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The Influence of Diet on Local Distributions of *Cypraea*[1]

THERESE HAYES[2]

ABSTRACT: The distribution of *Cypraea* in two habitat zones at Puako reef on the island of Hawaii was examined. Three species, *Cypraea gaskoini*, *C. cicercula*, and *C. scurra*, were found only in the reef face study site, and two species, *C. poraria* and *C. caputserpentis*, were found only in the reef top study site. Active individuals of all species were distributed nonrandomly with respect to substrate type. For reef face species the distribution of individuals appeared to be related to diet, with sponge the major dietary component of each of four reef face species. One cowrie was found to be prey specific for one species of sponge, and the distribution of *C. gaskoini* appeared to be dependent on the distribution of its prey sponge.

COWRIES OF THE GENUS *Cypraea* are nocturnally active gastropods found for the most part associated with coral reefs in which they occupy many different habitats. In Hawaii 34 species of the genus occur from the intertidal zone to depths of 100 m offshore (Kay 1979).

One factor that may influence the local distribution of *Cypraea* is food availability. If food availability does affect cowrie distribution, then the diets of individual cowries must show at least some degree of specialization.

Dietary specialization has been shown in other marine gastropods. *Conus*, a predatory gastropod genus, shows dietary specialization between its member species (Kohn 1959, 1967, 1968, 1971). Stenophagy has also been found in some members of the Terebridae (Miller 1966, 1970) and Buccinidae (Taylor 1978*a*). Some species of *Acmaea* on the coast of California have been found to have specialized algae diets (Test 1945, Craig 1968, Eaton 1968).

The habits of *Cypraea* are not as well-known. Although it is known that cowries feed by scraping a taenioglossan radula over hard substrates, information on the diet of cowries is scarce. That some species are algae grazers, eating both a wide variety of algal food and, alternatively, only one or two algae species, has been documented. A broad algal diet has been found in *Cypraea caputserpentis* in Hawaii (Kay 1960). *C. moneta* at Enewetak, Marshall Islands, on the other hand, has been found to feed primarily on two species of algae, *Jania capillacea* and *Schizothrix calicola* (Renaud 1976). Other cowries feed on a proteinaceous diet. *C. teres* is known to feed on sponge in Australia (Taylor 1975), and specimens of *C. spadicea* have fed on frozen shrimp in an aquarium (Darling 1965). Additional information on feeding habits is anecdotal but indicates that in general cowries are capable of feeding on a wide variety of foods (Kay, in press).

The following questions are addressed in this study:

1. What are the differences in species composition of *Cypraea* between two habitat zones on a shallow subtidal coral reef?
2. Do cowries exhibit dietary specialization with respect to substrate?
3. Are any differences in species composition related to dietary specialization?

In an attempt to answer these questions the distribution of cowries was examined and gut content analysis was performed. If cowries exhibit dietary specialization, this specialization should be reflected by nonrandom distribution of individuals on available substrates during feeding. Gut contents should also show

[1] Manuscript accepted 1 June 1982.
[2] University of Hawaii, Department of Zoology, 2538 The Mall, Honolulu, Hawaii 96822.

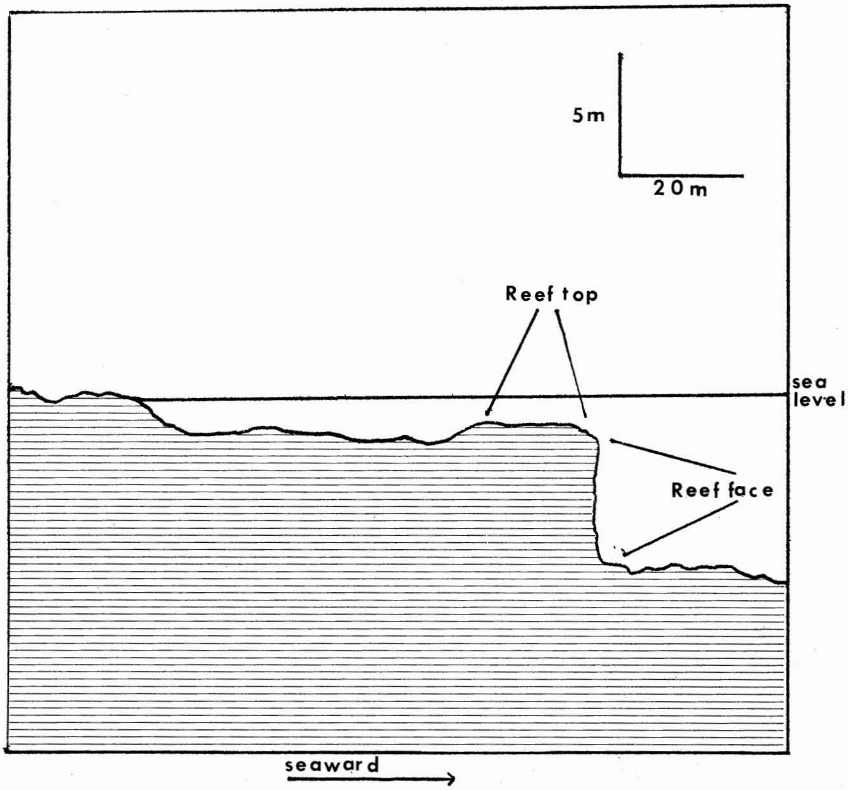


FIGURE 1. Typical reef profile depicting the positions of the reef face and reef top study sites.

a distribution of dietary items that differs from the distribution of available substrates.

SITE DESCRIPTION

This study was conducted at Puako on the west coast of the island of Hawaii (approximately 19°58′30″ N, 155°50′53″ W), an area of extensive coral reef development.

A typical profile of the reef is shown in Figure 1. The intertidal zone varies in width from a few meters to more than 50 m from shore. A shallow, subtidal basalt platform extends seaward to approximately 100 m from shore. The reef consists of filamentous algae, coralline algae (*Porolithon* spp.), and colonies of the corals *Pocillopora meandrina* and *Porites lobata*. Depth of the platform varies from 1 to 3 m.

At the seaward edge the reef drops to a depth of approximately 7 m in a vertical face, which is honeycombed with small caves and overhangs supporting the growth of a variety of sponges. This is a subset of the reef face habitat described by Hobson (1974) and will also be referred to as the cave habitat zone.

From the base of the reef face the reef slopes gently to a depth of about 13 m, and the major coral species is *Porites lobata*. The topography of the bottom is complex, and the average vertical relief is approximately 1 m. At approximately 13 m the slope becomes steeper and the reef drops to coral rubble and sand flats at depths ranging from 20 to 45 m. This area supports extensive colonies of *Porites compressa*.

METHODS

Two habitat zones were chosen for this study: the reef platform and the reef face. Both are characterized by a hard, nonporous substratum interrupted by numerous holes and crevices and they appear physically similar enough to allow comparisons between them.

A study site was established in each habitat zone. A section of the reef face was marked off at 5 m intervals for a distance of 40 m. The height of the reef face averaged approximately 5 m ($\bar{x} = 5.1, s = 1.1, n = 8$). On the reef platform an area 15 × 20 m was divided into 10 quadrats, 5 m on a side. The size of the quadrats was chosen based on preliminary observations of cowrie abundance and patchiness in the area and on personal experience of the size of an area a diver can work without losing orientation and concentration.

Observations were carried out every 7 to 10 nights from May through October 1980. Observation periods were usually 1 to $1\frac{1}{2}$ h in duration for each site. During each observation period divers recorded the number of each species of *Cypraea* per 25 m^2 quadrat.

Because diet may be indicated by substrate associations, the substratum occupied by each individual was recorded. Cowries often began to crawl away when a light was shined on them; observations were made on moving and stationary individuals, although this may have added error to estimation of substrate association with diet.

To facilitate field observations and to obtain a suitable sample size in each class, substrata were grouped into four major categories: (1) filamentous algae, (2) coralline algae, (3) sponge, and (4) miscellaneous (silt, bryozoans, hydroids, basalt rock, and live coral). If an individual was on heterogeneous substrata, it was noted as such under the miscellaneous category.

The proportion of each study site comprised of each substratum was photographically determined. Photographs of the reef, each covering an area 14.5 × 21.0 cm, were taken using a Nikonos II camera with a Novatek Plus 3 close-up lens and a Braun electronic flash in an Ikelite housing. Between 8 and 12 random sites were chosen in each of 18 quadrats for a total of 189 photographs. The position of each site was determined by obtaining random number pairs from a random numbers table (Rohlf and Sokal 1969). These pairs were used as coordinates on a 25 m^2 grid marked at 24 cm intervals. The grid was superimposed on each quadrat and photographs were taken. Different sets of random number pairs were used for each quadrat. The resulting slides were projected onto an 11 × 14 in grid with 140 points of intersection and the substrate at each point was determined. The results for each study site were tallied and a percentage was calculated for each substrate type in each study site.

For each study site the distribution of each species of *Cypraea* was compared with the distribution of substrates using the *G*-test for goodness-of-fit [also called the log likelihood ratio test (Sokal and Rohlf 1969)]. This test is used to predict how well an observed distribution fits a predicted distribution. A good fit of cowrie distribution to the specified distribution of substrata would indicate that the cowries were distributed irrespective of substrate. Conversely, a poor fit of a species distribution to the substrate distribution would indicate nonrandomness in the cowries' occupation of substrata.

Using the percentage of each species of cowrie observed on each substratum as a basis, cowries were collected from each substratum in proportion to the number observed on that substrate during the course of the study, for a total of 12 individuals collected per species. The proportions of substrata in the study site were assumed to be representative of the reef face habitat zone based on preliminary observations and estimation of substrata.

Samples were frozen and examined in the laboratory for stomach contents. Specimens of each species were dissected and material from the stomach was removed. For uniformity and to reduce the bias toward undigestible material, only the stomach contents were examined.

The material was squashed between a coverslip and a glass slide and examined at 100× total magnification. The proportion of each food type in each gut was determined using an ocular grid with 225 points of intersection and covering 0.5 mm^2. Twenty-five uniformly spaced fields were examined for each individual and a percentage of dietary items was calculated.

To determine whether the diet of each species was the result of random grazing on available substrate, the results of the stomach content analysis were tested against the distribution of substrate using the *G*-test for goodness-of-fit. The food items were grouped into the same classes as were the substrates: (1) filamentous algae, (2) coralline algae, (3) sponge, and (4) miscellaneous. A poor fit of the distribution of food items to the distribution of substrate indicates a nonrandom pattern of feeding.

To determine whether the amount of surge is different between the reef face and the reef top study sites, a plaster-of-paris block was fastened to the bottom in each of 8 quadrats in each study site. Each block weighed approximately 76.9 g (range: 67.7–88.7). After 24 h the blocks were recovered and allowed to dry for one week. Each block was then reweighed to determine the amount of erosion. Erosion of the plaster-of-paris blocks was assumed to be caused by wave action.

TABLE 1

ABUNDANCE OF *Cypraea* IN THE STUDY SITES AT PUAKO

SPECIES	RELATIVE ABUNDANCE
Reef face	
Cypraea fimbriata	.3715
C. maculifera	.1825
*C. gaskoini**	.1456
C. helvola	.1315
C. isabella	.1157
C. teres	.0141
C. sulcidentata	.0130
C. granulata	.0114
C. schilderorum	.0087
*C. tigris**	.0038
*C. cicercula**	.0016
*C. scurra**	.0005
Reef top	
C. fimbriata	.4633
*C. caputserpentis**	.2239
C. maculifera	.1282
C. helvola	.1155
C. isabella	.0268
*C. poraria**	.0169
C. teres	.0141
C. schilderorum	.0070
C. granulata	.0028
C. sulcidentata	.0014

*Found only in one site.

RESULTS

Estimation of Abundance

The abundance of *Cypraea* in the cave and reef top study sites is presented in Table 1 and in Figures 2*A* and 2*B*. *Cypraea fimbriata* Gmelin is the most abundant species and occurs in both habitats. Other species that occur in both habitats are *C. helvola* Linnaeus, *C. maculifera* Schilder, *C. granulata* Pease, *C. isabella* Linnaeus, *C. schilderorum* (Iredale), *C. sulcidentata* Gray, and *C. teres* Gmelin. Two of the reef platform species, *C. caputserpentis* Linnaeus and *C. poraria* Linnaeus, were never observed in the reef face study site; four reef face species, *C. gaskoini* Reeve, *C. cicercula* Linnaeus, *C. scurra* Gmelin, and *C. tigris* Linnaeus, were never observed in the reef top study site. Elsewhere on the reef, however, individuals of *C. tigris* were seen on the reef top.

The density of cowries in the reef top study site is 0.18 individuals per m^2 ($s = 0.042$, $n = 16$ periods of observation), and the density is 0.528 individuals per m^2 ($s = 0.124$, $n = 18$) in the reef face study site.

Substrate Observations

The relative abundance of individuals of each species observed on each substrate is shown in Table 2 (top) and Figure 3*A* for the reef face study site and in Table 2 (bottom) and Figure 3*B* for the reef platform. Also shown are the distribution of substrate in each habitat and the results of the *G*-test for goodness-of-fit. For every species the distribution of individuals with respect to substrate was significantly different from the distribution of substrates ($p < .005$ in all cases).

In the reef face study site some species were consistently observed on substrata that comprised only a small percentage of the study site. Specimens of *C. gaskoini* were consistently (47.7 percent) observed in association with one species of red sponge, and unidentified species of the genus *Prianos*. For individuals of *C. isabella*, 38.3 percent were observed on one species of yellow sponge, *Psammaplysilla*

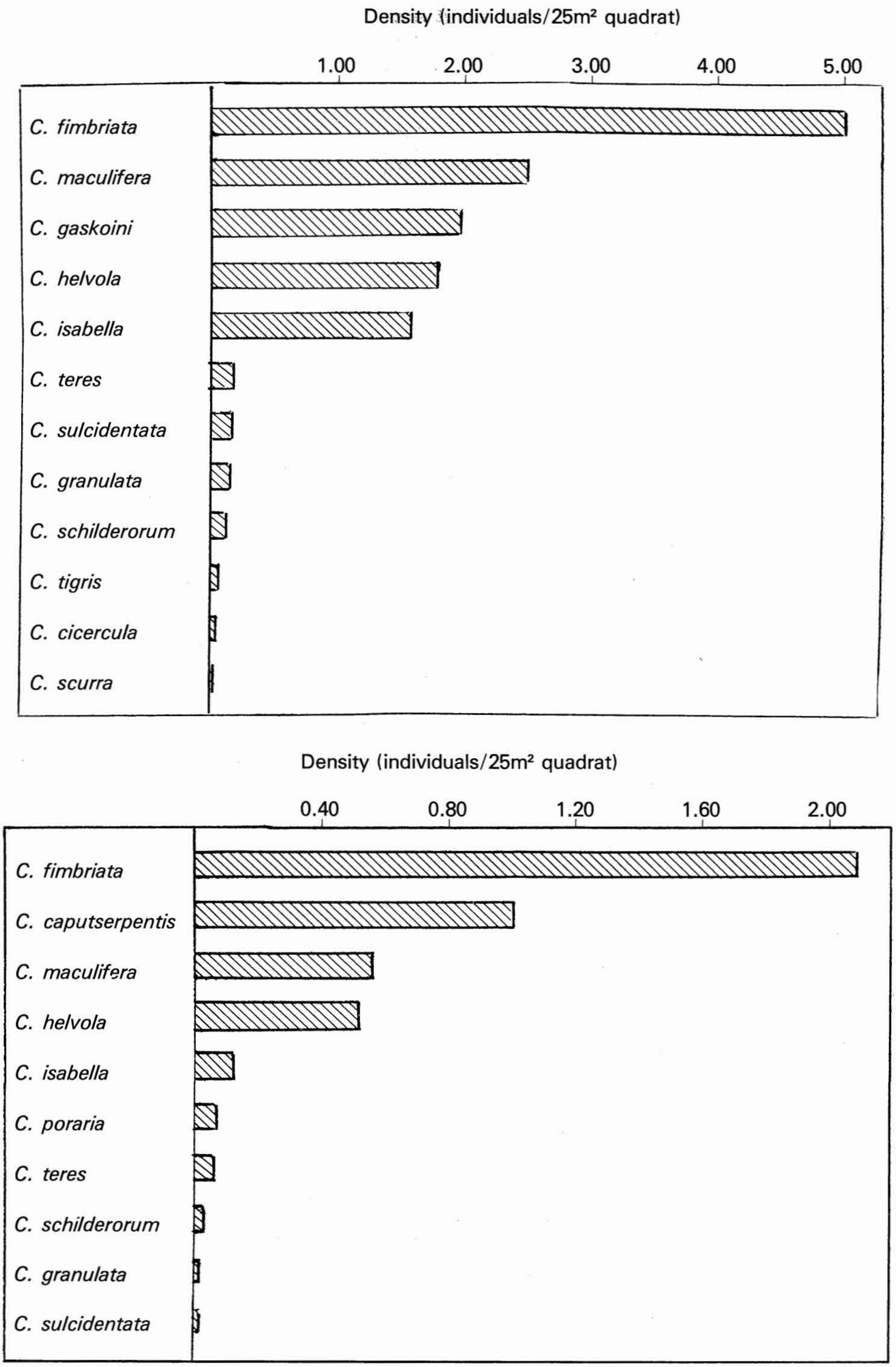


FIGURE 2. Density of *Cypraea*. *A*, at reef face study site ($n = 1841$ animals in 136 quadrats); *B*, at reef top study site ($n = 710$ animals in 157 quadrats).

TABLE 2

OCCURRENCE OF COWRIES BY SPECIES ON EACH SUBSTRATE TYPE COMPARED TO SUBSTRATE DISTRIBUTION*

	RELATIVE OCCURRENCE				
SPECIES	ALGAE	CORALLINE ALGAE	SPONGE	MISCELLANEOUS	G-TEST†
Reef face					
Cypraea helvola	.1957	.4681	.0511	.2851	97.718
C. maculifera	.0272	.5468	.0362	.3897	362.239
C. isabella	.0096	.4067	.3828	.2010	473.650
C. gaskoini	.0189	.3295	.4773	.1742	738.283
C. fimbriata	.1195	.7312	.0266	.1238	191.761
Substrate	.3476	.5491	.0209	.0842	
Reef top					
C. helvola	.6707	.2439	.0122	.0732	24.784
C. maculifera	.1573	.6742	0	.1685	188.537
C. fimbriata	.6489	.2571	0	.0940	78.614
C. caputserpentis	.3185	.6242	0	.0573	264.355
Substrate	.7201	.0962	.0005	.1850	

* Each species distribution is significantly different from substrate distribution ($X^2_{[.005]} = 12.838$; $df = 3$).
† Values for the G-test for goodness-of-fit.

purpurea. Total cover of all sponges in the study site was only 2.1 percent. Individuals of *C. maculifera* were usually found in areas of predominantly coralline algae, or else in very deep cracks and crevices in the reef face where precise identification of the substrate was difficult. These crevices supported colonies of hydroids and bryozoans and were often covered by a film of silt. No clear pattern of substrate association was evident for either *C. helvola* or *C. fimbriata*.

In the reef top study site all species were observed on coralline algae or filamentous algae most of the time. With the exception of *C. fimbriata*, individuals were usually found in crevices or in dead colonies of *Pocillopora meandrina*. Only individuals of *C. fimbriata* were found in the flat featureless areas of the reef top. In contrast, in the reef face study site individuals of all species of cowrie could be found in the open.

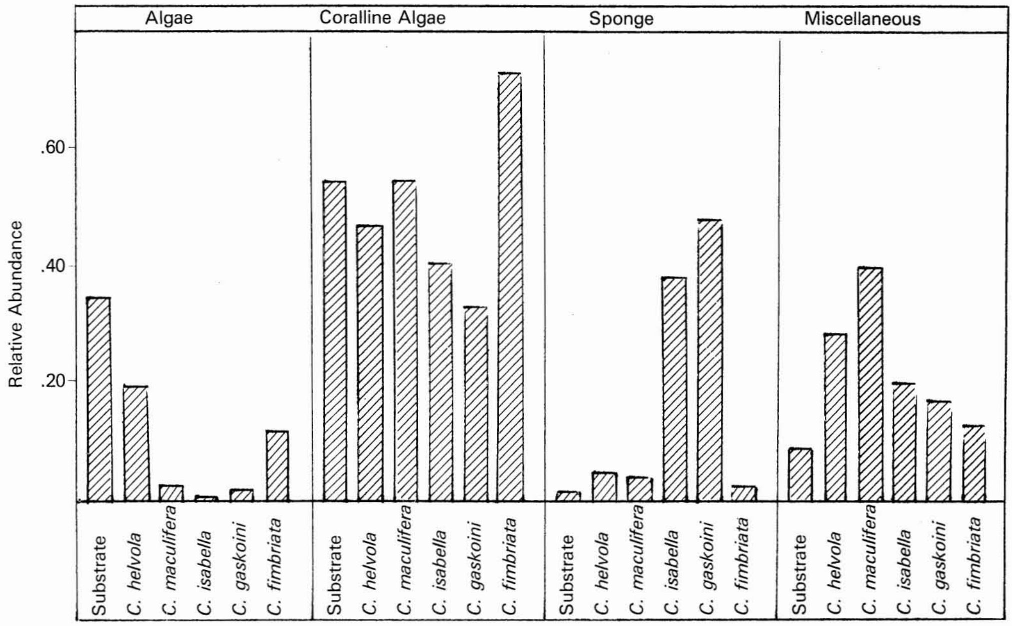
Stomach Contents

The diets of each of four selected species of *Cypraea* are summarized in Table 3. For each species the distribution of dietary items is significantly different from the expectation generated by the proportion of substrata ($p < .005$) in the habitat zone from which the specimen was taken.

The diet of *C. gaskoini* is composed almost entirely of red sponge, *Prianos* sp. No other cowrie showed this degree of specialization. For *C. helvola*, *C. isabella*, and *C. maculifera*, sponge species could not be identified with confidence from the gut contents alone. The diet of *C. isabella* is about equally split between filamentous algae and sponge. Based on field observation the sponge was identified as *Psammaplysilla purpurea*. *C. maculifera* was found to eat a variety of items; approximately 68.6 percent of its diet consisted of sponge and much of the remainder consisted of hydroids, algae, and bryozoans. *C. helvola* also feeds mainly on sponge (57.2 percent), much of which may be the same species as one found in the stomach of individuals of *C. maculifera*, based on spicule types. Almost 25 percent of the diet of *C. helvola* consisted of filamentous algae.

DISCUSSION

If diet influences the local distribution of *Cypraea*, individuals must exhibit some degree of dietary specialization. Results of this study



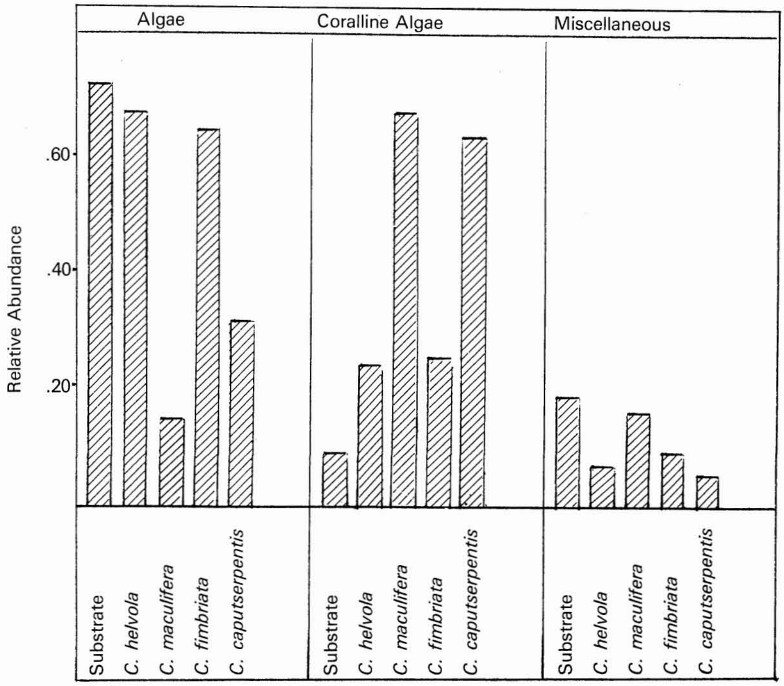


FIGURE 3. Abundance of *Cypraea* relative to substrate type at reef study sites. Each species distribution is significantly different from substrate distribution ($X^2_{[.005]} = 12.838$; $df = 3$): *A* (top), at reef face study site: *Cypraea helvola*, 97.718; *C. maculifera*, 362.239; *C. isabella*, 473,650; *C. gaskoini*, 738,283. *C. fimbriata*, 191.761. *B* (bottom), at reef top study site: *Cypraea helvola*, 24.784; *C. maculifera*, 188.537; *C. fimbriata*, 78.614; *C. caputserpentis*, 264.355.

TABLE 3

ABUNDANCE OF DIETARY ITEMS IN GUTS OF EACH SPECIES OF *Cypraea**

	DIETARY COMPONENTS								
SPECIES	ALGAE	CORALLINE ALGAE	SPONGE	DIATOMS	FORAMS	BRYOZOANS	HYDROIDS	OTHER	G-TEST†
C. gaskoini	.0162	.0288	.9473	0	0	0	0	0	149,060.58
C. isabella	.3694	.0965	.4562	.0081	.0028	0	0	.0665	13,070.62
C. helvola	.2403	.0025	.5723	.0626	.0021	0	0	.0572	143,850.30
C. maculifera	.0682	.0211	.6862	.0067	.0042	.0280	.0512	0	86,693.30

*The distribution of food items eaten by each species is significantly different from substrate distribution ($X^2_{[.005]} = 12.838$; $df = 3$).
† For the G-test, diatoms, forams, bryozoans, hydroids, and miscellaneous were combined.

show that at least 50 percent of the diets of the four species examined were composed of sponge. Only *C. gaskoini* seems restricted to sponge of one species, although *C. isabella* may also have a highly specialized diet. The prey sponge of *C. isabella* is heavily encrusted with coralline and filamentous algae, and the algae found in the stomach of the specimens examined may have been ingested in conjunction with the sponge in some instances. The relative ability of the cowries to digest plant or animal material has yet to be studied in detail.

Since most of the diet of all species examined was sponge, the factors that determine the distribution of sponge may be important in the lives of cowries by secondarily influencing their distribution. The occurrence of most species of sponge is governed by physical factors such as light intensity and surge (Johnson 1980). Levels of ultraviolet light encountered on the reef platform have been found to be detrimental to the growth of some sponges, as well as to bryozoans and tunicates, and ultraviolet light penetrates shallow water almost as well as does visible light (Jokiel 1980). Though measurements were not made, light intensity in the reef face study site was noticeably lower than on the reef top because of the greater depth and shading by the cliff face and overhangs.

Though moderate surge may bring food to the sponge and prevent siltation, too much surge may cause scouring by sand and stones and be detrimental to sponge growth (Johnson 1980). As can be seen in Table 4, surge is greater on the reef platform than in the reef face study site as measured by the plaster-of-paris blocks ($p < .05$). The stronger surge combined with the higher light intensity therefore may inhibit the growth of most species of sponge on the reef top. Neither the prey sponge of *C. gaskoini* nor that of *C. isabella* was ever observed on the reef top.

TABLE 4

SURGE IN REEF FACE AND REEF TOP HABITATS BY ONE-WAY MODEL I*

	SS	df	MS	F_S
Between habitats	219.506	1	219.506	6.401†
Within habitats	445.506	13	34.295	
Total	665.338	14		

*A comparison of surge data shows that there is a significant difference between the habitats in the amount of surge as measured by erosion of plaster-of-paris surge blocks ($n = 8$ for reef top; $n = 7$ for reef face). $F_{.05(1,13)} = 4.67$.
† Significant at $p = .05$.

As Table 2 shows, the cowries were nonrandomly distributed with respect to substrate type. Because all observations were made during the animals' active period, the substrates occupied were assumed to correspond to their diets. The occurrence of 47.7 percent of the individuals of *C. gaskoini* and 38.3 percent of the individuals of *C. isabella* on a substratum that comprised only 2.1 percent of the total of all substrate types suggests a strong substrate specialization. The dominance of sponge spicules in the stomachs of all species examined indicates that this substrate specialization is related to diet.

The absence of *C. gaskoini* and its prey sponge from the reef top suggests that food availability affects the distribution of *C.*

gaskoini, the most specialized in dietary requirements of the species studied. Such prey-dependent distribution has been observed in dorid nudibranchs, also sponge feeders (Johnson 1980).

The relationship between coralline algae and cowrie distribution on the reef top may not be related to diet. Coralline algae were often found in dead colonies of *Pocillopora meandrina* and in crevices on the reef top, all of which provide shelter on the otherwise featureless reef platform. Alternatively, dead coral and crevices may allow the growth of some sponges not easily visible to a diver.

Factors other than prey distribution may also influence cowrie distribution. Menge and Sutherland (1976) showed that on the New England intertidal shore, as one moves from areas of more to less stress, the community becomes dominated by predators. Distribution of prey species may be influenced by shelter space or by predator distribution. In the laboratory *Conus pennaceus* will feed on *Cypraea maculifera*, and *Conus textile* will feed on *Cypraea caputserpentis* and *Cypraea moneta* (Kohn 1959). Other cowries on which *Conus pennaceus* will feed in the laboratory include: *Cypraea cicercula*, *C. gaskoini*, *C. granulata*, *C. helvola*, *C. sulcidentata*, and *C. teres* (Jazwinski 1979). Though no individuals of *Conus textile* were found in either study site, shell fragments from individuals of *Conus pennaceus* were found on the reef top. Some fish also feed on *Cypraea*. During the study a *Diodon hystrix* was observed feeding on an individual of *Cypraea maculifera* (S. Jazwinski, personal communication). *Diodon holocanthus* and *Monotaxis grandoculis* are also nocturnal predators on prosobranch gastropods (Hobson 1974). Brachyuran crabs, both xanthid and portunid, are common at Puako, and some species are likely predators on *Cypraea*. In the reef face study site an individual of *Carpilius convexus* was observed carrying away individuals of both *C. isabella* and *C. maculifera*. An individual of *Portunus pubescens* was also observed carrying away a juvenile of *C. maculifera* from the reef face study site (S. Johnson, personal communication). Octopuses are also predators on *Cypraea*. An individual of *Octopus cyanea* was observed carrying away an individual of *Cypraea isabella* off Oahu (S. Jazwinski, personal communication).

Competition, a factor not included in this study, may also affect cowrie distribution. Herbivorous gastropods and sea urchins are common at Puako, especially in the reef top study site. Vertebrate sponge predators, such as *Zanclus cornutus*, *Centropyge potteri*, and *Ostracion meleagris*, are frequent (Hobson 1974). Some species of nudibranch also feed on sponge (Johnson 1980). Though few were observed on the reef top, nudibranchs are common in the reef face.

CONCLUSION

Though many species of *Cypraea* occur in both habitat zones studied at Puako, at least some species appear to be restricted to only one. *Cypraea poraria* and *C. caputserpentis* were never observed in the reef face study site, and *C. gaskoini*, *C. cicercula*, and *C. scurra* were never observed on the reef top. Within each study site cowries were distributed non-randomly with respect to substrate. This distribution may be mainly a function of diet, although other factors such as shelter also appear to be important, especially on the reef top. The diet of each of the four species examined consisted mainly of sponge. At least two species, *C. gaskoini* and *C. isabella*, appear to feed on a specific sponge. The absence of *C. gaskoini* and its prey sponge from the reef top indicates that the cowrie's distribution is influenced by the distribution of its prey sponge.

Information on the diet of the reef-top individuals, as well as that of *C. fimbriata*, is needed to further elucidate answers to the questions asked in this study. Data on inducers to larval settlement are also necessary before an answer is clear. Finally, information on rates of predation and utilization of shelter space is needed for a fuller understanding of the factors that influence the local distributions of *Cypraea*.

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