Marine Biology 101, 227–233 (1989)

Marine Biology

Life history of the golden ring cowry *Cypraea annulus* (Mollusca: Gastropoda) on Okinawa Island, Japan

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Abstract

Two mark-recapture studies, regular population censuses, field observations, and laboratory culture were used to study the life history of the tropical marine gastropod *Cypraea annulus* Linnaeus, 1758 from Cape Maeda, Okinawa Island, from April 1984 to March 1986. In the field, the average rate of increase in shell length of marked juvenile snails was 1.0 ± 0.3 mm wk^{-1} ($N = 13$), with a maximum of 1.5 mm wk^{-1} (initial shell length 10.6 to 17.2 mm). In the laboratory, the maximum growth rate of juveniles was 3.0 mm wk^{-1} with food *ad libitum*. Snails with primordial teeth on the shells grew at a rate of 0.1 to 0.5 mm wk^{-1} for about 2 wk. The adults continued to grow at a similar rate for an additional 3 to 6 wk, and ceased detectable growth when some females started spawning egg masses. In the littoral zone on Okinawa Island, snails reproduced throughout the year. Egg masses brooded by three females (shell length 17.4 to 21.3 mm) in the field contained 90 000 to 133 000 ova. In the laboratory, brooding periods of three females lasted 6, 8, and 9 d. The estimated average frequency of spawning was 5 egg masses $female^{-1}$ yr^{-1}. The mean shell length of adult females (20.3 mm) was significantly larger than that of adult males (19.6 mm). The life-history strategy of *C. annulus* is characterized by rapid growth, high fecundity, and repeated spawning throughout the year.

Introduction

The life histories of few tropical marine gastropods have been studied (e.g. Frank 1969, Kenny 1977, Yamaguchi 1977, Perron 1983, 1986, Burgett et al. 1987, Smith 1987). The family Cypraeidae especially has received little attention from scientists interested in life history strategies. Studies on the life histories of cypraeids have reported only spawning behaviors, fecundity, and morphology of veligers (e.g. Ostergaard 1950, Natarajan 1954, 1957, D'Asaro 1970, Renaud 1971, Bandel 1973, Taylor 1975, Tanaka 1980). Only one paper (Darling 1965) dealt with juvenile growth (on *Cypraea cinerea*). Little is known of the growth and reproduction of the common intertidal cowry *C. annulus* Linnaeus, 1758 in the Indo-West Pacific. Only a few field studies have been carried out on adult growth and male and female size in *C. annulus* (identified equivalently as *Monetaria annulus*). At Heron Island, Australia, Frank (1969) proved growth of *M. annulus* to be determinate by mark-recapture censuses. Female *C. annulus* are usually slightly larger in shell length than males (Orr 1959, Schilder and Schilder 1961).

The purpose of the present study was to examine sexual maturity, growth, breeding seasons, reproductive behaviors, fecundity, frequency of spawning, and male and female size in the golden ring cowry *Cypraea annulus*.

Materials and methods

The study site was located on an eroded limestone platform (ca. 20 to 70 m wide) of a fringing reef at Cape Maeda on Okinawa Island, Japan. Four small coves were chosen for the experiments (Fig. 1). The substratum consists of coral and limestone, and is usually exposed at low tide, except in tide pools. Wave action at the study site is mild during most of the spring and summer, except for the periods of occasional typhoons, but is harsh during most of the fall and winter because the site faces the dominant NW monsoon wind. One typhoon passed within 300 km of Okinawa Island in August 1984 (Okinawa Meteorological Agency 1985).

Three developmental stages after settlement were distinguished in *Cypraea annulus* Linnaeus, 1758 according to shell morphology (Fig. 2). The S1 stage begins at completion of metamorphosis. Kay (1985) called this stage an oliviform

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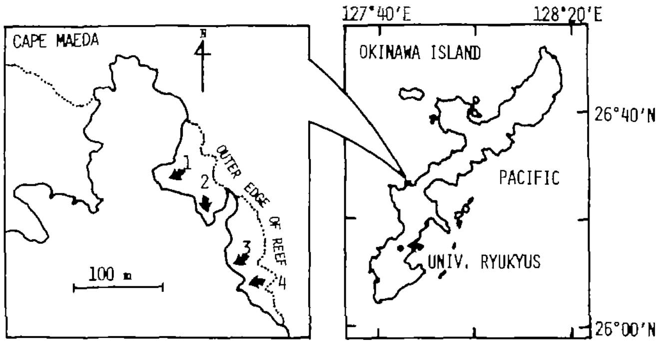

Fig. 1. Cape Maeda, Okinawa Island, Japan, showing locations of stations

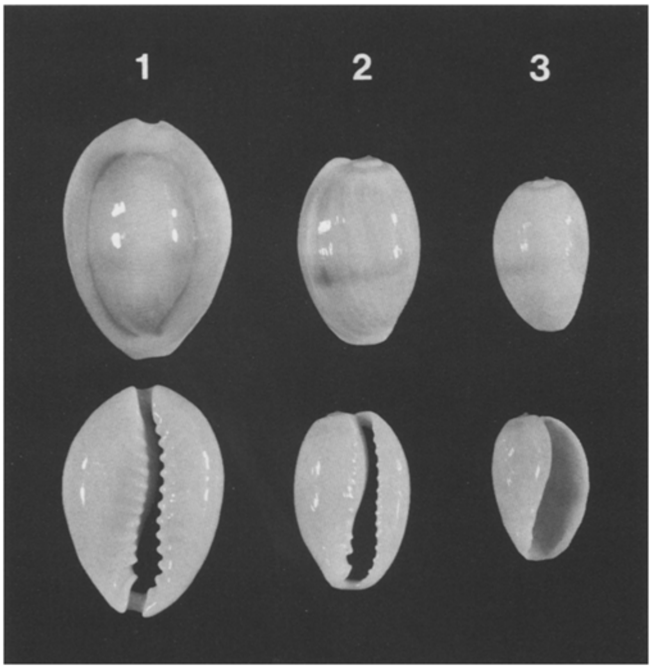

Fig. 2. *Cypraea annulus*. Shell morphology of three developmental stages. Top: dorsal view; bottom: ventral view. 1: S3, adults with complete rings on dorsal surfaces; 2: S2, snails with primordial teeth; 3: S1, juveniles

or "bulla" stage. The S2 snails have primordial or developing teeth on the shell aperture. The S3 stage is recognized by the completion of a bright orange-yellow ring on the dorsal surface.

Growth

Two mark-recapture studies of S1 and S3 snails, laboratory culture, and regular population censuses were used. The shell lengths were measured to the nearest 0.1 mm with vernier calipers. Shell widths and heights were also measured in the mark-recapture studies of S3 snails.

Mark-recapture studies of S1 snails were carried out from May to August 1984 in Cove 4 to determine growth rates. On each date, 19 to 51 S1 snails were collected, their outer lips were painted with nail polish, and they were released within 4 h. Snails painted at each census were distinguished by different colors. Six biweekly censuses were made, during which period 32 out of 198 marked cowries were recaptured. Growth was measured as the difference between the original and the present shell length, from the apex to the farthest point of the outer lip (Yamada 1987).

Seventeen S1 snails, collected from May to July 1984, were reared in laboratory aquaria until December 1984. Seawater temperatures varied in accordance with room temperature (21° to 29 °C). The cowries were fed fresh filamentous green algae (e.g. *Enteromorpha intestinalis*) from May to July. Since the filamentous algae were not found in situ after July, the preserved brown alga *Undaria pinnatifida* was given thereafter. Shell lengths of the S1 snails were measured weekly from May to September 1984.

Size-frequency distributions of S1 and S2 snails were ascertained in 22 biweekly or monthly samples between June 1984 and July 1985 at Coves 1 and 4. Samples 1 to 5 were made at Cove 4. No S1 snails were found in Sample 6 at Cove 4 because the cove was completely exposed during the summer midday low tides and the density of the snails had been reduced by a typhoon. Samples 6 to 18 were therefore made at Cove 1, which was less exposed.

S3 snails ($N = 676$) were marked with small numbered tags attached to the dorsal surface of their shells with a fast-drying adhesive at Cove 1 between June and August 1984, for mark-recapture studies used to examine the pattern of growth.

Breeding season

Counts were made of the number of snails sitting on egg masses, or "brooding" snails, during monthly 15 min searches at low tide from June 1984 to July 1985. The brooding snails were considered mature females, since all 13 collected at Cape Maeda were confirmed to be female by dissection. Furthermore, spawning females brooded their egg masses in aquaria. Size-frequency distributions in growth studies were also used to determine seasons of S1 snail recruitment.

Fecundity

Three brooding females and their brooded egg masses were collected from Cove 3. The number of egg capsules per egg mass and the number of eggs per capsule from ten haphazardly chosen capsules were counted. Heights and widths of the ten capsules were measured under a profile projector to the nearest 0.1 mm.

Spawning frequency

The spawning cycle of snails that brood eggs and reproduce without synchronization has the proportional relationship: (average no. of brooding females)/(total no. of fe-

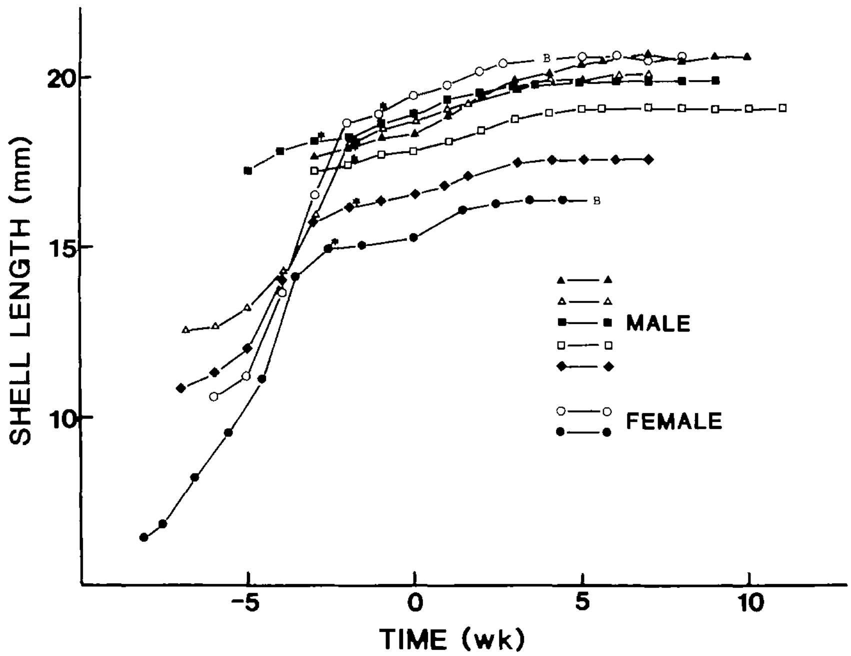

Fig. 3. *Cypraea annulus*. Individual shell growth in laboratory from May to September 1984. Shell length plotted as function of time; Stage S3 commences at Time 0. *: beginning of Stage S2; B: brooding

Table 1. *Cypraea annulus*, Growth rates ($\bar{x}$, mm wk^{-1}) of three developmental stages in field and in laboratory. *N*: no. of snails. –: no data

Stage	Field			Laboratory		
	$\bar{x}$	SD	*N*	$\bar{x}$	SD	*N*
S1	1.0	0.3	13	1.3[a]	0.7[a]	5
S1–S2	0.7	0.4	10	–	–	–
S1–S3	0.3		1	–	–	–
S2	–	–	–	0.3	0.1	7
S3	0.1[b]	0.1[b]	12	0.2[c]	0.1[c]	7[c]
				0.0[de]	0.0[de]	6[d]

[a] Excluding first week of observations
[b] mm yr^{-1}
[c] First 6 wk
[d] Subsequent 4 mo
[e] mm $(4\ mo)^{-1}$

males) = (brooding period)/(period of spawning cycle). Thus, the average period of the spawning cycle may be indirectly estimated from the first three variables. The average number of brooding females and total number of S3 snails were obtained by monthly 15 min searches in breeding season studies. The sex ratio was not significantly different from 1 : 1 in the field. Half of the total number of S3 snails were considered female. The brooding period was measured in the laboratory.

Male and female size

The size of male and female snails was measured on mating pairs and brooding females collected on 17 April 1984 at Coves 3 and 4, mating pairs on 4 May 1984 at Coves 3 and 4, and S3 snails collected haphazardly on 26 March 1986 at Cove 2. Mating snails were easily sexed by the presence of a penis which retracted when a male was disturbed. The S3 snails were dissected and sexed by the presence of penises. ANOVA was used for size comparison. Correlation coefficients between mating male and female sizes were calculated.

Results

Sexual maturity

Neither brooding nor copulating Stage S1 *Cypraea annulus* were found during the study periods. However, a few copulating snails of the late S2 stage were observed in the field. Most copulating snails and all brooding females were at the S3 stage. Snails, therefore, become mature at the late S2 stage.

Growth

Cypraea annulus grew very rapidly during the S1 stage in both the field and the laboratory, but growth declined with increasing stage (Table 1). In the field, 21 of 198 marked S1 juveniles were recaptured as S1 juveniles, 11 as S2 snails, and 1 as a S3 adult. Eight of these S1 juveniles and one S2 snail displayed unusually thick rims compare to the normal thin juvenile shell. Their growth rates were less than 0.3 mm wk^{-1}; the nail-polish marking may have disturbed shell growth. These snails were excluded from the calculations. In the laboratory, the juveniles' growth declined considerably one week before they became S2 snails (Fig. 3), as the labial edges began to extend toward the columellae. The maximum growth rate of the S1 stage in the laboratory was 3.0 mm wk^{-1} shell length. One S1 juvenile grew from 10.6 to 18.6 mm in 4 wk (i.e., 2.0 mm wk^{-1}).

S2 snails grew at reduced rates of 0.1 to 0.5 mm wk^{-1}, and advanced to the S3 stage in about 2 wk. After growing into S3 adults with rings on their dorsal surfaces, the adults

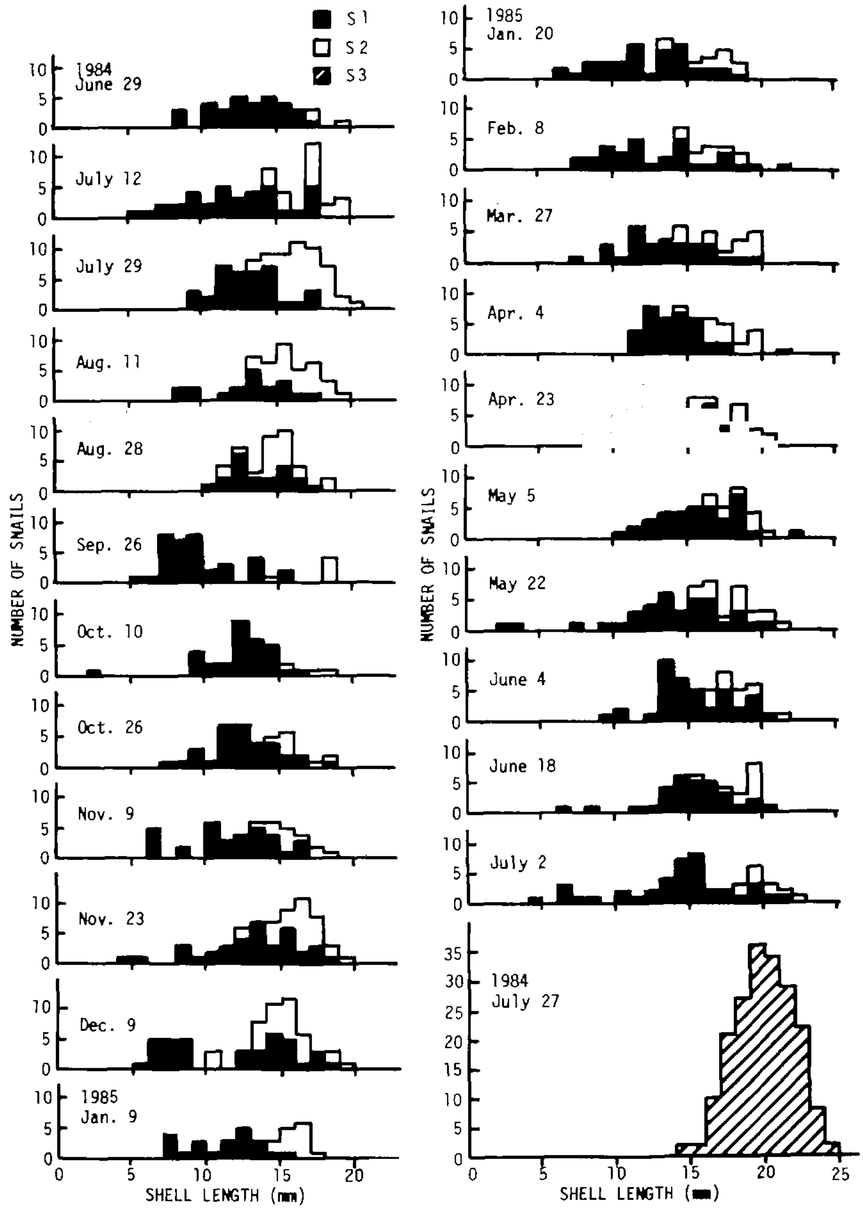

Fig. 4. *Cypraea annulus*. Size-frequency distributions of S1 juveniles and S2 snails from June 1984 to July 1985 and S3 adults in July 1984 at Cape Maeda, Okinawa Island. S2 snails were collected less extensively on 29 June and 12 July 1984. Site sampled on June to August 1984 was approx. 150 m away from other site

continued to grow at a rate similar to that of S2 snails for an additional 3 to 6 wk, thickening their shell and increasing their width during this period. During the subsequent 4 mo observation, these shells did not grow detectably in length, width, or height (Table 1). Two females spawned 4 and 5 wk after completion of the rings on their dorsal surfaces (Fig. 3).

Twelve of 676 tagged S3 adults were recaptured 9 to 21 mo after release in the field. Five had grown 0.2 to 0.4 mm in shell length, while the other seven had not increased more than 0.1 mm in size. Eight of the recaptured adults had been marked more than one year earlier. All recaptured snails had pale, or pale and irregular dorsal surfaces with fading rings (perhaps as a result of erosion).

Fig. 4 shows size-frequency distributions of S1, S2, and S3 snails from June 1984 to July 1985. The size-frequency of S1 juveniles in each sample displayed a similar distribution pattern without distinct modes throughout the year, with one exception on 26 September 1984. Because of continuous juvenile recruitment, growth rates could not be estimated from these histograms. The minimum and maximum shell length of S1 juveniles collected were 2.5 and 22.5 mm, respectively.

Breeding season

Brooding females were observed in the field throughout the study period (Table 2). Each search revealed the presence of both yellow and violet egg masses. Violet egg masses appear to be older than yellow ones, since egg-mass color changed from yellow to violet during the brooding period in the laboratory aquaria. Juveniles were collected throughout the year (Fig. 4). Therefore, the population of *Cypraea annulus* at Cape Maeda reproduced throughout the year without detectable peak periods in its breeding activity.

Table 2. *Cypraea annulus.* Number of brooding females found during 15 min search at Cape Maeda from June 1984 to July 1985. During each search, about 190 snails were examined

Date		No.
1984		
June	28	6
July	27	14
August	27	8
September	25	9
October	26	15
November	23	8
December	19	2[a]
1985		
January	9	7
January	20	3
February	8	3[a]
March	27	17
April	23	5
May	22	9
June	18	14
July	2	11

[a] On these dates, searches lasted less than 15 min

Table 3. *Cypraea annulus.* Shell length of mating pairs, brooding females, and adults at Cape Maeda, Okinawa Island. *N:* no. of snails

Snails	*N*	Mean length (mm)	SD	Range (mm)
17 April 1984				
Mating males	27	18.3	2.36	14.9–23.8
Mating females	27	20.4	1.81	16.8–24.1
Brooding females	25	20.1	2.17	15.0–23.6
4 May 1984				
Mating males	39	17.9	2.30	14.8–22.2
Mating females	39	19.2	2.31	14.5–22.5
26 March 1986				
Males	88	19.6	1.80	15.2–23.0
Females	105	20.3	2.30	15.4–26.7

Reproductive behavior and fecundity

One female *Cypraea annulus* spawned single egg capsules successively in August in a laboratory aquarium; complete spawning took ca. 24 h. Within 5 d of spawning, the color of the egg mass changed from yellow to violet, the color change at the center of the egg mass occurring earlier than that at the periphery; veliger larvae emerged after 8 d. The brooding periods of two other females were 6 and 9 d in October and December, respectively. Veligers emerged both in the morning and in the afternoon. The females nipped and tore off the egg capsules whilst the veligers emerged and, after emergence, moved away and left the emptied capsules on site. The size of veligers was 0.13 mm one day after emergence from the egg capsules.

Egg masses brooded by three females (shell length: 17.4, 21.3, and 20.1 mm) in the field contained 90 000, 127 000, and 133 000 ova, respectively.

Spawning frequency

The average brooding period in the laboratory (7.67 d) was used for calculations. The average number of S3 adults found during a 15 min search for brooding females at Cape Maeda was 187. With a sex ratio of 1:1, half (93.5) would be females. The mean number of monthly brooding females was 9.85 excluding the months of December 1984 and February 1985 (Table 2). Thus, the average spawning-cycle period $= 7.67 \times 93.5/9.85 = 72.8$ d, and the average spawning frequency $= 365/72.8 = 5$ egg masses female^{-1} yr^{-1}.

Male and female size

At Cape Maeda, the mean shell lengths of females were significantly larger than those of males between mating pairs on 17 April 1984 ($F = 13.75$; df $= 1, 52$; $p < 0.001$) and on 4 May 1984 ($F = 5.88$; df $= 1, 76$; $p < 0.05$), and between haphazardly collected S3 snails on 26 March 1986 ($F = 4.58$; df $= 1, 191$; $p < 0.05$) with a considerable overlap of the ranges (Table 3). The mean shell lengths of mating and brooding females on 17 April 1984 were not significantly different ($F = 0.22$; df $= 1, 50$; $p > 0.05$).

Correlation between sizes of mating males and females were not significant ($r = -0.094$, df $= 25$, $p > 0.05$ on 17 April 1984; $r = 0.021$, df $= 37$, $p > 0.05$ on 4 May 1984).

Discussion

Growth

A juvenile *Cypraea spadicea* grew rapidly at 3.3 mm wk^{-1} in an aquarium, except for no growth during the first 2 wk (Darling 1965). This rate is similar to the maximum growth rate of S1 juvenile *C. annulus* in the aquaria in the present study, although the adult size of *C. spadicea* (shell length 45 mm) is about twice that of *C. annulus*. Snails may enhance their fitness by rapid growth with fragile, thin, juvenile shells or by slow growth with strong, thick, juvenile shells; *C. annulus* choose the former.

In my laboratory observations, the juveniles grew more slowly during the first week after introduction into the aquaria than in subsequent weeks. Yamaguchi (1975) noted that young juveniles of many marine sedentary invertebrates grow slowly, and fitted their growth to logistic rather than to von Bertalanffy growth equations. Both juveniles introduced into the aquaria were not young (*C. spadicea*, 30 mm); therefore, both Darling's (1965) and my results may be attributable to differences between laboratory and field conditions rather than to slow growth of young juveniles.

Frank (1969) remarked that growth of *Cypraea annulus* ceased once they reached their adult shape, except for repairs to the shell. His growth comparisons, however, were based not on shell length but on the distance between notches at the top and bottom of the aperture. In my field study, six out of the twelve recaptured S3 adult cowries had ob-

Table 4. Cypraeidae. Life-history data. –: no data

Species	Capsule size (mm)	Capsules/ egg mass	Eggs/ capsule	Eggs/ egg mass	Days *in capsula*	Size at emergence (μm)	Month(s) of breeding	Locality	Source
Cypraea annulus	0.9–2.0 × 0.7–1.3	233–267	230–603	90 000–133 000	6–9	130[b]	All months[g]	Okinawa	Present study
C. caputserpentis	2	100	200	20 000	–	130	Oct.[d g]	Hawaii	Ostergaard (1950)
	1.1 × 0.9	100–200	200	20 000–40 000	18	100–120	All months[g]	Hawaii	Kay (1960)
C. carneola	4	1 000	500	500 000	14	220	July[d f]	Hawaii	Ostergaard (1950)
C. cinerea	2.0–2.5 × 1	400	200–300	–	–	–	June–July[d g]	Colombia and Curaçao	Bandel (1973)
C. errones (as *Erronea errones*)	1.45–3.25 × 1.40–1.80	481–546	20–76	–	–	373	Sep.–Mar.[g]	India	Natarajan (1957)
C. fimbriata	–	–	–	–	–	–	Mar.–Oct.[e g]	Hawaii	Taylor (1975)
C. helvola	2	1 000	200	200 000	–	140	July[d g]	Hawaii	Ostergaard (1950)
	–	–	–	–	–	–	June–July[e g]	Hawaii	Taylor (1975)
C. isabella	1.5	1 500	200	300 000	11	150	July[d f]	Hawaii	Ostergaard (1950)
	–	–	–	–	–	–	All months[e g]	Hawaii	Taylor (1975)
C. mauritiana	4 × 3	300[a]	1 000	–	–	235[c]	June[d f]	Hawaii	Ostergaard (1950)
C. moneta	2.20–3.00	34–596	500	17 000–298 000	14	145–155	–	Eniwetok	Renaud (1971)
C. poraria	–	–	–	–	–	140	May[d g]	Hawaii	Ostergaard (1950)
C. rashleighana	–	–	–	–	–	–	June[e g]	Hawaii	Taylor (1975)
C. spurca acicularis	2.6 × 1.6	140 and 290	1 100	154 000 and 319 000	–	–	May–June[d f]	Florida	D'Asaro (1970)
C. teres	–	–	–	–	–	–	May[e g]	Hawaii	Taylor (1975)
C. vitellus	2.5 × 1.5	380	600	228 000	12	190	July[d f g]	Japan	Tanaka (1980)

[a] Portion of an egg mass
[b] One day after emergence of veligers
[c] Unsuitable culture conditions
[d] Month(s) of observation
[e] Month(s) of occurrence of free-swimming veligers
[f] In vitro
[g] In situ

viously increased in shell length, width, and/or height by >0.1 mm but <0.7 mm during a period of about 9 to 21 mo. These individuals apparently continued to grow as adults with dorsal rings. In the laboratory, however, there was no detectable growth during the last 4 mo of adulthood, the S3 stage. It would seem, therefore, that the six S3 adults which had increased in shell length when they were recaptured had been tagged within 6 wk after completion of their dorsal rings. Consequently, the growth of *C. annulus* appears to be determinate.

Breeding season

Cypraea annulus reproduces all year around at Cape Maeda. At Heron Island, Frank (1969) found egg masses of *C. annulus* (as *Monetaria annulus*) in March, June, and July, and juveniles from July through February. Egg masses and juveniles might have been difficult to find at Heron Island because of the lower population density of snails (0.4 m^{-2}; Frank 1969). *C. annulus* at Cape Maeda (32.7 m^{-2}; own personal observation) were about 80 times as dense as at Heron Island. Judging from the occurrence of egg masses throughout the year, Kay (1960) suggested that there was no pronounced breeding season for *C. caputserpentis* in Hawaii. Taylor (1975) also found planktonic veligers of *C. isabella* throughout the year in Hawaii. On the other hand, Natarajan (1957) showed that the breeding season of *C. errones* (as *Erronea errones*) in India was from Sep. to March. Taylor (1975) noted that the greatest diversity and abundance of cypraeid larvae in plankton occurred during the spring and summer in Hawaii.

Reproductive behavior and fecundity

Brooding behavior has been reported for many *Cypraea* species: e.g. *C. isabella* and *C. helvola* by Ostergaard (1950), *C. errones* (as *Erronea errones*) by Natarajan (1954, 1957), *C. spurca acicularis* by D'Asaro (1970), and *C. vitellus* by Tanaka (1980). In the present study, female *C. annulus* were also observed brooding their egg masses.

Table 4 shows that the number of capsules per egg mass and number of eggs per capsule in *Cypraea annulus*, *C. moneta* (Renaud 1971), and *C. vitellus* (Tanaka 1980) are similar. The period of development within capsules ranged from 6 to 9 d in *C. annulus*, the shortest amongst the cypraeid species investigated. Veliger size at emergence averaged 0.13 mm, similar to that of *C. caputserpentis*, *C. helvola*, and *C. poraria* (Ostergaard 1950).

Spawning frequency

Tanaka (1980) reported that *in capsula* time for *Cypraea vitellus* increased by 75% when seawater temperature was reduced from 26° to 19 °C. The surface seawater temperature varied from 17.8° to 31.4 °C at Sesoko, just off Okinawa Island (Nakamura 1984). The brooding period in *C. annulus* may therefore vary considerably with season.

Five females in the aquaria spawned three to four times each between July and November 1984 under *ad libitum* food supply, equivalent to seven to ten times per year. High water-temperature and high food-availability may have caused these high frequencies, which are significantly higher than the estimated frequency of five times per year in the field.

Male and female size

Although he did not compare the difference statistically, Orr (1959) showed that shell length of female *Cypraea annulus* in Zanzibar was slightly larger than that of males, with a considerable overlap. On the other hand, in the central Pacific (the Ellice Islands to the Marshall Islands) and in the Indian Ocean (Mahé, Seychelles), Schilder and Schilder (1961) found that the shells of female *C. annulus* were not significantly larger than those of males ($p>0.2$). However, their data for specimens from these different localities were pooled, and may have obscured the actual, regional size-differences, between the two sexes. In the present study, the mean shell length of females was significantly larger than that of males, with a wide range of overlap.

Schilder and Schilder (1961) reported similar results for *Cypraea moneta* (as *Monetaria moneta*) and *C. helvola* (as *Erosaria helvola*). Griffiths (1961 b) reported female *C. angustata* to be significantly larger than the males, while differences in *C. errones* were not significant. Griffiths (1961 a), however, found that the mean shell length of the females was significantly less than that of the males in *C. hesitata* (as *Umbilia hesitata*). It appears, therefore, that in Cypraeidae females are not always larger than males.

No correlation was observed between sizes of mating male and female *Cypraea annulus*. Pairing in *C. annulus* would therefore appear to be random with respect to size. To my knowledge, no such observation has previously been reported for the Gastropoda.

Acknowledgements. I would like to express my appreciation to M. Yamaguchi and S. Katoh for their support and encouragement throughout this study and for their helpful comments on the manuscript. I am grateful to M. Horikoshi and M. Nishida for their helpful discussions. The manuscript has also benefited from reading by K. M. Brown, D. W. Foltz, J. M. Lawrence, K. J. Lupardus, M. T. Randall, H. Senou, S.-K. Wu, and two anonymous reviewers.

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Date of final manuscript acceptance: October 21, 1988.
Communicated by J. M. Lawrence, Tampa