STRANDED KELP — ITS FAUNA AND INFLUENCE ON SANDY BEACH ENERGETICS

by

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CONTENTS

ABSTRACT

This thesis presents results of studies conducted on banks of kelp stranded on a sandy beach at Kommetjie on the west coast of the Cape Peninsula. The physical and chemical character of the beach are related to variations in the standing stocks and productivity of macro-, meio-fauna and bacteria as determined from a quantitative survey conducted on a monthly basis throughout 1981. Tracer experiments were carried out to establish the partitioning of dissolved organic matter between the different faunal elements (namely bacteria and meiofauna) present in the sand below decomposing kelp. Finally, a description of the flow of energy through the wrack bed ecosystem is given.

Chapter 2 presents results on the physical and chemical character of the beach. The following aspects were investigated: temperature regime, saturation of the sediment, the range in size of sand grains, changes in the depth of the water table during a tidal cycle, the intertidal distribution of interstitial nutrients, the average volume of sea water filtered into the beach and finally, an estimate of the quantity of kelp cast ashore within one year.

Ambient temperatures at midday ranged between 14°C in winter to 26°C in summer, whilst in the wrack bed and sand below, temperatures were slightly lower, between 13°C and 21°C. The sediment was most saturated (40-100%) 30cm from the surface at the swash zone at the time of low spring tide. Higher upshore maximum saturation was reached 30cm above the water table (9-80%) and at the surface at the HW mark, the sand was never more than 9% saturated. The median particle diameter of sand grains ranged between 266-286μm with very low phi quartile deviation and near zero skewness values.

During an entire spring tide cycle, the water table lay just below the surface between the swash zone and the middle of the beach. However, from here landwards, the water table dropped dramatically from an average depth of less than 1cm to 62cms. Fluctuations in the groundwater profile lagged behind the incoming tide by 1 hour and behind the receding tide by 4 hours.

The total volume of sea water filtered into the beach during a single spring tide was $3,02m^3\ m^{-1}\ d^{-1}$ and this input was concentrated between mid and high water. The total volume per tidal cycle was $1,56m^3\ m^{-1}$. The surf zone at Kommetjie is approximately 40m wide with an average depth of 0,16m giving a total volume of $6,4m^3$ per metre of shore. This means that at a filtered volume of $3,02m^3\ m^{-1}\ d^{-1}$, the whole surf zone would be filtered every second day.

The flow and ebb of a spring tide had no obvious influence on the tidal distribution of dissolved interstitial nutrients. Meaned data show wide standard deviations, emphasising the patchy distribution of nutrients. There was a marked concentration of inorganic nitrogen at the high water mark where kelp accumulated. Here, at a depth of 60cm, ammonia-nitrogen was 538,59µg-at. l^{-1}, nitrites 4,46µg-at. l^{-1} and nitrates 11211,94µg-at. l^{-1} while downshore concentrations dropped to less than 1% of that at HW. Silicates reached a maximum of 5,66µg-at. l^{-1}, 10m above the low tide mark and inorganic phosphates ranged from 3,76 to 10,06µg-at. l^{-1}. Dissolved organic carbon (DOC) and total carbon reached maximae of 33,33µg ml^{-1} and 86,5µg ml^{-1} respectively. The concentrations of inorganic nitrogen and DOC in interstitial water beneath decomposing kelp are far higher than values found in the water of offshore kelp beds, surf water and on sandy beaches devoid of wrack.

Maximum kelp deposition on Kommetjie beach occurred in winter (240kg wet mass m^{-1}) and the mean standing stock was 83,5kg m^{-1}. The total deposition rate was calculated as 2179kg wet mass $m^{-1}\ yr^{-1}$ based on an estimate of 14 days for the complete replacement of kelp on the beach.

Chapter 3 presents results on the numbers and biomass of organisms utilizing stranded kelp on the beach. A total of 35 macrofaunal species (4 amphipods, 2 isopods, 7 molluscs, 4 dipterans and 18 coleopterans) were recorded amongst drift kelp. The amphipod, Talorchestia capensis dominated for most of the year both in terms of numbers and biomass. Variations in macrofaunal biomass closely followed the pattern of kelp input, indicating that the fauna migrates to areas of maximal food deposition. There is a reversal of the usual vertical distribution pattern in intertidal habitats, in which diversity and biomass both increase towards the sea. Here the highest biomass and greatest species diversity is rather found at the driftline, and progressively declined downshore. This can be attributed to the terrestrial origin of most faunal elements and the concentration of food at the top of the beach.

The meiofauna was dominated by nematodes and oligochaetes, which were concentrated in the mid- and high-tidal levels, where kelp lay on the surface or was buried in the sand. It appears that meiofauna are concentrated in these areas because of the availability of dissolved and particulate organic matter they utilize as food. Bacterial biomass showed an inverse relationship to that of meiofauna, indicating possible grazing pressure.

The mean standing stock estimates for macrofauna, meiofauna and bacteria were 2257; 623; 961g dry mass m^{-1} of shoreline respectively, giving a biomass ratio of 3,6:1:1,5. Turnover rates suggest that bacteria may account for 71% of annual productivity, meiofauna 15% and macrofauna, 14%. Despite the energetic importance of bacteria, amphipods, followed by fly larvae, are the most important primary consumers of surface kelp. However, much of this kelp is returned to the sand as faeces, since both forms have low assimilation efficiencies. The input of faeces, together with the mechanical breakdown of kelp by grazers, presents a rich supply of suitable particles to meiofauna and bacteria for further mineralization. The separation of the epifauna and infauna trophic elements is discussed.

Chapter 4 presents data from tracer experiments in which undisturbed sand cores, containing natural populations of bacteria and meiofauna, were extracted from beneath decomposing kelp and incubated with D-(1-^{14}C)mannitol, a polyol and primary photosynthate of the two dominant species of kelp stranded. In terms of carbon values, an inverse tidal distribution exists between meiofauna and bacteria in the field, suggesting a close trophic interrelationship where meiofauna graze heavily on bacteria.

The above observation was supported by tracer experiments in that, as meiofaunal uptake of label increased, that of bacteria decreased. However, in the sand cores grazing by meiofauna did not decrease bacterial numbers, but rather stimulated the maintenance of a stable population. Although bacterial activity decreased, the overall retension of label by these microbes was three times that of meiofauna per gram dry mass at the end of a 24h incubation period. This indicates that bacteria play the major role in absorbing dissolved organic matter in the beach sediment.

The uptake rates of meiofauna increased as the concentration of ^{14}C-mannitol was raised from 1μl to 4μl ml^{-1} sea water. In addition, there was a distinct partitioning of labelled material between different meiofaunal groups. Oligochaetes displayed the highest activity, followed by nematodes and turbellarians. This resource partitioning is closely related to differences in nutrition, although essentially all three groups seem to ingest dissolved organic matter via bacteria.

Chapter 5 presents a final synthesis of information in this thesis and from other sources on high kelp-input beaches and compares the composition, biomass and distribution of the fauna and the energy flow pattern with those described for open sandy beaches devoid of wrack.

In terms of energy values, kelp input onto Kommetjie beach represented 4×10^6 kJ m^{-1} yr^{-1}. This material profoundly effects the composition, biomass and distribution pattern of the fauna. The macrofauna consists primarily of semi-terrestrial amphipods, kelp fly larvae and Coleoptera, that are concentrated around the driftline, plus some carnivores isopods at lower levels. Herbivorous macrofauna are thought to consume 71% of the kelp deposited and are preyed upon by birds, isopods and carnivorous Coleoptera that together take 63% of herbivore biomass, or 25% of production, annually.

The remaining kelp, plus the faeces and excretory products of the macrofauna, enter the sand column and support a bacterial standing crop of 961g m^{-1} (dry mass). The food supply to the bacteria is sufficient to allow a turnover rate of 70 times per annum. Assuming the meiofauna, which has a standing stock of 624g m^{-1}, feeds entirely on bacteria, it would consume 32 times the bacterial standing stock per annum. Most of the carbon entering the system is respired as CO_2, while the nitrogen may ultimately be returned to the sea. Unlike some beaches, that have been shown to generate their own surf zone phytoplankton blooms, these rely almost entirely on imported materials and play little role in returning nutrients to support production in adjoining aquatic systems.

The thesis ends with an Appendix listing data not included in the main text.

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CHAPTER 1

General Introduction

Approximately seventy percent of the southern African coastline consists of long stretches of exposed sandy beaches (McLachlan *et al*, 1981*a*) which lack vast off-shore kelp beds due to the instability of the sandy sea-bed. However, from Cape Algulhas on the south coast to Lüderitz on the west coast, rocky shores are a common feature and here the coastal waters support dense beds of macrophytes and the adjacent shores receive large quantities of stranded kelp.

The topography of the Cape Peninsula, in the south-western Cape, consists largely of geological series of Table Mountain Sandstone and Malmesbury Shale which extend subtidally and provide a stable platform for the attachment of macrophytes. On the west coast of this peninsula, kelp beds dominated by *Ecklonia maxima* and *Laminaria pallida* have been a focus of study for the past eight years. This work was initiated by an interest in harvesting kelp on a commercial basis to provide fertilizer and alginic acid, an emulsion stablizer used extensively in industry. However, before commencing this enterprise, it was necessary to investigate the effect harvesting could have on several commercially exploited populations which form part of the kelp bed system (such as the rock lobster, an industry with an annual revenue of R19 million, pers. comm., Fisheries Development Corporation). Over the years much information has been gathered on the primary production of these beds and the biology and ecology of resident fauna, culminating in a review by Newell *et al* (1982). One of the key questions which arose from this work was: What is the fate of exported kelp material which is stranded on the adjacent shore?

Koop and Field (1980, 1981) have investigated the fate of kelp washed onto rocks and found that most of this material is consumed by a single organism, the supralittoral isopod, *Ligia dilatata*. Recent studies on kelp stranded on small sandy beaches between rocky headlands have shown that here a far more complex system is in existence as the sandy environment necessitates a three-dimensional approach. Two of the main primary consumers of this stranded material have been investigated, principally the amphipod *Talorchestia capensis* (Muir, 1977) and larvae of the kelp fly, *Fucellia capensis* (Stenton-Dozey and 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- and micro-fauna and recently the fluxes in material arising from decomposing kelp have been investigated (Koop *et al*, 1982*a*, *b*).

However, there is no information on the seasonal fluctuations within the system or on the flow of energy through the different trophic groups. This thesis provides data on the seasonal variations in composition, distribution, abundance and biomass of the macro-, meio-fauna and bacteria and their relative contributions to the beach economy in terms of standing stocks, productivity and energy flow. The role of stranded kelp in a sandy beach ecosystem is emphasised by comparing the data with that available on east coast beaches where the main energy input is in the form of phytoplankton.

CHAPTER 2

Description of the physical and chemical character of a sandy beach receiving stranded kelp

INTRODUCTION

The west coast of the Cape Peninsula is characterised by vast offshore kelp beds dominated by Ecklonia maxima Osbeck and Laminaria pallida (Grev.) J. Arg., with small patches of Macrocystis angustifolia and many understorey algal species (see Field et al, 1980a). Much of this kelp is ultimately uprooted and stranded on the nearby coastline where large banks of wrack accumulate at irregular intervals on both rocky and sandy shores. One such stretch of coast is the Kommetjie area (34°08'S, 18°19'E) where sandy beaches are indispersed between rocky headlands of Table Mountain Sandstone. The shoreline is aligned almost south-west/north-east and is exposed to onshore swells from the South Atlantic. The particular sandy beach under study in this thesis (fig. 2.1), is bordered to the south by a 200m long rocky peninsula which extends subtidally to provide a platform for the attachment of large macrophytes.

Wherever the supply of stranded kelp is regular and consistent, a characteristic intertidal fauna exists which depends on this material as a primary food source. The rocky intertidal isopod, Ligia dilatata survives solely on kelp (Koop and Field, 1980, 1981), while on the sandy beaches the trophic interrelationships of the rich intertidal community depends mainly on wrack as a source of primary production (see Chapter 3).

To help qualify the biotic component of a sandy beach at Kommetjie, certain physical and chemical parameters were recorded during a year-long survey. This chapter presents data on the temperature regime, saturation of the sediment, the size range of sand grains, the average volume of sea water filtered into the beach, changes in the depth of the water table during a tidal cycle, and the intertidal distribution of dissolved nutrients. Finally monthly estimates are made on the quantity of kelp cash ashore at Kommetjie.

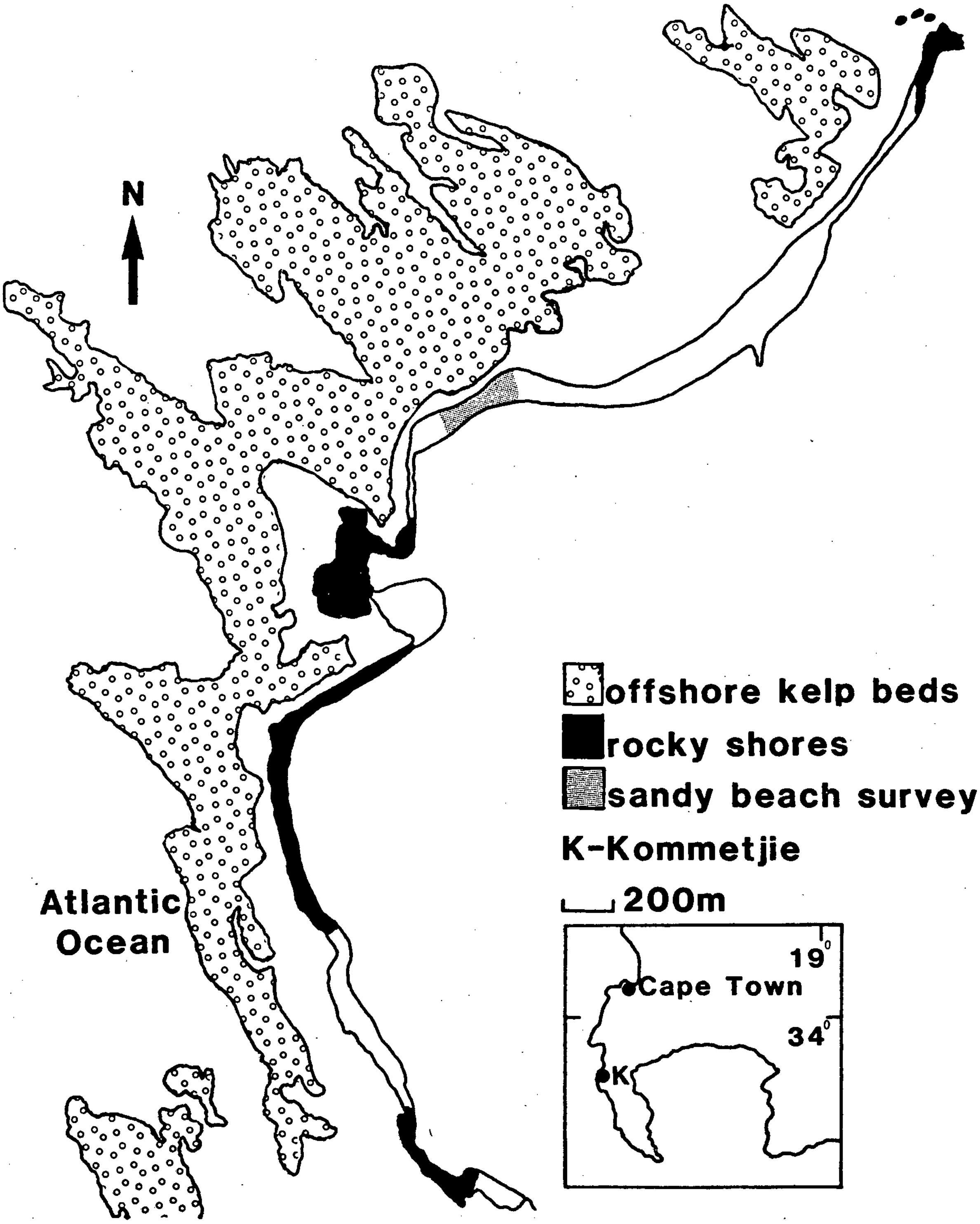


Fig. 2.1. The study area on a sandy beach at Kommetjie, Cape Peninsula, South Africa.

MATERIALS AND METHODS

Physical parameters

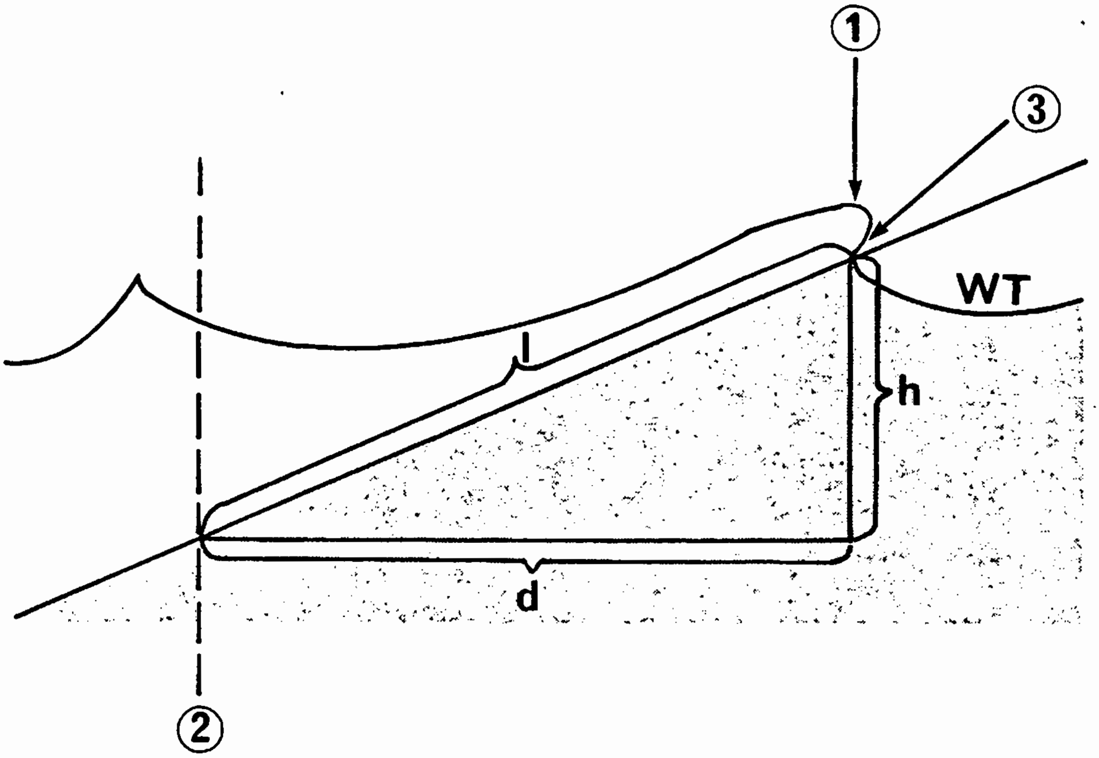
Each month, at the time of low spring tide, the noon temperature of the air, and under wrack banks, laying at LW, MW, and HW was taken. In addition, temperature and percentage saturation of the sand at 30cm depth intervals were measured whenever sampling the interstitial fauna. In determining the water content of the sediment, wet sand samples were weighed, dried at $60^{\circ}C$ for 4 days and then reweighed, the difference being expressed as a percentage of the maximum water loss (i.e. % saturation).

One set of dried sand samples was used to establish the size distribution of particles. The sediment from each tidal level and vertical depth, was passed through a series of sieves, ranging from coarse (2mm) to fine (212µm). Sub-samples thus separated were weighed and the cumulative percentage contribution from the coarse to fine size classes calculated. This plotted against phi values (McManus, 1963),provided information on median particle size (Md Ø), coefficient of sorting (QD Ø) and skewness (Skq Ø), (Morgans, 1956).

The volume of sea water filtered into the beach

This parameter was determined during a complete spring tidal cycle on 2/06/1981. The volume of sea water filtered through the beach was measured using the method of Riedl (1971) as modified by McLachlan (1979). This essentially involves measuring the volume of water flushed into the sand by a series of swashes at different points in the tidal cycle. Details of the methods used in the field are given by McLachlan (1979). Only the theory and mathematical interpretation of results are discussed here.

In theory, it is assumed that a wedge of unsaturated sand is completely filled with water from a single swash passing over it (fig. 2.2). The



①	edge of swash
②,③	old and new formed boundaries between saturated and unsaturated sand respectively
WT	water table
l,d,h	dimensions of the wedge shaped area of sand (FW) filled with water by the swash illustrated

Fig. 2.2. Diagrammatic representation of the filling, by an incoming swash, of a wedge of unsaturated sand positioned perpendicular to the shoreline on a sandy beach at Kommetjie, Cape Peninsula.

dimensions of the wedge, namely the distance the swash travels over the unsaturated sand (l) and the depth of the water table in this sand (h) are integrated with the amount of air space available for filling (termed the saturation gap (p(y))) to obtain the volume of water filtered. This relationship if expressed mathematically as follows:

$$\text{Total volume filled by a wedge forming swash} = \int_0^l \int_0^{hx/l} p(y)\,dy\,dx$$

(McLachlan , 1979)

where l = length of wedge forming swash

h = initial depth of the water table below the sand surface at the highest point of the swash

p(y) = (% saturation gap above the water-table)/$_{100}$

d = the base of the wedge along the initial water-table (d is assumed to equal l).

and the width of the wedge is taken as 1m.

The above double integration was computerised (Programme I, Appendix A) and the volume of water filtered through the beach expressed as cubic metres per metre of shoreline per hour. The total volume for one tidal cycle was obtained by integration using linear interpolation as shown in Programme II (Appendix A).

Beach profile

On the 3/06/1981, the depth of the water table was recorded each hour at 10m intervals up the shore. The beach slope was measured from the low tide mark to the highest swash line according to the method of Day (1969). A 3-dimensional diagram was then plotted relating changes in the depth of water table to time and tidal height.

Interstitial nutrients

Interstitial water samples were collected each hour at 10m tidal intervals to depths of 30cms to the water table during the spring tidal cycle of 3/06/1981. Two 20ml samples were extracted from each site using a stainless steel needle, 30cm in length and with an internal diameter of 3mm. The last 3cms of the needle were perforated with a series of 0,5mm diameter holes while at the opposite end, a 20ml syringe with a plunger was fitted to withdraw samples.

The interstitial water was filtered through 25mm Whatman GF/C filters and the filtrate frozen prior to analysis. Samples were analysed for ammonia (NH_4^{4+}-N), nitrite (NO_2^--N), nitrate (NO_3^--N), phosphate (PO_4^{3-}-P) and silicates (SiO^{4-}-Si) on a Technicon AutoAnalyser II. The results were expressed in μg -at. l^{-1} (=μmole l^{-1}). The analytical procedures are summarised in Table 2.1, together with the standards used.

In addition to the above nutrients, samples were analysed for the presence of DOC (dissolved organic carbon). An automated method, suitable for use on the Technicon AutoAnalyser II recently developed at the Sea Fisheries Institute and described by Mostert (1983) was followed. Briefly the method involves the oxidation of both organic and inorganic carbon compounds (i.e. total carbon) to carbon dioxide, using a solution of potassium persulphate and a low frequency ultra-violet light source. In a separate treatment the inorganic carbon fraction is oxidised to carbon dioxide using sulphuric acid. Carbon dioxide diffuses through a gas-permeable membrane into a highly coloured, weakly buffered phenolphthalein solution, which is proportionally discoloured and measured by inverse colourimetry. DOC (μg ml^{-1}) is found using the difference in total and inorganic carbon concentrations.

The total carbon standard used consists of 30mg oxalic acid and 30mg sodium carbonate made up to 1 litre with artificial sea water. The inorganic carbon standard consists solely of 30mg sodium carbonate l^{-1}.

Table 2.1 Summary of the methods for analysis of nutrients in sea water (see Stickland and Parsons, 1972; Grasshoff, 1976).

Nutrient	Method	Standard
NH_4^{4+}-N	reacts in alkaline medium with hypochlorite to form monochloramine which in presence of phenol and suitable catalyst (e.g. nitroprusside), yields indophenol blue read at 630nm	2 μg -at.l^{-1} ammonium sulphate in N- free water
NO_3^--N	conversion to nitrite using copper-cadmium reduction column - reacts with sulphanilamide to form diazo compound which couples with a diamine complex to form a red azo dye read at 520nm	15 μg -at.l^{-1} potassium nitrate in N- free water
NO_2^--N	as for nitrates, but without the reduction process	as for nitrates
PO_4^{3-}-P	reacts with molybdate reagent to form heteropoly-acid:- this is reduced to molybdenum - blue complex using ascorbic acid: interference from dissolved silicate avoided by maintaining pH below 1,0; absorbance measured at 660nm	1,5 μg-at.l^{-1} potassium dihydrogen phosphate in artificial sea water using ARISTAR (Merck) grade NaC1
SiO_4^{4-}-Si	silicomolybdic acid formed by similar reaction to one above; read at same frequency; interference from dissolved phosphates avoided by maintaining pH at 2,0	25 μg-at.l^{-1} sodium silicofluoride in artificial sea water made up using ARISTAR (Merck) grade NaC1

Collection of kelp

To establish the quantity of kelp cast ashore at Kommetjie during one year, monthly samples of fresh material in the process of being deposited at the swash line were collected at the time of low spring tide. Five random 1m^2 quadrants were removed from a large area, (a 300m stretch of beach) to compensate for patchy deposition. Each quadrant was wet weighed in the field. The mean weight times 300m was then regarded to represent the total quantity of fresh kelp present on the day of sampling. This value, expressed per running metre of beach, was later increased by an estimated rate for the total replacement of stranded kelp in order to reach a monthly figure.

RESULTS AND DISCUSSION

Temperatures

During the monthly visits to the study site, air temperatures varied from 26°C in January to 14°C in July with a mean of 19°C (Table 2.2). The temperature range in the wrack beds was lower, with a maximum of 21°C in summer and a minimum of 12,7°C in winter. The old, dried kelp piles lying upshore generally retained higher temperatures than those further downshore (see Appendix B). Temperatures in the sand column ranged between 13,3°C to 20,8°C during the year and little difference occurred with depth (Appendix B).

Water content of the sand

At the time of low spring tide, the sand was most saturated 30cm below the surface in the lower intertidal area (40 - 100%), thus illustrating the direct influence of the incoming waves on the water gradient here (Table2.3). Higher upshore the water from the previous tide has drained through the interstices and therefore maximum saturation was reached 30cm above the water table (33,4 - 79,8% at MW and 9,0 - 35,7% at HWS). At MW the deep wrack piles aid in retaining moisture in the surface layers of the sediment, while at HWS the thinly dispersed, dried wrack affords little protection and thus

Table 2.2 Mean monthly fluctuations in the temperatures of the air, in wrack banks and in the sand at Kommetjie beach, Cape Peninsula, during 1981. (See Appendix B for original data).

x = mean of temperatures measured in wrack at 3 tidal heights (n = 3).

+ = mean of temperatures measured in sand at 30cm depth intervals to the water table at 3 tidal heights (n = 6).

Month	Temperature (°C) at midday		
	ambient	in wrack x	in sand +
January	26,0	21,0	19,5
February	21,0	22,3	20,8
March	25,0	23,3	-
April	24,0	20,0	19,3
May	24,0	16,0	16,0
June	17,0	12,7	-
July	14,0	12,7	13,3
August	16,0	14,0	13,3
September	15,0	13,0	-
October	16,0	19,0	18,3
November	18,0	22,7	18,5
December	17,0	22,3	-

Table 2.3 Fluctuations in the water content (% saturation) of sand at different tide levels and vertical depths on Kommetjie beach, Cape Peninsula, during low spring tides.

Month	Tide level	% saturation of sand at 30cm depth intervals to the water table		
		0 - 30	30 - 60	60 - 90
January	LWS	67,4	48,7	
	MW	39,8	43,0	
	HWS	5,7	9,0	
February	LWS	40,2		
	MW	27,8	42,3	39,6
	HWS	1,3	27,2	35,5
April	LWS	60,9	54,7	
	MW	44,0	79,8	
	HWS	9,4	19,6	
May	LWS	64,0		
	MW	41,3	47,9	
	HWS	6,8	23,0	30,2
July	LWS	100,0	43,0	
	MW	31,3	44,3	
	HWS	9,4	29,4	
August	LWS	44,5		
	MW	37,2	34,9	
	HWS	13,2	20,2	35,7
October	LWS	83,6	42,8	
	MW	20,9	33,4	
	HWS	7,0	30,0	
November	LWS	41,1		
	MW	31,1	41,7	
	HWS	7,9	12,1	24,3

a saturation level of 9,4% was never exceeded.

Water table

Changes in the depth of the water table as a function of distance upshore (0 - 40m) and time (each hour within a spring tide cycle) are illustrated in figs. 2.3(a) and (b) as a 3-dimensional and corresponding contour plot respectively. Between the swash zone and the middle of the beach, 20 metres upshore, the sand was saturated just below the surface during the entire tide cycle (fig.2.3(a)). However, within the next 20 metres landwards, the water table dropped dramatically from an average depth of less than 1cm to 62cms (fig.2.3(b)). This change may be attributed to the steeper beach slope of 1/12 between the 20m and 40m stations as compared to 1/19 lower down the shore.

On the day measurements were taken (3/06/1981), early low tide was at 10.00h, high tide at 16.00h and the late low at 22.00h, four hours after the last data were recorded. At the uppermost station (40m), the peak water table level (32cm from surface) lagged behind tidal high water by one hour, while the water table low (77cm) lagged three to four hours behind early low tide (fig 2.3(b)). Lag periods decreased with distance downshore of the high water mark. The elevation of the groundwater profile is thus out of phase with the oceanic tidal flow.

A similar observation as above was made by Lanyon et al (1982) on sandy beaches in Australia using time-series curves and they suggested a reason for the assymmetrical change in the depth of the water table with tidal flow. As the tide rises, swash wave inundation of the unsaturated sand increases in frequency and in proportion with the groundwater recharge. However, on the falling tide the water-table is in an effluent state and fewer swashes inundate the unsaturated sand. This is supported by data collected when estimating the volume of sea water filtered

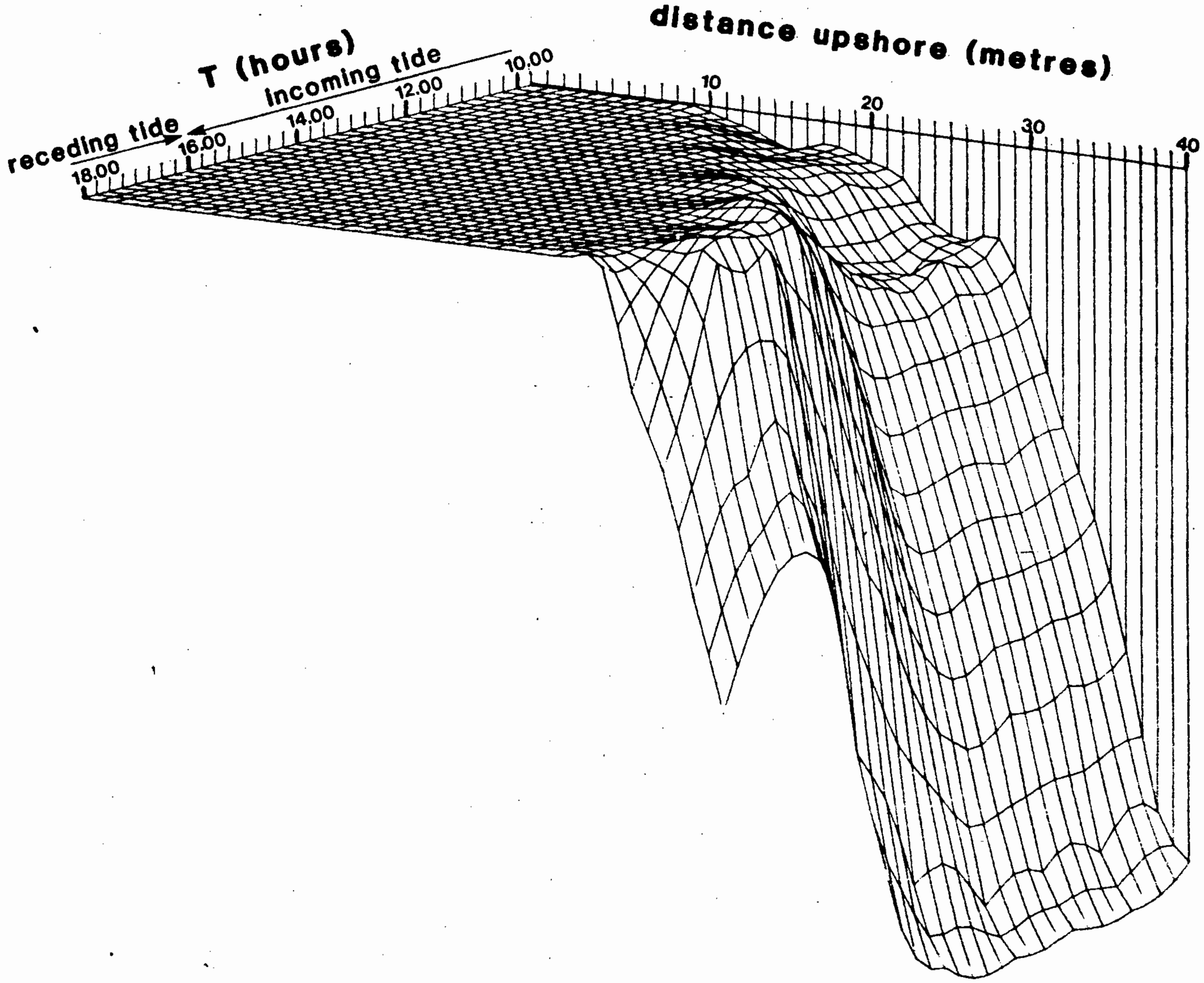


Fig. 2.3(a). A three-dimensional view of changes in the depth of the water table as a function of time and distance upshore at Kommetjie beach, Cape Peninsula.

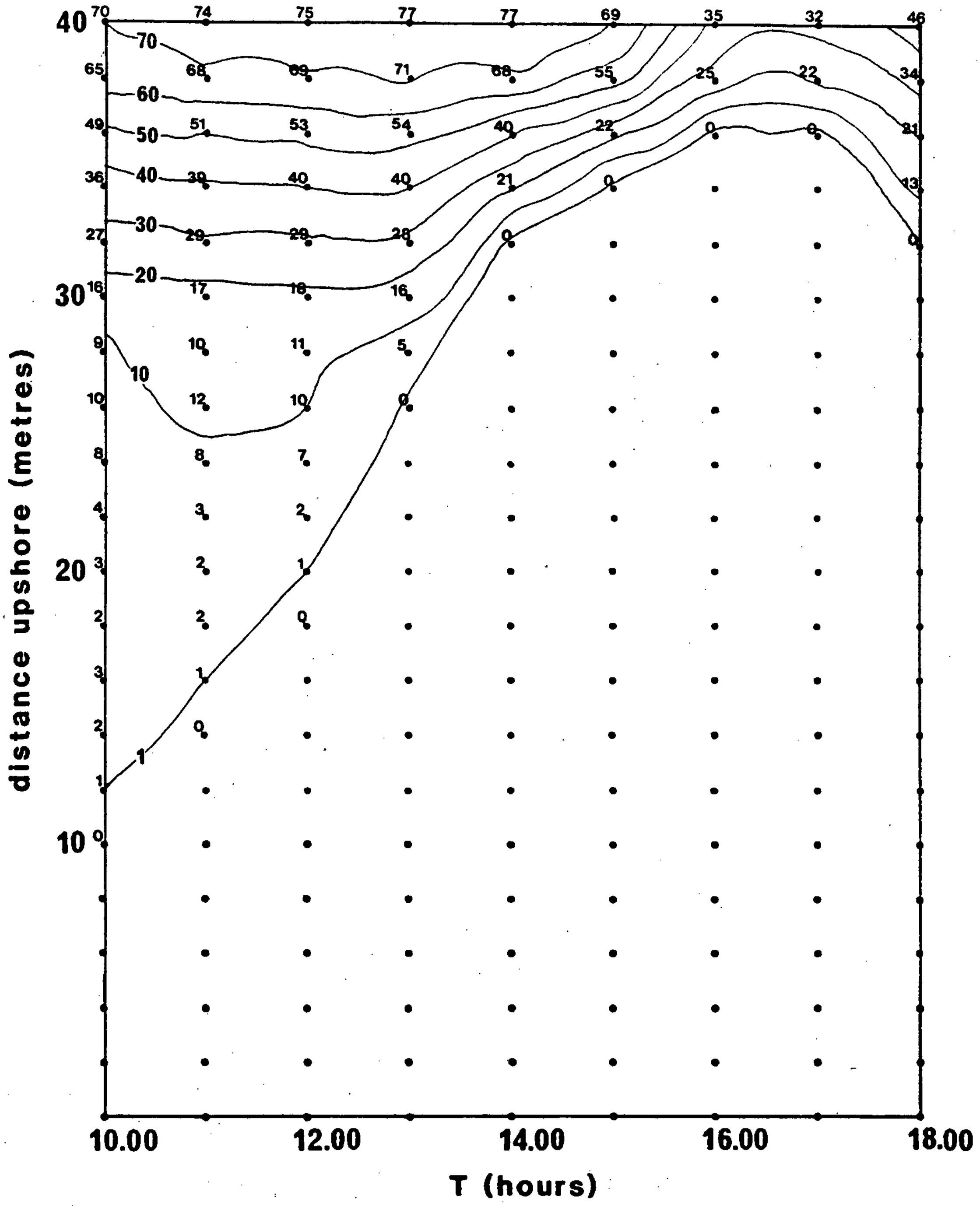


Fig. 2.3(b). Corresponding contour plot of fig.2.3(a) illustrating the depth of the water table in cms. as a function of time and distance upshore on Kommetjie beach, Cape Peninsula.

through Kommetjie beach (see Table 2.5). Here, the number of wave swashes passing over unsaturated sand on the incoming tide far exceeded the frequency on the outgoing tide.

Sediment characteristics

The median particle diameters of sand grains lying at all tidal levels to the depth of the water table were very similar, ranging from 266 to 286µm (Table 2.4). This falls in the category of medium sized grains (500 - 250µm or 1-2Ø) (McLachlan, 1977a). Very low phi quartile deviation (Qd Ø) and near zero skewness (Skq Ø) values indicate that for the entire beach a high proportion of the particles fell in a narrow range around the median and that there was equal sorting of particles both larger and smaller than the median. As there is good mixing of sand grains throughout, Kommetjie beach can be regarded as exposed (Cox, 1976).

The range of grain size does not preclude the existence of true interstitial life, as the values are far above the barrier of 200µm postulated by Wieser (1959) to separate burrowing forms from true interstitial meiofauna. Other authors suggest different limits. McIntyre and Murison (1973) suggested an optimum particle diameter of 230µm, while Hulings and Gray (1976) noted that an interstitial fauna can be found in sand with median particle diameters of 125 - 500µm.

The volume of sea water filtered into the beach

The saturation gaps in the beach sand at Kommetjie were given by the following linear regression:

$$\text{saturation gap (\%)} = 0{,}007h + 0{,}0017 \quad (r = 0{,}76;\ p < {,}01; 7\ \text{d.f.})$$

This showed that the saturation gaps ranged between 15-39% from 20cm above the water table to the surface whilst pore spaces were saturated just above the water table (0,02 - 2%).

Table 2.4 The horizontal and vertical distribution of different sized sand particles on Kommetjie beach, Cape Peninsula.

(Md μm = median particle diameter in μm; Md Ø = mean particle diameter in phi values; Qd Ø = sorting coefficient; Skq Ø = skewness)

Tide level	Depth into sediment (cms.)	Particle diameter			
		Md μm	Md Ø	Qd Ø	Skq Ø
LWS	0 - 30	280	1,85	0,25	0,00
	30 - 60	280	1,85	0,25	0,00
MW	0 - 30	268	1,92	0,23	0,00
	30 - 60	268	1,92	0,21	-0,06
	60 - 90	286	1,83	0,23	0,00
HWS	0 - 30	266	1,95	0,18	-0,03
	30 - 60	286	1,83	0,19	0,01
	60 - 90	285	1,82	0,18	-0,03

Table 2.5 follows the layout in McLachlan (1979) and presents results obtained during a day's observations of a spring tide. It can be seen that the frequency and dimensions of the wedges increase from a minimum on the incoming tide to a maximum before high tide. The greatest input of sea water ($0{,}8m^3m^{-1}hr^{-1}$) is thus on the late incoming tide and this coincides with the highest frequency in swashes (16,98 second intervals). The total input for the spring tide ($3{,}02\ m^3m^{-1}d^{-1}$) was concentrated between mid and high water, a distance of 20 - 35m. The total volume per tidal cycle was $1{,}56m^3m^{-1}$.

The surf zone at Kommetjie is approximately 40m wide with an average depth of 0,16m giving a total volume of $6{,}4m^3$ per metre of shore. This means that at a filtered volume of $3{,}02m^3m^{-1}d^{-1}$, the whole surf zone would be filtered every second day.

In deriving the volume of sea water filtered through Kommetjie beach, a number of points should be noted:

1) the values recorded are minimum, as the bottom of a wedge is often not straight as assumed in the calculations, but hollow (Riedl, 1971);
2) no allowance is made for small volumes of water pumped through saturated sand by the pressure of the waves (Riedl _et al_, 1972);
3) not all wedges considered in the calculations were necessarily filled with water by an incoming swash;
4) as measurements were taken when the tidal range was the greatest (spring tide) the volume filtered per day is greater than it would be at neap tides.

McLachlan (1979) estimated an average volume of $10m^3m^{-1}d^{-1}$ filtered through eastern Cape beaches with slopes between 1/20 and 1/29, mean wave heights of 1 - 1,2m and swash periods of about 16 - 25 seconds. Here the range in the volumes filtered per tidal cycle measured during spring tides was 3,73 -

Table 2.5 Summary of readings of frequencies, lengths (mean = $\bar{l}$) and heights (mean = $\bar{h}$) of wedge-forming swashes on Kommetjie beach during a spring tide on 2.06.1981, with the resultant volume of sea water (m^3) filtered through a 1m stretch of beach per hour. Readings were taken over 15mins., within each hour.

O = outgoing; I = incoming; E = early; M = mid; L = late.

Time start :	09h15	10h15	11h15	12h15	13h15	14h15	15h15	16h15	17h15	18h15	19h15
Time end :	09h30	10h30	11h30	12h30	13h30	14h30	15h30	16h30	17h30	18h30	19h30
Tide :	Low	EI	EI	MI	LI	LI	High	EO	MO	LO	LO
Number :	0	0	11	14	48	53	13	9	21	0	0
$\bar{l}$ (m) :	0	0	1,57	1,15	2,34	1,17	2,35	1,06	1,07	0	0
$\bar{h}$ (cm) :	0	0	3	16	40	63	23	15	12	0	0
Volume m^3 $hr^{-1}m^{-1}$:	0	0	0,0004	0,0141	0,4965	0,8045	0,0909	0,0443	0,0262	0	0

$5,43m^3m^{-1}$. At Kommetjie beach, with a steeper beach slope (1/15) and a mean wave height of 2m, the range in the time between swashes was far greater (17 secs. - 2 mins.), resulting in a lower volume input. This reduction in the number of swashes reaching the beach may be the result of the buffering effect of the offshore kelp beds and kelp debris in the surf. Inshore swells were often reduced from 2m to less than 0,5m before reaching the shore (pers. obs.). The Cape east coast lacks large kelp beds and hence no barrier exists between the shore and oceanic swells.

In considering the factors influencing filtration volumes on three Cape east coast beaches with difference physical properties, it was concluded that maximum input would be on a very exposed, steep beach of coarse sand with a narrow surf zone and high wave frequency during a stormy equinox spring tide (McLachlan, 1979). Under these conditions values may exceed $20m^3m^{-1}d^{-1}$. In relation to these characteristics, Kommetjie beach represents an environment with moderate physical properties, but the impact of the kelp beds on the expected input volume must also be considered as an influencing factor here.

Interstitial nutrients

In the initial sampling programme, the aim was to determine any influence tidal rhythm may have on nutrient concentrations in the sand column. Thus samples of interstitial water were extracted at hourly intervals during one tidal cycle. Unfortunately no pattern emerged and data were meaned for each site. This resulted in large standard deviations (Table 2.6), which indicate patchy distribution of nutrients in the interstitial environment of a beach covered with wrack. As kelp decays, pockets of organic material become buried in the sand and here bacterial activity creates irregular concentrations of the by-products of decomposition. The incoming and outgoing tide obviously had little effect in dispersing this material through the sediment.

Table 2.6 The horizontal and vertical distribution of interstitial nutrients on Kommetjie beach, Cape Peninsula. The results are meaned for samples extractd each hour during the spring tide cycle of June, 1981.

( ) = standard deviation from the mean

n = number of samples

vertical penetration of samples (cms) at 10cm intervals upshore

Nutrient	00	10	20		30		40		
	0-30	0-30	0-30	30-60	0-30	30-60	0-30	30-60	60-90
NH_4^{4+}-N	25,71	34,12	110,56	9,5	27,8	13,17	6,47	285,55	538,59
µg -at. l^{-1}	-	(29,74)	(84,74)	(9,6)	(20,19)	(8,35)	(2,79)	(251,61)	(190,8)
	n = 1	n = 2	n = 4	n = 3	n = 6	n = 6	n = 6	n = 6	n = 6
NO_2^--N	0,3	0,20	0,20	0,15	0,20	0,19	0,29	3,99	4,46
µg -at. l^{-1}	-	(0,03)	(0,17)	(0,06)	(0,06)	(0,16)	(0,12)	(2,86)	(2,38)
	n = 1	n = 2	n = 4	n = 3	n = 6	n = 6	n = 6	n = 6	n = 6
NO_3^--N	0,63	0,87	0,87	1,16	1,12	1,43	73,97	208,34	1211,94
µg -at. l^{-1}	-	(0,34)	(0,35)	(0,79)	(0,68)	(1,32)	(61,49)	(155,92)	(1351,85)
	n = 1	n = 2	n = 4	n = 3	n = 6	n = 6	n = 6	n = 6	n = 6
PO_4^{3-}-P	5,31	6,93	10,06	3,38	4,05	3,76	6,35	5,06	5,15
µg -at. l^{-1}	-	(6,77)	(3,69)	(1,07)	(1,52)	(2,19)	(1,25)	(2,71)	(2,27)
	n = 1	n = 2	n = 3	n = 3	n = 6	n = 6	n = 6	n = 6	n = 6
SiO_4^{4-}-Si	4,55	5,66	5,48	3,75	3,77	3,63	4,21	2,87	2,52
µg-at. l^{-1}	-	(2,04)	(1,24)	(o,59)	(0,51)	(0,96)	(0,66)	(0,90)	(0,46)
	n = 1	n = 2	n = 4	n = 3	n = 6	n = 6	n = 6	n = 6	n = 6

Contd.../

Table 2.6 continued

Nutrient	vertical penetration of samples (cms) at 10cm intervals upshore								
DOC	15,1	2,1	12,55	6,83	16,83	11,08	5,63	13,22	33,33
µg ml^{-1}	-	(2,97)	(11,33)	(3,87)	(15,48)	(20,34)	(4,56)	(7,48)	(13,21)
	n = 1	n = 2	n = 4	n = 3	n = 6	n = 6	n = 6	n = 6	n = 6
Total carbon	53,2	35,35	86,50	47,30	60,58	44,43	39,78	48,9	71,82
µg ml^{-1}	-	(11,95)	(34,57)	(6,85)	(21,97)	(25,02)	(5,64)	(7,64)	(15,52)
	n = 1	n = 2	n = 4	n = 3	n = 6	n = 6	n = 6	n = 6	n = 6

Nevertheless a clear pattern was observed in the intertidal distribution of the nutrients (Table 2.6). The most remarkable feature was the great concentration of all forms of inorganic nitrogen at the high tide mark (40m station), especially at depths below 60cm. Here ammonia-nitrogen reached a mean value of 538µg-at.l^{-1}, nitrites 4,46µg-at.l^{-1} and nitrates 1211,94µg-at.l^{-1}, while downshore concentrations dropped to less than 1% of that at HWS. From the 30m station seawards, nitrite levels remained relatively constant and no vertical gradient was observed. Nitrates, however, gradually declined downshore, although at each sampling site there was a slight increase with depth into the sand column. By contrast, concentrations of ammonia-nitrogen showed marked tidal variations. After a dramatic decline from the uppermost station to the next site 10m seawards, levels increased before declining once again towards the swash zone. Generally concentrations were highest 30cm from the surface, the inverse of the vertical gradient at HWS.

The concentration of dissolved organic carbon (DOC) followed a similar vertical and horizontal distribution as observed for ammonia-nitrogen and nitrate, although the the maximum, 33,33µg ml^{-1}, reached 60 - 90cm below the surface at HWS, was not so dramatically different from concentrations lower down the beach. The values for total carbon were similar at all tide levels, (35,35 - 86,50µg ml^{-1}), decreasing with depth except at HWS when, like DOC and inorganic nitrogen concentrations, there was an increase.

Silicates reached a maximum of 5,66µg-at.l^{-1}, 10m above the low tide mark and thereafter concentrations generally declined to HWS. Inorganic phosphates ranged from 3,76 to 10,06µg-at.l^{-1}. Values declined slightly with depth but no clear tidal distribution was observed.

At the time of sampling, the largest accumulations of stranded kelp were at the high tide mark (i.e. 40m station in Table 2.6). This coincides with the high levels of inorganic nitrogen and DOC recorded here and thus indicates the release of leachates from decomposing kelp at the surface. Koop et al (1982a) conducted a microcosm experiment at Kommetjie and found that total carbon can reach 5640 μg ml^{-1} directly below the decomposing kelp. Since no such concentration was recorded in this study, it appears that nearly all the carbon percolating from the surface is rapidly utilized by the interstitial fauna. Further, the marked increase in the concentrations of DOC and inorganic nitrogen with depth at HWS suggests that most of the leachates are utilized in the first 60cm of the sediment and that below this depth, there is an accumulation of both inorganic and organic material. Since nitrite and nitrate levels were exceptionally high here, it is evident that nitrifying bacteria can still oxidise ammonia-nitrogen. The accumulation of nutrients,especially nitrates, below 60cm may also be due to the scarcity of meiofauna (Koop and Griffiths, 1982) which are known to directly absorb dissolved matter (e.g. Chia and Warwick, 1969; Meyer-Reil and Faubel, 1980).

The high concentrations of inorganic nitrogen and DOC in interstitial water beneath decomposing kelp are in marked contrast to values found in kelp beds or oceanic water, surf water, and on sandy beaches devoid of wrack (see Table 2.7). Carter (1983) reports maximal values of 5 μg-at.l^{-1} for ammonia-nitrogen and 22 μg-at.l^{-1} for nitrates in kelp bed water during periods of upswelling on the west coast of the Cape Peninsula. Here,DOC levels reach 22 μg ml^{-1} when strong wave action fragments kelp fronds and subside to less than 1 μg ml^{-1} with the onset of calmer weather.

Low inorganic nitrogen concentrations were also observed in the surf and interstitial waters of some Cape south and west coast beaches and while values from the Natal coast were slightly higher, even these are not equal to the maximae at Kommetjie. Phosphate concentrations on these beaches and in off-shore kelp beds are similar to those at Kommetjie, whereas the silicates reach higher levels. Since the beaches presented in Table 2.7 receive offshore and surf phytoplankton as a nutrient source, the higher levels of silicates

Table 2.7 A comparison of the range of nutrients found associated with oceanic water and intertidal habitats on sandy beaches devoid of wrack. Standard deviations, when presented, are given in brackets.

		Nutrient range (minimae, maximae, mean and SD)						
Locality		NH_4^{4+}-N µg-at. l^{-1}	NO_2^--N µg-at. l^{-1}	NO_3^--N µg-at. l^{-1}	PO_4^{3-}-P µg-at. l^{-1}	SiO_4^{4-}-Si µg-at. l^{-1}	DOC µg ml^{-1}	Literature Source
SOUTH AFRICA								
Oudekraal (west coast)	oceanic water	1,6 - 5,1		0,7 - 21,9	0,6 - 5,2	2,0 - 22,1	0,1 - 22,0	Carter, 1983
10 Cape west coast beaches	surf water		0,3 (0,2)	11,7 (4,4)	1,7 (0,4)	13,6 (6,0)		Orren *et al*, 1981
	interstitial water		0,2 (0,1)	10,4 (8,7)	7,6 (5,7)	23,3 (17,2)		
10 Cape south coast beaches	surf water		0,2 (0,2)	5,8 (3,0)	1,2 (0,6)	5,2 (2,5)		
	interstitial water		0,2 (0,2)	27,7 (19,8)	3,2 (1,5)	18,3 (10,5)		
Brighton beach, Natal coast	surf water	54,0 (24,0)	3,9 (1,7)	33,0 (20,0)				Oliff *et al*, 1970
	interstitial water	56,0 (44,0)	2,8 (1,9)	72,0 (72,0)				
ENGLAND								
Llanddona beach	seawater	5,7 (9,2)	0,3 (0,2)	5,2 (5,3)	0,8 (0,2)			Pugh *et al*, 1974
	water table pool	7,9 - 70,9 (3,6 - 23,4)	0,1 - 0,6 (0,1 - 0,6)	0,6 - 3,3 (0,4 - 2,4)	0,5 - 3,5 (0,3 - 2,5)			
Newborough beach	seawater	2,6 (3,6)	0,1 (0,1)	3,5 (3,3)	0,6 (0,3)			
	water table pool	3,7 - 15,0 (5,2 - 9,9)	0,1 - 0,9 (0,1 - 1,3)	1,6 - 20,2 (2,0 - 9,4)	1,1 - 1,8 (0,2 - 0,4)			

may arise from the frustule remains of diatoms.

Included in Table 2.7 are examples of two clean sandy beaches in Anglesey, England (Pugh et al, 1974). The values recorded here show that even on a worldwide scale, the concentrations of inorganic nutrients on beaches which receive no kelp are all within the same order of magnitude. This further illustrates the impact that decaying wrack has on enhancing interstitial nutrient concentrations at Kommetjie. In Chapter 3 it will be seen that this in turn supports a very rich biomass of meiofauna and bacteria.

Kelp deposition

In attempting to determine the quantity of kelp cast ashore at Kommetjie during the course of one year, an estimate of turnover rates is required. Koop and Field (1980) and Koop et al (1982a) estimated an eight day cycle of replacement, in which period approximately 80% of 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.

Maximum kelp deposition occurred in winter (Table 2.8), a feature common along the Cape west coast (Muir, 1977; Koop and Field, 1980) when large offshore swells and onshore winds uproot whole plants and drive them ashore. The mean standing stock calculated from Table 2.8 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 and Field, 1980). The offshore kelp bed at Kommetjie is approximately 700ha in area (Koop et al, 1982a). It has a standing stock of 23030 tonnes of Ecklonia maxima and 17248 tonnes of Laminaria pallida (Field et al, 1980a) of which 10% (Simons and Jarman, 1981) and 15% (Jarman, pers. comm.[x]) respectively may be exported annually to the adjacent 3km shore. This represents 4890 tonnes of stranded kelp or 1630 m^{-1} yr^{-1}. This value is also similar to that recorded above and supports the estimate of turnover time.

Table 2.8 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 during 1981.

Months	Mass of kelp (kg m^{-1})
January	36
February	80
March	184
April	43
May	78
June	240
July	116
August	38
September	19
October	76
November	38
December	55

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[x] N.G. Jarman, Seaweed Laboratory, Sea Fisheries Institute, Sea Point, South Africa.

CHAPTER 3

A year-long survey of the fauna associated with stranded kelp on a sandy beach

INTRODUCTION

Seventy percent of the southern African coastline consists of sandy beaches (McLachlan *et al*, 1981*a*), but these received little attention until Brown's publications (1964, 1971*a,b*) on the general ecology of beaches around the Cape Peninsula. Since then McLachlan (1977*a-c*, 1980), Dye (1979), McLachlan *et al* 1979, 1981*a,b*), Dye *et al* (1981) and Woolridge *et al* (1981) have investigated the physical parameters and fauna of eastern and southern coast beaches and Bally (1981), those of 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 ecologial energetics of consumer organisms inhabiting these beds. Some of the uprooted kelp plants are stranded on nearby shores, providing a rich source of energy for the intertidal fauna. One particular area along this coastline, Kommetjie, has been a focus of study for the past few years. Several of the primary consumers of stranded kelp have been investigated, principally the amphipod *Talorchestia capensis* (Muir, 1977), the isopod *Ligia dilatata* (Koop and Field 1980, 1981) and larvae of the kelp fly *Fucellia capensis* (Stenton-Dozey and 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 have been investigated (Koop *et al.* 1981*a*,*b*).

This chapter 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.

MATERIALS AND METHODS

Beach zonation

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 (see Plate 3.1). 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.

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 via a stoppered inlet and left for 10 minutes before kelp and sand to a depth of 15cm were transferred to plastic bags (see Plate 3.2). Samples from each zone were pooled and the fauna indentified to species, counted and oven dried at 60^{0}C and then ashed at 460^{0}C for 5 hours to establish ash free dry mass (AFDM). A table of the mean individual dry mass of common species is given in Appendix D.

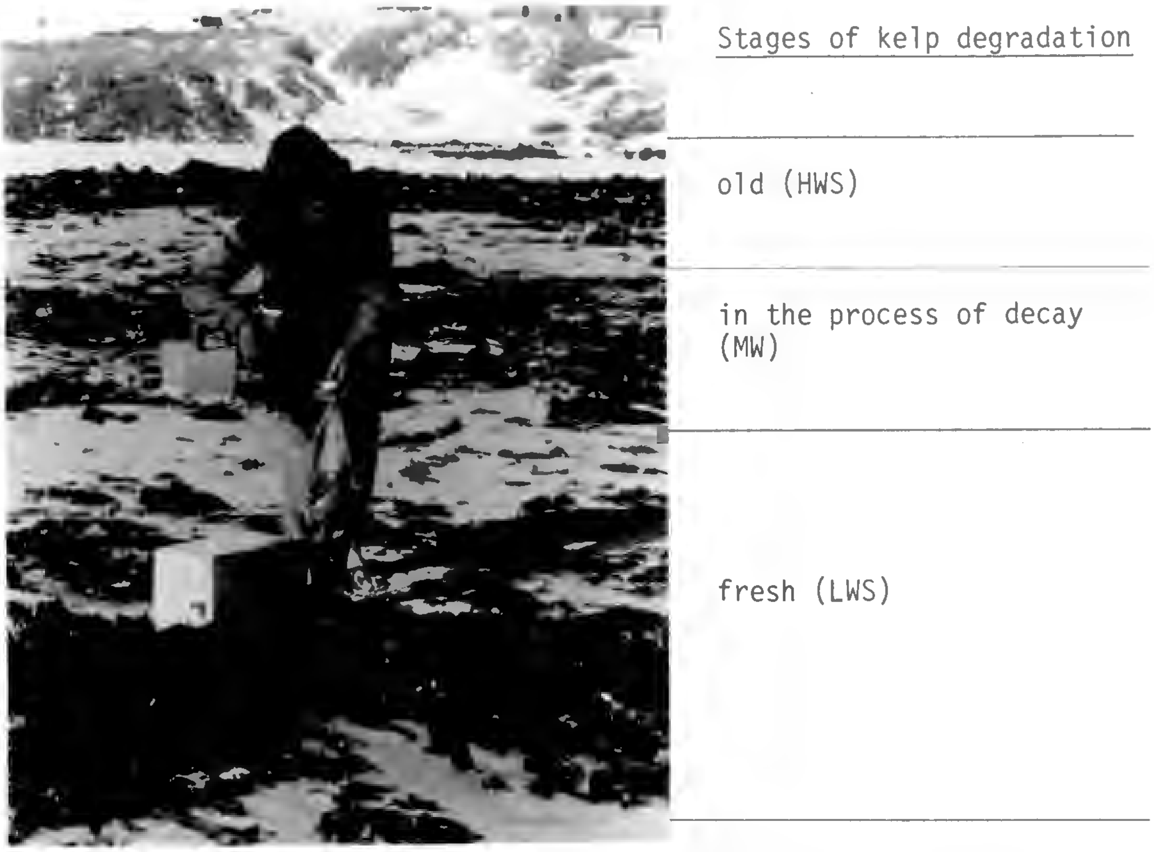

Plate 3.1. Zonation of Kommetjie beach. In zoning the beach, three stages of kelp degradation were recognised at the time of low spring tide, namely those in which deposits were old, in the process of decay and fresh. The position of these correspond to HWS, MW and LWS respectively.

Plate 3.2 Since many macrofaunal species are very motile, each site was enclosed with a plastic tank and then sprayed with insecticide before sampling.

Meiofauna

Once every three months, four random sand cores were extracted to depths of 30cm and 60cm from each zone using a stainless steel corer 30cm in length and 10cm^2 in cross section. It was not considered necessary to sample beyond this depth as Koop and Griffiths (1982) 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^{o}C to constant weight before ashing at 460^{o}C for 5 hours. All weights were determined using a Mettler ME 30 microbalance. The mean individual dry mass (Appendix D) was used to convert numbers to biomass. The less frequent meiofauna were given an arbitary mass of 0,5μg per individual (McLachlan 1977_b_, _c_).

Bacteria

Bacterial densities were established quarterly from four random sand cores extracted at 30cm depth interval to the water table in each zone using the same stainless steel corer described above. From the cores, which were mixed for a sampling site, a 10ml subsample was preserved in 10ml of 10% formalin in sterile seawater. To remove bacteria attached to sand grains, the samples were sonicated three times in a DAWE Sonicleaner type 6442A. After each sonication, a sample was shaken vigorously for five seconds and left for 10 seconds to allow sand and heavy debris to settle before the supernatant was decanted into a separate autoclaved vial. Hereafter 10ml of 10% formalin in sterile seawater was added. This resulted in 30ml of accumulated liquid which enabled numbers to be related back to the original sand volume. Few bacterial cells are damaged during sonication as Koop (1982) found that 98% of dislodged bacteria could still be counted.

The supernatant was analysed for bacterial numbers by the AODC (acridine orange direct count) method, which has been widely used elsewhere (Hobbie et al, 1977) and in work on the Cape west coast kelp beds (Field et al, 1980b; Linley et al, 1981; Koop, 1982; Stuart, 1982). However, recently a new method has been developed using 4'6-diamidino-2-phenylindole (DAPI) which enable better distinction between bacteria and background interference (Porter and Feig, 1980).

Polycarbonate nucleopore filters (47mm diameter; 0,2μm pore size) were used to retain bacteria for counting. These filters were prestained in a solution of 1g irgalan black in 1 litre of 2% acetic acid for 10 minutes (Hobbie et al, 1977) to reduce background fluorescence when viewed under an epifluorescent microscope. Each filter was rinsed three times in sterile distilled water and then placed on a millipore pad (AP1004751) which was kept moist by adding a few drops of 1% Photoflo (Kodak) surfactant both above and below.

A known volume of supernatant, stained in 5ml acridine orange for 10 minutes, was poured onto a prepared filter under vacuum (0,8atms). Half a filter was placed on a glass slide coated with a low viscosity immersion oil (Nikon) before adding more oil and a cover slip. The slide was viewed under a Zeiss standard 18 microscope fitted with a 1000X magnification oil immersion lens, an epifluorescent condenser, an HBO 50 Watt mercury burner, a 455-500 band pass exciter filter, a 510 beam splitter and a LP 520 barrier filter. The field diameter was adjusted to include 20-30 bacteria within each of 20 randomly chosen fields. Bacterial density was then calculated as follows:

$$\text{Bacterial density} = \frac{S.10^6.n}{s.v} \text{ cells ml}^{-1}$$

where S = working surface area of filter (mm^2)

n = mean number of cells per field

s = area of microscopic field (μm^2)

v = volume of sample filtered (ml)

from Mazure (1978)

Bacterial biomass was determined from 20ml samples of interstitial water collected from each zone with a sterile syringe. Each sample was fixed with 1ml of 2,5% glutaraldehyde and then incubated at 5°C for no more than fourteen days before processing. The samples were then prepared for scanning electron microscopy by a combination of methods outlined by Linley et al, (1981) based on work by Todd and Kerr (1972), Paerl (1975) and Bowden (1977). A portion of a 20ml sample was filtered onto a polycarbonate nucleopore filter (0,2µm pore size; 25mm diameter) under a slight vacuum. The filter paper was then supported between two magnets to enable transfer during desalination (passage through decreasing concentrations of sterile autoclaved seawater: 100, 75, 50, 25 and 10%, with 10 mins in each, ending with 2 washes in distilled water) and dehydration (passage through increasing concentrations of ethanol: 10, 20 .... 90,100% with 20 minutes in each, ending with two washes in ethanol).

The samples were kept immersed in ethanol before being critical point dried and mounted on stubs for coating with a 200 A° layer of gold/palladium under vacuum. The specimens were viewed on a Cambridge S180 scanning electron microscope and photographed. From the micrographs, the proportion and dimensions of rods ($\pi r^2 h \ \mu m^3$) and cocci ($^4/_3 \ \pi r^3 \ \mu m^3$) were estimated using vernier calipers. Using a specific gravity for bacterial cells of 1,1 (Luria, 1960) the biomass was calculated as follows:

$$\text{Wet biomass} = \frac{N.v.SG}{10^6} \text{ mgl}^{-1},$$

where N = number of cells ml^{-1}

v = mean bacterial cell volume (μm^3)

SG = specific gravity of bacterial cells

from Linley _et al_ (1981).

Wet mass was converted to dry mass and carbon equivalents by multiplication factors of 0,2 and 0,1 respectively (Luria, 1960; Troitsky and Sorokin, 1967; Sorokin and Kadota, 1972). The above wet to dry mass conversion factor should however be treated with caution as Davies (1981) has recently established two new factors of 0,068 for _Pseudomonas_ strains and 0,049 for _Vibrio_ strains among kelp-attached bacteria in the waters of the west coast kelp beds.

RESULTS AND DISCUSSION

Macrofauna

Thirty-five macrofaunal forms were recorded, comprising 4 species of amphipods, 2 isopods, 7 molluscs, 4 dipterans and 18 coleopterans (see Appendix C for complete list of species). The talitrid amphipod, _Talorchestia capensis_ was dominant for most of the year and accounted for over 90% of macrofaunal numbers (fig. 3.1(a)). This species is common in wrack beds and responsible for most of the primary consumption of surface material (see Chapter 5). Other amphipods present in order of abundance were _Talorchestia quadrispinosa_, _Paramoera capensis_ and _Gitanopsis pusilla_.

Both species of isopods, _Exospaeroma truncatitelson_ and _Eurydice longicornis_ were restricted to the low tide swash zone, where they feed on organic matter and prey on small living animals such as _Talorchestia_. Their numbers and biomass declined drastically during the winter as is reflected by their small contribution towards total macrofauna in figs 3.1(a) and (b). At this time large swells reaching the shore may have created inhospitable conditions in the swash zone, especially for the dominant species, *E. truncatitelson* which prefers sheltered beaches (Brown, 1973). The presence of these isopods is not directly related to wrack, as they are usually found in much greater densities on other beaches around the Cape Peninsula which are devoid of large kelp deposits (Brown, 1973). They never comprised more than 15% of the macrofauna during the year.

Of the seven mollusc species, two were common, a brown bivalve , 1mm in diameter (?*Neogaimardia kowiensis*) and a small grazing gastropod (*Eatoniella nigra*), both of which were abundant to a depth of 10cm at all tidal levels. These two animals were the dominant forms during September, comprising 85% of the total macrofauna, whereas during the previous two months they were present in only small numbers, less than 1% of all fauna (fig. 3.1(a)). This reflects the rapid manner in which some organisims can be re-established once environmental conditions are optimal. Other molluscs present were mainly juveniles of sublittoral forms (*Choromytilus meridionalis* and *Burnepena* sp.) which were probably washed ashore with kelp. The remaining species, *Kellia rotunda*, *Tricolia capensis* and *Tricolia neritina* were rare in samples. The beach lacked large molluscs, such as the filter feeding bivalves, *Donax* spp. and the scavenging gastropods, *Bullia* spp. found on beaches without wrack along the east and west coast of the South-western Cape (Brown, 1971*b*; Bally, 1981). Their absence is probably due to the disruptive forces created by the kelp being thrown ashore plus the lack of their natural food in the form of phytoplankton and carrion.

The adults of the two most common dipterans *Fucellia capensis* and *Coelopa africana* were always present, but exceptionally high numbers were recorded

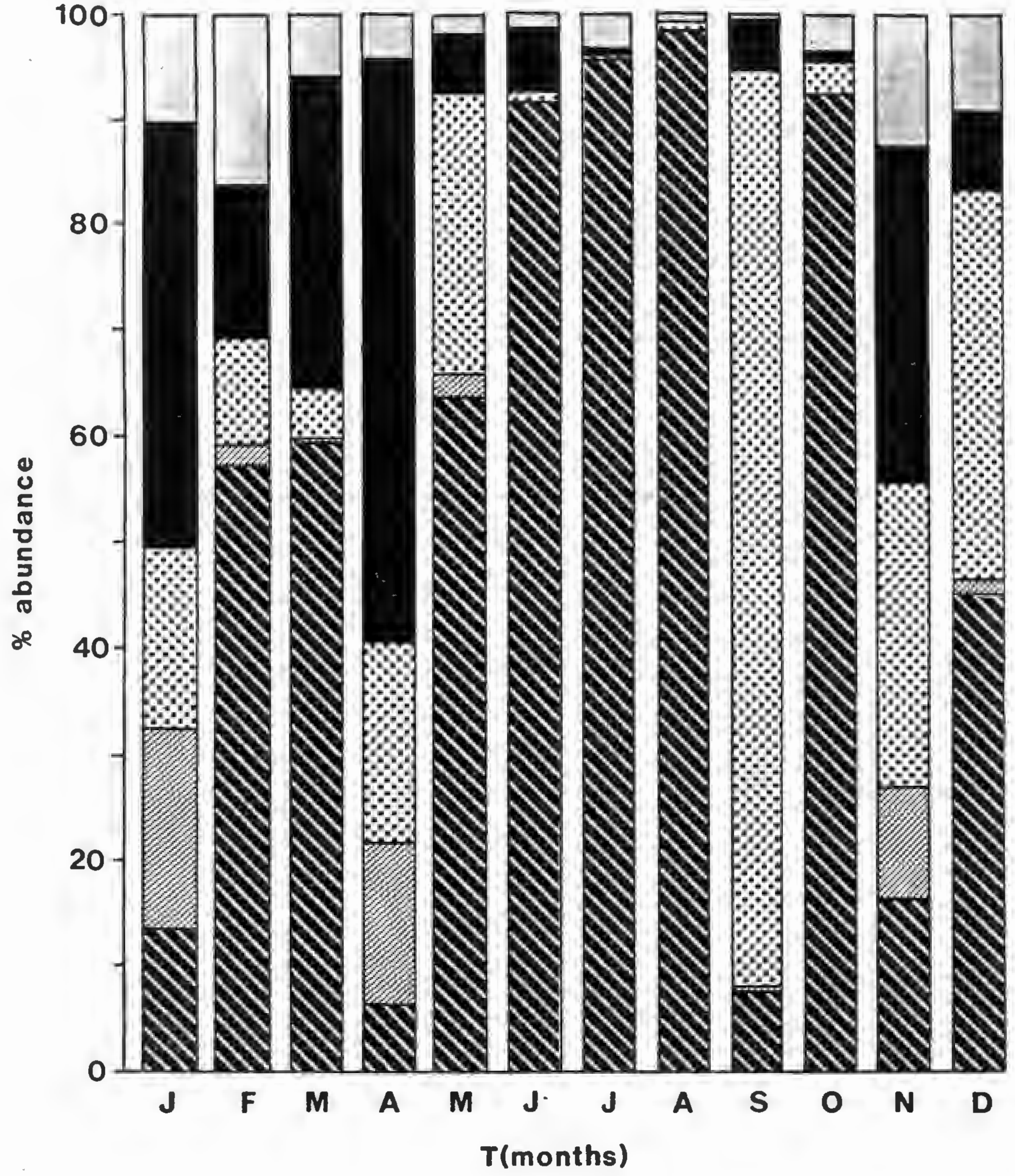

Fig. 3.1(a). Monthly fluctuations in the taxonomic composition of macrofauna, in terms of percentage abundance, found associated with kelp stranded on Kommetjie beach, Cape Peninsula.

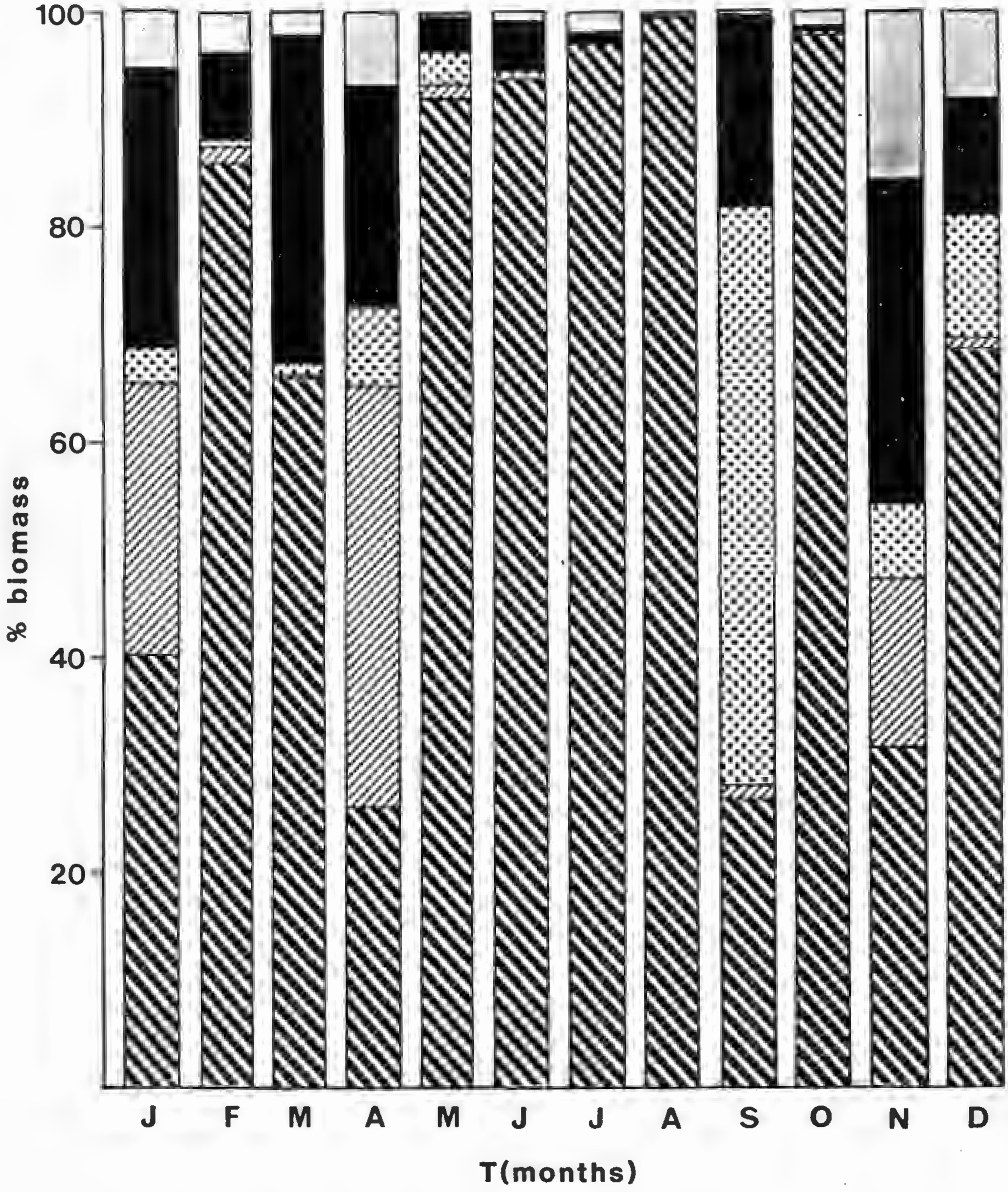

Fig. 3.1(b). Monthly fluctuations in the taxonomic composition of macrofauna, in terms of percentage biomass, found associated with kelp stranded on Kommetjie beach Cape Peninsula.

in summer and autumn, coinciding with the presence of many larvae (fig. 3.1(a)). This may reflect a summer/autumn breeding peak, this possibility being reinforced by the virtual absence of larvae from July to October (see Appendix C). When present, flies frequented kelp at all tidal levels, whereas the larvae were concentrated at mid-tide in large decaying banks of wrack upon which they feed. Two unidentified flies, one of which was fairly common, and an unidentified larval form were also recorded.

The two most abundant Coleoptera were carnivorous forms, Aleochara salsipotens (Staphylinidae) and Acritus lightfooti (Histeridae). The most common herbivore was Cercyon maritimus (Hydrophilidae). The genera Aleochara and Cercyon are frequently found associated with wrack on beaches in the northern hemisphere (Backlund, 1945; Doyen, 1976; Moore and Legner, 1976). Other typical intertidal forms were Pachyphaleria capensis, Bledius sp., Omalium sp., and Cafius xantholoma, a species present in Sweden (Backlund, 1945) and California (Moore and Legner, 1976). The beetles are generally restricted to HWS, although they may migrate down the beach during neap tides (Griffiths and Stenton-Dozey, 1981). Few larvae were recorded and those present were well adapted to survive inundation by the sea. For example, the larvae of Aleochara spp. are ectoparasites on the pupae of kelp flies, obtaining protection from the puparium (Moore and Legner, 1976).

The abundance of beetles through the year was erratic with no seasonal pattern. Like the isopods, their contribution towards total macrofaunal numbers seldom exceeded 10% (fig. 3.1(a)). 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, which are likely to be their breeding grounds.

The macrofauna as a whole were concentrated between mid-tide and HWS, while the lower intertidal remained far less colonised throughout the year (Table 3.1). Although the highest abundance (4 173 x 10^3 m^{-1}) and biomass (5 885,87g dry mass m^{-1}) were recorded in July at HWS, no definite seasonal preferance 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, 1977*c*). 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.3.2), hereby revealing the response of the animals towards the pulses in their food supply. Amphipods, which made up 92% of the mean annual standing stock, strongly influenced the trimodal pattern in total biomass observed during the year. The three peaks, February (1860g m^{-1}), July (6761g m^{-1}) and October (7324g m^{-1}) coincided with maximal contribution by amphipods, namely 85%, 97% and 94% respectively, while the troughs corresponded to minimal contribution.

The overall changes in faunal biomass are also influenced by the growth dynamics of *Talorchestia capensis*, which have been studied by Muir (1977). He attributed the June-July peak to the presence of a high density of overwintering juveniles and this was confirmed in the present study by the abundant contribution of 99% by juveniles at this time (see Appendix C). Muir found that the low biomass of amphipods in September was created by a drastic fall-off in the adult population (only 83 adults m^{-1} were sampled in this survey), while the increase in October was brought about by the entry of a juvenile cohort. In support of this latter point, the contribution of adults towards total abundance rose from 1% in August and Sep-

Table 3.1 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). Appendices C and D contain the original data.

Month	Zones and their respective widths in metres	Number x $10^3 m^{-1}$	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

Table 3.1 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
September	N LWS : 36	96,00	26,83	2
	D MW : 10	1,08	2,52	5
	O HWS : 7	18,64	36,56	5
October	N LWS : 17	327,82	371,53	6
	D MW : 9	583,80	2419,49	11
	O HWS : 8	1241,60	4532,54	10
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	19,77	9
	D MW : 13	111,69	140,30	15
	O HWS : 14	9,22	16,66	17

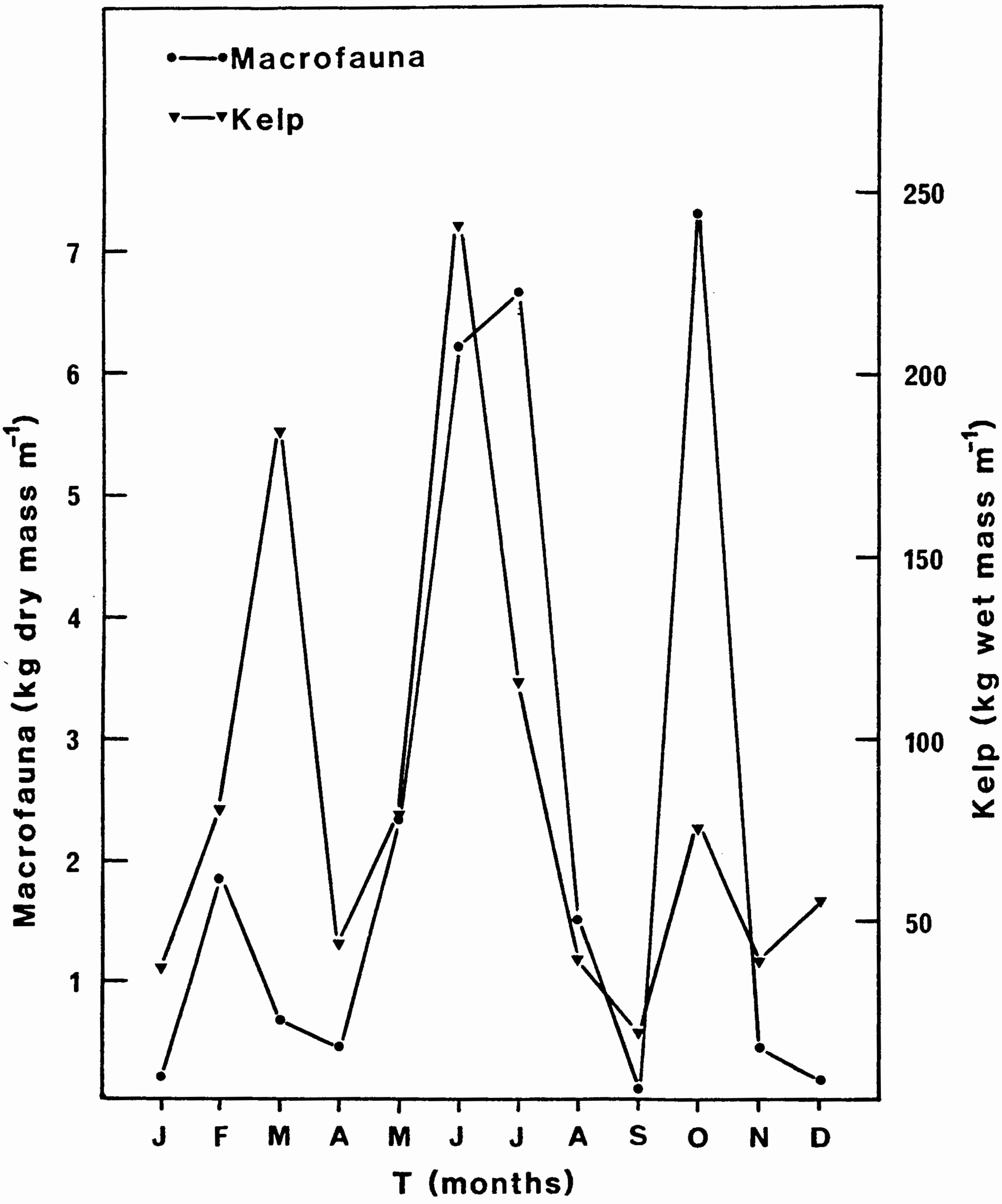

Fig. 3.2. Monthly fluctuations in the total biomass of macrofauna (g dry mass m^{-1}) in response to the quantity of kelp (kg wet mass m^{-1}) washed ashore at Kommetjie in the Cape Peninsula.

tember to 15% in October (see fig.3.1(a)). As these two surveys were four years apart, it appears that the population of T. capensis is permanently in residence on Kommetjie beach and the dynamics hereof are consistent from year to year.

Meiofauna

Insufficient taxonomic data on marine meiofauna in southern Africa are available for specific identification to be made. Nevertheless some distinct trends in basic taxonomic composition are evident. Figures 3.3(a) and (b) compare the percentage abundance and biomass 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 that 90%) followed by harpacticoid copepods and turbellarians (both less that 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 3,4 μg dry mass, Appendix D), made this group more important in terms of biomass. The great abundance of large oligochaetes on beaches with wrack was also noted in Finland where they are regarded as the most important decomposers of kelp (Giere, 1975).

On most other sandy beaches studied in southern Africa, nematodes are the dominant taxon and harpacticoid and mystacocarid crustaceans are next in importance (McLachlan, 1977 b,c; Dye et al, 1981; McLachlan et al, 1981a; Orren et al, 1981, Woolridge et al, 1981). Here oligochaetes contribute as little as 2% of the standing stock and have a mean individual dry mass of only 1,8μg.

This taxonomic difference may be attributed to two factors. Firstly, in comparison with the mean particle diameter of 277μm for sand at Kommetjie (see

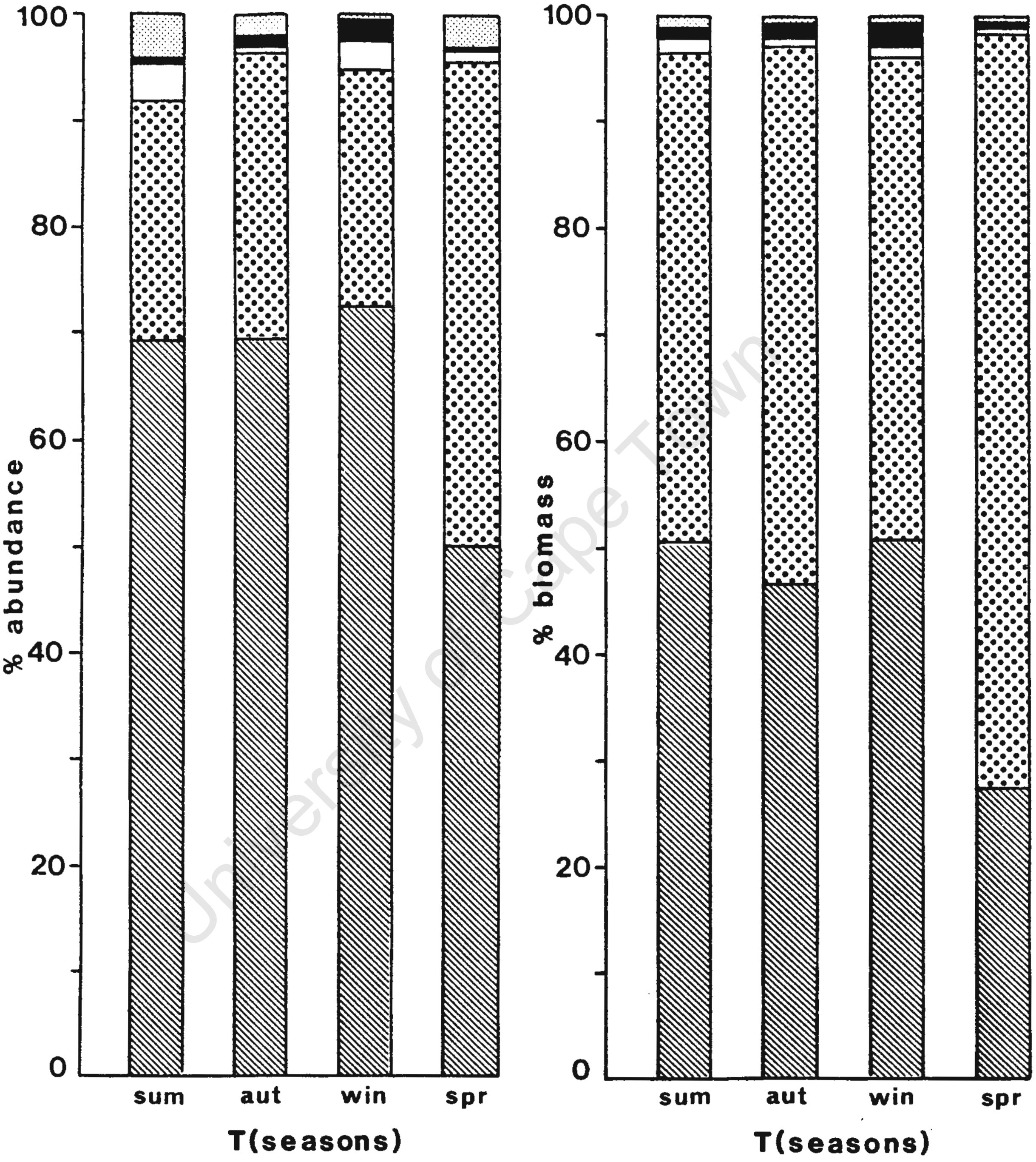

Fig. 3.3(a) and (b). Seasonal changes in the taxonomic composition of interstitial meiofauna, in terms of percentage abundance (a) and biomass (b), found associated with kelp stranded on Kommetjie beach, Cape Peninsula.

Chapter 2), other beaches have slightly coarser substrates. Orren et al (1981) reported a mean Mdμm of 287 on the west and south coasts of the Cape, while McLachlan et al (1981a) obtained a mean of 350μm for beaches stretching from the southern Cape to the Natal coast. Thus these areas are probably better oxygenated, a condition which favours high densities of meiofaunal crustaceans (McLachlan, 1977b). A second factor to be noted is that the beaches studied by the above authors are not fuelled by stranded kelp but rather by phytoplankton, mainly in the form of diatoms, a diet upon which harpacticoids thrive (McIntyre, 1969). The similarity in the dominance of nematodes can be expected because of the great species diversity in this group (see Chapter 4) and hence the ability to invade many varied microhabitats in the interstitial environment.

The seasonal changes in the densitities of the four major meiofaunal taxa are shown in figure 3.4 (see Appendix E for the original data). From summer to autumn, nematodes and harpacticoids decreased in numbers, whereas oligochaetes and turbellarians exhibited a gradual increase. During winter, greatest densities were attained in all groups except oligochaetes which reached a maximum in spring, when other taxa were on a decline.

Seasonal fluctuations in total numbers and biomass with respect to vertical and horizonal distribution are shown in Table 3.2. 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.

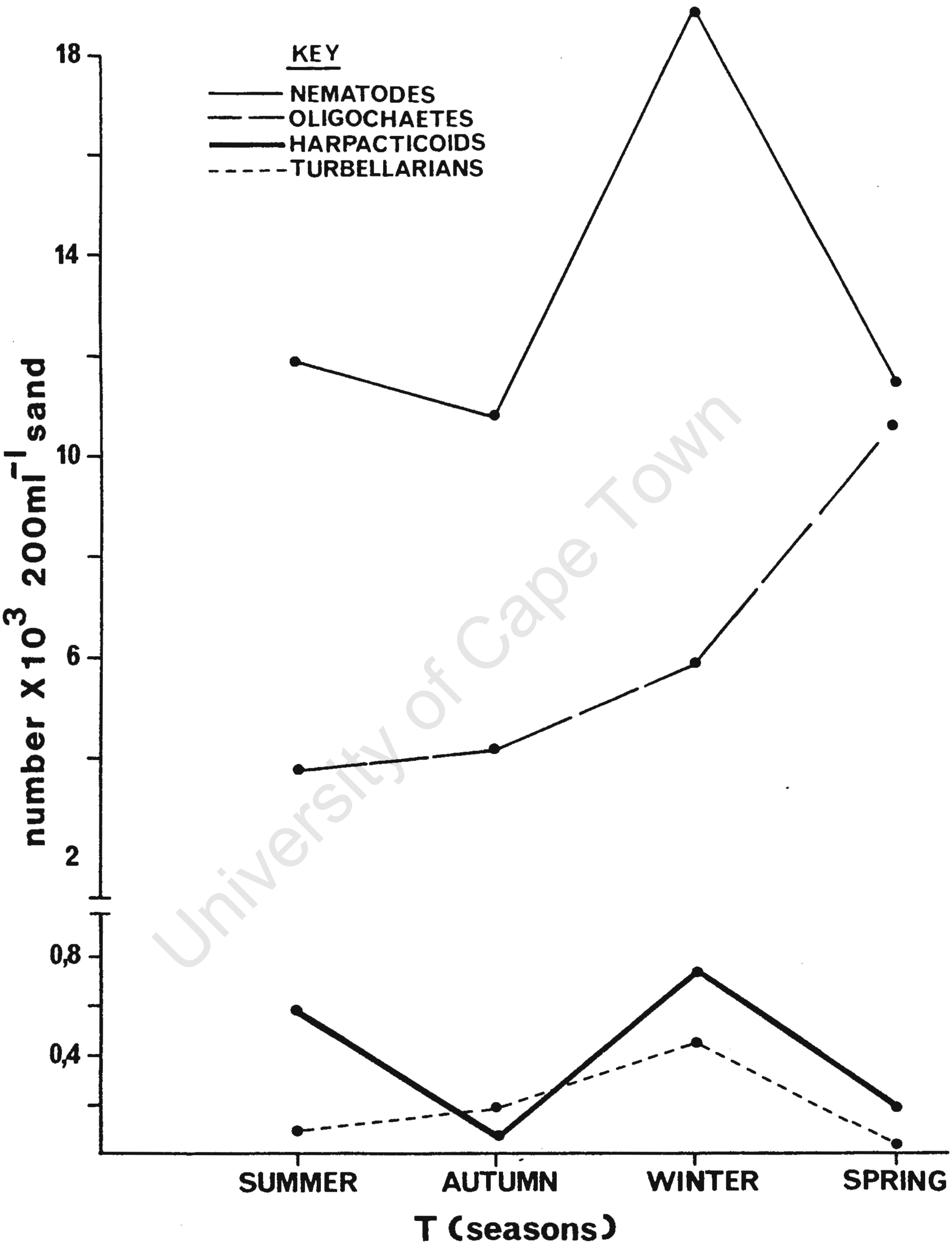

Fig. 3.4. Seasonal changes in the densities (number x 10^3 200ml^{-1} sand) of the four major meiofaunal groups (nematodes, oligochaetes, harpacticoid copepods and turbellarians) found in the interstitial environment beneath kelp stranded on Kommetjie beach, Cape Peninsula.

Table 3.2 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 3.1 for the abbreviations and widths of the different zones). Appendix E contains the original data.

		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
	O 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
	O HWS	109,25	220,32	95,36	156,15	204,60	376,47
						248,09	430,92
Winter	N LWS	12,00	18,30	3,81	5,79	15,81	24,10
	D MW	163,23	292,36	206,98	319,33	370,21	611,69
	O 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
	O HWS	46,54	101,30	14,27	20,03	60,80	121,33
						321,68	690,82

McLachlan (1980) has emphasised the necessity to view the zonation of meiofauna on sandy beaches three-dimensionally, because of their deep vertical penetration into the sediment. He concluded that while meiofauna densities on east coast beaches may be controlled mainly by available food (McLachlan, 1977c), the factors responsible for the vertical distribution of densities appeared to be dessication at low tide and dissolved oxygen in the interstitial water. As east coast beaches are physically similar, McLachlan (1980) has developed a generalised pattern in vertical strata coincidental to changes in meiofaunal distribution. From this, a typical pattern in intertidal abundance emerged when samples were collected during low tide in summer. Greatest densities were generally encountered between 20-60cm at HW extending to the surface at MW, while the lower shore was sparsely colonised (McLachlan, 1977c; Dye et al, 1981; McLachlan et al, 1981a; Woolridge et al, 1981). However certain changes in the environment, such as an increase in organic matter, will alter this generalised pattern (McLachlan, 1980), and indeed this was observed at Kommetjie.

At the time of low spring tides, maximal coverage by surface kelp was always observed at MW where deposits accumulate during the intermediate neap tides. It was therefore expected that this region would attract large densities of meiofauna by providing abundant food in the form of dissolved and particulate organic matter colonised by dense bacterial populations. Many authors have shown such attraction in meiofauna (e.g. McIntyre, 1969; Fenchel, 1970; Gerlach, 1977). However meiofauna were not always most abundant at MW, for during summer and autumn their numbers were greater at HWS (Table 3.2). This was due to a drastic alteration in the physical structure of the beach by the formation of two berms bordering the mid-tide level. The isolation and reduced drainage resulting from masses of buried material trapped in the sand, caused this area to become waterlogged. The sediment was 40 - 80% saturated as compared to 21-44% in winter and spring (see Table 2.3). A sulphide smell emerged from the rotting kelp at the surface and a reducing layer (noted by the dark colouration of the sand and the presence of hydrogen sulphide) was apparent at a depth of only 40cm. The temperature in the sediment was approximately $21^{0}C$ as compared to $12^{0}C$ in winter. These anoxia conditions indicated a high degree of microbial activity as is supported by the biomass maximae recorded for bacteria at this time (see Table 3.3.). Although there was a large potential food source, meiofauna were precluded from reaching high densities because of the drastically reduced oxygen tensions that must have been present at mid-tide. The only taxon to exceed 100 individuals $200ml^{-1}$ of sand were nematodes, which are notably more tolerant of anoxic conditions (Teal and Wieser, 1966; McIntryre, 1969). Meiofauna were thus restricted to the upper reaches of the beach. Although most animals avoid sediments less than 10% saturated (Cox, 1976), the great densities only 30cm below the surface where saturation averaged 7,6% (see Table 2.3) were presumably in response to the very high concentration of organics directly beneath decomposing kelp (Koop _et_ _al_, 1982_a_).

In winter and summer no berms existed on the beach and a reducing layer only appeared below the permanent water table some 90cm from the surface at mid-tide. Meiofauna were thus able to utilise the rich food supply and indeed reached their highest biomass at this level than at any other time during the year (Table 3.2).

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 3.3) of which approximately 63% were of coccoid form (see Appendix F). 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. In the northern hemisphere, Dale (1974) studied the incidence of intertidal bacterial popu-

Table 3.3 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 3.1 for abbreviations and widths of the respective zones). Appendix F contains the original data.

Sampling depths (cm)

		0 - 30		30 - 60		60 - 90			
Season Sampled	Zone	Numbers	Biomass	Numbers	Biomass	Numbers	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
	0 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
	0 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
	0 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
	0 HWS	1364,03	133,77	446,03	43,72	848,06	83,15	2658,12	260,64
								6789,46	749,28

lations colonising far finer sediments (particle diameters of 8µm-212µm) than found on southern African beaches (277µm-350µm) and arrived at much higher densities (approximately $0,15.10^9$ - 13.10^9 ml^{-1} of dry sand). This difference appears to support his hypothesis that the finer the sediment, the larger the surface area for bacterial colonization and hence the greater the density.

Bacterial cells found associated with wrack beds are generally larger than those in other ecosystems. Meyer-Reil *et al* (1978) reported volumes ranging from 0,01 to $0,18µm^3$ from sandy beaches in Kiel Bright, while even smaller volumes (0,04 to $0,07µm^3$) occurred in a salt marsh habitat studied by Wilson and Stevenson (1980). In a previous survey of wrack at Kommetjie, Koop and Griffiths (1982) recorded a mean cell volume of $0,57µm^3$ for rods and $0,2µm^3$ for cocci, while Koop *et al* (1982*a*) encountered a range of 0,18 to $0,41µm^3$ in an *in situ* microcosm experiment. In the present study, cocci ranged from 0,06 - $0,15µm^3$ and rods, 0,53 - $1,9µm^3$, the highest mean cell volumes for both forms being recorded in autumn. As biomass values are determined from numbers and cell volumes (see methods), the large number and size of bacteria in this season had an obvious influence on the extraordinary high biomass recorded at this time (Table 3.3).

The data on bacterial abundance and biomass show a seasonal trend in intertidal distribution (Table 3.3). In summer and autumn, values were highest at mid-tide with a marked decline towards LWS and HWS. In winter bacteria were concentrated at HWS, whereas in spring the greatest biomass was found at mid-tide and numbers peaked further upshore. The difference in density from one tide level to the next at this time was not as marked as in summer and autumn. During all seasons, numbers and biomass varied only slightly with depth and remained consistently high to the level of the water table.

The above seasonal distribution of bacteria was the reverse of the pattern observed for meiofauna (see Table 3.2), possibly indicating the influence of grazing pressure by meiofauna upon bacteria. It has been reported elsewhere that meiofauna may control bacterial densities (Jansson, 1968; Giere, 1975; Gerlach, 1978, see Chapter 4) and has also been suggested by Koop and Griffiths (1982) who found inverse patterns in the density distribution of these two forms in the sand. However, it should be noted that meiofauna densities alone cannot determine bacterial distribution in this wrack system. As mentioned earlier, meiofauna were probably excluded from mid-tide in summer and autumn because of the anoxic conditions which prevailed, even though the largest deposits of kelp were observed in this area. Bacteria have a far greater diversity and hence ability to utilise kelp debris under extreme conditions. Indeed Koop *et al* (1982*a*) have shown that as dissolved and particulate organic matter leach from decomposing kelp and accumulate in the sediment, bacterial biomass can rise 20 fold in 8 days. Thus in autumn, when a remarkable high value of 2644g dry mass m^{-1} was recorded, bacteria capitalised on the high levels of DOM and POM in a reduced environment and in the absence of an abundance of meiofauna. This is supported by the fact that meiofaunal biomass was at its lowest recorded value for this season (see Table 3.2).

The biomass of bacteria therefore appears to be influenced by the mean cell volume, particle diameter of the sand grains, grazing pressure by meiofauna and above all, the availability of food.

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.

Meiofaunal biomass showed the least fluctuation during the year, supporting the idea that small metazoans are able to maintain stable populations on sandy beaches (McIntyre, 1968, 1969; McLachlan, 1977b). Although bacterial standing stocks varied less than those of the macrofauna, they were still relatively dynamic, as revealed by the extraordinary high biomass recorded in autumn, believed to be in response to the particular conditions present on Kommetjie beach at this time. This emphasises the ability of bacteria to respond to environmental change by rapidly adjusting their rate of turnover.

Compared to the other intertidal sandy beaches in southern Africa, the biomass ranges encountered here are generally higher. On east coast beaches (Natal and Transkei), the maximum range recorded for macrofauna was 8 - 99g m^{-1} (Dye et al, 1981; Woolridge et al, 1981) while southwards towards Algoa Bay, biomass ranges from 7 - 6621g m^{-1} (McLachlan, 1977c). On the Cape west coast the mean annual value can reach between 92g and 683g per metre of beach (Bally, 1981). The fauna in these areas consist mainly of large filter-feeding and scavenging molluscs and is quite unlike that present in the wrack beds.

Previously recorded meiofaunal biomasses range from 10 - 156g m^{-1} on the east coast to 117 - 243g m^{-1} on the south coast (McLachlan et al, 1981a), values which are considerably lower than those given here. The only information available on bacteria in sandy beaches of southern Africa, provides data on densities which suggest a slightly lower biomass range (McLachlan et al, 1979).

Even on the basis of a worldwide comparison, the faunal biomass supported by stranded kelp material is high. Bally (1981) has extensively reviewed the literature on macrofauna of clean sandy beaches in countries other than

South Africa. He found a minimum of 10g m^{-1} on Whidbey Island, U:S.A:, and a maximum of 731g m^{-1} on the Pacific coast of Panama. McIntyre (1969, pg. 251) reviews meiofaunal densities around the world and judging from these values, standing stocks are unlikely to exceed those found in this study. Information on intertidal bacteria is scarce, but Dale (1974) reports that biomass estimates are similar in most sediment types ranging from 10g m^{-2} in lagoon sands to 57g m^{-2} in shallow muds, as compared to an approximate maximum of 59g m^{-2} at Kommetjie.

Comparison of the mean standing stock of macrofauna (2257g m^{-1}), meiofauna (624g m^{-1}) amd 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_ (1981_a_) 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.

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 (1977_b_,_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, 1977*b*,*c*; Koop and Griffiths, 1982), this value has been follwed here.

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 physical parameters (Dale, 1974), while interactions with larger fauna can stimulate productivity (Fenchel, 1970, 1972; Lopez *et al*, 1977; Robertson and Mann, 1980). At Kommetjie, a turnover of 70 times per year has been estimated on the basis of the conversion efficiency of available organics (see Chapter 5). 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 3.4. 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 even greater if samples penetrated beyond the depth of the water table and if kelp surfaces were analysed.

Table 3.4 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 ($P/\bar{B}$)	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	960,65	30,0	28819,5	70,4

The relative significance of bacteria is similar to that recorded by Koop and Griffiths (1982) for their wrack ecosystem, but here the meiofauna assumed a greater role, contributing some 10% as compared to only 2,6% for macrofauna. This difference may be due to the dominance of the amphipod *Talorchestia quadrispinosa* among the macrofauna, a species which is not as specialised as *T. capensis* in utilizing stranded kelp and therefore does not reach equivalent densities. Unfortunately studies to date have tended to exclude bacteria in productivity estimates in sandy beaches, concentrating on macrofauna or meiofauna or both (e.g. McIntyre, 1969; Brown 1971*a*,*b*; McLachlan, 1977*a*-*c*. Ansell *et al*, 1978; Tietjen, 1980; Bally, 1981). Considering only macro- and meio-fauna McLachlan (1977*a*,*c*) reported a great variation in their relative contributions towards the total secondary productivity on east coast beaches of South Africa, but on average each was of similar importance. In a salt marsh intertidal habitat dominated by *Spartina*, Wieser and Kanwisher (1961) studied the role of all three biotic components and found that bacteria contributed the most towards biological activity, some 53 - 65%, followed by macrofauna and then meiofauna at only 10 - 15%. If this example, and the results obtained here, can be regarded to represent the pattern of partitioned secondary productivity in the intertidal habitats with high organic input, it seems a gross mistake to exclude bacteria in any future work in this field.

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 via grazing and fragmentation (Griffiths and Stenton-Dozey, 1981; Chapter 5). The surface biota thus plays an important role in degrading whole kelp plants, thereby providing leachates and small organic particles to the interstitial fauna. As the dominant macrofaunal organisms, the amphipod _T. capensis_ and larvae of the kelp fly _F. capensis_, are characterised by low assimilation efficiencies (Muir, 1977; Stenton-Dozey and Griffiths, 1981) faeces production would greatly increase this input.

Many authors have shown that different amphipod species increase the decomposition rate of intertidal grasses by reducing particle size, thereby supplying a greater surface area for microbial action and through the excretion of nitrogen rich materials, enhance bacterial growth (Fenchel, 1970; Lopez _et al_, 1977; Harrison, 1977; Robertson and Mann, 1980). If the same is true for kelp-derived detritus, then fragmentation of kelp by surface organisms will maintain a long-term supply of particles for the support of bacterial populations and for animals further along the food chain, such as the meiofauna.

Evidence is presented in the literature of incidental grazing by macrofauna on meiofauna, such as grass shrimp predation in a salt march habitat (Bell and Coull, 1978; Bell, 1980) and juvenile fish which move in with the tides (McIntyre and Murison, 1973). Beside the fact that these faunal elements are lacking at Kommetjie, it is doubtful whether the macrofauna derives any energy from meiofauna, as kelp consumers dominate. Other than providing nutrients to the sub-surface environment, any further interaction between the macrofauna and meiofauna would be indirect. For example, burrowing activities can cause disturbance, but at the same time enhance oxygenation of the sediment (Gerlach, 1978; Bell, 1980). However, even this interaction would be restricted to the upper 15cm of substrate at Kommetjie, as no macrofauna were found beyond this depth. The surface biota thus appears to be largely isolated from the interstitial trophodynamics.

In contrast to the findings in Chapter 5, 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 role of bacteria in the initial decomposition of the kelp lying on an open beach is probably not as pronounced, their impact being shifted to the final degradation of kelp fragments.

Besides the role 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 supplememted by direct absorption of dissolved organic matter (e.g. Chia and Warwick, 1969; Meyer-Reil and Faubel, 1980), and since very high values of carbon have been recorded immediately beneath decomposing kelp (Koop et al, 1982a), the dense populations of nematodes and oligochaetes found at Kommetijie could directly utilise this energy source. In addition, certain groups such as nematodes, turbellarians and acarines are predatory on other meiofauna (Giere, 1975; Cox, 1976).

In Chapter 5 the energy flow through the Kommetjie wrack ecosystem has been quantified. On a qualitative basis, it appears that two isolated trophic levels are in existence, a feature noted in most intertidal sandy beaches (e.g. McIntyre, 1969; Gerlach, 1971; McIntyre and 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 phosphorous. 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.

CHAPTER 4

Utilization of the kelp leachate, D-mannitol, by sandy beach bacteria and meiofauna

INTRODUCTION

The principal primary photosynthate of the two dominant kelp species in the offshore water at Kommetjie, *Ecklonia maxima* and *Laminaria pallida*, is the acylic polyol, D-mannitol, which accounts for as much as 77% of the free reducing sugars and polyols in the mucilage exuded from fronds (Newell *et al*, 1980). This kelp component, plus laminarin and alginates, form the major carbon source available to bacteria, but above all mannitol is most rapidly metabolised by both kelp-attached bacteria and those in the water column (Davies, 1981; Newell and Lucas, 1981; Stuart *et al*, 1981). On the adjacent sandy beaches where large banks of rotting kelp accumulate, the bacterial assemblage associated with the surface of sand grains is also dominated by mannitol-fermenters (Koop, 1982). This illustrates the high degree to which bacteria in both ecosystems have adjusted their metabolism to the chemical nature of the two dominant primary producers.

In the sandy beach environment where kelp leachates are not diluted, they reach far higher concentrations than in the kelp bed waters (Koop *et al*, 1981*a*; Chapter 2). Although D-mannitol has so far not been detected in the sand below wrack, the decline in its concentration in decaying kelp on the surface of the beach, suggests that high levels would be present were uptake by the interstitial fauna not so rapid (Koop *et al*, 1982*a*).

Mannitol, plus other kelp exudates support a standing stock of bacteria which far exceeds that in the offshore waters (Mazure, 1978; Chapter 3). Bacteria share the high levels of organics with a rich meiofaunal community and it is the aim of this chapter to follow the partitioning of these organics in the form of D-(1-^{14}C) mannitol between bacteria and meiofauna and between the major meiofaunal taxa. The impact of meiofauna on bacterial densities is discussed.

MATERIALS AND METHODS

Collection of interstitial fauna

Interstitial meiofauna and bacteria were collected from Kommetjie beach during June and July, 1982. On each of three separate visits, plastic corers, 4,4cm in diameter and 4cm in length, were used to extract 17 x 30ml sand samples from a depth of 20 to 30cm below banks of rotting kelp. Such locations were known to contain high densities of interstitial fauna (Chapter 3). Samples were sealed with a screw-on lid at one end and a piece of parafilm at the other to ensure minimal disturbance of the sand.

In the laboratory, meiofauna were separated from one of the seventeen sand samples using a modified Oostenbrink separation funnel (Fricke, 1979). Counts hereof ensured that sufficient meiofauna were present in the remaining sixteen samples to determine uptake and incorporation of labelled mannitol.

Apparatus

The plastic corers containing undisturbed sand were connected to a vacuum flask and pump as shown in fig 4.1. To each core, 9ml of natural sea water (filtered and sterilized) and 1ml of Dextran 2000 (Pharmacia No. 170 360-01) were added with a known volume of D-(1-^{14}C) mannitol (see later). Dextran is a blue, inert dye used in this study to follow the passage of labelled sea water through the sand column when a slight vacuum of 15mm Hg was applied to substitute the interstitial water originally present.

In fig 4.1 it can be seen that a series of three sintered polyethylene discs (pore size approximately 200μm; diameters between 4-4,3cm) were placed one above and two below the sand core. These discs (numbers 1 to 3 in fig. 4.1) were used to:

1) disperse the added sea water evenly over the surface of the sand core;

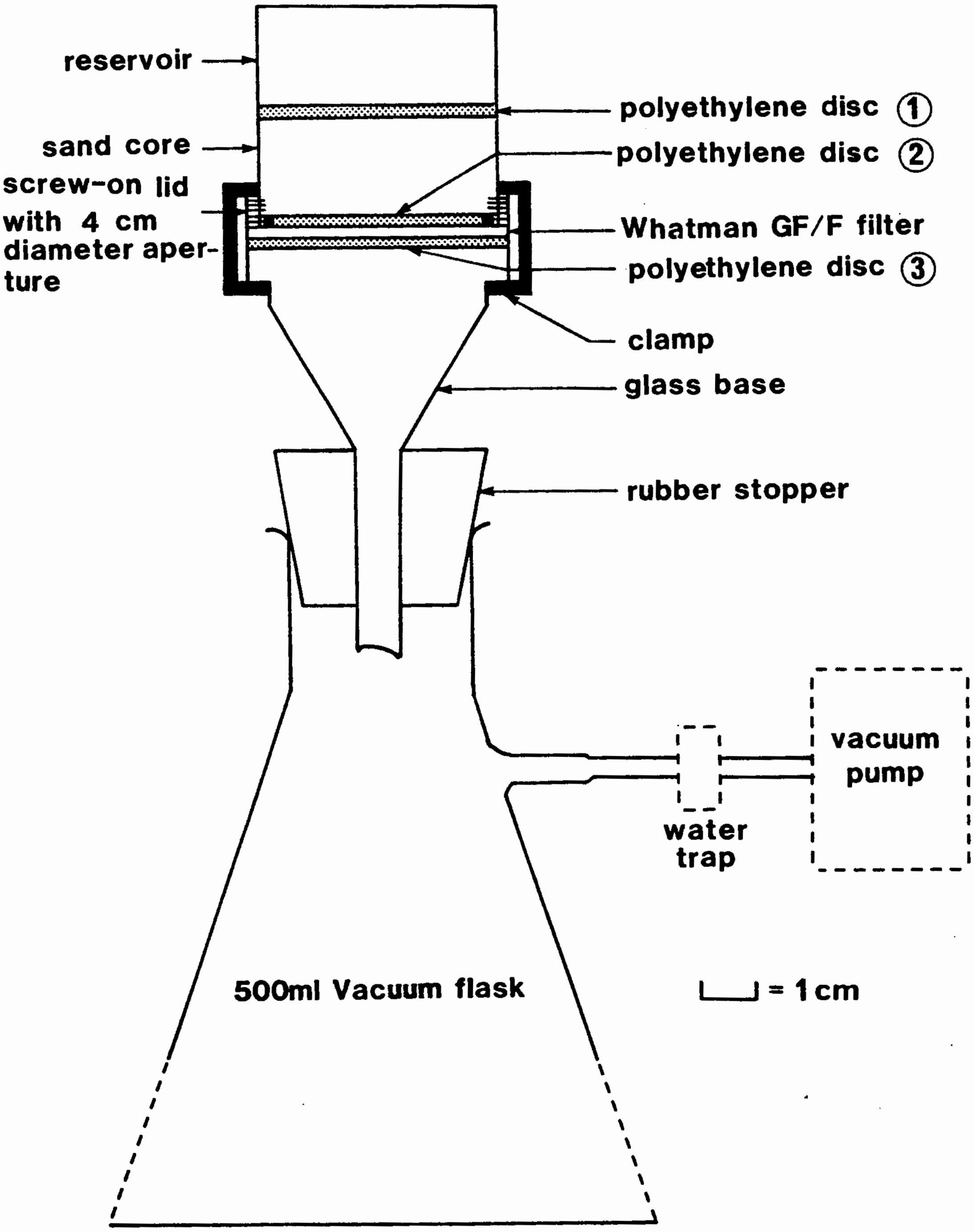

Fig. 4.1. Apparatus used to replace interstitial sea water originally present in a 30ml sand core extracted from beneath decomposing kelp on Kommetjie beach, Cape Peninsula, with sea water labelled with D-(1-^{14}C)mannitol.

2) capture any meiofauna which may escape the sand core when a vacuum was applied;

3) support a GF/F Whatman filter (pore size approximately 0,7µm; diameter 4,7cm) which in turn trapped bacteria escaping the sand core.

Experimental procedure

Increasing concentrations (1µl, 2µl and 4µl ml^{-1} sea water) of D-(1-^{14}C) mannitol (200µCi ml^{-1}; specific activity 59mCi mmol^{-1}; Amersham Buchner Co.) were used in three separate experiments designed to trace uptake and incorporation by bacteria and meiofauna simultaneously. For each concentration of label, sixteen sand cores were incubated in parallel at an *in situ* temperature of 13^{0}C in the dark for 3h, 6h, 12h and 24h. Thus for any one incubation period four sand cores were treated as follows:

I. Two sand cores for determining uptake and incorporation of label by bacteria and meiofauna.

Two sand cores were incubated in parallel to serve as duplicates in ascertaining average radioactive uptake by bacteria and meiofauna simultaneously. After incubation, further uptake was stopped by flushing the sand column, while under slight vacuum, with 50ml Bouins fixative (from a 1,05l stock of 750ml picrinic acid, 250ml formalin and 50 ml glacial acetic acid). Fixation greatly influences the retention of labelled material in meiofauna organisms, a phenomenon which is well known for the retention of label within bacteria (Meyer-Reil and Faubel, 1980). These authors found that fixation with Bouins solution yields a 5-fold higher retention of labelled material by meiofauna compared to fixation with formalin only and hence Bouins was used in this study.

Data on bacterial activity were obtained from 5 x 1ml aliquots of sand extracted at random from each core using a 1ml syringe with the tip removed. These subsamples were viewed under a dissecting microscope and any meiofauna present were removed. Two 1ml aliquots of sand were then set aside for counting bacteria (see Materials and Methods in Chapter 3), while the remaining three subsamples served as duplicates to determine the uptake of label by sand. Uptake by abiotic factors associated with this seston material (see below), was substracted from the total activity to give an estimate of bacterial uptake of labelled mannitol.

Meiofauna were separated from the remaining sand by swirling a core four times in distilled water. The accumulated supernatant was viewed under a dissecting microscope and nematodes, oligochaetes and turbellarians, which comprise more than 90% of the meiofaunal assemblage at Kommetjie (see Chapter 3), were counted. Meiofauna collected from the sand aliquots described above and from the sintered polyethylene disc (disc No. 2 in fig. 4.1) were added to these counts. Individuals from each taxon were transferred to separate Nucleopore membrane filters (pore size 0,45µm) with very fine forceps.

All aliquots of sand and filters with meiofauna were placed in separate scintillation vials to which 1ml Soluene-350 (Packard Instrument Co., code 600 3048) was added. This liquid is a fast acting proteinaceous tissue solubilizer with a high water holding capacity of 0,48ml H_2O ml^{-1} of Soluene-350 (Packard Manual, April 1976). The rate of solubilization was increased by warming the samples at 40°C for 24 hours. Hereafter, 10ml Dimilume-30 were added to each vial. This is a liquid scintillation cocktail manufactured by Packard (code 6013067) and specially formulated to inhibit chemiluminescence caused by alkaline substances or peroxides and to accomodate proteinaceous tissue solubilizers such as Soluene-350 (Packard Manual, April 1976). The Whatman GF/F filters used to trap bacteria escaping the sand column while under vacuum were also placed in 10ml Dimilume-30. Scintillation counts were read in disintegrations per minute (DPM) on a Packard Tricarb 460 scintillation counter.

II. Two sand cores for determining uptake by abiotic factors

One core was fixed at time zero with Bouins (see above), labelled and then incubated for a relative period. After incubation, the sand core and Whatman GF/F filter were treated as described above. This control accounted for uptake by inorganic and dead organic debris, sand grains and the glass fibre filter paper.

Another sand core was combusted at 550°C for 4 hours before adding the labelled mannitol. After incubation, 5 x 1ml aliquots of sand were removed and transferred directly to separate scintillation vials. The glass fibre filter used in conjunction with this sand core was also placed in a vial. Treatment hereafter was the same as described above. This control accounted for uptake by sterile sand and the glass fibre filter.

Scintillation counts for the two controls were substracted from those obtained for the two experimental sand cores, enabling a nett estimate of uptake by bacteria and meiofauna.

RESULTS AND DISCUSSION

Partitioning of D-mannitol between bacteria and meiofauna

Data from a year-long survey of standing stocks of fauna on Kommetjie beach revealed an inverse tidal distribution of interstitial bacteria and meiofauna, suggesting a close trophic-interrelationship between the two groups of organisms (see Chapter 3). This was further supported by comparing bacterial carbon with that of meiofauna occurring at the same locality on the beach. The biomass data presented in Appendices E and F were converted to carbon values for meiofauna and bacteria respectively using the following multiplication factors:

meiofauna:	nematodes	0,397
	oligochaetes	0,399
	harpacticoids	0,275
	turbellarians	0,333
		(from Hennig *et al*, 1983)
bacteria		0,5
		(from Luria, 1960)

A plot of bacterial carbon against meiofaunal carbon (fig.4.2) further emphasised the inverse relationship, where high biomass values of bacteria generally correspond to low values for meiofauna and visa versa.

Subsequent experiments carried out by incubating sand cores extracted from beneath decaying kelp with a labelled dissolved organic solute (D-(1-^{14}C) mannitol), provided information on the more intricate details of the above interrelationship. The numbers of individual meiofauna and bacteria per sample were converted to biomass values with reference to Appendix D. The uptake of labelled material was thus expressed as disintegrations per minute (DPM) per gram dry mass of organism and this plotted against increasing periods of incubation illustrated the relative uptake by meiofauna and bacteria at three different concentrations of mannitol (figs 4.3 and 4.4).

Meiofaunal activity increased considerably when supplied with mannitol above 1μl ml^{-1} sea water and was still on the increase when the experiment terminated

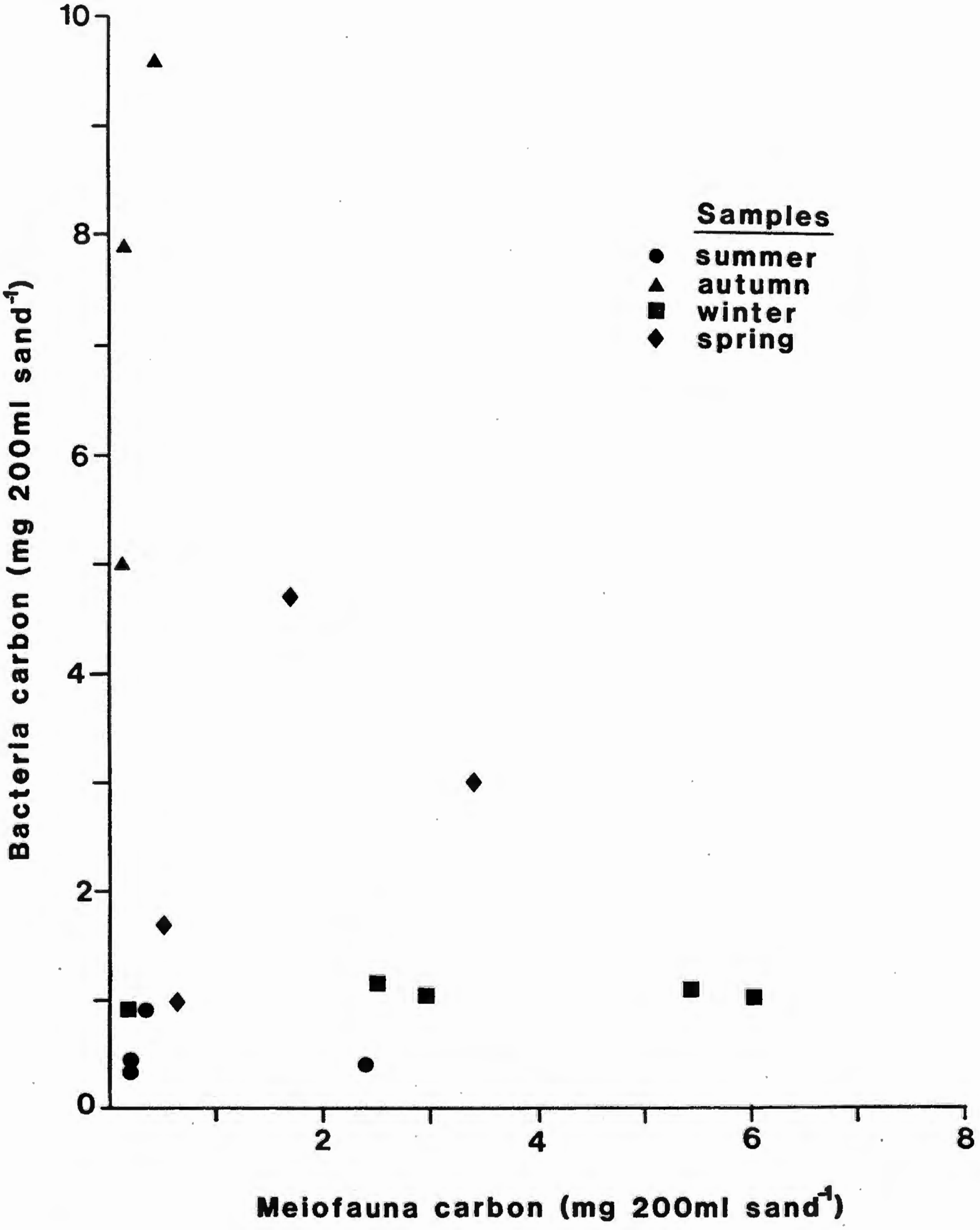

Fig. 4.2. Relationship between bacterial and meiofaunal carbon (mg 200ml sand^{-1}) in the sediment beneath stranded kelp on Kommetjie beach, Cape Peninsula. Data are derived from biomass values for meiofauna (Appendix E) and bacteria (Appendix F) occurring at the same sampling site on the beach during each season of 1981.

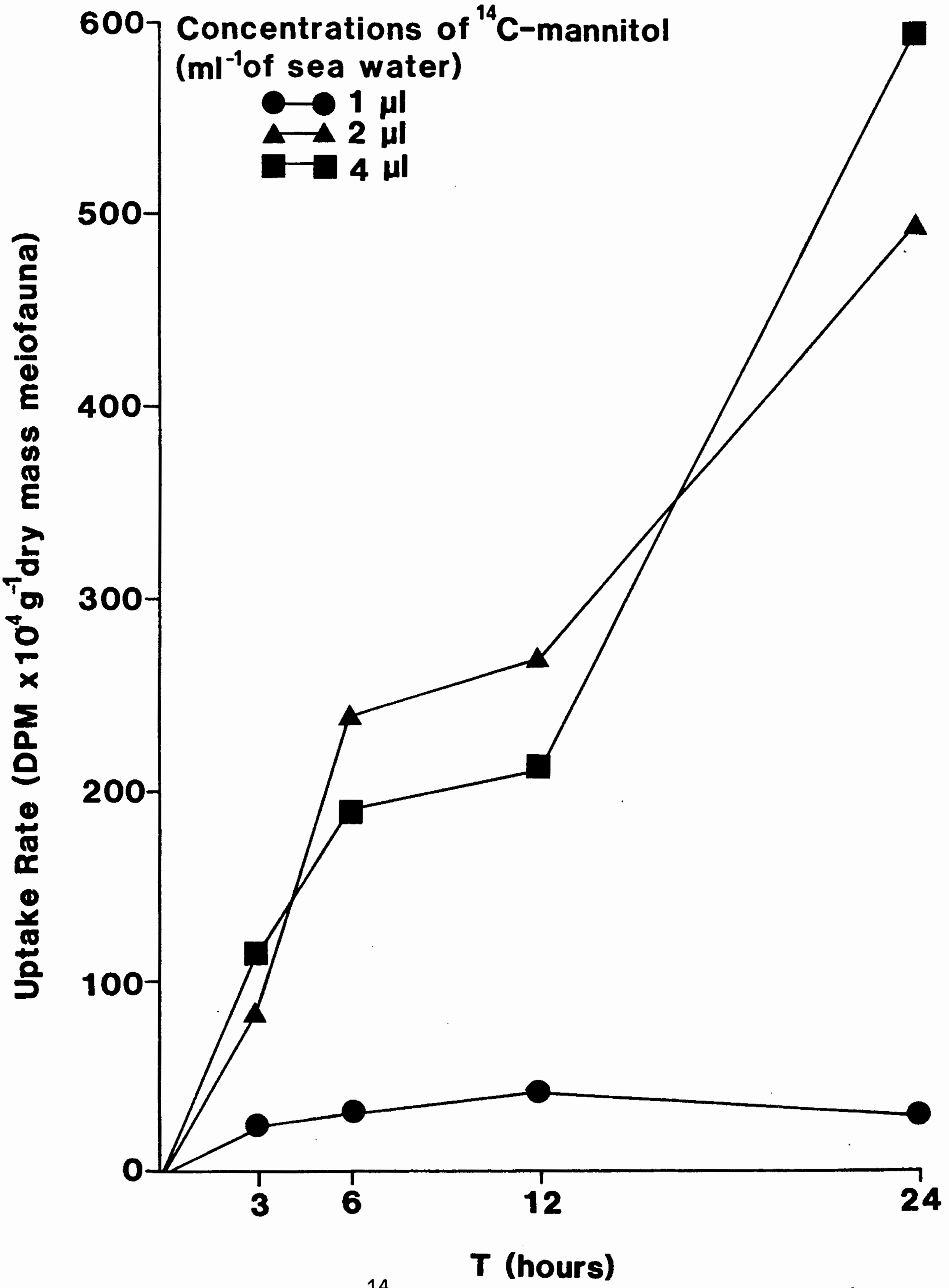

Fig. 4.3. Uptake rate of D-[1-^{14}C]mannitol by interstitial meiofauna (disintegrations per minute (DPM) x 10^{4} g^{-1} dry mass) in the presence of an _in situ_ population of bacteria extracted from beneath decomposing kelp on Kommetjie beach, Cape Peninsula. Uptake was monitored for 24 hours at three different concentrations of label (1µl, 2µl and 4µl ml^{-1} sea water).

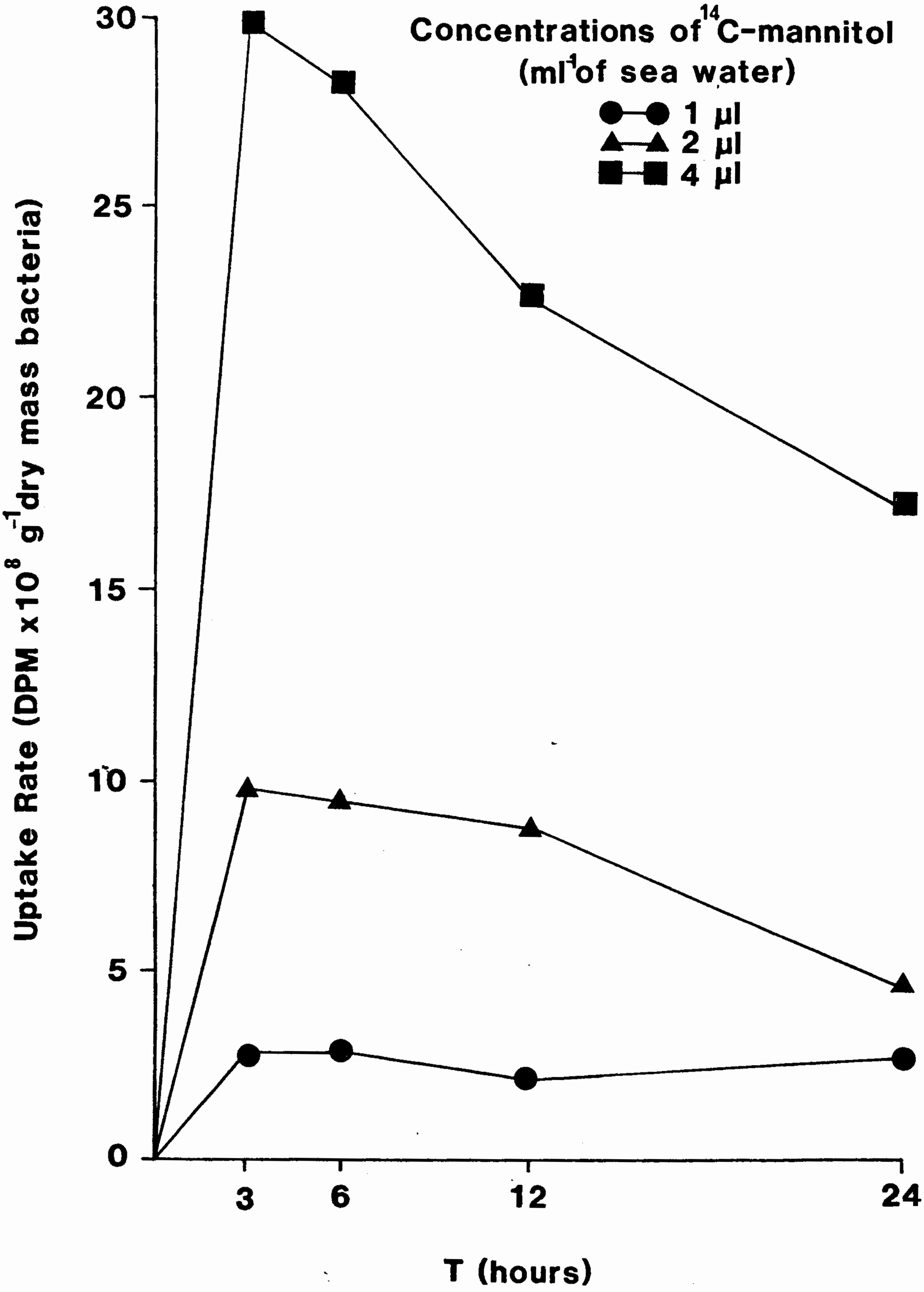

Fig. 4.4. Uptake rate of D-(1-^{14}C)mannitol by interstitial bacteria (disintegrations per minute (DPM) x 10^{8} g^{-1} dry mass) in the presence of a natural population of meiofauna extracted from beneath decomposing kelp on Kommetjie beach, Cape Peninsula. Uptake was monitored for 24 hours at three different concentrations of label (1µl, 2µl and 4µl ml^{-1} sea water).

after 24 hours (fig. 4.3). Since all values were corrected for abiotic absorption, the variation of DPM reflects biological activities and shows a general linear increase within the 24 hour incubation period. Bacterial activity, on the other hand, decreased markedly after incubation for 3 hours at concentrations of 2µl and 4µl of mannitol ml^{-1} sea water (fig.4.4). At 1µl ml^{-1} however, radioactive counts remained fairly stable. Once again an inverse relationship is shown between meiofauna and bacteria and this strengthens the hypothesis that meiofauna in the natural environment of the wrack bed ecosystem graze heavily on the bacterial assemblage. The same type of bacterial-meiofaunal interreaction was found by Meyer-Reil and Faubel (1980) when providing ^{3}H-glucose as a food source.

As kelp decays on Kommetjie beach, large quantities of organic matter leach into the interstitial environment and Koop et al (1982a) have detected dissolved carbon concentrations as high as 5640mg l^{-1} directly below surface wrack (see Chapter 2). The above authors also recorded high levels of alginates and reducing sugars other than mannitol, which was never chemically detected in the sand. However, by monitoring the mannitol content of decaying kelp on the surface of the beach over an eight day period, they recorded a loss of 70µg mg^{-1} dry mass. This indicates that high concentrations of the polyol are possible in the sand beneath kelp. It thus appears that D-mannitol is utilized by the interstitial fauna directly after leaching from surface wrack. From fig. 4.4 it can be seen that most of this uptake is by bacteria which were three orders of magnitude more radioactive per gram dry mass than meiofauna after 24 hours incubation in labelled mannitol. Such rapid uptake and incorporation of dissolved organic matter by sandy beach bacteria has been documented elsewhere especially for ^{3}H-glucose. (Meyer-Reil et al 1978, 1980). Further, Koop (1982) has found that 92% of the bacterial assemblage associated with the surface of sand grains on Kommetjie beach specifically ferment mannitol. This primary photosynthate of kelp is thus readily converted into bacterial biomass and must play a vital role in supporting the very high standing stocks recorded in Chapter 3.

The impact of meiofauna on bacterial densities

Generally two pathways are conceivable for the incorporation of dissolved organic matter (DOM) by meiofauna: direct uptake of DOM, in this study D-mannitol and/or particulate organic matter (POM) via bacteria and their extracellular products. In the former case, direct absorption can take place via the digestive tract (e.g. Chia and Warwick, 1969) and/or across the integument (e.g. Stewart, 1979; Tempel and Westheide, 1980). However, all investigations to date on direct utilization of dissolved organics are complicated by the additative uptake by bacteria attached to the body surface and gut lining of meiofauna. As long as a bacterial intermediary cannot be excluded, the importance of DOM as a major nutrient supply for meiofauna must remain doubtful. The alternative utilization of DOM via bacteria is far better substantiated in the literature (Jansson, 1968; Munro and Brock, 1968; McIntyre _et al_, 1969; Tietjen and Lee, 1977). In some of these investigations, reproducing populations of meiofauna have been maintained for over a year on a culture of DOM and bacteria only (e.g. McIntyre _et al_, 1969; Tietjen and Lee, 1977).

In this study the decrease in bacterial activity observed in fig. 4.4 cannot be explained by bacterial respiration and release of cell contents alone. Such a considerable loss of activity is obviously caused by meiofauna feeding on labelled bacteria. It seems therefore that in the natural environment beneath kelp on Kommetjie beach, dissolved organics are available to meiofauna mainly through bacteria and this is supported by the fact that approximately 90% of the nematode population is comprised of a selective bacterial feeder, _Rhabditis marina_ (see later).

Although fig. 4.4 strongly suggests that meiofauna feed heavily upon labelled bacteria, the actual number of bacteria in the experimental sand cores showed no corresponding decrease (Table 4.1). Densities from parallel experimental cores were fairly close to the matching controls, which had been fixed at time zero and thus represented a bacterial assemblage not fed upon by meiofauna (see Materials and Methods). It is therefore evident that the bacterial turnover rate was sufficient to sustain a stable population density while subjected to meiofauna predation for 24 hours. It is not valid to estimate this turnover rate, as the loss of bacterial radioactivity observed in fig. 4.4 does not reflect a decline in number alone, but also loss due to respiration, excretion and other metabolic processes.

Johannes (1965) promoted the idea that meiofauna play a vital role in preventing bacteria from reaching self-limiting numbers so that bacterial populations are kept in a "prolonged state of physiological youth". Although the data in Table 4.1 seem to support this hypothesis, it must be stressed that a 24 hour observation period is too short to make a similar generalization. Fig. 4.2 suggests that meiofauna actually reduce bacterial densities in the natural environment of the wrack bed ecosystem. The contradictory nature of these two sets of data serves to illustrate the diverse nature of bacterial-meiofaunal interactions. Meiofaunal predation cannot be considered to have a singular and negative effect on bacterial communities. Tietjen (1980) has stressed that the general activities of meiofauna in the beach sand have the potential to stimulate bacterial reproduction in several ways:

(a) Meiofauna may mechanically break down detrital particles, thereby increasing the surface area for bacterial colonization;

(b) Meiofauna may directly excrete inorganics such as nitrogen and phosphate for microbial utilization;

(c) Through the secretion of mucus, meiofauna may produce slime trials that attract and sustain bacterial growth (Riemann and Schrage, 1978);

Table 4.1 The number of bacteria ($X10^9$) associated with 30ml of sand in the presence of meiofauna and ^{14}C-mannitol for different incubation periods. C = controls; E1 and E2 = parallel experimental samples.

Incubation time (hrs)	Sample	Concentrations of D-(1-^{14}C) mannitol (μl ml^{-1} sea water) and corresponding bacterial densities ($x10^9$)		
		1 μl	2 μl	4 μl
3	C	11,06	7,99	10,12
	E1	9,20	11,10	11,49
	E2	10,03	10,10	10,94
6	C	13,60	12,10	9,06
	E1	12,46	15,39	10,64
	E2	10,64	12,29	7,74
12	C	11,11	14,92	14,19
	E1	11,15	17,45	12,06
	E2	10,86	13,79	9,95
24	C	9,32	15,47	14,38
	E1	12,46	20,68	15,91
	E2	9,74	16,34	13,09

(d) By their burrowing and swimming activities, meiofauna may act as vertical conveyors of nutrients and oxygen within the sediment (Gerlach, 1978).

Further investigation is thus necessary on the metabolic and physiological behaviour of the interstitial community at Kommetjie, before the quantitative impact of meiofauna on bacteria can be fully assessed.

Partitioning of D-mannitol between three meiofaunal groups

Figs 4.5, 4.6 and 4.7 illustrate the simultaneous uptake and incorporation of D-(1-^{14}C)mannitol by oligochaetes, nematodes and turbellarians respectively, when in the presence of an in situ bacterial population. The total activity retained by individuals in all three meiofaunal groups increased with elevated concentrations of D-mannitol, but there was a marked difference in the degree of radioactivity retained by different taxa. At the point of maximum uptake, oligochaetes were 5 times more active than either nematodes or turbellarians. This is not an indication of the relatively large size of oligochaetes (3,37μg indiv^{-1}) compared to nematodes (1,19μg indiv^{-1}) and turbellarians (2,24μg indiv^{-1}) as activity is expressed as DPM per gram dry mass of organism. A corresponding and even more contrasting situation results when activity is related to equal numbers of meiofauna, further emphasising the dominant role oligochaetes must play among the meiofauna in utilizing dissolved organics below stranded kelp.

Scintillation measurements of labelled meiofauna showed that uptake rates in all three groups depended on the period of incubation and the concentration of label. Maximum mannitol absorption occurred at a concentration of 14μl ml^{-1} after 24h in oligochaetes and nematodes, but only after 6h in turbellarians. The concentration of the food supply also had a marked effect on the pattern of uptake with time. At 2μl and 4μl ml^{-1} uptake over 24h was near linear in oligochaetes, but

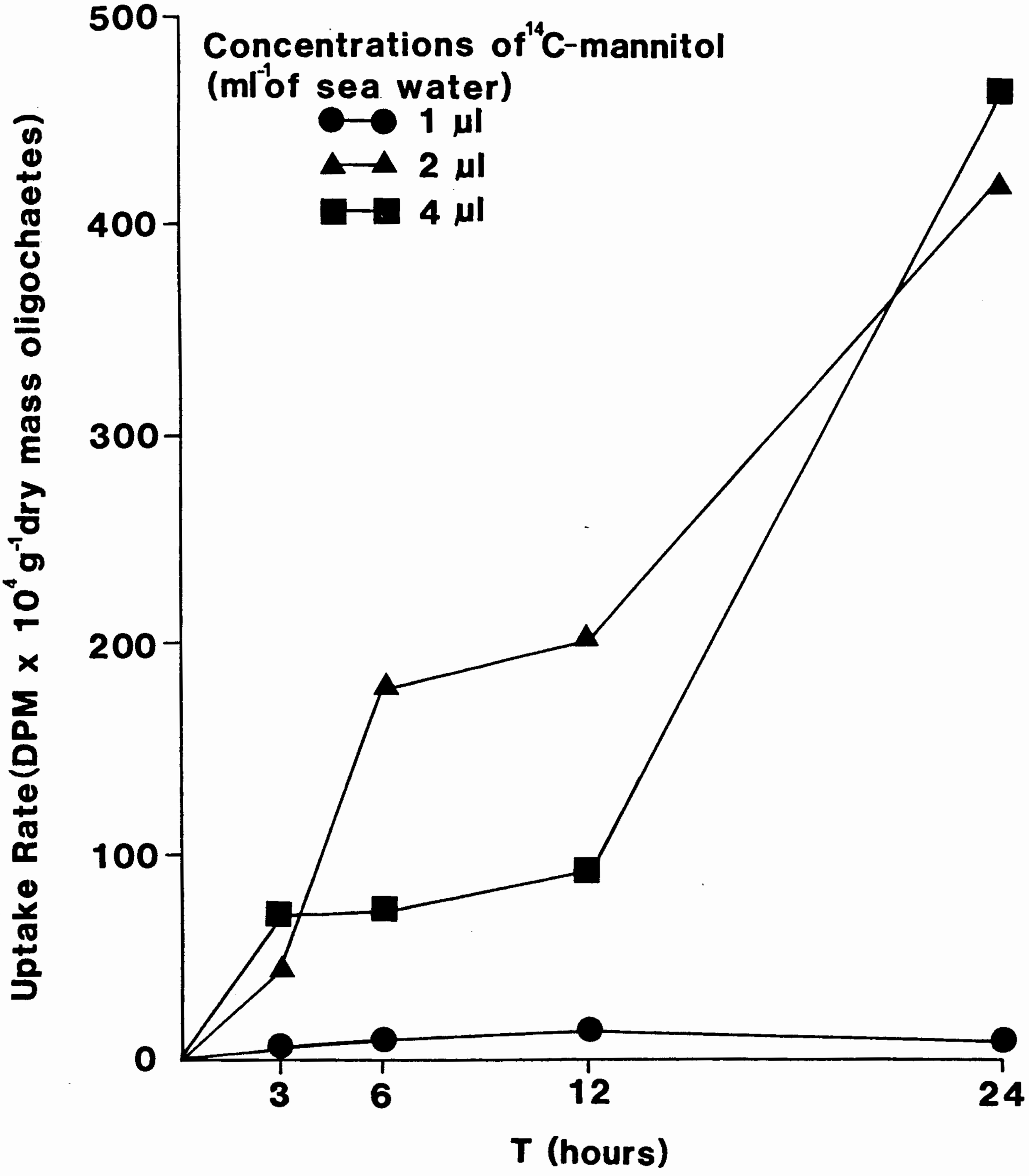

Fig. 4.5. Uptake rate of D-(1-^{14}C)mannitol by interstitial oligochaetes (disintegrations per minute (DPM) x 10^{4} g^{-1} dry mass) in the presence of an in situ population of bacteria and other meiofauna extracted from beneath decomposing kelp on Kommetjie beach, Cape Peninsula. Uptake was monitored for 24 hours at three different concentrations of label (1µl, 2µl and 4µl ml^{-1} sea water).

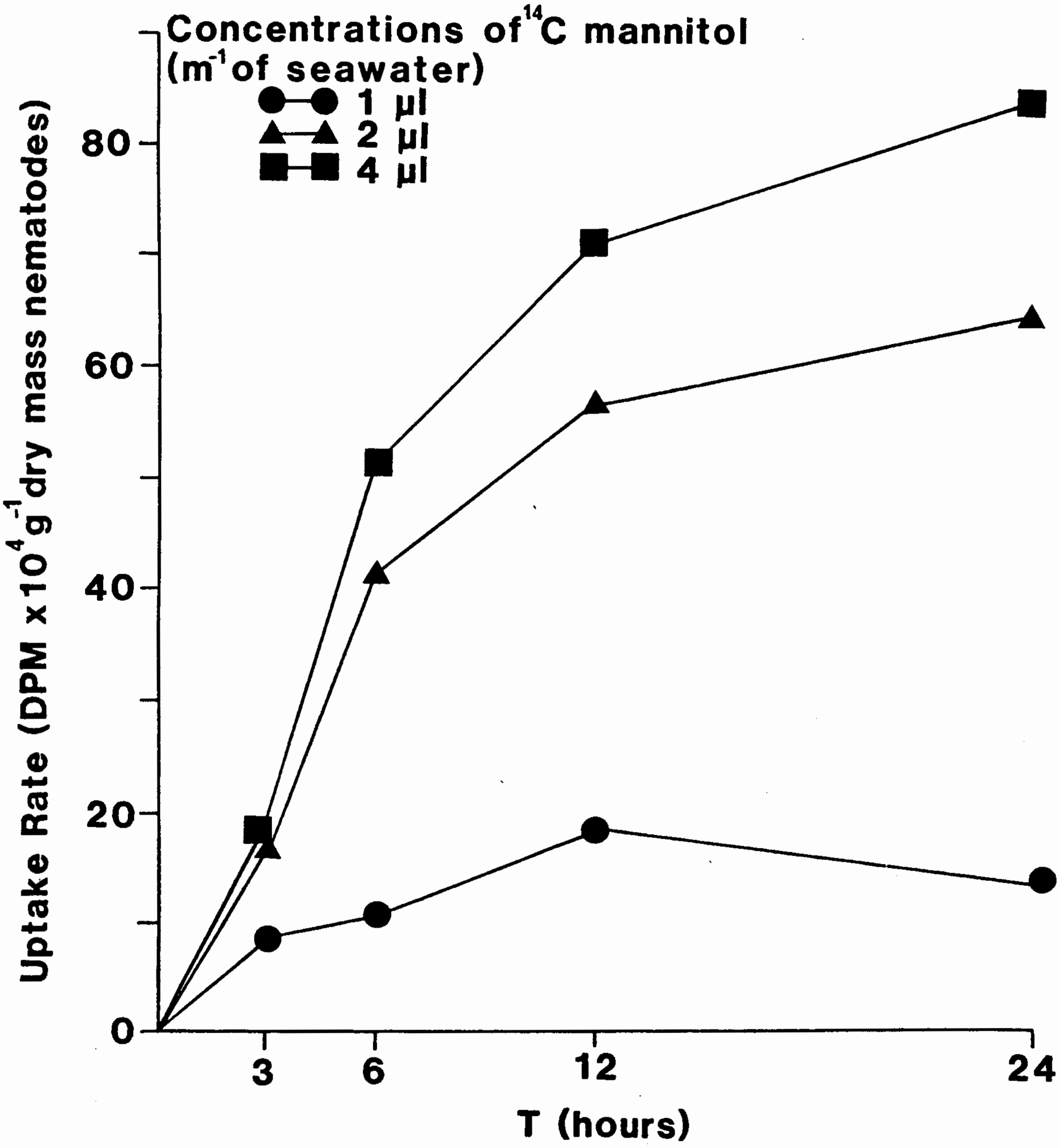

Fig. 4.6. Uptake rate of D-(1-^{14}c)mannitol by interstitial nematodes (disintegrations per minute (DPM) x 10^{4} g^{-1} dry mass) in the presence of an *in situ* population of bacteria and other meiofauna extracted from beneath decomposing kelp on Kommetjie beach, Cape Peninsula. Uptake was monitored for 24 hours at three different concentrations of label (1µl, 2µl and 4µl ml^{-1} sea water).

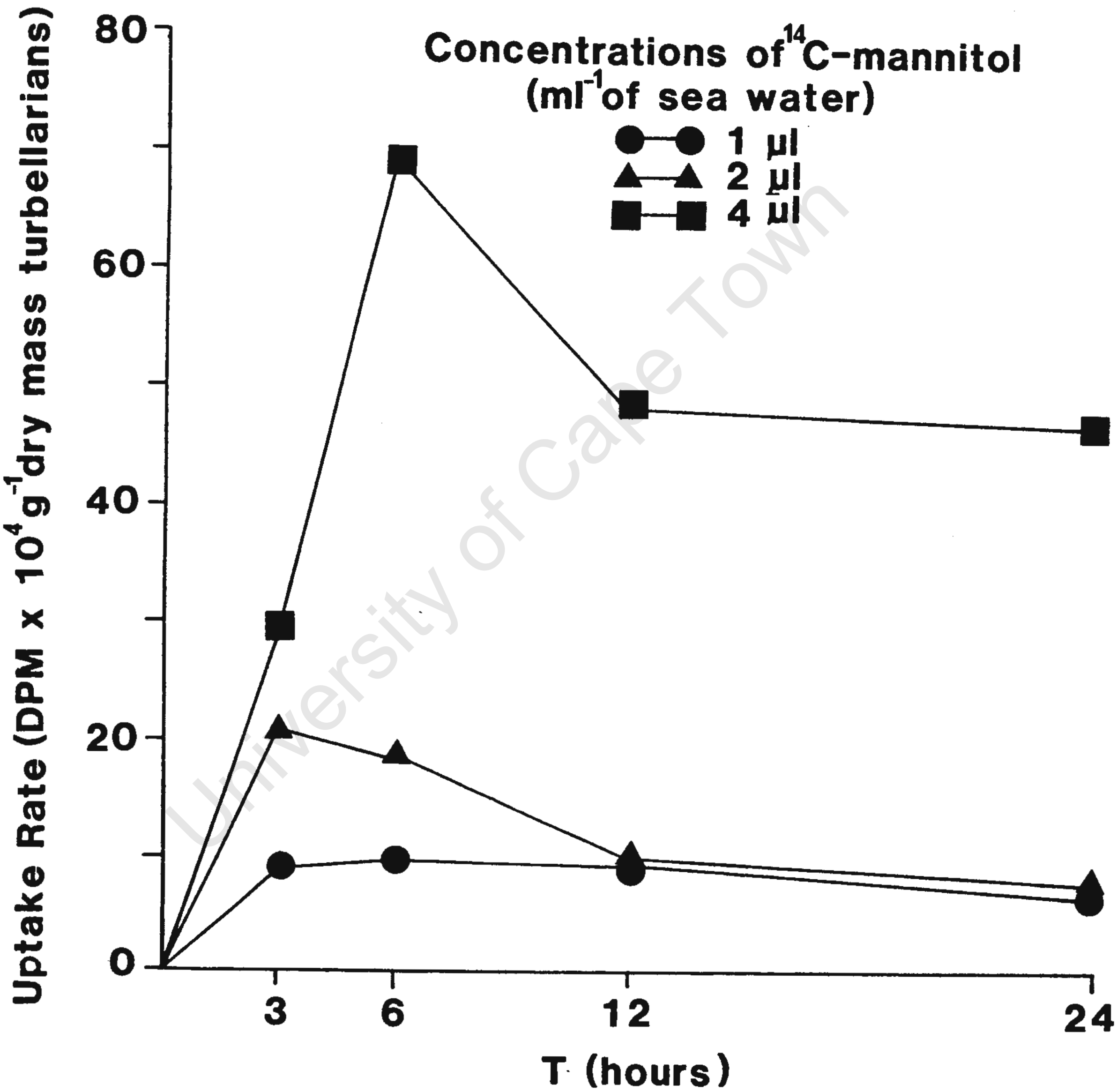

Fig. 4.7. Uptake rate of D(1-^{14}C)mannitol by interstitial turbellarians (disintegrations per minute (DPM) x 10^4 g^{-1} dry mass) in the presence of an *in situ* population of bacteria and other meiofauna extracted from beneath decomposing kelp on Kommetjie beach, Cape Peninsula. Uptake was monitored for 24 hours at three different concentrations of label (1µl, 2µl and 4µl ml^{-1} sea water).

increased exponentially in nematodes over the same time period. A linear increase occurred in turbellarians for the first 6h of incubation, whereafter activity declined. At the lowest concentration of ^{14}C-mannitol supplied (1μl ml^{-1}), activity in all meiofauna remained fairly stable, with a very small peak after 12 hours incubation.

The overall dominance of oligochaetes among interstitial meiofauna in the uptake of labelled DOM has been documented elesewhere. Meyer-Reil and Faubel (1980) incubated sand cores from beach sediments of the Western Baltic Sea in ^{3}H-glucose for 24h at 2μl ml^{-1} sea water and found that after oligochaetes, turbellarians and nematodes revealed similar rates of uptake per gram body mass and increase in activity was linear for all groups. Comparing the uptake of dissolved amino acids (^{14}C-glycine) between a different annelid group, Polychaeta and turbellarians, Tempel and Westheide (1980) found that polychaetes showed the highest activity and their uptake was linear over 26h, whereas turbellarian activity was similar to that in fig. 4.7.

Variations in the incorporation of D-mannitol by different groups of meiofaunal organisms can be related to differences in nutrition. Most of the work on feeding in meiofauna has been done on nematodes, probably because they represent the most diverse morphological group among meiofauna and thus provide a wide scope for comparative studies. Wieser (1953) proposed a classification of the types of feeding among the nematodes based on size of buccal cavity and whether armed or unarmed with teeth, and he suggested that there was a correlation between the type of buccal cavity and feeding pattern. Thus, species with large buccal cavities and no teeth may be non-selective deposit feeders; those with small buccal cavities and no teeth, selective deposit feeders; those with teeth and small buccal cavities, epigrowth feeders and those with large buccal cavities and teeth, omnivores and/or predators.

A fortuitous visit by Dr. Richard Warwick, from the Institute for Marine Environmental Research in Plymouth, U.K., enabled the identification of different feeding groups among the nematodes collected for the tracer experiments under discussion. He identified 8 genera composed of three feeding types in accordance with Wieser's classification (see Plates 4.1 - 4.8). The most striking feature of the nematode taxocene was the overwhelming dominance of Rhabditis marina (Plate 4.1). This species is cosmopolitan in distribution but is especially characteristic of conditions of fairly extreme decomposition (Inglis and Coles, 1961). The small narrow buccal cavity and lack of teeth suggest that R. marina is a selective deposit feeder, ingesting its food by means of the sucking power of the oesophagus. Tietjen et al (1970) and Tietjen and Lee (1977) have found however that this species has rather specific nutritional requirements which seem to be satisfied by a relatively restricted group of bacteria, especially Pseudomonas spp. Thus if R. marina can be considered a selective bacterial feeder, its great abundance in incubated sand cores correlates well with the high bacterial density beneath wrack (Chapter 3). It is interesting to note that in the sediment on Kommetjie beach, aerobic interstices are dominated by bacteria from the genus Pseudomonas (D. Muir, pers. comm.)+ and this coincides with areas favoured by interstitial nematodes.

One other selective deposit feeder, Haliplectus bichneri (Plate 4.2) was extremely rare in samples. Two non selective deposit feeders, Theristus sp. (Plate 4.3) and Axonolaimus sp. (Plate 4.4) were recognised by their large buccal cavities and lack of teeth. Axonolaimus spp. have been recorded to ingest large amounts of detrital material of which they utilise only a fraction, relying on associated bacteria to fulfill their nutritional requirements (Wieser and Kanwisher, 1961).

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The remaining nematode assemblage possess large buccal cavities and a varied number of teeth which suggests they are omnivores and/or predators - *Trissonchulus oceanus* (Plate 4.5), *Oncholaimus* sp. (Plate 4.6), *Haliochoanolaimus* sp. (Plate 4.7) and *Oxyonchus* sp. (Plate 4.8). In a later publication, Wieser (1960) has stressed that many nematodes that have been called "predators" on the basis of their buccal morphology actually behave as deposit feeders most of the time and hence the above classification of nematodes as omnivores/predators must be viewed with caution. For at least one of these genera however, *Haliochoanolaimus*, there are species in which predatory habits are better established than in any other species of marine nematodes (Wieser, 1960).

It is interesting to note that no epigrowth/epistrate feeders, which possess narrow buccal cavities with teeth according to Wieser's classification, were evident in samples. This may reflect the absence of diatoms in the interstitial environment below decomposing kelp on Kommetjie beach.

Unlike the diverse buccal morphology observed in Nematoda, marine littoral oligochaetes are generally similar in appearance and are mostly regarded as detrital feeders (see Giere, 1975 for review). The strong oesophageal musculature used to suck in detrital particles while burrowing through the substratum can be seen in specimens from Kommetjie beach (Plates 4.9(a), (b)). Although a large amount of detrital matter and sand grains are ingested by oligochaetes, it is believed, from both direct and indirect observations, that attached bacteria are the main food source (Giere, 1975).

Information on feeding in interstitial Turbellaria is extremely scarce but they are generally regarded as omnivores (Meyer-Reil and Faubel, 1980). Species from this taxon have been observed to feed on diatoms, detritus and the aufwuchs of sand grains (Tempel and Westheide, 1980), on the remains of dead meiofauna (McIntyre, 1969) and on living meiofauna (Jansson, 1968).

Plates 4.1 to 4.8 : Anterior views of interstitial Nematoda found associated with kelp stranded on a sandy beach at Kommetjie, Cape Peninsula. The feeding behaviour of each genus is based on the structure of buccal cavities according to Wieser's (1953) classification (see text).

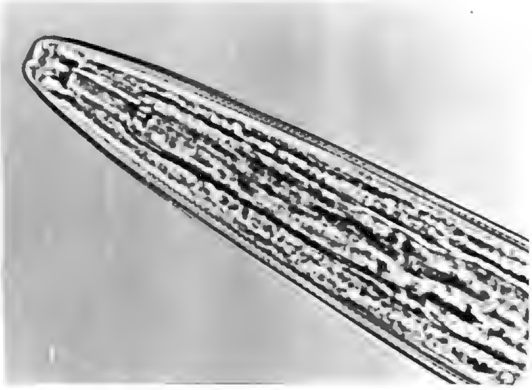

Plate 4.1. Rhabditis marina
(Scale : 1cm = 0,019mm)
selective deposit feeder

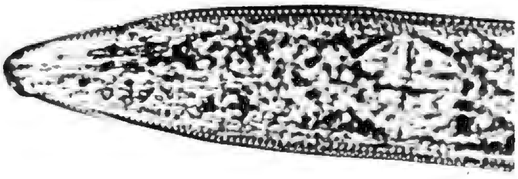

Plate 4.2. Haliplectus bichneri
(Scale : 1cm = 0,013mm)
selective deposit feeder

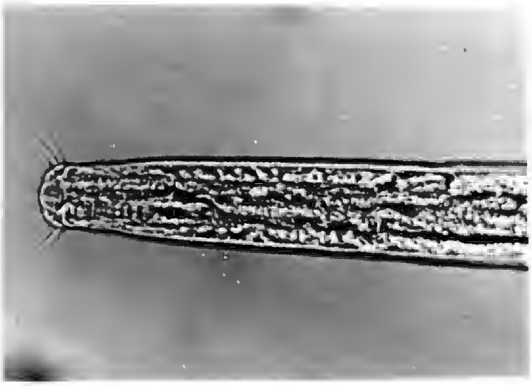

Plate 4.3. Theristus sp.
(Scale : 1cm = 0,019mm)
non-selective deposit feeder

Plate 4.4. Axonolaimus sp.
(Scale : 1cm = 0,019mm)
non-selective deposit feeder

Continued.../

Plate 4.5. Trissonchulus oceanus
(Scale : 1cm = 0,011mm)
omnivore and/or predator

Plate 4.6. Oncholaimus sp.
(Scale : 1cm = 0,025mm)
omnivore and/or predator

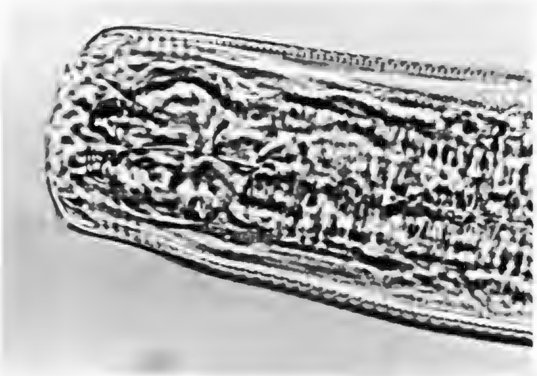

Plate 4.7. Halichoanolaimus sp.
(Scale : 1cm = 0,014cm)
omnivore and/or predator

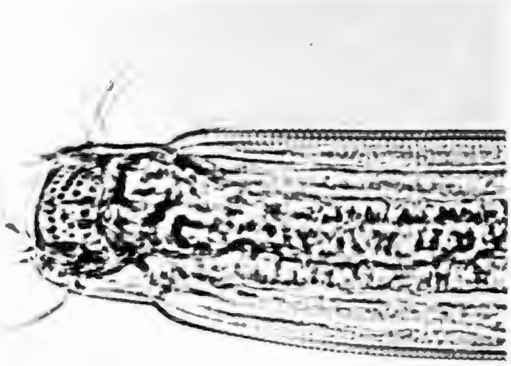

Plate 4.8. Oxyonchus sp.
(Scale : 1cm = 0,015mm)
omnivore and/or predator

Plate 4.9(a) and (b) : Antertior views of interstitial oligochaetes found associated with kelp stranded on a sandy beach at Kommetjie, Cape Peninsula. Note the well developed oesophageal musculature used to suck in detrital particles while burrowing through the sediment.

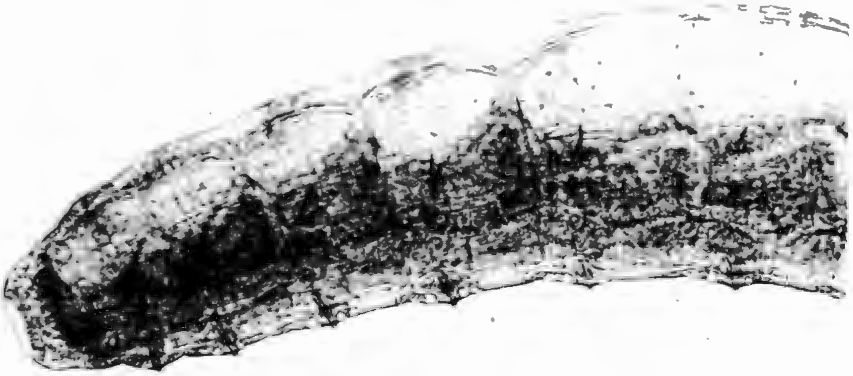

Plate 4.9(a) : Oligochaete - extended proboscis
(Scale : 1cm = 0,071mm)

Plate 4.9(b) : Oligochaete - retracted proboscis
(Scale : 1cm = 0,015mm)

The direct uptake of dissolved organics is well substantiated in nematodes (e.g. Chia and Warwick, 1969; Stewart, 1979) and turbellarians (Tempel and Westheide, 1980) but not in oligochaetes, although the latter authors have shown by autoradiography that another group within the Annelida, polychaetes, absorb dissolved amino acids across their body wall. However, as mentioned earlier in this chapter, it is doubtful whether dissolved organics taken up in this manner contribute significantly to the overall nutritional requirements of these organisms. For example, Tempel and Westheide (1980) found that in the interstitial polychaete, Hesionides arenaria, the nutritional profit of glycine absorption was only between 2% - 8%.

The above overview of feeding habits in interstitial littoral meiofauna shows that partitioning of D-mannitol is largely governed by the extent to which an intermediatory organism is incorporated into their diet. Oligochaetes, which displayed the highest radioactivity (fig. 4.5) appear to utilize only one intermediate, namely bacteria, whereas the far wider feeding habits in nematodes suggest two intermediates, namely bacteria and/or other meiofauna and thus the availability of D-mannitol is spread over a secondary and tertiary source. Turbellarians seem to fall into the same category as nematodes, which may explain why their levels of radioactivity were similar (figs. 4.6 and 4.7), but never reached those attained by oligochaetes.

CONCLUSIONS

1) Investigations of bacterial and meiofaunal distribution in the sandy beach sediment beneath decomposing kelp at Kommetjie (Cape Peninsula) indicates an inverse relationship in terms of biomass (carbon), suggesting that meiofauna graze heavily upon bacteria.

2) This relationship appears to be supported by tracer experiments in which sand cores extracted from beneath wrack were incubated with D-(1-^{14}C)mannitol, a polyol which is a primary photosyn-

thate of the dominant kelp species stranded on the beach. As the radioactivity of meiofauna increased with time, that of bacteria decreased. However, in incubated sand cores, grazing by meiofauna did not reduce bacterial density but rather stimulated the maintenance of a stable population.

3) Even though bacterial radioactivity decreased with time, their overall retention of ^{14}C-mannitol is far higher than in meiofauna, indicating that these microbes dominate the absorption of dissolved organic matter on the beach.

4) There is a clear difference in the partitioning of labelled material between the individual groups of meiofauna. Oligochaetes show the highest uptake of ^{14}C-mannitol, followed by nematodes and turbellarians. This difference is closely related to differences in nutrition. Essentially, however, all meiofauna in the wrack bed ecosystem are mainly utilizing kelp material which has been processed through heterotrophic micro-organisms before being made available as a food resource in the form of particulate and/ or dissolved organic matter.

CHAPTER 5

CONCLUSION : Kelp wrack and the flow of energy through a sandy beach ecosystem

INTRODUCTION

One of the most distinctive and frequently cited features of exposed sandy beaches as ecosystems is their almost complete lack of in situ primary production (e.g. Brown, 1964; Munro et al, 1978; McLachlan et al, 1981a). This results directly from the mobility of the sediments, which renders them unsuitable for the attachment of macrophytes or the development of dense benthic diatom communities. In the absence of these potential food resources macrofaunal organisms on exposed beaches must obtain their nutrition from imported materials. These may take the form of finely divided detritus or phytoplankton particles, many of which may originate from rich blooms of phytoplankton in the surf zone (McLachlan et al, 1981b), or large items of carrion. The macrofauna associated with these food resources normally comprises two major trophic elements, namely filter feeders, including bivalves (such as Donax) and crustacea (such as Emerita and Gastrosoccus) and predator/scavengers (e.g. Bullia, Ocypode, various isopods and polychaetes). The proportion of these two trophic elements differ widely, depending on the relative availability of plankton and detritus versus carrion (McLachlan et al, 1981a), but filter feeding bivalves are frequently the overwhelming dominants in terms of biomass (e.g. McLachlan et al, 1981b).

Certain beaches along the west coast of South Africa deviate from this generalized scheme in that they receive vast energy subsidies in the form of macrophytes uprooted from the highly productive kelp beds that dominate rocky shores along the coast (Field et al, 1980a; Newell et al, 1982). This material provides a rich food supply that is concentrated high up the beach (whereas the food supply of most intertidal organisms is more available lower down the the shore) and hence profoundly affects both the nature and distribution of the fauna. Various aspects of the ecology of high kelp-input beaches have recently received attention (Muir, 1977; Koop and Field, 1980; Stenton-Dozey and Griffiths, 1980; Griffiths and Stenton-Dozey, 1981; Koop et al 1981a,b; Chapter 3), making it possible to compute various aspects of energy flow through such a system.

This chapter aims to synthesise work presented in this thesis and other available information on high kelp-input beaches and to compare the composition, biomass and distribution of the fauna and the energy flow pattern, with those described for open sandy beaches in the Eastern Cape by McLachlan et al, (1981b). These authors suggest that the beach and surf zone may represent a more-or-less closed system in which surf zone phytoplankton, the main producers, are fed upon by a rich macrofauna dominated by filter feeding bivalves. Nutrients regenerated by the interstitial fauna and by the macrofauna are returned to the sea "in repayment of organic imports" and in turn support the surf zone phytoplankton.

RESULTS AND DISCUSSION

Rates of food supply to the beach

The estimated deposition rate of kelp on Kommetjie beach on the west coast of the Cape Peninsula is 2179kg wet mass $m^{-1} yr^{-1}$ (Chapter 2). This may be converted to energy equivalents on the basis of energy values derived from Newell et al (1982), assuming the wrack to comprise equal proportions of the kelps Laminaria pallida and Ecklonia maxima, and gives a value of 4,07 x 10^6kJ deposited per running metre of beach each year.

Trophic divisions of the macrofauna

The intertidal macrofauna of Kommetjie beach has been surveyed in Chapter 3 and the mean annual standing stocks of the major trophic groups derived from this data are presented in Table 5.1. The Amphipoda recorded in this survey consisted entirely of herbivorous species of the genus Talorchestia, and these made up over 90% of the total macrofauna. Since most of the insects were also primary consumers of kelp material, herbivores alone comprised 97% of the total intertidal macrofauna biomass.

Table 5.1 : Mean annual standing stocks of macrofaunal organisms on Kommetjie beach according to the different trophic groups.

Macrofaunal Group	Mean Annual Biomass (g dry mass m^{-1})
Herbivores	
Amphipoda	2083
Dipteran larvae	63
Herbivorous Coleoptera	28
Molluscs	11
Filter feeders	
Bivalve Molluscs	8
Carnivores	
Isopoda	42
Carnivorous Coleoptera	21
Total	2256

Consumption by primary consumers

Energy budgets are available for the two most important herbivores on Kommetjie Beach - the amphipod Talorchestia capensis (Muir, 1977) and the larvae of the kelp-fly Fucellia capensis (Stenton-Dozey and Griffiths, 1980).

The consumption rates of Talorchestia capensis given by Muir (1977) vary considerably both with temperature and animal size. At 17°C, for example, a 1 mg dry mass amphipod consumes 50% of its body mass in dry kelp per day, while one of 20 mg takes less than 20%. Equivalent figures at 21°C would be 70% and 25%. The mean mass of individual T. capensis on Kommetjie beach is about 8 mg (Appendix D) and the mean temperature beneath the wrack is 16,5°C (Appendix B). Using these figures, a mean consumption rate of 20% dry body mass d^{-1} was established. Given the energy equivalent for *Talorchestia* (Muir, 1977) of 18,13 kJ g^{-1}, the standing stock of amphipods on the beach thus has an energy value of 37,765 kJ m^{-1}. The consumption of kelp by this population would be 417g dry kelp d^{-1} or 152kg yr^{-1}. Using an energy equivalent for kelp of 14,12 kJ g^{-1} dry mass (Newell *et al*, 1982) this is equal to 2,146 x 10^{6} kJ m^{-1}yr^{-1}. From the energy budget equation of Muir (1977) this is apportioned by amphipods as shown in Table 5.2

Table 5.2 : Energy budgets for *Talorchestia capensis* and *Fucellia capensis* on Kommetjie beach (after Muir, 1977 and Stenton-Dozey and Griffiths, 1980).

	C	=	Pg	+	Pr	+	R	+	F	+	U
Talorchestia capensis											
kJ m^{-1}yr^{-1} x 10^{3}	4293		81		26		378		2095		1713
%	100		1,9		0,6		8,8		48,8		39,9
Fucellia capensis											
kJ m^{-1}yr^{-1} x 10^{3}	584		105		-		123		(356)		
%	100		18		-		21		(61)		

A similar analysis may be made for larvae of the kelp fly *Fucellia capensis* from data given by Stenton-Dozey and Griffiths (1980). Fly larvae have an energy value of 25,8 kJ g^{-1} and consume 1,8 times their dry mass in kelp d^{-1}.

Since the mean population of larvae is 63g m^{-1} (or 1625,4 kJ m^{-1}), total consumption is 63 x 1,8 x 365g or 41,4kg dry kelp $m^{-1}yr^{-1}$, which is equivalent to 0,584 x 10^6 kJ (27% of the figure of amphipods). Ingested energy is is expended as shown in Table 5.2.

There is no equivalent data for the herbivorous Coleoptera, which have a biomass of 28g m^{-1} of beach (1,3% of total herbivore biomass). For energy budgeting purposes it has been assumed that they have an energy equivalent of 15,0 kJ g^{-1} and eat their own body weight of kelp per day, i.e., 28 x 265g = 10kg $m^{-1}yr^{-1}$ or 141200 kJ $m^{-1}yr^{-1}$.

The mollusc fauna has also not received attention, since it makes up less than 1% of total consumer biomass (in contrast to the situation in areas studied by McLachlan _et al_, 1981_b_ and others). The only molluscs recorded were small ($<$1mm) bivalves, dominated by ?_Neogaimardia kowiensis_ and herbivorous gastropods, mostly _Eatoniella nigra_. For the purposes of this analysis it has once again been assumed that these organisms eat their own dry flesh mass in kelp per day. Assuming this to be 10% of the whole mass (flesh + shell) this would be 1,1 x 365g or 402g dry kelp $m^{-1}yr^{-1}$ for the herbivores and 292g dry mass for the filter feeders, giving a total of 694g or 9799 kJ $m^{-1}yr^{-1}$. For the energy value of small molluscs the value of 1,77 kJ g^{-1} whole dry mass given for mixed small molluscs by Field _et al_ (1980_a_), has been used. This gives a value of 34 kJ m^{-1} beach.

Consumption by carnivores

The herbivorous macrofauna on Kommetjie beach are preyed upon by a variety of wading and non-wading birds, by carnivorous isopods (mainly _Eurydice longicornis_ and _Exosphaeroma truncatitelson_) and by a variety of carnivorous Coleoptera of the families Staphylinidae, Histeridae, Tabaridae and Carabidae.

The distribution and numbers of coastal waders found along the beaches of the south-western Cape are given by Summers _et al_ (1977) and from their unpublished data it has been possible to extract figures specifically for Kommetjie beach. Equivalent counts for non-wading birds have been obtained from unpublished records of the Western Cape Wader Study Group. The feeding ecology, mass and energy requirements of each species are given by Hockey _et al_ (1983). From these figures the annual energy requirements of the avifauna can be calculated. A number of assumptions must be made as regards the lengths of time migratory species feed on South African beaches and the dependency of non-waders on intertidally collected foods, and Hockey _et al_ (1983) have been followed in this regard. The numbers, biomass and energy requirements of the avifauna of Kommetjie beach, as derived from the above sources, are given in Table 5.3. The total of 357 birds found per km of beach have a biomass of 54 738g (wet). Given a dry to wet mass conversion of 0,4 : 1 and energy value of 22,5 kJ g^{-1} dry mass (McLachlan _et al_, 1980) this is equal to 21,9g dry mass m^{-1} or 493 kJ m^{-1} beach. The total energy requirements of these birds derived from Table 5.3, is 16094 kJ $m^{-1} yr^{-1}$ which is 33 times their standing stock and represents 40% of the invertebrate biomass or 16% of production, assuming a $P/\bar{B}$ ratio of 2,5 (McLachlan, 1977_c_; Koop and Griffiths, 1982).

Since the assimilation efficiency of wading birds is approximately 73% (Hockey _et al_, 1983) they probably return some 4 000 kJ $m^{-1} yr^{-1}$ to the beach in the form of faeces.

Table 5.3 : Abundance, biomass and energy requirements of the avifauna of Kommetjie Beach. Abundance of wading birds after Summers _et al_ (1977) and for non-wading birds from unpublished data of Western Cape Wader Study Group. Biomass and daily energy requirements from Hockey _et al_ (1983). Only birds with an abundance of more than one individual per km are included in the analysis.

Species	No. birds per km	Biomass km^{-1} (g wet mass)	Energy expenditure per bird (kJ day^{-1})	Annual expenditure kJ $km^{-1}yr^{-1}$ x 10^3
Resident waders				
Black oystercatcher	4,8	3321	641,8	1124
White-fronted plover	9,3	418	107,5	365
Migrant waders				
Ringed plover	2,0	97	110,6 (x 150 days)	33
Curlew sandpiper	58,2	3259	124,0 (x 150 days)	1082
Sanderling	143,2	7876	122,6 (x 150 days)	2663
Common sandpiper	1,0	57	125,5 (x 150 days)	19
Non-waders				
Hartlaubs gull	133,8	39604	367,9 (x 60%)	10780
Cape wagtail	4,6	106	69,4 (x 50%)	58
Total	356,9	54738		16094

No energy budget data are available for the carnivorous isopods _Eurydice longicornis_ or _Exosphaeroma truncatitelson_, although various aspects of their ecology have been described by Brown (1973). Both species are known to feed on _Talorchestia_ and other amphipods, dead or dying molluscs and virtually any other available animal material. The only South African carnivorous isopod for which consumption estimates can be derived is the sublittoral _Cirolana_ imposita, which has been studied by Shafir and Field (1980). These authors give the following energy budget for a population with a mean standing stock of 394 kJ m^{-2} (26,8g dry mass) at Oudekraal, on the Cape Peninsula.

	C		Pg		Pr		R		F		U
kJ m^{-2}yr^{-1}	9899	=	1891	+	338	+	1822	+	977	+	-
%	100	=	19	+	3	+	18	+	10	+	(50 - by subtraction)

Note that the consumption estimate in this equation exceeds the combined total for energy expenditure by a factor of two, suggesting that C was considerably overestimated, a common failing in laboratory feeding experiments (Shafir and Field, 1980). In the light of this probable overestimate and Johnson's (1976) estimate that C in an intertidal species of Cirolana is only 6,78 x B, the annual consumption rate has been taken as ten times the standing stock, rather than the 25 times calculated from Shafir and Field (1980). Given the biomass of carnivorous isopods on the beach (42g m^{-1}) and using the energy equivalent for C. imposita given by Shafir and Field (1980), the standing stock of isopods is 617 kJ m^{-1} and total annual consumption is 6166 kJ m^{-1}yr^{-1}, which is equivalent to 15% of the standing stock of primary consumers on the beach or 6% of their annual production. This is considered to be a maximum estimate since both the major isopod species probably obtain a good percentage of their food in the form of carrion washed up on the beach and from prey which are of sublittoral origin.

No data are available for the carnivorous Coleoptera, other than descriptive accounts of the diets of various species (Backlund, 1945; Cheng, 1976). It has thus been assumed that their energy equivalent is 15 kJ g^{-1} dry mass, as for herbivorous forms, and their consumption rate is 10 times their standing stock per year. This gives a standing stock of 315 kJ m^{-1} and consumption estimate of 3150 kJ m^{-1}yr^{-1}.

Energy flow through the macrofaunal community

From the results presented above it is possible to construct an energy flow diagram for the high kelp-input beach at Kommetjie (Fig. 5.1). As in other beaches the macrofauna relies entirely on material imported from the sea to meet its nutritional requirements. The most important component of these imports at Kommetjie is undoubtably kelp wrack, which has an energy equivalent of over 4×10^6 kJ $m^{-1}yr^{-1}$. This is more than 30 times the combined input of detritus, phytoplankton and carrion reported for a beach near Port Elizabeth by McLachlan et al (1980b). Although small amounts of carrion (largely dead sponges and ascidians) were observed on Kommetjie beach, the presence of surf zone phytoplankton blooms was not recorded. It thus seems reasonable to assume that the enormous influx of kelp accounts for at least 95% of the food supply of the macrofauna in this area.

Since the major food resouces, kelp wrack, is deposited high on the beach, the macrofauna is concentrated around the drift line and is composed largely of terrestrial and semi-terrestrial species. For this reason species diversity, as well as biomass, tend to decline towards the low water mark (see Chapter 3). Amphipods of the genus Talorchestia are the major herbivores (95% by energy) and consume 52,7% of the kelp deposited on the beach, as opposed to 14,5% for kelp fly larvae and 3,5% for hervivorous Coleoptera. Total calculated consumption for the herbivores thus amounts to 70,7% of annual kelp deposition. The remaining 29,3% is thought to be degraded by bacteria and to either wash back into the sea at high tide or enter the sand column in dissolved or particulate form. The assimilation efficiency of both the major herbivores is, however, low, so that much of the material they eat is also returned to the beach in the form of faeces or excretory products. The organic input into the sand column is thus relatively insensitive to variations in the proportions of wrack decomposing or being eaten by macrofaunal herbivores (Koop et al, 1982a).

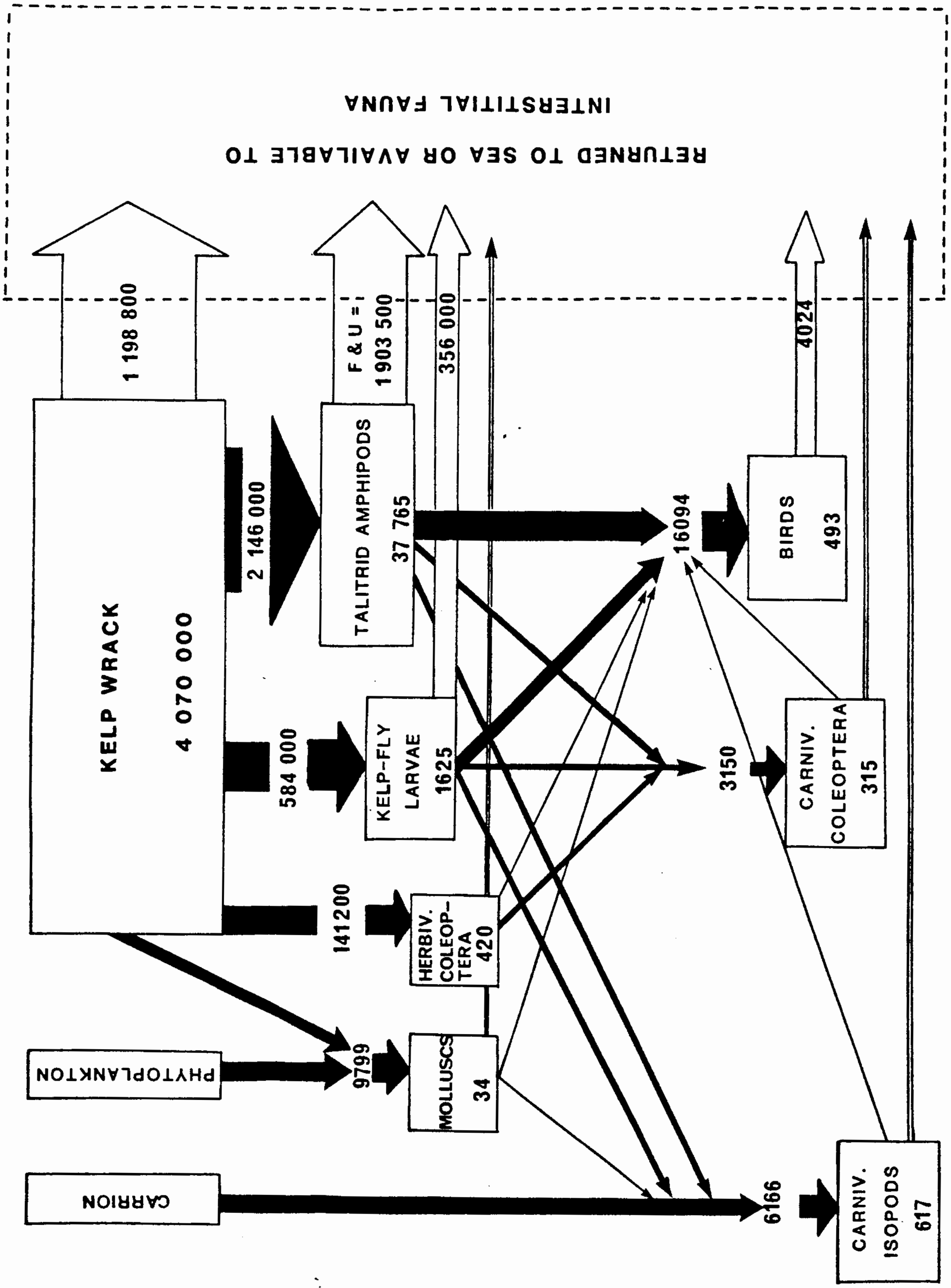

Fig. 5.1. Energy flow diagram for a sandy beach with high kelp input at Kommetjie, Cape Peninsula. Figures in boxes are mean annual standing stocks in kJ m^{-1}, or in the case of kelp wrack, annual input in kJ m^{-1} yr^{-1}. Arrows show annual flows in kJ m^{-1} yr^{-1}.

Three principal groups of macrofaunal predators occur on the beach - birds, isopods and carnivorous Coleoptera. All three groups have similar standing stocks, but the birds are the most important predators because of their high energy requirements. It is estimated that the avifauna removes some 40% of herbivore standing stock and the Coleoptera about 8%. Although the energy requirements of the isopods are equivalent to 15% of herbivore standingstock, much of this may be met by consumption of carrion deposited in the intertidal zone. Predation by fish has not been considered as this is thought to be low, because the fauna is so concentrated around the driftline. It may, however, become available to marine predators when flushed out of the wrack during storms. Since the assimilation efficiency of carnivores is high compared to that of herbivores, little of the food consumed by them finds its way back into the beach in the form of faeces.

This situation is very different from that depicted for open beaches in the Eastern Cape by McLachlan _et al_ (1981 _a_ and _b_). Here detritus and phytoplankton comprise over 90% of the food supply and support a fauna dominated by filter feeders such as _Donax_ and _Gastrosaccus_ (97,8%) and the scavenger _Bullia_ (1,75%). These in turn are preyed upon by fish, birds and crabs. Neither amphipods, isopods nor insects form significant components of the fauna and very few macrophytes are deposited on the beaches.

Interstitial fauna and energy flow

The standing stocks and distribution patterns of meiofauna and bacteria on Kommetjie beach are given in Chapter 3. To summarise, the mean annual standing stock of meiofauna was 624g m^{-1} and that of bacteria 961g m^{-1} (since the biomass of macrofauna was 2256g m^{-1}, this gives a biomass ratio of macrofauna : meiofauna : bacteria of approximately 3,5 : 1 : 1,5).

The energy supply to interstitial systems is in the form of particulate or dissolved organic matter that percolates into the sand, often in association with tidal or wave action or rainfall. In a high kelp-input beach this material consists predominantly of decomposed algae or the faeces and excretory products of its consumers. The rates of production of these materials are given in Fig. 5.1. Although an unknown proportion of this energy may be swept back into the sea during high tides (the first waves to inundate wrack banks often run brown with detritus), it is believed that most of it ultimately enters the sand column.

The total amount of organic material entering the sand is estimated as $3{,}5 \times 10^6$ kJ $m^{-1}yr^{-1}$, or 85% of the total input of the beach. The fate of this material has been investigated by Koop *et al* (1982*a* and *b*), who used a microcosm technique to show that over 90% of the carbon leaching from decomposing kelp was utilized by bacteria and/or meiofauna during drainage through a 1m long sand column. By comparing rates of utilization of carbon derived from kelp material with simultaneous increases in bacterial biomass in their microcosm they calculate that 28% of the carbon entering the sand is converted into bacterial carbon. Most of this carbon is respired by the bacteria and very little of it percolates back into the sea.

Extrapolating to the field survey, the mean annual standing stock of bacteria on the beach was 961g dry mass m^{-1}. At 28% conversion efficiency, production of this biomass of bacteria would require an input of $961 \times {}^{100}/_{28}$ or 3432g kelp debris, which is equivalent to 48462 kJ. The actual estimated input is $3{,}5 \times 10^6$ kJ, so that if this were all utilized by bacteria, sufficient energy would be available for them to have a production to biomass ($P/\bar{B}$) ratio of $\frac{3432}{48{,}5}$ or 70 times per year. This should be taken as a maximum figure, since bacteria may in fact suffer periods of food shortage interspersed with ones of surfeit and meiofauna may also compete with them for the available food resources (see Chapter 4). However in Chapter 3 it was stressed that the bacterial biomass at Kommetjie may have been substantially underestimated by considering bacteria in the sand column only and excluding those associated with the surface of decomposing kelp itself (Koop *et al*, 1981*a*). If the biomass were larger, the available energy would support fewer turnovers per year and thus the maximum estimate of a $P/\bar{B}$ of 70 for bacteria can be considered to correlate fairly well with the figure of 30 proposed by Koop and Griffiths (1982) from literature values.

The meiofauna are thought to feed principally upon bacteria (see Chapter 4) and have been estimated to have an annual food requirement of 50 times their biomass (Gerlach, 1978). Given the standing stock of meiofauna on Kommetjie beach (624g m^{-1}) this gives an annual consumption rate of 31,2kg $m^{-1}yr^{-1}$ bacteria, which could be supplied by a bacterial turnover of $\frac{31200}{961}$ = 32 times per year. This agrees well with the estimates of bacterial turnover and suggests that the interstitial environment is a relatively closed system in which bacteria absorb almost all of the available organic input and bacterial production is almost entirely consumed by the meiofauna.

CONCLUSIONS

1) The main source of energy for sandy beaches in the vicinity of kelp beds along the south west coast of South Africa is kelp wrack. Over 2 metric tons (wet mass) or 4 x 10^6 kJ of this material may be deposited on each metre of beach per annum.

2) Since this food resource is concentrated along the drift line, this is the zone of maximum macrofaunal species richness and biomass. The macrofauna consists predominantly of semi-terrestrial amphipods and insects and has a standing crop of over 2kg m^{-1} (dry mass), of which Talitrid amphipods comprise over 90%.

3) Calculated kelp consumption by herbivores on the beach amounts to 71%

of deposition. The remaining 29% of the wrack is degraded by bacteria and either enters the sand column or is washed back into the sea. Much of the material eaten by herbivores is also returned to the beach in the form of faeces or of excretory products.

4) Macrofaunal herbivores are consumed by predatory birds, isopods and Coleoptera. These are thought to take 40%, 15% (maximum) and 8% of overall herbivore standing stock per year, respectively, or a total of 63% of biomass, but since the production to biomass ratio of the macrofauna is approximately 2,5 this is only 25% of macrofaunal production.

5) Dissolved or particulate kelp debris that enters the sand column is rapidly utilized by bacteria and by a rich meiofauna that is dominated by nematodes and oligochaetes and is concentrated beneath the driftline.

6) Bacteria can convert kelp detritus into bacterial biomass with up to 28% efficiency and, given the available energy resources, may have a $P/\bar{B}$ ratio of 30 - 70. Meiofauna may directly absorb dissolved organic matter, but the inverse relationship of meiofaunal and bacterial biomass in the field and evidence from tracer experiments, indicate that they feed primarily on bacteria.

7) Meiofaunal food requirements total approximately 32 times the bacterial standing stock of 961g, indicating that they consume virtually all the bacterial production.

8) Most of the carbon in wrack deposited on the beach is ultimately dissipated as CO_2 through respiratory losses by bacteria or meiofauna. Nitrogen is efficiently retained by the bacteria and may thus ultimately find its way back to the sea. The amounts of nutrients returned to the nearshore zone are, however, insignificant in relation to the nutrient demands of the macrophytes and phytoplankton,

9) Beaches of this type are thus not closed ecosystem (cf. McLachlan *et al*, 1981*b*), but energy sinks, which rely upon imported debris to support internal food chains and which return only limited inorganic nutrients to the sea.

APPENDIX

APPENDIX A

Programme 1 : Calculation of the volume of sea water filtered into Kommetjie beach in one set of data collected over 15 minutes.

```
10    REM KOMMETJIE BEACH FILTRATION
20    REM RAW DATA
30    V=0
40    INPUT "INPUT NUMBER OF READINGS";N
50    INPUT "INPUT NUMBER OF MINUTES";T
60    FOR I=1 TO N
70    INPUT L,H
80    LPRINT L,H
90    REM CONVERT H FROM CM TO M
95    H=H/100
110   X=L*H*(.0071*H+.0017)
120   V=V+X
130   NEXT
140   V=60*V/T
150   LPRINT "  "
160   LPRINT "VOLUME";V
170   END
```

Programme 2 : The calculation of the volume of sea water filtered into Kommetjie beach per day by integrating the data of Programme 1 over a tidal cycle.

```
10    INPUT "INPUT NUMBER OF READINGS";N
20    V3=0
30    INPUT "INPUT T,V";T,V
40    LPRINT T,V
50    T1=T
60    V1=V
70    T=0
80    T2=0
90    V2=V
100   FOR X=2 TO N
110   INPUT "INPUT T,V";T,V
120   LPRINT T,V
130   T=T-T1
140   V3=V3+(V+V2)*(T-T2)/2
```

APPENDIX A

Programme 2 continued:

```
150  T2=T
160  V2=V
170  NEXT
180  T=12.43
190  V=V1
200  V3=V3+(V+V2)*(T-T2)/2
210  LPRINT "TOTAL VOLUME PER TIDAL CYCLE IS";
     V3 "CUBIC METRES PER METRE STRIP"
220  LPRINT " "
230  V4=V3*24/12.43
240  LPRINT "TOTAL VOLUME PER DAY IS " ;V4 "CUBIC
     METRES PER METRE STRIP"
250  END
```

```
 1            0
 2            4.12227E-03
 3            .0140657
 4            .496546
 5            .804459
 6            .0909356
 7            .044313
 8            .0261712
 9            0
 10           0
 11           0
 12           0
TOTAL VOLUME PER TIDAL CYCLE IS 1.48061 CUBIC METRES
PER METRE STRIP
TOTAL VOLUME PER DAY IS 2.85879 CUBIC METRES PER METRE
STRIP
```

APPENDIX B

Fluctuations in the temperature of the air, in wrack banks and in the sand at 30 cm depth intervals to the water table at different tide levels on Kommetjie beach, Cape Peninsula.

Month and tide level		Temperature (°C) at midday				
		ambient	in wrack	in sand at different depths (cms)		
				0 - 30	30 - 60	60 - 90
January	LWS	26	20	16	17	
	MW		19	17	17	
	HWS		24	26	24	
February	LWS	21	21	19		
	MW		22	21	21	21
	HWS		24	22	21	21
March	LWS	25	21			
	MW		22			
	HWS		27			
April	LWS	24	21	18	18	
	MW		21	20	19	
	HWS		18	21	20	
May	LWS	24	15	15		
	MW		14	15	15	
	HWS		19	17	17	17
June	LWS	17	11			
	MW		12			
	HWS		15			
July	LWS	14	12	13	14	
	MW		13	12	14	
	HWS		13	13	14	
August	LWS	16	14	14		
	MW		13	12	13	
	HWS		15	13	14	14

APPENDIX B continued

Month and tide level		Temperature (°C) at midday				
		ambient	in wrack	in sand at different depths (cms)		
				0 - 30	30 - 60	60 - 90
September	LWS	14	13			
	MW		13			
	HWS		13			
October	LWS	16	18	17	18	
	MW		18	18	18	
	HWS		21	20	19	
November	LWS	18	18	15		
	MW		20	16	20	
	HWS		30	20	20	20
December	LWS	17	21			
	MW		20			
	HWS		26			

APPENDIX C

Abundance (numbers m^{-1}) and tidal distribution of the species of macrofauna found associated with kelp stranded on Kommetjie beach

A = adult JUV = juvenile L = larva P = pupa

LWS = low water springs MW = mid water HWS = high water springs

				January		
CLASS	ORDER	FAMILY	SPECIES	LWS	MW	HWS
Crustacea	Amphipoda	Talitridae	Talorchestia capensis (A)	-	-	4500
			Talorchestia capensis (JUV)	-	-	9000
			Talorchestia quadrispinosa	-	-	-
		Eusiridae	Paramoera capensis	7375	-	-
		Amphilochidae	Gitanopsis pusilla	-	-	-
	Isopoda	Sphaeromatidae	Exosphaeroma truncatitelson	26375	167	188
		Cirolanidae	Eurydice longicornis	2500		563
Bivalvia	Veneroida	Gaimaridiidae	? Neogaimaridia kowiensis	11375	5250	6563
		Lasaeidae	Kellia rotunda	-	-	375
	Mytiloida	Mytilidae	Choromytilus meridionalis (JUV)	-	83	2250
Gastropoda	Mesogastropoda	Eatoniellidae	Eatoniella nigra	250	83	-
	Archaeogastropoda	Phasionellidae	Tricolia neritina	-	-	-
			Tricolia capensis	-	-	-
	Neogastropoda	Buccinidae	Burnupena sp. (JUV)	-	-	-
Insecta	Diptera	Anthomyiidae	Fucellia capensis (L)	125	167	25500
			Fucellia capensis (P)	-	-	-
			Fucellia capensis (A)	4000	2667	1313
		Coelopiidae	Coelopa africana (L)	-	-	-
			Coelopa africana (P)	-	-	1500
			Coelopa africana (A)	-	-	-
			Unidentified sp. (L)	125	167	17063
			Unidentified sp. (P)	-	-	5625
			Unidentified sp. 1 (A)	375	417	3000
			Unidentified sp. 2 (A)	-	-	-
	Coleoptera	Tenebrionidae	Pachyphaleria capensis (L)	125	-	-
			Pachyphaleria capensis (A)	-	-	375
		Staphylinidae	Aleochara salsipotens (A)	-	-	2812
			Bledius sp. (A)	-	-	-
			Cafius xantholoma (A)	-	-	-
			Omalium sp.	-	-	-
			Unidentified sp. (L)	-	-	375
		Histeridae	Acritus lightfooti (A)	-	-	2063
			Pachylopus sp. (A)	-	-	-
			Pachylopus sp. (L)	-	-	-
			Unidentified sp. (L)	-	-	1125
		Hydrophilidae	Cercyon maritimus (L)	125	-	-
			Cercyon maritimus (A)	-	-	750
		Melyridae	Colpometopus basicornis (A)	-	-	-
			Unidentified sp. (L)	-	-	938
		Tabaridae	Limata sp. (L)	-	-	563
		Empididae	Unidentified sp. (L)	-	-	-
		Hydrophilidae	Unidentified sp. (L)	-	-	6938
		Cossoninae	Curulionidae (sub-family) (A)	-	-	-
			Gymnetron sp. (A)	-	-	-
		Chrysomelidae	Phyllotreta sp. (A)	-	-	-
	Hemiptera	Cicadellidae	Unidentified sp.	-	-	-
Arachnida	Araneida	Philodromidae	Unidentified sp.	-	-	-

Appendix C continued : Monthly abundance (numbers m^{-1}) and tidal distribution of macrofaunal species.

SPECIES	February			March			April		
	LWS	MW	HWS	LWS	MW	HWS	LWS	MW	HWS
Talorchestia capensis (A)	-	43000	38250	-	9100	1350	-	-	137
Talorchestia capensis (JUV)	142	258250	7350	-	615314	22613	-	1733	2487
Talorchestia quadrispinosa	-	1500	-	-	-	-	-	867	37
Paramoera capensis	283	-	-	667	-	-	-	1733	-
Gitanopsis pusilla	142	-	-	-	-	-	-	-	-
Exosphaeroma truncatitelson	12892	250	-	1000	867	-	71333	4767	-
Eurydice longicornis	-	250	-	-	-	-	167	-	-
? Neogaimaridia kowiensis	9775	33750	2550	3500	12133	30713	19167	13433	112
Kellia rotunda	-	250	-	-	433	-	-	-	-
Choromytilus meridionalis (JUV)	-	2750	150	-	867	1688	-	-	25
Eatoniella nigra	4675	4500	-	1667	-	4050	57000	1733	12
Tricolia neritina	142	-	-	-	-	-	167	-	-
Tricolia capensis	-	-	-	-	-	-	-	-	-
Burnupena sp. (JUV)	-	-	-	-	-	-	167	-	-
Fucellia capensis (L)	708	2000	-	500	77997	-	-	-	-
Fucellia capensis (P)	142	7250	4500	-	5200	3038	-	-	700
Fucellia capensis (A)	3683	19000	18600	3167	26433	133988	167	11267	3750
Coelopa africana (L)	-	9250	900	-	17766	-	-	230534	250
Coelopa africana (P)	-	2000	16050	-	6066	4725	-	2600	9125
Coelopa africana (A)	-	-	-	-	3033	338	-	-	-
Unidentified sp. (L)	142	-	-	-	-	-	-	-	-
Unidentified sp. (P)	-	1000	450	-	-	1013	-	-	3125
Unidentified sp. 1 (A)	2267	750	-	333	1733	1688	-	433	125
Unidentified sp. 2 (A)	-	-	450	-	1300	31388	-	1300	250
Pachyphaleria capensis (L)	-	-	150	-	433	-	-	-	-
Pachyphaleria capensis (A)	-	-	-	-	-	-	-	-	125
Aleochara salsipotens (A)	-	9250	59400	-	16033	33750	-	-	4500
Bledius sp. (A)	-	250	-	-	-	-	-	-	-
Cafius xantholoma (A)	-	-	300	-	1733	-	-	-	-
Omalium sp.	-	250	-	-	-	-	-	-	125
Unidentified sp. (L)	-	-	-	-	-	-	-	-	-
Acritus lightfooti (A)	-	-	450	-	-	338	-	-	2750
Pachylopus sp. (A)	-	-	450	-	-	-	-	-	-
Pachylopus sp. (L)	-	-	-	-	-	-	-	-	250
Unidentified sp. (L)	-	-	900	-	-	-	-	-	-
Cercyon maritimus (L)	-	250	300	-	6500	-	-	-	750
Cercyon maritimus (A)	-	6750	17700	-	6066	-	-	867	1000
Colpometopus basicornis (A)	-	-	-	-	-	675	-	-	125
Unidentified sp. (L)	-	-	150	-	-	-	-	-	125
Limata sp. (L)	-	-	-	-	-	-	-	250	4500
Unidentified sp. (L)	-	-	-	-	-	-	-	3625	-
Unidentified sp. (L)	-	1000	1800	-	867	1688	-	2250	-
Curulionidae (sub-family) (A)	-	-	-	-	-	-	-	-	-
Gymnetron sp. (A)	-	-	-	-	-	-	-	-	-
Phyllotreta sp. (A)	-	-	-	-	-	-	-	-	-
Unidentified sp.	-	-	-	-	-	338	-	-	-
Unidentified sp.	-	-	-	-	-	-	-	-	125

Appendix C continued : Monthly abundance (numbers m^{-1}) and tidal distribution of macrofaunal species.

SPECIES	May			June			July		
	LWS	MW	HWS	LWS	MW	HWS	LWS	MW	HWS
Talorchestia capensis (A)	-	1933	59850	-	5600	41200	-	280	48000
Talorchestia capensis (JUV)	500	93767	315000	-	3398265	832000	-	581000	3960000
Talorchestia quadrispinosa	-	970	12600	-	2800	-	-	2800	-
Paramoera capensis	8667	-	-	1517	-	-	-	-	-
Gitanopsis pusilla	-	-	-	-	-	-	-	-	-
Exosphaeroma truncatitelson	16333	-	-	1517	-	-	-	-	-
Eurydice longicornis	-	-	-	233	-	-	-	-	-
? Neogaimaridia kowiensis	32167	84100	1050	3500	3733	-	-	467	-
Kellia rotunda	-	-	-	-	-	-	-	-	-
Choromytilus meridionalis (JUV)	-	-	-	-	-	-	-	-	-
Eatoniella nigra	13333	70567	3850	56350	3733	-	-	467	-
Tricolia neritina	167	-	-	116	-	-	-	-	-
Tricolia capensis	-	-	-	-	-	-	-	-	-
Burnupena sp. (JUV)	-	-	-	-	-	-	-	-	-
Fucellia capensis (L)	-	-	8750	-	244400	-	-	-	225
Fucellia capensis (P)	-	-	2450	-	-	-	-	5600	2400
Fucellia capensis (A)	1667	8700	-	-	10267	6800	-	2800	26400
Coelopa africana (L)	-	7733	-	-	-	-	-	467	-
Coelopa africana (P)	-	970	7000	-	-	400	-	3267	525
Coelopa africana (A)	-	-	-	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	800	-	-	1200
Unidentified sp. (P)	-	-	1050	-	-	-	-	-	1200
Unidentified sp. 1 (A)	-	-	-	-	-	-	-	-	1200
Unidentified sp. 2 (A)	-	-	-	-	-	1600	-	-	-
Pachyphaleria capensis (L)	-	-	-	-	-	-	-	-	-
Pachyphaleria capensis (A)	-	-	-	-	-	-	-	-	-
Aleochara salsipotens (A)	-	970	1750	-	59200	-	-	13533	69600
Bledius sp. (A)	-	-	-	-	-	-	-	-	-
Cafius xantholoma (A)	-	-	-	-	-	400	-	-	-
Omalium sp.	-	-	-	-	-	-	-	467	-
Unidentified sp. (L)	-	-	-	-	-	-	-	-	-
Acritus lightfooti (A)	-	-	-	-	-	-	-	1867	22800
Pachylopus sp. (A)	-	-	-	-	-	400	-	-	2400
Pachylopus sp. (L)	-	-	350	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	-	-	-	-
Cercyon maritimus (L)	-	-	700	-	-	-	-	467	-
Cercyon maritimus (A)	-	5800	-	-	-	9600	-	933	37200
Colpometopus basicornis (A)	-	-	-	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	-	-	-	1200
Limata sp. (L)	-	-	-	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	-	-	-	-
Unidentified sp. (L)	-	-	7600	-	-	-	-	-	3600
Curulionidae (sub-family) (A)	-	-	-	-	-	-	-	-	-
Gymnetron sp. (A)	-	-	-	-	-	-	-	-	-
Phyllotreta sp. (A)	-	-	-	-	-	-	-	-	-
Unidentified sp.	-	-	-	-	-	-	-	-	-
Unidentified sp.	-	-	-	-	-	-	-	-	-

Appendix C continued : Monthly abundance (numbers m^{-1}) and tidal distribution of macrofaunal species.

SPECIES	August			September			October		
	LWS	MW	HWS	LWS	MW	HWS	LWS	MW	HWS
Talorchestia capensis (A)	-	-	11900	-	83	-	-	97200	156800
Talorchestia capensis (JUV)	-	20767	1479000	-	167	10325	-	440400	1024000
Talorchestia quadrispinosa	-	117	850	-	-	88	-	2100	-
Paramoera capensis	305600	1983	-	-	-	-	144217	-	-
Gitanopsis pusilla	-	-	-	-	-	-	-	-	-
Exosphaeroma truncatitelson	1000	233	-	-	417	-	20417	3300	-
Eurydice longicornis	-	117	-	-	-	-	-	-	-
? Neogaimaridia kowiensis	-	167	-	13333	5250	-	6800	900	-
Kellia rotunda	-	-	-	-	-	-	-	-	-
Choromytilus meridionalis (JUV)	-	-	-	-	-	-	-	-	-
Eatoniella nigra	-	167	-	82667	18200	-	53833	11700	-
Tricolia neritina	-	-	-	-	-	-	-	-	-
Tricolia capensis	267	-	-	-	-	-	-	-	-
Burnupena sp. (JUV)	-	-	-	-	-	-	-	-	-
Fucellia capensis (L)	-	-	-	-	-	-	-	-	-
Fucellia capensis (P)	-	-	-	-	-	-	-	-	-
Fucellia capensis (A)	-	-	2550	-	-	7263	1133	4200	9600
Coelopa africana (L)	-	-	-	-	-	-	-	-	-
Coelopa africana (P)	-	-	-	-	-	-	-	-	-
Coelopa africana (A)	-	-	-	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	-	-	-	1600
Unidentified sp. (P)	-	-	-	-	-	-	-	-	-
Unidentified sp. 1 (A)	-	-	-	-	-	-	1417	600	1600
Unidentified sp. 2 (A)	-	-	-	-	-	-	-	-	-
Pachyphaleria capensis (L)	-	-	-	-	-	-	-	-	-
Pachyphaleria capensis (A)	-	-	-	-	-	-	-	-	4800
Aleochara salsipotens (A)	-	-	18700	-	-	350	-	15000	19200
Bledius sp. (A)	-	-	-	-	-	-	-	-	-
Cafius xantholoma (A)	-	-	-	-	-	-	-	-	-
Omalium sp.	-	-	-	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	-	-	-	-
Acritus lightfooti (A)	-	-	-	-	-	88	-	1180	19200
Pachylopus sp. (A)	-	-	-	-	-	-	-	900	-
Pachylopus sp. (L)	-	-	-	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	-	-	-	-
Cercyon maritimus (L)	-	-	-	-	-	-	-	-	-
Cercyon maritimus (A)	-	-	-	-	83	-	-	4500	4800
Colpometopus basicornis (A)	-	-	-	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	-	-	-	-
Limata sp. (L)	-	-	-	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	-	-	-	1600
Curulionidae (sub-family) (A)	-	-	-	-	-	-	-	-	1600
Gymnetron sp. (A)	-	-	-	-	-	-	-	-	-
Phyllotreta sp. (A)	-	-	-	-	-	-	-	-	278
Unidentified sp.	-	-	-	-	-	-	-	-	-
Unidentified sp.	-	-	-	-	-	-	-	-	160

Appendix C continued : Monthly abundance (numbers m^{-1}) and tidal distribution of macrofaunal species.

SPECIES	November			December		
	LWS	MW	HWS	LWS	MW	HWS
Talorchestia capensis (A)	-	1800	650	142	1625	-
Talorchestia capensis (JUV)	-	30500	2113	142	80925	233
Talorchestia quadrispinosa	-	600	-	-	-	-
Paramoera capensis	5733	-	-	-	-	-
Gitanopsis pusilla	-	-	-	-	-	-
Exosphaeroma truncatitelson	25333	1300	-	283	650	-
Eurydice longicornis	133	200	-	1700	-	-
? Neogaimaridia kowiensis	30933	3500	-	5667	1300	700
Kellia rotunda	-	-	-	-	108	-
Choromytilus meridionalis (JUV)	5467	2600	-	9208	5417	700
Eatoniella nigra	19733	9900	-	38675	3792	583
Tricolia neritina	267	-	-	-	-	-
Tricolia capensis	-	-	-	566	108	117
Burnupena sp. (JUV)	267	-	-	-	-	-
Fucellia capensis (L)	-	-	-	-	-	400
Fucellia capensis (P)	-	-	-	-	-	850
Fucellia capensis (A)	133	18100	7313	708	7475	933
Coelopa africana (L)	-	39700	163	-	325	-
Coelopa africana (P)	-	9900	1600	-	108	1200
Coelopa africana (A)	-	-	-	-	-	-
Unidentified sp. (L)	-	100	-	-	-	-
Unidentified sp. (P)	-	100	325	-	-	700
Unidentified sp. 1 (A)	133	200	-	425	433	233
Unidentified sp. 2 (A)	-	300	1950	-	-	117
Pachyphaleria capensis (L)	-	200	163	-	108	177
Pachyphaleria capensis (A)	-	-	975	-	-	233
Aleochara salsipotens (A)	133	2500	10563	-	7908	140
Bledius sp. (A)	-	-	-	-	-	-
Cafius xantholoma (A)	-	-	-	-	-	-
Omalium sp.	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	-
Acritus lightfooti (A)	-	100	2438	-	108	2567
Pachylopus sp. (A)	-	-	1138	-	-	467
Pachylopus sp. (L)	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	-	1989
Cercyon maritimus (L)	-	-	-	-	-	-
Cercyon maritimus (A)	-	1400	9588	-	1192	233
Colpometopus basicornis (A)	-	-	-	-	-	-
Unidentified sp. (L)	-	100	488	-	-	-
Limata sp. (L)	-	-	-	-	-	-
Unidentified sp. (L)	-	-	-	-	108	-
Unidentified sp. (L)	-	-	-	-	-	-
Curulionidae (sub-family) (A)	133	-	1463	-	-	233
Gymnetron sp. (A)	-	-	163	-	-	-
Phyllotreta sp. (A)	-	-	-	-	-	-
Unidentified sp.	-	-	-	-	-	-
Unidentified sp.	-	-	163	-	-	-

APPENDIX D : Dry mass and ash free dry mass (AFDM) per individual species or taxonomic group found associated with wrack on Kommetjie beach, Cape Peninsula.

A = adult
JUV = juvenile
L = larva
P = pupa

	dry mass (mg) per individual	AFDM (mg) per individual
MACROFAUNA		
AMPHIPODA		
Talorchestia capensis (A)	14,205	9,441
Talorchestia capensis (JUV)	1,258	0,889
Talorchestia quadrispinosa	28,470	20,103
Paramoera capensis	0,426	0,318
ISOPODA		
Exosphaeroma truncatitelson	1,748	0,784
Eurydice longicornis	0,533	0,372
MOLLUSCA		
Neogaimaridia kowiensis	0,239	0,035
Eatoniella nigra	0,286	0,037
Choromytilus meridionalis (JUV)	0,430	0,067
DIPTERA		
Fucellia capensis (L)	1,196	1,084
Fucellia capensis (P)	1,140	0,937
Fucellia capensis (A)	1,506	1,401
Coelopa africana (L)	1,020	0,921
Coelopa africana (P)	3,193	2,363
Coelopa africana (A)	3,180	2,428
Unidentified sp (L)	0,261	0,231
Unidentified sp (P)	0,164	0,158
Unidentified sp 1 (A)	0,120	0,109
Unidentified sp 2 (A)	0,710	0,649

APPENDIX D continued

	dry mass (mg) per individual	AFDM (mg) per individual
COLEOPTERA		
Pachyphaleria capensis (L)	3,102	2,900
Pachyphaleria capensis (A)	10,653	10,241
Aleochara salisipotens (A)	0,534	0,513
Cafius xanthaloma (A)	3,470	3,364
Acritus lightfooti	0,360	0,205
Pachylopus sp. (A)	6,505	6,270
Cercyon maritimus (L)	1,490	1,361
Cercyon maritimus (A)	1,821	1,505
Colpomelopus basicornis (A)	1,289	1,000
Limata sp. (L)	2,983	2,700

	dry mass (ug) per individual	AFDM (ug) per individual
MEIOFAUNA		
Nematodes	1,189	0,987
Oligochaetes	3,374	2,909
Harpacticoides	0,429	0,200
Turbellaria	2,243	1,885
"Others"	0,500	-
BACTERIA		
Mean for rods and cocci	$0,12756 \times 10^{-6}$	

APPENDIX E

The seasonal abundance (numbers 200ml sand^{-1}) and biomass (mg dry mass 200ml sand^{-1}) of interstitial meiofauna at different tidal levels on Kommetjie beach during 1981.

MEIOFAUNA TAXA

SEASON SAMPLED	ZONE	SAMPLING DEPTH (cms)	NEMATODES		HARPACTICOIDS		OLIGOCHAETES		TURBELLARIA		OTHERS		TOTAL	
			numbers	biomass	numbers	biomass	numbers	biomass	numbers	biomass	numbers	biomass	numbers	biomass
SUMMER	LWS	0-30	135	0,161	179	0,077	101	0,340	5	0,012	4	0,002	424	0,592
		30-60	97	0,115	60	0,026	7	0,024	6	0,016	6	0,003	176	0,182
	MW	0-30	381	0,453	13	0,006	39	0,131	4	0,001	1	0,001	438	0,600
		30-60	499	0,594	4	0,002	23	0,077	1	0,002	42	0,021	569	0,697
	HWS	0-30	6864	8,168	189	0,081	3195	10,767	80	0,194	509	0,255	10837	19,465
		30-60	3919	4,664	130	0,056	397	1,338	-	-	192	0,096	4638	6,154
AUTUMN	LWS	0-30	249	0,296	-	-	4	0,014	-	-	4	0,002	257	0,312
		30-60	456	0,543	-	-	45	0,152	9	0,022	36	0,018	546	0,735
	MW	0-30	786	0,935	-	-	3	0,010	-	-	-	-	789	0,945
		30-60	194	0,231	-	-	-	-	-	-	12	0,006	206	0,237
	HWS	0-30	4421	5,261	-	-	2786	9,389	-	-	76	0,038	7283	14,688
		30-60	4661	5,547	66	0,028	1285	4,330	173	0,419	172	0,086	6357	10,410
WINTER	LWS	0-30	271	0,322	16	0,007	59	0,198	19	0,046	16	0,008	381	0,581
		30-60	94	0,112	1	0,001	20	0,067	1	0,002	5	0,003	121	0,184
	MW	0-30	4867	5,792	430	0,184	2153	7,256	275	0,666	48	0,024	7773	13,922
		30-60	7945	9,455	158	0,068	1607	5,416	101	0,244	45	0,023	9856	15,206
	HWS	0-30	4106	4,886	52	0,022	727	2,449	26	0,063	53	0,027	4964	7,447
		30-60	1657	1,972	75	0,032	1265	4,263	11	0,027	-	-	3008	6,294

Appendix E continued

SEASON SAMPLED	ZONE	SAMPLING DEPTH (cms)	NEMATODES		HARPACTICOIDS		OLIGOCHAETES		TURBELLARIA		OTHERS		TOTAL	
			numbers	biomass	numbers	biomass	numbers	biomass	numbers	biomass	numbers	biomass	numbers	biomass
SPRING	LWS	0-30	425	0,506	-	-	188	0,634	18	0,044	89	0,045	720	1,229
		30-60	241	0,287	3	0,001	257	0,866	13	0,031	83	0,042	597	1,227
	MW	0-30	6236	7,421	18	0,008	7622	25,686	-	-	365	0,183	14241	33,298
		30-60	1742	2,073	130	0,056	612	2,062	-	-	111	0,056	2595	4,247
	HWS	0-30	2036	2,423	9	0,004	1774	5,978	4	0,009	55	0,028	3878	8,442
		30-60	955	1,136	29	0,012	146	0,492	-	-	59	0,029	1189	1,669

APPENDIX F

Bacterial NUMBERS ($\times 10^{6}$ ml sand^{-1}) at Kommetjie beach during 1981. LWS = low water springs; MW = mid water; HWS = high water springs.

Vertical depth (cms)

Season sampled	Zone	0 - 30		30 - 60		60 - 90	
		rods	cocci	rods	cocci	rods	cocci
summer	LWS	26,53	10,92				
	MW	14,01	34,31	46,76	114,57	18,91	46,32
	HWS	3,75	10,44	31,65	88,26	6,05	16,87
autumn	LWS	113,06	221,95				
	MW	258,44	475,54	134,72	247,88		
	HWS	129,80	246,42	146,21	277,59	100,81	191,39
winter	LWS	49,32	109,15				
	MW	48,08	103,27	45,07	96,80		
	HWS	54,77	155,08	57,17	161,88	38,40	108,72
spring	LWS	179,52	231,38				
	MW	186,39	113,75	186,04	113,54		
	HWS	174,88	174,88	57,18	57,18	108,73	108,73

Bacterial BIOMASS (mg dry mass 100ml sand^{-1}) at Kommetjie beach during 1981. See the above table for the abbreviations of the zones.

Vertical depth (cms)

Season sampled	Zone	0 - 30		30 - 60		60 - 90	
		rods	cocci	rods	cocci	rods	cocci
summer	LWS	0,391	0,084				
	MW	0,224	0,089	0,749	0,298	0,303	0,121
	HWS	0,036	0,012	0,306	0,104	0,058	0,020
autumn	LWS	8,622	0,384				
	MW	9,665	1,469	5,038	0,766		
	HWS	4,048	1,200	4,560	1,351	3,144	0,932

APPENDIX F continued

Season sampled	Zone	Vertical depths (cms) 0 - 30		30 - 60		60 - 90	
		rods	cocci	rods	cocci	rods	cocci
winter	LWS	0,937	0,152				
	MW	1,106	0,211	1,037	0,197		
	HWS	0,894	0,362	0,934	0,378	0,627	0,254
spring	LWS	1,596	0,415				
	MW	5,085	0,366	5,076	0,365		
	HWS	2,420	1,010	0,791	0,330	1,504	0,628

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