Prey preferences and browsing pressure of the butterflyfish *Chaetodon capistratus* on Caribbean gorgonians

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ABSTRACT: The Caribbean butterflyfish *Chaetodon capistratus* Linnaeus usually feeds on scleractinian corals , but at a site in the San Blas Islands, Panama, *C. capistratus* fed primarily on gorgonians; it fed mainly on polyps, did not feed on gorgonian colonies when the polyps were contracted, and fed primarily on large colonies. *Plexaura homomalla* was the most preferred prey species. An undetermined *Plexaura* sp., termed *Plexaura* A, and *Pseudopterogorgia americana* were also browsed heavily. During May, June and July 1981, 1982 and 1983, feeding on *Plexaura* A followed a lunar cycle in which large colonies were browsed during or shortly after full moon. Examination of *Plexaura* A gonad samples suggests that *C. capistratus* feeding was correlated with gorgonian spawning. During January 1984, when gonads were small, *Plexaura* A was rarely fed upon regardless of lunar phase. Extrapolation of feeding rates indicates that *Plexaura homomalla* colonies lose an average of 378 polyps d^{-1} to browsing and *Pseudopterogorgia americana* colonies lose 100 polyps d^{-1} to browsing by *C. capistratus*. These daily removal rates correspond to the number of polyps found on 5 to 10 cm of branch. The average *Plexaura* A colony lost only 19 polyps d^{-1}, but 1 colony suffered a maximum single-day loss of 1620 polyps. These data suggest that browsing by *C. capistratus* can cause a significant loss of biomass in a number of gorgonian species.

INTRODUCTION

Chaetodontids, common residents on Caribbean and Pacific coral reefs, are well known browsers on reef anthozoans (Caribbean: Randall, 1967; Birkeland and Neudecker, 1981; Pacific: Hiatt and Strasburg, 1960; Hobson, 1974, cited in Birkeland and Neudecker, 1981; Reese, 1975; Neudecker, 1977, 1979; Harmelin-Vivien and Bouchon-Navaro, 1983), and many species are known to browse on octocorals. Harmelin-Vivien and Bouchon-Navaro (1983) report that 2 of the 11 chaetodontids they studied at Moorea (French Polynesia) specialize on octocorals and that 6 additional species include octocorals in their diet. According to Randall (1967), the Caribbean chaetodontid *Chaetodon capistratus* feeds on gorgonians, and Birkeland and Neudecker (1981) found that gorgonians made up 9 % of the diet of *C. capistratus* at Salt River Canyon, St. Croix. Although many authors have examined the preferences of chaetodontids, few have considered the magnitude of damage to their prey. Harmelin-Vivien

and Bouchon-Navarro (1983) estimated the amount of scleractian tissue which chaetodontids at Moorea ingest, but there are no similar data on the consumption of octocorals nor are data available for Caribbean species.

In discussing predation on Caribbean gorgonians most authors have discounted the effects of chaetodontids and have concentrated on the effects of the snail *Cyphoma gibbosum* and the bristleworm *Hermodice carunculata* (Birkeland, 1974; Kinzie, 1974; Birkeland and Gregory, 1975; Preston and Preston, 1975; Harvell and Suchanek, 1983). These predators leave visible, identifiable evidence of feeding. Unlike those grazers, chaetodontids remove single polyps and the effects of chaetodontid browsing are not readily recognized.

In this study I report on the intensity of browsing of *Chaetodon capistratus* on a Caribbean gorgonian community. Detailed observations have revealed that in at least 1 locality, *C. capistratus* regularly feeds on certain species of gorgonians; that feeding on gorgonians follows species- and time-specific preferences; and

that the cumulative effect of the feeding is a high rate of polyp loss for some gorgonian colonies.

METHODS

Feeding by *Chaetodon capistratus* was studied at Korbiski Reef, a small backreef in the San Blas Islands, Panama. Located 1 km south of the Smithsonian Tropical Research Institute field station, the reef is composed of mixed sand and coral substrates rising from a silty-sand bottom at 20 m to a tidally exposed reef flat. The densest coral and gorgonian populations are located at the northern corner of the reef between 1 and 3 m depth. The reef is protected from heavy wave action by a barrier reef 3 km to the north.

A 10×10 m^2 area which had a particularly dense gorgonian fauna was selected for the study. The nature of substrate found at 100 uniformly distributed points was used to estimate the areal abundance of the coral and gorgonian species present. Feeding preferences were examined during July 1981, July–September 1982, May–August 1983, and January 1984.

During July 1981, single *Chaetodon capistratus* were followed and the number of bites taken from each species of gorgonian and coral was recorded. Observations were made on 18 d between July 7 and July 26 for 30 min periods between 0930 and 1300 h. The first fish observed in the 100 m^2 study area was followed for as long as it remained in the study area. If the individual left the area, observations were switched to the next individual sighted. It was common to collect data on 3 or 4 individual fish in the course of the 30 min period. Periods of time with no *C. capistratus* present were rare.

Analysis of the data from 1981 suggested that feeding preferences were specific to individual gorgonian colonies. Subsequent observations in July–September 1982 and January 1984 concentrated on identifying colony-specific preferences. We labelled 101 arbitrarily chosen colonies of the 5 most abundant gorgonian species. The colonies were chosen so that the full size range of each species was sampled. Maximum height, length and width of each colony were measured. Observations of the number of bites taken from each colony were made during 10 min periods in which groups of 10 to 20 labelled colonies were observed. All 101 colonies could be observed in a total of 8 such periods. This sequence was repeated twice on each of 21 d, between July 28 and September 8, 1982 and also on every fourth day in January 1984. All observations were made between 0900 and 1300 h.

The number of bites taken from each colony was analysed as a function of species, date and colony size.

Analysis of variance is the most powerful technique to use on such a data set since it can correct for a continuous variable such as size and simultaneously assess the effects of species, date and interactions. The data generated from the observations did not, however, meet the assumption of homoscedasticity inherent to analysis of variance. A log function was found to be the most effective transform for reducing heteroscedasticity, but transformed data were also heteroscedastic (Bartlett's Box F = 14.7, p<0.001). Unfortunately, nonparametric tests could not simultaneously test all hypotheses of interest in the data set. Therefore, both a parametric analysis of variance and nonparametric tests were used to analyse the data. The analysis of variance was performed using the ANOVA program from SPSS (Nie et al., 1975). The log-transformed data were first regressed against colony size and size-corrected feeding rates analysed with respect to species and date using a mixed model. The product of maximum height, length, and width was used as an estimator of colony size. Results of analyses using either area or height as size indices were virtually identical. In order to create replicates the observations were grouped into 7 sets of 3 consecutive days each. Days in which a colony's polyps were contracted were dropped from the analysis. Species effects and date effects were also tested in separate Kruskal-Wallis Tests (Siegel, 1956). The Kruskal-Wallis tests cannot be used to differentiate interaction effects nor to determine whether apparent species effects are independent of colony size.

Feeding on ten *Plexaura* A colonies was further monitored at approximately 4 d intervals between May 24 and August 26, 1983. *Chaetodon capistratus* had browsed heavily on 8 of the colonies during July–September 1982, but not on the other 2 colonies. All 10 colonies were similar in size, were within 5 m of each other, and no single colony was more than 1 m from the nearest of the ten. The 10 colonies were monitored during each of two 10 min observation periods spaced 30 min apart. A single branch from each of the colonies was also collected on each day. Sexual maturity of the colonies was assessed by dissecting out and measuring gonads of 20 polyps from each branch. These observations were repeated during January 1984.

Observations suggested that *Chaetodon capistratus* fed only on expanded polyps. Specificity for expanded polyps was determined by recording the number of visits by *C. capistratus* to a single colony and the number of bites taken during those visits. Following 10 min of observation, the colony was shaken until all of the polyps retracted. A second 10 min sequence of observations was then made to determine if *C. capistratus* continued to feed on colonies when their polyps were contracted.

Gut contents of 4 individuals were collected at the

study site on August 29 and September 5, 1983. The gut contents were examined microscopically and the frequency of polyps and other food items were determined.

RESULTS

Abundances of the dominant gorgonian and coral species are presented in Table 1. The species with the greatest areal abundance was an undetermined *Plexaura* sp., here termed *Plexaura* A. *Plexaura* A is similar in appearance to *Plexaura homomalla* forma *Kükenthali* (Moser), but can be distinguished by its reduced polyp armature, lack of a calicular lip and additional characteristics of its sclerites and skeleton (Lasker, 1984). *Pseudoplexaura porosa* (Houttuyn) and *Plexaura homomalla* (Esper) were also abundant. *Diploria strigosa* (Dana) and *D. labyrinthiformes* (Linnaeus) were the most abundant stony corals. Most of the remaining area was occupied by coral rock and sand.

Chaetodon capistratus prey preferences

In July 1981, *Chaetodon capistratus* took an average of 404 bites during each 30 min period, 341 of these from gorgonians. A comparison of the number of bites taken to the availability of living cover indicates a non random pattern of feeding ($X^2 = 31528$, df = 6, p < 0.001). *Plexaura homomalla* was the preferred species on most days, but *Plexaura* A was heavily grazed on 3 of the 18 d. The heavy feeding on *Plexaura* A and *P. homomalla* and the temporal variability of the

feeding is apparent in Fig. 1. Daily feeding rates were analysed in a species-by-day contingency table and the results indicated significant day to day changes in preferences ($X^2 = 5878$, df = 140, p < 0.0005). The changes in feeding on *Plexaura* A and *P. homomalla* account for the large chi-square value.

Observations made between July 28 and September 8, 1982, indicate that browsing on the 101 labelled colonies was dependent on the species, size of the colony, day of the observation and also differed among colonies of the same species. The differences in browsing on the different species are illustrated in Table 2 and Fig. 2. *Plexaura homomalla* and *Pseudopterogorgia americana* colonies were most heavily fed upon. Average browsing on *Plexaura* A was low but the *Plexaura* A sample (77 colonies) included a large number of small never-fed-upon colonies (30 colonies) which depressed the mean. Some *Plexaura* A colonies
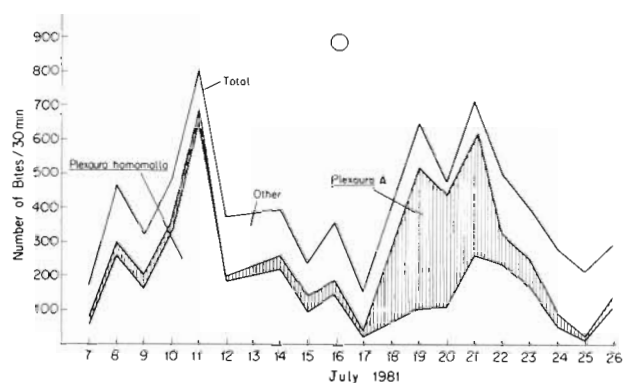

Fig. 1. *Chaetodon capistratus*. Feeding of individuals on gorgonians in a 100 m² area of Korbiski Reef, San Blas Islands during July 1981. Open circle at top of graph denotes full moon

Table 1. Relative abundances of substrate at the Korbiski study site and total bites taken by *Chaetodon capistratus* over 540 min of observation

Substrate	% of all substrates	% of living cover	% gorgonians	Number** of bites (%)
Gorgonians				
Gorgonia flabellum	0.8	1.5	1.8	348 (4.7)
Plexaura flexuosa	3.1	5.7	6.8	195 (2.7)
P. homomalla	6.3	11.5	13.8	3234 (44.0)
Plexaura A	25.0	45.8	54.8	1675 (22.8)
Pseudoplexaura spp.	7.1	13.0	15.6	239 (3.3)
Pseudopterogorgia spp.	3.3	6.0	7.2	529 (7.2)
Other				
Diploria spp.	6.7	12.3	–	540 (7.3)
Other coral and sponges	2.3	4.2	–	•*
Sand and rubble	45.4	–	–	592 (8.1)
				7352

* Feeding on other corals and sponges included with sand and rubble
** Total of number of bites in each of 18 30-min periods

Table 2. Mean number of bites removed from gorgonians colony^{-1} (20 min)$^{-1}$ during 20 min observation periods on 21 d during July–September 1982. N: sum of number of colonies observed on the 21 d. N is frequently less than the number of colonies × 21 because colonies whose polyps were contracted were excluded from analysis

Species	x̄	Standard error	N	Maximum	# of colonies
Plexaura A	1.26	0.18	1259	108	77
Plexaura flexuosa	1.55	0.45	55	24	5
Plexaura homomalla	25.17	3.12	136	259	8
Pseudoplexaura porosa	0.70	0.29	111	15	6
Pseudopterogorgia americana	9.65	2.25	101	153	5

were heavily fed upon at times (maximum data Table 2). The importance of variation in feeding between individual colonies is underscored by noting that 76 % of the bites taken from *Plexaura* A were restricted to 9 colonies. Regressions of feeding against colony size among *Plexaura* A colonies indicate that volume had a significant effect on feeding (F = 351.1; df = 1,1257; p < 0.001) but only accounted for 22 % of the total variance in per colony feeding rates. Temporal changes in preferences are illustrated in Fig. 2 & 3.

Results of the analysis of variance (ANOVA) are presented in Table 3. A significant proportion (20.7 %) of the variance was described by regressing the number of bites taken against colony volume. The ANOVA also indicates that predation on the colonies differed significantly between days and between species, but differences between days contributed only
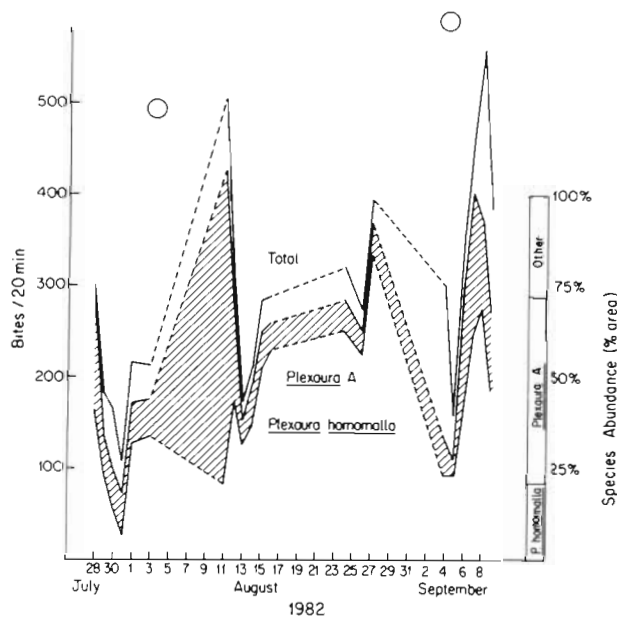

Fig. 2. *Chaetodon capistratus*. Feeding on marked gorgonian colonies during 21 d in July–September 1982. Relative abundance of gorgonian species among marked colonies differs somewhat from overall abundance (Table 1). Open circles at top of graph denote full moon

slightly to total variance. Differences between species were strongly influenced by date as indicated by the significant species-date interaction. In combination, the species effect and species-date interaction accounted for 46.4 % of the variance. The nonparametric Kruskal-Wallis tests were in close agreement with the ANOVA. The number of bites removed from colonies significantly differed between species (X^2 = 319.97, df = 4, p < 0.001) and significantly differed between days (X^2 = 16.36, df = 6, p = 0.012). The Kruskal-Wallis tests could not, however, test for interaction effects and pooled data across days and species.

Lunar periodicity in browsing

Temporal variation in feeding on *Plexaura* A weakly followed a lunar cycle. The peak in feeding on *Plexaura* A in July 1981 occurred July 18–23 which was 2 to 7 days after the full moon, and in 1982 occurred during the periods of August 11–13 and September 4–9, 8 to 10 and 2 to 7 d after full moon. That same periodicity is apparent in the data collected during May–August 1983 (Fig. 4). In both years, almost all of the feeding on *Plexaura* A colonies occurred from immediately before to 10 days after the full moon. However, feeding on each colony did not increase during each full moon period (Fig. 3). Some colonies were never subject to heavy feeding, some were subject to heavy feeding during only one of the full moons, and some were subject to increased feeding on more than one full moon. The most common pattern among the 10 colonies observed in both 1982 and 1983 was that of one major peak in browsing each summer.

Feeding in January 1984 (Fig. 5) followed a different pattern than that observed during the summer observation period. Feeding on *Plexaura* A colonies was low and no peak in feeding was observed (Fig. 5 vs Fig. 2 & 4). Total feeding on gorgonians ranged from 227 to 456 bites (20 min)$^{-1}$ which is comparable to the feeding rates observed both in 1981 and 1982 (Fig. 1 & 2; note that rates in Fig. 1 are for 30 min observation periods).

Lunar periodicity in browsing on *Plexaura* A was correlated with *Plexaura* A reproductive state. During May–August 1983 *Plexaura* A colonies contained large gonads with eggs up to 900 µm diameter. The decrease in mean values which occurred through the summer (Fig. 4) corresponded with the disappearance of the largest eggs, presumably through spawning. Observations of colonies in the field and in aquaria indicated that spawning occurs in the evening and is restricted to several day periods shortly after the full moon. The sudden decrease in gonad diameters in June and July 1983 (Fig. 4) was presumably due to spawning after full moon. Analysis of the data from individual colonies reveals that 11 of 14 cases of 250 µm decrease in gonad diameter occurred between Days 11 and 21 of

Fig. 4. *Chaetodon capistratus*. Feeding and maximum gonad diameter (mean ± standard error) of 10 *Plexaura* A colonies during May–August 1983. Open circles at top of graph denote full moon

the lunar cycle (where the new moon is Day 1). The binomial probability of such a distribution is < 0.01.

Heavy feeding on *Plexaura* A colonies correlated with drops in gonad diameter. A general correspondence can be observed in Fig. 4. Furthermore, 8 of 12 cases of heavy feeding (20 or more polyps removed) occurred within 4 d of observed 125 µm or more decreases in gonad diameter. Similarly 14 of the 23 instances in which 10 or more bites were observed, occurred within 4 d of 125 µm decreases in gonad size. The probability of a given feeding event occurring within 4 d of one of the 33 125-µm drops was 0.264 (66/250) and the binomial probabilities of the observed coincidence between feeding and drops in gonad diameters are 0.003 for cases of 20 or more bites and < 0.001 for cases of 10 or more bites.

The relevance of gonad state to the browsing rates is further supported by the observations from January 1984. Overall feeding on gorgonians during January 1984 was very similar to that observed during summer
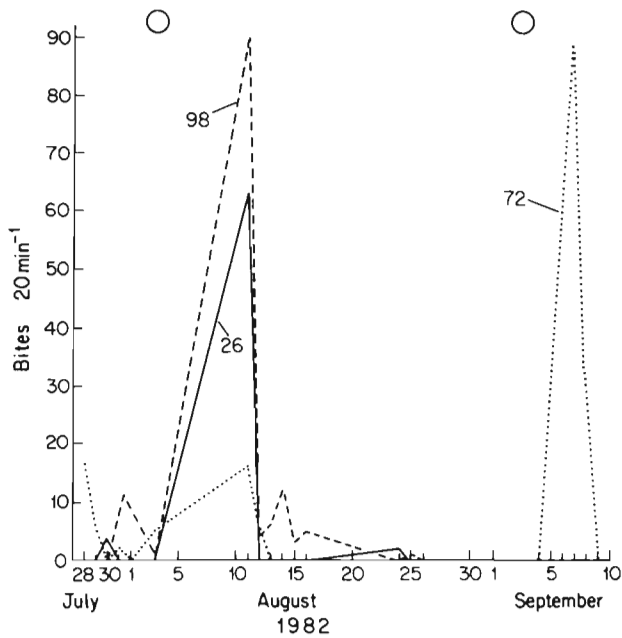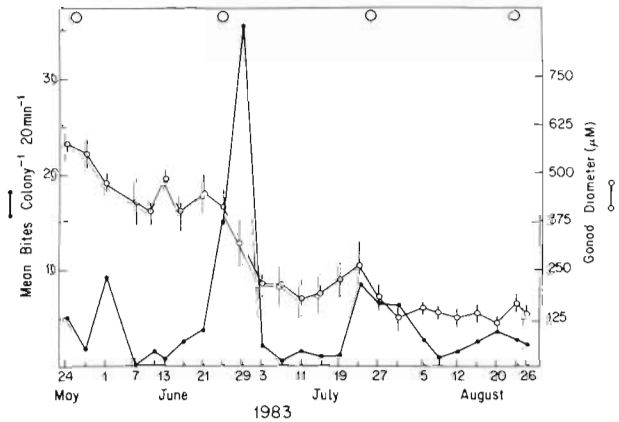

Fig. 3. *Chaetodon capistratus*. Feeding on select *Plexaura* A colonies during July–Sept. 1982. Numbers: labelled colonies. Open circles at top of graph denote full moon

Table 3. *Chaetodon capistratus*. ANOVA results for feeding rates on individual colonies in 1982

	df	MS	F*	P	% Total variance
Covariate					
volume	1	120.4	1070.2	0.001	20.7
Factor					
species	4	6.0	14.6	0.001	44.4
date	6	0.3	2.7	0.009	0.2
date × species	24	0.4	3.7	0.001	2.0
Residual	1620	0.1			32.7

* F-ratios were calculated using $MS_{residual}$ as denominator, except for the species effect for which $MS_{date \times species}$ was used

(Fig. 5). Unlike the May-August observations of previous years, there was no indication of a change in *Chaetodon capistratus* feeding behavior during the full moon (Jan 18). Feeding throughout the month was extremely low and feeding on the 10 colonies monitored during 1982 and 1983 averaged 0.8 bites colony^{-1} (20 min)$^{-1}$ (SE = 0.2, range = 0.0–1.7). The absence of a lunar pattern in feeding on *Plexaura* A during January 1984 corresponded to the small and unchanging size of gonads throughout the month (mean maximum diameter = 175 µm, SE = 50 µm, range 0 to 225 µm). *C. capistratus* appeared to inspect *Plexaura* A colonies more frequently on January 20 and 22, 2 and 4 d after full moon, but after inspecting the colonies the fish usually swam away.

Chaetodon capistratus feeding decreased dramatically when a colony contracted its polyps, indicating that *C. capistratus* feeds almost exclusively on gorgonian polyps and not on coenenchyme. *Plexaura homomalla* colonies with expanded polyps were regularly visited by *C. capistratus* (8 colonies, 71 visits). In 87 % of the visits (a visit is defined as a fish swimming among colony's branches) feeding was observed, and the mean feeding rate was 13.7 bites visit^{-1} (standard error = 2.84, n = 71). Visits continued after colonies were forced to contract their polyps (79 visits), but only 14 % of the visits resulted in feeding and the feeding

Fig. 5. *Chaetodon capistratus.* Feeding on marked gorgonian colonies during January 1984. See Fig. 2 and text for explanation. Mean feeding on the same 10 *Plexaura* A colonies as in Fig. 4 is plotted at bottom of graph. Open circle at top of graph denotes full moon

rate dropped to 0.7 bites visit^{-1} (SE = 0.3, n = 79). Furthermore, feeding on contracted polyps was restricted to the end of the 10-min observation periods when some polyps had begun to reexpand.

Chaetodon capistratus feeding preferences were further corroborated by the 4 gut samples. Two fish were collected on August 29, 1983, and a second pair on September 5, 1983. The fish were observed feeding on gorgonians prior to collection, but neither day was one of unusually heavy feeding. The number of food items found in the guts of the 4 fish were 102 and 115 on August 29, and 79 and 91 on September 5. The August samples contained 67 and 93 clearly recognizable gorgonian polyps and the September samples contained 60 and 54 gorgonian polyps. The remainder of food items were classified as either gorgonian fragments (8 % of all items), non-anthozoan invertebrates (11 %), or unidentifiable (8 %).

DISCUSSION

Chaetodon capistratus predation pressure on gorgonians was high at Korbiski Reef. Effects of *C. capistratus* browsing were calculated from the colony-specific feeding data collected over a 42 d period in 1982. The feeding rates observed in 1982 were similar to values obtained in June 1981 and May-August 1983 (*Plexaura* A only) and, with the exception of rates of feeding on *Plexaura* A, were comparable to values from January 1984 as well. Therefore, extrapolation of the 1982 data should provide a first approximation of predation pressure on gorgonians at Korbiski Reef. To calculate daily grazing I assumed each bite corresponded to the loss of a single polyp and extrapolated the observed 20 min bite rate over the 5 h (0800 to 1300 h) period during which *C. capistratus* feeding appeared to be heaviest. Extrapolation of the feeding rate over only the 5 h of heaviest feeding should provide a conservative estimate of daily browsing. The results of such an analysis (Table 4) illustrate the species- and colony-specific nature of the predation pressure exerted by *C. capistratus*. *Plexaura homomalla* was the preferred gorgonian prey. The 'average' *P. homomalla* observed in this study lost 378 polyps d^{-1} which is equal to all of the polyps from 9 cm of branch each day (41.3 polyps^{-1} cm^{-1} of branch, Lasker et al., 1983). Kinzie (1974) reports *P. homomalla* growth rates of 1.3 to 4.2 cm y^{-1}. Thus, the estimated number of polyps removed in a day by *C. capistratus* is greater than the net yearly accretion of polyps on a single branch. (Note, however, that a large colony contains hundreds of branches.) The severity of browsing on the *P. homomalla* colonies followed in this study is even more striking if maximum browsing rates are consi-
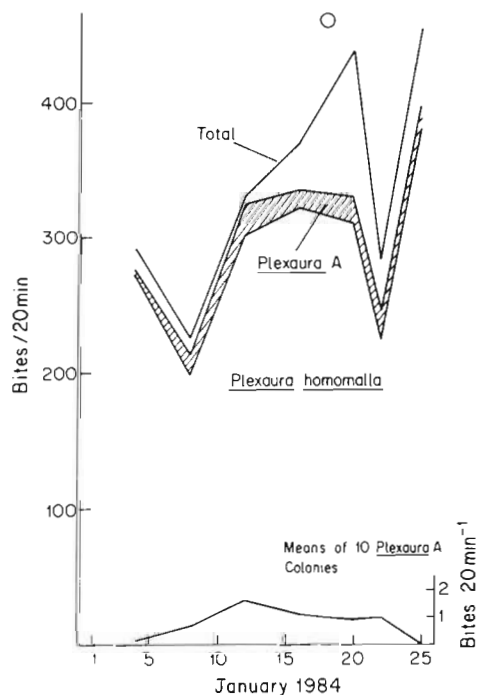
Table 4. *Chaetodon capistratus* grazing pressure on gorgonians at Korbiski Reef

Species	Mean daily number of polyps removed per colony	Range of mean daily removal rates among different colonies	Maximum single daily removal rate
Plexaura A	19	0–195	1620
Plexaura flexuosa	23	0– 32	180
Plexaura homomalla	378	10–968	3885
Pseudoplexaura porosa	12	0– 65	360
Pseudopterogorgia americana	100	0–493	2295

dered. One colony had an average of 968 polyps removed on each day of observation and 3885 polyps removed on one particular day.

If the browsing on *Plexaura homomalla* is extrapolated over 12 mo the mean number of polyps lost per colony becomes 1.11×10^5 polyps, the equivalent of all the polyps on a total of 3.4×10^3 cm of branch. The severity of predation on *P. homomalla* can then be estimated by comparing the loss of polyps to total colony size. There is no simple relation between colony size and number and length of branches (e.g. Kinzie, 1974). However, a first approximation of colony size may be estimated by assuming that *P. homomalla* colonies branch dichotomously every 5 cm. (Examination of colonies suggests that most colonies have fewer branches than expected from dichotomous branching and that branches are often greater than 5 cm apart.) Using such a model and assuming all branches grow equally, a 50 cm tall colony would contain 1.0×10^4 cm of branches. The yearly feeding rate on such a colony equals 34 % of the colony's polyps.

Pseudopterogorgia americana colonies also suffered large daily losses of polyps during the study. The *P. americana* colonies on the study site were all very large (mean height = 85 cm, n = 5) and each contained many meters of branches. The proportionate loss of polyps was not nearly as great as that which occurred among *Plexaura homomalla* colonies, but the single colony loss of as many as 493 polyps d^{-1} is high.

Some *Plexaura* A colonies were subject to intensive browsing, but browsing was variable among colonies, and was correlated with size. Mean browsing on colonies which were greater than 75 cm height was 66 polyps d^{-1} during May–August 1983. Those colonies suffered rates of feeding as great as 195 polyps d^{-1}, which is equivalent to the number of polyps contained in 4 cm of colony. However, feeding was restricted to only a few days each year and the yearly loss due to browsing is therefore a small fraction of the total number of polyps. The pattern of gonad size fluctuation and *Chaetodon capistratus* feeding suggest that *C. capistratus* concentrated on *Plexaura* A colonies when the polyps contained ripe eggs. *C. capistratus* regu-

larly took single bites from colonies at other times and the switch to more intense feeding after the full moon may have been triggered by changes in the taste or appearance of polyps containing mature eggs. *C. capistratus* appeared to inspect the colonies or substrates on which they browsed. Although eggs were not usually visible to human observers, they can be recognized shortly before release, and the most intense feeding on *Plexaura* A which I have observed occurred at dusk on July 19, 1984, on a colony in which eggs were clearly visible in the tops of polyps. Similarly, my only observations of heavy feeding on *Pseudoplexaura porosa* (July 22–23, 1981) corresponded to days in which large egg masses were visible. I have also observed *C. capistratus* feeding on planulae being released by *Montastrea cavernosa* (Linnaeus), but in that case the butterflyfish concentrated on the extruded planulae and not on the colony itself.

The presence of large egg masses in *Plexaura* A colonies was a necessary but not sufficient condition to heavy feeding. Many colonies ranging in height from 30 to 90 cm which had large egg masses (500 μm maximum diameter) were not heavily browsed. Finally, no trend between gonad size and grazing was observed among the heavily browsed *Plexaura homomalla* colonies. During the 1982 observations four heavily browsed *P. homomalla* were sampled for gonad condition. Two of the colonies had no visible gonads and the other 2 had gonad diameters of only 150 μm.

The preference of *Chaetodon capistratus* for gorgonians at Korbiski Reef was strikingly different from preferences at Salt River Canyon, St. Croix (Birkeland & Neudecker 1981), reflecting differences between coral faunas of the 2 areas. Agaricids, the preferred item at Salt River Canyon, were very rare in the 100 m^2 study site at Korbiski. Furthermore, although gorgonians are common at 3 of the 4 areas at Salt River, *Plexaura* A and *Plexaura homomalla* may be less common at Salt River than at Korbiski Reef.

Birkeland and Neudecker (1981) also found that *Chaetodon capistratus* is an active generalist, feeding in a manner which broadens its diet relative to the

abundance of prey. They suggested such a strategy could provide a more balanced diet and suggested feeding on nutrient-rich, non-anthozoan prey would further enhance the diet. At Korbiski Reef, *C. capistratus* fed less on the most abundant species (*Plexaura* A) and more on a less abundant species than expected (*P. homomalla*). However, the pattern of feeding observed at Korbiski Reef (Table 1) suggests dietary preferences which are independent of abundance. The basis for such preferences may relate to nutrient intake as Birkeland and Neudecker (1981) suggested. The shift in browsing on *Plexaura* A which correlates with *Plexaura* A spawning also suggests that *Chaetodon capistratus* preferences are based on prey quality, since polyps with eggs are likely to have greater nutritive value than those without eggs. Alternatively, preferences and fluctuating preferences may relate to the presence and concentration of toxic secondary compounds, which are found in many gorgonian species (Ciereszko and Karns, 1973; Tursch et al., 1978). These hypotheses are not mutually exclusive and detailed chemical analyses, toxicity tests, and comparisons between areas with different gorgonian abundances are all needed to test the hypotheses.

The data on *Chaetodon capistratus* from Korbiski Reef demonstrate that gorgonians can be a major component of the *C. capistratus* diet. The data also suggest that among species like *Plexaura homomalla* browsing by *C. capistratus* removes polyps at rates which have a substantial effect on the number of polyps a colony contains. However, the temporal variation in feeding preferences of *C. capistratus* reported here and the spatial variation observed between this study and that of Birkeland and Neudecker (1981) both suggest that assessments of predation pressure and diet require long-term data sequences and may be site specific. The degree of temporal specificity of *C. capistratus* also suggests that short-term studies and/or studies which randomize temporal data may fail to discern important aspects of feeding behavior.

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