

Ecological Relationships of Chaetodontid and
Pomacanthid Fishes at St. Croix

By

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Ecology

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Abstract

Chaetodontid and pomacanthid foraging patterns were examined by observing feeding and analysing stomach contents. Chaetodon capistratus browsed a diverse array of anthozoan corals, especially scleractinians, and other prey at the rate of 27 ± 8 bites per 5 min. C. aculeatus is a predator of cryptic invertebrates, particularly serpulid polychaetes and crustaceans, and feeds at a slower rate (12 ± 4 bites per 5 min).

The pomacanthids, Holacanthus ciliaris, H. tricolor, Pomacanthid arcuatus, and P. paru, are sponge specialists. H. tricolor feeds on sponges (98% of diet volume) at the rate of 10 ± 2 bites per 5 min.

Mating systems of Chaetodon aculeatus, C. capistratus, and Holacanthus tricolor were also investigated. Size dimorphism, reproductive behavior, and grouping patterns were examined. Differences in mating systems were related to differences in resource abundance and distribution, foraging patterns, and type of sex determination.

Chaetodon aculeatus forages solitarily during the day and mates a nearby individual at dusk. C. capistratus is monogamous, and pairs forage together in a home range during the day and mate there at night. Both species spawn only once per evening, and all reproduction appears to occur at the same site. Holacanthus tricolor forages solitarily during the day in male-defended territories. H. tricolor is a polygynist, protogynus

hermaphrodite. A dominant male spawns with up to three females a night, but females spawn only once.

Whether local populations of these fishes are at carrying capacity of different reef areas was investigated with removal experiments. Estimates of population size were made by visual censusing of four transects in two habitats which differ in coral cover and structural complexity.

C. aculeatus, C. capistratus, and H. tricolor accounted for the majority of these fishes at each site before they were removed in 1978.

Since total abundances had returned to preremoval levels after two years, they were probably at the carrying capacity of the sample sites. While total abundances did not change, there were some differences in species composition. Chaetodontid and pomacanthid fishes have broad food and habitat niches. Even though carrying capacity is predictable because densities depend on resource availability, species composition is more the result of chance associated with space availability and recruitment than fine niche partitioning.

**Foraging Behavior of Chaetodontid and Pomacanthid
Fishes at St. Croix**

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Abstract

Chaetodontid and pomacanthid foraging patterns were examined by observing feeding in situ and analysing stomach contents. Fishes of these families feed on abundant reef resources, corals and sponges, which few other fishes eat.

Chaetodon capistratus browsed a diverse array of anthozoan corals, especially scleractinians. Prey were ingested at a high rate (27 ± 8 bites/5 min) and processed quickly. C. aculeatus was a predator of cryptic invertebrates, particularly serpulid polychaetes and crustaceans, found on the undersurfaces of corals or ledges. C. aculeatus fed at a slower rate (12 ± 4 bites/5 min) on more calorific prey requiring more handling time. Both species co-occurred, and even though they preferred fish eggs when available, food resources appeared partitioned in such a manner that competition was avoided. The generalized foraging behavior of C. capistratus is adaptive for diet shifts according to prey availability, as evidenced by its high abundance and broad distribution in the western Atlantic. Conversely, the more specialized species, C. aculeatus, is restricted to well developed coral reefs.

The pomacanthid, H. tricolor, was a sponge feeding specialist. H. tricolor lived within specific territories, and fed on sponges (98% of diet volume), predominantly large, brightly colored species (65% of sponges eaten), and the rest were encrusting species. H. tricolor took 10 ± 5 bites per 5-min period.

Radiation of the chaetodontid and pomacanthid fishes has resulted in specialized adaptations to exploit prey which are noxious or toxic to older lineages of reef fishes. By ingesting significant quantities of corals and sponges, these fishes probably affect the growth, abundance,

and distribution of the major components of Caribbean coral reefs.

INTRODUCTION

Chaetodontid fishes feed primarily on anthozoans, polychaetes, and small crustaceans in both the Western Atlantic (Randall, 1967; Birkeland and Neudecker, 1981) and Pacific oceans (Hiatt and Strasburg, 1960; Hobson, 1974; Reese, 1975, 1977; Neudecker, 1977, 1979). Pomacanthids feed mainly on sponges in both oceans, but also consume some algae, ascidians, fish eggs, gorgonids, and zooantharians (Randall and Hartman, 1968; Hobson, 1974; Shen and Liu, 1976). Consumption of reef building corals and sponges, which are both somewhat noxious and structurally defended, is relatively uncommon among reef fishes. Coral reef fishes of the families Chaetodontidae and Pomacanthidae are highly specialized teleost families whose foraging patterns have probably evolved relatively recently in geologic time (Randall and Hartman 1968, Randall 1974). Corals and sponges (particularly in the Caribbean) comprise much of the structure and life-form of coral reefs and their consumption by fishes exerts considerable influence on reef community structure (Neudecker, 1979).

Some data has been given on the foraging behavior of Chaetodon aculeatus and C. capistratus and related prey preferences to relative abundance of prey species on reefs at St. Croix (Birkeland and Neudecker, 1981). This paper presents additional, but more detailed information on those two species and also examines the foraging and activity patterns of the pomacanthid Holacanthus tricolor. In this study, prey were ordered according to the total number of bites counted on each prey and the number of observation periods each particular prey was eaten. Observational data were verified with analyses of stomach contents of the three most abundant species. Since prey distribution and abundance were not measured during

the 1980 observations, the new data indicate what the fish actually ate, but not necessarily what prey they preferred. Foraging observations and specimen collections were all made in Salt River Canyon, where I measured the distribution and abundance of all chaetodontid and pomacanthid fishes along four 100 m transects. At all four sites combined, Chaetodon capistratus, C. aculeatus and Holacanthus tricolor were the most abundant species.

MATERIALS AND METHODS

Data Sources

Two main sources of data comprise the basis for my analyses of foraging patterns: (1) observations and collections made during National Undersea Laboratory System (NULS) Saturation Mission 78-1 (May and June 1978) during 13 scuba excursions (38 hrs) from underwater habitat Hydrolab at St. Croix, U.S. Virgin Islands; (2) observations made during NULS Mission 80-1 (February - March 1980) in 13 excursions yielding about 35 hrs of observation.

Study Sites

Hydrolab is located on a sand bottom in 15.5 m of water about 30 m north of the barrier reef fronting Salt River Estuary and about 5 m west of the east slope. Observations were made at 100 m transect lines established in 1978 (Birkeland and Neudecker, 1981) along the 15 and 30 m isobaths on the east slope and west wall of Salt River Canyon.

Both sides of the Canyon supported coral reef development but differed in submarine topography, species composition, and abundance of benthic invertebrates and fishes. West wall transects were located in a more structurally complex habitat than those on the east slope because of steep

faces, cracks, and overhangs resulting from slumping of large coral blocks from the canyon wall. Among anthozoans, scleractinian corals and antipatharians were far more abundant at both west wall transects (21% of surface cover at 15 m, 35% at 30 m) than at either depth on the east slope (15% at 15 m and 1% at 30 m; Birkeland and Neudecker, 1981). Corals were more abundant at the 15 m isobaths, except for Agaricia which was more prevalent at 30 m depths (Birkeland and Neudecker, 1981).

East slope transects had much less vertical relief and extended over a more gentle sloping bottom of 15-20 degrees. The substratum was more unconsolidated at east slope sites and contained many cobble-filled troughs (Adey et al., 1977). Whereas scleractinian corals were less abundant on the east slope, plexaurid gorgonids accounted for 80% of surface cover by anthozoans (Birkeland & Neudecker, 1981).

Foraging Patterns

Measurements of the distribution and abundance of all chaetodontid and pomacanthid fishes in Salt River Canyon during 1978 and 1980 indicated that Chaetodon aculeatus, C. capistratus and Holacanthus tricolor were the most abundant and widely distributed species of the 2 families studied (Neudecker and Lobel, in press). Consequently, the analyses of foraging behavior concentrated on those abundant species.

Foraging behavior and prey selection were quantified by following individual fishes for 5-min periods and tallying the number of bites on each prey item. Follows were made during the day when these fishes were actively foraging. Chaetodontid and pomacanthid fishes are generally unconcerned about the presence of divers and could be followed closely enough to determine most prey identities. However, when a fish foraged for

small prey in the algae, on the undersurfaces of corals or ledges, or in the plankton, prey species could not be visually identified and bites were recorded to location categories.

Stomach Content Analyses

When a fish bit a coral and left no obvious mark, it was difficult to determine by visual observation whether the intended prey was coral polyps, mucus, or associated crustaceans. Similarly, it was not possible to determine exactly what prey were taken from sponges, algal turf, or the plankton. Often the sought-after prey was a tiny associate of sponges or algal turf and therefore a recorded bite on a sponge may not have indicated that the sponge was the food item. In those cases, a simple description of location of the feeding activity and its associated behavior was recorded.

Stomach-content analyses were necessary to verify observations and to identify small prey items. Prey identifications were determined by spearing a representative sample of fishes and examining stomach contents. Because I personally speared every fish, I know what each one was purported to be eating when captured, and this information aided in the analysis.

Immediately after spearing, stomach contents were preserved by injecting a buffered 10-percent formalin solution into the gut cavity. Specimens were stored in formalin until analysis. Since food habits change over the life of most fishes (Randall, 1967; Hobson, 1974), all of the specimens selected were adults. In order to minimize biases toward less digestible prey organisms, only the stomach contents were examined. However, everything found in the stomach of a fish is not necessarily an item specifically sought as food.

Stomach contents were examined under a dissecting microscope, and

when greater resolution was needed a compound microscope was used. Visual estimates were made of the percent of the total stomach volume contributed by each prey species or category (Randall, 1967; Hobson, 1974). From these estimates the mean percent of that item in the diet volume for each fish species was calculated according to the method of Hobson (1974).

The presence of entire polyps with eight pinnate tentacles in a fish's stomach was considered to be evidence of browsing on octocorals. Masses of tissue and polyps with zooxanthellae were considered to be evidence of browsing on hexacorals. Stomach content analyses could only verify that coral polyps were fed up on, and when corals were eaten, the relative proportions of the species consumed could only be determined accurately from observations in the field.

RESULTS

Chaetodontids

Chaetodon capistratus. At Salt River Canyon capistratus was monogamous and 75 percent of all observed individuals were paired (Neudecker and Lobel, in press). Pairs foraged, rested, and mated within specific home ranges on the reef. From repeated follows of known pairs in their home ranges and by marking boundaries and measuring the enclosed areas, the home range size of C. capistratus was estimated to be about of 75 m². C. capistratus was active during the day and first appeared above the bottom at about 0600 hrs and began to feed by 0630 hrs. Foraging continued almost continually until about 1800 hrs and the latest foraging behavior observed occurred at 1842 hrs. Spawning occurred just before sunset before the pair sheltered in holes, crevices, or around the bases of

corals and gorgonids for the night (Neudecker and Lobel, 1982).

Chaetodon capistratus is a browser of anthozoans which feed mostly on the scleractinian corals Agaricia, Siderastrea, Madracis and Mycetophyllia at the study sites; bites on the plexaurid gorgonid, Pseudoplexaura, and foraging in algal turf, probably for polychaetes, were also frequently observed (Table 1). Of 2325 bites observed, 2067 or 89 percent were taken from scleractinian corals (Table 1).

Prey species eaten by C. capistratus are listed in Table 1 according to their importance in the diet. Importance was the combined rank of the number of 5-min periods a particular prey was eaten and the total number of bites on that prey. To test for differences in prey importance depending upon the measures of frequency and intensity of feeding, the measures were compared with a Kendall's tau correlation coefficient. Either measure alone may be indicative of prey importance in the diet, since the two measures were not significantly different (Kendall's tau, $r = 0.86$, $P < .001$, $N = 34$).

Stomach content analyses supported the foraging observations and demonstrated that 73.5 percent of the diet volume of C. capistratus consisted of anthozoan corals, while polychaetes and gorgonids constituted 11.25 and 9 percent, respectively (Table 2). The presence of intact scleractinian and gorgonian polyps indicated that C. capistratus was a browser of corals (sensu Neudecker, 1979), nipping off polyps without any skeletal material.

While foraging, on many different prey, individuals of a pair generally stayed within 0.5 m of each other as they swam around their home range. Although pair members were closely spaced, they seldom fed on the same coral colony simultaneously. The mean feeding intensity of C.

Table 1. Observed foraging behavior of *Chaetodon capistratus* at Salt River Canyon in 1978 (N = 61) and 1980 (N = 24) combined. Prey species or types were derived by combining the relative rank of the number of 5-min periods a prey was fed upon (occurrence) and the total number of bites on that prey (bites).

Prey or feeding location in descending order of importance	Common name of probable prey type	Occurrences (N = 85)	Bites (N = 2325)	$\bar{x} \pm SD$ bites per 5 min
Agaricia	(coral)	72	732	10.2 \pm 5.7
Siderastrea	(coral)	54	339	6.3 \pm 3.8
Pseudoplexaura	(gorgonid)	50	235	4.7 \pm 3.2
Madracis mirabilis	(coral)	23	148	6.4 \pm 3.7
Algal turf	(invertebrates)	37	44	3.4 \pm 1.4
Mycetophyllia	(coral)	21	85	4.0 \pm 2.7
Madracis decactis	(coral)	21	80	3.8 \pm 1.8
Porites asteroides	(coral)	11	75	6.8 \pm 3.6
Solenastrea	(coral)	16	74	4.6 \pm 2.4
Meandrina meandrites	(coral)	20	62	3.1 \pm 2.3
Dichocoenia stokesii	(coral)	7	46	6.6 \pm 3.4
Monastrea annularis	(coral)	16	41	2.6 \pm 1.6
Diploria	(coral)	8	40	5.0 \pm 2.9
Porites	(coral)	5	31	6.2 \pm 5.9
Fan sponge	(sponge)	5	25	5.0 \pm 1.9
Iciligorgia	(sponge)	2	25	12.5 \pm 10.6
Stephanocoenia stokesii	(coral)	8	22	2.8 \pm 1.4
Montastrea cavernosa	(coral)	6	21	3.5 \pm 1.4
Mussa	(coral)	3	12	4.0 \pm 1.0
Antipathes	(black coral)	2	11	3.0 \pm 1.4
Cirripathes	(black coral)	5	10	2.0 \pm 0.7
Sponges	(sponge)	4	9	2.3 \pm 1.5
Mancinia	(coral)	5	8	1.6 \pm 0.5
Plexaura	(gorgonid)	3	8	2.7 \pm 2.1
Helioceris	(coral)	3	7	2.3 \pm 0.6
Zooanthids	(zooanthid)	2	7	3.5 \pm 0.9
Bartholomea	(zooanthid)	2	7	3.5 \pm 2.1
Eusmilia fastigata	(coral)	2	7	3.5 \pm 0.7
Antipathes sp. 2	(black coral)	2	6	3.0 \pm 1.4
Sponge zooanthids	(sponge-zooanthid)	2	3	1.5 \pm 0.7
Muricia	(sponge)	1	2	2.0 \pm 0
Hydroid	(hydroid)	1	1	1.0 \pm 0
Verongia	(sponge)	1	1	1.0 \pm 0
Erythropodium	(sponge)	1	1	1.0 \pm 0

Table 2. Stomach contents of Chaetodon capistratus (N=10). Five specimens were collected near transects at 15 and 30 m on each the east and west walls of Salt River Canyon.

Prey	Frequency	\bar{X} Volume % of Diet
Anthozoan corals	10	73.50
Polychaetes - serpulids	3	11.25
Gorgonians	5	9.00
Unidentified material	4	3.00
Algae	3	2.00
Fish Eggs	2	0.75
Crustaceans	1	0.50

capistratus was 27.4 ± 8.4 bites per 5 min (N = 85), and the range was 13-63 bites in 5 min. Individuals fed on an average of 5.0 ± 1.4 (range = 2-9, N = 85) different species or types of prey per 5-min feeding bout. There was an average of 3.5 ± 1.3 (range = 1-7, N = 85) different species and 8.5 ± 2.3 (range = 4-13, N = 24) different colonies of scleractinian corals fed upon each 5-min period, and individuals took an average of 2.0 ± 1.8 bites per coral colony (range = 1-12, N = 24).

Chaetodon aculeatus: Activity patterns of C. aculeatus were similar to those of C. capistratus. C. aculeatus individuals appeared on the reef just after sunrise, circa 0600 hrs, and began to feed soon thereafter. Solitary individuals maintained exclusive use of home range areas where they foraged during the day and rested alone at night. Home ranges were, estimated to be about 115 m² in size. C. aculeatus appeared to feed almost continuously between 0630 and 1800 hrs, and the latest incidence of feeding was observed at 1835 hrs. C. aculeatus retired before C. capistratus and one evening the last individual out was seen at 1853 hrs compared to 1910 hrs for C. capistratus.

Chaetodon aculeatus was a generalized carnivore that fed mainly on serpulid worms, demersal crustaceans, and fish eggs (Tables 3, 4). Occasionally C. aculeatus was observed to feed on plankton about one meter above the bottom. Whereas Randall (1967:799) and Hubbs (1963:176) reported that pedicellariae and tubefeet of urchins were a major food of C. aculeatus, they were taken only twice (8 bites) during observations (N = 67) in Salt River Canyon. C. aculeatus was also observed to feed from sponges, three species of scleractinian corals, and some gorgonids (Table 3), but the absence of sponge spicules or coral polyps in their

stomachs (Table 4) suggests that tiny crustaceans associated with the larger animals were the prey rather than the sponges or corals themselves. Individuals hunted for the serpulid worms and crustaceans on the undersurfaces of corals and rocks and in the algal turf (Table 4).

C. aculeatus foraged in only eight different locations in the environment: undersurfaces, algal turf, sponges, fish eggs, corals, octocorals, echinoids, and plankton; most feeding occurred in the first four patch types (Table 3). The mean foraging rate was 12.3 ± 4.4 (range 9-63) bites per 5 min (N = 67). The most intense feeding was directed at fish eggs, such as those of Abudefduf saxatilis, and occurred opportunistically when unguarded eggs were encountered. Unlike C. capistratus, C. aculeatus was sometimes unsuccessful in catching prey since some lunges for prey were not followed by chewing. An average of 2.6 ± 0.8 (range 1-4) different types of prey or feeding locations were consumed during the 67 feeding bouts.

Pomacanthid

Holacanthus tricolor. Individuals of tricolor foraged solitarily, within male defended territories, between 0600-1800 hrs. All foraging observations were of solitary individuals, although other individuals were also feeding alone in the territory at the same time. Holacanthus tricolor is inactive at night and remained sheltered near the bottom under corals or gorgonids or in holes on the reef.

H. tricolor is generally the most abundant pomacanthid fish on reefs throughout the Caribbean (Randall, 1968; Allen, 1980). Holacanthus tricolor is a polygynous, protogynous hermaphrodite, and one male maintains a harem of 3-5 females (Neudecker and Lobel, in press).

Foraging of H. tricolor was observed during six 5 min periods. The

Table 3. Observed foraging behavior of *Chaetodon aculeatus* a: Salt River Canyon in 1978 (N = 43) and 1980 (N = 24) combined. Kendall's tau comparing the observation periods was not significant ($r = 0.91$, $P < .001$, $N = 12$).

Prey or feeding location in descending order of importance	Common name or probable prey type	Occurrences (N = 67)	Bites (N = 827)	$\bar{x} \pm SD$
Undersurfaces	(invertebrates)	56	270	4.8 \pm 1.9
Sponges	(invertebrates)	50	230	4.6 \pm 2.2
Turf	(invertebrates)	34	142	4.2 \pm 1.6
Abudefduf eggs	(fish eggs)	9	124	13.8 \pm 9.8
Verongia	(sponge-inverts)	6	19	3.2 \pm 1.9
Plankton	(plankton)	3	13	4.3 \pm 0.6
Siderastreaeidae	(coral)	4	10	2.5 \pm 0.6
Urchin spines	(urchins)	2	8	4.0 \pm 0
Agariciidae	(coral)	3	6	2.0 \pm 1.0
Montastrea	(coral)	1	2	2.0 \pm 0
Pseudoplexaura	(gorgonid)	1	2	2.0 \pm 0
Plexaurid	(gorgonid)	1	1	1.0 \pm 0

Table 4. Stomach contents of Chaetodon aculeatus (N = 12). Six specimens were collected from transects on each side of Salt River Canyon in 1978.

	Fish containing this prey (N = 12)	Mean % of diet volume
Polychaetes Serpulids <u>Spirobranchus</u> sp.	11	68.5
Crustaceans amphipods copepods isopods shrimps	8	25.0
Embryonic fishes and fish eggs	4	5.5
Unidentified animal material	1	1.0

Table 5. Foraging behavior and stomach contents of Holacanthus tricolor.

Feeding locations or prey type	Observed foraging activity		Stomach contents	
	Occurrence (N = 6)	Bites (N = 58)	Occurrence (N = 6)	Mean % of diet volume
Sponges	6	44	6	98.83
red sponges			4	52.50
yellow sponges			3	45.70
Algal turf	2	12	2	1.17
brown algae			2	0.75
red algae			1	0.42
Under coral	1	2		

majority of feeding was on large red and yellow sponges (44/68 bites, 65% of all bites; Table 5). The remainder of bites were taken in the algal turf (12/68, 18%) and occasionally under corals (2/68 bites; Table 5). H. tricolor fed at the rate of 9.7 ± 5.4 (range = 5-19) bites per 5 min period. Stomach content analyses indicated that sponges comprised 98 % of the diet volume, suggesting that smaller encrusting sponges were taken from the turf and under corals. The stomach content analyses are in close agreement with those of Randall and Hartman (1968), who reported that sponges of 30 species comprised 97% of the diet volume of H. tricolor (N = 24).

DISCUSSION

Chaetodontid Foraging Patterns

Chaetodon aculeatus and C. capistratus overlapped both spatially and temporally, but exhibited different foraging patterns.

C. aculeatus was a solitary predator of small, discrete prey such as polychaetes and crustaceans, whereas C. capistratus foraged in closely associated pairs that browsed mostly on scleractinian corals. Although food separation was clear between the two species, both preferred to eat fish eggs when available and fed at high rates when eggs were encountered. C. aculeatus took an average of half as many bites as C. capistratus. Part of the difference in foraging rates may be related to the body size of C. capistratus, which is on the average about 20% greater than that of C. aculeatus (Neudecker and Lobel, in press). Foraging rate differences may also be related to the fact that the main prey of C. aculeatus, polychaetes and crustaceans, are more calorific than coral polyps eaten by C. capistratus (Birkeland and Neudecker, 1961). Differences in foraging rates

also indicate that prey of C. aculeatus required more handling time. C. aculeatus often paused to chew its prey after capture, whereas chewing of prey was not obvious for C. capistratus. Further, on a few occasions, C. aculeatus was observed to attack a potential prey and miss, but misses by C. capistratus were not seen.

In conjunction with its higher foraging rate, C. capistratus fed on an average of twice as many (5.0 ± 1.4) different prey per 5-min period as C. aculeatus (2.6 ± 0.8). The size of the prey array of C. capistratus was probably larger than that of C. aculeatus (Table 1 vs Table 3). However, part of this difference may be the result of an inability to identify the species of polychaetes and crustaceans eaten by C. aculeatus.

Not only were prey of the two species different, but also the way in which each species foraged differed. Pairs of C. capistratus swam from coral to coral, took a few bites per colony, but did not feed on a colony simultaneously. Individuals of C. aculeatus spent most of their time foraging on the undersurfaces of corals and ledges.

The mouth morphologies of these two species reflect their relative foraging strategies. C. aculeatus has a longer and somewhat prostrusible snout which may be adapted to ingesting small, discrete prey from cracks and crevices (Hubbs, 1963; Burgess, 1978). C. capistratus exhibits mouth morphology more typical of Chaetodon species, and has fleshy lips that are well adapted for sucking up coral polyps and fine teeth to rip them off cleanly without scraping the corallum.

Whereas the distribution of C. capistratus is broad, throughout the tropical western Atlantic from Brazil to the Carolinas, Bermuda and occasionally Massachusetts (Burgess, 1978), that of C. aculeatus is more restricted, including islands off the northern coast of South America, and

through the Caribbean Island arc to southern Florida and the Bahamas (Burgess, 1978). The generalized foraging pattern and large number of different prey species eaten by C. capistratus makes possible use of widely distributed habitats. This trophic plasticity allows survival in areas far removed from coral reefs and accounts for the ease with which C. capistratus can be maintained in aquaria (Allen 1980).

C. aculeatus is probably less widely distributed because of its greater habitat and prey specialization. C. aculeatus inhabits coral reefs with high structural complexity and an abundance of cryptic environments. Although this species is generally thought to be a relatively deep-dwelling coral reef fish (Hubbs, 1963; Burgess, 1978; Allen, 1979), it sometimes occurs in very shallow water (Randall, 1967). The relatively high abundance of C. aculeatus at 15 m on the west wall of Salt River Canyon is probably the result of the high structural complexity there. Prey sought by C. aculeatus are associates of corals and other reef biota.

While tropical marine fishes are not expected to show seasonal variation in their diets, variation between areas might be expected to result from differences in local abundance of food organisms (Randall, 1967). Differences in relative abundances of scleractinian corals and zooantharians may account for the prevalence of the latter in Randall's (1967) specimens of Chaetodon capistratus. Scleractinians were prevalent in Salt River Canyon, zooantharians were not. Polychaetes were potentially available to C. capistratus, but the predominance of corals in their diets seems to indicate a preference for them. Further, the five specimens taken from the east wall, which had less coral coverage, contained a wider range of prey items. I would expect C. capistratus to be most abundant on reefs that have high surface coverage by scleractinian corals, and to consume

mainly corals at those sites.

The preference of serpulid polychaetes shown by C. aculeatus in Salt River Canyon is in agreement with Randall (1967). However, feeding on tube feet and pedicellariae of echinoids was seldom observed, even though it constituted a major prey item for individuals studied by Hubbs (1963) and Randall (1967). Urchins were not common at the Salt River sites. However, because small invertebrates comprise the bulk of the diet of C. aculeatus, foraging among urchin spines is probably directed at associated invertebrates, whereas urchin body parts are either ingested in lieu of or incidentally to crustaceans.

Lang (1971, 1973) has outlined an aggression hierarchy of Caribbean scleractinians based on their abilities to digest tissues of neighboring colonies by an extracoelenteric feeding response. She considered this behavior to be interspecific competition for space and light. Species of the most aggressive families (Mussidae, Meandrinidae and Faviidae) are generally not eaten by C. capistratus. These corals have large, fleshy polyps and perhaps more abundant and/or toxic nematocysts. Since these slow growing, aggressive species have sophisticated competition strategies (Lang 1971, 1973), they might also be expected to have well developed chemical defenses against predators. More directly, the three scleractinian genera most preferred by C. capistratus (Agricia, Siderastrea and Madracis) are the least aggressive species. These preferred species are abundant, fast growing, and have small polyps. I have already posited (Neudecker, 1979) that an efficient predation strategy for corallivores would be to eat abundant, fast growing species with rapid repair responses. However, the relationship is not perfect since the sixth most important prey (Table 1) was Mycetophyllia, a highly aggressive species.

Pomacanthid Foraging Patterns

During an investigation of the food habits of 212 species of reef fishes of the West Indies, Randall (1967) found sponges in the stomachs of only 21 species. This relatively low incidence of feeding on sponges has been attributed to the defensive mechanisms of the sponges, calcareous and siliceous spicules and toxins (Bakus and Green 1974) and to the fact that fishes which eat sponges are recently evolved teleosts (Randall and Hartman 1968; Bakus 1964, 1969). Randall and Hartman (1968) studied the sponge eating species and reported that the pomacanthids Holacanthus ciliaris, H. tricolor, Pomacanthus arcuatus and P. paru ate predominantly sponges.

At St. Croix, Holacanthus ciliaris, H. tricolor, Pomacanthus arcuatus and P. paru were all observed to feed mainly on sponges. These fishes ate a large number of sponge species, although their identities were not recorded. Randall and Hartman (1968) reported that H. ciliaris had the most diverse diet of sponges (40 spp.), while H. tricolor fed on 28 species and Pomacanthus arcuatus and P. paru fed on 26 and 24 species, respectively. At Salt River Canyon, H. tricolor fed on many species of macro- and encrusting sponges. Observed foraging patterns of H. tricolor indicated that macrosponges comprised 65% of all bites, whereas smaller encrusting species taken from undersurfaces and among the algal turf comprised the rest of the diet. It is probable that the small amount of algae found in the stomachs of specimens taken by me and those examined by others (Randall, 1967; Randall and Hartman, 1968) were ingested incidentally to encrusting sponges. At St. Croix, sponges comprised 98.3% of the diet of H. tricolor, which agrees with the 97.1% figure reported by Randall and Hartman (1968).

Although Randall and Hartman (1968) reported that there was no

compelling evidence to suggest that fish predation was of great importance in controlling sponge populations in the West Indies. The four species of pomacanthids considered here eat mainly sponges and thereby reduce sponge growth rates and may also restrict their distribution, as do some chaetodontids to corals (Neudecker, 1979). Bakus (1964) has presented some experimental evidence that fish predation restricted the distribution of some sponges at Fanning Island.

CONCLUSIONS

Chaetodon capistratus is a generalist that feeds primarily on scleractinian corals on well developed coral reefs, but its ability to make dietary shifts according to prey availability allows it to inhabit a broad spectrum of habitat types throughout the tropical and subtropical western Atlantic. On the other hand, the most specialized species of the chaetodontids examined, C. aculeatus, is restricted in distribution to well developed reefs which are structurally complex. The mouth morphology of C. aculeatus is adapted to ingesting elusive prey such as serpulid polychaetes and crustaceans that inhabit interstices of the reef or are associated with anthozoans, sponges, and the algal turf of coral reefs.

The pomacanthid, H. tricolor, was a sponge specialist. The diet of H. tricolor was almost entirely sponges, most of which were large, brightly colored species, and the rest were encrusting species found in the algal turf or on undersurfaces.

Chaetodontid and pomacanthid fishes feed on the corals and sponges which constitute most of the life form of Caribbean coral reefs. While corals and sponges are not eaten by most fishes because they are mechanically and chemically protected, chaetodontid and pomacanthid fishes

have evolved specialized morphologies and foraging behaviors to cope with the defenses of their prey. The many species differ from each other mainly through the utilization of different prey species by adjusting to their specific defense tactics (Bakus, 1964, 1969; Hobson, 1974). Utilization of corals and sponges by chaetodontid and pomacanthid fishes probably affects their growth, abundance and distribution, and thereby exerts considerable influence on Caribbean coral reef communities.

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LITERATURE CITED

- Adey, W., Gladfelter, W., Ogden, J., and Dill, R. 1977. Field guidebook to the reefs and reef communities of St. Croix, Virgin Islands. Atlantic Reef Committee, University of Miami, Miami Beach, Florida. 52 pp.
- Allen, G. R. 1980. Butterfly and Angelfishes of the World, Vol. 2. Wiley-Interspace, NY. 352 pp.
- Bakus, G. J. 1964. The effects of fish-grazing on invertebrate evolution in shallow tropical waters. Allan Hancock Found. Occas. Pap. 27:1-29.
- _____. 1969. Energetics and feeding in shallow marine waters. Int. Rev. Genet. Exp. Zool. 4:275-369.
- Bakus, G. J., and Green, G. 1974. Toxicity in sponges and holothurians: a geographic pattern. Science 185:951-953.
- Birkeland, C., and Neudecker, S. 1981. Foraging behavior of two Caribbean chaetodontids: Chaetodon capistratus and C. aculeatus. Copeia 1981(1): 169-178.
- Burgess, W. E. 1978. Butterfly fishes of the world. T. F. H. Publ., Neptune City, NJ. 832 pp.
- Hiatt, R. W., and Strasburg, D. W. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30:65-127.
- Hobson, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish Bull. 72:915-1031.
- Hubbs, C. L. 1963. Chaetodon aya and related deep-living butterfly fishes: their variations, distribution and synonymy. Bull. Mar. Sci. Gulf and Caribb. 13:133-192.

- Lang, J. 1971. Interspecific aggression by scleractinian corals, I. The rediscovery of Scolymia cubensis (Mile Edwards and Halme). Bull. Mar. Sci. 21(4):952-959.
- _____. 1973. Coral reef project-papers in memory of Dr. Thomas F. Goreau, II. Interspecific aggression by scleractinian corals, II. Why the race is not only to the swift. Bull. Mar. Sci. 23(2):260-279.
- Neudecker, S. 1977. Transplant experiments to test the effects of fish grazing on coral distribution. Proc. Third Int. Coral Reef Symp. 1:317-323.
- _____. 1979. Effects of grazing and browsing fishes on the zonation of corals in Guam. Ecology 60:666-672.
- Neudecker, S., and Lobel, P. S. In press. Mating systems of chaetodontid and pomacanthid fishes at St. Croix. Zeit. Tierpsychol.
- Randall, J. E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr., Miami 5:665-847.
- _____. 1968. Caribbean reef fishes. T. F. H. Publ., Jersey City, NJ. 318 pp.
- _____. 1974. The effect of fishes on coral reefs. Proc. Second Int. Coral Reef Symp. 1:159-166.
- Randall, J. E., and Hartman, W. D. 1968. Sponge-feeding fishes of the West Indies. Mar. Biol. 1:216-225.
- Reese, E. S. 1975. A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. Zeit. Tierpsychol. 37:37-61.
- _____. 1977. Coevolution of corals and coral feeding fishes of the family Chaetodontidae. Proc. Third Int. Coral Reef Symp. 1(Biology):267-274.

Shen, S. C., and Liu, C. H. 1976. Ecological and morphological study of the fish fauna from the waters around Taiwan and its adjacent islands, 17. A study of sex reversal in a pomacanthid fish Gemicanthus semifasciatus (Kamohara). Acta Oceanogr. Taiwanica Sci. Repts. 6:140-150.

