Community structure on sandy beaches: patterns of richness and zonation in relation to tide range and latitude

Estructura comunitaria de playas arenosas: patrones de diversidad
y zonación en relación a rango mareal y latitud

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ABSTRACT

Recent studies have shown a consistent increase in species richness, abundance and biomass of intertidal macrobenthos over a range of micro/mesotidal sandy beaches from reflective to dissipative conditions. However, beaches occur in a continuum of morphodynamic forms beyond mesotidal dissipative in macrotidal areas: these are ultradissipative beaches and tide flats, where tides take over from waves as the controlling force. This paper tests the hypotheses: 1) that species richness, abundance and biomass continue increasing and 2) that more than three faunal zones may be distinguished on beaches on the above continuum beyond the mesotidal dissipative type, and also examines the hypothesis: 3) that temperate beaches are richer in species than tropical beaches. Two temperate, microtidal, dissipative beaches and four tropical, macrotidal, ultradissipative to tidal flat beaches in Australia were quantitatively surveyed with a total sampling area of 4.5 m^2 each. The results, when plotted against an index of beach state, indicate that species richness continued to increase over this range of beach types and especially strongly towards the tidal flat. Abundance also increased, but only weakly towards the tidal flat and biomass showed a decreasing trend. The tropical beaches (15-30 species) supported richer faunas than the temperate (12 species) beaches. Similar response to an index of beach state by communities from widely differing regions and latitudes suggests that species richness is probably mainly a function of beach type and latitude may play a minor role. Zonation was indistinct in most cases and no more than three zones could be distinguished on any of the beaches. It appears that in macrotidal regimes, where tides take over from waves as the force controlling beaches, intertidal climate becomes more benign, leading to the presence of species that construct semi-permanent burrows, the attainment of high diversity and thus the development of suitable conditions for biological interactions to play a greater role in community organisation than on microtidal, wave-dominated beaches.

Key words: Sandy beaches, macrobenthos, community organization, Australia.

RESUMEN

Estudios recientes muestran un incremento consistente en la riqueza específica, abundancia y biomasa del macrobento intermareal a lo largo de un rango de playas arenosas micro/mesomareales, desde condiciones reflectivas a disipativas. Sin embargo, las playas ocurren en un continuum de formas morfodinámicas que van más allá de sitios disipativos mesomareales: estas son las playas ultradisipativas y planicies mareales de características macromareales, donde como fuerza de control las mareas son más importantes que las olas. Se ponen a prueba las siguientes hipótesis: 1) riqueza, abundancia y biomasa de especies sigue aumentando desde sitios disipativos mesomareales a macromareales, 2) más allá del tipo disipativo mesomareal se distinguen más de tres zonas faunísticas en el intermareal, y 3) playas temperadas tienen mayor riqueza de especies que playas tropicales. Dos playas temperadas, micromareales y disipativas, y cuatro sitios tropicales, macromareales, ultradisipativos a planicies mareales se muestrearon en Australia (área total de muestreo de 4,5 m^2 por playa). Los resultados indican que la riqueza de especies sigue aumentando a lo largo del rango estudiado y especialmente hacia la planicie mareal analizada. La abundancia también aumenta, pero débilmente hacia esa planicie, a la vez que la biomasa muestra una tendencia de disminución. Las playas tropicales (15-30 especies) presentan mayor riqueza de especies que las temperadas (12 especies). Similares respuestas a un índice del estado de una playa en comunidades de diferentes regiones y latitudes, sugieren que la riqueza de especies es probablemente una función del tipo de playa siendo la latitud un factor de menor importancia. La zonación no fue diferente en la mayoría de los casos y no se distinguieron más de tres zonas en todas las playas. Parece ser que en regiones macromareales, donde las mareas llegan a ser más importantes que las olas, el clima intermareal llega a ser más benigno, lo que resulta en la presencia de especies que construyen habitáculos semipermanentes y el logro de una alta diversidad, y por lo tanto el desarrollo de condiciones apropiadas que juegan un rol más importante en la organización comunitaria que aquél de playas micromareales dominadas por el oleaje.

Palabras clave: Playas arenosas, macrobentos, organización comunitaria, Australia.

INTRODUCTION

Being the most dynamic of soft bottom habitats, high energy ocean beaches provide an unique opportunity for ecologists to decipher the underlying influences of the two physical elements of marine depositional environments, sediment properties and hydrodynamics, on macrobenthic fauna. We envisage a continuum in hydrodynamic exposure levels of intertidal sediments that progresses from low energy tidal mud and sand flats via ultradissipative, dissipative and intermediate beaches to reflective beaches as the wave dominated extreme. Recent studies across a section of this continuum on micro- and mesotidal coasts have revealed consistent trends in intertidal macrobenthic community structure related to changes in sandy beach morphodynamic type. These trends principally take the form of increasing species richness, abundance and biomass and an increase in the number of recognisable faunal zones from reflective to dissipative beaches (McLachlan et al. 1993, Jaramillo et al. 1993). Thus communities increase in biological complexity from reflective to dissipative micro/mesotidal beaches, implying that environmental conditions on the beach face may become less harsh across this gradient.

Classification of beach types into reflective, intermediate and dissipative is adequate for microtidal situations. However, when tide range also varies tidal effects must be taken into account since elevated tidal energy increases the dissipative nature of beaches. Masselink & Short (1993) have developed a model of beach types which clarifies the role of tides by classifying beaches along two axes, each based on a dimensionless parameter: Dean's parameter (or the dimensionless fall velocity) is used as an index of the degree of dissipativeness of the surf zone, and the relative tide range is used as an index of the relative role of tides and waves in allowing swash, surf zone and shoaling wave processes to mobilise sediment. Utilizing this classification as a model, a series of beach states may be envisaged extending from the microtidal reflective through intermediate and micro/mesotidal dissipative to macrotidal ultradissipative beaches and beyond this to tide dominated flats. No ecological survey has been undertaken across this spectrum from fully wave-dominated to fully tide-dominated beaches to date.

Dexter (1992) proposed that tropical beaches harbour less diverse faunas than temperate beaches in general. This hypothesis arose from a literature review of surveys of beach fauna. However, since most tropical beaches are reflective, whereas increasing wave energy towards higher latitudes (Davies 1972) results in a greater prevalence of more dissipative states, richer fauna recorded in surveys of temperate beaches may simply be an artifact of the relative proportions of beach types investigated at different latitudes. Resolution of this issue requires a comparison of beaches of similar morphodynamic type (or a range of types) from different latitudes.

Zonation of the fauna is not as distinct on sandy beaches as on rocky shores and the number of recognisable zones has been much debated (Rafaelli et al. 1991, Peterson 1991). It has nevertheless been shown that the number of faunal zones and their distinctness on sandy beaches increases from reflective to dissipative conditions (Jaramillo & McLachlan 1993). McLachlan & Jaramillo (1994) reviewed studies of zonation on sandy shores and concluded that microtidal dissipative beaches support three zones recognisable by the presence of characteristic species, but that a fourth zone might become evident in more dissipative systems. They suggested a detailed quantitative survey of beaches encompassing tide dominated conditions, i.e. ultradissipative beaches and sand flats to resolve the question of the existence of three or four zones in this section of the spectrum of intertidal sandy sediments.

This paper tests the hypothesis that the increases in species richness, abundance and biomass recorded from reflective to dissipative beaches in micro/mesotidal conditions will continue through macrotidal ultradissipative systems to sand flats. It also examines the hypothesis that tropical beaches are species poor compared to temperate beaches, taking beach type into account. Finally it examines zonation patterns and other community responses to physical conditions along a gradient from microtidal dissipative

to macrotidal sand flat conditions, i.e. to the point on the intertidal sand habitat continuum where tides take over fully from waves as the major hydrodynamic factor. This is accomplished by quantitative surveys of six Australian beaches which span a wide range of wave and tide energy levels. Previous accounts of Australian beach faunal communities are limited (Dexter 1983, 1984, 1985, McLachlan 1985) and this is the first report covering South Australia or Queensland.

METHODS

Two temperate microtidal sites were studied on the extensive Coorong beach in South Australia, one named Coorong at the Granites, 150 km east of Goolwa and the other near Goolwa, 2 km from the western end of the beach (Fig. 1). Wave height decreased eastwards along this beach but surf conditions were fully dissipative at both sites, which are modally dissipative (Short, pers. comm.). The Queensland beaches were located in a tropical macrotidal regime near Mackay (Fig. 1) and were subject to moderate to low wave energy, which decreased slightly from Mackay Harbour through Grass Tree and Sarina to Cassuarina beaches.

At each beach 15 levels were fixed at equal horizontal distances along a transect perpendicular to the shore during spring low tide. The upper one or two levels were
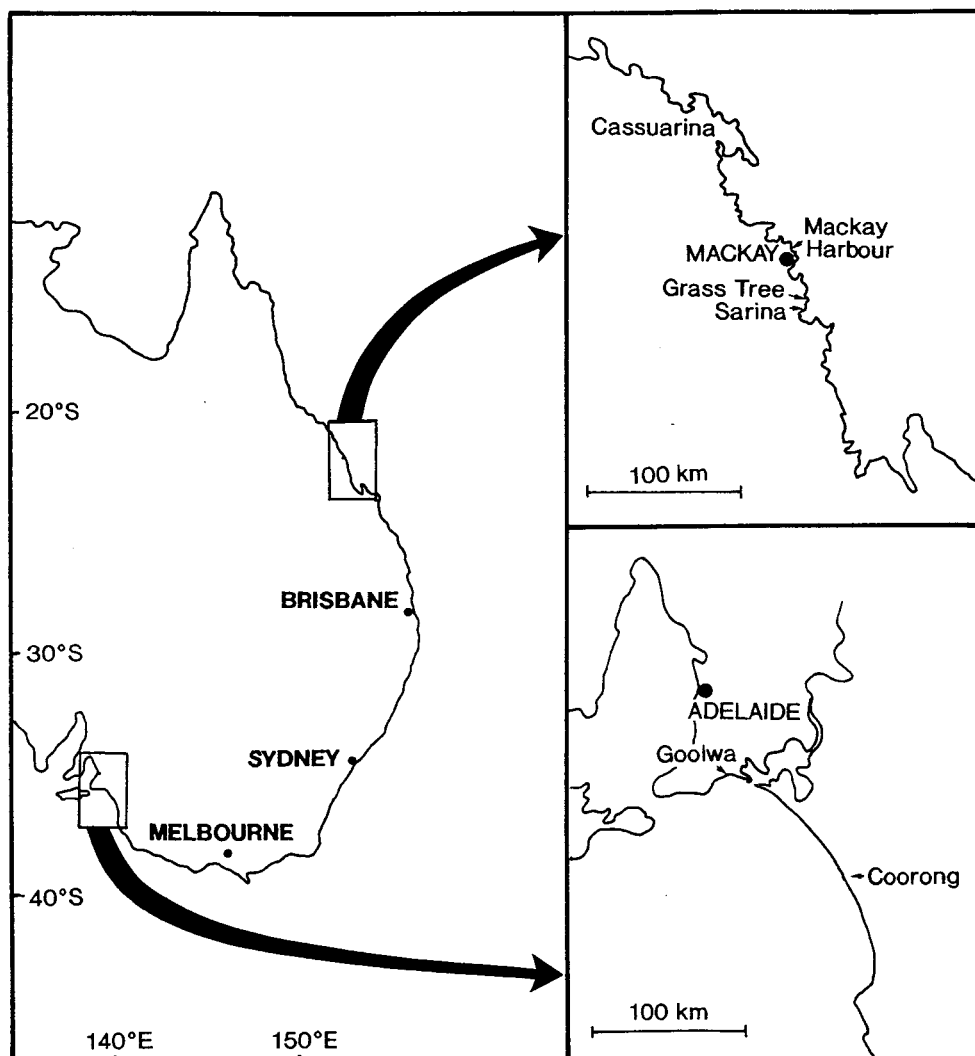

Fig. 1: Map of the Australian coast showing study sites.

Mapa de la costa Australiana indicando los sitios de muestreo.

located above the drift line and the lowest in the swash zone during low tide. At each level a sand sample was taken for analysis and the depth of the water table below the sand surface noted. Other physical measurements taken at the time of sampling included surveying the beach profile with a dumpy level and observations on breaker height and beach state. At each level three replicate quadrats of 0.1 m² were excavated to 25 cm and the sand passed through 1 mm mesh to extract the fauna. The total area sampled per beach was thus 4.5 m², the greatest yet reported for any beach survey. Specimens were preserved in 5-10% formalin and returned to the laboratory for identification. In addition to the quadrats, qualitative collections were undertaken in the supralittoral *for ghost crabs*, which were usually not sufficiently abundant to appear in the quantitative samples.

In the laboratory, sediment samples were analyzed in a settling tube and graphical particle size parameters estimated. All specimens were identified to species as far as possible, enumerated and shell-free biomass determined by drying at 60°C for 48 h. In cases where specimens had to be sent away for identification dry mass was taken as 25% of wet mass.

Beach state was calculated from the dimensionless fall parameter (Dean's parameter, which is based on breaker height divided by wave period and sand fall velocity) and the relative tide range (RTR, which is the mean spring tide range divided by breaker height) (Masselink & Short 1993). Values for tide range, breaker height and period and RTR for the Queensland beaches were obtained from Masselink & Short (1993) and for the South Australian beaches from Short (pers. comm.). Sand fall velocities were not taken from settling tube fall rates but from Gibbs et al. (1971) based on the estimated mean sand particle sizes per beach. This was done in order to allow comparison with previous studies (McLachlan et al. 1993) although it results in lower setting velocity values and thus higher Dean's values. Beach state index (BSI, McLachlan et al. 1993), which is the log of Dean's parameter multiplied by tide range, was also calculated for each beach.

Numbers and biomass were summed for running metres of shoreline by linear interpolation. Kite diagrams of ln abundance were constructed to show species distributions on all beaches and within each beach abundance data (untransformed and ln transformed) were subjected to classification analysis following construction of a Bray-Curtis similarity matrix. Clustering was performed using an unweighted pair-group method and arithmetic average linking (Field et al. 1982). Since groups resulting from cluster analyses were subjectively distinguished by eye, no standard level of dissimilarity was employed.

RESULTS

All beaches displayed relatively low gradients with slopes flatter than 1/20 (Figs 2-7), indicative of very fine to medium sands; no sands with mean particle diameters > 500 μm were encountered (Table 1). Sands were very fine to fine along the temperate beaches and more variable on the tropical beaches. The tropical beaches often had coarser layers underlying the surface sand, but this was largely missed in our sand samples which covered only the upper 5 cm. This surface sand ranged from medium sand in the case of Mackay Harbour to very fine sand at Casuarina beach. Coarsest sand occurred at the top of the shore and particles became finer downshore in all cases except Coorong Beach where there was a coarsening of the sand towards the bottom of the shore. Although there was some variability between levels, sand samples from all levels and beaches were well sorted and showed little skewness.

The key physical and biological variables for each beach are summarised in Table 2. Beach widths increased and beaches became flatter as wave height decreased and tide range increased from the temperate beaches to the tropical beaches. The former had tide ranges less than wave heights (RTR < 1) and were clearly wave dominated (RTR < 3, Masselink & Short 1993). The tropical Queensland beaches (RTR 8-16) fell in Masselink & Short's (1993) categories III (RTR 7-15, terraced and ultradissipative systems) and IV (the transition to tide

TABLE 1

Summary of substrate characteristics for six beaches. On each beach 15 levels were
sampled and sand taken for substrate analysis. Data from these 15 levels are grouped into sets of three
levels and values averaged. This yields five sets of values representing the supralittoral (levels 1-3),
upper shore (4-6), midshore (7-9), lower shore (10-12) and swash zone (13-15) on each beach

Resumen de las características del sustrato en las seis playas estudiadas. En cada playa se muestrearon 15 niveles
obteniéndose muestras de arena en cada uno para análisis de sustrato. Los datos de estos 15 niveles se agruparon en grupos de
tres niveles para obtenerse promedios. Esto originó cinco grupos de valores representando en cada playa al supralitoral (niveles
1-3), intermareal superior (4-6), intermareal medio (7-9), intermareal inferior (10-12) y zona de resaca (13-15)

Beach levels	Mean (phi)	Mean (mm)	Sorting (phi)	Skewness
Temperate beaches				
Coorong 1-3	2.3	210	0.31	-0.08
Coorong 4-6	2.7	160	0.3	-0.16
Coorong 7-9	3.1	120	0.26	0.12
Coorong 10-12	3.1	120	0.40	0.01
Coorong 13-15	2.7	160	0.51	-0.42
Goolwa 1-3	2.2	210	0.50	-0.07
Goolwa 4-6	3.2	110	0.12	0.18
Goolwa 7-9	3.2	110	0.14	0.10
Goolwa 10-12	2.9	130	0.21	-0.01
Goolwa 13-15	3.0	125	0.31	0.06
Tropical beaches				
Mackay H 1-3	1.2	430	0.45	0.17
Mackay H 4-6	1.7	320	0.59	-0.29
Mackay H 7-9	2.4	190	0.32	0.17
Mackay H 10-12	2.3	200	0.41	0.19
Mackay H 13-15	2.6	160	0.37	0.01
Grass Tree 1-3	2.8	140	0.20	0.02
Grass Tree 4-6	2.5	170	0.41	-0.24
Grass Tree 7-9	2.3	210	0.54	-0.49
Grass Tree 10-12	2.5	180	0.45	-0.56
Grass Tree 13-15	2.6	170	0.36	-0.29
Sarina 1-3	1.7	300	0.28	0.08
Sarina 4-6	2.2	220	0.20	0.06
Sarina 7-9	2.2	220	0.20	0.08
Sarina 10-12	2.2	220	0.20	-0.02
Sarina 13-15	2.3	210	0.24	0.00
Cassuarina 1-3	3.3	105	0.16	0.21
Cassuarina 4-6	3.4	100	0.17	0.25
Cassuarina 7-9	3.4	100	0.20	0.06
Cassuarina 10-12	3.2	110	0.25	0.07
Cassuarina 13-15	3.3	100	0.18	-0.06

dominated flats, RTR > 15). None of the beaches fell in category II with intermediate RTR values 3-7. The two temperate South Australian beaches were of the microtidal dissipative (barred dissipative - Masselink & Short 1993) type. The Queensland beaches were all macrotidal and of three morphodynamic types according to Masselink & Short (1993), low tide terrace (reflective upper shore and wide dissipative lower shore; Mackay Harbour, Grass Tree), ultradissipative (fairly flat and featureless; Sarina) and tidal flat (Cassuarina), with RTR increasing from 8 to 16 over this range.

However, our calculation of Deans parameter yielded higher values (3.2-7.5) than recorded by Masselink & Short (1993) (0.6 - 2.4), placing both Mackay Harbour and Grass Tree beaches into the ultradissipative category, although both these beaches and Sarina exhibited profiles of the low tide terrace type (Figs 4-6) along our transects when we sampled.

Coorong beach (Fig. 2) harboured 12 species, which were concentrated on the upper shore. Classification (at 70% dissimilarity) analysis suggested three zones: a supralittoral zone (levels 1-2) with dipteran larvae
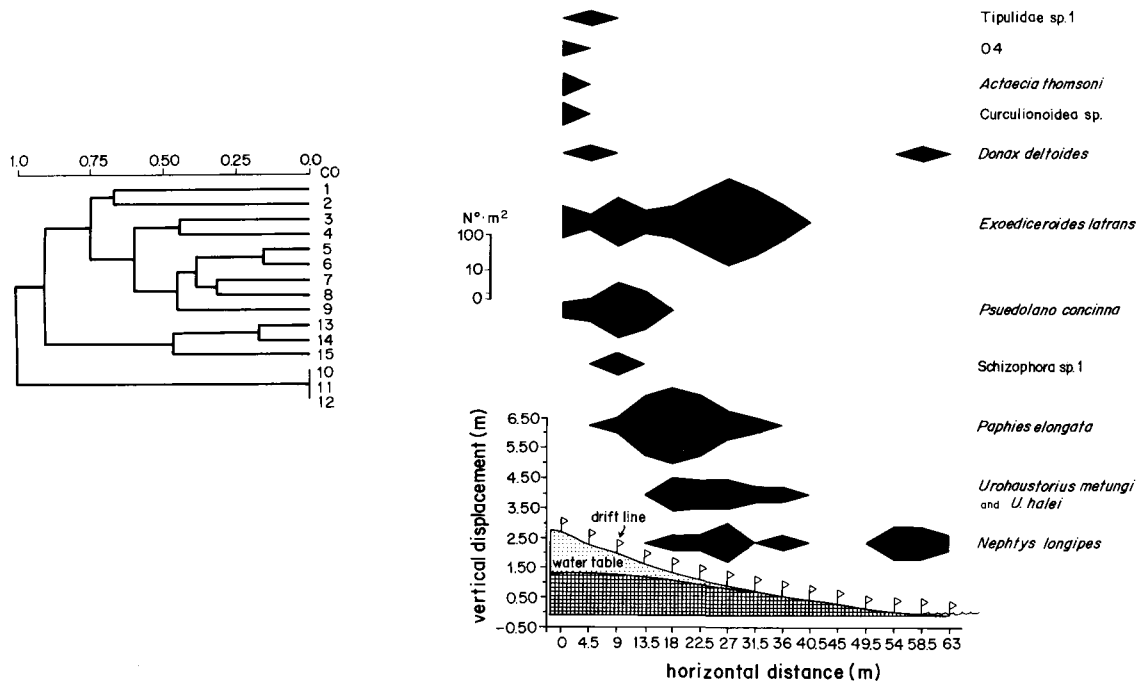
Fig. 2: Beach profile and faunal distribution (ln scale) on Coorong beach. Flags indicate sampling levels from 1 at the top of the shore to 15 at the swash line. Classification diagram group these 15 levels on the basis of similarities in faunal assemblages.

Perfil de playa y distribución faunística (escala en ln) en la playa de Coorong. Las banderas indican los niveles de muestreo desde 1 en la parte superior de la playa a 15 en la línea de resaca. El diagrama de clasificación agrupa estos 15 niveles sobre la base de similitudes faunísticas.

TABLE 2

Physical and faunal attributes of six Australian beaches. Hb = breaker height, Tide = maximum spring tide range, Mn = mean sand particle size, Dean's value is the dimensionless fall velocity (= breaker height/wave period X sand fall velocity), RTR = relative tide range (= mean spring tide range/breaker height), BSI = Beach State Index, abundance and biomass values are per running metre across each transect

Atributos físicos y faunísticos de seis playas Australianas. Hb = altura de la ola, marea = máximo rango mareal en sicigia, Mn = tamaño medio de la partícula, parámetro de Dean (= altura de la ola/período de la ola x velocidad de sedimentación de la arena), RTR = rango mareal relativo (= rango mareal medio en sicigia/altura de la ola), BSI = Indice del estado de la playa, valores de abundancia y biomasa por metro lineal a lo largo de cada transecto

Beach/Attribute	Coorong	Goolwa	Mackay Harbour	Grass Tree	Sarina	Cassuarina
H_b(m)	1.3	2	0.6	0.4	0.5	0.3
Tide (m)	1.2	1.2	6	6.5	6.5	6.5
Wave period (s)	12	12	5	5	5	5
Sand (mm)	152	139	261	172	237	101
Dean's value	6.4	12	3.4	4	3.2	7.5
RTR	1	0.6	8	12	10	16
1/slope	23	21	28	38	33	44
Beach width (m)	63	70	182	224	210	238
BSI	1.03	1.28	1.42	1.52	1.43	1.79
Number of spp.	12	12	15	20	22	30
Abundance (m^{-1})	5 875	4 752	26 756	8 693	31 288	32 857
Biomass (g.m^{-1})	213	5 453	2 208	559	1 880	234

(Tipulidae), curculionoid weevils and the isopod *Actaecia thomsoni*; a littoral zone on the upper shore (levels 3-9) with the amphipod Exoediceroides latrans, the isopod *Pseudolana concinna*, the clam *Paphies elongata* (= *Donacilla angusta*) and the amphipods *Urohaustorius metungi* and *U. halei* (not distinguisable during sample sorting); and a sublittoral fringe with Donax deltoides and *Nephtys longipes* extending over the lower shore (levels 10-15). Juveniles of D. deltoides occurred on the midshore. *P. elongata* and *E. latrans* dominated numbers and *P. elongata* dominated biomass (Table 3).

Goolwa beach (Fig. 3) harboured 12 species and, although classification (at 60% dissimilarity) indicated less clear groupings, three zones appear recognisable: a supralittoral zone (levels 1-3) with the isopod *Pseudolana concinna*; a littoral zone on the midshore (levels 3-9) dominated by the polychaetes *Hemipodus* sp. and Nephtys longipes and the amphipods *Urohaustorius metungi* and *U. halei*; and a sublittoral fringe on the lower shore (levels 10-15) dominated by Donax deltoides. D. deltoides exhibited intraspecific zonation, with adults on the lower shore and in the surf zone and juveniles in a band on the midshore. The latter wedge clam completely dominated the intertidal macro-

fauna of this beach in terms of abundance and biomass (Table 3).

Whereas the two temperate beaches exhibited fairly smooth concave slopes, three of the four tropical beaches had breaks in slope; steep upper (swash dominated reflective) shores above broad dissipative terraces or flats. Water tables usually intersected these beaches near the break in slope. In general the upper shores housed sparse faunas, whereas the terraces maintained many species in abundance.

Mackay Harbour beach supported 15 species (Fig. 4), seven of which were widely distributed over the terrace. No clear pattern of zonal segregation emerged from analysis of species distributions across the shore. *Ocypodid crabs* (*O. cordimana*) characterised the supralittoral (levels 1-3) with juveniles of this species occurring lower down. The terrace was dominated by haustoriids (*Urohaustorius* spp.), but polychaetes and the clam *Paphies elongata* were also common. At the bottom of the shore ghost shrimps *(Callianassa australiensis)* and crabs (*Matuta* sp). appeared. The isopod *Pseudolana cocinna*, typical of the upper littoral and supralittoral on the temperate beaches, again appeared high in the littoral. *Haustoriids dominated* faunal numbers but *Matuta* sp. contributed most to the biomass (Table 3).
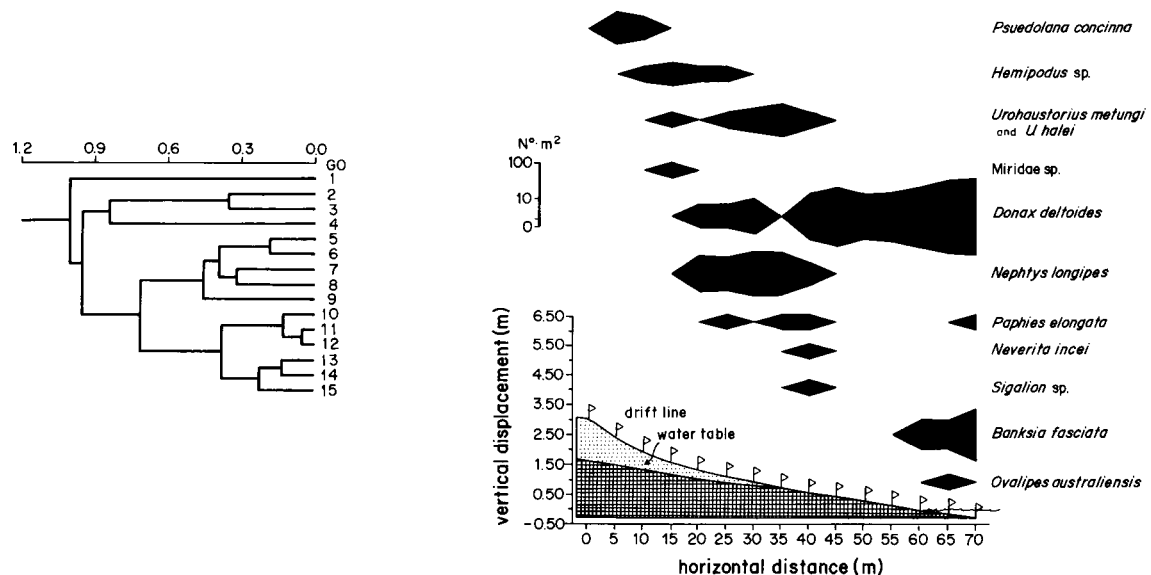

Fig. 3: Beach profile and faunal distribution on Goolwa beach with classification diagram.

Perfil de playa y distribución faunística en la playa de Goolwa con diagrama de clasificación.

TABLE 3

Abundance and biomass of the fauna on six Australian beaches

Abundancia y biomasa de la fauna en seis playas Australianas

Species	Code	Cassuarina Beach		Coorong Beach		Goolwa Beach		Grass Tree Beach		Mackay Harbour Beach		Sarina Beach	
		Abundance (m^{-1})	Biomass $(g.m^{-1})$	Abundance (m^{-1})	Biomass $(g.m^{-1})$	Abundance (m^{-1})	Biomass $(g.m^{-1})$	Abundance (m^{-1})	Biomass $(g.m^{-1})$	Abundance (m^{-1})	Biomass $(g.m^{-1})$	Abundance (m^{-1})	Biomass $(g.m^{-1})$
Annelida													
Scolelepis carunculata and Dispio glabrilamellata	P1	4632.50	70.55					533.33	1.97	352.08	2.19	2506.25	85.13
Hirsutonuphis sp.	P10	120.42	1.90									56.25	4.33
Spionidae sp.	P11	396.67	1.19									200.00	0.40
Paraonis gracilis gracilis	P12	127.50	0.16										
Armandia sp. 1	P13	184.17	0.50										
Megalona dakini	P14	63.75	0.06										
Lobochesis bibrancha	P15									265.42	4.40	1193.75	5.86
Perineris sp.	P16							106.67	0.24	43.33	0.52	100.00	18.70
Solomonereis marauensis	P17											150.00	0.65
Nephtys longipes	P18			265.00	32.25	466.67	54.22						
Hemipodus sp.	P19					83.33	11.65						
Scoloplos sp.	P2	290.42	0.43										
Sigalion sp.	P3					16.67	0.33						
Glycera sp.	P4	1069.58	13.61					960.00	8.96	606.67	24.30	1225.00	19.27
Glycera americana	PP							53.33	79.04				
Goniadidae sp.	P5	170.00	0.34										
Platynereis dumerilli antipoda	P7	368.33	2.03										
Unknown sp.	P8	113.33	2.32										
Armandia sp. 2	P9	56.67	0.11										
Mollusca Bivalvia													
Paphies elongata	B1	680.00	0.51	1725.00	105.80	68.75	8.82			1083.33	46.15	450.00	67.45
Donax faba	B2	113.33	0.03					53.33	0.04	43.33	18.07	500.00	71.50
Donax deltoides	B3			30.00	64.34	3479.17	4609.29						
Unknown sp.	B4							53.33	0.03				
Gastropoda													
Banksia fasciata	G1					337.50	18.15						
Conuber conicus	G4							53.33	6.83			50.00	6.40
Neverita incei	G5					16.67	29.58						
Arthropoda Insecta													
Curculionoidea sp.	INS1			30.00	0.11								
Tipulidae sp. 1	INS 2			15.00	0.06								

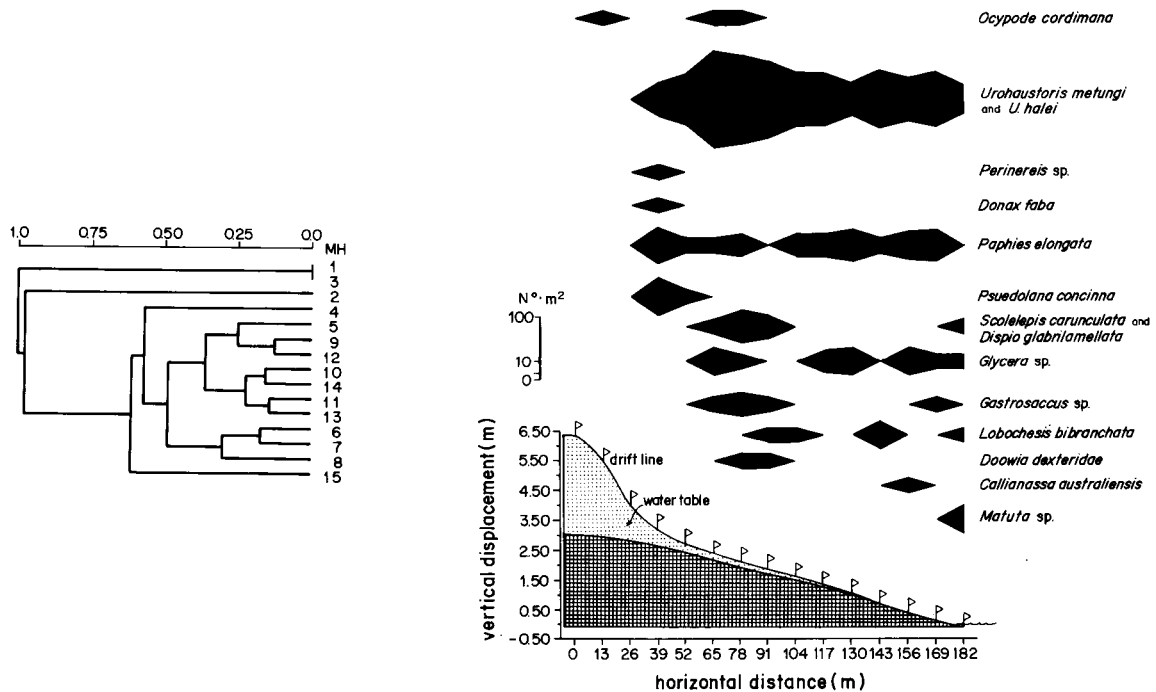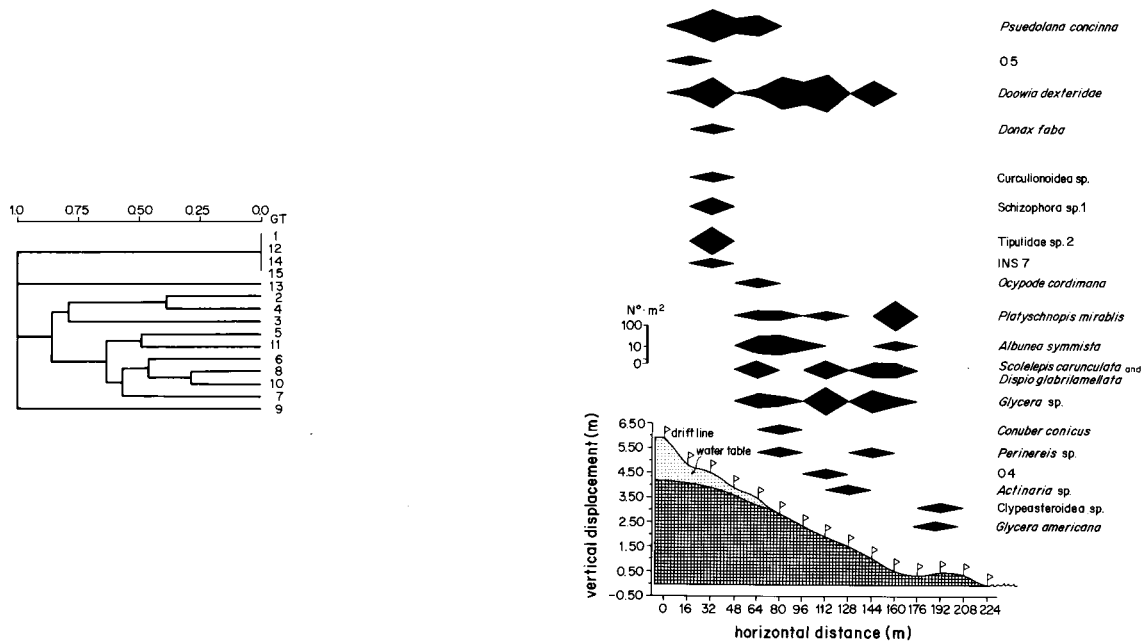| Species	Code	Cassuarina Beach Abundance (m⁻¹)	Biomass (g.m⁻¹)	Coorong Beach Abundance (m⁻¹)	Biomass (g.m⁻¹)	Goolwa Beach Abundance (m⁻¹)	Biomass (g.m⁻¹)	Grass Tree Beach Abundance (m⁻¹)	Biomass (g.m⁻¹)	Mackay Harbour Beach Abundance (m⁻¹)	Biomass (g.m⁻¹)	Sarina Beach Abundance (m⁻¹)	Biomass (g.m⁻¹)
Schizophora sp. 1	INS 3			30.00	0.09			160.00	1.97				
Unknown sp.	INS 4							53.33	0.21				
Tipulidae sp. 2	INS 6							480.00	0.16				
Schizophora sp. 2	INS 7							53.33	0.03				
Miridae sp.	INS 8					16.67	0.23						
Crustacea Amphipoda													
Urohaustorius metungi and U. halei	A1	8688.89	7.62	180.00	0.31	150.00	0.17	3413.33	1.87	23435.60	80.59	18650.00	48.35
Platyschnopis mirablis	A2	4080.00	1.87					746.67	0.61				
Doowia dexteridae	A3	233.75	0.21							86.67	0.04	250.00	0.50
Unknown sp.	A4	453.33	0.20										
Exoediceroides latrans	A6			3150.00	5.30								
Isopoda													
Pseudolana concinna	I1	680.00	2.89	405.00	3.30	100.00	0.47	1226.67	3.84	303.33	1.17	2450.00	13.18
Ulakanthura colac	I2	332.92	0.20										
Actaecia thomsoni	I4			30.00	0.32								
Decapoda													
Gastrosaccus sp.	D1	1133.33	2.04							216.67	0.48	150.00	0.45
Callianassa australiensis	D2	5610.00	63.86							43.33	23.49		
Ocypode cordimana	D3	396.67	35.70					53.33	8.91	130.00	140.14	550.00	147.15
Albunea symmista	D4	191.25	10.26					480.00	5.65			56.25	270.23
Mutata sp.	D6									146.25	1866.74	50.00	750.90
Ogyrides delli	D7											50.00	2.95
Ovalipes australiensis	D9					16.67	720.30						
Miscellaneous													
Nemertia sp.	N	1933.75	14.86										
Unknown sp.	O1	56.67	0.17										
Unknown sp.	O2											2150.00	26.76
Unknown sp.	O4			15.00	1.26			53.33	0.11				
Unknown sp.	O5							53.33	0.27				
Clypeasteroidea	SD1	120.42	0.12					53.33	12.37			500.00	340.20
Pycnogonida	SS1	559.58	0.21										
Actiniaria sp.	ANEM							53.33	425.76				
Total per metre		32857.23	233.95	5875.00	213.14	4752.10	5453.21	8693.30	558.87	26756.01	2208.28	31287.50	1880.36

Fig. 4: Beach profile and faunal distribution on Mackay Harbour beach with classification diagram.

Perfil de playa y distribución faunística en la playa de Mackay Harbour con diagrama de clasificación.

Grass Tree beach (Fig. 5) had 20 species, which exhibited patchy distributions vertically and horizontally and little clear zonation pattern emerged from the analyses. The steep upper beach (levels 1-4) was occupied by the ghost crab *O. cordimana* (with juveniles of this species extending lower on the shore), insects, the isopod *Pseudolana concinna* and the amphipod *Doowia dexteridae*; the terrace (levels 5-11) was dominated by *D. dexteridae*, a variety of polychaetes, the amphipod *Platyschnopis mirabilis* and the mole crab *Albunea symmista*; and the bar at the base of the terrace (level 13) was occupied by sand dollars and the polychaete *Glycera americana*. Haustoriids dominated numbers, whereas the anemone *Actiniaria* sp dominated biomass (Table 3).

Sarina beach (Fig. 6) supported 22 species. Other than for a sparse population of ghost crabs in the supralittoral (juveniles occurring lower down) all species recorded came from the terrace and most had wide distributions. Nevertheless the classification (at 85% dissimilarity) analyses suggest some pattern: a supralittoral zone (levels 1-2) with *O. cordimana* (not recorded in the quantita-

tive samples); a littoral (upper terrace, levels 3-6) with haustoriid amphipods, *Pseudolana concinna*, *Donax faba* and polychaetes; and a lower terrace (levels 7-15) or sublittoral fringe with polychaetes, crustaceans, urchins, the naticid *Conuber conicus* and mole and swimmming crabs. The classification hints at subdivision of the terrace, but separation is not distinct. Numbers were high and dominated by haustoriid amphipods and polychaetes but biomass was dominated by decapods, especially *Matuta* sp and *Albunea symmista* (Table 3).

Cassuarina beach (Fig. 7) had a smooth, wide (240 m) profile and yielded 30 species in the quantitative samples. Although most species exhibited extensive intertidal distributions, some zonation was evident in the classification (at 80% dissimilarity) diagram: adult ghost crabs (not in the quantitative samples) occurred in the supralittoral zone at level 1 which was otherwise devoid of fauna; the upper littoral zone (levels 2-4) was dominated by the isopod *Pseudolana concinna* with some amphipods and other species also present; and the rest of the shore was characterised by a variety of species,

Fig. 5: Beach profile and faunal distribution on Grass Tree beach with classification diagram.

Perfil de playa y distribución faunística en la playa de Grass Tree con diagrama de clasificación.
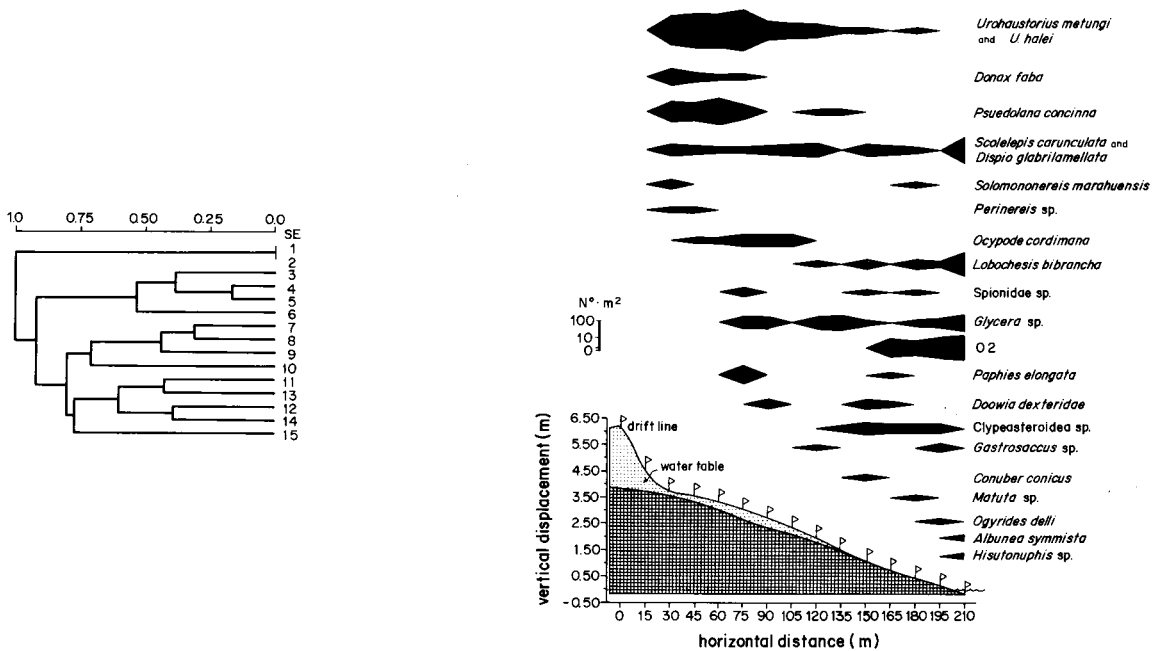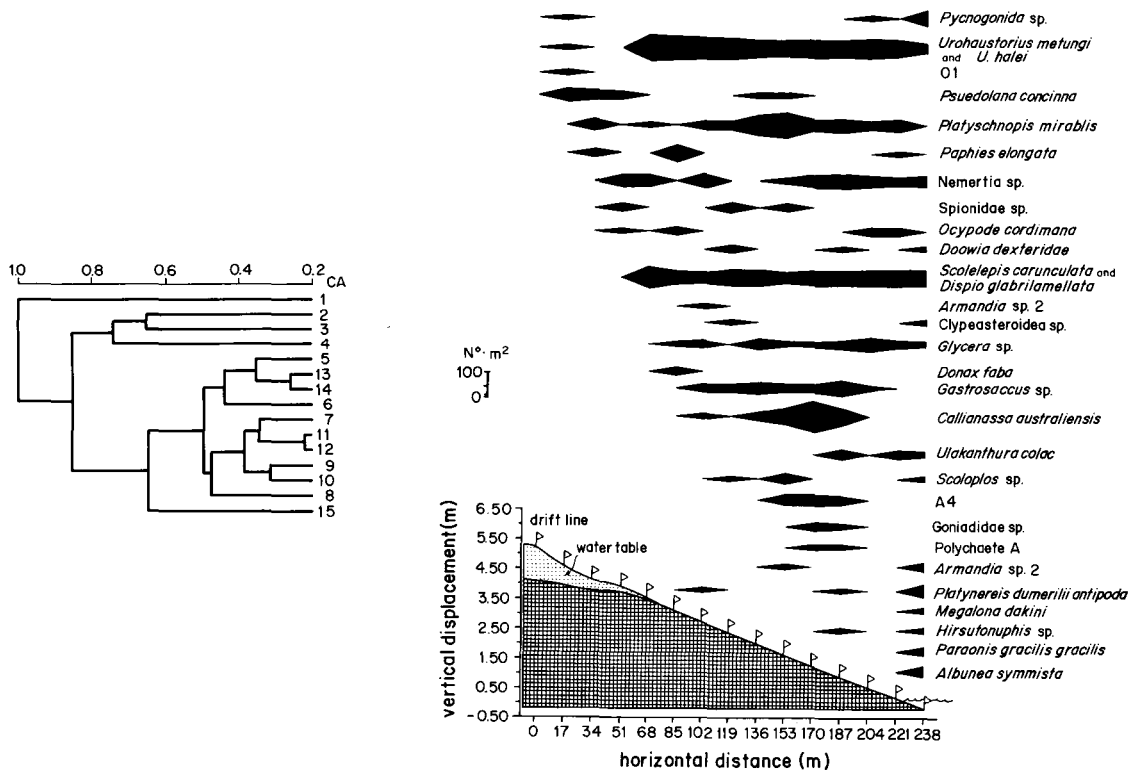

Fig. 6: Beach profile and faunal distribution on Sarina beach with classification diagram.

Perfil de playa y distribución faunística en la playa de Sarina con diagrama de clasificación.

mostly with extensive distributions. The abundant fauna was dominated by poly- chaetes, haustoriids and the ghost shrimp *Callianassa australiensis*, the latter, together with other decapods, contributing most to biomass (Table 3).

Abundance and biomass values for sandy beaches can broadly be classified as follows:

Fig. 7: Beach profile and faunal distribution on Cassuarina beach with classification diagram.

Perfil de playa y distribución faunística en la playa de Cassuarina con diagrama de clasificación.

abundance values < 1 000 m^{-1} are taken as low, 1 000 - 10 000 m^{-1} as medium and > 10 000 m^{-1} as high and for biomass < 100 g.m^{-1} low, 100 - 1 000 g.m^{-1} medium and > 1 000 g.m^{-1} high. On this basis the temperate beaches and Grass Tree beach supported moderate faunal abundance whereas the other three tropical beaches supported high faunal abundance. All beaches supported moderate biomass except Goolwa, where biomass was very high and Mackay Harbour and Sarina where biomass was fairly high. Division of abundance and biomass values by beach widths reveals that three of the four tropical beaches supported higher densities (147, 39, 149 and 138 m^{-2}) than the temperate beaches (68 and 93 m^{-2}). However, Goolwa beach (77.9 g.m^{-2}) supported greater biomass per unit area than any of the tropical beaches (12.1, 2.5, 9.0 and 1.0 g.m^{-2}) and Coorong (3.4 g.m^{-2}) was intermediate. Goolwa beach fauna displayed a greater mean individual size (1148 mg) because of the presence of numerous large Donax del-

toides, whereas the other beaches included more small (Coorong 34, tropical beaches 83, 64, 60 and 7 mg) forms. Molluscs dominated the temperate beaches (30% and 82% of numbers, 80% and 86% of biomass) and crustaceans and polychaetes the tropical beaches (crustceans: 91%, 68% 71% and 66% of numbers and 96%, 4%, 66% and 53% of biomass; polychaetes: 5%, 19%, 17% and 23% of numbers and 1%, 16%, 7% and 40% of biomass). Polychaetes were most diverse and abundant in the finest sands.

Faunal species richness, as measured by the total number of species recorded per beach (transect = 4.5 m^2), generally increased with increasing RTR and BSI from lowest values in the temperate beaches to highest at Cassuarina beach with 30 species (Table 2). A plot of these data (Fig. 8) together with those from six other biogeographic areas (McLachlan et al. 1993) reveals that the two temperate beaches and Mackay Harbour closely fit the general trend but the other three tropical beaches, especially Cassuarina,
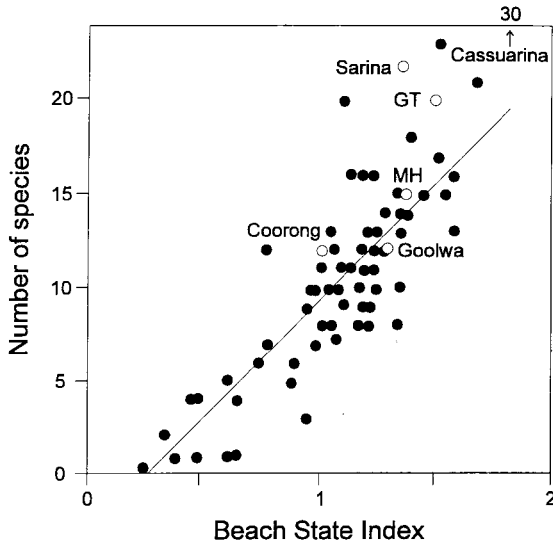
Fig. 8: Relationship between species richness recorded in beach transect surveys and BSI (see text). Each point represents one beach; after Mclachlan et al. (1993) with values for the beaches in this study as open circles. The regression (line) for the original data is Y = 12.8X - 3.5, r = 0.82.

Relación entre riqueza de especies registrada en cada muestreo y "BSI" (ver texto). Cada punto representa una playa (según McLachlan et al. 1993). Los círculos blancos representan las playas de este estudio. La línea de regresión para los datos originales es Y = 12.8X - 3.5, r = 0.82.

have elevated richness. The scatter suggests that above a BSI value of about 1.3, ie where tides play a greater role, richness may increase more rapidly than predicted by this regression model. A regression of the data for these six Australian beaches only (Y = 24.8X - 16.5, r = 0.90, p < 0.05) confirms the steeper increase in species richness over this part of the BSI scale (slope 24.8 versus 12.8 for the original data).

Abundance values exhibited a general increase from low to high BSI across this series of Australian beaches to a maximum at Cassuarina Beach. These data conform well to the regression developed by McLachlan et al. (1993) (Fig. 9), suggesting that abundance continues to increase logarithmically as BSI increases. If only the values for these six beaches are considered no significant regresion is obtained (Y = 2.66 + 1.05X, r = 0.68) but the trend is for a weak increase in abundance from Coorong to Cassuarina (slope 1.05 versus 2.55 for the original data).

Beach width increases linearly over this series from Coorong to Cassuarina beaches while abundance increases logarithmically, thus the increase in faunal density.

Biomass was greatest at Goolwa, Mackay Harbour and Sarina, in the center of this series and lowest at Coorong and Cassuarina. When plotted together with the data from McLachlan et al. (1993) (Fig. 10) the values for these beaches fall within the recorded range. If only these six beaches are considered, the trend is for total biomass to increase from Coorong (BSI = 1.03) to Goolwa (BSI = 1.28) and then decrease to Cassuarina (BSI = 1.79). A regression of log biomass against BSI for these six beaches is not significant (Y = 3.41 - 0.31X, r = 0.14). However, a highly significant fit is obtained if Coorong is omitted (Y = 7.15 - 2.72X, r = 0.96, p = 0.01), this showing a steep drop in biomass (slope - 2.72) from Goolwa to Cassuarina beaches.
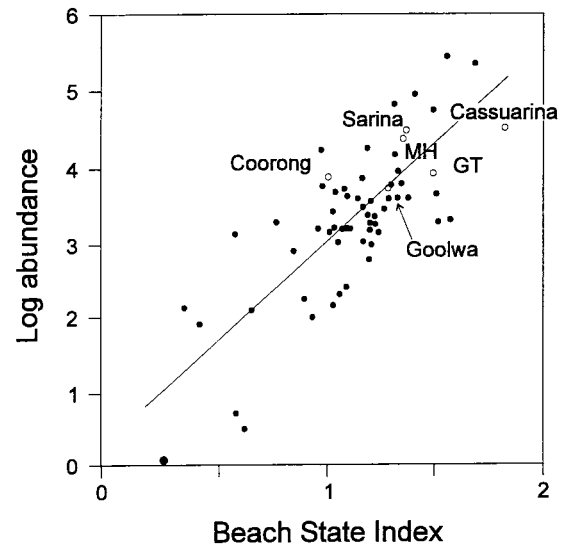

Fig. 9: Relationship between abundance of beach fauna per 1m transect and BSI. After McLachlan et al. (1993) with values for the beaches in this study as open circles. The regression (line) for the original data given by McLachlan et al. (1993) was incorrect and is correctly given by Y = 0.39 + 2.55X, r = 0.77.

Relaciones entre abundancia de la fauna de la playa por 1m de transecto y "BSI" (ver texto). Círculos negros corresponden a datos de McLachlan et al. (1993); los círculos blancos a las playas de este estudio. La línea de regresión para los datos originales fue incorrecta; la correcta es Y = 0.39 + 2.55X, r = 0.77.
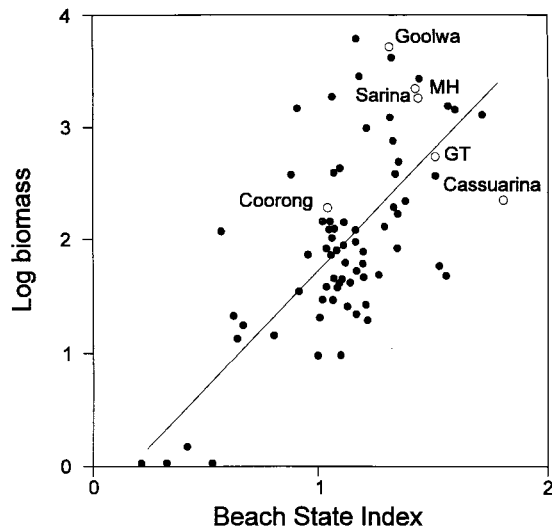
Fig. 10: Relationship between biomass of beach fauna per 1m transect and BSI. Solid circles data from McLachlan et al. (1993) with values for beaches in this study as open circles. The regression (line) for the original data was incorrect and is correctly given by Y = 2.12X - 0.34, r = 0.69.

Relaciones entre biomasa de la fauna de la playa por 1 m de transecto y "BSI" (ver texto). Círculos negros corresponden a datos de McLachlan et al. (1993); los círculos blancos a las playas de este estudio. La línea de regresión para los datos originales fue incorrecta; la correcta es Y = 2.12X - 0.34, r = 0.69.

DISCUSSION

If latitudinal differences are ignored, the six sites form a rough series (Table 2) with increasing widths, decreasing slopes and increasing BSI values from Coorong to Cassuarina beaches. Dean's values show a less clear trend because of the opposing influences of wave energy and sand particle size. A key part of the estimation of Dean's parameter lies in the value for sand fall velocity. The fall velocities that we obtained in our settling tube were well above those for similar sized particles as listed by Gibbs et al. (1971). Our use of values from Gibbs rather than our directly measured settling velocities has therefore resulted in higher Deans values (by a factor of two) and consequently higher BSI values. We did this deliberately because published information with which we compared our data had used values from Gibbs (Figs 8-10). The compa-

risons of trends in faunal richness, abundance and biomass with beach type are thus on the same scale, whereas our absolute values for Dean's parameter may be high. Additionally, since we used mean sand grain sizes across the entire shore, whereas Masselink & Short (1993) used only values from high tide levels, where the sand is coarser, this may further increase our Dean's values relative to theirs.

BSI values for these six beaches suggest a slightly different interpretation to that of McLachlan et al. (1993) in classifying beaches according to this index. Reflective beaches occur only in microtidal regimes and have BSI values < 0.6; values 0.6 - 1.0 indicate intermediate beaches in micro- or mesotidal regimes, values 1.0 - 1.5 indicate dissipative and high energy intermediate beaches in micro/mesotidal regimes, whereas values > 1.5 signify mesotidal to macrotidal dissipative to ultradissipative states to tide dominated flats. It is unlikely that any beach would score in excess of 2.0 and thus multiplication of this index by five may be useful in creating a simple ten point scale of beach types. A suggested classification on this scale is illustrated in Fig. 11. Further work on a wider range of beach types will enable refinement of this index and scale.

Sand particle sizes showed a trend unusual for exposed beaches (Brown & McLachlan 1990): decreasing downshore, especially on Coorong, Goolwa, Mackay Harbour and Sarina beaches. Coarser sand at high tide levels on these beaches is indicative of reflective conditions in these areas and the predominance of swash processes on the upper beach faces as opposed to shoaling wave effects over the lower shores or terraces (Masselink & Short 1993).

The beaches covered in this study fall into two distinct categories without any intermediate forms: temperate, microtidal dissipative and tropical macrotidal low tide terrace to tidal flat beaches. This creates the problem of ascribing differences in their faunal communities unequivocally to latitudinal or morphodynamic effects. This problem was resolved by placing the beaches at their respective positions on a morphodynamic continuum and comparing trends (Figs 8 - 10). This comparative approach showed
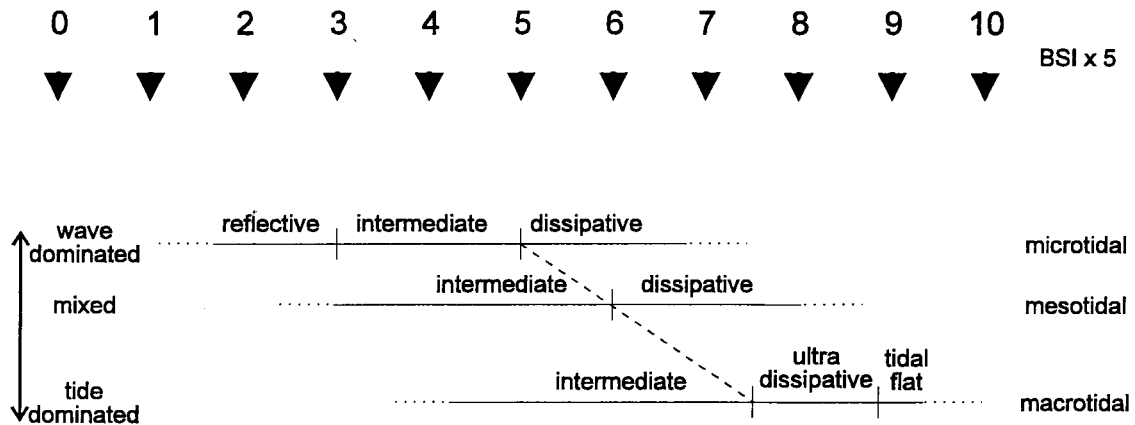
Fig. 11: Suggested classification of beach types against the BSI scale (see text).

Clasificación sugerida de tipos de playas versus escala "BSI" (ver texto).

species richness to increase greatly from the temperate microtidal to the tropical macrotidal beaches. Further, the six Australian beaches exhibited a steeper increase in species richness than micro- and mesotidal beaches previously examined. In addition to this a study of species/area curves for these six beaches (Jaramillo et al. 1994) indicated that sampling missed a significant proportion of species on the macrotidal beaches (especially Cassuarina) but not on the microtidal beaches. The increase in richness from the temperate to tropical beaches may therefore be considerably greater than recorded here. It thus appears that species richness not only continues to increase across the spectrum of beach types towards the tide dominated sand flat, but in fact accelerates.

There is no indication from the trends in the Australian beach data that diversity is lower in the tropics than temperate areas; rather it seems that diversity may be higher than the general trend, but it is not possible at this stage to determine to what extent this is due to the different beach types and the increased role of tides and to what extent it is due to latitude. Our results therefore refute the hypothesis of lower diversity on tropical beaches: all four tropical beaches supported more species than the two temperate beaches. The good fit of data sets from a variety of latitudes on four comtinents to a single regression model of species richness as a function only of beach type (Fig. 8) implies that species richness of intertidal sand communities is primarily determined by morpho-

dynamic type and its controlling physical factors, sand particle size, wave energy and tide range. The role of latitude is probably less than that of tides, but can only be deciphered by comparison of similar series of beach types from different latitudes. Current studies comparing temperate and tropical areas in Africa and South America and Australia should answer this in the near future.

Abundance increased over the range of beaches studied here in accordance with the regression model of McLachlan et al. (1993). However, the trend of increasing abundance for this Australian data set alone was not as steep as for the earlier data set, although the difference was not significant. The Queensland beach data do not therefore indicate that the trend of logarithmically increasing abundance with linear increase in BSI changes under macrotidal conditions. This logarithmic increase in abundance with a linear increase in beach width is also reflected in the finding that densities doubled on average from the temperate to the tropical beaches.

Biomass did not increase with BSI across these Australian beaches. All values fell within the recorded range which shows beach faunal biomass to be extremely variable (Fig. 10). In fact, the significant negative trend in biomass across the five Australian beaches with BSI values above 1.2 suggests that biomass may peak in micro-/mesotidal beaches and decrease towards macrotidal regimes. Goolwa was close to the maximum

recorded value for beach biomass which appears to have a ceiling around 5 x 10^3 g. m^{-1} (this study, Mclachlan et al. 1993).

Several interesting trends emerged in the zonation patterns of individual species. *Donax deltoides* exhibited size related zonation, juveniles apparently recruiting higher on the shore than adults. A similar situation has been described for a closely related species, *D. serra*, on the west coast of South Africa (Bally 1983). However, in warmer waters *D. serra* adults occur higher on the shore and juveniles lower down (Donn 1990) and *D. deltoides* may do the same in warmer parts of its range. The downward shift of adults in the South African species in colder waters may be a consequence of depressed burrowing rates at lower temperatures and thus inability to maintain position in the dynamic swash conditions on the higher shore (Donn & Els 1990). *Ocypode cordimana* displayed the opposite pattern on the Queensland beaches, juveniles occuring on the midshore and adults in the supralittoral.

Some species common to both the temperate and the tropical beaches displayed shifts in zonation: the high shore isopod *Pseudolana concinna* occupied an almost supralittoral position (at and above the drift line) on the temperate beaches but occured in the upper littoral below the drift line on the tropical beaches; the haustoriid amphipods *Urohaustorius* spp. occurred in the upper littoral just below the drift line on the temperate beaches but extended downshore to the sublittoral fringe on the tropical beaches; and the bivalve *Paphies elongata* occupied the upper littoral on the temperate beaches but extended down across the entire shore to the swash zone on the tropical beaches. These downward shifts in the tropics are probably in response to higher temperatures and greater desiccation of the sand on the upper shore.

The classification analyses failed to demonstrate four faunal zones on any of these beaches and in two cases even three zones were difficult to distinguish. Since Goolwa and Coorong are two points 150 km apart on a continuous dissipative beach, and differ only in wave energy and particle size to a small extent, their zones should correspond. Although neither site exhibited

extremely clear zonation we suggest that they may share three zones in common: a supralittoral zone inhabited by insects, a littoral zone with haustoriid amphipods and the bivalve *Paphies elongata*, and a lower zone extending into the sublittoral, with *Donax deltoides* dominant; the cirolanid isopod *Pseudolana concinna* occurs at the junction between the supralittoral and littoral zones.

On the tropical beaches the pattern is more complex. The reflective upper beach supports an impoverished fauna, primarily ocypodid crabs, and can be termed the supralittoral zone. Below this, because of the high position of the water table, the broad terrace is saturated, resulting in little moisture gradient across the rest of the shore. The bottom of the upper beach and the upper terrace constitute a littoral zone with the isopod *Pseudolana concinna*, haustoriids and other species. A lower zone with many species, notably decapod mole crabs, ghost shrimps and swimming crabs, spans most of the terrace. In a seasonal study of a tropical mesotidal sand flat near Singapore Vohra (1971) recorded exceptional species richness, 140 species, but zonation difficult to characterise.

In both the temperate and tropical cases zonation corresponds roughly to Dahl's (1952) tripartite scheme, which identifies a supralittoral zone by the presence of talitrid amphipods or ocypodid crabs, a midshore zone with cirolanid isopods and a lower shore with many species. None of the beaches displayed any pattern which could be related back to Salvat's (1964) four moisture zones of dry sand (= supralittoral), retention (= littoral), resurgence and saturation (= lower shore). We emphasise that the intertidal distribution patterns described and discussed in this paper are for the low tide period only and many species populations shift upshore on the rising tide.

The macrotidal beaches were distinguished from the microtidal beaches in this survey by the presence of species establishing semi-permanent burrows *(Callianassa australiensis)* and forms with low mobility (sand dollars, anemones). Anemones have also been recorded in surveys of low energy, tide dominated sandy shores by Vohra

(1971) and Peterson & Black (1986). Apparently sufficient substrate stability in macrotidal conditions allow addition of a small suite of relatively immobile forms to the normal complement of highly motile species typical of sandy beaches. This addition both adds to species richness and provides scope for greater community complexity, biological structure and interspecies interactions on the tide dominated beaches.

We conclude from this study that macrotidal beaches support more species rich faunas than their microtidal counterparts, that tropical beaches are not poorer in species than temperate beaches of similar morphodynamic types and that it is not possible to distinguish more than three distinct zones on sandy beaches over a very wide range of conditions. We suggest that the attainment of high diversity, likely increased stability of the substrate and the presence of species constructing semi-permanent burrows on the macrotidal beaches are conditions which indicate that biological interactions may begin to play a greater role in community organisation than on wave dominated microtidal beaches.

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