Temporal and Spatial Variability in Community Structure of a Sandy Intertidal Beach, Cape Paterson, Victoria, Australia

D. Haynes[A] and G. P. Quinn[B]

[A]*Gippsland Water, PO Box 348, Traralgon, Vic. 3844, Australia.*
[B]*Department of Ecology and Evolutionary Biology, Monash University, Clayton, Vic. 3168, Australia.*

Abstract. The infauna of a sheltered sandy intertidal beach at Cape Paterson, Victoria, was sampled on a three-monthly basis over a two-year period. In total, 116 495 individuals comprising 41 species were collected over this time. Common species collected included the dipteran *Chaetocoelopa sydneyensis*, the coleopteran *Sphargeris physodes*, the isopods *Pseudolana concinna* and *Actaecia thomsoni*, the amphipods *Talorchestia* cf. *novaehollandiae* and *Exoediceroides maculosus*, and the polychaetes *Magelona* sp. and *Scolelepis lamellicincta*. There were significant differences in infaunal densities and species richness between the beach heights sampled, with both factors increasing with decreasing beach height over the intertidal zone. In general, insects were confined to upper beach heights, polychaetes were confined to lower beach heights, and different crustacean species spanned the entire intertidal beach. Significant temporal differences also existed in infaunal densities and species numbers at most of the beach heights sampled. These temporal differences were related to changes in the densities of common intertidal species. Only four of these common species (*S. physodes*, *C. sydneyensis*, *T.* cf. *novaehollandiae* and *E. maculosus*) exhibited any seasonal pattern in this temporal variation in density. Multivariate analysis of infaunal data failed to consistently separate beach heights into the universal zones previously proposed for sandy intertidal habitats. The unpredictable nature of biotic and abiotic influences on sandy intertidal infauna makes it unrealistic to expect to be able to consistently separate faunal assemblages on any given sampling occasion, with the exception of a characteristic fauna with terrestrial affinities that is confined to the upper beach. Any zonation patterns identified as being present on sandy beaches need to be qualified by the time of year in which data were collected.

Introduction

The vertical distribution of intertidal animals is rarely, if ever, random (Russell 1991). Non-randomness may be manifested in a variety of ways, but its most frequent expression is zonation. Maintenance of a characteristic tidal level (or zonation) on sandy shores by infauna was first noted by Stephen (1929, 1930) on Scottish beaches and was subsequently observed on other shores by various workers over the next 20 years (Bally 1983). A universal zonation scheme for beaches was subsequently proposed by Dahl (1952), who suggested that there were three sandy beach intertidal zones (which were essentially equivalent to the three zones recognized for rocky shores at the time) defined by the fauna living in each of those zones. The zones comprised: *(1)* a subterrestrial fringe characterized by the presence of air-breathing crustaceans, *(2)* a mid-littoral zone characterized by cirolanid isopods, and *(3)* a sublittoral fringe with a mixed fauna often characterized by oëdicerotid and phoxocephalid amphipods in the Southern Hemisphere and by a diversity of molluscs and polychaetes on all beaches. An alternative zonation scheme based on the degree of moisture in beach sediments was proposed by Salvat (1964, 1966, 1967). Salvat defined four zones: *(1)* a zone of drying or dry

sand wetted only by spray or by large waves at high-water spring tides, *(2)* a zone of retention reached by all tides where some moisture is always retained in the sand, *(3)* a zone of resurgence that is subject to considerable water movement during the rise and fall of the tide, and *(4)* a zone of saturation that is permanently saturated with water but has little interstitial water flow. Salvat's zonation scheme was confirmed and refined by Pollock and Hummon (1971), who further divided the zone of drying on a semi-protected beach into zones of dry and drying sand. More recently, Brown (1983) has suggested that there are only two indisputably universal zones present on sandy shores: an upper zone inhabited by *air-breathing* animals and a lower zone inhabited by *water-breathing* animals.

The application of universal zonation schemes to the infaunal distribution of a number of beaches worldwide has met with only limited success (e.g. Trevallion *et al.* 1970; Withers 1977; McLachlan 1980*a*, 1990; McLachlan *et al.* 1981; Shelton and Robertson 1981; Bally 1983; Wendt and McLachlan 1985; Allen and Moore 1987; Raffaelli *et al.* 1991), and this may be a consequence of temporal variation in the distribution of infauna on sandy shores. Many temperate sandy intertidal invertebrate species reproduce

seasonally (Crocker 1967; Holland and Polgar 1976; Dexter 1985), and as a consequence the structure of intertidal communities will vary seasonally depending on recruitment and mortality of dominant species (Holland and Polgar 1976; Dexter 1979; Shelton and Robertson 1981; Underwood 1981; Leber 1982). As a result, infaunal zonation patterns derived from data collected over a short time period (i.e. weeks or months) will not necessarily reflect the distribution of infauna at other times of the year. This temporal restriction on the applicability of a universal zonation scheme for sandy intertidal beaches has rarely been acknowledged when studies of sandy intertidal zonation have been undertaken (Shelton and Robertson 1981; Dexter 1984).

Approximately 1100 km of the 1700 km of Victorian coastline comprises sandy beaches (Fairweather 1990), so these represent an important component of the Australian marine ecosystem. However, there have been few ecological studies of Australian sandy beaches and most have emphasized the spatial distribution of infaunal assemblages across the beach face over a short time period (Dorsey 1982; Dexter 1983; McLachlan and Hesp 1984; McLachlan 1985; Shepherd et al. 1988; Wilson et al. 1990). The only Australian studies to include both spatial and temporal components are those by Dexter (1984, 1985), who investigated the spatial and temporal variability of fauna of New South Wales sandy beach habitats and the life histories of common intertidal species. This paucity of studies on sandy beaches is in marked contrast to Australian rocky intertidal shores, where detailed studies of the vertical distribution and population ecology of common species and their interactions have been carried out. These studies have made major conceptual contributions to the understanding of community ecology (reviewed by Underwood 1994). There is an urgent need for similar quantitative ecological studies on Australian sandy beaches, not just to understand the biodiversity of these habitats, but also to compare the spatial and temporal variability in biota with that recorded for rocky shores. In this study, the temporal (seasonal and annual) and spatial (vertical height on the beach face) patterns of the fauna on a Victorian sandy intertidal beach are described and the suitability of a universal zonation scheme to describe sandy intertidal infaunal distribution is discussed after consideration of the temporal variation.

Materials and Methods

Study Area

The study site is located in a sandy bay at Cape Paterson on the eastern Victorian coastline (Fig. 1). The bay is approximately 150 m long and has an average width of 50 m. The study site faces south-west to Bass Strait, although the oceanic swell is attenuated by a series of broken reefs that run out perpendicular to the shore, creating a wide, offshore surf zone. These subtidal reefs support dense algal communities that contribute highly variable quantities of wrack deposits to the upper sandy beach. The beach is morphodynamically dissipative (Short 1983) and has a slope of approximately 1:10. Wave action on the beach is slight and wave height

rarely exceeds 1 m. The spring tidal range is approximately 2 m and exposes up to 40 m of intertidal sand beach. The bay is one of several within the boundaries of the Bunurong Marine Park and is situated between eroding Cretaceous sandstone and mudstone cliffs.

Infaunal Sampling

A pilot study carried out in December 1988 indicated that five replicate samples, each of 0.38 m^2 surface area, would provide a good estimate (i.e. with a standard error less than 20% of the mean; Elliott 1979) of population densities of species collected from the sandy intertidal from all heights sampled on the beach. The sandy intertidal beach was subsequently sampled at three-monthly intervals on eight occasions over the period from March 1989 to December 1990. Infauna were collected at low spring tides along a transect running perpendicular to the beach. Most other sandy intertidal studies have also used a single transect sampled down the beach (Ansell et al. 1972; Withers 1977; McLachlan et al. 1979, 1981; Dye et al. 1981; Shelton and Robertson 1981; McLachlan 1985, 1990; Wendt and McLachlan 1985; Allen and Moore 1987; Eleftheriou and Robertson 1988). The main limitation to this approach is that the single transect cannot be used to represent the distribution and abundance of the infauna of the rest of the beach. The temporal and spatial (height) changes in community structure can, however, be described for this single transect location. Five replicate samples were collected at nine beach heights along the transect at 5-m intervals from 10 m above the high-tide swash line down to the low-water line during each survey. A circular sampling quadrat with a surface area of 0.38 m^2 was pushed into the sand to a depth of 15 cm at each of the 45 sampling points and the sand within each quadrat was excavated and washed through a 1-mm mesh. Retained organisms were preserved in buffered 4% formaldehyde in sea water for counting and identification in the laboratory. In March 1990, 15 replicates from Beach Heights 1, 4 and 5 were unable to be sampled, and as a consequence 345 samples (of a possible 360) were collected for infaunal analysis during the study.

Beach Profiles

The slope of the beach from the foredunes to the subtidal was measured on four occasions between December 1988 and June 1990 with a surveyor's level and staff, and beach profiles were constructed from this data. These profiles represent a dynamic equilibrium of offshore, onshore and longshore sediment movements occurring on the beach (McIntyre 1977). Observations were also made of wave action, the depth of any reduced (anaerobic) layer in the sand, and the presence of any permanent intertidal animal burrows. This information describing the physical and biological nature of the study site was used to rate the beach on the basis of exposure according to the scale proposed by McLachlan (1980b) and modified by Dexter (1983). A single sediment sample was collected from each beach height during each infaunal survey for grain size analysis.

Data Analysis

Data were inspected for gross deviations from normality and appropriate transformations were carried out ($\log_{10}$, $\log_{10}(x + 0.1)$ or square root) where necessary prior to analysis. All statistical computations were carried out with the aid of the SYSTAT V5.03 package (Wilkinson 1990). Two-factor analyses of variance (ANOVAs) by beach height and time showed significant interactions for both number of species ($F_{48, 252} = 6.48$, $P < 0.001$) and total infaunal density ($F_{48, 252} = 21.52$, $P < 0.001$). As recommended by Kirk (1995), simple main effects were analysed with one-way ANOVAs to compare species numbers and infaunal density between times for each height separately and between heights for each sampling time separately. Tukey HSD (honestly significant difference) multiple comparison tests, with an experiment-wise Type 1 error probability of 0.05, were used to locate any significant temporal and spatial differences.

Two-factor ANOVAs by height and time were not possible for individual species because none occurred at all heights, so one-way
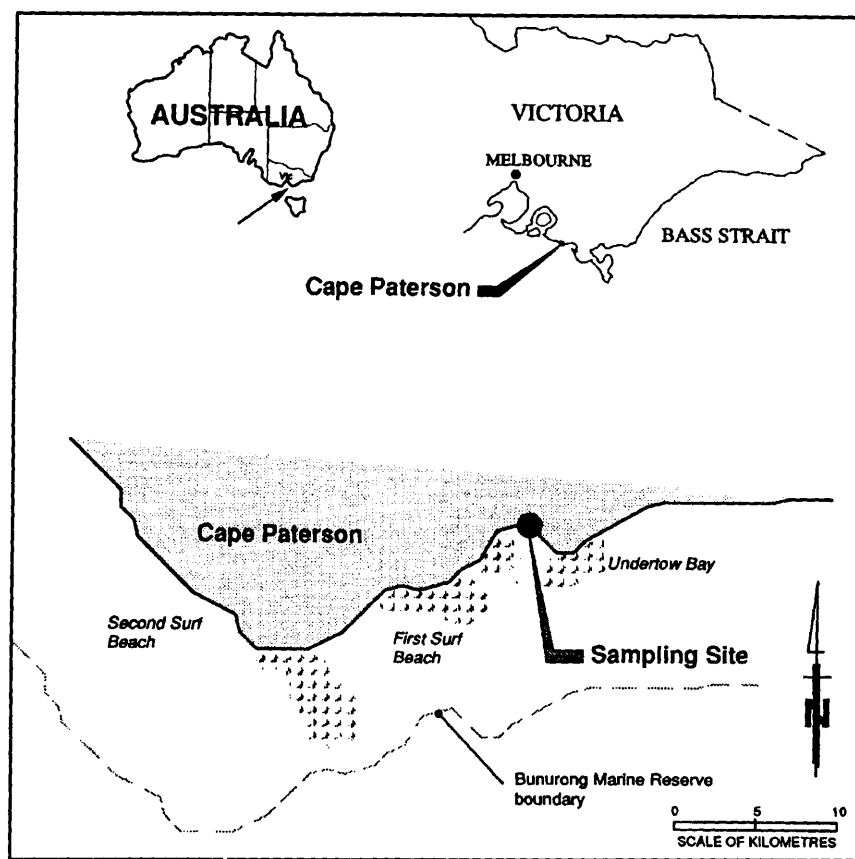
Fig. 1. Cape Paterson sampling site.

ANOVAs were used to compare the densities of common species over time, pooling samples from all beach heights where each species occurred. Multivariate techniques were applied to detect any natural groupings of beach heights for the infaunal data. Both cluster analysis (unpaired group mean averages, or UPGMA) and ordination (non-metric multidimensional scaling, or NMDS) on a Bray–Curtis distance matrix derived from root–root transformed means (Raffaelli et al. 1991) were used.

Results

Sediment Analysis

Cape Paterson beach sediments are composed predominantly of well sorted, medium sands that have an average median grain size of 0·376 mm. Well sorted beach sediments are typical of foreshore environments (Davis 1989). The study site scored 10 on the exposure scale of McLachlan (1980b) and Dexter (1983), rating as a sheltered environment. The beach profile at the study site was consistent over time (maximum change in sand height at any one location along the transect approximately 1 m), providing further evidence of the relatively protected nature of the intertidal foreshore, with little sand transport being detected during the survey period (Fig. 2).

Infaunal Community Structure

In total, 116495 individuals representing 41 species were collected during the period from March 1989 to December 1990. Eighteen of the species each contributed more than 0·01% of the total number of individuals collected over the sampling period (Table 1). The fauna of the site was numerically dominated by insects, particularly the dipteran *Chaetocoelopa sydneyensis*, which accounted for 75% of the total number of individuals collected. The isopod *Pseudolana concinna* was the second most abundant organism and accounted for over 11% of the total number of individuals collected. Other species collected in relatively high numbers included the isopod *Actaecia thomsoni*, the polychaetes *Magelona* sp. and *Scolelepis lamellicincta*, the coleopteran *Sphargeris physodes* and the amphipods *Talorchestia* cf. *novaehollandiae* and *Exoediceroides maculosus*. The intertidal habitat ranges of these species are presented in Table 1. Of the 18 relatively common species, only 11 were collected on all sampling occasions. None of these characteristic species spanned the entire intertidal zone, although some were more restricted than others. These

11 ubiquitous species may be used to characterize different tidal zones present along the sampling transect. In general, polychaetes (e.g. *Nephtys longipes* and *S. lamellicincta*) were restricted to lower beach heights, insects (e.g. *Sartallus signatus*, *Sphargeris physodes* and *C. sydneyensis*) were restricted to higher beach heights, and different crustacean species (e.g. *P. concinna*, *A. thomsoni*, *E. maculosus* and *Bumeralius buchalius*) spanned the entire intertidal.

Infaunal Zonation Patterns

There was a general pattern of greatest species richness and highest infaunal densities occurring at upper beach heights and the lowest densities and species richness occurring in the centre of the beach, immediately below the high-tide line (Fig. 3). Infaunal densities and species richness tended to increase with decreasing beach height over the true intertidal zone (Beach Heights 4 to 9) (Fig. 3). Significant differences in infaunal densities and species
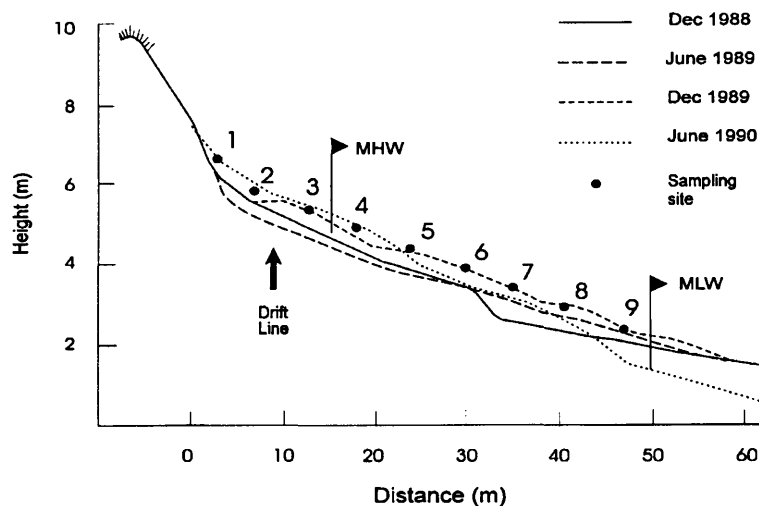
Fig. 2. Changes through time (December 1988 to June 1990) in the vertical profile of the Cape Paterson sampling site. MHW, mean high water; MLW, mean low water.
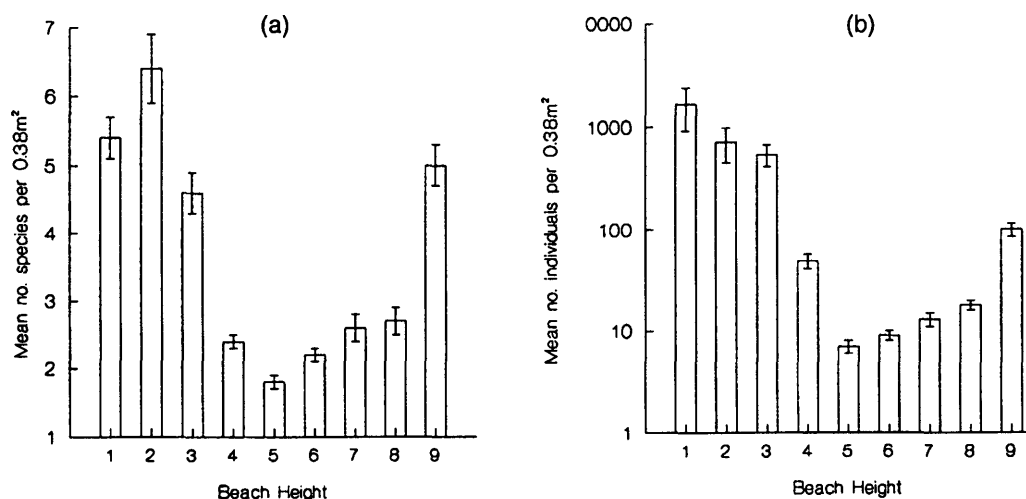
Fig. 3. Mean number (and standard error) of *(a)* species and *(b)* individuals at different beach heights, combining sampling times.

Table 1. Density and habitat range of species contributing > 0·01% of total individual numbers

Data set excludes March 1990 sample; total sampling area is 131·1 m²; intertidal range indicates where a species was found on the beach over the survey period; 100% occurrence indicates where a species was found on every survey

Species	Faunal group	Total no. individuals collected	% total no. individuals	Average density (no. m⁻²)	Total wet wt (g)	% total biomass	Intertidal range (beach height)	100% occurrence (beach height)
Chaetocoelopa sydneyensis	Diptera	86873	74·6	662	608	47·5	1–3	2
Pseudolana concinna	Isopoda	13348	11·5	102	140	10·9	1–6	3–6
Talorchestia cf. *novaehollandiae*	Amphipoda	5447	4·7	41	168	13·1	1–6	1
Actaecia thomsoni	Isopoda	2057	1·8	15·7	23	1·8	1–4	1–3
Scolelepis lamellicincta	Polychaeta	1518	1·3	11·6	53·8	4·2	6–9	8–9
Exoediceroides maculosus	Amphipoda	1502	1·3	11·5	3·3	0·3	5–9	7–9
Magelona sp.	Polychaeta	1436	1·2	10·9	117	9·1	8–9	
Sphargeris physodes	Coleoptera	1127	1·0	8·6	33	2·6	1–3	1–2
Talorchestia sp.	Amphipoda	583	0·5	4·4	6	0·5	1–3	
Bumeralius buchalius	Amphipoda	538	0·5	4·1	3·3	0·3	5–9	8–9
Glycera sp.	Polychaeta	265	0·2	2·0	71	5·6	4–8	4–6
Staphylininae sp. (larvae)	Coleoptera	235	0·2	1·8	0·1	0·01	1–3	
Leodamas fimbriatus	Polychaeta	137	0·1	1·0	1·2	0·1	9	
Sartallus signatus	Coleoptera	107	0·1	8·0	1·3	0·1	1–3	1
Anchistylis waitei	Cumacea	61	0·05	0·5	0·02	<0·01	7–9	
Cafius australis	Coleoptera	49	0·04	0·4	1·3	0·1	1–3	
Lumbrineris sp.	Polychaeta	40	0·03	0·3	5·5	0·4	7–9	
Nephtys longipes	Polychaeta	26	0·02	0·2	37·8	2·9	8–9	9

richness existed between beach heights on each sampling occasion (Table 2). *P. concinna* was the numerically dominant species on all sampling occasions except June and September 1990, when *C. sydneyensis* occurred in very high numbers (Table 2). A cluster analysis and NMDS were derived separately for each sampling occasion to examine the natural groupings of beach heights at different times. The cluster and ordination analyses produced very similar patterns that were reasonably consistent through time, and only the NMDS results representing the most different times are presented in Fig. 4. Interpretation of ordination plots (and cluster dendograms) is necessarily subjective (Kent and Coker 1992), although the first axis of the NMDS was consistent with beach height for all sampling times. A grouping of the upper three beach heights (i.e. Heights 1 to 3) separately from the rest was apparent, from both the cluster and the ordination analyses (Fig. 4a), at all times except December of both years, and this group occasionally included Height 4 (e.g. June and September 1989). Separation of beach heights within these groups (i.e. 1 to 3, rest) by cluster analyses varied through time, although the two lowest heights (8 and 9) tended to remain separated from the other heights on most occasions. In December 1989 and 1990, beach heights were spread along Axis 1 with no clear groupings (Fig. 4b).

Temporal Infaunal Variation

Greatest species richness and highest infaunal densities tended to occur in autumn and spring (Fig. 5). Significant temporal differences in average infaunal densities existed at each of the beach heights sampled over the survey period (Table 3). Significant differences in average species richness were also present at all beach heights sampled except Heights 5 and 8 (Table 3). Tukey tests indicated that there were no consistent seasonal patterns associated with temporal changes in either species richness or infaunal densities at any of the beach heights sampled. Any significant temporal change in average infaunal densities that occurred over the two-year sampling period at each beach height was related to significant changes in the densities of common species (Fig. 6). These species included *S. physodes* ($F_{6,98} = 3.00$, $P = 0.010$), *C. sydneyensis* ($F_{6,98} = 7.12$, $P < 0.001$), *T.* cf. *novaehollandiae* ($F_{6,98} = 9.48$, $P < 0.001$), *E. maculosus* ($F_{6,168} = 6.54$, $P < 0.001$), *S. lamellicincta* ($F_{7,152} = 2.67$, $P = 0.012$) and *Magelona* sp. ($F_{7,72} = 2.84$, $P = 0.011$). Only four of these species exhibited any apparent seasonal pattern in this temporal variation. Average densities of *S. physodes* were highest in autumn and spring samples collected in both years, although these peak values were not significantly different from densities recorded at other times of the year (Fig. 6a).

Table 2. Summary of ANOVAs comparing species richness and total abundance across transect heights for each sampling date separately
*$0.01 < P < 0.05$, **$0.001 < P < 0.01$, ***$P < 0.001$

| Sampling date	Mean (s.d.) number of species per 0.38 m²	Mean (s.d.) number of individuals per 0.38 m²	ANOVA F test, change in species numbers over height	ANOVA F test, change in infaunal densities over height	Dominant species (% total for sampling date)
Mar. 1989	4.6 (2.8)	243 (458)	$F = 24.26$***	$F = 97.11$***	*P. concinna* (61%) *C. sydneyensis* (24%)
June 1989	3.6 (1.7)	99 (116)	$F = 21.90$***	$F = 35.81$***	*P. concinna* (32%) *Magelona* sp. (21%) *T.* cf. *novaehollandiae* (11%) *S. lamellicincta* (12%)
Sept. 1989	3.9 (2.5)	146 (234)	$F = 13.89$***	$F = 36.93$***	*P. concinna* (33%) *C. sydneyensis* (23%) *T.* cf. *novaehollandiae* (22%)
Dec. 1989	3.4 (1.8)	46 (53)	$F = 30.51$***	$F = 33.53$***	*P. concinna* (52%) *E. maculosus* (14%) *S. lamellicincta* (8%)
June 1990	3.1 (2.2)	324 (774)	$F = 13.19$***	$F = 35.92$***	*T.* cf. *novaehollandiae* (7%) *C. sydneyensis* (87%)
Sept. 1990	4.0 (2.4)	1628 (4130)	$F = 18.58$***	$F = 118.09$***	*T.* cf. *novaehollandiae* (2%) *C. sydneyensis* (95%)
Dec. 1990	3.6 (1.9)	79 (101)	$F = 19.74$***	$F = 33.43$***	*P. concinna* (28%) *E. maculosus* (27%) *T.* cf. *novaehollandiae* (21%) *A. thomsoni* (9%)
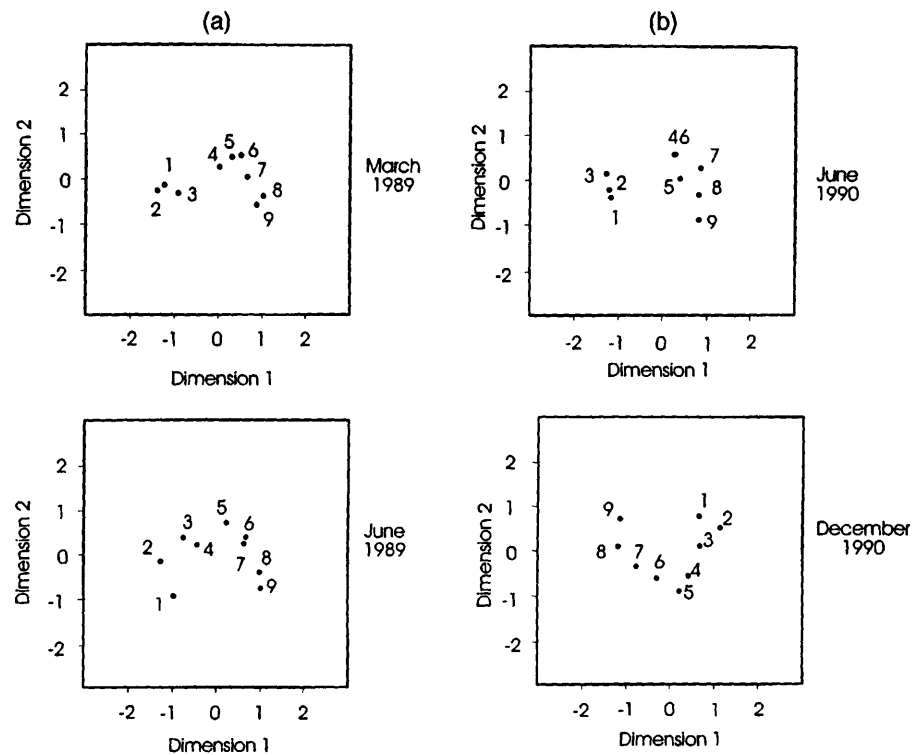
Fig. 4. (a) NMDS plots for March (stress 0·04) and June (stress 0·02) 1989. (b) NMDS plots for June (stress 0·02) and December (stress 0·05) 1990.
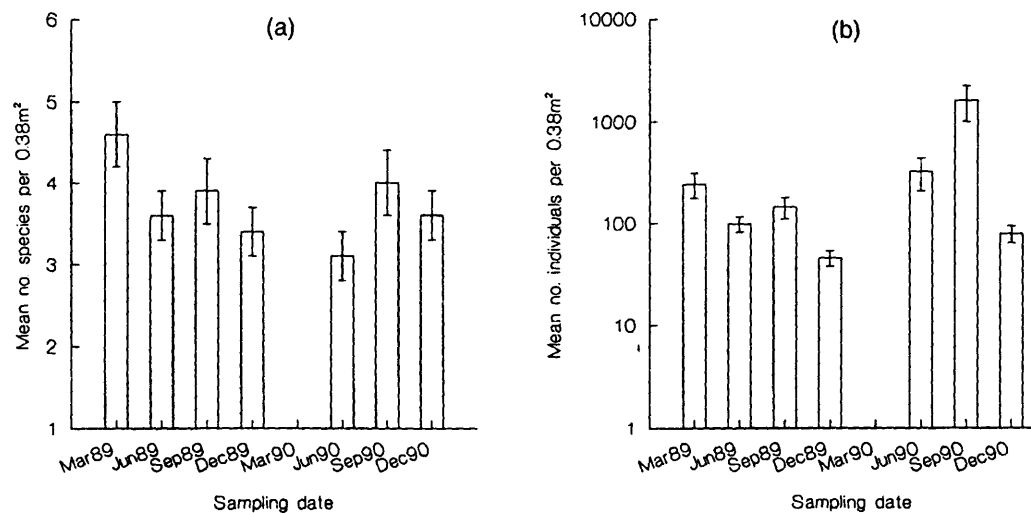

Fig. 5. Mean number (and standard error) of (a) species and (b) individuals at different sampling times, combining beach heights.

Average densities of *C. sydneyensis* were lowest in the December samples and exhibited wide fluctuations at other times of the year (Fig. 6b). Average densities of *T.* cf. *novaehollandiae* increased over the period June to September in both sampling years, with minimum numbers being recorded in both December samples (Fig. 6c). Similarly, average densities of *E. maculosus* tended to increase over the period June to December in both years (Fig. 6d).

Table 3. Summary of ANOVAs comparing species richness and total abundance across sampling dates for each transect height separately
$*0.01 < P < 0.05$, $**0.001 < P < 0.01$, $***P < 0.001$

Beach height	Mean (s.d.) number of species per 0.38 m^2	Mean (s.d.) number of individuals per 0.38 m^2	ANOVA F test, change in species numbers over time	ANOVA F test, change in infaunal densities over time	Dominant species (% of total for beach height)
1	5.0 (1.9)	1542 (4131)	$F = 4.64**$	$F = 92.52***$	C. sydneyensis (93%) T. cf. novaehollandiae (4%) P. concinna (1%)
2	6.0 (3.1)	643 (1593)	$F = 34.92***$	$F = 35.92***$	C. sydneyensis (79%) T. cf. novaehollandiae (11%) P. concinna (3%) A. thomsoni (3%)
3	4.8 (1.7)	511 (762)	$F = 7.15***$	$F = 19.28***$	C. sydneyensis (44%) T. cf. novaehollandiae (6%) P. concinna (46%)
4	2.2 (0.9)	43 (46)	$F = 10.71***$	$F = 41.07***$	P. concinna (90%) A. thomsoni (3%) Glycera sp. (5%)
5	2.1 (1.0)	9 (8)	$F = 0.85$	$F = 4.01**$	B. buchalius (50%) P. concinna (32%) Glycera sp. (11%)
6	2.4 (0.8)	9 (7)	$F = 2.94*$	$F = 13.70***$	P. concinna (26%) Glycera sp. (24%) B. buchalius (28%) E. maculosus (18%)
7	2.6 (1.2)	13 (11)	$F = 8.51***$	$F = 9.25***$	E. maculosus (16%) B. buchalius (37%) S. lamellicincta (30%)
8	2.8 (1.1)	17 (15)	$F = 0.86$	$F = 9.47***$	S. lamellicincta (73%) E. maculosus (19%) B. buchalius (9%)
9	5.0 (1.7)	96 (93)	$F = 8.13***$	$F = 55.52***$	Magelona sp. (38%) S. lamellicincta (3%) E. maculosus (23%)

Discussion

Infaunal Zonation

The spatial characteristics of the macrofauna of the study site at Cape Paterson are similar to those found on sheltered beaches at other coastal locations around Australia and elsewhere. Similarities with other beaches include: *(1)* an increase in species diversity with decreasing tidal height (McLachlan 1977; Dexter 1979, 1983, 1984), *(2)* an increase in infaunal density with decreasing tidal height (Dexter 1979, 1983, 1984), *(3)* differences in faunal composition at different beach heights (Dexter 1979, 1984; Bally 1983; McLachlan 1983, 1990; Eleftheriou and Robertson 1988), and *(4)* the occurrence of characteristic groups of animals at different tidal heights down the beach slope (Dahl 1952; Trevallion *et al.* 1970; Dexter 1983, 1984). Characteristic faunal groups at the Cape Paterson study site include coleopterans, amphipods and a cirolanid isopod species above the high-tide swash line, the same cirolanid isopod and an exoedicerotid amphipod at mid-tidal heights, and a relatively diverse fauna, including polychaetes, at lower tidal heights.

Differences in community structure between seasons in this study cannot be unambiguously interpreted as real seasonal patterns because, as in most marine benthic studies, only a single time was sampled in each season (see critical review of this problem by Morrisey *et al.* 1993). This notwithstanding, the significant variation over time in infaunal densities at the Cape Paterson site was a result of change in the density of dominant species present at each beach height sampled. Only four of the common species (*C. sydneyensis, S. physodes, T. cf. novaehollandiae* and *E. maculosus*), which varied significantly in density over time at all beach heights, showed any consistency between years in the variation in densities between seasons. Large fluctuations in the density of *C. sydneyensis*, with smallest numbers present in December, is consistent with observations of a similar European species (*Coelopa* sp.) (Dobson 1976). Dobson noted that high densities of *Coelopa* sp. were associated with winter storm wrack and that entire insect populations could be wiped out when wrack was washed away by storm activity. Densities of *E. maculosus* tended to increase from June to December at
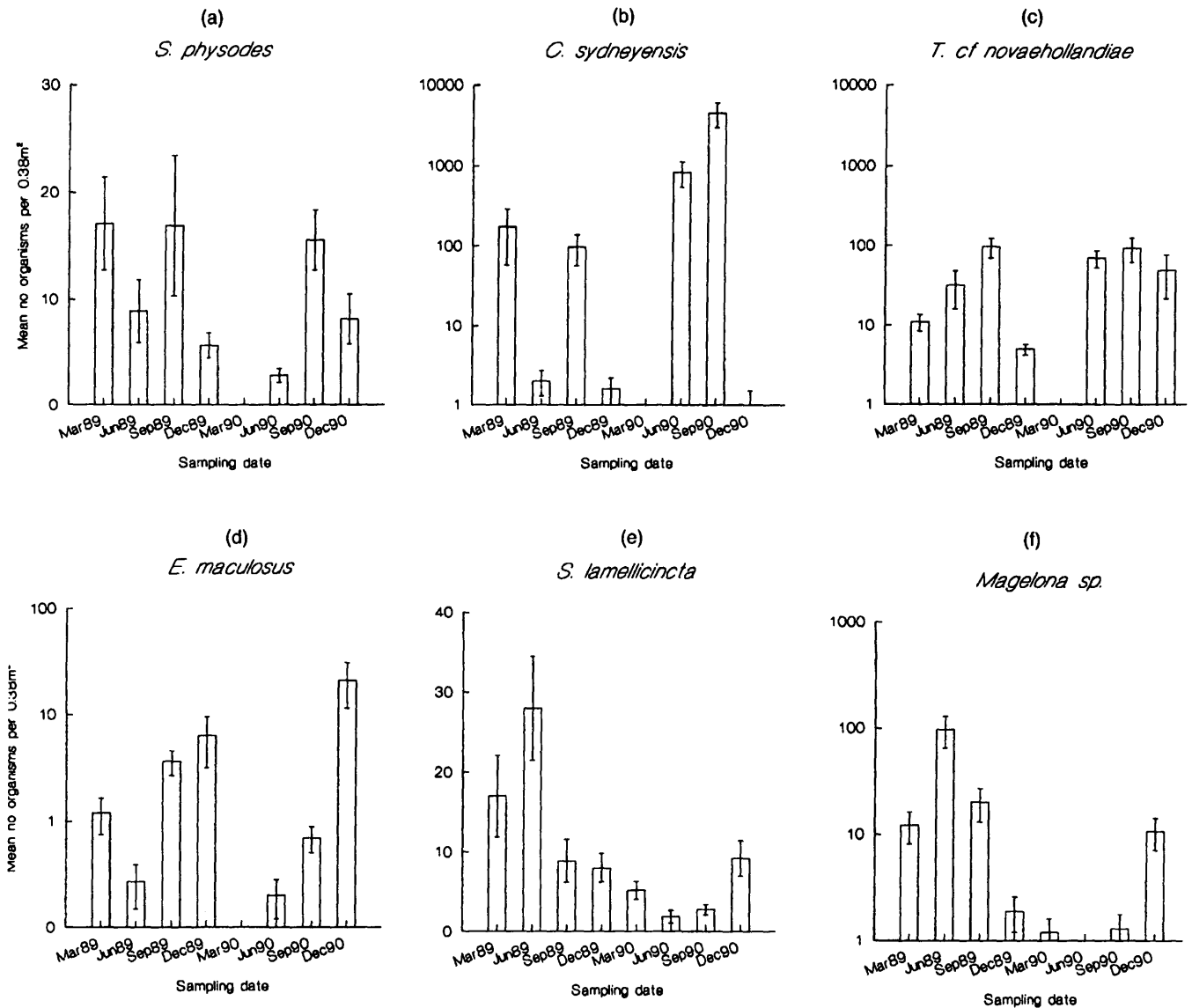
Fig. 6. Mean number (and standard error) of (a) *S. physodes*, (b) *C. sydneyensi*, (c) *T.* cf. *novaehollandiae*, (d) *E. maculosus*, (e) *S. lamellicincta* and (f) *Magelona* sp. at different sampling times, combining beach heights.

Cape Paterson, suggesting that recruitment was occurring over this period. This species is reproductively active in spring and autumn on New South Wales beaches, although gravid females may be recovered at other times of the year (Dexter 1985). Only one other study (Dexter 1984) has examined seasonal variation in intertidal community structure on Australian beaches. Dexter (1984) also found that, when present, temporal variation in infaunal densities occurred as a result of changes in the densities of dominant (amphipod, isopod and polychaete) species present at her study sites. However, Dexter (1984) concluded that the limited data available on the physical characteristics of the study sites did not suggest predictable seasonality in changes in infaunal populations.

Universal zonation schemes proposed for sandy intertidal habitats to date by Dahl (1952), Salvat (1967) and Brown (1983), defined by either the characteristic fauna or the moisture content of beach sands, can be compared with intertidal zones identified at Cape Paterson (Fig. 7). Both multidimensional scaling and cluster analysis clearly distinguished an upper zone on the Cape Paterson beach characterized by the presence of a fauna dominated by insects, notably the dipteran *C. sydneyensis,* the tenebrionid beetle *S. physodes* and the staphylinid beetle *S. signatus.* An actaecid isopod (*A. thomsoni*) and two talitrid amphipods (*T.* cf. *novaehollandiae* and *Talorchestia* sp.) were also present in the upper beach heights at Cape Paterson. The relatively rich fauna at high-tide levels on the Cape Paterson beach is
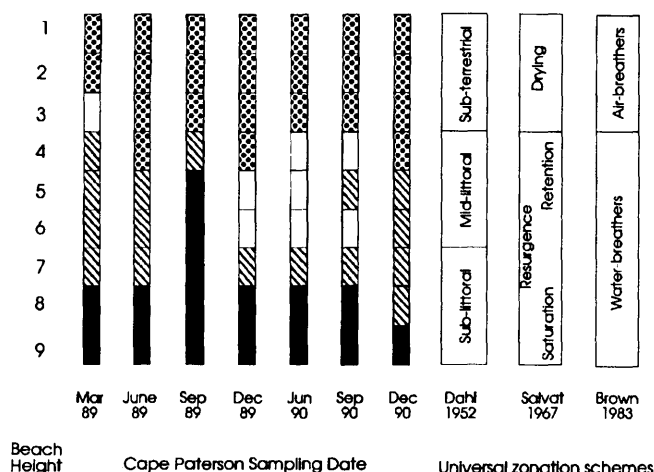
Fig. 7. Comparison of zonation pattern of the fauna at the site at Cape Paterson with the proposed universal infaunal zonation schemes for sandy beaches.

probably related to the presence of wrack, as another study has shown increased species richness when beach wrack was present (Griffiths *et al.* 1983). The genus *Talorchestia* is restricted to the zone of drying (Brown and McLachlan 1990), and upper beach heights sampled at Cape Paterson, with a fauna with terrestrial affinities, are therefore equivalent to Dahl's (1952) subterrestrial fringe, Salvat's (1967) zone of drying and Brown's (1983) zone of air-breathers.

Separation of zones lower down the beach face at Cape Paterson is difficult. On most occasions (except September 1989 and December 1990), the two lowest sampling sites characterized by the presence of polychaetes (notably *Lumbrineris* sp., *Nephtys longipes*, *Magelona* sp. and *Leodamas fimbriatus*) separated out from other mid to low intertidal sites. The comparatively high species richness and the dominance of polychaete species at the lower beach heights equates this lower zone to Dahl's (1952) sublittoral fringe and Salvat's (1967) zone of saturation. In contrast to Dahl's (1952) prediction, phoxocephalid amphipods were not usually found in this zone at Cape Paterson.

Subdivision of the central intertidal region at Cape Paterson is also problematic. On four of the seven sampling occasions (March 1989, June 1989, June 1990 and December 1990), the central beach sampling heights grouped as one zone. In September 1989, the central sampling heights grouped with the lower intertidal sampling sites, and in December 1989 and September 1990, no clear group was apparent in the central intertidal area (see Fig. 7). The dominant species of the central intertidal zone were the cirolanid isopod *P. concinna* (which equates the central intertidal region at Cape Paterson with Dahl's 1952 mid-littoral zone) and the polychaetes *Glycera* sp. and *S. lamellicincta*. *Glycera* is a cosmopolitan polychaete genus

found on sandy beaches in both Northern and Southern Hemispheres (Brown and McLachlan 1990) and is most commonly found in the lower tidal resurgence and saturation zones (Brown and McLachlan 1990). *Scolelepis* is characteristically found in the zone of retention (Brown and McLachlan 1990). The distribution of these two polychaetes on the beach at Cape Paterson is therefore the reverse of that commonly encountered elsewhere. Similarly, studies by Dexter (1984) also found that the distribution of *Scolelepis carunculata* on other Australian beaches did not conform to the typical zonation pattern described by Brown and McLachlan (1990).

This study indicates clearly that Cape Paterson beach fauna community structure is dynamic and variable, and as a consequence zonation patterns are not necessarily clearly defined; two zones are always distinguishable, three zones are often distinguishable, but four zones are unlikely to be distinguishable. The study also indicates that any zonation patterns present need to be qualified by the time of year in which the data were collected. Large temporal variation (over a few years) in the abundance of dominant species has also been described for rocky intertidal shores (Underwood 1994), and seasonal variations in abundance on these shores have been well documented (Underwood 1981). This variability can result from temporal patchiness in settlement and recruitment patterns (Underwood and Denley 1984) and from seasonal variations in interactions (Underwood 1994). In the current study, fluctuations through time at the community level in species diversities and infaunal densities are clearly influenced by the population dynamics of the numerically abundant species (Holland and Polgar 1976; Dexter 1984). Zonation patterns will also be complicated by the mobility of the fauna preventing zones having sharp boundaries (McLachlan 1983) and by storms creating random, abiotic physical disturbance resulting in removal (or movement) of individuals (Tamaki 1987; McLachlan 1988), depletion of species diversities (Lake 1990), and differences in sediment characteristics (Thrush *et al.* 1989). In particular, the seasonal occurrence of small waves in summer and heavy waves in winter is a general phenomenon found on many temperate intertidal sand beaches (Tamaki 1987) and may be an important factor in determining seasonal change in the distribution of macrobenthic animals living in these environments. Resource heterogeneity (including localized food concentrations caused by the movement and deposition of drift algae) can also contribute to the creation of a highly dynamic mosaic of habitat patches on a beach. Spatial patterns of infaunal distribution may also be influenced by a variety of biotic factors, including active biological aggregations and larval settlement. Underwood (1994) has emphasized that zones containing sets of species do not really exist on rocky intertidal shores, and except for a few

characteristic faunal species with terrestrial affinities confined to the upper beach, consistent zonation was not apparent at the sandy beach site sampled in the present study. Further studies are now needed to examine the influences of temporal and spatial variability in patterns of larval settlement, aggregation and interactions between faunal species on sandy beach ecology.

Acknowledgments

References

Allen, P. L., and Moore, J. J. (1987). Invertebrate macrofauna as potential indicators of sandy beach instability. *Estuarine, Coastal and Shelf Science* 24, 109–25.

Ansell, A. D., Sivadas, P., Narayanan, B., Sankaranarayanan, V. N., and Trevallion, A. (1972). The ecology of two sandy beaches in south west India. I. Seasonal changes in physical and chemical factors, and in the macrofauna. *Marine Biology (Berlin)* 17, 38–62.

Bally, R. (1983). Intertidal zonation on sandy beaches of the west coast of South Africa. *Cahiers de Biologie Marine* 24, 85–103.

Brown, A. C. (1983). The ecophysiology of sandy beach animals—a partial review. In 'Sandy Beaches as Ecosystems'. (Eds A. McLachlan and T. Erasmus.) pp. 575–605. (Junk: The Hague.)

Brown, A. C., and McLachlan, A. (1990). 'Ecology of Sandy Shores.' (Elsevier: Amsterdam.)

Crocker, R. A. (1967). Niche diversity in five sympatric species of intertidal amphipods (Crustacea:Haustoriidae). *Ecological Monographs* 37, 173–200.

Dahl, E. (1952). Some aspects of the ecology and zonation of the fauna on sandy beaches. *Oikos* 4, 1–27.

Davis, R. A. (1989). Texture, composition and provenance of beach sands, Victoria, Australia. *Journal of Coastal Research* 5, 37–47.

Dexter, D. M. (1979). Community structure and seasonal variation in intertidal Panamanian sandy beaches. *Estuarine and Coastal Marine Science* 9, 543–58.

Dexter, D. M. (1983). Community structure of intertidal sandy beaches in New South Wales, Australia. In 'Sandy Beaches as Ecosystems'. (Eds A. McLachlan and T. Erasmus.) pp. 461–72. (Junk: The Hague.)

Dexter, D. M. (1984). Temporal and spatial variability in the community structure of the fauna of four sandy beaches in south-eastern New South Wales. *Australian Journal of Marine and Freshwater Research* 35, 663–72.

Dexter, D. M. (1985). Distribution and life histories of abundant crustaceans of four sandy beaches of south-eastern New South Wales. *Australian Journal of Marine and Freshwater Research* 36, 281–9.

Dobson, T. (1976). Seaweed flies (Diptera:Coelopidae, etc.). In 'Marine Insects'. (Ed. L. Cheng.) pp. 447–63. (North Holland Publishing: Amsterdam.)

Dorsey, J. H. (1982). Intertidal community offshore from the Werribee sewage-treatment farm: an opportunistic infaunal assemblage. *Australian Journal of Marine and Freshwater Research* 33, 45–54.

Dye, A. H., McLachlan, A., and Wooldridge, T. (1981). The ecology of sandy beaches in Natal. *South African Journal of Zoology* 16, 200–9.

Eleftheriou, A., and Robertson, M. R. (1988). The intertidal fauna of sandy beaches—a survey of the east Scottish coast. Scottish Fisheries Research Report No. 38.

Elliott, J. M. (1979). 'Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates.' 2nd Edn. Freshwater Biological Association Scientific Publication No. 25. (Ambleside, UK.)

Fairweather, P. G. (1990). Ecological changes due to our use of the coast: research needs versus effort. *Proceedings of the Ecological Society of Australia* 16, 71–7.

Griffiths, C. L., Stenton-Dozey, J. M. E., and Koop, K. (1983). Kelp wrack and the flow of energy through a sandy beach ecosystem. In 'Sandy Beaches as Ecosystems'. (Eds A. McLachlan and T. Erasmus.) pp. 547–56. (Junk: The Hague.)

Holland, A. F., and Polgar, T. T. (1976). Seasonal changes in the structure of an intertidal community. *Marine Biology (Berlin)* 37, 341–8.

Kent, M., and Coker, P. (1992). 'Vegetation Description and Analysis.' (CRD Press: London.)

Kirk, R. E. (1995). 'Experimental Design: Procedures for the Behavioural Sciences.' (Brooks/Cole: USA.)

Lake, P. S. (1990). Disturbing hard and soft bottom communities: a comparison of marine and freshwater environments. *Australian Journal of Ecology* 15, 477–88.

Leber, K. M. (1982). Seasonality of macroinvertebrates on a temperate, high wave energy sandy beach. *Bulletin of Marine Science* 32, 86-98.

McIntyre, A. D. (1977). Sandy foreshores. In 'The Coastline'. (Ed. R. S. K. Barnes.) pp. 31–47. (Wiley: Chichester.)

McLachlan, A. (1977). Composition, distribution, abundance and biomass of the macrofauna and meiofauna of four sandy beaches. *Zoologica Africana* 12, 279–306.

McLachlan, A. (1980a). Intertidal zonation of macrofauna and stratification of meiofauna on high energy beaches in the Eastern Cape, South Africa. *Transactions of the Royal Society of South Africa* 44, 213–23.

McLachlan, A. (1980b). The definition of sandy beaches in relation to exposure: a simple rating system. *South African Journal of Science* 76, 137–8.

McLachlan, A. (1983). Sandy beach ecology—a review. In 'Sandy Beaches as Ecosystems'. (Eds A. McLachlan and T. Erasmus.) pp. 321–80. (Junk: The Hague.)

McLachlan, A. (1985). The biomass of macro- and interstitial fauna on clean and wrack-covered beaches in Western Australia. *Estuarine, Coastal and Shelf Science* 21, 587–99.

McLachlan, A. (1988). Behavioural adaptions of sandy beach organisms: an ecological perspective. In 'Behavioural Adaption to Intertidal Life'. (Eds G. Chelazzi and M. Vannini.) pp. 449–75. (Plenum: New York.)

McLachlan, A. (1990). Dissipative beaches and macrofauna communities on exposed intertidal sands. *Journal of Coastal Research* 6, 57–71.

McLachlan, A., and Hesp, P. (1984). Faunal response to morphology and water circulation of a sandy beach with cusps. *Marine Ecology Progress Series* 19, 133–44.

McLachlan, A., Wooldridge, T., and Van der Horst, G. (1979). Tidal movements of the macrofauna on an exposed sandy beach in South Africa. *Journal of Zoology (London)* 187, 433–42.

McLachlan, A., Wooldridge, T., and Dye, A. H. (1981). The ecology of sandy beaches in southern Africa. *South African Journal of Zoology* 16, 219–31.

Morrisey, D. J., Underwood, A. J., Howitt, L., and Stark, J. S. (1993). Temporal variation in soft-sediment benthos. *Journal of Experimental Marine Biology and Ecology* 164, 233–45.

Pollock, L. W., and Hummon, W. D. (1971). Cyclic changes in interstitial water content, atmospheric exposure and temperature in a marine beach. *Limnology and Oceanography* **16**, 522–35.

Raffaelli, D., Karakassis, I., and Galloway, A. (1991). Zonation schemes on sandy shores: a multivariate approach. *Journal of Experimental Marine Biology and Ecology* **148**, 241–53.

Russell, G. (1991). Vertical distribution. In 'Intertidal and Littoral Ecosystems; Intertidal Ecosystems of the World 24'. (Eds A. C. Mathieson and P. H. Nienhuis.) pp. 43–65. (Elsevier: Amsterdam.)

Salvat, B. (1964). Les conditions hydrodynamiques interstitielles des sédiments meubles intertidaux et la répartition verticale de la fauna endogenée. *Compte rendu hebdomadaire des Séances de l'Academie des Sciences Paris* **259**, 1576–9.

Salvat, B. (1966). *Eurydice pulchra* (Leach 1815) et *Eurydice affinis* (Hansen 1905) (Isopodes:Cirolanidae): taxonomie, éthologie, répartition verticale et cycle réproducteur. *Actes de la Société Linnénne de Bordeaux A* **193**, 1–77.

Salvat, B. (1967). La macrofauna carcinologique endogenée des sédiments meubles intertidaux (Tanaidaces, Isopodes et Amphipodes): éthologie, bionomie et cycle biologique. *Mémoires du Muséum National d'Histoire Naturelle, Série A* **45**, 1–275.

Shelton, C. R., and Robertson, P. B. (1981). Community structure of intertidal macrofauna on two surf-exposed Texas sandy beaches. *Bulletin of Marine Science* **31**, 833–42.

Shepherd, R. A., Knott, B., and Eliot, I. G. (1988). The relationship of juvenile southern mole crabs *Hippa australis* Hale (Crustacea:Anamura:Hippidae) to surficial swash water-circulation over several diurnal spring-tide cycles during winter conditions on a micro-tidal sandy beach. *Journal of Experimental Marine Biology and Ecology* **121**, 209–25.

Short, A. D. (1983). Sediments and structures in beach–nearshore environments, south east Australia. In 'Sandy Beaches as Ecosystems'. (Eds A. McLachlan and T. Erasmus.) pp. 145–56. (Junk: The Hague.)

Stephen, A. C. (1929). Studies on the Scottish marine fauna: the fauna of the sandy and muddy areas of the tidal zone. *Transactions of the Royal Society of Edinburgh* **56**, 291–306.

Stephen, A. C. (1930). Studies on the Scottish marine fauna: additional observations of the fauna of sandy and muddy areas of the tidal zone. *Transactions of the Royal Society of Edinburgh* **56**, 521–35.

Tamaki, A. (1987). Comparison of resistivity to transport by wave action in several polychaete species on an intertidal sand flat. *Marine Ecology Progress Series* **37**, 181–9.

Thrush, S. F., Hewitt, J. E., and Pridmore, R. D. (1989). Patterns in the spatial arrangements of polychaetes and bivalves in intertidal sandflats. *Marine Biology (Berlin)* **102**, 529–35.

Trevallion, A., Ansell, A. D., Sivadas, P., and Narayanan, B. (1970). A preliminary account of two sandy beaches in south west India. *Marine Biology (Berlin)* **6**, 268–79.

Underwood, A. J. (1981). Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *Journal of Experimental Marine Biology and Ecology* **51**, 57–85.

Underwood, A. J. (1994). Rocky intertidal shores. In 'Marine Biology'. (Eds L. S. Hammond and R. N. Synnot.) pp. 272–96. (Longman Cheshire: Melbourne.)

Underwood, A. J., and Denley, E. J. (1984). Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In 'Ecological Communities: Conceptual Issues and the Evidence'. (Eds D. J. Strong Jr, D. Simberloff, L. G. Abele and A. B. Thistle.) pp. 151–80. (Princeton University Press: Princeton.)

Wendt, G. E., and McLachlan, A. (1985). Zonation and biomass of the intertidal macrofauna along a South African beach. *Cahiers de Biologie Marine* **26**, 1–14.

Wilkinson, L. (1990). 'SYSTAT: The System for Statistics.' (Systat, Inc.: Evanston, IL.)

Wilson, R. S., Poore, G. C. B., and Gomon, M. F. (1990). Marine habitats at Wilsons Promontory and the Bunurong Coast, Victoria: report on a survey, 1982. Victorian Marine Science Laboratories Technical Report No. 73.

Withers, R. G. (1977). Soft shore macrobenthos along the south-west coast of Wales. *Estuarine and Coastal Marine Science* **5**, 467–84.