

The feeding ecology of three species of Caribbean angelfishes (family Pomacanthidae)

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Synopsis

The foraging behavior and associated morphology of the feeding apparatus of three sympatric species of angelfishes, *Holacanthus tricolor*, *Pomacanthus arcuatus* and *Pomacanthus paru* were studied at St. Croix, U.S. Virgin Islands. All three had overlapping diets, consisting of algae and numerous species of sponges. The two *Pomacanthus* species also fed on gorgonians. The morphology of the dentition, jaws and gill rakers was similar in all three species. Male *Holacanthus tricolor* defended territories overlapping the foraging areas of two to four females. Within the male's territory, females defended smaller territories against other females of the same size, but tolerated smaller females. In contrast, both *Pomacanthus* spp. formed pairs which defended intraspecific feeding territories.

Introduction

Tropical fishes exhibit a wide variety of behavioral and morphological adaptations enabling them to exploit the food resources available on coral reefs. Despite the abundance of sponges, the biology of the fishes which feed on this resource has not been well studied as compared to that of fishes which feed on algae and coral.

The rock beauty, *Holacanthus tricolor*, the gray angelfish, *Pomacanthus arcuatus* and the french angelfish, *P. paru*, all feed primarily on sponges (Randall & Hartman 1968), and occur sympatrically throughout the Caribbean (Allen 1979). In this study, we investigated the use of space by individuals, the feeding behavior, and the morphology of the feeding apparatus in relation to foraging on sponges.

Material and methods

Study site

The behavior and ecology of *Holacanthus tricolor*, *Pomacanthus arcuatus* and *P. paru* were studied during the months of May, 1981 and September, 1982. Data were primarily collected during two, 1 week National Undersea Laboratory System (NULS-1, Hydrolab) Saturation Missions at the Salt River Submarine Canyon, St. Croix, U.S. Virgin Islands.

The study site was located along the east wall of the canyon beginning at a shelf, 10 m deep, and sloped down at a 15°–45° incline to depths below 50 m. The wall was covered with gorgonians, especially plexaurids, as well as scleractinian corals and sponges. Quadrat studies of sessile invertebrates in this area by Suchanek et al. (1984) revealed that

hard corals comprised approximately 20% of the bottom cover at 10 m and 30 m depths, while sponges comprised 8% and 18.3% respectively. Over 20 species of sponges were reported in their study.

Methods

The abundance of pomacanthids at the Salt River study site was determined by replicate censuses (1981: N = 14 censuses; 1982: N = 16) along two 100 m transect lines set at 20 m and 25 m isobaths. Two divers swam parallel to each transect line, one on each side. Divers counted all pomacanthids occurring within five meters of their side of the line. The total area sampled was 2000 m².

Holacanthus tricolor were captured using hand nets, and anesthetized (Quinaldine[®], 1:10 in ethanol). The fish were sexed underwater by cannulation using a non-destructive technique (adapted for underwater use from Ross 1984). Each fish was measured to obtain its standard length (SL), then finclipped and released. No ill effects were observed from the anesthesia or handling. *Pomacanthus arcuatus* and *P. paru* were not captured or sexed, but individual fishes were identified by distinctive body markings.

Individuals of each species were followed for five or more 5 min periods, and bites on different prey items were counted. Dietary similarity (D) was calculated using Schoener's (1968) index of niche overlap in prey type between species x and y such that:

$$D = 1 - 0.5 \sum_{i=1}^n |P_{x_i} - P_{y_i}|$$

where P_{x_i} = proportion of bites on i by species x, and P_{y_i} = proportion of bites on i by species y.

The occurrence of swimming, sheltering and feeding activities, as well as interactions with other fishes were noted during each minute interval. Colored markers were dropped where feeding occurred to allow the determination of the foraging area. The positions of these markers were mapped in relation to the transect lines. Samples of food items were collected for later identification.

The movements of two female *H. tricolor* which had overlapping home ranges were simultaneously mapped at 1 min intervals for 60 min to examine their foraging patterns and use of space. The locations of shelters used by each female were marked.

The removal of specimens was not allowed within the Salt River Canyon, so specimens for dissection were collected by spearing in a similar habitat at nearby Cane Bay. Specimens were immediately injected with 10% buffered formalin, stored on ice, and later measured and weighed. The gut contents and gonads were removed and placed in formalin within six hours, and later transferred to 70% isopropyl alcohol. Gut contents were sorted roughly, and the volume of the major taxa was measured.

One representative adult specimen of *H. tricolor* (SL = 160 mm) and *P. paru* (SL = 198 mm) and one young adult *P. arcuatus* (SL = 132 mm) were used to investigate the morphology of the feeding apparatus. Frozen specimens were thawed and, using a camera lucida, illustrations were made of the head with the mouth in the resting, retracted position and also with the mouth maximally open and protruded. The premaxilla and dentary bones and gill rakers of each specimen were then surgically removed. Premaxilla and dentary bones were cleaned manually and ultrasonically with 2% sodium hypochlorite solution, then passed through an ethyl alcohol series and air dried. Dried specimens were coated to 300 Å with gold palladium and examined under a (Zeiss Novascan 30[®]) scanning electron microscope at 15kv. Photographs were taken with Polaroid[®] Type 55 P/N film. Further observations were made of the teeth and gill rakers using a dissecting microscope.

Results

Holacanthus tricolor

The rock beauty, *Holacanthus tricolor* was the smallest and most abundant pomacanthid in the study area. We observed an average of 1.46 individuals per 1000 m² in censuses along the transect lines. Five females and two males were fin-clipped

in 1981 and 14 females and 5 males in 1982. Three females and one male from the 1982 collection were positively identified as individuals fin-clipped in 1981.

Foraging areas. The foraging areas of five females and two males were mapped in May 1981, and 14 females and six males in September 1982 (1982 shown in Fig. 1). Males maintained large, non-overlapping home ranges, averaging 1053 m² (SD = 294) in area (N = 5, data from 1982; a sixth male had home range borders which were too deep to map accurately). Areas between male home ranges were often unoccupied or lightly used. On two occasions, encounters between males at shared borders were observed, and resulted in vigorous chasing. On a third occasion, a marked male was observed to leave his feeding range and enter the range of another male. The intruding male showed distinct blackening of the yellow facial area, and fled back to his own area when chased by the resident. Males within their home ranges swam close to the substratum, feeding, and occasionally sheltering under ledges. Individuals spent 62% of all 1 min observation intervals concealed under ledges, apparently sheltered. Although observations were difficult during these times, it appeared that little feeding occurred while sheltered. Feeding was recorded during forays from these shelters. There were no significant differences in feeding rates or time spent sheltered between males and females (t-test, $p > 0.5$).

The home range of each male encompassed the ranges of two to four smaller females (mean home range area of females = 354 m², SD = 123 N = 19, data from 1981 and 1982). Males visited females several times during the day, sometimes feeding beside one or two females. No agonistic behavior or other overt displays were observed between the sexes. Males spent an average of 1.8 min h⁻¹ (SD = 3.2) with each individual female within his home range.

Females of very different sizes (mean percent size difference = 15.4%, N = 5) had foraging areas which overlapped extensively, approaching 100% in several cases. No agonism was observed among these females which spent an average of 4.0 min h⁻¹

(SD = 3.7) together, and often fed on the same sponges. In contrast, females of similar sizes within the same male's home range, showed little or no overlap in home ranges (Table 1), and two chases were observed between such females associated with different males.

Simultaneous observations of females with overlapping home ranges revealed that these females followed specific paths, and often revisited the same sponges and shelters. Ten of the 16 shelters were used by both fish though usually at different times. Two other females with overlapping home ranges used 11 of 14 of the same shelters during two hours of observations. Interactions between females with shared home ranges were non-aggressive and short in duration (less than 10% of the observation periods). At night, marked individuals were found in separate shelters.

Four juveniles of approximately 35 mm to 60 mm were found within the ranges of the adults in 1982. Juveniles restricted their movements to 1 to 2 m² during the period of observation. Adults of both sexes completely ignored juveniles when they encountered them.

Feeding behavior. Individual *H. tricolor* fed during 46% of all 1 min intervals, with an average feeding rate of 2.74 bites per minute. Table 2 shows that most feeding bites were directed toward algae (49.9%) and 14 species of sponges (42.6%). Common species of sponges in the diet (greater than 5% of all bites were directed toward these sponges) were *Verongula* sp., *Desmacella meliorata*, and an unidentified, black sponge with a gray cortex. Examination of sponges showed large areas with bite marks, but in no case was the whole sponge consumed at one time. Individuals frequently made repeated visits to the same sponge during a 25 min observation period.

Stomach contents. Stomach contents of 18 *H. tricolor* collected at Cane Bay were analyzed by percent volume of food items. Sponges comprised 95%, algae 4% and other invertebrates and eggs 1%. Most sponge fragments in the guts were not identified to species, however, clumps of *Myrmekeioderma styx* and *Verongula* sp. were recognized.

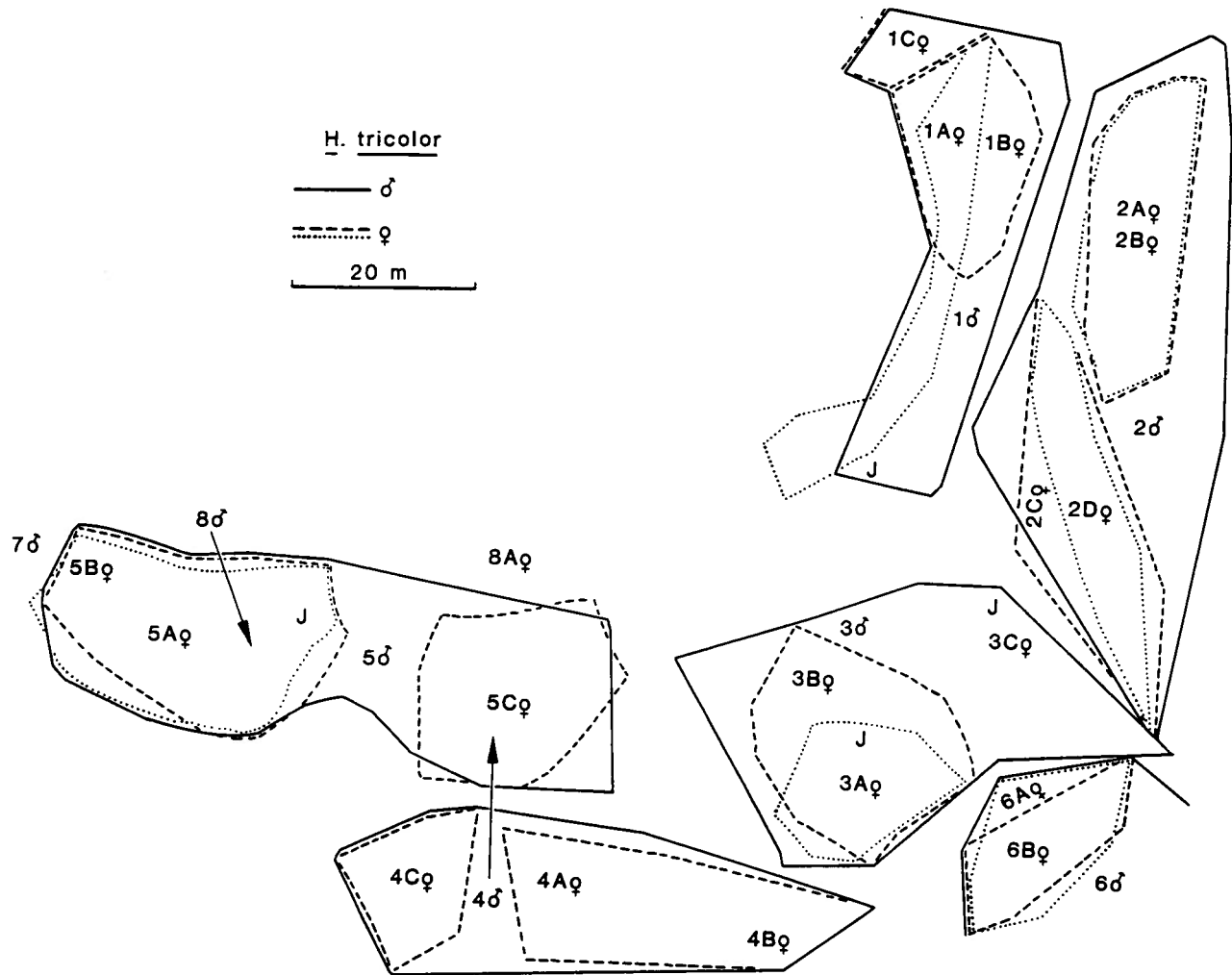


Fig. 1. Territories of male and female *Holacanthus tricolor* at the Salt River submarine canyon study site in 1982. Numbers refer to harems, with male territories outlined in solid lines, and associated female territories designated by letters and outlined with dotted or dashed lines. Note overlapping and non-overlapping female territories within each harem. Arrows indicate intrusions by males into neighboring male territories. J = juveniles.

Table 1. Body sizes (SL in mm) of males and females within each harem of *Holacanthus tricolor* (data from 1982). Females with overlapping home ranges are grouped together. Harem numbers refer to Figure 1; (*) was a female undergoing sex change.

	Harem number					
	1	2	3	4	5	6
Male	145	174	132	160	167	Large
Large female	128*	122	125	120	135	126
Small female	85	Small	115	103	122	107
Large female	130	122	Large	—	132	—
Small female	—	Small	117	—	—	—

Functional morphology of the feeding apparatus. Analysis of the feeding apparatus of *Holacanthus tricolor* revealed that its jaws were protractile during jaw opening, and formed a symmetrical biting surface (Fig. 2a). The premaxilla and dentary jaw teeth lay in distinct rows. The labial teeth were larger and tricuspid with well developed lateral cusps, while the lingual teeth were smaller with poorly developed or no lateral cusps. The teeth with better developed cusps lay side by side and overlapped laterally such that a series of cutting edges was formed (Fig. 3a). The large central teeth, lateral labial teeth and anterior labial replacement teeth all had pointed central cusps, except the anterior labial teeth which were worn. The pharyngeal teeth were unicuspid, numerous and villiform, with slightly curved tips pointing posteriorly. The gill rakers were relatively short, having numerous spines or lateral processes (Fig. 4a). The anterior and posterior rakers of adjacent gill arches interdigitated to form an effective sieve. The anterior rakers of the first arch were the longest, and those of the two posterior arches the smallest.

Pomacanthus arcuatus and *Pomacanthus paru*

The gray and french angelfishes, *Pomacanthus arcuatus* and *P. paru* were larger than the rock beauty and were observed less frequently during censuses along the transects. An average of 0.57 *P. arcuatus* and 0.21 *P. paru* per 1000 m² were observed in 1981 and 0.56 and 0.31 per 1000 m² in 1982 respectively. Observations of known individuals and mapping of territories, however, indicated that both species were approximately equal in abundance in the study area. Five pairs of each species were observed, and quantitative data on feeding and social behavior were recorded from seven *P. arcuatus* and six *P. paru*.

Foraging areas. All adult *P. arcuatus* and *P. paru* were paired with conspecifics, presumably of the opposite sex. Members of a pair were evenly matched in size. Pairs ranged over wide areas and spent little or no time sheltered. Unlike *H. tricolor*, individuals of both species swam 1–3 m above the

substratum, where their movements were less strongly influenced by aspects of the bottom topography. Both *Pomacanthus* spp. spent considerable amounts of time posing for cleaning by other fishes and shrimp (10% of all 1 min intervals).

Pairs of *P. arcuatus* frequented intraspecifically exclusive foraging areas. These foraging areas were large, but each occupied a narrow isobath range, giving the appearance of bands of adjacent shallow, intermediate and deep home ranges (Fig. 5a). The lack of intraspecific overlap in home ranges, suggested that pairs were intraspecifically territorial. This was supported by an observation of two pairs chasing each other at the boundary of their home ranges. Pair members swam together during 46% of all minute observations, usually staying less than four body lengths apart. When two members of a pair were re-united after a period of separation, they occasionally exhibited a carouselling display, consisting of approaching each other one to two meters above the bottom, followed by rapid head to tail circling. The most extensively studied pair ranged over a measured area of 2200 m² (Fig. 5a), extending between 18 to 29 m in depth.

Pomacanthus paru pairs, like *P. arcuatus*, inhabited large, intraspecifically exclusive home ranges with similar patterns of shallow, medium depth, and deep bands of contiguous home ranges (Fig. 5b). The most extensively studied pair of *P. paru* covered an area of 2300 m². Pair members spent 51% of their time together. Carouselling between pair members was also observed. No interspecific agonism was observed between gray and french angelfishes, and the home ranges of the two species overlapped completely.

No juvenile french or gray angelfishes were observed in the study area in either 1981 or 1982. During the second year, one observation was made of a sub-adult (approx. 200 mm in total length) *P. paru* within the area of an adult pair. Both members of the pair vigorously chased the sub-adult which finally sheltered in a hole. The sub-adult was not seen in the area on subsequent dives. Numerous juveniles and small sub-adults were observed in shallow water near Fredriksted Pier, St. Croix, an area where adults were absent.

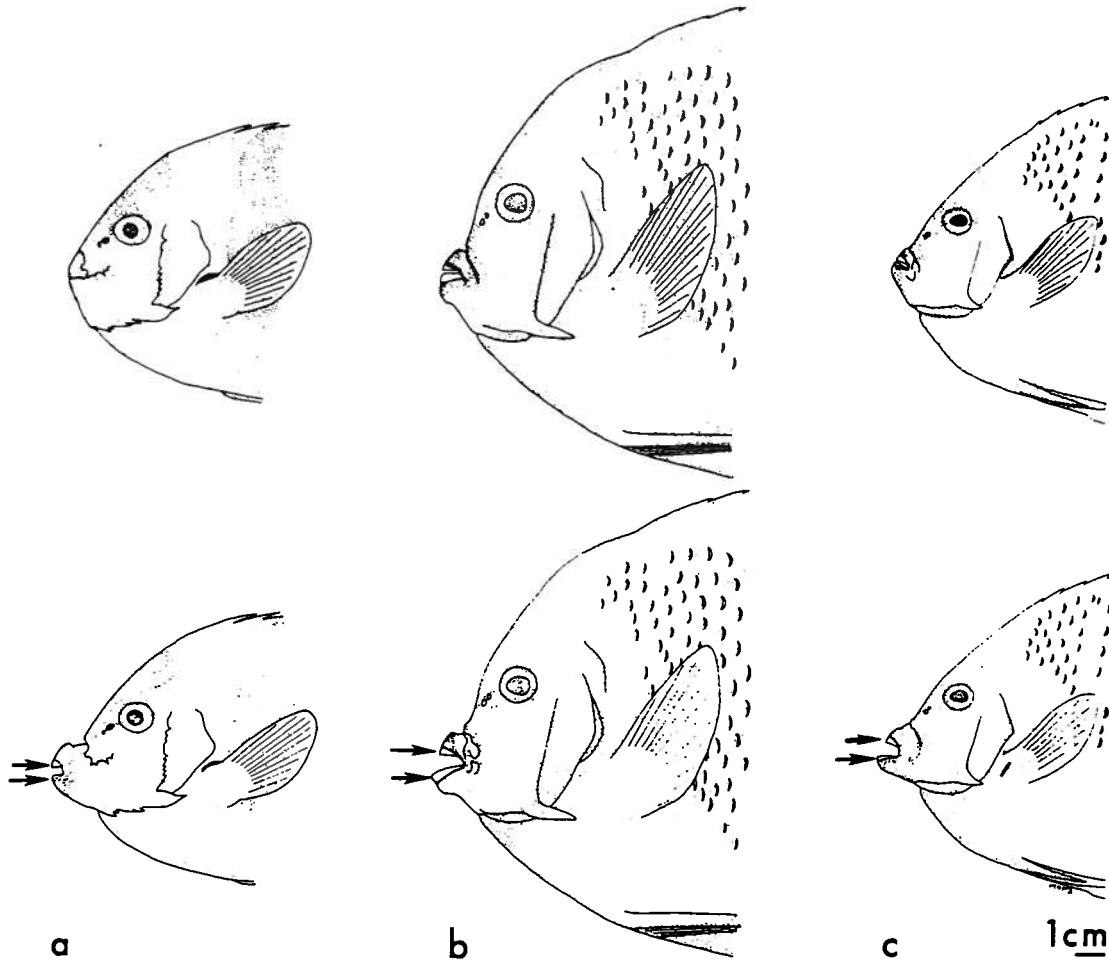


Fig. 2. The heads and jaws of (a) *Holacanthus tricolor*, (b) *Pomacanthus paru*, and (c) *P. arcuatus*. In the upper row, jaws are shown in the relaxed, retracted positions and in the lower row, jaws are in maximally protruded positions. Arrows indicate the exposed portions of the upper and lower jaw teeth, showing the symmetrical biting surface formed by the teeth of *H. tricolor*, compared to the asymmetrical biting surfaces formed by the teeth of the two *Pomacanthus* species. Jaws were manually protruded by pushing the angular-interopercular joint dorsally.

Feeding behavior. Both the gray and french angel-fishes fed on a variety of sponges as well as algae and gorgonians (Table 2). Insufficient specimens of either species were collected for quantitative gut content analyses but feeding observations revealed apparent differences between the diets of the two species. Sample sizes were too small for tests of significance on individual food items. *Pomacanthus arcuatus* fed largely on algae (33.9% of feeding bites) and on four species of gorgonians (43.1% of bites). Fourteen species of sponges constituted 26.7% of all bites, with the predominant species

(>5% of bites) being *Myrmekioderma styx*.

Pomacanthus paru fed less on algae (10.4% of all feeding bites) than *P. arcuatus* and not at all on the gorgonian *Icilogorgia schramii*. Twelve sponges occurred in the diet, with more than 25% of all feeding bites directed toward *Desmacella meliorata*, a species mostly absent from the diet of the gray angel. *Myrmekioderma styx* and an unidentified yellow sponge also occurred prominently in the diet. Feeding rates were similar for *P. arcuatus* and *P. paru*, averaging 2.67 bites per min (SD 1.5) and 2.99 bites per min (SD 2.0), respectively.

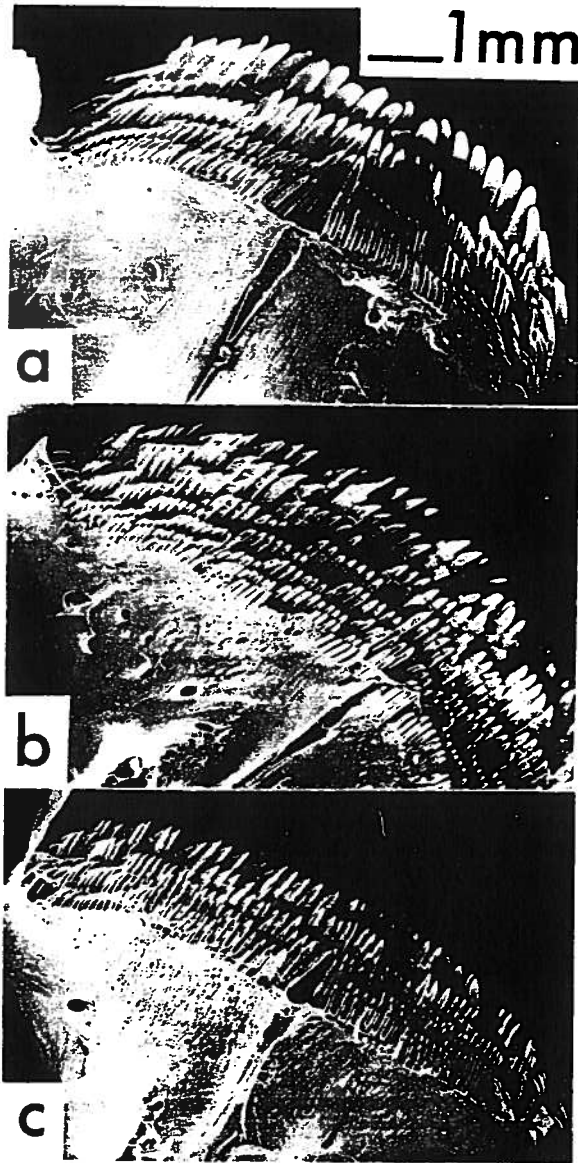


Fig. 3. Ventral view of the teeth of the premaxilla of (a) *Holacanthus tricolor*, (b) *Pomacanthus paru* and (c) *P. arcuatus*. In all three species, teeth are tricuspid and occur in distinct rows. The teeth of *H. tricolor* are relatively larger and more robust than those of the other two species.

The three species differed in the distribution of feeding bites among major food types (Kruskal-Wallis test; $p < 0.05$). The two *Pomacanthus* spp. differed from *H. tricolor* in the quantity of gorgonians in the diet. *Holacanthus tricolor* fed significantly more on algae and sponges than *P. arcua-*

tus, whereas *P. paru* fed less on algae and more on sponges than the other two species. The two *Pomacanthus* species showed the greatest dietary similarity (Schoener's similarity coefficient $D = 0.496$) followed closely by *H. tricolor* and *P. arcuatus* ($D = 0.490$) with *H. tricolor* and *P. paru* having the least overlap in diet ($D = 0.352$).

Functional morphology of the feeding apparatus. The jaws of *Pomacanthus arcuatus* and *P. paru*, like *H. tricolor*, were protractile during jaw opening. In the *Pomacanthus* spp. the lower jaw lay anterior to the upper jaw during maximal jaw opening, and formed an asymmetrical biting surface (Fig. 2b, c). The premaxilla and dentary teeth of the *Pomacanthus* species were similar to those described for *H. tricolor* above. The species differed, in that the gray and french angelfishes had more rows of teeth on the premaxilla and the dentary than *H. tricolor*. *Holacanthus tricolor* had more robust teeth than either *P. arcuatus* or *P. paru* (Fig. 3b, c). The pharyngeal teeth and gill rakers were similar in the three species (Fig. 4b, c).

Discussion

These three species of angelfishes ranged over large areas and fed extensively on sponges, which are a relatively unusual food source for fishes (Randall & Hartman 1968). The morphology of the jaws and dentition, as well as the foraging behavior of these fishes may be understood, in part, as adaptations to this unusual food resource.

Foraging areas

Foraging patterns and use of space differed between *H. tricolor* and the two *Pomacanthus* spp., despite similar feeding habits. In the former species, females of different sizes shared overlapping territories. Each male defended a territory containing a harem of two or more females. In contrast, in both *Pomacanthus* spp. pairs defended intraspecifically exclusive areas.

Harem polygyny as exhibited by *H. tricolor* may

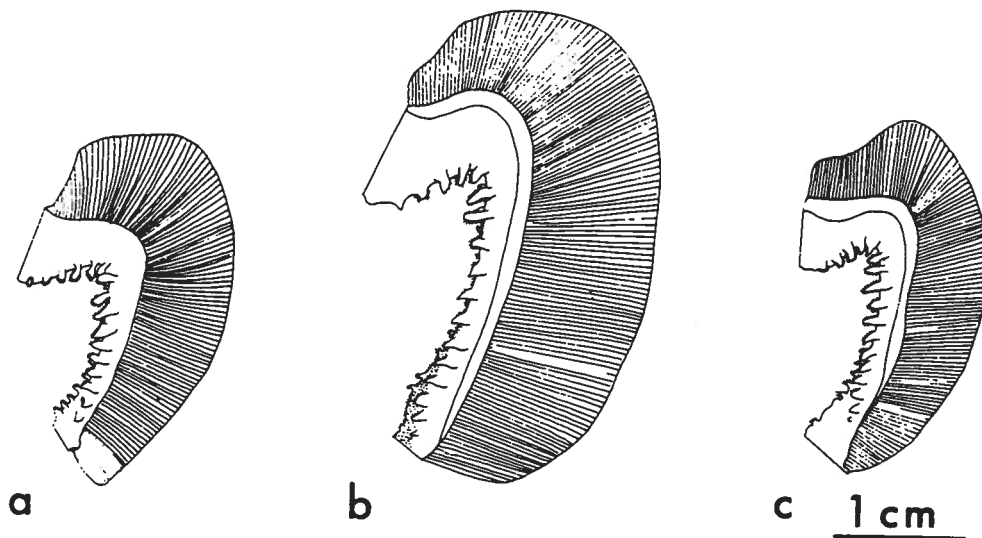


Fig. 4. The anterior left gill arch with gill rakers and filaments of (a) *Holacanthus tricolor*, (b) *Pomacanthus paru* and (c) *P. arcuatus*. Upper and lower portions are surgically cut resulting in the unnaturally straight edges.

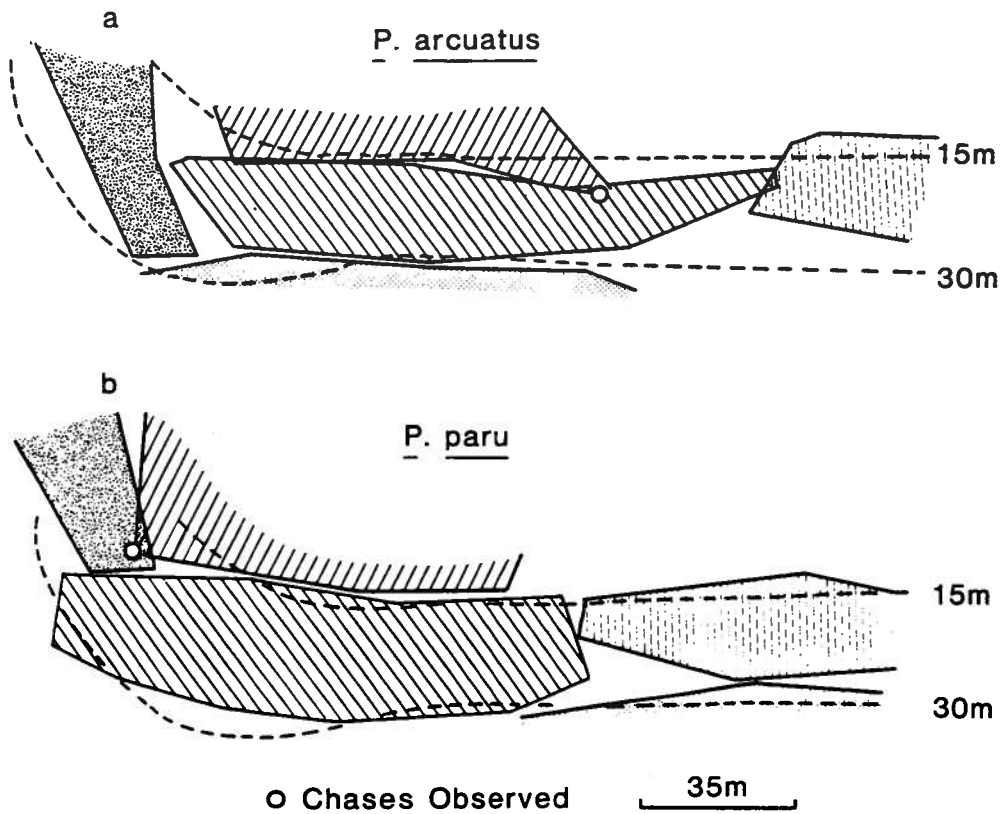


Fig. 5. Home ranges of pairs of (a) *Pomacanthus arcuatus* and (b) *P. paru* at the Salt River submarine canyon study site. There was little overlap of conspecific ranges, but nearly complete overlap of ranges of different species. Open circles represent the locations of observed intraspecific chases.

result if individual males are able to monopolize limited resources necessary for more than one female. The most likely limiting resources necessary for female reef fishes are food and shelter (Sale 1980). To properly test whether these factors are indeed limiting in any one situation, requires long

term field experimentation. However, several lines of evidence from our study indicated that neither was limiting for female rock beauties at Salt River Canyon. Females spent only a fraction of their available time feeding, and seldom consumed all of any individual sponge. Home ranges were

Table 2. Diets of the three species of angelfishes at Salt River Submarine Canyon, St. Croix, U.S. Virgin Islands, based on observed feeding bites on different substrata.

Prey item	<i>Holacanthus tricolor</i>		<i>Pomacanthus arcuatus</i>		<i>Pomacanthus paru</i>	
	% of all bites	bites per min	% of all bites	bites per min	% of all bites	bites per min
Number of fish:	N = 16		N = 8		N = 6	
Total minutes observed:	500		340		300	
Algae	49.9%	(1.42)	33.9%	(0.89)	10.4%	(0.31)
Sponges (Total)	42.6%	(1.21)	26.7%	(0.70)	62.6%	(1.87)
<i>Angelus</i> sp.	2.2%	(0.06)	0	0	0	0
<i>Anthosigmella varians</i>	0	0	0.2%	(<0.01)	1.3%	(0.04)
<i>Callyspongia vaginalis</i>	0	0	1.1%	(0.03)	0	0
<i>Chondrilla nucula</i>	3.2%	(0.09)	0	0	0	0
<i>Cliona</i> sp.	1.8%	(0.05)	2.2%	(0.06)	3.6%	(0.11)
<i>Cribochalina vasculum</i>	0	0	2.3%	(0.06)	0	0
<i>Dasychelina</i> sp.	0.1%	(<0.01)	0	0	0	0
<i>Desmacella meliorata</i>	5.8%	(0.16)	0.7%	(0.02)	26.4%	(0.78)
<i>Ectyoplasia ferox</i>	0.5%	(0.02)	0	0	0.7%	(0.02)
<i>Haliclona compressa</i>	0.8%	(0.02)	1.1%	(0.05)	1.3%	(0.04)
<i>Iotrochata birotula</i>	1.1%	(0.03)	0.2%	(<0.01)	1.3%	(0.04)
<i>Ircinia strobilina</i>	0.6%	(0.02)	0.2%	(<0.01)	0	0
<i>Mycale laevis</i>	0	0	0.1%	(<0.01)	0	0
<i>Myrmekioderma styx</i>	2.9%	(0.08)	5.9%	(0.16)	9.7%	(0.29)
<i>Niphates digitalis</i>	0	0	2.6%	(0.12)	0	0
<i>Plakortis angulospiculatus</i>	0.7%	(0.02)	2.3%	(0.10)	1.3%	(0.04)
<i>Pseudoceratina crassa</i>	3.2%	(0.09)	2.2%	(0.06)	3.0%	(0.09)
<i>Ulosa ruetzleri</i>	0	0	1.6%	(0.04)	0	0
<i>Verongula</i> sp.	8.5%	(0.24)	0	0	0	0
Unid. black sponge sp.	5.0%	(0.14)	0	0	0	0
Unid. gray sponge sp.	1.4%	(0.04)	0	0	0	0
Unid. yellow sponge sp.	0	0	0	0	6.0%	(0.18)
Other sponge spp.	3.5%	(0.10)	4.7%	(0.27)	8.0%	(0.24)
Gorgonians (Total)	0.2%	(<0.01)	34.1%	(0.87)	26.0%	(0.78)
<i>Icilogorgia schramii</i>	0	0	12.4%	(0.33)	0	0
<i>Muracea</i> sp.	0	0	0.5%	(0.01)	0	0
<i>Plexaura</i> sp.	0.2%	(<0.01)	15.6%	(0.38)	14.4%	(0.43)
<i>Pseudoplexaura</i> sp.	0	0	5.6%	(0.15)	11.6%	(0.35)
Antipatherians						
<i>Stichopathes</i> sp.	0	0	1.5%	(0.04)	0	0
Scleractinians						
<i>Montastrea cavernosa</i>	0.2%	(<0.01)	0	0	0	0
Eggs	0.2%	(<0.01)	0	0	0	0
Unidentified	7.0%	(0.20)	3.8%	(0.17)	1.0%	(0.03)
Total	100%	(2.84)	100%	(2.67)	100%	(2.99)

very large, but were usually not contiguous, with adjacent areas rich in sponges and algae that were apparently used little or not at all. Finally, if food resources were limiting, one might expect a female to exclude other females from the feeding range regardless of size, since females of very different sizes still fed on the same sponges and algae. This was not the case, nor did we find increased aggression when females fed on or near the same food source. These observations suggest that food was not a major limiting resource for females at this site at the time of the study.

Females spent a great amount of time during the day in shelters. Observations of females in shared home ranges, however, showed that up to 16 shelters were used by the females. Over 90% of the shelters were used by both females at the same or different times. This circumstantial evidence suggests that shelters were also not limiting.

Feeding behavior

All three species of angelfishes in this study fed on a variety of sponges and algae, with considerable overlap in diet among them. These findings agreed with gut content analyses by Randall & Hartman (1968) in the Virgin Islands and Puerto Rico and Feddern (1968) in the Bahamas, although the predominant species of sponges which they observed in the diets of these fishes differed from those in the present study.

Each individual fed on a variety of sponges. Qualitative estimates of the abundance of sponges in the habitat differed from their abundance in the diet, suggesting some feeding preference. A tolerance for a wide variety of sponge species in the diet may be adaptive to a site attached species with widely dispersed pelagic larvae. Settlement areas and areas of growth would thereby not be limited by the availability of one or a few species of food items.

We found, as did Randall & Hartman (1968), that algae made up only a small portion of gut contents, compared to the larger sponge fragments. From behavioral observations however, it was clear that 10–50% of all feeding bites recorded

were on algae. These results demonstrate the problems in analyzing feeding data from stomach contents alone. Algae were an important constituent of the diet of these three species at Salt River Canyon, considering the relative amount of time and energy which was spent in feeding on this food source.

Pomacanthus arcuatus and *P. paru* differed from *H. tricolor* in their use of gorgonians as a food source. Gut content studies show only small amounts of polyps in the diet compared to other foods (Randall & Hartman 1968). This suggests, that like algae, these polyps may not contribute substantially to the caloric intake of these fishes, but they may provide essential proteins or other nutrients.

Both *Pomacanthus* species were very similar in size and diet. Eight of ten sponge species found in the diet of *P. paru* were also found in the diet of *P. arcuatus*. This dietary overlap was also reflected in the values of Schoener's similarity coefficients for these two species. In spite of this, there was almost complete spatial overlap of territories, and no observations of interspecific aggression. This morphological, spatial and dietary overlap suggests at least two possibilities: (1) food resources at this time are not limiting at the densities of these fishes at the St. Croix study site, or (2) the differences described above are sufficient to allow spatial overlap without competition. Defense of large, intraspecific territories lowers the density of each population, and may allow coexistence by reducing interspecific competition (Vance 1985). Without experimental manipulations, it cannot be determined if competition occurs at the densities observed in this study. These species also co-occur in other areas in the Caribbean (Feddern 1968, Clarke 1977, Moyer et al. 1983).

Functional morphology of the feeding apparatus

Overall, the similarities in the feeding apparatus of these species were greater than the differences. In all three species, the numerous rows of interdigitating tricuspid teeth presented a grasping and shearing surface that could effectively crop sponge and

algal material. Shearing is effective on hard, elastic and tough materials (Sibbing 1982) such as sponges and algae. The peripheral teeth of *H. tricolor* were more robust than those of either *P. arcuatus* or *P. paru*. It is perhaps significant therefore, that *H. tricolor* fed proportionately more on algae than did the other two species, as robust shearing teeth may be required for scraping tough algal material off hard surfaces. Consequently, the peripheral teeth showed more wear than those of the other two species. Similarly robust and worn teeth have been observed in the butterflyfish *Chaetodon unimaculatus*, which grazes on coral tissue, also biting the underlying calcareous corallite (Motta 1985). The gill rakers of all three species were similar.

The most notable difference in jaw structure among the species was that the maximally open and protruded jaws of *Pomacanthus arcuatus* and *P. paru* formed an asymmetrical biting surface, while those of *Holacanthus tricolor* formed a symmetrical biting surface.

These species showed only slight modifications in the jaw and teeth morphologies, but they exhibited a considerable degree of plasticity in their prey choice. Similar comparisons among Hawaiian butterflyfishes show much greater morphological divergence, although most species still maintained considerable plasticity in prey choice (Motta 1985). Similar findings have led Keast & Webb (1966) to state that whereas divergence in structure does not prevent food overlaps in cohabiting species, it may serve to reduce interspecific competition because the species have specializations which place them at an advantage in certain situations, or in obtaining certain foods.

It seems doubtful that the morphological differences among the species would allow resource partitioning or explain differences in resource use and foraging behavior. Alternately, the differences in foraging behavior may reflect differences in reproductive biology and social systems among these fishes, rather than differences in feeding ecology.

Reproductive biology and use of space

Holacanthus tricolor exhibits monandric protogyn-

ny, in which all males are secondarily derived from females (Hourigan & Kelley 1985). In this type of mating system, females are an important and defendable resource. Regardless of whether food resources are presently limiting or not, sponges and algae are a spatially and temporally stable and predictable resource, favoring site attachment by the females feeding on them. This site attachment may therefore allow large males to monopolize more than one female (Emlen & Oring 1977). If males are able to control harems and reproduce with more than one female as indicated by spawning observations (Neudecker & Lobel 1982, Moyer et al. 1983), then their average reproductive success will be greater than that of any one female. If the male disappears, it is therefore advantageous for the largest female to change sex and gain a similar advantage. Likewise, it would be adaptive for large females to allow other smaller females in their home range, since these individuals would then form the nucleus of its harem when it changed sex (Hourigan & Kelley 1985, Hourigan 1986). This grouping of females will favor polygyny by facilitating male defense of these groups (Emlen & Oring 1977). Females should exclude other females of similar size which might compete for the chance to change sex, and for subsequent mating with the smaller remaining females (Hourigan 1986). Kuwamura (1984) suggested a similar system for *Labroides dimidiatus*. He found no evidence of food as a limiting resource.

The reproductive biology of the *Pomacanthus* spp. is not known. The defense of intraspecific feeding territories by pairs closely resembles the behavior of monogamous pairs of coral-feeding butterflyfishes (Reese 1975, Hourigan 1987). These fishes were found to be gonochoristic, with male-female pair mates closely matched in size. Pairs defended territories and excluded juveniles. If female *Pomacanthus* are gonochoristic (i.e. not sex changing), there would be no advantage to allowing smaller females within their home ranges. Likewise males should exclude other conspecific males. Gonochorism is consistent with the observed lack of size differences between pair mates.

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