AN ABSTRACT OF THE THESIS OF Robert F. Myers for the Master of Science degree in Biology presented 5 December 1983.

Title: The Comparative Ecology of the Shallow-Water Species of
Canthigaster (Family Tetraodontidae) of Guam

Approved: ______________________________
Steven S. Amesbury, Chairman, Thesis Committee

The utilization of resources of food and space and possible mechanisms of avoiding competitive exclusion among sympatric species of *Canthigaster* were investigated. Species of *Canthigaster* were not homogeneously distributed between habitats or within habitats. One species, *Canthigaster solandri*, occurred in all habitats investigated and was the most abundant species in each habitat. Seven other species were variously encountered less frequently and in fewer habitats than *C. solandri*. For every possible species pair, one species was consistently found in one or more habitats not inhabited by the other, and many were entirely separated spatially. Some species utilized microhabitats rarely exploited by congeners occurring in the same habitats.

The only relevant morphological difference between species is a significantly shorter gut in *Canthigaster epilampra*, the only species that fed primarily on animals.

All species fed on a wide variety of both plant and animal food. Although there were few notable qualitative dietary differences among species based on frequency of occurrence of diet categories, numerous and consistent quantitative differences were found. Each species consistently fed on one or more diet categories absent, or nearly absent, in the diets of its congeners. Diet differed significantly

between most species, but not between individuals of the same species from different habitats, indicating that species-specific selectivity of certain diet items may be more important than differences in food availability between habitats. Diet differed less between individuals of different species collected in the same habitat and site than between all individuals of different species collected. The interspecific differences in niches may reduce competition between species.

THE COMPARATIVE ECOLOGY OF THE SHALLOW-WATER SPECIES OF CANTHIGASTER (FAMILY TETRAODONTIDAE) OF GUAM

By

ROBERT F. MYERS

A Thesis Submitted in Partial Fulfillment of

the Requirements for the Degree of

MASTER IN SCIENCE
in
BIOLOGY

UNIVERSITY OF GUAM

1983

TO THE GRADUATE SCHOOL:

The members of the committee approve the thesis of Robert F. Myers presented December 5, 1983.

Steven S. Amesbury, Chairman

Charles Birkeland

Charles E. Birkeland

Stephen G. Nelson

Patricia J. Hoff

Patricia J. Hoff

ACCEPTED:

Roy T. Tsuda
Dean of the Graduate School

ACKNOWLEDGEMENTS

I would like to thank the faculty and staff of the University of Guam Marine Laboratory and Biology Program and the many fellow graduate students and visiting biologists for their criticism, advice and assistance throughout this project. Terry Donaldson was particularly helpful in sharing logistical support; Robert L. Kock assisted in the collection of some of the specimens; Russell Clayshulte and Mitchell Colgan assisted in the data processing; and Michael E. Molina and Drs. Gerald R. Allen, John E. Randall and Patrick L. Colin provided useful literature and encouragement.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Coral reefs are highly diverse and complex environments which may contain several hundred species of fishes living in close proximity to one another. A given reef community may contain groups of several closely related species with similar, if not identical, morphologies that seemingly share the same resources of food and habitat. This is particularly evident among certain groups of herbivores such as scarids and acanthurids which frequently occur in large heterotypic schools (Jones, 1968; Choat and Robertson, 1975; Alevison, 1976).

The competitive exclusion principle predicts that no two species with the same ecological requirements can coexist indefinitely on the same limiting resource. In the coral reef environment where often shelter (Randall, 1965) and, in some cases, food (Tsuda and Bryan, 1973) may limit populations of certain species groups of fishes, and where the number of resident species often appears to greatly exceed the number of observed niches, violations of this principle seem to occur. This has led to a multitude of studies of factors determining diversity and community structure of coral reef fishes over the last decade and a half. Many of these studies support one of two divergent, yet not entirely mutually exclusive, schools of thought: one maintaining that competitive exclusion is avoided by specialization in which available resources are finely partitioned between species (Smith and Tyler, 1972), the other predicting that competitive exclusion is avoided because unpredictable "random" events such as disturbances, recruitment, or even predation prevent a superior competitor from eliminating inferior ones (Sale, 1978). Other recent studies have indicated that specializations may be very subtle and easily overlooked, leading one to believe that unpredictable events are the sole means of avoiding competitive exclusion (Greenfield and Greenfield, 1982; Gladfelter and Johnson, 1983).

With the exception of color, most species of *Canthigaster* are morphologically indistinguishable from one another. Their systematics and zoogeography are well known, having been recently reviewed (Allen and Randall, 1977; Lubbock and Allen, 1979). All are small, most less than 100 mm standard length (SL), and, for the most part, all inhabit coral reefs and adjacent marine environments. All but two are known from depths of 30 m or less. All species studied to date are diurnal omnivores that feed on a wide variety of benthic plants and invertebrates. They are well protected from most piscivorous predators by possessing toxic skin (Eger and Starkus, 1973), toxic flesh or toxic internal organs (Halstead, 1967), and by their ability to inflate their abdomen by swallowing water when frightened. Presumably adult *Canthigaster* are not predator limited. However there are at least two literature accounts of predation on *Canthigaster* by piscivorous fishes indicating that protection is not universal (Hobson, 1974; Morgans, 1982).

At least eight species -- *Canthigaster amboinensis* (Bleeker), *C. bennetti* (Bleeker) *C. coronata* (Valliant & Sauvage), *C. epilampra* (Jenkins), *C. janthinoptera* (Bleeker). *C. leoparda* (Lubbock & Allen), *C. solandri* (Richardson) and *C. valentini* (Bleeker) -- occur in Guam's waters (Appendix A). Preliminary observations indicate that many areas contain as many as three or four species of *Canthigaster* living in close proximity to one another. At least one species, *C. solandri*, appears to be nearly ubiquitous in shallow reef habitats.

If resources of food or space limit Canthigaster populations, the competitive exclusion principle predicts that sympatric species will exhibit species-specific differences in diet or habitat. If resources of food and space are not limiting, or if coexistence of species with identical ecological requirements is made possible by unpredictable events, one would expect to find no significant differences in the utilization of resources between species. This study was undertaken to determine the extent to which Guam's species of Canthigaster partition resources of food and space.

MATERIALS AND METHODS

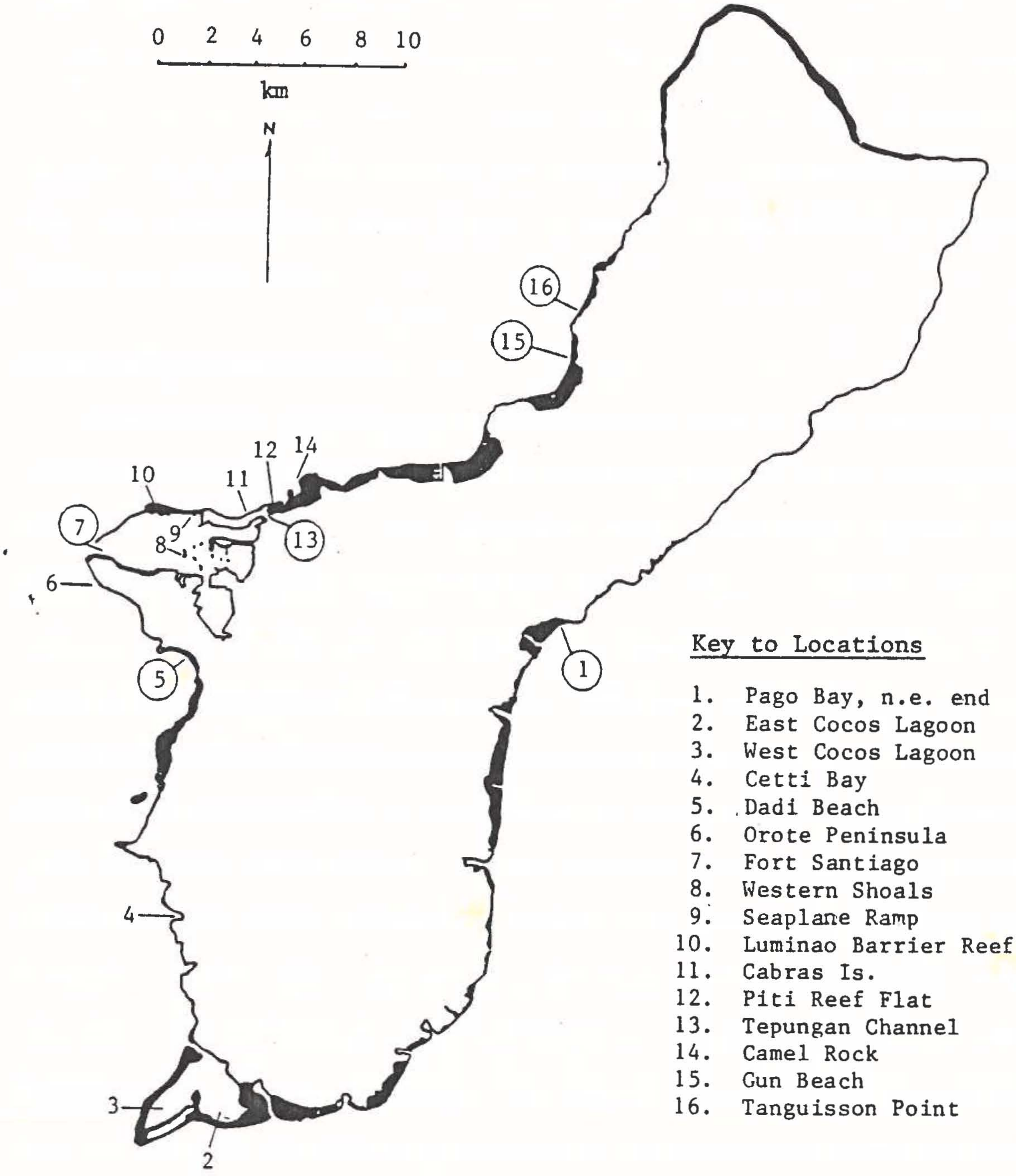
Distribution and Abundance

Distributions and abundances of species of Canthigaster from near shore to depths of 33 m were determined by means of standardized timed counts supplemented by collections of specimens and incidental observations.

The term habitat is generally synonymous with reef zone in the context of this study since habitat types tended to follow zonal lines at the sites investigated. The term microhabitat as used herein refers to small scale differences in bottom cover or topography on the order of a few meters at the most in any given dimension. Since individuals of Canthigaster tend to move over a much wider area, spending time in or crossing a number of microhabitats, a microhabitat more meaningfully constitutes a place visited than a place of residence.

Timed counts were made by swimming within a given habitat or parallel to depth contours and enumerating all species of Canthigaster observed within three meters of the observer in time intervals of three minutes each. An attempt was made to maintain a steady pace in order to ensure that approximately equal areas were covered during each count. Distance was calibrated by measuring the distance covered in selected three minute counts and using an average value to calculate the area covered. A total of six sites in a variety of habitats were chosen (Figure 1). Resulting distributions and abundances were tested by means of the G-test (Sokal & Rohlf, 1981).

Records of Canthigaster sightings were kept on numerous other dives if sufficient time and effort were spent to be reasonably certain of



Key to Locations

1. Pago Bay, n.e. end
2. East Cocos Lagoon
3. West Cocos Lagoon
4. Cetti Bay
5. Dadi Beach
6. Orote Peninsula
7. Fort Santiago
8. Western Shoals
9. Seaplane Ramp
10. Luminao Barrier Reef
11. Cabras Is.
12. Piti Reef Flat
13. Tepungan Channel
14. Camel Rock
15. Gun Beach
16. Tanguisson Point

Figure 1. Map of Guam showing the locations of the collecting sites.

encountering all resident Canthigaster species within a given habitat. Taken together with timed counts and collecting dives, a total of 114 visits in 12 habitats were considered. Unbiased collecting data, when all species were collected with equal effort, were used to provide information on size distributions and demography. Relationships between size and distribution were tested by means of the student's t-test (Sokal and Rohlf, 1981).

Morphological Observations

Specimens of Canthigaster were collected from a wide variety of reef habitats around Guam by means of hand nets or, in a few instances, with a small spear. All specimens were immediately placed in individually numbered, tightly sealed plastic bags. Location, depth, habitat, time of day and any noteworthy behavioral observations were recorded on underwater plastic slates. Specimens were placed on ice as soon after collection as possible (generally within one hour) to ensure rapid death which results in curtailment of digestive processes (Hobson, 1974) and were then frozen. At the earliest opportunity, they were dissected and their alimentary canals and gonads were examined. Standard length (SL), wet weight, sex and reproductive state were recorded. The alimentary canal was dissected by cutting as close to the esophagus and anus as possible. The general term "gut" is henceforth used to refer to the removable portion of the alimentary canal and the term "gut contents" is used to refer to all material present in the gut. The gut was then removed, laid flat, and measured. Relative percent fullness was visually estimated. The gut was then assigned a code number and set aside in a refrigerator while other guts were similarly prepared. Following dissection of approximately ten specimens, the contents of each gut were analyzed.

Feeding Ecology: Gut Content Analysis

Gut contents were examined for the following species with numbers of specimens of each indicated in parentheses: *Canthigaster amboinensis* (36), *C. bennetti* (10), *C. epilampra* (10), *C. janthinoptera* (10), *C. solandri* (162) and *C. valentini* (36). Because few juveniles were collected of species other than *Canthigaster solandri*, and because evidence suggests a high degree of habitat segregation between juveniles and adults of *C. solandri* (as well as some differences in diets between juveniles and adults), interspecific comparisons were made only between adults, unless otherwise indicated.

Field observations made of feeding by each species were generally limited to the type and orientation of the substrate fed on since it was usually not possible to determine *in situ* what, specifically, was taken as food.

The gut of each species of *Canthigaster* is long and looped and lacks a well-defined stomach. Since food remains were found to be generally identifiable throughout the gut, its entire contents were examined. Following removal of the gut, its contents were squeezed out and spread evenly in a shallow dish for viewing under a dissecting microscope. Occasionally a more powerful microscope with a resolving power to 400 x was used to determine the identity of specific food items. Diet items were identified to the finest taxonomic unit possible, then placed in one of the following 20 general categories: Cyanophyta, Chlorophyta, Phaeophyta, fleshy Rhodophyta, coralline Rhodophyta, Anthophyta, unidentified plant material, scleractinian coral, Bryozoa, Porifera, Tunicata, Brachiopoda, Mollusca, Foraminifera, Echinodermata, Polychaeta and other worms, Crustacea, unidentified or other animal material, unidentified organic material and detritus, and sand and inorganic material. A visual estimate of the relative volume of each distinguishable food item or general dietary category as a percentage of the entire contents was recorded. This value was multiplied by the estimated percent fullness of the gut to yield the diet volume of each item or diet category in each gut. Percent diet volumes for dietary items in each species or size class and habitat group of a particular species were calculated by summing the diet volumes of individuals and dividing by the sum of all diet volumes of all dietary categories. Frequency of occurrence of dietary categories was also calculated.

Feeding Ecology: Statistical Treatments

The following statistical procedures were employed to compare dietary patterns between and within species:

1. Comparisons based on the single most voluminous diet category in each gut were made between inter- and intraspecific groups and tested with the Kolmogorov-Smirnoff two sample test (Tate & Clelland, 1957). Comparisons were set up as follows: For each group compared, for example species A and species B, each individual was tallied under the diet category most voluminous in its gut. A table was set up with each of the two groups to be compared heading columns, and diet categories heading rows. Thus if 31 of 35 individuals of species A and 9 of 30 individuals of species B each had more of the <u>ith</u> diet

category in its gut than any other diet category, 31 and 9 would be listed under the *i*th row of columns A and B, respectively. The cumulative frequencies of diet categories were then tested. Significance indicates a lack of similarity between most voluminous diet categories in individuals of the two groups compared. Normally the Kolmogorov-Smirnoff two sample test utilizes the X^2 distribution tables which are not valid for multiple comparisons. However, for *a priori* comparisons, a level conservative enough to compensate for the increase in probability of making a type I error when making multiple comparisons between k sample can be calculated by the formula $\alpha' = 1-(1-\alpha)^{1/k}$ (Sokal and Rohlf, 1981). Thus if six sets of data (for example data on six species) are to be cross-compared, the new critical value of $\alpha' = 0.085$ would have to be exceeded in order to reject the null hypothesis of no difference between single most voluminous diet categories at the 95% probability level.

2. Multiple comparisons of total plant volume were made between species or intraspecific groups within a species with the approximate test of equality of means by the method of Games and Howell (Sokal and Rohlf, 1981). Since volumes were previously weighted according to total volume of a given gut, the degree of influence of a particular gut's contents is directly related to its relative fullness.

3. Proportional diet overlap, $P_{xy}=1-.5(\sum_i |P_{xi}-P_{yi}|)$ based on Hurlbert (1978) where P_1 equals the proportion (or mean diet volume) of diet category i, was used as a measure of judging

the degree of quantitative similarity between diets of two sets of individuals (either between species or within a species). Theoretical values range from zero in diets that are entirely different to 1.0 for identical diets.

4. The Shannon-Weiner diversity index, H', where $H' = \left[-\sum_{i} p_i \ln p_i\right] - \left[\frac{s-1}{2n}\right]$ (Poole, 1974), was employed as a measure of relative feeding niche breadth for each species. This was based on the diet volume of each category in each specimen. Multiple comparisons of mean H' values between species were made using the approximate test of equality of means using the method of Games and Howell (Sokal and Rohlf, 1981).

RESULTS

Distribution and Abundance

Results of timed counts indicate that *Canthigaster* species are not homogeneously distributed between habitats or within habitats (Figure 2). Results of the G-test were highly significant (p .001) for total G, heterogeneous G (between habitats), pooled G (between species), and all individual G's between species within each of the habitats (based on raw counts after lumping the 15 and 21 m counts and the 27 and 30-33 m counts, respectively). In all habitats *C. solandri* was the most abundant species, far outnumbering all of its congeners, except in the reef front where *C. amboinensis* was nearly as numerous. No other species was found in all habitats and two, *C. amboinensis* and *C. bennetti*, were counted in only one habitat each. The collective density of *Canthigaster* species ranged from a mean of 3.8 individuals per 1,000 m^2 at 15 m on the outer reef slope to a mean of 12.9 individuals per 1,000 m^2 in moats and shallow channels.

Frequency of occurrence of all species of *Canthigaster* based on presence or absence during a given visit to a particular habitat was determined for 12 habitats from observations made during 114 visits (Table 1). Results support those of timed counts, with *C. solandri* encountered on nearly every visit in all habitats. Other species were variously encountered in fewer habitats and usually less frequently. Certain habitats were visited in which timed counts were not conducted. Two habitats, the inner and outer intertidal reef flats (at Pago Bay), contained only juvenile *C. solandri* and *C. amboinensis* (the latter rarely on outer reef flats only). In addition, two rare species not

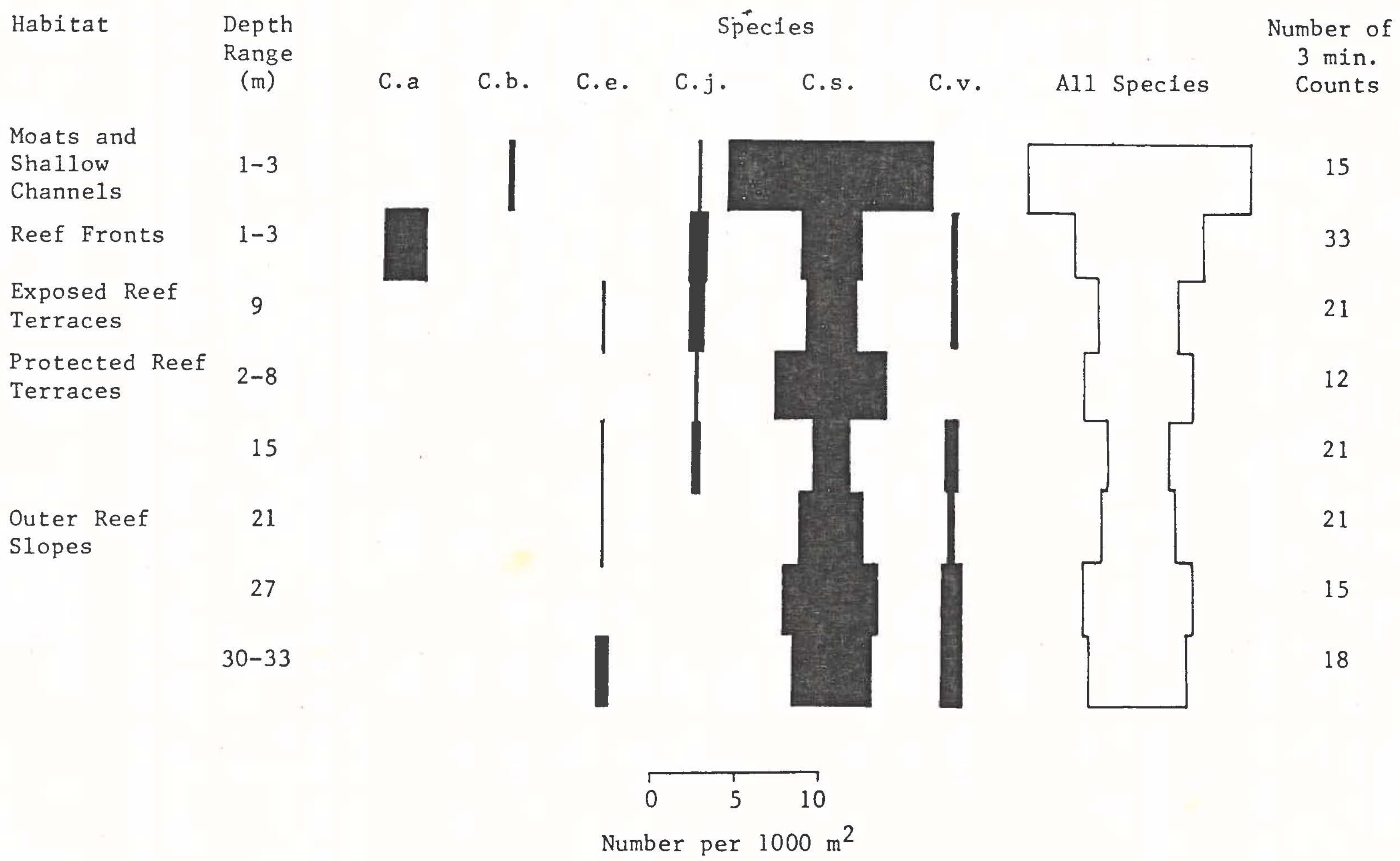


Figure 2. Density of Canthigaster species by habitat and depth based on timed counts at six sites on Guam.

Table 1. Frequency of occurrence of species of *Canthigaster* in various reef habitats of Guam based on presence or absence of a given species during a given visit. Duration of visits exceed 15 minutes and were judged sufficient to encounter all species in the immediate area. Only dives in which a conscious effort was made to note all *Canthigaster* species present are included.

Habitat and depth range	No. of visits			% frequency of occurrence						No. Spp.
		C.a.	C.b.	C.e.	C.j.	C.s.	C.v.	C.c.	C.l.	
Lagoon patch reef top, 0-3 m.	2					100				1
Lagoon patch reef slope, 3-25 m.	4					75	100			2
Moat, 0.5-1.5 m.	10		60		20	100	30			4
Shallow channel, 1-4 m.	15	7j	73		60	100	47			5
Inner reef flat, 0-1 m.	10					100j				1
Outer intertidal reef flat, 0-1 m.	11	64j				100j				2
Protected bay slope, 3-12 m.	3					100	67			2
Reef front, 1-4 m.	18	100			22	94	11			4
Exposed outer reef terrace, 3-9 m.	15	13	7		27	100	13			5
Protected outer reef terrace, 3-10 m.	2				100	100	50			3
Outer reef slope, 8-36 m.	16			44	6	100	56	6		5
Deep dropoff & adjacent shelf, 18-36 m.	8			100		100			13	3
Observed depth range in m:		0-9	1-3	9-36	1-21	0-36	1-36	11	27-36	
No. of habitats inhabited:		4	3	2	6	12	8	1	1	
% of habitats inhabited:		33.3	25.0	16.7	50.0	100	66.7	8.3	8.3	

C.a. = *C. amboinenensis*
C.b. = *C. bennetti*
C.e. = *C. epilampra*
C.j. = *C. janthinoptera*
C.s. = *C. solandri*
C.v. = *C. valentini*
C.c. = *C. coronata*
C.l. = *C. leoparda*
j = juveniles only

seen during timed counts, *C. coronata* and *C. leoparda*, were each encountered once, on visits to the outer reef slope and a deep dropoff, respectively.

Distribution and relative abundances are given in greater detail, by species, below. The number of specimens collected, followed by their size range in standard length, is given in parentheses after the species name. Natural history observations are included when considered relevant to this study.

Canthigaster amboinensis (37:19.4 - 81.8 mm SL)

This, the largest member of the genus at Guam, has one of the most restricted distributions. Although observed in four of the twelve habitats visited it was consistently present only along reef fronts exposed to wave induced surge between depths of one and four meters. It was the only species to rival *Canthigaster solandri* in abundance in any given habitat. Juveniles were observed on the outermost reaches of reef flats of exposed coasts as well as the reef front and were secretive, usually remaining under ledges and in holes. Adults spent most of their time out in the open. This was clearly the strongest swimmer of the genus encountered, its swimming ability an adaptation undoubtedly related to its preference for areas subject to strong water movement and to wide-ranging foraging habits. Some individuals were observed to cover an area as large as 35 m on its longest axis in a time span as short as five minutes, occasionally stopping to nip at the substrate.

Canthigaster bennetti (12:36.0 - 66.8 mm SL)

This species also has a relatively restricted distribution, usually limited to moats, shallow channels, and lagoon environments to a depth of four meters. Even in these areas it was not consistently encountered, being observed on 17 of 25 visits. It was observed only once in an outer reef environment, at a depth of three meters on an exposed terrace off the Orote Point cliffline. It was also observed only once during the timed counts when a pair was seen in the moat off Tanguisson Point. Juveniles less than 35 mm SL were observed in Tepungan Channel and in the inner reaches of the Tanguission power plant effluent channel. This species was always observed out in the open, but usually within a few centimeters of the substrate where its coloration often rendered it quite cryptic.

Canthigaster _coronata_ (1:76.8 mm SL)

This is the rarest species of _Canthigaster_ encountered during this study. Only one specimen was observed and collected, at a depth of 11 m along the outer reef slope of Pago Bay in an area of barren limestone covered with low-profile algae and scattered sandy depressions.

Canthigaster _epilampra_ (10:45.0 - 78.3 mm SL)

This is a relatively uncommon species with a fairly restricted distribution. It was observed only along the outer reef slope and deep dropoffs from depths of 9 to 36 m. It was encountered on all eight deep dropoff dives, often in or near large caves, but was less frequent in areas of moderate slopes or at depths shallower than 20 m.

The two smallest individuals (less than 50 mm SL) were collected above 24 m and none this size were observed deeper. None less than approximately 40 mm SL were observed at all. The largest adults were associated with steep dropoffs and large caves. Individuals of this species were generally found in the open rather than hidden within the substrate, but they readily disappeared into holes and crevices when pursued.

Canthigaster janthinoptera (13:27.1 - 53.0 mm SL)

This, the smallest member of the genus at Guam, is moderately widespread, occurring in six of the twelve habitats investigated. It was not consistently present in any particular habitat type, but was consistently present at certain sites. Adults were observed in reef front, reef terrace and outer reef slope environments from depths of three to 21 m, while juveniles less than 35 mm SL were observed only in moats and shallow channels. It is probably the most secretive species at Guam, being found in or near recesses and holes. Its secretive habits made observation difficult, which may have resulted in underestimates of its true abundance being derived from timed counts, although an effort was made to look in all likely places.

Canthigaster leoparda (1:46.8 mm SL)

This is the deepest dwelling and one of the least frequently encountered species known from Guam. It was observed only in the "Blue Hole", a large cave adjacent to a steep dropoff, at a depth of 27 m on one occasion during the course of this study and on three previous occasions to depths of 36 m or more. It was always solitary and remained close to the sides of the cave, in or near recesses.

Canthigaster solandri (267:25.0 - 72.2 mm SL)

This is the most abundant and ubiquitous species of *Canthigaster* at Guam. It occurred in all habitats investigated and was observed on all but two of 114 visits. Timed counts indicated a mean density of 4.7 individuals per 1,000 m^2 for all areas surveyed, with a high of 18.7

individuals per 1,000 m^2 at the Tanguisson Point moat to a low of none at the Pago Bay reef front (however it was observed there on all other occasions, except during the timed counts). Measurements and reproductive data indicate that individuals from the shallow intertidal and subtidal reef flat of Pago Bay are significantly smaller than those collected elsewhere (Figure 3; $t=17.47$, $p < 0.001$ and $t=14.66$, $p < 0.001$, for comparison with other exposed coast and protected habitats, respectively) and were immature. Juveniles less than 35 mm SL were observed only on similar reef flats and shallow protected areas such as the Agana Boat Basin and the Tanguisson power plant effluent channel where they were seen throughout the year. All individuals greater than 50 mm SL examined from other habitats were mature. No relationship between depth of capture and size was apparent.

Canthigaster solandri was generally found in the open, often over sandy substrates several meters from the nearest shelter. Most of those observed appeared to be site-oriented, swimming slowly and covering an area of a few meters during short observation periods (usually five minutes or less); however, a few were clearly moving from one site to another, swimming steadily in one direction from one end of the observer's limit of visibility to the other.

Canthigaster valentini (41:29.9 - 74.0 mm SL)

This is the second most abundant and ubiquitous species at Guam, occurring in eight of the twelve habitats investigated. It was consistently observed along lagoon patch reef slopes but less frequently observed along outer reef slopes, outer reef terraces, protected bay slopes, shallow channels and moats. It was not seen in shallow reef flats, patch reef tops or deep dropoffs.

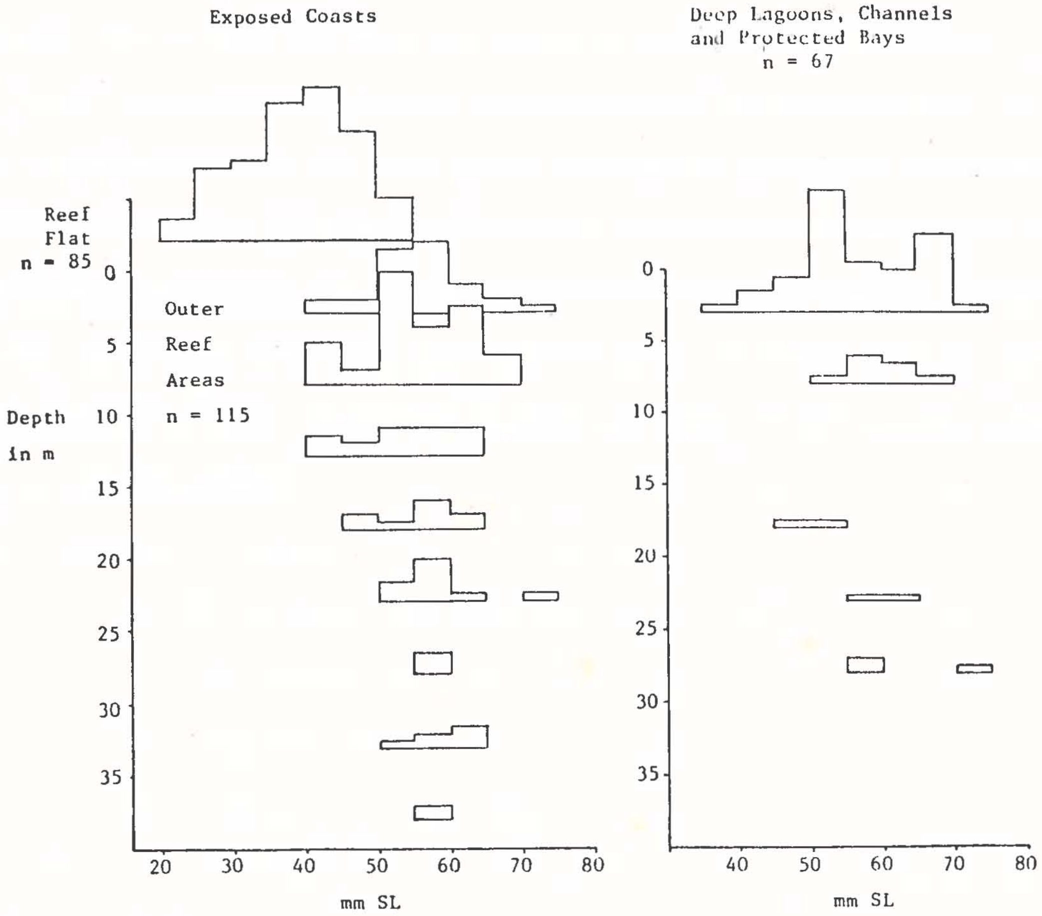


Figure 3. Size distribution of <u>Canthigaster</u> <u>solandri</u> with habitat and depth. Reef flat specimens are significantly smaller than those from beyond the reef margin on exposed coastlines (t = 17.47***) and those from deep lagoons, channels and protected bays (t = 14.6***). Based on collections made at N.E. Pago Bay, Tanguisson Pt., Gun Beach, Camel Rock, and Orote Peninsula for exposed coasts, and Cocos Lagoon, Apra Harbor and Cetti Bay for protected coasts.

Juveniles less than 35 mm SL were observed only in the shallower portions of the species' range in sheltered habitats such as the upper lagoon slope at Western Shoals and between one and two meters in Tepungan Channel and the subtidal moats of Luminao and Piti Reefs.

Both juveniles and adults were generally encountered out in the open, frequently over or near sandy patches or channels, occasionally several meters from the nearest shelter. The Batesian monacanthid mimic *Paraluteres prionurus* was closely associated (it maintained a distance of one meter or less from its model) with at least six of the *C. valentini* individuals collected, and it was seen in the general area of many of the remainder.

Morphology

All species of Canthigaster are characterized by an elongate snout with a strong terminal beak consisting of two fused plates in each jaw. This allows them to selectively seize individual algal tips, invertebrates, or parts of invertebrates and break them off or wrench them from the substrate. All species possess a long and looped intestine and lack a well defined stomach (Figure 4).

Internal alimentary morphologies appeared quite similar among the six species examined for gut content analysis. Relative gut length was the same for all species except C. epilampra which possessed a somewhat shorter gut than did its congeners ($t=2.67$, $P < 0.05$).[1] This may be an adaptation for its primarily carnivorous dietary habits.

Although no specimens were measured, C. leoparda appears to possess a relatively longer snout than do its congeners. This, together with its deep, cave-dwelling habits, strongly suggests that it is a carnivore even more specialized than C. epilampra.

Few external morphological differences are useful in separating the species of Canthigaster other than color pattern. Fin ray counts are of limited use since they overlap for all species occurring at Guam, although modal differences in dorsal and anal fin ray counts may be useful in separating C. amboinensis from its congeners (Allen and Randall, 1977). The greater number of dorsal and anal fin rays

---

[1] Based on the ratio SL/gut length between C. epilampra (n=6) and its sympatric congeners C. amboinensis (n=10), C. bennetti (n=8), C. janthinoptera (n=6), C. solandri (n=10), and C. valentini (n=10) pooled (n=44). All specimens were in the size range of 45-78 mm SL except C. janthinoptera which ranged from 40-52 mm SL.

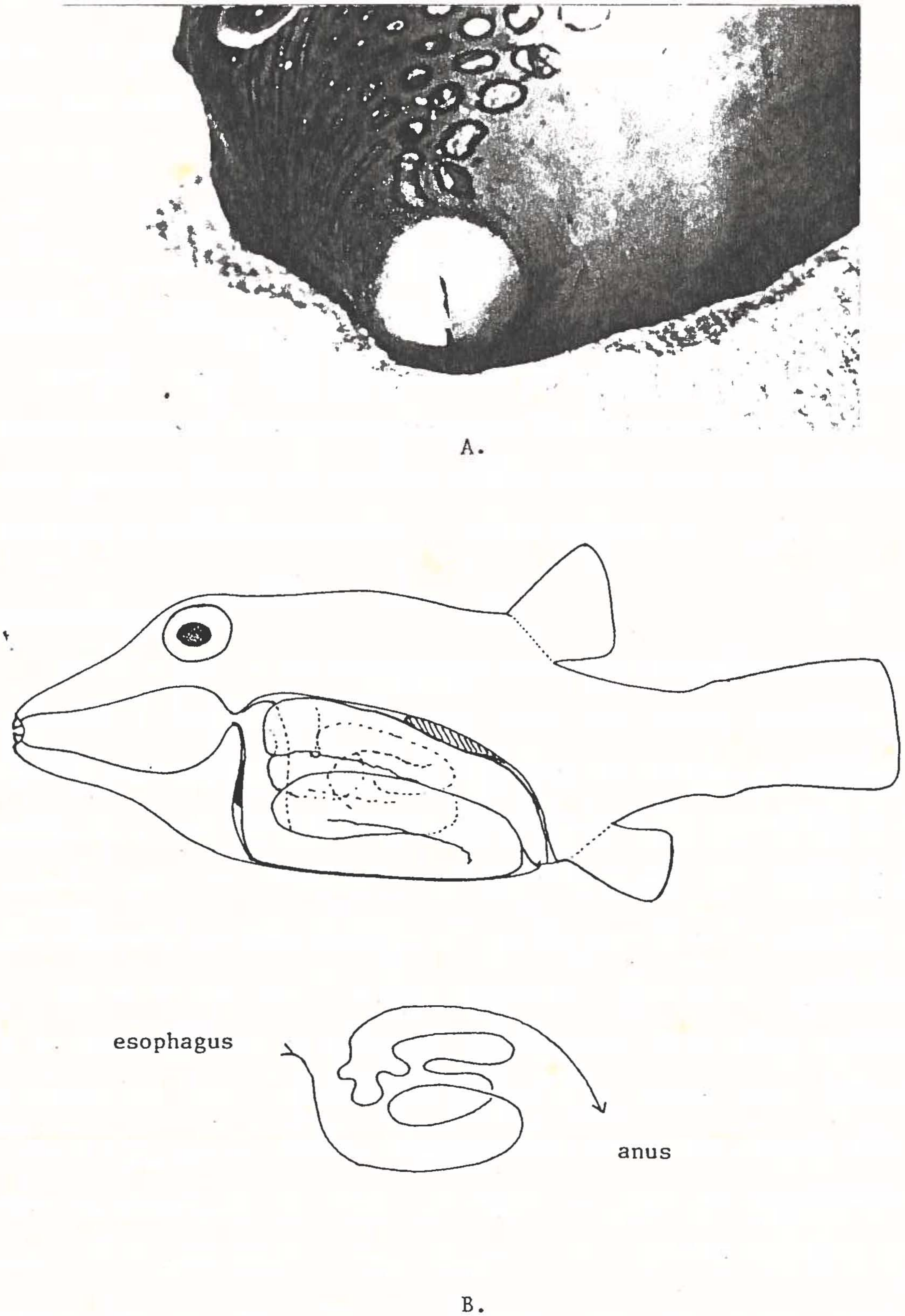


Figure 4. Alimentary anatomy of a representative species of <u>Canthigaster</u>, <u>C</u>. <u>solandri</u>, 50 mm SL. A. Dentition. B. Position and coiling of the alimentary canal.

possessed by *C. amboinensis* may strengthen the fins to facilitate its greater swimming ability and thus be an adaptation for living in surge swept habitats. In addition, Allen and Randall (1977: figures 9 and 10) showed that the ratio of body depth to standard length is slightly greater for *C. epilampra* than for *C. bennetti* and that the caudal peduncle length is slightly greater for *C. bennetti* than for *C. epilampra*. Since none of the above characteristics are directly related to feeding ecology, they were not examined further. Color pattern alone proved sufficient for easily separating the species in the field. The eight species known to inhabit Guam's waters may be distinguished according to the key and plates I - IV of Appendix A.

Feeding Ecology

All six species of *Canthigaster* whose gut contents were examined contained a wide variety of both plant and animal material. The contents of each gut invariably consisted of dozens to hundreds of individually snipped bits and pieces of plants and animals of a wide range of taxa. This resulted in a high frequency of occurrence of most diet categories in each species, giving the superficial appearance of a high degree of interspecific diet similarity. This is in sharp contrast to proportions based on relative diet volumes, which show substantial interspecific dietary differences (Figure 5). Nearly every individual of each *Canthigaster* species consumed both plants and animals, but the relative proportions of plant and animal material and their component taxa varied considerably among species. Most species fed to a great extent upon at least one diet category that was either absent or occurred in small quantities in the diets of its congeners (Table 2).

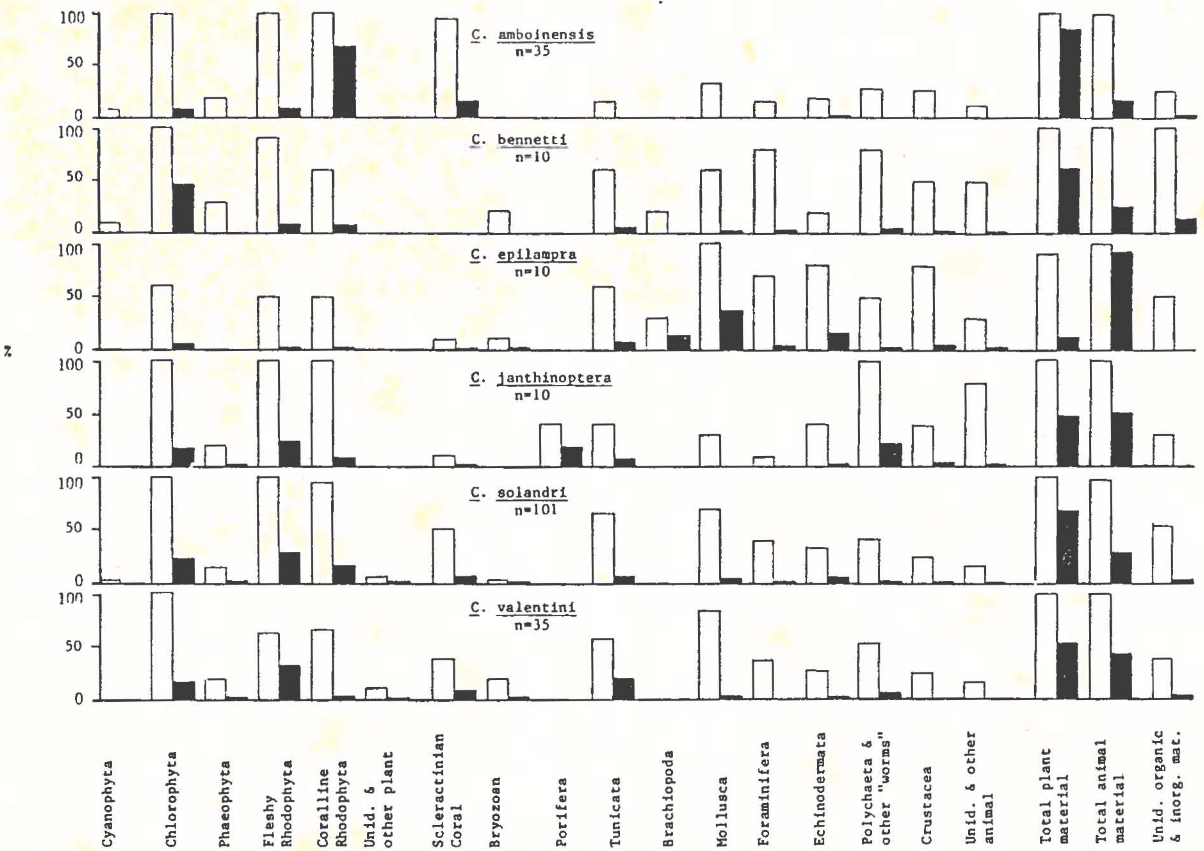


Figure 5. Proportional representation of diet categories in the guts of adults of six species of Canthigaster. Open bars represent the percentage of individuals of each species of Canthigaster in which the diet category is present. Filled bars represent the mean percent diet volume of a given diet category in each species. Total plant material and total animal material are represented on the right.

Table 2. Major diet categories of adult Canthigaster species and their contribution to the diets of their most important exploiter species. Those absent, or found only in small quantities, in the diets of the named species' congeners are indicated with an asterisk. Sample size is indicated in parenthesis.

DIET CATEGORY	MOST IMPORTANT EXPLOITER SPECIES	MEAN % DIET VOLUME
Coralline Rhodophyta*	*C. amboinensis* (35)	66.6
Scleractinian corals*		13.5
Chlorophyta	*C. bennetti* (10)	44.3
Mollusca*	*C. epilampra* (10)	37.1
Echinodermata*	"	16.8
Brachiopoda*	"	12.1
Crustacea	"	5.9
Foraminifera	"	4.4
Polychaeta & other worms*	*C. janthinoptera* (10)	22.4
Porifera*	"	8.0
Fleshy Rhodophyta	*C. valentini* (35)	31.0
Tunicata	"	18.6

Degree of herbivory was examined by comparing the percent diet volumes of plant material among species and testing by the approximate test of equality of means. Results show differences (Table 3) between a number of species. Most notable are for *Canthigaster epilampra* which fed on significantly less plant material than did any of its congeners, *C. amboinensis* which fed on significantly more plant material than did four out of five of its congeners, and *C. solandri* which fed on significantly more or less plant material than did four out of five of its congeners. The dominant diet category in individual guts was compared between species, and their relative frequencies were tested by Kolmogorov-Smirnoff two-sample tests (Table 4). The results clearly show that the dominant diet category in individuals of *Canthigaster* differ between most species. The only cases in which diets, based on every specimen examined, were similar between species, were the *Canthigaster janthinoptera*-*C. valentini*, *C. janthinoptera*-*C. epilampra*, and *C. solandri* - *C. valentini* comparisons. It is notable that in two comparisons (*C. bennetti*-*C.solandri* and *C. epilampra*-*C. solandri*), in which diets were significantly different based on all specimens examined, the diets were not significantly different when considering only specimens collected in the same habitat and site.

Comparisons of mean proportional diet overlap between species support the foregoing results (Table 5). As might be expected, the two species with relatively specialized diets, *Canthigaster amboinensis* and *C. epilampra*, had the lowest mean interspecific diet overlap. Diet overlap between species that occurred in the same habitat was generally higher than that between all possible species pairs (.57 vs, .41; Tables 5 and 6, respectively). In five out of seven possible comparisons, mean

Table 3. Result of the approximate test of equality of means of adjusted diet volumes of total plant material between adults of six species of <u>Canthigaster</u> from Guam using the Games and Howell method. The differences between means, $Y_i - Y_j$, are given below the diagonal. Differences between means significant at the 0.05 level are indicated with an asterisk and tallied by species in the right hand column.

	Ca	Cb	Ce	Cj	Cs	Cv	no. *
Ca	0	-	-	-	-	-	4
Cb	30.48	0	-	-	-	-	1
Ce	70.62*	40.14*	0	-	-	-	5
Cj	46.84*	16.36	23.78*	0	-	-	3
Cs	19.32*	11.16	51.30*	27.52*	0	-	4
Cv	38.80*	8.32	31.82*	8.04	19.48*	0	3

Table 4. Results of Kolmogorov-Smirnoff two-sample tests between diets of adults of six species of *Canthigaster*. Results are based on comparisons utilizing only the single most voluminous diet category in each gut. Details of methodology are given in the text. Sample size is indicated in parentheses. The second of paired sample sizes or results refers to comparisons between individuals collected in the same habitat and site, all others refer to comparison based on all individuals examined. Significance indicates a difference in diet. An asterisk indicates significance at the 95% level. All results are for two-tailed tests.

C. amboinensis (35/35)	*	*	*	* / *	*
C. bennetti (10/10)	-	*	*	* /ns	*
C. epilampra (10/10)	-	-	ns	* /ns	*
C. janthinoptera (10/10)[1]	-	-	-	* / *	ns/ns
C. solandri (101/53)[2]	-	-	-	-	ns/ns
C. solandri (- /22)[1]	-	-	-	-	-/ns

[1] Only individuals from habitats and sites where *C. janthinoptera*, *C. solandri*, and *C. valentini* co-occur are included in the second of each comparison.

[2] Includes all *C. valentini* and *C. solandri* co-occurring in the same habitat and site regardless of the presence or absence of *C. janthinoptera*.

[@] Sample sizes are 30, 6, 4, and 22 for each of the second comparisons, respectively.

[@@] Samples sizes are 6, 35, and 6 for each of the second comparisons, respectively.

Table 5. Proportional diet overlaps between adults of six species of *Canthigaster* at Guam.

	Mean proportional diet overlap with other species	*C. bennetti*	*C. epilampra*	*C. janthinoptera*	*C. solandri*	*C. valentini*
C. amboinensis	.28	.24	.11	.28	.40	.30
C. bennetti	.43	-	.28	.49	.54	.49
C. epilampra	.26	-	-	.28	.31	.29
C. janthinoptera	.48	-	-	-	.64	.63
C. solandri	.52	-	-	-	-	.73
C. valentini	.49	-	-	-	-	-

Overall interspecific mean proportional diet overlap: .41

Table 6. Proportional diet overlaps between collections of *Canthigaster* species occurring in the same habitat and site compared to proportional diet overlaps of all specimens in a given comparison.

Comparison	A Proportional diet overlap between all specimens collected	B Proportional diet overlap between individuals occurring in the same habitat and site	Proportional difference between (A) and (B)
C. amboinensis & *C. solandri*	.40	.48	.08
C. bennetti & *C. solandri*	.54	.47	-.07
C. epilampra & *C. solandri*	.31	.47	.16
C. janthinoptera & *C. solandri*	.64	.65	.01
C. janthinoptera & *C. valentini*	.63	.58	-.05
C. valentini & *C. solandri*	.73	.86	.13
C. valentini & *C. solandri* occurring with *C. janthinoptera*	.73	.76	.03
Mean proportional diet overlap and net change in (A) from (B):	.57	.61	±.08

diet overlap increased even further when only specimens occurring in the same habitat and site were compared (Table 6).

Shannon-Weiner diversity, after lumping similar diet taxa into their respective diet categories, was similar for the diets of all species except *Canthigaster amboinensis*, the species with the least diverse diet (Table 7).

Detailed intraspecific comparisons between diets of different size classes or between groups from different habitats were possible only for *Canthigaster solandri* and *C. valentini*. Although some significant differences were found between intraspecific, interhabitat diets of *Canthigaster solandri* and *C. valentini*, these differences were considerably fewer, proportionately, than those found for all possible interspecific comparisons (4% vs. 80% respectivley, of Kolmogorov-Smirnoff tests significant for these two sets of comparisons, reef flat specimens excluded; Tables 4 and 8). Mean proportional dietary overlap was higher for intraspecific comparisons between habitat groups of *Canthigaster solandri* and *C. valentini*, respectively, than for all possible interspecific comparisons (.64 vs .41), also indicative of higher dietary consistency within a species than between species.

Detailed accounts of feeding ecology by species with pertinent behavioral observations are given below:

Canthigaster amboinensis (35:42.8 - 81.8 mm SL)

Canthigaster amboinensis, while omnivorous, fed on significantly more plant material, which comprised 82% of its diet volume, than any other species examined. Crustose and articulate coralline red algae (primarily *Amphiroa fragilissima*) were the most important dietary items, followed by scleractinian corals which were the most important animal

Table 7. Result of approximate test of equality of means of the Shannon-Weiner diversity indices, H', between adults of six species of *Canthigaster* from Guam using the Games and Howell method. Interpretation follows that of Table 3.

	Ca	Cb	Ce	Cj	Cs	Cv	no. *
Ca	0	-	-	-	-	-	3
Cb	.5326	0	-	-	-	-	0
Ce	.4228	.1098	0	-	-	-	0
Cj	.7185*	.1859	.2957	0	-	-	1
Cs	.4467*	.0859	.0239	.2718	0	-	1
Cv	.5049*	.0277	.0821	.2136	.0582	0	1

Table 8. Results of Kolmogorov-Smirnoff two-sample tests between diets of <u>Canthigaster</u> <u>solandri</u> from different habitats. A dashed line separates comparisons involving reef flat individuals which were all juveniles. Explanation of methods and results is the same as for Table 4.

	Moats, shallow channels (8)	Lagoon reef slopes (11)	Reef fronts (30)	Exposed outer reef terraces (29)	Protected outer reef terraces (4)	Outer reef slopes (14)	Deep dropoff (4)
Reef flats (61)	ns	ns	ns	ns	ns	ns	ns
Moats, shallow channels (8)	-	ns	ns	ns	ns	ns	ns
Lagoon reef slopes (11)	-	-	ns	ns	ns	ns	ns
Reef fronts (30)	-	-	-	ns	ns	*	ns
Exposed outer reef terraces (29)	-	-	-	-	ns	ns	ns
Protected outer reef terraces (4)	-	-	-	-	-	ns	ns
Outer reef slopes (14)	-	-	-	-	-	-	ns

materials consumed. Chlorophytes and coralline rhodophytes occurred in every specimen examined. Animal remains occurred in 97% of those examined, the most frequent taxon being scleractinian corals which were found in 94% of the specimens.

In the field *Canthigaster amboinensis* was observed to move over a larger area of substrate per unit time than were any of its congeners. It was observed to stop and feed on the algal encrusted surface of the sides and tops of surge channels and to feed on the living surface of the corals *Leptoria phrygia* and *Acropora* spp. (2 species).

Canthigaster amboinensis has the least diverse diet of all the species investigated. Its diet was significantly less diverse than that of three out of five of its congeners (Table 7). The single most voluminous diet category in each gut differs significantly between *Canthigaster amboinensis* and each of its congeners. Mean interspecific diet overlap between *Canthigaster amboinensis* and its congeners was the second lowest.

Canthigaster solandri was the only congener collected, or found consistently, in the same habitat and site as *C. amboinensis*. Diets still differed significantly between individuals of the two species collected together, although diet overlap was somewhat higher than that between the two species based on all specimens collected (.48 vs. .40).

Canthigaster bennetti (10:45.0 - 66.8 mm SL)

Canthigaster bennetti relies heavily on both plant and animal material for its diet with plant material comprising the bulk of its diet volume (61%) and animal material somewhat less (26%). It fed more heavily on chlorophytes than did any of its congeners. Chlorophytes were the most voluminous dietary category, greatly exceeding all others.

and occurred in every specimen examined. Every specimen examined also contained some animal remains, with foraminiferans and annelids each occurring in eight of ten guts. In the field, *Canthigaster bennetti* was observed feeding on algal-covered limestone, rubble and loose sand substrates.

The diet of *Canthigaster bennetti*, based on the most voluminous diet category in each gut, differed significantly from that of all of its congerners, except for individuals of *C. solandri* collected in the same habitat and site.

Canthigaster epilampra (10:45.0 - 78.3 mm SL)

Canthigaster epilampra, while omnivorous, is more carnivorous than any of the other species studied with 91% of its diet volume consisting of animal material. This unusually high degree of carnivory is consistent with its relatively short alimentary canal, the only noteworthy morphological adaptation differentiating the species studied. The most important prey were molluscs, primarily small gastropods, which occurred in every specimen examined. *Canthigaster epilampra* fed more heavily on molluscs, echinoderms, brachiopods, crustaceans, foraminiferans and bryozoans than did any of its congeners. Plant material, primarily chlorophytes, comprised only 8% of its diet volume (significantly less than that of any other congener) and occurred in nine of the ten guts examined. In the field it was observed to nip at encrusted limestone surfaces, frequently under ledges or in holes.

The diet of *Canthigaster epilampra*, based on the most voluminous diet category in each gut, differed significantly from that of all its congeners except *C. janthinoptera*, the only other species with 50% or more of its diet volume consisting of animal material. While the diet of Canthigaster epilampra differed significantly from that of C. solandri based on all specimens collected, it did not differ significantly from that of the four C. solandri specimens collected with C. epilampra. Canthigaster epilampra had the lowest mean interspecific diet overlap. Among congeners, its mean diet overlap was highest for the Canthigaster epilampra-C. solandri comparison (.32), and somewhat higher between specimens of the two species collected together (.47).

Canthigaster janthinoptera (10:35.0 - 53.0 mm SL)

Canthigaster janthinoptera relies nearly equally on both plant and animal material for its diet, with the diet volume of animal material slightly exceeding that of plant material (51% vs. 48%) and both occurring in every specimen. The most important diet categories were polychaetous annelids and fleshy rhodophytes which each comprised 22% of its diet volume. The former occurred more abundantly in Canthigaster janthinoptera than in any of its congenors. Canthigaster janthinoptera was the only species to contain Porifera remains which comprised 8% of its diet volume. In the field it was frequently seen picking at the sides and roofs of small caves and overhangs.

The most voluminous diet category in individual guts differed significantly between Canthigaster janthinoptera and all of its congeners except C. epilampra and C. valentini, the latter of which occurred in the same habitats and sites as C. janthinoptera and C. solandri. Based only on specimens collected from the same habitats and sites, diets still differed significantly between Canthigaster janthinoptera and C. solandri, but not between C. janthinoptera and C. valentini. Interspecific diet overlap was higher for all possible comparisons between *Canthingaster janthinoptera*, *C. solandri*, and *C. valentini*, than for any other species-species comparison.

Canthigaster solandri (162:25.0 - 72.2 mm SL)

Canthigaster solandri is omnivorous, feeding most heavily on a wide variety of fleshy and coralline algal tips. Based on all specimens examined, plant material comprised 76% of its diet volume; animal material, 21%. The three most important constituents diet were fleshy rhodophytes, chlorphytes, and coralline rhodophytes. Tunicates were the most important animal constituent. Plant material occurred in every specimen examined, animal material in 86% of them. In the field *C. solandri* was observed feeding on a wide variety of substrates ranging from algal encrusted limestone to rubble, loose sand, thick algal mats, and clumps of macroalgae.

Enough specimens were obtained to examine diet composition by size class (Figure 6) and by habitat. Possible ontogenetic dietary patterns are apparent, among them, a general decrease in the diet volume of chlorophytes with size, and a generally larger diet volume of animal material and greater diversity (H') in individuals greater than 50 mm SL than in individuals less than that size. Since nearly all individuals less than 50 mm SL were obtained from the reef flat, dietary patterns of individuals from this habitat are essentially the same as those for smaller size class individuals.

Among the individuals not found on reef flats (essentially all adults), plant material comprised 69% of the diet volume of *C. solandri*, animal material, 29%. The three most important diet constituents were fleshy rhodophytes, chlorophytes, and coralline rhodophytes. The most important animal constituents were echinoderms, tunicates, and

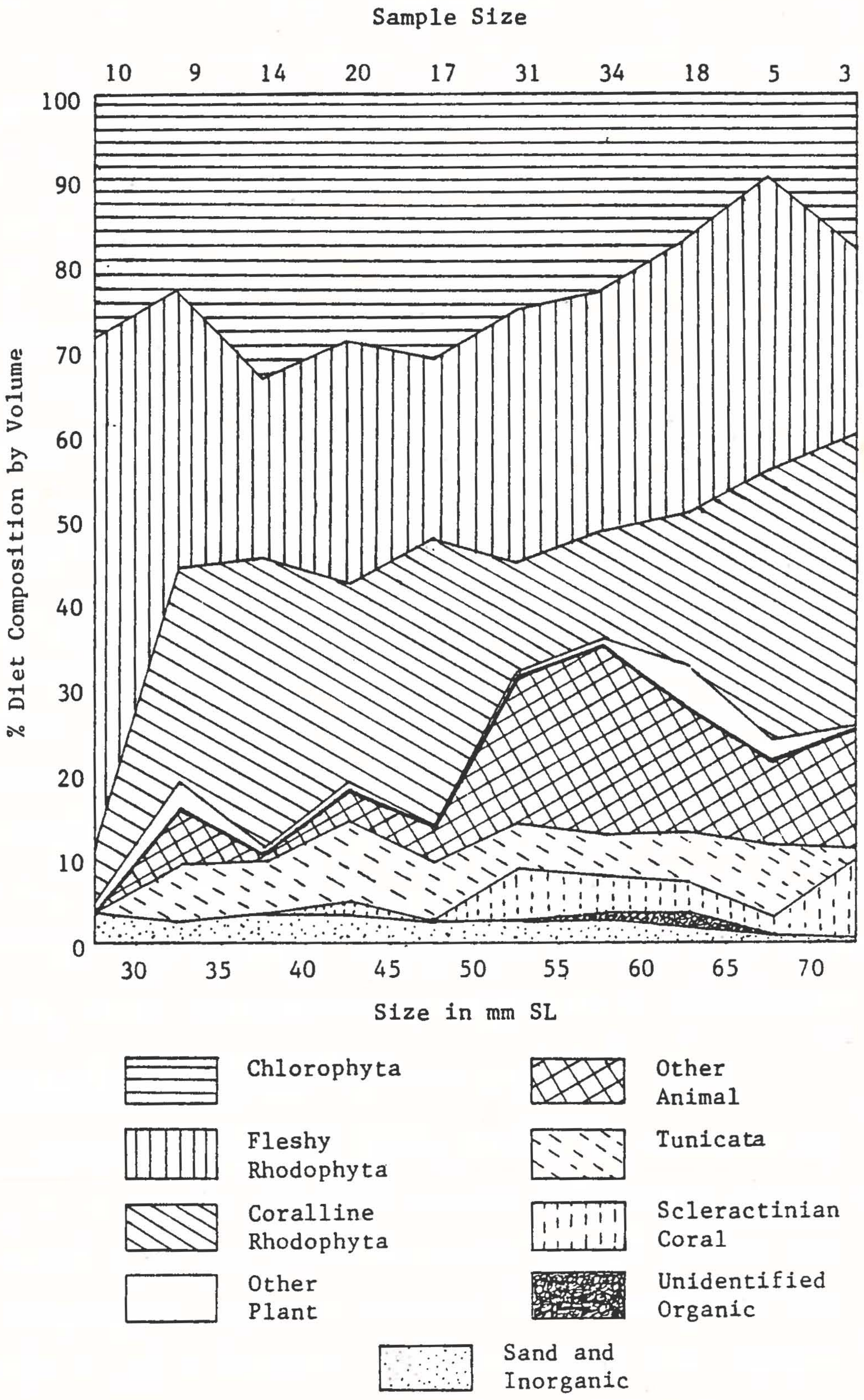


Figure 6. Diet composition of <u>Canthigaster solandri</u> by size class.

scleractinian corals. Every specimen contained plant remains and all but two contained animal remains. Mean diet volume of plant material differed significantly between *C. solandri* and all of its congeners except *C. bennetti*. The diet of *C. solandri*, based on the most voluminous diet category in each gut, differed significantly from that of all its congeners except *C. valentini* when all specimens are considered. However, among specimens collected together, it did not differ significantly from that of *C. bennetti*, *C. epilampra*, and *C. valentini*. Mean interspecific diet overlap was higher for *C. solandri* than for any other species. Diet overlap was higher among species collected together than among all specimens of each species in four out of five comparisons involving *C. solandri* (Table 7).

Intraspecific comparisons among specimens of *C. solandri* from different habitats indicate that there is considerably less within-species than between-species dietary variability. Few significant differences were found among the diets of *C. solandri* from different habitats (Table 9), and diet overlap between groups of individuals from different habitats was higher than it was between species (.63 vs. .41, respectively; Tables 9 and 5, respectively).

Canthigaster valentini (35:42.3 - 74.0 mm SL)

Canthigaster valentini relies heavily on both plant and animal material for its diet with plant material comprising a slightly greater percentage of its diet volume than animal material (52% vs. 43%). As in *C. janthinoptera*, the most important plant constituents were fleshy rhodophytes and chlorophytes. Tunicates were the most voluminous animal constituent, and, along with fleshy rhodophytes and phaeophytes, occurred in greater volume in C. valentini than in any other species.

Table 9. Proportional diet overlaps between collections of *Canthigaster solandri* from different habitats. Sample size is indicated in parentheses.

	Mean proportional diet overlap woth other habitats	Moats, shallow channels	Lagoon patch reef slopes	Reef fronts	Exposed outer reef terraces	Protected outer reef terraces	Outer Reef slopes	Deep dropoffs
Reef flats (61)	.67	.51	.67	.76	.64	.83	.73	.56
Moats, shallow channels (8)	.54	-	.64	.50	.58	.47	.48	.63
Lagoon reef slopes (11)	.63	-	-	.55	.70	.60	.62	.66
Reef fronts (30)	.66	-	-	-	.73	.73	.65	.68
Exposed outer reef terraces (29)	.66	-	-	-	-	.67	.66	.61
Protected outer reef terraces (4)	.64	-	-	-	-	-	.62	.53
Outer reef slopes (14)	.61	-	-	-	-	-	-	.53
Deep dropoffs (4)	.61	-	-	-	-	-	-	-
Overall mean proportional dietary overlap:	.63							

Every specimen contained both plant and animal material with chlorophytes occurring in all specimens and molluscs occurring in 83% of them. In the field this species was observed picking at the surface of encrusted hard substrates, loose sand, algal clumps and living corals.

The most voluminous diet category in individual guts of C. valentini differed from those of all its congeners except C. janthinoptera and C. solandri when all individuals are considered. Numerous C. solandri and all C. janthinoptera were collected from the same habitats and sites as C. valentini. For specimens collected together, diet, based on the most voluminous diet category in each gut, did not differ significantly between C. valentini and C. janthinoptera, and C. valentini and C. solandri, respectively (the latter comparison barely not significant). However, the diets of C. solandri and C. janthinoptera did differ significantly, indicating that C. valentini's diet may be somewhat intermediate between the two.

The most voluminous diet category in each gut did not differ significantly among individuals of C. valentini from three different habitats. Mean diet overlap was higher between individuals of C. valentini from different habitats than between C. valentini and its congeners (.66 vs. .49).

DISCUSSION

A number of studies of the ecology of closely related sympatric species of fishes have shown significant differences between the niches of each species (Robertson et al., 1979; Vivien, 1975; Gladfelter and Johnson, 1983; Greenfield and Greenfield, 1982). As pointed out by Gladfelter and Johnson (1983), feeding studies that only consider frequency of occurrence of, or simply catalogue, food items (for example, Hiatt and Strasburg, 1961) may be misleading since differences in diet or behavior sufficient to prevent competitive exclusion are often overlooked. Sale's (1977) statements that "...many reef fishes do not finely partition resources of food or living space..." and "...among food specialists it is common for two or three sympatric species to show nearly identical specialization, thus overlapping greatly in the foods they consume..." seem inspired by such studies as well as his own studies (Sale, 1975). Although Sale's statements may have been too generally applied, or are easily misinterpreted, it should be pointed out that for certain guilds of fishes they have merit. Among territorial herbivorous damselfishes (Sale, 1975) and planktivorous damselfishes (Tribble and Nishikawa, 1982; Shipgel, 1982) interspecific differences in habitat, microhabitat or diet often cannot be found. It should be noted that the subjects of these studies are all strongly site-attached, spending their entire post-larval lives in small discrete areas and subject to intense predation. Indeed, their site orientation itself may be an adaptation to intense predation or competition. For these guilds and others like them, competitive exclusion could be prevented if equilibrium is never reached. If this were the case with

Canthigaster, one could expect to find a number of sympatric species with indistinguishable or broadly overlapping niches. The degree of niche overlap between *C. solandri*, *C. janthinoptera* and *C. valentini* in habitats where they coexist might partially be the result of equilibrium not being attained because of unpredictable events possibly in the early life history of *Canthigaster*, of which nothing is known.

Distributions and abundances vary significantly among the species of *Canthigaster*. *C. solandri* far outnumbers all but one of its congeners in every habitat investigated while its congeners occupy narrower ranges of habitats. For every possible species pair, one species is consistently found in a habitat or habitats not utilized by the other. This would make it possible for a more broadly distributed species (e.g. *C. solandri*) to maintain itself in a situation in which a narrowly distributed species (for example *C. amboinensis* or *C. epilampra*) is a superior competitor by adopting a fugitive strategy during periods of scarce resources and intensive competition (Dale, 1978). A number of species have mutually exclusive habitat ranges (such as *C. amboinensis*, *C. bennetti* and *C. epilampra*), partitioning this resource completely among themselves. Others utilize microhabitats rarely exploited by their congeners. *C. janthinoptera* and *C. leoparda* are secretive, remaining in or near holes and crevices, while *C. amboinensis*, *C. bennetti*, *C. solandri* and *C. valentini* generally remain out in the open, and *C. epilampra* occasionally occupies caves or holes.

All species examined fed on a wide variety of food, but each consistently fed on one or more diet categories absent, or nearly absent, in the diet of all of its congeners. In all but three comparisons, diet differed significantly between all possible species pairs. Two species, C. amboinensis and C. epilampra, can be termed specialists, since they each feed primarily on a single diet category or group of related categories (coralline red algae and sessile invertebrates, respectively). The other species, to varying degrees, can be termed generalists. Only C. janthinoptera has a diet that does not differ significantly from that of all of its congeners, the two with similar diets being C. epilampra and C. valentini. In the C. epilampra - C. janthinoptera comparison, each species occupied a mutually exclusive range of habitats. In the C. janthinoptera - C. valentini comparison both species occurred together in the same habitats as C. solandri, but C. janthinoptera consistently fed on one food, sponges, not fed on by any of its congeners, although its diet as a whole was not significantly different from that of C. valentini. Although diets based on all specimens examined were significantly different between species in nearly every case, diets between populations of species occurring in the same habitat and site were not usually different. With the exceptions of C. janthinoptera and C. valentini, such comparisons were possible only between C. solandri and each of its congeners, respectively. C. amboinensis, C. bennetti, C. epilampra and C. janthinoptera had mutually exclusive distributions. The question of why two species, with different but overlapping distributions, would have more similar diets where they coexist than where they do not coexist may be explained as follows: The relative abundance of different foods in different habitats influences the composition of the diets, accounting for the differences between diets of populations of species that do not occur in the same habitat. The wide ranging generalist, C. solandri, could be a fugitive species where it occurs with a specialist that is a superior competitor (possibly *C. bennetti* or *C. epilampra*) and may be forced to habitats not used by the superior competitor during times of scarce resources. When food is not limiting they coexist, and their diets are similar. Continuous movement between areas, which would seem quite plausible for the abundant and ubiquitous *C. solandri*, may prevent competitive exclusion. The situation involving *C. valentini*, *C. janthinoptera*, and *C. solandri* may be more complex, since all three coexist in a number of habitats. Among specimens collected together, the diet of *C. valentini* did not differ significantly from that of *C. solandri* or *C. janthinoptera*, but the diet of *C. solandri* did differ significantly from that of *C. janthinoptera*, suggesting that the diet of *C. janthinoptera* may be intermediate between that of the other two species. In any case, for every possible species pair, whether or not their diets differed, at least one occurs in habitats not occupied by the other, potentially preventing competitive exclusion.

There are a number of indications that niche diversification has resulted from competitive interactions in the evolutionary history of *Canthigaster*. One is that most of the characteristics of their niches are consistent across site, habitat, and in some cases, geographic lines. The few available literature accounts mentioning the ecological distribution (Table 10) or diets of species of *Canthigaster* are in general agreement with the results of this study. Another indication of past competitive interactions is that within-species diet similarity tends to be greater than between-species dietary similarity (Tables 4 and 8). This is an indication that species-specific selectivity of certain diet items is more important in shaping a given species' diet than are differences in food availability between habitats.

Table 10. Comparison of the ecological distribution and abundances of the species of *Canthigaster* observed during this study with observations of these and other species in the literature.

Species	This Study: Ecological Distribution and Abundance	Depth Range	Other Observations: Ecological Distribution and Abundance	Depth Range	Source	Location[1]
C. amboinensis	exposed reef fronts where it may be the most abundant *Canthigaster*; occasionally in exposed areas of adjacent habitats	0-9m	primarily in the lower surge zone (approx. = reef front)		Allen & Randall, 1977	----
			shallow surge-swept basalt boulder habitat	0-15m	Hobson, 1974	Hawaiian Is.
			uncommon	2-15m	Allen & Steene, 1979	Christmas Is.[2]
C. bennetti	shallow sandy protected moats, subtidal reef flats, lagoons and channels; generally uncommon	1-3m	shallow, sandy areas	0-10m	Allen & Randall, 1977	----
			uncommon	6-12m	Allen & Steene, 1979	Christmas Is.
C. coronatus	rubble and sand area of outer reef slope; rare	12m	reef face and outer dropoff	10->25m	Hobson, 1974	Hawaiian Is.
			areas of mixed sand, rubble and boulders with sparse algae	6-36^{+}m	personal observ.	Hawaiian Is.
			areas of sand, rubble and boulders with sparse algae	8-121m	Tyler, 1967	----
			----	6->15m	Allen & Randall, 1977	----
C. epilampra	outer reef slope and deep drop-offs, often in areas of high vertical relief; uncommon to moderately common locally	9-36^{+}m	uncommon	12-20m	Allen & Steene, 1979	Christmas Is.
			outer reef slopes, near caves or ledges; uncommon	20m	personal observ.	Hawaiian Is.
			outer reef slopes, near caves or ledges; uncommon	25m	Allen & Randall, 1977	----
C. janthinoptera	shallow, semi-exposed areas with considerable shelter; common but secretive	1-21m	common	4-30m	Allen & Steene, 1979	Christmas Is.

Table 10. (continued)

Species	This study: Ecological Distribution and Abundance	Depth Range	Other Observations: Ecological Distribution and Abundance	Depth Range	Source	Location
C. leoparda	cave in deep dropoff; rare	27-36^{+}m	vicinity of caves along vertical dropoffs	30-50m	Lubbock & Allen, 1979	Philippines, Indonesia & Christmas Is.
C. solandri	ubiquitous and generally the most common member of the genus in most habitats	0-36^{+}m	most common member of the genus in a wide variety of habitats	1-16m	Allen & Randall, 1977	----
C. valentini	most habitats except intertidal reef flats; moderately common below 3m	1-36m	wide variety of habitats; common	0-30m	Tyler, 1967	----
			more common than most spp.	to > 20m	Allen & Randall, 1977	----
				5-15m	Allen & Steene, 1979	Christmas Is.
C. jactator	not present in Guam		all habitats except reef flat; most common member of genus except in boulder habitat where *C. amboinensis* is the most common member	0->25m	Hobson, 1974	Hawaiian Is. (endemic)
			ubiquitous, including reef flats; very common	0-30^{+}m	personal observ.	Hawaiian Is.
C. rostrata	not present in Guam		coral reefs and seagrass beds; common		Randall, 1967	West Indies
			"many observations"	to 160m	Colin, 1974	Jamaica

[1] Specific localities are not given by Allen & Randall (1977). Tyler (1967) lists numerous localities and habitats under "material examined".

[2] Christmas Is., Indian Ocean, for all Allen & Steene (1979) citations.

In addition to competition among congeners it seems possible that competition with certain species of grazers such as acanthurids, scarids or siganids that crop algal mats (consequently removing the habitat of some of the invertebrates eaten by Canthigaster as well as the algae) or territorial pomacentrids which exclude Canthigaster from their territories, has played a role in the evolution of Canthigaster. Certain specialists, such as the cave-frequenting C. janthinoptera, C. epilampra, or C. leoparda, may have evolved in response to competitive pressure from non-canthigasterine herbivores as well as from some of their own congeners or other omnivorous tetraodontiforms. The generalists, such as C. solandri and C. valentini, may be able to respond to competitive pressure by altering their diets by living in adjacent habitats, or by exploiting microhabitats such as small holes and irregularities of the substrate not accessible to larger grazing herbivores, during times of scarce resources. Although not quantified or directly comparable, observations at other island groups in the tropical Pacific lend this hypothesis credibility. During visits to Enewetak, Kosrae, Truk, Palau, Pagan and Saipan, I noted that species of Canthigaster were strikingly less abundant than they were at Guam and in the Hawaiian Islands, where grazing herbivores are highly exploited by man, particularly on reef flats. Each of these islands has a much larger reef area per capita and is relatively unexploited. At Saipan, an island subject to perhaps intermediate exploitation, Canthigaster species were notably less abundant than at Guam, but more abundant than at Kosrae or Pagan where, during a week of diving in a variety of habitats, fewer than four or five individuals were observed (personal observation). To test this hypothesis, quantitative information on the relative abundances of species of Canthigaster, grazing herbivores and territorial herbivorous pomacentrids, as well as fishing pressure would have to be obtained for a number of islands subject to various degrees of exploitation.

Guam's species of Canthigaster are for the most part morphologically indistinguishable and would thus seem potentially equally suited to a given niche. Yet they partition resources of food and space to the extent that each species occupies a niche that is at least partially species-specific. Specificity of niches varies among the species along one or more axes of diet, habitat or microhabitat. Niche separation along any one of these axes ranges from total separation to none at all, but collectively, there is always some separation.

The patterns of resource partitioning of Guam's sympatric species of Canthigaster has much in common with that of the Caribbean holocentrids studied by Gladfelter and Johnson (1983). Quantitative diet composition and habitat or microhabitat distribution differed significantly between most species. Intraspecific dietary consistency of major food items was found across site and habitat lines and both groups contained species that could be termed specialists and species that could be termed generalists. For these species, existing differences between their niches alone are adequate to permit their coexistence.

LITERATURE CITED

Alevison, W. S. 1976. Mixed schooling and its possible significance in a tropical western Atlantic parrotfish and surgeonfish. Copeia 1976:352-356.

Allen, G. R., and J. E. Randall. 1977. Review of the sharpnose pufferfishes (subfamily Canthigasterinae) of the Indo-Pacific. Rec. Australian Museum 30:475-517.

Allen, G. R., and R. C. Steene. 1979. The fishes of Christmas Is., Indian Ocean. Aust. Nat. Parks and Wildlife Serv. Spec. Publ. No. 2. v + 81 pp.

Choat, J. H., and D. R. Robertson. 1975. Protogynous hermaphroditism in fishes of the family Scaridae. Pages 263-283 in R. Reinboth, ed. Intersexuality in the Animal Kingdom. Springer-Verlag, Heidelberg.

Colin, P. L. 1974. Observation and collection of deep-reef fishes off the coasts of Jamaica and British Honduras (Belize). Mar. Biol. 24:29-38.

Dale, G. 1978. Money-in-the-bank: A model for coral reef fish coexistence. Env. Biol. Fish. 3:103-108.

Eger, W. H., and J. G. Starkus. 1973. Morphological aspects of the skin from toxic Caribbean pufferfishes (Tetroadontiformes). Proc. Assoc. Island Mar. Lab. Carib. 8:20-21.

Gladfelter, W. B., and W. S. Johnson. 1983. Feeding niche separation in a guild of tropical reef fishes (Holocentridae). Ecology 64: 552-563.

Greenfield, D. W., and T. A. Greenfield. 1982. Habitat and resource partitioning between two species of Acanthemblemaria (Pisces: Chaenopsidae), with comments on the chaos hypothesis. Pages 499-507 in K. Rutzler and I. G. Macintyre, eds. The Atlantic barrier reef ecosystem at Carrie Bow Cay, Beliz, I: Smithsonian Contrib. Mar. Sci. vol. 12.

Halstead, B. W. 1967. Poisonous and venomous marine animals of the world. Vol. 2 - Vertebrates. U.S. Gov. Print. Off. Washington, D.C. 1070 pp.

Hiatt, R. W., and D. W. Strasburg. 1961. 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.

Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59:67-77.

Jones, R. S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (Surgeonfishes). Micronesica 4:309-361.

Lubbock, R., and G. R. Allen. 1979. *Canthigaster leoparda*, a new sharpnose pufferfish (Teleostei: Tetraodontidae) from the Indo-Pacific. Rev. Fr. Aquariol. 6:87-90.

Morgans, J. F. C. 1982. Serranid fishes of Tanzania and Kenya. Ichthyol. Bull. J. L. B. Smith Inst. Ichthyol., No. 46. 44 pp.

Poole, R. W. 1974. An introduction to quantitative ecology. McGraw Hill. x + 532 pp.

Randall, J. E. 1965. Grazing effect on seagrasses by herbivorous reef fishes in the West Indies. Ecology 46:255-260.

________. 1967. Food habits of reef fishes of the West Indies. Studies in Tropical Oceanography No. 5. pp. 665-847.

Robertson, D. R., N. V. C. Polunin, and K. Leighton. 1979. The behavioral ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus*, *A. leucosternon* and *Zebrasoma scopas*): Their feeding strategies, and social and mating systems. Env. Biol. Fish. 4:125-170.

Sale, P. F. 1975. Patterns of use of space in a guild of territorial reef fishes. Mar. Biol. 29:89-97.

________. 1977. Maintenance of high diversity in coral reef fish communities. Amer. Naturalist 111:337-359.

________. 1978. Coexistence of coral reef fishes - a lottery for living space. Env. Biol. Fish. 3:85-102.

Shipgel, M. 1982. Niche overlap among two species of coral dwelling fishes of the genus *Dascyllus* (Pomacentridae). Env. Biol. Fish. 7:65-68.

Smith, C. L., and J. C. Tyler. 1972. Space resource sharing in a coral reef fish community. Bull. Nat. Hist. Mus. Los Angeles County 14:125-170.

Sokal, R. R. and F. J. Rohlf. 1981. Biometrics. 2nd ed. W. H. Freeman and Co., San Francisco. ix + 859 pp.

Tate, M. W., and R. C. Clelland. 1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publ., Danville, Ill. 171 pp.

Tribble, G. W., and M. Nishikawa. 1982. An analysis of the diets of four spartially overlapping damselfishes of the genus _Chromis_. Japan. J. Ichthyol. 29:267-271.

Tsuda, R. T., and P. G. Bryan. 1973. Food preferences of juvenile _Siganus_ _rostratus_ and _S_. _spinus_ in Guam. Copeia 1973:604-606.

Tyler, J. C. 1967. A diagnosis of the two transversely barred Indo-Pacific pufferfishes of the genus _Canthigaster_ (_valentini_ and _coronatus_). Proc. Acad. Nat. Sci. Philad. 119:53-73.

Vivien, M. L. 1975. Place of apogonid fish in the food webs of a Malagasy coral reef. Micronesica 11:185-198.

APPENDIX A

Key to the species of *Canthigaster* of Guam[1]

1 Dorsal rays usually 12, ground color uniformly dark brown, with numerous white and black spots (Indo-W. Pacific and Eastern Pacific).. *amboinensis*

-- Dorsal rays 8 to 10; if ground color uniformly dark, black spots absent...2

2 Caudal fin evenly spotted .... *solandri*

-- Caudal fin not evenly spotted..3

3 Upper portion of head and body with four dark bars, each wider than pale interspaces 4

-- Upper portion of head and body without dark bars.................5

4 First two bars of body with narrow extensions continuing down middle of sides; dorsal rays usually 9 (Indo-W, Pacific, excluding Hawaiian Is.)[2]

.... *valentini*

-- First two bars on body terminate at about middle of sides; dorsal rays usually 10 (Indo-W. Pacific, including Hawaiian Is.)

.... *coronata*

5 Spots on body or sides rounded and relatively large, the largest at least 2/3 the size of pupil; ground color uniformly dark; dorsal and anal rays usually 9 6

---

[1] Based in part on Allen and Randall (1977).

[2] This species is also sexually dichromatic with males possessing a dusky area along the midline of the belly and more numerous yellow spots and and streaks on the chin and anterior portion of the belly than the female.

-- Spots on body or sides tiny, less than ¼ the diameter of pupil; dorsal portion of body darker than adjacent region on sides; dorsal rays 9 or 10, anal rays usually 9 7

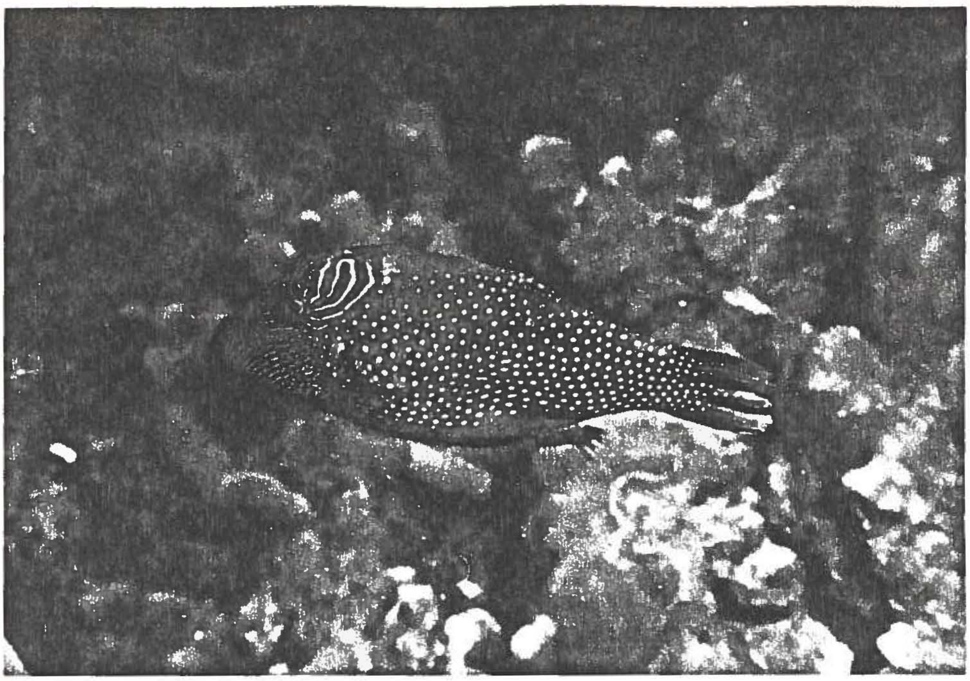
6 Spots on head and body pale, ground color dark brown to black (Indo-W. Pacific, excluding Hawaiian Is.) .... *janthinoptera*

-- Spots on body dark and arranged in clusters; ground color light yellowish-tan (Guam, Philippine, Indonesia and Christmas Island, Indian Ocean) .... *leoparda*

7 Numerous tiny red and white spots interspersed over most of body; red and light blue lines radiating from eye; no conspicuous ocellus above pectoral axil; pectoral rays 15 or 16 (Indo-W. Pacific, excluding Hawaiian Is.) .... *bennetti*

-- Numerous tiny blue spots and lines over most of body except parts of back; blue lines over yellow ground color radiating from eye, one of these terminating in a small yellow-centered ocellus above pectoral axil; pectoral rays usually 17, rarely 16 (W. and Central Pacific, including Hawaiian Is., and Christmas Is., Indian Ocean) .... *epilampra*

A.



B.

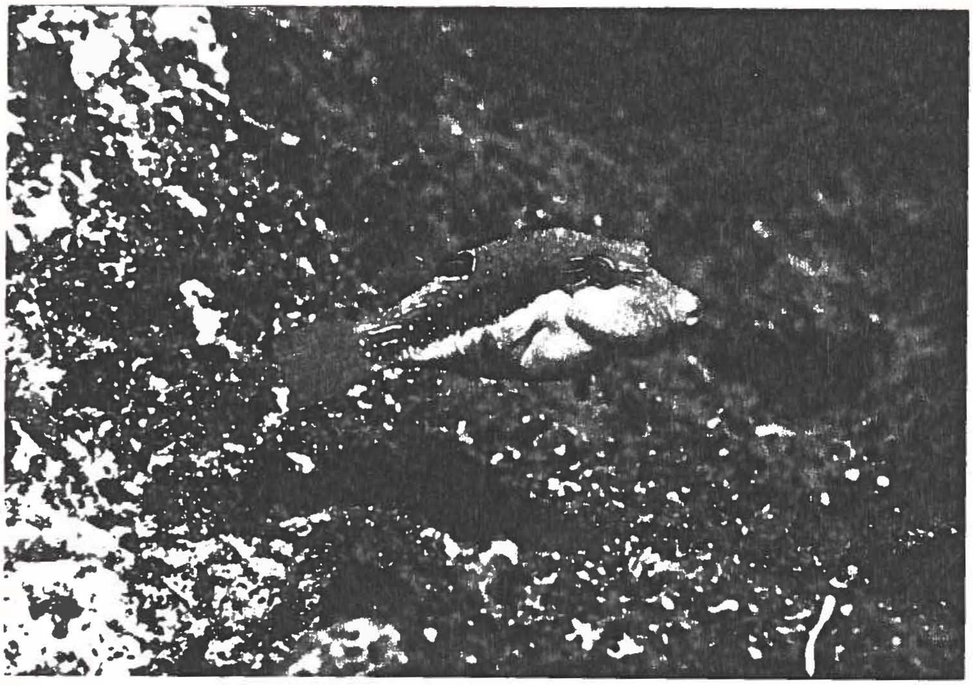
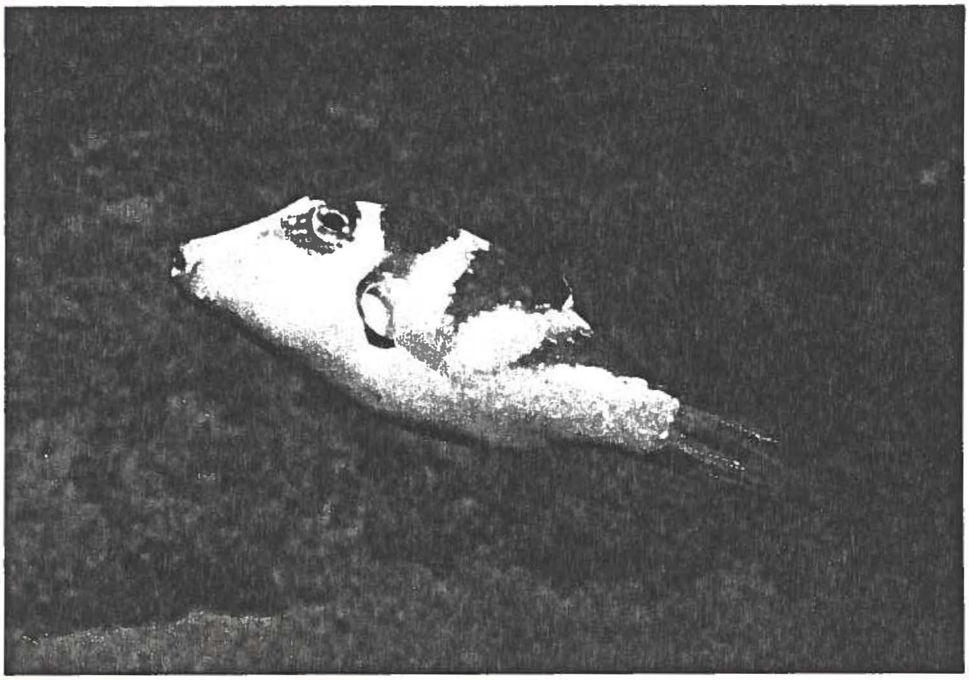


Plate I. A. Canthigaster amboinensis, 10 m, Oahu, Hawaiian Islands.
B. C. bennetti, 3 m, Orote Peninsula, Guam.

A.



B.

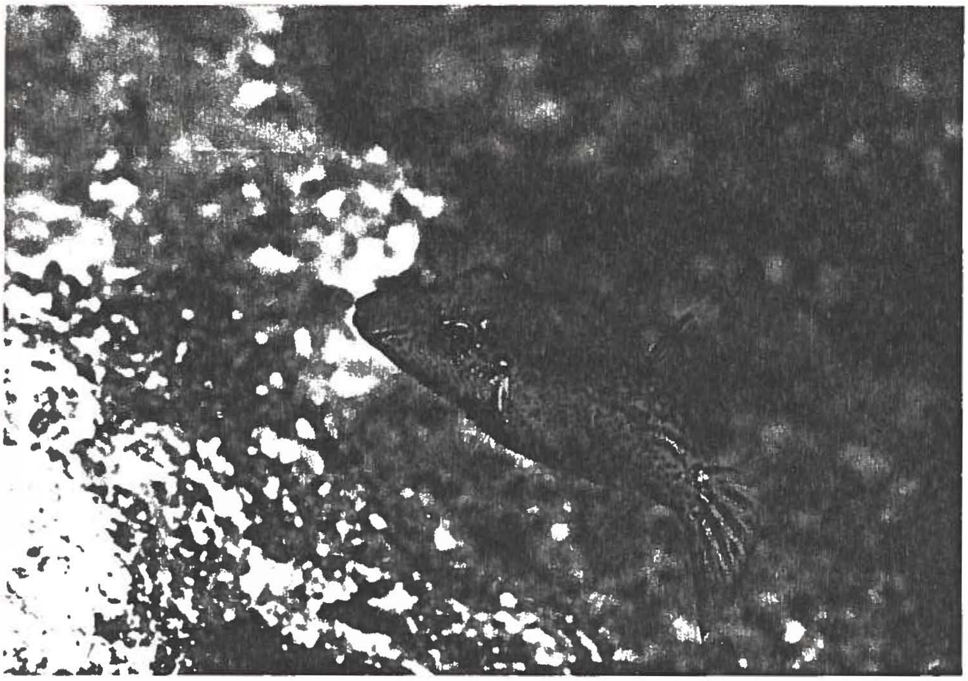
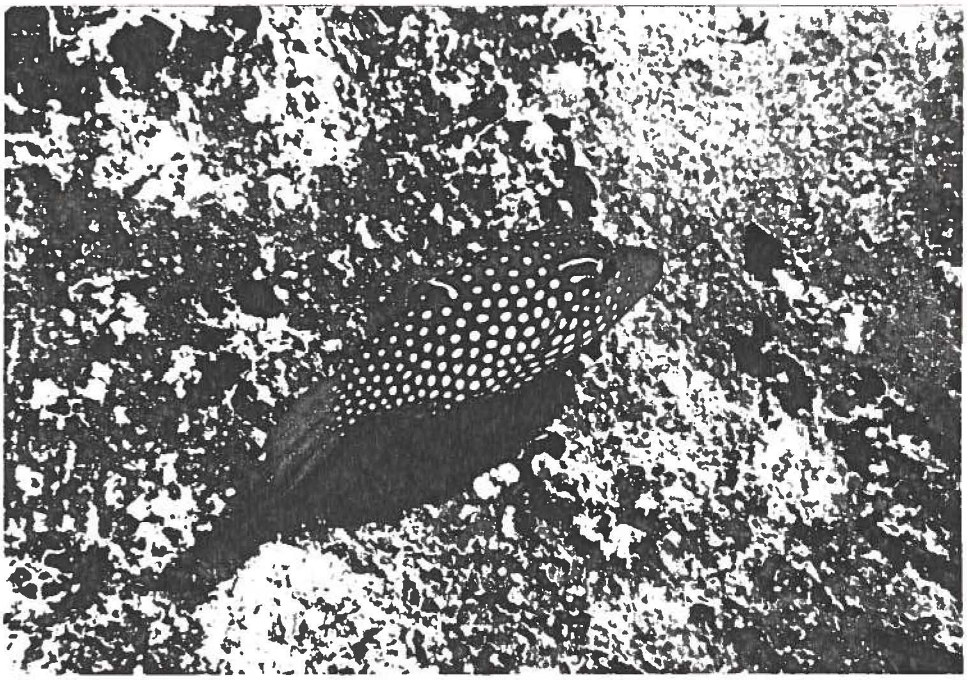


Plate II. A. Canthigaster coronata, 12 m, Oahu, Hawaiian Islands.
B. C. epilampra, 24 m, Orote Peninsula, Guam.

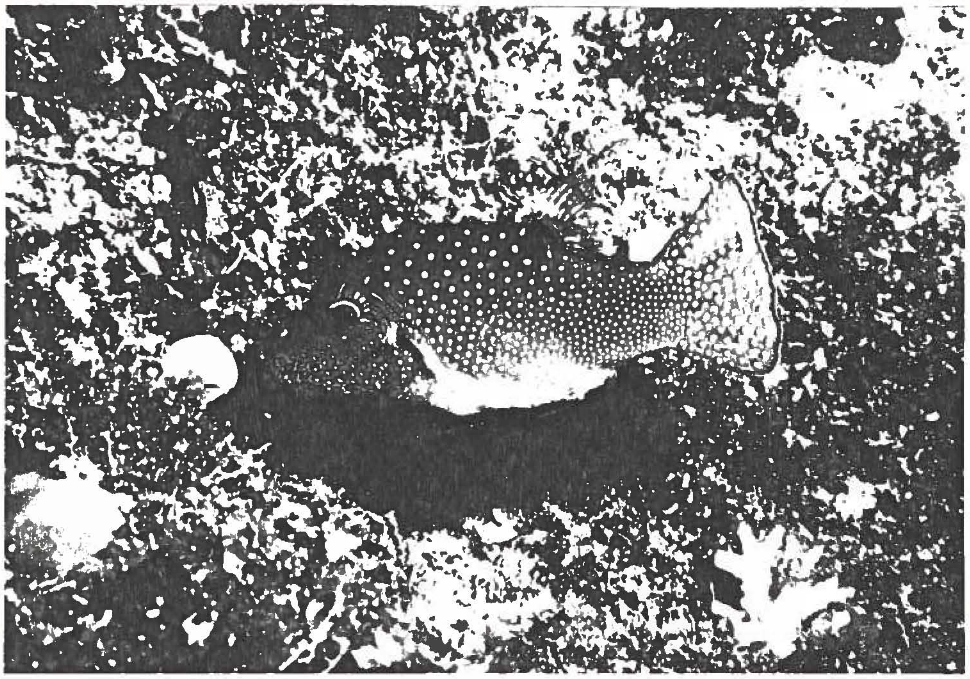
A.



B.

Plate III. A. *Canthigaster janthinoptera*, 1 m, under Tepungan Channel bridge, Guam.
B. *C. leoparda*, 30 m, Orote Peninsula, Guam.

A.



B.

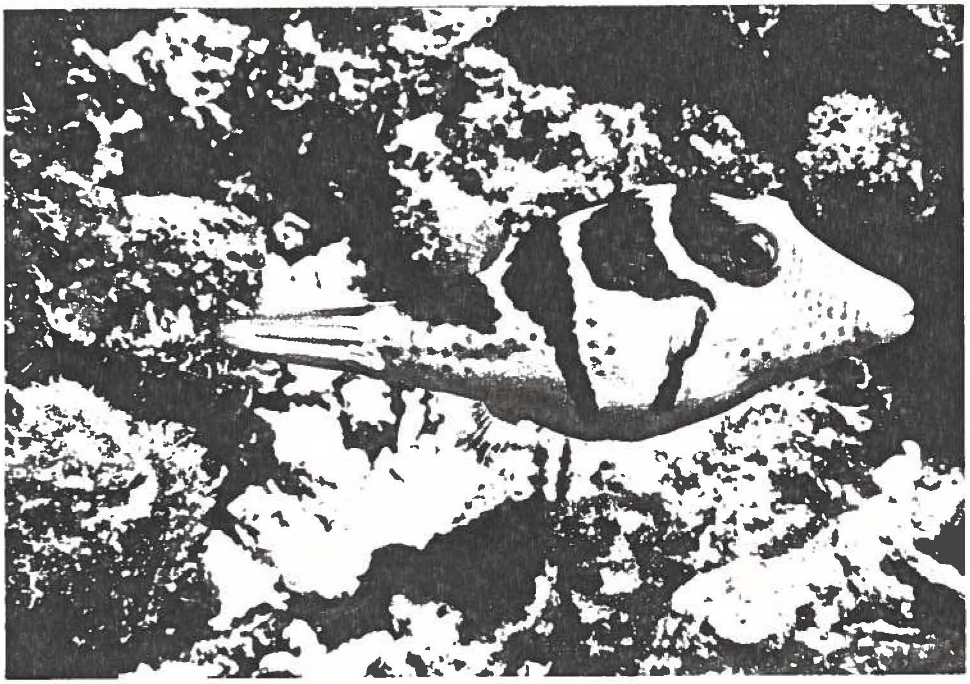


Plate IV. A. *Canthigaster solandri*, 6 m, Gun Beach, Guam.
B. *C. valentini*, 1.5 m, Agana Bay, Guam.