Dissipative Beaches and Macrofauna Communities on Exposed Intertidal Sands

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ABSTRACT ▮

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This study was undertaken primarily to test the hypotheses that (1) the intertidal fauna of exposed sandy beaches occupy four distinct zones and (2) that dissipative (flat) beaches support faunas of high abundance and diversity. The benthic macrofauna of three high energy, dissipative beaches on the Oregon coast was quantitatively surveyed and found to comprise an assemblage of 16-21 species and $50\text{-}290*10^9$ individuals per meter per beach. This fauna exhibited zonation, four zones being distinguished by 3-4 characteristic species each. Zonation appeared to be related to both interstitial moisture levels in the sand at low tide and tide levels or inundation times. These data, together with similar data from a range of beaches in southern Africa and western Australia, were analyzed for changes in faunal diversity, total abundance and biomass and mean individual mass in response to physical changes in sand particle size, wave height, beach slope and beach type. The biological parameters showed good correlations with all the physical parameters, but beach slope and type gave the best fits for abundance and diversity. Biomass was, however, best correlated with wave energy. This is interpreted as meaning (1) that wave energy, which may control surf zone productivity and food availability, controls intertidal biomass and (2) that, although sand particle size and wave climate may have some direct effects, the type of fauna developing on a beach is primarily determined by the total swash "climate" of the beach face as reflected in beach slope and beach type.

ADDITIONAL INDEX WORDS: *Sand, benthos, waves, fauna, zonation, biomass, amphipods. Topic sentences: faunal zonation on flat beaches; global patterns in beach fauna diversity, abundance and biomass; ecology of Oregon sandy beaches.*

INTRODUCTION

The zonation of species and communities on exposed rocky shores has been widely described and a variety of explanations, based on manipulative experimentation involving both physical factors and biological interactions, has been elevated to the status of paradigms (PETERSON, 1979; UNDERWOOD and DENLEY, 1984). Exposed sandy beaches, which make up the greatest proportion of most open shores, have received no such thorough treatment. Indeed, few authors have examined general or global zonation schemes and most literature on faunal zonation on exposed sandy beaches is autecological (*e.g.* CROKER, 1967; DEXTER, 1967; BOSWORTH, 1977; HALEY, 1982; and HUGHES, 1982). Two general zonation

schemes have, however, been proposed for sandy beaches: DAHL (1952) defined three biological zones and SALVAT (1964, 1966, 1967) defined four physical zones.

DAHL's (1952) top zone, the subterrestrial fringe, was characterised by talitrid amphipods in temperate areas and ocypodid crabs in warm areas. His midlittoral was characterised by cirolanid isopods and his sublittoral fringe by a mixed fauna in which hippid crabs and haustorid amphipods could be represented. Some authors applied this scheme to their beaches with reasonable agreement, although the lowest zone remained difficult to define (*e.g.* PHILIP, 1972; VOHRA, 1972; JARAMILLO, 1978; and MCLACHLAN *et al.*, 1981a). SALVAT's (1964) scheme was based on pore moisture changes to distinguish the following zones: a zone of drying at the top of the shore with little moisture, a zone of resurgence wetted on every tide but retaining only capillary water

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during low tide, a zone of resurgence marked by discharge of water on the outgoing tide and associated with the groundwater table at low tide, and a zone of saturation, at the bottom of the shore, with limited circulation of the groundwater. POLLOCK and HUMMON (1971) expanded this by subdivision of the zone of drying. Few authors have attempted to apply this scheme but where they have it has proved useful (WITHERS, 1977; BALLY, 1983; and WENDT and MCLACHLAN, 1985).

These schemes represent only the position during low tide and, because of the movement of the fauna, such zones would not be expected to have sharp boundaries (MCLACHLAN, 1983). As exposed sandy beaches are amongst the most physically controlled of all marine ecosystems, an underlying physical basis would be expected for any scheme of animal distribution in such systems. It is therefore not surprising that DAHL's subterrestrial fringe and midlittoral zones correspond exactly to SALVAT's zones of drying and retention, but the position on the lower shore is far less clear.

Such zonation patterns must be strongly affected by physical changes which affect water content and drainage across different beach types and it may be questioned how widely valid they are. On a global scale, exposed sandy beaches may be divided into three broad types based on their "morphodynamics;" reflective, intermediate and dissipative (SHORT and WRIGHT, 1983). Reflective beaches, occurring where there is coarse sand, low wave energy and often also small tide ranges, have steep faces, no surf zones and reflect wave energy back to sea. At the other extreme, dissipative beaches develop under conditions of fine sand, heavy wave action and often also larger tide ranges; they have flat slopes and wide surf zones in which most wave energy is dissipated. Between these two extremes, intermediate beaches have fine to medium sands, moderate to heavy wave action and a range of tide types; they have intermediate slopes and surf zones characterized by bars, channels and rip currents. Under conditions of very large tides the situation is more complex and macrotidal beaches have reflective upper shores and dissipative lower shores (WRIGHT et al., 1982). The changes in drainage, water retention and other beach face processes that occur across this spectrum of beach types must exert a strong influ-

ence on beach faunal zonation, abundance and diversity.

Several of the individual factors which make up the beach environment have been considered to directly affect the distribution and abundance of beach fauna. These include sand particle size, wave action, beach slope, sand moisture and food in the surf water (e.g. RAPSON, 1954; BROWN, 1964; SALVAT, 1964; MCINTYRE, 1970; ELEFTHERIOU and NICHOLSON, 1975; and MCLACHLAN et al., 1981a). As slope is determined by the interaction between wave action and grain size, it may be expected to give a more complete picture of a beach than grain size alone. Nevertheless, wave action and grain size have generally been considered the most important (ELEFTHERIOU and NICHOLSON, 1975), but only one study has succeeded in demonstrating a quantitative relationship between biological and physical parameters: this showed an increase in both total abundance and species diversity with a decrease in grain size or slope over a range of intermediate beaches in southern Africa (MCLACHLAN et al., 1981a). From this correlation for African beaches, it was predicted that steep reflective beaches should support impoverished faunas (0-5 species, <100 animals.m^{-1}), whereas flat, dissipative beaches should support the richest faunas (15-20 species. > 10000 animals.m^{-1}). Surveys of reflective beaches in south-west Australia showed this to be the case (MCLACHLAN, 1985). No deliberate test has been carried out on dissipative beaches.

Access to the extensive, high energy, dissipative beaches on the north-west coast of the USA allowed the simultaneous examination of two fundamental questions in beach ecology: (1) Do dissipative beaches support faunas of high abundance and diversity? and (2) Does this fauna exhibit zonation and how is this displayed on the lower shore in particular? Resolution of the latter question should be facilitated on dissipative shores because of the predicted high number of species which could act as indicators of zones and also because of the expansion of the lower zones as a result of flat slopes and fine sand retaining much moisture. Despite this expected richness of the fauna of the beaches of Oregon and Washington, they have received little ecological attention. Previous work has been limited to unpublished

theses (BOSWORTH, 1976; DUPRE, 1978; KEMP, 1979, 1985; LLEWELLYN, 1982) and autecological studies (BOSWORTH, 1973; HUGHES, 1982; KEMP, 1988).

METHODS

Study Area

The Oregon coast experiences mixed tides, with a maximum daily amplitude of 3.6 m and a mean of 2 m. Wave action exhibits strong seasonal variation, being severe in winter and moderate in midsummer, with average significant breaker heights of 4-5 m and 1-2 m respectively (KOMAR et al., 1976). As beach sands typically range 200-300 μm, this corresponds to modally dissipative beaches that may become intermediate in midsummer. Three beaches on the central Oregon coast between Newport and Bandon were selected for study (Table 2), all being fully open to the sea and extensive enough not to be strongly influenced by headlands, i.e. at least 5 km in length. Sampling was carried out during minus tides when the lower shore was well exposed.

Sampling and Sorting

Each beach was sampled once in May-July. A single transect was surveyed across the shore. Sand samples for particle size analysis were taken at three levels on the shore and the positions of the low tide groundwater table and driftline noted. Sand samples were oven dried at 60°C and dry sieved through a nest of screens at 1Φ intervals to determine mean particle size (Mz) and sorting parameters (FOLK, 1968). Two replicate 0.1 m² quadrats were excavated to 25 cm depth at 11-12 points across the shore from the water to above the driftline or the base of the dunes. The sand was passed through a sieve of 1.5 mm mesh and all the fauna retained, fixed in formalin, identified within 10 days using SMITH and CARLTON (1975) and KOZLOFF (1987), counted and dry mass determined by drying at 60°C for 72 h. In addition to the quantitative sampling, qualitative collections were made over the shore for about 30 min per beach to record rarer species that might have been missed. Seine nets were used on one occasion to sample icthyofauna.

Data Analysis

To aid interpretation of zonation patterns, kite diagrams were plotted of distribution patterns across the intertidal and the abundance data subjected to multivariate analysis. Abundance values by sampling level were log transformed and similarity values calculated between stations using the Bray-Curtis coefficient. Clustering was performed using both nearest neighbour and group average linkages and ordination using multi dimensional scaling according to the Kruskal method (FIELD et al., 1982; SYSTAT, 1987).

The abundance and biomass data were calculated for metre-wide transects at each beach. In the case of species only recorded in the qualitative samples, an abundance value of $10.m^{-1}$ was used. These data were combined with data I gathered using similar techniques in southern Africa and Australia. This composite data set was analyzed for changes in total abundance and biomass, mean individual biomass (total biomass/total abundance) and species diversity in response to changes in morphodynamic state, slope, particle size and wave energy over 23 beaches by linear regression analysis. As particle size had been measured in all surveys, the mean value was used for each beach. Wave height and period values (mean annual significant breaker height and period) were obtained from STEEDMAN et al. (1977) for the Australian beaches and KOMAR et al. (1976) for the Oregon beaches, but for the southern African coast values were estimated on the basis of 15 years experience of this coast, the data of Dr. T. E. DONN (pers. comm.) and some published values (MCLACHLAN, 1979). Morphodynamic state is expressed by Dean's parameter which is dimensionless and is <1 for reflective beaches, 1-6 for intermediate beaches and >6 for dissipative beaches (SHORT and WRIGHT, 1983). Dean's parameter is given as $\Omega = Hb/Ws.Tb$, where Hb is the significant breaker height in cm, Tb the wave period in seconds and Ws the fall velocity of the sand in $cm.s^{-1}$. Fall velocity was obtained from particle size and GIBBS et al. (1971).

RESULTS

Fauna and Zonation

The three beaches all had well sorted fine to medium sands with mean grain sizes, 230–

270 μm at Threemile, 150–220 μm at Whiskey Run and 260–300 μm at Moolach, decreasing upshore in all cases. They were flat (slopes 1/57, 1/80 and 1/57 respectively) and dissipative with high water table positions and diverse and abundant faunas (Figures 1-3). Whisky Run, the finest grained and flattest beach, had the most diverse fauna with 21 species, not includ-

ing coleopterans and pupae of uncertain origin encountered in the supralittoral region. Threemile and Moolach had 16 and 17 species respectively.

Table 1 lists the species recorded and their abundance and biomass values across the entire transects in sequence from the top of the shore down. This coast falls into the Oregonian Prov-
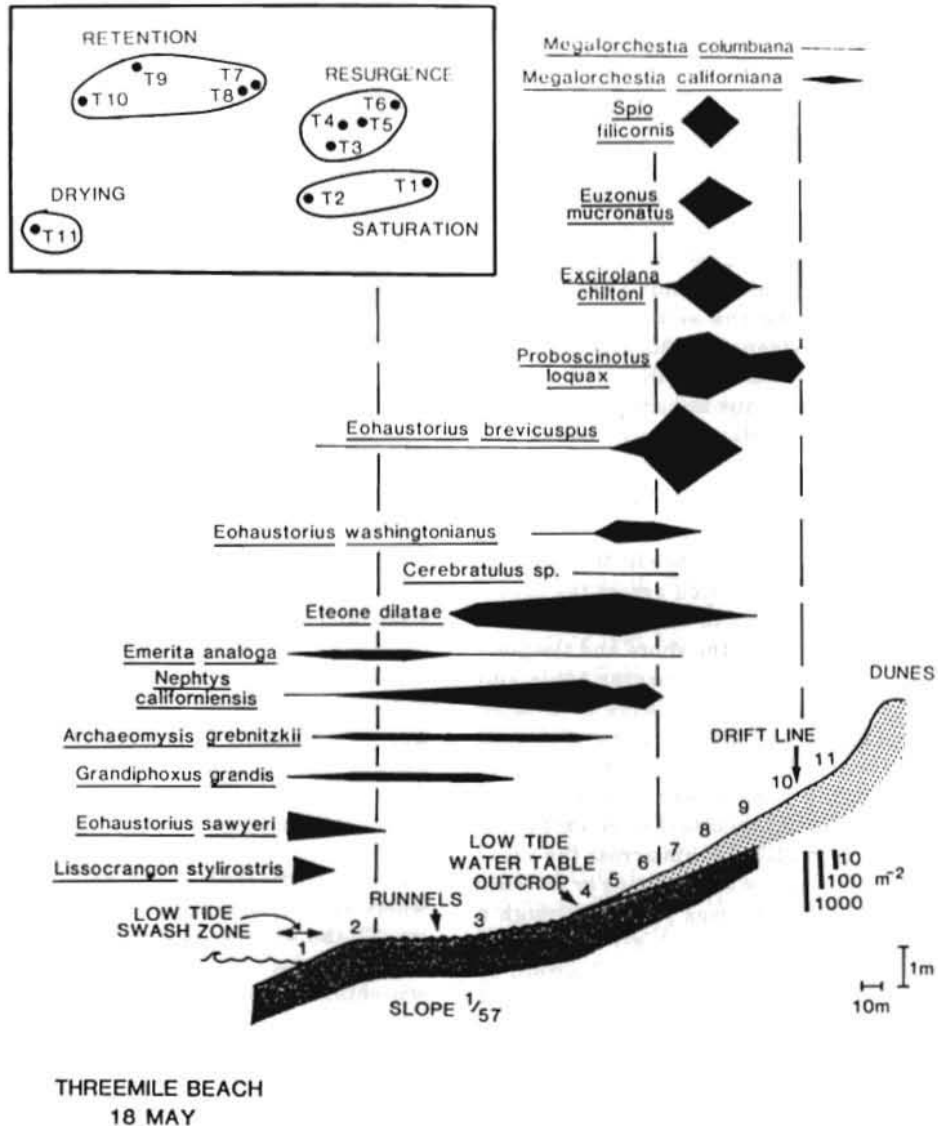

THREEMILE BEACH
18 MAY

Figure 1. Profile of Threemile Beach showing faunal distribution, sampling sites (1-11) and boundaries of zones as identified by multi-dimensional scaling (inset).
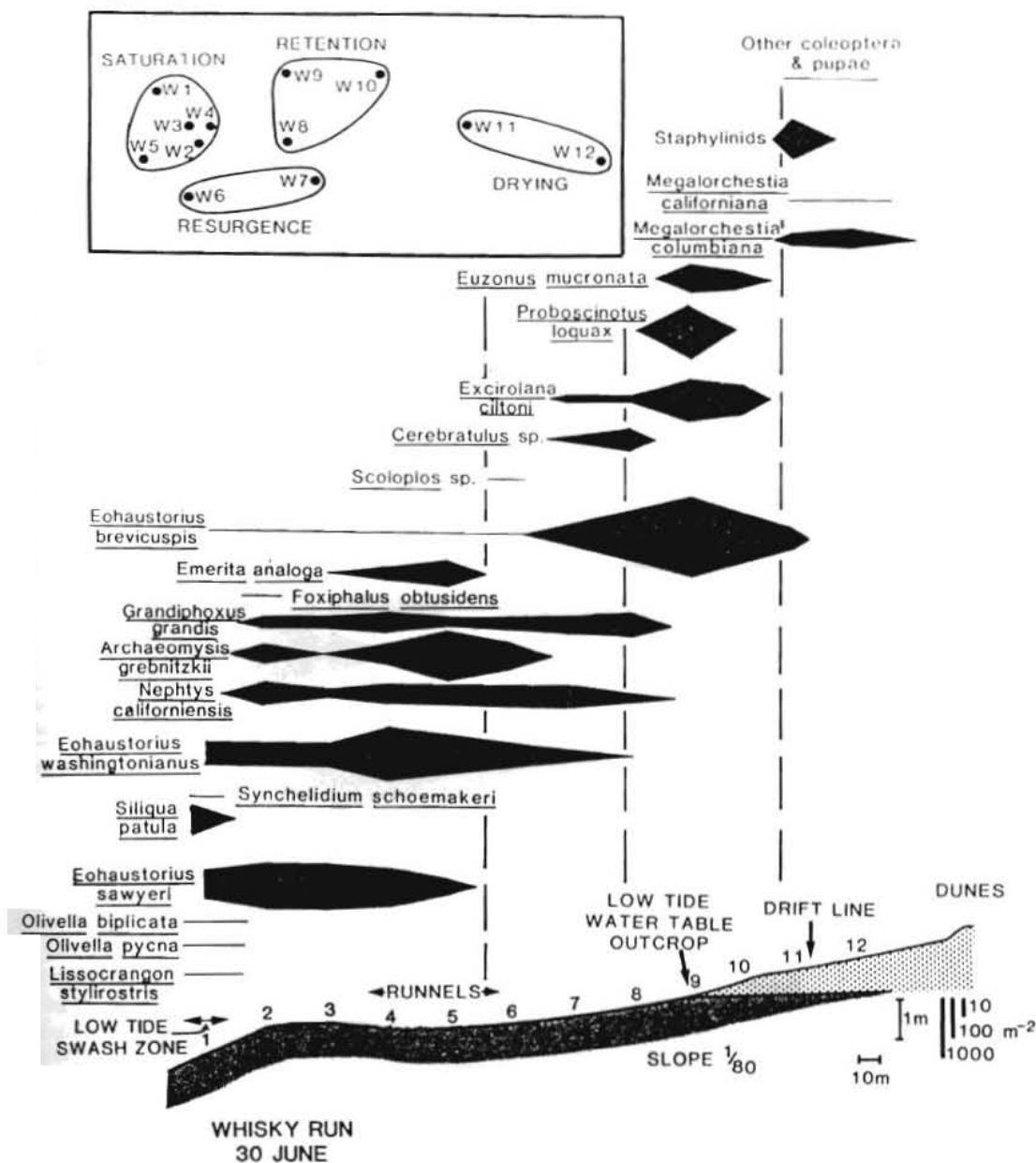
Figure 2. Profile of Whisky Run Beach showing faunal distribution, sampling sites (1-12) and boundaries of zones as identified by multi-dimensional scaling (inset).

ince, which extends from northern British Columbia to southern California (FOSTER *et al.*, 1988). The fauna was dominated by gammarid amphipods, particularly haustoriids,

which also dominate beaches on the east coast (HOLLAND and POLGAR, 1976; DONN and CROKER, 1983). Polychaetes filled the second slot with the deposit feeder *Euzonus mucronata*,
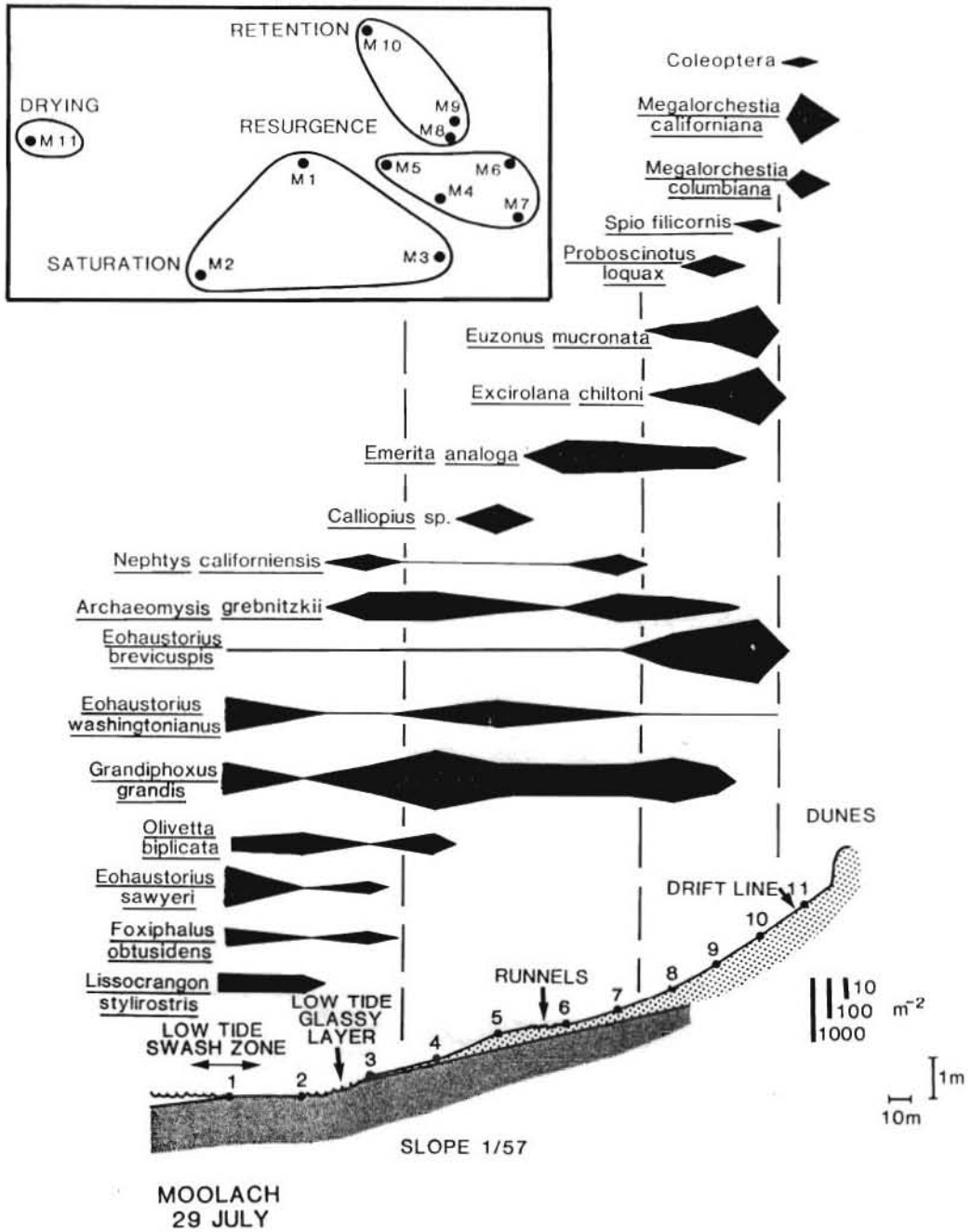
Figure 3. Profile of Moolach Beach showing faunal distribution, sampling sites (1-11) and boundaries of zones as identified by multi-dimensional scaling (inset).

Table 1. *Abundance and dry biomass of the fauna on three Oregon beaches.*

Zone	Species (and taxon)		Threemile N	Threemile S	Beach Whiskey Run N	Beach Whiskey Run S	Moolach N	Moolach S
D	Coleoptera: unidentified spp.	(I)	0	0	53	0.05	70	4.76
D	Pupae	(I)	0	0	525	0.68	0	0
D	Coleoptera: Staphylinidae	(I)	0	0	3300	1.32	0	0
D	Megalorchestia californiana Brandt 1851	(C)	120	2.40	10	0.07	2600	30.68
D	M. columbiana (Bousfield 1958)	(C)	10	0.20	113	0.77	450	1.53
R	Euzonus mucronata (Treadwell 1914)	(P)	6000	79.79	1500	187.50	4583	779.16
R	Proboscinotus loquax (Barnard 1967)	(C)	28770	152.48	25400	60.96	200	0.50
R	Excirolana chiltoni (Richardson 1905)	(C)	6930	26.51	5550	29.97	5600	49.52
R	Spio cf. filicornis (O.F. Muller 1766)	(P)	2700	20.00	0	0	75	0.27
R	Scoloplos? sp.	(P)	0	0	75	5.11	0	0
R	Eohaustorius brevicuspis Bosworth 1973	(C)	209431	383.99	160727	273.24	8250	13.78
R/G	Cerebratulus? sp.	(N)	45	0.27	500	9.15	0	0
G	E. washingtonianus (Thorsteinson 1941)	(C)	17163	31.57	17767	30.20	2250	3.83
G	Calliopius sp.	(C)	0	0	0	0	600	0.30
G	Eteone dilatae Hartman 1936	(P)	6965	92.63	0	0	0	0
G	Nephtys californiensis Hartman 1938	(P)	4925	515.50	3771	77.31	375	17.63
G	Grandiphoxus grandis (Stimpson 1856)	(C)	2080	19.76	2100	11.97	18144	139.71
G	Archaeomysis grebnitzkii Czerniavsky 1882	(C)	2825	3.32	11400	23.94	2402	9.37
G	Emerita analoga (Stimpson 1857)	(C)	409	147.24	750	387.38	1463	700.54
S	Eohaustorius sawyeri Bosworth 1973	(C)	500	1.20	10500	17.87	1867	3.12
S	Foxiphalus obtusidens (Alderman 1936)	(C)	0	0	75	2.48	231	0.11
S	Synchelidium schoemakeri Mills 1962	(C)	0	0	38	0.11	0	0
S	Siliqua patula (Dixon 1788)	(B)	0	0	56	91.97	0	0
S	Lissocrangon stylirostris (Holmes 1900)	(C)	125	27.69	10	2.22	150	17.10
S	Olivella biplicata (Sowerby 1825)	(G)	0	0	10	1.19	630	24.57
S	O. pycna Berry 1935	(G)	0	0	10	0.46	0	0
Total Numbers			288998		244240		49940	
Total Biomass				1504.65		1215.92		1796.48

N = numbers.m − 1, B = biomass (g.m − 1). Under zone D = drying, R = retention, G = resurgence, S = saturation. Under taxon I = Insecta, C = Crustacea, P = Polychaeta, N = Nemertea, B = Bivalvia, G = Gastropoda.

the carnivore *Nephtys californiensis* and the suspension feeder *Eteone dilatae.* Together, amphipods and polychaetes made up 65% of the species recorded. Donacid bivalves were absent, being replaced by the Pacific razor clam *Siliqua patula,* which occurred mainly in the surf zone (LEWIN *et al.,* 1979), but extended up onto the lower shore. Were this species more intertidal, the biomass would be much higher. Indeed, a feature of this fauna is the small mean body size and relatively low biomass, a consequence of the scarcity of molluscs. *Excirolana chiltoni,* an active scavenger of the retention zone, was recorded by DUPRE (1978) and BOSWORTH (1976) as *Cirolana harfordi.* Insects were commonly encountered above the driftline; a variety of coleopterans and pupae of uncertain origin and, at Whisky Run, an abundant resident population of staphylinids.

About half the species were common to all three beaches and displayed some zonation. Examination of the kite diagrams, dendrograms and ordination plots all suggested the same zonation patterns and therefore only the multi-dimensional scaling plots are illustrated (Figures 1-3) to show affinities and groups among stations for each beach. Pooling the stations for all beaches resulted in the same groupings but less clarity because of inter-beach differences. This confirms subdivision of the shore into four zones, the boundaries of which are indicated in Figures 1-3.

At the top of the shore the zone of drying (subterrestrial fringe), characterized by the talitrid amphipods *Megalorchestia* spp., was most distinct and extended from the drift line to the top of the backshore. Below this the zone of retention (midlittoral) was also distinct and characterized by the cirolanid isopod *Excirolana chiltoni,* the amphipod *Proboscinotus loquax,* the

bloodworm *Euzonus mucronata* and the abundant haustoriid amphipod *Eohaustorius brevicuspis*. The latter species was not confined to this zone, however, and occurred in low numbers over much of the shore.

The lower zones were less sharply defined, but nevertheless evident. The resurgence zone was centered around the low tide water table outcrop on Threemile, but situated below it on Whisky Run and above it on Moolach, suggesting that tidal level might be at least as important as sand moisture in defining zones. Species characteristic of this zone ranged widely over the shore but had their distributions centered here, the widest zone on two of the three beaches: the polychaetes *Nephtys californiensis* and *Eteone dilatae*, the mysid *Archaeomysis grebnitzkii*, the haustoriid amphipod *Eohaustorius washingtonianus*, the phoxocephalid amphipod *Grandiphoxus grandis* and the mole crab *Emerita analoga*. Finally, the zone of saturation was restricted to the area between the low tide water table outcrop and swash regions. Characteristic species included the scavenging gastropod *Olivella biplicata*, the haustoriid *Eohaustorius sawyeri* and the shrimp *Lissocrangon stylirostris*. Besides *E. analoga*, other species observed migrating included the haustoriids and *E. dilatae*.

Global Trends

For the analysis of "global" trends in biological features of beaches in relation to physical changes, data from 23 beaches were used (Table 2). Three Australian beaches are reflective and experience low wave energy and microtides, three Oregon beaches are dissipative with high wave energy and mesotides and 17 southern African beaches are mostly intermediate, being subject to moderate to heavy wave action and micro- to mesotides. This series is unique in covering a range from reflective beaches, devoid of macrofauna, to dissipative beaches with exceptionally rich faunas. Significant correlations (p <0.05) were found between all four physical parameters used (wave height, sand particle size, Dean's parameter and beach slope) and the four biological variables, diversity, total abundance and biomass and mean individual biomass (Table 3, Figure 4). No attempt was made to correlate tide range with biological parameters as a significant relation-

ship had already been found between biological parameters and slope and particle size for southern African beaches subject to a uniform tide range (MCLACHLAN *et al.*, 1981a).

Dean's parameter gave the best correlation with diversity and abundance, followed closely by slope, but wave height best explained changes in biomass. As Dean's parameter is in reality little more than a sophisticated average measure of slope, the good agreement between these two parameters is logical: slope values reflect a single point in time, whereas the values for Dean's parameter give an annual mean based on mean wave data. Species diversity increased linearly and total abundance logarithmically from steep reflective to flat dissipative beaches. Although biomass showed the same general trend, it seems most closely related to wave energy, which may directly control food inputs. The size of the average organism on a beach, mean individual biomass, increased from dissipative to reflective beaches, from fine to coarse sand and from flat to steep beaches, with slope giving the best fit. Particle size also gave good correlations, but, like wave energy it represents only part of the physical forces operating on the beach, whereas Dean's parameter and slope are more integrated measures of the result of all these interactions.

DISCUSSION

Ecology of Oregon Beaches

The beaches surveyed in this study are typical of the Oregon coast in being modally dissipative and composed of sands chiefly in the range 200–300 μm. They experience extreme wave action in winter when they become ultra-dissipative ($\Omega > 10$). They are bathed by highly productive surf waters which support dense "blooms" of surf diatoms for much of the year and provide abundant food for filter and deposit feeders. Indeed, surf diatom blooms are characteristic of high energy, flat beaches worldwide (LEWIN and SCHAEFER, 1983). The permanence of well developed surf zones, with high productivity in the form of surf diatom "blooms," indicates that these beaches should not be seen in isolation but, rather as part of a larger ecosystem, the beach/surf zone ecosystem (MCLACHLAN *et al.*, 1981b) extending to the limit of surf circulation cells at about 16 m

Table 2. *Summary of beach surveys used for analysis of global trends.*

Beach, Location & Coordinates	Physical						Biological			
	Tide Type & max. range (m)	Wave Height Hb (m)	Period (sec)	Sand Mz (um)	Slope	Hb/ WsT	No. spp	Abund. (m−1)	Biomass (g.m−1)	Ref.
Whisky Run, U	mixed									
4310N12425W	3.6	2.4	9.5	200	1/80	10.5	21	244240	1216	1
Threemile, U	mixed									
4345N12412W	3.6	2.4	9.5	250	1/57	7.9	16	288998	1505	1
Moolach, U	mixed									
4440N12405W	3.6	2.4	9.5	275	1/57	6.8	17	49940	1796	1
Maitlands, S	semi-diurnal									
3357S2520E	2.1	2.0	9.0	300	1/35	5.4	12	6569	6622	2
Stillbaai, S	semi-diurnal									
3433S2140E	2.1	1.5	9.0	222	1/23	5.9	11	624	23	3
Cebe, S	semi-diurnal									
3231S2835E	2.1	1.4	8.5	215	1/33	6.1	12	2206	56	4
Sundays, S	semi-diurnal									
3335S2555E	2.1	1.7	9.0	260	1/34	5.6	13	2520	991	5
Gulu, S	semi-diurnal									
3310S2740E	2.1	1.5	8.5	242	1/36	5.7	8	3041	19	4
Mpande, S	semi-diurnal									
3145S2921E	2.1	1.3	8.5	225	1/26	5.5	8	2790	99	4
Keurbooms, S	semi-diurnal									
3402S2339E	2.1	1.5	9.0	304	1/12	4.1	7	1510	36	3
St. Lucia, S	semi-diurnal									
2815S3225E	2.1	1.3	8.0	279	1/14	4.3	9	250	9	6
Sardinia, S	semi-diurnal									
3403S2526E	2.1	1.4	9.0	285	1/25	4.0	7	213	53	2
Struisbay, S	semi-diurnal									
3436S2010E	2.1	1.8	9.0	364	1/23	3.8	12	2555	108	3
Wildernes, S	semi-diurnal									
3401S2259E	2.1	2.0	9.0	394	1/13	3.8	8	1309	37	3
St George, S	semi-diurnal									
3348S2538E	2.1	1.2	8.0	285	1/32	3.9	8	1096	108	2
Kings, S	semi-diurnal									
3355S2536E	2.1	0.8	8.0	215	1/25	3.8	8	173	41	7
Thompsons, S	semi-diurnal									
3105S3010E	2.1	1.3	8.5	362	1/10	2.9	3	105	9	4
Sodwana, S	semi-diurnal									
2725S3244E	2.1	1.3	8.0	431	1/18	2.5	5	201	87	6
Blythdale, S	semi-diurnal									
2916S3116E	2.1	1.4	8.5	876	1/5	1.2	1	3	18	6
Kelso, S	semi-diurnal									
3016S3040E	2.1	1.4	8.5	936	1/8	1.1	1	5	33	6
Sorrento, A	mixed									
3134S11537	0.9	0.4	6.5	310	1/9.5	1.4	4	92	–	8
Quinns, A	mixed									
3120S11537E	0.9	0.4	6.5	370	1/7	1.1	2	155	1	9
Scarborough, A	mixed									
3135S11535E	0.9	0.4	6.5	610	1/5	0.6	0	0	0	9

Under location U = USA, S = South Africa, A = Australia. References: 1 = this study, 2 = McLachlan 1977a, 3 = McLachlan et al. 1981. 4 = Wooldridge et al. 1981, 5 = Wendt and McLachlan 1985, 6 = Dye et al. 1981, 7 = McLachlan 1977b. 8 = McLachlan and Hesp 1984, 9 = McLachlan 1985.

depth (LLEWELLYN, 1982). Wave energy seems to control surf diatom productivity (CAMPBELL, 1987; LEGENDRE and DEMERS, 1984) and thus is the most important factor influencing the dimensions of this system, its productivity and most other biological

Table 3. *Regression equations for data in table 2.*

Equation	r^2	n
Number of species $= 2.1\Omega - 0.6$	0.89 **	23 a
Log $(N + 1) = 0.51\Omega + 0.69$	0.83 **	23 a
Log $(B + 1) = 0.29\Omega + 0.56$	0.51 **	22
Log (ind. B) $= -0.23\Omega - 0.08$	0.32 **	21
Number of species $= 0.26$ (1/slope) $+ 1.74$	0.83 **	23 a
Log $(N + 1) = 0.06$ (1/slope) $+ 1.27$	0.76 **	23 a
Log $(B + 1) = 0.04$ (1/slope) $+ 0.81$	0.58 **	22
Log (ind. B) $= -0.02$ (1/slope) $- 0.53$	0.20 *	21
Log (no. species $+ 1$) $= 0.46$Mz $(\phi) + 0.13$	0.67 **	23 a
Log $(N + 1) = 1.64$ Mz $(\phi) + 0.19$	0.53 **	23
Log (ind. B) $= -1.04$ Mz $(\phi) + 0.61$	0.46 **	21
Number of species $= 7.3$ Hb (m) $- 2.15$	0.61 **	23
Log $(N + 1) = 1.77$ Hb (m) $+ 0.30$	0.58**	23
Log $(B + 1) = 1.46$ Hb (m) $- 0.34$	0.69 **	22 a

N = total numbers.m -1, B = total dry biomass (g.m -1), ind. B = mean individual biomass (g), Ω = Dean's parameter, Mz(ϕ) = mean sand particle size in phi units, Hb = significant breaker height (m). * = $p<0.01$. a = displayed in Figure 4.

processes. These Oregon beaches would therefore be expected to support high abundance and biomass of benthos.

Zonation

This study has confirmed the presence of four zones in the intertidal of these high energy dissipative beaches. Although the boundaries between zones were not sharp (as on rocky shores), and many species had wide distributions, all four zones were evident and had characteristic species whose populations were always centered in that zone. This is the first time that zonation has been applied to the fauna of an American beach, barring DUPRE's (1978) unpublished study of the upper intertidal areas of two Oregon beaches. Previous evaluation of SALVAT's (1964) scheme was confined to uncritical use of it by WITHERS (1977) and BALLY (1983) and one critical evaluation (WENDT and MCLACHLAN, 1985) in which four zones were not always clear—on two beaches only three groups could be distinguished based on fauna but four groups based on moisture levels. More recently, ALLEN and MOORE (1987) were not able to distinguish SALVAT's zones on Welsh beaches. DUPRE (1978) studied the retention and saturation zones on two Oregon beaches, but did not distinguish them or refer to SALVAT's scheme.

Although the two lower zones, which correspond to SALVAT's zones of resurgence and saturation, or DAHL's sublittoral fringe, are not as distinct as the two upper zones, they do appear valid, harboring species clearly not centered in other zones. Species occupying the saturation zone also extend into the sublittoral and may more appropriately be called surf zone species whose upper limits of distribution are on the lower shore. Similarly, some of the resurgence zone species extend into the sublittoral, *e.g. A. grebnitzkii* (LLEWELLYN, 1982). As this latter species is represented in the intertidal mainly by small juveniles (LLEWELLYN, 1982) that would pass through the sieve used in this study, it was probably undersampled. *Emerita analoga*, which occupies the top of the swash zone (PERRY, 1980), was also found in the zone of saturation at Threemile beach, a result of its high mobility and tidal migrations rather than an indication that it is a resident of the latter zone.

The fauna recorded in the saturation zone in this study is similar to that recorded in the shallow subtidal off California, with species like *Foxiphalus obtusidens, Eohaustorius sawyeri* and *Synchelidium schoemakeri* (OLIVER *et al.*, 1980). Saturation zone species are thus subtidal forms at the upper limits of their distribution; resurgence zone species are intertidal forms that require wet sand during low tide; retention zone species are also intertidal forms, but capable of remaining in sand only slightly damp during the low tide period; and drying zone species are air-breathers that are supralittoral, not intertidal.
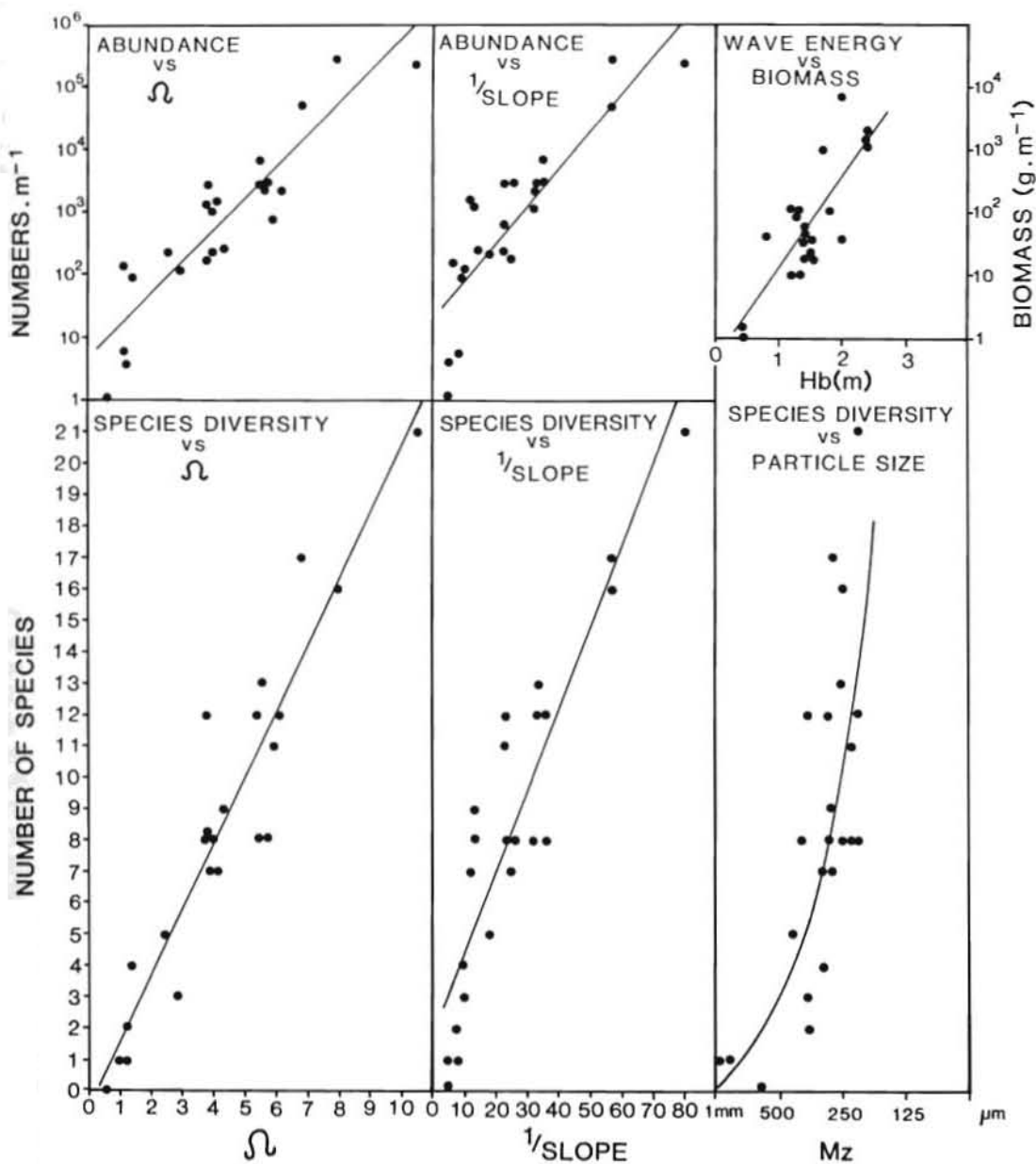
The true intertidal, between the zones of

Figure 4.   Scatter diagrams for selected regressions from Table 3.

drying and saturation, has been shown to consist of two zones in this study and it is suggested that the underlying cause is physical rather than biological. PETERSON (1979) has reviewed reasons why competition is ineffective as a means of structuring communities on soft

bottoms, but shown that predation can be a factor, especially in low energy situations. The polychaetes recorded were all monospecific representatives of their families, whereas the phoxocephalid and haustoriid amphipods were represented by two and three species respec-

tively. Some of the zonation of these amphipods may be the product of competitive interactions between closely related species, *e.g. Eohaustorius* (BOSWORTH, 1976). This has been extensively discussed in terms of the haustoriid fauna of less exposed shores (*e.g.* CROKER, 1967; and DEXTER, 1967). However, sediments at the high energy end of the spectrum should be least affected by either competitive or predatory interactions.

SALVAT's original description suggested that pore moisture in the sand at low tide and exposure time controlled zonation. Besides sediment properties, pore moisture is influenced by two hydrodynamic processes, groundwater seepage (JOHANNES, 1980) out of the beach and water filtration (RIEDL and MACHAN, 1972) through the beach driven by waves and tides. Filtered volumes for these beaches are in the range $0.1\text{-}7\text{m}^3 \text{ m}^{-1} \text{ d}^{-1}$ (MCLACHLAN, 1989). Groundwater discharge rates are well above these values, meaning that each beach is probably underlain by a freshwater lens and experiences elevated water tables. The day-to-day positions of these biological zones on the shore may therefore be determined by (1) low tide moisture levels related to rain and groundwater flow, the tidal cycle, beach slope, permeability and wave action, (2) tide levels and associated inundation or exposure times and (3) the responses of the fauna which may lag behind physical changes and further be modified by tidal, diel and semilunar migrations and storm/calm cycles. Finally, this study suggests that SALVAT's zones, although defined physically, may also be identified biologically.

Responses of Beach Fauna to Global Changes in Beach Types

The effects of wave energy on the bottom, controlling faunal gradients in the subtidal off exposed beaches, has been well documented (*e.g.* DAVIS and VON BLARICOM, 1978; VON BLARICOM, 1982; and MCLACHLAN *et al.*, 1984). Such effects in intertidal beaches are less clear. BALLY (1981) dispelled the simple notion that the fauna becomes increasingly impoverished along a gradient from sheltered to exposed beaches, summarizing 105 beach studies to show that many exposed beaches had extremely rich faunas. However, like many other authors who have looked for trends across

a range of beaches, he was not able to demonstrate any quantitative relationships or single out the key parameters.

Meaningful analysis of faunal changes over a full range of beach types depended on (1) access to a complete spectrum of beaches from fully reflective to fully dissipative and (2) collection of data by one person using the same techniques to reduce methodological differences as far as possible. The data set in Table 2 is unique in these respects. The only beach types not covered by this survey are macrotidal beaches which have more complex morphodynamics but are usually associated with low energy or protected situations. Regression analysis of individual parameters indicated that they all influenced the fauna. However, the better fit of regressions based on composite parameters (Dean's parameter and slope—both measures of overall beach state) rather than isolated factors (such as particle size or wave action), indicates that the control of beach fauna is complex and determined by the overall morphology and dynamics of a beach. Wave action and particle size are the two primary factors that essentially determine the character of a beach. Individually, however, they cannot characterize a beach (ELEFTHERIOU and NICHOLSON, 1975; BROWN, 1971). For example, many species can live and burrow in a much wider range of sand sizes than those in which they are found in nature (BROWN, 1973). Only biomass was better correlated with a simple parameter (wave energy) than a compound parameter. It has already been pointed out that there is strong evidence that wave action controls surf zone productivity (LEGENDRE and DEMERS, 1984; CAMPBELL, 1987). Abundance and diversity of the fauna, however, are best explained by beach state or slope although no cause-and-effect relationship is proved. What are the implications of this?

Both beach slope and morphodynamic state are measures of the way in which wave energy is dissipated on the beach face. The flatter a beach the longer and more even the swashes that traverse its face. Furthermore, the wider and more dissipative the surf zone, the more wave energy is modified and the dominant period converted from the incident gravity period to infragravity periods. What this means is that for waves of say 10 s period, reflective beaches will experience a swash every 10 s,

whereas dissipative beaches will only experience an infragravity bore every 40–60 s and intermediate beaches will be in between. Thus a flat beach on its own will mediate the swash, but a flat beach and wide surf zone together, as found in fully dissipative beaches, will cause maximum modification of the swash periods and lengths (SHORT and WRIGHT, 1983).

This clearly has major implications for the fauna. Animals make use of swashes to move about the beach face and to feed. The longer (in length and period) the swashes, the better these animals can move and feed. For filter feeders, for example, swashes of 5 s period on a reflective beach make feeding virtually impossible. Similarly, molluscs, which rely almost exclusively on swash currents to transport them about the beach, can usually not respond fast enough, in terms of burrowing time, to utilize swashes of periods <10–20 s (MCLACHLAN and YOUNG, 1982). Beaches towards the dissipative end of the spectrum (with swash periods >30 s) are thus conducive to macroscopic intertidal life. They presumably also have more varied beach face processes generating more niches and resulting in greater diversity. The small mean body sizes of the fauna also suggest that, despite high wave energy, dissipative beaches may be more hospitable to smaller and less robust macrofauna, *e.g.* haustoriid amphipods. The "autecological hypothesis" (NOY-MEIR, 1979) states that in physically-controlled environments animal populations have little influence on each other and communities are structured by each species responding independently to the physical environment rather than biological interactions. The good correlations found between purely physical parameters and faunal abundance, diversity, biomass and individual size on exposed sandy beaches suggest that this hypothesis is broadly valid in such systems.

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