

Spatial and temporal patterns of polychaete communities in a subtropical mangrove swamp: influences of sediment and microhabitat

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ABSTRACT: Spatial and temporal patterns of polychaete communities in 2 intertidal flats were examined in a subtropical mangrove swamp, Tan-Shui estuary, Taiwan from 1991 to 1993. The 2 sites appear as distinct microhabitats, differing mainly in sediment granulometry, and consequently in community structure. The 'Creek' site was sandy (0.10 to 0.26 mm, 2 to 30% silt/clay content), while the 'River' site was muddy (0.06 to 0.14 mm, 16 to 60% silt/clay content). A total of 9 species were collected, with 6 species found at both sites. Indices of species diversity and evenness were greater at the Creek site than at the River site, but averaged density was 2 times lower (8317 vs 23325 ind. m⁻²). Dominance at the Creek site was shared by 2 to 3 species, whereas at the River site a single species, the sabellid *Laonome albicingillum*, was dominant. Population densities and physical parameters were closely correlated. *Malacoceros indicus* occurred with large particles, while *L. albicingillum* increased with small grains. Population densities at both sites varied seasonally, but the timing for increases in densities was 1 to 2 mo earlier at the River site. Effects of shading by mangrove trees at the Creek site were the likely causes of such subtle differences. Abundance in this swamp was greater than those in other tropical mangrove systems. The polychaete populations here may have experienced an environment which was not only nourished by sufficient detrital food, but was also less subject to fluctuation in terms of physical factors. *L. albicingillum* had high reproductive rates, similar to those of opportunistic species, but differed in its large size and in its life history traits.

KEY WORDS: Polychaetes · Subtropical mangrove swamp · Sediment

INTRODUCTION

Mangrove systems offer an extremely diverse array of benthic substrates for infauna, from soft mud, mud or sand mixed with mangrove-, river- and tide-derived detritus, to hard substrates, such as prop roots (e.g. Macnae 1968, Woodroffe 1985, Alongi 1989, 1990, Day et al. 1989). With such complexity, the sediment in mangrove systems is expected to harbor a high diversity of infaunal communities, as positive correlations between diversity of infauna and sediment grain size often occur in non-vegetated habitats (Whitlatch 1981, Etter & Grassle 1992).

Mangrove sediment is characterized not only by its habitat complexity, but also by its highly enriched

organic detritus (e.g. Macnae 1968, Alongi 1989, Day et al. 1989). In organically enriched, but non-vegetated, sediment in temperate regions, certain polychaete species or groups of species, called opportunistic species, are the most dominant component, often occurring in densities of 100 000s of ind. m⁻² (e.g. Grassle & Grassle 1974, Pearson & Rosenberg 1978, Levin 1984). Furthermore, based on sediment grain size alone, deposit feeders are dominant in mud substrates, while suspension feeders are dominant in sand (e.g. Sanders 1958, Rhoads & Young 1970). However, the patterns of relations in infauna sediment and infauna-trophism sediment have only been cursorily assessed in mangrove systems. Whether mangrove systems also possess certain distinct infauna assemblages and whether the sediment properties play decisive roles in determining the infaunal community structure, as in temperate systems, is largely unknown.

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Among available data from mangrove systems, Sasekumar (1974) found that the species composition of infauna, particularly molluscs and crabs, in a Malayan mangrove system resembled that of a Javan mangrove system, and proposed that mangrove infauna was similar throughout the Indo-Pacific region. Alongi (1989) generalized the patterns of infaunal species composition in which very few polychaetes were found in mangrove systems in the Indo-West Pacific region. However, in some localities in Southeast Asia, polychaetes may be abundant, with the most frequently encountered families being the Aphroditidae, Nereidae, Eunicidae, Capitellidae and Maldanidae (Alongi 1989). Reise (1991) also noticed that polychaetes in mangrove systems in Thailand and Malaysia were faunistically poor and their densities were much lower than those in temperate regions.

In northern Taiwan, the estuary of the Tan-Shui River is vegetated by the mangrove *Kandelia candel* (L.) Druce. This mangrove swamp is a riverine type and located within the tropical-subtropical climate zone (Wester & Lee 1992). A preliminary survey of the Tan-Shui mangrove swamp found that the infauna was dominated by polychaetes, with a large population of the sabellid *Laonome albicingillum* (Hsieh 1995) occurring at a density of about 19 000 ind. m⁻². Molluscs and oligochaetes were rare. These findings differ from the generalizations and patterns derived from temperate regions and from other tropical mangrove areas.

The purposes of the present study were to: (1) characterize the spatial and temporal patterns of sediment granulometry and polychaete community structure; (2) assess the relationships between sediment characteristics and community structure; (3) examine the heterogeneity of a mangrove swamp in terms of sediment granulometry and polychaete assemblages; and (4) verify the generalizations in abundance derived from the benthic infaunal communities found in temperate regions and other tropical mangrove habitats.

MATERIALS AND METHODS

Study area. The study area was located in the mangrove swamp (ca 60 ha) in the Tan-Shui estuary, Chu-Wei (25° 10' N, 121° 27' E), Taipei County, Taiwan (Fig. 1). Polychaete communities from 2 sites in the swamp were studied. One site, named the 'Creek' site, was an intertidal flat of a creek, entirely surrounded by mangrove trees. The other site, named the 'River' site, was an open, intertidal flat, with the main river channel on its west and mangrove trees on the east. The creek was quite shallow, less than 1.5 m deep, while

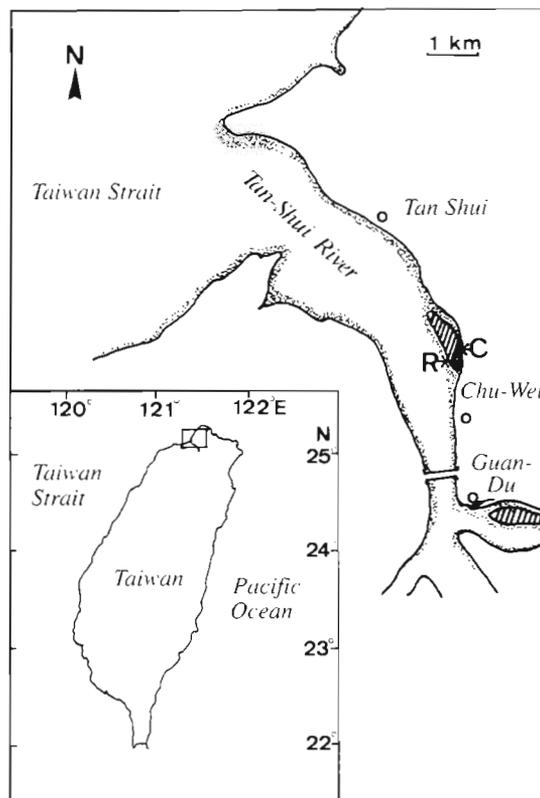


Fig. 1. Location of the Tan-Shui mangrove swamp in northern Taiwan. Hatched areas indicate mangrove forests. C: Creek site; R: River site

the river ranged from 2 to 10 m deep (Chang et al. 1987). The creek runs into the river in the northwest. The salinity of overlying waters ranged from 2 to 22‰ S.

Sampling in the field. Bimonthly samples were taken from September 1991 to September 1993. At each site, 3 transects, each separated by about 10 m, were set up arbitrarily, yet perpendicular to the river or the creek. At each transect, 2 infaunal cores were taken, 1 m above and 1 m below mean low tide level. The vertical distance between these 2 cores was less than 20 cm. Two smaller sediment cores were also taken immediately adjacent to the infaunal cores and were collected only from below mean low tide levels.

For the collection of infauna, PVC corers with an inner diameter of 8.2 cm were pushed about 30 cm deep into the sediment, after which the contained sediment was sieved through a 0.5 mm screen. Specimens retained on the screen were relaxed in 0.2% 2-phenoxyethanol and then fixed in 10% formalin. In the laboratory, polychaetes were sorted, counted and identified.

For the collection of sediment, PVC corers with an inner diameter of 2.6 cm were pushed 15 cm deep into the sediment. One of the 2 sediment samples collected

was fixed with 10% formalin and used for analysis of granulometry, while the other was refrigerated at 12°C and used for analysis of organic content. Temperatures of the sediment at a depth of 10 cm were recorded at ebb tide, when no water covered the sediment.

Measurement of environmental and biotic parameters. For granulometric analysis, sediment samples were wet-sieved through the Wentworth series of screens with mesh openings from 1.0 mm to 63 µm. Silt and clay content was measured using pipette methods (Buchanan & Kain 1971), with a slight modification by Hsieh & Chang (1991). Median grain sizes and sorting coefficient were calculated following Folk (1966). Organic content of the sediment was determined as the percentage of ash-free dry weight of sediment following Crisp (1971).

For each collection date, population density of each species at each site was expressed as the mean density of 6 cores, and density of the community at each site was the sum of population densities of each species. For all collections over the study period ($n = 12$), at each site, the grand mean density of each species was calculated as the mean of population densities of that particular species, whereas the grand mean densities of the community were the sums of grand mean densities of the constituent species.

Community structures at the 2 sites were characterized in terms of species richness, species diversity and evenness. Species richness was determined using direct counts of species numbers, and was expressed as the mean number of species per core. Direct count was chosen because samples of equal sizes were taken from both sites (Ludwig & Reynolds 1988). Species diversity and evenness were expressed using the Shannon index (H') and the Pielou index (J') (Pielou 1966), respectively. Similarity of communities between 2 sites was analyzed using a similarity index following Bray & Curtis (1957).

Statistics and analyses. Population densities of each species were compared between the 2 sites using the Wilcoxon 2 sample test (Sokal & Rohlf 1981). How the communities differed and which species contributed to such differences were determined using analysis of ordinations by Factor Analysis (Press 1972). The relationships between biotic and environmental parameters were determined using Canonical (Digby & Kempton 1987) and Spearman rank correlations (Sokal & Rohlf 1981). The population densities used in these multivariate analyses were taken only from the 3 infaunal cores collected below mean low tide levels, which were adjacent to where the sediment samples were taken (see above). Environmental parameters included median grain size, silt and clay content, sorting coefficient and organic content; the biotic parameters included population densities of each species

except *Manayunkia* sp. (see Table 1), and indices of species diversity and evenness. All statistical calculations were produced using SAS software (SAS Institute 1985) and a Sparc 10 computer.

RESULTS

Temperature of sediment

Temperatures of sediment at 10 cm depth at the Creek site ranged from 14.7 to 31°C, and from 16.2 to 31°C at the River site (Fig. 2). At both sites, the highest temperatures occurred in July, and the lowest occurred in January. Temperatures in winter were consistently lower at the Creek site than at the River site (Fig. 2).

Granulometry

The median particle sizes at the Creek site (0.10 to 0.26 mm in diameter) were larger than those at the River site (0.06 to 0.14 mm) (Fig. 3), indicating a fine sand and a mud to very fine sand environment, respectively. The silt and clay content of the sediment at the Creek site (about 2 to 30%) was lower than that at the River site (16 to 60%) (Fig. 3). The sorting coefficients of the sediment at both sites mostly fell within the range 0.85 to 1.65, indicating a moderately to poorly sorted sediment. The organic content of the sediment at both sites was similar, usually about 1.5 to 6%. A strong negative correlation occurred between the grain size and content of silt and clay (Spearman's $r = -0.94$, $p = 0.0001$).

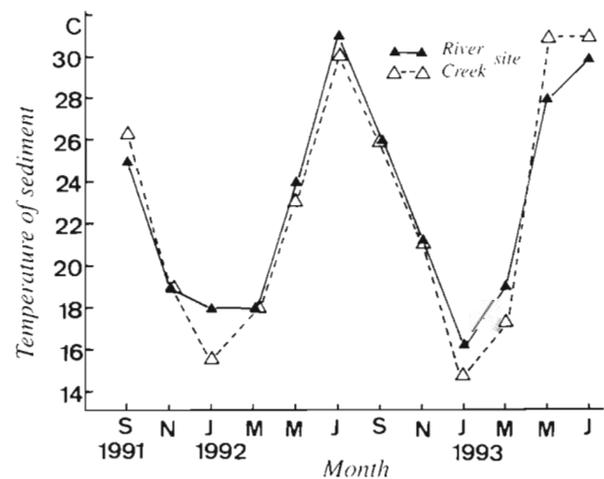


Fig. 2. Temporal changes of sediment temperatures (at 10 cm depth) at the Creek and River sites

Table 1. Comparisons of composition, density (ind. m^{-2}) and relative abundance (%) of each species at the Creek and River sites in the Tan-Shui mangrove swamp. ns: not significant, ** $p < 0.01$ (highly significant); -: absent; nd: test not done

Species	Creek site			River site			Wilcoxon test p
	Mean	SE	%	Mean	SE	%	
Capitellidae							
<i>Capitella</i> l sp.	3401.5	732.71	40.9	1001.1	331.01	4.3	0.0068 **
<i>Capitellides</i> sp.	466.5	161.22	5.6	212.3	62.91	0.9	0.1697 ns
Goniadidae							
<i>Goniada</i> cf. <i>emerita</i>	-	-	0.0	31.4	7.74	0.1	nd
Nereidae							
<i>Neanthes glandicincta</i>	914.6	226.85	11.0	904.1	226.27	3.9	0.8192 ns
Sabellidae							
<i>Laonome albicingillum</i>	639.4	82.05	7.7	19219.1	2048.42	82.4	0.0004 **
<i>Manayunkia</i> sp.	183.4	158.74	2.2	-	-	0.0	nd
Spionidae							
<i>Malacoceros indicus</i>	1933.9	172.87	23.2	340.7	125.48	1.5	0.0005 **
<i>Prionospio japonicus</i>	778.3	270.13	9.4	1331.2	785.39	5.7	0.5856 ns
<i>Polydora ligni</i>	-	-	0.0	285.6	241.81	1.2	nd
Grand mean density	8317.6	1124.24		23325.5	2408.31		0.0015 **

Species composition and abundance

A total of 5 families, 9 genera and 9 species were collected. Six species were found at both sites (Table 1).

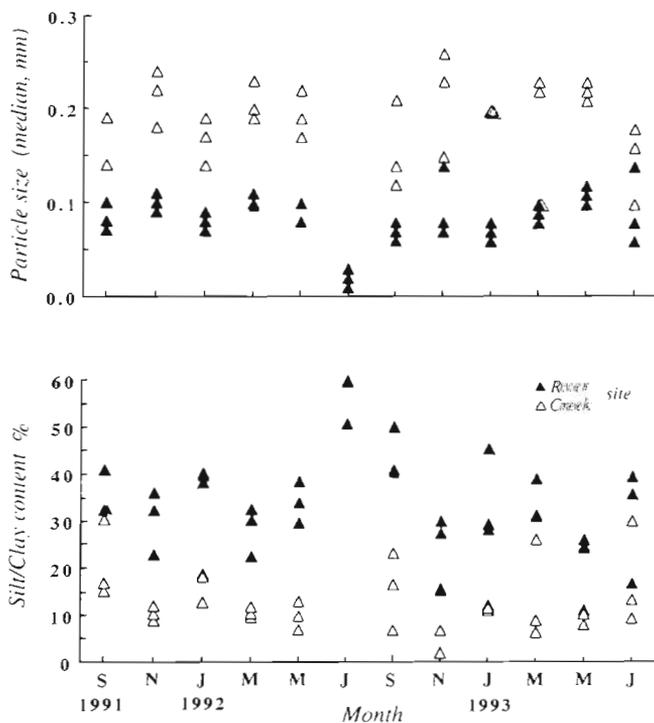


Fig. 3. Temporal changes of particle size (median diameter, mm) and silt and clay content (% dry weight) of the sediment at the Creek and River sites. Note that sorting coefficient and organic content are not shown

The grand mean density of the community was about 2.5 times lower at the Creek site than at the River site (8318 vs 23325 ind. m^{-2} ; Table 1, Fig. 4). There was no species at the Creek site with a density greater than 50% of total community abundance. In contrast, the most dominant species, *Laonome albicingillum* Hsieh, alone comprised 82.4% of total community abundance at the River site (Table 1).

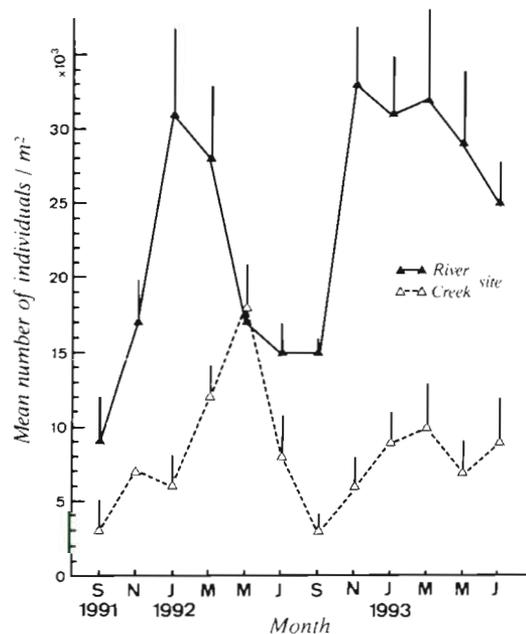


Fig. 4. Temporal changes in the density (mean + 1 SE, ind. m^{-2}) of the total polychaete community at the Creek and River sites

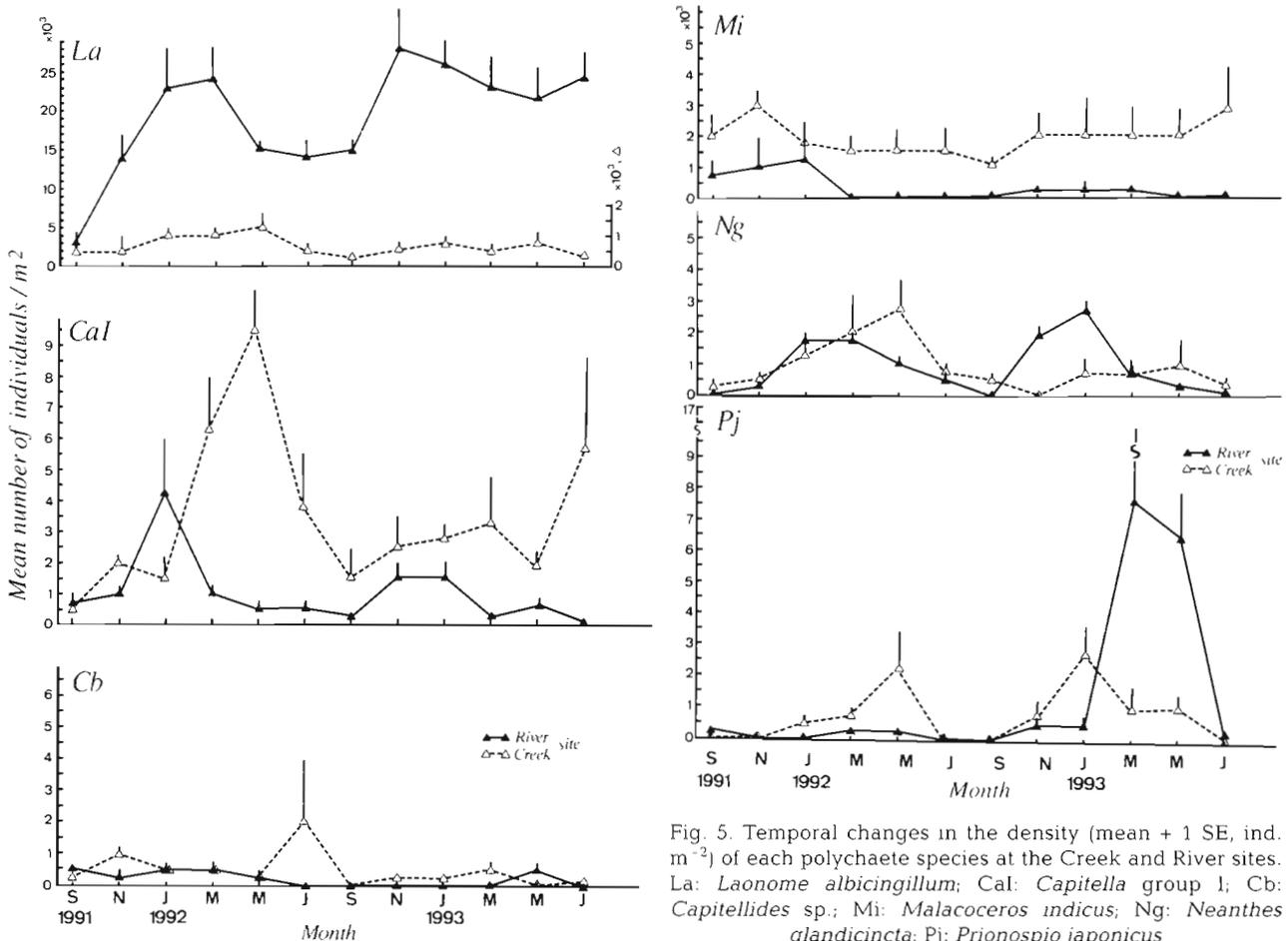


Fig. 5. Temporal changes in the density (mean + 1 SE, ind. m^{-2}) of each polychaete species at the Creek and River sites. La: *Laonome albicingillum*; Cal: *Capitella* group I; Cb: *Capitellides* sp.; Mi: *Malacoceros indicus*; Ng: *Neanthes glandicincta*; Pj: *Prionospio japonicus*

Among the 6 species shared by both sites, 2 species, *Malacoceros indicus* (Fauvel) and *Capitella* I sp., had significantly higher densities at the Creek site than at the River site (*M. indicus*: $p < 0.01$, 1934 vs 341 ind. m^{-2} ; *Capitella* I sp.: $p < 0.01$, 3401 vs 1001 ind. m^{-2} ; Table 1, Fig. 5). Three species, *Capitellides* sp., *Prionospio japonicus* Okuda and *Neanthes glandicincta* (Southern), had approximately equal abundances at the 2 sites ($p > 0.05$; Table 1, Fig. 5). Only 1 species, *Laonome albicingillum*, had significantly higher densities at the River site than at the Creek site ($p < 0.01$, 19219 vs 639 ind. m^{-2}) (Table 1, Fig. 5).

Community structure

The overall averaged species richness was 4.2 species $core^{-1}$ (range 2.5 to 5.8) at the Creek site and 3.9 species $core^{-1}$ (range 2.2 to 5.2) at the River site. Species richness did not significantly differ between sites ($p = 0.581$) except in September 1991 (River >

Creek site) and in May 1992 and March 1993 (Creek > River site) (Fig. 6).

Indices of species diversity at the Creek site ($H' = 1.03$ to 1.74) were greater than those at the River site ($H' = 0.13$ to 1.45) except in September 1991 (Fig. 6). Evenness (J') was also higher at the Creek site ($J' = 0.53$ to 0.89) than at the River site ($J' = 0.06$ to 0.70), except in September 1991 (Fig. 6).

These results show a stronger tendency of dominance at the River site. The distribution patterns of relative abundances among species illustrate how dominance differed between the 2 sites. At the Creek site, 70 to 80% of community abundance was shared over the study period by 2 or 3 species, most often by *Capitella* I, *Malacoceros indicus* or *Neanthes glandicincta*. The first 2 species held the top rank of dominance 11 times (out of a total 12 times), while the 3 species combined took the second rank 10 times. In contrast, at the River site *Laonome albicingillum* persistently held the top rank of dominance (12/12). In September 1991, the relative abundance of *L. albicingillum* decreased, and more species occurred at

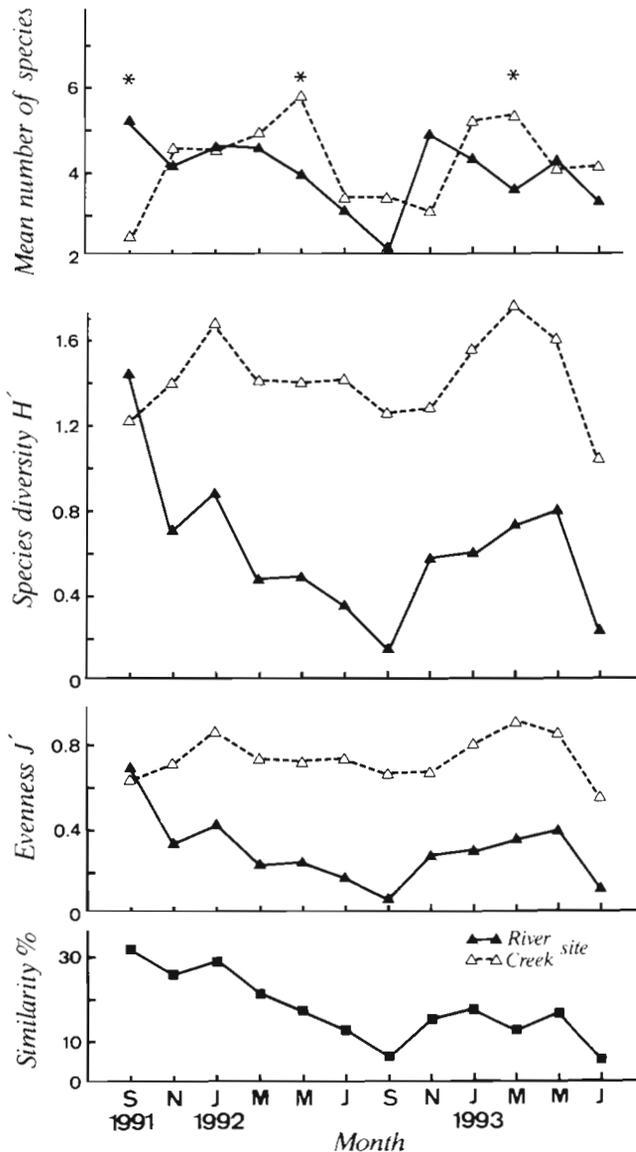


Fig. 6. Temporal changes of species richness (mean number of species per core), species diversity (H') and evenness (J') indices at the Creek and River sites and temporal changes in similarity (% similarity) between the 2 sites

the River site, resulting in a greater diversity and a more even distribution than at the Creek site (Fig. 6). The similarity of community structure between the 2 sites was low, with only 5.50 to 32.45% resemblance (Fig. 6).

Seasonality

Densities of the communities at both sites showed similar seasonal variations with high levels in winter to spring (January to May) and low levels in summer

(July to September) (Fig. 4). With respect to each species, similar trends occurred in *Laonome albicingillum*, *Capitella* I, *Malacoceros indicus*, *Neanthes glandicincta* and *Prionospio japonicus* (Fig. 5). The seasonal changes of densities were not exactly synchronous between sites, as the timing for density increases was often delayed 1 or 2 mo at the Creek site (Fig. 4). In particular, population densities of *L. albicingillum*, *Capitella* I, and *N. glandicincta* peaked from November to March at the River site, but from March to May at the Creek site (Fig. 5). For *M. indicus*, densities did not vary greatly among seasons other than being slightly lower in September 1992. For *P. japonicus* the seasonal changes of population densities at both sites were not consistent between years, but the general trend was still present (Fig. 5). The species richness, species diversity and evenness indices at both sites, along with similarity indices, showed similar seasonal changes with the lowest values occurring in the summer (Fig. 6).

Representative species of each community

Among the 9 species, relative importance in differentiating the 2 communities was demonstrated by Factor Analysis (Figs. 7 & 8). The first 2 principal factors together explained 43% of total variations of the abundances in the 2 communities pooled, while the first factor alone explained 26%. On axis factor 1, *Laonome albicingillum* and *Malacoceros indicus* were the most important elements, having high positive or negative correlation with the axis (factor loading = 0.76 and -0.64, respectively) (Fig. 7). On axis factor 2, *Neanthes glandicincta* and *Capitella* I were important with high positive correlations (factor loading = 0.68 and 0.60, respectively) (Fig. 7). When all samples were ordinated by axis factors 1 and 2 (Fig. 8), the 2 communities were well separated on axis factor 1, in which the community of the Creek site was characterized by the presence of a large population of *M. indicus*, whereas that of the River site was distinguished by a very abundant population of *L. albicingillum* (Figs. 7 & 8).

Relations of biotic and environmental parameters

In the overall relationships, particle size and silt/clay content had strong effects on community indices and population densities. Organic content and sorting coefficient were relatively unimportant (Table 2). Species diversity (H') and evenness (J') indices and the population densities of *Capitella* I, *Malacoceros indicus* and *Prionospio japonicus* increased when particle size

became larger and decreased when sediment contained more silt/clay (Table 2). The population densities of *Neanthes glandicincta* and *Laonome albicingillum* showed a reverse trend, decreasing with particle size but increasing with silt and clay content (Table 2). Only the population density of *Capitellides* sp. and *Goniada* cf. *emerita* were not correlated with any environmental parameters measured (Table 2).

The first 2 canonical correlations between 10 biotic and 4 environmental parameters were both significant (cumulative proportions = 0.71 and 0.88, respectively; $r_1 = 0.79$, approx. $F_{(40, 199)} = 3.32$, $p = 0.0001$; $r_2 = 0.49$, approx. $F_{(27, 155)} = 1.74$, $p = 0.0191$). In the first canonical variable, species diversity, evenness and population densities of *Malacoceros indicus*, *Capitella* I and *Capitellides* sp. were positively correlated with particle size, but negatively correlated with silt/clay content, organic content, sorting coefficient and density of *Laonome albicingillum* (Fig. 9). In the second canonical variable, the density of *L.*

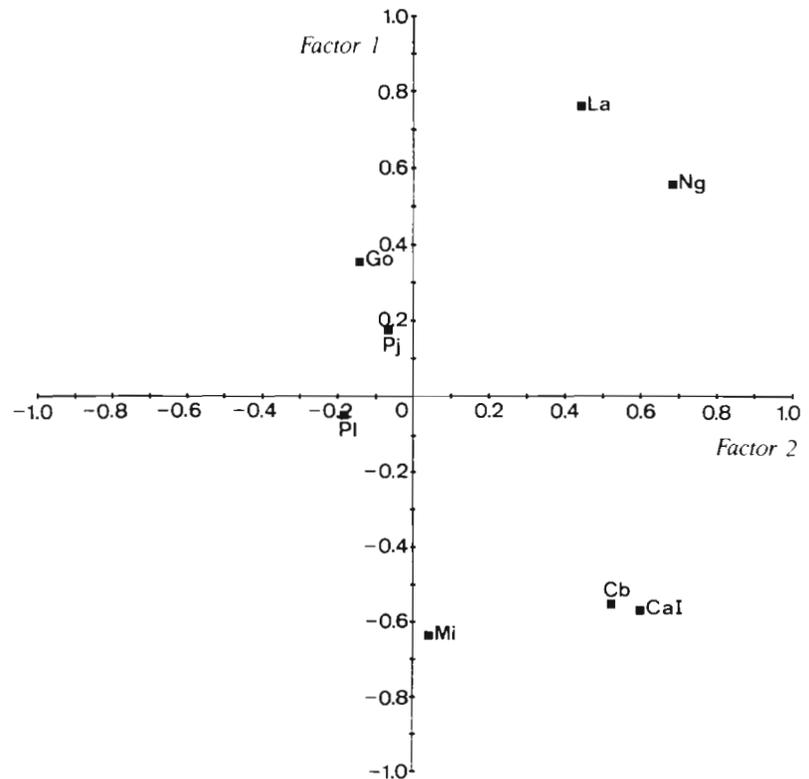


Fig. 7. Ordinations of polychaete species based on their population densities by the first 2 factor axes, Factors 1 and 2, using Factor Analysis. Pl: *Polydora ligni*; Ma: *Manayunkia* sp.; Go: *Goniada* cf. *emerita*; other species abbreviations as in Fig. 5

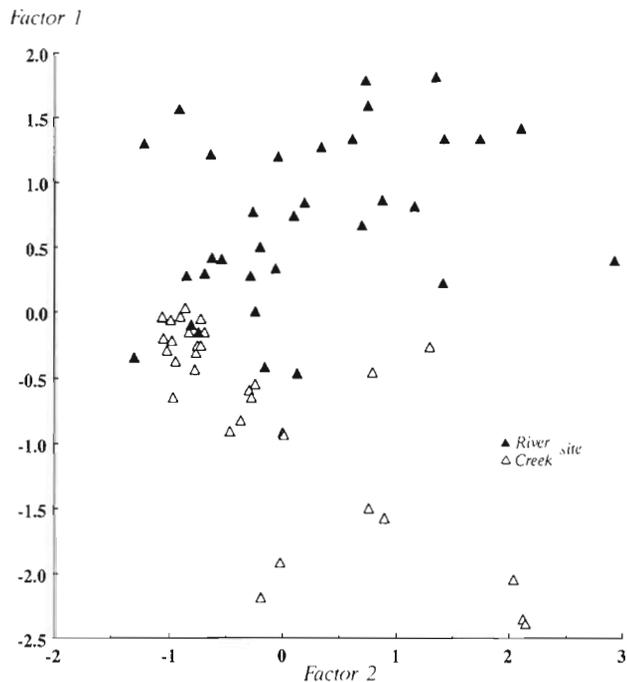


Fig. 8. Ordinations of the Creek and River polychaete community by the first 2 factor axes, Factors 1 and 2, using Factor Analysis

albicingillum and *N. glandicincta* were positively correlated with sorting coefficient but negatively correlated with organic content (Fig. 9). The spatial and temporal patterns of the polychaete communities in relations to environmental parameters are summarized in Table 3.

DISCUSSION

The importance of granulometry

The spatial distribution of infaunal assemblages constrained by sediment granulometry has been well documented from non-vegetated areas in temperate regions, where sand and mud infauna are separated (e.g. Sanders 1958, Rhoads & Young 1970). Similarly, in tropical reef lagoons, crustacean faunas are distinguished as fine sand and coarser sand communities (Jones 1984). The present study also clearly demonstrates that in this subtropical mangrove swamp in Taiwan, the infaunal communities are separated on the basis of the sediment grain size and silt and clay content, recognizing a spatial distribution pattern in which the community of the Creek site is associated

with fine sand and less silt/clay content, and that of the River site is closely related to mud, with much more silt and clay (see Figs. 3, 7 to 9). Within distances of only about 600 m in the swamp, in various and distinguishable intertidal flats, the sediment environment in the Tan-Shui mangrove system is quite heterogeneous, agreeing with similarly diverse array found in benthic substrates of many other mangrove swamps (e.g. Macnae 1968, Alongi 1989).

Relationships between feeding assemblage and sediment

In the Tan-Shui swamp, the deposit feeders, such as the spionids, the capitellids and the nereids (Fauchald & Jumars 1979), predominantly inhabit the fine sand environment (0.10 to 0.26 mm, Creek site), while the suspension feeders, such as the sabellids, dwell in the mud substrate (0.06 to 0.14 mm, River site). These patterns do not correlate with those found in non-vegetated areas, where an opposite trend has been found (Sanders

Table 2. Spearman's correlations between biotic and environmental parameters in Tan-Shui mangrove swamp. *Manayunkia* sp. was not included due to absence from the samples. +: positive correlation; -: negative correlation; ns: no significant correlation; * $p < 0.01$, ** $p < 0.001$

Biotic parameters	Environmental parameters			
	Particle size	Silt/clay content	Sorting coefficient	Organic content
Community index				
Shannon H'	+**	-**	ns	ns
Evenness J'	+**	-**	ns	ns
Population density				
<i>Capitella</i> I sp.	+**	-**	ns	-**
<i>Capitellides</i> sp.	ns	ns	ns	ns
<i>Goniada</i> cf. <i>emerita</i>	ns	ns	ns	ns
<i>Neanthes glandicincta</i>	-**	+*	ns	ns
<i>Laonome albicingillum</i>	-**	+**	ns	ns
<i>Malacoceros indicus</i>	+**	-**	ns	ns
<i>Prionospio japonicus</i>	+*	-*	ns	ns
<i>Polydora ligni</i>	ns	ns	-*	+*

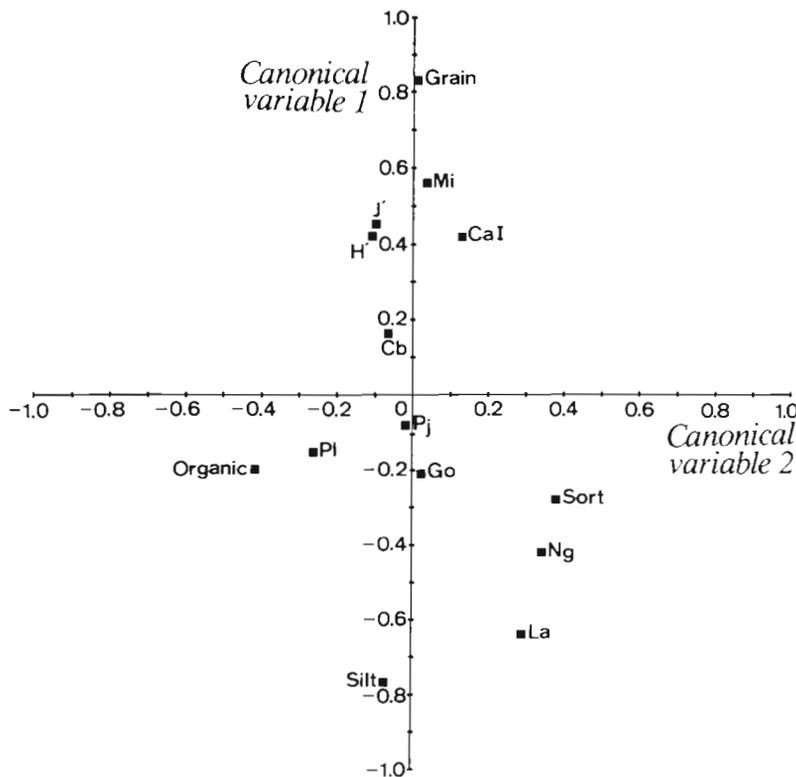


Fig. 9. Ordinations and relationships among biotic and environmental parameters by the first 2 canonical variables using Canonical Correlation Analysis. Grain: median particle size; Silt: silt/clay content; Organic: organic content; Sort: sorting coefficient; H' : species diversity; J' : evenness; species abbreviations as in Fig. 7

1958, Rhoads & Young 1970). Thus, from the aspect of feeding modes, sediment particle sizes alone do not fully explain the establishment of populations at either site. For particle feeding, the feeding processes depend on the dynamics of bottom fluid, particulate motions, food supply rate and interactions among infauna, trophisms and sediment (Rhoads 1970, Rhoads & Young 1970, Jumars & Nowell 1984).

A sandy environment suggests a faster flow regime. In addition, grains ca 0.1 to 0.4 mm in size are considered to be transported or eroded more easily than smaller grains (Sanders 1958, Rhoads 1970). Fast flow and easy transportation and erosion may prevail at the Creek site, and consequently increase the chance of bedload transportation and mixing, thus favoring deposit feeding. As for the River site, the muddy sediment there suggests a slower current, resulting in the settling of materials. In addition, runoff and tides continuously occur along the river bank, bringing in large quantities of materials, but broader tidal fluctuations may cause these materials to be resuspended. Settling, continuous supply and resuspension of the materials benefit suspension feeding. Furthermore, the mud substrate at the River site is slippery and firm (pers. obs.), and transport of particles <0.1 mm is

difficult along such a consolidated surface (see above), thus diminishing the abundance of the deposit feeders. It is also possible that the suspension feeders effectively take out materials from the water column, resulting in insufficient food for the deposit feeders (Rhoads & Young 1970).

Seasonality

Seasonality of abundances occurs in the Tan-Shui mangrove swamp, reaching a high in winter and spring and falling to a low in summer. Population densities decrease dramatically in summer at both sites, probably due to high mortality caused by high temperatures in summer (e.g. Hsieh & Simon 1991a, b).

The exact time when the population densities increase or decrease varies between the 2 microhabitats by 1 or 2 mo (see Figs. 4 & 5). A subtle difference in winter temperatures between the 2 sites was detected. Temperatures from November to March were 0.5 to 2.5°C lower at the Creek site than at the River site (see Fig. 2). Both sites are intertidal flats and are not directly under the canopies of the mangroves. However, the River site is more open, as only the east side is adjacent to the mangroves, whereas the Creek site is

entirely surrounded by mangroves. That mangrove canopies provide a cool, stable and humid environment for macrofauna communities was noticed in a Malayan mangrove swamp (Sasekumar 1974). Thus, shading makes the Creek site cooler, especially in winter. It is likely that the increase in abundance at the Creek site slows down in the winter due to lower temperatures, which suppress reproductive success (e.g. Hsieh and Simon 1991a, b), whereas temperatures are higher at the River site.

Comparisons of species composition and abundance with other habitats

The species composition of polychaetes in the mangrove systems has not been extensively studied in southeast Asia, the Indo-West Pacific or northern Australia. Since species composition varies widely among habitats and zones (e.g. Alongi 1989), comparisons of species richness between the Tan-Shui mangrove system and other similar habitats cannot be done until more data are available.

The abundance of polychaete community in the present study area is greater (average >5000 ind. m^{-2}) than those recorded in other mangrove systems in southeast Asia and the Indo-West Pacific (average <500 ind. m^{-2}) (Sasekumar 1974, Wells 1983, Alongi 1989). Although detailed studies are needed to analyze why population densities are greater in the Tan-Shui mangrove system, some of the main causes can be attributed to the quality of the habitat, particularly with regard to climate, temperature regime, status of heavy metals and activities of microbial decomposition. In mangrove systems in southeast Asia and northern Australia, habitats are subject to climatological disturbances, resulting in extreme fluctuations in salinity, erosion of sediment or excessive heat (Sasekumar 1974, Wells 1983, Alongi 1989, 1990, Reise 1991). Comparatively, variations in temperature (15 to 32°C), salinity (2 to 22‰ S) and granulometric characteristics (e.g. particle sizes do not change seasonally; see Fig. 3) in the Tan-Shui mangrove swamp are smaller (Chou & Bi 1990, Anon 1991, this study). In regard to the status and impact of heavy metals, Chiu & Chou (1991) found that a large proportion were fixed to organic mat-

Table 3. Summary of the characteristics of granulometry, winter temperatures and polychaete community at the Creek and River sites of the Tan-Shui mangrove swamp

Characteristics	Creek site	River site
Granulometry		
Particle size	Large (0.10–0.26 mm)	Small (0.06–0.14 mm)
Silt/clay content	Low (2–30%)	High (16–60%)
Winter temperature	Low (0.5–2.5°C lower)	High
Community structure		
Species diversity H'	High	Low
Evenness J'	High	Low
Species composition	7 species (6 species in common)	8 species
Abundance of community	Low (2× lower)	High
Relative distribution of abundance among species	Even	Uneven
Tendency of dominance	Weak	Strong
Persistency of dominance	Low, by 2–3 species	High, by 1 species
Timing for abundance increase	Spring	Winter
Representative species in each community	<i>Malacoceros indicus</i>	<i>Laonome albicingillum</i>

ter which was found in large quantities in the mangrove system. These fixed forms are refractory and stable, and therefore are not toxic to the organisms (Chiu & Chou 1991). Moreover, the clean-up of waste materials from the Tan-Shui mangrove swamp system is evident by the presence of various and abundant microbial communities. Wu (1993) found that these microorganisms produced various enzymes, which could break down accumulated detritus. The microorganisms also facilitated floc formation by precipitating polypeptides and cellulose, resulting in a clean environment (Wu 1993). The polychaete populations can maintain high densities in the Tan-shui mangrove system, not only because they are nourished by sufficient organic detritus generated in the mangrove swamp or carried into the estuary by river or tides, but also because they live in a clean and healthy habitat which does not experience severe fluctuations or heavy metal poisoning.

In comparison with the abundances of individual species in other organically enriched habitats, only *Laonome albicingillum* has a density comparable to those of opportunistic species, such as the *Capitella* group and *Streblospio benedicti*, found in temperate regions (Grassle & Grassle 1974, Pearson & Rosenberg 1978, Levin 1984). *L. albicingillum* has some reproductive characteristics similar to those of the opportunistic species. *L. albicingillum* is a simultaneous hermaphrodite, has a long reproductive season (approximately from fall to early summer of the following year), can self fertilize, has a rapid development rate (i.e. less than 33 h from fertilized eggs to settlement), and has a low dispersal ability (Hsieh 1995, unpubl. data). These characteristics contribute to increasing the reproductive rate (e.g. Grassle & Grassle 1974, Levin 1984, 1986). However, *L. albicingillum* differs from the opportunistic species in its large size (adults are 3 to 5 cm long) and its lack of brood protection (Hsieh 1995). Larger size indicates longer generation time and late maturation; lack of brood protection indicates high mortality in early development stages. These latter constraints contribute to lowering the reproductive rate (Stearns & Crandall 1984). Reproductive rate is an intrinsic control of reproductive capability, that, in turn, contributes to the success of *L. albicingillum* in the mangrove swamp.

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