

Diel and tidal migrations of the sand-burrowing mysids, *Archaeomysis kokuboi*, *A. japonica* and *Liella ohshimai*, in Otsuchi Bay, northeastern Japan

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ABSTRACT: Diel and tidal changes in distributions of the 3 species of sand-burrowing mysids, *Archaeomysis kokuboi* Li, *A. japonica* Hanamura, Jo & Murano and *Liella ohshimai* (Li), were studied during summer on a sandy beach in Otsuchi Bay, on the Pacific coast of northeastern Honshu, mainland Japan. During the day *A. kokuboi*, the closest dweller to the shoreline, showed remarkable tidal migrations that differed among the developmental stages and sexes. During the daytime, intraspecific zonation of *A. kokuboi* relative to the shoreline was maintained during the habitat shift with tide. However at night *A. kokuboi* emerged from the sand and swam in the water column. The swimming activities became progressively less with growth through juveniles, immatures, mature males, non-brooding females to brooding females. *A. japonica*, which occurred just below the intertidal zone, showed no tidal migration, but also emerged into the water column at night. Its swimming activities differed among developmental stages, i.e. adults were inactive, while immatures and juveniles swam into the water column to expand their horizontal distribution offshore. Likewise, *L. ohshimai*, mostly juveniles or immatures <3.0 mm standard length, showed no tidal migration, but emerged into the water column at night. The spatiotemporal distribution patterns of the 3 mysid species of various developmental stages showed very little overlap. The daytime behaviors of sand-burrowing mysids, such as tidal migration or burrowing, are unique among mysidaceans, and may be adaptations to avoid visual predators. On the other hand distribution patterns of the different species and stages at night seem well adapted to ensuring feeding or reproduction.

KEY WORDS: Sand-burrowing mysids · *Archaeomysis* · *Liella* · Diel migration · Tidal migration · Northeastern Japan

INTRODUCTION

Mysids belonging to the genus *Archaeomysis*, subfamily Gastrosaccinae, consist of sand-burrowers found in temperate and subarctic waters of the North Pacific (Mauchline & Murano 1977, Hanamura 1992). They are abundant in Japanese waters and considered to play an important role in sandy beach ecosystems (Itô 1985, Jo & Hanamura 1993, Takahashi & Kawaguchi 1995). Studies of their ecology have been extremely restricted in spite of their abundance on sandy beaches. Three sand-burrowing mysids, *Archaeomysis kokuboi* Li, 1964, *A. japonica* Hanamura, Jo & Murano, 1996 and

Liella ohshimai (Li), 1964, occur on the sandy beach at Otsuchi Bay, northeastern Honshu. *A. japonica* was formerly regarded as *A. grebnitzkii* Czerniavsky, 1882 until recently (see Li 1964), when Hanamura et al. (1996) discussed the systematic status of this species and concluded that the Japanese population of *A. grebnitzkii* was actually a new species, *A. japonica*. These mysids are known to show clear interspecific bathymetric zonation in nearshore waters and their habitats shift seasonally and according to development in species-specific ways (Takahashi & Kawaguchi 1995). However, the diel shift of their habitat still remains to be studied inter- and intraspecifically. Many other freshwater or marine mysids have spatiotemporal distributional patterns that are key factors in, for example, their life strategies, ecological role in the

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communities and population dynamics (Mauchline 1970, Grossnickle 1979, Beeton & Bowers 1982, Webb et al. 1988, Moen & Langeland 1989, Webb & Wooldridge 1990). This is also true of the sand-burrowing species and information on tidal and diel distribution patterns are important in understanding their ecology. This paper examines the diel and tidal changes of distributional patterns in the 3 sand-burrowing mysid species, *A. kokuboi*, *A. japonica* and *I. ohshimai*, on a sandy beach in Otsuchi Bay.

MATERIALS AND METHODS

The study was done at Koshirahama Beach in Otsuchi Bay. A detailed description of the study site was given in Takahashi & Kawaguchi (1995). Samples were taken every 3 h for 24 h on 18–19 August 1993. The weather was fine and sea conditions were calm throughout sampling. Times of sunset and sunrise were 18:27 and 04:48 h respectively. The phase of the moon was new and times of low tide were 09:54, 21:57 and 10:30 h, while high tides were at 16:26 and 03:50 h (MSA 1993).

A sledge net (30 cm width, 10 cm height, 330 μ m mesh) was employed to investigate the benthic distribution. This sledge net is designed to agitate the upper 1.5 cm of sand with the 2 chains, and skim the benthic organisms by a plankton net fixed behind the sledge. Sampling was done at 11 stations from the shoreline to a point 20 m offshore (1.3 m deep) which were marked by buoys fixed at 2 m intervals (Fig. 1). At each station, a 5 m tow was made parallel to the shoreline. Two additional offshore stations located 50 and 100 m offshore from the shoreline were also established as

shown in Fig. 1 (Stns 12 and 13) and 40 m tows were made parallel to the shoreline. A conical plankton net of 30 cm in mouth diameter and 330 μ m mesh was towed horizontally for 40 m parallel to the shore to collect mysids swimming in the water column at Stns 11, 12 and 13. The sampling layers were: surface at Stn 11; surface and 1 and 2 m above the bottom at Stn 12; surface and 1, 2 and 4 m above the bottom at Stn 13 (Fig. 1). Attachment positions of the plankton nets on the wire were preset on the basis of the desired sampling depth and the wire angle, which was maintained at 45° during a haul. When the nets were lowered and retrieved, the wire was kept vertical to minimize sampling contamination from undesired layers.

Sampling with an ordinary sledge net (single-layered) cannot distinguish whether captured mysids were burrowing in the sand or swimming just above the bottom. Therefore, to investigate diel change in the vertical microdistribution pattern near the bottom, sampling with a 2-layered sledge net (30 cm width, 10 + 10 cm height, 330 μ m mesh) was done (to try to collect the burrowing and swimming mysids separately) at 4 points: just beyond the shoreline (0.3 m deep), 20 m (1.3 m deep), 50 m (3.3 m deep), and 100 m (5.3 m deep) offshore from the shoreline on 8–9 September 1994.

The samples were fixed in 10 % formalin and sorted into species and different sexual maturity stages based on Mauchline (1980). Juvenile and immature mysids of *Archaeomysis* species, which are very similar in morphology, were identified according to Takahashi & Kawaguchi (1996). Standard length (SL) was measured as a distance from the base of the eyestalk to the posterior end of the 6th abdominal segment with a profile projector.

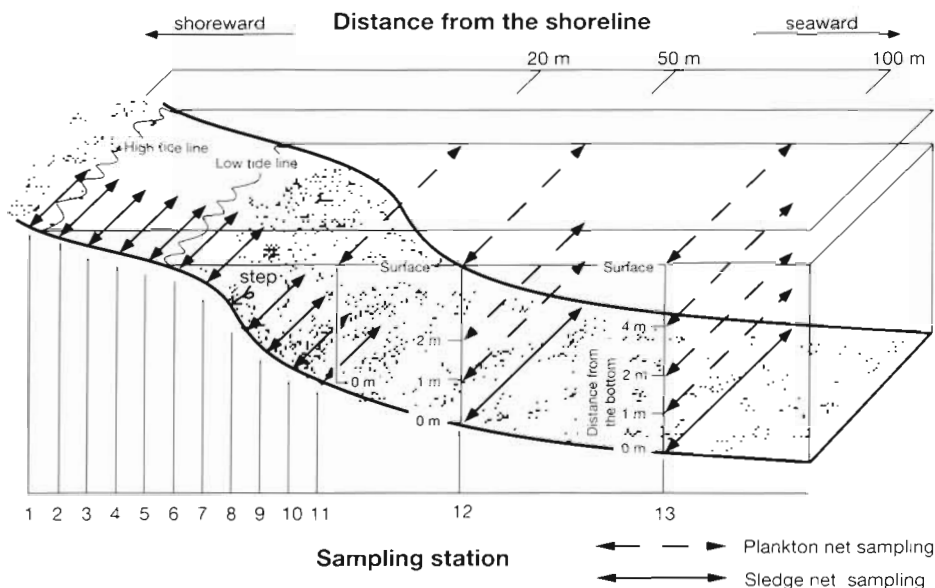


Fig. 1. Schematic representation of sampling coverage with sledge and plankton nets at Koshirahama Beach, Otsuchi Bay, Japan

RESULTS

Diel and tidal change in the distribution patterns of *Archaeomysis kokuboi*

Macroscale change in the benthic and planktonic distribution patterns

Shifts of the benthic distribution patterns of different developmental stages are shown in Figs. 2 & 3 and those of planktonic distribution in Fig. 4. During the

day, *Archaeomysis kokuboi*, the closest dweller to the shoreline, showed remarkable tidal migration following the tidal shift of the shoreline, but the migration behavior was different among the developmental stages and sexes. The structure of the intraspecific zonation was maintained during the daytime tidal shift of its habitat as a whole, but at night the mysids emerged into the water column. Nocturnal swimming activities were also different among the developmental stages and sexes. The pattern of each stage can be described as follows:

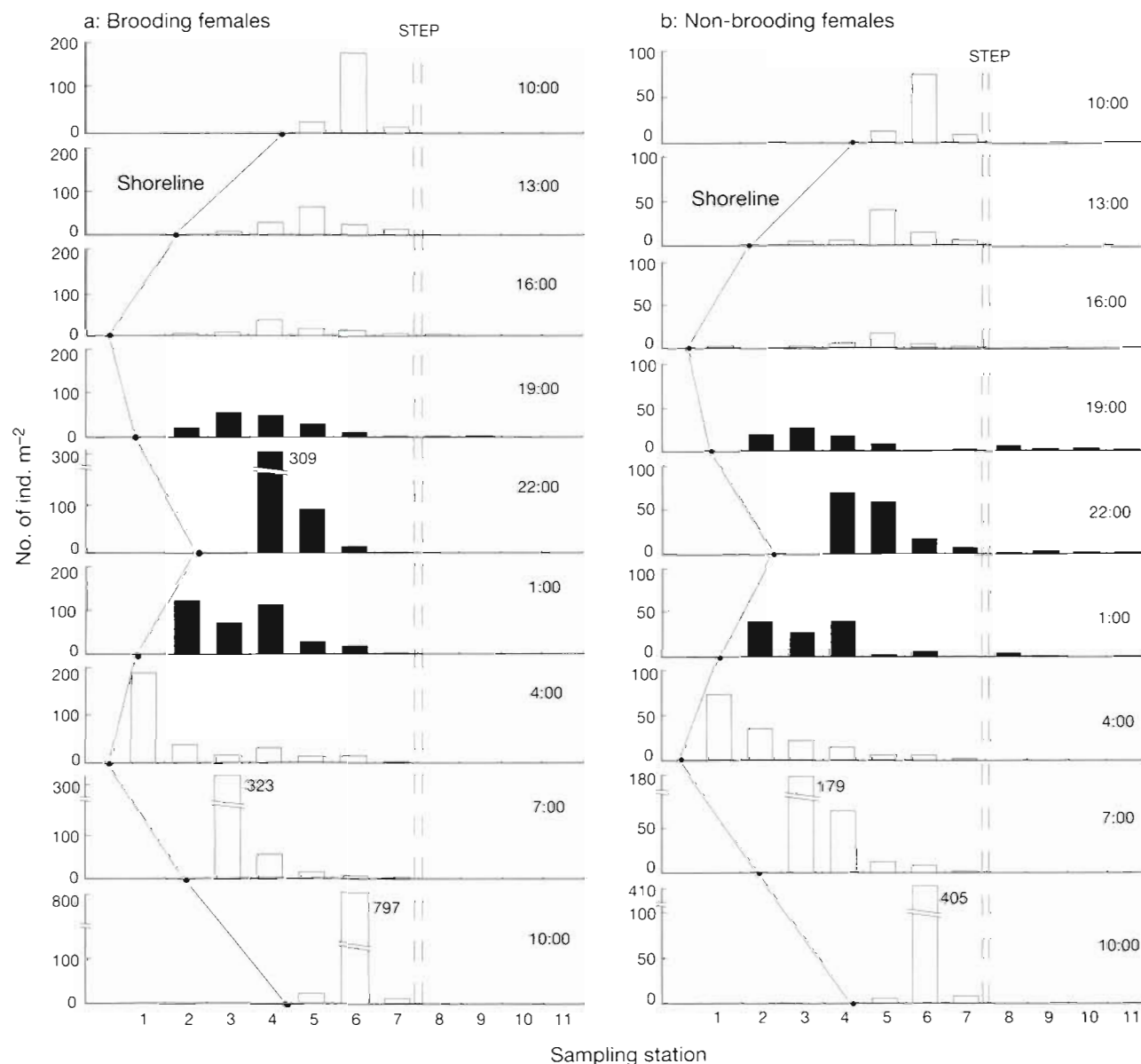


Fig. 2. *Archaeomysis kokuboi*. Benthic distribution pattern of mature females over 24 h, 18–19 August 1993 at Koshirahama Beach. (a) Brooding females, (b) non-brooding females. Open bars: day collection; black bars: night collection; shaded bars: dawn collection. Dot on the horizontal axis indicates the position of the shoreline (swash line) at each sampling time. Broken lines indicate the position of the step

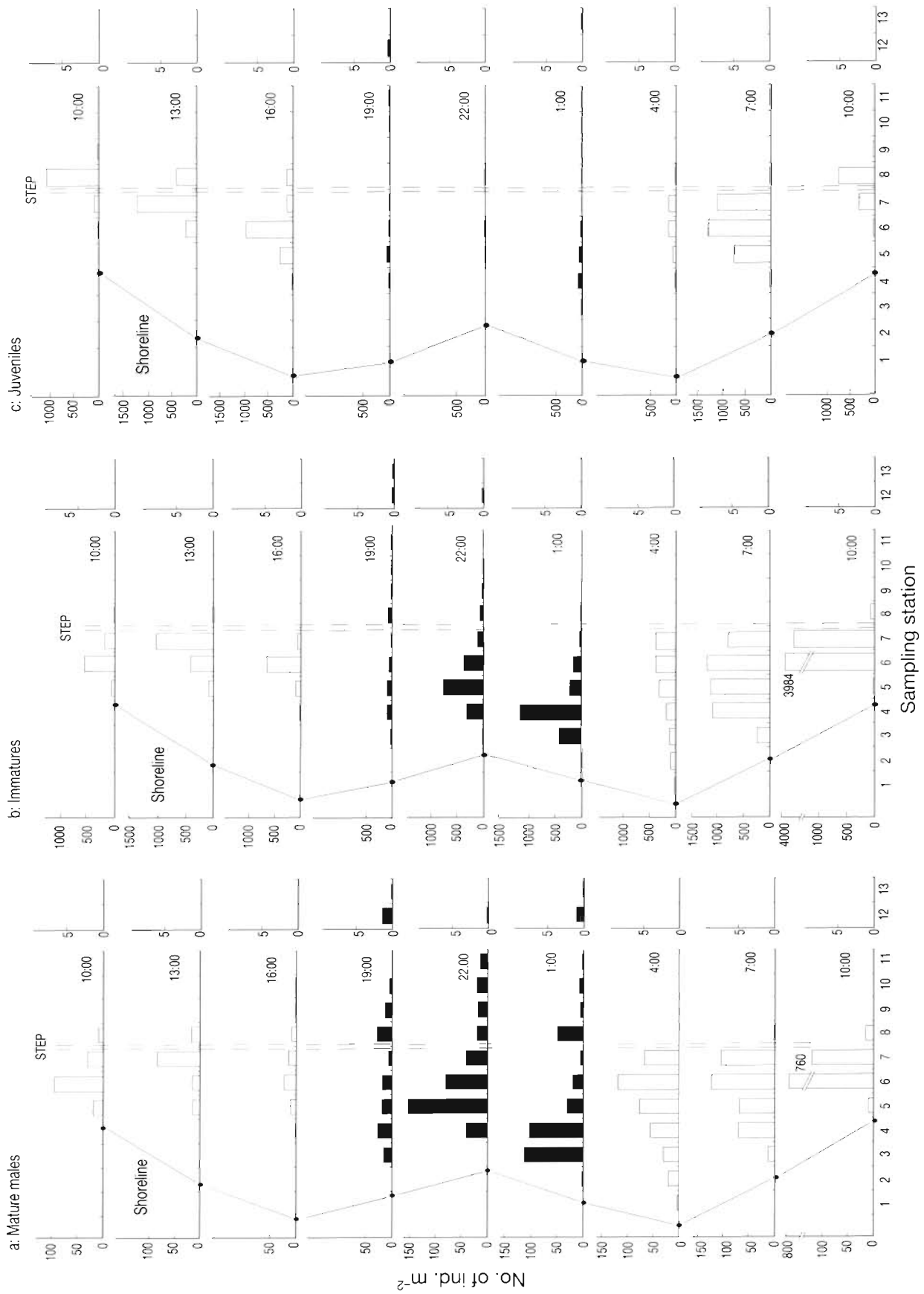


Fig. 3. *Archaeomysis kokuboi*. Benthic distribution pattern of (a) mature males, (b) immatures, (c) juveniles over 24 h, 18–19 August 1993 at Koshirahama Beach. Details as for Fig. 2

Mature females (brooding and non-brooding): The peak abundance of mature females was always located rather close to the shoreline when compared with those of other categories such as mature males, immatures and juveniles, except for the low tide period (Fig. 2). Among mature females, brooding females tended to distribute slightly closer to the shoreline compared with non-brooding females. Daytime distribution patterns on the bottom changed according to tidal phase, i.e. the peak abundances were located slightly more seaward during flooding tide (13:00 to 16:00 h) and more shoreward during the ebbing tide (04:00 to 07:00 h). On the other hand, during the night flood tide, peak abundances were located close to the shoreline and more closely followed the tidal shoreline shift than was the case during the daytime flooding tide. Mature females, brooding or not, were rare beyond the step during the day, but at night only a small portion of non-brooding females occurred beyond the step (Fig. 2b). However, no mature females occurred at the bottom of the offshore Stns 12 and 13 throughout the sampling period, and no brooding females were taken there in the plankton. A few non-brooding females occurred at 19:00 h near the surface layer at Stn 11 and 4 m above the bottom at Stn 13 with a density of 2.1 and 0.4 ind. m^{-3} , respectively (Fig. 4), suggesting that they had dispersed offshore into the water column at night.

Mature males: During the day the peak abundance was always observed 2 to 4 m shoreward from the step (Stns 6 and 7), regardless of the tidal shift of the shoreline (Fig. 3a), but at night the peak shifted shoreward. The seaward limit of their distribution was located just below the step at Stn 8 during the daytime, but at night their

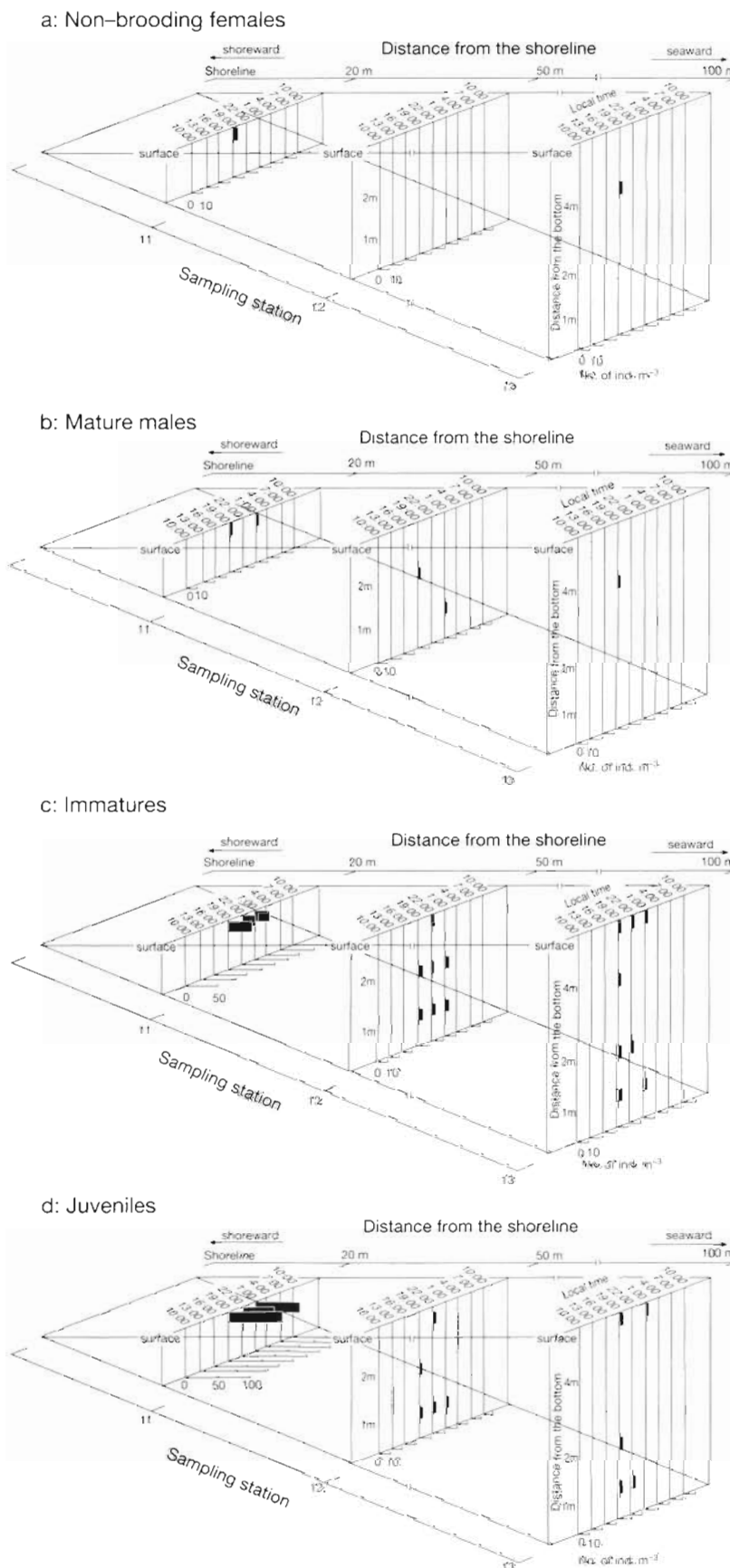


Fig. 4. *Archaeomysis kokuboi*. Distribution of (a) non-brooding females, (b) mature males, (c) immatures and (d) juveniles in the water column over 24 h, 18–19 August 1993, Koshirahama Beach. Brooding females were not captured in the water column by plankton net. Sunset 18:27 h; sunrise 04:08 h

benthic distribution extended seaward to Stn 13, 100 m distant from the shoreline. Mature males were not collected by plankton net sampling during the daytime, but a few individuals occurred at Stns 11 to 13 at night, and 19:00 to 01:00 h, with a density of 0.4 to 0.7 ind. m^{-3} (Fig. 4b).

Immatures: The diel and tidal-shift pattern of distribution for immatures was similar to that of mature males (Fig. 3b). The distribution of immatures in the water column, however, was different from those of mature males and females, i.e. they swam up into the water column more actively at night (Fig. 4c). These swimming immatures consisted of smaller size classes, <5.0 mm SL, and those >5.0 mm SL remained near/on the bottom at night (Fig. 5). Throughout the night highest densities of swimming juveniles were always recorded at the surface at Stn 11, suggesting that their main swimming area was limited to the nearshore area (Fig. 4c).

Juveniles: Differently from other developmental stages, juveniles showed peak abundance just beyond the step during the daytime at low tide (Fig. 3c). This peak moved shoreward following the tidal shift of the shoreline and was located above the step during the flooding tide (Fig. 3c). Total catches by the sledge net in the nearshore area (Stns 1 to 11) decreased drastically at night and dawn. On the other hand, average densities in the water column increased at night (Fig. 4d). Almost all juveniles <3.0 mm SL took part in nighttime swimming in the water column (Fig. 5). During the nighttime the highest densities of swimming juveniles always occurred in surface layers at Stn 11, indicating that their swimming area is limited to the nearshore area just as for immatures (Fig. 4d).

Diel change in vertical microdistribution in near-bottom habitat close to the shoreline

In the 2-layered sledge net samples, which examined the near bottom microdistribution, more than 90% of total individuals were captured by the lower net, within the 10 cm layer above the bottom during the day (Table 1). At night, however, 53.6% of the total catch was collected by the upper net, 10 to 20 cm above the bottom. The proportions of different developmental stages were different between upper and lower net night samples; i.e. the catch of brooding females was always higher in the lower net than in the upper ($p < 0.05$, chi-square test), those of immatures was higher in the upper net than the lower net ($p < 0.01$, chi-square test). The catches of non-brooding females and mature males were almost equal in both nets ($p < 0.05$, chi-square test)

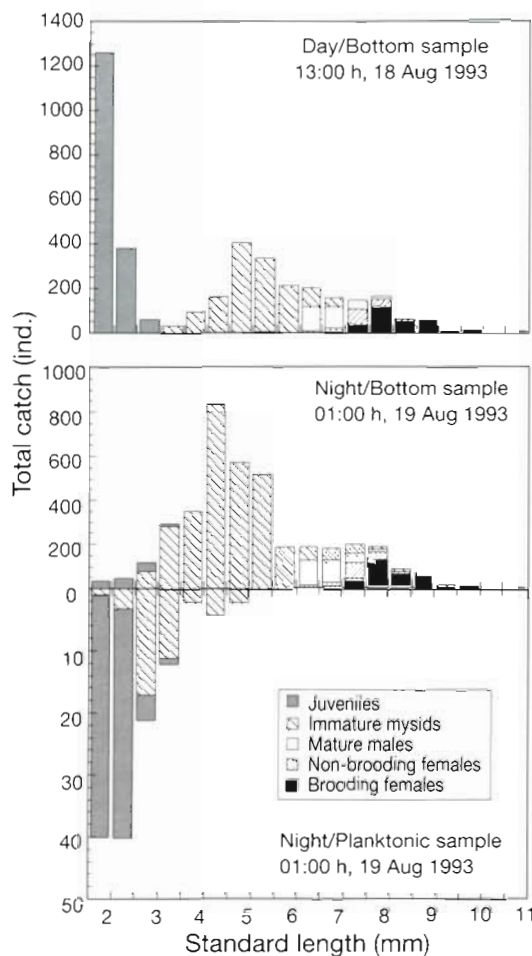


Fig. 5. *Archaeomysis kokuboi*. Diel change in standard length distribution of individuals collected at the bottom with sledge net and in the water column with plankton net in Koshirahama Beach, showing the nighttime emergence of juveniles and smaller immature mysids into the water column. No mysids were collected by daytime sampling with plankton net

Table 1 *Archaeomysis kokuboi*. Diel vertical distribution pattern near the bottom in the shoreline area of 0.3 m depth. –: no mysid collected

Category	Height from the bottom (cm)	No. of ind. m^{-2}	
		Day (08:00 h)	Night (21:00 h)
Brooding female	10–20	1.3	53.3
	0–10	18.0	81.3
Non-brooding female	10–20	0.7	54.7
	0–10	18.7	49.3
Mature male	10–20	0.7	99.3
	0–10	6.0	93.3
Immature	10–20	2.0	103.3
	0–10	26.7	47.3
Juvenile	10–20	–	4.7
	0–10	–	–

Diel and tidal change in distribution patterns of *Archaeomysis japonica*

Macroscale change in the benthic and planktonic distribution patterns

Benthic and planktonic distribution patterns of *Archaeomysis japonica* at different developmental stages are shown in Figs. 6 & 7, respectively. All adult *A. japonica* were grouped as a whole, because total catches were too small to detect sexual or developmental differences. This species, which inhabits the subtidal zone, showed no tidal migration, but emerged into the water column at night in different ways according to developmental stage. The pattern of each stage is described as follows:

Adults: Adults were almost always distributed seaward beyond the step, from Stns 9 to 13 regardless of tidal phase and time, with a peak at Stn 11, 20 m distant from the shoreline, except for 16:00 h when the peak was observed at Stn 10 (Fig. 6a). They were not collected in the water column during the day, but a few individuals occurred there at 19:00 h, at a density of 0.3 to 0.7 ind. m^{-3} (Fig. 7a).

Immatres: During the day almost all immatures were found beyond the step regardless of tidal phase, with peaks just below the step at Stn 8, except at 04:00 h, when the peak shifted to Stn 11 (Fig. 6b). At night almost all of the immature population disappeared from the bottom habitat (Fig. 6b) and occurred in the water column (Fig. 7b). Immatres swam up regardless of body size, but individuals 3.5 to 6.0 mm SL were not captured by either sledge or plankton nets at night (Fig. 8), presumably because they were several decimeters above the bottom where no sampling was made. Highest average density in the water column at night was 2.3 ind. m^{-3} in the layer 2 m above the sea bottom at Stn 12, followed by 2.1 ind. m^{-3} in the layer 1 m above the sea bottom at Stn 13 and 1.4 ind. m^{-3} in the layer 1 m above the sea bottom at Stn 12, indicating that immatures swam into the layer 1 to 2 m above the bottom. No immatures occurred in the plankton sample at the most shoreward Stn 11 at night (Fig. 7 b), indicating that at night immatures migrate seaward beyond the daytime habitat and disperse into the water column in the 50 to 100 m offshore area.

Juveniles: During the daytime, peak abundances were always observed just below the step at Stn 8 and did not

show tidal shift (Fig. 6c). At night and dawn, total catches with the sledge net in the area just beyond the step (Stns 8 to 11) decreased drastically and juveniles, like the immatures, occurred in the water column (Fig. 7c). Highest average density at night in the water column was 5.3 ind. m^{-3} in the layer 2 m above the sea bottom at Stn 13 and in the surface layer at Stn 11 (1.5 to 2.0 m above the bottom), followed by 4.2 ind. m^{-3} in the layer 2 m above the bottom at Stn 12, indicating that they swim up slightly higher than immatures at night.

Diel change in the vertical microdistribution in the near bottom habitat

Diel change in the microscale vertical distribution pattern of *Archaeomysis japonica* in the near-bottom habitats were revealed by the 2-layered sledge net (Table 2). All individuals were captured within 10 cm from the bottom during the daytime, but at night 39.1% were collected 10 to 20 cm above the bottom and the proportions in the upper and lower net differed among developmental stages. Adults were always higher in the lower net ($p < 0.01$, chi-square test), while juveniles were more common in the upper net ($p < 0.01$, chi-square test). Vertical distribution of immatures at night differed among the sampling stations. The lower net catches were larger than the upper ones in the shallowest station ($0.05 < p < 0.01$, chi-square test), while individuals were higher in the upper net at the other 2 offshore stations, 50 to 100 m distant from the shoreline ($p < 0.01$, chi-square test).

Table 2. *Archaeomysis japonica*. Diel vertical distribution pattern near the bottom at 3 stations which were 1.3, 3.3 and 5.3 m deep and about 20, 50 and 100 m offshore from the shoreline, respectively. -: no mysid collected

Time	Category	Height from the bottom (cm)	No. of ind. m^{-2}		
			Distance from the shoreline 20 m	50 m	100 m
Day (13:00 h)	Adult	10–20	–	–	–
		0–10	0.8	0.2	0.2
	Immature	10–20	–	–	–
		0–10	0.7	0.3	–
	Juvenile	10–20	–	–	–
		0–10	1.1	–	–
Night (01:00 h)	Adult	10–20	0.9	0.4	–
		0–10	3.0	2.1	0.9
	Immature	10–20	7.0	2.6	3.1
		0–10	17.6	1.8	1.3
	Juvenile	10–20	0.7	0.4	2.2
		0–10	0.2	–	–

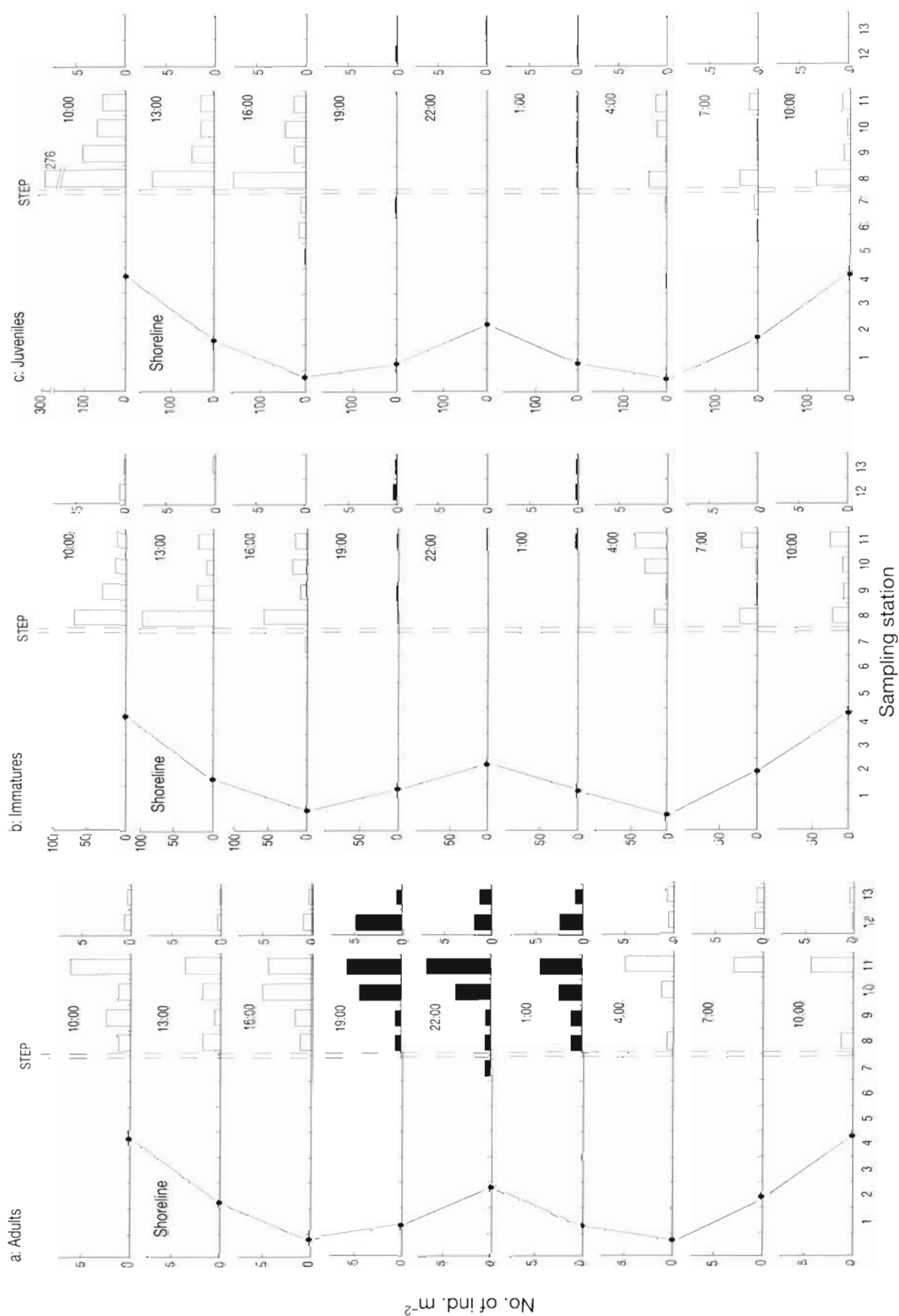


Fig. 6. *Archaeomysis japonica*. Benthic distribution pattern of (a) adults, (b) immatures, and (c) juveniles over 24 h, 18–19 August 1993 at Koshirahama Beach. Details as for Fig. 2

Fig. 7. *Archaeomysis japonica*. Distribution of (a) adults, (b) immatures and (c) juveniles in the water column over 24 h, 18–19 August 1993 at Koshirahama Beach. Sunset 18:27 h; sunrise 04:08 h

Diel and tidal change in distribution pattern of *Iella ohshimai*

Iella ohshimai only occurred at the 2 offshore stations, Sins 12 and 13 (Table 3). They showed no tidal migration throughout the 24 h sampling period. Collected individuals consisted only of juveniles or immatures at an average density of 1.3 ind. m⁻², but at night sledge net catches decreased greatly, while considerable numbers appeared in the plankton, especially 1 to 2 m above the bottom (Table 3).

Occurrence patterns of the 3 species in the water column at night

Spatiotemporal distribution patterns of *Archaeomysis kokubol*, *A. japonica* and *Iella ohshimai* in the water column are summarized in Fig. 9, in which both sexes and all developmental stages are combined (although almost all were juveniles and immatures < 3 mm SL). Emergence into the water column was limited to night in all species. However,

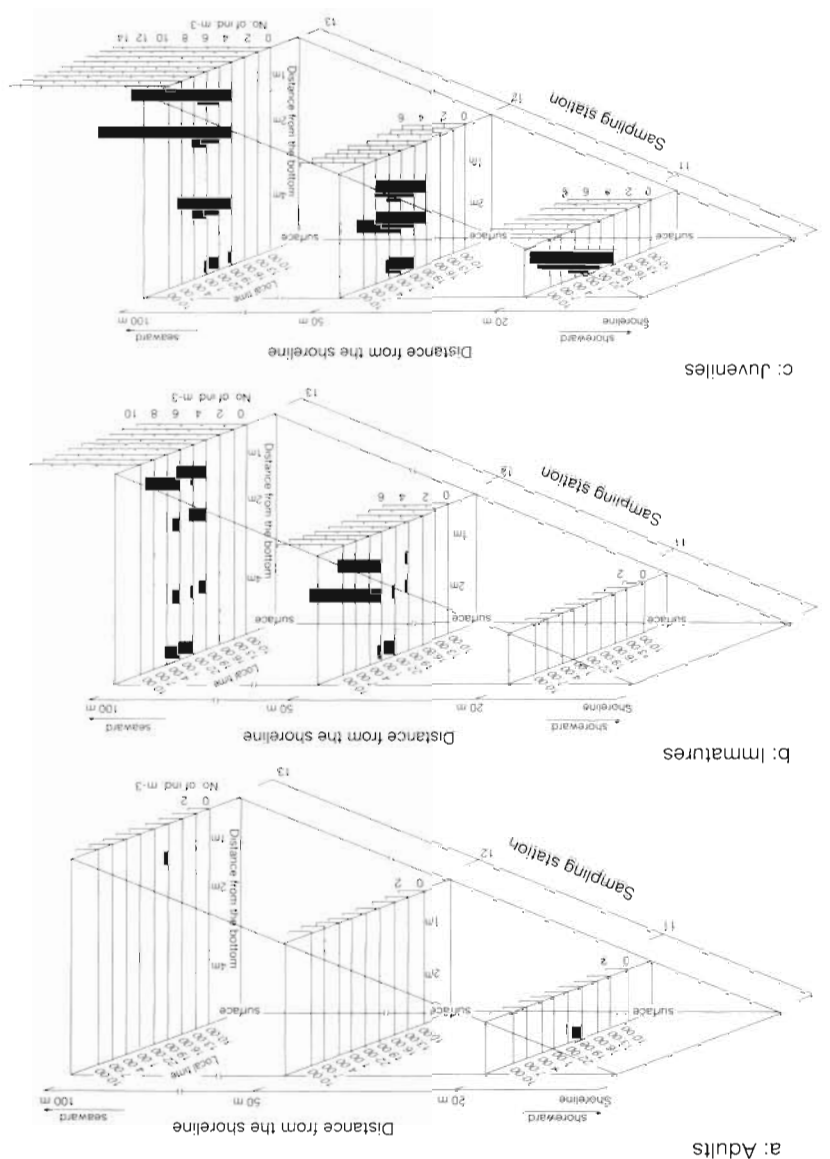


Table 3. *Iella ohshimai*. Vertical distribution of total mysids collected at 3 stations. All individuals collected were juveniles and immatures. Values for the bottom samples are expressed as number of individuals per m². Other values, from water column samples, are expressed as number of individuals per m³. —: no mysid collected

Sampling station	(distance from the shoreline)	Day		Night		Day		Night		Day		Night	
		10:00	13:00	16:00	19:00	22:00	1:00	4:00	7:00	10:00	Day	10:00	10:00
Stn 11 (20 m offshore)	Surface	—	—	—	—	—	—	—	—	—	—	—	—
	Bottom	—	—	—	—	—	—	—	—	—	—	—	—
	1 m above the bottom	—	—	—	0.3	1.0	—	—	—	—	—	—	—
Stn 12 (50 m offshore)	Surface	—	—	—	—	—	—	—	—	—	—	—	—
	Bottom	—	—	—	—	—	—	—	—	—	—	—	—
	1 m above the bottom	—	—	—	0.3	1.4	4.2	—	—	—	—	—	—
Stn 13 (100 m offshore)	Surface	—	—	—	—	—	—	—	—	—	—	—	—
	Bottom	—	—	—	—	—	—	—	—	—	—	—	—
	1 m above the bottom	—	—	—	—	—	—	—	—	—	—	—	—
	4 m above the bottom	—	—	—	0.3	0.7	2.1	—	—	—	—	—	—
	2 m above the bottom	—	—	—	2.4	2.8	2.4	—	—	—	—	—	—
	Bottom	1.5	0.1	0.7	1.7	1.7	2.4	2.4	—	—	—	—	—

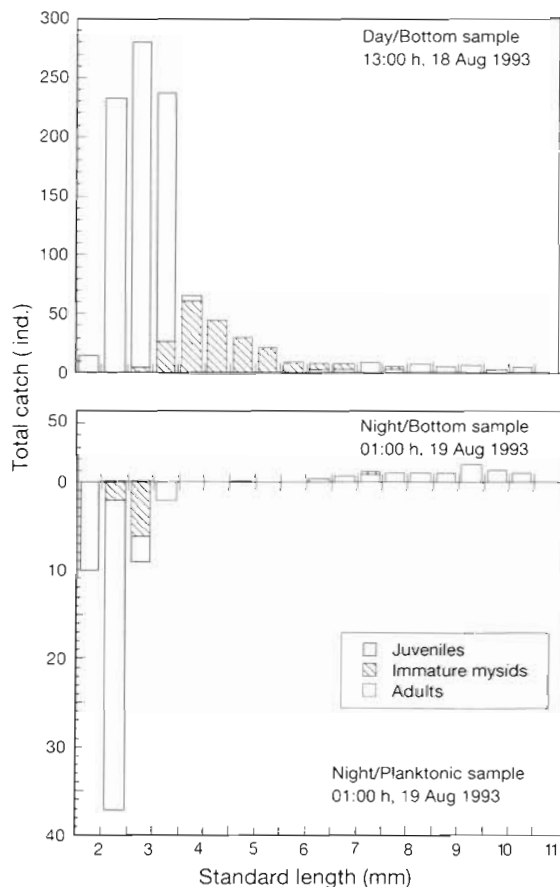


Fig. 8. *Archaeomysis japonica*. Diel change in standard length distribution of individuals collected at the bottom with sledge net and in water column with plankton net in Koshirahama Beach, showing the nighttime emergence of juveniles and smaller immature mysids into the water column. No mysids were collected by daytime sampling with plankton net

the areas of peak abundance did not overlap each other for the 3 species. The shallows were dominated by *A. kokuboi* throughout the night, since more than 93 % occurred at Stn 11, 20 m far from the shoreline. In *A. japonica* such an extreme peak abundance was not observed. They occurred at the 3 sampling stations, Stns 11, 12 and 13, at night at >10 ind. m^{-2} , except at 01:00 h at Stn 11, but 55.4 ind. m^{-2} , which occupied 32.7% of the total catch, were recorded at 19:00 h at the deepest Stn 13. *I. ohshimai* occurred only at the 2 deeper stations, Stns 12 and 13. At 01:00 h, 24.9 ind. m^{-2} , 49.8% of the total catch, were collected, indicating swimming activities of this species were higher late at night than early in the night. This is in contrast to the 2 *Archaeomysis* species, which had peak swimming activities at around 19:00 h (Fig. 9).

DISCUSSION

The daytime habitat of *Archaeomysis kokuboi* shifted according to the shoreline movement (Fig. 10a). A similar tidal migration for this species has been reported on the Pacific coast of northeastern Japan (Matsudaira et al. 1952) and in *Gastrosaccus psammodytes* which inhabits sandy beaches in South Africa (McLachlan et al. 1979). This tidal migration during the daytime was more pronounced in mature females and juveniles, and rather less so in mature males and immatures. The habitat of *A. kokuboi* is limited near the shoreline and its distribution pattern is considered to be controlled by factors such as flow regime near the shoreline (Takahashi & Kawaguchi 1995). Mature

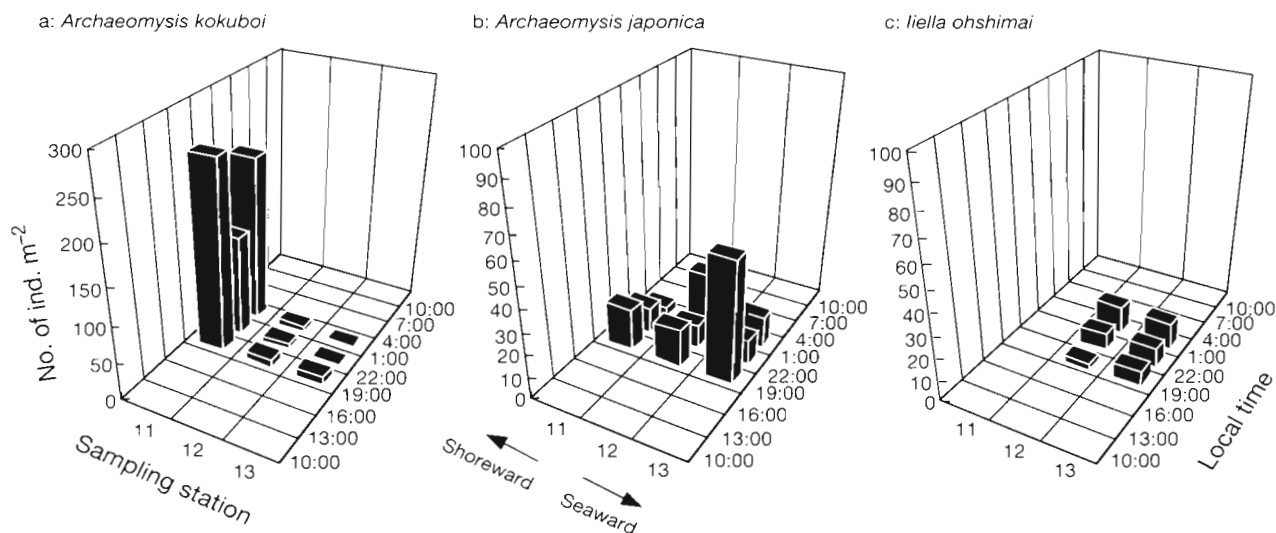


Fig. 9. (a) *Archaeomysis kokuboi*, (b) *Archaeomysis japonica* and (c) *Liella ohshimai*. Spatial and temporal distribution patterns in the water column of the offshore area, Koshirahama Beach. Stns 11, 12 and 13 were located 20, 50 and 100 m distant from the shoreline

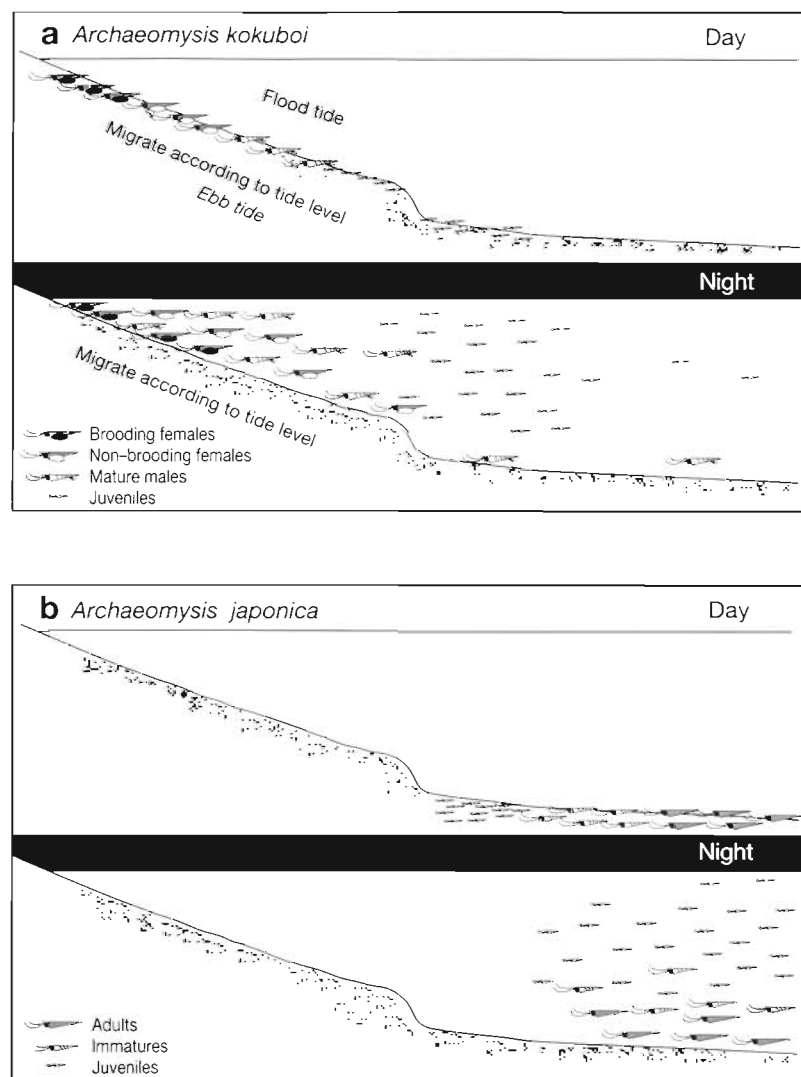


Fig. 10. (a) *Archaeomysis kokuboi* and (b) *Archaeomysis japonica*. Schematic diagram showing day-night distribution patterns at Koshirahama Beach

females and juveniles occupy both seaward and shoreward edges of their intraspecific zonation (Takahashi & Kawaguchi 1995). Therefore environmental factors limiting their distribution are presumed to shift according to tidal movement. On the other hand, mature males and immatures occupy the central part of their distributional range, and show little tidal migration by day, implying that environmental factors limiting their distribution may not be severe compared with those of mature females and juveniles. The positions of the peak abundance were different between the flooding and ebbing tides for all developmental stages even at the same tide level, i.e. the peaks were located slightly seaward at flood, but closer to the shoreline at ebb. These phenomena suggest that there is a time lag for mysids responding to tidal movements. They also indi-

cate that the mysids persist in the bottom layer during daytime even during tidal migration.

Archaeomysis kokuboi swam up into the water column at night (Fig. 10a). This is the first description of nocturnal behavior of this species, but many other beach mysids, such as *Gastrosaccus sanctus*, *G. psammodytes* and *G. mediterraneus*, have been known to exhibit planktonic phases at night (Moran 1972, Wooldridge 1981, Macquart-Moulin & Ribera Maycas 1995). Nocturnal swimming of *G. psammodytes*, which inhabits sandy beaches in South Africa, is known to be related to the diel distribution of their main diet, the surf-zone diatom *Anaulus australis* (Drebers & Schulz) according to Webb et al. (1988) and Wooldridge (1989). This species is known to feed more actively at night than during the daytime (Brown & Talbot 1972). *A. kokuboi* exhibits a nocturnal feeding rhythm regardless of developmental stage or sex (Takahashi & Kawaguchi unpubl.), and thus its nocturnal swimming seems to be related to feeding behavior. Almost all mature *A. kokuboi* emerged into the water column and remained in the shallower area just inshore of the step at night. However, detailed distribution patterns at night indicated that brooding females swim less than non-brooding females and mature males. Our laboratory observations in Otsuchi Marine Research Center showed that brooding females became poor swimmers

with the development of embryos in their brood pouch. In the summer season, Japanese flounder *Paralichthys olivaceus* and Japanese anchovy *Engraulis japonica* frequently fed on *A. kokuboi* at night in the study area, but brooding females were rarely found in the stomach contents of these predators (Takahashi 1996). These observations imply that nocturnal swimming behavior of brooding females may represent a trade-off between advantages of feeding and disadvantages of predation, or waste of energy, or mechanical damage of embryos from swimming in the shore zone. The nocturnal swimming activity of mature males was higher than that of mature females, and only a few mature males were found as far as 100 m distant from the shoreline. The peak abundance of mature males at night shifted shoreward where the non-brooding

females are abundantly distributed. These behavior patterns may increase the chance of mating.

Archaeomysis japonica is mainly distributed seaward and scarcely occurred shoreward of the step during the daytime (Fig. 10b). Their distribution range was not affected by the tide level. The peak abundance of juveniles of this species was always located just below the step where juvenile *A. kokuboi* were concentrated at the lowest tide level. Although juvenile *A. kokuboi* showed a noticeable tidal migration, juvenile *A. japonica* did not, indicating that the response to the tidal bottom-water movement, i.e. flow regime near the bottom, innately differed between the 2 species.

Archaeomysis japonica also emerged into the water column at night (Fig. 10b). Nocturnal swimming may be common in *A. japonica*, since Hanamura et al. (1996) collected a large number of this species in the water column at night in coastal waters off western Hokkaido. Nocturnal swimming behavior was different among developmental stages in Otsuchi Bay. Adults did not migrate so much horizontally and emerged into the water column within 10 cm or so from the bottom, i.e. just above the daytime bottom habitat. In the field, adult *A. japonica* fed more at night than during the day, and benthic harpacticoid copepods were one of their main prey (Takahashi & Kawaguchi unpubl.), also indicating that they swam up and fed at night just above the bottom.

Many marine and freshwater mysids molt, mate (spawn) and release larvae during nocturnal swimming (Murano 1964, Pezzack & Corey 1979, Mauchline 1980). In both *Archaeomysis* species, we always observed molting at night, especially just after sunset in laboratory rearing, and also frequently found exuviae in field-collected night samples in this study. Therefore, in nature, molting is considered to occur during the night when the mysids leave the bottom.

In both *Archaeomysis* species, small individuals, including juveniles and immatures, disappeared at night from their daytime benthic habitat and occurred in the water column offshore from their daytime habitats (Fig. 10a, b). The environment just above their daytime habitat, slightly offshore of the step, may be too rough for small mysids and they risk being stranded by wave action (Nagata 1964). Almost all juveniles and immatures (<3.0 mm in SL) of the 3 species entered the water column, but the spatio-temporal distribution patterns differed among them. Juveniles of both *Archaeomysis* species fed actively at night and their main diets were similar (Takahashi & Kawaguchi unpubl.), suggesting that small mysids segregate for feeding at night. Peracarids, including Mysidacea, lack planktonic larval stages, and nocturnal swimming may also play an important role in their dispersal (Alldredge & King 1980, Kaartvedt

1989). This may also be true for the sand-burrowing mysids in the present study. It is believed that nocturnal migration patterns in Peracarids such as amphipods and cumaceans that live in Masfjorden, Norway (Kaartvedt 1989) may well be related to the trade-off between short-distance dispersal (within habitat) and long-distance dispersal (out of habitat). The daytime habitat of *A. kokuboi* is limited to the narrow range around the shoreline throughout the year at Koshirahama Beach (Takahashi & Kawaguchi 1995). Thus at night, juveniles of *A. kokuboi* do not migrate seaward and avoid transportation offshore, whereas *A. japonica* and *Liella ohshimai* show ontogenetic migration to deeper water (Takahashi & Kawaguchi 1995), possibly through the nocturnal swimming recognized in this study. A similar behavior is known in *Gastrosaccus spinifer*, *Mesopodopsis slabberi* and *Schistomysis kervillei* in the North Sea (Van der Baan & Holthuis 1971).

Intertidal species, including *Archaeomysis kokuboi*, have not been listed in the literature as the main prey of the fishes of sandy beaches, although such mysids are abundant there. Moreover *A. kokuboi*, especially mature individuals, were rarely preyed on by fish such as Japanese flounder during daytime at Koshirahama Beach (Takahashi 1996). In the Japan Sea juvenile Japanese flounder exploited mainly pelagic mysids, although sand-burrowing *A. japonica* were dominant in the same habitat (Hirota 1990). Daytime distribution pattern of sand-burrowing mysids, such as tidal migration, and burrowing behavior may be effective adaptations for predator avoidance. Therefore, sand-burrowing mysids may succeed in escaping visual predators by this unique behavior among mysidaceans, i.e. burrowing in sand or invading the intertidal area by day. On the other hand, their distribution patterns at night are well adapted to ensure feeding or reproduction during the dark period.

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