

Comparison of resistivity to transport by wave action in several polychaete species on an intertidal sand flat

Akio Tamaki*

Amakusa Marine Biological Laboratory, Kyushu University, Tomioka, Reihoku-cho, Amakusa, Kumamoto-ken 863-25, Japan

ABSTRACT: Passive transport by waves and tidal inflow currents was examined as one of the physical factors determining the distribution of adults of 5 polychaete species – *Armandia* sp. (family Opheliidae), *Spio filicornis* (Müller) (fam. Spionidae), *Rhynchospio glutaea* (Ehlers) (fam. Spionidae), *Nephtys polybranchia* Southern (fam. Nephtyidae), *Scoloplos uschakovi* Wu (fam. Orbiniidae) – inhabiting an intertidal sand flat in west Kyushu, Japan. On the tidal flat, the year can be divided into 2 periods due to seasonally changing wind direction: a period of large waves from autumn to spring and a calm period during summer. A significant landward shift of the adult distribution center was observed only for the overwintering population of *Armandia* sp.; this could be ascribed to passive transport of individuals by large incoming waves based on the results of a trapping experiment in the field. *Armandia*'s shallow-dwelling position below the sediment-water interface (within 1 cm), inability to adhere to large materials, and habit of curling up in a circle when disturbed by waves are considered to be the main causes of its susceptibility to large waves. Adults of *Spio filicornis*, *R. glutaea* and *N. polybranchia* can reach the deeper layers in the sediment (5 to 10 cm), and may hence be less affected by wave action. This also applies to *S. uschakovi* adults, but even juveniles of this species, which occur in the shallow layers of the sediment (within 1.4 cm), were resistant to wave disturbance. One reason may be that their winding abdomen acts as an anchor in the sediment.

INTRODUCTION

Following recruitment, the adult distributions of macrobenthic animals inhabiting marine soft sediments are determined by the following 3 major processes: survival of individuals; active migration of individuals; passive transport of individuals by waves and currents. Particularly in habitats affected by strong waves and/or currents, the importance of the role of passive transport has been recognized in determining the distributions of several macrofaunal species such as molluscs (Matthiessen 1960, Gilbert 1968, Edwards 1969, Thompson 1982, Donn et al. 1986), polychaetes (Dales 1952, Reise 1981, Brown 1982, McDermott 1983), peracarid crustaceans (Fincham 1970, Grant 1980, 1981) and an echinoderm (Mukai et al. 1986).

I have studied some factors which determine the distribution of macrobenthic animals inhabiting an

intertidal sand flat in west Kyushu, Japan, and found that adults of the 3 most numerically abundant polychaete species (2 spionids and an opheliid) showed a common zonal distribution pattern along the tidal axis in summer (Tamaki & Kikuchi 1983). In winter, however, the distributions of the spionids and the opheliid were different, with the center of the opheliid zone displaced landward (Tamaki 1984a). There is a seasonal change in the intensity of incoming waves due to seasonally changing wind direction (Tamaki 1984b). Large incoming waves disturb the sediment surface over the whole flat. In terms of the degree of sediment disturbance, the year can be divided into 2 periods: a period of disturbance from autumn to spring and a calm period during summer (Tamaki 1984b). Thus, one of the possible factors inducing the difference in the distributions of the spionids and the opheliid in winter is differential resistivity to landward transport by strong wave action. The present study examines this possibility in the above 3 polychaetes plus 2 other numerically abundant poly-

*Present address: Faculty of Fisheries, Nagasaki University, Bunkyo-machi 1–14, Nagasaki 852, Japan

chaete species. The study is composed of 3 parts: (1) description of the seasonal (mainly summer and winter) change in the distribution of both juveniles (newly settled larvae) and adults along the tidal axis; (2) field investigations of which species are uprooted and washed into the water column by strong wave action and transported landward; (3) an examination of the relationship between the resistivity to transport by wave action and the vertical distribution of individuals in the sediment for each species.

STUDY SITE

The study site is a moderately protected intertidal sand flat facing Tomioka Bay at the northwestern corner of Amakusa Shimoshima Island, west Kyushu, Japan (see Fig. 1 in Tamaki 1985). The flat is exposed for a distance of 335 m offshore at extreme low spring tide. A rectangular area delimited by 2 lines perpendicular to the coastline, 300 m wide, was selected for routine sampling (the black-colored area in Fig. 1 in Tamaki 1985). A preliminary survey revealed that the macrobenthic community on the sand flat was subdivided into 4 zonal assemblages parallel to the coast line (Tamaki & Kikuchi 1983). They were named after characteristic species, and are, from the uppermost flat to the lowest margin, the spionid polychaete *Prionospio krusadensis* Fauvel zone, the ghost shrimp *Callianassa japonica* Ortmann zone, the razor clam *Solen strictus* (Gould) zone and the gastropod *Umbonium (Suchium) moniliferum* (Lamarck) zone, respectively. The habitat of *C. japonica* expanded in autumn 1980 in 2 ways: gradual extension of the original habitat offshore, and generation of an exclave zone in the lower *Umbonium* zone (see Fig. 1 to 5).

The tidal flat is open northeastward to the sea. Thus, when strong northerly or northeasterly winds (here defined as those of Beaufort scale 2 or more) blow, large incoming waves disturb the sediment surface over the whole flat.

STUDY ORGANISMS

The present study deals with 5 polychaete species which were within the top 16 numerically abundant smaller macrobenthos collected in a distribution survey over the whole study site in July 1979 (Table 1; data from Tamaki & Kikuchi 1983). The top 16 species included 95% of the total number of individuals. The following description is extracted from that given in Tamaki (1984a).

All the polychaetes other than *Pseudopolydora paucibranchiata* (Okuda) appear on the tidal flat

throughout the year. *P. paucibranchiata* is the only transient member, found from June to October, and is therefore eliminated from the present paper which focuses on a comparison of summer and winter distributions on the tidal flat. *Prionospio krusadensis* appears throughout the year only in the *Prionospio* zone, which is situated in the most landward ca 10 m wide zone, due to a spatially restricted larval recruitment. No landward transport of individuals was detected for this polychaete, and hence it is also excluded. Thus, the remaining 5 polychaete species are examined in this paper: *Armandia* sp. (family Opheliidae), *Spio filicornis* (Müller) (fam. Spionidae), *Rhynchospio glutaea* (Ehlers) (fam. Spionidae), *Nephtys polybranchia* Southern (fam. Nephtyidae) and *Scoloplos uschakovi* Wu (fam. Orbiniidae). Their main recruitment season, except for *S. uschakovi*, is summer, and overwintering is by adult forms. Both juveniles and adults of *S. uschakovi* overwinter.

MATERIALS AND METHODS

Natural abundance pattern of polychaetes. In a survey of the macrobenthos conducted in July 1979, the distributions of the numerically dominant species were found to be zoned parallel to the coastline (Tamaki & Kikuchi 1983). Thus, representative sampling can be carried out along 1 transect. Spatial and temporal changes in the densities of the macrobenthos were examined along a transect situated 120 m southeast of the northwestern edge of the sampling area (the white line in Fig. 1 in Tamaki 1985). Sampling was conducted at every or every other spring tide from March 1980 to March 1981. A maximum of 22 sampling stations were placed between the shoreline and mean low water spring tide level (MLWS). The distance between stations varied from 10 to 30 m. Adult macrobenthos were collected using a quadrat frame (25 × 25 × 10 cm, n = 1), and sediment was sieved through a 0.5 mm mesh sieve. Cores to sample juvenile macrobenthos as well as adults were collected with a short corer (88 cm² × 1.4 cm deep PVC corer, n = 6 or 3). Both kinds of samples were fixed in the field with 10% neutralized formalin solution containing Rose Bengal. In the laboratory, one sample for juveniles was washed through a sieve of 0.125 mm mesh. All macrofaunal individuals were sorted out under a dissecting microscope. Animals were identified to species level and the number of individuals of each species was counted. The body length of all unbroken specimens in each juvenile-sample was measured by tracing the dorsum under a dissecting microscope with a drawing apparatus (× 25).

Vertical distribution of polychaetes. To examine the

Table 1. Characteristics of the 7 numerically most abundant polychaete species on the sand flat. Density (no. of individuals retained on a 1 mm mesh sieve; 625 cm²) was examined at a total of 120 sampling stations (n = 1 at each station) over the whole flat in Jul 1979 (Tamaki & Kikuchi 1983)

Species (family)	Order of numerical abundance among all smaller macrobenthos*	No. of ind. pooled for all stations*	Mobility**	Recruitment period** (peak)
<i>Pseudopolydora paucibranchiata</i> (Okuda) (Spionidae)	1	4382	Sedentary; tube (made of detritus and sand particles) builder	Jun-Sep (Jul-Aug)
<i>Armandia</i> sp. (Opheliidae)	5	963	Highly mobile; burrower	Apr-Nov (Jun; Aug; Oct)
<i>Spio filicornis</i> (Müller) (Spionidae)	6	879	Sedentary; inhabitant of simple burrow	Apr-Nov (Jul)
<i>Rhynchospio glutaea</i> (Ehlers) (Spionidae)	10	294	Sedentary; inhabitant of simple burrow	Apr-Oct (Jul)
<i>Prionospio krusadensis</i> Fauvel (Spionidae)	12	200	Sedentary; inhabitant of ramified burrow	Jun-Sep (Jul)
<i>Nephtys polybranchia</i> Southern (Nephtyidae)	15	112	Highly mobile; burrower	Jul-Sep (Jul)
<i>Scoloplos uschakovi</i> Wu (Orbiniidae)	16	97	Moderately mobile; burrower	Apr-May; Dec (May; Dec)

* After Table 1 in Tamaki & Kikuchi (1983)
 ** After Tamaki (1984a)

vertical distribution of smaller macrobenthos in the sediment, sediment cores were taken with an acrylic corer having a cross-sectional area of 100 cm², and each core was subdivided into several sections. Subdivision was achieved by pushing the whole sediment core in the corer upward from underneath and cutting it at fixed depths from the sediment surface. The depth intervals examined were as follows: 0 to 1, 1 to 2, 2 to 3, 3 to 5 and 5 to 10 cm; it had been found in a previous sampling that very few smaller macrofaunal species inhabited depths below 10 cm (Tamaki 1984a). The sampling was done at a point near the shore 700 m southeast of the fixed transect during low tide on 2 May 1984. All sectioned cores were treated in the same manner as samples taken in the routine sampling for adults along the transect. Data from 3 sediment cores were pooled for each depth interval.

Trapping of passively transported macrobenthos. A trap was established on the sand flat to confirm which infaunal species are uprooted from the sediment and transported landward by large incoming waves. During low tide, a rectangular pyramid-shape bag made of 0.5 mm opening nylon net with aperture 50 × 30 cm and length 100 cm was placed in the uppermost part of the sand flat (*Prionospio* zone). To prevent the entry of animals through crawling or rolling on the sediment surface, the bag was fixed horizontally 2 cm above the sediment surface. It was fastened with ropes to wooden stakes placed at the side of the bag with its opening

facing offshore. Surveys were undertaken for 1 d intervals both on a day with northerly winds and on another day with no northerly winds in February 1982. All materials trapped in the bag were treated in the same manner as those collected in routine sampling for juveniles along the transect.

RESULTS

Natural abundance patterns

The life-history information included in the following descriptions has been extracted from Tamaki (1984a).

Armandia sp.

This species has a planktonic larval stage. After settlement on the substratum, it passes through a benthic juvenile stage (e.g. 6.5 to 10 d in early summer), and metamorphoses once more to attain adult form. The shape of individuals before the second metamorphosis (juveniles) is vermiform. After metamorphosis (adults), the shape becomes spindle-like. In 1980, the recruitment of larvae began in April and ended in November. The largest recruitment was observed at the end of June. Spatial and temporal changes in the density of *Armandia* sp. juveniles and

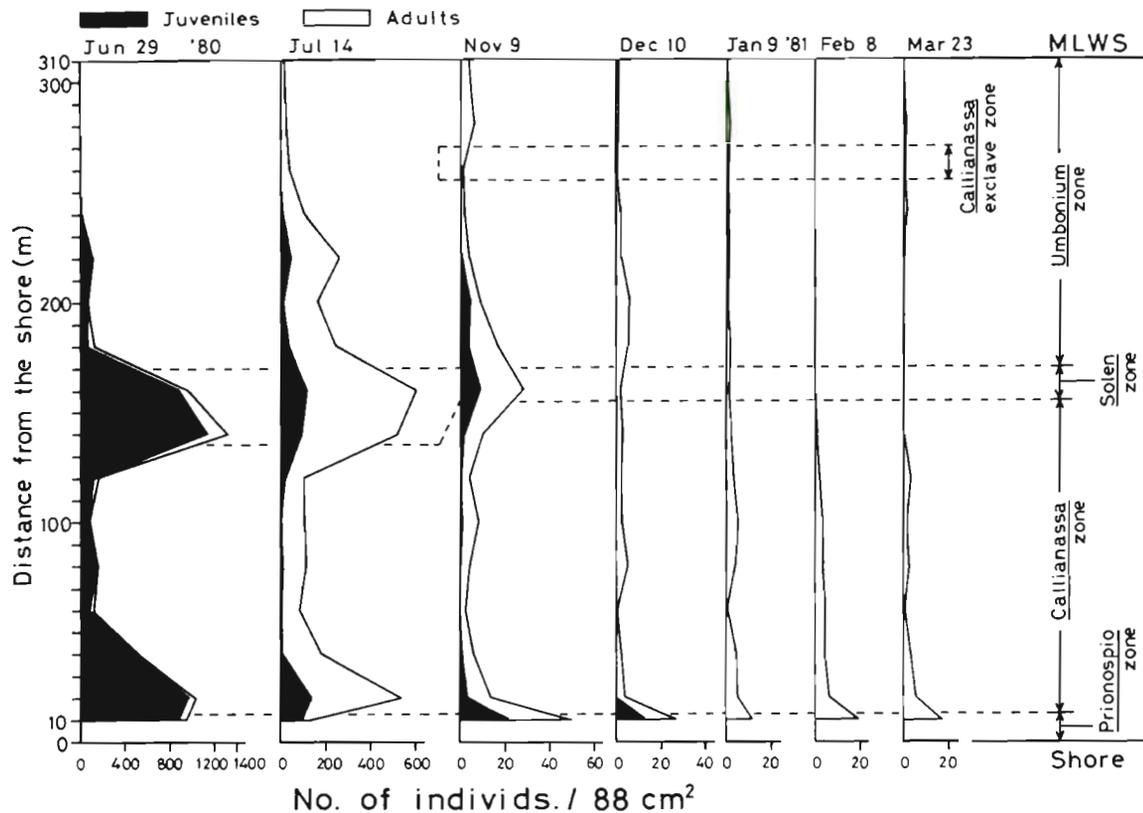


Fig. 1. *Armandia* sp. Spatial and temporal changes in densities of juveniles and adults (from core sampling; ≥ 0.125 mm) along the fixed transect in early summer 1980 and during late autumn 1980 to early spring 1981. Almost all individuals could be collected by core sampling due to their shallow-dwelling habit in the sediment (see Table 2 and text). Two facts suggest that the low density of adults in the *Prionospio* zone on 14 Jul 1980 was due to sampling error: (1) on 29 Jun, juvenile density in the *Prionospio* zone was as high as that in the uppermost *Callianassa* zone; (2) on 28 Jul 1980, adult density in the *Prionospio* zone was higher than that in the uppermost *Callianassa* zone (see Fig. 4 in Tamaki 1985)

adults along the fixed transect during the end of June to mid-July 1980, and during November 1980 to March 1981, are shown in Fig. 1. At the end of June, *Armandia* larvae settled almost exclusively in the *Solen* zone and in the neighborhood of the *Prionospio* zone. A part of the population had emigrated from the settlement zones mainly in an offshore direction with concurrent growth of body size by July 14 (Tamaki 1985). The distribution pattern of juveniles and adults in November was similar to that in summer, i.e. bimodal along the transect. The overwintering individuals were derived from the cohorts that were recruited during September to November and had a maximum 6 mo life span. The distribution of the overwintering population shifted gradually landward. In December and January, an appreciable number of individuals were still present in the *Umbonium* and *Solen* zones, while subsequently, in February and March, only a few individuals were found there. In March 1981, the center of distribution was situated in the uppermost part of the tidal flat, i.e. the *Prionospio* to uppermost *Callianassa* zone with density decreasing offshore.

Spio filicornis

In 1980, the larval recruitment of this species occurred during April to November. There were 3 temporal maxima in the density of recruits, occurring in June, July and September, with the highest density at the end of July. Spatial changes in the density of *Spio filicornis* along the fixed transect are shown in Fig. 2 for juveniles on the 2 dates of highest larval recruitment and for adults on a summer and a winter date. At the end of July 1980, the juvenile distribution pattern was bimodal along the transect with highest densities in the *Solen* and uppermost *Callianassa* zones. The pattern at the end of September 1980 was different from that in July with the density differences between stations not as great. Only a few or no juveniles were collected in the samples from October 1980 through March 1981; this was due to the cessation of recruitment and to the migration of already recruited juveniles down into the deeper sediment layers (Table 2). The distribution pattern of adults reflected that of juveniles in summer, i.e. bimodal along the transect both in summer and in

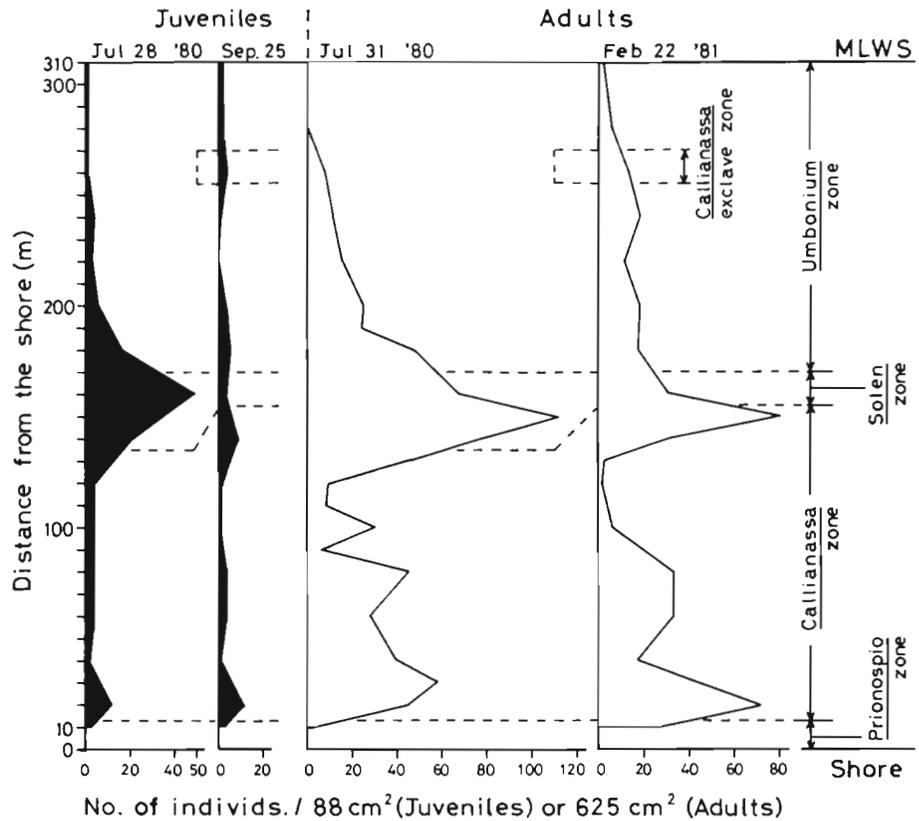


Fig. 2. *Spio filicornis*. Spatial and temporal changes in the densities of juveniles (from core sampling; ≥ 0.125 mm) and adults (from quadrat sampling; ≥ 0.5 mm) along the fixed transect; for juveniles, on the 2 dates of highest larval recruitment, and for adults, on a summer and a winter date. Juvenile body length: 0.72 to 2.84 mm (28 Jul); 0.68 to 4.40 mm (25 Sep)

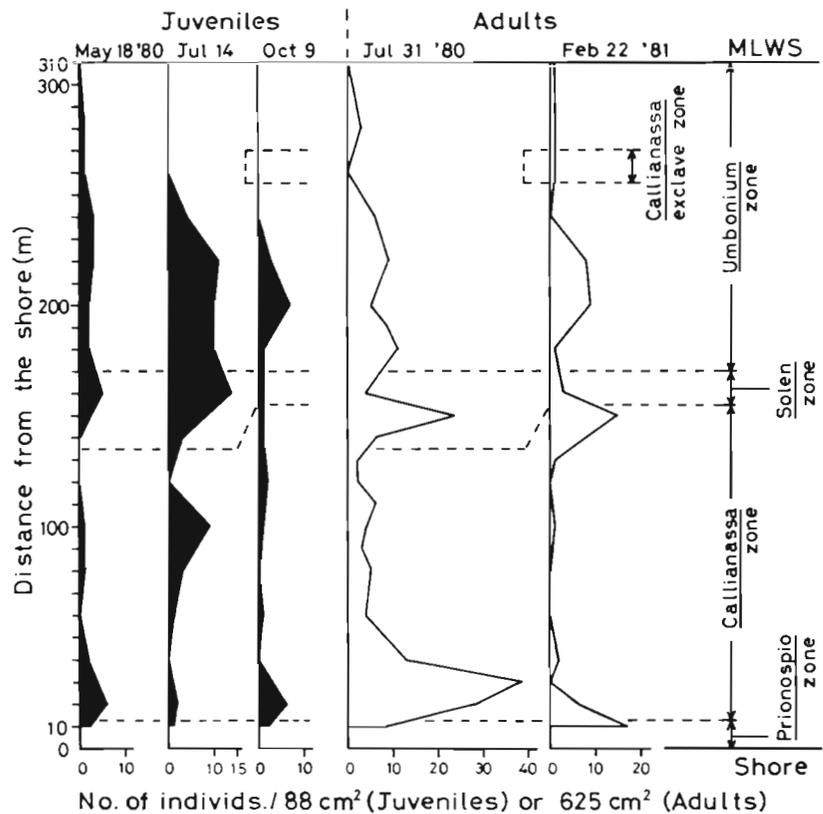


Fig. 3. *Rhynchospio glutaea*. Spatial and temporal changes in the densities of juveniles (from core sampling) and adults (from quadrat sampling) along the fixed transect; for juveniles, on the 3 dates of highest larval recruitment, and for adults, on a summer and a winter date. Juvenile body length: 0.56 to 3.56 mm (18 May); 0.58 to 3.80 mm (14 Jul); 0.48 to 3.44 mm (9 Oct)

winter. However, the density in the lowest *Umbonium* zone was higher in February 1981 than in July 1980. Migration of individuals from the *Solen* and upper *Umbonium* zones or spatially expanded settlement of larvae in September as compared with July may be responsible for this phenomenon.

Rhynchospio glutaea

In 1980, the larval recruitment of this species occurred during April to October. Temporally, there were 3 maxima in the density of recruits, i.e. in May, July and October. Spatial changes in the density of *Rhynchospio glutaea* along the fixed transect are shown in Fig. 3 for juveniles on the 3 dates of highest larval recruitment and for adults on a summer and a winter date. The distribution pattern of juveniles was basically bimodal with the highest densities in the *Solen* to middle *Umbonium* zone and in the uppermost *Callianassa* zone, but there was variation between months. On 14 July 1980, a large number of individuals were also found in the lower *Callianassa* zone, and the density in

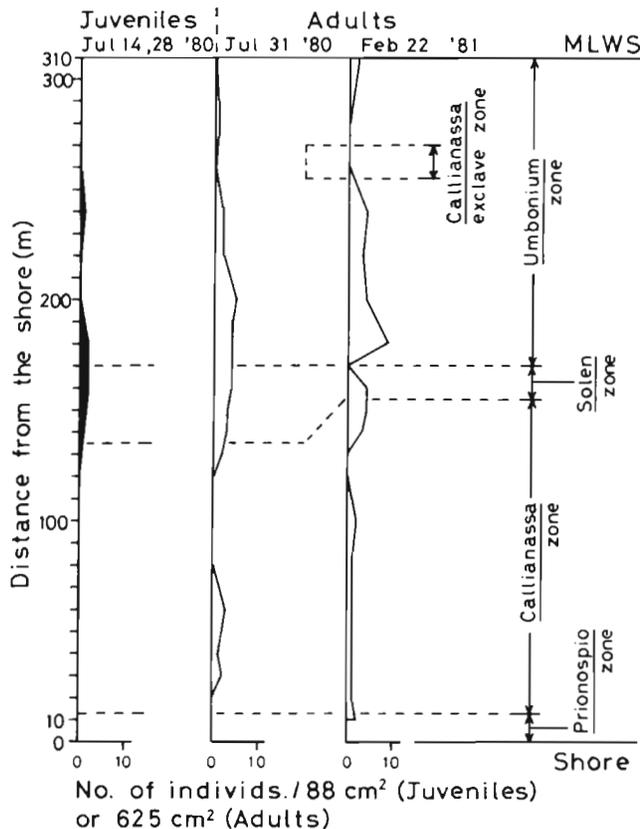


Fig. 4. *Nephtys polybranchia*. Spatial and temporal changes in the densities of juveniles (from core sampling) and adults (from quadrat sampling) along the fixed transect; for juveniles, data on 2 dates in Jul pooled, and for adults, on a summer and a winter date. Juvenile body length: 0.84 to 2.40 mm

the uppermost *Callianassa* zone was lower. On 9 October 1980, the density in the *Solen* zone was much lower. Only a few juveniles were collected in the samples from November 1980 through March 1981, which is ascribed to the same processes as in *Spio filicornis*. The distribution pattern of adults was bimodal along the transect both in summer and in winter reflecting that of juveniles.

Nephtys polybranchia

In 1980, the larval recruitment of this species occurred during July to September. Highest recruitment was found in July. Spatial changes in the density of *Nephtys polybranchia* along the fixed transect are shown in Fig. 4. Samples for juveniles for 2 dates in July were pooled due to the low number of individuals, and data for adults are shown for a summer and a winter date. Juveniles were distributed in the *Solen* to middle *Umbonium* zone. The center of distribution of adults was also found in this zone both in summer and in winter, but an appreciable number of individuals were also found in the lowest *Umbonium* zone and in the *Prionospio* to *Callianassa* zone. Those in the lowest *Umbonium* zone had probably migrated actively from the larval settlement zone. Those in the *Prionospio* to *Callianassa* zone could be due either to active migration or to passive transport by wave action.

Scoloplos uschakovi

In 1980, there were 2 temporal maxima in the density of recruits of this species: in May–June and December. Recruitment was short on both occasions lasting for 2 wk to at most 1 mo. Spatial changes in the density of *Scoloplos uschakovi* along the fixed transect are shown in Fig. 5 for juveniles on the dates with highest larval recruitment in 1980 and in March 1981, and for adults on a summer and a winter date. On 18 May 1980, juveniles were found in the *Umbonium* zone and in the uppermost *Callianassa* zone. However, most of the juveniles in the latter zone died by June 1. On 10 December 1980, almost all the juveniles were found only in the *Umbonium* zone except at MLWS and in the exclave zone of *Callianassa japonica* in the lower *Umbonium* zone. Juveniles were continuously found in the surface 1.4 cm layer until March 1981. The center of distribution of the population, which was landward of the *C. japonica* exclave zone, shifted a little landward by March 1981. Most of the adults were found in the *Solen* to *Umbonium* zone both in summer and in winter reflecting the distribution of juveniles. On 22 February 1981, the center of distribution was found more landward than that on 31 July 1980.

Vertical distribution of polychaetes

The vertical distributions of the 5 polychaete species in the sediment are shown in Table 2. Only 8 *Armandia*

Table 2. Vertical distribution of the 5 most abundant polychaete species (retained on a 0.5 mm mesh sieve) in the sediment. Pooled data from 3 core samples of 100 cm²

Species	Depth interval (cm)				
	0-1	1-2	2-3	3-5	5-10
<i>Armandia</i> sp.	6	1	0	1	0
<i>Spio filicornis</i>	1	6	11	5	2
<i>Rhynchospio glutaea</i>	40	29	7	2	0
<i>Nephtys polybranchia</i>	2	1	0	4	3
<i>Scoloplos uschakovi</i>	1	1	2	1	0

sp. individuals were collected (all adults), and 6 of them were found in the surface 1 cm layer. In a previous examination of vertical distribution, 98 % of juveniles (45/46) and 97 % of adults (36/37) of *Armandia* were found in the top 1 cm sediment (Tamaki 1984a). *Spio filicornis* was found as deep as the 5 to 10 cm layer, but the center of distribution was at 2 to 3 cm. The largest number of *Rhynchospio glutaea* was found in the top 1 cm layer, but these worms could reach 5 cm. *Nephtys polybranchia* dwelled in the deepest layer (5 to 10 cm) as well as in the shallowest layer. *Scoloplos uschakovi* dwelled uniformly from the surface to the 3 to 5 cm layer.

Trapping of passively transported macrobenthos

The results of the trapping experiment performed both on a stormy and a calm day in February 1982 are shown in Table 3. Sixteen *Armandia* sp. individuals

Table 3. Field trapping of macrobenthos uprooted and transported by incoming waves and tidal inflow current. No. of individuals of the 5 polychaete species trapped in the bag are shown

Species	13-14 Feb 1982	22-23 Feb 1982
Wind direction and force (Beaufort scale)	NE 2-4*	E 0-2**
<i>Armandia</i> sp. (adults)	16	0
<i>Spio filicornis</i>	2	1
<i>Rhynchospio glutaea</i>	0	0
<i>Nephtys polybranchia</i>	0	0
<i>Scoloplos uschakovi</i>	0	0

* Large incoming waves were present
 ** No large wave surges were present

were trapped when large incoming waves occurred while none were trapped when the sea was calm. Apart from *Armandia*, only 1 or 2 individuals of *Spio filicornis* were trapped on the calm and stormy days, respectively.

DISCUSSION

For 4 of the 5 polychaete species studied here – *Armandia* sp., *Spio filicornis*, *Rhynchospio glutaea* and *Nephtys polybranchia* – the distribution patterns of adults along the tidal axis in summer were similar, that is, bimodal with centers of distribution in the *Solen* to upper *Umbonium* zone and in the *Prionospio* to upper *Callianassa* zone (Fig. 1, 2, 3 & 4), basically reflecting the common distribution pattern of settled larvae in spring to summer. In winter to early spring, however, there was a difference in the adult distributions; *S. filicornis*, *R. glutaea* and *N. polybranchia* maintained basically the same distribution pattern as in summer (Fig. 2, 3 & 4), while the center of distribution of *Armandia* sp. was restricted to the *Prionospio* to uppermost *Callianassa* zone (Fig. 1). For both juveniles and adults of *Scoloplos uschakovi*, the center of distribution was in the *Solen* to *Umbonium* zone both in summer and in winter (Fig. 5).

An appreciable number of only *Armandia* sp. individuals were trapped in the bag placed in the field for collecting macrobenthos uprooted and suspended in the water column, and this was restricted to the stormy day (Table 3). This suggests that on stormy days in winter and spring, *Armandia* adults were uprooted and washed into the water column by strong wave action and transported landward. Since *Armandia* adults live only within the top 1 cm of the sediment (Table 2), they may be the most susceptible to resuspension by waves; their inability to adhere to large materials such as shell fragments and their habit of curling up in a circle when disturbed by waves (pers. obs.) should also promote this passive transport process. In fact, I have observed many times in laboratory aquaria that *Armandia* adults buried in the sediment could easily be dispersed by vibrating the water column above the sediment. This may explain the mechanism through which the center of the distribution of *Armandia* adults shifted to the neighborhood of the shore during autumn to spring. On the other hand, in summer, active migration of *Armandia* adults mainly in an offshore direction could prevail (Fig. 1; Fig. 4 in Tamaki 1985) as there was little or no landward transport of individuals in the absence of strong northerly winds (see Fig. 2 in Tamaki 1984b).

Because adults of the other 4 polychaete species (i.e. *Spio filicornis*, *Rhynchospio glutaea*, *Nephtys poly-*

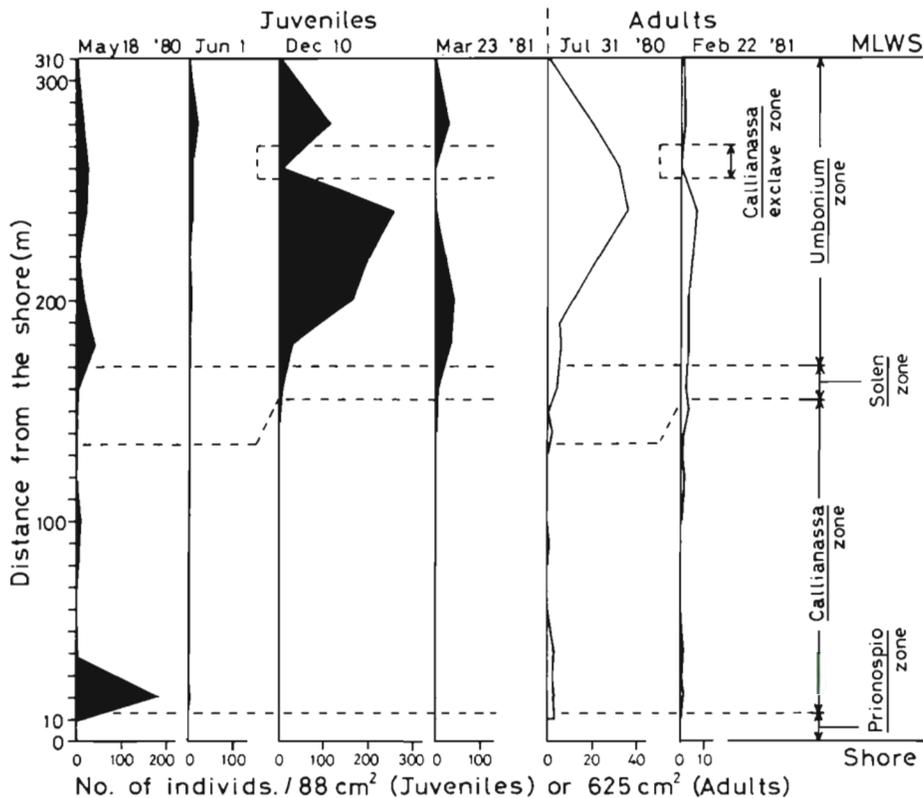


Fig. 5. *Scoloplos uschakovi*. Spatial and temporal changes in the densities of juveniles (from core sampling) and adults (from quadrat sampling) along the fixed transect; for juveniles, on the dates with highest larval recruitment in 1980 and a date in March 1981, and for adults, on a summer and a winter date. Juvenile body length: 0.42 to 4.32 mm (18 May and 1 Jun 1980); 0.48 to 4.24 mm (10 Dec 1980); 1.20 to 4.16 mm (23 Mar 1981)

branchia, *Scoloplos uschakovi*) inhabit or can reach sediment layers deeper than *Armandia* sp. (Table 2), it may be expected that they are less susceptible to sediment disturbance by waves (see Grant 1981 for an example of haustoriid amphipods, in which a deeper-living species is more resistant to current disturbance). In contrast to adults, juveniles of these polychaetes inhabit the top 1.4 cm of the sediment, and hence may be more easily affected by wave action than adults. However, most of the larval recruitment of these polychaetes, except *Scoloplos uschakovi*, is completed by early October (Table 1; Fig. 2, 3 & 4), and juveniles moved into deeper sediment layers afterward as was revealed in the remarkably reduced densities of individuals collected in the juvenile sampling during late autumn to spring. In this way, *Spio filicornis*, *Rhynchospio glutaea* and *Nephtys polybranchia* may be able to maintain a relatively constant distribution pattern along the transect throughout the year. As mentioned in 'Results', adults of *Nephtys polybranchia* found in the *Prionospio* to *Callianassa* zone could have been brought from the larval settlement zone through passive transport by wave action. Based on the above considerations, however, this possibility may be slight.

For *Scoloplos uschakovi*, a large number of juveniles were found within the top 1.4 cm of the sediment during winter to spring, and a part of the population might have been transported landward (Fig. 5). Brown

(1982) reported that small individuals of *Scoloplos fragilis* inhabiting a sandy beach were transported by waves. However, the juvenile population of the present *S. uschakovi* did not experience such a thorough passive transport as *Armandia* sp. This difference can be ascribed to a differential resistivity to wave action, which may come from differences in the body structure: the body of *Armandia* is straight from head to tail, whereas that of *S. uschakovi* consists of a straight thoracic section and a winding abdominal one. The abdominal section of *S. uschakovi* may act as an anchor by holding it to the sediment.

Two kinds of measurements would substantiate the above-proposed mechanism through which differences in the distributions of the present 5 polychaete species in winter and spring could be brought about: (1) measuring to what depth large waves can disturb the sediment in the field; (2) measuring the resistivity of each polychaete species to such wave forces in a laboratory flume (cf. Grant 1980).

In this study, the importance of passive transport of individuals by waves and currents in determining the distribution of adult macrobenthos was confirmed especially for the overwintering population of *Armandia* sp. when subjected to large incoming waves. Conversely, in summer, when the sea was calm, active migration of individuals of *Armandia* was conspicuous (Fig. 1) with little or no passive transport taking place

(Tamaki 1985). Up to now relatively few studies have taken into consideration which benthic life stages of each species are most susceptible to passive transport by waves and currents with seasonally varying intensities (e.g. Matthiessen 1960, Edwards 1969, Fincham 1970, Reise 1981, Brown 1982, Thompson 1982, Mukai et al. 1986). Since the seasonal occurrence of gentle waves in summer and heavy ones in winter is a general phenomenon found in many temperate-zone intertidal sand flats (e.g. Komar 1976, Gray 1981), we should note the mobility and resistivity to wave action of each species for understanding the seasonal change in the distribution of macrobenthic animals living in such localities of high wave energy.

Acknowledgements. I thank Mr I. Goto for field assistance, Dr. M. Nishihira for discussions and Professor T. Kikuchi and Dr. H. Mukai for critical reading of the manuscript. This is contribution No. 313 from the Amakusa Marine Biological Laboratory, Kyushu University.

LITERATURE CITED

- Brown, B. (1982). Spatial and temporal distribution of a deposit-feeding polychaete on a heterogeneous tidal flat. *J. exp. mar. Biol. Ecol.* 65: 213–227
- Dales, R. P. (1952). The larval development and ecology of *Thoracophelia mucronata* (Treadwell). *Biol. Bull. mar. biol. Lab., Woods Hole* 102: 232–242
- Donn, T. E., Jr., Clarke, D. J., McLachlan, A., du Toit, P. (1986). Distribution and abundance of *Donax serra* Röding (Bivalvia: Donacidae) as related to beach morphology. I. Semilunar migrations. *J. exp. mar. Biol. Ecol.* 102: 121–131
- Edwards, D. C. (1969). Zonation by size as an adaptation for intertidal life in *Olivella biplicata*. *Am. Zool.* 9: 399–417
- Fincham, A. A. (1970). Amphipods in the surf plankton. *J. mar. biol. Ass. U.K.* 50: 177–198
- Gilbert, W. H. (1968). Distribution and dispersion patterns of the dwarf tellin clam, *Tellina agilis*. *Biol. Bull. mar. biol. Lab., Woods Hole* 135: 419–420
- Grant, J. (1980). A flume study of drift in marine infaunal amphipods (Haustoriidae). *Mar. Biol.* 56: 79–84
- Grant, J. (1981). Sediment transport and disturbance on an intertidal sandflat: infaunal distribution and recolonization. *Mar. Ecol. Prog. Ser.* 6: 249–255
- Gray, J. S. (1981). *The ecology of marine sediments*. Cambridge University Press, Cambridge
- Komar, P. D. (1976). *Beach processes and sedimentation*. Prentice-Hall, Englewood Cliffs
- Matthiessen, G. C. (1960). Intertidal zonation in populations of *Mya arenaria*. *Limnol. Oceanogr.* 5: 381–388
- McDermott, J. J. (1983). Food web in the surf zone of an exposed sandy beach along the mid-Atlantic coast of the United States. In: McLachlan, A., Erasmus, T. (ed.) *Sandy beaches as ecosystems*. Junk, The Hague, p. 529–538
- Mukai, H., Nishihira, M., Kamisato, H., Fujimoto, Y. (1986). Distribution and abundance of the sea-star *Archaster typicus* in Kabira Cove, Ishigaki Island, Okinawa. *Bull. mar. Sci.* 38: 366–383
- Reise, K. (1981). Ökologische Experimente zur Dynamik und Vielfalt der Bodenfauna in den Nordseewatten. *Verh. dt. zool. Ges.* 1981: 1–15 (cited from Reise, K. [1985]. *Tidal flat ecology*. Springer-Verlag, Berlin)
- Tamaki, A. (1984a). Study on dynamics of the benthic community on an intertidal sand flat, with special reference to biological interactions in the same trophic level. Doctoral dissertation, Kyushu University, Fukuoka
- Tamaki, A. (1984b). Structural characteristics of an intertidal sand flat in Tomioka Bay, Amakusa, west Kyushu. *Publ. Amakusa Mar. Biol. Lab., Kyushu Univ.* 7: 125–150
- Tamaki, A. (1985). Zonation by size in the *Armandia* sp. (Polychaeta: Opheliidae) population on an intertidal sand flat. *Mar. Ecol. Prog. Ser.* 27: 123–133
- Tamaki, A., Kikuchi, T. (1983). Spatial arrangement of macrobenthic assemblages on an intertidal sand flat, Tomioka Bay, west Kyushu. *Publ. Amakusa Mar. Biol. Lab., Kyushu Univ.* 7: 41–60
- Thompson, J. K. (1982). Population structure of *Gemma gemma* (Bivalvia: Veneridae) in south San Francisco Bay, with a comparison to some northeastern United States estuarine populations. *The Veliger* 24: 281–290

This article was submitted to the editor; it was accepted for printing on February 24, 1987