SANDY BEACH ECOLOGY - A REVIEW

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1. INTRODUCTION

Sandy beaches dominate most temperate and tropical coastlines where they represent both important recreational assets and buffer zones against the sea. In some areas they are very productive and are exploited commercially. However, they have been regarded as marine deserts by many biologists and were largely neglected until Remane (1933) began studies on the coasts of Germany. The work of Pearse et al (1942) was also pioneering and represented the first qualitative attempt to evaluate a whole beach system. Since then sandy beach ecology has advanced considerably, though it has always lagged behind other aspects of coastal marine ecology in the attention it has enjoyed. During this period biological research on beaches has spread from early taxonomic and qualitative studies through quantitative ecology and physiology of important species towards a more holistic systems approach today.

The term sandy beach has been loosely used in the literature to cover a range of environments from high energy open ocean beaches to extremely sheltered estuarine sand flats. For the purposes of this review a sandy beach is considered to be a sandy littoral area open to the sea. This does not include sand flats in estuaries or closed lagoons but only open marine beaches. Nevertheless, such beaches may differ considerably in their degree of exposure to wave action. On a 20 point exposure scale, developed for studies on intertidal fauna (McLachlan, 1980a), beaches scoring 11 to 18 are considered exposed and are characterised by continuous, often heavy, wave action, the absence of silt, a mobile fauna and a high degree of oxygenation of the sand. Sheltered beaches (scores 5-10) have less, often intermittent wave action, fauna which may construct semi-permanent burrows and reduced layers present and sometimes close to the surface. Beaches scoring below 5 points on this rating scale are not open ocean beaches and fall outside the scope of this review. Wright, Short (1982) have developed a six point scale classifying beaches from dissipative to reflective extremes based on morphodynamics.

As the sandy beach occupies a dynamic interface position between sea and land, its boundaries with the adjacent terrestrial and marine environments are not always clear and the functional extent of the beach itself has seldom been discussed. The sand beach is considered here to be part of a system

comprising i) the sand body from the highest drift line near the dune/beach boundary out to beyond the break point of the waves and ii) the moving water envelope of the surf zone to the outer limit of surf circulation cells where they exist. This dynamic environment, which I call the beach/surf zone ecosystem, is of great extent in both tropical and temperate areas. It does not include the dunes typical of many sandy coasts, although dune/beach interactions are important. Its landward boundary is clearer than its seaward boundary where, in exposed situations, surf circulation cells, driven by breaking waves, mix with inshore water. The basic topography and features of this system are illustrated in Fig. 1.

been written on sediments, wave action and relationships between sedimentary parameters, beach slope and wave action, considerably less attention has been focused on the important processes relating to water movement in the surf zone. The significance of surf circulation cells, rip current systems etc., has still to be realized in beach ecological studies.

Biological work to date has concentrated on the fauna of the intertidal sand body and most other aspects of beach ecology, including the surf zone as a whole, have been neglected. The intertidal sand body of open sandy beaches is characterized by a mobile substratum and the absence of attached plants. Normally the substratum provides two
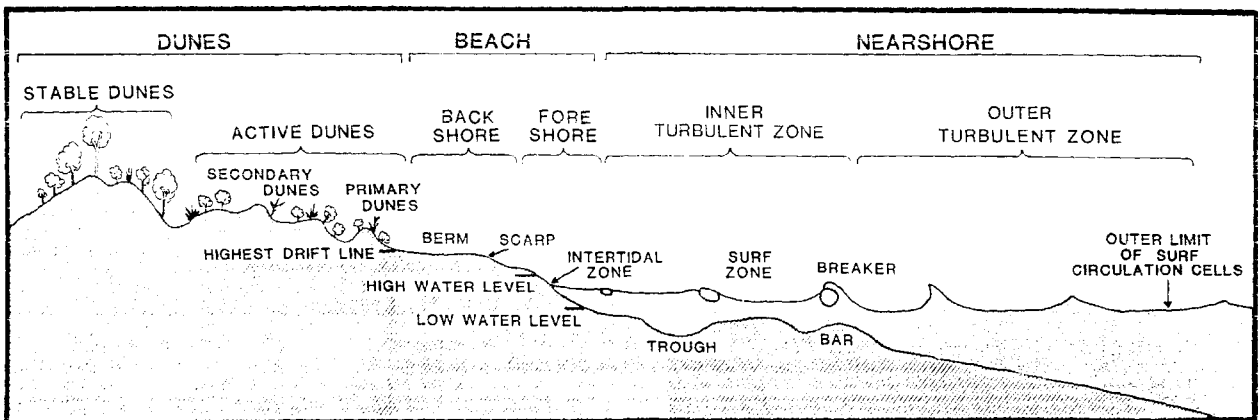

FIGURE 1. Profile of a typical sandy beach environment, showing areas referred to in the text.

The physical features of this system will not be examined here. Besides other papers in this volume, descriptions of physical features of beaches important to ecologists may be found in many publications, including Bascom (1964), King (1972), Davies (1972) and Inman, Brush (1973). Though much has

habitats suitable for faunal population. These are i) the macrofauna habitat consisting of the sand surface and upper layer of sediment and ii) the interstitial habitat consisting of the porous system of the sand body. The former, particularly on exposed beaches, is a uniform but dynamic and unstable,

essentially two dimensional system. The latter is a more stable and complex habitat with clear vertical gradients and is essentially a three dimensional system (McLachlan, 1977a). It has great vertical extent on exposed beaches or high energy 'windows' where strong hydrodynamic forces introduce oxygen deep into the sediment. Elsewhere its base consists of reduced layers (Fenchel, Riedl, 1970).

The macrofauna of sandy beaches and the meiofauna (and microfauna) of their interstices comprise two entirely separate faunal components with virtually no overlap or exchanges of energy. This is because the meiofauna are extremely small interstitial forms while the macrofauna are several orders of magnitude larger (McIntyre, 1971; McIntyre, Murison, 1973; McLachlan, 1977a). Schwinghamer (1981) distinguished three biomass peaks in intertidal sediments corresponding to bacteria, interstitial meiofauna and macrofauna. As sediments become finer below 200 um mean grain size, large burrowing forms of meiofauna become increasingly important and tend to bridge the size gap between macrofauna and meiofauna. This makes separation into two components less marked in finer sediments and facilitates better energy flow between these components. Energy flow between these components also increases because the meiofauna are concentrated near the surface and macrofauna deposit feeders increase in abundance in finer sediments. In coarser sediments such intermediate forms are absent, probably because they represent a size range selected against by the physical forces of the beach environment. Thus although meiofauna-macrofauna interactions may occur (Hummon et al., 1976; Reise, 1979) these are generally of negligible significance in terms of energy flow on exposed sandy beaches.

The only review on sand beach ecology as a whole is that of Hedgpeth (1957), although some aspects of beach ecology are covered by Eltringham (1971). Both these works are outdated and there is a distinct need for a synthesis of information on sandy beaches. The aim of this review is to outline our knowledge of the ecology of individual components of sandy beach biotas and the structure and function of beach ecosystems as a whole. It progresses through the interstitial fauna and macrofauna of the sand body, phytoplankton, zooplankton and fishes of the surf zone and birds of the beach and dune margin to functional aspects within the framework of energy flow and nutrient cycling.

2. THE INTERSTITIAL SYSTEM

The porous system between the sand grains generally averages about 40% of the total sediment volume. Most physical properties of this system are directly determined by the sediment properties which in turn are related to the wave and current regime as well as the geological history of an area. Grain size, shape and sorting are most important in fixing porosity and permeability which influence drainage. Drainage is critical in determining the moisture content, oxygen and organic input and the depth of reduced layers. Permeability increases with coarser substrate and better sorting and

drainage also increases on steeper beaches. The interactions between these factors are well documented and covered in several papers (Webb, 1958; Hulings, Gray, 1971; Crisp, Williams, 1971).

The major process involving the interstitial system on open beaches is the filtration of sea water. This water is introduced into the sediment either by flushing by waves and tides in the intertidal (Riedl, 1971; Riedl, Machan, 1972; McLachlan, 1979a) or the pumping effects of waves in the subtidal (Steel et al., 1970a; Riedl et al., 1972). In exposed situations filtered volumes may average 5-10 m^3 per metre strip of intertidal beach per day and be several times on very steep, coarse grained beaches. In the subtidal surf zone off open beaches wave pumping may filter $0.05-5.00m^3$ $m^{-2}.d^{-1}$. This flushing or pumping concentrates dissolved and particulate organics in the sand. Under high energy conditions, however, the input of oxygen and the high drainage rates maintain this system fully oxygenated and there are no steep vertical gradients in oxygen and oxidation states of sulphur or nitrogen (Riedl, MacMahan, 1969; McLachlan et al., 1979a). Permeability and flushing generally decrease with increasing shelter until drainage is so poor that the sand is constantly saturated. Vertical chemical gradients are then steep and reduced layers occur close to the surface (Fig. 2).

The interstitial system is subject to cyclic changes related to tidal and diurnal cycles and the seasons. In high energy beaches this mainly results in fluctuations in the water table, pore
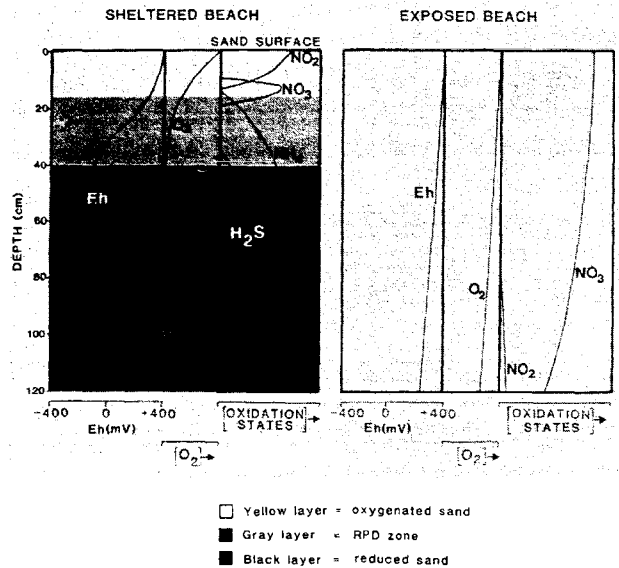

FIGURE 2. Schematic representation of vertical chemical gradients in a sheltered and an exposed beach. (After Fenchel, Riedl, 1970; McLachlan et al., 1979a)

moisture content and surface temperature (Pollock, Hummon, 1971; McLachlan et al., 1977a) while in very sheltered situations it can result in sharp changes in chemical gradients, for example pH changes coupled to temperature changes (Gnaiger et al., 1978). In sheltered beaches with reduced layers three vertical zones (Fig. 2) may be distinguished, namely clean (oxygenated) sand, a gray (or RPD) transition zone and black (reduced) conditions (Fenchel, Riedl, 1970). Horizontal zones may also be distinguished down the beach from the relatively constant conditions of the sublittoral to the backshore with large temperature and salinity fluctuations (Salvat, 1964, 1967; Schmidt, 1970; Mielke, 1976). On exposed beaches, because of its greater vertical extent

and better drainage, the interstitial system lends itself to subdivision into strata. Pollock, Hummon (1971) recognized five strata in a coarse grained (Md = 660 um) Massachusetts beach which they could relate back to Salvat's (1964) horizontal zones. McLachlan (1980b) distinguished four strata on East Cape beaches (Md = 250 um) which closely parallel those of Pollock and Hummon. In both cases the strata range from surface dry sand at the top of the beach down through moist layers to the permanently saturated zone below the water table (Fig. 3 and Table 1).
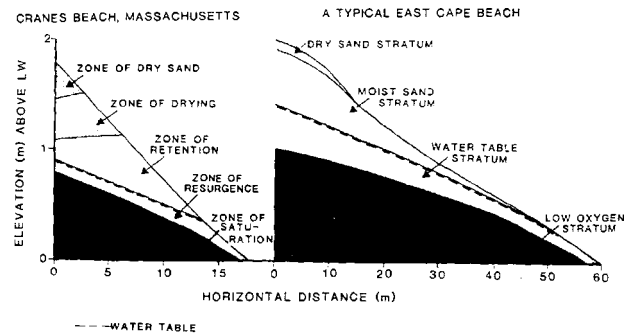

FIGURE 3. Stratification of intertidal sand based on interstitial moisture content during low tide for a beach in Massachusetts and the East Cape, South Africa. (After Pollock, Hummon, 1971; McLachlan, 1980). See also Table 1.

Table 1. Summary of stratification of exposed sandy beaches based on interstitial water content (Modified from Pollock, Hummon 1971; McLachlan, 1980). See also Fig.3.

Zone/Stratum	Moisture Content & Water Circulation	Degree of Oxygenation	Temperature
Zone of dry sand/ Dry sand stratum	Low, loses capillary water	High	Highly variable
Zone of drying/ Dry sand stratum	Low, loses capillary water	High	Variable
Zone of retention/ Moist sand stratum	Loses gravitational water but retains capillary water	High	Little variation
Zone of resurgence/ Water table stratum	Gravitational water from zone of retention drains through here during ebb tide	Moderate to low	Stable
Zone of saturation/ Low oxygen stratum	Permanently saturated, little water circulation	Low to very low	Very stable

Large numbers of microscopic organisms occupy the interstices: fungi, algae, bacteria, protozoans and metazoans. Amongst the animals, metazoans that pass undamaged through a 1mm screen are considered meiofauna and the rest microfauna. Individual dry weights are $10^{-5}-10^{-8}$g for meiofauna, $10^{-6}-10^{-11}$g for protozoans and $10^{-10}-10^{12}$g for bacteria (Fenchel, 1978; Warwick, pers. comm.) Fungi in sandy beaches are generally concentrated at higher tide levels and have been little studied (Upadhyay et al., 1978). A flora of diatoms or flagellates only develops in sheltered beaches and is absent on very exposed beaches (Steel et al., 1970a; Brown, 1971a). This also appears to be more characteristic of temperate than tropical beaches (Munro et al., 1978). In sheltered sands the diatom flora may be locally important and, due to mixing by wave action, may occur to some depth in the sand (Steele, Baird, 1968; McIntrye, 1977; Anderson, Meadows, 1978). Munro, Brock (1968) recorded numerous living bacteria and diatoms attached to sand grains up to 10cm below the sand surface and Round (1979) described a diatom assemblage living below the sand surface. Amspoker (1977) described the intertidal distribution of epipsammic diatoms on a Californian beach. Where sand is permanently saturated diatoms generally occur closer to the surface. Pearse et al., (1942) recorded Chrysophyta, Chlorophyta, Pyrrophyta and Cyanophyta on sandy beaches.

Bacteria are abundant and important in beach sediments, mostly being attached to the sand grains (Meadows, Anderson, 1966, 1968). Numbers range 10^8-10^{10} cells per gram dry sand and increase with finer sediment and greater surface area (Dale, 1974; Meyer-Reil et al., 1978; Mazure, Branch, 1979). Khiyama, Makemson (1973) recorded 362 bacterial strains in beach sand, many associated symbiotically with metazoans. Those on sand grains made up 54-78% of the total numbers of 10^7-10^8 per gram of wet sand. Wicks (1974) demonstrated the presence of Azotobacter in marine sand beaches while Rheinheimer (1977) isolated 31 strains from beach sand, of which the majority showed salinity optima at $30-50^o/_{oo}$ and were gram negative rods that could decompose proteins, carbohydrates and fats. Andrews et al., (1976) studied microbial development in a model sandy beach, recording greatest abundance near the high and low tide marks.

Organic carbon and nitrogen in the sand have been found to correlate with bacterial biomass and abundance (Dale, 1974; Anderson et al., 1981; Bolter et al., 1981) which can be up to four times the biomass of the meiofauna (Meyer-Reil, Faubel, 1980). Munro et al. (1978) estimated microbial production at $15gC.m^{-2}$ for a temperate beach and $72gC.m^{-2}$ for a tropical beach, the higher latter value due to greater water percolation. Mazure, Branch (1979) estimated an average bacterial biomass of $14.2gm^{-2}$ dry weight in the sands of Langebaan Lagoon. Dye (1979a) showed that disturbance caused greatly increased bacterial activity in beach sand. McLachlan et al., (1979a) recorded bacterial numbers around 10^8 per gram dry sand down to more than 1m in the sediment of an exposed beach. Dye

(1980a) was able to show tidal fluctuations in oxygen uptake by beach sand. Maximum uptake coincided with maximum water percolation through the sand and maximum fluctuation occurred at higher tide levels. Desiccation of the sand caused a severe drop in oxygen uptake or bacterial activity. Dye (1981) also attempted to partition total benthic oxygen uptake on exposed East Cape beaches and concluded that bacteria were responsible for most of the oxygen consumption except where there was a very rich macrofauna. Meyer-Reil et al., (1980) estimated microbial turn-over time of 100h with daily microbial carbon production of $43mg.m^{-2}$ in sheltered beaches in the Baltic. They concluded that 50% of microphytobenthos primary production was fixed by micro-organisms. Koop, Griffiths (1982) found a high bacterial biomass on an exposed beach receiving high kelp input on the west coast of South Africa, bacteria being found to 1.2 m in the sediment. Koop et al., (1982a, b) estimated that bacteria were responsible for over 90% of carbon utilization of these kelps. Annual turnover (P/B) of bacteria in this system was estimated to be 30 times (Koop, Griffiths, 1982; Stenton-Dozey, Griffiths, 1983). Despite this information we still know nothing about the ecology of individual species of micro-organisms on sandy beaches.

All groups of protozoans may be present in the interstitial system but ciliates and foraminiferans have been best studied as they are usually relatively large and quite abundant, especially on sheltered beaches with fine sands (Swedmark, 1964; Fenchel, Jansson, 1966; Panikkar, Rajan, 1970; Hartwig, Parker,

1977; Fenchel, 1978; Hartwig, 1982). Small protozoans have also been enumerated on exposed beaches in the Eastern Cape (Dye, 1979b; McLachlan et al., 1979a; Dye, 1981). Their numbers ranged 10^1-10^3 per gram dry sand and they were found to more than 1m depth in a well oxygenated beach. Their contribution to total benthic oxygen consumption was significant, accounting for 15-25% of interstitial oxygen uptake.

Meiofauna have received considerable attention on sandy beaches and several reviews cover aspects of meiofauna ecology (Delamare-Deboutteville, 1960; Swedmark, 1964; Fenchel, Riedl, 1970; Wieser, 1975; Giere, 1975; Fenchel, 1978).

Small metazoans occurring on sandy beaches may be either temporary meiofauna, i.e., larval forms of macrofauna, or permanent meiofauna. As we are mainly dealing with interstitial meiofauna here, the temporary component is generally not of importance on open beaches. The dominant components of sandy beach meiofauna are nematodes and harpacticoid copepods with several other taxa of variable importance. These include turbellarians, oligochaetes, ostracods, mystacocarids, gastrotichs, halacarid mites, tardigrades, gnathostomulids, hydrozoans and bryozoans. There is a well established relationship between the relative proportions of nematodes and harpaticoids and grain size. Nematodes tend to dominate in finer sediments, harpacticoids in coarser sediments and in sediments with mean grain size around 300-350 um they are about equally important (Gray, 1971; McLachlan et al., 1981b; Raffaelli,

Mason, 1981; Hockin, 1982). Fricke, Fleming (1983) have demonstrated experimentally the neamtode preference for finer sediments.

In sands above 200 um the meiofauna is usually entirely interstitial while below 200 um burrowing forms become increasingly important due to pore size restrictions (Wieser, 1959). Interstitial harpacticoids may occur down to 160 um (McLachlan et al., 1977b; Moore, 1979a) while nematodes can pursue an interstitial mode of life down to 125-100 um (Wieser, 1959; McIntyre, Murison, 1973; Fenchel, 1978). In noncapillary sediments nematodes dominate (Fenchel, 1978). As most open sandy beaches have grain sizes in the range 200-500 um, interstitial nematodes and harpacticoids are almost always dominant. McIntyre, Murison (1973) considered sands of 230 um to be optimum for the development of interstitial fauna while Gray, Rieger (1971) suggested that meiofaunal diversity increases as sands get finer. In South Africa richest meiofauna occurs in sands of 250-350 um (McLachlan et al., 1981b).

On a vertical basis meiofauna distribution is related to the degree of drainage and oxygenation of the sediment (see Fig. 3 and Table 1). Meiofauna abundance drops off drastically in the RPD and reduced layers (Fenchel, Riedl, 1970; McLachlan, 1978) and a deep vertical distribution therefore only occurs on exposed beaches where reduced layers are absent (Renaud-Debyser, 1963; Fenchel, Riedl, 1970; McLachlan et al., 1979a) (see also Fig. 2). Different species and taxa show well defined vertical distribution patterns related to differing tolerances to reducing conditions (Fenchel, Riedl, 1970). Vertical distribution is generally shallower in the surf zone than on the beach but high numbers may still occur 10-30 cm into the sediment (McLachlan et al., 1977b). Dean (1981) looked at the effects of wave action on meiofauna abundance.

Horizontal distribution may take the form of layers, horizontal zones, bathymetrical steps and geographical regions (Fenchel, Riedl, 1970). Horizontal zones of meiofauna distribution have been described from some beaches, particularly under relatively sheltered conditions (Coull, 1970; Schmidt, 1972a, b; Harris, 1972a; Moore, 1979b) where the meiofauna is close to the surface and the distribution tends to take on a more two-dimensional character (Fig. 4).

Seasonality has been documented in several cases in temperate areas with the meiofauna occurring in lower abundance and moving deeper into the sediment in winter (Renaud-Debyser, 1963; Harris, 1972b; Schmidt, 1972a, b,; Hulings, 1974; Mielke, 1976; Faubel, 1976; Nodot, 1976; Feder, Paul, 1980). In warmer areas seasonality is less clear (McLachlan, 1977b) and in sublittoral areas it may be more complex (Emberton, 1981). Vertical migrations other than seasonal have been recorded as response to factors such as heavy rains (Bush, 1966), wave disturbance (Boaden, 1968), tidal factors (Rieger, Ott, 1971; Meineke, Westheide, 1979) and changes in moisture and oxygen over the tidal cycle (McLachlan et al., 1977a).

(a) SHERTALLAI BEACH, INDIA

HWS

Arenopontia orientalis
Arenopontia acantha
Psammopsyllus operculatus

ALL INTERSTITIAL FORMS

1 m

WATER TABLE

10 m

(b) A TYPICAL MANX BEACH

3 EURYHALINE UPPER SHORE SPECIES (ALL INTERSTITIAL)

HWS

3 EULITTORAL SPECIES (1 EPIBENTHIC 2 INTERSTITIAL)

HWN

6 SUBLITTORAL FRINGE SPECIES (EPIBENTHIC)

1 m

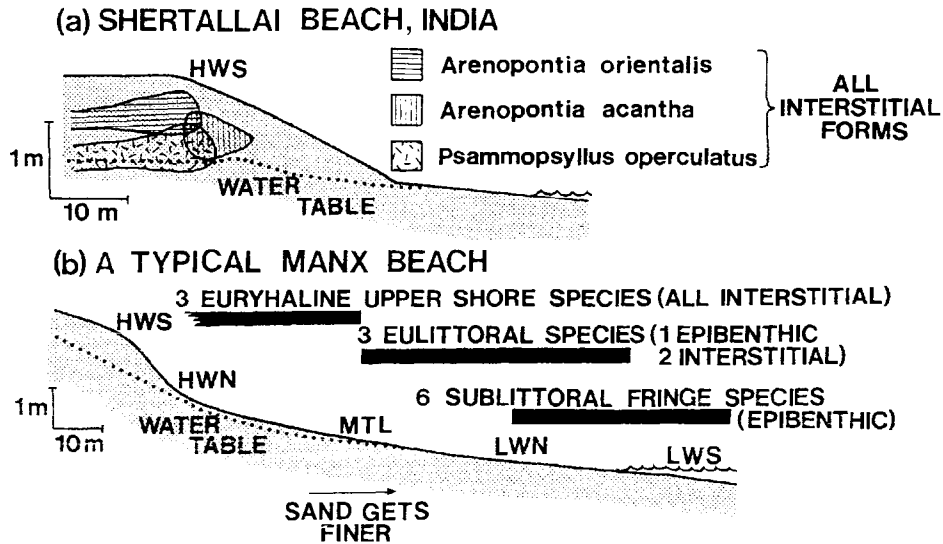WATER TABLE   MTL

10 m

LWN

LWS

SAND GETS FINER

FIGURE 4. Comparison of vertical and horizontal distribution patterns of harpacticoid copepods in a well drained, exposed beach (a) and a sheltered beach (b) where distribution patterns tend to be very three-dimensional and rather two-dimensional respectively. (After (a) Munro et al., 1978 and (b) Moore, 1979b). In all cases the copepods are concentrated above the low tide water table. On the sheltered beach interstitial fauna are mostly concentrated high on the shore where some drainage occurs. Nevertheless zonation in this case is still mostly across the shore and not vertically in the sediment.

seasonality are becoming clearer as a result of ecophysiological studies on responses, preferences and tolerances of important meiofaunal species (Jansson, 1967, 1968a; Wieser et al., 1974; Wieser, 1975; Hartwig et al., 1977; Wieser, Scheimer, 1977).

A wide range of food items has been recorded for meiofauna including diatoms, bacteria, protozoa, detritus, other meiofauna and dissolved organics (Jansson, 1968b; McIntyre, 1969; Fenchel, 1978; Giere, 1975, 1982). Feeding categories include bacterial

feeders, non-selective deposit feeders, diatom feeders, carnivores and even filter feeders. Various studies have shown aggregation of meiofauna in response to specific bacterial strains (Gray, Johnson, 1970) or where there are high levels of organics generally or localized small scale concentrations (Lee et al., 1977; McLachlan et al., 1977b; Moore, 1979a; Hogue, Miller, 1981) or concentrations of prey (Fenchel, 1978). Feeding rates have been estimated directly for a copepod (Rieper, 1978). There have also been studies on growth, production and

population dynamics of important species (Pawlak, 1969; Lasker et al., 1970; Hall, Hessler, 1971; McLachlan 1977c; Feller, 1980). Most species have year round reproduction with generation times ranging 1-3 months (McIntyre, 1969; Lasker et al., 1970; Giere, 1975; Bartsch, Schmidt, 1979).

Over the past decade ecological studies on sandy beach meiofauna have advanced from the more general surveys of the sixties. More attention has been paid to the complex of factors composing the interstitial system and results have been better analysed statistically (Gray, Rieger, 1971; Hulings, 1971; Hulings, Gray, 1976; McLachlan, 1978; Hogue, Miller, 1981). The basic pattern of meiofaunal response to different sediment types is well documented and responses to chemical features of the interstitial system are clearer. More work is needed on biotic interactions including competition, feeding and predation.

With regard to energetics and benthic metabolism the interstitial system has still largely been regarded as a black box and few authors have progressed beyond the estimation of abundance or biomass. On exposed beaches, and in most other sediments, meiofaunal numbers fluctuate within an order of magnitude of $10^6 m^{-2}$ and dry biomass values range 20-4400 $mg.m^{-2}$. Some figures are compared in Table 2.

Clearly biomass tends to be higher in the intertidal on exposed beaches because the great vertical extent of these systems provides greatest habitat availability and high percolation rates

supply adequate dissolved and particulate organic food. Meiofauna are generally considered to subsist on the microfauna which in turn are largely fuelled by dissolved and particulate organics flushed into the sand (McIntyre et al., 1970). Measurements of benthic metabolism have attempted to partition oxygen uptake between these different components of the interstitial fauna (Munro et al., 1978; Dye, 1980a; 1981). Rates of mineralisation of organics by the interstitial system have also been measured in experimental sand columns in an attempt to understand these processes better and estimate nutrient cycling (McIntyre et al., 1970; Boucher, Chamroux, 1976; McLachlan et al., 1981c).

Vernberg, Coull (1974) estimated the ratio of metabolic activities of ciliates to meiofauna to macrofauna as 1:0.5:2.1 for a sandy sublittoral sediment and 1:0.54:0.04 for an exposed beach. Dye (1981) partitioned benthic metabolism between microfauna, meiofauna and macrofauna on two exposed beaches in the ratios 1:0.23:0.04 and 1:0.27:1.85, the latter beach having an exceptionally rich macrofauna. McLachlan et al., (1981a) partitioned benthic metabolism on East Cape beaches amongst the interstitial fauna and macrofauna as 1:0.4. On a west Cape beach receiving a high kelp input, biomass ratios of macrofauna: meiofauna: bacteria were 3.5:1:1.5 (Griffiths et al., 1983) while these ratios for productivity were 1:1:4.7.

It may be concluded that our knowledge of the interstitial system of open sandy beaches has advanced considerably over the past two decades. We have a good

Table 2. Abundance and dry biomass values for meiofauna recorded from marine sands.

Source	Locality	Abundance	Biomass
Wieser (1960)	Buzzards Bay	sublittoral $10^6.m^{-2}$	$100 - 600$ mg.m^{-2}
Coull (1970)	Bermuda	sublittoral $10^6.m^{-2}$	$33 - 259$ mg.m^{-2}
McIntyre, Murison (1973)	South Africa	exposed intertidal $10^6.m^{-2}$	$279 - 1\ 092$ mg.m^{-2}
McLachlan (1977a, b)	South Africa	exposed intertidal $10^6.m^{-2}$	$20 - 3\ 360$ mg.m^{-2}
McLachlan et al., (1977b)	South Africa	sublittoral $10^6.m^{-2}$	$350 - 1\ 045$ mg.m^{-2}
Fenchel (1978)	sublittoral	sand $10^5-10^6.m^{-2}$	$50 - 1\ 700$ mg.m^{-2}
McLachlan et al., (1981b)	South Africa	exposed intertidal $10^6.m^{-2}$	$400 - 4\ 000$ mg.m^{-2}
Stenton-Dozey, Griffiths (1983)	South Africa	exposed intertidal $10^6-10^7.m^{-2}$	$1\ 000 - 44\ 000$ mg.m^{-2}

general idea of the distribution patterns of interstitial fauna in relation to many features of inter-stitial climate. However, in this respect the excellent work of Riedl and co-workers in describing water flow through beach sand has not received the attention it deserves. The patterns of water input, percolation and pulsing disturbance described by Riedl, Machan (1972) (Fig. 5) add a considerable degree of comprehension to distribution patterns of meiofauna and most other interstitial processes in intertidal sands (e.g. Figs. 3 and 4a). This water flow is the superparameter controlling interstitial climate and the distri-bution of interstitial fauna in beach sands. Both meiofauna and bacteria therefore tend to concentrate in the moist sand at and above MTL and below the sand surface where there is high water input, percolation and aeration, minimum stagnation and pulsing currents

are not too severe. Under sheltered conditions the aerated strata become much flatter, the interstitial fauna concentrates close to the sand surface and the overall dimensions of the system take on a more two dimensional nature.
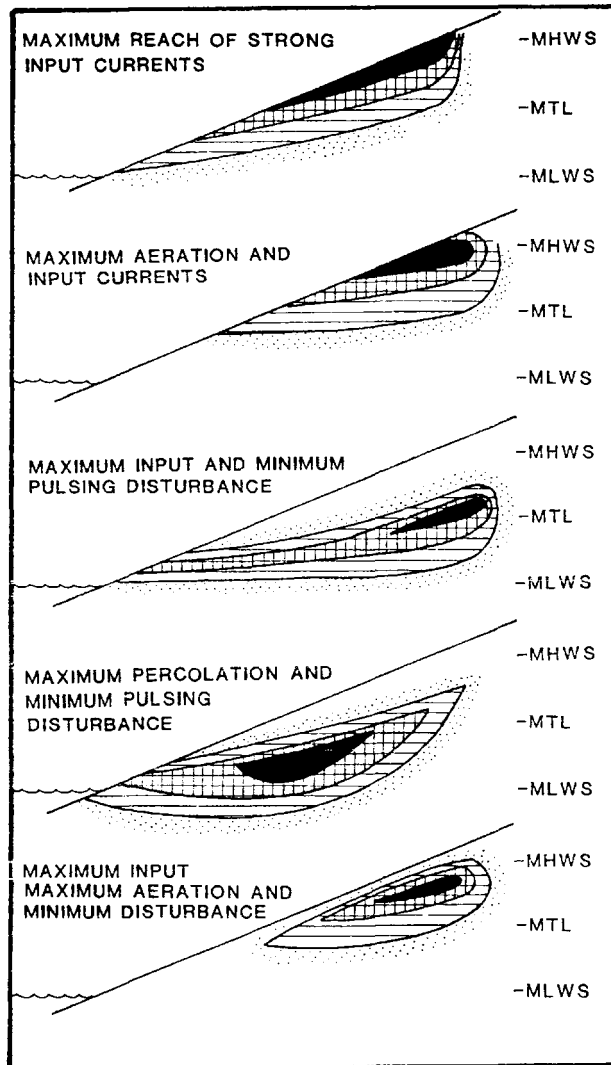

FIGURE 5. Diagrammatic representation of some important interstitial parameters related to water flow in an intertidal high energy beach. (After Riedl, Machan, 1972).

The interstitial system appears to be very efficient at mineralising virtually all organic materials it receives, whether these be dissolved or particulate. In this process bacteria are most important, with meiofauna mostly at the top of the interstitial food chain. There is little exchange with higher trophic levels, especially on exposed beaches. By the removal and mineralisation of organic materials and the release of inorganic nutrients the micro- and meiofauna are responsible for the 'purification' of large volumes of sea water flushed through the interstitial system.

3. THE MACROFAUNA

While not usually as quantitatively important in energy flow as the interstitial fauna, the macrofauna of sandy beaches are often abundant and, in some cases, attain exceptionally high densities. Their main feature on open beaches is the high degree of mobility displayed by all species. These animals may vary from a few mm in length to 10cm and consequently a variety of methods have been used to sample them. Generally sand is passed through a 0.5mm or 1mm screen, though in areas of coarse sand, screens of 2mm or even 4mm have been used. Thus not all workers have sampled the same components of the community.

The macrofauna community consists of those organisms too large to move between the sand grains and generally in the size range 1mg-2g dry tissue mass. Such species make up shifting populations in the intertidal and surf zones of open beaches. When evaluating them it is best to consider the population across an intertidal strip of beach as a whole, this unit contracting and expanding as beach profile changes and

tides pass from springs to neaps. Consequently all further discussion of abundance and biomass of macrofauna populations will consider metre wide strips of beach and not square metres, unless stated otherwise. All authors should present their results in this way, at the same time stating the width of the beach.

The macrofauna of sandy beaches includes most major invertebrate taxa although it has long been recognised that molluscs, crustaceans and polychaetes are the most important (Rees, 1939; Watkin, 1942; Southward, 1953; Schuster-Diedricks, 1956; Sourie, 1957; Pichon, 1967; Dexter, 1969, 1972). There is a tendency for crustaceans to be more abundant on tropical beaches or more exposed beaches and molluscs to be more abundant on less exposed and/or temperate beaches (McIntyre, 1968, 1970; Seed, Lowry, 1973; Dexter, 1981) although there are many exceptions to this and polychaetes are sometimes more abundant than either of these taxa (Brown, 1981; McDermott, 1983). Indeed, Dexter's (1983) work suggests that crustaceans dominate the most exposed beaches and polychaetes the most sheltered beaches with molluscs reaching maximum abundance in intermediate situations (Fig. 6). In terms of biomass, however, molluscs are usually most important (Trevallion et al., 1970; Dexter, 1974, 1976; Eleftheriou, McIntyre, 1976; McLachlan, 1977a; Ansell et al., 1972a; Bally, 1981; Shelton, Robertson, 1981).

There have been many studies on the biology and ecology of dominant bivalves and gastropods of sandy beaches
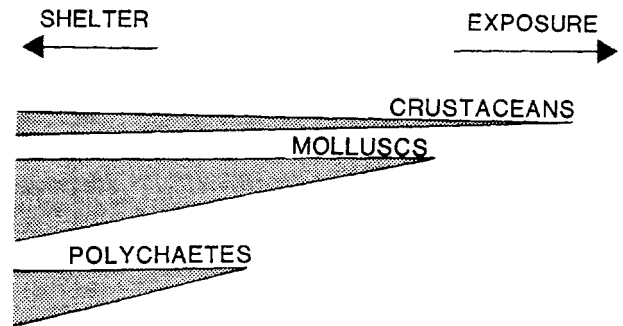
SHELTER ← EXPOSURE →

CRUSTACEANS
MOLLUSCS
POLYCHAETES

FIGURE 6. Responses of the major invertebrate groups to the exposure gradient on sandy beaches.

(Stephen, 1928, 1931, 1932; Rapson, 1952, 1954; Holme, 1954; Figueras, 1956; Edgren, 1959; Ansell, 1961; Wade, 1967; McIntyre, 1970; Smith, 1971; Brown, 1971b; Ansell et al., 1972b; Irwin, 1973; de Villiers, 1974; McLachlan, Hanekom, 1979; McLachlan, Van der Horst, 1979; McLachlan et al., 1979b; Leber, 1982b). Brown (1982) reviewed work on whelks of the genus Bullia and Ansell (1983) has covered the genus Donax.

There have been some general accounts of crustaceans on sandy beaches (McIntyre, 1963; Epelde-Aguire, Lopez, 1975; Kamihira, 1979) and many studies on individual species or groups. Amphipods have been extensively studied on the east coast of the United States (Croker, 1967a, 1967b, 1968, 1970; Dexter, 1967, 1971; Sameoto, 1969a, 1969b; Bousefield, 1970; Craig, 1973; Croker et al., 1975; Scott, Croker, 1976; Holland, Polgar, 1976; Donn, 1980) and elsewhere (Williamson, 1951; Barnard, 1963; Fincham, 1971, 1974, 1977; Kamihira, 1981). Isopods, both air- and water-breathers, have also been widely studied (Fish, 1970; Jones, 1971, 1974,

1979; Dexter, 1977a; Klapow, 1972; Fish, Fish, 1972; Kensley, 1972, 1974; Holdich, Brown, 1973; Ferrara, 1974; Glynn et al., 1975; Johnson, 1976a, 1976b; Chelazzi, Ferrara, 1978; Eleftheriou et al., 1980; Holanov, Hendrickson, 1980). Mysids have been investigated by Fishelson, Loya (1968), Brown, Talbot (1972) and Wooldrigde (1981) and cumaceans by Pike, Le Sueur (1958) and Corey (1970).

Hippid crabs have been extensively studied. Efford (1976) reveiwed distribution in the genus Emerita while other studies include Alikunhi (1944), Matthews (1955), Thomassin (1969), Efford (1965, 1966, 1972), Dillery, Knapp (1970), Wenner (1977), Wenner, Fusaro (1979) and Subramoniam (1979). Ocypodids have also been widely studied (Crane, 1941; George, Knott, 1965; Fellows, 1975; Jones, 1972; Hill, Hunter, 1973; Vannini, 1976; Wolcott, 1978; McLachlan, 1980c; Robertson, Pfeiffer, 1981; Robertson, Pheiffer, 1981; Hill, 1982; Wada, 1982; Hails, Yaziz, 1982) and Caine (1974) and du Preez (1981) have studied portunids. There have also been studies on cnidarians (Kastendiek, 1982), echinoderms (Buchanan, 1966; Laurence, Ferber, 1971; Scheibling, 1982; Dexter, Ebert, 1975; Dexter, 1977b), polychaetes (Clark et al., 1962; Longbottom, 1970; Mock, 1981; Wilson, 1981; Brown, 1982) and insects (New, 1968; Craig, 1970; Orth et al., 1977; Stenton-Dozey, Griffiths, 1980; Chelazzi et al., 1983).

Bally (1981) summarised the results of all beach macrofauna surveys to 1981. The number of species found on a beach ranges from one (Gauld, Buchanan, 1956; McLachlan et al., 1981b) to 82 (Vohra, 1971), this number increasing with decreasing exposure. Bally (1981) divided beaches into three degrees of exposure and, based on a literature survey of 105 beach studies, listed average numbers of species, abundances and dry biomass values for these (Table 3).

TABLE 3. Summary of mean macrofaunal abundance and dry biomass values based on 105 beach surveys.(After Bally, 1981).

	High energy	Medium energy	Low energy
No. spp.	11	17	30
Abundance m^{-2}	400	752	1710
Abundance m^{-1}	20045	34571	2797867
Biomass g.m^{-2}	2.26	1.97	6.23
Biomass g.m^{-1}	871	170	63
Sand particle diameter um	310	257	238

While diversity and abundance decrease with exposure (Angus, 1979; McLachlan et al., 1981b) individual size increases, yielding high biomass values even at lower abundances in some cases. Though most classifications of beach exposure are very subjective, the above trends remain clear. The highest biomass values come from very exposed dissipative beaches, e.g. 6621 g ashfree dry mass.m^{-1} in the East Cape (McLachlan, 1977a) and 25735g dry mass m.$^{-1}$ in Peru (Penchaszadeh, 1971). These high biomass values are, without exception, due to filter feeders (Donax, Emerita). Exposed beaches are thus not necessarily sparsely inhabited.

Species diversity normally increases from high to low tide marks (McLachlan, 1977a) and may decrease again around the break point (McGwyyne, 1980) and then increase offshore (Field, 1971; Day et al., 1971; Christie, 1976). However, on a beach dominated by kelp input, maximum macrofauna diversity occurred around the drift line at the top of the beach (Stenton-Dozey, Griffiths, 1983).

The distribution of macrofauna along the beach is generally patchy, the combined result of movement and sorting by the swash, localized food concentrations or biological aggregations of species (Loesch, 1957; Thum, Allen, 1975; Achutankutty, 1976; Moueza, Chessel, 1976; Hayes, 1977; Saloman, Naughton, 1978; Fusaro, 1980; Brown, 1982). Bally (1981) investigated patchiness in detail on west Cape beaches and showed it to be a common occurrence in all species at all tide levels, often having proportions of 10^1-10^2m. This suggests that line transect sampling strategies may be unreliable, particularly if not replicated. Dauer, Simon (1975), however, showed that by pooling the results of a whole line transect, error due to patchiness can be reduced by 10-15%. Hartnoll (1983) has quantified the species area relationship on a sheltered sandy beach. He found little increase in diversity as sample size increased above $0.25m^2$ and suggested that for accurate sampling an aggregate area of $0.5m^2$ is adequate.

Distribution and abundance of organisms on the beach has been related to many factors. Factors said to influence the macrofauna include sand grain size and/or organic content (Longbottom, 1970;

McIntyre, 1970; Lawrence, Ferber, 1971; Alheit, 1978; Bally, 1981, McLachlan et al., 1981b; Lopez-Cotelo et al., 1982) beach slope (McLachlan et al., 1981b) sand moisture (Hayes, 1977; Salvat 1964, 1966, 1967; Bally, 1981; Withers, 1977) food in the surf water (Brown, 1964; Rapson, 1954; Wade, 1968; McLusky et al., 1975; Ansell et al., 1972a; Nair, 1978; McLachlan et al., 1981a; Hutchings et al., 1983) and dynamic changes such as due to storms (Scott, 1960; Brown, 1971a). Effects of dredging and beach nourishment have also been investigated in the inter- and sub-tidal (Reilly, Bellis, 1978; Turbeville, Marsh, 1982; Culter, Mahadevan, 1982; Saloman et al., 1982), while effects of disturbance predation have been assessed experimentally in a sheltered sand flat by Woodin (1981). Many authors have monitored organic or chlorophyll levels in the surf without being able to demonstrate correlations with faunal abundance. Undoubtedly, however, beaches with high biomass must receive high inputs of particulate organics and it is noticeable that on most beaches where very rich filter feeding populations occur, phytoplankton blooms have been recorded in the surf (New Zealand - Rapson, 1954; Washington - Lewin et al., 1979a; South Africa - McLachlan et al., 1981a; South America - Gianuca, 1983). Alternately, rich populations develop in upwelling regions, probably feeding on phytoplankton advected shorewards after upwelling cycles (Hutchings et al., 1983).

Of the physical factors, wave action and particle size have generally been considered the most important although

Eleftheriou, Nicholson (1975) show that grain size alone can not characterize a beach. As particle size, beach slope and wave action are closely related, defining the former two fixes the latter (Davies, 1972; McLachlan, 1980a). McLachlan et al., (1981b) obtained significant correlations between macrofauna species numbers and abundance and both grain size and beach slope, but not with wave action estimates for beaches on the south and east coast of South Africa (Fig. 7). This suggests that it is not wave action but rather steep slope and coarse sands that limit the fauna. Very exposed beaches (in terms of wave height) often have richer faunas than less exposed beaches where the latter have coarse grains and steep slopes. Finer sands result in flatter slopes as does heavier wave action. The flatter the slope of a beach the more evenly wave energy is dissipated in the surf zone and intertidal and this is the crucial factor. Thus a very exposed beach can support a rich macrofauna if it is dissipative as opposed to relective (e.g. Maitland beach, McLachlan, 1977a; Copalis beach, Lewin et al., 1979a). Indeed, high energy dissipative conditions seem optimal for the development of a high biomass of filter feeders.

Much less is known of macrofauna ecology below the intertidal. Fauna is generally absent around the break point but increases in abundance and diversity onshore and offshore in accordance with less turbulent conditions, less coarse substrates and higher organic levels (Clark, Milne, 1955; Morgans, 1962; Barnard, 1963; Field, 1971; Day et al., 1971; Christie, 1976; Masse,
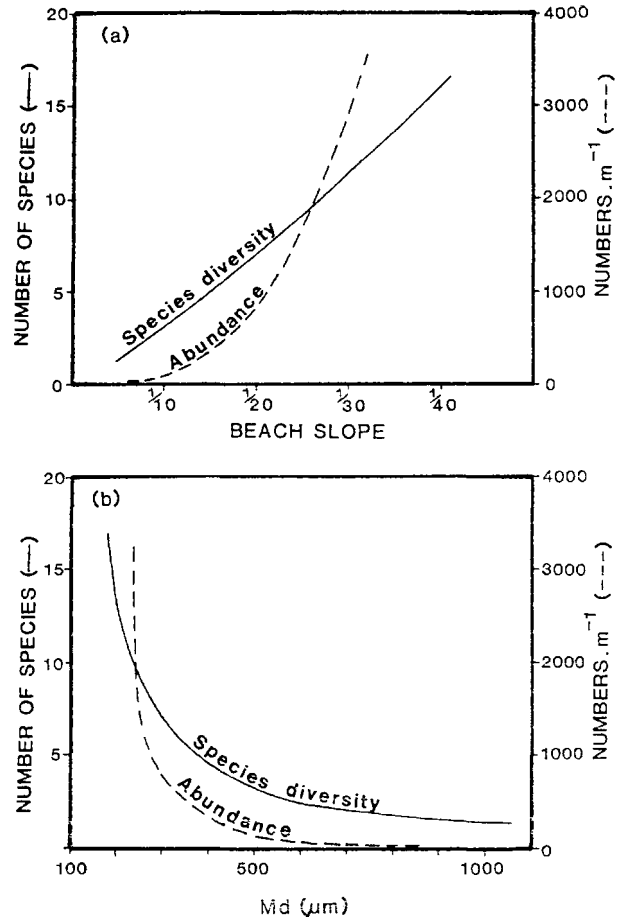
FIGURE 7. The relationships between macrofaunal species diversity and abundance and the slope (a) and particle size (b) of beaches in South Africa. (After McLachlan et al., 1981b).

1970, 1971, 1972; Dexter, 1978; Hill, Hunter, 1979; Shin, 1981, 1982; Kastendiek, 1982). The zone inside the break point has been termed the inner turbulent zone and the area outside this (out to where wave effects on the bottom are negligible) the outer turbulent zone. Biomass values are seldom high. Masse (1970, 1971) recorded number of $1048 - 10031$ m^{-2} and biomass $2.5-11.7g$ dry mass m^{-2} at various localities in the Mediterranean at depths $1,5 - 5m$. McIntyre, Eleftheriou (1968) recorded an

average dry biomass of $1.3g.m^{-2}$ in the intertidal and $3.7g.m^{-2}$ in the subtidal with 62 species on the beach and 116 off the Scottish shore. The poorest zone was just below LWS.

Much has been written on intertidal distribution patterns. The earliest serious attempt at providing a zonation scheme for sandy beaches was that of Dahl (1952)(Fig. 8). This was very similar to an earlier suggestion by Davenport (1903). Based on the distribution of crustaceans in northern temperate and South American beaches he proposed three zones essentially equivalent to the three zones of rocky shores. These zones were: the subterrestrial fringe characterized by ocypodid crabs in warm areas and talitrid amphipods in cold areas; the midlittoral zone characterized by cirolanid isopods (although these may be absent in cold temperate areas); and the sublittoral fringe with a mixed fauna often characterized by hippid crabs in the tropics and haustorid and other amphipods in temperate areas. Dahl's zones were thus defined biologically.

Subsequently many authors have tried this scheme with varying results. Gauld, Buchanan (1956) found an overlap of talitrids and ocypodids on west African shores and also recorded Excirolana in this zone. Lower zones showed less correspondence. Philip (1972) in India, Vohra (1972) in Singapore and Jaramillo (1978) in Chile found Dahl's scheme useful and Escofet· et al., (1978) found it fairly suitable for beaches in Brazil, Uruguay and Argentina. Wood (1968), however, found circolanids replaced by a sphaeromid on

the midshore in New Zealand. In South Africa Dahl's scheme, with modifications, has been found acceptable (McLachlan, 1980b; McLachlan et al., 1981b).
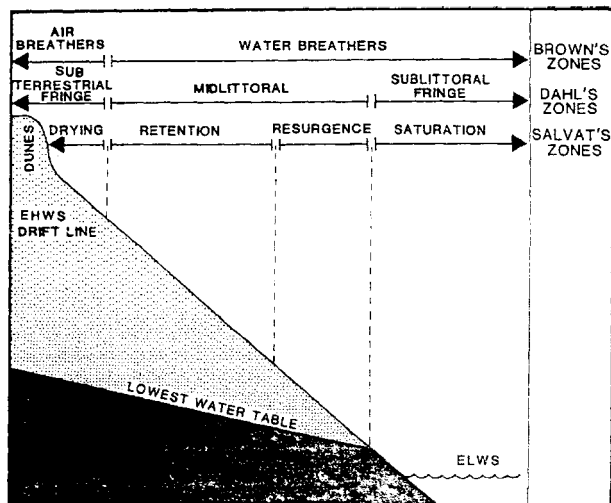
FIGURE 8. Diagrammatic representation of schemes of macrofauna zonation on sandy beaches.

Salvat (1964, 1966, 1967) described an alternate scheme based on physical factors. He delineated four zones on the beach, based on water saturation (Fig. 8). Pollock, Humon (1971) used this system for a Massachusetts beach they were studying, except that they subdivided the zone of drying and they extended their zones into strata covering the whole interstitial system (see Table 1 and Fig. 3). Salvat's system has been found reliable in describing zonation of macrofauna, particularly isopods (Withers, 1977; Bally, 1981). Both these authors admitted, however, that boundaries are not sharp and that zones grade into each other. Eleftheriou, Jones (1976) pointed out that differences in inter-

tidal distribution between different areas and species make eurydicid isopods unreliable indicators of zonation as proposed by Dahl. They did not, however, attempt to use Salvat's scheme.

Views on zonation of macrofauna on sandy beaches are thus highly conflicting, a situation not surprising in a dynamic environment with a highly mobile fauna. It may safely be said that zonation, in the classical sense, has never been proved on a sandy beach, i.e. sharp boundaries have not been demonstrated. Further, individual species show much clearer zonation than the fauna as a whole. Indeed, Brown (pers. comm.) is of the opinion that only two zones are distinguishable on sandy shores - air breathers in the supralittoral and water breathers below them. However, two boundaries are clearly and indisputably visible on open beaches, namely the drift line and the edge of the saturated sand where the water table reaches the surface. These correspond to Dahl's boundaries. However, although the boundary between Salvat's zones of retention and resurgence are not obvious there is considerable evidence that meaningful subdivision of the midlittoral can be made on many beaches. These zonation schemes are summarized in Fig. 8. Within these zones most species show subzones and there is often blurring of boundaries. Isopod species usually exhibit a clear zonation near the top of the shore and midlittoral (Withers, 1977; Eleftheriou, Jones, 1976; Bally, 1981; McLachlan et al., 1981b; Dexter, 1983). Bivalves, also exhibit zonation, often with two species occupying a beach, the smaller species in the sublittoral fringe and

the larger one in the eulittoral (e.g. Amphidesma spp. in New Zealand, Rapson, 1952; Donax spp. in India, Ansell et al., 1972b; Donax spp, in the East Cape, McLachlan, 1980b).

Besides zonation patterns at community level, intraspecific zonation has been recorded in several species. This generally takes the form of zonation of size classes and has been recorded in most taxa typical of open beaches, including molluscs and crustaceans (Alikunhi, 1944; Glynn et al., 1975; McLachlan et al., 1979b; Wooldridge, 1981; Ansell, Lagardere, 1980; Brown, 1982; Haley, 1982). This may be due to differential sorting of the sizes in the swash or to active migration to areas differentially suitable to the organism at different life stages.

Zonation as the researcher records it is, however, only the distribution of the psammolittoral fauna at an instant in time and most species undergo tidal migrations of some sort. Typically this involves a simple movement up and down the beach with the tides allowing the animal to stay in the swash zone where conditions for feeding are opitmal and predation minimal. In molluscs this movement involves no endogenous rhythms but simply a series of responses to changing physical conditions, most notably the degree of saturation and thixotropy of the sand (Mori, 1938; Turner, Belding, 1957; Ansell, Trevallion, 1969; Trueman, 1971). In some molluscs it may be more complex, e.g. Donax serra in the East Cape, where there is not normal tidal migration but rather semilunar movement up and down the shore to occupy a position near mean

tide level during springs and near low tide during neaps (McLachlan et al, 1979c). Movements related to periods of storm and calm have also been recorded (Leber, 1982a).

In crustaceans these rhythms are generally endogenous and more complex. They have been shown to include entry into the plankton at night (e.g. mysids, anphipods and isopods), increased activity during springs as opposed to neaps, and orientation behaviour (Papi, Pardi, 1963; Enright, 1963, 1965, 1972; Hammer et al., 1968, 1969; Cubit, 1969; Fincham, 1970, 1973; Alheit, Naylor, 1976; MacQuart-Moulin, 1977; McLachlan et al., 1979c; Marsh, Branch, 1979; Hager, Croker, 1980; Fusaro, 1980; Jaramillo et al., 1980; Scapini, Ugolini, 1981). The advantage of increased activity during springs is that it prevents the animals being stranded as the tides retreat.

Ansell, Trueman (1973) calculated the energy costs of migration in Donax and Emerita and concluded that it was more profitable for the animals to migrate than to attempt to maintain position. Tidal migratory behaviour has several advantages; it allows animals to stay in the zone optimal for feeding, i.e. the edge of the swash zone; it keeps them too shallow for many fish predators but just immersed enough not to be fully open to birds; it helps to prevent animals being stranded on the shore; in supralittoral forms, e.g. Tylos, it enables them to move down the beach during the low tide to feed on debris.

This migration naturally has marked effects on zonation and all zones compress so that at high tide most of the invertebrate population on the beach may be compressed into a narrow strip with considerable overlap between species. Further, in addition to normal tidal migration, movement into the subtidal has been recorded in winter in Donax parvula (Leder, 1982b).

Temporal changes in beach macrofauna have been recorded both in whole communities (Sanchez et al., 1982) and in individual species populations. The most dramatic of these are those associated with the monsoon in India where most of the fauna disappears during this period (Ansell et al., 1972a; Dwivedi et al., 1973; McLusky et al., 1975). Longer term fluctuation spanning several years have also been recorded (Rapson, 1954; Coe, 1955; Davis, Von Blaricom, 1978). Dramatic changes in the long term may also take the form of occasional mass mortalities, e.g. Donax spp. (Orton, 1929; Fitch, 1950; Loesch, 1957; Johnston, 1966, 1968; Grindley, Nel, 1968; de Villiers, 1974) such as related to poisonous dinoflagellate blooms. Seasonal changes have been reported in most species studied and for several communities.

In an unstructured and physically controlled habitat like a sandy beach, most species tend to be unspecialized generalists with board niches (Brown, Talbot, 1972; Brown, 1982; McGwynne, 1980; Bally, 1981). Because of this, the physical nature of the environment and the mobility of the fauna, competition amongst the sandy beach fauna is unlikely, though the possibility of exploitation competition can not be ruled out. Wilson (1981)

demonstrated negative interactions in a dense assemblage of deposit feeding polychaetes, but this was in a very sheltered beach. Trophic groups among the macrofauna include scavenger/ predators, filter feeders (suspension) and, on less exposed shores, deposit feeders. Filter feeders usually dominate and consist mostly of bivalves. The tellinaceans of high energy beaches, Donax spp., are, unlike most other members of the family, suspension feeders (Ansell, 1983). Deposit feeding is not common in sandy beach filter feeders, except in very sheltered situations. In cases where the fauna is impoverished, however, such as on very coarse, steep beaches, supralittoral scavengers may dominate as a result of the virtual absence of other species (Gauld, Buchanan, 1956; Dye et al., 1981; Wooldridge et al., 1981). On sheltered beaches deposit feeders, e.g. Arenicola, Callianassa and Scolelepis, may be very important or even dominate (e.g. Saloman, Naughton, 1978; McDermott, 1983).

The tropic structure of the beach macro-fauna is therefore normally dominated by mobile filter feeders. Even where other forms may be more abundant, filter feeders usually dominate biomass (Dexter, 1979; Eleftheriou, McIntyre, 1976). As there is little or no primary production on the beach, the macrofauna is dependent on food imports from adjacent systems, i.e. the land and the sea (Brown, 1964; Ansell et al., 1972a; McLachlan et al., 1981a; Griffiths et al., 1983). The sea is the most important and supplies particulates for filter and deposit feeders and carrion and macrodebris for scavengers and predators.

As the bulk of the fauna are usually filter feeders, the size of beach populations is probably closely related to the richness of inshore waters in particulate organic material (Ansell et al., 1972a; Hutchings et al., 1983). In some areas large amounts of macrodebris may be cast ashore, particularly adjacent to kelp beds. In such situations vast populations of supra-littoral scavengers develop (Hayes, 1974; Griffiths, Stenton-Dozey, 1981). In other areas carrion input may be high, e.g. in the form of cnidarians, and in such cases midlittoral scavengers such as Bullia reach high abundance (McGwynne, 1980; Brown, 1982).

Macrofaunal food webs have been given for beaches in South America (Koepcke, Koepcke, 1952; Gianuca, 1983), the Cape Peninsula (Brown, 1964; Griffiths et al., 1983) and the East Cape (McLachlan et al., 1981a). The main predators on the macrofauna as listed by several authors are birds, fishes and crabs (Coe, 1955; Loesch, 1957; Masse, 1963; Wade, 1967; Penshaszadeh, Olivier, 1975). The former two will be discussed later. Crabs, being part of the benthos, represent a form of predation resident in the beach/surf system. Du Preez (1981) has made a detailed study of the swimming crab Ovalipes on East Cape beaches and shown it to be an important predator on Donax and Bullia. Several other authors mention the importance of both ghost crabs and swimming crabs as predators on beaches (Loesch, 1957; Koepcke, 1953; Ansell et al., 1972a). Virnstein (1977) showed the importance of crabs in controlling macrofauna

communities by predation in subtidal sand in Chesapeake Bay. Naticid gastropods are important predators on burrowing bivalves but are not generally found on open ocean beaches.

Besides predation, "natural" mortality can at times be important on sandy beaches. This includes not only mass mortalities due to poisoning (de Villiers, 1974) but also being cast above the shore by storms (Brown, 1971a; Penshaszadeh, Olivier, 1975; McLachlan et al., 1981a). McLachlan, Young (1982) suggested the importance of upwelling and sudden temperature drops in retarding mobility as a factor contributing towards this. Ansell et al., (1978) have shown that where the mortality rate is fairly constant, the mortality coefficient, longivity and production are related. Ansell (1983) lists cases of commercial exploitation of Donax where heavy mortality may be caused by man.

It may be concluded that the distribution and diversity of beach macrofauna is largely determined by physical factors, prime among which are wave action, particle size and beach slope. Food input probably determines abundance of both scavengers and filter feeders. The most pronounced feature of macrofauna animals is a high degree of mobility and tidal migrations on exposed beaches. The main rôle of the macrofauna is to process food imports, coming mainly from the surf, and in turn to be consumed by terrestrial and marine predators. They are thus in the middle of the food chain.

4. PHYTOPLANKTON

Blooms of diatoms in surf zones, persistent or sporadic, now appear to be a typical feature of many sandy beach surf zones. Rich surf phytoplankton blooms have been reported from the Washington coast, U.S.A., (Thayer, 1935; Lewin, Norris, 1970), the Gulf coast of the U.S.A., (Gunter, 1979; Gunter, Lyles, 1979), New Zealand (Rapson, 1954; Cassie, Cassie, 1960; Lewin, Norris, 1970), South Africa (McLachlan, Lewin, 1981) and the east coast of South America (Gianuca, 1983). These blooms are mostly composed of masses of cells of one or two species belonging to the genera Chaetoceros, Asterionella, Aulacodiscus and Anaulus.

The blooms described by Gunter (1979) and Gunter, Lyles (1979) are Chaetoceros dominated strips hugging the beaches. Heavy rains leach nutrients from the land and these, being retained near the beach by calm seas, apparently cause the blooms. These blooms take the form of strips 5-6m wide for miles along the shore. All the other reported surf zone blooms occur as patches of phytoplankton within well developed surf zones. Of these, those off the Washington coast have been most intensively studies and reviewed by Lewin, Schaefer (1983).

Lewin, Norris (1970) first described the similarities between blooms on the Washington and New Zealand coasts where Chaetoceros and Asterionella were dominant. Lewin, Hruby (1973) described the diel periodicity in buoyancy of Chaetoceros, this species dispersing at night and rising to the surface during the day. Floating at the surface, they create a stable foam which is then

retained in the surf by wave action and often stranded on the beach. This clearly appears to be a mechanism for retention in the surf zone. Lewin (1974) described long term changes in species composition of the blooms with _Aulacodiscus littorii_ dominant before 1950 and _Chaetoceros armatum_ dominant after 1950. Other studies looked at light utilization (Lewin, Mackas, 1972), nitrate reductase activity (Collos, Lewin, 1974), daily periodicity (Lewin, Rao, 1975), C:N ratio (Collos, Lewin, 1976), respiration (Robertson, Lewin, 1976), chemical composition (Lewin et al., 1979a) and the clay coat (Lewin et al., 1980) of the surf diatoms _Chaetoceros_ and _Asterionella_.

Lewin et al., (1975) analysed environmental conditions associated with the blooms over two years, finding the diatom populations relatively constant over this period. Lewin (1978) evaluated factors controlling the seasonal cycle of nitrate in the surf. Nitrate concentrations fluctuated widely in relation to season, upwelling and phytoplankton growth and ammonium seemed to be an important nitrogen source, particularly during summer. Lewin et al., (1979b) measured ammonia excretion by _Siliqua_ and concluded that the razor clam populations of Washington beaches could regenerate significant amounts of ammonium into the surf zone. Lewin (1977) summarised knowledge of these blooms, pointing out the interdependence of the diatoms and the razor clams. Diatoms are the main food of the razor clams while the clams in turn regenerate inorganic nitrogen which is utilized by the diatoms.

Subsequently more attention has been paid to the ecology and distribution of the blooms. Jijina, Lewin (in prep. a, b) described physical features of the coastal zone in relation to blooms at 13 beaches in Washington and Oregon. Blooms were best developed on long flat beaches while steeper beaches and beaches near rocks has poorer blooms. Low air and water temperatures were associated with increased diatom densities while nutrient concentrations were inversely proportional to densities. They concluded that the type of beach and its physical characteristics were very important in bloom development.

McLachlan (1980d) suggested that blooms form where surf circulation cells develop and trap beach generated nutrients, pointing out that this is most likely on long beaches of flat slope (i.e. dissipative beaches). McLachlan, Lewin (1981) described blooms of _Anaulus birostratus_ from the East Cape, South Africa, and showed that the blooms were positioned over rip currents by day. All surf bloom forming species show a daytime buoyancy and this results in the collection of diatom cells as a foam or scum over rip currents. Presumably the opposing forces of incoming waves and outgoing rip current keep them in position. While diatom cells may travel all around the surf circulation cells, the rip current area may act as a bottle-neck for buoyant material.

McLachlan, Lewin (1981) also showed that blooms developed in water not very high in nutrients. Though nutrient concentration is low, supply is constnat as inorganic nutrients are continually

draining out of the beach. Nutrients are generated on the beach both by the filtration of water and mineralisation of organics by the interstitial fauna (McLachlan, 1980a, 1982; McLachlan et al., 1981a) and by excretion of the macrofauna (Prosch, McLachlan, 1983). Both of these sources are important and have been shown to generate significant amounts of nitrogen on East Cape beaches. Subsequently wind has been shown to be of overriding importance in controlling short term changes in blooms in the surf (Romer, Sloff, pers. comm.).

Estimates of primary production in surf zones off beaches have been made by Cassie, Cassie (1960) and Edwards (1973a). The latter obtained figures of 10495 and 5597 $kcal.m^{-2}.y^{-1}$ for phytoplankton primary production in the shallow off two sheltered Venezuelan beaches. Estimates of primary productivity in surf phytoplankton blooms are now under way (Lewin, Schaefer, 1983) and we should soon have figures for biomass and production of these rich algal communities.

Recently Wilce et al., (1982), Wilce, Quinlan (1983) and Quinlan et al. (1983) reported on masses of free living ball-like algae, Pilayella, on sand bottoms and in the surf off beaches in Nahant bay, Massachusetts. This species reached peak biomass in summer and proliferated by fragmentation and re-generation. It's nutrient source is uncertain but nutrient recycling within the beach/surf system is considered important.

It may be concluded that rich surf diatom blooms consisting of one or two species commonly occur in well developed surf zones on gently shelving beaches. Diurnal buoyancy of the diatoms results in their concentration over rip currents by day. Nutrients are derived from many sources, but the beach is probably most important. Inorganic nitrogen generated as ammonium by macrofauna and zooplankton excretion and as nitrate by the interstitial fauna is constantly draining into the surf and passing through rip currents where the blooms are situated. In this way the blooms are positioned in a site of steady nutrient supply. Wind has a pronounced influence on bloom development by controlling wave action and surf circulation patterns. We need to know more of the interaction between wind, waves, nutrients and blooms. We also need more reports on the sources of primary production in surf zones that do not support these diatom blooms.

5. ZOOPLANKTON

Studies on surf zone zooplankton are virtually absent from the literature. While several taxonomic papers list species taken off sandy beaches, few were sampled in the surf zone or include ecological notes. Brattegard (1969 and subsequent works) described mysids from shallow water off the Bahamas including some from sandy habitats and similar accounts are given by Wigley, Burns (1971) for the Atlantic coast of the U.S.A. and Bacescu (1975) for Tanzania.

Bowman (1971) described copepods off the southeast coast of the U.S.A. and recognised a 'coastal association' dominated by one'coastal' and one 'estuarine' species. Outside this lay 'shelf' and 'oceanic' associations

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dominated by four and seven species respectively. Sander, Moore (1978) studied inshore and offshore copepods around the West Indies as shallow as 10m and recorded average numbers of 100-500.m^{-3} with other groups making up 11-22% of total zooplankton numbers. Youngbluth (1979) studied zooplankton within 1km of the coast of Puerto Rico at about 10m depth. He recorded numbers of 41-7568.m^{-3} of which 65-84% were copepods. Settled volume biomass values averaged 0.086ml.m^{-3} and highest numbers were recorded at night.

Moran (1972) found the benthic mysid, Gastrosaccus sanctus, to occur in shoals along the shore in the top 1cm of sand, but moving into the top 1-2m of water at night in the Mediterranean. It exhibited a clear zonation offshore. Fincham (1970), studying amphipods in Britain, Macquart-Moulin (1977), studying two benthic mysids and an isopod in the Mediterranean, and Wooldridge (1981), studying a benthic mysid in the East Cape, found similar patterns. Night time planktonic activity of benthic crustaceans, particularly mysids, amphipods and isopods, is well known (Alheit, Naylor, 1976).

The most detailed account of surf zone zooplankton yet published is the work of Clutter (1967) at La Jolla. He studied the nearshore zonation of four benthic and five pelagic mysids out to 17m depth. All species formed schools and occupied clear zones, occurring on or near the bottom. A large species dominated inside the surf while the most abundant species, Metamysidopsis elongata, peaked where rip currents dispersed and had its

outer limit of distribution near the outer limit of rips. He postulated that detrital food in suspension decreases outside this zone and that zonation was mainly related to the nearshore, wave-induced circulation patterns.

Several studies have recently been done on surf zone zooplankton in the East Cape. In most of this work the use of large nets has attempted to avoid the normal loss of large forms such as mysids, a problem often not appreciated by workers using small nets. Cockcroft (1979) sampled inside the breakers at 1m depth, just outside at 3m and further out at 10m off a moderately exposed beach. Greatest biomass occurred just outside the breakers (although netting efficiency was very low in the surf). Abundance increased considerably after dark when dry biomass values ranged 6-980mg.m^{-3}. Mysids dominated biomass (21% at 1m, 83% at 3m and 84% at 10m; mean 63%) with copepods averaging only 13%. At the 1m site the prawn, Macropetasma africana, was very important although poorly sampled. The dominant species overall was the mysid, Mesopodopsis slabberi. Biomass was distinctly higher than offshore in Algoa Bay and about the same as recorded in local estuaries, indicating the general richness of zooplankton in the surf zone.

Subsequently Cockcroft (1983) has made a detailed study of Macropetasma, which occurs in vast shoals in East Cape surf zones. Growing up to 7cm in length, this prawn is really a nektonic form. It exhibits a clear zonation with juveniles inshore and adults out as far as 20m depth. They shoal near the bottom by day and disperse at night,

being most abundant inside the breakers. Numbers recorded averaged 21-37.m^{-3} giving a dry biomass of 0.9-1.8g.m^{-3}. This species uses the surf zone as a nursery area and, being an opportunistic omnivore, it feeds on detritus, phytoplankton and small crustaceans. Shoals tend to move inshore at night and to concentrate around phytoplankton blooms by day.

Romer (pers. comm.) is investigating food chains around surf phytoplankton blooms, including small and large zooplankton. He finds that zooplankton is concentrated around blooms by day but more dispersed at night, this resulting in a slight decrease in biomass after dark. Crustaceans (Macropetasma, mysids, copepods) account for about 85% of biomass and siphonophores, chaetognaths, and others for the remainder. Mean total numbers in a bloom during the day are about 2000 zooplankters.m^{-3} with a dry biomass of 0.8g.m^{-3}. However, higher values, up to 750g.m^{-3}, have been recorded in dense swarms of plankters, particularly where prawns were abundant.

Wooldridge (1983) studied the zooplankton of Algoa Bay from just behind the breakers to about 4km offshore (20m depth) using a net of 1.5m diameter. While salps, medusae, ctenophores and others were often common, crustaceans dominated, making up about 80% of biomass. Fifteen species of mysids accounted for more than 90% of crustacean biomass, with copepods second in importance. A single species of mysid, Mesopodopsis slabberi, was by far the dominant species, especially close inshore, with average numbers around

1000.m^{-3} just behind the breakers and 10.m^{-3} further offshore. It even reached densities exceeding 15000.m^{-3} (mainly juveniles, dry biomass 1.02g.m^{-3}) behind the breakers at times. Other mysid species seldom totalled more than 10.m^{-3}. Dry zooplankton biomass averaged about 0.25g.m^{-3} behind the breakers and 0.015g.m^{-3} offshore, an order of magnitude lower.

Mesopodopsis formed vast shoals which virtually disappeared by day (presumably moving to deeper water) and then became abundant at night. This inshore population consisted largely of juveniles and breeding occurred at sea even though large numbers often moved into estuaries. This study indicates that the inshore area and surf zone has a mysid dominated zooplankton community of very high biomass. Abundance and biomass in this region are an order of magnitude higher than offshore and even higher than recorded in most estuaries. Many authors have probably underestimated the contribution of the larger and more mobile zooplankton through using small nets.

Clearly our knowledge of surf zone zooplankton is abysmal. Few papers go beyond species lists or counts of abundance. While it is difficult to extrapolate from the small amount of hard data currently available, three points seem clear: i) the zooplankton of exposed surf zones may be very rich with high biomass values, ii) large crustaceans (e.g. mysids, penaeids) dominate the biomass (as they can cope with the turbulence of these areas) but are difficult to sample, iii) there are

clear offshore zonation patterns and diurnal changes in abundance. Much work remains to be done in this field, in particular relating distribution and abundance to wave induced circulation patterns and available food in the near-shore zone.

6. FISHES

Though far better studied than zooplankton, we still know comparatively little of the ecology of fishes from surf zones off open beaches, largely because of the difficulties of sampling in these environments. Pearse et al., (1942) list fish caught by seine net off North Carolina beaches and more extensive reports of fishes in surf zones of the United States are given by Gunter (1958) et al. (1960), McFarland (1963), Schaeffer (1967, 1970), Cupka (1972) and McDermott (1983). Around the coasts of Britain and Europe much attention has been paid to juvenile flatfish using beaches as nursery grounds (Macer, 1967; Edwards, Steele, 1968; Edwards et al., 1970; Steele, Edwards, 1970; Steele et al., 1970b; Jones, 1973; Gibson, 1973; Thijssen et al., 1974; Lockwood, 1974; Poxton et al., 1982). In South Africa Rossouw (1983) has studied elasmobranchs from surf zones with particular emphasis on the sandshark Rhinobatos annulatus, Lasiak (1982, 1983) has made a detailed investigation of surf zone ichthyofauna communities and Romer, (pers. comm.) has investigated food chains around surf phytoplankton blooms.

In the cold temperate waters of Britain and Europe shallow sandy bays are important as nursery areas for flatfish and several authors have studied recruitment, growth and feeding of juveniles in the shallow subtidal off sandy beaches (Riley, Corlett, 1966; Macer, 1967; Edwards, Steele, 1968; Lockwood, 1974; Poxton et al., 1982). Among these fish, plaice (Pleuronectes platessa), dabs (Limandia limandia) and turbot (Scophthalmus maximus) are the most important. In summer, after metamorphosis, large numbers move into fine sand bays where the water is less than 3-5m deep. There they feed on demersal plankton and benthos, including mysids and the siphons of Tellina and tentacles of polychaetes. Mortality is high and the populations of these juveniles generally decline rapidly through autumn until they move into deeper water again at the onset of winter.

In the United States Gunter (1958) sampled surf fish off the Texas coast, recording fewer species off open beaches than inside the barrier. He mostly caught small and juvenile fish which were most abundant in spring and summer. McFarland (1963) found that zooplankton was the primary food source for the surf fish at Mustang Island, Texas. Planktivores were the most abundant trophic group and even mullett (Mugil cephalus) and benthic feeders took large amounts of zooplankton at times. He recorded 47 species with an average of four in winter (biomass 25.81b/acre) and 16 in summer (biomass 103.21b/acre). High primary production in the surf, he concluded, was more than sufficient to support the fish community. Moddle, Ross (1981) also recorded midwater planktivorous fish dominating the surf zone in the northern Gulf of Mexico. Armitage, Alevizon (1980)

recorded the diet of the Florida pompano (Trachinotus carolinus) and found Donax to be an important item.

Carlisle et al., (1960) recorded 71 species off Californian beaches with an average of 284 specimens per beach seine haul. The surfperch, Amphistichtus argenteus, and the orbina, Menticirrhus undulatus, were dominant but flatfish, skates, rays and sandsharks (Rhinobatos) were also common. Best catches were taken on the low tide. They made a detailed study of the biology of the surfperch including reproduction, growth and feeding and found the mole crab, Emerita analoga, to be the main item in the diet.

Schaefer (1970) studied feeding of the striped bass, Morone saxatilis, in the surf at Long Island. Amphipods and mysids were the dominant foods though fishes, particularly anchovies, were also important. During sampling 71 species of fish were recorded.

McDermott (1983) sampled the fauna of a barrier beach in New Jersey by means of cores and seine netting. The dominant benthic organism and main food for the fish was the polychaet, Scolelepis squamata, which reached densities up to $40000.m^{-2}$ (=50g dry mass.m^{-2}) in a band approximately 20m wide. Of 26 fish species only seven were common and one resident. This species, Menidia menidia, the silverside, made up 85% of fish numbers and 40% of fish mass and Scolelepis formed 70-80% of its diet. Leber (1982a) recorded four fish species feeding on beach macrofauna, including the silverside. Donax and Emerita were the main prey items.

Edwards (1973b) sampled with a beach seine net off two Venezuelan beaches and recorded 49 species (31 at one beach and 32 at the other) which he divided into plankton feeders, fish carnivores, benthos feeders and herbivores (Mugil). Fish biomass was estimated at $5g.m^{-2}$ dry mass at the unpolluted beach and $1g.m^{-2}$ at at a polluted beach. Plankton feeders and benthos feeders were most important. Penchaszadeh (1983) found mysids and other motile crustaceans to be the main prey of fishes off Venezuelan beaches.

In Australia Lenanton et al. (1982) described the utilization of surf zone accumulations of macrophytes and their associated amphipods as nursery feeding areas for 0+ year classes of three fish species.

In the Eastern Cape, South Africa, Rossouw (1983) has studied elasmobranchs with particular reference to the biology of the sandshark, Rhinobatos annulatus. This species comes into the surf to give birth in summer. Juveniles stay in the surf but adults move offshore in winter. They feed on mysids, small Donax and other benthic prey. Amongst various other elasmobranchs, duckbill rays, Myliobatis spp., come into very shallow water to prey on Donax spp. These, together with other large rays are very important predators on the benthos. As in the case of flatfishes in European waters, the great success of skates and rays in these environments is probably due to their flattened shape allowing them to forage in very shallow water, thus being able to take even the macrofauna that undergo tidal migrations.

Romer (pers. comm.) is investigating food chains around surf phytoplankton blooms. He has found that mullett, Liza richardsoni, grazed directly on the phytoplankton and are taken in turn by larger predatory fishes. The mullett as well as other juvenile fish in the surf also prey extensively on zooplankton.

Lasiak (1982, 1983) has made the most detailed study to date of surf fish communities, seining on two Algoa Bay beaches over a period of three years. At the less exposed beach she recorded 66 species and 29 at the more exposed site with teleosts dominating numbers and elasmobranchs dominating biomass. Seven common species were resident while other species were intermediate or sporadic in occurrence. The community showed no overall seasonal trends but a very high degree of short term variability which seemed to be largely coupled to the effects of wind on the surf zone as several biological parameters were closely correlated to wind direction and intensity prior to sampling. Studies over 24h showed no clear trends though maximum abundance, biomass and diversity often tended to occur around twilight. Sampling on consecutive days proved to be very variable. She concluded that the surf zone fish assemblage was a highly variable community whose structure and dynamics were probably dominated by abiotic factors while biological interactions were of secondary importance. As most food organisms were highly motile, their availability would be strongly influenced by surf conditions which in turn are determined by wind effects on the wave regime. Hence short term variability is largely controlled by winds.

Lasiak (1982) distinguished six feeding categories, namely: benthic feeders, planktivores, detritivores, piscivores, herbivores and omnivores. Herbivores owed their occurrence to the presence of some rocky reefs near the sampling site at the less exposed beach, and were virtually absent at the more exposed beach. The mullet, Liza richardsoni, was the only detritivore, but in Lasiak's study fed mainly on zooplankton and may thus be considered a planktivore. Her feeding groups may thus be simplified to include, benthic feeders, planktivores, piscivores and omnivores. At both beaches motile organisms (mysids, prawns, fish, cephalopods and zooplankton) dominated the food base and these foods were taken by all feeding groups including benthic feeders. Almost all species employed opportunistic feeding strategies. Table 4 summarises the biomass, composition and food consumption of this surf zone fish assemblage.

We still know very little of surf zone ichthyofauna and the danger of sampling in heavy surf will probably keep the situation that way. To really understand resource partitioning and niche structure of surf zone fishes some more accurate means of sampling is necessary whereby the actual location of fish within different parts of the surf can be made. Perhaps SCUBA counts are the solution. In this way the distribution and feeding of fish in the surf could be better understood in terms of spatial partitioning of this zone in three dimensions. However, zooplankton as food for fish will be more important

Table 4. Biomass, composition and food consumption of fishes in less exposed surf zones in the East Cape. (After Lasiak, 1982).

Feeding group	Biomass g.m^{-1} (dry mass)	FISH Number of Species Dominants	Other	TOTAL PREY TAKEN Species or group	Amount consumed g.m^{-1}.y^{-1}
Benthic feeders	78	3	6	Macrobenthos	269
Planktivores	60	4	5	Mysids/prawns	657
Piscivores	10	2	4	Zooplankton	200
Omnivores	10	2	0	Fish	672
Total	158			Total	1798

at night and studies not employing after dark sampling will miss this.

Surf zone fish communities are highly dynamic assemblages with few resident species. They are variable in space and time and short term variations in wind, controlling surf conditions, are probably a major factor controlling these communities. Most species show a high degree of opportunism in feeding, and consequently all feeding types may predate heavily on zooplankton and larger schooling crustaceans when they are locally abundant. Planktivores, and benthic feeders with opportunistic planktivore tendencies, are therefore a major component of surf zone ichthyofauna. Fish are important as energy transformers in surf zones and, because they are highly motile, are also important in the export of energy from the beach/surf zone system.

7. BIRDS
While some authors have made brief mention of birds as predators on sandy beach benthos (Koepcke, Koepcke, 1952; Brown, 1964; Leber, 1982; Vader, 1982)

there are few published reports on the ecology of birds on sandy beaches. Most papers simply record counts of waders and other birds along sandy shorelines.

Fitch (1950) recorded gulls dropping clams to break them and Brunton (1978) recorded gull predation of toheroa clams. Veitch (1980) recorded dead birds on beaches in New Zealand and similar records have been made in Belgium (Kuyken, 1978) and Britain (Cadbury, 1978). Prater, Davies (1978) recorded sanderling overwintering on British beaches, while Schneider, Harrington (1981) demonstrated depletion of benthic prey at a migratory stopover for shorebirds. Burger et al. (1977) compared the utilization of an open beach, a sheltered beach and a salt marsh by migrating birds. There are several reports of birds breeding on or adjacent to beaches, particularly terns (Fuchs, 1977; Davies, 1981; Randall, McLachlan, 1982) and plovers (Summers, Hockey, 1980).

In South Africa there are several count records for the western Cape. Pringle,

Cooper (1977) conducted counts over 18 months which revealed eight migrant and seven resident species. Summers et al. (1977) recorded higher bird numbers on the west coast than the south coast of the western Cape, presumably due to greater food abundance in the former area. They recorded 1267 birds over 99,6km of sandy beaches and 8319 birds over 120,4km of mixed shores. Twelve wader species occurred on the beaches with sanderling (Calidris alba), white-fronted sandplovers (Charadrius marginatus) and black oystercatchers (Haematopus moquini) most important. Resident species averaged 7,3km^{-1} and migrants 15,2km^{-1} in summer. Summers, Cooper (1977) recorded fewer oyster-catchers on beaches than rocky shores and Summers, Waltner (1979) recorded mass changes in waders, showing most species to be heavier in winter. On the Natal coast Joubert (1981) made counts over 10 months, recording 14 species and densities of 39km^{-1}, with waders making up only 0,52km^{-1}. Terns roosted on the beach in relatively high numbers.

In the Eastern Cape McLachlan et al. (1980) counted birds on three beaches over 12 months, recording 17 species with average numbers of 18,9km^{-1} of which waders accounted for 47%. They estimated bird biomass and also food consumption from standard metabolic rates for four dominant species which made up 95% of numbers. From this they estimated that birds were taking 32% of available macrobenthic production from these beaches each year. This was mainly· in the form of sand mussels (Donax spp.), mussel siphons, and mysids. Birds also took significant amounts of insects blowing onto the beach and carrion cast ashore. On kelp dominated beaches on the west coast birds are the main predators and were estimated to take 40% of herbivore standing stock (Griffiths et al., 1983). Hockey et al. (1983) summarised the rôle of shorebirds on sandy beaches in South Africa. They found diversity and abundance of shorebirds to increase with latitude. Birds consumed 10-49% of macrobenthic production in different areas and return significant amounts of faeces, feathers and carcases to the beach system.

Moran, Fischelson (1971) recorded two plovers, Charadrius hiaticula and C. alexandrius, feeding on the mysid Gastrosaccus sanctus. They found these plovers to hunt at random, regardless of the size of the mysids, preferring areas where mysids were densest. However, Schneider (1981) reanalysed their data to show that C. hiaticula selectively takes larger mysids. Schneider (1982) studied the foraging behaviour of turnstones (Arenaria interpres) feeding on Donax variabilis on a florida beach and Pienkowski (1982) described diet and feeding of two plovers on a sand flat in Northumberland. They fed during day and night and polychaet worms and crus-taceans dominated in the diet.

Myers et al. (1980) analysed the predation of sanderlings on beach crustaceans in detailed laboratory experiments. They showed how several variables affect a sanderling's capture rate. Capture is determined by prey density, the sampling rate and sampling efficiency. Sampling rate depends on penetrability of the substrate and

sampling efficiency depends on prey size, depth and substrate penetrability. Prey risk varied inversely with prey depth, 60% of prey 10mm or shallower being taken and very much less below 10mm. Larger prey were more vulnerable than smaller prey but small prey were never rejected. Prey risk was higher where prey organisms occurred close together. Capture rate could be predicted on the basis of prey size, density and sand penetrability. For prey it was best to be small, deep in the substratum and not near other individuals. Prey species had no effect (Excirolana vs. Emerita). However, this was all done with dead prey. Most feeding was /done without visual cues although sanderling may use visual cues at times, e.g. when feeding on beach wrack insects. Although probe location was random it could also be affected by the feeding patterns of nearby birds.

Wading birds are important predators on sandy beaches, being efficient croppers of the macrobenthos during periods of low tide. On beaches where high inputs of macrodebris concentrate macrofauna along the drift line above the reach of marine predators, birds may be the most important predators. Even birds that only roost on the beaches may be important where the faecal deposits of large flocks may add significant amounts of nutrients locally.

8. FOOD WEBS AND ENERGY FLOW

8.1 Introduction

The macrofauna and interstitial fauna of open sandy beaches form two separate communities with little or no energy flow between them. The macrofauna are part of a larger food web including zooplankton, fishes and birds, while the interstitisal fauna constitute their own food web in the sand (McIntyre, Murison, 1973; McLachlan, 1977a; McLachlan et al., 1981a). The only links between these two food webs is the common input of particulate (and probably dissolved) organics to both and the possible washing of micro-organisms from the sand (Munro et al., 1978) to provide food for filter feeders. In more sheltered situations, however, deposit feeders and sand swallowers may take in large amounts of interstitial fauna. Oliver et al., (1982) recorded phoxocephalid amphipods feeding on a variety of foods including nematodes and Croker (1967b) recorded a haustorid amphipod feeding on meiofauna, both cases being in sheltered sands. On a lagoon beach Alheit, Scheibel (1982) recorded juvenile demersal fish feeding on harpacticoid copepods. However, as these exchanges are mostly negligible on open beaches I look separately at the macrofauna food web and interstitial energetics.

8.2 Macrofauna

Several authors have mentioned aspects of predation or food chains relating to sandy beaches (Pearse et al., 1942; Bonnet, 1946; Koepcke, Koepcke, 1952; Hedgpeth, 1957; Brown, 1964; Steele et al., 1970b; Philips, 1970; Edwards, 1973a, 1973b; Reilly, Bellis, 1978; Ansell et al., 1978; Reilly, 1979; McLachlan et al., 1981a; Leber, 1982; Gianuca, 1983). Macrofauna food chains start and end in the sea, with the land playing only a negligible rôle, mainly in the form of insects blowing onto the beach and land crabs, birds and mammals

moving onto the beach to feed. Open beaches are characterized by the absence of attached plants (Brown, 1964) and primary production by the benthic microflora is generally negligible. On a sheltered temperate beach, however, Steele, Baird (1968) found viable diatoms mixed to 20cm depth in the sand and primary production low but measurable. They considered vertical mixing due to wave action to be the main limiting factor. In the shallow subtidal off two Venezuelan beaches, Edwards (1973a) recorded significant benthic primary production due to both micro- and macro-algae (2943 and 6500 kcal.m^{-2}y^{-1} at two beaches) but these areas are hardly typical of open beaches and the latter area was subject to heavy pollution. Primary production in the water column may be very important, particularly where surf phytoplankton blooms occur. Unfortunately primary production figures for a surf phytoplankton bloom have yet to be published. Edwards (1973a) estimated primary production in the water column off Venezuelan beaches as 2934mgC.m^{-2}.d^{-1}.

Different authors have partitioned food sources for sandy beaches in a variety of ways. Brown (1964) distinguished an erratic supply of macrodebris and a regular supply of particulates while Hayes (1974) recognised dissolved and microparticulate organics, stranded plankton and large organic masses. Edwards (1973a) distinguished three main pathways by which energy travels from primary foods to fishes; (1) via zooplankton to plankton feeding fish, (2) via benthos to demersal fishes and (3) directly from benthic algae to

herbivorous fishes. Ansell et al., (1978) distinguished two groups of macrofauna, (1) herbivores and detritivores and (2) carnivores. McLachlan et al., (1981a) separated only filter feeders and scavengers/predators on East Cape beaches, where deposit feeders were of negligible importance. On kelp dominated beaches Griffiths et al. (1983) distinguished herbivores, carnivores and filter feeders. The possible food sources and trophic groups of macrofauna on sandy beaches are listed in Table 5.

Zooplankton, which are extremely important in surf water, although largely ingored to date, would fall in categories (1) and (4). On most sandy beaches food source (1) is by far the most important, with food sources (3) and (4) being next. On sheltered shores, however, particulate detritus and living microflora and fauna may be of most importance once incorporated in the sediments, and under such conditions deposit feeders such as Arenicola, Callianassa and Scolelepis may be abundant.

While inputs of particulate matter to beaches have yet to be measured, some estimates are available based on the requirements of the macrofauna. In India particulate feeders accounted for 56141 kJ.m^{-2}y^{-1} and carnivores for 4291 kJ.m^{-2}y^{-1} on Shertallai beach and 38765 kJ.m^{-1}.y^{-1} and 235kJ. m^{-1}y^{-1} at Cochin beach respectively. Particulate feeders thus accounted for 91% of the food consumption on average (Ansell et al., 1978). In the East Cape, filter feeding macrofauna were estimated to assimilate

Table 5. Food sources and trophic groups of macrofauna on open sandy beaches.

FOOD SOURCE	FEEDING GROUP
1. Particulate organics including phytoplankton	Filter feeders
2. Deposited detritus, benthic diatoms, interstitial fauna	Deposit feeders

3. Stranded debris – plants
         – animals
	Scavengers – herbivores
	         – carnivores

4. Other fauna	Predators

109421 $kJ.m^{-1}.y^{-1}$, 93% of the total for the beach macrofauna, with scavenger/predators making up the remaining 7% (McLachlan et al., 1981a). This does not include zooplankton organisms which are mainly filter feeders and very abundant. Scavengers are only important where there are large inputs of debris or where filter feeders are absent because of unstable physical conditions or the absence of food (e.g. East Coast of South Africa, Dye et al., 1981; Wooldridge et al., 1981).

Huge inputs of macrophytes characterize beaches adjacent to kelp beds or similar areas. In southern California Hayes (1974) estimated these inputs to amount to 473kg wet (ca.78kg dry) algae $m^{-1}.y^{-1}$ (Macrocystis), while on West Cape beaches adjacent to kelp beds values range around 2000kg wet Ecklonia $m^{-1}.y^{-1}$ (Koop, Kield, 1980; Koop et al., 1982a; Stenton-Dozey, Griffiths, 1983; Griffiths et al, 1983). While Hayes (1974) found Tylos punctatus to consume only 4-5% of the edible kelp input, estimates for macrofauna consumption in the West Cape range 9-74%, this being taken by isopods, amphipods and fly larvae (Muir, 1977; Koop, Field, 1980, 1981; Stenton-Dozey, Griffiths, 1980; Griffiths, Stenton-Dozey, 1981; Koop et al., 1982a; Griffiths et al., 1983). Biodegradion of macrophytes by the macrofauna is thus very important.

In sheltered localities or where large amounts of particulate organics are deposited, deposit feeders may reach high biomass values (Eleftheriou, McIntyre, 1976; McDermott, 1983). On most beaches organic content of the sand is very low, e.g. $0,2-0,4mg.g^{-1}$ sand in Scotland and India (Steele, 1976) and undetectable amounts in the West Cape and East Cape (Brown, 1971a; McLachlan, 1977a).

Predators on the other benthos include crabs, starfish and gastropods. These normally occur in relatively low abundance, making up 5-10% of biomass. As many are supralittoral forms, e.g. Ocypode, they may be the only macrofauna where swash conditions are too dynamic for intertidal macrofauna to survive (Gauld, Buchanan, 1956; Dye et al., 1981). They generally take both living benthic prey and stranded carrion.

Energy flows through different species and trophic efficiencies vary widely. Turnover (P/B) ranges from 0.3 for Tellina tenuis on a temperate beach (Trevallion, 1971) to 10.3 for Donax spiculum on a tropical Indian beach (Ansell et al., 1972b). Ansell et al., (1978) found turnover on these tropical beaches generally ten times higher than on cold temperate Scottish beaches. Edwards (1973a) recorded average P/B's of 2.8-3.5 for the macrobenthos, McLachlan et al., (1981a) used P/B's of 0.5-5.0 for somatic production of molluscs and crustaceans, and Koop, Field (1981) estimated the P/B for Ligia dilatata at 3.75 times per year.

Assimilation efficiencies ($^A/_C$ X 100%) vary widely, commonly being very low for scavengers/grazers feeding on abundant macroalgae, e.g. 64% for Tylos (Hayes, 1974), 5.5% for Ligia (Koop, Field, 1981) and 30-50% for Talorchestia and fly larvae, (Stenton-Dozey, Griffiths, 1980). Koop et al., (1982a) estimated an overall average assimilation efficiency of 22% for invertebrate kelp grazers while Ansell et al., (1978) and Edwards (1973a) assumed assimilation efficiencies of 80% for carnivores and 60% for herbivores. Ansell et al., (1978) estimated efficiencies of transfer of energy through the food chain ($^P/_A$ X 100%) as 15-16% for herbivores and detritivores and 25-30% for carnivores in India while Edwards (1973a) estimated $^P/_C$ X 100% as 15% for benthos, 17% for demersal fish and 11-15% for other fish at his unpolluted site. Ecological efficiencies calculated from McLachlan et al. (1981a) were 9-19% for the macro-fauna with a mean of 17%.

These food chains end in fishes, birds, crabs and other invertebrate predators and man. Very few studies have estimated the importance of these different predators. In Scotland juvenile flatfish are the most important predators, cropping siphons of bivalves, palps of polychaetes and whole prey. Bivalves may then put more energy into regeneration of siphons and less into reproduction. Trevallion (1971) estimated that up to 1.3% of total annual energy expenditure in Tellina tenuis may go into regenerating siphons. In India crabs were considered the most important predators, with fishes and man less important and birds virtually absent (Steele, 1976; Ansell et al., 1978). Edwards (1973a) estimated fish to account for 71-89% of production at his two beaches, starfish accounting for 13% on one and crabs for 13% on the other beach. McLachlan et al., (1981a) partitioned predation on east Cape beaches. Birds took 32% of intertidal macrofauna production (McLachlan et al., 1980), fishes were estimated to take 55% and benthic predators (mainly crabs, Ovalipes) 10% with man accounting for less than 3%. Du Preez (1981) has subsequently made a detailed investigation of the predation of Ovalipes on Donax and Bullia and Lasiak and Rossouw (1983) have studied fish predation. On kelp dominated beaches of the West Cape, however, birds are the major predators (Griffiths et al., 1983).

Evaluating our knowledge of sandy beach food chains as a whole is made difficult by not only the small number of quantitative studies, but also the absence of data on zooplankton. The

macrofauna cannot be considered in isolation when describing these food chains. Surf zone zooplankton production, also untimately falling prey to fishes and being exported from the system, is probably more important in terms of energy flow. In the East Cape for example, where we have some idea of surf zone zooplankton biomass, a different pattern emerges if larger mobile crustaceans, such as mysids and prawns, are included with zooplankton out to 500m from the beach (Table 6).

Table 6. Summary of approximate faunal dry biomass for an average beach and surf zone in the East Cape. (From McLachlan, 1983)

CATEGORY	BIOMASS $g.m^{-1}$
Macrobenthos	1500
Zooplankton	1100
Birds	5
Fishes	300

The food chain is centred around filter feeding benthos and zooplankton feeding on particulate detritus and phytoplankton and being taken in turn by fishes, birds and crabs. As zooplankton turnover is 6-7 times that of the macrofauna, the centre of gravity of the food chain is clearly in the surf and not on the beach. McFarland (1963) came to a similar conclusion, showing that plankton was the predominant fish food off Texas beaches, greatly exceeding the benthos as an available food source. The surf zones he studied were characterized by high primary productivity in summer.

To conclude this section on macrofauna energetics it appears that five main beach types can be recognised in terms of macrofauna energy flow patterns (Table 7). Information on surf zone zooplankton in different zoogeographic regions is unfortunately not available to allow incorporation into this scheme. It may be expected, however, that as zoopolankton and macrobenthic filter feeders utilize the same food resources, their total biomass would be roughly similar in many cases.

8.3 Interstitial Fauna

Less attention has been paid to interstitial energetics, although as early as 1942, Pearse et al., proposed that the interstitial systems of sandy beaches had digestive and incubating functions, the microfauna mineralising organic materials in the sand. Little attempt was made subsequently to evaluate or quantify this until quite recently. This system consists typically of bacteria, protozoans and meiofauna constituting their own food web in the sand.

Dissolved and fine particulate organics form the base of this food chain, although in sheltered situations the benthic microflora might also play a rôle. McIntyre et al., (1970) were the first to demonstrate that interstitial fauna could subsist on dissolved organics. Using two experimental sand columns, they maintained viable micro- and meiofaunal populations in the second column on the effluent leaving the first column. They suggested that bacteria were the prime utilizers of dissolved organics, utilizing these organic molecules when they adsorb onto sand grains

Table 7. Major beach types in terms of macrofauna energetics.

Type	Latitude	Predominant Food Sources	Macrofaunal Biomass	Dominant Trophic Group	Predators
1. High turnover, particulate-based food chain	Tropical	Particulates	Low to moderate	Filter Feeders	Invertebrates Fishes
2. Low turnover, particulate-based food chain.	Temperate	Particulates	Low to high	Filter Feeders	Fishes, Birds Invertebrates
3. Macrodebris-based food chain.	Temperate	Stranded macrophytes	Moderate	Scavengers/ Grazers	Birds
4. Sediment-based food chains in sheltered beaches.	Temperate or Tropical	Deposited detritus microorganisms and benthic microflora	Low to high	Deposit Feeders	Birds, Fishes Invertebrates
5. Carrion-based food chains in extremely ex-posed steep beaches.	Temperate or Tropical	Stranded carrion	Low	Scavengers/ Predators	Birds, Crabs

where they can be digested with extra-cellular enzymes. The meiofauna in turn fed mainly on these bacteria, accounting for approximately 5% of bacterial con-sumption.

Fenchel (1972) considered bacteria the only primary decomposers of particulate plant detritus with their decomposition rate limited by oxygen and nutrients. Consequently he suggested that higher trophic levels in the interstitial food web are dependant on initial processing of plant detritus by bacteria. Although

some meiofaunal species may feed directly on detritus, microflora or dissolved organics, in a broad sense meiofauna do form the top of the inter-stitial food web as most species feed on bacteria, protozoa or other meiofauna (McIntyre, Murison, 1973; McLachlan et al., 1981a). The position of protozoans in this system has been little studied in open beaches; while some forms may have a similar trophic status to bacteria, others are even predatory on meiofauna. However, in a broad sense they probably occupy a position inter-

mediate between, and overlapping with, bacteria and meiofauna in interstitial food chains.

Three trophic types may be recognised within the meiofauna, predators, herbivores and bacterivores, with only the Hydrozoa and Turbellaria exclusively predatory (Tietjen, 1980). Swedmark (1964) however, listed four categories, predators, diatom and epigrowth feeders, detritus eaters and suspension feeders. Besides direct grazing of meiofauna on the microfauna, Tietjen (1980) considered that meiofauna stimulate bacterial activity in the interstitial system by (1) mechanical breakdown of detritus, making it more susceptible to bacterial colonisation, (2) excretion of nutrients for microbial use, (3) secretion of mucous thereby attracting bacterial growth and (4) movement conveying nutrients and oxygen. Assimilation efficiencies ($^A/_C$ X 100%) for meiofauna have been estimated in the range 6-26% while transfer efficiencies ($^P/_A$ X 100%) were 79-97% for three nematode species (Tietjen, 1980). For turnover ($^P/_B$) a ratio of 10 has been widely used for meiofauna (Gerlach, 1971).

Because of the difficulty of scale when working with the minute inhabitants of the interstitial fauna, investigations of interstitial energetics have generally taken the form of 'black box' studies of the system as a whole. This has commonly been done by measuring interstitial or benthic oxygen consumption in situ and then attempting to partition this. Benthic oxygen consumption measurements have been discussed and reviewed by Lassere (1976), Pamatmat

(1977) and Dye (1983). Another approach has been the study of experimental sand columns in the laboratory.

Several authors have maintained laboratory sand microcosms for extended periods (McIntyre et al., 1970; Pugh, 1976; Boucher, Chamroux, 1976; Chamroux et al., 1977; Wormald, Stirling, 1979; McLachlan et al., 1981c). A closed circuit system has been successfully maintained for 16 months on soluble amino acids (Boucher, Chamroux, 1976) confirming the utilization of dissolved organics by microorganisms and their subsequent consumption by the meiofauna. However, changes in meiofaunal community structure (decreased diversity) indicated that the utilization of soluble organics via bacteria was not the only trophic path to the meiofauna. In this case bacteria and meiofauna were estimated to account for 95% and 5% of the carbon input respectively, the same proportions as found by McIntyre et al. (1970).

There have been few detailed studies of interstitial energy budgets in situ on open beaches. The three cases that warrant attention concern a comparative study of Scottish and Indian beaches, studies on high energy beaches in the Eastern Cape and studies on beaches receiving high kelp inputs in the Western Cape.

Munro et al. (1978) made a detailed comparative investigation of interstitial dynamics on tropical Indian beaches (Md 150-190um) and Scottish beaches (Md 250um) using small and large sand columns and in situ measurements. The tropical beach lacked epipsammic

diatoms which were common on the temperate beach. Dissolved organics were estimated to make up 80% of the input on the Scottish beach and 39% on the Indian beaches. Interstitial community respiration on the tropical beach ($164gC.m^{-2}.y^{-1}$) was nine times the winter values and twice the summer values for the temperate beach (mean = $42gC.m^{-2}.y^{-1}$) with microbial production estimated to be 72 $gC.m^{-2}.y^{-1}$ in the former and an annual average of $15g.C.m^{-2}.y^{-1}$ in the latter (using respiration figures based on an assumed conversion efficiency of 45% and the assumption that the contribution of meiofauna was negligible). Meiofauna biomass was, however, much higher on the Scottish beach ($273-523mg.\ m^{-2}$) than the Indian beach ($24-60mg.m^{-2}$)(Table 8). They postulated that more vigorous flushing of the sand on the tropical Indian beach both boosted respiration and striped bacteria from the sand grains.

The tropical beach received more organics and had a higher interstitial oxygen consumption rate than the Scottish beach as a result of increased water flow by wave flushing. Surf

organic levels were 500-1000 ug $C.l^{-1}$ in Scotland and 900-3700 $ug.l^{-1}$ in India. However, surf flushing of the Indian beaches may remove significant quantities of bacteria, thus making them available to macrofauna filter feeders and decreasing the quantity available to the meiofauna.

In the East Cape the interstitial fauna consists essentially of meiofauna, protozoans and bacteria to considerable depth in the sand (Dye, 1979a; McLachlan et al., 1979a). Dye (1980) showed tidal fluctuations in benthic oxygen consumption as a result of tidally induced changes in pore moisture and interstitial water flow, lowest values being recorded when the sand dried out. Dye (1979a) investigated biological oxygen demand in beach sand, using intact sand cores in the laboratory as these gave higher values than in situ techniques. He showed that disturbance caused a significant increase in oxygen uptake.

In a more detailed study Dye (1981) later partitioned this oxygen uptake between bacteria, protozoans and meiofauna on two beaches (Table 9).

Table 8. Biomass, production and respiration of interstitial organisms on Scottish and Indian beaches. (After Munro et al., 1978). All values in $gC.m^{-2}.y^{-1}$.

| | INDIA | | | SCOTLAND | | |
	Respiration	Production	Biomass	Respiration	Production	Biomass
Algae	0	0	0	–	7	–
Microfauna	160	72	–	31	15	–
Meiofauna	4	2	0.02	4	2	0.2

Table 9. Partitioning of interstitial oxygen uptake on two East Cape beaches. (After Dye, 1981).

	MODERATELY EXPOSED BEACH		VERY EXPOSED BEACH	
	Biomass %	O_2 uptake %	Biomass %	O_2 uptake %
Meiofauna	75	18	79	21
Protozoa	19	18	17	24
Bacteria	6	64	4	55

In the West Cape very rich interstitial populations develop on beaches with high kelp inputs. Koop, Griffiths (1982) recorded dry biomass of 241, 200 and 663 $g.m^{-1}$ of macro- meio- and microfauna respectively. Bacteria were concentrated at lower tide levels, probably subsisting on small particles of broken down kelp resulting from feeding and faeces of macrofauna and meiofauna. Koop et al., (1982a) quantified carbon flow through this system. Bacteria on the stranded fronds were responsible for much initial degradion. Breakdown of the kelp resulted in high concentrations of leachates (up to 5640 $mgC.l^{-1}$) in the sediment below the kelp. Over 90% of this was utilized by bacteria after seeping through 1m of sand and 23-27% of carbon in the kelp was converted to bacterial carbon. The ratio of increase in bacterial biomass to kelp carbon used was 58.7%, giving a conversion efficiency of 29.4% if bacterial biomass is 50% carbon (Koop et al., 1982a). Much of the faeces of invertebrate grazers were also converted to bacterial carbon as these grazers have low assimilation efficiencies. The remaining 73-77% of the kelp was mineralised by the microbes quite rapidly. The great significance of these microbes indicates why Hayes (1974) recorded such little kelp breakdown in California where he looked at only one grazer, Tylos punctatus.

8.4 Conclusions

It may be concluded that intertidal sandy beaches are important in the processing of organics whether these be as DOM, POM or larger animal and plant remains. These foods generally come from the sea and in turn most production returns there. The interstitial fauna are always more important than the macrofauna in this mineralisation of organic materials, even where a rich macrofauna occurs (Table 10).

The interstitial system is driven by inputs of soluble and particulate organics, the main path being via bacteria attached to sand grains to meiofauna. The intermediate rôle of protozoans is uncertain. On exposed beaches there is little exchange between this sytem and the macrofauna although the importance of microorganisms flushed from the sand as food for the macrofauna needs further investigation. The concentrations of meiofauna flushed from

360

Table 10. Approximate partitioning of total benthic assimilation between macrofauna and interstitial fauna in four geographic areas based on data in Munro et al. (1978) Ansell et al. (1978), McLachlan et al. (1981a) and Koop, Griffiths, (1982).

ASSIMILATION [kJ.m^{-1}.y^{-1} (%)]

LOCALITY AND BEACH TYPE	Macrofauna	Interstitial fauna	BEACH WIDTH (m)
Scotland, temperate	30 000 (23)	99 000 (77)	60
India, tropical	427 000 (38)	703 000 (62)	60
East Cape, warm temperate	116 000 (37)	236 000 (63)	60
West Cape, temperate with high kelp input	42 000 (3)	1599 000 (97)	63

the sand of exposed beaches were measured by McLachlan (1977a) and found to be negligible. On sheltered beaches a greater size spectrum of organisms may occur, filling the gap between interstitial fauna and larger macrofauna and thereby facilitating energy flow by predation. In such environments deposit feeders may also ingest significant quantities of interstitial fauna. Inshore food chains in beach environments are however centred in the surf zone rather than the intertidal, even where rich intertidal macrofaunas occur. Our area of least understanding at the moment is these dynamic food chains of the surf zone and in particular the role of zooplankton and larger motile crustaceans.

9. NUTRIENT CYCLING
It has long been speculated that beaches may be of importance in recycling nutrients by mineralising organic materials coming from the sea (Pearse et al., 1942). This is effected by the fauna consuming organic nutrients including nitrogen and phosphorous and then excreting this in inorganic form, e.g. NH_4, PO_4. In some areas groundwater seepage can, however, also supply considerable amounts of inorganic nutrient via the beach to the surf zone. This can take the form of both artesian aquifers and general seepage around the area where the permanent water table meets the sea. Johannes (1980) found this to be very important in Western Australia where submarine groundwater

discharge ranged 1-5m.y^{-1} and contained up to 380 ug at l^{-1} NO$_3$-N.

Nutrient regeneration by the macrofauna, zooplankton, birds and fishes has been virtually ignored. Lewin et al., (1979b) and Prosch, McLachlan (1983) respectively investigated ammonia excretion in bivalves of the genera Siliqua and Donax on beaches in Washington and the East Cape, South Africa. In both cases very large populations of these bivalves develop and nutrients regenerated by them could be of significance in supplying phytoplankton requirements in the surf zone. Hayes (1974) found Tylos to consume only 4-5% of kelp input on Californian beaches while Griffiths, Stenton-Dozey (1981) and Koop et al. (1982a) estimated that 9-74% of stranded kelp was consumed by the macrofauna. Not all of this is assimilated, however, and low assimilation efficiencies may result in a comparatively small proportion of kelp nitrogen being regenerated directly by the macrofauna. The contribution of other faunal components must also be important in this regard but have yet to be investigated.

Generally the interstitial system of sandy beaches has been thought more important in nutrient regeneration than the macrofauna. Water filters through the sand, as a result of tides and waves both in the intertidal and the subtidal, and DOM and POM are removed by the interstitial fauna and mineralised.

Several studies of experimental systems of sand columns or model beaches have looked at mineralisation and/or nutrient regeneration, mostly concentrating on nitrogen (Chamroux, 1965; McIntyre et al., 1970; Pugh, 1976; Boucher, Chamroux, 1976; Cahet, 1976; Wormald, Stirling, 1979; Munro et al., 1978; McLachlan et al., 1981c). Generally nitrification is the dominant activity in beach sand and organic nitrogen is efficiently mineralised to nitrate. Increasing organic loading tends to raise equilibrium levels and it is usually only at very high levels that a beach can not cope and anoxic conditions and ammonia appear (Oliff et al., 1970; Pugh, 1976). Boucher, Chamroux (1976) recorded total mineralisation of amino acids added to their sand columns while Munro et al., (1978) recorded 70% mineralisation of natural organics, mostly in the top 5cm of their columns. McLachlan et al. (1981c) found 35% mineralisation of natural organics in 50cm sand columns and this increased to 65% when amino acids were added.

Most of these sand column studies have been somewhat artificial as water flow has been unrelated to in situ flow rates, there has been continuous submergence, and inputs have been constant rather than tidal or pulsing. Exceptions are Pugh (1976) and McLachlan et al. (1981c), although even these experiments did not incorporate pulsing flows. Filtration rates have ranged 25-1000 l.m^{-2}.d^{-1}, covering a variety of flows both intertidal and subtidal.

McLachlan (1982) followed up earlier sand column work with a model of water filtration and nutrient regeneration by sandy beaches. This was based on a regression model predicting filtration volume as a function of sand particle size, beach slope and tide range.

Coupled to this was an estimate of the degree of mineralization of organics in relation to sand particle size and the filtration distance. The average filtration distance is about 35% of the horizontal intertidal distance (Riedl, Machan, 1972) and average mineralisation was estimated to be at least 60-80%. At a filtration rate of $10^4 1.m^{-1}.d^{-1}$ and an organic nitrogen level of 0.15mg. 1^{-1} this predicted regeneration of 0.9g NO_3-N $m^{-1}.d^{-1}$. An attempt to estimate total nutrient production by beaches in the East Cape was made by McLachlan et al. (1981a). They estimated nitrogen excretion by the macrofauna and interstitial fauna of the beach and surf zone at 350gN.$m^{-1}.y^{-1}$ and 591gN. $m^{-1}.y^{-1}$ respectively. Thus, even on beaches such as these with very high macrofauna biomass, the interstitial fauna are more important in nutrient regeneration, accounting for 63%. While only approximate, the above figures suggest that the mineralising activities of the benthos alone can replenish the nutrient pool of the surf zone in a matter of days or weeks.

Koop et al. (1982b) quantified microbial regeneration of nitrogen from stranded kelp over an eight day cycle. In this time the microbes incorporated 94% of the kelp nitrogen, which normally strands at an average input of 12gN.$m^{-1}.d^{-1}$. However, in the long term the beach can not act as a nitrogen sink and this must return to the sea. In this case this could supply roughly one quarter of the nitrogen requirements of phytoplankton in the adjacent kelp beds. While hardly typical of open beaches, even on the west coast (Bally, 1981), these figures for beaches adjacent

to rocks and subject to large kelp inputs are interesting for comparison.

It may therefore be concluded that sandy beaches can mineralize most organics they receive, the bulk of this being done very efficiently (80-100%) by the interstitial fauna. This is accomplished by the process of water filtration through the beach and will be greatest where steep beaches and short period waves result in high filtration volumes (e.g. in the tropics). Where vast macrofauna populations occur they may also contribute significantly to nutrient regeneration. Zooplankton, birds and fishes must also be very important.

Most organic nitrogen and phosphorous supplied to a beach will rapidly be returned to the surf as nitrates, ammonia and phosphates. Thereafter the fate of these nutrients will depend on physical conditions in the surf zone. Where cellular circulation patterns occur there may be a high degree of retention, while on irregular coasts or reflective beaches, exchange with the open sea may be much more rapid. As many surf zones are characterized by high primary productivity, utilization of beach generated nutrients in the surf zone may be very important and is in need of more attention. Hayes (1974) and Koop et al. (1982b) consider such nutrients of little importance in the surf while McLachlan et al. (1981a) suggest that these nutrients may be sufficient to maintain surf phytoplankton blooms on long open beaches.

10. TOWARDS A MORE HOLISTIC APPROACH
This review has attempted a functional

look at our present knowledge of the ecology of beach/surf zone environments as a whole, incorporating all aspects of fauna and flora, energy flow and nutrient cycling. Unfortunately, most published studies of beach environments have not attempted such a holistic approach and have tended to investigate one or more components in isolation.

In the East Cape research on beach environments has been unique in attempting a holistic approach towards the quantification of energy flow and nutrient cycling under the concept of a beach/surf zone ecosystem. This is based on two contentions (McLachlan, 1980c): (1) that the sand body of the beach together with the water envelope of the surf zone form an ecosystem where internal energy flows are greater than exchanges across boundaries and (2) that this system has definable boundaries, these being the drift line on the landward margin and the outer limit of surf circulation cells on the seaward margin. The central concept is that the circulation cells that typify the surf zones of open beaches (Inman, Brush, 1973) imply a certain measure of integrity of surf zone water and retention of materials within this zone. This is in opposition to the idea that beaches are purely high energy interfaces between sea and land. Clearly, however, this can not apply to pocket beaches, beaches associated with rocky shores or beaches dropping directly into deep water where there is no real surf zone. The kelp input beaches of the South African west coast, for example, function as interfaces between adjacent kelp beds and the land.

Energy flow and nutrient cycling in a long open beach typical of the East Cape is illustrated in Fig. 9. This is a rich system with considerable flows of energy and nutrients. It includes producers (phytoplankton), consumers (benthos, zooplankton, fishes) and decomposers (interstitial fauna). Energy flows within this system appear to be greater than across its boundaries. However, although exchange across the dune/beach boundary is negligible, exchanges across the outer boundary of the surf cells remain to be quantified. The main trophic pathway is from fine organic materials (POM and phytoplankton) via zooplankton and filter-feeding macrofauna to fishes. The interstitial fauna is also extremely important in mineralising POM and DOM. The total amount of inorganic nitrogen regenerated by the beach and surf zone fauna is not yet known, but must be substantial as the macrofauna and interstitial fauna alone can regenerate enough to replenish the surf zone nutrient pool within a few weeks to days. Although not indicated in Fig. 9, wave action probably represents the most important factor controlling this system, as it is responsible for transporting water, sediment and biological materials, driving surf circulation cells and pumping water through beach sand.

Clearly, not only biological and chemical information is needed to understand beach/surf ecosystems. Water movement, the key to all dynamic processes occurring here, is the realm of the physical oceanographer. The discreteness of surf circulation boundaries and exchanges across them
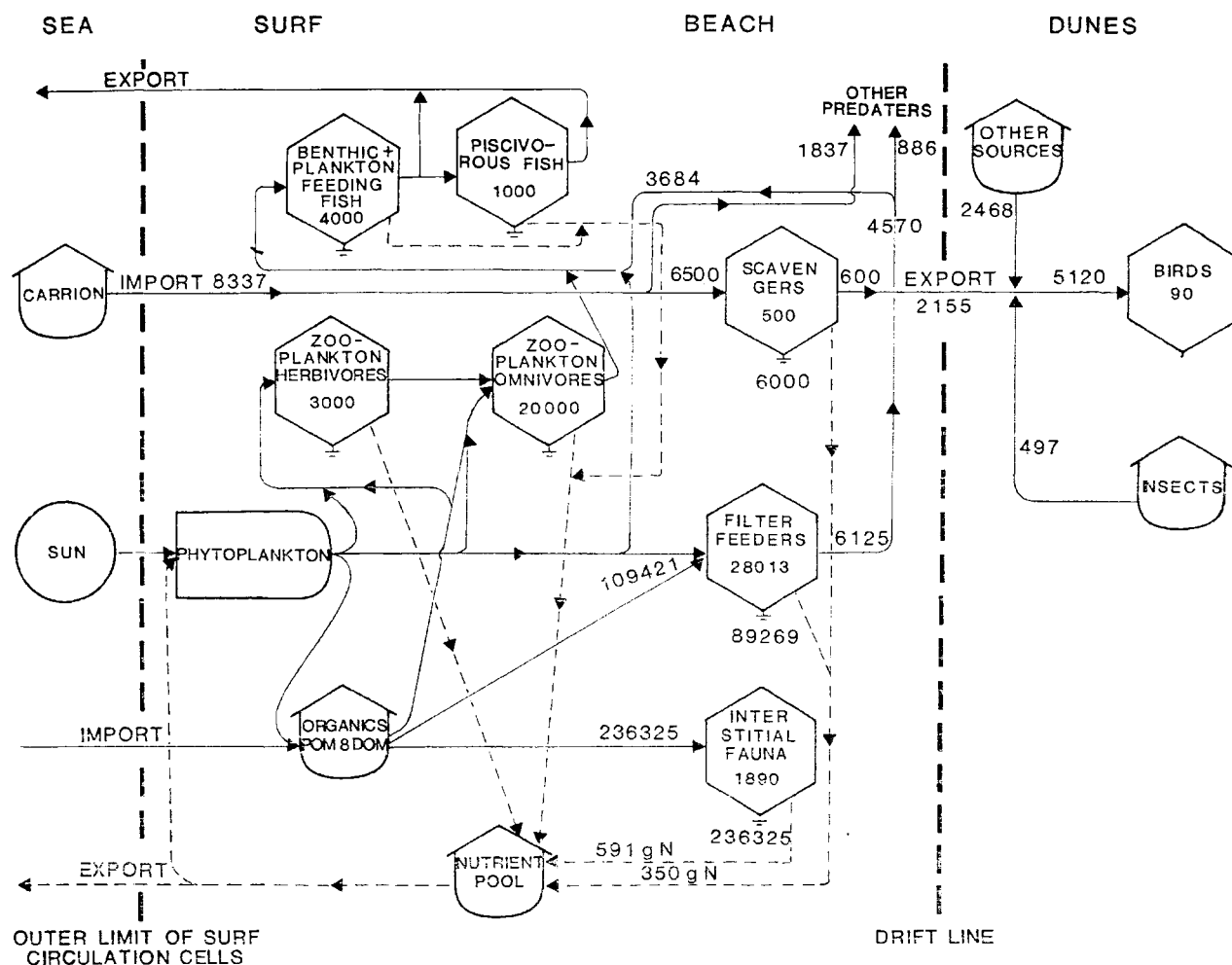
SEA   SURF   BEACH   DUNES

EXPORT

BENTHIC +
PLANKTON
FEEDING
FISH
4000

PISCIVO-
ROUS FISH
1000

OTHER
PREDATERS

1837   886

OTHER
SOURCES

3684

4570

2468

CARRION   IMPORT 8337

6500   SCAVEN
GERS
500

600   EXPORT
2155

5120   BIRDS
90

ZOO-
PLANKTON
HERBIVORES
3000

ZOO-
PLANKTON
OMNIVORES
20000

6000

497

SUN   PHYTOPLANKTON

FILTER
FEEDERS
28013

6125

INSECTS

109421

89269

IMPORT   ORGANICS
POM & DOM

236325   INTER
STITIAL
FAUNA
1890

236325

591 g N

350 g N

EXPORT   NUTRIENT
POOL

OUTER LIMIT OF SURF
CIRCULATION CELLS

DRIFT LINE

FIGURE 9. Energy flow (solid lines) and nutrient cycles (broken lines) for a typical East Cape beach, largely after McLachlan et al. (1981a). All values in $kJ.m^{-1}.y^{-1}$ except nutrient values in g inorganic N.

need to be quantified. It is therefore essential that physical oceanographers, biologists and chemists work together. Beaches in different geographic areas need to be studied in this fashion. Biologists in particular must not only study the intertidal fauna, but must venture out into the surf zone. In the dynamics of fine organic materials, phytoplankton and zooplankton lies the key to a more realistic understanding of the function of sandy beach/surf zone

ecosystems, and this can only be evaluated in the presence of a detailed knowledge of the physical and chemical environment.

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