

Diet of *Cypraea caputdraconis* (Mollusca: Gastropoda) As It Relates to Food Availability in Easter Island¹

C. OSORIO,² F. JARA,³ AND M. E. RAMIREZ⁴

ABSTRACT: Diet and food preferences of Easter Island's endemic cowrie, *Cypraea caputdraconis* (Melvill), are reported. Gut content analyses of specimens from different rocky intertidal localities around the island revealed that *C. caputdraconis* is primarily an herbivore. Algae composed >90% of the cowrie's diet in all cases. Five algal genera, *Cladophora*, *Sphacelaria*, *Ceramium*, *Galaxaura*, and *Pterocladia*, were the most frequent and abundant items in the diet of *C. caputdraconis*. The feeding habits of *C. caputdraconis* are most similar to those of *C. caputserpentis* L. from Hawaii in that both have clearly herbivorous diets. Both species share the R-1 type of taenioglossan radula, which also supports their close phylogenetic relationship. Indo-West Pacific populations of *C. caputserpentis* have been suggested as ancestral to *C. caputdraconis* from Easter Island.

PREVIOUS OBSERVATIONS on trophic relationships of intertidal and shallow subtidal communities at Easter Island have centered primarily on carnivorous invertebrates such as gastropod mollusks and starfish (Kohn 1978*a,b*). Knowledge of herbivore-plant interactions for the benthic fauna of Easter Island is scant, however. The endemic cowrie *Cypraea caputdraconis* (Melvill) (locally known as *pure*) inhabits rocky intertidal habitats around the island (Osorio and Cantuarias 1989). Their shells are widely exploited for making ornaments by local craftsmen, and the cowrie constitutes a valuable economic resource for the islanders.

Information about the feeding habits of cowries is available for some *Cypraea* spp. from the North Pacific (Kay 1960*b*, Renaud 1976, Morris et al. 1980, Hayes 1983). These reports show that cowries, as a group, are

capable of feeding on a wide spectrum of resources. Thus, the group includes herbivores, carnivores, and scavengers (Renaud 1976, Hayes 1983). However, different species achieve some degree of specialization on particular foods. One factor that may influence the local distribution of cowries is food availability (Hayes 1983). Because intertidal gastropods may strongly determine the structure and organization of littoral communities (Lubchenco 1978, Underwood 1980, Jara and Moreno 1984), knowledge of their diet can greatly contribute to understanding their ecological role.

In this study we documented the diet of *C. caputdraconis* based on gut content analyses of cowries from different rocky intertidal localities around Easter Island and assessed its food preferences with respect to food availability in the field.

¹Funds for this work were provided by the Departamento Técnico de Investigación, Universidad de Chile. Proyecto No. 3046-9012. Manuscript accepted 15 March 1992.

²Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile.

³Facultad de Pesquerías y Oceanografía, Universidad Austral de Chile, Casilla 1327, Puerto Montt, Chile.

⁴Laboratorio de Botánica, Museo Nacional de Historia Natural, Casilla 787, Santiago, Chile.

MATERIALS AND METHODS

Observations were carried out at various rocky intertidal localities around Easter Island (27° 07' S, 109° 22' W) in two consecutive summer field seasons (January 1989 and January 1990). We also analyzed a sample obtained from one locality in the fall (May 1989).

Cowries were collected manually during low tides from the intertidal in the manner described by Osorio and Cantuarias (1989).

A total of 123 adult *C. caputdraconis* were used for gut content analyses. Upon collection in the field, cowries were immediately preserved in 7% formaldehyde. The specimens were later dissected in the laboratory to obtain the guts and their contents. Except for the degree of digestion, we found no differences between the contents of the anterior, middle, and posterior gut; therefore, we examined only the stomach contents using a stereomicroscope. Algae were determined to the generic or lowest possible taxonomic level.

To obtain an initial identification of the components, we first examined qualitatively the contents of samples from Mauku Roa and Hanga Nui in 1989. For the remaining samples, we utilized both occurrence and numerical methods (Windell 1971). Given the small gastric volume, all pieces and structures found were identified and counted. Initially, the abundance of blue-green algae and diatoms was estimated qualitatively as rare, common, and abundant. Later, counts of the number of fragments were also made for these two groups in the manner described above.

To obtain a measure of food preferences, we gathered data on food availability in areas associated with cowries collected at two sites in January 1990. Two specimens from Anakena and three specimens from Hanga

Vare Vare were examined. Using a metallic frame (5 by 5 cm), we collected all the material scraped from the substratum with a sharp knife at distances 0, 10, and 25 cm from each of the snails. The 5-cm² samples of scrapings were preserved in 7% formaldehyde and later examined in the laboratory in a manner similar to that used in analyzing the stomach contents. The results from the different quadrats around each snail were later pooled to obtain the total abundance of each item. The percentage relative abundance of items available from the substrate was calculated from the totals obtained from all the quadrats sampled. The percentage relative abundance of items in the diet was calculated from the totals obtained from all five snails examined.

To determine food preferences, the relative abundances of items in the field and in the diet were used to calculate Ivlev's (1961) electivity index. This index ranges from -1 to $+1$; zero indicates no preference. Because the confidence limits for this index are unknown, we arbitrarily assigned electivity values to three categories: Neg., Pos., and None. Values ranging between ± 0.35 were assigned to the None selectivity category. Electivity values greater than $+0.35$ (Pos.) were interpreted as positive selection (e.g., item was taken in a proportion much greater than its abundance in the environment). Conversely, electivity values lower than -0.35 (Neg.) were interpreted as negative selection.

TABLE 1

Cypraea caputdraconis FROM EASTER ISLAND: LOCALITIES, DATES, AND TIMES OF COLLECTION, AND NUMBER OF SPECIMENS EXAMINED IN THIS STUDY

LOCALITY	DATE COLLECTED	TIME OF DAY	TOTAL EXAMINED	EMPTY (n)	HIDIG (n)	TYPE OF ANALYSIS
Mauku Roa	17 Jan. 1989	0900–1100	55	10	16	Qualitative
Hanga Nui	19 Jan. 1989	1000–1200	4	0	1	Qualitative
La Perouse	17 Jan. 1989	0900–1100	15	2	5	Quantitative
Motu Kainga Rere	27 Jan. 1989	1300–1400	15	0	5	Quantitative
Anakena	10 May 1989	1200–1300	17	1	6	Quantitative
Tepito Te Cura	09 Jan. 1990	1400–1600	12	0	2	Quantitative
Anakena	10 Jan. 1990	1200–1300	1	0	0	Quantitative
Hanga Vare Vare	26 Jan. 1990	0900–1100	4	0	0	Quantitative
Total			123	13	35	
%				10.6	28.5	

NOTE: EMPTY, the number of stomachs without content; HIDIG, the number of stomachs with contents highly digested.

RESULTS

Feeding

Of the 123 *C. caputdraconis* examined, 10.6% had empty stomachs and 28.5% had highly digested contents that we were unable to identify with certainty (Table 1). Qualitative analysis of two samples (Mauku Roa and Hanga Nui) indicated that 36 different items were present in the stomach contents of this cowrie (Table 2).

Quantitatively, algae were the most abundant and the most frequent components of the diet of *C. caputdraconis*, composing over 93% of the contents (Table 3). Blue-green algae, although not counted in this analysis, were neither abundant nor frequent. Diatoms, on the other hand, were both abundant (qualitatively) and frequently found (Table 3).

Cladophora sp. was the most abundant of the five taxa of Chlorophyta, *Sphacelaria* sp. the most abundant of the four taxa of Phaeophyta, and Rhodophyta were found in all gut contents examined (Table 3). The Rhodophyta were the most diversified group, represented in the contents by at least 10 taxa (Table 2). The abundance of the different taxa varied from place to place, however. Thus, *Pterocladia capillaceae* (Gmel.) Born. & Thur., followed by *Hypnea* sp., were the most abundant taxa at La Perouse; *Ceramium skottsbergii* Peters, followed by *P. capillaceae*, were the most abundant taxa at Motu Kainga Rere; at Anakena *C. skottsbergii*, followed by *Hypnea* sp., were most abundant; and at Tepito Te Cura *P. capillaceae*, followed by *Herposiphonia* sp., were most abundant (Table 3). The relative abundance of the three main groups of algae also varied from sample to sample. Thus, Rhodophyta were least abundant at both La Perouse and Motu Kainga Rere, while Chlorophyta were least abundant at both Anakena and Tepito Te Cura (Figure 1). The most discordant of the samples was that from Anakena collected in the fall (May); all other collections were made in summer (January). The discordance was significant (Kendall's coefficient of concordance; $W = 0.0625$) (Gibbons 1985).

At most, invertebrates accounted for < 8% of the contents (Tepito Te Cura); but some,

TABLE 2

Cypraea caputdraconis FROM EASTER ISLAND:
IDENTIFICATION OF THE ITEMS FOUND BY QUALITATIVE
ANALYSIS OF STOMACHS OF SPECIMENS FROM TWO SAMPLES

Cyanophyta
Undetermined blue-green algae
Chrysophyta
Undetermined diatoms
Chlorophyta
<i>Caulerpa webbiana</i> Mont.
<i>Cladophora</i> sp.
<i>Enteromorpha</i> sp.
<i>Ulva</i> sp.
<i>Ventricaria ventricosa</i> (J.Ag.) Olsen & West
Phaeophyta
<i>Ectocarpus</i> sp.
<i>Lobophora variegata</i> (Lamour) Wom.
<i>Sphacelaria</i> sp.
<i>Zonaria</i> sp.
Rhodophyta
Calcareous (coralline)
<i>Ceramium skottsbergii</i> Peters
<i>Falkenbergia rufolanosa</i> (Harv.) Schmitz
<i>Galaxaura</i> sp.
<i>Gelidiopsis</i> sp.
<i>Herposiphonia</i> sp.
<i>Hypnea</i> sp.
<i>Laurencia claviformis</i> Børg.
<i>Lophosiphonia cristata</i> Falk.
<i>Pterocladia capillaceae</i> (Gmel.) Born. & Thur.
Mollusca
Bivalvia (larvae)
Gastropoda (larvae)
Arthropoda
Amphipods
Copepoda
Unidentified crustaceans
Isopoda
Ostracoda
Diptera (larvae)
Other Invertebrates
Foraminifera
Bryozoa
Porifera (spicules)
Nematoda
Coelenterata (Hydroida)
Polychaeta
Ascidiacea
Remains
Sand grains
Shell fragments
Coral fragments
Sea urchin spines

such as Foraminifera, occurred in as many as 90% of the stomachs (Table 3, Anakena). Sponges, represented in the contents by their spicules, were neither frequent nor abundant.

TABLE 3

Cypraea caputdraconis FROM EASTER ISLAND: NUMBER OF FRAGMENTS,^a AND ABSOLUTE (*n*) AND RELATIVE (%) FREQUENCY OF OCCURRENCE OF ITEMS FOUND IN STOMACH CONTENTS OF SPECIMENS FROM FOUR SAMPLES

STOMACH CONTENTS	LOCALITIES											
	LA PEROUSE (<i>n</i> = 8)			MOTU KAINGA RERE (<i>n</i> = 10)			ANAKENA (<i>n</i> = 10)			TEPITO TE CURA (<i>n</i> = 10)		
	Frag.	<i>n</i>	%	Frag.	<i>n</i>	%	Frag.	<i>n</i>	%	Frag.	<i>n</i>	%
Cyanophyta												
Blue-green algae (undetermined)				+	1	10	++	2	20	+	1	10
Chrysophyta												
Diatoms (undetermined)	+++	8	100	+++	9	90	+++	9	90	++	7	70
Chlorophyta												
<i>Cladophora</i> sp.	1,096	8	100	322	10	100	243	8	80	167	3	30
Phaeophyta												
<i>Sphacelaria</i> sp.	959	8	100	291	6	60	579	8	80	231	4	40
<i>Zonaria</i> sp.				48	5	50	51	3	30			
Rhodophyta												
Calcareous (coralline)	10	2	25	5	2	20	26	2	20	2	1	10
<i>Ceramium skottsbergii</i>	68	4	50	150	1	10	591	6	60			
<i>Galaxaura</i> sp.				1	1	10	10	1	10			
<i>Herposiphonia</i> sp.							267	2	20	60	2	20
<i>Hypnea</i> sp.	117	3	38				347	6	60			
<i>Pterocladia capillaceae</i>	169	6	75	62	2	20	10	3	30	188	5	50
Mollusca												
Bivalvia (larvae)												
Gastropoda (larvae)	5	2	25	5	4	40	5	2	20	45	3	30
Arthropoda												
Ostracoda	28	3	38	6	4	40	9	4	40	2	1	10
Other Invertebrates												
Foraminifera	1	1	12	23	8	80	55	9	90	8	1	10
Bryozoa										1	1	10
Porifera (spicules)				+	4	40	+	3	30	+	2	20
Coelenterata (Hydroida)	24	1	12	11	1	10						
Nematoda				3	2	20				2	1	10
Grand Total	2,476			927			2,193			706		

^a +, rare; ++, common; +++, abundant.

Food Preferences

Five algal genera, *Cladophora*, *Sphacelaria*, *Ceramium*, *Galaxaura*, and *Pterocladia* were most preferred by the cowries (Table 4, column Pos., range 91–99%). These algae, with the exception of *Galaxaura* sp., were the most frequent and abundant items found in the contents (Table 3).

Of the other 33 items available, 10 were taken more or less according to their abundance in the environment and showed no particular preference (Table 4, column None). In general, these items were those that could

be incidentally rasped along with the preferred algae. This seemed particularly true for diatoms, which were frequent and abundant in both the stomach contents and in the field, but were not selected for or against. Most of the diatoms were either epilithic or epiphytic and thus were rasped from the substratum or ingested along with other food items. The Foraminifera can be similarly explained; they were frequent but not abundant in the stomach contents and were ingested in about the same proportion as they were available (Table 4).

The remaining 23 items (Table 4, column

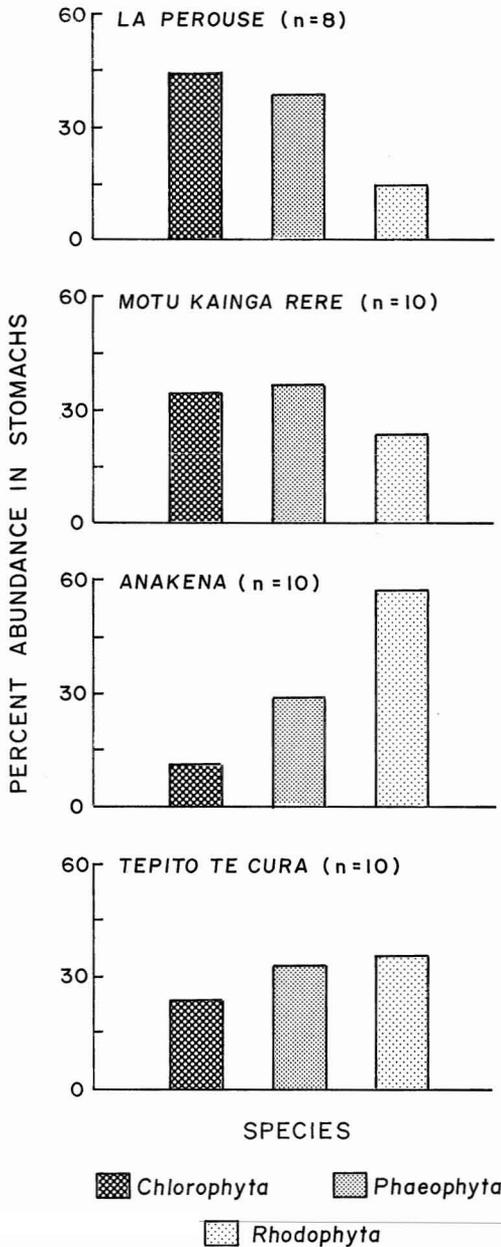


FIGURE 1. *Cypraea caputdraconis* from Easter Island: relative abundance of the major groups of algae found in samples of stomach contents of specimens from four rocky intertidal localities.

Neg.) were either consumed in much lower proportions than available or not taken at all (12 items). Some items were clearly selected against. Among the algae were *Caulerpa webbiana* Mont., *Ventricaria ventricosa* (J. Ag.) Olsen & West, *Ectocarpus* sp., *Falkenbergia rufolanosa* (Harv.) Schmitz, and *Lophosiphonia cristata* Falk. Eggs of *C. caputdraconis* were not ingested. Other items such as Amphipoda, Isopoda, Diptera (larvae), Polychaeta, and Ascidiacea were also clearly selected against. In general, mollusks, arthropods, and other invertebrates, which were neither frequent nor abundant in the stomach contents (Table 3), were consumed in much lower proportion than their availability (Table 4) and may have been ingested incidentally or rasped from the substratum when feeding on other items.

DISCUSSION

The data presented here establish the strictly herbivorous trophic status of *C. caputdraconis* at Easter Island. Qualitative and quantitative analyses clearly demonstrate that algae compose >90% of the cowrie's food. This is the first herbivorous invertebrate from Easter Island for which a detailed knowledge of its diet is known. Previous observations on the trophodynamics of marine benthic communities at Easter Island have reported exclusively on carnivorous invertebrates such as mollusks (*Mitra flavocingulata* Lamy, *Neothais nesiotis* Dall, *Pisania decapitata* engleri [Hertlein], and *Conus miliaris* Hwass) (Kohn 1978a,b), starfish (*Leiaster leachii* [Gray], *Astrostele paschae* [Clark]) (Garth 1973, Kohn 1978a), and ophiuroids (*Ophiocoma dentata* Muller and Troschel) (Osorio and Cantuarias 1989).

Available information on the feeding habits of cowries indicates that most species exhibit a proteinaceous diet (Hayes 1983). Along the California coast, *Cypraea spadicea* Swainson is a carnivore and a carnivorous scavenger (Morris et al. 1980; F. J., pers. obs.). At Puako reef, Hawaii, the distribution of at least four species of *Cypraea* seemed to be closely associated with the distribution of sponges, their

TABLE 4

FOOD PREFERENCES OF *Cypraea caputdraconis* BASED ON THE RELATIVE ABUNDANCE (%) OF FOOD ITEMS CONSUMED AND THOSE AVAILABLE IN THE ENVIRONMENT

ITEMS	IN DIET (%)	AVAILABLE (%)	ELECTIVITY ^a		
			POS.	NONE	NEG.
Algae (91–99%)					
Cyanophyta					
Blue-green algae (undetermined)	3.6	13.4			0.58
Chrysophyta					
Diatoms (undetermined)	37.0	30.6		+0.09	
Chlorophyta					
<i>Caulerpa webbiana</i> Mont.	0.0	0.1			1.00
<i>Cladophora</i> sp.	13.6	0.4	0.94		
<i>Enteromorpha</i> sp.	0.1	1.7			0.89
<i>Ulva</i> sp.	0.7	1.7			0.41
<i>Ventricaria ventricosa</i> (J.Ag.) O. & W.	0.0	0.8			1.00
Phaeophyta					
<i>Ectocarpus</i> sp.	0.0	1.1			1.00
<i>Lobophora variegata</i> (Lamour) Wom.	0.1	1.9			0.99
<i>Sphacelaria</i> sp.	5.8	2.0	0.49		
<i>Zonaria</i> sp.	0.1	0.9			0.98
Rhodophyta					
Calcareous (coralline)	2.4	13.1			0.69
<i>Ceramium skottsbergii</i>	3.5	0.1	0.97		
<i>Falkenbergia rufolanosa</i> (Harv.) Schmitz	0.0	0.2			1.00
<i>Galaxaura</i> sp.	2.1	0.1	0.97		
<i>Gelidiopsis</i> sp.	1.6	1.8		-0.06	
<i>Herposiphonia</i> sp.	1.7	2.0		-0.08	
<i>Hypnea</i> sp.	0.1	0.2			0.71
<i>Laurencia claviformis</i> Børg.	2.0	1.6		+0.11	
<i>Lophosiphonia cristata</i> Falk.	0.0	0.3			1.00
<i>Pterocladia capillaceae</i>	4.7	1.8	0.45		
Mollusca (0–2.0%)					
<i>Cypraea</i> (eggs)	0.0	0.4			1.00
Bivalvia (larvae)	0.1	0.2		-0.30	
Gastropoda (larvae)	0.2	0.4		-0.31	
Veliger larvae	0.0	0.1			1.00
Arthropoda (0–4.7%)					
Amphipoda	0.0	0.1			1.00
Copepoda	0.1	0.1		-0.05	
Crustacea (undetermined)	0.0	0.1			1.00
Isopoda	0.0	2.3			1.00
Ostracoda	0.4	4.0			0.78
Diptera (larvae)	0.1	1.3			0.97
Other Invertebrates (0–2.5%)					
Foraminifera	1.8	3.0		-0.25	
Bryozoa	0.6	1.2		-0.34	
Porifera (spicules)	0.2	0.1		+0.33	
Nematoda	0.1	3.8			0.94
Polychaeta	0.0	5.8			1.00
Echinoidea (spines)	0.1	0.2			0.90
Ascidiacea	0.0	0.1			1.00

^a Food selection (Ivlev 1961) indicated as follows: POS., positive selection, item consumed in greater proportion than its abundance in the environment; NEG., negative selection, item consumed in lower proportion than its availability in the environment. The relative abundance of the major groups in the diet of the specimens examined is indicated in parentheses. Items resulting in electivity values between ± 0.35 were arbitrarily assigned to the NONE preference category.

main dietary component (Hayes 1983). That sponges are also important prey items for cowries elsewhere was shown by Taylor (1975) for *C. teres* Gmelin in Australia. Herbivorous cowries are less commonly cited. A stenophagous diet was reported by Renaud (1976) for *C. moneta* L., which feeds mainly on two algal species at Enewetak. On the other hand, *C. caputserpentis* L. in Hawaii feeds on a broad variety of algae (Kay 1960b), similar to *C. caputdraconis* at Easter Island. Both species also share the R-1 type of taenioglossan radula (Kay 1960a, Osorio 1989), which supports the close phylogenetic relationship proposed by Rehder (1980).

Because cowries feed by scraping the substrate with their radulae, some of the items identified in their stomachs are probably ingested with the main food items. This argument was used to explain the presence of filamentous algae in the stomachs of the spongivorous specialist *C. isabella* L. and other cowries from Hawaii (Hayes 1983). The presence of most invertebrate items reported here from the stomachs of *C. caputdraconis* can be similarly explained. In general, the algae of Easter Island are short and turfy in appearance (Santelices and Abbott 1987), and the most important algae in the diet of *C. caputdraconis* share similar characteristics. Intertidal macroalgae provide habitats to a wealth of small invertebrates (e.g., copepods, amphipods, etc.) (Colman 1940, Hagerman 1966, Gunnill 1982a,b, 1983). The presence of invertebrates in the stomach of *C. caputdraconis* is thus explained and is corroborated by the lack of preference shown for those items (Table 4). Larval Diptera were available but were clearly rejected. Dipterans are common inhabitants of intertidal algae and are usually taken by herbivores in conjunction with plant material (Robles and Cubit 1981, Robles 1982), but that was not the case for *C. caputdraconis*. Although diatoms were ingested in much the same proportion as they are available, their relevance in the diet has yet to be ascertained although siliceous material is an important part of the cowrie shell.

The composition of the marine vegetation around Easter Island has been described as

monotonous with a high degree of similarity among sites (Santelices and Abbott 1987). Assuming that this is a generalized phenomenon, the relative abundance of the three major algal groups in the diet of *C. caputdraconis* from different localities might be expected to be similar also (Figure 1). In fact, results from two localities (La Perouse and Motu Kainga Rere) both show a lower abundance of Rhodophyta compared with the other two localities (Anakena and Tepito Te Cura) where Rhodophyta predominate (Figure 1). However, differences with respect to Tepito Te Cura, although not striking, suggest that algal composition among sites around the island might not be as homogeneous as previously thought. The major and significant (Kendall's $W = 0.0625$) disagreement with respect to the other sites was shown by the sample collected from Anakena in the fall (Figure 1). La Perouse and Anakena are close to each other and floristic affinities between these sites were found to be high during a summer survey (Santelices and Abbott 1987). Thus, this temporal difference in the diet of *C. caputdraconis* might well be a response to seasonal changes in the algal composition. Although seasonal changes in the feeding behavior of *C. caputdraconis* might also be a plausible explanation for the lack of concordance, we have no evidence to support such an alternative. Rather, populations of *C. caputdraconis* did not seem to migrate seasonally up and down the shore as our sampling was done, and local collectors work at much the same tidal levels throughout the year.

ACKNOWLEDGMENTS

We thank the shell collectors of the Pakarati family and also Felipe Teao and Hugo Atan from Easter Island, whose assistance and enthusiasm in the field made our work there most enjoyable. We are grateful to A. San Martin and E. Villouta for collecting the May 1989 sample for us. The assistance provided by M. Ríos and M. Bustos during the early part of this research is greatly appre-

ciated. We thank P. Morales for quantifying the abundance of items available. N. Bahamonde, C. Moreno, and V. Marín provided valuable advice, suggestions, and criticism, which improved an early version of the manuscript. The final paper benefitted greatly from the comments and editorial suggestions made by J. Stimson and two unknown reviewers. To all of them we remain most thankful.

LITERATURE CITED

- COLMAN, J. 1940. On the faunas inhabiting intertidal seaweeds. *J. Mar. Biol. Assoc. U.K.* 24: 129–183.
- GARTH, J. S. 1973. The brachyuran crabs of Easter Island. *Proc. Calif. Acad. Sci.* 39: 311–336.
- GIBBONS, J. D. 1985. Nonparametric statistical inference, 2d ed. Marcel Dekker, New York.
- GUNNILL, F. C. 1982a. Macroalgae as habitat patch islands for *Scutellidium lamellipes* (Copepoda: Harpacticoida) and *Amphithoe tea* (Amphipoda: Gammaridae). *Mar. Biol. (Berl.)* 69: 103–116.
- . 1982b. Effects of plant size and distribution on the numbers of invertebrate species and individuals inhabiting the brown alga *Pelvetia fastigiata*. *Mar. Biol. (Berl.)* 69: 263–280.
- . 1983. Seasonal variations in the invertebrate faunas of *Pelvetia fastigiata* (Fucaceae): Effects of plant size and distribution. *Mar. Biol.* 73: 115–130.
- HAGERMAN, L. 1966. The macro- and micro-fauna associated with *Fucus serratus* L., with some ecological remarks. *Ophelia* 3: 1–43.
- HAYES, T. 1983. The influence of diet on local distribution of *Cypraea*. *Pac. Sci.* 37(1): 27–36.
- IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven.
- JARA, F., and C. A. MORENO. 1984. Herbivory and structure in a midlittoral rocky community: A case in southern Chile. *Ecology* 65(1): 28–38.
- KAY, E. A. 1960a. Generic revision of the Cypraeidae. *Proc. Malacol. Soc. Lond.* 33: 278–287.
- . 1960b. The functional morphology of *Cypraea caputserpentis* L. and an interpretation of relationships among the Cypraeacea. *Int. Rev. Gesamten Hydrobiol.* 45(2): 175–196.
- KOHN, A. J. 1978a. Gastropods as predators and prey at Easter Island. *Pac. Sci.* 32(1): 35–37.
- . 1978b. Ecological shift and release in an isolated population: *Conus miliaris* at Easter Island. *Ecol. Monogr.* 48: 323–336.
- LUBCHENCO, J. 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. *Am. Nat.* 112: 23–39.
- MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.
- OSORIO, C. 1989. La radula de *Cypraea caputdraconis* Melvill, 1888 (Mollusca: Gastropoda). *Rev. Biol. Mar.* 24(2): 149–153.
- OSORIO, C., and V. CANTUARIAS. 1989. Vertical distribution of mollusks on the rocky intertidal of Easter Island. *Pac. Sci.* 43(4): 302–315.
- REHDER, H. 1980. The marine mollusks of Easter Island and Sala y Gomez. *Smithson. Contrib. Zool.* 289: 1–167.
- RENAUD, M. 1976. Observations on the behavior and shell types of *Cypraea moneta* (Mollusca: Gastropoda) at Enewetak, Marshall Islands. *Pac. Sci.* 30(2): 147–158.
- ROBLES, C. 1982. Disturbance and predation in an assemblage of herbivorous Diptera and algae on rocky shores. *Oecologia (Berl.)* 54: 23–31.
- ROBLES, C., and J. D. CUBIT. 1981. Influence of biotic factors in an upper intertidal community: Effects of grazing Diptera larvae on algae. *Ecology* 62: 1536–1547.
- SANTELICES, B., and I. A. ABBOTT. 1987. Geographic and marine isolation: An assessment of the marine algae of Easter Island. *Pac. Sci.* 41(1–4): 1–20.
- TAYLOR, J. D. 1975. The living cowries. Pages 7–49 in J. D. Taylor and J. G. Walls,

- eds. Cowries. T.F.H. Publications, Neptune, New Jersey.
- UNDERWOOD, A. J. 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. *Oecologia (Berl.)* 46:201-213.
- WINDELL, J. T. 1971. Food analysis and rate of digestion. Pages 215-226 in W. E. Ricker, ed. *Methods for assessment of fish production in fresh waters*. Int. Biol. Programme Handb. 3.