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Ecological Relationship Between Body Size and Fecundity in the Slipper Shell, *Crepidula onyx* Sowerby (Gastropoda: Calyptraeidae) in Korean Waters

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The aim of the present study was to investigate the ecological relationship between female body size (=shell length) and fecundity in a Korean population of protandric hermaphrodite, *Crepidula onyx* Sowerby, using 6 reproductive variables (the number of capsules per brood, capsule size, the number of embryos per capsule, total number of embryos per brood, egg size, and larval size). The investigation was based on 32 females, 107 egg capsules, 263 eggs, and 250 veliger larvae sampled in January 2000, from Yangpo, the southeastern coast of Korea. All foregoing reproductive variables, except larval size, were significantly correlated with the female body size ($p<0.001\sim0.01$). There was a significant increase both in the number of capsules per brood and the number of embryos per capsule with female body size ($p<0.001$). Consequently, the fecundity of the female *C. onyx* increased with female body size to over 14.65 mm (the minimum size of egg brooding in the present study). This investigation, therefore, provides additional evidence that female fecundity of protandric hermaphrodites is positively correlated with female body size.

Key words: Reproductive ecology, Body size, Fecundity, *Crepidula onyx*, Korean water

Introduction

Female fecundity in gastropods is often closely correlated with size (Hughes, 1986), and protandry (sex change from male to female) is advantageous in many species in which female fecundity is related to large body size (Hoagland, 1975). *Crepidula* species are typical protandric hermaphroditic gastropods (Webber, 1977). Females of many species belonging to the genus *Crepidula* alter fecundity by controlling the number and/or size of the capsules and the number of eggs each capsule contains (Gallardo, 1976; Chaparro et al., 1999). The theory of sex allocation (Werren, 1980) predicts that large hermaphrodites, including *Crepidula* species, should increase egg production rather than sperm production to maximize their reproductive success. Consequently, a positive correlation between egg production and female body size is expected in most protandric hermaphroditic species.

In many *Crepidula* species, a positive correlation between egg production and female body size was reported by several workers (e.g. Hoagland, 1975), although the number of embryos per capsule was independent of the parent female body size in a few species with nurse eggs (Chaparro et al., 1999). For instance, a strong relationship between female fecundity and female body size was reported by Hoagland (1975), who observed that the number of eggs produced per season rose steeply with body size in *C. fornicata*. Also, Gallardo (1977) found that, in *C. dilatata*, the larger females produced more eggs per capsule and more capsules per egg mass.

With reproductive ecology of *C. onyx*, some observations were made by a few workers (e.g. Coe, 1942 on the presence of nurse eggs; Hoagland, 1978 on social behavior). However, there is no direct evidence in *C. onyx* to support the general assumption that female fecundity of the protandric hermaphrodites is positively correlated to female body size (Hoagland, 1978). A protandric hermaphroditic slipper shell, *C. onyx* is a sedentary filter feeder (Charnov, 1982). Along the coast of Korea, it is commonly found on live and empty shells of the gastropods *Kelletia lischke*, *Neptunea cumingi* and *N. arthritica*.

The purpose of the present study is (1) to examine the relationship between the body size of brooding females and their fecundity in *C. onyx*, in terms of the number of capsules per brood, capsule size, the number of embryos per capsule, total number of embryos per brood, egg size, and larval size based

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on specimens sampled from the southeastern coast of Korea and (2) to compare the present results with existing information in the literature for other congeneric species.

Materials and Methods

Sampling

Thirty-two brooding female *Crepidula onyx*, adhering to the 3 host gastropod species, *Kelletia lischkei*, *Neptunea cumingi* and *N. arthritica*, were collected in January 2000 from a subtidal site (ca. 35 m in depth) with bait traps (35×35×70 cm) in Yangpo on the southeastern coast of Korea (35°50'20"N, 129° 30'25"E). Samples were collected from a single site to avoid inter-population variation of female body size because sex-changing invertebrates show individual variation in size at sex change that may be due to population structure and environmental heterogeneity (Collin, 1995).

The host gastropods and *C. onyx* at the sampling site were usually sympatric with *Petalomera wilsoni*, *Ceratostoma fournieri*, *Asterina pectinifera* and *Asterias amurensis versicolor.* The bottom structure of the site consisted of a number of boulders (ϕ30-100 cm; SCUBA observation). Bottom water temperature and salinity, which were recorded in the field with a T-S meter (Orion Model 135) during sampling, were 11.8℃ and 33.7‰, respectively.

Inspection and treatment

The host gastropod samples were brought to the laboratory, where individual *C. onyx* was detached from their host with a small spatula and inspected foot-up. After detachment and inspection, the brooding female specimens were gently washed at least 2 times with tap water to remove ambient mucus prior to fixation in a 10% neutral formalin solution individually with its egg mass.

Female body size (=shell length of female; SLF) (Fig. 1A,B) was measured with a Vernier caliper (precision 0.01 mm). In order to observe the presence of nurse eggs, I examined all capsules containing embryos with different developmental stages (eggs or veliger larvae). In each of the brooding females examined, the number of capsules per brood was counted directly with the naked eyes. At least 5 capsules in each brood were measured (magnified by 10) (Fig. 2A). After measuring, the capsules were broken open with a fine needle, and the number of embryos, eggs or larvae, were counted directly

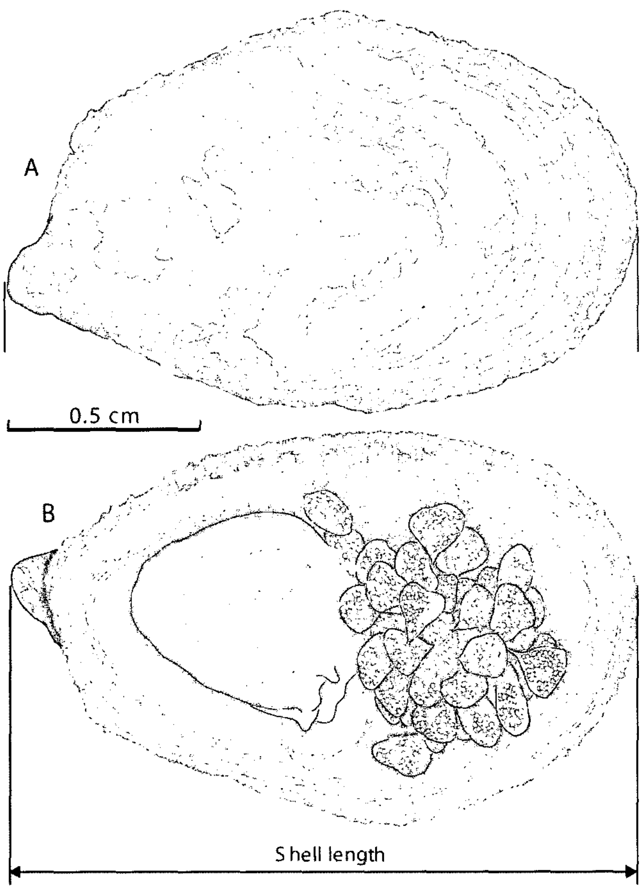

Fig. 1. Linear dimension of the shell of *Crepidula onyx*. Dorsal (A) and ventral (B) views. The ventral view showing a few brooding egg capsules within the mantle cavity of a female.

(magnified by 25). Of the embryos within the capsules, at least 10 embryos were measured (magnified by 40). In the present study, egg size was measured as the longest dimension of the egg diameter (Fig. 2B); larval size was measured as the longest dimension of the protoconch (Fig. 2C). All measurements and counts were made under a dissecting microscope using a calibrated ocular micrometer (precision 0.001 mm) at different magnifications, except the female body size and the number of capsules per brood. Drawings were made using the dissecting microscope with a drawing tube.

Since there was no nurse egg in *C. onyx*, the embryos in the present study are identical to early developmental stage eggs and to late developmental stage larvae. The fecundity of individual females was expressed as the total number of embryos per brood. This number was calculated for each female by multi-

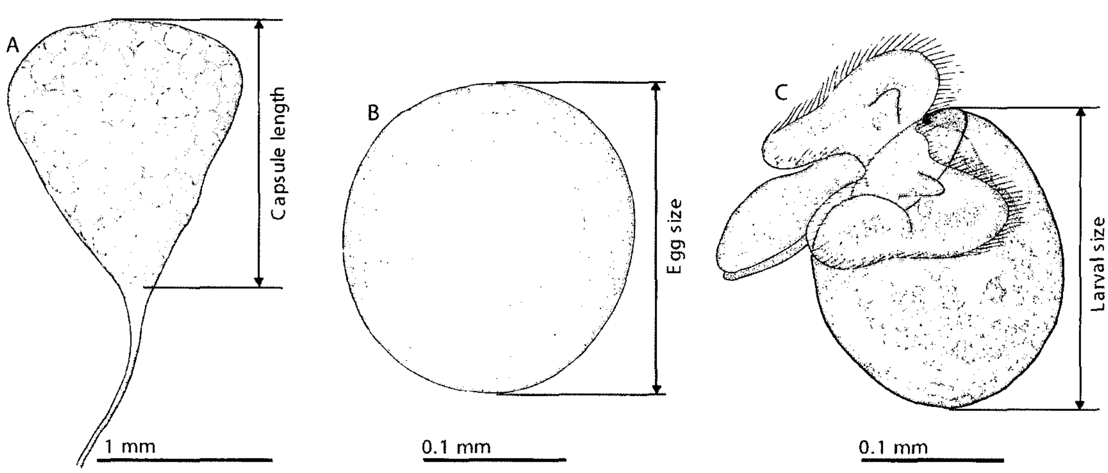

Fig. 2. Linear dimension of an egg capsule containing a few eggs (A), an egg (B) and a veliger larva bearing protoconch and ciliary velum (C) used in the present study for *Crepidula onyx*. Egg diameter represents longest dimension in diameter; larval size represents maximum length of the protoconch in the veliger larva.

plying the number of capsules per brood by the average number of embryos in 5 of its capsules that were randomly chosen. However, in the statistical analysis related to embryo size, the embryo was classified into 'the egg' or 'the larva' because there was a significant correlation ($r=-0.268$, $p<0.001$) between developmental stage and embryo size.

With the aid of the computer program SPSS PC+ and MINITAB, correlation coefficients were calculated using Pearson's correlation coefficient, and regression analysis was made using the least-squares method.

Voucher specimens of the adults and the broods have been deposited at the Korea Inter-University Institute of Ocean Science, Pukyong National University, Korea.

Results

Among the 3 major host gastropods, *Kelletia lischkei*, *Neptunea cumingi* and *N. arthritica*, *Crepidula onyx* was found predominately on *K. lischkei*. Bryozoans and spirobid polychaetes were frequently encountered as epibioants on the surface of the shell of *C. onyx*.

Of the 32 females of *C. onyx* sampled, 4 individuals formed 2 stacks (each 2 females formed a stack) and the others (28 individuals) attached on the host shells singly; 27 (ca. 84%) females brooded egg capsules. The females deposited a cluster of stalked egg capsules on the shell surface of the host gastropods and brooded them within their mantle cavity (Fig. 1B). Mean shell length of the females was 19.9 mm (Table 1). Within this sample, the minimum size of a sexually mature female, which was determined by egg brooding, was 14.6 mm in the mean shell length (Table 1). Each female produced approximately 22 capsules and each capsule contained approximately 70 embryos (Table 2). The two individuals forming stacks on the females were identified as non-brooding females and were considerably smaller than the females below (lower/upper female in shell length (mm): 20.28/9.41 and 20.55/9.78).

The egg capsule, which was thin and cream-colored, was a flattened triangular sac with a round vertex. Its lateral margins were longer than its distal one (Figs. 1B, 2A). A laminar peduncle, which was an extrusion of the capsular membrane (Fig. 2A), extended from the proximal vertex of each capsule. It was united in a branch by its stalks on a common stem fastened to a shell that was covered by the parent. The morphology of the common stem, however, was usually not prominent. The mean size of the capsule was 1.714 mm (Table 1).

The creamy white eggs floated in a gelatinous fluid within their own membrane (Figs. 1B, 2A). Mean egg size was 0.24 mm; mean larval size was 0.22 mm (Table 1). All eggs within a capsule were nearly the same shape and developmental stage. The eggs were generally spherical (Fig. 2B); the larvae were veliger-shaped with a ciliated velum and a nearly transparent protoconch (Fig. 2C). Within a capsule, there was no difference in the morphology of the eggs and larvae that could be discriminated visually

Table 1. Number of specimens and size examined in the present study. Samples of *Crepidula onyx* were collected from the outer shell surface of the 3 gastropod species, *Kelletia lischkei*, *Neptunea cumingi* and *N. arthritica*, which were collected by the bait traps (ca. 35 m in depth) in January 2000 from Yangpo, southeastern Korea. In the present study 'egg' represents all developmental stage until veliger stage, and 'larva' represents veliger larva with protoconch and velum within the egg capsule. For measuring of the egg and larva, see Fig. 2. SD=standard deviatio

		Number of specimens	Mean (Min.-Max.) (mm)	SD
Female brooded		27	19.9 (14.6-25.9)	2.71
Capsule		107	1.7 (1.2-2.5)	0.28
Embryo	Egg	263	0.2 (0.1-0.3)	0.02
	Larva	250	0.2 (0.1-0.2)	0.02

Table 2. Data on the reproductive variables. Samples of *Crepidula onyx* were collected from the outer shell surface of the 3 gastropod species, *Kelletia lischkei*, *Neptunea cumingi* and *N. arthritica*, which were collected by the bait traps (ca. 35 m in depth) in January 2000 from Yangpo, southeastern Korea. SD=standard deviatio

Reproductive variable	Mean (Min.-Max.)	SD
Number of capsules/ Brood	22.0 (7-38)	7.67
Number of embryos/ Capsule	69.7 (24-135)	24.77
Total number of embryos/Brood	1627.2 (294-4455)	983.60

as nurse eggs.

The female body size was significantly correlated with the 4 following reproductive variables ($p<0.001$) (Table 3): the number of capsules per brood, capsule size, the number of embryos per capsule and total number of embryos per brood. All foregoing variables significantly increased with increasing the female body size ($p<0.001$) even though the slopes varied between variables. Also, the capsule size, the number of the embryos per capsule, and the total number of the embryos per brood were significantly correlated to (Table 3, $p<0.001$) and increased with increasing number of capsules per brood ($p<0.001$). Capsule size was significantly correlated to (Table 3, $p<0.001$) and increased with increasing number of embryos per capsule and/or total number of embryos per brood.

Although the probability varied from 0.001 to 0.01, egg size was significantly correlated with the female body size (Fig. 3) and the following 4 reproductive variables: the number of capsules per brood, capsule size, the number of embryos per capsule and total number of embryos per brood (Table 4). However, no significant relationship was observed between the larval size and the female body size and the foregoing 4 variables at $p=0.05$ (Table 4).

Discussion

Crepidula onyx, in the present study, rarely formed stacks (4/32 individuals). Collin (2000) observed that some species of *Crepidula* form semi-permanent stacks of many individuals, others make small stacks or pairs, and some do not stack. Hoagland (1978), however, frequently found stacked populations of C. onyx in muddy bays, where recruitment and population densities were high. Thus a discrepancy in the frequency of stacks in *C. onyx* between the present study and Hoagland's (1978) observation was probably caused by environmental heterogeneity between the two study sites, mud vs. boulder, and may implicate that the degree of stack formation in *C. onyx* is correlated with local environmental conditions. According to Collin (2000), the local population of *C. onyx*, which was examined in the present study, may be classified into the second category, "make small stacks or pairs in its social habits."

The brooding females examined in the present study showed considerable intraspecific variation in the shell length (SL) (14.65-25.90 mm) (Table 1). The largest one was approximately two times larger than that of the smallest one. In addition, the mean size (ca. 20 mm) of the females in the present study was remarkably smaller than that of the same species as reported by Hoagland (1986) (33 mm). Size variation of the female in protandric hermaphrodites (e.g. *Crepidula* species) may be explained by the fact that individual variation in size at sex change may be due to population structure and environmental heterogeneity (Collin, 1995). However, since Hoagland (1986) reported only a brief description of his sampling site (Balboa Island, California, USA), the author could not compare in detail the environmental heterogeneity between the present sampling site and Hoagland's to explain the possible size discrepancy between the two allopatric populations of *C. onyx*. Even though the female body size in the present study was considerably smaller than that in Hoagland (1986), egg size (=egg diameter in Hoagland, 1986)

Table 3. Correlations between the reproductive variables of *Crepidula onyx* used in the present study. 'S' represents significant correlation between two related variables at p<0.001. Values in the parenthesis represent Pearson's correlation coefficient (MINITAB)

Variable	Shell length of female (mm)	Number of capsules/Brood	Capsule size (mm)	Number of embryos /Capsule
Number of capsules/Brood	S (0.56)			
Capsule size (mm)	S (0.54)	S (0.34)		
Number of embryos /Capsule	S (0.68)	S (0.48)	S (0.62)	
Total number of embryos/Brood	S (0.72)	S (0.84)	S (0.54)	S (0.89)

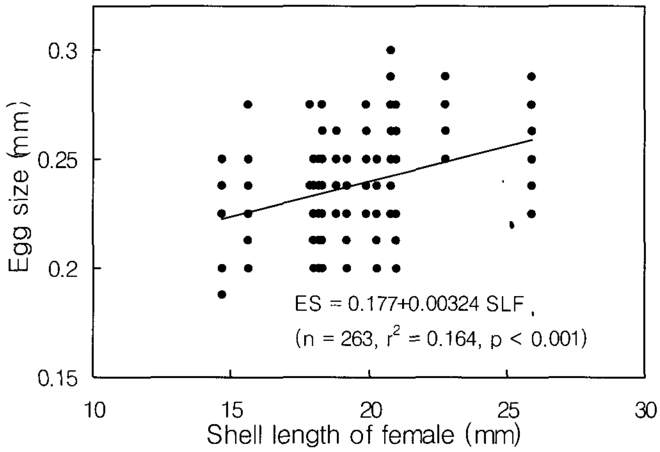

Fig. 3. Regression of egg size (ES) against shell length of female (SLF) of *Crepidula onyx* sampled in January 2000 from Yangpo, southeas

in the present study (0.241 mm) was larger than that in Hoagland (1986) (0.172 mm). Therefore, there may be a difference in the reproductive strategy of the two allopatric populations. The present population probably produces a small number of larger eggs while Hoagland's population presumably produces a large number of smaller eggs (the number of eggs/capsule=70 vs. 220; egg size (mm)=0.241 vs. 0.172).

The mean size of the eggs (0.241 mm, Table 1) of this population of *C. onyx* was very similar to that of a congeneric species, *C. adunca* (0.24 mm; Strathmann, 1987), even though it was considerably different from that of an allopatric population of *C. onyx* (Hoagland, 1986). Hoagland (1986) suggested that egg size could be used as a species character in Calyptraeid species since he found that egg size was far more stable within the species than the size of the capsule, the number of capsules per brood, or the number of embryos per capsule within species. Similarly, Gallardo (1977) found relatively stable egg

Table 4.Correlations between egg or larval size (mm) and shell length of the female, and 4 reproductive variables of *Crepidula onyx* used in the present study. In the present study 'egg' represents all developmental stage until veliger stage, and 'larva' represents veliger larva with protoconch and velum within the egg capsule. 'S*' represents significant correlation between two related variables at p<0.001; 'S' at p<0.01; 'NS' represents no significant correlation between two related variables at p=0.05. Values in the parenthesis represent Pearson's correlation coefficient (MINITAB)

	Classification	
	Egg size (mm)	Larval size (mm)
Shell length of female (mm)	S* (0.405)	NS
Number of capsules/Brood	S* (0.243)	NS
Capsule size (mm)	S* (0.270)	NS
Number of embryos/Capsule	S (0.191)	NS
Total number of embryos/ Brood	S* (0.246)	NS

size (0.204-0.238 mm) in a Chilean population of *C. dilatata*. Collin (2000), however, found large intraspecific variation in egg size in *C. adunca*, ranging from 0.262 to 0.315 mm for one female. In addition to Collin's observation, intraspecific variation of egg size (0.190-0.300 mm, Table 1) was also found in the present study for *C. onyx* and in the comparison of the two allopatric populations of *C. onyx* (the present result and Hoagland (1986)). Therefore, there may not be enough data to accept Hoagland's suggestion of egg size as a species character in Calyptraeid species.

Egg size in *Crepidula onyx* was significantly correlated with the female body size (Table 4, Fig. 3). However, larval size was not significantly correlated with the female body size (Table 4). Presumably, this inconsistency, therefore, means that larger eggs might not necessarily develop into larger larvae in this species. Generally, larger eggs containing more yolk hatch into large juveniles, which survive better than smaller ones (Spight, 1976). However, to test this general concept of a significant relationship between egg size and juvenile survival rate in *C. onyx*, the author must extend the scope of the study to obtain data on the correlation between larval size and survivorship in this species.

The egg capsules of *C. onyx* contained remarkably fewer embryos (ca. 70/capsule) than those of *C. fornicata* (240/capsule in Costello and Henley, 1971). However, minimum and maximum values (24-135/capsule) were similar to those of *C. adunca* (50-100/capsule in Strathmann, 1987) and *C. plana* (65-170/capsule in Costello and Henley, 1971).

The relationship between the female body size and fecundity in *Crepidula* species is controversial, although there was a significant correlation between the two variables in the present study (Table 3). Gallardo (1976) found significant relationships between the female body size and the number of eggs per brood and between the female body size and the number of encapsulated embryos in *C. dilatata*. Also in *C. dilatata*, Chaparro et al. (1999) found a significant positive correlation between capsule size and the female body size and the number of eggs per capsule and the female body size, even though the number of embryos per capsule was independent from the female body size since not all the eggs developed (some were nurse eggs). The controversy seems to be caused by the presence of nurse eggs only in some species. If a species does not have nurse eggs, the female body size usually shows a significant positive relationship with fecundity in terms of the number of eggs per capsule and/or brood (e.g. *C. onyx* in the present study; *C. dilatata* in Gallardo, 1976; *C. dilatata* in Chaparro et al., 1999). If a species has nurse eggs, the female body size is usually independent of fecundity (e.g. *C. dilatata* in Chaparro et al., 1999).

The trend of increasing numbers of embryos per capsule with increasing the female body size shown in the present study seems to be common in gastropod species (Gallardo, 1977, 1979, 1981; Perron and Corpuz, 1982). However, it does differ from the other gastropod species examined by Gallardo (1977, 1979, 1981) and Perron and Corpuz (1982). Since *C. onyx* does not make nurse eggs, a significant positive correlation between the number of embryos per capsule and the number of capsules per brood and the female body size may implicate that fecundity is higher in larger females than in smaller ones. The increasing reproductive output with increasing the female body size, as reported in this study, is additional evidence to support that protandry, which is characteristic of most species of *Crepidula* (Hughes, 1986), may be favored when female reproductive output increases with size (Collin, 1995). This significant positive correlation was also reported in a congeneric species in which the number of capsules, eggs per capsule and total eggs per brood clearly increased with increasing the female body size (e.g. *C. fornicata* in Hoagland, 1975; *C. adunca* in Collin, 2000). Also, the theory of sex allocation (Charnov, 1982; Werren, 1980) predicts that large hermaphrodites should increase egg production rather than sperm production to maximize their reproductive success (Yusa, 1994). Consequently, it should be a common phenomenon that female fecundity is positively related to age and size of the female in *Crepidula* species. The positive correlation, as seen in C. onyx, between body size and egg production is likely to occur in a number of gastropod species. For instance, the same phenomenon in field populations of hermaphroditic *Aplysia* spp. was found by Kandel and Capo (1979), Switzer-Dunlap and Hadfield (1979) and Yusa (1994). Even though the author did not examine movement and/or behavior of *C. onyx*, Coe (1938) noted that the movement of immature and small males could increase the reproductive potential of this species.

The presence of nurse eggs and/or "embryonic cannibalism" seems common in Calyptraeid species (e.g. Thorson, 1940 in *Crepidula* (*=Ergaea*) walshi; Chaparro and Paschke, 1990 in *C. dilatata*). Although Coe (1942) found that in capsules of *C. onyx*, half of the embryos frequently disintegrated and used as food by the survivors, the author could not identify any embryos as nurse eggs in the present study. This discrepancy between the two studies may implicate intraspecific variation of embryonic cannibalism. The intraspecific variation of embryonic cannibalism in *Crepidula* species was also observed by Fretter and Graham (1994), who reported that it was not a common occurrence in the genus *Crepidula* and could only have been accidental. In addition, Gallardo (1977) did not observe any nurse eggs or embryonic cannibalism in a congeneric species, *C. dilatata*, with indirect development. Therefore, the females in the present population may provide their embryos with other extraembryonic food sources other than nurse eggs, such as nutritive fluids and yolk material, as shown in many other marine gastropod species (Chaporro et al., 1999).

In conclusion, the larger females of *C. onyx* in the present study produced more egg capsules and eggs than the smaller ones. This Korean population showed a positive correlation between female body size and fecundity, as . shown in many protandric hermaphroditic calyptraeid species without nurse eggs (Hoagland, 1978). However, because the author's data was limited to a local population, sampling at other sites will be needed to get a more generalized relationship between the fecundity and the female body size in *C. onyx*.

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