Habitat zonation of the sand-burrowing mysids (*Archaeomysis vulgaris*, *Archaeomysis japonica* and *Iiella ohshimai*), and diel and tidal distribution of dominant *Archaeomysis vulgaris*, in an intermediate sandy beach at Fukiagehama, Kagoshima Prefecture, southern Japan

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Abstract: Distribution patterns of the three species of sand-burrowing mysids, *Archaeomysis vulgaris*, *Archaeomysis japonica* and *Iiella ohshimai* were investigated, and also the diel and tidal distribution patterns of the dominant mysid *A. vulgaris* were investigated in the surf zone of an exposed and mesotidal sandy beach at Fukiagehama, Kagoshima Prefecture, southern Japan. The morphodynamic state of the beach was an intermediate type with a low-tide terrace or ridge/runnel. Habitat zonation was recognized among the three species during the entire study period (May and October of 2002 and 2003). *A. vulgaris* occurred from the high-water shoreline to the low-water shoreline during the daytime, whereas *A. japonica* was observed off the low-water shoreline and *I. ohshimai* was found far from the longshore bar. Habitats of *A. vulgaris* shifted along the beach slope, depending on the tidal changes at the shoreline. However, at low water in May of 2002 and 2003, most individuals of *A. vulgaris* were distributed in the intertidal runnel and on the low-tide terrace, rather than off the low-water shoreline. *A. vulgaris* had the highest population density of the three species, and fluctuations in its total mean density in the surf zone were estimated at each tide in May of 2003. These ranged from 2,956 indiv. m⁻² at low water at night to 172 indiv. m⁻² at middle water during the daytime. Distribution patterns characteristic of *A. vulgaris* are ecologically interpreted in relation to beach morphology, water flow regimes in the surf zone, and avoidance of fish-predation pressure.

Key words: *Archaeomysis*, *Iiella*, intermediate sandy beach, intertidal runnel, low-tide terrace

Introduction

Of the sand-burrowing mysids occurring in the surf zone of sandy beaches of various beach-types throughout the world (Brown & McLachlan 1990), the genus *Archaeomysis* is typical and abundant all along Japan's sandy coastline (Hanamura 1997). Six species presently comprise this

genus. Five species of the species (*Archaeomysis vulgaris*, *Archaeomysis kokuboi*, *Archaeomysis articulata*, *Archaeomysis japonica*, *Archaeomysis ochotensis*), excluding *Archaeomysis grebnitzkii* in the USA, have been found in Japan (Hanamura 1997). Despite *A. vulgaris* being dominant in southern Japan, biological and ecological information about it is very scarce. Although early taxonomic and biogeographic studies suggested differences in habitat types between *A. vulgaris* and *A. japonica* (Jo & Hanamura 1993, Hanamura 1997), detailed distribution patterns of the con-

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genera remain uncharacterized.

To understand the distribution patterns of these mysids, it is necessary to know the beach morphodynamic states of each individual sandy beach, because changes in beach morphodynamic states directly determine the microdistribution patterns of macroscopic animals (McLachlan & Hesp 1984, Brown & McLachlan 1990, Harvey 1998, Layman 2000, Marcomini et al. 2002). The term “beach morphodynamics” was defined as the mutual adjustment of topography and fluid dynamics involving sediment transport (cf. Wright & Thom 1977). Therefore, this term implies mutual interaction between waves (tides/currents) and beach morphology, such that the wave action modifies the beach morphology, which in turn will modify the waves and so on (Short 1999). In terms of the beach morphodynamic states, sandy beaches have been roughly categorized into reflective (steep), intermediate and dissipative types, which are related to beach morphology and beach slopes characteristic of each sandy beach.

With the exception of some ecological studies on sand-burrowing mysids in high-energy dissipative sandy beaches facing open coasts (McLachlan 1990, Hanamura 1999), most previous studies have been carried out on low-energy reflective beaches which are found inside estuaries, bays and harbors (Matsudaira et al. 1952, Takahashi & Kawaguchi 1995, 1997, Kaneko & Omori 2003). So, it is also necessary to understand their distribution patterns on high-energy intermediate sandy beaches that are found on open coasts, because the distribution patterns of mysids, one of the most abundant prey organisms on sandy beaches, are of ecological importance.

In order to present ecological information about sand-burrowing mysids in an intermediate sandy beach, this paper describes (1) the horizontal distribution patterns of *A. vulgaris* and *A. japonica*, together with the less abundant sand-burrowing mysid, *Iiella ohshimai*, and also deals with (2) details of the diel and tidal distribution patterns of the dominant mysid *A. vulgaris* at Fukiagehama. Distribution patterns characteristic of *A. vulgaris* from the results are ecologically interpreted in relation to beach morphology, water flow regimes in the surf zone, and avoidance of fish-predation pressure.

Materials and Methods

Study area and beach morphology

The study was done at Fukiagehama on the western coast of Kagoshima Prefecture, Kyushu, southern Japan (31°29' N, 130°19'E) (Fig. 1). Fukiagehama is one of the longest sandy beaches in Japan and has a ca. 45 km coastline, opening broadly to the East China Sea. The bottom substratum was largely composed of medium grained and well-sorted sand (the mean of median particle diameters, $Md\phi$: 295 μm ; the mean of sorting coefficients: 0.57), and the intertidal zone was ca. 100 m in width with a 1:45 beach

Fig. 1. Map showing the study area in Fukiagehama, Kagoshima Prefecture, Kyushu, southern Japan.

slope ratio (Nonomura et al. unpubl.).

Figure 2 introduces beach morphology for all the sampling stations in the study area on each sampling date (15–16 May 2002, 23 October 2002, 17 May 2003 and 27 October 2003), because of seasonal changes in beach morphology. Sampling stations in the surf zone were coded as follows: H1–H5: high-water shoreline; HM1–HM5: higher middle-water shoreline; LM1–LM5: lower middle-water shoreline; R1–R4: intertidal runnel; LTT: low-tide terrace; HL1–HL5: higher low-water shoreline; LL1–LL5: lower low-water shoreline; B: longshore bar. In this study, ‘surf zone’ refers to the area between the shoreline and breaker zone over the longshore bar, the usual width of the surf zone being approximately 100 to 200 m. Beach slope was steeper at Stns H1–H5 than at any other stations. Thus, wave condition adjacent to the high-water shoreline was harsh during high water. In contrast, waves were of low energy from middle water to low water. The study area has been reported as an intermediate type characterized by a low-tide terrace or ridge/runnel (cf. Nakane et al. 2005), according to the beach morphodynamic state classification by Short (1999). The maximum tidal range was ca. 3 m at spring tide. The low-tide terrace often appeared above the water level at low water. Off the low-tide terrace, the longshore bar was found running parallel to the coastline. Two shallow troughs emerged at low water, the intertidal runnel between the backshore and the low-tide terrace, and the in-

Fig. 2. Beach morphology at low water (left) and profiles (right) of the line A–A' on each sampling date. Distances (m) from the high-water shoreline are shown on the left and top, respectively. Height (m) from high-water level is also shown to the left of the beach profile.

fralittoral runnel between the low-tide terrace and the longshore bar. The intertidal runnel, the low-tide terrace and the infralittoral runnel are typical of the morphology of intermediate sandy beaches (cf. Short 1999). Seepage of groundwater was observed in the intertidal runnel during low water. The infralittoral runnel was often observed to

have a connection with the open sea. The water-depth in the intertidal runnel was less than 5 cm at low water, while that in the infralittoral runnel was more than 40 cm at low water. The intertidal runnel sometimes lacked surface water depending on the low-water level and/or beach morphology, while the infralittoral runnel remained covered with sea water. These structures seasonally occurred in spring and fall. Mean salinity and mean water-temperature at low water was 18.6 psu and 23.2°C in the intertidal runnel, and 32.2 psu and 22.2°C in the infralittoral runnel, because of the low salinity of the groundwater seepage (Nonomura et al. unpubl.).

Mysid sampling and data analysis

Sampling was conducted at approximately 3-hr intervals according to changes in tidal levels (Fig. 3). In 2002 sampling was conducted three times, from high water to low water later during the daytime; with one extra sampling for practice in the use of the sampling gear at low water on 15 May. In 2003 sampling was conducted five times, from low water in the nighttime to low water in the daytime. The tidal phase was a spring tide and the weather was fine throughout the sampling. Tidal levels and local time came from the data of Kushikino City (31°43'N, 130°16'E) (JCG 2001, JCG 2002).

Figure 4 is a schematic representation of sampling coverage with three kinds of sampling gear. Sampling was done between the high-water shoreline and the longshore bar. Mean water-depths h_s of Stns H3, LM3/HM3, R3, LL3/HL3 and B at high water were 0.4, 1.3, 1.5, 2.7 and 3.6 m, respectively. The mean distance from the high-water shoreline to the longshore bar was 200 m. Stations adjacent to the shoreline (e.g. Stns H1–H5) were set at intervals of 3 m in 2002 and 6 m in 2003. A sledge net, a NORPAC net and a quadrat were used for the mysid sampling. A 50 cm wide and 10 cm high sledge net (mesh size of 335 μ m) with a chain was used to collect mysids just above and burrowing in the sandy bottom. A NORPAC type plankton net (mesh size of 335 μ m; 45 cm mouth diameter; 1.8 m long) was towed to collect mysids in the water column. After the ebb tide went out, a quadrat (0.04 m²) was used in the intertidal zone to collect mysids on the surface of the sandy bottom or buried in sand up to 5 cm depth, because most individuals of *Archaeomysis vulgaris* were in the intertidal runnel at low water (as will be mentioned later). Around the shoreline, the sledge net and the plankton net were towed once each over a distance of 3 m. At offshore stations, the nets were towed twice over a distance of 5 m because of the low density of mysids. The plankton net was towed in two ways: a surface tow and an oblique tow from the bottom to the water surface to cover the whole water column. All the tows were made parallel to the shoreline.

Mysids were fixed in 10% sea-water formalin and sorted into species and different sexual maturity stages (mature female, immature female, mature male, immature male and

Fig. 3. Tidal level and sampling time. Arrows indicate the sampling carried out. Black, white and mesh bars indicate night, day and dusk/dawn, respectively.

juvenile) after Takahashi & Kawaguchi (1996) and Nonomura et al. (2005). The distance (m) from the high-water shoreline for each individual mysid and the density (indiv. m^{-2}) of mysids were calculated, with the data being examined using a Wilcoxon–Mann–Whitney test, a Kruskal–Wallis test with a nonparametric multiple comparison and a Chi-square test for proportions after Zar (1999).

Calculation of weighted mean distance from high-water shoreline

In addition, the weighted mean distance from the high-water shoreline (WMDi, m), adapted from Shimode & Shirayama (2006), was used to examine differences in horizontal distribution among mysids, the diel and tidal distribution of the dominant species *A. vulgaris*, and the developmental stage-specific distribution of *A. vulgaris*. The WMDi was calculated as follows:

$$TMDe = \frac{\sum n_i d_i}{\sum d_i}$$

where n_i is the observed density (indiv. m^{-2}) at d_i , distance (m) from the high-water shoreline.

Estimation of total mean density of *Archaeomysis vulgaris* in the surf zone

Total mean density (TMDe, indiv. m^{-2}) was calculated to estimate fluctuations of the total population of *A. vulgaris*, collected by a sledge net, a NORPAC net and a quadrat, in the surf zone. If *A. vulgaris* individuals only migrated inside the surf zone without any losses or gains, the population would be conserved and the TMDe would be nearly constant at each tide. On the other hand, if individuals were transported out of the surf zone by surf zone currents (bed return currents, rip currents and longshore currents), patchily distributed and/or also subjected to high predation-pressure by fishes and crabs, the TMDe could fluctuate considerably. Therefore in order to assess the fluctuation in distribution patterns of *A. vulgaris*, it is necessary to estimate its TMDe in the surf zone at each tide. This will also help to evaluate the accuracy of density measurements in this perturbed surf zone environment. The TMDe was calculated as follows:

$$WMDi = \frac{\sum n_j d_j}{\sum n_j}$$

where n_j is the observed density (indiv. m^{-2}) at d_j , representative distance (m) covered by each sampling station. The representative distance d_j is equivalent to a half distance between adjacent sampling stations. The summation of d_j is nearly equal to the surf-zone distance (ca. 200–300 m).

Results

Horizontal distribution patterns of *Archaeomysis vulgaris*, *Archaeomysis japonica* and *Iiella ohshimai*

The three species of sand-burrowing mysids, *Archaeomysis vulgaris*, *Archaeomysis japonica* and *Iiella ohshimai* occurred throughout the study period. Figure 5 indicates the horizontal distribution patterns of the three species at each

Fig. 4. Schematic representation of sampling coverage at each tide at Fukiagehama. *: sampling stations in May, **: stations in October, and the others are common stations.

station. Averaged density in Fig. 5 was not the TMDe, but was calculated from the observed density, only when the species occurred. It was shown that most *A. vulgaris* occurred in the intertidal zone from the high-water shoreline (Stns H1–H5) to the higher or lower low-water shoreline

(Stns HL1–HL5/LL1–LL5), and few were observed off the longshore bar (Stn B). *Archaeomysis japonica* occurred mainly in the infralittoral zone off the higher or lower low-water shoreline (Stns HL1–HL5/LL1–LL5), where it was often more abundant than *A. vulgaris*, but was scarce in the

Fig. 5. Horizontal distribution patterns of *Archaeomysis vulgaris*, *Archaeomysis japonica* and *Liella ohshimai* in the surf zone at Fukiagehama. Numbers in parentheses are the distance from the high-water shoreline. Note that values are averaged densities on a logarithmic scale, except for zero. The WMDi of year 2003 was calculated from the data for daytime only, and this excluded data from night and dawn.

intertidal zone. *A. vulgaris* and *A. japonica* distributions often overlapped in the higher or lower low-water shoreline (Stns HL1–HL5/LL1–LL5). Differences in distance from the high-water shoreline between *A. vulgaris* and *A. japonica* were supported by Wilcoxon–Mann–Whitney tests

($p < 0.05$) for each sampling date. *Liella ohshimai* was found only off the longshore bar (Stn B). The mean WMDi of *I. ohshimai* (202 m) was larger than for *A. vulgaris* (35 m) or *A. japonica* (121 m), but nonparametric comparisons of *I. ohshimai* to *A. vulgaris* and *A. japonica* were not carried

out because the sample size was small. These results suggest habitat zonation among the three species in the surf zone at Fukiagehama.

Diel and tidal horizontal distribution patterns of *Archaeomysis vulgaris*

WMDi during the daytime for the population of *A. vulgaris* at high water, middle water and low water is shown in Table 1. No significant difference (Kruskal–Wallis test, $p > 0.05$) in the WMDi was noted among sampling dates (May 2002, October 2002, May 2003 and October 2003). The mean WMDi for each tide during the daytime was

Table 1. WMDi (weighted mean distance) from the high-water shoreline for the population of *Archaeomysis vulgaris* at high water, middle water and low water during the daytime.

	High water	Middle water*	Low water*
May 2002	11	19	55
October 2002	13	31	51
May 2003**	20	29	31
October 2003**	18	48	78
Mean	16	32	54

* Middle water is used as a synonym of higher or lower middle water, and the same applies to low water.

** Night-down data of Year 2003 was excluded from this table, because of nonparametric comparisons among sampling dates.

16 m at high water, 32 m at middle water and 54 m at low water. These results suggest that the habitat of *A. vulgaris* shifted along the beach slope, depending on the tidal changes in the shoreline.

An example of diel and tidal horizontal distribution patterns of *A. vulgaris* at different sexual maturity stages in May of 2003 is shown in Fig. 6. During flood tide from night (02:00) to dawn (05:00), the position of peak abundance of *A. vulgaris* shifted shoreward in accordance with the tidal movement of the shoreline and the WMDi also changed from 67 m to 27 m. However, during ebb tide during the day (08:00–14:30), *A. vulgaris* showed slight tidal shifts and the WMDi was 20 m at high water, 29 m at lower middle water and 31 m at lower low water. At nighttime low water (WMDi: 67 m), *A. vulgaris* had a wider distribution than during daytime low water (WMDi: 31 m) because of its nocturnal swimming activity in the water column.

At higher low water, at night (02:00), 87% of *A. vulgaris* were found in the intertidal runnel (Stns R1–R4) above the tide level, rather than at Stns HL1–HL5 beneath the tide level, with the greatest abundance at Stn R4. At higher middle water, at dawn (05:00), the peak abundance shifted shoreward from Stns R4 to HM5, moving with the flood tide. At high water, at about 08:00 in the morning, most *A. vulgaris* occurred at stations H3, H5 and LM3, which were off Stn H1. At lower middle water, just before noon, the peak abundance was at Stn LM1. Later at lower low water, 99.9% of *A. vulgaris* were found in the intertidal

Fig. 6. Diel and tidal horizontal distribution patterns of *Archaeomysis vulgaris* in May 2003 at Fukiagehama. Note that values observed are on a logarithmic scale, except for zero. Arrow: peak abundance position; +: < 1 indiv. m^{-2} ; -: no mysids collected.

Fig. 7. Diel and tidal vertical distribution patterns of *Archaeomysis vulgaris* in May 2003 at Fukiagehama. Blanks indicate no mysids collected, but sampling of mid layer was not carried out at Stn HL5 of HL or Stn LL5 of LL because of the shallow water-depth. Note that values in each layer are on a logarithmic scale, except for zero. T: total; Mf: mature female; Mm: mature male; If: immature female; Im: immature male; J: juvenile.

runnel (Stns R1–R4), with the peak at the shoreward station (Stn LM3) above the tide level.

Although there were no marked differences in distribution between the WMDi of the five sexual maturity stages of *A. vulgaris* (Kruskal–Wallis test, $p > 0.05$), mature females (mean WMDi: 30 m) had a tendency to occur more shoreward than the other stages (juveniles: 40 m, mature males: 39 m, immature males: 36 m and immature females: 35 m in mean WMDi).

The diel and tidal horizontal distribution patterns of *A. vulgaris* in May of 2002 were similar to those during May of 2003. However, the patterns in October differed from those in May because at low water *A. vulgaris* occurred mainly in the low-tide terrace (Stn LTT) and the higher or lower low-water shorelines (Stns HL1–HL5/LL1–LL5), instead of the intertidal runnel, without differences in the WMDi between sampling dates (Table 1; Kruskal–Wallis test, $p > 0.05$).

Diel and tidal vertical distribution patterns of *Archaeomysis vulgaris*

Vertical distribution patterns of *A. vulgaris* were examined using the data of May and October of 2003, but the sample size in October was small. Figure 7 shows the vertical distribution patterns in relation to diel and tidal changes for *A. vulgaris* in May of 2003, where the densities (indiv. m^{-2}) in the surface, mid and bottom layers are calculated from the total individuals estimated in each layer, and according to the tides. Data from the surface and mid layers are from the NORPAC net, and those at the bottom from the sledge net. As shown at higher low water (HL), at night (02:00), 86% of *A. vulgaris* were found in the surface layer, whereas at higher middle water (HM), at dawn (05:00), 85% were in the bottom layer. After dawn, 71–100% were collected in the bottom layer

Table 2. Comparing vertical distributions of the five sexual maturity stages of *Archaeomysis vulgaris* in the water column, using the data collected in May 2003 by sledge net sampling (0–10 cm layer from bottom) and NORPAC net sampling (higher than 10 cm layer from bottom). Numbers in parentheses are density values (indiv. m^{-2}).

Category*	Height from the bottom (cm)	Proportion (%)	
		Night (02:00)	Day (08:00)
Mature ♀	more than 10	74.0 (409)	18.3 (175)
	0–10	26.0 (144)	81.7 (780)
Juvenile	more than 10	95.1 (135)	34.9 (91)
	0–10	4.9 (7)	65.1 (170)
Mature ♂	more than 10	86.0 (1095)	33.5 (92)
	0–10	14.0 (178)	66.5 (183)
Immature ♀	more than 10	88.6 (1246)	30.7 (318)
	0–10	11.4 (161)	69.3 (717)
Immature ♂	more than 10	86.5 (734)	40.3 (186)
	0–10	13.5 (115)	59.7 (275)

* Partitions between categories were based on comparisons at night.

(08:00–14:30). In October 2003, also, nocturnal swimming activity was observed in the water column for *A. vulgaris*, and swimming activities were also observed for *A. japonica* and *I. ohshimai*.

For the data at night (02:00) at higher low water (HL) and the data during the day (08:00) at high water (H) in May 2003, a comparison of the vertical distribution of the five different sexual maturity stages of *A. vulgaris* was carried out (Table 2). There were marked differences in the vertical distributions among the developmental stages (Chi-square tests, $p < 0.05$). At night (02:00), the population of *A. vulgaris* was divided into three groups (mature females, juveniles and others) (Tukey-type multiple comparisons, $p < 0.05$). During the day (08:00), the population was divided into two groups (mature females and others) (Tukey-type multiple comparisons, $p < 0.05$). Mature females of *A. vulgaris* had a higher proportion of the population in the 0–10 cm layer altitude from the bottom than the others, while the juveniles had a higher proportion of the population in the water column at an altitude higher than 10 cm.

Changes in total mean density (TMDe) of *Archaeomysis vulgaris* in the surf zone

Total mean density (TMDe) of *A. vulgaris* at each developmental stage fluctuated at each tide (Fig. 8). For example, the TMDe in May of 2003 of animals from juvenile to mature stages was estimated to be 2,956 indiv. m^{-2} at higher low water in the nighttime, compared with 241, 190 and 172 indiv. m^{-2} at higher middle water (dawn), high water

Fig. 8. Changes in Total mean density (TMDe) of *Archaeomysis vulgaris* in the surf zone at Fukiagehama. Note that values are on a logarithmic scale, except for zero. Black bar: night; mesh bar: dawn; white bar: day; +: <1 indiv. m⁻².

(daytime) and lower middle water (daytime), respectively. By the time of lower low water later in the daytime, the TMDe was 1,342 indiv. m⁻². Estimated TMDe during each tide usually fluctuated several times, up to 17 times at most, throughout the study period.

TMDe of *A. vulgaris* was higher than *A. japonica* during the study period (Wilcoxon–Mann–Whitney test, $p < 0.05$). In addition, for both species the TMDe in May 2003 (*A. vulgaris*: 172–2956 indiv. m⁻², *A. japonica*: 13–709.0 indiv. m⁻²) was higher than in October 2003 (*A. vulgaris*: 3–55 indiv. m⁻², *A. japonica*: 0.2–25.5 indiv. m⁻²) (Wilcoxon–Mann–Whitney test, $p < 0.05$).

Discussion

The daytime distribution of *Archaeomysis vulgaris* was observed from the high-water shoreline to the low-water shoreline, while *Archaeomysis japonica* occurred mainly off the low-water shoreline. This suggested that *A. vulgaris* was an intertidal species and *A. japonica* was an infralittoral one, showing habitat zonation. Distributions of the two species overlapped off the low-water shoreline, because a portion of the *A. vulgaris* population moved to the infralittoral runnel zone during ebb tide. This might be the reason why the two species were able to coexist in the surf zone (cf. Jo & Hanamura 1993). Habitat types of *A. vulgaris* and *A. japonica* agreed with earlier results of Jo & Hanamura (1993) and Hanamura (1997). Habitat zonation

between intertidal *Archaeomysis kokuboi* and infralittoral *A. japonica* has also been reported at Koshirahama Beach in northeastern Japan, and *A. japonica* was found in the area more than 10 m from the high-water shoreline, which followed a seasonal movement in the position of a step structure (Takahashi & Kawaguchi 1995). At Fukiagehama Beach in southern Japan, *A. japonica* was found in the area more than 60 m from the high-water shoreline, which corresponded to seasonal changes in the position of the low-tide terrace structure, which was in turn related to seasonal changes in the width of the intertidal zone. *Iiella ohshimai* was found further away from the two *Archaeomysis* species, and this also agreed with results by Takahashi & Kawaguchi (1995). These results suggest that the habitat boundaries of sand-burrowing mysids depend on the morphodynamic state of each individual sandy beach.

Takahashi & Kawaguchi (1995, 1997) suggested habitat zonation among different sexual maturity stages for *A. kokuboi* and *A. japonica* at a low-energy reflective beach, Koshirahama Beach, and emphasized differences in their responses to wave action or flow regimes near the bottom. Various developmental stages of *A. vulgaris* were found to overlap in their distribution at high-energy intermediate beach at Fukiagehama. At high-energy intermediate beaches, the microdistribution patterns of mysids might be disturbed and therefore show few differences among developmental stages because the wave action is stronger than at low-energy reflective beaches.

The horizontal and vertical distribution patterns, in relation to diel and tidal rhythms, for *A. vulgaris* described in this study were similar to those for *A. kokuboi* (cf. Matsudaira et al. 1952, Ii 1964, Takahashi & Kawaguchi 1997), *A. vulgaris* (cf. Kaneko & Omori 2003) and *Archaeomysis grebnitzkii* (cf. McLachlan 1990). At nighttime low water, *A. vulgaris* had a wider distribution than at daytime low water, and there were differences in the vertical distribution patterns among developmental stages. *A. vulgaris*, like *A. kokuboi* and *A. japonica*, has been reported to feed in the water column at night (cf. Takahashi & Kawaguchi 1998, Kaneko & Omori 2003, author pers. obs.). Our laboratory observations (unpub.) at night showed that mature females became poor swimmers and are sensitive to artificial stimulation (e.g. light, percussion) because of having embryos or larvae in the marsupium, while the others are active swimmers and are insensitive to such stimulation. In fact, mature females burrowed into the sand immediately when they appeared in the water column, but the others swam about actively. Feeding activity and swimming behavior related to light conditions seems to be one of the reasons why their distribution expands offshore at night.

Fluctuations in total mean density (TMDe) at each tide suggested that non-conservative factors may influence the population of *A. vulgaris*, such as surf zone currents (bed return currents, rip currents and longshore currents), fish predation and other biological processes. In addition, the variability of measured TMDe suggests sand-burrowing mysids were probably patchily distributed in the rapidly changing surf zone, and thus it was difficult to accurately estimate their density.

In May of 2002 and 2003 at Fukiagehama, the total density of *Archaeomysis vulgaris* was greater at low water in the intertidal runnel than off the low-water shoreline (Fig. 6). Since salinity at low water in the intertidal runnel (mean: 18.6 psu) was lower than that in the infralittoral runnel or at the low-water shoreline (mean: 32.2 psu), it might be necessary for *A. vulgaris* to be tolerant of low salinities. Our unpublished data show that both *A. vulgaris* and *A. japonica* had a high tolerance to low salinity. All individuals of the two species survived in seawater of 8 and 16 psu for 24 hr at 20°C. However, *A. vulgaris* and *A. japonica* were unable to survive in freshwater (0 psu) for one hr at 20°C. This suggests that *A. vulgaris* and *A. japonica* can live in the intertidal runnel during low water. *Gastrosaccus* spp., which are also sand-burrowing mysids that occur in the intertidal zone, have been reported to have a high tolerance to low salinities (cf. Mauchline 1980), and thus the ability to tolerate low salinities might be common to sand-burrowing mysids occurring in the intertidal zone of sandy beaches. Differences in distribution patterns between sand-burrowing mysids do not depend on their tolerances to low salinities but may depend on differences in their responses to surf zone currents such as the bed return current, offshore movement near the bottom, and/or be related to differences in their ability to burrow into the sandy bottom.

There are two possible ecological factors that may explain the distribution patterns of *A. vulgaris* in the intertidal runnel at low water. The first is food availability (cf. Clutter 1966, Webb et al. 1988, Webb & Wooldridge 1990, Takahashi & Kawaguchi 1997). Webb & Wooldridge (1990) have interpreted the greater nocturnal presence of some mysids behind the breaker zone, compared to their daytime distribution, as a response to the increased concentration of phytoplankton caused by rip currents. At night, *A. vulgaris* collected at the low-water shoreline had guts containing food, whereas all of those collected in the intertidal runnel had empty guts (author's pers. obs.). Therefore, the intertidal runnel was not a major feeding area for *A. vulgaris* because they fed at night. The second hypothesis is predation avoidance (cf. Webb & Wooldridge 1990, Takahashi & Kawaguchi 1997). The most powerful ichthyo-predators of surf-zone mysids on southern Japan's sandy beaches, are *Paralichthys olivaceus*, *Paraplagusia japonica*, *Heteromyceteris japonica*, *Sillago japonica*, *Takifugu niphobles* and *Latolabrax latus* (Suda et al. 2002, 2004, Inoue et al. 2005, Nakane et al. 2005). According to our field observations (unpub.), such ichthyo-predators were not found in the intertidal runnel at low water. Certain species of fishes utilize the infralittoral runnel as a habitat for feeding or as a nursery, but rarely the intertidal runnel (cf. Harvey 1998, Layman 2000). Therefore, the predation avoidance hypothesis could be applicable for *A. vulgaris*, since it could survive buried in the sand in the intertidal runnel with very little seawater during low water.

Takahashi & Kawaguchi (2004) stated that *A. kokuboi* and *A. japonica* had adapted differently to their respective intertidal and infralittoral beach habitats. The high reproductive potential of intertidal *A. kokuboi* was an adaptation to its high mortality rate caused by unpredictable events such as storms, or extreme changes in temperature or salinity. In contrast, the efficient reproduction of *A. japonica* during the high water temperature season was an adaptation to the infralittoral habitat where more predictable events such as seasonal variation of temperature prevailed. To understand the distribution patterns characteristic of *A. vulgaris*, the reproductive biology of *A. vulgaris* must be studied. Beach morphodynamic states also should be taken into consideration to better understand the distribution patterns of mysids on sandy beaches.

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