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1. 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 Gastrosaccus); and predator/scavengers (e.g. Bullia, Ocypode, various isopods and polychaetes). The proportion of these two trophic elements differs 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., 1980; 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 shore) and hence profoundly affects both the nature and distribution of the fauna. Various aspects of the ecology of beaches with high kelp input have recently received attention (Muir, 1977; Koop, Field, 1980; Stenton-Dozey, Griffiths, 1980; Griffiths, Stenton-Dozey, 1981; Koop et al., 1982 a,b), making it possible to compute various aspects of energy flow through such a system.

In this study we aim to synthesize the 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.

- 2. RESULTS AND DISCUSSION
- 2.1 Description of study site

The data presented here were all collected from one of a number of short beaches interspersed between rocky headlands at Kommetjie (34°08'S. 18°19'E) on the west coast of the Cape Peninsula, South Africa. The profile and sediment characteristics of one such beach are described by Koop and Griffiths (1982) and the fauna and flora of the adjacent kelp beds by Field et al. (1980). Wave characteristics of a nearby site are given by Velimirov et al. (1977). average the intertidal zone is some 45 m wide, with a slope of about 1:20, and the median grain size of the sand varies between about 240 μm and Wave height is normally between 1 and 4 m and water temperatures between 8 and 15° C. During our monthly visits to the study site air temperatures varied from 26°C (Jan.) to 13.7°C (July) with a mean of 19,3°C. The temperature range beneath the wrack was lower, with a maximum of 21°C, a minimum of 12°C and a mean of 16,5°C.

2.2 Rates of food supply to the beach

Rates of wrack deposition at Kommetjie beach have been estimated by Koop and Field (1980) and by Stenton-Dozey and Griffiths (1983). Two main factors complicate these measurements. Firstly the wrack is extremely unevenly deposited along the length of the beaches, and secondly an estimate of residence time is required if standing stock estimates are to be converted into annual rates of input.

Koop and Field (1980) measured the wet mass of wrack lying on a randomly chosen 5 m wide strip of beach at monthly intervals for 17 months. Minimum values of about 2 kg m $^{-1}$ occurred in summer and maxima of over 40 kg m $^{-1}$ during winter. Using an 8 day residence time Koop et al. (1982a) have used these figures to calculate the yearly input of kelp as 1200 - 1800 kg wet mass m $^{-1}$ y $^{-1}$. In an attempt to verify these figures and to correct for the extreme patchiness of wrack deposits a further 12 months data have been

collected by Stenton-Dozev and Griffiths (1983) at an adjacent site. In this case overall estimates were made of the volume of wrack deposited over a 300 m stretch of beach and supplemented by weighings at selected sites. The results show a similar seasonal cycle of deposition, with high values in autumn and winter and lower ones in summer. The mean standing stock of kelp on the beach was 25.07 kg m^{-1} . a residence time of 14 days, based on degradation experiments conducted by Griffiths and Stenton-Dozey (1981), this gives a total deposition rate of 2179 kg wet mass m^{-1} y^{-1} . 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 4.07×10^6 kJ deposited per running metre of beach each year.

2.3 Nature, distribution and biomass of the macrofauna

The intertidal biota of Kommetjie beach has been surveyed by Koop and Griffiths (1982) and the macrofauna within the wrack beds described by Griffiths and Stenton-Dozey (1981) and Stenton-Dozey and Griffiths (1983). The macrofaunal distribution patterns obtained by Koop and Griffiths (1982) are typical and are summarized in Table 1.

Of the fifteen species (7 Coleoptera, 2 Diptera, 2 Amphipoda, 2 Isopoda, 1 Oligochaeta, 1 Polychaeta) recorded overall, all but three were directly associated with kelp wrack on the driftline. As a result there was a marked increase in species diversity as one moved up the beach from the low water mark, which is the reverse of the normal pattern. Recent results by Stenton-Dozey and Griffiths (1983) have increased the number of species recorded amongst kelp wrack at Kommetjie to 35 (of which 22 are insects), suggesting that the increase in diversity