SPATIAL DISTRIBUTIONS AND POPULATION STRUCTURES IN *SCOPIMERA GLOBOSA* AND *ILYOPLAX PUSILLUS* (DECAPODA: OCYPODIDAE)[1)2)]

KEIJI WADA

Seto Marine Biological Laboratory, Kyoto University

With Text-figures 1–5 and Tables 1–5

Abstract

Spatial distributions and population structures of *Scopimera globosa* De Haan and *Ilyoplax pusillus* (De Haan) (Decapoda: Ocypodidae) were investigated at four stations established on the intertidal flat of Waka River Estuary, middle Japan. In *S. globosa*, large males tended to be restricted to the upper level, while small males and juveniles were distributed more evenly. This feature is explained in connection with repulsive interactions between individuals. Juveniles of *I. pusillus* showed higher densities at upper levels inhabited by many conspecific sexable crabs, and the spatial associations between these juveniles and sexable crabs within the upper levels were highly positive. These spatial features of juvenile *I. pusillus* are attributable to their special habit that they can dwell in the adult burrows together with the adults. At the stations inhabited by both *S. globosa* and *I. pusillus*, juvenile *S. globosa* appeared to be restricted within rather upper levels, although no such tendency was detected at the stations devoid of *I. pusillus*. Thus, it is suggested that the distribution patterns of these two species are influenced by intraspecific or interspecific relations.

Introduction

For the two intertidal ocypodid crabs, *Scopimera globosa* De Haan, 1835 and *Ilyoplax pusillus* (De Haan, 1835), the spatial distribution of their population members have been studied by several workers (Harada & Kawanabe, 1955; Ono, 1957, 1960, 1962, 1965; Wada & Tsuchiya, 1975; Wada, 1976). In any of these works, however, neither size nor sex was taken into consideration. Recently, the difference in the distribution pattern between newly settled juveniles and adults of *S. globosa* was pointed out by Wada (1981a) in relation to the granularity of substratum. In addition, the difference in size structure and sex ratio of *S. globosa* between upper and lower areas was reported by Wada (1981b).

In the present paper, distribution patterns of these two ocypodid crabs are studied with regard to their life stages and sex. The significance of the spatial association of different life stages or of different species for the determination of their distribution pattern is also discussed on the basis of the observations at separate

1) Contribution from the Laboratory of Animal Ecology, Department of Zoology, Kyoto University, No. 448.
2) Contributions from the Seto Marine Biological Laboratory, No. 686.

stations of different species composition.

Materials and Methods

Four stations (Sts. A, B, C and D) were selected on tidal flat in Waka River Estuary (34°10′N, 135°10′E), middle Japan (Fig. 1). *S. globosa* occurred at Sts.

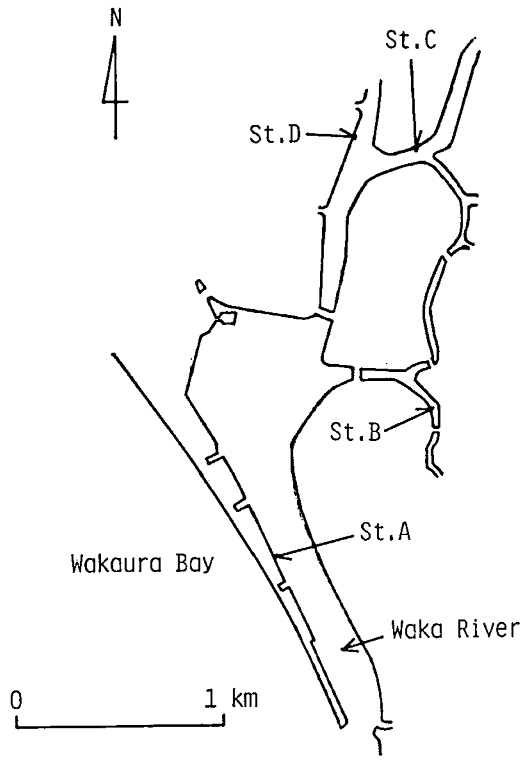

Fig. 1. Waka River and its tributaries with four sampling stations (Sts. A–D).

A, C and D, and *I. pusillus* at Sts. B, C and D. Samples of crabs were collected at spring low tides in August and October–November 1973, January–February and April 1974 at Sts. A–C, and in July 1973 at St. D. At each station, two to four quadrats were set apart on a line crossing their distribution zone, and thc quadrats were numbered serially from the uppermost one as, for example, A–1, A–2 and so on. The quadrats measured 50 cm × 50 cm except that used for D–3, which measured 1 m × 1 m. The substrate within each quadrat was dug up by a shovel to a depth of 20 cm, and was sieved by a net with 1 mm opening to capture crabs. In July and August 1973, numerous unsexable juveniles which had newly settled were encountered together with sexable crabs. Some quadrats (A–1; B–1, 2; C–1, 2, 3) were further divided into sub-quadrats of 10 cm × 10 cm and crabs were sampled separately for each sub-quadrat for the examination of spatial association between the unsexable and the sexable crabs in each quadrat.

Crabs were fixed in 10% sea-water formalin. The sex and the reproductive condition of females were recorded. Carapace breadth was measured to the nearest 0.1 mm with a micrometer under a binocular microscope. In *S. globosa*, the breadth, which does not mean the maximum, was measured across the anteriolateral incisions, whereas in *I. pusillus* the widest part was measured.

At Sts. A, B and C in August, the surface 1–2 cm of substrate sand was collected in each quadrat. The samples were dried at a temperature of 100°C for 5–10 hours, and then sieved with the standard series of sieves and weighed for each fraction. The level of water table in each quadrat was also measured at Sts. A–C at low tide of the sampling day.

Results

Environmental Conditions

Intertidal heights of all the stations were around the mean tide level, St. A being slightly lower than the rest (Figs. 2–5). Since the traverses in each station were slightly shifted in order to avoid the sampling sites already disturbed in preceding observations, the slopes or heights of the traverses were not always identical even in the same station (Figs. 2–4). Granularities of the substratum at Sts. A, B and C are shown in Table 1. Silt-clay percentage and sorting (σ_ϕ) were lowest at St. A and highest at St. B, while the other indices showed similar values among the stations. Within a given station, the silt-clay percentage increased gradually

Table 1. Silt-clay percentage, median diameter (Mdϕ), mean diameter (Mϕ), sorting ($\sigma\phi$), and skewness (α_ϕ) of the surface 1–2 cm sand in sampling quadrats at Sts. A–C. Each index of the granularity was calculated according to Mogi (1971).

	St. A		St. B		St. C		
	1	2	1	2	1	2	3
Silt-clay %	0	0.15	5.26	7.23	2.83	3.78	4.90
Mdϕ	1.90	1.95	1.90	2.00	1.95	2.05	1.80
Mϕ	1.95	1.95	1.88	2.00	1.90	2.00	1.88
$\sigma\phi$	0.55	0.55	0.93	0.95	0.70	0.75	0.78
α_ϕ	0.09	0	−0.02	0	−0.07	−0.07	0.10

Table 2. Water table in sampling quadrats at low tide.

	St. A		St. B		St. C		
	1	2	1	2	1	2	3
Aug.	10 (cm)	5	10	5	—	21	9
Oct. – Nov.	14	4	10	8	12	9	7
Jan. – Feb.	10	3	9	6	8	8	—
Apr.	8	5	—	—	13	9	6

from the upper to the lower quadrats. This was true for all of the three stations, though at St. A its difference between quadrats was very slight. The level of water table at low tide was usually deeper in an upper quadrat than in a lower one at every station, while it was similar in the uppermost quadrat among the different stations (Table 2).

Cross-shore Distribution of *S. globosa* and *I. pusillus*

The density of *S. globosa* at Sts. A and C was higher in the uppermost quadrat than in the succeeding lower ones during the four seasons (Figs. 2 & 4). *I. pusillus* showed the same tendency at St. B (Fig. 3), but at St. C it was very few in the uppermost quadrat supporting many *S. globosa* and rather abundant in the quadrats

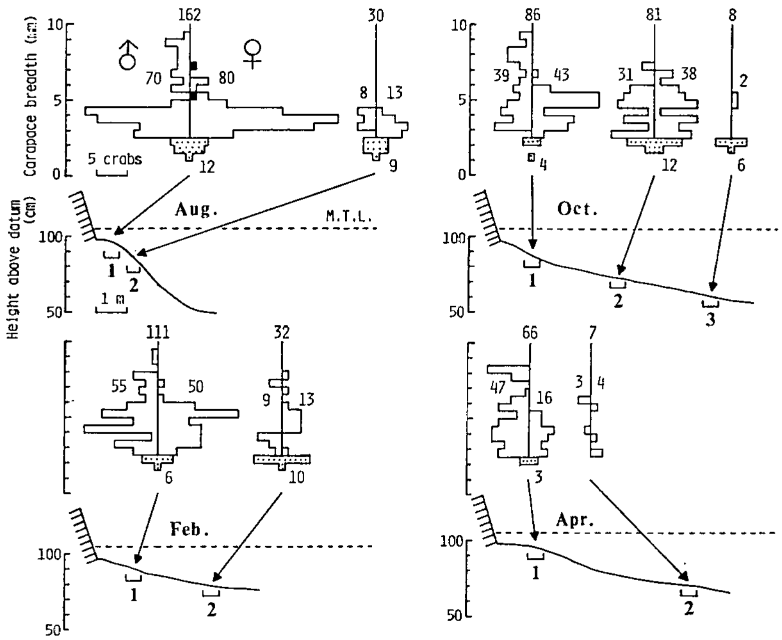

Fig. 2. Size compositions of *Scopimera globosa* in respective sampling quadrats at St. A with profiles showing sites of the quadrats. The solid histograms indicate ovigerous females and the dotted ones unsexable juveniles. Number of collected crabs in each quadrat is shown by figures separately for the males (left), the females (right), the unsexable juveniles (lowermost) and the total of them (uppermost). M.T.L.: mean tidal level.

C–2 and C–3 (Fig. 4). At St. D, the uppermost and the lowermost quadrats were occupied by *I. pusillus*, while in the quadrat D–2 and the upper half of the quadrat D–3 *S. globosa* was dominant, and in the lower half of D–3 the densities of the both species were similar each other.

Cross-shore Variation of Population Structure

Cross-shore variations of population structure will be considered from the size-frequency distributions obtained at the quadrats of Sts. A–C for four seasons and

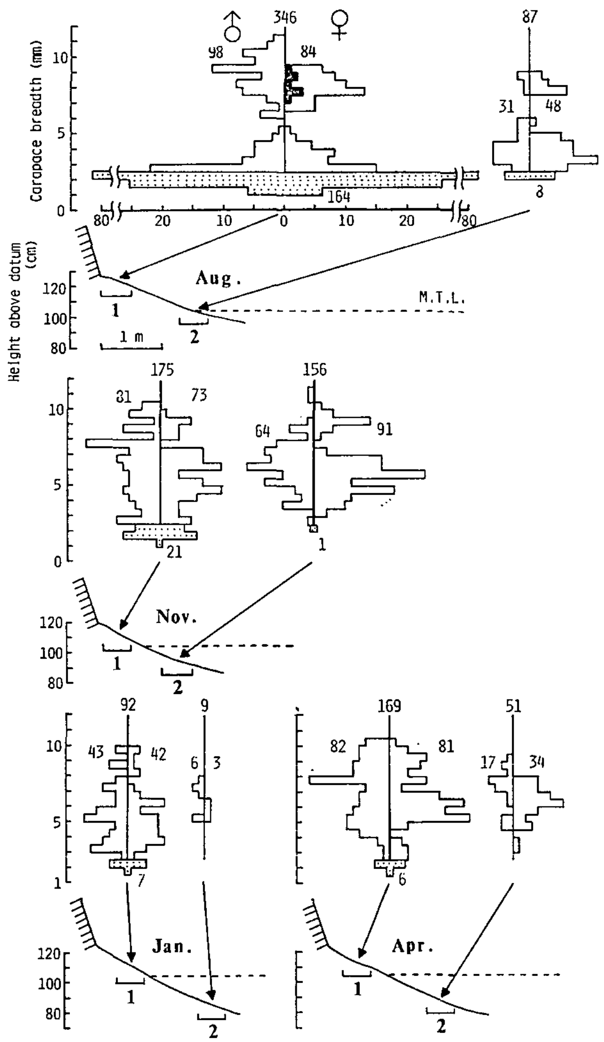

Fig. 3. Size compositions of *Ilyoplax pusillus* in respective sampling quadrats at St. B with profiles showing sites of the quadrats. Details as for Fig. 2.

of St. D for summer (Figs. 2–5).

(I) *S. globosa*

Both sexable males and females were more abundant in upper quadrats than in lower ones, not only at St. A where *S. globosa* solely occurred, but also at Sts. C and D where *I. pusillus* occurred together, except for D–1 occupied by *I. pusillus*. In each quadrat, densities of the both sexes were generally similar, except for A–1 in April where the density of the males was three times higher than that of the females. As seen at Sts. A and C in August and October, large males were restricted to the upper level, whereas small males were widely distributed from the upper to

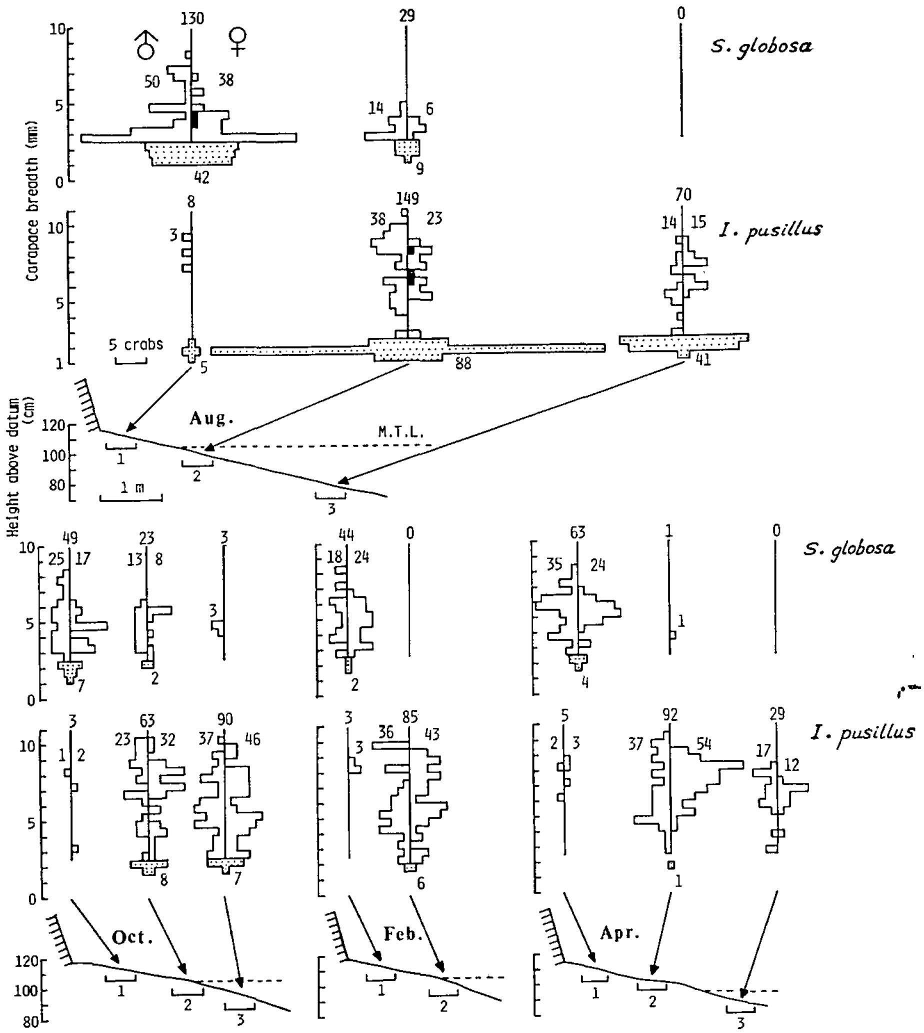

Fig. 4. Size compositions of *Scopimera globosa* and *Ilyoplax pusillus* in respective sampling quadrats at St. C with profiles showing sites of the quadrats. Details as for Fig. 2.

the lower levels, with their density being higher at the upper. On the other hand, difference of the female size structure between quadrats was not so evident on any traverse as in the males. Ovigerous females were few and were found only in the uppermost quadrat at Sts. A and C in August.

Unsexable juveniles smaller than 2.5 mm co-occurred with sexable crabs. At St. A, where no *I. pusillus* occurred, their density was not so much different between the uppermost quadrat and the succeeding lower ones, as compared with the density of sexable crabs. In October and February, the density of unsexable juveniles was higher in the lower quadrats A–2 or A–3 than in the uppermost one, in contrast with sexable crabs which were more abundant in the uppermost. At Sts. C and D,

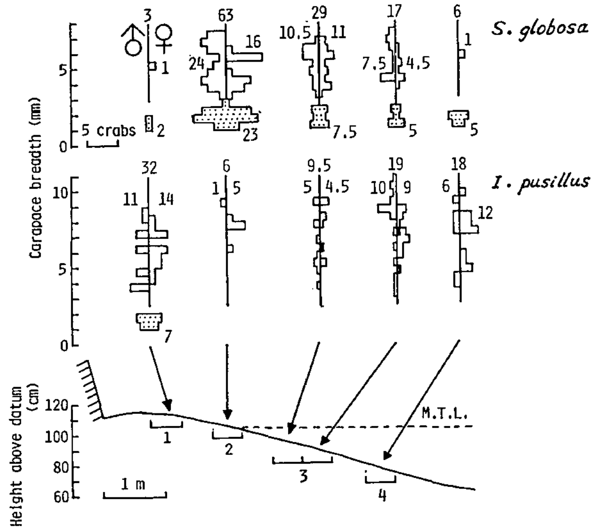

Fig. 5. Size compositions of *Scopimera globosa* and *Ilyoplax pusillus* in respective sampling quadrats at St. D with profiles showing sites of the quadrats. Details as for Fig. 2, and in the quadrat D–3 (1 m × 1 m) the number of crabs as well as the size compositions per 0.25 m^2 is shown separately for the upper and the lower half of the quadrat.

where *I. pusillus* co-occurred, juveniles of *S. globosa* were more abundant in the upper quadrats inhabited by many conspecific sexable crabs and few *I. pusillus* than in the lower ones which were occupied rather by *I. pusillus*.

(II) *I. pusillus*

Both sexable males and females were more abundant in upper quadrats than in lower ones not only at St. B where *I. pusillus* solely occurred, but also at Sts. C and D where *S. globosa* occurred together, except for C–1 and D–2 occupied by *S. globosa*, though in autumn the females at St. B and both sexes at St. C were more abundant in the lower quadrat. In each quadrat, densities of both sexes were generally similar. In the males at St. B, large crabs, as well as small crabs, tended to occur mainly in the upper quadrat, whereas in the lower quadrat the population was composed mostly of middle-sized crabs. Such tendency in the males could be recognized also in the quadrats C–2 and C–3. In the females, difference of the size structure between upper and lower quadrats was not so evident as in the males. Ovigerous females were found in the quadrats B–1 and C–2 in August and D–3 in July, but none from the lowermost quadrats at any station.

Unsexable juveniles smaller than 2.5 mm appeared much more abundantly in summer than in other seasons, co-occurring with sexable crabs. At St. B, their density was higher in the upper quadrat than in the lower as in sexable crabs. At Sts. C and D where *S. globosa* occurred together, they showed higher density in the quadrat inhabited by many conspecific sexable crabs and few *S. globosa*.

Spatial Association between Unsexable Juveniles and Sexable Crabs in Each Quadrat

For the analysis of the spatial associations between newly settled juveniles and sexable crabs of a single species and between two species, the samples obtained in August when the juveniles occurred abundantly were examined with two indices (γ & ω) proposed by Iwao (1977) based upon interspecies mean crowding.

The overlap index γ between two groups takes the maximum value of 1.0 when the both occur completely overlapped and the minimum value of 0 when their distributions are completely exclusive with each other. The correlation index ω between two groups changes from its maximum of $+1$ for complete overlapping, through 0 for independent occurrence, to the minimum of -1 for complete exclusion.

The values of γ and ω between unsexable juveniles and sexable crabs of *S. globosa* in A–1 and C–1 and of *I. pusillus* in B–1, 2 and C–3 are shown in Table 3. Though the values of *S. globosa* in C–1 were similar to those of *I. pusillus* in C–3,

Table 3. Values of γ and ω representing the spatial associations between unsexable juveniles and sexable crabs of the same species in respective five quadrats in August.

	S. globosa		*I. pusillus*		
	St. A–1	St. C–1	St. B–1	St. B–2	St. C–3
γ	0.395	0.638	0.827	0.663	0.603
ω	−0.190	−0.071	0.067	0.376	0.006

Table 4. Values of γ and ω representing the spatial associations of four groups of crabs, i.e. sexable *S. globosa* (Ss), unsexable *S. globosa* (Su), sexable *I. pusillus* (Is), and unsexable *I. pusillus* (Iu) in C–2 in August.

		γ			
		Ss	Su	Is	Iu
ω	Ss		0.342	0.487	0.459
	Su	0.020		0.338	0.325
	Is	−0.206	−0.157		0.847
	Iu	−0.230	−0.165	0.431	

I. pusillus showed larger values in the both indices than *S. globosa* for the quadrats A–1 and B–1, 2 occupied solely by each species. On the other hand, for C–2 where the both species co-occurred in similar densities, the interspecies γ and ω were calculated as well as the intraspecies γ and ω (Table 4). The intraspecies γ and ω of *I. pusillus* showed remarkably larger values than any other pair, while among the other pairs the values of the both indices were similar to each other.

Discussion

In *S. globosa*, while sexable crabs of both sexes co-occurred in similar densities at both the upper and the lower level, the large males tended to be restricted to the upper level and the small males occurred rather evenly from the upper to the lower level. A similar example was already reported by Wada (1981b). In addition, the unsexable juveniles were also distributed widely as in small males, being distinctly abundant in some cases at the lower level. The same tendency in the cross-shore distribution of large and small crabs has been reported in other ocypodids; e.g. *Scopimera inflata* Milne Edwards by Fielder (1971), *Dotilla fenestrata* Hilgendorf by Hartnoll (1973) and *Ocypode quadrata* (Fabricius) by Fisher and Tevesz (1979), in which the differences between upper and lower levels in substratum, water condition and duration of exposure time have been pointed out as factors influencing such distributional feature.

It may easily be anticipated that the water table descends deeper at low tide at the upper level of the shore, as is actually demonstrated in Table 2, and the deeper burrows for water supply are needful there. The fact, reported by Utashiro and Horii (1965), that the burrows of *S. globosa* are generally deeper landward appears to support this. If the small crabs need their burrows reaching down to the same depth as in large crabs for water supply, the upper level would be less favorable site for them to burrow. However, as shown in the present survey, many small crabs inhabited also the upper level, and the burrows of small crabs were generally shallower than those of large crabs at the same upper level (Table 5). These evidences do not support the supposition.

Table 5. Burrow depths of different size groups in male *S. globosa*. The data were obtained at an area of the same level near St. C in 14:30–15:00 on 25 May, 1982.

Carapace breadth (mm)	N	Burrow depth (cm)		
		Max.	Min.	Mean
3 – 5	8	5.6	2.4	4.2
5 – 7	8	8.0	3.3	5.9
7 – 9	9	9.5	6.2	8.0

It may also easily be anticipated that the upper level is the place where surface activities are allowed for longer time. Both large and small crabs have been witnessed to appear on the surface and continue their surface activities throughout the whole exposure time, though many cease to come out of their burrows at the late exposure time. For those crabs requiring longer surface activity, the upper level is naturally favorable, but there is no evidence to suppose that this is particularly applicable to large crabs.

As is shown in Table 1, the granularity of the substratum was similar between the upper and the lower level of the same station, particularly of St. A. Accordingly, it is also unlikely that the granularity of the substratum has some connection with the cross-shore variation in the size structure of *S. globosa* population. On the contrary, the size difference itself appears to act as the factor governing the difference in size structure. The small crabs have been often observed to be attacked by large crabs and driven away. If the large crabs burrow at and occupy the upper level, as is the case in the present study, presumably because, for instance, they can construct firm large burrows there, the small crabs are more or less forced to occur at the lower level. The distributional difference between large males and small males or between juveniles and sexable crabs in *S. globosa* may thus be attributable principally to the repulsive interaction between the individuals.

In *I. pusillus*, the distribution of large males tended to be biased to the upper level, while middle-sized males occurred more evenly. This feature may be also related to the repulsive interaction between the individuals, because the same situation as mentioned above for *S. globosa* is applicable also to male *I. pusillus*, particularly the larger ones. In females of both *S. globosa* and *I. pusillus*, on the other hand, the difference of size structure between upper and lower levels was not so evident as in males. The repulsive interaction may not be intensive among the females and the exclusive action of large males may not be directed to small females, which is to be examined and confirmed in the future study.

In contrast to small males and juveniles of *S. globosa*, the density of small males and juveniles of *I. pusillus* was higher at the upper level where many conspecific large crabs burrowed. As has been reported by Wada (1981a), many of small *I. pusillus* dwell in large burrows made by adults, cohabiting with the adult and some other small crabs. The repulsive interaction has been seldom noticed between large and small crabs in *I. pusillus*. This situation naturally results in the highly positive correlation in occurrence between them, as is exemplified in each quadrat, and allows small crabs to inhabit abundantly the upper level large crabs occupy.

Between stations inhabited only by single species and by both species, no evident difference was found in cross-shore distributions of sexable crabs of either species or juveniles of *I. pusillus*. As to juvenile *S. globosa*, on the other hand, the following difference was recognizable: at St. A not inhabited by *I. pusillus*, the density of juveniles in the upper quadrat was almost the same as the density in the lower quadrat or rather lower than the latter, but at Sts. C and D where *I. pusillus* co-occurred, the density of juvenile *S. globosa* was high in the upper quadrat inhabited also by many sexable crabs of *S. globosa* and low in the lower quadrat inhabited by many crabs of *I. pusillus*. This fact suggests that the occupation of the lower quadrat of C and D by many crabs of *I. pusillus* may have an effect to keep off juvenile *S. globosa* from the lower quadrat. This supposition means that the distribution of juvenile *S. globosa* is also influenced by the existence of *I. pusillus*. As has already been stated, juvenile *S. globosa* are often attacked and driven away by conspecific sexable crabs. In contrast to this, interspecific fight between *S. globosa* and *I. pusillus* has not been so frequent even in co-occurring areas, and it has been rare case that juvenile *S. globosa* are driven away by sexable *I. pusillus*. Thus, it seems that the distribution of juvenile *S. globosa* is influenced by sexable *I. pusillus* differently from the conspecific sexable crabs.

Acknowledgments

I wish to express my thanks to Dr. M. Morisita (Professor Emeritus of Kyoto University) for his encouragement and advice for this study, and to Prof. E. Harada, Prof. H. Kawanabe, Dr. T. Itô, Mr. A. Taki (Kyoto University), Prof. M. Nishihira (University of the Ryukyus), and Prof. I. Maki (Wakayama University) for their many constructive criticisms at various stages during the research and preparation of the manuscript. Dr. Y. Maruyama (Kyoto University) generously provided the computer program for the spatial association. The members of Animal Ecology and of the Seto Marine Biological Laboratory of Kyoto University provided much enlightening discussion.

REFERENCES

Fielder, D.R. 1971. Some aspects of distribution and population structure in the sand bubbler crab *Scopimera inflata* Milne Edwards, 1873 (Decapoda, Ocypodidae). Aust. J. mar. Fresh. res., Vol. 22, pp. 41–47.

Fisher, J.B. and Tevesz, M.J.S. 1979. Within-habitat spatial patterns of *Ocypode quadrata* (Fabricius) (Decapoda Brachyura). Crustaceana, Suppl. 5, pp. 31–36.

Harada, E. and Kawanabe, H. 1955. The behavior of the sand-crab, *Scopimera globosa* De Haan, with special reference to the problem of coaction between individuals. Jap. J. Ecol., Vol. 4, pp. 162–165. (in Japanese with English summary).

Hartnol, R.G. 1973. Factors affecting the distribution and behaviour of the crab *Dotilla fenestrata* on East African shores. Est. Coast. Mar. Sci., Vol. 1, pp. 137–152.

Iwao, S. 1977. Analysis of spatial association between two species based on the interspecies mean crowding. Res. Popul. Ecol., Vol. 18, pp. 243–260.

Mogi, A. 1971. Shoreline and Breaker Zone, pp. 109–252. In: Geology of Sublittoral Zone. Ed. M. Hoshino. Tokai University Press. Tokyo. VII+445 pp. (in Japanese).

Ono, Y. 1957. The interrelation among individuals of a fiddler crab *Ilyoplax pusillus* De Haan. Jap. J. Ecol., Vol. 7, pp. 45–51. (in Japanese with English summary).

——— 1960. Interrelation among individuals of a fiddler crab, *Ilyoplax pusillus* De Haan (II): The regulatory mechanism at high population density. Jap. J. Ecol., Vol. 10, pp. 161–168. (in Japanese with English summary).

——— 1962. On the habitat preference of ocypoid crabs in the estuary. Mem. Fac. Sci. Kyushu Univ., Ser. E (Biol.). Vol. 3, pp. 143–163.

——— 1965. On the ecological distribution of ocypoid crabs in the estuary. Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol.), Vol. 4, pp. 1–60.

Utashiro, T. and Horii, Y. 1965. Ecology and burrows of *Scopimera globosa* and *Ilyoplax pusillus*: Biological studies in "Lebensspuren" Part VII. Mem. Fac. Education, Niigata Univ., Takada Sch., Vol. 10, pp. 110–143. (in Japanese with English abstract).

Wada, K. 1976. The distribution of three species of ocypodid crabs in the estuary of Waka River, mainly examined in relation to the granularity of substratum. Physiol. Ecol. Japan Vol. 17. pp. 321–326. (in Japanese with English synopsis).

——— 1981a. Growth, breeding, and recruitment in *Scopimera globosa* and *Ilyoplax pusillus* (Crustacea: Ocypodidae) in the estuary of Waka River, middle Japan. Publ. Seto Mar. Biol. Lab., Vol. 26, pp. 243–259.

——— 1981b. Wandering in *Scopimera globosa* (Crustacea: Ocypodidae). Publ. Seto Mar. Biol. Lab., Vol. 26, pp. 447–454.

——— and Tsuchiya, M. 1975. Distribution of ocypodid crabs in relation to tidal level and the substratum in the Gamo Lagoon. Jap. J. Ecol., Vol. 25, pp. 235–238. (in Japanese).