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Population persistence of *Capitella* sp. (Polychaeta; Capitellidae) on a mud flat subject to environmental disturbance by organic enrichment

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ABSTRACT: The exclusive domination of several sibling species of the polychaete complex *Capitella capitata* in organically enriched areas has been recognized to reflect their opportunistic characteristics, especially production of planktonic larvae with widespread dispersal ability. In the present study it was found that a population of *Capitella* sp. in an organically enriched mud-flat habitat subject to environmental disturbance was, by contrast, maintained without reliance on recolonization from other habitats throughout 1 yr. Although the population declined markedly after the development of reducing conditions in the sediment in early summer, very small patches with extremely low densities (< 100 ind. m^{-2}) were preserved in restricted areas with moderate organic enrichment within a gradient of organic enrichment. These remnant populations rapidly reconstructed dense patches in the most organically enriched areas during recovery of sediment conditions from late autumn to winter. Although the most enriched areas allowed *Capitella* sp. to establish dense patches, these areas were accessible only during parts of the year. Nevertheless, the distribution was concentrated in enriched areas, since this deposit-feeder required organically enriched sediment for normal growth. The population size structure was apparently influenced by the level of sediment organic matter, and individuals large enough for reproduction were rare in less enriched areas. Thus, the association with organically enriched sediment and the population dynamics, as characterized by the dramatic seasonal fluctuations in population size, are attributable to the physiological requirement of this species for organically enriched sediment, the dramatic seasonal fluctuations in the carrying capacity of habitats subject to catastrophic environmental disturbance, and the extraordinarily large potential of *Capitella* sp. for rapid population growth.

INTRODUCTION

Organic enrichment of soft bottom sediment tends to be accompanied by the development of reducing conditions in the sediment and deoxidization of bottom water, as a result of decomposition of abundant organic matter. Benthic communities in such organically enriched areas are subject to catastrophic environmental disturbances, and often exhibit an annual cycle of temporal defaunation in summer and recolonization from autumn to winter (Kolmel 1979, Tanaka & Kikuchi 1979, Santos & Simon 1980a, b, Tsutsumi & Kikuchi 1983). There is a general pattern of distribution of benthic macrofauna along a gradient of organic enrichment of the sediment (Pearson & Rosenberg 1976, 1978). Benthic communities in the most organically enriched sediment with the most disturbed environment are occupied solely by small, thread-like polychaetes, which include several species belonging to the sibling species complex of *Capitella capitata*. Such polychaetes often reach very high densities (Kitamori 1975, Pearson & Rosenberg 1978, Kikuchi 1979, Reish 1979). These simple benthic communities, lacking in diversity, are gradually replaced by more diverse communities after a decrease in the additional organic discharge into the bottom environment.

In the past decade, the association of *Capitella* species with organic enrichment of the sediment has come to be considered as a reflection of the opportunistic characteristics of their life history (production of planktonic larvae with widespread dispersal ability, early maturation, 'big-bang' reproduction, high potential for population growth, poor ability to compete with other benthic fauna, etc.). The population dynamics of these species are characterized by a very rapid response to environmental variability, early recolonization, explosive increases in the population during the faunal recovery process, and a rapid decline in the

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density of the population after the subsequent recolonization of the environment by other fauna or the occurrence of an environmental disturbance (Grassle & Grassle 1974, Kikuchi & Tanaka 1976, McCall 1977, Rosenberg 1976, Pearson & Rosenberg 1978, Kikuchi 1979, Kolmel 1979, Gray 1981, Tsutsumi & Kikuchi 1983).

The production of planktonic larvae with the ability to disperse over a wide area has been considered one of the most important life-history characteristics of an opportunistic species that can persist as a population in disturbed habitats, since it allows the organism to escape from an environmental disturbance and to discover new, open habitats with great speed (Grassle & Grassle 1974, McCall 1977). Recent life-history studies have, however, revealed that the *Capitella* species that exhibits the most opportunistic population dynamics possesses rather restricted dispersal ability since it produces lecithotrophic larvae with a very brief planktonic stage (Grassle 1980, Tsutsumi & Kikuchi 1984). Furthermore, Tsutsumi (1987) reported that, in the initial stages of the faunal recovery process, after defaunation in organically polluted areas, a seed population of the *Capitella* species was supplied from very small populations that remained somewhere in the close vicinity of the azoic areas. Thus, it appeared that the *Capitella* population was maintained within a habitat subject to environmental disturbance by organic pollution without any reliance on widespread dispersal ability. Although life-history adaptation to disturbed habitats has been emphasized in the association of several species within the sibling species complex of *Capitella capitata* with organic enrichment of the sediment, it seems appropriate to review the factors that allow *Capitella* species to inhabit only the most organically enriched areas, in terms of a precise description of their population dynamics.

Since 1979, I have studied the life history and population dynamics of *Capitella* species in Tomioka Bay, Amakusa Shimoshima Island, Kyushu, South Japan. In this study area, 2 types of *Capitella* species occur, each with a different mode of reproduction. One type produces a large number of small eggs (less than 100 µm in diameter; author's unpubl. data), and the other produces a restricted number of large eggs (less than 300 eggs of about 280 µm in diameter; Tsutsumi & Kikuchi 1984). The former type is extremely rare and is easily distinguished from the latter type, since the former has a markedly slender and yellowish body. The latter type occurs in large numbers in the areas that are organically polluted as a result of fish farming (Tsutsumi 1983, 1987) and on a muddy flat where the sediment is also organically enriched by a large amount of organic discharge from the luxuriant growth of sea lettuce on the flat (Tsutsumi 1983). Field and laboratory studies of this latter *Capitella* species indicate a marked consistency in the size of mature eggs and the modes of larval development throughout the year, with no marked changes in brood size per female that cannot be explained by concomitant changes in the body size of brooding females (Tsutsumi & Kikuchi 1984). I have, therefore, concluded that the latter type of *Capitella* species consistes of a single species, which is referred to as *Capitella* sp. in the present paper and which is equivalent to *Capitella capitata* in the reports by Tsutsumi (1983, 1987) and by Tsutsumi & Kikuchi (1983, 1984). In general, the features of the life history of *Capitella* sp. closely resemble those of *Capitella* sp. I, which responds extremely rapidly to environmental disturbances (Grassle & Grassle 1976, Grassle 1980).

The purpose of the present study was to generate a description of environmental conditions in the habitat and the population dynamics of *Capitella* sp. on the mud flat; to analyze the environmental factors that influence the density and distribution of *Capitella* sp.; and to elucidate the mechanisms that allow *Capitella* sp. to maintain its population in organically enriched areas subject to environmental disturbance.

STUDY AREA

Shioiri Flat is a mud flat adjacent to Tomoe Cove, which is a subsidiary cove of Tomioka Bay on the northwestern corner of Amakusa Shimoshima Island on the west coast of Kyushu, Japan (32°32′ N, 130°02′ E) (Fig. 1). This flat is about 200 m in length and 100 m in width at low tide during spring tides, and is divided into 2 parts, Upper Flat and Lower Flat, by a bank parallel to the shoreline. Tidal flow between the 2 flats is maintained by a narrow gap in the bank. The chlorinity of the bottom water on the flat in flood never falls below 1.8 % except during the rainy season. The annual range of surface temperatures of the sediment on the flat varies between 3.2 °C (February) and 36.0 °C (late August).

MATERIALS AND METHODS

Fifteen sampling stations were arranged in a grid at 20 m intervals on Upper Flat, while 45 sampling stations were set at 10 m intervals on Lower Flat (Fig. 1). Assessment of environmental conditions and quantitative sampling of the *Cpitella* population were carried out twice at all stations on the flat (1 April and 9 September 1983), and an additional twice on Lower Flat only (13 June and 21 December 1983). At 2 sampling stations on Lower Flat, namely Stns C1 and F2, which were 0.85 m and 0.90 m above MLWS, respectively (Fig. 1), environmental conditions were assessed

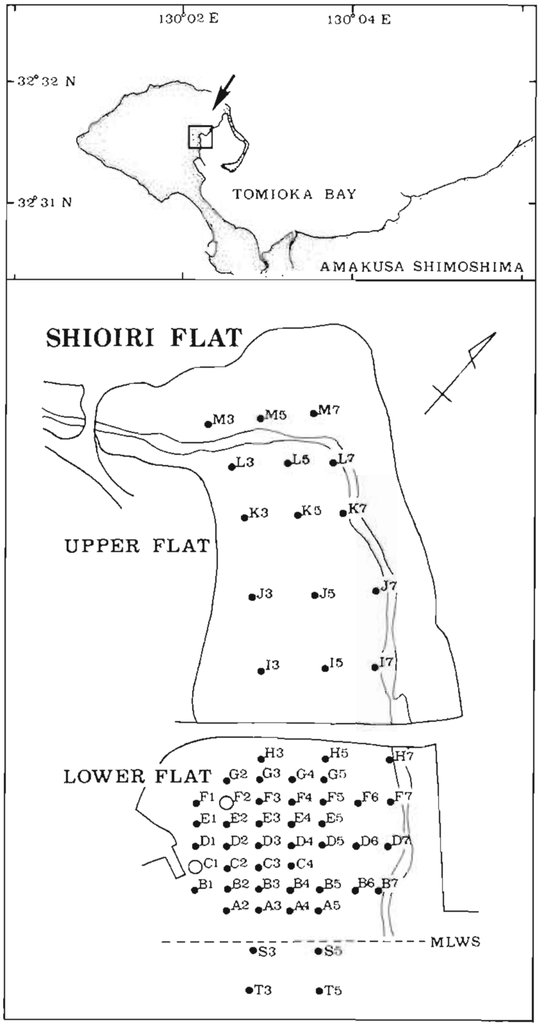

Fig. 1 Study area, Kyushu, Japan. Topography and locations of sampling stations on Shioiri Flat. (○) Routine-sampling stations used for the population study

at fortnightly or monthly intervals, and a quantitative survey of the *Capitella* population was repeated 85 times and 40 times at these stations, respectively, from April 1983 to April 1984.

The environmental assessments included physicochemical analyses of the sediment (grain size, total sulfide content and organic matter content of the surface layer of the sediment, to a depth of about 1 cm), measurement of the vertical profile of redox potential values in the sediment, and observation of the extent of coverage of the sediment by sea lettuce *Ulva pertusa*.

The samplings and assessments of environmental conditions on the flat were performed during low tide. Sediment samples for population studies of *Capitella* sp. were taken with small core samplers (4 × 4 × 5 cm, 6.25 × 6.25 × 5 cm or 10 × 10 × 5 cm). The size of the core sampler and the number of samples taken at each station were appropriately adjusted on each sampling occasion, being based on the abundance of *Capitella* sp. on the previous sampling occasion, since the density of *Capitella* sp. changed dramatically from month to month or even from week to week. However, at least 3 samples were taken at all sampling stations. At Stns C1 and F2, more than 10 samples were collected to permit more precise estimations of the density and size-structure of the *Capitella* population on each sampling occasion. Samples were fixed and preserved in a 10 % solution of formalin containing Rose Bengal. After sieving of each sample through a 0.125 mm mesh sieve, the worms were sorted under a stereoscopic microscope in the laboratory and preserved in 10 % formalin. The number of *Capitella* sp. in each sample was counted, and the sex of adult worms determined. The body size of the worms was represented by the maximum width of thoracic segments. Most of the specimens were broken into pieces during sampling and sieving, but their thoracic segments were never injured. The maximum width was closely correlated with the dry body weight (Tsutsumi & Kikuchi 1984).

Sediment samples for chemical analyses and analysis of particle size were collected from the surface of the sediment with a spoon. The total sulfide content of the sediment was determined with an H_2S-absorbent column. The amount of organic matter in the sediment was expressed in terms of the protein content, based on the organic nitrogen content, which was estimated by extracting and measuring levels of a number of amino acids with chloric acid (Buchanan & Longbottom 1970). Since protein is required for individual growth, the protein content of the sediment should be representative of the abundance of available food resources for a deposit-feeding polychaete, such as *Capitella* sp., as it attempts to establish a population (e.g. Tenore 1977). The vertical profile of redox potential values in the sediment was measured with a portable redox meter, by insertion of the platinum electrode into the sediment at different depths. Coverage of sea lettuce on the sediment was estimated by visual inspection.

RESULTS

Organic enrichment of sediment by sea lettuce

Fig. 2 shows the seasonal variations in coverage by sea lettuce of Shioiri Flat. Sea lettuce *Ulva pertusa* grew luxuriantly on Lower Flat throughout almost the entire year, while it was generally sparse on Upper Flat. Coverage of sea lettuce reached 100 % in the central area of Lower Flat, which included one of the routine sampling stations (Stn F2), and the standing crop exceeded 400 g dry wt m^{-2} throughout almost the entire year. Another routine sampling station (Stn C1) was at the edge of or outside the area of sea lettuce.

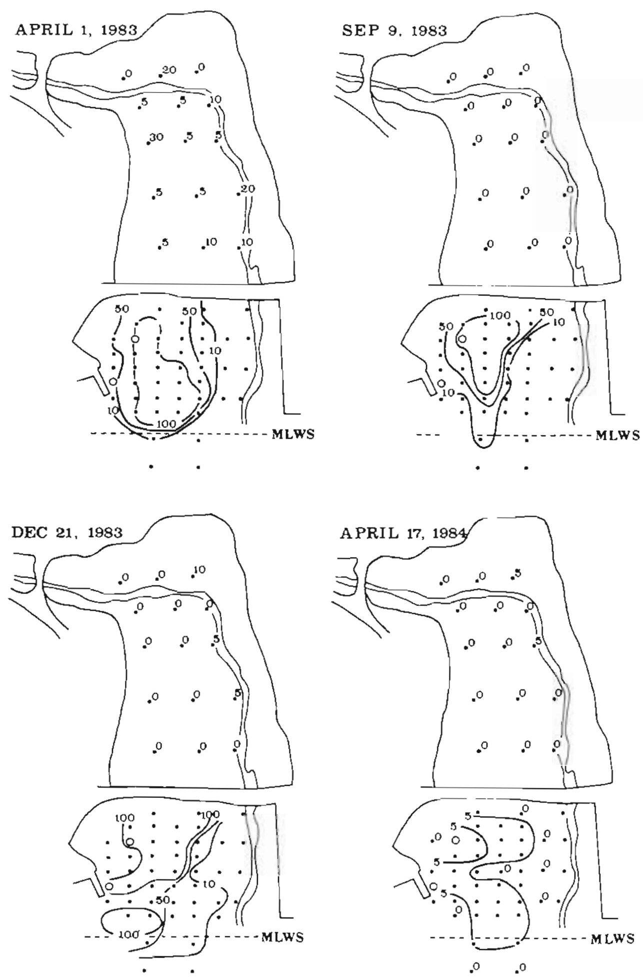

Fig. 2. *Ulva pertusa*. Seasonal variations in the distribution of sea lettuce, expressed as coverage (%) of the sediment, on Shioiri Flat

This pattern of distribution of sea lettuce on the flat was maintained from April 1983 until January 1984. The sea lettuce began to wither in February, and it had almost entirely disappeared from Lower Flat by April 1984.

Sediment thickly covered by sea lettuce tended to be organically enriched by the accumulation of a large amount of algal debris in the sediment. Fig. 3 shows the distribution of protein content of the surface layer of the sediment on the flat on 1 April 1983. Highest protein contents (over 0.50 %) were noted on Lower Flat, where the sediment was thickly covered by sea lettuce. The mean protein content of the sediment at 15 stations with 100 % coverage by sea lettuce on Lower Flat was 0.43 % ± 0.19 (mean ± SD), while at 13 stations where the coverage was below 10 % the mean protein content was 0.29 % ± 0.16. Thus, the level of organic matter in the sediment increased significantly as a result of the luxuriant growth of sea lettuce. Algal production was responsible for the additional organic discharge onto the sediment on Lower Flat.

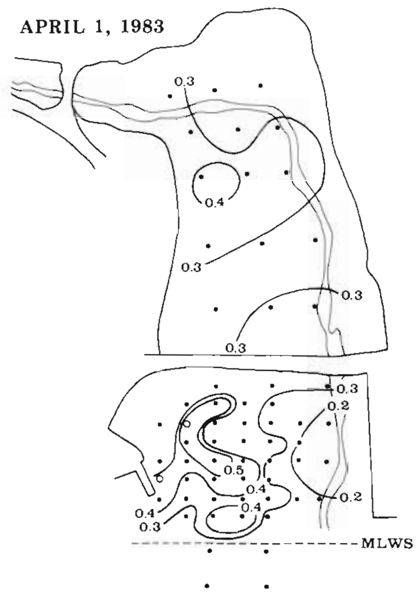

Fig. 3. Distribution of protein content of the sediment surface layer (%) on Shioiri Flat on 1 April 1983

Environmental disturbance by organic enrichment of sediment

The sediment that was organically enriched by the luxuriant growth of sea lettuce on Lower Flat turned black, smelling of H_2S, during high-temperature conditions in the summer. The development of reducing conditions in the sediment was evaluated by measurement of the total sulfide content of the sediment. Fig. 4 shows the pattern of distribution of the total sulfide content of the surface layer of the sediment on Lower Flat. In April 1983, the total sulfide content was less than 0.4 ppt at all stations except F2 and E3, indicating that the sediment on the flat was still aerobic. In June 1983, the total sulfide content of the sediment exceeded 0.4 ppt at 13 stations, all of which were located in areas with a luxuriant growth of sea lettuce. In particular, at 4 stations (F2, E2, D4 and C3), a high concentration of total sulfide of above 0.8 ppt was recorded. Fig. 5 shows the relationship between the protein content and the total sulfide content of the surface layer of the sediment in June 1983. A significant positive correlation was observed between these parameters ($r = 0.604$, $p < 0.01$, F-test). Open circles in Fig. 5 indicate the stations at which 100 % of the surface of the sediment was covered by sea lettuce. These stations were distributed in areas with a protein content of more than 0.4 % and a total sulfide content of more than 0.4 ppt. These data also demonstrate that reducing conditions were prevalent even in the surface layer of the sediment that was organically enriched by the luxuriant growth of sea lettuce in June 1983.

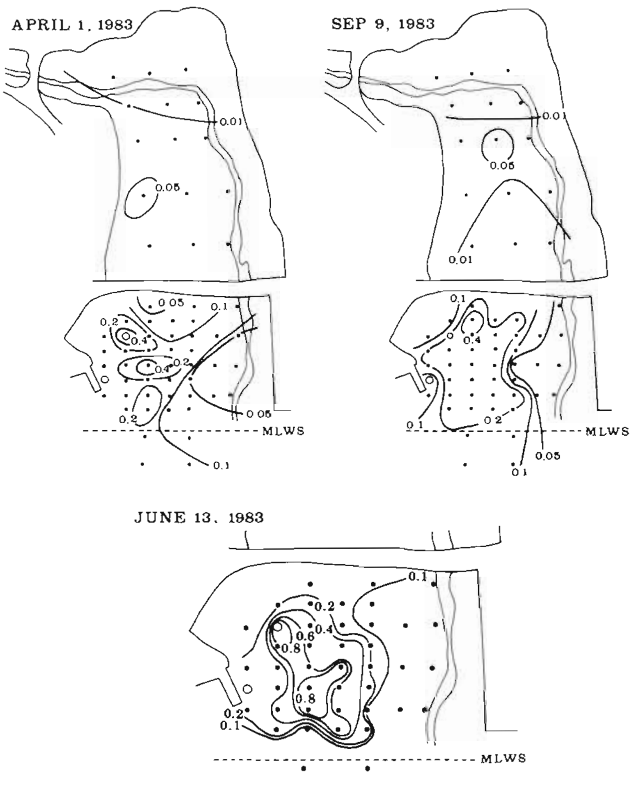

Fig. 4. Seasonal variations in distribution of total sulfide content of the sediment surface layer (ppt) on Shioiri Flat

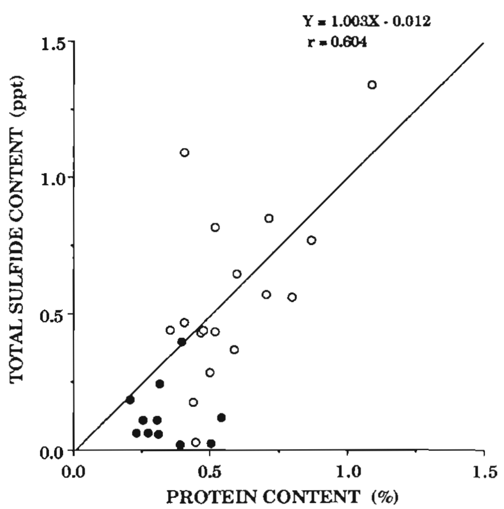

Fig. 5. Relationship between protein content (%) and total sulfide content (ppt) of the sediment surface layer on Lower Flat on 13 June 1983. Open circles: stations where 100 % of the surface of the sediment was covered by sea lettuce

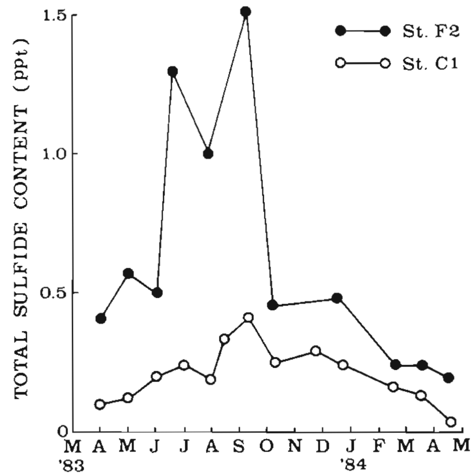

Fig. 6. Seasonal fluctuations in total sulfide content (ppt) of the sediment surface layer at 2 routine-sampling stations (C1 and F2) on Lower Flat

Figs. 6 and 7 show the seasonal variations in the total sulfide content of the surface layer of the sediment and variations in the vertical profiles of redox potentials in the sediment at 2 routine-sampling stations. At Stn F2, with the most organically enriched sediment, the total sulfide content of the surface layer of the sediment increased rapidly and exceeded 1.0 ppt in June, and at that time there was a −150 mV isopleth that extended 4 to 5 mm beneath the surface of the sediment. The black anaerobic layer reached the surface of the sediment. Such reducing conditions in the surface layer of the sediment lasted for about 3 mo. Re-oxidation of the reduced sediment was initiated at the beginning of September, following a dramatic decrease in the total sulfide content. This phenomenon occurred simultaneously throughout the organically enriched sediment on Lower Flat. No sediment with a total sulfide content of more than 0.6 ppt in the surface layer was observed at any station on 9 September 1983 (Fig. 4).

At another routine-sampling station, C1, the deterioration of the sediment conditions during the summer was rather mild, as a result of diminished discharge of organic matter from the sea lettuce that grew sparsely on the sediment. The −150 mV isopleth of redox potential in the sediment fluctuated at a depth of between 1 and 2 cm and, consequently, the total sulfide content of the surface layer of the sediment never exceeded 0.5 ppt during the summer (Fig. 6).

Seasonal variations in the distribution and population density of *Capitella* sp.

The seasonal variations in the distribution of *Capitella* sp. on Shioiri Flat are shown in Fig. 8. In April 1983, when the surface layer of the sediment still remained rather oxidative, even in the areas of Lower Flat that were thickly covered by sea lettuce (Fig. 4), dense patches of *Capitella* sp. were found in the organically enriched sediment with luxuriant growth of sea lettuce. As illustrated in Fig. 9, the density of *Capitella*

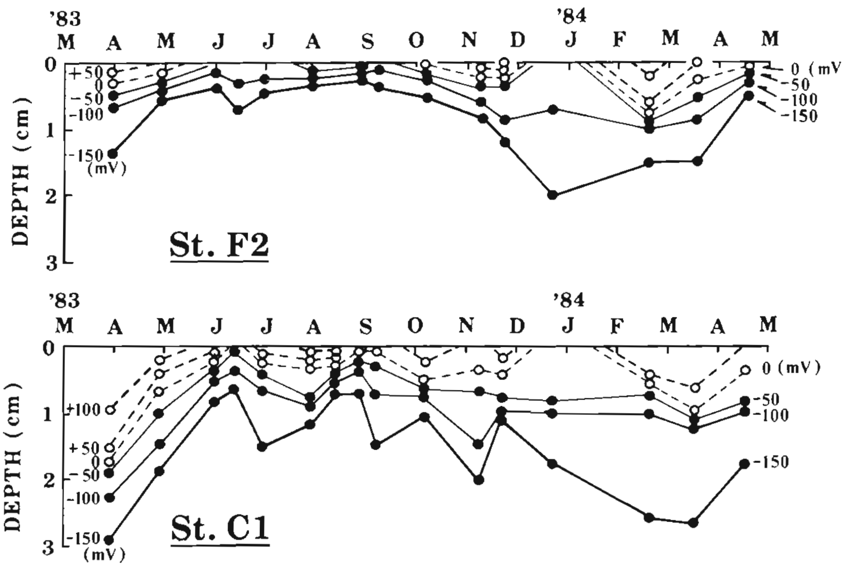

Fig. 7. Seasonal variations in vertical profiles of redox potential in the sediment at 2 routine-sampling stations (C1 and F2) on Lower Flat

sp. on Lower Flat was significantly correlated with the protein content of the sediment ($r = 0.604$, $p < 0.01$, F-test). Highest densities of over 40 000 ind. m^{-2} were recorded at 3 stations (D2, E2 and F3), where the sediment contained organic matter with a protein content of more than 0.38 %. By contrast, densities of less than 10 000 ind. m^{-2} were noted at stations where the sediment protein content ranged from 0.13 to 0.35 %. On Upper Flat, the sediment was sparsely covered by sea lettuce (Fig. 2), and the protein content of the sediment was less than 0.40 % at all stations except K3 (Fig. 3). Although *Capitella* sp. was found at 9 stations, densities were generally much lower than those on Lower Flat. Only at 2 stations, I3 and K3, were small patches with relatively high densities (about 23 000 ind. m^{-2}) observed.

Thus, the *Capitella* population was concentrated in organically enriched areas with luxuriant growth of sea lettuce on Lower Flat in early spring. However, reducing conditions developed in the organically enriched areas on the flat from late spring to summer (Figs. 4, 5 and 6). The size of the *Capitella* population declined dramatically after the development of reducing conditions in the sediment. At Stn F2, representative of the most organically enriched areas, a very dense patch of worms (ca 55 000 ind. m^{-2} in late April) had disappeared by mid-June, and no individuals were collected

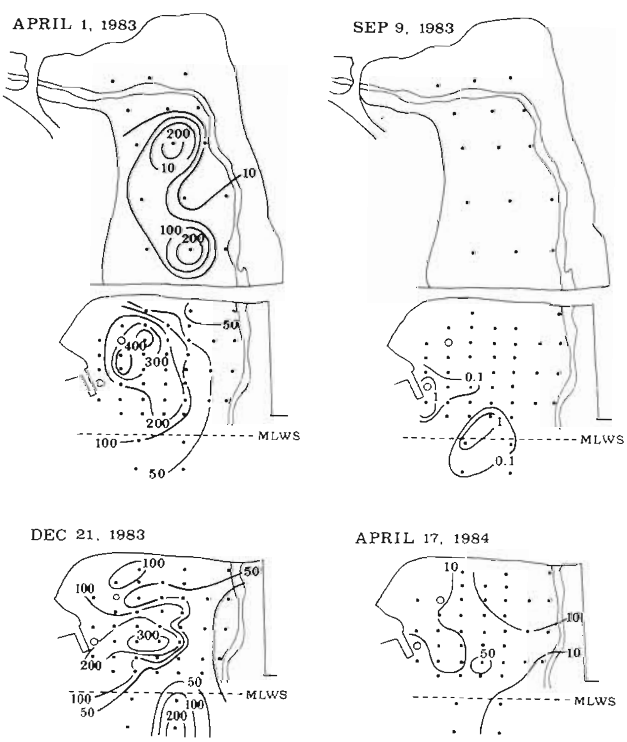

Fig. 8. *Capitella* sp. Seasonal variations in distribution (ind. 0.01 m^{-2}) on Shioiri Flat

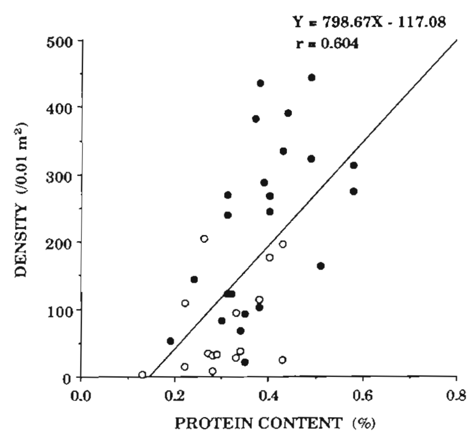

Fig. 9. *Capitella* sp. Relationship between protein content of the sediment surface layer (%) and density (ind. 0.01 m^{-2}) of worms on Lower Flat on 1 April 1983. (○) Stations at which no brooding females were collected

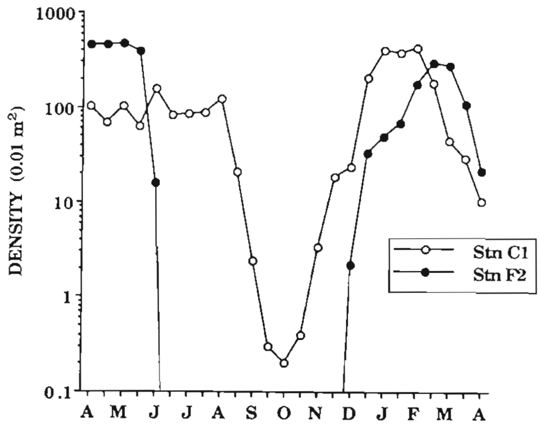

Fig. 10. *Capitella* sp. Seasonal fluctuations in density of distribution (0.01 m^{-2}) at 2 routine-sampling stations (C1 and F2) on Lower Flat

at this site from then until mid-November (Fig. 10). At this station, the black anaerobic layer with a high concentration of sulfides extended as far as the sediment surface from June to August (Figs. 6 and 7). *Capitella* sp., a subsurface deposit-feeding polychaete, burrows in the sediment. However, it does not stay in a fixed burrow. The worms are apt to expose themselves to the sediment without the creation of a microoxygenated area around them. Therefore, they are subject to the influence of the development of reducing conditions in the surface layer of the sediment during the summer. The total sulfide content of the surface layer of the sediment and the vertical profile of the sediment at Stn F2 indicated that barely any habitable space for *Capitella* sp. remained at this station during the summer.

In summer, the *Capitella* population on the flat was preserved as very small patches in restricted areas with transitional environments, adjacent to the most organically enriched where there was luxuriant growth of sea lettuce (Fig. 8). In September, *Capitella* sp. was found with remarkably low densities of less than 100 ind. m^{-2} at only 10 stations (including one of 2 routine sampling stations, C1) on Lower Flat. As represented by the chemical characteristics of the sediment at Stn C1 (Figs. 4 and 6), the surface layer of the sediment at these stations remained relatively oxidative, even in summer, due to the diminished organic enrichment by sparsely growing sea lettuce (sediment coverage was less than 30%). Thus, a small habitable space for *Capitella* sp. was preserved in the surface layer of the sediment at these stations.

These very small patches with extremely low densities of worms were maintained throughout the summer and autumn (Fig. 10), and they served as the seed population for the re-establishment of dense patches in the most organically enriched areas, with luxuriant growth of sea lettuce, on the flat in winter.

The process of recovery of the *Capitella* population on the flat was initiated in November. The remnant small patches on Lower Flat exhibited explosive population growth, as observed at Stn C1 (Fig. 10), and the distribution of the organisms expanded toward the neighboring, organically enriched areas with luxuriant growth of sea lettuce (Fig. 8). Dense patches, with densities of more than 20 000 ind. m^{-2}, were once again found on the flat within 3 mo of initiation of the recovery process of the population. However, the *Capitella* population rapidly declined again from late winter to the next spring, after the withering of sea lettuce on the flat (Fig. 2). The dense patch of *Capitella* sp. disappeared suddenly at the end of January at Stn C1 and at the end of February at Stn F2 (Fig. 10). Two different landscapes were evident on Lower Flat between spring 1983 and spring 1984. In 1983 the flat was thickly covered by a luxuriant growth of sea lettuce, and *Capitella* sp. was found at high density in the sediment. By contrast, in 1984, the flat was bare, and very few individuals of *Capitella* sp. were found on the flat.

Thus, the establishment of dense populations of *Capitella* sp. was restricted to the areas with organically enriched but relatively oxidative sediment. The population dynamics revealed the annual repetition of the establishment of dense patches, rapid decline, explosive increase, and re-establishment of the dense patches, apparently under the influence of the abundance of sea lettuce and the development of reducing conditions in the sediment on the flat. Although the *Capitella* population was extremely reduced in size in summer, it was self-sustaining within the flat, relying only on its extraordinary potential for rapid growth of the population.

Relationship between sediment protein content and population structure

The open circles in Fig. 9 indicate that the *Capitella* population included no brooding females. Such a population structure was observed in the low-density patches (fewer than 20 000 ind. m^{-2}) established at stations with sediment protein content below 0.42%. The data in Fig. 9 predict that the distribution of *Capitella* sp. on Lower Flat would be restricted to areas where the sediment contains organic matter with a protein content of more than 0.20%, and that habitats with conditions suitable for reproduction of *Capitella* sp. are further restricted to areas where the organic matter in the sediment contains more than 0.30 to 0.40% protein.

The composition by size of the *Capitella* population on 1 April 1983 was compared between 2 stations (F2 and D1) with different levels of organic matter in the

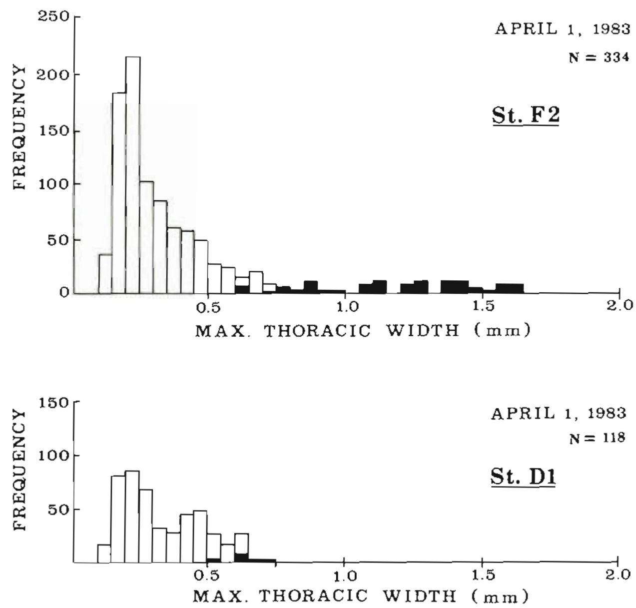

Fig. 11. *Capitella* sp. Size-frequency distributions at Stns F2 and D1 on Lower Flat on 1 April 1983. Filled bars: brooding females

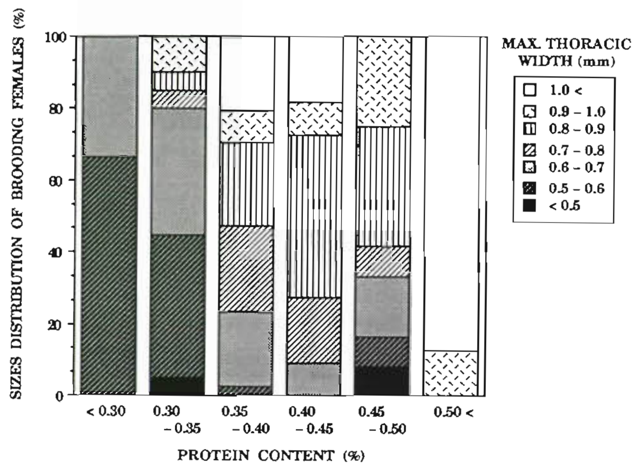

Fig. 12. *Capitella* sp. Relationship between protein content of the sediment surface layer (%) and distribution sizes of brooding females (%) on Lower Flat on 1 April 1983

sediment (protein contents of 0.581 % and 0.311 %, respectively) to examine how the level of protein in the sediment influences the population structure of this species (Fig. 11). Stn F2 was located in one of the most organically enriched areas, with luxuriant growth of sea lettuce (100 % coverage), and the *Capitella* population here consisted of dense patches of over 30 000 ind. m^{-2}. The width of the thoracic segments ranged from 0.10 to 1.65 mm, and the majority of mature individuals were larger than 1.0 mm in maximum thoracic width. At Stn D1, by contrast, the sediment was sparsely covered by sea lettuce (10 % coverage), and *Capitella* sp. occurred at rather low density (14 000 ind. m^{-2}). *Capitella* individuals had body sizes of below 0.75 mm in maximum thoracic width, and there were a small number of mature individuals with body sizes of 0.50 to 0.75 mm in maximum thoracic width. Since *Capitella* sp. usually becomes sexually mature after reaching more than 0.5 mm maximum thoracic width, it appears that these mature individuals possessed only the minimum, or slightly larger than minimum, body size prerequisite for reproduction.

The depression of growth following the decrease in levels of organic matter in the sediment was also clearly apparent in the size-composition pattern of brooding females along a gradient of organic enrichment of the sediment. Fig. 12 illustrates the size composition of brooding females collected at 38 stations, with various levels of organic matter in the sediment, on Lower Flat on 1 April 1983. Since *Capitella* sp. is semelparous, the body size of a brooding female represents the body size at reproduction. Brooding females collected at stations where the sediment contained organic matter of protein content less than 0.30 % had body sizes of less than 0.70 mm in maximum thoracic width, and this is the smallest size reported for reproductively competent *Capitella* sp. The proportion of these smallest females in the entire population of brooding females tended to decrease significantly at stations with higher levels of organic matter in the sediment. At stations where the sediment contained organic matter with a protein content of 0.35 to 0.50 %, fewer than 30 % of brooding females reproduced with the smallest competent body sizes. At stations with the most organically enriched sediment, with a protein content of more than 0.50 %, none of the brooding females reproduced with body sizes of less than 0.90 mm maximum thoracic width.

Thus, on the Shioiri Flat, body sizes at reproduction were influenced to a large extent by the level of organic matter in the sediment. These data indicate that *Capitella* sp. suffered from a depression of growth in areas with less organically enriched sediments, and that very few individuals of *Capitella* sp. could reach the minimum reproductively competent body size in sediment with a protein content of less than 0.30 %. *Capitella* sp. is, therefore, a polychaete that can establish a population only in organically enriched sediment, as a result of its requirement for sediment with rather high levels of organic matter content for its normal growth.

DISCUSSION

The reconstruction of a dense patch of *Capitella* sp. in the organically enriched areas was brought about by the explosive increase in size of tiny remnant patches, which were preserved in restricted areas with transitional environments, adjacent to the organically enriched areas. Such a process of recovery of the *Capitella* population was first suggested by a population study in a cove that was organically polluted by fish farming (Tsutsumi 1987). The present study has identified the seed populations for the recovery process and has revealed where they were maintained throughout the summer. Although the ability to disperse over a wide area has been emphasized with respect to the persistence of populations of *Capitella* species that occur in disturbed habitats (Grassle & Grassle 1974, McCall 1977), the results of the present study indicate that the persistence of a population of *Capitella* sp. was achieved within a single habitat without reliance on a supply of larvae from other habitats.

In previous benthic studies of the population dynamics of *Capitella* species that predominate in organically enriched areas, sampling sites were set up several hundred meters to several kilometers apart (Grassle & Grassle 1974, Pearson 1975, Rosenberg 1976, Tsutsumi & Kikuchi 1983), and population studies on *Capitella* species have even been carried out by analysis of data obtained at only one or a few sampling sites in the habitat (Warren 1976, Oyenekan 1983, Zhang & Wu 1986). Present results strongly suggest that very precise and detailed benthic samplings within a single habitat are required for the monitoring of the dramatic dynamics of changes in the size of populations of *Capitella* species. The opportunistic persistence of populations of *Capitella* species through widespread dispersal by planktonic larvae, as suggested in previous studies, seems to be an incorrect interpretation of the population dynamics of these species. Such an interpretation reflects the difficulties in finding the source populations that re-establish the dense populations using field surveys at a rather limited number of sampling stations.

The absence of *Capitella* species with opportunistic life histories in healthy areas has been ascribed to poor ability to compete against other infauna (Grassle & Grassle 1974, Kikuchi & Tanaka 1976, Pearson & Rosenberg 1976, 1978, Kikuchi 1979). These *Capitella* species showed a rapid increase in the size of populations in azoic areas in the absence of any competition, while their populations crashed during the subsequent faunal recovery process (Grassle & Grassle 1974, Rosenberg 1976, McCall 1977). The crash was, however, followed by a decrease in organic pollution (Grassle & Grassle 1974, Rosenberg 1976), and the sudden appearance or expansion of distribution of the *Capitella* species occurred with the progress of organic pollution (Pearson 1975, Tsutsumi & Kikuchi 1983). The present study indicates that *Capitella* sp. requires sediment with additional organic input, for example from the luxuriant growth of sea lettuce, if females are to grow to reproductive capacity (Figs. 9, 11 and 12). The concentration of the *Capitella* population in the organically enriched areas seemed to be ascribable to the physiological requirements of this species for sediment containing abundant organic matter, rather than to competitive exclusion by other infauna from healthy areas with less organically enriched sediment. It is very likely that future studies of the populations and physiology of the *Capitella* species that predominate in organically enriched areas will establish still more rigorously that the physiological requirement for organically enriched sediment for normal growth is the factor most responsible for the concentration of the *Capitella* species in organically enriched areas.

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