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Spatial Variation of Intertidal Macrofauna on a Sandy Ocean Beach in Australia

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Spatial variation of macrofauna on a sandy beach was examined simultaneously over two scales across-shore (among and within zones) and three nested scales along-shore over the entire length of the beach. Prior to the main study, pilot studies were performed to determine: (1) the relative efficiency, accuracy and precision of combinations of core size, depth of sampling, and sieve mesh size; and (2) the likely distribution of macrofauna across-shore so that stratification of sampling in the main study would be meaningful. From this, three zones were defined across-shore, namely: (1) the high-shore zone which extended 10 m downshore of the drift line and was dominated by two species of isopod; (2) the mid-shore zone which extended across the beach from the bottom of the high-shore zone to the top of the swash zone and was dominated by the glycerid polychaete *Hemipodus* sp.; and (3) the swash zone which contained more species than the other two zones and was dominated by amphipods, *Hemipodus* sp., the bivalve *Donax deltoides* and a species of cumacean. In the main study, multivariate analyses confirmed that assemblages of macrofauna varied significantly among zones despite smaller scale variation within zones and along-shore variation. Significant along-shore variation was detected in assemblages of macrofauna from each zone and occurred at different scales for different zones. Only assemblages in the swash zone showed a pattern of along-shore variation that was consistent with a gradient in wave exposure along the beach. Univariate analyses showed that significant variation in populations of individual taxa occurred at both large and small scales. Significant variation was detected across-shore within zones for nearly all variates and this demonstrated the importance of formally assessing variation *within* zones when making comparisons *among* zones. Significant variation was also detected along-shore in analyses of particular taxa, and interactions of across- and along-shore variation also occurred. These results illustrate the necessity of considering both across- and along-shore variation for describing spatial patterns in assemblages or individual species of macrofauna. Unfortunately, sampling a single transect across a beach, which is common in many published descriptions of spatial patterns, will not provide an adequate nor representative description of the macrofauna of that beach because this approach fails to consider all important sources of variation and confounds large- and small-scale variation. The authors conclude that a better understanding of small-scale variation, both

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along- and across-shore within beaches, is required in order to provide better descriptions of patterns, provide a basis for larger scale studies, allow unconfounded comparisons among beaches and, ultimately, to improve our understanding of the ecology of sandy beaches.

Introduction

The ecology of macrofauna (defined as invertebrates retained on 0·5 mm or coarser meshs) on sandy beaches has been examined in many countries including Chile (Jaramillo & McLachlan, 1993; Jaramillo *et al.*, 1993), India (Trevallion *et al.*, 1970; Ansell *et al.*, 1972; McLusky *et al.*, 1975), North America (e.g. Leber, 1982; Larsen & Doggett, 1990; McLachlan, 1990), South Africa (e.g. McLachlan, 1977; Dye *et al.*, 1981; McLachlan *et al.*, 1981; Wooldridge *et al.*, 1981), Uruguay (e.g. Defeo *et al.*, 1992) and the U.K. (e.g. Allen & Moore, 1987; Rafaelli *et al.*, 1991; Bamber, 1993). The ecology of macrofauna on sandy beaches in Australia, however, has received little attention (Robertson, 1994). For example, in New South Wales (NSW) where sandy beaches make up 65% of the length of the coast, most ecological work on intertidal marine organisms has been done on rocky shores (Fairweather, 1990). Published work on sandy beach macrofauna in Australia is limited to that of Dexter (1983, 1984, 1985) and Jones *et al.* (1991) in NSW, while Shepherd *et al.* (1988), McLachlan and Hesp (1984) and McLachlan (1985) have studied aspects of sandy beach macrofauna in Western Australia. Thorough quantitative descriptions of Australian sandy beach macrofauna are required both for basic knowledge of these ecosystems and as a basis for further studies into processes that direct patterns in distribution and abundance.

The importance of spatial and temporal scales chosen for ecological investigations is now well known (e.g. Dayton & Tegner, 1984; Levin, 1992). It is thus widely acknowledged that there is no single scale at which spatial or temporal variation in the distribution and abundance of organisms should be investigated or at which processes structuring assemblages operate. The distribution and abundance of many organisms, including soft-sediment macrofauna, is known to be patchy at a variety of spatial scales (e.g. Thrush, 1991; Morrisey *et al.*, 1992; James *et al.*, 1995). The distribution and abundance of the macrofauna of sandy beaches is patchy (e.g. McLachlan, 1983; Brown & McLachlan, 1990), and thus descriptions of sandy beach macrofauna should be based on sampling designs that are properly replicated at each of several scales. Unfortunately, this is rarely the case. A common approach to describing the macrofauna of sandy beaches in studies published over the past 20 years has been to sample one shore-normal transect per beach with one or more samples at each of several levels on the beach (e.g. Trevallion *et al.*, 1970; McLusky *et al.*, 1975; Dye *et al.*, 1981; McLachlan *et al.*, 1981; Wooldridge *et al.*, 1981; McLachlan, 1985, 1990; Allen & Moore, 1987; Jaramillo & McLachlan, 1993; Jaramillo *et al.*, 1993). The sampling designs used in these types of studies include few spatial scales, are usually poorly replicated at each scale and are often inadequate for addressing the questions asked. For example, in seeking to make unequivocal, overt comparisons among beaches, adequate descriptions of spatial variation within beaches are not provided by the type of sampling design outlined above and unconfounded comparisons among beaches are impossible (see Hurlbert, 1984; Morrisey *et al.*, 1992).

Sandy beaches have both *across-shore*, defined as perpendicular to the water line, and *along-shore*, defined as parallel to the water line, dimensions (across- and along-shore are used in this sense throughout this paper). Much emphasis has been placed on across-shore variation and zonation in assemblages of sandy beach macrofauna (e.g. McLachlan, 1990; Rafaelli *et al.*, 1991; Defeo *et al.*, 1992; Jaramillo *et al.*, 1993) at the expense of along-shore variation. Studies of zonation are often poorly designed because they fail to consider variation among different levels across-shore but within zones (e.g. Dexter, 1983, 1984, 1985), and therefore any differences among zones are confounded with the likely smaller scale variation within zones. Further, studies of across-shore variation and other descriptions of sandy-beach macrofauna are usually done at only one site which necessarily covers only a very small proportion of the total length of the beach (e.g. Defeo *et al.*, 1992; Jaramillo *et al.*, 1993; McLachlan, 1990; Raffaelli *et al.*, 1991). Thus along-shore variation was not considered. Nevertheless, across-shore variation seems to occur commonly in assemblages of sandy beach macrofauna. Sampling designs for thorough descriptions of sandy beach macrofauna should, however, consider both across- and along-shore variation. The need to assess variation at several spatial scales with proper replication at each scale means sampling designs may necessarily be quite complex.

There has been limited use of modern statistical techniques in descriptions of the distribution and abundance of sandy beach macrofauna. Kite diagrams are commonly used (e.g. Ansell *et al.*, 1972; McLusky *et al.*, 1975; Dye *et al.*, 1981; McLachlan, 1990; Defeo *et al.*, 1992), but these do not allow authors to determine whether the abundances of macrofauna vary significantly in space or time, and are of little assistance for interpreting the results of complex sampling programmes. Rarely have analyses of variance (ANOVA) been used despite their widespread use in other areas of marine ecology and their utility in providing a logical framework for the design of sampling programmes (e.g. Underwood, 1981). Multivariate analyses have been used in studies of zonation (e.g. McLachlan, 1990; Raffaelli *et al.*, 1991; Jaramillo *et al.*, 1993), but usually without statistical comparisons of zones using appropriate techniques, for example the ANOSIM test (Clarke, 1993) which requires zones to be defined *a priori*.

Nested sampling designs have proven useful for descriptions of spatial variation in soft-sediment macrofauna (e.g. Morrisey *et al.*, 1992). In these designs, one or more smaller spatial scales are sampled within each spatial scale of interest (see Green, 1979; Underwood, 1981). Nested designs allow unconfounded, statistical comparisons among each spatial scale. Such designs, which are rare in studies of organisms on sandy beaches, are likely to be especially useful for descriptions of both across- and along-shore variation in the macrofauna of sandy beaches.

There has been little discussion also of appropriate sizes of sampling units, depths of sampling or sieve mesh sizes for sampling assemblages of macrofauna on sandy beaches. A range of sizes and types of sampling units from $<0{\cdot}005$ m^2 corers (e.g. Leber, 1982) to $0{\cdot}25$ m^2 quadrats (e.g. Larsen & Doggett, 1990) have been used. Sampling depths range from 10 cm (e.g. Dexter, 1983, 1984, 1985) to 30 cm (e.g. McLachlan, 1977) or deeper for studies of particular species [e.g. to 40 cm for a cirolanid isopod, (de Alava & Defeo, 1991), to 50 cm for a bivalve, (Defeo *et al.*, 1986)]. The mesh size of sieves used for assemblages of macrofauna ranges from 0·5 mm (e.g. Dexter, 1983, 1984, 1985) to 4 mm (e.g. Dye *et al.*, 1981; McLachlan *et al.*, 1981). Usually no justification is given for the choice of these sampling variables. It is, however, important to determine whether the chosen sampling units and protocols are accurately, precisely and efficiently sampling the organisms targeted, otherwise resources are wasted, analyses lack power and the patterns detected may be erroneous (see Andrew & Mapstone, 1987).

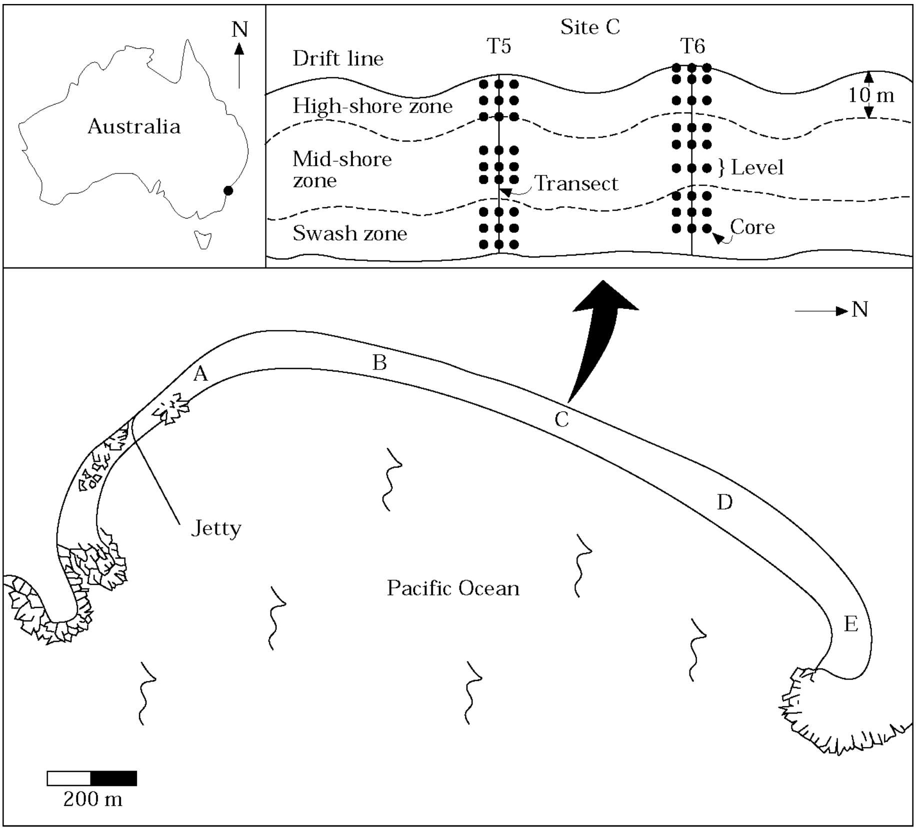

Figure 1. Regional location and map of Catherine Hill Bay showing the position of sampling sites A–E along the beach and an example of the sampling design (only shown for Site C).

The aim of this paper is to describe patterns of spatial variation of intertidal macrofauna sampled on single occasions in cusp bays on an exposed ocean sandy beach in NSW. The main study is unique because it is the first study of sandy beach macrofauna that simultaneously considers both across- and along-shore variation and interactions of these at several spatial scales. Results from two pilot studies are also reported because there is little published background work on which to base decisions about sampling variables for macrofauna on Australian or other sandy beaches.

Methods

Study site

Studies were performed on the sandy ocean beach at Catherine Hill Bay (CHB; 33°09′S, 151°38′E) located 90 km north of Sydney and 28 km south of Newcastle, NSW. The aspect of the northern half of the beach is south-easterly while that of the southern half of the beach is easterly (Figure 1). East to south-easterly swells and moderate waves (1–2 m) predominate in this region of the NSW coast (Short & Trenaman, 1992; Short, 1993). At CHB, there is a gradient of exposure from the southern end of the beach to the more exposed northerly parts. Waves at CHB average 1·5 m, decreasing in size slightly towards the southern end of the beach (Short, 1993). Mean grain size of sand at CHB is 0·27 mm (C. Hogan, pers. comm.). The beach at CHB is characterized by variable configurations of sand bars and rips and the modal beach state is intermediate (*sensu* Wright & Short, 1983). Within this intermediate state, the southern parts of the beach at CHB have a modal transverse bar and rip configuration. This is the most common modal beach state in NSW where it occurs on 33% of all beaches (Short, 1993). The northern parts of the beach at CHB have a modal rhythmic bar and beach configuration. This is the highest energy modal beach state present in NSW where it occurs on 10% of beaches (Short, 1993). The highest energy, intermediate beach state (longshore bar and trough) only occurs on outer bars on 7% of NSW beaches and there are no modally dissipative beaches in NSW (Short, 1993). Tides in NSW are semi-diurnal and unequal. High tides range from 1·0 m to 2·0 m above Indian Springs Low Water (ISLW), and low tides range from 0·1 m to 0·8 m above ISLW. The beach at CHB does not seem to receive regular nor large quantities of kelp wrack (pers. obs.).

General methods

The high-tide drift line (DL) and the top and bottom of the swash zone were the major reference points used in this study. All sampling was done during spring low tides. The DL used was that left by the highest of the previous two high tides. All distances were measured across the beach face from the DL. Cusps were present on the upper beach face on all occasions that sampling was done. All transects were laid and all sampling was done in the bays of cusps.

Samples were collected using corers because this method is considered superior to digging quadrats (see Straughan, 1982). Adjacent core samples at each level sampled on the beach were spaced randomly 0·5–2 m apart, along-shore in each study. Unless otherwise indicated, all samples were sieved through a 0·5 mm mesh and the residue was preserved with 10% formalin in seawater and stained with Biebrich Scarlet *in situ*. Macrofauna were sorted from the samples with the aid of a magnifying lamp (approximately 2 ×). Ten randomly chosen samples from Pilot Study 2 (see below) were scanned under a binocular microscope (12 ×) after sorting with the aid of the magnifying lamp and no additional macrofauna were found. The only animals found with the binocular microscope were copepods and nematodes which, together with other meiofauna (e.g. nemerteans), were not included in this study. Macrofauna were identified to species where possible and counted. The volume of sediment retained on the 0·5 mm mesh was measured in Pilot Study 2 and the main study after samples were sorted, and this volume was used as a guide to variation in sediment coarseness.

Pilot Study 1: Appropriate core size, depth of sampling and sieve mesh size

This pilot study was done to determine the relative accuracy, relative precision and efficiency (as defined by Andrew & Mapstone, 1987) of combinations of three sizes of cylindrical corer (50 mm, 105 mm and 195 mm diameter), two depths of coring (10 cm and 20 cm), and two sieve mesh sizes (0·5 mm and 1 mm) for providing estimates of macrofaunal abundance. These depths of coring and sieve mesh sizes were chosen for comparisons because they seemed the most commonly used in the literature. Similarly, the diameter of corers chosen covered most of the range of diameters of those commonly used in other studies of sandy beach macrofauna. Samples were collected from a site towards the northern end of CHB on 7 May 1993 (approximately Site D of the main study, see below). The distance between the DL and the top of the swash zone at low tide (0·4 m above ISLW) was approximately 32 m. Samples were collected from about the middle of the intertidal zone at 19 m downshore of the DL, and from low on the shore approximately 2 m above the top of the swash zone at low tide. Maximum penetration of the corers into the sediment was about 20 cm and separate core samples were taken to 10 cm or 20 cm below the surface. After the corer was pushed to the desired depth in the sediment, a hole was dug down the outside of the corer and a steel plate inserted under the sample to prevent it sliding out. In practice, this plate was only required to obtain complete cores for the 195 mm corer on the mid-shore and the 105 mm and 195 mm corers low on the shore in wet sand, but the plate was used for each size of corer.

Three replicate samples were taken for each combination of size of corer and depth of sampling at both levels on the beach. The combination of size of corer and depth of sampling was chosen at random for each position across the beach. Maximum penetration into the sediment achieved using the 195 mm diameter corer was 10 cm on the mid-shore and 15 cm low on the shore instead of the desired 20 cm. Thus, only the 195 mm/10 cm samples were collected from the mid-shore while both 195 mm/10 cm and 195 mm/15 cm samples were collected from low on the shore. The time taken to collect each core sample was recorded. Samples were taken from the beach, stored overnight in plastic bags and sieved the next morning. Each sample was first sieved through a 1 mm mesh and both the fractions passing through the mesh and that retained on the mesh were kept. The >1 mm fraction was preserved in 10% formalin and freshwater, and stained with Biebrich Scarlet. The <1 mm fraction was then washed over a 0·5 mm sieve and the residue preserved as for the >1 mm fraction. Times for sieving and sorting macrofauna from the samples were recorded separately for each fraction. Times for the 1 mm fraction were used as estimates for the 1 mm mesh, whereas times for the 0·5 mm and 1 mm fractions were summed and used as estimates for the 0·5 mm mesh. Total time per replicate was then estimated as the sum of coring (same for each mesh size), sieving and sorting times. Mean total times for each combination of core size and depth were used in calculations of efficiency.

Comparisons of accuracy among the combinations of core size and core depth were done using a one-way ANOVA on standardized abundances (number per 2000 cm^3). Abundances were standardized because samples could not be taken to 20 cm using the 195 mm corer and therefore a balanced set of data was not obtained. The greatest estimate of mean density was taken as the most accurate. Estimates of precision (SE/mean) were calculated from the unstandardized abundances. The number of replicates required to achieve precisions of 0·1, 0·15 and 0·2 were calculated (see Andrew & Mapstone, 1987) and used to determine the total amount of time required for estimates of abundance at each level of precision. Efficiency was calculated for each level of precision as total time=time per replicate × number of replicates.

Pilot Study 2: Distribution of macrofauna across the beach (zonation)

This pilot study was done to determine the likely distribution of macrofauna across-shore in order to meaningfully stratify sampling in the main study. Macrofauna were sampled on two shore-normal transects at CHB. A transect towards the northern end of the beach (similar area to Pilot Study 1 and Site D of the main study, see below) was sampled on 30 June 1993, and one towards the southern end of the beach (at approximately Site B of the main study, see below) was sampled the next day. Three 105 mm diameter core samples were collected at 2-m intervals across-shore, both upshore and downshore of the DL. Sampling continued upshore of the DL until the berm of the foredune was reached (10 m upshore for the northern transect, 8 m for the southern transect). Sampling continued downshore until the lowest part of swash zone that it was practical to sample was reached (50 m downshore for northern transect, 42 m for southern transect). All samples for each transect were collected during the 6 h around low tide (0·5 m above ISLW on both days) and samples from the swash zone and immediately above the swash zone were collected within 2 h either side of the time of low tide.

Extra samples were taken along ' litter lines ' (along-shore strips of stranded organic matter) left up to about 10 m below the DL by the ebbing tide to see whether these areas contained aggregations of animals associated with the stranded organic matter. Three replicate samples were taken along each litter line (at 0·2, 5·3 and 8·7 m below the DL on the northern transect and at 0, 1·5 and 2·2 m below the DL on the southern transect) (i.e. there was no obvious organic matter stranded on the DL on the northern transect but there was on the southern transect).

Main Study: Spatial variation of intertidal macrofauna

Samples were collected during the period 22 February 1994 to 25 Februry 1994 inclusive. On the basis of the groups of macrofauna that occurred at different levels of the beach in the second pilot study (see Results), the intertidal beach exposed at low tide was divided into high-shore, mid-shore and swash zones. The high-shore zone extended between the DL and 10 m downshore of the DL, the mid-shore zone extended from the bottom of the high-shore zone down to the top of the swash zone, and the swash zone extended between the maximum level of wave run-up and the most seaward point exposed during backwashes. The positions of the top and bottom of the swash were determined during a 5–10-min period prior to sampling the mid-shore and/or swash zones.

Five sites were chosen at about 300–400 m intervals along the entire beach (Figure 1). Two shore-normal transects within each site were laid in adjacent cusp bays and were 40–50 m apart (Figure 1). Transects were marked at 2-m intervals from the uppermost limit of each zone and three levels were chosen randomly within each combination of zone, site and transect. Adjacent levels were separated by at least 2 m and a different set of levels was chosen at random for each combination of zone, site and transect. Three replicate samples were collected from each level using a 105 mm diameter corer to 20 cm depth. For the mid-shore and swash zones, the uppermost or ' zero ' level was not sampled because it corresponded to, or was <2 m from, the lowest level of the zones upshore of these. If any particular level within the swash zone was too low on the shore to be sampled because of wave surge, a level higher in the swash zone was chosen at random in its place. This occurred only for the lowest level in the swash zone on Transects 3, 5 and 8.

Overall, the sampling design had two spatial scales across-shore (zones and levels nested within zones) and three spatial scales along-shore (sites, 100s of metres apart; transects nested within sites, 10s of metres apart; and replicate cores at each level, metres apart). The sampling design was orthogonal with respect to zones, sites and transects (i.e. each zone was sampled on each transect at each site), so interactions between across-shore (zones) and along-shore (sites and transects) variation were assessed formally using a mixed-model ANOVA (Underwood, 1981). Further, the sampling design was balanced so that the number of samples and the total sample area were the same for each of the three zones, each of the five sites, each of the 10 transects and each of the three levels per zone, site and transect.

The slope of the beach at most transects was relatively constant between the DL and the bottom of the swash zone, and the average slope of each transect was measured using a clinometer. At Transects 7 and 8, however, there was a weak berm present on the upper mid-shore and the upper levels of the beach were flat. For Transect 7, the slope was measured between the crest of the berm and the bottom of the swash zone. The DL was only 2 m behind the crest of the berm on Transect 8 and the slope was measured between the DL and bottom of the swash zone as for most other transects.

The two transects from each site were not sampled during the same day (Table 1). All zones on individual transects were sampled during the same low tide on 1 day but zones were sampled within different periods of time around low tide (Table 1). Some combinations of zone, site and transect were sampled while the tide was ebbing and others while the tide was flooding.

Statistical analyses

The spatial scales (zones, sites, transects, levels) over which significant variation occurred was determined using ANOVA for the abundance of particular taxa, the total abundance of individuals, the number of species and the volume of sediment retained on the 0·5 mm mesh. For taxa that occurred in more than one zone, a four-factor ANOVA with zones, sites, transects nested within sites, and levels nested within the interaction of zones and transects within sites was used. Zones was a fixed factor and all other factors were considered random. For taxa that occurred in one zone only, a fully-nested three-factor ANOVA with sites, transects within sites, and levels within sites and transects was used (all random factors). Cochran's Test was used to check the assumption of homogeneity of variances prior to ANOVA and abundances were transformed where appropriate to homogenize variances (Underwood, 1981). *Post-hoc* multiple comparison tests were done using Student–Newman–Keuls (SNK) tests for three means or Ryan's tests for four or more means (Day & Quinn, 1989).

Multivariate analyses were used to detect patterns in the distribution of assemblages of macrofauna. The methods of Clarke (1993) and PRIMER software (Plymouth Marine Laboratory) were used. The total abundance of each species at each level (sum of the three replicate cores per level) was used in these analyses to restrict the ordination plot to a reasonable number of points (90 instead of 270). This summation to levels still allowed variation within zones and within transects to be estimated and used in comparisons among each of these two factors. Four levels in the high-shore zone (one each of Transects 4 and 10, and two on Transect 7) had no macrofauna and were not included in the multivariate analyses. A fourth-root transformation was applied to the summed abundances so that analyses considered both abundant and rarer taxa, a matrix of Bray–Curtis similarities was generated, and the technique of non-metric multidimensional scaling (MDS) was used on the matrix. Similarity percentage analyses (SIMPER) were used to identify the species contributing most to average similarity. Analyses of similarities (ANOSIM) tested the significance of any apparent differences among spatial scales.

Results

Pilot Study 1: Appropriate core size, depth of sampling and sieve mesh size

Four species and a total of 72 individuals were collected from the 33 samples (total from both meshes). The 1 mm mesh retained varying proportions of the total abundance of

TABLE 1. Day, slope, width of mid-shore and swash zones, and time periods (to nearest 0·25 h) of sampling for each transect in the main study (see Methods for details of slope and width measurements)

Site	A		B		C		D		E	
Transect	1	2	3	4	5	6	7	8	9	10
Day	3	1	4	2	2	4	1	3	2	1
Slope (°)	4	3	4	4	5	5	5	6	5	4·5
Widths (m)										
Mid-shore	20	25	26	21	14	16	11	12	18	20
Swash zone	7	12	10	15	13	11	16	14	12	16
Times										
High-shore	− 1·75	− 1·5	− 2·5	− 2·5	− 2·25	− 1·75	+ 2·5	− 2·5	− 1·5	+ 3·25
	− 2·25	− 2	− 3	− 3	− 2·5	− 2·25	+ 2·75	− 3	− 2	+ 3·5
Mid-shore	− 1	− 1	+ 1·25	+ 1·75	+ 0·5	− 1	+ 2	+ 1	− 1	+ 1
	− 1·75	− 1·5	+ 2	+ 2	+ 1	− 1·75	+ 2·5	+ 2	− 1·5	+ 1·25
Swash zone	− 0·25	− 0·25	+ 0·75	+ 1	− 0·25	− 0·25	+ 1·5	+ 0·25	− 0·5	+ 0·25
	− 1	− 1	+ 1·25	+ 1·75	+ 0·5	− 1	+ 2	+ 1	− 1	+ 1

The starting and finishing times of sampling (relative to the time of low tide) are shown for each combination of zone, site and transect. Sampling before low tide is indicated by a − and after low tide by a + (e.g. the high-shore zone on Transect 2 was sampled 1·5 to 2 h before low tide).

each species. Although all individuals of the bivalve *Donax deltoides* and the amphipod *Zobracho canguro* were retained on the 1 mm mesh only, on average, 57% (SE=10%, n=21) of individuals of the glycerid polychaete, *Hemipodus* sp., and 50% (SE=29%, n=4) of individuals of the amphipod, *Exoediceroides maculosus*, were retained on the 1 mm mesh. In a similarly designed study at Avoca Beach (35 km south of CHB), all individuals of the cumacean, *Gephyrocuma pala*, retained on the 0·5 mm mesh had passed through the 1 mm mesh and only, on average, 50% (SE=22, n=5) of individuals of the amphipod, *Tittakunara katoa*, were retained on the 1 mm mesh. According to Dexter (1983, 1984), *G. pala* and *T. katoa* are common on sandy ocean beaches in NSW. Since the main study was to be a general survey of assemblages and there has been little work of this type done on Australian beaches, the authors decided to use a 0·5 mm mesh. Thus, estimates of accuracy, precision and efficiency were calculated using total abundances and times for the 0·5 mm mesh.

Mean abundance (accuracy) did not vary significantly among the combinations of core size and depth of sampling for any variates (Figure 2; one-way ANOVAs on numbers per 2000 cm^3, P>0·05, untransformed abundance except for *Z. canguro* (fourth-root), variances homogeneous at P>0·05). Trends in estimates of accuracy and precision showed that the 50 mm core samples gave relatively accurate, but variable and imprecise, estimates (Figure 2). The 105 mm corer gave relatively accurate and precise estimates for both depths of sampling. The 195 mm corer gave relatively inaccurate but usually precise estimates for the samples obtained. Efficiency for each level of precision differed among variates and combinations of core size and core depth (Figure 2). Efficiency of the 50 mm corer to either depth was poor in all cases. Efficiency of the other combinations was similar for most variates but, overall, the 105 mm corer sampling to 10 or 20 cm was the most efficient. Since sampling to a depth of 10 or 20 cm was similarly efficient for the 105 mm corer, and because the authors wanted to do a detailed general survey, sampling to 20 cm with this corer was chosen.

The 105 mm diameter corer was also chosen over the 195 mm corer for other reasons. The smaller corer: (1) was easier to use (cores can be reliably taken to 10 or 20 cm depth without having to insert the metal plate under the corer if samples are taken above the water table); (2) was quicker to use, which is an important consideration in the swash zone and allows macrofauna less time to escape by burrowing; and (3) allowed more replicate samples to be taken per unit time, which has benefits in statistical analyses (e.g. Green, 1979).

Pilot Study 2: Distribution of macrofauna across the beach (zonation)

Ten species of macrofauna and 346 individuals were collected from 186 samples. One species, *Mysta* sp. (Polychaeta: Phyllodocidae), was represented by only two individuals on the southern transect.

Assemblages of macrofauna varied with height on the shore (Figure 3). Kelp fly larvae were collected mainly in the 10 m upshore of the DL and were most common on the southern transect [Figure 3(a)]. Two species of isopod, *Actaecia pallida* and *Pseudolana concinna*, occurred mainly between the DL and 10 m downshore of the DL on the northern transect [Figure 3(b)]. Only one *A. pallida* was collected from the southern transect. Isopods (or other macrofauna) were not aggregated around the ‘ litter lines ’ sampled high on the shore [Figure 3(b)].

The glycerid polychaete *Hemipodus* sp. dominated abundance on the mid-shore [Figure 3(c)]. This species also occurred in the swash zone with the cumacean *G. pala*

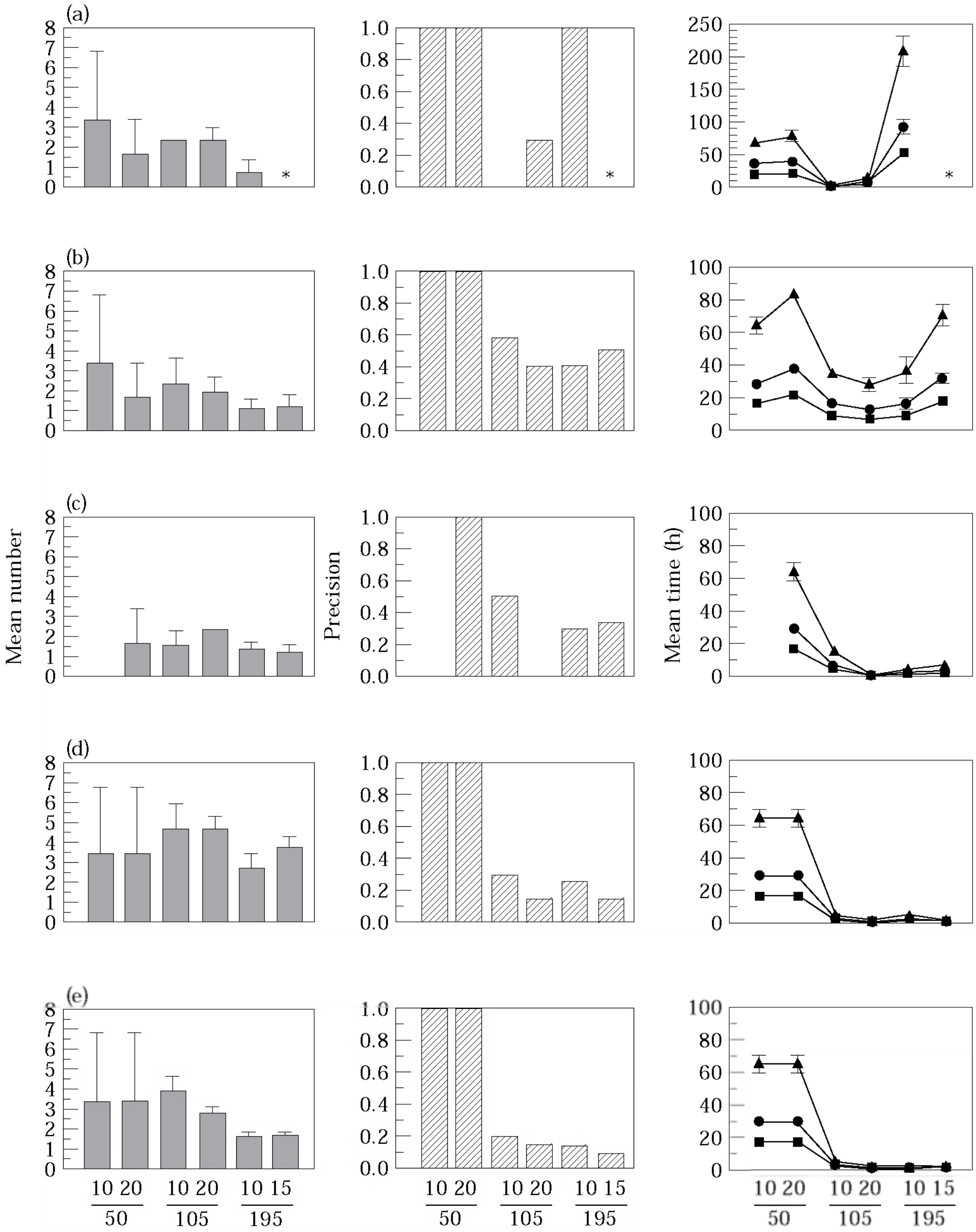

Figure 2. Results of Pilot Study 1 for comparisons of core size (50, 105 and 195 mm diameter) and depth of sampling (10 or 20 cm, but some only to 15 cm) from samples taken on the mid-shore and low-shore. Comparisons are of accuracy (left column, mean number per 2000 cm^3+SE, n=3), precision (middle column, SE/mean, n=3) and efficiency [right column, mean time ± SE for precisions of 0·1 (▲), 0·15 (●) and 0·2 (■)]. *These samples could not be taken. The abundances, numbers of species and estimated times used are for samples sieved using a 0·5 mm mesh. (a) *Hemipodus* sp. (mid-shore); (b) *Hemipodus* sp. (low-shore); (c) *Zobracho canguro* (low-shore); (d) total abundance (low-shore); (e) number of species (low-shore).

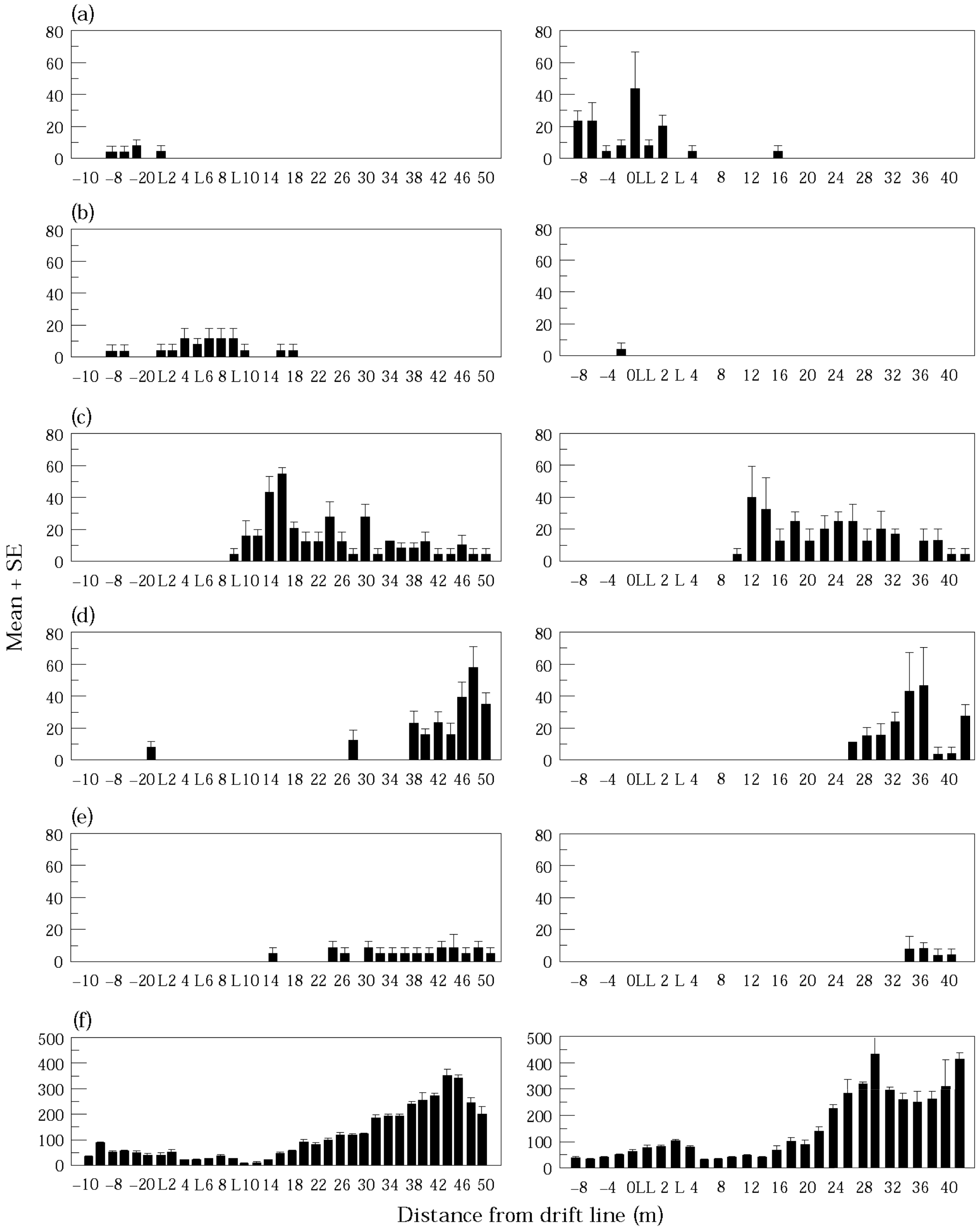

Figure 3. Results of Pilot Study 2 for across-shore variation in the mean abundance (per 0·1 m^2, $n=3$) of groups and species of macrofauna and the volume of sediment retained on a 0·5 mm mesh for two shore-normal transects. Sampling was done at 2-m intervals across-shore and extra samples were taken along ‘ litter lines ’ (L). The top of the swash zone at low tide on the northern (left column) and southern (right column) transects was at about 40 m and 30 m below the DL, respectively. (a) Kelp fly larvae; (b) Isopoda; (c) *Hemipodus* sp.; (d) Amphipoda and Cumacea; (e) *Donax deltoides*; (f) volume of sediment (ml).

and the amphipods *Z. canguro*, *E. maculosus* and *T. katoa* [Figure 3(d)]. One individual each of *E. maculosus* and *G. pala* were collected at the DL on the northern transect and these had probably been stranded by the ebbing tide. Small numbers of *D. deltoides* occurred in the swash zone on both transects and also on the mid-shore on the northern transect [Figure 3(e)], most were <15 mm long.

The volume of sediment retained on the 0·5 mm mesh increased down-shore [Figure 3(f)]. The largest and most variable volumes of sediment occurred in samples from the swash zone on both transects. The sediment in the swash zones was coarser and not as well sorted as that in the zones higher on the shore (pers. obs.). The volume of samples tended to be larger for the southern transect than for the northern transect.

The results of this pilot study were used to stratify sampling in the main study of spatial variation. For the main study, the shore was divided into high-shore, mid-shore and swash zones on the basis of the distribution of isopods, glycerid polychaetes, amphipods and cumaceans (see Methods). Further, the results suggested that adjacent sampling levels within these zones could be at ≥ 2-m intervals across-shore because smaller scale patchiness was negligible and, with three or more sampling-levels within zones, this interval would achieve adequate across-shore coverage for sampling zones.

Main Study: Spatial variation of intertidal macrofauna

Assemblages of macrofauna

Multivariate analyses confirmed that assemblages of macrofauna differed among zones as expected from the definition of zones and stratification of sampling which was based on groups of macrofauna [Figure 4(a)]. Assemblages changed from high on the shore through the mid-shore zone to the swash zone, but assemblages from adjacent zones overlapped and there was no clear-cut discontinuity between any zones [Figure 4(a)]. Despite this overlap, significant differences in assemblages were detected among zones and between each pair of zones [ANOSIM, Table 2(a)]. SIMPER analysis among zones showed that the isopods *A. pallida* and *P. concinna* dominated assemblages in the high-shore zone (43 and 40% contribution to average similarity, respectively, over all sites, transects and levels), *Hemipodus* sp. dominated assemblages in the mid-shore zone (82% contribution) whereas *Hemipodus* sp., *D. deltoides* and *T. katoa* dominated assemblages in the swash zone (43, 21 and 16% contribution, respectively). Other taxa were also collected from various zones (Table 3).

Significant along-shore variation in assemblages of macrofauna occurred among sites in the high-shore and swash zones. In the high-shore zone, significant differences in assemblages were detected among sites but not between transects within sites [ANOSIM, Table 2(b)]. There was a large amount of variation within most sites in the high-shore zone and the only obvious difference was between Sites A and C [Figure 4(b)]. Assemblages at Site A were dominated by *P. concinna* (SIMPER, 94% contribution to average similarity of high-shore assemblages at Site A), whereas those at Site C were dominated by *A. pallida* (88%). Both these species of isopod were abundant at Site E and this site bridged the gap between Sites A and C on the ordination plot [Figure 4(b)]. The structure of assemblages in the high-shore zone at Sites B and D was variable compared to the other sites, nevertheless *P. concinna* was common at Site B which tended to group with Site A towards the top left hand corner of the ordination plot, and *A. pallida* was common at Site D which tended to group with Site C towards the bottom right hand corner of the ordination plot [Figure 4(b)].

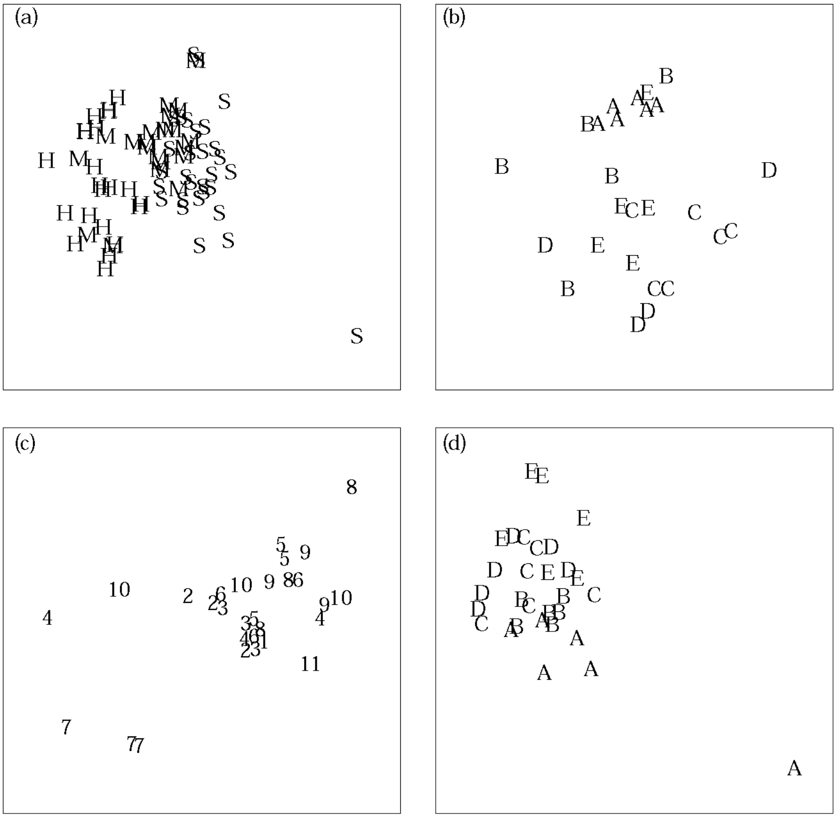

Figure 4. MDS ordination plot (stress=0·08) for the main study showing (a) differences in assemblages among zones (H, high-shore; M, mid-shore; S, swash zones); (b) along-shore variation among Sites A–E of assemblages in the high-shore zone; (c) along-shore variation among Transects 1–10 of assemblages in the mid-shore zone; and (d) along-shore variation among Sites A–E of assemblages in the swash zone. Plots (b), (c) and (d) are parts of the original MDS plot expanded and relabelled to show along-shore variation separately for each zone. Overlapping symbols in Plots (b), (c) and (d) have been offset by hand for clarity.

Significant along-shore variation occurred between transects within at least one site in the mid-shore zone but no significant differences were detected among sites [ANOSIM, Table 2(c)]. The largest differences between transects within sites occurred between Transects 7 and 8 in Site D and, indeed, between Transect 7 and all other transects [Figure 4(c)]. *Hemipodus* sp. was abundant in assemblages on all transects except Transect 7 within the mid-shore zone but the isopod *A. pallida*, which occurred in the high-shore zone on all other transects, was abundant in the mid-shore zone on Transect 7 (Table 3).

In the swash zone, significant differences were detected among sites but not between transects within sites [ANOSIM, Table 2(d)]. Sites A and E were the most obviously different, and this was the only zone where along-shore variation corresponded with the gradient of increasing wave exposure from Site A nearest the southern end of the beach through Sites B, C and D to Site E nearest the northern end of the beach [Figure 4(c), gradient from Site A near the bottom of the plot to Site E near the top]. The outlying point from Site A on the MDS plot represents the assemblages from one level on

TABLE 2. Results of four separate ANOSIM tests from the main study. (a) A one-way ANOSIM among zones (over all sites and transects) with subsequent pairwise tests between Zones (i, ii, iii). A two-way nested ANOSIM among sites and transects nested within sites for each of: (b) assemblages in the high-shore zone; (c) assemblages in the mid-shore zone; and (d) assemblages in the swash zone

ANOSIM test among	Possible permutations	*P*
(a) All zones (global test)	$4{\cdot}269 \times 10^{38}$	<0·001
(i) High- *vs.* mid-shore zone	$6{\cdot}646 \times 10^{15}$	<0·001
(ii) High-shore *vs.* swash zone	$6{\cdot}646 \times 10^{15}$	<0·001
(iii) Mid-shore *vs.* swash zone	$5{\cdot}913 \times 10^{16}$	<0·001
(b) High-shore		
Sites	945	<0·005
Transects (sites)	$4{\cdot}000 \times 10^{4}$	>0·80 n.s.
(c) Mid-shore		
Sites	945	>0·10 n.s.
Transects (sites)	$1{\cdot}000 \times 10^{5}$	<0·04
(d) Swash zone		
Sites	945	<0·005
Transects (sites)	$1{\cdot}000 \times 10^{5}$	>0·08 n.s.

The number of possible permutations was less for comparisons involving the high-shore zone than those involving the mid-shore and/or swash zones because four of the 30 levels sampled in the high-shore zone contained no macrofauna and were therefore not included in the multivariate analyses, whereas all levels in the other zones were used. Where the number of possible permutations was >20 000, a random sample of 20 000 permutations was used for each permutation test. Non-significant (n.s.) results (P>0·05) are indicated.

TABLE 3. Total abundance of taxa collected in the main study for each zone; high-shore, mid-shore and swash zones, total of 90 cores for each zone (=0·78 m^2 sampled per zone), three cores at each of three levels on each of 10 transects

Taxon	High-shore	Mid-shore	Swash
Actaecia pallida (Isopoda: Actaeciidae)	79	33[a]	—
Pseudolana concinna (Isopoda: Cirolanidae)	91	30	—
Kelp fly larvae (Insecta: Coleopidae)	15	2	—
Staphylinid beetle larvae (Insecta: Staphylinidae)	11	1[a]	—
Adult beetles (Insecta)	3	1[a]	—
Juvenile *Mictyris* sp. (Decapoda: Mictyridae)	11	4	—
Hemipodus sp. (Polychaeta: Glyceridae)	10	182	67
Zobracho canguro (Amphipoda: Urohaustoriidae)	—	21	27
Donax deltoides (Bivalvia: Donacidae)	—	12	47
Lobochesis longiseta (Polychaeta: Opheliidae)	—	9[a]	2
Gephyrocuma pala (Cumacea: Diastylidae)	—	1[a]	32
Tittakunara katoa (Amphipoda: Platyschnopidae)	—	—	75
Exoediceroides maculosus (Amphipoda: Oedicerotidae)	—	—	19
Scolelepis carunculata (Polychaeta: Spionidae)	—	—	4[a]
Pisione sp. (Polychaeta: Pisionidae)	—	—	2[a]

[a] These animals occurred on only one transect in that particular zone.

Transect 1 which was the only place where the spionid polychaete *Scolelepis carunculata* occurred. Assemblages at Site A were dominated by the bivalve *D. deltoides* (SIMPER, 80% contribution to average similarity of swash zone assemblages at Site A), those at

Site B were dominated by *D. deltoides*, *Hemipodus* sp., and the amphipods *T. katoa* and *E. maculosus* (38, 35, 12 and 12%, respectively), those at Site C by *Hemipodus* sp., *T. katoa* and *D. deltoides* (51, 21, 11%), those at Site D by *Hemipodus* sp. and the cumacean *G. pala* (76, 18%) and, finally, those at Site E by the amphipods *Z. canguro* and *T. katoa* plus the glycerid *Hemipodus* sp. (72, 11, 11%).

Individual species of macrofauna

Significant variation in abundance occurred at all spatial scales examined in one or more of the analyses of individual taxa (Table 4). There was significant variation among the levels within some combinations of zones, sites and transects for nearly all variates {significant levels [Z × T(S)] terms, Table 4}. This indicates that the distribution of macrofauna and other variates was usually not homogeneous across-shore within zones.

Hemipodus sp. occurred in all zones and the abundance of this polychaete varied significantly among zones despite the significant small-scale variation among levels [Z × T(S)] [Table 4(a)]. *Hemipodus* sp. was most abundant in the mid-shore zone followed by the swash zone and, finally, was least abundant in the high-shore zone [Figure 5(a), SNK Test on zone means]. Along-shore, significant differences in the abundance of *Hemipodus* sp. occurred among sites [Table 4(a)]. *Hemipodus* tended to be most abundant at Site C in the middle of the beach [Figure 5(b), Ryan's test on site means was inconclusive]. No significant variation in the abundance of *Hemipodus* sp. occurred between transects within each site [Table 4(a)].

The total abundance of macrofauna varied among sites [Table 4(b)]. Most macrofauna occurred at Site C (in part because of the large numbers of *Hemipodus* sp. at this site) and similar numbers occurred at all other sites [Figure 5(c)] but Ryan's test was inconclusive on the significance of these differences. The total abundance of macrofauna also varied among levels [Z × T(S)] but no significant differences were detected among zones nor transects within each site [Table 4(b)].

The number of species per sample varied significantly among zones [Table 4(c)] and increased down-shore with the greatest number of species occurring in the swash zone compared with the high- and mid-shore zones which had similar numbers of species [Figure 5(d), SNK test on zone means].

Patterns of variation among zones in the volume of sediment retained on the 0·5 mm mesh differed among transects [a significant Z × T(S) interaction, Table 4(d)]. In general, however, the volume of sediment retained increased down-shore [Figure 6(a)]. On Transects 2, 7 and 10 there was relatively little difference in sediment coarseness among zones compared to Transects 3–6 where sediments in the swash zone were coarse and gravel was observed beneath the top 5 cm of sand. This gravel appeared to be from the rocky shores at either end of the beach which are composed of conglomerate. Patches of gravel beneath the sand in the swash zone are common at CHB (per. obs.).

The isopod, *A. pallida*, tended to be most abundant in the high-shore zone except on Transect 7 where it was most abundant in the mid-shore zone [Figure 6(b)]. Less than 50 m along the shore, at Transect 8, it was most abundant in the high-shore zone. Both Transects 7 and 8 crossed a weak berm that extended along the beach much of the way between Sites C and E (Figure 1). The DL located at Transect 7, however, occurred 10 m behind the crest of the berm on a flat part of the beach, whereas the DL at Transect 8, which was sampled 2 days later (Table 1), occurred almost on the crest of the berm. Thus, the different pattern of zonation of *A. pallida* on Transect 7 compared with all

TABLE 4. Summary of ANOVA results for selected variates over the zones in which they occurred in main study

		(a) *Hemipodus* sp. H, M, S			(b) Total abundance H, M, S			(c) No. of species H, M, S			(d) Sediment volume H, M, S		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Zones (Z)	2	13·92	12·32	<0·005	17·12	1·35	>0·30	10·37	9·07	<0·01	120·0	33·53	—
Sites (S)	4	2·283	5·34	<0·05	31·38	5·82	<0·05	3·546	4·29	>0·05	14·01	1·27	>0·35
Transects (sites) [T(S)]	5	0·4276	1·26	>0·25	5·389	0·46	>0·80	0·8259	0·67	>0·60	11·00	13·12	—
Z × S	8	1·130	1·90	>0·15	12·66	1·13	>0·40	1·144	0·97	>0·50	3·580	1·95	>0·15
Z × T(S)	10	0·5944	1·75	>0·05	11·19	0·95	>0·45	1·182	0·96	>0·45	1·840	2·19	<0·05
Levels [Z × T(S)]	60	0·3391	2·97	<0·001	11·76	3·25	<0·001	1·237	2·61	<0·001	0·8386	17·95	<0·001
Residual	180	0·1143			3·622			0·4741			0·0467		

		(e) *Actaecia pallida* H, M			(f) *Pseudolana concinna* H, M			(g) *Zobracho canguro* M, S					(h) *Tittakunara katoa*		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	Source	df	MS	*F*	*P*
Zones	1	4·652	1·56	>0·25	3·667	2·56	>0·15	0·0390	0·84	—	Sites	4	0·3306	0·30	>0·85
Sites	4	1·975	5·12	>0·05	3·316	27·44	<0·005	1·535	3·73	>0·05	Transects (sites)	5	1·1097	1·58	>0·20
Transects (sites)	5	0·3858	1·94	>0·10	0·1208	0·31	>0·90	0·4119	2·71	—	Levels [T(S)]	20	0·6956	4·48	<0·001
Z × S	4	2·987	3·65	>0·05	1·434	2·12	>0·20	0·0464	0·11	>0·95	Residual	60	0·1554		
Z × T(S)	5	0·8192	4·13	<0·005	0·6752	1·76	>0·10	0·4080	2·69	<0·05					
Levels [Z × T(S)]	40	0·1985	2·25	<0·001	0·3845	4·30	<0·001	0·1520	1·30	>0·10					
Residual	120	0·08811			0·08932			0·1171							

H, high-shore; M, mid-shore; S, swash zone. Data for all variates except total abundance and number of species were transformed to fourth-root (X) prior to analysis. Variances were homogeneous (P>0·05) for all variates except *P. concinna* where variances were homogeneous at P>0·01 and so a=0·01 was used (Underwood, 1981), and *A. pallida* where variances were heterogeneous (P<0·01). —, main effect was not tested because it was involved in a significant interaction (Underwood, 1981).

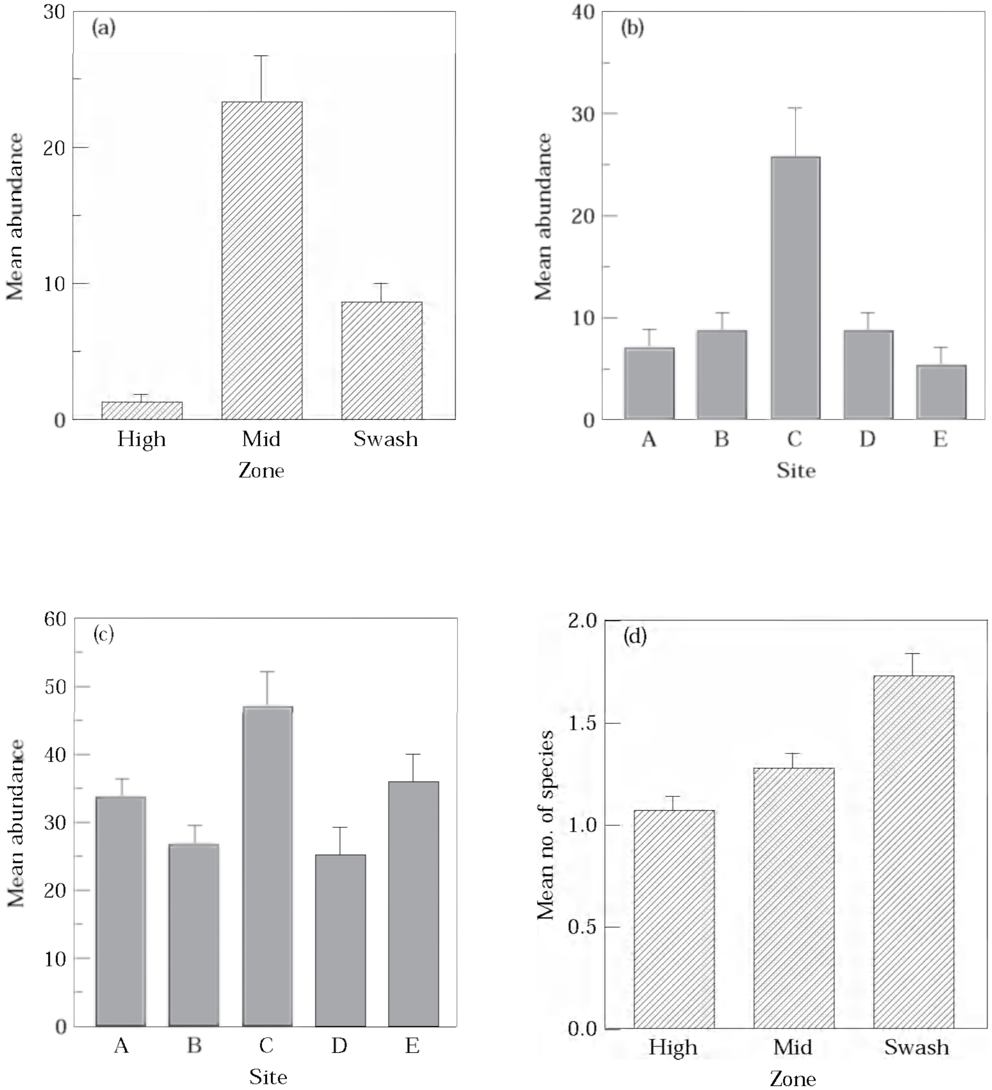

Figure 5. Variation in the mean (+SE) number of: (a) *Hemipodus* sp. per zone (mean per 0·1 m^2; averaged over sites, transects, levels and replicate cores; n=90); (b) *Hemipodus* sp. per site (mean per 0·1 m^2; averaged over zones, transects, levels and replicate cores; n=54); (c) total macrofauna per site (mean per 0·1 m^2; averaged over zones, transects, levels and replicate cores; n=54); and (d) species per zone (mean per core sample; averaged over sites, transects, levels and replicate cores; n=90).

other transects is probably an artefact of using the DL as a reference point. Abundance data for *A. pallida* had heterogeneous variances (Cochran's test, P>0·01) and the ANOVA results should therefore be treated with caution [Table 4(e)].

The cirolanid isopod *P. concinna* was most abundant at Site A and no consistent differences in abundance were detected among the other sites (Ryan's test on site

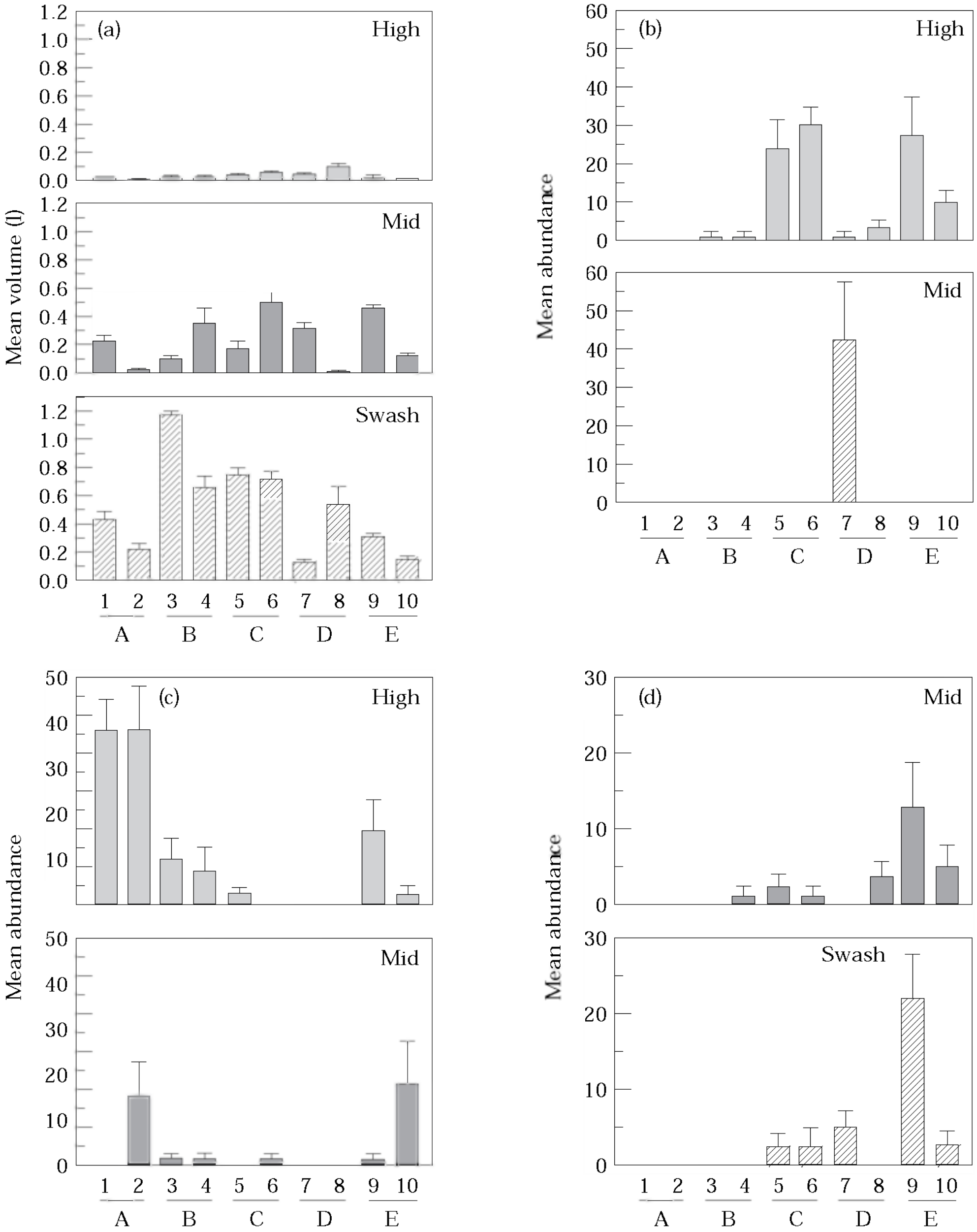

Figure 6. Variation among zones and Transects 1–10 within Sites A–E in the mean: (a) volume of sediment retained on the 0·5 mm mesh (mean per core); (b) abundance of *Actaecia pallida* (none collected from the swash zone); (c) abundance of *Pseudolana concinna* (none collected from the swash zone); and (d) abundance of *Zobracho canguro* (none collected from the high-shore zone). All means+SE per 0·1 m^2 (except volume, mean+SE per core) from *n*=9 cores (three replicates per level from three levels per transect per zone).

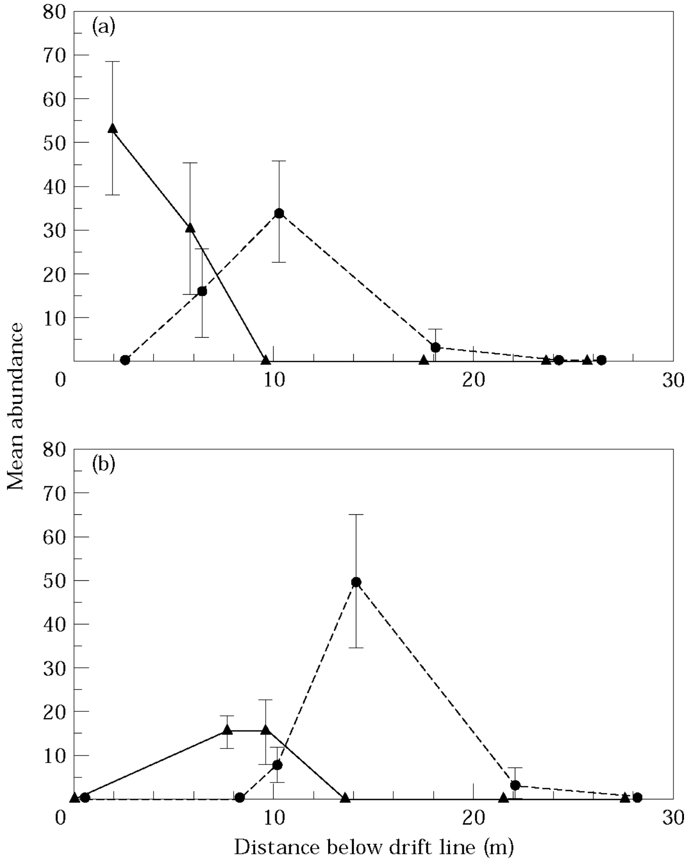

Figure 7. Mean abundance (per 0·1 m^2, ± SE, n=3) of the isopods *Actaecia pallida* (▲) and *Pseudolana concinna* (●) across-shore in the high- and mid-shore zones on Transects (a) 9 and (b) 10. Symbols are offset for clarity.

means). The abundance of *P. concinna* also varied significantly among levels but not between the high- and mid-shore zones [Table 4(f)]. *P. concinna* occurred in the high- and mid-shore zones at most sites [Figure 6(c)], but it mainly occurred near the top of the mid-shore zone (per. obs.). There was some evidence that *A. pallida* occurred higher on the shore than *P. concinna* (Figure 7) and they only occurred together in reasonable numbers on Transects 9 and 10 near the northern end of the beach.

The relative abundance of the amphipod *Z. canguro* in the mid-shore and swash zones varied among transects [significant Z × T(S) interaction, Table 4(g), Figure 6(d)]. Along-shore, *Z. canguro* was most abundant on Transect 9 and, overall, was more abundant on the more wave-exposed northern half of the beach than on the southern half of the beach [Figure 6(d)].

The amphipod *T. katoa* only occurred in the swash zone (Table 3) and no significant differences in abundance were detected among sites or between transects within sites along-shore [Table 4(h); mean abundance was 9·62 individuals per 0·1 m^2 (SE=2·03, n=90)]. Significant variation in abundance occurred only among levels [T(S)] indicating a patchy distribution across the swash zone.

Discussion

Zonation and along-shore variation of assemblages

Assemblages of sandy-beach macrofauna varied among zones across the beach and similar patterns of zonation occurred along the entire beach. The high-shore zone which extended 10 m downshore of the DL was dominated by isopods, the mid-shore zone which extended downshore of the high-shore zone to the top of the swash zone was dominated by glycerid polychaetes, and the swash zone was dominated by amphipods, glycerids, bivalves and cumaceans. Dexter (1983, 1984) reported that the isopod *P. concinna*, the amphipod *T. katoa*, the cumacean *G. pala*, and the bivalve *D. deltoides* were the characteristic macrofauna of sandy ocean beaches in NSW. These species were common in the present study but the isopod, *A. pallida*, was also abundant and the glycerid polychaete, *Hemipodus* sp., was the most abundant animal collected.

Dahl (1952) described three zones on temperate beaches based on the distribution of crustacean macrofauna. These were the supralittoral zone with ghost crabs or talitrid amphipods, the midlittoral zone with cirolanid isopods, and the sublittoral fringe with amphipods from the families Haustoriidae, Phoxocephalidae and Oedicerotidae. Jaramillo *et al.* (1993) reported similar patterns of zonation for intermediate and dissipative beaches in Chile. The authors did not sample the supralittoral areas of the beach but the burrows of ghost crabs were commonly observed there. Cirolanid isopods did dominate the upper intertidal and amphipods from the above families or similar were abundant in the swash zone. The polychaete *Hemipodus* sp. dominated the mid-shore zone in the present study and two zones (high-shore and mid-shore) were identified within the midlittoral zone of Dahl (1952). Further subdivision of the high-shore zone may be possible because, where they occurred together, the isopod *A. pallida* tended to occur higher on the shore than *P. concinna* (Figure 7). Similarly, Raffaelli *et al.* (1991) concluded that up to three zones based on assemblages of macrofauna could be identified within the midlittoral zone defined by Dahl (1952). Trevallion *et al.* (1970) described a similar pattern of zonation for a beach in India to that found in the present study.

The zones distinguished in the present study were a good basis for stratification of sampling and are probably useful for further work. Other authors have, however, found less evidence of zonation. For example, Defeo *et al.* (1992) concluded that no consistent patterns of zonation occurred for several beaches in Uruguay and no consistent patterns of zonation were reported by McLachlan (1990) for four dissipative beaches in North America. Thus, although the use of zones to stratify sampling appears useful in individual cases such as the present study, application to several beaches or through time would require thorough preliminary work to ascertain any spatial variation in patterns of zonation within and among other beaches, or temporal fluctuations in zonation at several scales. For example, subsequent work (James & Fairweather, 1995) at CHB has shown that large temporal changes may occur in the across-shore distribution of the bivalve *Donax deltoides* sampled during low tides. Also, different size classes of *Donax deltoides* may occur in different zones (James, unpubl. data), thus casting doubt on the utility of this species in defining zones in future studies.

Significant along-shore variation in assemblages of macrofauna occurred in all zones but at different scales in the present study. Significant differences occurred among sites but not between transects within sites in the high-shore and swash zones, whereas the opposite pattern occurred in the mid-shore zone. For assemblages in the swash zone, there was evidence of along-shore variation consistent with the gradient in wave exposure from the sheltered southern end of the beach to the more exposed northern end, but this was not apparent for assemblages in the other two zones. The along-shore variation in assemblages of macrofauna was due to changes in the relative abundance of similar species among transects or sites and changes in species composition of assemblages among transects or sites. Species typical of each zone did not occur in similar numbers on all transects nor at all sites along the beach. Further, these species were not necessarily present on every transect nor at every site. These results indicate the importance of assessing along-shore variation. The authors recommend that all descriptive and comparative studies of assemblages of sandy beach macrofauna (including those concerned with across-shore variation) examine along-shore variation at appropriate spatial scales, determined from pilot studies or relevant previous work, to give unequivocal results that are more likely to be generally applicable.

Spatial variation of individual taxa along- and across-shore

The abundances of individual taxa varied at several spatial scales both along- and across-shore in the present study. Across-shore, differences were detected among levels within combinations of zones, sites and transects for the number of species and abundances of almost all taxa. Differences among zones also occurred for some variates. These results indicate the importance of sampling more than one across-shore level per zone when making comparisons among zones on sandy beaches. Otherwise, any differences observed among zones will be confounded with the smaller scale differences that are likely to occur within zones. The sampling design used by Dexter (1983, 1984, 1985) illustrates this type of confounding. A further implication is that sampling only one level within a zone or on a beach is likely to give misleading results because of small-scale, across-shore variation. For example, Bonsdorff and Nelson (1992) sampled two species of *Donax* in the swash zone of a beach by taking replicate cores along-shore at one level of the swash zone at approximately monthly intervals. Not surprisingly, they described large peaks of abundance during some sampling occasions but otherwise few animals were found. It is impossible to tell whether these results reflect real temporal increases in the abundance of populations of *Donax* or merely occasions when these mobile bivalves happened to be very abundant at the single level that was sampled.

In the present study, significant along-shore variation in the abundances of individual taxa occurred mainly among sites but also the smaller scale of among transects within sites (manifest through interactions). There were various patterns with, in general, *A. pallida* and *Z. canguro* being most abundant towards the northern end of the beach, *P. concinna* being most abundant near the southern end of the beach, *Hemipodus* sp. being most abundant near the middle of the beach, and *T. katoa* being similarly abundant along the length of the beach. Also, not all species occurred on all transects or at all sites. For example, the two species of isopod that occurred in the high-shore zone were not both present on every transect. This significant along-shore variation suggests that sampling single sites or transects is very unlikely to give representative results for the distribution or abundance of macrofauna on any particular beach. The representativeness of results for particular beaches and the validity of comparisons among beaches should be questioned when only one site or transect is sampled per beach in studies of macrofauna.

The few studies to consider quantitative along-shore variation in sandy beach macrofauna have only considered variation at one or perhaps two spatial scales. Defeo *et al.* (1986) sampled sites spaced at 1-km intervals on a beach, but no properly replicated sampling was done along-shore at any smaller scales. Similarly, Jaramillo *et al.* (1994) sampled sites at intervals of 100 m along-shore, but with only one quadrat per site they did not consider smaller spatial scales. The differences in abundance among sites that were observed in these studies are confounded with the likely differences at any scale smaller than sites. Donn (1987) sampled bivalves at two spatial scales along-shore, using two shore-normal transects laid 50 m apart within each of several sites which were spaced at about 5-km intervals. However, only graphical analyses of abundances among sites with no estimates of variance within sites (across-shore or between transects) were presented, and thus there was no indication of the relative size and statistical significance of variation at spatial scales smaller than sites. Although significant along-shore variation did not occur at a scale smaller than sites for most variates in the present study (except *Z. canguro* and *A. pallida*), sampling and adequate replication at the two along-shore scales smaller than sites (i.e. transects and replicate cores) has allowed the authors to assess this explicitly and to perform unconfounded comparisons among sites. Likewise, the use of sampling designs and analyses which incorporate several spatial scales and adequate replication at each scale are necessary for unconfounded comparisons in all studies of sandy beach macrofauna. Fully nested sampling designs are obviously appropriate in this situation.

Significant interactions between along-shore and across-shore variation occurred in the abundance of some individual taxa (e.g. *Z. canguro*). These interactions occurred between zones and transects but not zones and sites. Thus, despite the patterns of zonation described for assemblages in multivariate analyses, differences among zones for particular taxa are not necessarily consistent along the entire beach. This casts further doubt upon the results of studies that describe the across-shore distribution and abundance of sandy beach macrofauna, or compare these among beaches using samples from only one transect or site per beach. The authors recommend adequate assessment of both across- and along-shore variation for studies of particular taxa (and, as pointed out above, for assemblages of macrofauna).

Utility of pilot studies

The present results indicate the importance of pilot studies in designing optimal sampling programmes for the macrofauna of sandy beaches. Pilot Study 1 allowed selection of an efficient combination of corer size, depth of sampling and sieve mesh size with regards to the aims of the main study. It was important to choose an efficient combination of these variables because this enabled properly replicated studies at many spatial scales in minimal time. Pilot Study 2 allowed meaningful stratification of sampling effort in the main study. Across-shore patterns of variation detected in Pilot Study 2 were evident in the more extensive main study of the entire beach. The authors urge more widespread use of pilot studies to improve the efficiency, rigour and power of sampling strategies for sandy-beach macrofauna (see also Green, 1979; Andrew & Mapstone, 1987; James *et al.*, 1995).

Precision for abundant taxa in the main study varied widely among zones for individual species but much less for the total abundance and the number of species (Table 5). For taxa that occurred in more than one zone (e.g. *A. pallida*, *P. concinna* and *Hemipodus* sp.), precision was best (i.e. smallest) in those zones which were defined on the basis of the presence of these taxa in Pilot Study 2 (e.g. high-shore zone for *A. pallida* and *P. concinna*, mid-shore and swash zones for *Hemipodus* sp.) and where these species

TABLE 5. Estimates of precision for each zone based on results of the main study

	High-shore	Mid-shore	Swash
Actaecia pallida	0·18	0·46	—
Pseudolana concinna	0·18	0·35	—
Hemipodus sp.	0·48	0·14	0·16
Zobracho canguro	—	0·30	0·28
Donax deltoides	—	0·38	0·17
Tittakunara katoa	—	—	0·21
Total abundance	0·09	0·09	0·09
No. of species	0·08	0·05	0·07

Precision (SE/mean) was calculated from 90 cores per zone (three replicates from each of three levels on each of 10 transects). —, the species did not occur in that zone.

were most abundant. The precision of estimates of total abundance and number of species was good for all zones. The pilot studies were obviously done before patterns of distribution were known, and choices among sampling variables were made based on the need to sample fauna from all zones over both large and small spatial scales for the authors' description. It is very unlikely that one size of corer or one size of sieve mesh will sample all species optimally in sandy-beach assemblages because of their different sizes and habits. Any future work that targets particular species or assemblages would benefit from pilot studies specific to those species or assemblages. For example, a $0{\cdot}1\ m^2$ sampling unit has been used by the authors in subsequent studies (James & Fairweather, 1995) of the large bivalve, *Donax deltoides* which grows up to 60 mm long.

Other considerations for further work

The results of the present study suggest much about how one should distribute sampling effort among spatial scales in further studies of macrofauna at CHB. Although significant spatial variation occurred at all scales, sites were more often significant sources of variation than transects. Across-shore, levels were more often significant sources of variation than zones. These results imply that more effort could usefully be put into sampling sites (i.e. by having more sites) but sampling more transects per site would be unnecessary. Across-shore, more effort could be put into sampling levels within zones. Note that without properly replicated sampling at spatial scales smaller than sites or zones, unconfounded comparisons among sites or zones would have been impossible and adequate replication within sites and zones should be maintained in all future work on assemblages. However, to cut down on sampling effort for subsequent studies at CHB, one could argue to do without replicate transects within sites because these seem less significant sources of variation than sites. This decision would be a trade-off between sampling effort and logical rigour but does have support from the present results. The authors feel that researchers must base such decisions on the results of pilot studies or relevant previous work. Otherwise, studies are prone to strong criticism that they ignore variation at important spatial scales and the decisions are made in ignorance of what the results of any trade-offs are likely to be.

The results of the present study are not meant to be representative of all intermediate beaches in NSW, even though about 70% of NSW beaches are modally intermediate and 93% of the total length of beaches in NSW is made up of intermediate beaches (Short, 1993). The patterns described in the present study only apply to the distribution and abundance of macrofauna in cusp bays during spring low tides at CHB. Different patterns may be found for horns of cusps (McLachlan & Hesp, 1984), reflective beaches (e.g. McLachlan, 1985; Jaramillo *et al.*, 1993) or beaches with similar morphodynamics but at other places along the coast of NSW. Examining these possibilities is an avenue for further research.

The patterns described in the present study provide part of the background information required to formulate hypotheses and design experiments to investigate processes directing the distribution and abundance of macrofauna on this sandy beach. Patterns were detected both at relatively broad scales and finer scales within the beach and, also, both along- and across-shore. It is likely that different processes operate at these different scales and dimensions. Therefore, a variety of further studies are required to elucidate the relative importance and function of ecological processes for sandy-beach macrofauna.

The importance of good descriptions of spatial patterns can not be overestimated because they form the basis for further work and should therefore be rigorous. For exposed sandy ocean beaches where the physical nature of the environment and the mobility and cryptic nature of the macrofauna pose severe challenges to field-based, experimental manipulations designed to shed light on processes, good descriptive studies are even more essential because they will form at least part of the basis of our understanding and management of these ecosystems for the foreseeable future.

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