

Aspects of the Reproductive Activity of *Cypraea caputdraconis* from Easter Island (Mollusca: Gastropoda: Cypraeidae)¹

CECILIA OSORIO,² DONALD BROWN,³ LIGIA DONOSO,² AND HUGO ATAN²

ABSTRACT: *Cypraea caputdraconis* Melvill, 1888 (commonly known as *pure*), endemic to Easter Island, is an important mollusk in Easter Island handicrafts. Knowledge about its reproduction is necessary for sustainable management of this resource. Data presented here are from 14 monthly samples taken between 1989 and 1991. As in other species of the genus, *C. caputdraconis* populations sampled at Easter Island had a higher proportion of females (60.28%) than males. Females averaged slightly larger than males, but there was a large degree of size overlap between the sexes and lengths were not significantly different. Reproductive activity occurs year-round, as evidenced by the presence of all three gonadal stages at every sampling date, suggesting a reproductive cycle with continuous gametogenic activity, either lacking or with a very brief period of gonadal rest. Egg mass surveys indicate agreement between egg mass presence and gonadal maturity. Egg masses were recorded throughout the year. A decrease in the percentage of animals with egg capsules corresponded to a decrease in water temperature toward winter. Observations on behavioral sex expression in relation to brooding clearly point to the female as incubator, although in one instance a male was observed on the egg mass. The reproductive activity of the Easter Island *pure* may be tentatively characterized by a continuous reproductive cycle, with increased activity during spring and summer. We recommend closing this fishery during the period of peak reproductive activity to prevent overexploitation.

THE GENUS *Cypraea* Linnaeus, 1758, includes about 202 Recent species, mostly inhabiting tropical waters at less than 30 m depth (Kay 1985). Current knowledge of cypraeid reproduction includes information on sexual dimorphism (Griffiths 1961, Schilder and Schilder 1961), sex ratios (Schilder and Schilder 1961), anatomy of the reproductive system (Fretter 1946, Kay 1960*a,b*), characteristics of egg masses (Kay 1960*a*, Bandel 1973, Wilson 1985), nesting behavior (Kay 1960*a*), incubation times and developmental patterns (Ostergaard 1950, Kay 1960*a*,

Wilson 1985), and periods of reproductive activity for *C. caputserpentis* Linnaeus, 1758, from Hawai'i (Kay 1960*a*) and for *C. annulus* Linnaeus, 1758, from Japan (Katoh 1989).

Cypraea caputdraconis Melvill, 1888, from Easter Island (commonly known as *pure*) was recorded by Burgess (1985), who reported the shell length range and said that *C. caputdraconis* and *C. engleri* Summers & Burgess, 1965, have the most restricted range of any cowries. Lorenz and Hubert (1993) also reported shell length range. *Cypraea caputdraconis* has been studied with respect to its vertical distribution (Osorio and Cantuarias 1989), radular morphology (Osorio 1989), feeding (Osorio et al. 1993), and characteristics of its egg masses and larval stages (Osorio et al. 1992).

This study reports evidence of reproductive activity in *C. caputdraconis*, obtained by macro- and microscopic analysis of gonadal

¹This study was supported by Departamento de Investigación y Desarrollo de la Universidad de Chile. Manuscript accepted 1 May 1998.

²Departamento de Ciencias Ecológicas, Universidad de Chile, Casilla 653, Santiago, Chile.

³Facultad de Ciencias, Universidad de Valparaíso, Gran Bretaña 1111, Valparaíso, Chile.

stages and from egg mass frequencies. This preliminary knowledge of the reproductive cycle will aid in the establishment of management decisions for the protection of this species, an important resource for the artisans of Easter Island.

MATERIALS AND METHODS

Samples of *C. caputdraconis* were collected at random from the intertidal zone at Easter Island (25° 09' S, 109° 23' W) from 1989 to 1991 and fixed in 10% formalin-seawater. Sampling sites and dates, sample sizes, and the types of analyses are listed in Table 1.

For each specimen measured, maximum shell length was determined with calipers to the nearest 0.05 mm. Results were expressed as ranges and the arithmetic mean \pm SD for males and females separately. After dissec-

tion of the soft body from the shell, individuals were separated by sex according to presence or absence of a penis and also by gonad color (orange gonads in males, yellow gonads in females). The presence of a penis correlated with male gonad color in all cases.

The degree of gonadal development was evaluated microscopically on specimens representing various macroscopic gonadal stages selected from each monthly sample. Sections of gonad from 339 previously fixed individuals were dehydrated in ethanol, clarified in xylol, and embedded in paraffin. Sections 7 μ m thick were stained with hematoxylin and eosine, dehydrated, clarified, and mounted in Canada balsam, following a commonly used histological technique (Lopez et al. 1982). Histological preparations were examined with a microscope (Nikon Optiphot). Each individual was assigned to one of the following gonadal stages:

TABLE 1

SAMPLES OF *C. caputdraconis* ANALYZED, SITE, DATE, SAMPLE SIZE, AND TYPE OF ANALYSIS PERFORMED

SITE	DATE	SAMPLE SIZE	TYPE OF ANALYSIS		
			SHELL SIZE	EGG MASS COUNT	GONADS HISTOLOGY
Easter Island ^a	16 Jan. 1989	55	X		X
Karava Viviri	28 Feb. 1989	23	X		X
Anakena	May 1989	26	X		X
Ovahe	Sept. 1989	35	X		X
Tepito Tecura	9 Jan. 1990	12	X		X
Vaihu	30 Jan. 1991	161		X	
Hanga Nui	12 Mar. 1991	29	X		X
HN-V-PA ^b	12 Mar. 1991	17	X		
Prai Ahure	13 Mar. 1991	261		X	
Vaihu	25 May 1991	103		X	
Prai Ahure	13 June 1991	86		X	
Vaihu	15 June 1991	33	X		X
Prai Ahure	July 1991	78		X	
Prai Ahure	3 Aug. 1991	40	X		X
Prai Ahure	17 Sept. 1991	28	X	X	X
Prai Ahure	5 Oct. 1991	141		X	
Prai Ahure	10 Oct. 1991	31	X		X
Prai Ahure	14 Nov. 1991	147		X	
Prai Ahure	14 Nov. 1991	36	X		X
Total		1,342			

^a Several unspecified sites.

^b HN, Hanga Nui; V, Vinapu; PA, Prai Ahure.

STAGE 0 (UNDIFFERENTIATED STAGE). Specimens with terminal juvenile shell. Penis is absent and color of the gonad cannot be identified. Microscopically, the gonadal outline is difficult to locate and germinal cells are undifferentiated.

Females

STAGE F1 (STAGE OF INITIAL MATURITY). Gonad yellow, incipiently covering the visceral mass. Gonadal acini with active initial oogenesis. Germinal line represented mostly by small oogonia and initial previtellogenic oocytes bearing germinal vesicle.

STAGE F2 (STAGE OF PEAK MATURITY). Gonad yellow, completely covering the visceral mass. Gonadal acini with complete oogenesis. In the germinal line, vitellogenic oocytes predominantly free and very large (due to their high content of vitelline platelets), thus filling the acini. Acini rarely deviate from this condition.

STAGE F3 (STAGE OF REGRESSION OR POST-GAMETE RELEASE, WITH OCCASIONAL GONADAL RECOVERY). Gonad cream or brown, partially covering the visceral mass. Gonadal acini contracted, with few free, residual vitellogenic oocytes or containing oogonia and initial previtellogenic oocytes in their walls only, the last considered evidence of gamete release but in some cases followed by recovery of gametogenic activity.

Males

STAGE M1 (STAGE OF INITIAL MATURITY). Gonad orange, incipiently covering the visceral mass, or apparently absent. Acini with early germinal line, indicating the beginning of active spermatogenesis. Spermatogonia and spermatocytes predominate; early spermatids rare. Penis present.

STAGE M2 (STAGE OF PEAK MATURITY). Gonad orange, completely occupying the visceral end. Complete germinal line in gonadal acini. Elongate spermatids arranged in tiers predominating, filling the lumen of the acini.

STAGE M3 (STAGE OF REGRESSION OR MAXIMUM RELEASE). Gonad translucent, inconspicuous. Gonadal acini with large spaces, occupied by few residual spermatids of a prior release.

Egg Masses

Monthly egg mass counts were made in 1991 during low tides on the rocky intertidal at Prai Ahure and Vaihu. Randomly chosen individuals were briefly lifted off the rock to determine whether egg masses were present. In January 1990 and March 1991 egg masses and their incubator were collected from 9 and 11 nests, respectively. The egg masses were found in concave depressions called "marine pots." All capsules were counted. The intracapsular developmental stage was determined for all full capsules (Osorio et al. 1992).

RESULTS

Shell Size and Sex Frequencies

Data on shell sizes are presented in Figure 1. Juveniles ranged from 20.3 to 36.3 mm (average 27.9 ± 3.14), males from 21.6 to 37.7 mm (average 28.2 ± 2.6), and females from 19.8 to 40.1 mm (average 28.8 ± 2.6) long. Although juvenile shells (22 specimens, Table 2) may be as long as adult shells, they can be distinguished easily by the color of the shell and the absence or small size of the teeth surrounding the aperture. The sex ratio for all individuals identified to sex from

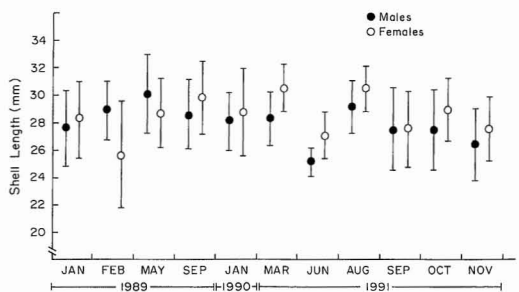


FIGURE 1. Shell size of *Cypraea caputdraconis* females and males (mean \pm SD) from 11 samples collected at Easter Island.

TABLE 2
SEX PROPORTION IN *C. caputdraconis* FOR SAMPLES COLLECTED BETWEEN 1989 AND 1991

SITE	DATE	NO. OF INDIVIDUALS ^a					% F
		TOTAL	F	(j)	M	(j)	
Easter Island ^b	16 Jan. 1989	55	27	1	27		50.9
Karava Viviri	28 Feb. 1989	23	12		11		52.2
Anakena	May. 1989	26	13		13		50.0
Ovahe	Sept. 1989	35	18		16	1	51.4
Tepito Tecura	9 Jan. 1990	12	9		3		75.0
Hanga Nui	12 Mar. 1991	29	14	1	14		51.7
HN-V-PA ^c	12 Mar. 1991	17	12	1	4		76.5
Vaihu	15 June 1991	33	21	7	3	2	84.8
Prai Ahure	3 Aug. 1991	40	20	1	19		52.5
Prai Ahure	17 Sept. 1991	28	12	6	10		64.3
Prai Ahure	10 Oct. 1991	31	13		18		41.9
Prai Ahure	14 Nov. 1991	36	24	2	10		72.2
Total		365	195	19	148	3	
Average							60.28

^a (j), juveniles; F, females; M, males.

^b Several sites.

^c HN, Hanga Nui; V, Vinapu; PA, Prai Ahure.

various sites between 1989 and 1991 was 1.14:1—60.28% were females, 39.72% males, and 6% juveniles (Table 2).

Gonadal Maturity

Table 3 lists the monthly distribution of *C. caputdraconis* males and females in the various stages of gonadal maturity (as defined in *Materials and Methods*).

Females in stage 1 were present at each sampling date, except for January 1989. However, males were only found during May and September 1989, in January 1990, and in March and June 1991. Exceptionally high frequencies of females were observed in March, June, August, and November of 1991.

Females in stage 2 were well represented in the 1989 samples, with high frequencies in January, May, and September. High frequencies of males were observed in January and September 1989 and March, August, and October of 1991. Females at peak maturity were conspicuously absent in 1991.

Females in stage 3 were also present during the entire sampling period, reaching

TABLE 3
MONTHLY DISTRIBUTION OF *C. caputdraconis*, WITH NUMBER OF MALES (M) AND FEMALES (F) AT THE VARIOUS STAGES OF GONADAL MATURITY

DATE	GONADAL STAGE							Total
	Stage 0	F1	M1	F2	M2	F3	M3	
Jan. 1989	1			11	26	20	5	63
Feb. 1989	2	1		1	1		2	7
May. 1989		2	3	7	8	4	2	26
Sept. 1989		5	1	7	20	2		35
Jan. 1990		3	2	4	1	2		12
Mar. 1991		12	4		10	2		28
June 1991	6	15	2		3	7		33
Aug. 1991	1	18		1	14	1	5	40
Sept. 1991	6	10			7	2	3	28
Oct. 1991		11			17	2	1	31
Nov. 1991		22		1	7	3	3	36
Total	16	99	12	32	114	45	21	339

NOTE: For a description of gonadal stages refer to *Materials and Methods*.

maximum values in January 1989. Although in 1991 there were fewer individuals at this stage of postgamete release (which may indicate recovery of gametogenic activity), it is

TABLE 4
 COUNTS OF *C. caputdraconis* EGG MASSES FROM EASTER ISLAND IN 1991

SITE	DATE	NO. OF INDIVIDUALS			
		TOTAL	WITHOUT EGGS	WITH EGGS	(%)
Vaihu	30 Jan.	161	141	20	12.4
Prai Ahure	13 Mar.	261	244	17	6.5
Vaihu	21 May.	103	95	8	7.8
Prai Ahure	13 June	86	81	5	5.8
Prai Ahure	July	78	77	1	1.3
Prai Ahure	17 Sept.	28	27	1	3.6
Prai Ahure	5 Oct.	141	125	16	11.3
Prai Ahure	14 Nov.	147	130	17	11.6
Total		1,005	920	85	
Average					7.54

noteworthy that the highest frequency of individuals in this stage occurred in June, August, and November. Because of the high incidence of males in stage 1, there were no males in stage 3 in samples from September 1989, January 1990, and March and June 1991.

Egg Masses

Results of egg mass surveys at the various intertidal sampling sites are presented in Table 4.

Figure 2 shows results from surveys in 1991, with average monthly sea-surface temperatures reported for 23 yr at Hanga Roa (Figure 2a). Egg masses were counted at various sites, and adult individuals associated with egg masses were found on all sampling dates. Between March and September, winter in the Southern Hemisphere, there was a decrease in sea-surface temperatures, along with a decrease in egg mass frequency (from 7.8% to 1.3%). In spring and summer, as temperatures rose, a greater frequency of individuals associated with egg masses was found (11.3–19.6%) (Figure 2b).

All 20 nests (9 collected in January 1990 and 11 in March 1991) and their egg masses were found in "marine pots," holes bored by the urchin *Echinometra insularis* (Rehder 1980, Osorio and Cantuarias 1989). A total

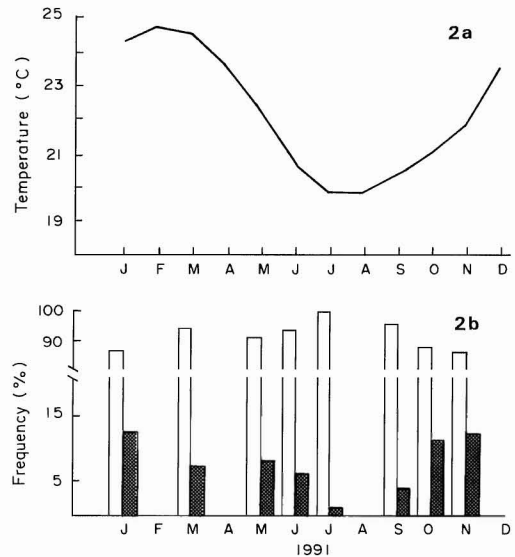


FIGURE 2. (a) Average monthly sea-surface temperature at Hanga Roa (1957–1978), recorded by the Chilean Navy. (b) Monthly egg mass surveys at Easter Island during 1991. White columns, without eggs; black columns, with eggs.

of 12 adults was found incubating in the first nine nests (Table 5); three of the males coexisted with females, but in all cases a female was covering the egg mass. The gonadal analysis of brooding adults revealed that, of nine females, two were in stage F1 (with active initial oogenesis), five were in stage F2

TABLE 5

NUMBER OF CAPSULES PER EGG MASSES (NEST) OF *C. caputdraconis* AT TEPITO TECURA, 9 JAN. 1990

NEST NO.	ADULT PRESENT		EGG CAPSULES ^a					OBSERVATIONS
	SHELL SIZE (mm)	SEX	STAGE 1	STAGE 2	STAGE 3	EMPTY	TOTAL	
1	24.0	F			45	48	93	Gonad in stage F3; larvae hatched upon fixation; algae
2	26.0	F			203		203	Gonad in stage F1; larvae hatched upon fixation; algae
3	28.0	F	260			43	303	Gonad in stage F2
4	30.9	F	55			27	82	Gonad in stage F2
	26.0	M						Gonad in stage M1
5	30.6	F	242	11		62	315	Gonad in stage F2
6	31.5	F	175			34	209	Gonad in stage F3
	26.9	M						Gonad in stage M2
7	27.2	F			192	46	238	Gonad in stage F1
8	24.9	F	178			50	228	Gonad in stage F2
	31.7	M						Gonad in stage M1
9	35.7	F		23	400		423	Gonad in stage F2
Total							2,094	
Average							233 capsules/nest	

^a Stage 1, with eggs at early cleavage; stage 2, with embryos at preveliger; stage 3, with veliger.

(peak maturity), and the two in stage F3 exhibited an early germinal line. Two males were in stage M1 and one in stage M2 (peak maturity, Table 5).

The number of capsules per nest ranged from 82 to 423, with an average of 232.6 ± 77.4 . On 9 January 1990 most of the nests contained capsules at an early developmental stage (white eggs in early cleavage) and empty capsules, the latter making up between 14.2 and 32.9% (average 44.3 ± 8.2) of the egg mass. Only four of the nests contained veliger larvae, at the final stage of intracapsular development (brown). The veligers were released from the capsules during fixation. There were no empty capsules in nest 9, containing preveliger and veliger larvae, nor in nest 2, which contained veliger larvae (Table 5).

In the March 1991 (Table 6) sample, the number of capsules per nest ranged from 112 to 320, with a average of 183 ± 61 . Again,

the females were usually covering the egg mass; an exception was nest 6, which was covered by a male. On this date, three nests were occupied by more than one individual: two in nest 6 (M-F), three in nest 7 (F-M-M), and four in nest 10 (F-F-F-M). However, there was no increase in number or diversity of capsular stages. Supernumerary individuals were usually found surrounding the cowry covering the egg mass. The female in nest 1 was apparently an advanced juvenile, as shown by the absence of teeth around the aperture, in spite of its considerable size (36.3 mm, Table 6). In this sample there was a predominance of nests (8 out of 11) with capsules containing eggs at the initial stages of cleavage. All nests contained empty capsules, composing from 9 to 63% of the egg mass. Only nest 3 exhibited two developmental stages in separate capsules: initial cleavage and veliger larvae. All capsules in nest 4 were empty.

TABLE 6
EGG MASSES (NESTS) OF *C. caputdraconis* SURVEYED IN MARCH 1991

SITE ^a	DATE	NEST NO.	ADULT		NO. OF CAPSULES ^b					OBSERVATIONS	
			SIZE (mm)	SEX	STAGE 1	STAGE 2	STAGE 3	EMPTY	TOTAL		
HR	4	11	30.5	F	41				71	112	
V	5	5	29.4	F	93				45	138	
V	5	6	28.5	M	233				68	301	
			28.7	F							
V	5	7	40.1	F				263	57	320	
			28.3	M							(*)
			32.5	M							(*)
HN	12	1	36.3	F	108				18	126	Late juvenile
HN	12	2	35.5	F	140				93	233	
HN	12	3	31.2	F	45			49	45	139	
HN	12	4	31.1	F					100%		
PA	13	8	28.3	F			123		18	141	
PA	13	9	39.1	F	132				13	145	
PA	13	10	31.2	F	125				50	175	
			29.4	F							(*)
			25.1	F							(*)
			21.8	M							(*)
Total										1,830	
Average ^c	183 ± 61 capsules/egg mass										

^a HN, Hanga Nui; HR, Hanga Roa; PA, Prai Ahure; V, Vaihu.

^b Stage 1, capsule at early cleavage; stage 2, capsule with preveliger larvae; stage 3, capsule with veliger larvae.

^c For 10 nests.

(*), surrounding individual covering egg mass.

DISCUSSION

Shell Size and Sex Frequencies

Sexual dimorphism is not pronounced among archaeogastropods. However, in mesogastropods with internal fertilization (e.g., the genus *Cypraea*), the male can be distinguished from the female by the penis, apparent behind the right tentacle (Webber 1977). Male/female differences in other characters (e.g., size, proportions, and morphology of the shell) have also been reported (Webber 1977). Evidence of sex-related differences in shell color has been reported for *C. gracilis* Gaskoin, 1848 (Griffiths 1961). In addition, females are usually more abundant and larger than males (Webber 1977).

Size distributions of cypraeid populations indicate that females tend to be larger than males. In *C. annulus* from Okinawa, Japan,

mean shell length is significantly greater in females than in males, with a large degree of size overlap between sexes (Katoh 1989). Other studies also indicate that in *C. annulus*, *C. moneta*, and *C. helvola* the females are slightly larger (Schilder and Schilder 1961). In our study the size distribution of *C. caputdraconis* samples from Easter Island indicates that females are slightly larger than males. Because of considerable size overlap, female and male sizes are not significantly different ($P = 0.09$). Juveniles were also found in a wide range of lengths (20.3–36.3 mm; average 27.9 ± 3.14), overlapping in size with the adult population, composed of individuals ranging from 21.0 to 40.1 mm in length (average 28.53 ± 2.6).

In a previous study (Riveros 1951) shell sizes for adults of *C. caputdraconis* (24–34 mm) were similar to those found in our study. Rehder (1980) reported an average

shell length of 28.9 mm (15.74–42.31 mm). Rehder also suggested that there may be a dwarf race in Hanga Nui, but in 29 individuals from there we found that the average length (29.15 ± 1.89 mm) and range of size were similar to other samples. Burgess (1985) and Lorenz and Hubert (1993) reported shell length range from 16 to 45 mm, so shells longer than the ones in our study have been reported. In our study maximum lengths suggest the beginning of a decline, possibly related to overexploitation of the species.

A slight dominance of females (55%) has been reported for *C. moneta* and *C. helvola* (Schilder and Schilder 1961). In 365 randomly chosen individuals of *C. caputdraconis* analyzed in our study, 60.28% were females, 39.72% males. The prevalence of females is significant ($P < 0.05$). However, it is important to note that these animals were obtained at various sites and dates.

Gonadal Maturity

The tropical cypraeids *C. caputserpentis* in Hawai'i (Kay 1960a,b) and *C. annulus* in Okinawa (Katoh 1989) are reproductively active year-round. Seven other cypraeid species from temperate Australian waters have short reproductive periods (Wilson 1985), and *C. errones* Linnaeus, 1758, from India has been found to have a long reproductive period, from September to March (Natarajan 1957). Our study of the reproductive cycle in *C. caputdraconis* by macroscopic and histological analysis of gonadal maturity reveals the occurrence of all three gonadal stages at each sampling date. Our observations showed that occurrence of gonadal stage 2 (peak maturity) exceeded 50% in January, May, and September 1989 and October 1991; that all three gonadal stages were usually present in the same month; and that animals that recently released gametes exhibited a new maturity wave in the germinal line, strongly suggesting a reproductive cycle with continuous gametogenic activity, either lacking or with a very brief period of gonadal rest.

Egg Masses

Results from egg mass counts are in agreement with observations of gonadal maturity and support the possibility that *C. caputdraconis* reproduces year-round, as is known in some other tropical species (Kay 1960a, Katoh 1989). However, *C. caputdraconis* differs in its increased reproductive activity during summer and the decrease in the proportion of animals associated with egg masses as sea-surface temperatures declined toward winter.

Our observations that (1) on all sampling dates there were individuals on egg masses, (2) embryos and larvae in various stages of intracapsular development coexist in the same egg mass, and (3) the majority of nests contain both capsules in early developmental stages and empty capsules further support our conclusion that *C. caputdraconis* seems to have a continuous reproductive cycle, with an increase in activity during spring and summer that coincides with a rise in sea-surface temperature.

Our observation that some nests were occupied by more than one female raises the possibility that these nests contain egg masses produced by different females, which could be explained as gregarious behavior around the brooding female in such a peculiar nest as a marine pot. Nest sharing with other females cannot, however, be disregarded. On the other hand, more than one male could copulate with a female, and in one nest two males were found next to a female.

Although the reproductive pattern may favor a stable level of abundance for the future, human intervention by local harvesters may already be causing a decline in adult sizes. A recommendation pertaining to the control and management of the fishery is thus necessary, with harvest quotas based on studies of population structure and prevention of harvesting during periods of reproduction peak. Overfishing this endemic species could have serious consequences because of its restricted range (endemic to Easter Island and Sala y Gomez) and the potential risk to the stability of the population of *C. caputdraconis*.

ACKNOWLEDGMENTS

We thank Professors S. Aviles and E. Lozada for their valuable comments on the manuscript. We also thank M. Bustos, V. Romero, and J. Mella for their technical collaboration and all the islanders who helped us during fieldwork on Easter Island. We acknowledge with thanks the review of this work and the recommendations made by Dr. F. Moretzsohn.

LITERATURE CITED

- BANDEL, K. 1973. Notes on *Cypraea cinerea* G. and *Cyphoma gibbosum* L. from the Caribbean Sea and description of their spawn. *Veliger* 15(4): 335–337.
- BURGESS, C. M. 1985. Cowries of the world. Gordon Verhoef, Seacomber Publication, Cape Town.
- FRETTER, V. 1946. The genital ducts of *Theodoxus lamellaria* and *Trivia* and a discussion on their evolution in the prosobranchs. *J. Mar. Biol. Assoc. U.K.* 26: 312–351.
- GRIFFITHS, R. J. 1961. Sexual dimorphism in Cypraeidae. *Proc. Malacol. Soc. Lond.* 34: 203–206.
- KATO, M. 1989. Life history of the golden ring cowry *Cypraea annulus* (Mollusca: Gastropoda) on Okinawa Island, Japan. *Mar. Biol.* 101: 227–233.
- KAY, E. A. 1960a. The functional morphology of *Cypraea caputserpentis* Linn. and an interpretation of the relationships among the Cypraeacea. *Int. Rev. Hydrobiol.* 45: 175–196.
- . 1960b. Generic revision of the Cypraeinae. *Proc. Malacol. Soc. Lond.* 33: 278–287.
- . 1985. About the cowries. Pages 4–14 in C. M. Burgess, Cowries of the world. Gordon Verhoef, Seacomber Publication, Cape Town.
- LOPEZ, M. L., C. LEYTON, and M. E. GRAF. 1982. Técnicas de Histología y Citología. Departamento de Biología Celular y Genética, Facultad de Medicina, Universidad de Chile, Santiago, Chile.
- LORENZ, F., and A. HUBERT. 1993. A guide to worldwide cowries. Verlag Ch.H.
- NATARAJAN, A. V. 1957. Studies on the egg masses and larval development of some prosobranchs from the Gulf of Manor and the Palk Bay. *Proc. Indian Acad. Sci. Sect. B* 46: 170–228.
- OSORIO, C. 1989. La rádula 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: 302–315.
- OSORIO, C., C. GALLARDO, and H. ATAN. 1992. Egg mass and intracapsular development of *Cypraea caputdraconis* Melvill, 1888 from Easter Island (Gastropoda: Cypraeidae). *Veliger* 35(4): 316–322.
- OSORIO, C., F. JARA, and M. E. RAMIREZ. 1993. Diet of *Cypraea caputdraconis* (Mollusca: Gastropoda) as it relates to food availability in Easter Island. *Pac. Sci.* 47: 34–42.
- OSTERGAARD, J. M. 1950. Spawning and development of some Hawaiian marine gastropods. *Pac. Sci.* 4: 75–115.
- REHDER, H. A. 1980. The marine mollusks of Easter Island and Sala y Gomez. *Smithson. Contrib. Zool.* 289: 1–167.
- RIVEROS, Z. F. 1951. *Cypraea (Aricia) caputserpentis* L. en Isla de Pascua. *Rev. Biol. Mar. Montemar* 3(1–2): 154–157.
- SCHILDER, F. A., and M. SCHILDER. 1961. Sexual differences in cowries. *Proc. Malacol. Soc. Lond.* 34: 207–209.
- WEBBER, H. H. 1977. Gastropoda: Prosobranchia. Pages 1–114 in *Reproduction of marine invertebrates*. Vol. 4. Mollusks: Gastropods and Cephalopods. Academic Press, New York.
- WILSON, B. R. 1985. Direct development in southern Australian cowries (Gastropoda: Cypraeidae). *Aust. J. Mar. Freshwater Res.* 36: 267–280.