, including comparisons between fished and protected areas established in 1997 in the Florida Keys National Marine Sanctuary. Two general questions are addressed. First, are there significant differences in the distribution and density of *C. gibbosum* in the Florida Keys between shallow fore reef habitats, among geographic regions, and between fished and protected areas? Second, are spatial variations in gorgonian host occupancy related to which gorgonian species are preferred hosts, occupied in proportion to their availability, or under-occupied by *C. gibbosum*?

MATERIALS AND METHODS

Study area

The Florida Keys are an archipelago of limestone islands extending approximately 360 km from Key Biscayne to the Dry Tortugas (Fig. 1). Along the seaward edge or platform margin of the south Florida shelf is the reef tract, a semi-continuous series of offshore bank-barrier reefs. Bank-barrier reefs are separated from the islands by Hawk Channel, a V-shaped basin 5 m to 12 m deep that is dominated by sand, seagrass beds, and patch reefs (FDEP, 1998). Twenty-three no-fishing zones, most 1-2 km^2, were established in 1997 in the Florida

Keys National Marine Sanctuary (NOAA, 1996) and encompass many of the best-developed offshore bank-barrier reefs. The no-fishing zones provide an opportunity to evaluate the direct and indirect effects of fishing in the Florida Keys (Bohnsack and Ault, 1996). Most of the offshore no-fishing zones extend seaward to only 13-15 m depth, with the fore reef environment within the zones characterized by high-relief spur and groove topography or low-relief hard-bottom (Chiappone and Sullivan, 1997). Acroporid corals historically dominated the shallower areas of the fore reef in some locations, but they no longer form extensive thickets of live colonies (Dustan and Halas, 1987; Porter and Meier, 1992). The upper Keys region, excluding Pickles Reef sampled in this study, was formerly encompassed within the Key Largo National Marine Sanctuary (established in 1975) and the Pennekamp Coral Reef State Park (established in1960), which prohibited spear-fishing and collecting for marine aquaria. The remaining area of the Florida Keys, from southwest of Molasses Reef to Key West, excluding Looe Key, has not been protected from spear-fishing and marine aquarium collecting except within the Sanctuary zones established in 1997.

Survey methods

Cyphoma gibbosum densities, gorgonian densities, and gorgonian host-occupancy patterns were assessed by habitat type, geographic region, and between protected areas and fished sites in the Florida Keys (Table 1). Surveys were undertaken as part of an ongoing assessment of the community structure and condition of coral reef and hard-bottom benthos in relation to the zoning plan for the Sanctuary (Miller et al., in press). Sixty-three sites were surveyed from southwest of Key West to northern Key Largo during June to September 2001, spanning over 200 km of the reef tract (Fig. 1). The shallow platform margin (1-7 m depth) was stratified with respect to two habitat types (high-relief spur and groove and low-relief hard-bottom), three regional sectors, and 10 of the Sanctuary's 23 no-
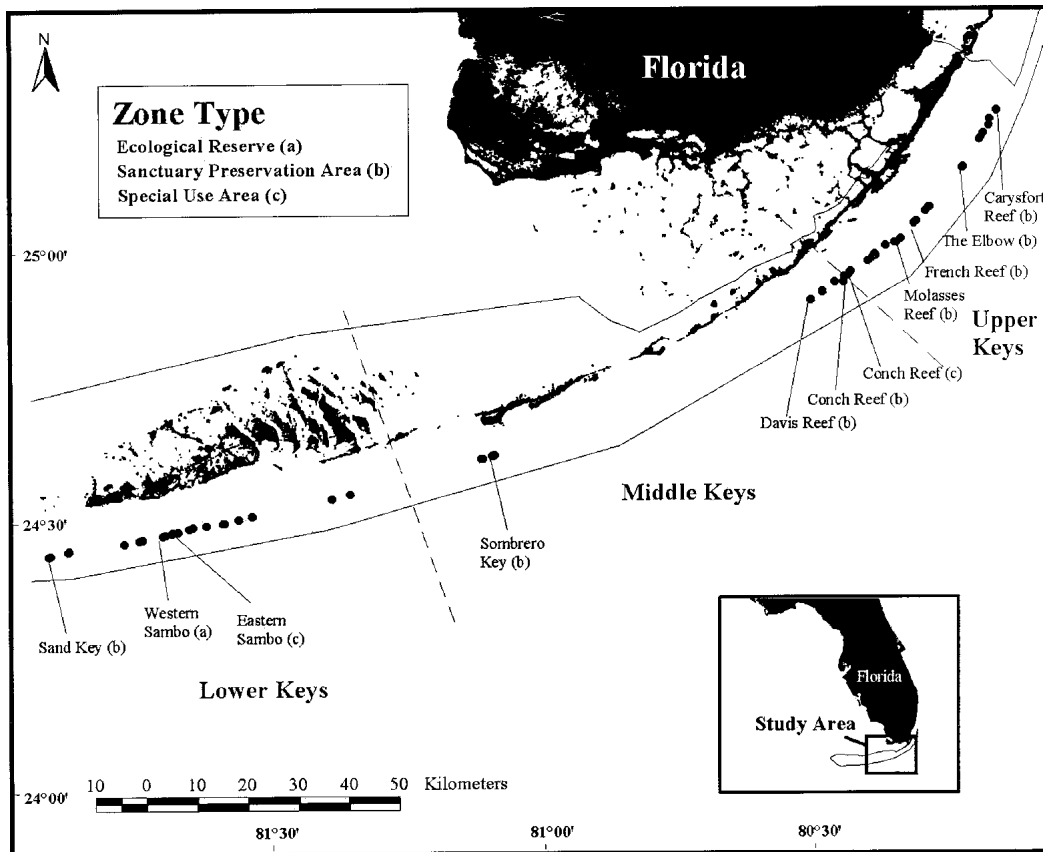
FIG. 1. Low-relief hard-bottom and spur and groove sites sampled for *Cyphoma gibbosum* on the Florida Keys shallow platform margin during June-September 2001. Closed dots (●) represent individual survey sites and zone types represent different name designations for no-fishing zones in the Florida Keys National Marine Sanctuary.

fishing zones (Table 1). The fore reef habitat types sampled represent considerable variability in geomorphology, topographic complexity, benthic community structure, and gorgonian density patterns. Sites open to fishing in the spur and groove habitat included Western Dry Rocks, Marker 32, Middle Sambo, No Name Reef, Pelican Shoal, American Shoal, Delta Shoal, Pickles Reef, and Sand Island. Sites open to fishing in the hard-bottom habitat included Marker 26, Maryland Shoal, Big Pine Shoal, Delta Shoal, Crocker Reef, Little Conch Reef, Northeast of French Reef, and Dixie Shoal.

A two-stage, stratified sampling design was used to assess density differences in *C. gibbosum* and gorgonian host availability,

following procedures outlined in Cochran (1977). Spatial areas comprising each of the sampling strata were constructed in a geographical information system (GIS) with a grid of 200 × 200 m "blocks" or sites that served as the primary sampling units. Calculations of stratum areas and random allocations of sampling stations within strata were performed with the GIS. Each site that contained spur and groove or low-relief hard-bottom, as determined from FDEP (1998) habitat mapping, was assigned a unique number and randomly selected for sampling from a discrete uniform probability distribution to ensure that each primary unit had equal selection probability. Second-stage sampling units (i.e., transect locations) were then randomly positioned

TABLE 1. Mean (± 1 standard error) densities (no. individuals per m²) of *Cyphoma gibbosum* and branching gorgonians by habitat type, geographic region, and management zone in the Florida Keys. Four 20 m² plots were surveyed for *C. gibbosum* and two 10 m² plots were surveyed for gorgonians at each site. Total gorgonian densities do not include the encrusting gorgonian *Erythropodium caribaeorum* (F. Anthothelidae). No-fishing zones are indicated with asterisks (*).

Strata/site location (no. sites)	*C. gibbosum* no./m²	Briareidae no./m²	Gorgoniidae no./m²	Plexauridae no./m²	Total gorgonians no./m²
High-relief spur & groove (34)	0.031 ± 0.008	0.04 ± 0.02	4.24 ± 0.56	0.91 ± 0.17	5.18 ± 0.63
Lower Keys Region (17)	0.042 ± 0.012	0.01 ± 0.01	1.02 ± 0.30	0.96 ± 0.32	1.99 ± 0.61
No-fishing zones (8)	0.016 ± 0.006	0.03 ± 0.02	0.55 ± 0.12	0.48 ± 0.13	1.06 ± 0.21
Sand Key* (2)	0.013 ± 0.005	0.03 ± 0.03	0.90 ± 0.39	0.50 ± 0.33	1.43 ± 0.71
Eastern Dry Rocks* (2)	0.013 ± 0.013	0 ± 0	0.48 ± 0.09	0.15 ± 0.06	0.63 ± 0.11
Western Sambo* (2)	0.03 ± 0.013	0.07 ± 0.06	0.68 ± 0.05	0.43 ± 0.19	1.18 ± 0.21
Eastern Sambo* (2)	0.025 ± 0.025	0.03 ± 0.03	0.15 ± 0.06	0.83 ± 0.36	1.00 ± 0.44
Fished areas (9)	0.065 ± 0.019	0 ± 0	1.44 ± 0.54	1.39 ± 0.59	2.83 ± 1.12
Middle Keys Region (3)	0.013 ± 0.013	0 ± 0	2.87 ± 0.99	1.43 ± 0.41	4.30 ± 1.33
No-fishing zones (2)	0.019 ± 0.019	0 ± 0	1.43 ± 0.28	0.88 ± 0.29	2.30 ± 0.53
Sombrero Key* (2)	0.019 ± 0.019	0 ± 0	1.43 ± 0.28	0.88 ± 0.29	2.30 ± 0.53
Fished areas (1)	0 ± 0	0 ± 0	5.75 ± 1.35	2.55 ± 0.45	8.30 ± 0.90
Upper Keys Region (14)	0.021 ± 0.012	0.09 ± 0.04	8.43 ± 0.78	0.73 ± 0.12	9.25 ± 0.85
No-fishing zones (8)	0.008 ± 0.006	0.08 ± 0.04	7.95 ± 1.16	0.64 ± 0.13	8.68 ± 1.21
Molasses Reef* (2)	0.006 ± 0.006	0 ± 0	6.38 ± 0.69	0.68 ± 0.29	7.05 ± 0.53
Elbow Reef* (2)	0.025 ± 0.022	0 ± 0	9.60 ± 3.80	0.55 ± 0.18	10.15 ± 3.91
Carysfort Reef* (4)	0 ± 0	0.16 ± 0.07	7.91 ± 1.48	0.68 ± 0.21	8.75 ± 1.62
Fished areas (6)	0.038 ± 0.025	0.09 ± 0.07	9.08 ± 0.98	0.84 ± 0.21	10.01 ± 1.17
Low-relief hard-bottom (29)	0.019 ± 0.005	0.02 ± 0.01	8.79 ± 0.80	2.21 ± 0.25	11.01 ± 0.86
Lower Keys Region (7)	0.025 ± 0.009	0 ± 0	5.31 ± 0.51	3.68 ± 0.45	8.99 ± 0.88
Fished areas (7)	0.025 ± 0.009	0 ± 0	5.31 ± 0.51	3.68 ± 0.45	8.99 ± 0.88
Middle Keys Region (13)	0.015 ± 0.006	0.01 ± 0.01	8.83 ± 0.83	2.14 ± 0.40	10.98 ± 0.91
No-fishing zones (4)	0.013 ± 0.007	0.03 ± 0.02	7.90 ± 0.78	0.96 ± 0.19	8.89 ± 0.87
Davis Reef* (2)	0.013 ± 0.007	0 ± 0	7.88 ± 1.10	0.63 ± 0.21	8.50 ± 1.15
Conch Reef* (2)	0.013 ± 0.013	0.05 ± 0.03	7.93 ± 1.28	1.30 ± 0.22	9.28 ± 1.45
Fished areas (9)	0.017 ± 0.008	0.01 ± 0.01	9.24 ± 1.14	2.67 ± 0.52	11.92 ± 1.21
Upper Keys Region (9)	0.019 ± 0.012	0.03 ± 0.02	11.43 ± 2.10	1.16 ± 0.26	12.62 ± 2.33
Fished areas (9)	0.019 ± 0.012	0.03 ± 0.02	11.43 ± 2.10	1.16 ± 0.26	12.62 ± 2.33

within each primary unit. The small sizes of most of the no-fishing zones permitted the random allocation of two replicate sites for a particular habitat stratum. Within each site, four pre-generated, random sampling points were located using differential GPS. Two paired, 25 m transects were deployed at each sampling point per site, typically from inshore to offshore. Using a 40 cm scale bar, a 0.4 m swath or band along each transect (each 10 m² in area) was surveyed for *C. gibbosum*, and for the species, number, and maximum colony height of gorgonians occupied by the snail. Two of the 0.4 m × 25 m transects were surveyed for the species and colony numbers of all gorgonians. One observer completed all the surveys.

Data analysis

Statistical comparisons of mean densities were performed by calculating confidence intervals (CI) based on the equation CI = mean ± $t_{[\alpha, df]}$* standard error. Standard errors were estimated by the two-stage, stratified random sampling design (Cochran, 1977). Confidence intervals were adjusted for multiple comparisons using the Bonferroni procedure (Miller, 1981). The experiment-wise error was held at $\alpha = 0.05$ and the comparison-wise error was adjusted based on the number of multiple comparisons (comparison-wise error rate = α/c, where c = {k (k-1)}/2 and k = number of comparisons). Mean densities of *C. gibbosum* and gorgonians were compared sta-

tistically for differences between habitat types, among geographic regions, and between protected and fished areas.

Goodness of fit procedures using chi-square analysis was used to address the following questions. First, is occurrence frequency of *C. gibbosum* independent of habitat type, geographic region, and management zone in the Florida Keys? Second, are snails randomly distributed on gorgonian hosts? Third, is the distribution of *C. gibbosum* on gorgonian hosts independent of gorgonian family and species? For the first hypothesis, the frequency of snails was compared to the expected distribution by habitat type, geographic region, and management zone, assuming the null model that distribution was proportional to sampling effort. For the second hypothesis, the number of individuals per gorgonian prey was evaluated against the expected number if *C. gibbosum* was randomly distributed, using the equation $P(X) = (\mu^X)/e^\mu X!$ to compute the expected Poisson frequencies (Zar, 1996). For the third hypothesis, the pattern of gorgonian host occupancy by *C. gibbosum* among gorgonian families and species was compared against the expected distribution, calculated by multiplying the total number of snails occupying gorgonians by the proportional availability of gorgonians by family and species. Prey selection was assessed using Ivlev's index of electivity (e) = $(r_i - P_i)/(r_i + P_i)$, where r_i is the proportion of prey species i utilized and P_i = proportion of prey species i available. This index rates species utilization from −1 to +1, with −1 indicating total rejection, 0 indicating that prey are taken in proportion to their abundance, and +1 indicating a preference of host species to the exclusion of others (Manly et al., 1993). Correlation analyses using the Spearman rank correlation coefficient were used to explore the relationships between gorgonian occupancy by *C. gibbosum* and gorgoninan availability (Zar, 1996).

RESULTS

Spatial distribution and density patterns

Surveys yielded 129 snails and all except one occurred on gorgonian colonies (99.2 %).

Of the 128 individuals occupying gorgonians, one was on the basal attachment and the others were on the upper regions of the colonies. Occupied gorgonians ranged in maximum height from 8-106 cm.

The first part of this study searched for significant differences in the distribution and density of *C. gibbosum* in shallow fore reef habitats. Site density was very variable, ranging from no individuals recorded (40 % of sites) to 0.2 individuals/m² (Table 1). Chi-square indicated that more snails (66 %) occurred in all spur and groove sites compared to hard-bottom ($X^2 = 7.38$, df = 1, $0.01 > P > 0.005$). Mean *C. gibbosum* density was 1.6 times greater in spur and groove than in hard-bottom, but the difference was not significant (t-test; $P > 0.05$). The discrepancy between both statistical tests reflected the substantial inter-site variability in density within the spur and groove habitat stratum. Within this habitat, more snails than expected were recorded from the lower Keys region ($X^2 = 13.22$, df = 2, $0.005 > P > 0.001$) (Fig. 2A). Mean densities among geographic regions were 0.042 individuals/m² in the lower Keys, 0.013 individuals/m² in the middle Keys, and 0.021 individuals/m² in the upper Keys (Table 1), but the variations were not significant. Less regional variation was apparent in the hard-bottom habitat, where mean *C. gibbosum* densities were 0.025 individuals/m² in the lower Keys, 0.015 individuals/m² in the middle Keys, and 0.019 individuals/m² in the middle Keys.

A significant difference in the frequency of *C. gibbosum* ($X^2 = 33.997$, df = 1, $P < 0.001$) was found between all protected and fished areas within the spur and groove habitat type. Specifically, 81 % of all individuals found within the spur and groove habitat were recorded from fished areas, despite representing only 47 % of the sampling effort within this habitat stratum (Fig. 2B). Differences in snail frequency between protected and fished areas were most obvious in the lower Keys ($X^2 = 19.12$, df = 1, $P < 0.001$), where the mean density from fished areas (0.067 individuals/m²) was 3.9 times greater than from protected areas (0.017 individuals/m²) (Table 1). Similarly, mean density was greater in upper Keys fished
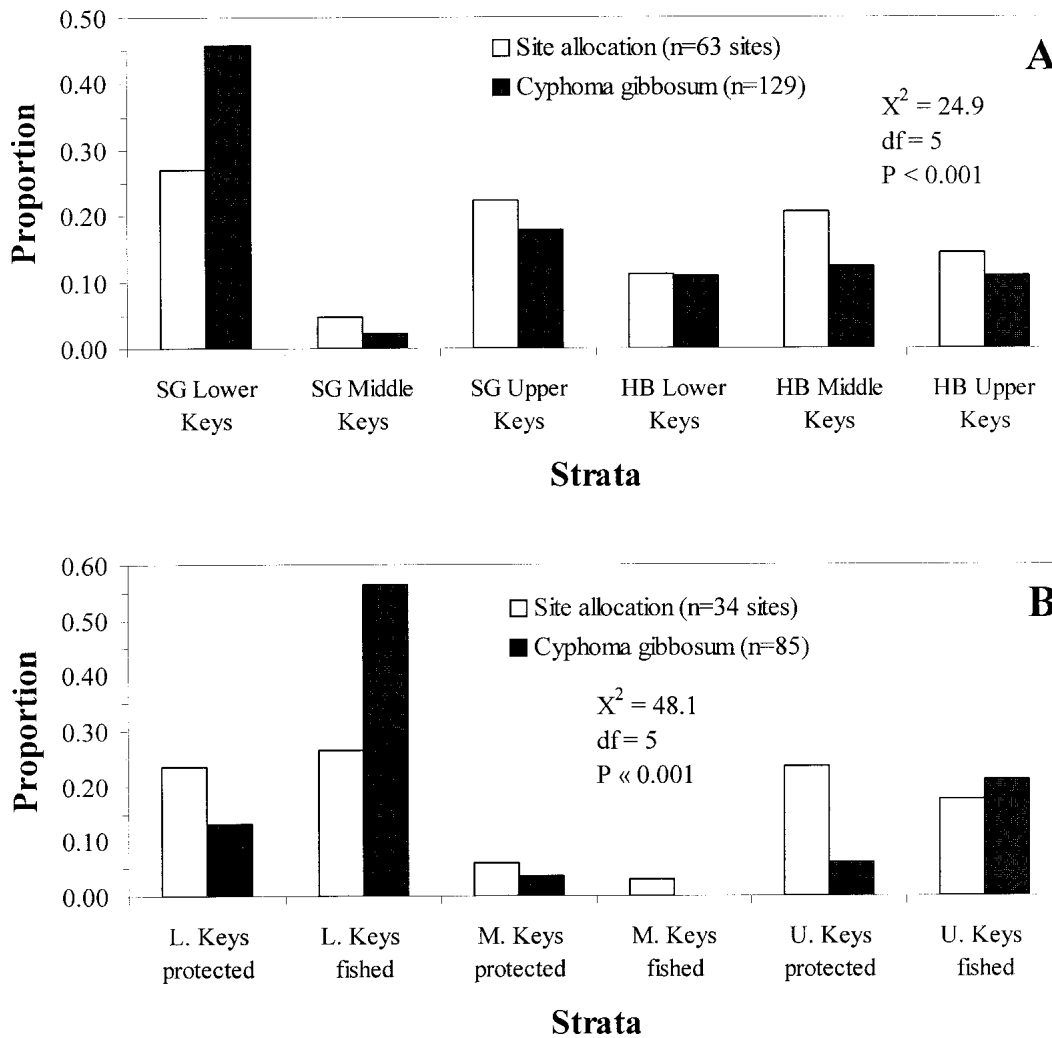
FIG. 2. Distribution of *Cyphoma gibbosum* by (A) habitat type and regional sector and (B) geographic region and management type for spur and groove. SG = spur and groove, HB = hard-bottom, NTZ = no-fishing zones, and ref = fished areas. Site allocation refers to the proportion of sites sampled in each stratum defined by habitat type, regional sector, and protection from fishing.

areas (0.038 individuals/m^2) compared to protected areas (0.008 individuals/m^2). Spur and groove habitat is not common in the middle Keys and only one fished and one non-fished sites were sampled.

Gorgonian host occupancy

The second part of this study addressed the gorgonian occupancy patterns of *Cyphoma gibbosum* in the Florida Keys to determine which species are preferred hosts,

occupied in proportion to their availability, or under-occupied relative to availability. Occupancy patterns were then evaluated to assess if spatial variations were related to the availability of preferred gorgonian hosts. From the 63 sites, 126 transects were sampled for gorgonian species composition and density. Twenty-four gorgonian taxa (not including the encrusting *Erythropodium caribaeorum*), and 9911 branching colonies were counted, represented by the families Briareidae (38 colonies or 0.38 %),

Gorgoniidae (7977 colonies or 80.5 %), and Plexauridae (1896 colonies or 19.1 %) (Table 1). Mean densities of Plexauridae, Gorgoniidae, and total gorgonians were significantly greater (P < 0.05) in low-relief hard-bottom, a pattern opposite that of snail densities. Geographic variations in mean gorgonian density were apparent in the spur and groove habitat, with mean densities of Gorgoniidae and total gorgonians significantly greater (P < 0.02) in the upper Keys compared to the middle and lower Keys. This pattern contrasted with the snail density patterns found in the spur and groove habitat.

   Cyphoma gibbosum was found on 11 gorgonian species belonging to three families (Table 2). Most snails occurred individually (58 %) or in pairs (31 %) (Fig. 3A), thus departing significantly (X^2 test; P < 0.001) from the Poisson distribution. The Spearman rank correlation coefficient test found no significant correlation between *C. gibbosum* densities and total gorgonian densities among the 63 sites (r = -0.218, P > 0.05). There was no significant correlation (P > 0.05) between snail density and density of gorgonian families or individual species, except for *Plexaura homomalla* (r = 0.337, P < 0.01). When only spur and groove reefs were considered (34 sites and where 66 % of all *C. gibbosum* were found), there was no significant correlation between *C. gibbosum* densities and particular gorgonian families and species.

   The family Plexauridae was the most

TABLE 2. Gorgonian host occupancy (r_i) by *Cyphoma gibbosum* on Florida Keys offshore spur and groove and hard-bottom habitats relative to prey availability (P_i). Host availability data do not include the encrusting gorgonian *Erythropodium caribaeorum* (Anthothelidae). Selectivity was calculated using Ivlev's electivity index (Ivlev, 1961). f = frequency of occupancy or availability, r_i = proportion of gorgonians occupied, P_i = proportion of hosts available.

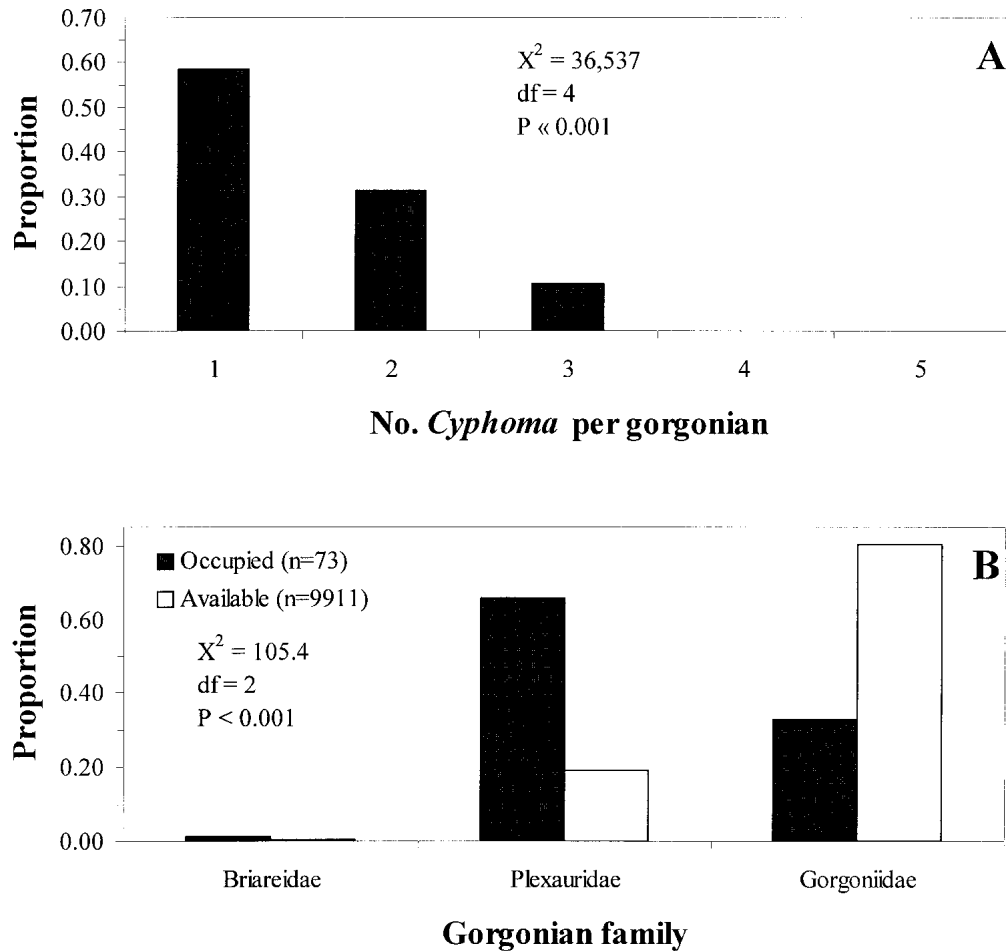| Gorgonian family/species	Gorgonian occupancy		Gorgonian availability		Electivity index $(r_i - P_i)/(r_i + P_i)$
	f	r_i	f	P_i	
Briareidae					
Briareum asbestinum	1	0.0137	38	0.0038	+0.57
Plexauridae					
Eunicae calyculata	0	0	37	0.0037	−1.00
E. fusca	0	0	241	0.0243	−1.00
E. laciniata	0	0	37	0.0037	−1.00
E. mammosa	8	0.1096	396	0.0400	+0.47
E. succinea	0	0	9	0.0009	−1.00
E. tourneforti	8	0.1096	206	0.0208	+0.68
Muricae atlantica	0	0	44	0.0044	−1.00
M. muricata	2	0.0274	181	0.0183	+0.20
Muriceopsis flavida	0	0	33	0.0033	−1.00
Plexaura flexuosa	23	0.3151	394	0.0398	+0.78
P. homomalla	4	0.0548	109	0.0110	+0.67
Plexaurella dichotoma	1	0.0137	49	0.0049	+0.47
P. grisea	0	0	14	0.0014	−1.00
Pseudoplexaura spp.	0	0	83	0.0084	−1.00
P. porosa	2	0.0274	63	0.0064	+0.62
Gorgoniidae					
Gorgonia ventalina	14	0.1918	2370	0.2391	−0.11
Pseudopterogorgia acerosa	2	0.0274	428	0.0432	−0.22
P. americana	8	0.1096	4064	0.4100	−0.58
P. bipinnata	0	0	877	0.0885	−1.00
P. rigida	0	0	6	0.0006	−1.00
Pterogorgia anceps	0	0	9	0.0009	−1.00
P. citrina	0	0	222	0.0224	−1.00
P. guadalupensis	0	0	1	0.0001	−1.00
Total	73	1.0000	9911	1.0000	

FIG. 3. (A) Proportional incidence of the number of *Cyphoma gibbosum* per gorgonian colony and (B) proportional occupancy of *C. gibbosum* by gorgonian family. In the lower figure, available gorgonians refers to the total number of colonies sampled (9911) and white bars refer to the proportion of this total represented by three different families. The proportion of gorgonians occupied by *C. gibbosum*, indicated by the filled bars, represents the proportion of the 73 cases of occupancy among the three gorgonian families. For example, although only about 20 % of the 9911 gorgonians sampled were represented by Plexauridae, over 60 % of the 73 *C. gibbosum* incidences were found on Plexauridae.

commonly occupied (66 %) by *C. gibbosum*, followed by Gorgoniidae (33 %) and Briareidae (< 2 %) (Fig. 3B). The distribution of snails on gorgonians was dependent upon the family ($X^2 = 105.4$, df = 2, P < 0.001) and species of gorgonians ($X^2 = 213.8$, df = 10, P < 0.001). Fewer Gorgoniidae and more Plexauridae were occupied than expected, assuming the null model that occupancy was proportional to availability ($X^2 = 170.8$, df = 2, P < 0.001).

The most common gorgonians occupied by *C. gibbosum* were *Plexaura flexuosa* Lamouroux (31.5%), *Gorgonia ventalina* Linnaeus (19.2%), *Eunicea mammosa* Lamouroux (11%), *E. tourneforti* Milne Edwards and Haime (11%), and *Pseudopterogorgia americana* (Gmelin) (11%) (Table 2). Among the 63 sites, selectivity indices indicated preference for *P. flexuosa, E. tourneforti, P. homomalla, Pseudoplexaura porosa* (Houttuyn), and *Briareum asbestinum* (Pallas) (Table 2). The sea fan *G. ventalina*, although commonly encountered with *C. gibbosum*, was occupied only in proportion to its availability. The remaining gorgonians

(e.g., the sea plume *P. americana*) were not occupied or were under-occupied in proportion to their availability. Comparisons among geographic regions, between preferred gorgonians and their availability between habitat types, and between fished and protected areas, yielded unexpected results (Table 3). The gorgonians more commonly occupied by *C. gibbosum* were generally the most abundant (up to ten times more) in hard-bottom compared to spur and groove sites, while *C. gibbosum* densities exhibited an opposing pattern.

DISCUSSION

This study encompassed many sites, stratified with respect to habitat type, geographic region, and management zone, to evaluate the density and gorgonian host-occupancy patterns of *C. gibbosum*. Although considerable variability occurred between sites and years, density values were similar to those reported by Lasker and Coffroth (1988). Snails exhibited a clumped distribution on gorgonian hosts, mirroring previous results from the Virgin Islands (Birkeland and Gregory, 1975; Hazlett and Bach, 1982) and Panama (Lasker and Coffroth, 1988). Although more solitary individuals were found than pairs or aggregations, it is possible that these individuals were searching for mates (Ghiselin and Wilson, 1966). Lasker and Coffroth (1988) propose that the clumped distribution of *C. gibbosum* could be due to intra-colony variation in secondary metabolite content of gorgonians, while Gerhart (1986) proposes that gregariousness is due to mucous trail following. All but one snail found during our study occupied gorgonians. Birkeland and Gregory (1975) found only 1 % of individuals on the substratum, and Harvell and Suchanek (1987) showed that *C. gibbosum* generally avoids even the basal regions of gorgonians. Our results indicate that gorgonian hosts are readily available and that *C. gibbosum* is probably not food limited.

The distribution patterns of *C. gibbosum* are produced by at least two independent processes: the movement of individuals to colonies (Lasker et al., 1988) and the time spent on a colony (Gerhart, 1986; Lasker and Coffroth, 1988). Considering the differences in gorgonian density patterns and management histories of the various regions surveyed in the Florida Keys, we expected greater snail densities in low-relief hard-bottom areas with higher gorgonian densities. However, more snails were

TABLE 3. Comparisons of mean (± 1 standard error) densities (no. colonies per m^2) of selected gorgonians occupied by *C. gibbosum* by habitat type, geographic region, and management zone in the Florida Keys.

Strata/site location (no. sites)	E. tourneforti	P. flexuosa	P. porosa	G. ventalina	P. americana
High-relief spur and groove (34)	0.08 ± 0.02	0.25 ± 0.04	0.06 ± 0.03	1.59 ± 0.19	1.14 ± 0.21
Lower Keys Region (17)	0.05 ± 0.03	0.23 ± 0.07	0.08 ± 0.05	0.60 ± 0.12	0.33 ± 0.15
No-fishing zones (8)	0.02 ± 0.02	0.14 ± 0.05	0 ± 0	0.42 ± 0.09	0.13 ± 0.05
Fished areas (9)	0.08 ± 0.05	0.30 ± 0.12	0.16 ± 0.09	0.77 ± 0.20	0.50 ± 0.28
Middle Keys Region (3)	0.05 ± 0.02	0.43 ± 0.25	0.22 ± 0.09	0.98 ± 0.17	1.30 ± 0.53
No-fishing zones (2)	0.02 ± 0.02	0.13 ± 0.13	0.28 ± 0.13	0.83 ± 0.18	0.50 ± 0.09
Fished areas (1)	0.10 ± 0.00	1.05 ± 0.55	0.10 ± 0.10	1.30 ± 0.30	2.90 ± 0.50
Upper Keys Region (14)	0.11 ± 0.04	0.23 ± 0.04	0.01 ± 0.01	2.91 ± 0.31	2.10 ± 0.40
No-fishing zones (8)	0.03 ± 0.01	0.23 ± 0.05	0.01 ± 0.01	2.69 ± 0.26	1.13 ± 0.41
Fished areas (6)	0.23 ± 0.07	0.23 ± 0.06	0.01 ± 0.01	3.22 ± 0.64	3.39 ± 0.59
Low-relief hard-bottom (29)	0.26 ± 0.03	0.39 ± 0.05	0.03 ± 0.01	2.22 ± 0.26	5.67 ± 0.54
Lower Keys Fished Areas (7)	0.43 ± 0.08	0.74 ± 0.07	0.10 ± 0.04	1.33 ± 0.23	3.21 ± 0.37
Middle Keys Region (13)	0.24 ± 0.03	0.33 ± 0.06	0.02 ± 0.01	2.28 ± 0.28	5.71 ± 0.71
No-fishing zones (4)	0.21 ± 0.04	0.19 ± 0.04	0 ± 0	2.23 ± 0.42	5.04 ± 0.53
Fished areas (9)	0.25 ± 0.04	0.39 ± 0.08	0.03 ± 0.02	2.31 ± 0.36	6.01 ± 1.00
Upper Keys Region (9)	0.17 ± 0.05	0.21 ± 0.06	0 ± 0	2.84 ± 0.69	7.52 ± 1.25
Fished areas (9)	0.17 ± 0.05	0.21 ± 0.06	0 ± 0	2.84 ± 0.69	7.52 ± 1.25

found in spur and groove sites, and without considering preference for particular gorgonian hosts, this result markedly departed from our expectations.

Snails were more abundant in areas with low gorgonian densities, and this lack of correspondence, while not unexpected in a prey-rich environment, indicates that factors in addition to host availability affect *C. gibbosum* densities. For example, if fishing affects snail predators (such as hogfish, *Lachnolaimus maximus*) (Randall and Warmke, 1967) it is possible that higher snail densities within the spur and groove habitat could be explained by protection from fishing. However, snail densities were lower in the upper Keys, which have been long-protected from spear-fishing, than in the lower Keys. This is interesting because spear-fishing is the preferred method for capturing *L. maximus* in the Florida Keys (Harper et al., 2000), and most snails within the upper Keys region were recorded from three sites at Pickles Reef, just southwest of the former Key Largo National Marine Sanctuary, where spear-fishing is permitted.

Predation may have also affected the results. For example, fishery independent surveys of *L. maximums* during 2001 indicated a mean density of 0.122 individuals per sample in spur and groove, and 1.38 individuals per sample in hard-bottom, a pattern inversely related to *C. gibbosum* densities (D. McClellan, NOAA/NMFS, pers. comm.). Similar patterns were observed in the spur and groove habitat between fished and protected sites for the upper and lower Keys, where *C. gibbosum* densities were greater in fished sites and *L. maximus* densities were greater in protected sites.

Most gorgonians were occupied in proportion to their abundance or were under-occupied, while a few species were occupied in disproportion to their availability, indicating possible host preference. The plexaurids *E. tourneforti*, *P. flexuosa*, *P. homomalla*, *P. dichotoma*, and *P. porosa* were occupied preferentially relative to their densities. These results agree somewhat with previous studies, although increasing densities of these gorgonian hosts did not correlate with increased snail densities. The most common gorgonians occupied in Panama were *P. homomalla*, *Pseudoplexaura* spp., and *Pseudopterogorgia* spp. (Lasker and Coffroth, 1988; Lasker et al., 1988), and Lasker and Coffroth (1988) found a strong bias for sea plumes and lesser preferences for other species. Strong preferences for Gorgoniidae, especially sea plumes and *G. ventalina*, were also documented in the Virgin Islands (Birkeland and Gregory, 1975; Harvell and Suchanek, 1987) but in the Florida Keys there was no strong preference for Gorgoniidae despite relatively high densities.

Several mechanisms have been proposed to explain the host occupancy patterns of *C. gibbosum*, principally among them structural and chemical defenses of gorgonians. Harvell and Suchanek (1987) observed that foraging times were negatively correlated with the proportion and size of component sclerites in gorgonians. *Cyphoma gibossum* seems capable of tolerating the unusually high levels of gorgonian chemical defenses (Pawlik et al., 1987; Sammarco and Coll, 1992). For example, this snail is immune to prostaglandins produced by *Plexaura homomalla* (Gerhart, 1986), one of the commonly occupied gorgonians in the Florida Keys.

Water depth (Bayer, 1961), light levels (Muzik, 1982), habitat type (Kinzie, 1970; Opresko, 1973; Lasker and Coffroth, 1983), frequency and severity of disturbances such as storms (Yoshioka and Yoshioka, 1987), predation (Birkeland and Gregory, 1975; Lasker, 1985; Lasker et al., 1988), and variable recruitment (Yoshioka, 1996) can affect the spatial pattern of gorgonians. Previous studies have concluded that predation, especially by *C. gibbosum*, imposes a minor effect on gorgonians relative to other factors such as colony toppling during storms (Kinzie, 1970), structural failure of the underlying substratum (Wahle, 1985), and sediment scouring and burial (Yoshioka and Yoshioka, 1987). Predation by *C. gibbosum* played a negligible role in gorgonian mortality during a five-year study at two reefs on the southwest coast of Puerto Rico, even though individuals were noted fre-

quently (Yoshioka and Yoshioka, 1991). In the Florida Keys, of the 9911 colonies assessed during this study, approximately 0.5% were occupied by *C. gibbosum*. When spur and groove and low-relief hard-bottom habitats are considered separately, the percentage occupancy was 7.7% and 0.13% for each habitat type, respectively. These estimates, especially for spur and groove reefs, are within the range reported for the Virgin Islands, where 4.7% of the 5483 gorgonians sampled were occupied by *C. gibbosum* (Birkeland and Gregory, 1975).

Our results also provide baseline data to assess the affects of no-take protection within marine protected areas in the sanctuary. These areas produce more and larger fish but effects on the benthos are not well documented. Targeted studies on the relationships between predators and prey, such as hogfish (*Lachnolaimus maximus*) and *C. gibbosum*, including detailed censuses of fishes and snails in multiple habitat types, and experimental work to document predation, will provide important insight into how changing fish communities in marine reserves help to structure the benthos. Other factors that may influence patterns of ovulid gastropods in the Florida Keys, and thus warrant further study, include recruitment variability and diver poaching patterns.

Literature Cited

Bayer, F.M. 1961. The Shallow-water Octocorallia of the West Indian Region: A manual for marine bi-ologists. The Hague, Martinus Nijoff, Netherlands, 373 pp.

Birkeland, C. and B. Gregory. 1975. Foraging behavior and rates of feeding of the gastropod, *Cyphoma gibbosum* (Linnaeus). Bull. Nat. Hist. Mus. Los Angeles Co. 20: 57-67.

Bohnsack, J.A. and J.S. Ault. 1996. Management strategies to conserve marine biodiversity. Oceanography 9: 73-82.

Chiappone, M. and K.M. Sullivan. 1997. Rapid assessment of reefs in the Florida Keys: Results from a synoptic survey. Proc. 8th Int. Coral Reef Symp., Panama 2: 1509-1514.

Cochran, W.G. 1977. Sampling techniques, 3rd edition. Wiley & Sons, NY.

Coll, J.C., D.M. Taprolas, B.F. Bowden, L. Webb and H. Marsh. 1983. Transformation of soft coral (Coelenterata: Octocorallia) terpenes by *Ovula ovum* (Mollusca: Prosobranchia). Mar. Biol. 74: 35-40.

Dustan, P. and J.C. Halas. 1987. Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. Coral Reefs 6: 91-106.

FDEP (Florida Department of Environmental Protection). 1998. Benthic habitats of the Florida Keys. FMRI Technical Report TR-4, St. Petersburg, FL, 53 pp.

Gerhart, D.J. 1986. Gregariousness in the gorgonian-eating gastropod *Cyphoma gibbosum*: tests of several possible causes. Mar. Ecol. Prog. Ser. 31: 255-263.

Ghiselin, M.T. and B.R. Wilson. 1966. On the anatomy, natural history and reproduction of *Cyphoma*, a marine prosobranch gastropod. Bull. Mar. Sci. 16: 132-141.

Harper, D.E., J.A. Bohnsack and B. Lockwood. 2000. Recreational fisheries in Biscayne National Park, Florida, 1976-1991. Mar. Fish. Rev. 62: 8-26.

Harvell, C.D. and W. Fenical. 1989. Chemical and structural defenses of Caribbean gorgonians (*Pseudopterogorgia* spp.): Intracolony localization of defense. Limnol. Oceanogr. 34: 383-389.

Harvell, C.D. and T.H. Suchanek. 1987. Partial predation on tropical gorgonians by *Cyphoma gibbosum* (Gastropoda). Mar. Ecol. Prog. Ser. 38: 37-44.

Hazlett, B.A. and C.H. Bach.1982. Distribution pattern of the flamingo tongue snail (*Cyphoma gibbosum*) on its gorgonian prey (*Briareum asbestinum*). Mar. Behav. Physiol. 8: 305-309.

Kinzie, R.A. 1970. The ecology of the gorgonians (Cnidaria, Octocorallia) of Discovery Bay, Jamaica. Ph.D. Dissertation, Yale University, New Haven, CT.

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. and M.A. Coffroth. 1983. Octocoral distributions at Carrie Bow Cay, Belize. Mar. Ecol. Prog. Ser. 13: 21-28.

Lasker, H.R. and M.A. Coffroth. 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., M.A. Coffroth and L.M. Fitzgerald. 1988. Foraging patterns of *Cyphoma gibbosum* on octocorals: The roles of host choice and feeding preference. Biol. Bull. 174: 254-266.

Lewis, J.C. and E. Von Wallis. 1991. The function of surface sclerites in gorgonians (Coelenterata, Octocorallia). Biol. Bull. 181: 275-288.

Manly, B.F.J., L.L. McDonald and D.L. Thomas. 1993. Resource selection by animals: Statistical design and analysis for field studies. Chapman & Hall, NY, 177 pp.

Miller, R.G. 1981. Simultaneous statistical inference. Springer-Verlag, NY, 200 pp.

Miller, S.M., D.W. Swanson and M. Chiappone. In press. Multiple spatial scale assessment of coral reef and hard-bottom community structure in the Florida Keys National Marine Sanctuary. Proc. 9th Int. Coral Reef Symp, Bali.

Muzik, K. 1982. Octocorallia (Cnidaria) from Carrie Bow Cay, Belize. Pp. 303-310 *In* K. Rutzler and I.G. Macintyre (Eds.), The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize. I. Structure and Communities, pp. 303-310. Smithsonian Institution Press, Washington, D.C.

Neudecker, S. 1985. Foraging patterns of chaetodontid and pomacanthid fishes at St. Croix, U.S. Virgin Islands. Proc. 5th Int. Coral Reef Congr., Tahiti 5: 415-420.

NOAA (National Oceanic and Atmospheric Administration). 1996. Final management plan/environmental impact statement. Volume II: Development of the management plan: environmental impact statement. NOS/SRD, Silver Spring, MD, 245 pp.

Opresko, D.M. 1973. Abundance and distribution of shallow-water gorgonians in the area of Miami, Florida. Bull. Mar. Sci. 23: 535-557.

Pawlik, J.R. and W. Fenical. 1989. A re-evaluation of the ichthyodeterrent role of prostaglandins in the Caribbean gorgonian coral *Plexaura homomalla*. Mar. Ecol. Prog. Ser. 52: 95-98.

Pawlik, J.R., M.T. Burch and W. Fenical. 1987. Patterns of chemical defense among Caribbean gorgonian corals: A preliminary survey. J. Exp. Mar. Biol. Ecol. 108: 55-66.

Porter, J.W. and O.W. Meier. 1992. Quantification of loss and change in Floridian reef coral populations. Amer. Zool. 32: 625-640.

Randall, J.E. and G.L. Warmke. 1967. The food habits of the hogfish (*Lachnolaimus maximus*), a labrid fish from the western Atlantic. Carib. J. Sci. 7: 141-144.

Sammarco, P.W. and J.C. Coll. 1992. Chemical adaptations in the Octocorallia: evolutionary considerations. Mar. Ecol. Prog. Ser. 88: 93-104.

Shoup, J.B. 1968. Shell opening by crabs of the Genus *Calappa*. Science 160: 887-888.

Van Alstyne, K.L. and V.J. Paul. 1992. Chemical and structural defenses in the sea fan *Gorgonia ventalina*: effects against generalist and specialist predators. Coral Reefs 11: 155-159.

Vrolijk, N.H. and N.M. Targett. 1992. Biotransformation enzymes in *Cyphoma gibbosum* (Gastropoda: Ovulidae): implications for detoxification of gorgonian allelochemicals. Mar. Ecol. Prog. Ser. 88: 237-246.

Wahle, C.M. 1985. Habitat-related patterns of injury and mortality among Jamaican gorgonians. Bull. Mar. Sci. 37: 905-927.

West, J.M. 1997. Plasticity in the sclerites of a gorgonian coral: Tests of water motion, light level, and damage cues. Biol. Bull. 192: 279-289.

Yoshioka, P.M. 1996. Variable recruitment and its effects on the population and community structure of shallow-water gorgonians. Bull. Mar. Sci. 59: 433-443.

Yoshioka, P.M. and B.B. Yoshioka. 1987. Variable effects of Hurricane David on the shallow water gorgonians of Puerto Rico. Bull. Mar. Sci. 40: 132-144.

Yoshioka, P.M. and B.B. Yoshioka. 1989. A multispecies, multiscale analysis of spatial pattern and its application to a shallow-water gorgonian community. Mar. Ecol. Prog. Ser. 54: 257-264.

Yoshioka, P.M. and B.B. Yoshioka. 1991. A comparison of the survivorship and growth of shallow-water gorgonian species of Puerto Rico. Mar. Ecol. Prog. Ser. 69: 253-260.

Zar, J.H. 1996. Biostatistical analysis, 3rd edition. Prentice Hall, Upper Saddle River, NJ, 918 pp.