

Sexual Dimorphism on the Shell of *Littorina brevicula* (Philippi) (Gastropoda: Littorinidae)

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Study on sexual dimorphism in *Littorina brevicula* should be interesting to examine that how the species prevent niche-overlap between the sexes? and how the species act differently in the reproductive roles of the sexes?

Sexual dimorphism on the shell of *L. brevicula* was examined with 211 periwinkles larger than 5 mm shell length in Pusan, Korea. Sexual dimorphism was detected in the aperture length only. Aperture length of the female was longer than that of the male.

A difference in the sexual role in the reproduction seems to be a probable explanation for the sexual dimorphism in the aperture length. The reproductive role of the male is to choose the best female and to transfer the sperm successfully by copulation, and the role of the female is to spawn their fertilised eggs into the seawater successfully. Perhaps females migrate to lower elevations on the shore than the males, so that they are submerged when they spawn. Because wave action at the lower area of the shore is stronger than that at the higher area on the shore, the females might need larger aperture size than the males to avoid dislodgement.

Key words : *Littorina brevicula*, sexual dimorphism, reproductive role, shell morphology

Introduction

Sexual dimorphism is a wide-spread phenomenon in the animal kingdom (Slatkin, 1984). When discussing the origin of sexual dimorphism, Hedrick and Temeles (1989) suggested that sexual dimorphism might be evolved from intrinsic differences - dimorphic niche - between the reproductive roles of males and females. Sexual dimorphism, therefore, is important in preventing the niche-overlap between the sexes (Voight, 1995).

In molluscs, it is not easy to tell the sex of a specimen from its shell (Hallers-Tjabbes, 1979), and also in prosobranch gastropods, sex difference of the same species are generally not pronounced (Webber, 1977; Hughes, 1986). Very few gastropod species has been reported to be sexually dimorphic in shell morphology (e.g., Cotton, 1905 in *Strombus* sp.; Pelseneer, 1926 in *Nucella* sp.) and/or shell size (e.g., Abbott, 1960 in *Strombus* sp.; Reid, 1986 in *Littoraria* spp.).

Of the morphological elements of the shell, size and shape of the shell aperture are the most important sex-related elements. For instance, Reid (1986) reported that in *Littoraria* species, aperture shape was sometimes more elongate in males than in females, and Cazzaniga (1990) noted that in *Pomacea canaliculata*, the Argentine apple

snail, relative widths of aperture were significantly different between sexes. In addition to these, there were several studies on the sexual dimorphism of the family Littorinidae: Moore (1937) in *Littorina littorea*, Lenderking (1954) in *L. angulifera*, Daguzan (1977) in *Littorina* spp. However, there has been virtually no reports on sexual dimorphism, and its ecological and adaptive significance of *Littorina brevicula* so far.

The present study attempted to: (1) determine whether sexual dimorphism exist in the shell of *L. brevicula*, and if it exist (2) discuss its ecological and adaptive significance.

Materials and Methods

For the present study, in August 1993, 211 periwinkles larger than 5 mm shell length were collected from a rocky shore in Pusan, Korea (35° 02' N, 129° 02' E), and were preserved with 5% neutralise formalin. Linear shell characters (Fig. 1) - shell length (SL), shell height (SH), shell width (SW), whorl height (WH), aperture length (AL), and aperture width (AW) - were measured with a vernier callipers to the nearest 0.01 mm. The periwinkles were then dissected to ascertain their sex based on

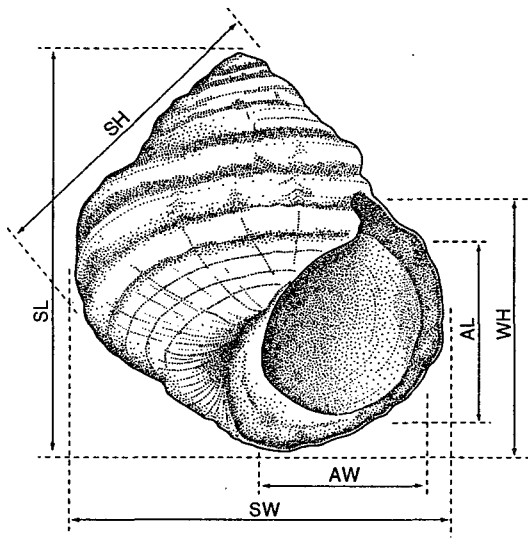


Fig. 1. Measurements of the morphometric shell characters. SL, shell length; SW, shell width; WH, whorl height; AL, aperture length; AW, aperture width; SH, shell height.

morphology of their internal reproductive organs. Ten mm SL was applied to a size criterion to classify the young and the adult group, because size of the main mating group in the field (> 70% of all mating pairs observed, $n=240$) was more than 10 mm SL (Son, in press).

Student *t*-test was applied to test sexual difference of the mean value of the measured characters. Analysis of Covariance (Zar, 1984) was applied for testing for significant differences between slopes and elevations of 2 linear regression lines (male and female) of all morphometric characters. ELEFAN (Electric Length Frequency Analysis) (Pauly and Cody, 1985) was used to calculate the mean frequency of the sexes.

Results and Discussion

Of the 211 periwinkles collected, 104 individuals (49.3%) were identified as males and 107 individuals (50.7%) were identified as females. It was noted that the specimens consisted of two size groups in the present study, the young group (SL < 10 mm) and the adult group (SL > 10 mm) both with the males and females (Fig. 2). The young group are more abundant than the adult group (Fig. 2). Sexual differences in mean size (in SL), however, were not statistically significant (student *t*-test, $p > 0.01$) in the young group as well as in the adult group. Mean sizes (in SL) of the male were 8.51 mm (6.37~9.98 mm, $n=70$) in the young group and 11.29 mm (10.01~13.33 mm, $n=34$) in the adult group; those of the female were 8.46 mm (7.08~9.70 mm, $n=66$) in the young group and 11.37 mm (10.04~14.27 mm, $n=41$) in the adult group. Table 1 summarises the measured values on the 6 morphometric characters of the shell.

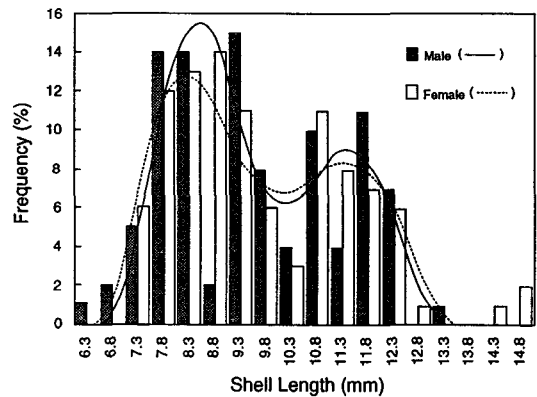


Fig. 2. Size frequency composition of the males and females. The sample ($n=211$) (> 5 mm in shell length) was collected randomly from Pusan, Korea in August 1993.

Table 1. *Littorina brevicula*. Summary of the measured values (mm) on the six morphometric characters of the shell. Samples were collected randomly from Pusan, Korea in August 1993

Characters		SL	SW	WH	AL	AW	SH
Male ($n=104$)	Mean	9.42	8.91	6.86	4.48	3.50	6.12
	SD	1.52	1.37	0.98	0.72	0.55	0.94
	Min.	6.37	5.90	4.49	2.96	2.34	4.07
	Max.	13.33	13.50	9.45	6.46	5.06	8.66
Female ($n=106$)	Mean	9.58	9.08	7.06	4.63	3.62	6.28
	SD	1.63	1.49	1.09	0.79	0.61	0.99
	Min.	7.08	6.42	5.13	3.12	2.59	4.68
	Max.	14.27	13.00	10.01	6.65	5.28	8.74

SL, shell length; SW, shell width; WH, whorl height; AL, aperture length; AW, aperture width; SH, shell height.

Table 2. *Littorina brevicula*. Summary of the coefficients of regression resulted with the model $y=ax+b$. Samples were collected randomly from Pusan, Korea in August 1993

Variables		Coefficients					
		Males (n=104)			Females (n=106)		
x-axis	y-axis	a	b	r ²	a	b	r ²
SL	SW	0.8738	0.6795	0.9318	0.8794	0.6708	0.9348
SL	WH	0.6213	1.0061	0.9322	0.6478	0.8614	0.9378
SL	AL	0.4583	0.1610*	0.9478	0.4693	0.1452*	0.9365
SL	AW	0.4376	0.2232	0.9150	0.3584	0.1872	0.9124
SL	SH	0.6038	0.4337	0.9618	0.5883	0.6508	0.9472

*These intercepts were significantly different between the sexes $p<0.01$.

SL, shell length; SW, shell width; WH, whorl height; AL, aperture length; AW, aperture width; SH, shell height.

Among the seven morphometric characters, the sexual differences were detected only from aperture length (AL). The aperture length (Fig. 3) of females was longer than that of males. There were no significant differences (student t-test, $p>0.01$) between the male and the female in the SW, WH, AW, and SH (Table 1).

When these measured characters were regressed on shell length (SL), all the slopes and intercepts showed no significant difference between the sexes except the case of intercept of regression of aperture length (AL) on SL ($p<0.01$, Table 2).

In this population of *L. brevicula*, sexual dimorphism appeared in the aperture length. This character of the female was slightly greater than that of the male. Size of circular-shaped aperture can be calculated approximately from a geometrical equation (πr^2). In this population of *L. brevicula* long aperture length meant large aperture size, and short aperture length meant small aperture size.

Demian and Ibrahim (1972) suggested that shell aperture provided the most significant sex-related differences in a mesogastropod species, *Marsia cornuarietis*. Sexual dimorphism of shell morphology involving the shape of the aperture was also observed by Cazzaniga (1990) in *Pomacea canaliculata*. Reid (1986) reported that the aperture shape of *Littoraria* species living in the mangrove forest was sometimes more elongate in males especially in the adult shells.

Discussing morphological differences between the sexes, Kitching et al. (1966) suggested that the difference could be related with their respective reproductive function such as the role in sexual intercourse. Among the elements of the shell, the aperture can be one of the most important feature probably because the aperture

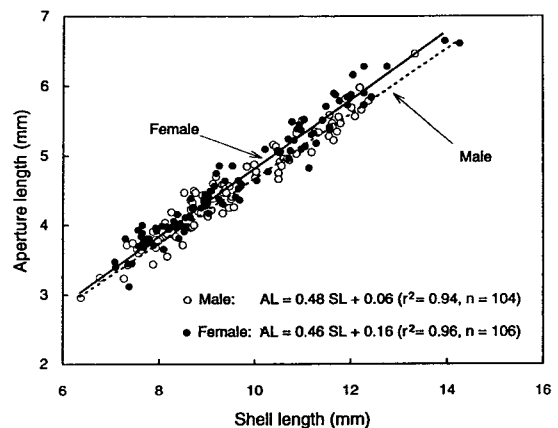


Fig. 3. Relationship between shell length (SL) and aperture length (AL) in the male and the female. For the present study, the samples (>5 mm in SL) were collected randomly from Pusan, Korea in August 1993. There was significant difference between elevation of the two regression lines ($p<0.01$).

size needed to be different for the performance of their sexual acts as suggested by Hallers-Tjabbes (1979). Kitching et al. (1966) and Struhsaker (1968) noted already that aperture size of a gastropod shell was proportional to the foot size by which the gastropod crept on the substrate.

It has been reported by several authors that high-intertidal species of Littorinidae including *L. brevicula* migrate to lower elevation on the shore in their breeding season (Kojima, 1959; Hannaford Ellis, 1985; Takada, 1992, 1995). Downward migration during the reproductive season has been regarded as an adaptive behaviour for the increase of the chance of spawning during immersion (Ohkagi, 1988). In the recent study on the

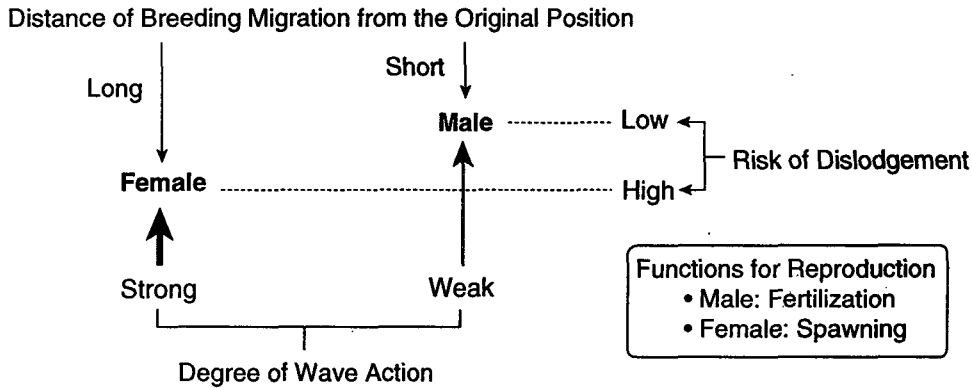


Fig. 4. A schematic model of the environmental differences facing to the male and female. A sexual dimorphism in the aperture size may be caused by the difference in sexual role.

seasonal migration pattern of *L. brevicula* in the southern Japan (Amakusa), Takada (1995) reported a dimorphic migration pattern that might be the result from the presence of two reproductively isolated sub-populations in the same area. It seems to be a common phenomenon in the littorinid species that they migrate down the shore in their breeding seasons. Migratory behaviour of *L. brevicula* was believed to be related with the different sexual role of the sexes for successful reproduction. For the sexual discrepancy in the aperture size of *L. brevicula*, breeding migration of the species related to its reproductive role seems to give a probable explanation (Fig. 4).

The reproductive role of the male is to choose the best female and to transfer the sperm successfully by copulation, and the role of the female is to receive the sperm successfully and to spawn their fertilised eggs into the seawater successfully. Although it has not been interested yet, perhaps females migrate to lower elevations on the shore than males, so that they are submerged when they spawn. Because wave action at the lower area of the shore is stronger than that at the higher area on the shore, the females might need larger aperture size than the males to avoid dislodgement.

Under the severe conditions of strong wave-action there appears to be intense selection in the females for a large foot size. Kitching et al. (1966) and Struhsaker (1968) reported that aperture size of a gastropod shell was positively correlated with the foot size. This ecological difference could help maintain sexual dimorphism in the aperture size. Boulding and Van Alstyne (1993)

showed the positive relationships between the degree of wave action and the foot size of the two *Littorina* species. If sexual difference in the aperture size was formed during ontogenic development to increase survival-rate of the spawning female after sexual maturation, the sexual difference might not be noticeable at the young stages but be noticeable at the adult stages. However, in the present study periwinkles showed the sexual difference in the aperture size between the male and female, therefore, may be fixed genetically already. For the conformation of the suggestion that the female may migrate to seaward area for successful spawning, it will be needed to study relative sex-ratio of *L. brevicula* along the vertical transect of the intertidal area in the breeding seasons.

L. brevicula did not show the difference in mean shell size between the male and female in the present study (Fig. 2). Pelseneer (1926) and Struhsaker (1966), however, had reported the larger mean size of female than that of male in the *Littorina* species (*L. pintado*, *L. picta* and *L. scabra*). The difference in mean shell size between the sexes, therefore, in the family Littorinidae is not a consistent pattern.

Acknowledgements

I am most grateful to my supervisor, Prof. S. Y. Hong, for his guidance and encouragement throughout my Ph.D. course. My deep thanks are also due to Dr. B. Johannesson, Tjärnö Marine Biological Laboratory, Sweden, for his critical comments and suggestions on

an earlier draft of this manuscript.

References

- Abbott, R.T. 1960. The genus *Strombus* in the Indo-Paific. Indo-Pacific Mollusca, 1, 33~146.
- Boulding, E.G. and K.L. Van Alstyne. 1993. Mechanisms of differential survival and growth of two species of *Littorina* on wave-exposed and on protected shores. J. Exp. Mar. Biol. Ecol., 169, 139~166.
- Cazzaniga, N.J. 1990. Sexual dimorphism in *Pomacea canaliculata* (Gastropoda: Ampullariidae). The Veliger, 33, 384~388.
- Cotton, H.S. 1905. Sexual dimorphism in *Strombus pugilis*. Nautilus, 3, 139~140.
- Daguza, J. 1977. Analyse biometrique du dimorphisme sexuel chez quelques Littorinidae (Mollusques, Gastropodes, Prosobranches). Halictis, 6, 17~40.
- Demian, E.S. and A.M. Ibrahim. 1972. Sexual dimorphism and ratio in the snail *Marisa corruarietis* (L.). Zool. Soc. Egypt, Bull., 24, 52~63.
- Hallers-Tjabbes, C.C. 1979. Sexual dimorphism in *Buccinum undatum* L. Malacologia, 18, 13~17.
- Hannaforde Ellis, C.J. 1985. The breeding migration of *Littorina arcana* Hannaforde Ellis, 1978 (Prosobranchia: Littorinidae). Zool. J. Linn. Soc., 84, 91~96.
- Hedrick, A.V. and E.J. Temeles. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. Trend Ecol. Evol., 4, 136~138.
- Hughes, R.N. 1980. Population dynamics, growth and reproductive rates of *Littorina nigrolineata* Gray from a moderately sheltered locality in North Wales. J. Exp. Mar. Biol. Ecol., 44, 211~228.
- Kitching, J.A., L. Muntz and F.J. Ebling. 1966. The ecology of lough ine. XV. The ecological significance of shell and body forms in *Nucella*. J. Anim. Ecol., 35, 113~126.
- Kojima, Y. 1959. The relation between seasonal migration and spawning of a periwinkle, *Littorina brevicula* (Philippi). Bull. Mar. Biol. St. Asamushi, 9, 183~186.
- Lenderking, R.E. 1954. Some recent observations on the biology of *Littorina angulifera* Lam. Of Biscayne and Virginia Keys, Florida. Bull. Mar. Sci. Gulf and Carib., 3, 273~296.
- Moore, H.B. 1937. The biology of *Littorina littorea* (L.). Part 1. Growth of the shell and tissues, spawning, length of life and mortality. J. Mar. Biol. Ass. U.K., 21, 721~742.
- Ohgaki, S. 1988. Vertical migration and spawning in *Nodilittorina exigua* (Gastropoda: Littorinidae). J. Ethol., 6, 33~38.
- Pauly, D. and J.F. Cody. 1985. A modification of Bhattacharyas method of mixture of normal distributions. FAO Fisheries Report, 781, 1~16.
- Pelseneer, P. 1926. La proportion relative des sexes chez les animaux et particulièrement chez les mollusques. Acad. R. Belgique, Clas. Sci., Coll. 48, 1~258 (in Dutch with English abstract).
- Reid, G.R. 1986. The Littorinid Molluscs of Mangrove Forests in the Indo-Pacific Region. Brit. Mus. (Nat. Hist.), 227 pp.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution, 38, 622~630.
- Struhsaker, J.W. 1966. Breeding, spawning, spawning periodicity and early development in the Hawaiian *Littorina*: *L. pintado* (Wood), *L. picta* Philippi and *L. scabra* (Linne). Proc. Malacol. Soc. London, 37, 137~166.
- Struhsaker, J.W. 1968. Selection mechanisms associated with intraspecific shell variation in *Littorina picta*. Evolution, 22, 459~480.
- Takada, Y. 1992. The migration and growth of *Littorina brevicula* on a boulder shore in Amakusa, Japan. Proc. Int. Symp. Littorinid Biol., 3, 277~280.
- Takada, Y. 1995. Seasonal migration promoting assortative mating in *Littorina brevicula* on a boulder shore in Japan. Hydrobiologia, 309, 151~159.
- Voight, J.R. 1995. Sexual dimorphism and niche divergence in a mid-water octopod (Cephalopoda: Bolitaenidae). Biol. Bull., 189, 113~119.
- Webber, H.H. 1977. Gastropoda: Prosobranchia. In: Reproduction of Marine Invertebrates (eds. A.C. Giese and J.S. Pearse). Academic Press, London and New York, Vol. 4, pp. 1~97.
- Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J., 2nd ed., 718 pp.

Received October 2, 1997

Accepted November 10, 1997