

**FORAGING BEHAVIOR OF TWO CARIBBEAN CHAETODONTIDS:
Chaetodon capistratus and *C. aculeatus***

Charles Birkeland and Steve Neudecker

[Converted to electronic format by Damon J. Gomez (NOAA/RSMAS) in 2002. Copy available at the NOAA Miami Regional Library.]

Foraging Behavior of Two Caribbean Chaetodontids: *Chaetodon capistratus* and *C. aculeatus*

CHARLES BIRKELAND AND STEVE NEUDECKER

Chaetodon capistratus is a browser on anthozoans, preferring hexacorals (scleractinians, anemones and zoantharians) over octocorals and antipatharians. Within its preferred group of prey, *C. capistratus* is an active generalist, taking more of a certain prey than expected when the prey is scarce and less than expected when the same prey is common. This foraging for evenness among items in the diet results in the diet being more diverse than the available prey. The local abundance of *C. capistratus* is significantly correlated with local coral surface cover and/or with local coral diversity, perhaps because *C. capistratus* forages for evenness of diet. The abundance of *Chaetodon (Prognathodes) aculeatus*, a predator, does not correlate with these aspects of coral cover. *C. aculeatus* preys upon small discrete items (polychaetes, crustaceans, eggs), probably more calorific than anthozoans. *C. aculeatus* is considered very selective not only because its prey occupy small areas, but also because these prey are effectively defended (e.g., eggs) or have effective predator avoidance mechanisms (e.g., tubeworms). *C. capistratus* bit prey more frequently and regularly over the exposed corals (29.4 ± 8.4 bites per 5-min period) than did *C. aculeatus*, which bit in spurts (12.2 ± 4.6 bites per 5-min period) when it found hidden items of higher caloric value than anthozoans. *C. aculeatus* spent a greater proportion of time searching for fewer items of higher caloric value.

Coral tissue is abundantly available throughout the year on coral reefs, and the process of using it as a major source of food energy provides additional feeding niches, thereby contributing to the potential diversity of coral reef fishes and the carrying capacity for fishes by the coral reef habitats. Coral tissue appears to be an adequate source of food energy by its abundance, but chaetodontids tend to feed on a variety of scleractinians and must still occasionally obtain a few worms, crustaceans or fish eggs to augment this diet with essential nutrients. Although *C. capistratus* and *C. aculeatus* obtain most of their food energy from different sources, both may be limited in growth or reproduction by the same essential nutrients.

DIETS of chaetodontids consist predominantly of anthozoans, polychaetes and small crustaceans in both the Caribbean (Randall, 1967) and Pacific (Hiatt and Strasburg, 1960; Hobson, 1974; Reese, 1975, 1977). The relative importance of these items and the manner in which they are obtained varies between species. In the Pacific, some chaetodontids browse coral polyps while others graze coral colonies (Hiatt and Strasburg, 1960; Neudecker, 1977, 1979) and others take mostly mucus from the corals (Hobson, 1974). Some chaetodontids obtain crustaceans mostly from the plankton while others obtain them mostly from the benthos (Hobson, 1974). The degree of specialization, in terms of the relative proportions of food categories in the diet, also varies by species.

This paper examines dietary generalization in terms of the degree to which the proportions of prey species in the diet correspond to the proportions of prey species in the environment. A "passive generalist" is defined as a species that takes prey in the proportions in which they are available in the environment. Whether a species fits this definition is determined by a goodness of fit test where the "observed" is the diet and the "expected" is calculated by the relative abundance of prey in the environment. We conclude that a species is a passive generalist when there is no significant difference. Obtaining prey at random (within the relevant taxa) implies that the prey are taken in proportion to their availability and that the choice is not influenced by previous meals or bites. We assume that the proportions of prey available

do not change between bites because we have never observed a chaetodontid to alter the relative abundance of coral species or plankters.

An "active generalist" seeks a varied diet. When a prey is particularly common, it is taken less than expected by chance. When the same prey is relatively scarce, it is taken more than expected by chance. In other words, an active generalist is defined as a species for which the proportions of species in the diet differ significantly from the proportions available in such a way that the diet tends to be more diverse than the array of available prey because of increased evenness.

A "specialist" tends to favor certain prey species, whether common or rare. A specialist is defined as a species for which the proportions of prey species in the diet differ significantly from the proportions available in such a way that the prevalent items in the diet tend to vary in a consistent direction from the expected at all sites. Degree of specialization is compared by using both the number of species in the diet and the degree of deviation from the expected. To decide whether a species is a specialist or an active generalist requires observing the diet of the chaetodontid in different areas among which the relative abundances of the available prey differ.

SITE DESCRIPTION

This study was undertaken at St. Croix, U.S. Virgin Islands. Field observations were made from the NOAA Underwater Laboratory System-I (NULS-I), operated by the Manned Undersea Science and Technology Office of NOAA in cooperation with the West Indies Laboratory of Fairleigh Dickinson University. Observations were made during 15 diving excursions (38 h) between 25 May and 1 June 1978.

The laboratory (Hydrolab) was located at a depth of 16 m on a sandy channel in Salt River Canyon, St. Croix. The two areas chosen for sample transects were along the west and east walls of the canyon. Transects began 220 m and 260 m, respectively, from the laboratory.

The west wall was very steep, often vertical, with many overhangs and caves. The east wall had a more gentle slope and generally more sediment. Scleractinian corals and antipatharians were far more prevalent on the west wall at both 15 and 30 m depth, than on the east wall at either depth (Table 1). Gorgonaceans, especially plexaurids, were more common on

the east wall at both depths (Table 1). On both walls, *Agaricia* was more prevalent at 30 m than at 15 m although it was still the predominant coral at 15 m on the west wall (Table 1). Most other coral species were more common at 15 m on both walls.

METHODS

In order to define areas in which diet was compared with prey availability, four areas were marked off with 100 meter transect lines laid out along the 15 and 30 m isobaths on both the east and west walls of Salt River Canyon. The abundance of chaetodontids was measured by swimming along the transect lines and counting all chaetodontids seen within 1 m to either side and within 2 m above the transect line. Although all species of chaetodontids were counted, this paper reports only on *Chaetodon capistratus* and *Chaetodon (Prognathodes) aculeatus* because they were the only two species common enough to provide adequate data. (*Prognathodes* has recently been reduced from a genus to a subgenus by Burgess [1978].)

Measurement of surface areas for prey availability.—The relative abundances of potential prey species along transects were measured in terms of surface areas. The dimensions of large colonial animals were measured in centimeters and the areas were calculated. The occupation of horizontal surfaces were also measured by tallies from point intersection quadrats.

To assess the relative proportions of different large (>1 cm diameter) prey species at each of the four sites, we repeatedly tossed a 0.0625 m² quadrat haphazardly along the transect lines and measured all the animals larger than 1 cm in diameter within each quadrat. Height, maximum width or horizontal diameter, and greatest width or horizontal diameter perpendicular to the maximum diameter were measured for each individual sampled. Encrusting sponges, *Erythropodium*, corals and tunicates were measured as circular areas if the greater diameter was less than or equal to 1.5 times the perpendicular diameter. Half the geometric mean diameter was used as the radius in the calculation. If the greater diameter was larger than 1.5 times the perpendicular diameter, the area was measured as a rectangle by simple multiplication.

Sea fans, such as *Gorgonia* and *Iciligorgia*, were measured on one surface and the calculated area was doubled. The doubling of the

TABLE 1. RELATIVE PROPORTIONS OF ANTHOZOAN SURFACE AREAS ON THE WALLS OF SALT RIVER CANYON, ST. CROIX. The surface areas of scleractinian genera are presented as relative proportions of the scleractinians.

Area (wall) Depth (m)	West 15	East 15	West 30	East 30
Scleraxonians	.1028	.0070		
Plexaurids	.3457	.8286	.0437	.7983
Gorgoniids	.0349	.0109		.0364
Antipatharians	.2961		.5799	.1455
Anemones	.0028	.0013	.0031	.0037
Zoanthids in sponges	.0070	.0058	.0236	.0085
Free zoanthids	.0054			.0001
Scleractinians	.2053	.1464	.3497	.0075
<i>Stephanocoenia</i>	.0220	.0036	.0550	.0032
<i>Madracis</i>	.1074	.0373	.0076	
<i>Agaricia</i>	.3406	.0460	.7144	.8396
<i>Siderastrea</i>	.1600	.1409	.0866	.0256
<i>Porites</i>	.0903	.1049	.0064	.0312
<i>Diploria</i>	.0590	.1265		
<i>Colpophyllia</i>	.0046	.1051		
<i>Solenastrea</i>	.0044	.0063		.0051
<i>Montastraea</i>	.1453	.3588	.0662	.0082
<i>Meandrina</i>	.0062	.0205		.0523
<i>Dichocoenia</i>	.0010	.0332	.0048	.0316
<i>Mussa</i>		.0026		
<i>Scolymia</i>		.0002		
<i>Mycetophyllia</i>	.0564	.0124	.0590	
<i>Eusmilia</i>	.0028	.0017		.0032

area was done because fish can encounter the sea fans and browse them from both sides rather than from one side (as on encrusting organisms).

Surface areas of bushy gorgonaceans and antipatharians, and of tubular or finger-like sponges, were estimated by calculating the vertical surface area of a cylinder, circumference times height. Although the actual surface area was less for the bushy gorgonaceans and antipatharians, which were in the form of many thin and separated branches, the fish could still be considered to encounter a large cylindrical area.

Some sponges were spherical. The estimated surface area of the sphere ($4\pi r^2$) was calculated by using half of the geometric mean of the three diameters (height, width, and perpendicular width) as the radius.

A total of 254 quadrats (0.0625 m^2 each) were examined from which about three thousand animals were measured (two or three dimensions each). The surface areas occupied by algal turf, crustose coralline algae, etc., were difficult to measure by dimensions and so a tally was made of the organisms occupying the substrata

under the points of intersection of strings tied across the 0.0625 m^2 quadrats. Four strings tied from both sides of the quadrat gave 16 intersecting points for each quadrat. Point intersection data were used to assess horizontal surface coverage. A total of 254 quadrats provided a total of 4,064 points of intersection data.

The surface area was proportioned among the phyla by averaging the horizontal areal estimates from point-intersection and horizontal dimension measurement data (which were in close agreement for all major taxa). Within each taxon (sponge, gorgonacean, etc.), the relative vertical and horizontal dimensions were calculated. The vertical areas for each taxon were then added to the total for the community by taking their vertical areas relative to their horizontal areas and multiplying this by the proportion of their horizontal area in the community. When all vertical and horizontal areas were summed for the entire community, the proportions of the total made up by each species were calculated.

Field feeding observations.—Foraging behavior and prey selection were observed by following

TABLE 2. THE OBSERVED DIET OF *Chaetodon capistratus* AT THE FOUR STUDY SITES IN TERMS OF THE NUMBER OF BITES TALLIED FOR EACH MAJOR GROUP OF ANTHOZOANS. The expected frequency of bites in each group was calculated from the data in Table 1. The "+" and "-" signs indicate the direction of deviation of the observed from the expected.

	West wall 15 m		East wall 15 m		West wall 30 m		East wall 30 m					
	<i>f</i> obs	\bar{f}	<i>f</i> obs	\bar{f}	<i>f</i> obs	\bar{f}	<i>f</i> obs	\bar{f}				
Scleractinians	+	555	132	+	314	51	+	373	155	+	184	2
Scleraxonians	-		66	-		2	+	25				
Plexaurids	-	58	223	-	34	291	+	23	19	-	52	196
Gorgoniids	-		23	-		4				-		9
Antipatharians	-	8	191				-	13	257	-	1	36
Anemones	-		2	-		1	+	5	1	+	5	1
Zoanths in sponges	+	21	5	+	3	2	-	4	11	-		2
Free zoanths	0	3	3							+	4	
Total number of bites in the area			645			351			443			246

individual chaetodontids for 5-min periods and tallying the number of bites on each prey item. Individuals were not followed over successive 5-min periods. Observations were obtained twice each day: in the morning (0730 to 1200) and afternoon (1530 to 1830). Fish were followed as closely as possible without influencing their behavior. While this "discreet distance" (Reese, 1975) varied, the fishes did not appear to be affected by the observer.

The prey species could not be visually identified when the fish foraged for small prey in algal turf, on undersurfaces, or in the plankton. In those cases, the bites were tallied in categories of location.

Stomach content analysis.—When a fish pecked at a coral and left no obvious toothmarks, it was difficult to tell whether the fish was eating tissue from the coral polyp, mucus from the coral, microscopic debris or microscopic animals such as copepods associated with the coral. We also could not determine exactly what the fish was taking from the algal turf, undersurfaces or plankton. To determine the kinds of food taken from these surfaces, we speared at least ten adults of each fish species under study and preserved the stomachs with a buffered 10% formalin solution and later examined the stomach contents.

The stomach contents were examined under both dissecting and compound microscopes. A visual estimate was made of percent of the total volume of stomach contents contributed by

each prey category (Randall, 1967; Hobson, 1974) for each fish stomach.

The presence in the stomachs of entire polyps with eight pinnate tentacles was considered evidence for browsing on octocorals, and masses of tissue with zooxanthellae were considered as evidence for browsing on hexacorals. Stomach contents were examined only to verify that polyp tissue was actually taken. The relative proportions of anthozoan taxa in the diet were determined more accurately from field observations.

RESULTS AND DISCUSSION

C. capistratus was a browser of anthozoans (Table 2). This was verified by stomach content analysis (Table 3). In a total of 1,795 feeding observations for *C. capistratus*, 1,681 (93.6%) were on anthozoans. The other 114 observations probably involved predation by *C. capistratus* on small polychaetes and crustaceans (Table 3) from the algal turf ($N = 107$), from the surface of sponges ($N = 6$) or from off a hydroid ($N = 1$). When the anthozoans were considered as a class, *C. capistratus* was a specialist on hexacorals (scleractinians, anemones and zoanths), significantly preferring them over octocorals and antipatharians (Table 4). Although plexaurid gorgonaceans were prevalent in the diet at all sites, they were almost always taken considerably less than expected by chance. The proportions of different groups of anthozoans in the diet differed significantly

TABLE 3. CONTENTS OF THE STOMACHS OF *Chaetodon capistratus* AND *C. aculeatus* COLLECTED FROM SALT RIVER CANYON, HALF FROM THE EAST WALL AND HALF FROM THE WEST WALL, ALL BETWEEN THE DEPTHS OF 15 AND 30 M.

Items	Number of fish containing this item		Mean percent of diet volume	
	<i>C. capistratus</i> (N = 10)	<i>C. aculeatus</i> (N = 12)	<i>C. capistratus</i>	<i>C. aculeatus</i>
Hexacorals ¹	10		73.5	
Octacorals ²	5		9.0	
Serpulid polychaetes	3	11	11.25	68.5
Crustaceans	4	8	3.0	25.0
Eggs	2	4	.75	5.5
Algae	1		.5	
Unidentified animal material	3	1	2.0	1.0

¹ Tissues with zooxanthellae found.

² Polyps with eight pinnate tentacles found.

from the proportions expected (Table 4), and scleractinians were always taken more than expected (Table 2).

Among the hexacorals, the scleractinian corals, anemones and zoanthids all were generally favored by *C. capistratus*, but anemones and zoanthids were too scarce in the study areas to rank them with any certainty. Randall (1967:795) found much of the diet (38.6%) of *C. capistratus* to be made up of zoantharians, but "food habits may differ profoundly from area to area" (1967:671). However, *C. capistratus* prefers hexacorals to octacorals and antipatharians.

C. capistratus was an active generalist when feeding on scleractinians. The proportions of different groups of scleractinians in the diet of *C. capistratus* (Table 6) differed significantly from the expected proportions (Table 7), but the direction of deviation observed from the expected generally varied for the prevalent genera (Table 5). The difference between sites was indicated by the large interaction term (Table 7). *Madracis* was the only genus that appeared to be consistently selected. Mussids, especially *Mycetophyllia*, and *Solenastrea* were consistently taken in proportions greater than expected by chance, but this was possibly an artifact of the matter that they were not really prevalent at any of the study sites. Because the tendencies to select less abundant prey and to feed on a variety of prey promote evenness among

TABLE 4. G-TEST OF GOODNESS OF FIT OF PROPORTIONS OF THREE GROUPS OF ANTHOZOANS (SCLERACTINIANS, PLEXAURIDS, AND OTHER ANTHOZOANS) IN THE DIET COMPARED WITH THE PROPORTIONS EXPECTED (CALCULATED FROM TABLE 2). FOR THE STATISTICAL TEST OF GOODNESS OF FIT, THE EXPECTED MUST BE ≥ 5 IN MORE THAN 80% OF THE CELLS. THEREFORE, WE COMBINED THE CATEGORIES IN TABLE 2 INTO THREE GROUPS FOR THE TEST.

Test	df	G	
Pooled	2	4.261.988**	
West 15 m	2	1,278.586**	$\chi^2_{.005(2)} = 10.6$
East 15 m	2	988.848**	
West 30 m	2	499.902**	
East 30 m	2	1,494.652**	
Interaction	6	79.384**	$\chi^2_{.005(6)} = 18.5$
Total	8	4,341.372**	$\chi^2_{.005(8)} = 21.9$

proportions of items in the diet, the diet is usually more diverse than the available prey. This greater diversity in diet over available prey may not necessarily be the case if the available prey are very diverse. Note at the bottom of Table 5 that the diversity of items in the diet remains relatively constant despite greater variation in the diversity of available prey. A varied diet might be desirable for all but the most specialized of species.

Each individual *C. capistratus* appeared to be an active generalist on anthozoans, moving from coral colony to colony, usually taking from 1 to 5 bites from each colony. In the 5-min foraging observations (N = 61), each individual *C. capistratus* usually browsed on four to six species of anthozoans (4.9 ± 1.4). Observation periods with fewer prey species were also those with fewer bites taken and the periods with more prey species were those with more bites taken ($r = 0.95$, N = 61, $P < 0.001$). There were no significant differences between morning and afternoon foraging rates ($F_{s(1,31)} = 3.5$) or between foraging rates in the four transect areas ($F_{s(3,31)} = 0.6$).

The foraging of *C. aculeatus* differed from that of *C. capistratus* in several fundamental ways. *C. aculeatus* was generally a predator rather than a browser, feeding on entire discrete individuals of polychaetes, crustaceans, and eggs (Table 3). (However, nipping tentacles from tubeworms and pedicellariae and tube feet from echinoids should be categorized as browsing.) *C. aculeatus* tended to forage over the un-

TABLE 5. THE OBSERVED DIET OF *Chaetodon capistratus* AT THE FOUR STUDY SITES IN TERMS OF THE NUMBER OF BITES TALLIED FOR EACH OF THE GENERA OF SCLERACTINIANS. The expected frequency of bites on each genus was calculated from the data in Table 1. The "+" and "-" signs indicate the direction of deviation of the observed from the expected.

	West wall 15 m		East wall 15 m		West wall 30 m		East wall 30 m					
	<i>f</i> obs	\hat{f}	<i>f</i> obs	\hat{f}	<i>f</i> obs	\hat{f}	<i>f</i> obs	\hat{f}				
<i>Stephanocoenia</i>	-	4	12	-		1	-	20	-		1	
<i>Madracis</i>	+	102	59	+	19	12	+	29	3	+	29	0
<i>Agaricia</i>	+	214	188	+	92	14	-	183	266	-	75	154
<i>Siderastrea</i>	-	72	88	+	70	44	+	85	32	+	28	5
<i>Porites</i>	0	49	49	-	23	33	-	1	3	+	28	6
<i>Colpophyllia</i>	-		3	-		33						
<i>Diploria</i>	-	9	32	-	29	40	+	2	0			
<i>Solenastrea</i>	+	32	3	+	24	2	+	12	0	+	4	1
<i>Montastraea</i>	-	8	80	-	7	113	-	10	25	+	11	1
<i>Meandrina</i>	+	17	3	+	21	6				-	6	9
<i>Dichocoenia</i>	-		1	+	20	10	+	7	2	-		6
<i>Scolymia</i>										-		1
<i>Mussa</i>	+	12		-		1						
<i>Mycetophyllia</i>	+	32	31	+	6	4	+	44	22	+	3	0
<i>Eusmilia</i>	-	4	2	+	3	1						
		555			314			373			184	
Simpson's Index of Diversity, D (diet/nature)		.781/.811 = .963			.832/.807 = 1.031			.685/.473 = 1.448			.757/.294 = 2.575	

dersurfaces of coral shelves and hidden crevices rather than over the exposed substratum (Table 8). As with *C. capistratus*, there were no significant differences for *C. aculeatus* between morning and afternoon foraging rates ($F_{s(1,3)} = 2.1$) or between foraging rates in the four transect areas ($F_{s(3,3)} = 7.8$).

The most intense feeding activity of *C. aculeatus* was directed towards a large patch of eggs of the sergeant major *Abudefduf saxatilis*. The *A. saxatilis* left the eggs undefended for only a few minutes, so the eggs not only occupied a small area in the environment (were relatively scarce), but they were also frequently unavailable because they were defended.

The discrete food items sought by *C. aculeatus* (polychaetes, crustaceans, eggs) were probably of higher average caloric value, but were generally more difficult to obtain, than were the tissues of anthozoans browsed by *C. capistratus*. The sessile items in the diet of *C. aculeatus* often had either predator avoidance mechanisms (tubeworms) or were defended (fish eggs). These sessile items were so scarce on exposed surfaces that they did not show up in the prey availability survey. Therefore, the expected propor-

tions of these items in the diet were zero and the *C. aculeatus* was highly selective. Thus, the predatory *C. aculeatus* was highly selective for hidden resources. The browser, *C. capistratus*, was an active generalist, tending to broaden its diet. The list of items in the diet of *C. aculeatus* was a subset of the list for *C. capistratus* (Table 3).

Anthozoans generally have a much lower caloric value (494 cal/g wet wt, Cummins and Wuycheck, 1971) than do polychaetes and crustaceans (639 and 817 cal/g wet wt, Cummins and Wuycheck, 1971), so it seems reasonable to observe a coral-browsing chaetodontid consistently taking in more bites of food than a predatory chaetodontid. *C. capistratus* moved along the face of the reef, browsing on corals at a fairly regular pace, taking 29.4 ± 9.8 (61) bites per 5-min period. *C. aculeatus* moved from patch to patch, tending to bite in spurts, taking 12.2 ± 4.6 (44) bites per 5-min period. *C. capistratus* took significantly more bites ($t_{s(103)} = 11.95^{***}$) than did *C. aculeatus*, and there was significantly less variation in number of bites taken per 5-min interval ($F_{s(60,43)} = 3.65^{***}$).

Eggs generally have the greatest caloric value

TABLE 6. THE OBSERVED DIET OF *Chaetodon capistratus* AT THE FOUR STUDY SITES IN TERMS OF GENERAL GROUPS OF SCLERACTINIAN CORALS. For the statistical test of goodness of fit, the expected must be ≥ 5 in more than 80% of the cells. Therefore, we combined the genera in Table 5 into six groups for testing.

	West Wall 15 m		East wall 15 m		West wall 30 m		East wall 30 m					
	<i>f</i> obs	<i>f</i>	<i>f</i> obs	<i>f</i>	<i>f</i> obs	<i>f</i>	<i>f</i> obs	<i>f</i>				
<i>Agaricia</i>	+	214	188	+	92	14	-	183	266	-	75	154
<i>Siderastrea</i>	-	72	88	+	70	44	+	85	32	+	28	5
Other small polyp ¹ families	+	155	120	-	42	46	+	30	26	+	57	7
<i>Montastraea</i>	-	8	80	-	7	133	-	10	25	+	11	1
Other large ² polyp families	+	58	42	+	94	91	+	21	2	-	10	16
Highly aggressive ³ families	+	48	33	+	9	6	+	44	22	+	3	1
		555			314			373			184	

¹ Astrocoeniidae (*Stephanocoena*), Pocilloporidae (*Madraxis*), Poritidae (*Porites*).

² Faviidae (*Solenastrea*, *Colpophyllia*, *Diploria*), Meandrinidae (*Dichocoenia*, *Meandrina*).

³ Mussidae (*Mycetophyllia*, *Scolymia*, *Mussa*), Caryophyllidae (*Eusmilia*).

of the food we considered (1,492 cal/g wet wt, Cummins and Wuycheck, 1971) and probably contain a reasonably complete set of nutrients because the early stages in the lives of damselfishes are supported entirely within the eggs. The eggs are usually defended, and crustaceans and polychaetes are hidden, so it is not surprising that the predatory *C. aculeatus* tends to feed in spurts when the opportunities arise. The generalist, *C. capistratus*, also eats eggs, crustaceans and polychaetes (Table 3), and probably prefers them, but it appears less competent in obtaining such guarded resources.

C. capistratus appears to occur in a wider range of habitats (including mangrove and "back reef" areas) than does *C. aculeatus*. *C. capistratus* might be able to obtain polychaetes and eggs more easily in the absence of *C. aculeatus*. Randall (1967) reported the gut contents from his specimens of *C. capistratus* to contain a greater proportion of polychaete tentacles (31.4%) and eggs (6.4%) than ours (Table 3). This is not surprising, since his *C. capistratus* were collected in areas away from *C. aculeatus* (J. E. Randall, pers. comm.), while our *C. capistratus* and *C. aculeatus* were collected along the same transect lines.

The aspect of foraging behavior that is most in need of explanation is the consistent tendency of *C. capistratus* to broaden its diet. Generalists such as *Zanclus* and coral-browsing chaetodontids will feed actively in aquaria for a few months, but eventually die of apparent mal-

nutrition unless given a varied diet of corals and scuzz (John R. Eads and R. Sakamoto, pers. comms.). This dependence on a varied diet is in contrast to predators of crustaceans and polychaetes that can be maintained in aquaria on a relatively uniform diet (J. R. Eads and R. Sakamoto, pers. comms.). Fish malnutrition results usually from a lack of essential nutrients, not from too few calories. Fish are very dependent on certain nutrients being present in their diet. Serious symptoms of deficiencies of each of 14 essential vitamins are listed by Phillips (1969). Some amino acids may be synthesized by fish, but at least ten essential amino acids must be obtained in the diet (Phillips, 1969). "Protein requirements of fish are two to four times

TABLE 7. G-TEST OF GOODNESS OF FIT OF PROPORTIONS OF CORAL GENERA IN THE DIET COMPARED WITH THE PROPORTIONS EXPECTED (CALCULATED FROM TABLE 6).

Tests	df	G	
Pooled	5	740.575**	
West 15 m	5	131.800**	$\chi^2_{.005(5)} = 16.75$
East 15 m	5	378.239**	
West 30 m	5	179.203**	
East 30 m	5	277.575**	
Interaction	15	226.242**	$\chi^2_{.005(15)} = 32.8$
Total	20	966.817**	$\chi^2_{.005(20)} = 40$

TABLE 8. THE FREQUENCY WITH WHICH FORAGING ACTIVITY OF *C. aculeatus* (BITES) OCCURRED ON DIFFERENT PATCHES OF THE ENVIRONMENT. Frequency is the proportion of 5-min observation intervals (N = 43) in which bites were taken within the category of patch.

Patch of environment	Frequency ($\Sigma f = 43$)	No. bites
Undersurfaces ¹	35	180
Algal turf ¹	11	54
Sponges ¹	37	190
Corals (<i>Siderastrea</i>) ¹	2	6
Octocorals (plexaurids) ¹	2	3
Fish eggs (<i>Abudefduf saxatilis</i>)	3	66
Echinoids ²	2	8
Plankton	3	13

¹ Stomach content analysis (Table 3) implies that microscopic crustaceans or polychaetes are being picked from these surfaces (Randall, 1967:799).

² Pedicellariae and tubefeet were probably being picked from the echinoids (Randall, 1967:799; Hubbs, 1963:176).

higher than those of birds and mammals" (Love, 1970:207). Since individual food items usually do not contain all the essential kinds of macromolecules, the chaetodontids may need to eat at least small amounts of several foods to survive.

Food categories vary in their contents of essential amino acids. Omnivorous fishes utilize animal food for growth and plant food for metabolic energy (Migita and Hashimoto, 1949; Menzel, 1959; Fischer, 1970, 1972a, b, 1973). The grass carp grows ten times faster on animal food (Fischer, 1970), although its diet in the natural habitat often consists mostly of plant material (Fischer, 1973). For many herbivorous fishes, plant food supplies sufficient metabolic energy but traces of animal material are required for growth (Menzel, 1959; Fischer, 1972b, 1973; Mathavan et al., 1976). Fishes that are herbivorous as adults are often carnivorous in the juvenile stages of their life history (Fischer, 1973; Lowe-McConnell, 1977; Lassuy, 1979); this is probably because amino acids and other essential nutrients are necessary for early stages when development and growth are most important. As the fish matures and its growth rate slows, the fish can maintain itself on plant food. However, many of these herbivorous fishes will readily accept animal food if made available (Menzel, 1959; Fischer, 1973; Mathavan et al., 1976).

We suggest that anthozoan tissue is also a source of low quality food that is readily avail-

TABLE 9. SOME CHARACTERISTICS OF THE FOUR STUDY AREAS IN TERMS OF POPULATIONS OF *Chaetodon capistratus*, *C. aculeatus*, CORAL COVER AND CORAL GENERIC DIVERSITY.

Area	Depth	Percent coral cover	Coral generic diversity (Simpson's Index of Diversity)	Mean no./200 m ²	
				<i>Chaetodon capistratus</i>	<i>Chaetodon aculeatus</i>
West wall	15 m	41.47	.811	5.3	1.1
East wall	15 m	29.46	.807	2.2	0.3
West wall	30 m	17.10	.473	1.5	2.0
East wall	30 m	15.10	.294	1.0	1.0

able around coral reefs. Caribbean chaetodontids that ordinarily feed on anthozoan tissue would readily accept fish eggs, worms or crustaceans when these foods are accessible. By using foods from anthozoan tissue to provide most of their metabolic energy needs, chaetodontids can use foods from eggs, worms and crustaceans for more specific nutrient requirements. Laboratory experiments are required to determine whether some Indo-Pacific chaetodontids have the ability to feed exclusively on scleractinian tissue.

A second advantage of a broad diet arises in increased assimilation efficiencies from mixed diets. Bluegills, *Lepomis macrochirus*, can grow faster on a combination of worms and algae than on worms alone, but they lose weight on algae alone (Kitchell and Windell, 1970). Herbivorous fishes, such as *Tilapia mossambica*, require traces of animal food for adequate nutrient absorption efficiency (Mathavan et al., 1976). The grass carp, *Ctenopharyngodon idella*, grows on animal food and little, if at all, on plant food; but a mixed diet improves food utilization (Migita and Hashimoto, 1949; Fischer, 1973). Dietary problems of fish often arise from imbalance, rather than lack of essential nutrients (Buhler and Halver, 1961).

Whether a mixed diet is selected to provide essential nutrients or to provide a balanced diet for assimilation efficiency or both, our results suggest that individual eggs, crustaceans and polychaetes all tend to contain a greater variety of nutrients than do individual anthozoans. This hypothesis needs to be tested.

Since *C. capistratus* attempts to diversify its diet of corals, we were not surprised to find the local abundance of *C. capistratus* to correlate

significantly ($r_s = 1.0$, $P < 0.05$) with the local generic diversity of coral cover (Table 9). However, the abundance of *C. capistratus* also correlates with the total amount of the coral cover. The abundance of *C. aculeatus* does not correlate with either coral diversity or coral cover (Table 9).

Small crustaceans, serpulid polychaetes and eggs make up parts of the diets of both *C. capistratus* and *C. aculeatus*. *C. aculeatus* obtains most of its caloric intake from those food categories by searching for them on undersurfaces and in crevices and feeding in spurts when it finds them. *C. capistratus* obtains much of its caloric intake from exposed and apparently readily available anthozoans, but it has to take in more than twice as many bites to obtain an adequate caloric intake.

Chaetodontids do not appear to overexploit anthozoans as prey. Although anthozoans may be a superabundant food source for *C. capistratus*, some essential nutrients may be in short supply and available only in items that are hard to obtain such as fish eggs. Although *C. capistratus* is mainly a browser of anthozoans and *C. aculeatus* is a predator of polychaetes and crustaceans for caloric intake, these two chaetodontids may still be under competition for essential nutrients in hard to obtain items such as fish eggs. That an overlap in diet is small does not imply that competition is slight if the small overlap concerns essential nutrients.

Although fish populations may be limited by the same essential nutrients in eggs, crustaceans and worms, the bulk of the diets or the main sources of caloric intake may still come from different sources. Using abundant and easily obtained anthozoans as a primary source of food, taking only a few eggs, crustaceans or worms as they happen to be available increases the "carrying capacity" of fishes in the coral reef habitat, thereby contributing to the potential diversity of coral reef fishes.

ACKNOWLEDGMENTS

We wish to thank the staff of the NULS-I project for the very good support which they gave to us. Dennis K. Hubbard coordinated the project and Barry Walden kept the operation running smoothly the entire time. We sincerely appreciate all the air fills and scuba deliveries provided in the field by Mike Canfield, Rod Cattanaach, Steve McGowen and Dough Langhorst. Robert Dill and Sonia Dill were generous

with topside logistics. The West Indies Laboratory loaned us a compound microscope and a dissecting microscope for our stomach content analyses. John E. Randall, W. J. Hamilton III, Harry Kami, Henry Tucker and Ron Strong made helpful comments on this manuscript.

LITERATURE CITED

- BUHLER, D. R., AND J. E. HALVER. 1961. Nutrition of salmonoid fishes. IC. Carbohydrate requirement of chinook salmon. *J. Nutr.* 74:307-318.
- BURGESS, W. E. 1978. Butterfly fishes of the world. T. F. H. Publ., Neptune City, N.J.
- CUMMINS, K. C., AND J. C. WUYCHECK. 1971. Caloric equivalents for investigations in ecological energetics. *Internat. Verein. Theor. Angew. Limnol.* 18.
- FISCHER, Z. 1970. The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.). Part 1. *Pol. Arch. Hydrobiol.* 17:421-434.
- . 1972a. The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.). Part 2. Fish fed with animal food. *Ibid.* 19:65-82.
- . 1972b. The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.). Part 3. Assimilability of proteins, carbohydrates, and lipids by fish fed with plant and animal food. *Ibid.* 19:83-95.
- . 1973. Physiology and bioenergetics of grass carp. *Ibid.* 20:521-557.
- HIATT, R. W., AND D. W. STRASBURG. 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.
- KITCHELL, J. F., AND J. T. WINDELL. 1970. Nutritional value of algae to bluegill sunfish *Lepomis macrochirus*. *Copeia* 1970:186-190.
- LASSUY, D. R. 1979. The relation of diet, intestinal morphology and nitrogen assimilation in the damselfish *Eupomacentrus lividus*. Unpubl. MS Thesis, Univ. Guam.
- LOVE, R. M. 1970. The chemical biology of fishes. Academic Press, New York.
- LOWE-McCONNELL, R. H. 1977. Ecology of fishes in tropical waters. *Studies in Biology* 76. Edward Arnold, London.
- MATHAVAN, S., E. VIVEKANADAN AND T. J. PANDIAN. 1976. Food utilization in the fish *Tilapia mossambica* fed on plant and animal foods. *Helgoländer Wiss. Meeresunters* 28:66-70.
- MENZEL, D. W. 1959. Utilization of algae for growth by the angelfish, *Holocanthus bermudensis*. *J. Cons. Perm. Int. Explor. Mer* 24:308-313.

- MIGITA, M., AND V. HASHIMOTO. 1949. On the digestion of higher carbohydrates by zsuanihi (*Ctenopharyngodon idella*). Bull. Jap. Soc. Scient. Fish. 15.
- 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.
- PHILLIPS, A. M., JR. 1969. Nutrition, digestion, and energy utilization, p. 391-432. In: Fish physiology. W. S. Hoar and D. J. Randall (eds.). Academic Press, New York.
- RANDALL, J. E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. Miami 5:665-847.
- REESE, E. S. 1975. A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. Z. Tierpsychol. 37:37-61.
- . 1977. Coevolution of corals and coral feeding fishes of the family Chaetodontidae. Proc. Third Internat. Coral Reef Symp. 1. Biology:267-274.
- MARINE LABORATORY, UOG STATION, MANGILAO, GUAM 96913 AND INSTITUTE OF ECOLOGY, DIVISION OF ENVIRONMENTAL STUDIES, UNIVERSITY OF CALIFORNIA AT DAVIS, DAVIS, CALIFORNIA 95616. Accepted 18 Dec. 1979.