Zonation by size in the *Armandia* sp. (Polychaeta: Opheliidae) population on an intertidal sand flat*

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ABSTRACT: Spatial and temporal changes in the body-size composition of a population of *Armandia* sp. (Opheliidae), a burrowing polychaete species with a planktonic larval phase, are described for an intertidal sand flat in west Kyushu, Japan. From spring to summer 1980, the recruitment of *Armandia* was by discrete settlement of larvae (every spring tide), which allowed the fate of a particular cohort to be followed easily. At the end of June, when the largest recruitment in the year occurred, the larvae settled exclusively in 2 particular zones. A part of the population emigrated from the settlement zones mainly in an offshore direction with growth of body size generating a size zonation, and the densities of *Armandia* adults became spatially uniform through July and August. The significance of following migration processes of mobile benthos for understanding the structure of soft-sediment benthic communities is discussed.

INTRODUCTION

For macrobenthic organisms inhabiting marine soft sediments, the observed distribution of adults (usually individuals retained on a 0.5 or 1 mm mesh sieve) is a complex interaction of the settlement of planktonic larvae or brooded juveniles onto substrata and the following 3 processes after recruitment: survival of individuals; active migration of individuals; passive transport of individuals by waves and currents. Particularly for mobile benthic species, the role of active migration should be important in determining their distributions. One of the habitats where this process can be most easily followed is the intertidal zone, due to its accessibility. In intertidal zones, separate distribution patterns for juveniles and adults along the tidal axis or zonation by body-size (or age) have sometimes been found and ascribed to the active migration of individuals. However, most of the investigations were either for crustaceans (e.g. Bowers 1964, Trevallion et al. 1970, Glynn et al. 1975, Wooldridge 1981, Haley 1982, Wada 1983) or for molluscs (e.g. Edwards 1969, Ansell & Legardère 1980, Leber 1982, Berry & Othman 1983, Nishino et al. 1983, Price 1984); studies relating to polychaetes, the other constituent of the 3 major taxonomic groups of macrofauna, are few (e.g.

Dales 1952, Reise 1978), and their evidence for migration was not conclusive because temporal changes in the population structure were not examined. The present study describes the migration process of a mobile polychaete population, *Armandia* sp. (Opheliidae), on an intertidal sand flat, which was achieved through intensive sampling in time and space.

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 (Fig. 1). The flat is exposed for a distance of 335 m offshore at the extreme low spring tide. The highest elevation of the flat is close to the MLWN (mean low water neap tide) level, and the inclination along the tidal axis is small (1/300). A rectangular area delimited by 2 lines perpendicular to the coast, 300 m wide, was selected for routine sampling (the black-colored area in Fig. 1). A preliminary survey revealed that the community of the macrobenthos 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 gas-

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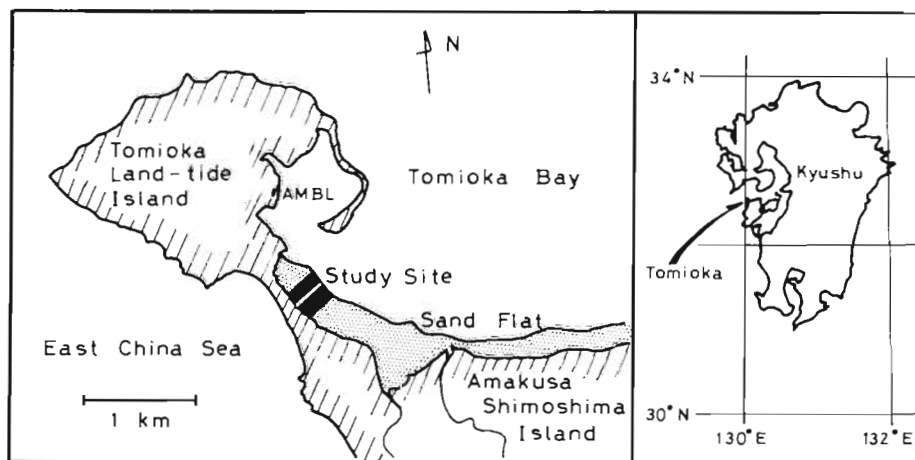* Contribution No. 307 from the Amakusa Marine Biological Laboratory, Kyushu University

Fig. 1. Location of the study site: the fixed transect is shown by a white line

tropod *Umbonium (Suchium) moniliferum* (Lamarck) zone.

The tidal flat is open to the sea to the northeast. Thus, when strong northerly or northeasterly winds blow, large incoming waves generated by these winds disturb the sediment surface over the whole flat. In terms of 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).

STUDY ORGANISM

The following description is extracted from that given in Tamaki (1984a). *Armandia* sp. is a deposit feeder, burrowing within the top 1 cm of the sediment (98 % of individuals were found in the top 1 cm layer). It has a planktonic larval stage. The larvae are ready to settle on the substratum when they attain the 6-setiger stage. Given a suitable sediment at this stage, they settle on it and complete metamorphosis to reach the 7-setiger stage. The minimum body size of benthic juveniles is 65 μm width and 280 μm length. After settlement, when individuals reach the 24-setiger stage, they metamorphose again and attain adult form. The maximum body length of adults is 8 (exceptionally 11) mm (summer) to 13 mm (overwintering) (see Fig. 3a, b). The shape of individuals before the second metamorphosis (hereafter called juveniles) is ver-miform. After metamorphosis (hereafter called adults), the shape becomes spindle-like. Thus it is easy to distinguish juveniles and adults from each other.

FIELD SAMPLING AND PROCESSING OF SAMPLES

In a survey of the macrobenthos conducted in July 1979, the distributions of the numerically dominant

species including *Armandia* sp. were found to be zoned parallel to the coast line (Tamaki & Kikuchi 1983). Thus, representative sampling can be carried out along only 1 transect. Spatial and temporal changes in the density of the *Armandia* sp. population were examined along a transect (Fig. 1) situated 120 m southeast of the northwestern edge of the sampling area, and sampling was carried out at every (as a rule) spring tide from March 1980 to March 1981. A maximum of 16 sampling stations were placed between the shoreline and the mean low water spring tide level (MLWS). 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). The corer did not have a lid on the first 4 sampling occasions (Mar 5 to May 3, 1980), and some water which may have contained specimens (particularly juveniles) was lost. From May 18, 1980, a corer with a rubber lid was used to prevent the water from running off. The samples were fixed in the field with 10 % neutralized formalin solution containing Rose Bengal. In the laboratory, 1 sample was washed through a sieve of 0.125 mm mesh. All macrofaunal animals were sorted out under a dissecting microscope. Individuals were identified to species level and their number was counted. The body length of *Armandia* sp. was measured by tracing the dorsum under a dissecting microscope with a drawing apparatus (× 25).

RESULTS

Large incoming waves generated by strong northerly winds in autumn to spring greatly disturb the sediment of this tidal flat. This disturbance affects the distribution of the benthos in a manner different from the gentle waves that occur in summer: some benthic animals, particularly those which live near the sediment surface including *Armandia* sp., are uprooted and washed into the water column by the strong wave

action, and further transported landward (Tamaki 1984a). Thus I think it appropriate to treat here only the summer distribution of *Armandia* sp. in examining active migration of the population.

Temporal abundance change at recruitment and size-structure of whole population

The yearly change in the densities of juvenile and adult *Armandia* sp. (data pooled for all the stations, Mar 1980 to Mar 1981) is shown in Fig. 2. In 1980, the
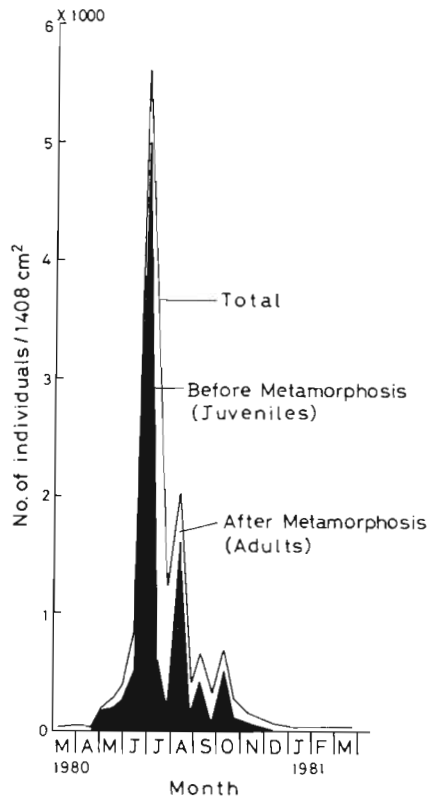

Fig. 2. *Armandia* sp. Temporal change in the density of the population (adults and juveniles) from March 1980 to March 1981. Densities at all 16 stations were pooled

recruitment of larvae began in April and ended in November. The largest recruitment was observed at the end of June, followed by much smaller recruitments in the succeeding 1½ mo. From the middle of August through October, large recruitments occurred 3 times at monthly intervals. This suggests that the recruitment pattern was discrete, not continuous. To examine the temporal change in size structure of the *Armandia* population, size histograms for each sampling date in the spring and summer period were made (Fig. 3a, b). Further, I separated the size histogram into

normal distribution groups according to Taylor's (1965) method.

The overwintering populations from 1979 survived at most until May 18, 1980 (Fig. 3a). They were the source of recruits in the spring to early summer of 1980. Hereafter, each recruitment group is designated by its corresponding sampling date. The first apparent recruit in 1980 was found on April 18. In the histograms after May 3, however, we can find a group which must have settled before April 18. Because recruitment seems to have taken place in accordance with the cycle of spring tides at least until June 14, and as the origin of each 'cohort' can be traced as a temporal sequence of normal distribution groups, the group derived from the recruit before April 18 can be attributed to that of April 2. So why were only few or no juveniles collected on April 2 and 18? One reason may have been the ineffectiveness of the sampling corer used in April (see preceding section).

On June 29, 1980, the largest recruitment in that year was observed (Fig. 2 & 3b). Although, until June 14, recruitment was completed within a relatively short time at every spring tide, the recruitment at the end of June took place over a longer period; on July 14, the 'cohort' from the June 29 recruitment group can be subdivided into 2 normal distribution groups (the groups named June 29, 1st and 2nd at the top of Fig. 3b). This subdivision seems justified, and will be discussed in the next section.

To estimate the dates of larval settlement of the two June 29 recruitment groups from the size-histogram data on July 14, we need to know the growth rate of individuals during the juvenile and adult stages. The growth rate during the juvenile stage was 6/15 of a size-class per day, since the mode in the recruitment group on June 14 shifted by 6 size-class intervals from June 14 to June 29 (Fig. 3a, b). The growth rate during the adult stage (just after metamorphosis) was 7/15 of a size-class per day, since the mode in the cohort from the June 14 recruitment group shifted by 7 size-class intervals from June 29 to July 14 (Fig. 3b). On July 14, the mode of the June 29 2nd group is found at size-class number 6.0. Taking into consideration the growth rate in the juvenile stage, we can conclude that the June 29 2nd group originated from larvae which settled around June 29. The June 29 1st group can then be traced to larvae which settled around June 21, because there is a gap of 4 size-class intervals (= 8 to 9 d in the stage of adults just after metamorphosis) between the modes of the 2 groups of the June 29 cohort on July 14. Thus, at the end of June, recruitment also took place at neap tides, but the temporal discreteness in recruitment was preserved. The life span of individuals of the spring to summer generations was ca 2½ mo (Fig. 3a,b).
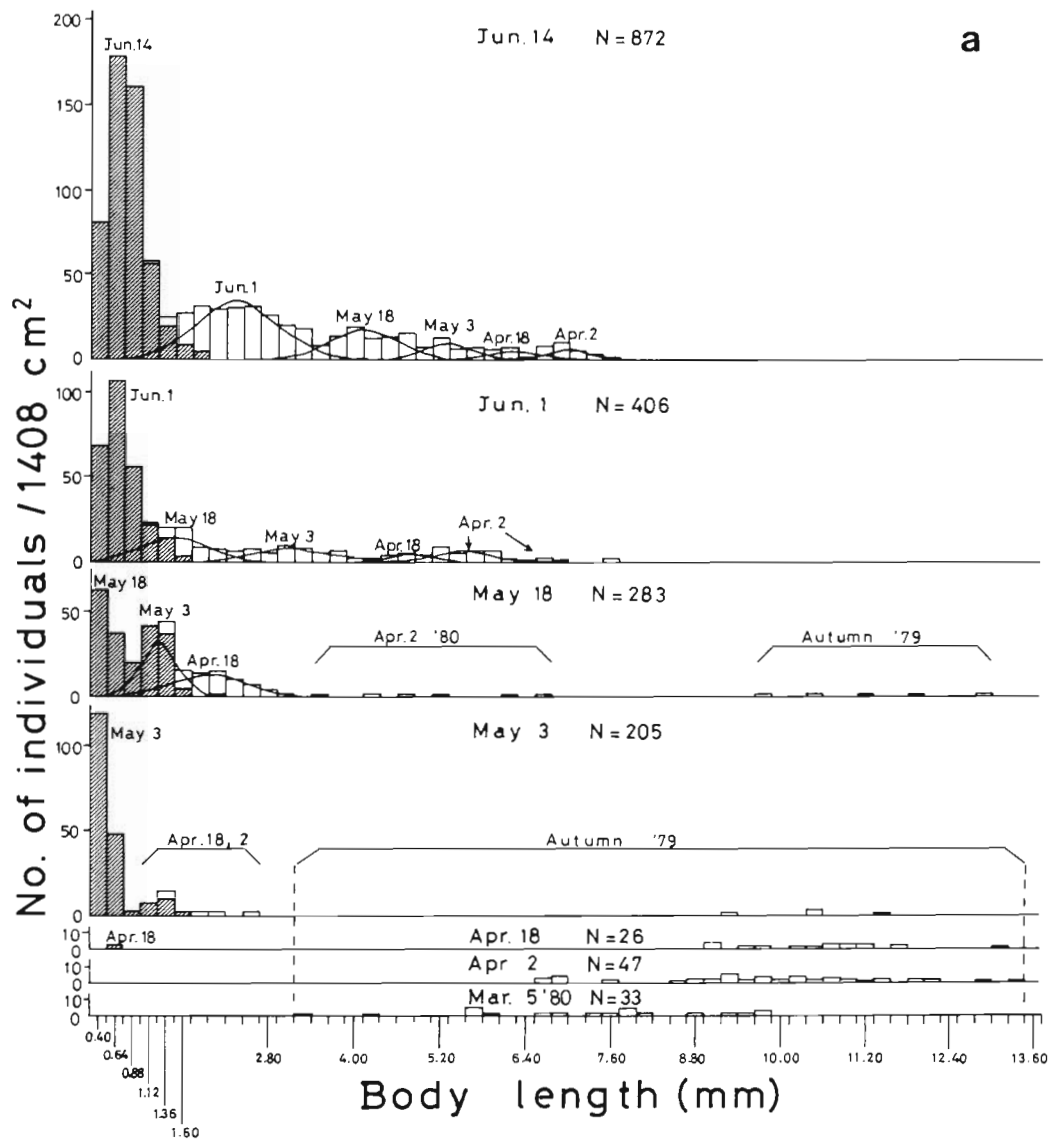
Fig. 3 (a: above) (b: opposite). *Armandia* sp. Temporal change in the size-structure of the population from March to July in 1980. Data at all 16 stations were pooled. Hatched parts: juveniles; blank parts: adults. A spring-tide cycle of recruitment can be seen. Cohorts are separated according to Taylor's (1965) method. Each recruitment group is designated by its corresponding sampling date. At the end of June, recruitment was not limited to around the spring tide (June 29); another 'pulse' of recruitment prior to June 29 is recognized, and these 2 'pulses' are labelled June 29 1st and 2nd at the top of Fig. (b): the former is actually the June 21 recruitment group consisting mainly of the emigrant population from larval settlement zones on July 14 (Fig. 4 & 5), while the latter corresponds to the June 29 recruitment group (see text). On April 2 and 18, data for settled larvae was not clearly consistent with data for their corresponding cohort groups recognized in May and June (see text)

Summer population distribution: larval settlement and movement after settlement

In order to examine the process of recruitment and subsequent changes in distribution, it is easiest to follow the fate of the cohort recruited at the end of June; the density of these larvae was the highest, followed by a far lower recruitment in the succeeding 1½ mo (Fig. 2). The body-size frequency composition of the population for each station on the transect in this period is shown in Fig. 4. The most conspicuous feature in the settlement of *Armandia* sp. on June 29, 1980 was that the location of settlement was confined within the most landward area from the *Prionospio krusadensis* zone to the uppermost *Callianassa japonica* zone, and in the middle of the tidal flat within the *Solen strictus* zone. Far lower densities were found in the remainder of the *C. japonica* zone and in the *Umbonium moniliferum* zone.

Armandia sp. juveniles and adults moved from the

b
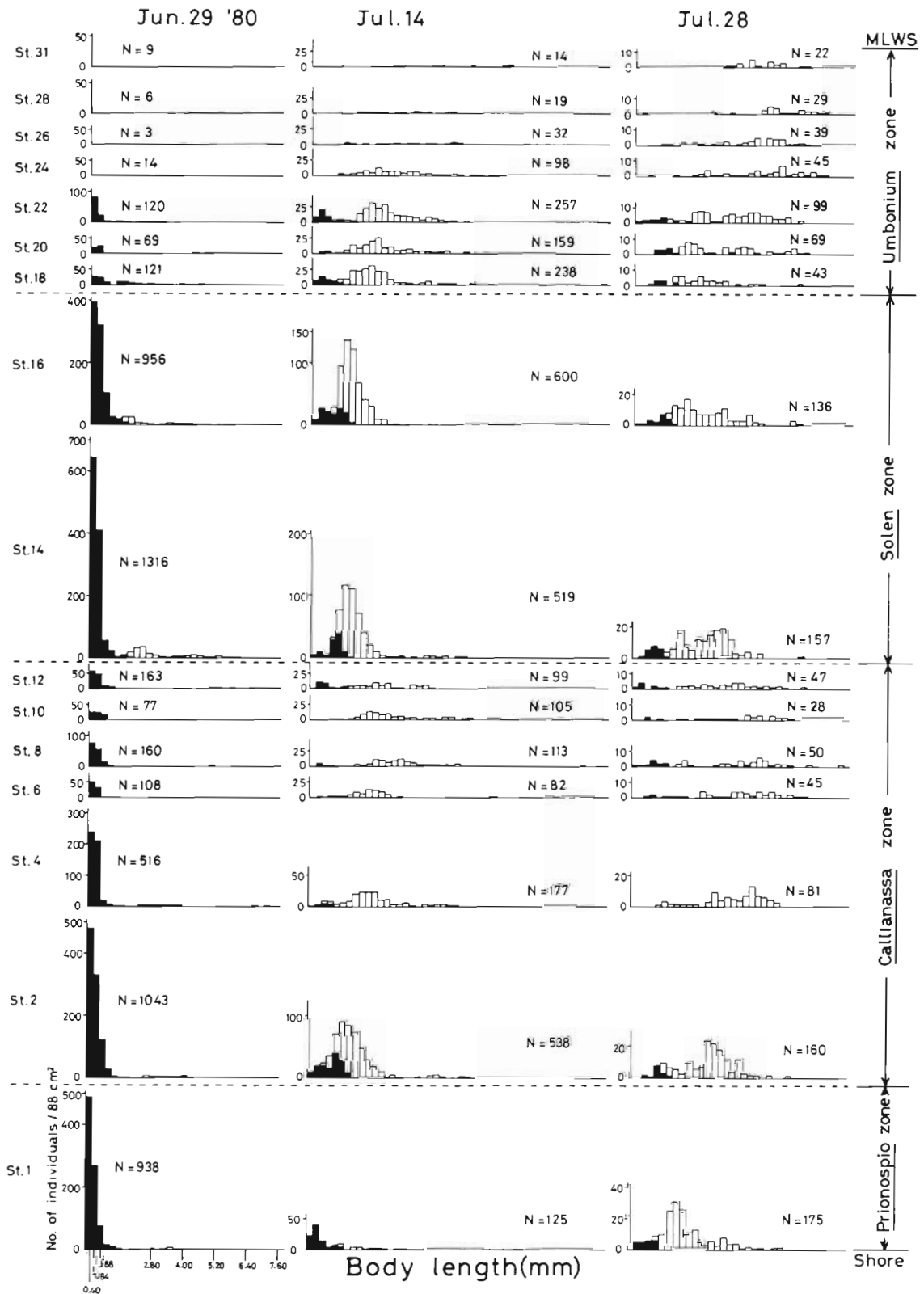
Jul.14
N = 3175

Jun.29 '80
N = 5619
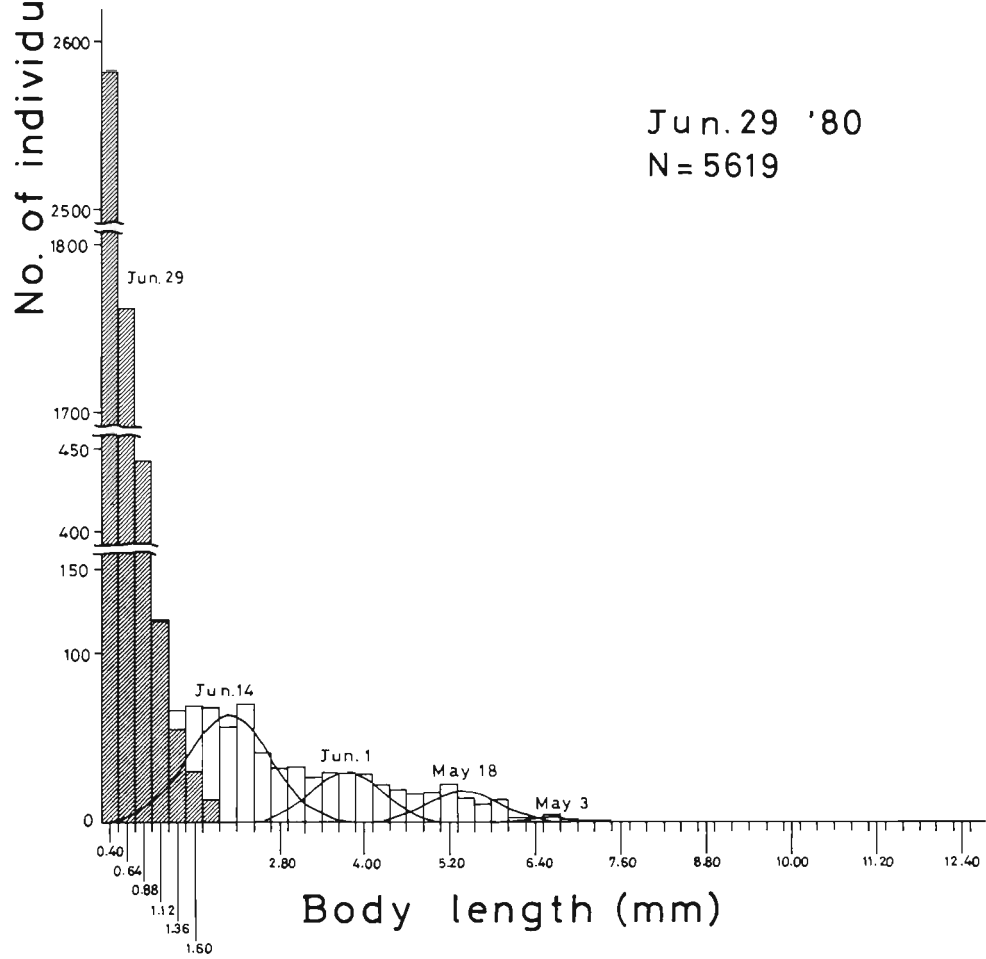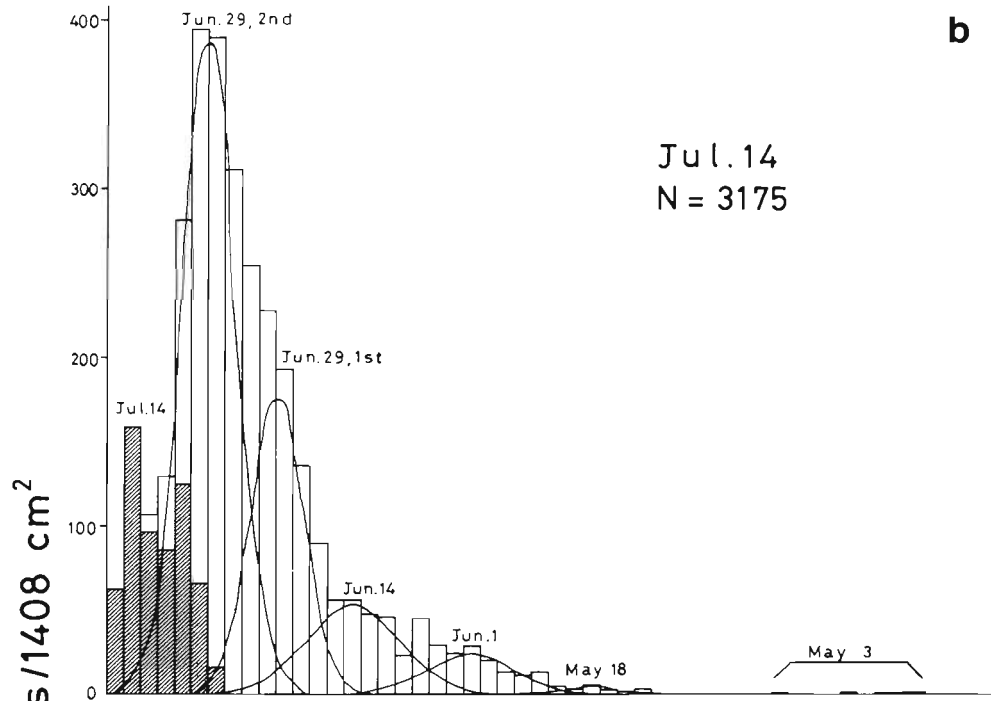
Fig. 4. *Armandia* sp. Body-size frequency composition of population for each sampling station along the fixed transect from end of June through July 1980. Distances between adjacent stations were 10 m (St. 1 to 2), 20 m (St. 2 to 28), and 30 m (St. 28 to 31). The low density at St. 1 on July 14 may be due to sampling error, since on July 28, density at this station was higher than those at St. 2 and 4

settlement zones in various degrees after June 29. In fact, the most apparent evidence of emigration was obtained in July when an appreciable number of adults was recorded in the lower *Umbonium moniliferum* zone (St. 24 to 31), where almost no larval settlement occurred at the end of June. Several characteristics could be recognized in the emigration of the population:

(1) The body-size data of the emigrants maintains the temporal sequence of larval settlement (see also [4]). This is more clearly recognized when the body-size data on July 14 for each station at which the largest larval-settlement occurred at the end of June (i.e. St. 1, 2, 14 & 16) are summed up separately from all

other stations (Fig. 5). The body-length mode for the 'other' stations (= June 29 1st recruitment group: actually June 21 recruitment group; see preceding section and Fig. 3b) is larger than that for the largest larval-settlement stations (= June 29 2nd recruitment group). This suggests that emigration occurred from the earlier cohorts in an orderly fashion.

(2) The influx from the *Solen strictus* zone (St. 14 & 16) to the *Umbonium moniliferum* zone (St. 18 to 31) (Influx 1) was the most conspicuous. The influx from the *S. strictus* zone to the lower *Callianassa japonica* zone (St. 8, 10 & 12) (Influx 2) and that from the (*Prionospio krusadensis* + uppermost *C. japonica*) zone (St. 1 & 2) to the middle *C. japonica* zone (St. 4, 6
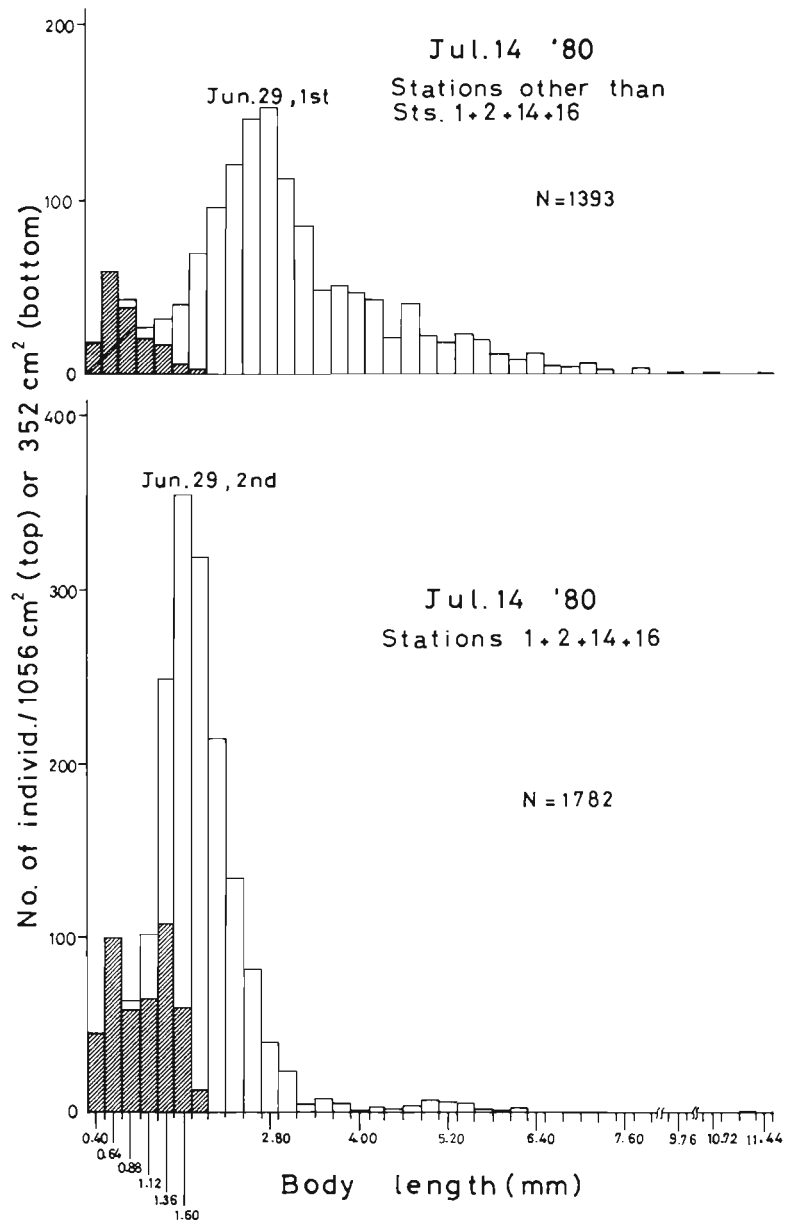

Fig. 5. *Armandia* sp. Subdivision of the body-size frequency composition of the population on July 14, 1980 into the populations at the stations where the larval settlement occurred exclusively on June 29, 1980 (bottom) and at all the other stations (top); hatched: juveniles; blank: adults. The June 29 1st recruitment group is the cohort recruited around June 21, while the June 29 2nd recruitment group is that recruited around June 29 (see text)

& 8) (Influx 3) were smaller. This can be confirmed by calculating a minimum estimate for the amount of Influx 1 and maximum estimates for the amounts of Influxes 2 and 3 during the period from June 29 to July 14.

The minimum estimate for Influx 1 is obtained on the assumption that all the individuals in the *Umbonium moniliferum* zone on June 29 remained in this zone with no mortality until July 14 and that only the remainder of the population (other than the July 14 recruitment individuals) in the zone on July 14 were derived from the population in the *Solen strictus* zone. The proportion of individuals of the July 14 recruitment group in each size-class can be calculated from Fig. 3b, from which, together with Fig. 4, we can obtain the total number of individuals other than the July 14 recruitment individuals in the *Umbonium moniliferum* zone on July 14. Thus the minimum estimate for the amount of Influx 1 is 407 individuals.

The maximum estimate for Influx 2 is obtained on the assumption that all the individuals in the lower *Callianassa japonica* zone on June 29 had died by July 14 and that all the individuals here on July 14, other than the July 14 recruitment individuals, were derived from the population in the *Solen strictus* zone. St. 8, 10 and 12 lie in the lower *C. japonica* zone, as the population which advanced to here from the *S. strictus* zone was found to have reached as far as St. 8 by July 14 (Fig. 4). Thus the maximum estimate for the amount of Influx 2 is 292 individuals, which is smaller than the minimum estimate for Influx 1.

The maximum estimate for Influx 3 is obtained in a similar way to that for Influx 2. On June 29, the total number of individuals in the (*Prionospio krusadensis* + uppermost *Callianassa japonica*) zone was comparable to that in the *Solen strictus* zone (1981 and 2272, respectively). St. 4, 6 and 8 fall in the middle *C. japonica* zone, as the population which advanced from the (*P. krusadensis* + uppermost *C. japonica*) zone into the middle *C. japonica* zone is found to have reached as far as St. 8 by July 14 (Fig. 4). Thus the maximum estimate of the amount of Influx 3 is 350 individuals. If the total number of individuals in the (*P. krusadensis* + uppermost *C. japonica*) zone had been as many as that in the *S. strictus* zone on June 29, the estimate would be 350 × (2272/1981) = 401, which is smaller than but very close to the minimum estimate for Influx 1.

(3) Influx 1, from the *Solen strictus* zone to the *Umbonium moniliferum* zone, was the fastest (speed of the June 29 1st recruitment group was at least 80 m in 23 d: from St. 16 to St. 24 during June 21 to July 14; see preceding section). Influxes 2 and 3 were slower (60 m, from St. 14 to St. 8, and, at the very most, 70 m, from St. 1 to St. 8 in 23 d, respectively).

(4) In each of the above influxes, most of the larger individuals were found at stations further from the *Solen strictus* or *Prionospio krusadensis* zone.

As a result of such emigration from the larval-settlement zones, the spatially concentrated distribution of *Armandia* sp. juveniles on June 29 became more and more uniform, particularly throughout the lower half of the flat through July and August (see Fig. 2 in Tamaki [1985]), creating a size-zonation along the tidal axis.

DISCUSSION

Active migration by benthic animals inhabiting marine soft sediments will yield various degrees of changes in the originally set spatial arrangement of individuals such as the distribution of juveniles, sometimes creating segregation of individuals by body size or age. However, observations of such spatial patterns on only 1 sampling occasion cannot give conclusive evidence for migration. The following 3 possible processes can also produce a spatially different body size or age composition in a population: (1) locally differential recruitment of different cohorts (Jumars 1978, Thompson 1982, Tamaki 1985); (2) passive transport of individuals in a size- or age-specific fashion by waves and/or currents (Dales 1952, Matthiessen 1960, Gilbert 1968, Brown 1982, Thompson 1982); (3) locally differential growth and/or mortality of individuals (Stephen 1928, Gibbs 1968, Green & Hobson 1970, Thompson 1982, Omori et al. 1984). Thus, to confirm migration in a population, it is at least necessary to examine temporal change in the spatial distribution of the size (age) classes of the population. None of the studies that suggested migration of natural polychaete populations have satisfied this requirement (e.g. Dales 1952 [*Thoracophelia mucronata*], Amouroux 1974 [*Ophelia neglecta*], Reise 1978 [*Arenicola marina*]).

The present study, through intensive sampling not only in space but in time, has succeeded in quantifying to some extent the process of migration in an *Armandia* sp. population with growth of body size. This success is partly because the study was planned during the period where possibilities (1) and (2) above are remote. Possibility (3), however, cannot be ruled out. In July, the body-sizes of the adult population of *Armandia* in the middle to lowest *Callianassa japonica* zone were larger than those in the zones with the largest settlement of larvae at the end of June, i.e. the *Prionospio krusadensis* to uppermost *C. japonica* zone and the *Solen strictus* zone (Fig. 4). This phenomenon was ascribed to the migration of individuals with growth of body size from the latter zones to the former zone in an orderly fashion, following the temporal sequence of larval settlement (see 'Results'). Another explanation

may be possible: the growth rate of individuals recruited in the middle to lowest part of the *C. japonica* zone may have been higher than that of individuals in the zones of the largest recruitment. However, 2 observations indicate that the first explanation is more reasonably acceptable: (1) emigration of individuals did occur from the *S. strictus* zone to the *Umbonium moniliferum* zone; (2) the increase in body size along the stations followed a similar trend in sequence from the *S. strictus* zone to the *U. moniliferum* zone, from the *S. strictus* zone to the lower *C. japonica* zone, and from the (*P. krusadensis* + uppermost *C. japonica*) zone to the middle *C. japonica* zone.

Examination of the 4 characteristics in the emigration of the *Armandia* sp. population (see 'Results') will make clear some possible trends in the population movement or factors regulating the emigration, which should be experimentally analysed. As previously mentioned, Characteristics (1) and (4) suggest that emigration occurred from the earlier cohorts in an orderly fashion. Another explanation may be possible: individuals which grew more rapidly may have attained greater mobility and advanced more quickly. A laboratory experiment suggests, however, that this is not the case (Tamaki 1984a): diffusion of a population of *Armandia* sp. composed of several different body-size classes was examined in a homogeneous sediment, and the advancing speeds of all the size-class groups were identical.

Alldredge & King (1980) found that a congeneric species of the present *Armandia* sp., *Armandia brevis*, swims in the water and returns to the sediment. In the present case, the body-size gradient found along the tidal axis from the larval settlement zones indicates that the emigration of the population was achieved not through such swimming behavior for long distances followed by random resettlement of individuals onto the sediment, but through the gradual advance of individuals in the sediment or through swimming for only short distances if at all.

Generally, in the analysis of factors regulating the emigration of mobile benthos, the following 2 aspects should be distinguished: (1) factors inducing emigration from original areas; (2) factors determining abundance in the areas at which emigrants arrive. One possible factor, which was striking on examining the spatial and temporal changes in the body-size composition of the *Armandia* sp. population (Fig. 4), is a negative influence of the activity of the ghost shrimp *Callianassa japonica* on the immigration of *Armandia* individuals (Category 2). For example, from the end of June to July 14, the influx from the *Solen strictus* zone to the *C. japonica* zone (Influx 2) was smaller than that from the *S. strictus* zone to the *Umbonium moniliferum* zone (Influx 1). This phenomenon may suggest lethal

and/or excluding effects of *C. japonica* on *Armandia* individuals in a direct or an indirect (e.g. by conditioning the properties of sediment) way. Tamaki (1984a) explained the cause of this phenomenon, on the basis of a laboratory experiment, as a mechanical interference of the feeding behavior of *Armandia* individuals through sediment-deposition by *C. japonica*; no lethal effects of *C. japonica* were detected. The sediment-deposition activity of *C. japonica* was an effective barrier rejecting the immigration of *Armandia* individuals into its habitat. However, the observation that not all *Armandia* individuals were prevented from entering the *C. japonica* zone indicates that the negative effect of *C. japonica* was incomplete.

In contrast to the small influx of the *Armandia* population into the *Callianassa japonica* zone, the interference by *C. japonica* does not necessarily delay the population advance through this zone when compared to the speed in the *Umbonium moniliferum* zone. Instead it is possible that the interference causes the *Armandia* population in the *C. japonica* zone to advance faster rather than slower. In general, the rate of dispersion of benthic animals should be higher under 'bad' sedimentary conditions and lower under 'good' conditions. In the case of the diffusion of mobile benthos, such a trial-and-error diffusion process may be common (e.g. Wieser 1956, Bowers 1964, Meadows 1964, Gray 1971, Ravenel & Thistle 1981, Wilson 1983). Tamaki (1984a) found through a laboratory experiment that the activity of *C. japonica* can also be beneficial to *Armandia* individuals by conditioning the properties of sediment (e.g. quality of food particles; softening of the sediment for penetration). In this case, the period of stay of *Armandia* individuals which had managed to enter the *C. japonica* zone should have been longer because of the favorable conditions: this influence may be more dominant than the interference through sediment-deposition. This would account for the reduced speed of advance of the invading population.

The importance of immigration and emigration of adults of mobile macrobenthos on the structure of soft-sediment benthic communities has been pointed out by several field experiments (e.g. McCall 1977, Peterson & Andre 1980, Wilson 1981, VanBlaricom 1982, Gallagher et al. 1983, Ambrose 1984). In all these studies, however, examination of the variation in the densities of mobile adults in experimental and control plots established in the vicinity of each other was only little backed up by attention to the migration process of species populations under natural conditions. The example of the interaction between *Armandia* sp. and *Callianassa japonica* highlighted in this study has indicated that following the movement of a natural population by intensive sampling in time and space should also be useful in clarifying the impact of biolog-

ical interactions on the abundance pattern of mobile benthic species.

LITERATURE CITED

Alldredge, A. L., King, J. M. (1980). Effects of moonlight on the vertical migration patterns of demersal zooplankton. J. exp. mar. Biol. Ecol. 44: 133–156

Ambrose, W. G. Jr. (1984). Influences of predatory polychaetes and epibenthic predators on the structure of a soft-bottom community in a Maine estuary. J. exp. mar Biol. Ecol. 81: 115–145

Amouroux, J.-M. (1974). Étude des peuplements infralittoraux de la côte du Roussillon II. Faunistique et caractéristiques bionomiques. Vie Milieu 24, fasc. 1, sér. B: 209–222

Ansell, A. D., Legardère, F. (1980). Observations on the biology of *Donax trunculus* and *D. vittatus* at Ile d'Oléron (French Atlantic coast). Mar Biol. 57: 287–300

Berry, A. J., Othman, Z. b. (1983). An annual cycle of recruitment, growth and production in a Malaysian population of the trochacean gastropod *Umbonium vestiarium* (L.). Estuar. coast. Shelf Sci. 17: 357–363

Bowers, D. E. (1964). Natural history of two beach hoppers of the genus *Orchestoidea* (Crustacea: Amphipoda) with reference to their complemental distribution. Ecology 45: 677–696

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

Edwards, D. C. (1969). Zonation by size as an adaptation for intertidal life in *Olivella biplicata*. Am. Zool. 9: 399–417

Gallagher, E. D., Jumars, P. A., Trueblood, D. D. (1983). Facilitation of soft-bottom benthic succession by tube builders. Ecology 64: 1200–1216

Gibbs, P. E. (1968). Observations on the population of *Scoloplos armiger* at Whitstable. J. mar biol. Ass. U. K. 48: 225–254

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

Glynn, P. W., Dexter, D. M., Bowman, T E. (1975). *Excirolana braziliensis*, a Pan-American sand beach isopod: taxonomic status, zonation and distribution. J. Zool., Lond. 175: 509–521

Gray, J. S. (1971). Factors controlling population localization in polychaete worms. Vie Milieu 22 Suppl.: 707–722

Green, R. H., Hobson, K. D. (1970). Spatial and temporal structure in a temperate intertidal community, with special emphasis on *Gemma gemma* (Pelecypoda: Mollusca). Ecology 51: 999–1011

Haley, S. R. (1982). Zonation by size of the Pacific mole crab, *Hippa pacifica* Dana (Crustacea: Anomura: Hippidae), in Hawaii. J. exp. mar Biol. Ecol. 58: 221–231

Jumars, P. A. (1978). Spatial autocorrelation with RUM

Leber, K. M. (1982). Bivalves (Tellinacea: Donacidae) on a North Carolina beach: contrasting population size structures and tidal migrations. Mar. Ecol. Prog. Ser 7: 297–301

Matthiessen, G. C. (1960). Intertidal zonation in populations of *Mya arenaria*. Limnol. Oceanogr. 5: 381–388

McCall, P. L. (1977). Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. mar. Res. 35: 221–266

Meadows, P. S. (1964). Substrate selection by *Corophium* species: the particle size of substrates. J. Anim. Ecol. 33: 387–394

Nishino, T., Nojima, S., Kikuchi, T. (1983). Quantitative studies of the life history and interspecific relationship of two gastropod species, *Odostomia* sp. (ectoparasite) and *Umbonium (Suchium) moniliferum* (Lamarck) (host). I. Life history and population dynamics of *Odostomia* sp. Publ. Amakusa Mar. Biol. Lab., Kyushu Univ. 7: 61–79

Omori, K., Mori, K., Nishino, T. (1984). The variation of life history traits of *Macrophthalmus japonicus* De Haan (Ocypodidae: Decapoda) according to environmental heterogeneity I. The problems to be solved. Benthos Res. 27: 28–37 (in Japanese with English abstract)

Peterson, C. H., Andre, S. V. (1980). An experimental analysis of interspecific competition among marine filter feeders in a soft-sediment environment. Ecology 61: 129–139

Price, C. H. (1984). Tidal migrations of the littoral salt marsh snail *Melampus bidentatus* Say. J. exp. mar. Biol. Ecol. 78: 111–126

Ravenel, W. S., Thistle, D. (1981). The effect of sediment characteristics on the distribution of two subtidal harpacticoid copepod species. J. exp. mar. Biol. Ecol. 50: 289–301

Reise, K. (1978). Experiments on epibenthic predation in the Wadden Sea. Helgoländer Meeresunters. 31: 55–101

Stephen, A. C. (1928). Notes on the biology of *Tellina tenuis* da Costa. J. mar. biol. Ass. U. K. 15: 683–702

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 Univ., 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). Inhibition of larval recruitment of *Armandia* sp. (Polychaeta: Opheliidae) by established adults of *Pseudopolydora paucibranchiata* (Okuda) (Polychaeta: Spionidae) on an intertidal sand flat. J. exp. mar Biol. Ecol. 87: 67–82

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

Taylor, B. J. R. (1965). The analysis of polymodal frequency distributions. J. Anim. Ecol. 34: 445–452

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

Trevallion, A., Ansell, A. D., Sivadas, P., Narayanan, B. (1970). A preliminary account of two sandy beaches in South West India. Mar Biol. 6: 268–279

VanBlaricom, G. R. (1982). Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. Ecol. Monogr. 52: 283–305

Wada, K. (1983). Spatial distributions and population struc-

tures in *Scopimera globosa* and *Ilyoplax pusillus* (Decapoda: Ocypodidae). Publ. Seto Mar. Biol. Lab., Kyoto Univ. 27: 281–291

Wieser, W. (1956). Factors influencing the choice of substratum in *Cumella vulgaris* Hart (Crustacea, Cumacea). Limnol. Oceanogr. 1: 274–285

Wilson, W. H. Jr. (1981). Sediment-mediated interactions in a densely populated infaunal assemblage: the effects of the polychaete *Abarenicola pacifica*. J. mar. Res. 39: 735–748

Wilson, W. H. Jr. (1983). The role of density dependence in a marine infaunal community. Ecology 64: 295–306

Wooldridge, T. (1981). Zonation and distribution of the beach mysid, *Gastrosaccus psammodytes* (Crustacea: Mysidacea). J. Zool., Lond. 193: 183–189