DISTRIBUTION OF JUVENILE AND ADULT GHOST SHRIMPS, *CALLIANASSA JAPONICA* ORTMANN (THALASSINIDEA), ON AN INTERTIDAL SAND FLAT: INTRASPECIFIC FACILITATION AS A POSSIBLE PATTERN-GENERATING FACTOR

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ABSTRACT

On an intertidal sand flat in western Kyushu, Japan, adults of the ghost shrimp *Callianassa japonica* Ortmann inhabited the upper tidal zone in 1979. Their distribution later expanded greatly to occupy almost the entire sand flat by 1983, the situation remaining unchanged until the end of the study in 1990. Both larval settlement and adult migration accounted for the expansion of the distribution. The positions of the tidal zones, which had the highest densities of newly settled juveniles, shifted, along with the distribution expansion of adults, but were always around the seaward margin of the adult habitat, with densities gradually decreasing shoreward. After maximum distribution expansion was attained, the densities of adults were higher seaward along the elevation gradient, reflecting spatial variations in juvenile density. Occupation of deep-sediment layers by juveniles and hence their escape from mortality-causing factors near the sediment surface might be facilitated through the bioturbation of sediments and by the presence of burrows of established adults. This appears to be responsible for the observed distribution patterns.

The maintenance of local populations may in good part depend on their recruitment success. For marine soft-sediment systems it has been reported that adults of some macrobenthic species lower recruitment of conspecific juveniles, while those of others promote it (for reviews, see Woodin, 1976; Reaka, 1987; Wilson, 1991; Tamaki, in press). Compared with the number of documented examples of negative intraspecific influences, only a few studies have demonstrated the occurrence of positive ones (Highsmith, 1982; Gallagher *et al.,* 1983). However, it may be natural for researchers studying soft bottom benthos to consider that local recruitment will be enhanced if larvae or juveniles settle on or near protective adults or if adults modify the surrounding environment so that juveniles can survive better there (e.g., Reaka, 1987). For the thalassinidean ghost shrimp genus *Callianassa,* the results of Posey (1986) suggested that the presence of adults of *Callianassa californiensis* Dana ensures the recruitment success of conspecific juveniles.

On an intertidal sand flat in western Kyushu, Japan, *Callianassa japonica* Ortmann dominated the macrobenthic community (Tamaki and Kikuchi, 1983). The distribution of adults of *C. japonica* within the sand flat has recently expanded extensively (Tamaki, 1984, 1987; Tamaki and Suzukawa, 1991; Tamaki *et al.,* 1992). The first aim of this paper is to describe both spatial and temporal changes in the densities and distributions of juveniles and adults of *C. japonica* associated with population expansion on the sand flat. The second is to identify possible mechanisms responsible for the distribution patterns observed, with particular emphasis on intraspecific facilitation by adults on settling larvae (=decapodid larvae, Y. Fukuda, personal communication; cf. Konishi *et al.,* 1990) or settled juveniles as related to both maintenance and expansion of the population.

MATERIALS AND METHODS

Study Area

The study area was an intertidal sand flat facing Tomioka Bay at the northwestern corner of Amakusa-Shimoshima Island, western Kyushu, Japan (Fig. 1). A rectangular area , approximately 300 m wide alongshore, was selected as the sampling site. It was exposed for a distance of 335 m seaward at extreme low water spring tide (ELWS). The elevation of the upper one-third to one-half of the site was close to the level of mean low water neap tide (MLWN), from which it gradually lowered to the mean low water spring tide (MLWS) level (=310 m from the shore) (Fig. 2).

Ecology of *Callianassa japonica*

Callianassa japonica is an obligate burrower. Ovigerous females of the species, which spawn planktonic
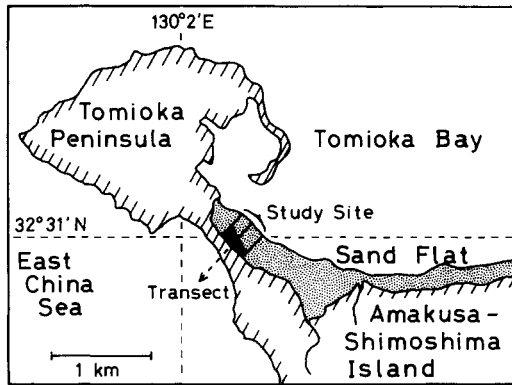
Fig. 1. Location of the study site and transect on the sand flat (dotted area) in western Kyushu. The distribution range of adults of *Callianassa japonica* in July 1979 is shown in black (from Tamaki and Kikuchi, 1983).
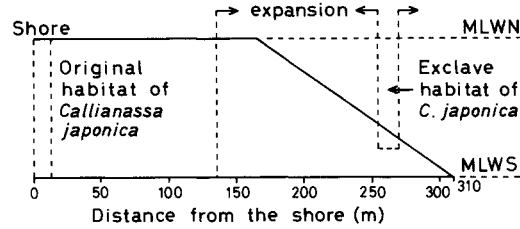

Fig. 2. Schematic representation of the adult distribution zones (=habitats) of *Callianassa japonica* along an elevation gradient (along the transect in Fig. 1) of the sand flat in late summer and autumn of 1980 (after Tamaki and Suzukawa, 1991). MLWN: mean low water neap tide; MLWS: mean low water spring tide.

zoeal larvae, occur from June–October, with newly recruited juveniles appearing between July and December (Ingole et al., in preparation). Females attain maturity at the age of approximately 1 year (Ingole et al., in preparation). A survey of macrobenthos distribution in early July 1979 revealed that adults of *C. japonica* inhabited the upper (approximately 80–150 m wide) zone of the study site, except for the uppermost approximately 10-m wide zone (Tamaki and Kikuchi, 1983; Fig. 1). From 1979 on, the distribution range of adults of *C. japonica* expanded seaward. During late summer and autumn, 1980, both gradual seaward extension of the original distribution zone and generation of a separate zone in the lower sand flat (around 260 m distant from the shoreline; hereafter called the exclave zone) occurred (Fig. 2). Expansion of these two zones continued after 1980, and by 1983 almost the entire sand flat (except for the uppermost zone) was densely populated by *C. japonica*. Since 1983, no reduction in the distribution range has been recorded. Accompanying the distribution expansion described above, several marked changes were observed in the sediment characteristics owing to the intense bioturbation by the occupants: decrease in the silt-clay content, softening (loosening) of formerly firm sediments, and deepening of the oxidized surface sediment layers into the formerly reduced region, extending as far as the bottom of the sediment column (Tamaki and Suzukawa, 1991). The initial noncolonization of the uppermost zone of the sand flat by *C. japonica* may have been due to the thin sediment layer (approximately 5–10 cm; Tamaki, 1984), which prevented adults of *C. japonica* from constructing deep burrows within it. After 1984, however, as sediment accumulated and eventually attained thicknesses greater than 10 cm, some adults successfully invaded the area (personal observation).

Sampling of Populations of *Callianassa japonica*

The presence of *Callianassa japonica* could be confirmed by the evidence of both burrow openings (3–6 mm in diameter for adults) on the sediment surface and the presence of the sediment softened so that one's

feet sank easily into it. Since the presence of zoned distributions (i.e., parallel to the shoreline) for *C. japonica* at the study site had already been confirmed (Tamaki and Kikuchi, 1983), sampling was conducted along one representative transect running from the shore to around the MLWS level (Fig. 1) during low tide at several spring tides during the period from September 1979 to July 1990. Sampling dates were grouped into 2 periods according to the degree of the distribution expansion of adults of *C. japonica*: before (September and October 1979, July, August, and September 1980, and February 1981) and after (September 1984, August 1986, July 1988, August 1989, and July 1990) overall distribution expansion. Specimens of *C. japonica* were collected using either a cylindrical corer [100 cm^2 × 35 cm high (during 1980–1984) or 50 cm high (after 1984) acrylic tube] or a metal quadrat frame (25 × 25-cm area × 12-cm height throughout the study period).

For core sampling, 3 stations [60 m, 160 m (140 m in February 1981), and 260 m distant from the shore] were placed, the number of samples (N) at each station varied from 6–20 (Table 1). Hereafter, St. X denotes a station which is X m distant from the shore. On one occasion (St. 260, February 1981) all samples (N = 6) were pooled in the field to yield 1 sample. On nearly every occasion, the entire sediment column, which overlay an accumulation of large-shell remains, was obtained by the corer. It was 1–3.5 cm short of the bottom of the sediment layer for 9 samples only at St. 60 in February 1981. Overall, the sediment thickness varied from 18.5–46 cm. After removal of the sediment column, it was sieved through a 0.5-mm mesh sieve and fixed with 10% neutralized Formalin solution. For examination of the vertical distribution of *C. japonica* in samples taken on 26 September 1980, each sediment column was subdivided into upper and lower sections (0–10 cm from the sediment surface and the remaining sediment column; 18.5–30.5-cm total depth), these being sieved through 0.5- and 1-mm mesh sieves, respectively.

For quadrat sampling, 16–22 stations were placed throughout the transect, the distance between adjacent stations varying from 10–30 m. The sampling dates are shown in Fig. 5. A single sample was taken at each station, except for St. 310, August 1986 (N = 5). The surface sediment was excavated to a depth of 10 cm within the frame, but on several occasions at the lowest stations (St. 320, August 1986; St. 330, July 1988; St. 310, August 1989), which were covered by water con-

Table 1. Dates, stations, and number of core samples (*N*) taken for *Callianassa japonica* before (A) and after (B) the overall distribution expansion of adults. Station 60 during 1980 to 1981 was situated in the middle of the original distribution zone. In February 1981, St. 140 was in the newly extended part of the original zone (15 m shoreward from its seaward limit), and St. 260 was in the newly generated exclave zone in the lower sand flat.

(A) Before overall expansion			
Date	30 July 1980	12 September 1980	26 September 1980	22–23 February 1981
Station (*N*)	60 (20)	60 (20)	60 (20)	60 (20), 140 (16), 260 (6)

(B) After overall expansion			
Date	23–24 September 1984	6–8 August 1986	2 August 1989	23 July 1990
Station (*N*)	60 (16), 160 (16), 260 (16)	60 (16), 160 (13), 260 (26)	60 (16), 160 (18), 260 (14)	60 (16), 160 (16), 260 (16)

cealing the quadrat frame, 6 core samples to a depth of 10 cm from the sediment surface were collected and pooled, the area covered (600 cm²) being nearly equivalent to that of one quadrat sample (625 cm²). After removal, the sediment was treated in the same manner as for core samples, the single difference being the use of a 1-mm mesh sieve only in 1979.

Laboratory Treatment of *Callianassa japonica*

For the separation of juveniles from adults of *Callianassa japonica*, body-size histograms were used. Among specimens collected from the core samples, those with undamaged bodies and those represented only by undamaged carapaces were measured for total length (TL: along the middorsum from the tip of the rostrum to the posterior margin of the telson) and carapace length (CL: along the middorsum from the tip of the rostrum to the posterior margin of the cardiac region), respectively, under a stereomicroscope to the nearest 0.1 mm. The total lengths for the latter specimens were estimated using a linear regression equation of TL on CL obtained for specimens collected on 13–14 October 1989 as follows: TL = 4.68 CL − 1.09 (*N* = 604; *r* = 0.99; *P* < 0.001) (from Ingole *et al.*, in preparation). Body-size histograms with a 1-mm interval were made from both directly measured and estimated TLs on each sampling date, and were arranged by the same months for different years. From these histograms, recruitment cohorts were tracked and defined, individuals being subsequently referred to as juveniles or adults, depending on body size.

For the core samples, densities of *Callianassa japonica* were calculated separately for juveniles and adults, by counting the number of not only unfragmented whole bodies but also detached heads and telsons. The allocation of heads and telsons to either juveniles or adults was done subjectively. The difference in densities among the 3 stations on each date was tested for significance by the Kruskal-Wallis test, except for the February 1981 data, to which the Mann-Whitney *U*-test between St. 60 and St. 140 was applied. For the quadrat samples, densities of juveniles only, whose body-size range was defined from the body-length histograms (Fig. 3) available for the closest dates in the same or different years, were calculated, because it was anticipated from results for vertical distribution that

only juveniles would have been obtained in representative numbers in contrast to the relatively low efficiency of collection of adults by this method.

RESULTS

Definition of Juveniles and Adults

The total length of *Callianassa japonica* from all the core samples ranged from 4.1–41.0 mm. Body-size (TL) histograms are shown in Fig. 3, in which 6.2% of the total TL data was estimated from CL data. The timing of recruitment of larvae and the growth of juveniles appears to have followed a similar pattern irrespective of year. Between late July and early September, juveniles (individuals which were recruited from early July to early September of the same year) and adults (those which were recruited in previous years) could be easily distinguished from each other by gaps in the size-frequency data, i.e., at the 11.05-mm TL point in July [although no juveniles were present in the core samples on 30 July 1980, such were collected during quadrat sampling on 31 July 1980 (see Fig. 5)] and at the 13.05-mm TL point in August and early September. Late September juveniles and adults could be separated at the 16.05–17.05-mm TL points, with two major size groups being recognizable within juveniles, i.e., the earlier and later recruitment cohorts. These were especially apparent in 1984. With regard to the February 1981 data, although it was difficult to conclusively separate juveniles [individuals which were recruited in the preceding year (=1980)] and adults (those which were recruited prior to 1980) based only on the shape of the
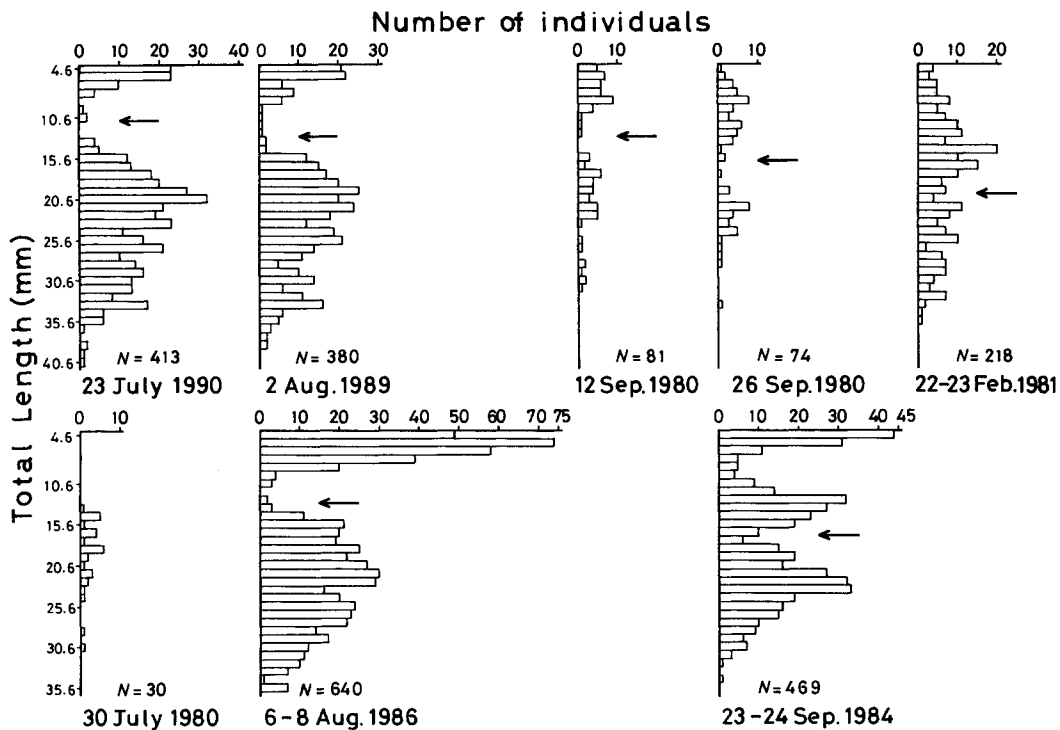
Number of individuals

Fig. 3. Body-size (TL) histograms of *Callianassa japonica* based on core samples (Table 1). Arrows indicate points at which juveniles (individuals of recruitment cohorts) and adults (those of the other cohorts with larger body sizes) are separated from each other. N = total number of individuals.

histogram, the separation point was taken as 20.05-mm TL, after consideration of both the presence of a valley at this point in the size-frequency data and results on cohort analysis obtained for other years (Ingole *et al.*, in preparation).

Vertical Distribution of Juveniles and Adults in the Sediment

Combining data from 20 samples taken at St. 60 on 26 September 1980 (Fig. 3), 55% of juveniles and all of the adults of *Callianassa japonica* were found in the lower sediment columns, i.e., from 10 cm below the sediment surface to the bottom.

Densities of Juveniles and Adults at Three Stations

Temporal changes in the densities of both juveniles and adults of *Callianassa japonica* at three stations along the transect, based on core sampling, are shown in Fig. 4. Combining the results of both the core and quadrat samples (see also Fig. 5), detached heads or telsons accounted for 6.8% of the total number of individuals. In 1979, the sea-

ward, approximately 10-m extension of the original distribution zone of adults of *C. japonica*, indicated by both the appearance of new burrow openings and the softening of the formerly firm sediment, was first noticed in late September. In 1980, extension of the original zone by 20 m and the generation of an exclave zone on the lower sand flat (approximately 15-m wide zone around St. 260) were first recorded in late September and late October, respectively. However, the colonization of these zones by a lower number of adults may have begun somewhat earlier in the years concerned. On 22–23 February 1981, both adults and juveniles were collected in the extended zone (St. 140) and the exclave zone (St. 260). This indicates that the generation of these new habitats was accomplished by the emigration of adults from their original habitat as well as by the settlement of larvae. On this date, the highest mean density of juveniles was observed at St. 140, the difference between St. 60 and St. 140 being significant ($P < 0.001$; Table 2). Following the maximum expansion of the distribution of *C.*
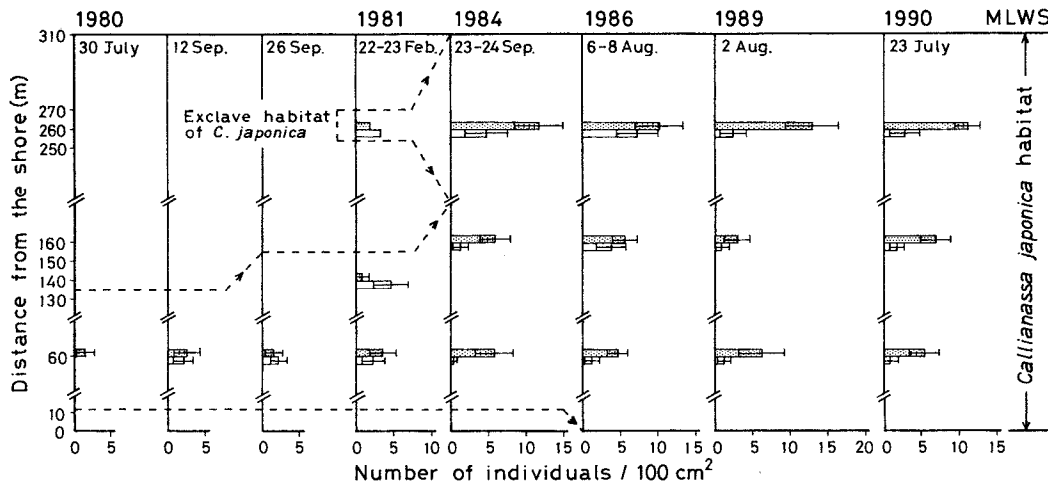
Fig. 4. Densities (mean ± SD number of individuals/100 cm²; number of samples shown in Table 1) of juveniles (blank columns) and adults (dotted columns) of *Callianassa japonica* at three stations on each occasion of core sampling. For St. 260 on 22–23 February 1981, densities per 600 cm² are converted to those per 100 cm². For each of the juvenile and adult categories on every occasion, the difference in densities among the stations was statistically significant (Table 2). Broken lines = limits of adult habitat of *C. japonica*.

japonica (i.e., during the period from 1984–1990), several characteristics were found concerning adult and juvenile densities: (1) the mean density of adults at St. 60 had increased from those recorded in 1980 and 1981 by a factor of 1.3 to 4; (2) the mean density of adults at each station was stable throughout the period, except at St. 160 in 1989, with the higher values being recorded at the more seaward stations on each sampling occasion [approximately 5–6, 6–7, and 10–13/100 cm² at Sts. 60, 160, and 260, respectively; the difference between the stations was significant (P < 0.001; Table 2)]; (3) the difference in juvenile densities between the stations was significant on each sampling occasion (P < 0.001 or 0.001 < P < 0.01 or 0.01 < P < 0.05; Table 2), with the higher mean densities being recorded at the more seaward stations, except at St. 160 in 1989. This followed the adult pattern.

Distribution of Juveniles along the Transect

The distribution patterns of juveniles of *Callianassa japonica* along the transect, based on quadrat sampling, were different between before and after the overall expansion of the distribution of adults (Fig. 5). Between 1984 and 1990, juvenile density was always highest at the most seaward station with a tendency to decrease shoreward.

This pattern was found also during core sampling, St. 200 appearing to approximate the point between the higher (seaward) and lower (shoreward) densities. Before the overall expansion of the distribution of adults (i.e., in 1979 and 1980), juveniles occurred both within the adult habitat and in the zone outside it, their densities in the two areas being comparable, especially so in 1980. As far as the distribution of juveniles within the adult habitat was concerned, a pattern similar to that following 1984 was observed, with the higher densities at the more seaward stations. This was consistent with the results of the core sampling in February 1981 (Fig. 4). However, looking at the distributions throughout the transect, the highest densities were not located around the most seaward stations. Before giving further statements on this point, the observed density values have to be corrected in light of the fact that the depth of sediment occupied by juveniles differed between different parts of the transect as shown below: (1) within the adult habitat, approximately half of the juveniles inhabiting each sampling area would escape collection due to their presence in sediment layers deeper than 10 cm (=quadrat-frame depth) (see above); (2) at the stations seaward of St. 160, in the zone outside the adult habitat, oxidized sediment was found close to the sediment surface (i.e., shallower than 10 cm),
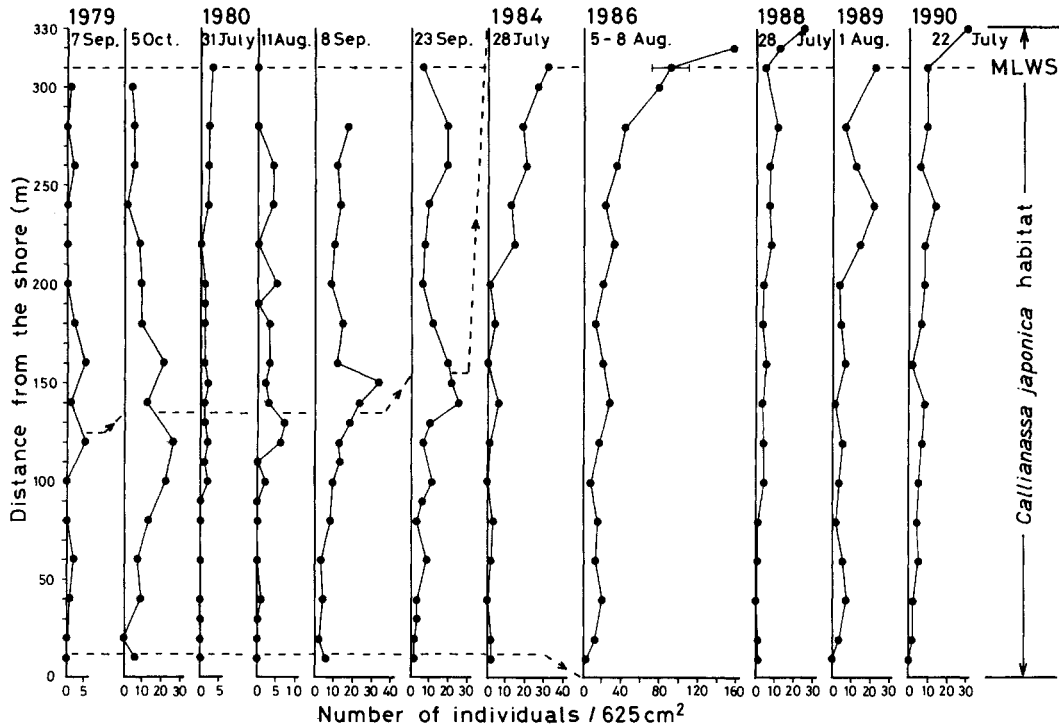
Fig. 5. Distributions [number of individuals/625 cm²; number of samples (N) = 1] of juveniles of *Callianassa japonica* along the transect on each occasion of quadrat sampling. On 8 September 1980, no samples were collected around the MLWS level. For St. 310 on 5–8 August 1986, the mean ± SD value (N = 5) is shown.

under which black, reduced layers existed (fig. 8 in Tamaki, 1984; fig. 6 in Tamaki and Suzukawa, 1991). At these stations, no juvenile burrows were found to penetrate beyond the reach of the quadrat frame (personal observation). This was expected following a laboratory experiment which demonstrated that *C. japonica* could not survive longer than 63 h under anoxic conditions (Mukai and Koike, 1984); (3) in the zone between the adult habitat and St. 160 [i.e., from St. 130 (in 1979) or St. 140 (in 1980) to St. 160], the oxidized surface sediment reached fairly deeply (greater than 10 cm) (Tamaki, 1984; Tamaki and Suzukawa, 1991), irrespective of the absence or presence of only a few adults (Figs. 4, 5). This might have been caused by the lateral permeation of oxygen originating from the underground sediment of the adult habitat (Tamaki, 1984). As a result, juveniles in this zone might also have been able to occupy deep sediment layers, and therefore escape collection. After considering the above factors, it was concluded that in 1979 and 1980, stations with the highest densities of juveniles along the transect were, in fact, those

situated in the seaward marginal zone of the adult habitat and an adjacent, narrow zone on the seaward side. Irrespective of the occurrence of larval settlement over the entire transect, the survival of juveniles thereafter was spatially different. At the beginning of each breeding season (June), only individuals that had settled in the adult habitat during the previous year still survived, whereas those in the other zones had disappeared. For example, from quadrat sampling performed as above on 12 June 1980,

Table 2. Statistical significance of the difference in densities of juveniles and adults of *Callianassa japonica* among the stations on each occasion of core sampling (Fig. 4). Either the Mann-Whitney U-test (between Sts. 60 and 140 in February 1981) or the Kruskal-Wallis test (among Sts. 60, 160, and 260 on the other occasions) was performed. * = 0.01 < P < 0.05; ** = 0.001 < P < 0.01; *** = P < 0.001.

	Sampling occasion				
	February 1981	September 1984	August 1986	August 1989	July 1990
Juveniles	***	***	***	*	**
Adults	***	***	***	***	***

a total of 15 and 0 individuals representing 1979 recruitment were collected in the adult habitat and the zone outside it, respectively (unpublished data).

DISCUSSION

Although various ecological aspects of members of *Callianassa* have been studied, there are only a few documented examples describing distribution expansion. It occurred on a small scale in populations of *C. californiensis* in response to the experimental exclusion of either predators (Posey, 1986) or sea grass (Harrison, 1987), and on a large scale under natural conditions in *C. australiensis* (verbal account in Hailstone and Stephenson, 1961). Since (1) migration of juveniles and/or adults has been reported for several species of *Callianassa* (Monod, 1927; Hailstone and Stephenson, 1961; Forbes, 1978; Bird, 1982; Posey, 1986; Harrison, 1987) and (2) settlement of planktonic larvae outside the adult bed reported for *C. californiensis* (see Posey, 1986), the colonization of new areas may not be a rare phenomenon in species of *Callianassa* other than *C. japonica* on the present sand flat.

On the sand flat, the positions of the stations giving the highest densities of juveniles of *Callianassa japonica* shifted as the distribution range of adults expanded, such stations always being situated around the seaward margin of the main distribution zone of adults, with densities gradually decreasing shoreward (Figs. 4, 5). In general, such spatial differences in juvenile density can result from settling larvae and/or juveniles' differential (1) passive accumulation in, (2) preference for, and (3) survival between, different areas. The possibility of differing rates of passive accumulation due to changing hydrodynamic forces or periods of submergence along the elevation gradient was not examined in the present study, and is left for future investigation. Thus, only the latter two alternatives are discussed in detail in the following sections. It was observed that, although larvae settled in both the adult habitat and the zone outside it, only those in the former zone survived until the next breeding season (Figs. 4, 5; unpublished data). This suggests that adults might have some positive effect on recruitment success. A corollary of this is that larvae which settled outside the adult habitat would

not become established unless some adult migration accompanied such larval settlement (Fig. 4). Accordingly, the following discussion is focused on the possible effects of adults on settling larvae and juveniles, based on (1) a comparison of juvenile densities in both the presence and absence of adults (before the overall expansion of the adult distribution zone) and (2) the examination of spatial variation in juvenile densities within the adult habitat (throughout the study period).

From examination of juvenile densities along the transect before the overall expansion of the distribution range of adults of *Callianassa japonica* (Fig. 5), it appears that sediments outside the adult habitat were not avoided by settling larvae, preference being comparable to that for the adult habitat. A field experiment in which adults of *C. japonica* were excluded from 2 × 2-m plots on the sand flat during April to August in 1986 also supported this view (table 4 in Tamaki and Suzukawa, 1991), the densities of newly settled juveniles of *C. japonica* being in fact a little higher in the exclusion plots than in the intact plots. Thus, only the possibility of spatially different survival rates of settling larvae and juveniles is examined below.

Under the softened sediment conditions of the habitat of adults of *Callianassa japonica* (Tamaki, 1984; Tamaki and Suzukawa, 1991), faster penetration of sediments, compared with that in firmer sediments in which *C. japonica* was absent, was suggested for two other burrowing, infaunal species (Tamaki and Suzukawa, 1991; Tamaki et al., 1992), the cirolanid isopod *Eurydice nipponica* Bruce and Jones, and the snake eel *Pisodonophis cancrivorus* (Richardson). Brenchley (1982) demonstrated that sediments reworked initially by some large-sized burrowers were more easily penetrated by other burrowers, including *Callianassa californiensis*, than intact sediments. A similar situation may also apply to different life stages of *C. japonica*, with burrowing of settling larvae and juveniles into deeper sediment layers being facilitated by the already-reworked adult habitat. In addition, settling larvae and juveniles sometimes enter the surface openings of adult burrows to later branch off on their own (Tamaki et al., in preparation). A sim-

ilar phenomenon was noted for *C. californiensis* (see Swinbanks, 1981). In the study area, probably owing to such mechanisms, juveniles of *C. japonica* in the adult habitat could reach deeper sediment layers than if adults were absent. Another obstacle to juvenile penetration of deep sediment layers without adults is the absence of oxygen (Tamaki, 1984; Tamaki and Suzukawa, 1991), because *C. japonica* is intolerant of long-term anoxic conditions (Mukai and Koike, 1984). This is not a problem in the adult habitat, in which oxygen reaches the sediment bottom.

Then how can the survival chances of settling larvae and juveniles, associated with faster arrival to and occupation of deeper sediment layers, be increased? At least three possibilities exist. (1) Escape from epibenthic predation. Epibenthic predators of juveniles of *Callianassa japonica* identified to date on the sand flat include the hermit crab *Diogenes nitidimanus* Terao, and several demersal fishes such as the goby *Favonigobius gymnauchen* (Bleeker), the puffers *Takifugu niphobles* (Jordan and Snyder) and *T. poecilonotus* (Temminck and Schlegel), the whiting *Sillago japonica* Temminck and Schlegel, and the stingray *Dasyatis akajei* (Müller and Henle), all of which utilize the lower sand flat as a feeding ground (Tamaki and Kikuchi, 1983; unpublished data). Posey (1986) demonstrated that the seaward limit of distribution of *Callianassa californiensis* on tidal flats on the west coast of North America was determined by effective epibenthic predation on both juveniles and adults, thus preventing distribution expansion. (2) Nonsusceptibility to disturbance of the sediment surface by large waves occurring from autumn to spring (Tamaki, 1984). According to Tamaki (1987), polychaetes living close to the sediment surface in the study area were more easily disturbed by wave action than those inhabiting deeper sediment layers. Juveniles of *C. japonica* inhabiting shallow sediment layers in the zone lacking adults might also suffer similar disturbance. (3) Avoidance of large fluctuations in temperature near the sediment surface (for example, at St. 60, the extremes of temperature at 1 cm below the sediment surface throughout the year were 36.6°C and 1.0°C, while those at the 10-cm level were 31.3°C and 5.7°C; Tamaki, 1984). During

low tide on hot sunny days, carcasses of *C. japonica,* which had died because of the heat, were often found on the sediment surface (personal observation). Such low tolerance to high temperatures could explain the lower survival rate of juveniles present in the shallower sediment layers in the zone lacking adults. Posey (1986) suggested that the decline in the density of juveniles of *C. californiensis* inhabiting the area outside the adult bed in winter reflected reduced burrowing activity, resulting in the collapse of their burrows. This might also occur in the present case.

The abundance pattern of juveniles within the adult habitat of *Callianassa japonica* (Figs. 4, 5) suggests that settling larvae crossing the sand flat with the incoming tide successfully burrowed en masse into the adult-inhabited substrate as soon as it was encountered, with the remaining larvae settling progressively shoreward. Such a larval settlement pattern seems to be unrelated to whether the adult density at the seaward limit of the habitat was lower (February 1981 data in Fig. 4; Table 2) or higher (1984–1990 data) than those in the more shoreward zone (Figs. 4, 5; Table 2). Thus, sediment conditions resulting from adult inhabitation (including even those in the narrow zone adjacent to the seaward margin of the adult habitat in 1979 and 1980, such as the thicker, oxidized surface sediment caused by the permeation of oxygen from the adult habitat) (Tamaki, 1984; Tamaki and Suzukawa, 1991) might be more important for larval settlement than simply the presence of adults. The above distribution pattern of newly settled juveniles would be maintained throughout the transect, at least for a short period, such juveniles all benefiting from the increased survival chances afforded by the habitat. In fact, it was observed that after the overall expansion of the adult distribution zone, spatial differences in juvenile density were reflected by those in adult density (Fig. 4; Table 2). A decline in both postlarval and adult densities up an estuary from near its mouth was observed for *C. californiensis* inhabiting a large tidal flat (Bird, 1982). In the present study, irrespective of fluctuations in juvenile density in different years, the density of adults was fairly stable at each station, especially after 1984 (Fig. 4). This suggests

that some density-regulating, physical and/ or biological factors operate as individuals grow. Intraspecific competition for space may be one such factor, unsuccessful adults being expelled to the sediment surface, where they may either die of predation or overheating or emigrate into other areas, as suggested for *C. californiensis* (see Bird, 1982). Such density-dependent emigration could be a mechanism causing some adults to migrate from their original habitat (Fig. 4). However, mere random movement of individuals could also be important, and further investigation is needed to clarify the factors responsible for adult migration.

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