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レイシガイダマシモドキの繁殖と発生の様式

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Mode of Reproduction and Larval Development of the Tide Pool Dwelling Whelk *Muricodrupa fusca*

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Abstract: The mode of reproduction and development of the muricid snail, *Muricodrupa fusca*, which inhabits tide pools was investigated on the Pacific coast of central Japan. This species has direct development and produces a small number of large eggs compared with the related species *Thais clavigera*. *M. fusca* breeds from March to August leaving egg capsules in small crevices in tide pools. During mating behavior, males mount females for many hours, but the duration of copulation seems to be short. Females of *M. fusca* are much larger than their mates, and the size ratio of female to male is greater than that of *T. clavigera*. Adaptive implications of their mode of reproduction and development are discussed with reference to the environmental conditions of tide pools in which the risk of desiccation and predation seems to be small.

Keywords: *Muricodrupa fusca*, reproduction, larval development, predation.

Introduction

Marine gastropods show a broad variety of reproductive and life-history patterns. Even among related species, there are large differences not only in the mode of larval development in which some species hatch as planktonic larvae and others hatch as fully formed snails, but also in the number and size of eggs or juveniles produced by an individual female (Mileikovsky, 1975; Grahame, 1977; Webber, 1977; Giangrande *et al.*, 1994). The ecological relevance of this broad variety has been much discussed in the context of optimal strategies. Several authors have detailed the mode of development of gastropods (Thorson, 1965; Mileikovsky, 1971), especially the Littorinidae (Mileikovsky, 1975) and the Muricidae (Spight, 1977a; Gallardo, 1979) with regard to their latitudinal distribution and habitat types. However, so far the relation between the mode of development and the environ-

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ment of their habitat, such as physical conditions, availability of resources and predation pressure, has not been fully clarified.

The main habitat of the Muricidae is rocky intertidal shores consisting of heterogeneous habitats. Especially tide pools show quite different physical and biological environments from surrounding rock surface (see Metaxas and Scheibling, 1993). *Muricodrupa fusca* (Küster), a common muricid of central Japan exclusively inhabits tide pools, while *Thais clavigera* (Küster), a related species to*M. fusca*, is abundant on open rock surfaces and utilizes the pools only temporarily (Abe, 1980). *M. fusca* shows no clear change in foraging activity in accordance with the rise and fall of the tide (Yamamoto, 1993) in contrast with most animals in the intertidal area such as *T. clavigera* (Abe, 1989). The unique foraging rhythm of *M. fusca* seems to be adaptive to its life in tide pools in which environmental conditions are more stable than on exposed rock surfaces (Yamamoto, 1993). Although several authors have investigated the reproductive ecology of *T. clavigera* (Amio, 1963; Spight, 1976; Lin and Hsu, 1979; Abe, 1983), there has been little study on the mode of reproduction of *M. fusca* with reference to tide pool environments.

The present study describes the mode of reproduction and development of *M. fusca* in comparison with other species of the Muricidae, especially *T. clavigera*. Some notes on the breeding behavior of *M. fusca* are also made. The ecological implications of their mode of reproduction are discussed in relation to the environmental conditions of their main habitat, tide pools.

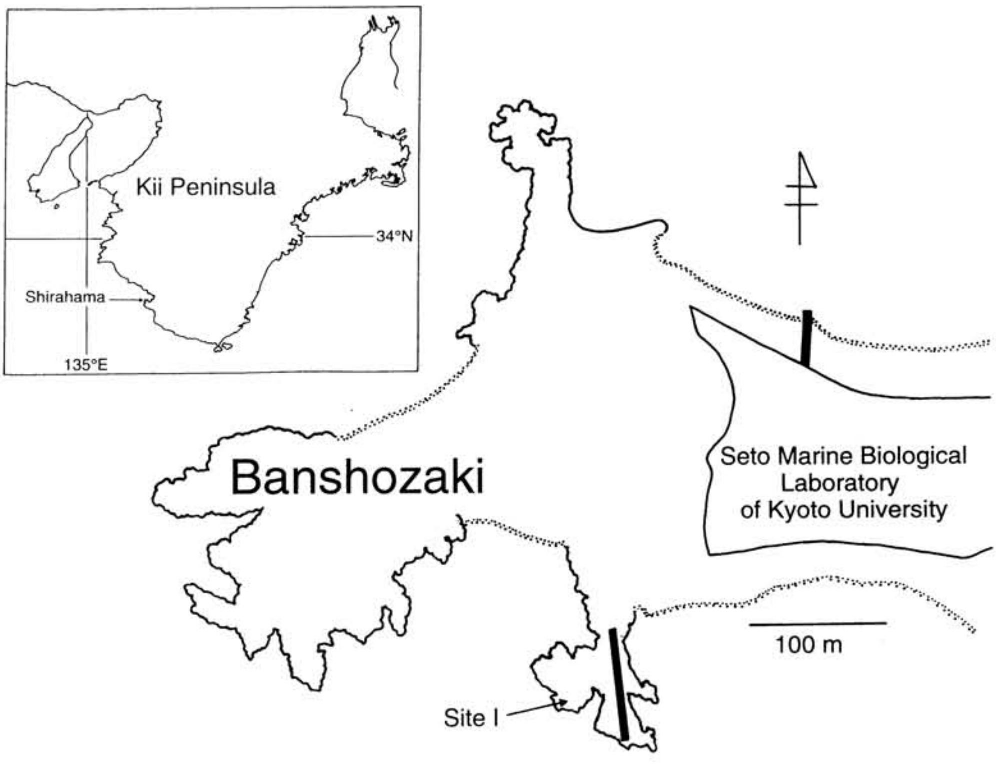

Fig. 1. Map of the study area. 調査地地図

Study Site and Methods

Study site was a rocky intertidal shore at Banshozaki, Shirahama on the west coast of the Kii Peninsula, the central Honshu (33°42′N, 135°21′E) (Fig. 1). Tidal range at the site during spring tide is 200 cm extending 100 cm above to 100 cm below the mean tide level (MTL). The breeding behavior and spawning site of *M. fusca* were investigated in the central part (Site I; area of 17.5 m^2) on a rock platform in a wave exposed shore (Fig. 1). Site I was located at 25 cm above MTL, and contained eight tide pools (Pools A to H). The size and shape of each tide pool are given in Table 1 together with the water temperature and salinity measured during a day of, fine weather on 13/8/91.

Observable breeding behaviors of this species are mounting which includes copulating, and spawning. During the mounting behavior, usually pairs form, but sometimes two or three whelks mount on one whelk. The latter case is termed multi-pairing and the former as single pairing in this study. It is assumed that mounting individuals are males. 'Copulating' was recorded only in the case in which the male inserts his genitalis into the female's apertures.

The survey of breeding activities at Site I was carried out almost every month from March 1991 to October 1992, and at 2- to 6-month intervals from February 1993 to February 1994. In all the tide pools at Site I, the number of whelks in mounting and copulating were counted every day at daytime low tide within a 1- to 3-week period around the spring tides. Once in every survey month, the shell height of all *M. fusca* found at Site I was measured and notes taken on the breeding behavior.

During the survey for breeding activity and also in July and August 1994, the spawning sites of *M. fusca* were investigated. All whelks and the substrate of tide pools at Site I

Table 1. Shape and physical conditions of the tide pools in Site. I. 調査タイドプールの形態と物理的環境条件

Mean depth is the average for the values of more than five random points in each pool. Max. and min. water temperature show the highest (around 14:00) and the lowest (around 3:00) value of each tide pool on 13 August 1991. Values for salinity are the highest around 17:00. Temperature and salinity of sea water in the morning are shown under 'Seawater' and did not vary during the day.

Pool	Area (m^2)	Mean depth (cm)	Max. depth (cm)	Water temperature (C°) Max.	Water temperature (C°) Min.	Salinity (%)
A	0.40	3.20	8.40	35.5	27.0	3.4
B	0.36	1.80	4.00	35.0	26.2	3.8
C	0.78	2.20	4.00	35.0	26.2	4.1
D	0.60	2.30	2.50	35.0	26.2	4.0
E	0.95	1.20	2.00	35.5	26.0	4.2
F	0.69	2.60	4.80	36.0	26.8	3.5
G	1.03	1.80	2.50	36.0	26.1	3.5
H	0.40	1.90	2.50	36.0	26.0	3.5
Seawater				30.0		3.0

were examined during the daytime low tide. When egg capsules or spawning females were found, the locations were recorded.

Besides the survey for breeding activities, egg capsules samples of *M. fusca* were collected in all parts of the rocky coast shown in Fig. 1 excluding Site I in July and August of both 1994 and 1995. The egg capsules of this species can be easily distinguished from those of other muricids on the basis of their distinctive shape which had been ascertained from their spawning in a laboratory. The substrate of conglomerate in the tide pools was broken to collect capsules. After fixation in 10% seawater formalin, each capsule was measured as shown in Fig. 2. Then, the capsules were dissected and eggs or juveniles in each capsule counted and measured. Fresh capsules were dissected in order to observe live juveniles and measure their shell heights.

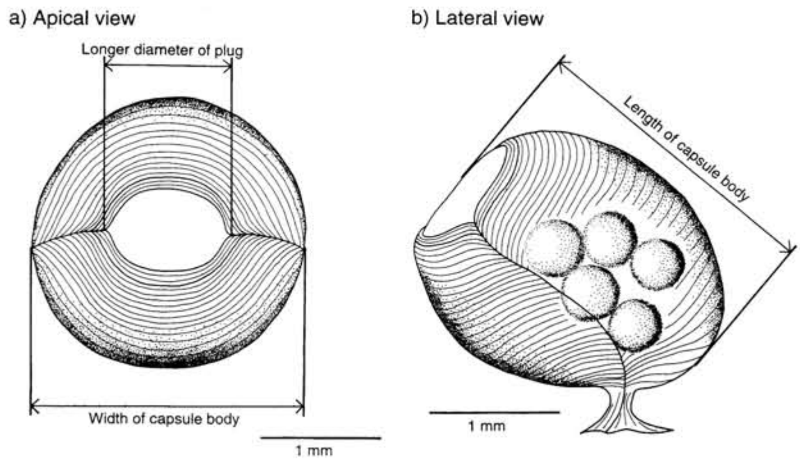

Fig. 2. Egg capsule morphology of *M. fusca* and dimensions measured. レイシガイダマシモドキの卵嚢の形態および測定部位

a) Apical view. b) Lateral view. Length of capsule body: the longest length of the capsule in the lateral view. Width of capsule body: the broadest width of the capsule as viewed from the plug. Longer diameter of plug: length between two meeting points of the upper and lower lines of the plug.

Results

Egg capsules, eggs and larvae: Some egg capsules of *M. fusca* were found in clumps, whilst others were laid singly. The maximum number of capsules in a clump was five. Egg capsules have an ellipsoid shape with a short stalk (Fig. 2). A flat pedal disk at the tip of stalk attaches to the substrate. There is an oval-shaped plug on the top of capsule. Many fine ridges encircle the surface of capsule body (Fig. 3b). The mean length and width of the capsule body are 2.30 mm ($\pm$0.22 SD, N = 19) and 2.25 mm ($\pm$0.15), respectively. The longer diameter of the plugs averaged 0.96 mm ($\pm$0.12).

Observations of the capsules spawned in the laboratory showed that the capsule was filled with a transparent gelatinoid material, and several yellow eggs could be seen inside the capsule just after being spawned (Fig. 3a). The capsules changed their color from

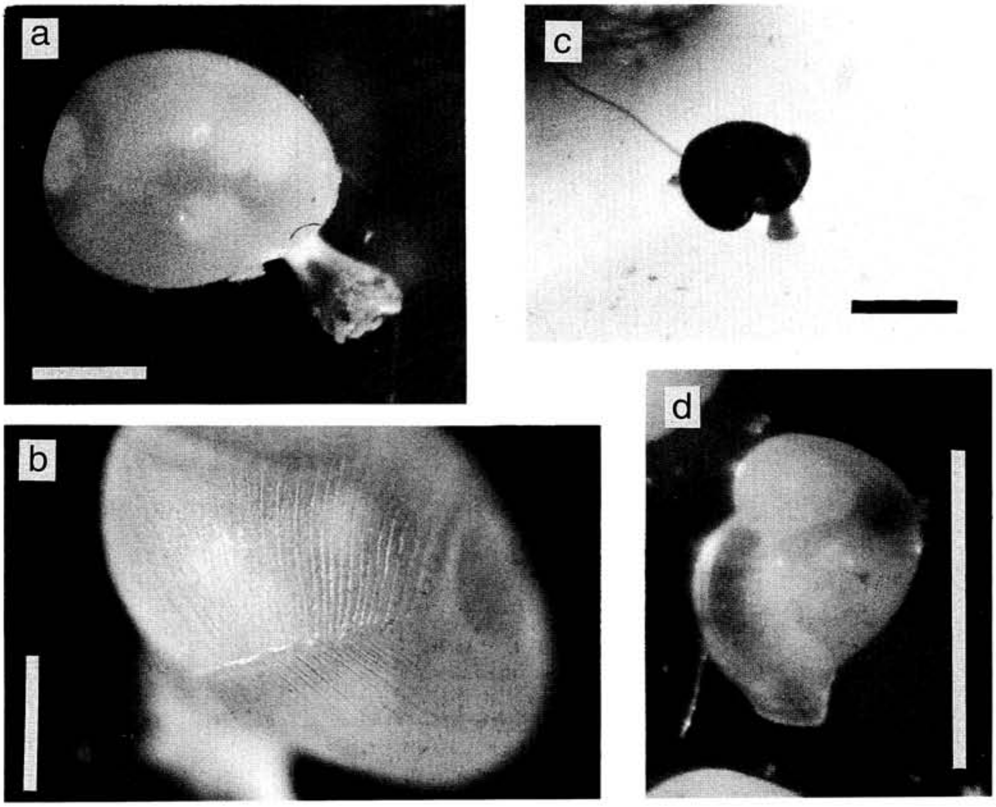

Fig. 3. Egg capsules and young of *M. fusca.* レイシガイダマシモドキの卵嚢と仔貝
a) An egg capsule soon after spawned with a stalk. b) A plug and encircling ridges of an egg capsule. c) A young snail crawling from a dissected capsule. d) A dead young snail extracted from a capsule. Bars represent 1 mm.

transparent white, semitransparent white, cream-colored and finally to light brown with development. Among the 19 egg capsules of *M. fusca* sampled from the field, 9 capsules were semitransparent white, and 3 were light brown. Eggs in the 7 other capsules seemed to have died before cleavage.

Egg capsules of a semitransparent white color had 9 to 14 eggs before the cleavage stage (Fig. 4a) with an average of 11.56 ($\pm$1.88, N = 9) eggs. The mean egg diameter showed no significant correlation to the number in each capsule (Kendall's rank correlation; N = 9, t = −0.303, p = 0.255). The diameter of all eggs from these capsules ranged from 0.10 to 0.50 mm with a mean of 0.40 mm ($\pm$0.09, N = 103). A few very small eggs (0.1 – 0.3 mm in diameter) were contained in some capsules, mixed with larger eggs. The mode of egg size was in the size class of 0.40 – 0.45 mm in which 55.3% of all eggs were included (Fig. 4b).

When capsules with light brown color were dissected, fully mobile young snails (Fig. 3c) or dead snails (Fig. 3d) were observed, and the mean size was 0.97 mm in shell height. Thus, *M. fusca* was shown to have direct development. The number of young snails in

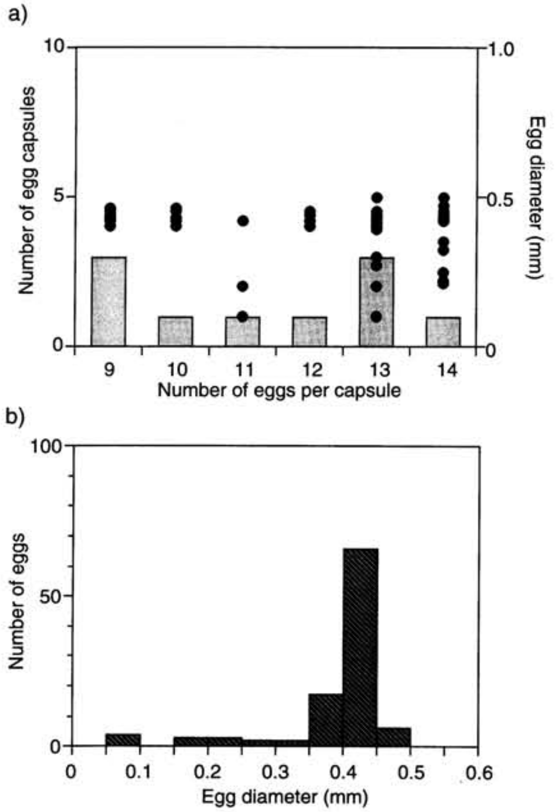

Fig. 4. Number of eggs per capsule and size of eggs of *M. fusca*.
レイシガイダマシモドキの卵嚢あたりの卵数と卵サイズ
a) Frequency of egg capsules (histograms) and egg sizes (solid circles) in relation to the number of eggs per capsule. b) Size distribution of all eggs from all capsules sampled.

each capsule was 3, 7 and 7.

Breeding behavior and breeding season: Mounting behavior was observed from October to July (Fig. 5a). The percentage of whelks showing mounting behavior gradually increased from March and reached a maximum, ca. 35% in June, and then decreased abruptly in July in each year from 1991 to 1993. The percentage fluctuated from October to February during the study period. In most pairs, males were observed to mount females, but copulation activity was not observed. Copulating pairs were found from April to July, but the percentage was less than 1% of all the mounting pairs at any one time (Fig. 5b). This low percentage indicates that males mount females for a much longer time than the actual copulating time. Spawning was observed in July or August in 1992 and 1993, but not in 1991.

Figure 6 compares the frequency distribution of the shell height between females and males showing mounting behavior from April to June 1992. Females were significantly

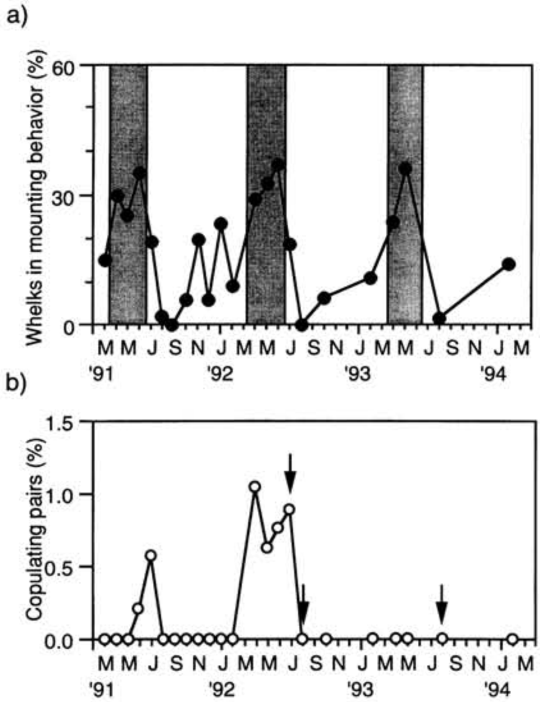

Fig. 5. Seasonal change in the frequency of breeding behavior of *M. fusca* in tide pools at Site I. Site I内のタイドプールにおける配偶行動の頻度の季節変化
a) The percentage of whelks (male and female) in mounting behavior (both single pairing and multi-pairing) to the total number of whelks in each survey month. The shaded areas indicate from April to June. b) Percentage of copulating pairs to all mounting pairs in each survey month. Arrows show the month when spawning was observed.

larger than the mounting males. Shell height of females and males ranged from approximately 12 to 18 mm and from 7 to 12 mm, respectively, and they rarely overlapped with each other. Females were always much larger than their mates (ca. 1.45 times on average, N = 42) in single pairs (Fig. 7). Shell heights of females were not correlated with those of their mates. This tendency was found in all months from April to June.

Spawning site: Egg capsules of *M. fusca* were found in small crevices between rocks in the conglomerate substrate of the tide pools, behind the tubes of the sedentary polychaete, *Pomatoleios kraussi* (Baird), or beneath empty oyster shells in tide pools. On several occasions, females were observed with their foot extending into small crevices, laying an egg capsule. No aggregations were observed during spawning. Among the 30 egg capsules which were found at Site I, 16 capsules were spawned in particular tide pools, i.e., Pools C and D (Table 2).

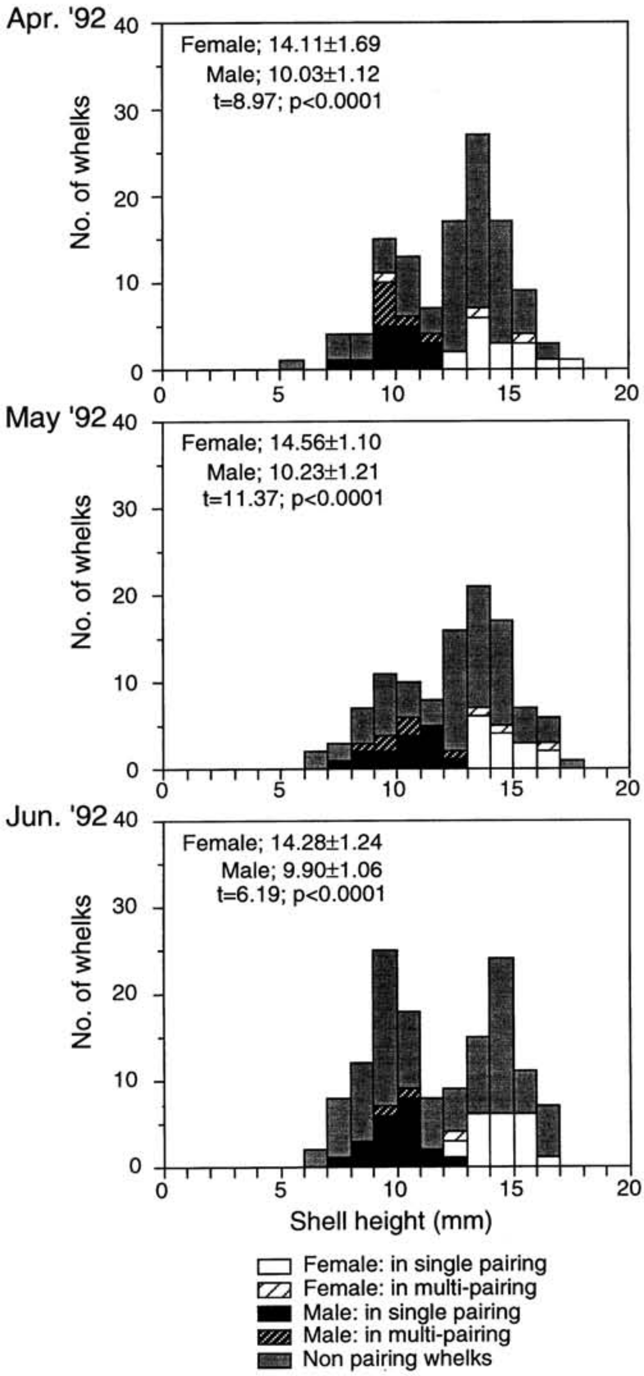

Fig. 6. Size histograms of *M. fusca* in tide pools at Site I from April to June, 1992.
レイシガイダマシモドキのサイズ分布（1992年4～6月）
Mean size (mm) ± SD of females and males in mounting groups are given as well as results from t-test between their sizes.

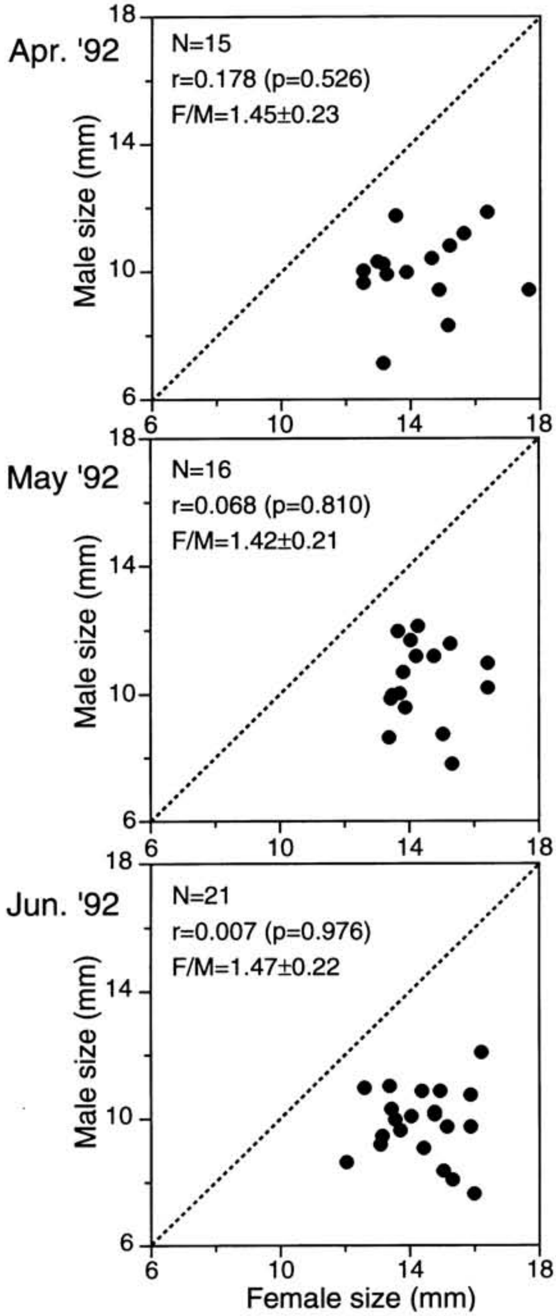

Fig. 7. Comparison of size (shell height) between females and males in each single pair from April to June, 1992.
1対1ペア内の雌雄のサイズ比較（1992年4～6月）
Sample size (N), correlation coefficient (r) and mean ratio (± SD) of female size to her mate size (F/M) are also given in each chart.

Table 2. Number of egg capsules newly found in each tide pool at Site I during each survey day.
調査日ごとに各タイドプールで新たにみられた卵嚢の数
Figures in parentheses indicate the area (m^2) of each tide pool.

Date	Pool and Area ($/m^2$)							
	A (0.40)	B (0.36)	C (0.78)	D (0.60)	E (0.95)	F (0.69)	G (1.03)	H (0.40)
1992 20 Jul.	—	—	1	—	—	—	—	—
21 Jul.	—	—	—	—	1	—	—	—
22 Jul.	—	2	—	1	—	—	1	—
15 Aug.	—	—	—	3	—	—	—	—
16 Aug.	—	—	—	2	—	—	—	1
17 Aug.	—	—	1	1	—	—	—	—
1993 7 Aug.	—	—	—	—	—	—	1	—
1994 20 Jul.	—	—	1	—	1	—	1	—
25 Jul.	1	—	1	1	1	1	2	—
2 Aug.	—	—	1	—	—	—	—	—
8 Aug.	—	—	1	2	—	—	—	1
Total	1	2	6	10	3	1	5	2

Discussion

The present study found that *M. fusca* develops directly, i.e., crawling young snails emerge from egg capsules lacking a planktonic stage. There are many reports on muricids with direct development, e.g., *Thais emarginata, T. canaliculata* (Houston, 1971), *T. lamellosa* (Spight, 1976), *Ocenebra japonica* (Amio, 1963) and other species (e.g., Spight, 1977a; D'Asaro, 1991). In contrast, *T. clavigera* shows indirect development in which larvae hatch as veligers (Lin and Hsu, 1979; Abe, 1983) as well as some muricids (Amio, 1963; Spight, 1977a; Barkati & Ahmed, 1983; D'Asaro, 1991). It is common among gastropods that are related species, even within the same genus, to have different modes of development from each other (Mileikovsky, 1975; Gallardo, 1977; Grahame, 1977).

In general, muricid species with direct development produce larger eggs than those with indirect development, i.e., 0.16 to 0.92 mm for the former vs. 0.08 to 0.32 mm for the latter (Spight, 1976). Mean egg size of *M. fusca* (0.43 mm) is intermediate among the species of direct development and much larger than that of *T. clavigera* (0.19 mm; Amio, 1963).

The number of eggs per capsule of *M. fusca* (9 to 14: Fig. 4) is clearly less than that of other species with direct development such as *O. japonica* (more than 1000: Amio, 1963), and also less than *T. clavigera* (160 to 220: Amio, 1963). The egg number per capsule does not necessarily indicate the number of juveniles that will hatch per capsule, because in some muricid species nurse eggs do not develop but supply yolk material to the other embryos. Among muricids with direct development, the percentage of nurse eggs varies from 60% (*Acanthina spirata*) to more than 99% (*O. japonica*) (see Spight, 1976). In *M. fusca*, 3 or 7 young snails grow up in each capsule, while capsules before the cleavage stage had 9–14 eggs (Fig. 4a). So, it is probable that the small eggs (0.1–0.3 mm in diameter) in the capsules are nurse eggs. Since *T. clavigera* has no nurse eggs (Spight, 1976), the number of viable offspring per capsule of *M. fusca* is far fewer than *T. clavigera*. However the number may be comparable with that of *T. emarginata* (ca. 10: Houston, 1971) and *T. canaliculata* (ca. 6: Houston, 1971) and also that of *O. japonica* in which less than 1% of more than 1000 eggs are viable.

Assuming that the capsules in one egg mass were spawned by a single female, the number of capsules per spawning event of *M. fusca* seems to be as low as *T. emarginata* and *T. canaliculata* (i.e., 6–9; Houston, 1971). This assumption is supported as *M. fusca* does not form any aggregations for spawning, and they spawned in small crevices, where due to physical size limitations only one female is thought to be able to extend her foot for spawning. From this *M. fusca* appears to produce larger-sized but a smaller number of offspring per spawning than *T. clavigera*, and has medium sized and comparable number of offspring in each spawning to other muricid species with direct development.

Emson (1985) has pointed out that direct development is favored among tide pool specific species. However, he did not discuss the relationship between the environmental factors in the tide pools and their mode of development. Any mode of development will be a result which derived from a balance between the advantages and disadvantages of that mode of reproduction within the physical and biological environment of the tide pools. One of disadvantages of direct development is the restriction for dispersal, but it can be said that the restriction enables offspring to stay in the patch habitat where their parents inhabit. A long period of pre-hatching is necessary for direct development and this may be disadvantageous where the predation on eggs by other carnivorous gastropods (Abe, 1983) or some physical stress, e.g., desiccation are apparent. *T. emarginata* which develops directly requires 60 days from spawning to hatching (Rawlings, 1995), while 4 *Thais* species with indirect development take only 16–22 days for this process (Barkati and Ahmed, 1983). In tide pools, predation and physical stress are less severe than outside the pools (Yamamoto, 1993). Therefore, the disadvantages of direct development seem to be less for *M. fusca* which mainly inhabits tide pools than for other muricids living on open surfaces of the rocky intertidal.

Site selection for spawning may be crucial for species with small numbers offspring which show direct development requiring a long period prior to hatching (see Spight, 1977b). Concentration of their spawning on particular tide pools, Pools C and D in Site I (Table 2), suggests a deliberate selection of spawning sites. Although water temperature and salinity were very similar among the eight tide pools at Site I (Table 1), the substrate of Pools C and D appeared to offer a more complex substrate compared with other pools owing to the abundance of sessile animals and the uneven surface of the conglomerate (Yamamoto, unpublished). Females seemed to spawn preferentially in the interstices between the tubes of polychaetes and in small crevices between rocks in the conglomerate substrate. These sites must be adequate for eggs as a shelter from predators. It is necessary to survey for abundance of sessile animals and the fine topographic features of the substrate with detailed data of the spawning site in tide pools in order to clarify the site selection for spawning in this species.

Although the size and age at maturity of *M. fusca* was not examined in the present study, sizes of females and males in mounting behavior suggest that they mature at the size of about 12 mm and 7 mm in shell height, respectively. Pairing females were larger than their mates as noted in other gastropods (see Webber, 1977). The mean ratio of female size to her mate's (ca. 1.45: Fig. 7) is a much larger than that of *T. clavigera* (1.14: Abe, 1983). Small males might be favored in species such as *M. fusca*, which require much longer time for mounting than copulation time. This explanation is acceptable under the condition where there is no competition among males for females. Although no competitive interactions among males of *M. fusca* were observed in the field and laboratory (Yamamoto, unpublished), multi-pairing in which two or three males mounted one female suggests that there are some interactions among males for females. This argument, however, is made assuming that the mounting whelks were always males. This assumption must be clarified by an anatomical and histological study before further clarification of the reproductive tactics of *M fusca* is possible.

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要　旨

タイドプールに棲む肉食性巻貝レイシガイダマシモドキ（アクキガイ科）の，繁殖と発生の様式を調査した。本種は，直達発生であり，近縁種であるイボニシに比べて大卵少産である。繁殖期は３月から８月ごろまでであり，タイドプールの小さなくぼみの中に卵嚢を産みつける。繁殖行動中は，雄が雌にマウントするが，マウンティングの時間は実際の交尾時間に比べて極端に長いと考えられる。雌は雄に比べて大きく，雌雄のサイズ比はイボニシよりかなり大きい。このような繁殖と発生様式の適応上の意味について，乾燥や捕食による危険が少ないであろうタイドプールの環境と関連づけて議論した。

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