THE FAUNA ASSOCIATED WITH KELP STRANDED ON A SANDY BEACH

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1. INTRODUCTION

Seventy percent of the southern African coastline consists of sandy beaches (McLachlan et al. 1981), but these received little attention until Brown's publications (1964, 1971a,b) on the general ecology of beaches around the Cape Peninsula. Since then McLachlan (1977a-c, 1980), Dye (1979), McLachlan et al. (1979, 1981), Dye et al. (1981) and Wooldridge et al. (1981) have investigated the physical parameters and fauna of eastern and southern coast beaches and Bally (1981), those of sandy beaches along the west coast north of the Cape Peninsula. All these are clean open beaches which receive only erratic deposits of macrophytes. The only form of primary production arises from offshore blooms of phytoplankton with the occasional stranding of carrion.

By contrast the west coast of the Cape Peninsula has extensive offshore kelp beds dominated by *Ecklonia maxima* and *Laminaria pallida*. Newell et al. (1982) have reviewed the available information on primary productivity, standing stocks and ecological energetics of consumer organisms inhabiting these beds. Much of the kelp material is ultimately uprooted and stranded on nearby shores, providing a rich source of energy for the intertidal fauna. One particular area along this coastline, Kommetjie (34°08'S, 18°19'E), has been a focus of study for the past few years. The beach is approximately one kilometre in length with sandy pockets bordered by rocky outcrops. Several of the primary consumers of stranded kelp have been investigated, principally the amphipod *Talorchestia capensis* (Muir 1977), the isopod *Ligia dilatata* (Koop, Field 1980,1981) and larvae of the kelp fly *Fucellia capensis* (Stenton-Dozey, Griffiths 1980). A one month survey of the macrofauna associated with stranded kelp and the rate at which this material was degraded was also undertaken by Griffiths and Stenton-Dozey (1981). Koop and Griffiths (1982) studied the relative significance of the macro-, meio-fauna and bacteria and recently the fluxes in material arising from decomposing wrack has been investigated (Koop et al. 1982a,b).

This paper presents results of a year-long survey conducted at Kommetjie to establish the seasonal pattern in composition, distribution, abundance and biomass of macro-, meio-fauna and bacteria and their relative contributions to the beach economy in terms of standing stock and productivity. Fluctuations in the fauna are correlated with the deposition rate of kelp material.

2. MATERIALS AND METHODS

2.1 Beach zonation and collection of wrack

In zoning the beach, three stages of kelp degradation were recognised at the time of low spring tide, namely those in which deposits were old, in the process of decay and fresh. The position of these corresponded to HWS, MW and LWS respectively and this zonation generally followed the pattern suggested by Dahl (1952), but in this case it was subjected to the condition of surface wrack rather than using indicator species of the fauna to determine zones.

To establish the quantity of material cast ashore, each month five 1m^2 quadrants were removed from fresh deposits along the 300m stretch of beach. A large area was covered to compensate for patchy deposition. The mean wet weight of these samples, times 300m was then regarded to represent the total quantity of new material present on the day of sampling. This value was later increased by an estimated rate for the total replacement of stranded kelp in order to reach a monthly figure.

2.2 Macrofauna

Four random 0,2m^2 quadrants were collected monthly from each zone at the time of low spring tide. Since many species, notably kelp flies and beetles, are very motile, each quadrant was initially enclosed with a plastic tank, sprayed with insecticide and left for 10 minutes, whereafter kelp and sand to a depth of 15cm were transferred to plastic bags. Sandpiles from each zone were pooled and the fauna identified to species, counted and oven dried at 60^{0}C.

2.3 Meiofauna

Once every three months, four random sand cores were extracted from each zone using a stainless steel corer 30cm in length and 10cm^2 in cross section to depths of 30cm and 60cm. It was not considered necessary to sample beyond this depth as Koop and Griffiths (1981) found that 97% of the meiofauna associated with a nearby wrack bed at Kommetjie was concentrated in the upper 60cm. A 200ml subsample was removed from the pooled cores and fixed in 5% formalin. Animals were separated from the sand in a modified Oostenbrink apparatus (Fricke 1979), stained with rose bengal and counted under a dissecting microscope, a distinction being made between the major taxonomic groups. Counts were increased by 10% to account for extraction loss (Fricke 1979). Biomass for a taxon was determined by placing a hundred representative individuals on each of three silicon glass cover slips which were oven-dried at 60^{0}C to constant weight. The mean individual dry mass was used to convert numbers to biomass.

2.4 Bacteria

Bacterial densities were established quarterly from four random sand cores extracted at 30cm depth intervals to the water table in each zone. From the cores, which were mixed for a sampling site, a 10ml subsample was preserved in 10ml of 10% formalin in sterile seawater. Bacteria were firstly removed from sand grains by shaking the samples in a DAWE Sonicleaner type 6442A, and then stained with acridine orange and counted under an epifluorescent microscope (Hobbie et al. 1977; Linley et al. 1981). Bacterial densities were calculated using the formula in Mazure (1978). The proportion of rods to cocci and the dimensions of these cells were determined from scanning electron micrographs. Volume was converted to wet weight assuming a specific gravity of 1,1 and wet weight to dry weight using a ratio of 0,23 (Luria 1960).

3. RESULTS AND DISCUSSION

3.1 Kelp deposition

In attempting to determine the quantity of kelp cast ashore, an estimate of turnover rate is required. Koop and Field (1980) and Koop et al. (1981a) estimated an eight day cycle of replacement in which period approximately 80% of the kelp present passed through the grazer and microheterotrophic pathways. Although an initial rapid loss in kelp mass was also observed by Griffiths and Stenton-Dozey (1981), total degradation was only completed after two weeks. It is therefore believed that the total replacement of kelp has a fourteen-day cycle, coinciding with spring tides and this has been used to estimate the quantity of kelp cast ashore annually.

Maximal kelp deposition occurred in winter (Table 1), a feature common along the Cape west coast

(Muir 1977 ; Koop, Field 1980) when large offshore swells uproot whole plants and drive them ashore. The mean standing stock calculated from Table 1 was 83,5kg wet mass m^{-1}, with a total deposition rate of 2179kg $m^{-1} yr^{-1}$, a value very similar to that established for a nearby rocky shore, namely 1200-1800kg $m^{-1} yr^{-1}$ (Koop, Field 1980). The offshore kelp bed at Kommetjie is approximately 700ha in area (Koop et al. 1982a). It has a standing stock of 23 030 tonnes of *Ecklonia maxima* and 17 284 tonnes of *Laminaria pallida* (Field et al. 1980), of which 10% (Simons, Jarman 1981) and 15% (N .Jarman, personal communication) respectively may be exported annually to the adjacent 3km shore. This represents 4 890 tonnes of stranded kelp or 1 630kg $m^{-1} yr^{-1}$. This value is also similar to that recorded above and supports our estimate of turnover time.

TABLE 1. The wet mass of kelp (kg m^{-1}) sampled at monthly intervals from the swash zone along a 300m stretch of beach at Kommetjie, Cape Peninsula.

Month	Mass of kelp (kg m^{-1})
January	36
February	80
March	284
April	43
May	78
June	240
July	116
August	38
September	19
October	76
November	38
December	55

3.2 Macrofauna

Thirty-five macrofaunal forms were recorded, comprising 4 species of amphipods, 2 isopods, 7 molluscs, 4 dipterans and 18 coleopterans. The talitrid amphipod, *Talorchestia capensis* was dominant for most of the year and accounted for over 90% of macrofaunal numbers (Fig. 1). This species is common in wrack beds and responsible for most of the primary consumption of surface material (Griffiths et al. 1983). Other amphipods present in order of abundance were *Talorchestia quadrispinosa*, *Paramoera capensis* and *Gitanopsis pusilla*. The isopods, *Exosphaeroma truncatitelson* and *Eurydice longicornis* were restricted to the waters' edge, where they feed on organic matter and prey on small living animals such as *Talorchestia* (Brown 1973). Their numbers declined in winter (Fig. 1) when the swash zone became inhospitable due to heavy wave action.

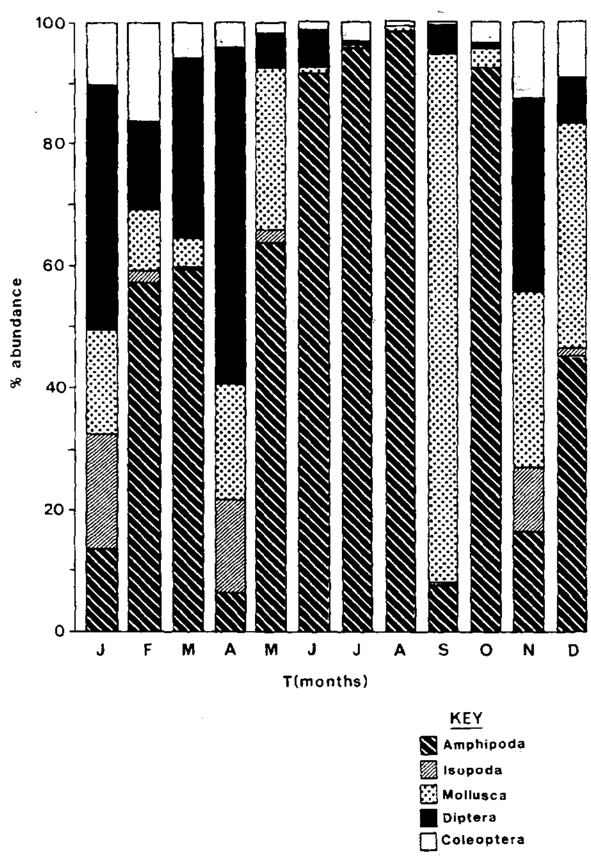

FIGURE 1. The taxonomic composition of macrofauna (percentage abundance) associated with kelp deposited on Kommetjie beach, Cape Peninsula.

Of the seven mollusc species, two were common, a brown bivalve, 1mm in diameter (*? Neogaimardia kowiensis*) and a small grazing gastropod (*Eatoniella* sp.) both of which were abundant to a depth of 10cm at all tidal levels. These two organisms were the dominant forms during September, comprising 85% of the total macrofauna (Fig. 1). Other molluscs present were mainly juveniles of sublittoral forms such as *Choromytilus meridionalis* and *Burnupena* sp. which were probably washed ashore with kelp.

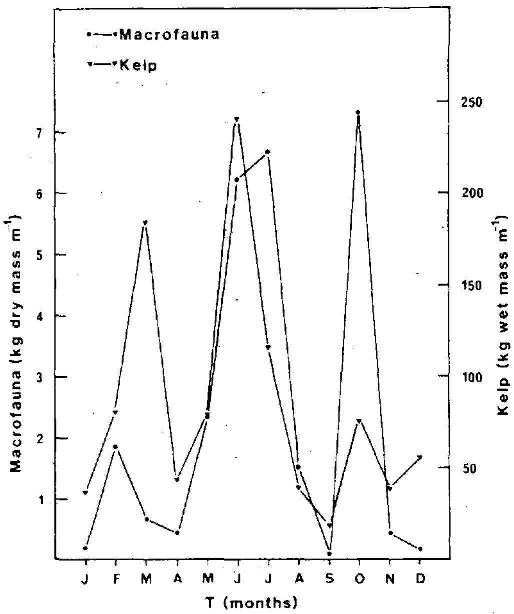

FIGURE 2. Monthly fluctuations in total biomass of the macrofauna (g dry mass m^{-1}) in response to the quantity of kelp cast ashore at Kommetjie beach, Cape Peninsula.

The adults of the two most common dipterans *Fucellia capensis* and *Coelopa africana* were always present, but exceptionally high numbers were recorded in summer and autumn, coinciding with the presence of many larvae (Fig. 1). This may reflect a summer/autumn breeding peak, this possibility being reinforced by the virtual absence of larvae from July to October.

The Coleoptera were dominated by two carnivorous forms, *Aleochara salsiipotens* (Staphylinidae) and *Acritus lightfooti* (Histeridae). The most common herbivore was *Cercyon maritimus* (Hydrophilidae), while other typical intertidal forms were *Pachyphaleria capensis*, *Bledius* sp., *Omalium* sp. and *Cafius xantholoma*. The abundance of beetles through the year was erratic with no seasonal pattern. Like the isopods, their contribution towards total numbers seldom exceeded 10% (Fig. 1). Both orders are not permanent residents of the intertidal habitat, the isopods entering from the sublittoral environment, while the beetles migrate down from the landward sand-dunes.

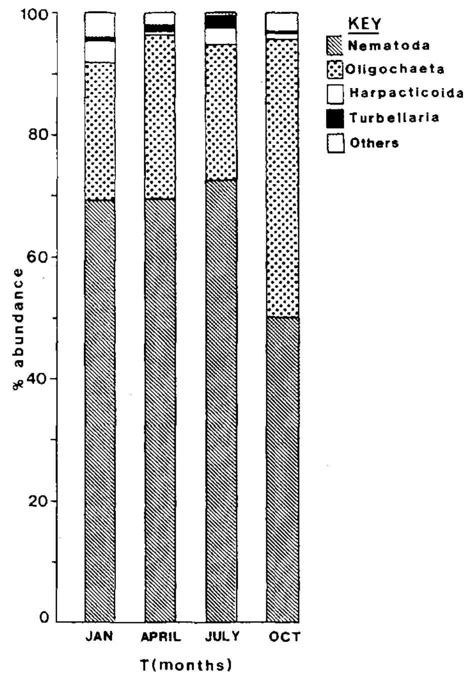

FIGURE 3. The taxonomic composition of meiofauna in terms of percentage abundance present on Kommetjie beach, Cape Peninsula for different seasons of the year.

The macrofauna as a whole were concentrated between mid tide and HWS, while the lower intertidal remained sparsely colonised throughout the year (Table 2). Although the highest abundance

(4 173 x $10^3 m^{-1}$) and biomass (5 885,67g dry mass $^{-1}$) were recorded in July at HWS, no seasonal pattern was evident for either MW or the upper intertidal. Species diversity generally declined down the beach, a phenomenon which is the reverse of the usual pattern (McLachlan 1977c). A similar observation was made by Koop and Griffiths (1982) and they attributed this to increased food availability in the form of stranded kelp at higher beach levels and to the fact that many of the species at HWS are essentially of terrestrial origin.

Monthly fluctuations in standing stocks of macrofauna corresponded closely to the pattern of kelp deposition recorded during the year (Fig. 2). Overall biomass fluctuations were controlled by variations in the biomass of amphipods which in turn are a function of the lifecycle of *T. capensis* as described by Muir (1977).

3.3. Meiofauna

Insufficient taxonomic data on marine meiofauna in southern Africa is available for specific identification to be made. Nevertheless some distinct trends in basic taxonomic composition are evident. Fig. 3 compares the percentage abundance of the four major taxonomic groups, the less frequent meiofauna being grouped under 'others'. The meiofauna were dominated by nematodes and oligochaetes (their joint contribution never being less than 90%) followed by harpacticoid copepods and turbellarians (both less than 3%). Other forms such as gastrotrichs, acarines, archiannelids and polychaetes were found in extremely low numbers. Although nematodes generally contributed 50% or more of numbers the relatively large size of individual oligochaetes (mean 3,4µg dry mass) made this group equal to or more important in terms of biomass.

Seasonal fluctuations in total numbers and biomass with respect to vertical and horizontal distribution are shown in Table 3. In summer and autumn the meiofauna were concentrated at HWS, especially in the first 30cm below the surface. Densities declined dramatically towards the sea, although similar values were obtained for the mid tide zone and the lower intertidal. During winter and spring the concentration of organisms shifted to the middle of the beach where again densities were greatest 30cm into the sand. From this area the decline towards HWS was more gradual than towards the sea, indicating a more even distribution between MW and HWS than found in summer and autumn.

On the east and south coast beaches of southern Africa, a similar distribution of meiofauna exists as that observed during winter and spring at Kommetjie (McLachlan 1977c; Dye et al. 1981; McLachlan et al. 1981; Wooldridge et al. 1981). The shift away from MW to HWS during summer and autumn was likely to be in response to the extremely anoxic conditions which were prevalent in surface wrack and 40cm below the surface in the mid tide area at this time.

3.4. Bacteria

Bacterial densities ranged from $25.10^{12} m^{-1}$ to $6\ 386.10^{12} m^{-1}$ or 14.10^6 to 734.10^6 per ml of dry sand (Table 4) of which approximately 63% were of coccoid form. This range is slightly greater than found by Koop and Griffiths (1982) in a nearby wrack bed and McLachlan et al. (1979) for east coast sandy beaches devoid of wrack. Numbers varied through the year but were consistently high to the depth of the water table.

In summer and autumn numbers and biomass were highest at the mid-tide level with a marked decline towards LWS and HWS (Table 4). In winter bacteria were concentrated at HWS whereas in spring the greatest biomass existed at MW and numbers peaked at HWS. This seasonal distribution pattern was the reverse of that observed for meiofauna (see Table 3) possibly indicating the influence of grazing pressure by meiofauna. This was especially evident in

TABLE 2. Monthly estimates of the numbers and biomass of macrofauna present on Kommetjie beach, Cape Peninsula, with respect to tidal distribution. The data can be expressed m^{-2} by dividing the values by the width of the respective zones. (N LWS = zone of fresh kelp deposition at low water springs; D MW = zone of decaying kelp at mid-tide; O HWS = zone of old kelp deposits at high water springs).

Month	Zones and their respective widths in metres				Number $\times 10^3 m^{-1}$	Biomass g dry mass m^{-1}	Total number of species
January	N	LWS	:	15	52,88	35,15	9
	D	MW	:	10	9,00	8,57	7
	O	HWS	:	15	100,88	146,06	19
February	N	LWS	:	17	37,12	23,55	9
	D	MW	:	15	403,75	1171,39	17
	O	HWS	:	6	169,95	664,96	16
March	N	LWS	:	20	10,83	7,90	6
	D	MW	:	13	809,87	582,92	14
	O	HWS	:	27	273,38	193,87	13
April	N	LWS	:	20	147,83	68,25	7
	D	MW	:	13	271,27	228,37	15
	O	HWS	:	10	72,50	170,30	19
May	N	LWS	:	20	74,67	49,07	8
	D	MW	:	29	276,48	337,39	9
	O	HWS	:	14	414,40	1956,12	11
June	N	LWS	:	14	63,12	20,58	6
	D	MW	:	14	3424,40	4588,44	6
	O	HWS	:	16	1203,60	1592,36	8
July	N	LWS	:	21	0,00	0,00	0
	D	MW	:	14	615,35	875,30	10
	O	HWS	:	6	4173,83	5885,67	11
August	N	LWS	:	16	411,87	137,76	3
	D	MW	:	14	46,67	26,15	7
	O	HWS	:	17	1513,85	1342,52	4
September	N	LWS	:	38	96,00	26,83	2
	D	MW	:	10	1,38	2,52	5
	O	HWS	:	7	18,64	36,56	5
October	N	LWS	:	17	327,82	371,53	6
	D	MW	:	9	563,80	2419,49	11
	O	HWS	:	8	1241,60	4532,54	10

TABLE 2. continued:

Month	Zones and their respective widths in metres				Number $\times 10^3 m^{-1}$	Biomass g dry mass m^{-1}	Total number of species
November	N	LWS	:	16	88,27	49,06	12
	D	MW	:	12	123,10	312,93	17
	O	HWS	:	13	37,38	78,86	14
December	N	LWS	:	17	56,95	19,17	9
	D	MW	:	13	111,69	140,30	15
	O	HWS	:	14	9,22	16,66	17

autumn, when bacterial biomass reached its peak at 2 644g m^{-1} when meiofauna was at its minimum (see Tables 3 and 4). It has been reported elsewhere that meiofauna may control bacterial densities (Jansson 1968; Giere 1975; Gerlach 1978).

3.5. Standing stocks

The greatest range of monthly standing stocks occurred in the macrofauna (66 - 7 324g dry mass m^{-1}) as compared to 431 - 759g m^{-1} and 115 - 2 644g m^{-1} for meiofauna and bacteria respectively. As most of the macrofauna are restricted to surface habitats, they are more susceptible to environmental fluctuations and hence a wide range in biomass can be expected over the year. By contrast, the interstitial fauna occupies a more stable environment, relatively free from external influences.

Comparison of the mean standing stock of macrofauna (2 257g m^{-1}), meiofauna (624g m^{-1}) and bacteria (961g m^{-1}) shows a biomass ratio of 3,6:1:1,5. Thus whereas the biomass of meiofauna and bacteria per metre of beach are similar, together they make up some 42% of the total biomass, with macrofauna accounting for the remaining 58%. Bacterial standing stocks are, however, minimal values since estimates were based on bacteria associated with the surface of sand grains only. The population colonising the surfaces of stranded kelp plants was not included although Koop et al. (1982a) found that 99% of the increase in bacterial biomass in a microcosm experiment over an eight day period was associated with the surface of the kelp itself. Although the equivalent figure in an open sandy beach would be far lower (the kelp in the microcosm was placed on rock draining into a shallow basin of sand), it does emphasise that kelp surfaces may support a significant bacterial biomass.

3.6. Productivity

As standing stocks only provide information on the quantity of the different biotic components present on the beach at any one time, it is more meaningful to establish the significance of each fauna in terms of productivity. McIntyre (1969) suggests a turnover rate of 2 for macrofaunal species living one year and longer, and 5 for shorter-lived forms. McLachlan (1977b,c) used values between 2,5 and 3,5 for species from South African east coast beaches, while Koop and Griffiths (1982) applied a mean $P/\bar{B}$ ratio of 2,5 to the macrofauna of a wrack bed. This latter value was used in this study to convert the mean standing stock of the macrofauna to an estimate of productivity.

The life histories of different species of meiofauna are very diversified but since most authors have accepted a $P/\bar{B}$ ratio of 10 (McIntyre 1964; Gerlach 1978; McLachlan 1977b, c; Koop, Griffiths 1981), this value has been followed here.

TABLE 3. The seasonal abundance (numbers x 10^6 m^{-1}) and biomass (g dry mass m^{-1}) of meiofauna with respect to different tide levels and vertical gradients on Kommetjie beach, Cape Peninsula (see Table 2 for the abbreviations and widths of the different zones).

		Sampling depth (cm)					
		0 - 30		30 - 60			
Season Sampled	Zone	Numbers	Biomass	Numbers	Biomass	Total Number	Total Biomass
Summer	N LWS	9,54	13,32	3,96	4,10	13,50	17,42
	D MW	6,57	9,00	8,54	10,45	15,11	19,45
	D HWS	243,83	437,96	104,36	138,47	348,19	576,43
						376,79	613,29
Autumn	N LWS	7,71	9,35	16,38	22,05	24,09	31,40
	D MW	15,39	18,43	4,02	4,62	19,40	23,05
	D HWS	109,25	220,32	95,36	156,15	204,60	376,47
						248,09	430,92
Winter	N LWS	12,00	18,30	3,18	5,79	15,81	24,10
	D MW	163,23	292,36	206,98	319,33	370,21	611,69
	D HWS	44,68	67,02	27,07	56,64	71,75	123,67
						457,77	759,45
Spring	N LWS	18,36	31,34	15,22	31,29	33,58	62,63
	D MW	192,25	449,52	35,03	57,34	227,29	506,86
	D HWS	46,54	101,30	14,27	20,03	60,80	121,33
						321,68	690,82

As pointed out by Gerlach (1978) it is not possible to estimate bacterial productivity from laboratory cultures as conditions are optimum, resulting in astronomical figures. In the field turnover rates are influenced by many parameters (Dale 1974), while interactions with larger fauna can stimulate productivity (Fenchel 1970, 1972; Lopez et al. 1977; Robertson, Mann 1980). At Kommetjie, a turnover of 70 times per year has been estimated on the basis of the conversion efficiency of available organics (Griffiths et al. 1983). However, as already mentioned, bacterial standing stocks at this locality have probably been underestimated and therefore this value should be reduced probably to the range of 30 to 40, which is close to that suggested by Gerlach (1978). To arrive at a conservative estimate of bacterial productivity, the $P/\bar{B}$ ratio of 30 was applied.

From the biomass and $P/\bar{B}$ ratios for each component of the biota annual production estimates have been calculated and are presented in Table 5. In contrast with the biomass figures, productivity estimates show that bacteria are of paramount importance, accounting for some 71% of productivity of the beach, while macrofauna and meiofauna contribute equally to the remaining productivity. The importance of bacteria would have been greater if samples penetrated beyond the depth of the water table and if kelp surfaces were analysed.

3.7. Trophic interrelationships of the fauna

At Kommetjie, the major part of the macrofaunal biomass is composed of primary consumers, which are responsible for 72% of the surface kelp lost

TABLE 4. The seasonal abundance (numbers x $10^{12} m^{-1}$) and biomass (g dry mass m^{-1}) of bacteria at different tide levels and sampling depths to the water table on Kommetjie beach, Cape Peninsula (see Table 2 for abbreviations and widths of the respective zones).

Season Sampled	Zone	0 - 30 Numbers	0 - 30 Biomass	30 - 60 Numbers	30 - 60 Biomass	60 - 90 Numbers	60 - 90 Biomass	Total Number	Total Biomass
Summer	N LWS	190,99	24,22					190,99	24,22
	D MW	217,42	14,09	726,01	47,12	239,52	19,08	1236,95	80,29
	O HWS	25,54	0,86	215,82	7,38	41,25	1,40	282,61	9,65
								1710,55	114,16
Autumn	N LWS	2010,04	540,36					2010,04	540,36
	D MW	6385,62	968,66	3328,56	504,95			9714,18	1463,61
	O HWS	1580,12	220,42	1779,96	248,26	2030,21	171,20	5390,29	639,88
								17114,51	2643,85
Winter	N LWS	760,62	52,27					760,62	52,27
	D MW	635,57	55,31	595,83	51,82			1231,40	107,13
	O HWS	1070,25	64,05	1117,19	66,91	750,33	44,93	2937,77	175,89
								4929,79	335,29
Spring	N LWS	1972,34	96,53					1972,34	96,53
	D MW	1080,49	196,24	1078,51	195,88			2159,00	392,11
	O HWS	1364,03	133,77	446,03	43,72	848,06	83,15	2658,12	260,64
								6789,46	749,28

via grazing and fragmentation (Griffiths, Stenton-Dozey 1981; Griffiths et al. 1983). The surface biota thus plays an important role in fragmenting whole kelp plants, thereby providing leachates and small organic particles to the interstitial fauna. As the dominant macro-faunal organisms, the amphipod *T. capensis* and larvae of the kelp fly *F. capensis* are characterised by low assimilation efficiencies (Muir 1977; Stenton-Dozey, Griffiths 1980), faeces production would greatly increase this input.

In contrast to the findings cited above, where macrofauna were responsible for most of the initial loss of kelp mass, Koop et al. (1982a) concluded from their microcosm study that bacteria degraded 90% of this material within eight days after stranding. However, this study took place in the absence of natural densities of macrofauna and meiofauna. The rôle of bacteria in the initial decomposition of kelp lying on an open beach is probably not as pronounced, their impact being shifted to the final degradation of kelp fragments.

Besides the rôle of decomposing kelp, bacteria probably constitute the major food source for the meiofauna, as detrital residues on their own provide a poor source of nitrogen and other essential minerals (McIntyre 1969; Fenchel 1970). There is evidence that this food source is supplemented by direct absorption of dissolved organic matter (eg. Chia, Warwick 1969; Meyer-Reil, Faubel 1980). In addition certain groups such as nematodes, turbellarians and acarines are

TABLE 5. The productivity of the components of the sandy beach biota at Kommetjie, Cape Peninsula, estimated from standing stocks and annual turnover rates.

	Mean annual standing stock (g dry mass m^{-1})	Annual turnover (P/B)	Annual production (g dry mass m^{-1})	Percentage of total production
Macrofauna	2256,97	2,5	5642,4	14,3
Meiofauna	623,62	10,0	6236,2	15,2
Bacteria	960,85	30,0	28819,5	70,4

predatory on other meiofauna (Giere 1975; Cox 1976).

Griffiths et al. (1983) have quantified the energy flow through the Kommetjie wrack ecosystem. On a qualitative basis, it appears that two isolated trophic levels are in existence, a feature noted in most intertidal sandy beaches (eg. McIntyre 1969; Gerlach 1971; McIntyre, Murison 1973). The macrofauna occupy a two dimensional environment, their stability being influenced by trophic interactions from within and by kelp supply and predation by birds from the outside. The infauna are relatively free from external factors and their only connection with the surface environment is related to the amount of nutrients arising from the wrack beds. The major impact of this isolated interstitial ecosystem on the economy of the beach is its consumption of organic carbon and production of waste products such as faeces and CO_2 and the remineralization of nitrogen and phosphorus. The beach appears therefore to act as an 'energy sink' which is fuelled by vast quantities of imported kelp and from which little is returned to the sea.

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