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PATTERNS OF POLYCHAETE COMMUNITIES IN TROPICAL SEDIMENTARY HABITATS: A CASE STUDY IN SOUTH-WESTERN THAILAND

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ABSTRACT. **–** Few studies have compared macrofaunal assemblages (organisms retained on a 0.5 mm sieve) between different tropical sedimentary habitats. The present study aims to address this issue, investigating vegetated (seagrass), non-vegetated organic mud and exposed beach habitats. Polychaetes were the dominant taxonomic group at all sampling sites, followed by crustaceans and molluscs. Thirty-six polychaete families were recorded, 31% of which were present in all three habitats. All families were represented in non-vegetated habitats. Polychaete family and functional group assemblages did not differ greatly between vegetated and non-vegetated habitats despite varying densities. Differences in polychaete assemblage structure were most pronounced between exposed beach and non-vegetated habitats. Polychaete assemblages were also negatively affected by the onset of the wet monsoon season. Overall, macrofaunal density (29 - 2,629 ind. m^{-2}) fell within the range of that reported by other authors in the region. Small-scale physical and environmental factors are thought to be responsible for the large variation in polychaete assemblage structure within habitats. Identification of polychaetes to species, together with further analysis of small-scale physical data should provide a deeper understanding of the spatial and temporal changes reported in this study. A call is made for the standardisation of future sampling efforts and techniques to allow meaningful comparisons amongst sedimentary habitats across large spatial scales.

KEY WORDS. **–** seagrass, polychaete, macrofaunal density, inter-habitat.

INTRODUCTION

Tropical sedimentary habitats, though visually simple, are diverse and complex. They comprise a variety of substrata: from non-vegetated soft mud, sand and coarse shingle, to algal mats, seagrass beds and mangrove swamps, all sustained by varying supplies of terrestrial- and marine-derived detritus. They may also be extremely dynamic (Alongi, 1990; Dittmann, 2000; Hall, 1994; Reise, 2002). Many studies (e.g., Ellingsen & Gray, 2002; Kendall & Widdicombe, 1999; Zajac et al., 1998) have shown how environmental factors, such as vegetation, sedimentary characteristics and organic enrichment, affect benthic biodiversity at local scales. However, to address the growing interest in broad-scale patterns of biodiversity (Gray, 2002; Kendall et al., 2003), assessment needs explicitly-structured, comparably-collected data sets, which are largely lacking in the tropics.

The benthic biota of the Andaman Sea coast of Thailand is poorly known in comparison with inshore benthic habitats in Europe or North America but it has recently been the subject of a number of scientific studies: Dexter (1996), Hylleberg & Nateewathana (1983; 1991a; 1991b), Meksumpun & Meksumpun (1999), Nateewathana (1988), and Petersen & Curtis (1980). Despite this body of work, there is still a lack of data sets comparable with those from higher latitudes. The present study builds on earlier work in the region and provides the much-needed, purpose-collected data, which will enable small and broad-scale comparisons of benthic biodiversity.

To address all the issues concerning broad-scale patterns for the fauna of the Andaman Sea is a substantial undertaking, but a first approximation can be achieved by bringing together existing data with information collected during a series of studies undertaken from Ranong Coastal Resource Research Station. In this paper we will: (i) investigate the effects of vegetation/habitat on polychaete assemblages in the region, (ii) identify the extent of seasonal variability in polychaete abundance, and (iii) compare our data to those reported in similar habitats throughout the tropics and beyond. This is the first comparative study of benthos from different sedimentary habitats to be carried out in Thailand.

MATERIALS AND METHODS

Site selection. – Collections have been made from an approximately 50 km long stretch of the Andaman coast of southwestern Thailand (Fig. 1) as part of a three-year baseline biodiversity survey. The shoreline is characterised by mangrove forests, small estuaries with patchy seagrass beds and long sandy beaches. Poorly developed fringing reefs are also present around islands and rocky outcrops (Chansang & Poovachiranon, 1994). Eleven sites were sampled between March 2000 and November 2001 and selected to represent three major sedimentary habitat types observed in the area: non-vegetated organic-rich mud, vegetated (seagrass) sediments, and exposed sandy beaches (Table 1). Distinctions between these three habitats were made on visual and physical criteria.

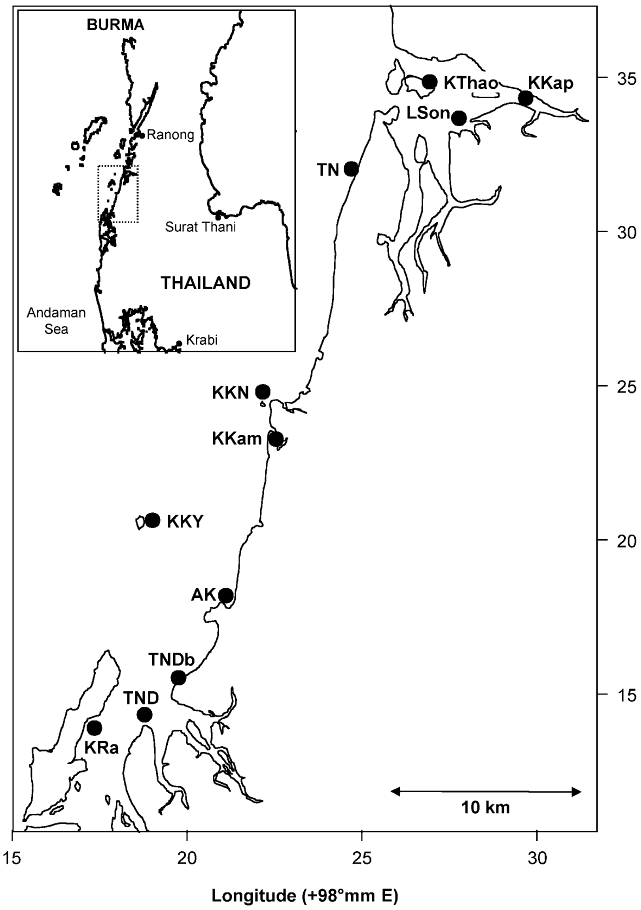

Fig. 1. Map of study area showing the location of each sampling site. Site abbreviations: AK = Ao Khoei, KKam = Khlong Kamphuan, KKap = Khlong Kapoe, KKY = Ko Kai Yai, KKN = Ko Kam Nui, KRa = Ko Ra, KThao = Ko Thao, LSon = Laem Son, TN = Thale Nok, TND = Thung Nang Dam, TNDb = Thung Nang Dam beach.

Environmental regime of the study area. – There are two seasons: the southwest monsoon season prevails between May and October, and the northeast monsoon between November and April. The southwest monsoon is characterised by heavy rainfall and strong onshore winds, which create continual moderate to high wave action. In contrast, during the northeast monsoon season, or dry season, this stretch of coastline experiences no significant rain, limited wind and a reduced intensity, frequency and height of waves. The semidiurnal tidal amplitude ranges from 1.1 to 3.2 m with a mean of about 2.2 m (Chansang & Poovachiranon, 1994). Five sites (of the 11) covering the three types of habitat were sampled during both the southwest (wet) monsoon and the northeast (dry) monsoon (Table 1).

Quantitative sampling. – Sampling was carried out on exposed flats nearest the water's edge at 11 selected locations during low tide using a 30 cm diameter (area: 0.07 m^2) plastic tube corer, inserted to a maximum depth of 40 cm. Adjacent surface samples were taken for sediment granulometric analysis. Granulometry samples were dried, sieved on a stack of graded sieves ranging from 63 μm to 2000 μm mesh, and the residue on each weighed (Buchanan & Kain, 1971). Faunal samples were washed through a 500 μm gauge sieve. All sieving residue was fixed in 8 % formalin and later transferred to 70 % alcohol before sorting under a dissection microscope and identification of macrofauna. All animals were identified to the lowest practical taxonomic level. Thailand has a rich polychaete fauna (Kendall et al., 2000), much of which cannot presently be fully identified as many species remain undescribed. The lack of taxonomic information inhibits full species by species comparison of all available data. Until more, fully comparable species information becomes available, initial investigation of patterns of polychaete distribution will be carried out at family level. Functional implications of patterns in faunal abundance were examined by an analysis of feeding category, in which food preference, motility pattern and feeding structure morphology are considered, as developed for polychaete families by Fauchald & Jumars (1979).

Analytical procedures. – Differences in the density of polychaetes between habitats and sampling seasons were examined using the non-parametric Mann-Whitney (U) test. Spatial patterns in the distribution of the polychaete population sampled were analysed using the PRIMER software package (Clarke & Warwick, 1997). To detect possible differences in polychaete assemblage composition (i.e., in the number and identity of families with or without the influence of their relative abundance) between habitats, multivariate analyses were carried out on untransformed and transformed family abundance data. Bray-Curtis index and group average linkage were used for cluster analysis and non-

Table 1. Physical information and sampling regime pertaining to each site sampled. Shaded months are those falling in the comparatively dryer northeast monsoon.

	Position				Number of samples taken						
					2000			2001			
Site	Latitude (N)	Longitude (E)	Habitat	% Sand	Mar	Sep	Nov	Mar	Apr	May	Nov
AK	9.178	98.227	EB	72		15			3		
KKam	9.229	98.239	NV	-		4		5		1	
KKap	9.346	98.296	SG$^{Ho, Hb}$	-			2				
KKN	9.241	98.238	EB	-						3	
KKY	9.201	98.195	NV	67				10			
KRa	9.157	98.185	NV	51		3					12
KThao	9.577	98.491	NV	-							6
LSon	9.556	98.496	SG^{Hb}	-							6
TN	9.276	98.259	EB	90		6					
TND	9.135	98.201	SG$^{Ho, Cr}$	52	5						12
TNDb	9.135	98.201	NV	62				2		1	

Site abbreviations as in Fig. 1. Habitat abbreviations: EB = Exposed Beach; NV = Non-vegetated sediment; SG = Seagrass. % Sand refers to the combined proportion of sediment retained on 250 µm and 125 µm mesh-size sieves; no values appear where granulometry data has been lost. Ho = *Halophila ovalis*, Hb = *Halophila beccarii*, Cr = *Cymodocea rotundata*.

metric multidimensional scaling (MDS) ordination. One-way ANOSIM (analysis of similarities) was carried out to test differences found in polychaete communities between habitats, and families typifying each habitat were identified using the SIMPER (similarity percentages) programme.

RESULTS

Granulometry analysis of the study sites indicated little differentiation in particle size ratios between seagrass, non-vegetated and exposed beach habitats, all falling within the 'muddy gravelly sand' category defined in the Habitat Identification Manual for Ranong (Kendall et al., in prep.).

Macrofauna. **–** A total of 6,774 macrofaunal individuals were collected in 96 cores at all 11 sites (Appendix). Polychaete worms were numerically dominant, accounting for over 75% of the total macrofauna sampled. Crustacea and Mollusca followed, together constituting around 14% of all macrofauna. Mean density of macrofaunal organisms core^{-1} was (± SE) 68.4 ± 17.1 (n = 91). There was a high degree of variability in mean macrofaunal density between sites, ranging from 2.0 ± 0.0 individuals core^{-1} (n = 3) at Ko Kam Nui (KKN) to 184.0 ± 35.0 individuals core^{-1} (n = 6) at Laem Son (LSon). Macrofauna were present at a higher density (Fig. 2) in seagrass (1,614 ± 571 m^{-2}) and in non-vegetated habitats (1,127 ± 211 m^{-2}) than in exposed beach habitats (90 ± 44 m^{-2}) (Mann-Whitney test: $z > P_{0.01}$). Differences in mean macrofaunal density values between non-vegetated and seagrass habitats were not significant. The polychaete component of the macrofauna mirrored these relationships (Fig. 2).

Polychaeta. **–** A total of 5,260 individuals belonging to 36 families were collected (Table 2). Numerically, families Capitellidae, Paraonidae, Nereididae, Spionidae, Goniadidae and Orbiniidae dominated in that order. Together they constituted over 64% of the individuals. Most other families were less common, with approximately one quarter of the total number of families encountered being represented by less than 10 individuals. Orbiniidae was the most widespread family, present at all 11 sites sampled, followed by the Capitellidae, Spionidae, Lumbrineridae, which were present at 10 of the 11 sites. Cossuridae, Dorvilleidae, Onuphidae and Pholoidae were present only at non-vegetated sites, which, as a habitat, contained all 36 families encountered. Non-vegetated sites harboured a greater number of rare families than did seagrass sites. Seagrass sites contained 30 families whilst exposed beach sites had only 12 families, none exclusive to any habitat. Eleven families (31% of the total) were found in all three habitats. Overall, there is a general increase in the number of families sampled with the number

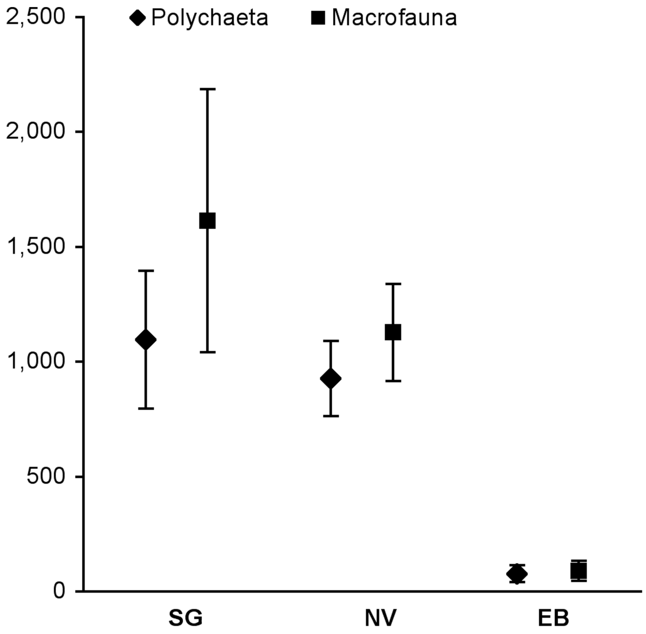

Fig. 2. Mean density (± SE) for polychaetes and macrofauna at each sampled habitat. EB = Exposed Beach, NV = Non-vegetated sediment, SG = Seagrass.

of replicate cores taken (Fig. 3) but the numbers of families appear to be highest at Ko Khai Yai (KKY) (n = 10) and Ko Ra (KRa) (n = 15) than at other sites. There is not, however, a significant trend of increasing polychaete density with an increase in the number of replicate cores taken, suggesting that the area sampled during the present study is not faunistically under-represented. The difference in polychaete density between monsoon seasons, though variable from habitat to habitat, is significant (Mann-Whitney test: $z >> P_{0.01}$), being higher in the dry season than in the wet monsoon season when the whole area under investigation is considered (Fig. 4). This trend was reversed in seagrass habitats.

The functional composition of the polychaete fauna of the study area has been examined in terms of: (i) the most abundant families within each habitat (i.e., those contributing cumulatively > 40% of individuals in their habitat), (ii) the families accounting for 95% of all individuals within each habitat, and (iii) the total number of families present in each habitat (Table 3). When only the most abundant families are examined (group (i)), all feeding categories except filter feeders were equally represented. When groups (ii) and (iii) are considered, carnivores were the most represented feeding category, followed by surface and sub-surface deposit feeders, in that order. Differences in the abundance of each feeding category between seagrass and non-vegetated habitats were not significant (Table 3). Significant differences in the relative abundance of the different feeding categories were detected between exposed beach and the other two habitats for all but the herbivore and filter feeding polychaete families.

Analysis of community structure. – Polychaetes, the most abundant and well-characterised component of sampled macrofauna, have been used exclusively in the following interhabitat comparisons. Tests for differences in polychaete community structure – performed using multivariate analysis on untransformed data, thus taking into account relative family abundance – indicated an overall lack of dissimilarity between habitats (ANOSIM result global R statistic: 0.292, P = 0.05), i.e., there were no distinct polychaete family assemblages in any habitat. Pairwise comparisons between habitats were equally indistinct. Only with severe transformation of the data, i.e., by only assigning families presence/absence (+/-) values, thus eliminating the effect of relative abundance and relying on similarities in polychaete family diversity, did any significant difference appear (Table 4), yet only between non-vegetated and exposed beach habitats (ANOSIM result for pairwise EB-NV +/- comparison R statistic: 0.764, P < 0.02). No differences in polychaete family diversity were found between non-vegetated and vegetated habitats. The relationships here highlighted are illustrated with the MDS plots in Figs. 5a and 5b, where resolution between vegetated and non-vegetated habitats is lacking, even when exposed beach habitats are omitted from the analysis.

This pattern of overall similarity amongst habitats yet weak differences in pairwise comparisons between exposed beach and non-vegetated habitats is also reflected when using polychaete feeding group abundance figures (Table 4). The relative contribution of families and feeding categories typifying each habitat was identified using SIMPER analysis (Table 5). The variation in proportion of sub-surface deposit feeders to carnivores was responsible for the differentiation between the two most dissimilar habitats.

DISCUSSION

Ecological comparisons. – In-depth analysis of community structure and function has revealed subtle patterns of variation between the habitats under investigation.

Previous studies (e.g., Turner & Kendall, 1999; Somaschini et al., 1994; Edgar et al., 1994; Ansari et al., 1991; Sheridan, 1997) have all – using slightly differing methodology and analyses – reported a greater diversity and abundance of infauna in vegetated than in adjacent non-vegetated areas. Most attribute this difference quantitatively to habitat modification by emergent seagrass plants altering local biological, chemical and/or physical conditions, which in turn

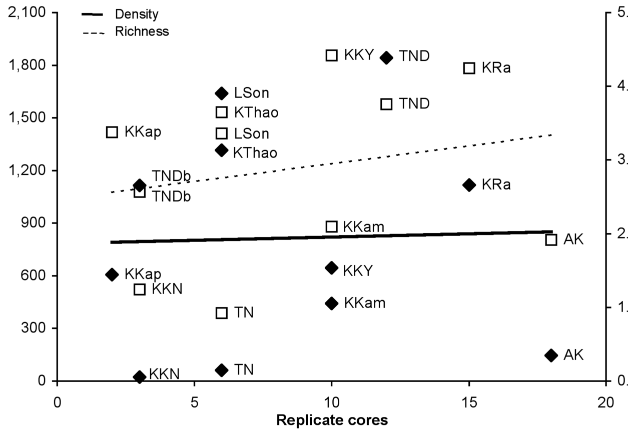

Fig. 3. Relationships between family richness (Margalef's d = (S-1)/Log(N)) (☐), density (◆) and sample replicates at the 11 sites sampled. Site abbreviations as in Fig. 1.

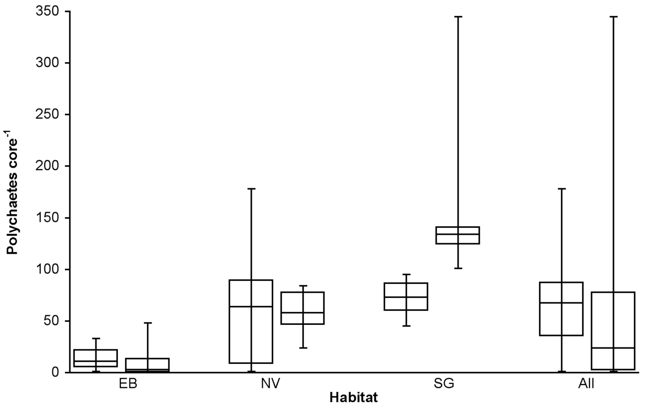

Fig. 4. Box and whisker plot of seasonal variation at each habitat and for all habitats considered together. Left-hand side boxes represent dry season sampling; right-hand side boxes represent wet season sampling. Habitat abbreviations as in Fig. 2.

Table 2. Total numbers of individuals belonging to major macrobenthic taxa at each habitat sampled on the north-western coast of southern Thailand. Polychaete families are followed by a three-letter feeding category code.

		Habitat			
		SG	NV	EB	Σ
Replicate cores (n)		20 (25)	44	27	91 (96)
Polychaeta		1,646 (2,323)	2,721	216	4,583 (5,260)
Ampharetidae	sst	69	22	0	91
Amphinomidae	cmx	83	55	0	138
Capitellidae	bmx	305	460	32	797
Chaetopteridae	fsp	1	1	0	2
Chrysopetalidae	cmx	9	5	0	14
Cirratulidae	smt	40	152	1	193
Cossuridae	bmx	0	8	0	8
Dorvilleidae	smj	0	2	0	2
Eunicidae	cmj	14	17	0	31
Flabelligeridae	sdt	4	1	0	5
Glyceridae	cdj	43	60	18	121
Goniadidae	cdj	218	124	0	342
Hesionidae	hmj	6	2	0	8
Lumbrineridae	cmj	49	113	8	170
Magelonidae	sdt	16	52	0	68
Maldanidae	bsx	65	35	0	100
Nephtyidae	cmj	52	60	0	112
Nereididae	cmj	293	379	2	674
Oenonidae	cmj	2	1	0	3
Onuphidae	cmj	0	6	0	6
Opheliidae	bmx	9	21	2	32
Orbiniidae	bmx	169	104	32	305
Oweniidae	sdt	91	69	0	160
Paraonidae	hmx	163	440	91	694
Pholoidae	cmj	0	3	0	3
Phyllodocidae	cmx	12	26	1	39
Pilargidae	cmj	33	108	0	141
Poecilochaetidae	sdt	6	11	0	17
Polynoidae	cmj	8	3	0	11
Sabellidae	fst	62	11	0	73
Spionidae	sdt	333	236	25	594
Sternapsidae	bmx	13	44	0	57
Syllidae	cmj	131	68	1	200
Terebellidae	sst	3	9	0	12
Trichobranchidae	sst	21	2	0	23
Unknown		0	11	3	14
Crustacea		347	302	27	676
Mollusca		326	51	6	383
Sipuncula		148	93	0	241
Echinodermata		20	10	4	34
Other taxa		37	141	2	180
Total		2,524 (3,201)	3,318	255	6,097 (6,774)
Polychaety density (m^{-2})		1,327	883	114	783
Macrofauna density (m^{-2})		1,803	1,077	135	957

Feeding category three-letter code: first letter (major food) – b = sub-surface deposit feeder, c = carnivore, f = filter feeder, h = herbivore, s = surface deposit feeder; second letter (motility) – d = discreetly motile, m = motile, s = sessile; third letter (feeding structure) – j = jaws, p = pump, t = tentacles, x = other, such as eversible pharynges (Fauchald & Jumars, 1979). 'Other taxa' include Enteropneusta, Anthozoa, Turbellaria, Cephalochordata, small vertebrates and insect larvae. Numbers in parentheses indicate the addition of five replicate samples for which there are only polychaete data; numbers outside parentheses have been used for macrofaunal density calculations. Habitat abbreviations as in Table 1.

Table 3. Distribution of families by feeding category and habitat, related to the number of families examined. Habitat and feeding category abbreviations as in Tables 1 & 2, respectively.

		Most abundant families			95% of families			All families		
Feeding category		SG	EB	NV	SG	EB	NV	SG	EB	NV
Sub-surface deposit feeders	bmx	1	0	1	2	2	3	4	3	5
	bsx	0	0	0	1	0	1	1	0	1
Carnivores	cdj	0	0	0	2	1	2	2	1	2
	cmj	1	0	1	5	1	5	8	3	10
	cmx	0	0	0	1	0	2	3	1	3
Filter feeders	fsp	0	0	0	0	0	0	1	0	1
	fst	0	0	0	1	0	0	1	0	1
Herbivores	hmj	0	0	0	0	0	0	1	0	1
	hmx	0	1	1	1	1	1	1	1	1
Surface deposit feeders	sdt	1	0	0	2	1	3	5	1	5
	smj	0	0	0	0	0	0	0	0	1
	smt	0	0	0	1	0	1	1	1	1
	sst	0	0	0	1	0	0	3	0	3
All categories		3	1	3	17	6	18	31	11	35

Interhabitat comparison of the numbers of families within each polychaete feeding category.

	SG-NV	NV-EB	EB-SG
Sub-surface deposit feeders	n.s.	*	*
Carnivores	n.s.	*	*
Filter feeders	n.s.	n.s.	n.s.
Herbivores	n.s.	n.s.	n.s.
Surface deposit feeders	n.s.	*	*

Most abundant families are those contributing cumulatively > 40 % of individuals within their habitat. Lord's Range test used where n < 5 (i.e. for Filter feeders and Herbivores). Asterisk (*) indicates a significant difference (z or L ≥ $P_{(0.01)}$), n.s. = not significant.

Table 4. PRIMER output summary for ANOSIM tests carried out on presence/absence transformed polychaete family data and feeding category abundance at each habitat. Habitat abbreviations as in Table 1.

	Family (+/-)		Feeding category	
	R statistic	Sig. level (%)	R statistic	Sig. level (%)
Global	0.405	1.8	0.304	3.3
Pairwise comparisons				
EB-NV	0.764	1.8	0.631	1.8
EB-SG	0.556	10.0	0.259	30.0
NV-SG	-0.041	57.1	0.067	37.5

Table 5. Polychaete families and feeding categories typifying each habitat resulting from SIMPER analysis ranked in decreasing order of their importance to the similarity within their habitat. Figures alongside each entry indicate total % contribution. Only families cumulatively contributing c. 50 % to the similarity are listed. Habitat abbreviations as in Table 1.

SG		NV		EB	
Family	Feeding cat.	Family	Feeding cat.	Family	Feeding cat.
Spionidae 19.6	carnivore 46.9	Capitellidae 30.2	carnivore 40.1	Orbiniidae 74.1	ss-deposit 71.0
Capitellidae 19.2	ss-deposit 24.0	Paraonidae 15.2	ss-deposit 33.6		carnivore 17.0
Nereididae 11.0	s-deposit 24.0	Spionidae 9.9	s-deposit 15.8		s-deposit 11.0
	herbivore 2.1		herbivore 10.0		
	filter 1.0		filter 0.5		

enhance deposition of material in suspension (e.g., fine sediments, detritus, plankton and invertebrate larvae) with concomitant effects on the structure of benthic communities (Eckman, 1983). Differences in macrofaunal density between seagrass and non-vegetated habitats in the present study may not be supported statistically, yet the sheer variability of macrofaunal density figures between cores at seagrass sites reflects the increased heterogeneity and complexity of this habitat when compared with non-vegetated habitats. It is this high degree of variation in macrofaunal density within and across sites vegetated with differing seagrass species yet belonging to the same habitat that has likely reduced the level of significance of the difference between habitats. Data transformation and allocation of polychaete families into functional groups reduced variability and revealed stronger and slightly significant relationships between habitats.

Habitat complexity is compounded from quantitative (the variety in types of substrata) and qualitative (the amount of above-ground substratum) elements. Qualitative complexity can be contributed in the form of different plant architectures, food sources, or habitat topography and attachment sites. In the present study it was found that at small spatial scales (< 1 m), neither seagrass nor non-vegetated sites were faunistically or topographically homogeneous, both being greatly influenced by intensive small-scale bioturbation (e.g., by burrowing sipunculans, crabs and shrimp), thus augmenting within-habitat physical variability. The negative R statistic resulting from the ANOSIM analysis between these habitats (Table 4) is indicative of greater variation between samples within a habitat than between habitats (Chapman & Underwood, 1999), thus supporting this observation. It has been assumed that at small scales there is a relationship between faunal similarity and the separation of any pair of samples but there is no basis for such an assumption (Kendall & Widdicombe, 1999). Macrofauna were found not to be randomly distributed within a habitat but were reflecting this small-scale spatial patchiness. Identification of polychaetes to a lower taxonomic level and subsequent analysis may alter the significance of this relationship and work is presently underway to investigate this.

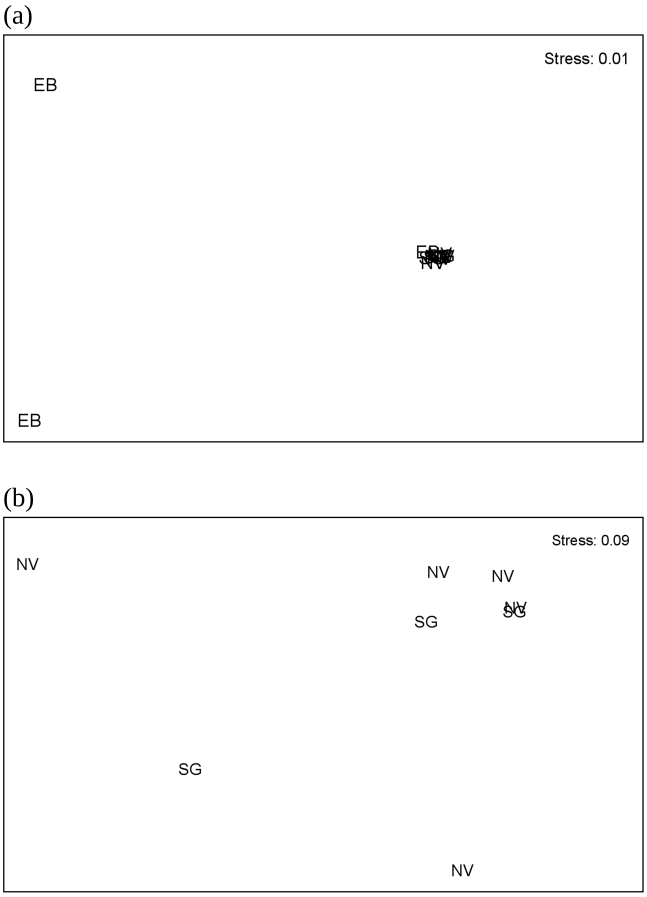

Fig. 5. Multivariate analysis output using presence/absence transformed polychaete data: (a) MDS plot showing all sites arranged by habitat, (b) MDS plot excluding Exposed Beach habitat. Habitat abbreviations as in Fig. 2.

Several authors report negative effects of monsoon rain on intertidal benthic fauna (see review by Alongi, 1990), listing increased levels of sediment disturbance by stronger wave action as the major responsible factor. This study does not contradict these findings as regards changes in overall polychaete density between seasons. However, variation of response to changes in season between habitats is, at best, erratic (Fig. 4). Vegetated sites, contrary to expectation, had a higher abundance of macrofauna during the wet monsoon. This may be due to seagrass fronds buffering most of the potentially damaging wave action and simultaneously trapping more of the increased suspended particulate matter present in the water column. Since all granulometry values fell within the same sediment category regardless of habitat or time of sampling, further investigation is needed before any process affecting this particular seasonal change can be identified.

Sheridan (1997) related benthic macrofaunal abundance to community function by allocating taxa into feeding groups. He found that the total faunal community in southwest Florida's intertidal substrates did not show major differences in feeding group composition between relatively stable sedimentary habitats (mangrove, seagrass and non-vegetated) despite these habitats differing in species composition. Similarly, in the present study, no great differences were observed between seagrass and non-vegetated habitats. Carnivores were most abundant in both these habitats, followed in turn by sub-surface and surface deposit feeders (Table 5). This pattern of distribution of trophic categories points to an established community with an evolved food chain reflecting a relatively stable environment in these habitats. Exposed sandy beach habitats, on the other hand, had an exclusive and overwhelming dominance of pioneering and opportunistic motile sub-surface deposit feeders (Table 5), thus reflecting a more dynamic, less stable environment, refractory to the settlement of a diverse and mature community. Interestingly, in the present study only non-vegetated habitats had a significant proportion (> 10%) of rare and herbivorous families. This could reduce the relative importance of vegetation as a stabilising influence of benthic macro-infaunal communities, as well as strengthening the relative value of non-vegetated habitats against vegetated habitats when considering their importance in coastal zone management and conservation. Conservation bodies targeting

Table 6. Comparison of intertidal macrofaunal (as retained on a 500 µm sieve) density from different locations.

Location	Density (ind. m^{-2})	Reference
Tropical		
Coleroon Estuary, Bay of Bengal	50 - 2,500	Patterson Edward & Ayyakkannu (1992)
Thale Sap Songkhla, Gulf of Thailand	374 - 2,420	Angsupanich & Kuwabara (1995; 1999)
Mlonggo Bay, Java	463 - 1,069	Warwick & Ruswahyuni (1987)
Bowling Green Bay, Australia	113 - 3,898	Dittmann (2000)
Crooked Harbour, Hong Kong	3,200 - 40,700	Lee et al. (2001)
Ala Wai canal, Hawaii	4,910 - 47,430	McCarthy et al. (2000)
Jaltepeque Estuary, El Salvador	259 - 23,852	Lara & Zamora (1994)
Temperate		
Isles of Scilly, UK	7,194 - 26,706	Bowden et al. (2001)
Cellars Beach, UK	16,616 - 71,141	Turner & Kendall (1999)
Yealm Estuary, UK	1,911 - 12,229	Webster et al. (1998)

non-vegetated habitats containing greater numbers of rare families may ensure a bigger representation and protection of infaunal diversity. As the most extensive habitat around the coast in the region, efforts to conserve small parts of it may not encounter as much opposition as other, more contentious and productive vegetated habitats.

Geographical comparisons. – Aungtonya et al. (2002) list a total of 37 polychaete families known to occur in Thai waters. Representatives of eight of those families (Acoetidae, Eulepethidae, Pectinariidae, Pisionidae, Sabellariidae, Serpulidae, Sigalionidae and Trochochaetidae) have not been encountered in the present study; however, it has generated five additional families to those already collected. These are Cossuridae, Oenonidae, Paraonidae, Pholoidae and Phyllodocidae. It would thus appear that no fewer than 42 polychaete families have been recorded in Thai waters, 78% of the total of 54 families reported to occur in and around the South China Sea (Paxton & Chou, 2000).

Total macrofaunal density for the study area (29 - 2,629 ind. m^{-2}) was within the broad limits of macrofaunal density found elsewhere in the Indo-Pacific region (Table 6). However, much higher and more variable densities have been found in other tropical settings, as well as in the temperate coastal waters of Europe (e.g., Junoy & Vieitez, 1992; Reise et al., 1994; Turner & Kendall, 1999), southern Africa (e.g., Allanson et al., 2000; Bursey & Wooldridge, 2002) and North America (e.g., Mattila et al., 1999). Differing definitions of faunal size categories prevent meaningful comparisons between all authors and locations; however, works referred to in Table 6 are comparable with the present study and give an indication of the density of polychaetes at their respective locations. Values obtained in this study fall within the ranges recorded by authors quoted in Table 6, yet most closely resemble figures presented by Angsupanich & Kuwabara (1995): 630 - 1,121 ind. m^{-2}, and Angsupanich & Kuwabara (1999): 120 - 575 ind. m^{-2} in Thai waters.

Reise (1991) reports a trend of decreasing macrofaunal density with decreasing latitude and supports his findings with a brief literature survey supporting his conclusions. Tropical studies from which he quotes low macrofaunal densities are, however, limited to mangrove swamps, thus omitting other varied and highly variable tropical intertidal habitats. Moreover, Sheridan (1997) reports total macrofaunal densities to be highest in mangrove peat (22,591 - 52,914 ind. m^{-2}) when compared with seagrass (6,347 - 23,545 ind. m^{-2}) and mudflat (3,611 - 22,465 ind. m^{-2}) sites. All of these tropical data are broadly similar to those reported for temperate sites for fauna retained on a 0.5 mm gauge sieve (Table 6). Since sampling and sample-processing techniques are so variable amongst researchers, temporal variation in faunal abundance so volatile, and habitat heterogeneity so pronounced at different locations over small spatial scales, extrapolation of macrofaunal density from individuals $core^{-1}$ to individuals m^{-2} can be misleading. A more standardised approach to benthic sampling across the scientific community is required before any generalisation can be made about an area under study. Only when fully representative and comparably collected data sets are available can meaningful relationships between areas be sought.

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Appendix. Total macrofauna sampled during March 2000 – November 2001 in 96 cores over 11 sites.

	AK	KKam	KKap	KKY	KKN	KRa	KThao	LSon	TN	TND	TNDb	Σ
Polychaeta												
Capitellidae	28	194	13	36	0	143	38	79	4	213	49	797
Cossuridae	0	0	0	0	0	0	8	0	0	0	0	8
Opheliidae	2	0	0	10	0	9	2	1	0	8	0	32
Orbiniidae	15	12	2	18	3	49	5	14	14	153	20	305
Sternapsidae	0	0	13	0	0	40	4	0	0	0	0	57
Maldanidae	0	3	3	15	0	8	1	26	0	36	8	100
Glyceridae	17	0	1	6	1	33	21	34	0	8	0	121
Goniadidae	0	6	11	2	0	86	6	9	0	198	24	342
Eunicidae	0	0	0	2	0	7	0	1	0	13	8	31
Lumbrineridae	7	5	1	61	1	27	12	1	0	47	8	170
Nephtyidae	0	2	0	7	0	50	1	0	0	52	0	112
Nereididae	2	6	7	16	0	29	326	239	0	47	2	674
Oenonidae	0	0	0	0	0	1	0	1	0	1	0	3
Onuphidae	0	0	0	5	0	0	0	0	0	0	1	6
Pholoidae	0	0	0	0	0	3	0	0	0	0	0	3
Pilargidae	0	57	0	2	0	40	9	24	0	9	0	141
Polynoidae	0	0	0	2	0	1	0	2	0	6	0	11
Syllidae	1	0	0	32	0	18	1	55	0	76	17	200
Amphinomidae	0	0	0	1	0	26	28	26	0	57	0	138
Chrysopetalidae	0	0	1	5	0	0	0	7	0	1	0	14
Phyllodocidae	0	4	0	3	0	14	5	4	1	8	0	39
Chaetopteridae	0	0	0	0	0	1	0	0	0	1	0	2
Sabellidae	0	0	0	5	0	1	2	0	0	62	3	73
Hesionidae	0	0	3	0	0	2	0	0	0	3	0	8
Paraonidae	91	2	4	70	0	285	23	27	0	132	60	694
Flabelligeridae	0	0	0	1	0	0	0	0	0	4	0	5
Magelonidae	0	2	10	34	0	12	4	0	0	6	0	68
Oweniidae	0	0	5	34	0	7	11	7	0	79	17	160
Poecilochaetidae	0	0	2	1	0	8	2	4	0	0	0	17
Spionidae	18	14	5	57	0	131	26	116	7	212	8	594
Dorvilleidae	0	0	0	2	0	0	0	0	0	0	0	2
Cirratulidae	1	0	4	20	0	120	8	6	0	30	4	193
Ampharetidae	0	2	0	0	0	11	6	6	0	63	3	91
Terebellidae	0	0	0	2	0	3	2	0	0	3	2	12
Trichobranchidae	0	0	0	0	0	2	0	0	0	21	0	23
Unknown	3	0	0	2	0	7	2	0	0	0	0	14
Crustacea	27	13	1	42	0	185	35	75	0	271	27	676
Mollusca	5	0	0	9	1	16	22	295	0	31	4	383
Sipuncula	0	3	0	3	0	37	37	23	0	125	13	241
Echinodermata	4	0	1	2	0	6	1	6	0	13	1	34
Other taxa	0	5	2	50	0	60	14	10	2	25	12	180
Σ	221	330	89	557	6	1,478	656	1,104	28	1,337	291	6,774

Macrofaunal data for TND are only available for 12 replicate cores. ‘Other taxa’ include Enteropneusta, Anthozoa, Turbellaria, Cephalochordata, small vertebrates and insect larvae. Site abbreviations as in Fig. 1.