

Habitat utilization and seasonal pattern of movement of the intertidal whelk *Muricodrupa fusca*

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ABSTRACT

The micro-habitat, size composition, and movement pattern of the muricid snail *Muricodrupa fusca* were investigated. In contrast to two other muricids, *Morula musiva* and *Thais clavigera*, this species exclusively inhabits tidepools and its shell size is small. The adaptive implications of its small size are discussed in relation to the environmental conditions of its main habitat. Small size presents some advantages for living in tidepools with limited food resources. The major disadvantages of a small size, namely low tolerance to desiccation and increased vulnerability to predators, appear to be avoided by inhabiting tidepools. *Mu. fusca* moved landward in September and seaward in February, and reproduction is proposed as the reason for this migration.

Key words: tidepool, intertidal, habitat, seasonal migration, *Muricodrupa fusca*

INTRODUCTION

Rocky intertidal shores consist of heterogeneous habitats, which are distributed not only along a vertical gradient (Connell 1961) but also in patches (see Newell 1970). A tidepool is one of patchy habitats and shows quite different environment conditions from the surrounding rock surface. Some intertidal organisms utilize tidepools as their permanent habitat (Dethier 1980; Huggett & Griffiths 1986; Grahame & Hanna 1989; Metaxas & Scheibling 1993; Trowbridge 1994), while other organisms use both tidepools and other habitats (Emson 1985). Some herbivorous gastropods permanently inhabit tidepools due to the presence of abundant algae (Underwood 1975, 1976). Many carnivorous gastropods are reported to use tidepools as shelter from wave action, desicca-

tion, or predation (Menge 1978; Moran 1985b; Fairweather 1988), but there are no reports of carnivorous gastropods that spend their entire lives in tidepools. The lack of such reports may be due to the tendency of papers on the ecology of rocky intertidal predators to concentrate on predators preying on sessile animals on exposed rock surfaces (Menge 1976; Hughes & Burrows 1991, 1993).

Three species of Muricidae, *Muricodrupa fusca* (Küster), *Morula musiva* (Kiener), and *Thais clavigera* (Küster), are common species along the rocky coasts of central Japan. Abe (1983, 1989a, b) presented the distribution, seasonal migration, reproduction, and foraging ecology of *Mo. musiva* and *T. clavigera*, and Yamamoto (1993, 1997) reported the reproduction and foraging ecology of *Mu. fusca*.

Muricodrupa fusca occurs in the upper and middle intertidal zones (highest of all eight species of Muricidae on this study site), and *Mo. musiva* and *T. clavigera* inhabit a wide range of intertidal zones (Abe 1980). *Mu. fusca* has

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direct development, hatching as crawling snails (Yamamoto 1997), while *T. clavigera* hatches as veligers (Abe 1983).

Muricodrupa fusca does not show any clear changes in foraging activity with change in tide (Yamamoto 1993), in contrast to the other two muricids (Abe 1989a). Yamamoto (1993) discussed the adaptive implications of this unique foraging pattern of *Mu. fusca* in light of the environmental conditions found in tidepools (low risk of desiccation and predation). This species feeds on gastropods, especially limpets (Yamamoto 1992), while the other two muricids prey on barnacles and mytilids (Abe 1980). *T. clavigera* especially prefers the barnacle, *Chthamals challengerii* (Hoek), and *Mo. musiva* favors the mytilid *Septifer virgatus* (Wiegman) (Abe, 1989a).

Abe (1980) reported that *Mu. fusca* mainly inhabits tidepools; however, there are no quantitative studies on the micro-distribution of this species. This study analyzed the micro-distribution of *Mu. fusca* in relation to the presence of tidepools. The results are compared with data from the two other mentioned muricids in order to determine *Mu. fusca*'s pattern of habitat use. Shell height frequency was also compared among the three species. The seasonal movement patterns of *Mu. fusca* between tidepools and the ecological importance of this movement in relation to reproduction are described in this paper. The ecological advantages of the behavioral and morphological characteristics exhibited by *Mu. fusca* are discussed in relation to a permanent life in tidepools.

MATERIALS AND METHODS

Materials

At the study site, the following putative prey species of the muricids were found: several species of limpets and littorinids, *C. challengerii*, and a mytilid, *Hormomya mutabilis* (Gould).

Abe (1985) distinguished two forms of *T. clavigera*, Form C and Form P, based on differences in their shell morphology. However, the two forms were not distinguished in the present study, because some individuals had on intermediate morphology.

Study Site

The study site was a wave-exposed rocky shore at Banshozaki in Shirahama on the west coast of the Kii Peninsula in central Japan (33°42'N, 135°21'E). The tidal range at spring tide extends from 100 cm above to 100 cm below the mean tide level (MTL). The above-mentioned studies on three muricids (Abe 1980, 1983, 1989a, b; Yamamoto 1992, 1993, 1997) have been conducted along the shore that includes the study site of this paper.

Six cross-shore transects (Transects a to f) were set from 15 cm above MTL to 70 cm below MTL. The highest points of Transects a, e and f were on the upper margin of the rocky shore. The transects varied in length, from 8 to 16 m depending on the slope.

The main observation area for intensive surveys was set up on a rock platform in a wave-exposed area from 25 cm above to 15 cm below MTL. The area was separated into two sub-areas, Sites I and II (Fig. 1). Site I was a flat region in the center of the platform at 25 cm above MTL with an area of 17.5 m², and Site II comprised the remaining portion of the main observation area. There were eight tidepools in Site I (Pools A to H) and 29 pools in Site II (Fig. 1). The depths of Pools A to H were similar

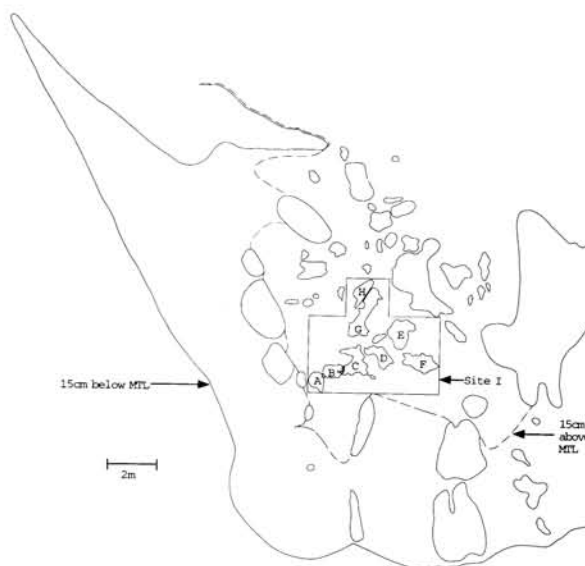


Fig. 1. Map of tidepools in the main observation area. Isoclines for shore heights of 15 cm above and 15 cm below MTL, the borders of Site I, and outlines of every tidepool are shown. A-H: 8 tidepools in Site I.

Table 1. Shape and physical condition of tidepools studied in Site I. Mean depth is an average of the values at more than five random points in each pool. Max. and Min. water temperatures show the highest (around 14:00) and the lowest (around 3:00) value for each tidepool on one day of summer and winter. Salinity is the highest value recorded on each day (around 17:00). Temperature and salinity of sea water in the morning of each day are shown at the bottom, and did not vary during the day.

Pool	Area (m ²)	Mean depth (cm)	Max. depth (cm)	Water temperature (C°)				Salinity (%)	
				Summer (13 Aug. '91)		Winter (18 Feb. '92)		Summer (13 Aug. '91)	Winter (18 Feb. '92)
				Max.	Min.	Max.	Min.		
A	0.40	3.20	8.40	35.5	27.0	19.0	9.8	3.4	3.6
B	0.36	1.80	4.00	35.0	26.2	16.8	7.9	3.8	4.1
C	0.78	2.20	4.00	35.0	26.2	18.2	8.9	4.1	3.9
D	0.60	2.30	2.50	35.0	26.2	17.1	9.0	4.0	4.0
E	0.95	1.20	2.00	35.5	26.0	17.2	8.1	4.2	4.0
F	0.69	2.60	4.80	36.0	26.8	17.0	8.3	3.5	3.6
G	1.03	1.80	2.50	36.0	26.1	18.1	7.8	3.5	3.6
H	0.40	1.90	2.50	36.0	26.0	18.0	7.9	3.5	3.5
Sea water				30.0		15.0		3.0	3.1

and shallow (Table 1). The physical conditions, water temperature and salinity were very similar among the eight tidepools. Four transects (Transects p to s) were set in Site I, with Transects p and q running along the landward-seaward axis of the shore and Transects r and s making right angles with Transects p and q.

The main observation area and the highest regions of the transects included the tidal range containing the main population of *Mu. fusca*. No muricids other than the focal three species occurred in the main observation area.

Field Study

Field surveys to measure the habitat use of the three muricids were carried out in June and December, 1994. All whelks of the three species were sampled at intervals of 1 m on Transects a to c, e, and f using a 1 m² quadrat (1 m × 1 m). Transect d had a very high density of whelks, so the sampling on this transect was conducted at intervals of 0.5 m using a 0.25 m² quadrat (0.5 m × 0.5 m). Data was collected on each whelk's location (inside or outside of a tidepool) and shell height.

The density of each muricid species was measured at Site I almost every month from

May, 1991, to August, 1992, and again in May, 1993. The number of whelks in the tidepools and on the surrounding rocky surface at Site I was counted during every survey. In addition, the number of *Mu. fusca* in the tidepools was counted every month from June, 1990, to January, 1991, and at 2- to 6-month intervals from October, 1992, to February, 1994. The shell height of all *Mu. fusca* found was measured once almost every month from February to October, 1992.

The movement of *Mu. fusca* between tidepools was investigated with a marking experiment conducted from April, 1991, to February, 1992. All whelks found in the pools of Site I were individually marked with a color code using vinylose paint ('Paint Marker', Mitsubishi Paint Co., Ltd.). The marks were coated with cyano-acrylate adhesive ('Aron-Alpha', Konishi Co., Ltd.) to prevent them from peeling off. The whelks were returned to the tidepools where they were caught and observed every day during a 1- to 3-week period around one or two spring tides. New whelks (without marks) in the survey site were marked once during every survey month. The numbers of *Mu. fusca* that moved between tidepools were calculated to

match changes in the density in each tidepool with the migration. These numbers were calculated by multiplying the total number of whelks in each tidepool by the migration rate of marked whelks.

The abundance of putative prey species was surveyed along the four transects (Transects p to s) set in Site I. Two to six quadrats of $2 \times 10^{-4} \text{ m}^2$ ($0.01 \text{ m} \times 0.02 \text{ m}$) were placed in the pools and on open rock surfaces at intervals of 0.5 m along each transect. All quadrats were photographed in December, 1994, and sessile animals such as barnacles and mytilids were counted on the photographs. The mobile prey of *Mu. fusca*, were counted littorinids and limpets, in each quadrat along Transects p and q during the same month.

RESULTS

Abundance of prey species

Limpets mainly inhabited the tidepools, while barnacles were exclusively distributed on open rock surfaces (Table 2). Littorinids were found mainly outside the pools. The density of mytilids did not differ significantly between the pools and open rock surfaces. Mytilids occurred on Transect d, along which the micro-distribution of the three muricids was surveyed. Mytilids covered 11.4% of the substrata outside the tidepools, but were not found inside the

pools.

Distribution of three muricid species

Densities of all three muricids were higher in the tidepools than outside the pools (Fig. 2ab) in June and December, 1994, and these differences were significant except for *T. clavigera* in June (Table 3). The density of *Mu. fusca* in the pools was much higher than for the two other species. *Mo. musiva* and *T. clavigera* were abundant outside the pools in the lower intertidal zone (Transects b and d), especially in June, while *Mu. fusca* was very rare outside the pools (Fig. 2ab). When *Mu. fusca* were found outside the pools, it mostly occurred in the beds of the mytilid *H. mutabilis*. No distinct differences in vertical distribution could be found among the three species.

At Site I, the density of *Mu. fusca* ranged from 10 to $80/\text{m}^2$ in the tidepools, which was much greater than outside the pools (i.e., $0-10/\text{m}^2$) except in December, 1991 (Fig. 3). *Mo. musiva* and *T. clavigera* were rare (i.e., $2.3/\text{m}^2$ and $0.4/\text{m}^2$ at the maximum, respectively) in both habitats.

Size composition of three muricid species

The mean shell height of each species did not differ significantly between the pools and open rock surfaces during June and December, 1994, except that *Mu. fusca* showed a significant difference along Transect d in December ($12.29 \pm$

Table 2. Comparison of mean prey density ($/10 \times 20 \text{ cm}^2$) between tidepools (in) and open rock surface (out) in December, 1994. Limpets and littorinids were not surveyed along Transects r and s.

Transect		Limpets			Barnacles			Littorinids			Mytilids		
		N	Mean \pm SD	U-test	N	Mean \pm SD	U-test	N	Mean \pm SD	U-test	N	Mean \pm SD	U-test
p	in	2	38.0 \pm 2.8	U=8	2	0	U=8	2	6.5 \pm 9.2	U=8	2	7.0 \pm 9.9	U=7
	out	4	10.8 \pm 6.8	P>0.05	4	522.8 \pm 188.6	P>0.05	4	201.0 \pm 186.7	P>0.05	4	56.8 \pm 47.2	P>0.05
q	in	5	39.6 \pm 8.6	U=20	5	0.8 \pm 0.5	U=20	5	3.6 \pm 7.0	U=20	5	60.4 \pm 54.8	U=12
	out	4	13.8 \pm 16.0	P<0.05	4	462.0 \pm 105.7	P<0.05	4	251.0 \pm 71.5	P<0.05	4	36.3 \pm 20.3	P>0.05
r	in	-	-	-	2	0	U=12	-	-	-	2	16.0 \pm 15.6	U=11
	out	-	-	-	6	654.5 \pm 122.6	P<0.05	-	-	-	6	63.0 \pm 27.3	P>0.05
s	in	-	-	-	3	12.3 \pm 20.5	U=9	-	-	-	3	81.3 \pm 67.5	U=6
	out	-	-	-	3	513.7 \pm 123.3	P<0.05	-	-	-	3	38.0 \pm 17.8	P>0.05
Total	in	7	39.1 \pm 7.2	U=56	12	3.4 \pm 10.3	U=204	7	4.4 \pm 4.0	U=56	12	49.3 \pm 53.1	U=119
	out	8	12.3 \pm 11.5	P<0.01	17	553.4 \pm 147.7	P<0.001	8	226.0 \pm 133.6	P<0.01	17	50.8 \pm 30.2	P>0.05

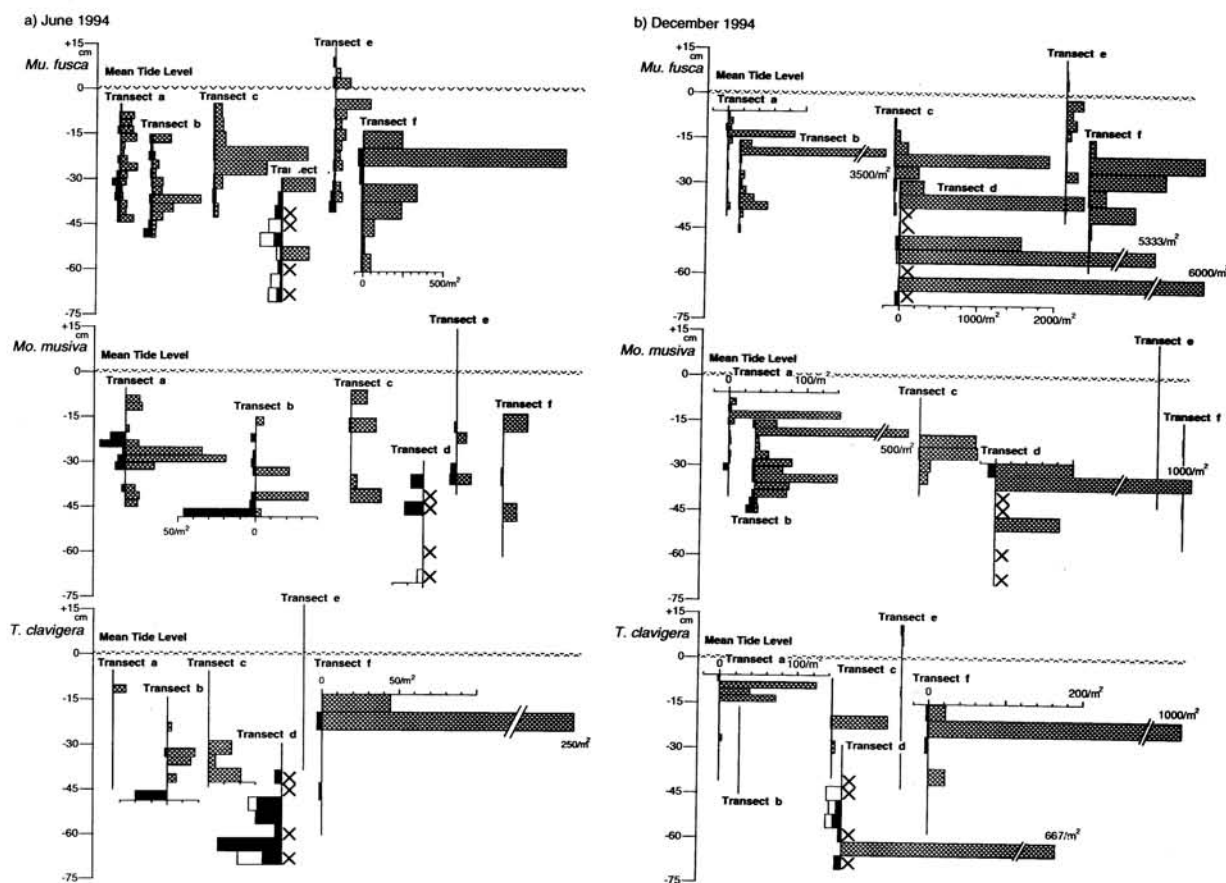


Fig. 2. Densities of three muricids, *Muricodrupa fusca*, *Morula musiva*, and *Thais clavigera*, along 6 transects in a) June, 1994, and b) December, 1994. Bars to right of each vertical line show densities inside tidepools. Solid and open bars to left of each line indicate densities on open rock surfaces and on mussel beds outside the pools, respectively. × indicates a quadrat with no pools.

Table 3. Comparison of density of three muricids between the pools (in) and open rock surfaces (out). 'Result of test' refers to Wilcoxon signed-rank test.

in>out ; Number of quadrats in which density was greater inside than outside the pools.

out>in ; Number of quadrats in which density was lower inside than outside the pools.

Month	Total No. of quadrats	<i>Muricodrupa fusca</i>		<i>Morula musiva</i>		<i>Thais clavigera</i>	
		in>out	out>in	in>out	out>in	in>out	out>in
Jun.1994	68	49	15	20	11	10	5
				-5.15	-2.65	-8.52	ns
				p<0.001	p<0.01		
Dec.1994	68	54	4	25	5	12	5
				-6.43	-3.96	-2.25	p<0.05
				p<0.001	p<0.001		

2.81 mm (N=131) in pools vs. 10.99 ± 2.72 mm (N=36) on open rocks, $t=3.07$, $p<0.05$). Whelk size showed no significant correlation or very small coefficients of correlation with height on the shore (Table 4).

Muricodrupa fusca had the lowest shell

height of the three species (Fig. 4), ranging from 3 to 19 mm and exhibiting a bimodal distribution with peaks at 10 mm and 15 mm. The shell height of *Mo. musiva* ranged from 5 to 25 mm and was unimodal, although whelks smaller than 10 mm were very rare. The size

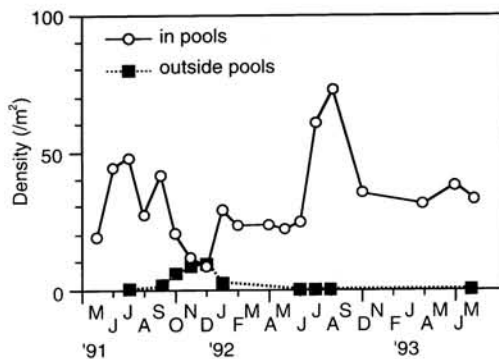


Fig. 3. Densities of *Muricodrupa fusca* at Site I from 1991 to 1993. Densities inside and outside the pools are shown separately.

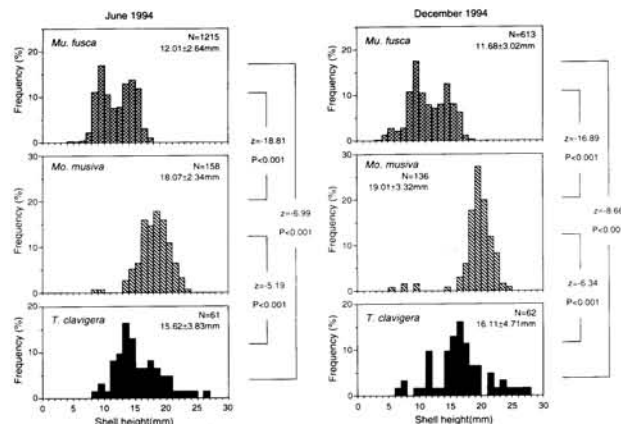


Fig. 4. Size distributions of three muricid species, *Muricodrupa fusca*, *Morula musiva*, and *Thais clavigera*, along 6 transects in a) June, 1994, and b) December, 1994. Sample size and mean \pm SD are shown in each chart. Results of Mann-Whitney U-test are also indicated.

Table 4. Correlation between the shell height of whelks and the shore height of the site where they were found : results of Kendall's rank correlation. Data for whelks inside and outside the tidepools were lumped together except for *Mu. fusca* along Transect d in December, where its mean shell height was significantly different between the two habitats.

Month	Transect	<i>Muricodrupa fusca</i>			<i>Morula musiva</i>			<i>Thais clavigera</i>			
		N	τ	P	N	τ	P	N	τ	P	
Jun.1994	Total	1215	0.03	ns	158	0.07	ns	61	0.10	ns	
Dec.1994	Transect d	(in)	131	-0.04	ns	12	0.30	ns	20	-0.17	ns
		(out)	36	0.04	ns						
	Total (without d)	613	0.16	p<0.001	136	-0.05	ns	62	0.18	p<0.05	

distribution of *T. clavigera* was also unimodal, with a peak at 15 mm, but it had a wider range of shell heights (i.e., 6-28 mm) than *Mo. musiva*. Although the maximum size of *T. clavigera* was larger than that of *Mo. musiva*, the average shell height of the latter species was larger by the Mann-Whitney U-test.

Movement of *Mu. fusca*

The density of *Mu. fusca* changed seasonally in the tidepools of Site I and varied between tidepools (Fig. 5). Almost no whelks were found in Pools A to D from August/September to February; while whelks occurred in Pools E to H during every season from 1990 to 1992, densities decreased from September, 1991, to February, 1992. For the sake of convenience,

the periods from September to February and from March to August will hereafter be referred to as the 'cool period' and 'warm period', respectively.

Table 5 shows the movement of *Mu. fusca* between the tidepools at Site I and the surrounding area. In late July and August when the whelk density decreased in Pool D (Table 5a, b and c); calculation indicate that 22 whelks arrived to Pool D from Pools A, B, and C, and 52 whelks moved from Pool D to Pools E, F, and G. During this period when the whelk density increased in Pools E, F, and G; a large number of whelks moved from Pools C and D, and remained in Pools E, F, and G. These results indicate that many whelks moved from seaward pools to landward pools (Fig. 1). The density

Habitat of *Muricodrupa fusca*

Table 5. Movements of individuals of *Muricodrupa fusca* between tidepools in and around Site 1. N : total number of whelks in each tidepool on the first day of each survey period. Figures in right nine columns show estimated numbers of whelks that moved from pools shown in left column to pools shown in the column headings during each period. Numbers of moved whelks were calculated by multiplying 'N' by the migration rate of marked whelks between the two pools. The summed total of figures in the right columns does not equal 'N' in each column of some tables (e.g., the second column of Table a) because of this method. "?" indicates no data of movement because there were no marked whelks in the pool on the first day.

a) 24 Jul.-25 Jul. 1991											d) 20 Aug.-7 Sep. 1991											
from	N	A	B	C	D	E	F	G	H	Site 1	from	N	A	B	C	D	E	F	G	H	Site 1	
A	28	16	4	4	4	0	0	0	0	0	A	0										
B	27	0	14	8	3	0	3	0	0	0	B	0										
C	41	0	2	32	4	2	0	2	0	0	C	0										
D	82	0	0	4	50	18	7	4	0	0	D	0										
E	28	0	0	0	9	19	0	0	0	0	E	1	?	?	?	?	?	?	?	?	?	?
F	50	0	0	0	4	0	46	0	0	0	F	21	0	0	0	0	4	17	0	0	0	0
G	58	0	2	0	0	0	0	51	5	0	G	36	0	0	0	0	18	0	14	5	0	0
H	13	0	0	0	0	0	0	0	13	0	H	13	0	0	0	0	7	0	7	0	0	0

b) 30 Jul.-31 Jul. 1991											e) 23 Jan.-12 Feb. 1992											
from	N	A	B	C	D	E	F	G	H	Site 1	from	N	A	B	C	D	E	F	G	H	Site 1	
A	3	3	0	0	0	0	0	0	0	0	A	0										
B	9	0	0	9	0	0	0	0	0	0	B	0										
C	16	0	0	0	11	0	5	0	0	0	C	3	?	?	?	?	?	?	?	?	?	?
D	37	0	0	0	16	8	8	4	0	0	D	2	?	?	?	?	?	?	?	?	?	?
E	24	0	0	0	0	24	0	0	0	0	E	65	0	0	0	5	58	0	2	0	0	0
F	47	0	0	5	5	0	38	0	0	0	F	18	0	0	0	0	0	18	0	0	0	0
G	36	0	0	0	0	0	0	18	18	0	G	20	0	0	0	0	0	0	14	6	0	0
H	10	0	0	0	0	0	0	0	0	10	H	10	0	0	0	0	0	0	3	7	0	0

c) 12 Aug.-13 Aug. 1991											f) 15 Feb.-16 Feb. 1992											
from	N	A	B	C	D	E	F	G	H	Site 1	from	N	A	B	C	D	E	F	G	H	Site 1	
A	1	0	0	0	0	0	0	0	0	1	A	0										
B	1	0	0	0	0	0	0	0	0	1	B	0										
C	2	0	0	0	0	0	0	0	0	2	C	3	0	0	3	0	0	0	0	0	0	0
D	13	0	0	0	3	0	3	0	0	7	D	8	0	0	0	8	0	0	0	0	0	0
E	19	?	?	?	?	?	?	?	?	?	E	63	0	0	0	2	61	0	0	0	0	0
F	65	0	0	0	0	0	39	13	0	13	F	21	0	0	0	0	0	21	0	0	0	0
G	105	0	0	0	0	0	0	87	0	18	G	19	0	0	0	3	0	0	13	3	0	0
H	72	0	0	0	0	0	0	24	48	0	H	7	0	0	0	0	0	0	4	4	0	0

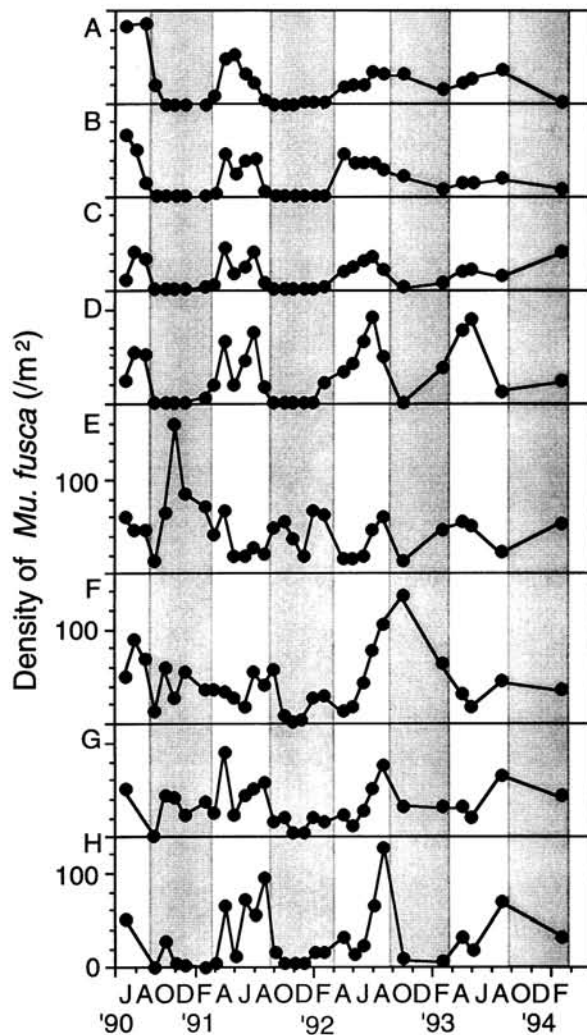


Fig. 5. Seasonal changes in densities of *Muricodrupa fusca* in 8 tidepools of Site I. Shaded areas cover the 6 months from September to February, which is referred to in the text as the cool period.

in Pool D increased from January to February, when 10 whelks evidently moved from Pool E or G to Pool D, although movement between tidepools was very rare (Table 5e and f). Most marked whelks stayed within Site I during the study period (Table 5). However on August 12 and 13, 1991, the weather was stormy and many whelks moved out of Site I. Except for these few days, the weather was either fine or cloudy with light winds.

During the cool period, the mean densities of *Mu. fusca* in Pools A to D and other tidepools within the seaward area were lower than $10/m^2$ (Fig. 6). These same pools during the

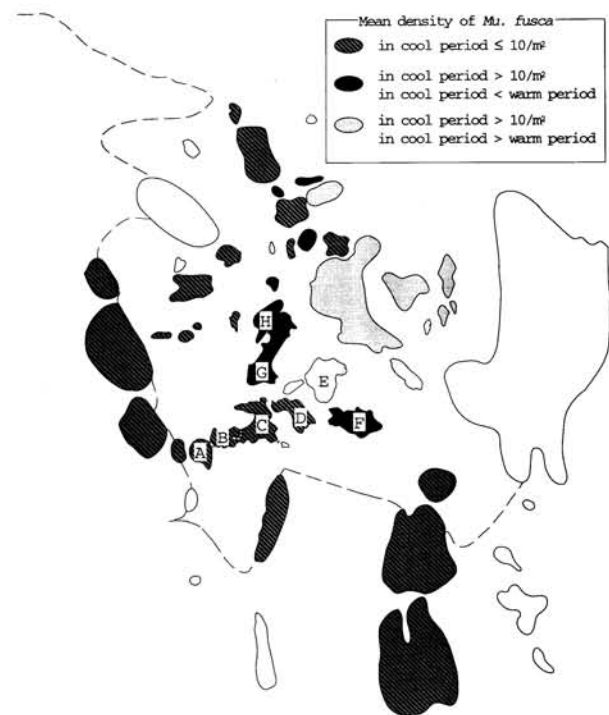


Fig. 6. Comparison of the mean density of *Muricodrupa fusca* between the cool and warm periods from 1991 to 1993 in each tidepool of the main observation area.

warm period always had higher densities of whelks (Fig. 5). The density in Pool E was lower during the warm period than in the cool period, and several other pools in the landward area showed the same pattern. Several pools, including Pools F, G, and H, had higher densities during the warm period than in the cool period, even though the densities there during the cool period exceeded $10/m^2$. These pools were located between the two previously mentioned groups.

Figure 7 shows the density of small (<12 mm in shell height) and large (≥ 12 mm in shell height) *Mu. fusca* among eight tidepools during the warm period. Whelks larger than 12 mm were presumed to be mature females (Yamamoto 1997). The density of large whelks in Pools A-D increased from February and attained its highest level in August, the spawning season of *Mu. fusca* (Yamamoto 1997). The density of small whelks fluctuated slightly in these pools at the lower levels during this period. However, small whelks in Pools E, G, and

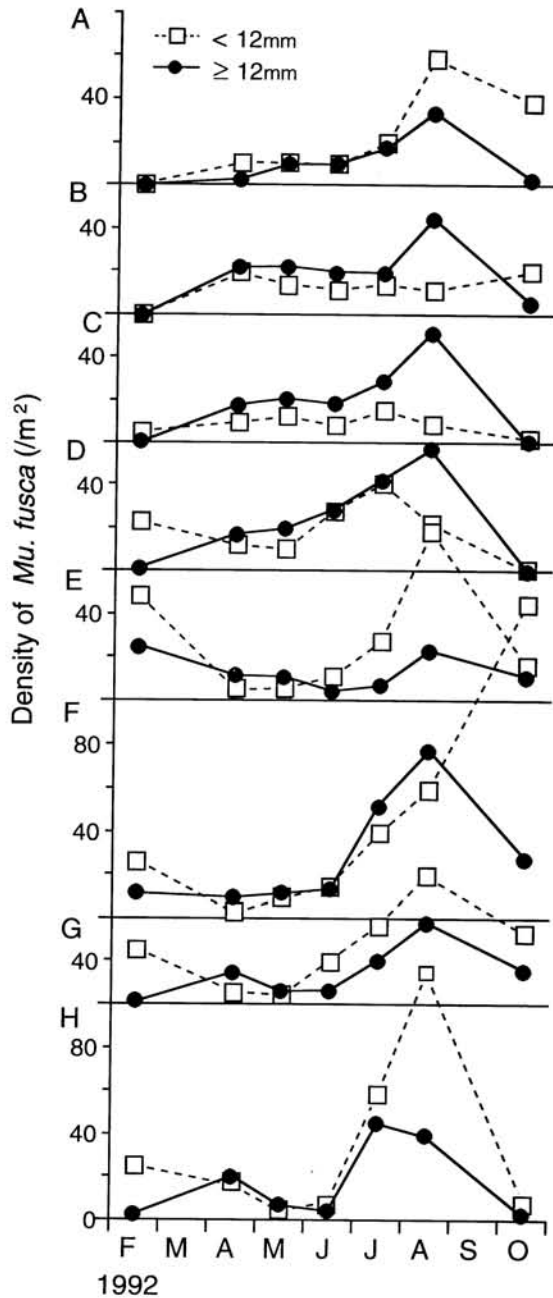


Fig. 7. Changes in the density of *Muricodrupa fusca* in two size classes in 8 tidepools of Site I in 1992.

H increased from June to August until their density was greater than that of the large ones. In Pool F, the increase in the density of large whelks was a little greater than the increase in the small ones in August.

DISCUSSION

Habitat utilization of *Mu. fusca*

Densities of the three muricids in and outside tidepools showed no clear interspecific differences in this study. All three species were more abundant in tidepools than on open rock surfaces (Fig. 2). However, *Mu. fusca* was the most abundant of the three muricids in the tidepools, and was rarely found outside the pools. The finding of differences in the microhabitats of the three muricids seems to be supported by differences in the micro-distribution of the favorite prey species of each muricid (Table 2). Barnacles, the favorite prey of *T. clavigera* (Abe 1989a), occurred exclusively on the open rock surfaces, and mytilids, the putative prey of *Mo. musiva* (Abe 1989a), inhabited both pools and open rock surfaces (on Transects p to s) or mainly open rock surfaces (Transect d). However, the favorite prey (limpets) of *Mu. fusca* (Yamamoto 1992) was more abundant inside the pools. This species forages exclusively in tidepools irrespective of the tidal level at low tide (Yamamoto 1993), whereas *Mo. musiva* rests in crevices or tidepools (Abe 1989b). *Mu. fusca* also spawns inside the pools, and juveniles hatch as crawling snails (Yamamoto 1997). Moreover, the abundance of *Mu. fusca* in the mussel beds (Fig. 2) suggests that this species tends to avoid dry habitats even when it occurs outside the pools. These results indicate that *Mu. fusca* depends more strongly on tidepools than the two other muricids in this study.

Several authors have studied the distribution of muricids in relation to shore level (Taylor 1976), wave exposure (Kohn & Leviten 1976; Moran 1985a), and density of their favorite prey item (Morgan 1972; Fairweather 1988). However, there have been no studies on tidepools as permanent habitats of muricids. The present study is the first report of a muricid species that spends most of its life inside tidepools.

There were no clear differences in the vertical distributions of the three species (Fig. 2), but Abe (1980) reported that *Mu. fusca* occurs higher in the intertidal zone than the other two species. This discrepancy is probably due to the present study area not including areas in

the lower intertidal zone which is expected as main habitat of *Mo. musiva* and *T. clavigera*.

Some species of muricids have been reported to show a vertical migration with increased shell height (Feare 1970; Butler 1979; Moran 1985a). However, the species in this study did not undergo any strong correlation between shell size and shore height of habitat during either summer or winter (Table 4), which suggests that these species have no habit of such vertical migration. Young *Mu. fusca* with a shell height of 3 mm (juveniles are 1 mm at hatching; Yamamoto 1997) were also found in the study site (Fig. 4). The small number of this size class must be due to the fact that young *Mu. fusca* just after hatching inhabit the small crevices where they were spawned (Yamamoto 1997). Therefore, it seems very likely proposed that *Mu. fusca* spends its entire life within the tidal range surveyed.

Size differences were clearly observed between the species, and *Mu. fusca* was smaller than the other two species (Fig. 4). Emson (1985) states the environment in tidepools favors smaller species because they can easily find shelter within the limited space of this habitat. However, *Mu. fusca* was not so much smaller than *Mo. musiva* and *T. clavigera* as to make it significantly better at finding shelter in tidepools.

Smaller species may benefit from other factors in habitats with limited resources. Although it may be difficult to accurately compare the amount of resources available to carnivorous gastropods between tidepools and open rock surfaces, a limited space certainly restricts the amount of available benthic animals. The main food resource for *Mu. fusca* is limpets (Yamamoto 1992), which occur more abundantly in the tidepools than on open rock surfaces and more sparsely than sessile animals outside the pools (Table 2). A small size probably gives some advantages to *Mu. fusca* because its food supply is more limited than those of the other two muricids.

One of the disadvantages of a small size in an intertidal animal is a decreased tolerance of desiccation at low tide. However, *Mu. fusca* does not experience desiccation since it inhabits tidepools. Another disadvantage may be an increased vulnerability to predators, but no

predators of *Mu. fusca* were found in the tidepools at the study site (Yamamoto unpublished). Therefore, *Mu. fusca* seems to be able to avoid the main disadvantages of a small size by inhabiting tidepools.

Movement pattern of *Mu. fusca* in relation to reproduction

The density of *Mu. fusca* in some tidepools changed drastically in early autumn and early spring. Whelks were not found in the seaward pools (Pools A-D) during the cool period from September to February, although whelks were found in the other pools during all seasons (Figs. 5 and 6). The seasonal movement of *Mu. fusca* between the seaward and landward pools is demonstrated by the estimated number of whelks moving toward landward pools from July to September and, conversely, toward seaward pools from January to February (Table 5). This movement occurred between pools at the almost same height. For each of the transects, no clear seasonal change in the distribution among different shore heights was found (Fig. 2ab). Due to seasonal migration, the density of *Mu. fusca* sometimes varied between neighboring tidepools having similar physical conditions (Table 1).

Accurate interpretation is difficult whether this movement resulted from active positive movement of whelks or random passive translocation due to strong waves. Long-distance movements of whelks out of Site I occurred when the weather was stormy with strong winds and high waves. Two days after the stormy weather, 85% of the whelks that had moved out of Site I and all of those moving from Pool F and G were found in the landward pools (Yamamoto unpublished). Therefore, movement landward at the end of the warm period (season of strongest wave action) might be caused by waves. However, because the transport by waves cannot occur in the opposite direction, it seems reasonable to suppose that the movement at the beginning of the warm period is due to *Mu. fusca*'s own efforts.

One possible explanation for this movement is the difference in prey density. Abe (1989b) reported that *T. clavigera* migrates to higher shores in winter due to the abundance of its favorite prey. However, there was no correlation

between the densities of *Mu. fusca* and its prey species. The most favorite limpet of *Mu. fusca*, *Siphonaria japonica* (Donovan) (Yamamoto 1992), exhibited a lower density in the landward pools than in the seaward pools (Yamamoto unpublished).

Another possible explanation is reproductive behavior. *Mu. fusca* breeds from March to August and concentrates its spawning in specific pools such as Pools C and D, which had higher densities of *Mu. fusca* during the spawning season (Yamamoto 1997). There were more large whelks (≥ 12 mm shell length), which were presumed to be females, in Pools C and D than in Pool E during the spawning season (Fig. 7).

Yamamoto (1997) suggested that *Mu. fusca* selects Pools C and D as spawning sites. Most whelks in Pool B were females, so the increase in whelk density in Pools A and B (even though few egg capsules were found in the pools) was probably due to the active movement of females searching for favorable spawning sites (Fig. 7). Therefore, it is highly probable that *Mu. fusca* migrated toward seaward pools for favorable spawning sites in the breeding season. If we assume this to be true, we can say that the environmental conditions preferred by this species for spawning are neither shore height, physical conditions such as water temperature and salinity, nor prey abundance.

In conclusion, *Mu. fusca* spends most of its life within tidepools and depends exclusively on the pools. Being the smallest of the three muricids in this habitat, this species seems to have some advantages related to the environmental conditions in tidepools. Its seasonal migration appears to be for the reproduction (Yamamoto 1997), and causes the seasonal changes in density and the great differences in densities of *Mu. fusca* between nearby pools (Fig. 5). These differences should have a strong influence on the populations of prey species in the tidepools.

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