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The ecology of kelp bed communities in the Benguela upwelling system

Analysis of biomass and spatial distribution

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ABSTRACT: Cool nutrient rich waters combined with a rocky coastline extending infratidally make the west coast of South Africa well suited to growth of kelp species. The kelp bed community is compared with the main kelp beds studied elsewhere (Nova Scotia, W. Europe, California). All these areas have cool, nutrient-rich water but the Benguela region differs in that large swells prevail. This paper deals with the determination of faunal and algal boundaries in these kelp beds (composed mainly of *Ecklonia maxima* and *Laminaria pallida*), as well as their biomass, in order to build a descriptive model of the food web. The main components of a site representative of the variable kelp beds on the west coast of the Cape Peninsula (Oudekraal) have been identified and quantified in terms of ash-free dry weight and Joules. The study covered an area from the rocky intertidal zone to the rock/sand interface found at a depth of 20 m. The site was divided into different areas (offshore, intermediate, inshore), and these were subdivided into depth zones of 4 m to show up any differences with depth. Different sampling techniques using SCUBA were combined to cover a wide range of organisms in the survey. Horizontal and vertical surfaces were differentiated. Kelp holdfasts were removed as a sampling unit for the infauna study. The distribution data of the organisms, other than kelp, were studied by means of multivariate methods which confirmed the division into inshore, mediate and offshore associations. Differences in faunal and floral composition could be detected between horizontal and vertical surfaces. Kelp biomass data showed high average standing crop in the inshore and mediate locality compared to the low offshore values. Maximum standing crop values, however, were not reduced. Mechanisms regulating the kelp bed structure are discussed. In the inshore and intermediate areas, algal biomass is much higher than animal biomass. A fact emerging from the data is that there is relatively little biomass of grazers; the major primary consumers are filter feeders. Problems of turnover rates are mentioned and an energy flow diagram for the area is proposed and its validity discussed.

INTRODUCTION

The west coast of southern Africa, from Cape Agulhas to Lüderitz, is characterized by kelp beds which dominate the rocky infratidal zone wherever cold Benguela water exerts its influence. These beds are composed mainly of *Ecklonia maxima* and *Laminaria pallida*, although *Macrocystis angustifolia* occurs sporadically in sheltered bays.

Similar kelp beds in other parts of the world, with their multilayered algal canopies, are major sources of nutrition for the whole inshore system (Aleem, 1956; North, 1971; Mann, 1972). Standing crops of the order of 10 kgm^{-2} wet mass (North, 1971; Mann, 1972; Aleem, 1973) and up to 50–60 kgm^{-2} (Westlake, 1963; Bellamy et al., 1968) and rates of primary productivity between 1000–2000 g Cm^{-2}y^{-1} have been recorded (Westlake, 1963; Bellamy et al., 1968; North, 1971; Mann, 1973),

Similarly high rates of production might be expected in the South African

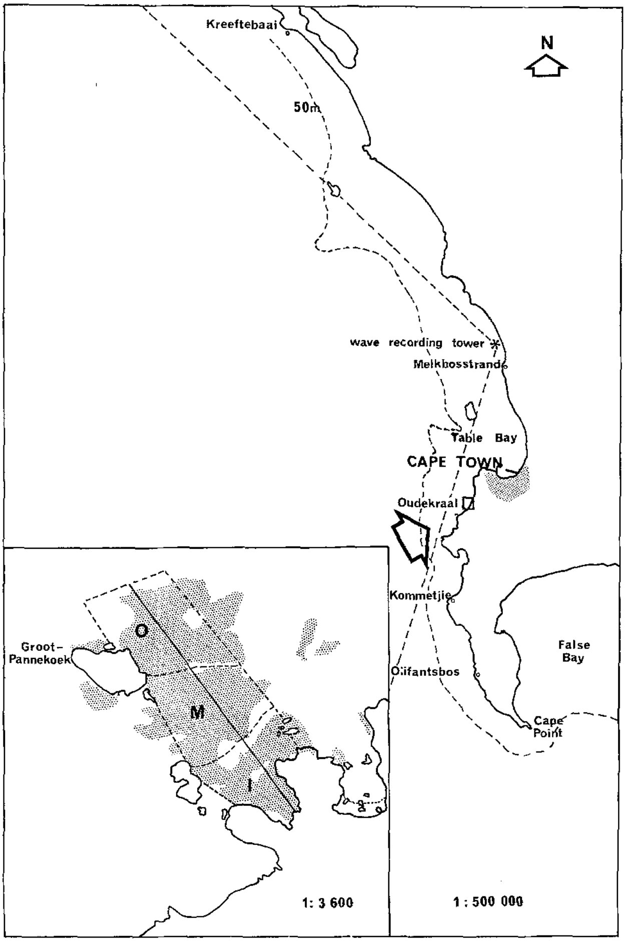

Fig. 1: Cape Peninsula and vicinity with position of the wave tower. Angle of reception for wave recorder indicated by dashed lines (see text). Inset shows study area divided into inshore (I) mediate (M) and offshore (O) locality. Coverage of kelp bed stippled

situation since nutrient concentrations in upwelled water off the Cape Peninsula are high: 20 μgat l^{-1} for NO_3 and SiO_4 and 1–1.5 μgat l^{-1} for PO_4 (Andrews, 1974). Moreover, rates of upwelling, powered by strong offshore winds (up to 32 $msec^{-1}$), particularly between September and April, are exceptionally high at up to 30 m day^{-1} (Bang, 1974; Bang & Andrews, 1974). By comparison upwelling rates off Peru have been estimated at 58 m $month^{-1}$ (Zuta et al., 1975) while for the Californian coast figures of 68 m $month^{-1}$ are given by Cushing (1971). Using the relevent figures for upwelling rate and defining the upwelling zone as the area within the 10° C isotherm, turnover volume and potential productivity can be calculated. If this is done for the Cape Peninsula area alone, estimates range between 6,192 and 9,029 tons C per upwelling day – equivalent to 0.38×10^6 to 0.93×10^6 tons Cy^{-1} depending upon wind conditions (Andrews & Cram, 1969; Andrews et al., 1970).

In addition to their remarkable potential for production South African kelp beds are notable for their exposure to large swells, often up to 6 m high or with periods up to 18 sec. Under these conditions the kelp exerts a breakwater effect, dissipating the energy of incoming swells and allowing animals and algae which could not withstand their full impact to occupy the area.

These factors, together with the association of a number of commercially important species with kelp, has led to an investigation of the dynamic relationships between environment and biota and between species populations within the community.

After a preliminary survey, Oudekraal, a site on the west coast of the Cape Peninsula (Fig. 1) was chosen for detailed analysis. The results of the initial survey of this site are presented here.

METHODS

The study area was defined as extending from the rocky intertidal zone to the seaward end of the kelp bed – a rock sand interface at a depth of 20 m. Echosoundings from a light boat were used to obtain a rough bottom profile and estimate the extent of the kelp. On this basis the site was divided into three sub-units (Fig. 1): (1) An inshore locality from the intertidal zone down to 8 m. (2) A mediate locality of 4–8 m depth characterized by granite boulders. (3) An offshore locality from the surface abutting a large granite outcrop (Groot Pannekoek), northwards for 200 m to a depth of 20 m.

Sampling methods

Each locality was subdivided into depth zones to test for depth stratification. Different sampling techniques using SCUBA were combined to cover the wide range of organisms encountered:

(1) For densely packed and slow moving organisms on rock surfaces, quadrats of 1/10 m^2 were cleared. The quadrats were laid in a stratified random basis; four quadrats being taken on vertical and four on horizontal surfaces in each depth zone.

The samples were returned to the laboratory, sorted, and either dried to constant weight and ashed (550° C for 5 h) or homogenized and redried for ignition in a ballistic bomb calorimeter (Gallenkamp) under 25 atmospheres of oxygen. Ash-free dry mass figures were used in the numerical analysis to overcome errors due to inclusions of sand in stomach contents and to avoid excessive weighting of organisms with calcium carbonate skeletons of little nutritive value. For animals with calcareous skeletons Paine's (1966) correction for endothermy of $CaCO_3$ was applied, or the animals were separated from the shell, which was weighed, dried and treated with HCl to remove $CaCO_3$, the remaining organics being burnt in the calorimeter to obtain a value for shell. The value for the whole organism was calculated using the dry weight flesh/shell ratio.

(2) Large, widely dispersed and faster moving animals were recorded by means of belt counts. A bottom line of length 15–30 m was laid through the area to be sampled. In each depth range 4–6 counts were made. Depending on visibility and species densities, animals were counted along a belt 2–5 m broad, using the rope as a guide, giving a coverage of 30–150 m^2. The counts were recorded on plastic underwater slates. A representative collection covering the size range of each species (a minimum of 10 specimens) was made to be dried or burnt in the calorimeter.

(3) Kelp holdfasts were used as sampling units and removed whole for the infauna study. Four holdfasts were collected in each depth zone, brought to the laboratory and the infauna treated as above. The basal area of the kelp holdfasts was estimated from the mean of 4 measured diameters, assuming the holdfast to have a circular base.

(4) An estimate of kelp biomass was derived from another related sampling programme at the same site. The method used involved laying a line from the shore to the end of the kelp bed. Plants within 0.5 m of the line were cut and the crop derived from successive 2 m steps along the line packed into labelled bags. Once ashore individual plants were measured and weighed wet with a spring balance, while representative samples were taken to the laboratory for measurement of dry weight, ash weight and calorific values. Substrate type and water depth were simultaneously recorded along the whole transect.

(5) Waves were recorded by a Wemelsfelder float type wave recorder, situated on a sea tower in 11 m deep water, one kilometer offshore near Melkbosstrand. All waves approaching between 202 and 312° East of North (Fig. 1) could be detected. Half hour records, taken twice daily, have been analysed for maximum wave height, upper one tenth wave height and zero crossing periods (Shillington, 1976). Additional information was obtained from Darbyshire (1974).

(6) Temperature was recorded at Oudekraal in 15 m depth using a thermoscript (Goerz Electric) fitted into a casing (Fricke & Thum, 1975). The instrument recorded over a period of 30 days, and was exchanged monthly, weather permitting.

Numerical methods

Two sets of raw data were subjected to multivariate analysis. The data obtained from quadrats were initially arranged in a matrix of 64 columns (quadrats) by 114 rows (taxa). Each set of four replicates was pooled to give a matrix of 16 × 114, ignoring the variability between replicates but giving more representative units for analysis. The holdfasts were treated individually in a matrix of 32 × 37. To analyse relationships between samples a similarity measure ($S = 1\text{-}D$, where D = dissimilarity) was used. The Canberra metric was chosen.

$$D_{jk} = \frac{1}{n} \sum_{i=1}^{n} \frac{| X_{ij} - X_{ik} |}{(X_{ij} + X_{ik})}$$

where X_{ij}, X_{ik} are the ash-free dry biomass values of the i^{th} taxon (or species) in the j^{th} and k^{th} samples respectively. This was selected in preference to the widely used measure of Bray & Curtis (1957) because the data are biomass values rather than numbers (Field & Velimirov, in prep.).

The similarity matrix obtained was summarised in two ways: by classification using group-average sorting (Lance & Williams, 1967) to arrange the samples into a dendrogram and by ordination using multidimensional scaling (Kruskal, 1964). The latter technique represents samples as points on a graph in such a manner that closely related samples are shown grouped together while dissimilar samples are far apart. The technique and its rationale will be discussed separately (Field & Velimirov, in prep.). Each of the methods of presentation has disadvantages and distorts the relationships between samples to some extent, but the use of both together gives a good idea of the validity of groupings.

The taxa (or species) characteristic of sample-groups were revealed by information statistic tests (Field, 1969, 1971). Comparing cluster 1 with cluster 2 for any one taxon (species), i:

$$2 \triangle I_i = 2 \, (I_{ti} - I_{1i} - I_{2i})$$

where I_{ti} is the total information content of both clusters together

$$I_{ti} = N_t \log N_t - A_{ti} \log A_{ti} - (N_t - A_{ti}) \log (N_t - A_{ti})$$

where N_t ist the number of quadrats (or holdfasts) in both clusters together ("potential presences"), A_{ti} ist the number of quadrats in which species i is actually present and $(N_t - A_{ti})$ is the number of quadrats from which species i is absent. Similarly, the information contents I_{1i} and I_{2i} are obtained for clusters 1 and 2 respectively.

RESULTS AND DISCUSSION

Wave action

Wave records for over two years (Fig. 2) reveal that 80 % of the waves occurring within one year exceed 1.5 m in height, ranging from 2 m to 7 m, while for 5 % of the period, waves higher than 4 m were recorded. Minimum wave height was 0.5 m. The most common wave periods recorded were between 7 and 9 seconds (Shillington, 1976). Measurements up to 1976, as yet unpublished, agree closely with those given above. This wave action, keeping the kelp bed in constant movement, is one of the most characteristic features of the Cape west coast.

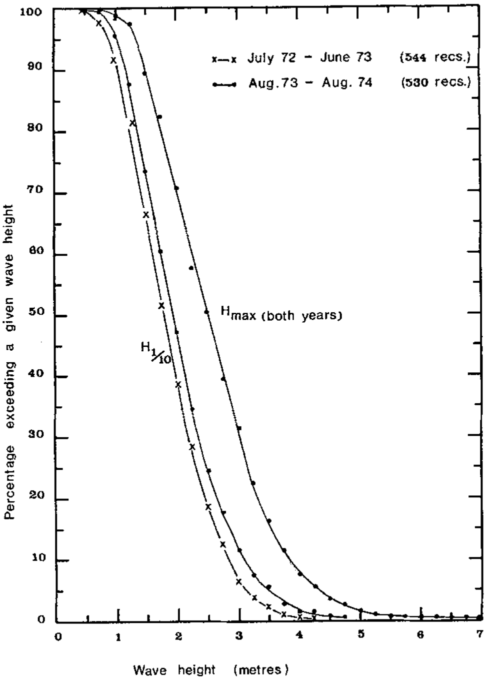

Fig. 2: Exceedence curves of wave heights. (After Shillington, 1975)

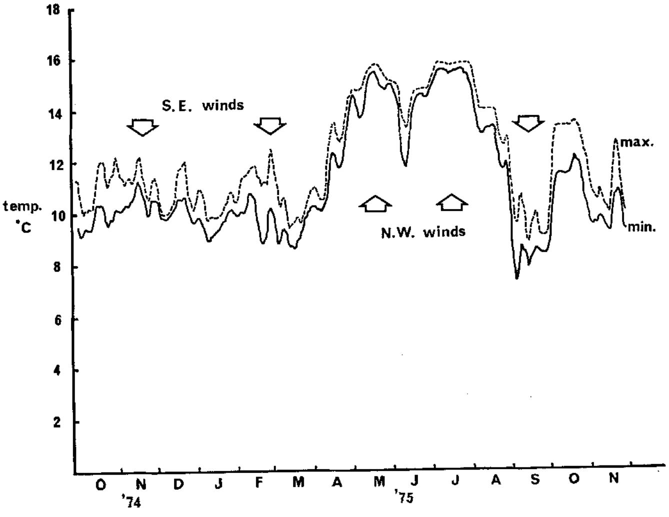

Fig. 3: Maximum and minimum temperature records, (running mean of 5 days) at Oudekraal, depth 15 m. Dominant wind patterns indicated

Table 1

Total kelp over 499 m transect – 4,555,091.0 kJ (407.476 kg dry mass)

Locality	Depth (m)	Species	Total area (m^2)	Rock area (m^2)	Mean standing crop (kJ m^{-2})	Max. standing crop (kJ m^{-2})	Total standing crop (kJ)
Inshore	0–4	*Laminaria pallida*	35	29	7,436.9	21,113.3	215,671.2
		Ecklonia maxima	35	29	17,567.6	39,919.5	509,487.0
	4–8	*Laminaria pallida*	115	60	6,632.8	30,521.6	397,979.1
		Ecklonia maxima	115	60	6,628.0	36,814.1	397,682.5
Mediate	4–8	*Laminaria pallida*	175	133	10,253.53	30,858.3	1,363,729.2
		Ecklonia maxima	175	133	9,766.8	78,452.1	1,298,985.7
Offshore	8–12	*Laminaria pallida*	60	52	6,244.5	20,039.4	324,718.5
		Ecklonia maxima	60	52	0	0	0
	12–16	*Laminaria pallida*	79	65	4,450.0	23,063.8	289,312.8
		Ecklonia maxima	79	65	2.2	42.3	118.5
	16–20	*Laminaria pallida*	35	30	3,200.0	27,765.5	96,022.5
		Ecklonia maxima	35	30	0	0	0

Temperature

Temperature conditions (Fig. 3) for 1974 show a minimum of 8.2° C between January and March, the peak of the upwelling season which occurs during the southern summer. The minimum temperature in 1975 (7.3° C) occurred at the end of August with the first south-east wind of the season, blowing the coastal water offshore. Maximum temperatures up to 15.5° C occur during winter, from April to mid-August. Occasionally the south-easter blows for very short periods in winter (compare month of June in Fig. 3) which immediately causes a brief unseasonal upwelling.

Kelp biomass, distribution and size

A total of 3.557 metric tons fresh weight of kelp was collected along the 499 m transect; the breakdown is shown in Table 1. The conversion factors from grams dry mass to kilo Joules (based on a summertime survey and therefore ignoring seasonal variations) are 12.26 ± 0.14 for *Ecklonia maxima* and 10.51 ± 0.22 for *Laminaria pallida.*

In the 0–4 m depth range inshore *E. maxima* formed 70 % of the kelp standing crop, reducing to 50 % in the 4–8 m range. In the mediate locality, which is confined

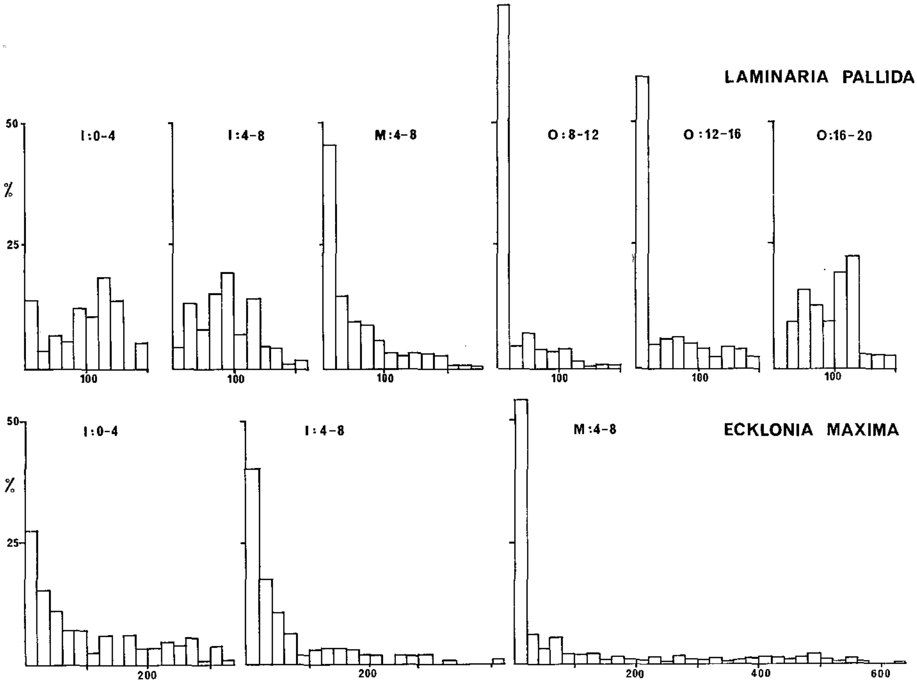

Fig. 4: Stipe-length percentage frequency distributions of *Laminaria pallida* and *Ecklonia maxima* by locality (I = inshore, M = mediate, O = offshore) and depth range. The x-axis represents stipe lengths (in cm)

to the 4–8 m depth range, *E. maxima* formed 49 % of the standing crop while in the offshore area only 3 juvenile *E. maxima* of insignificant energy content were recorded. Thus the proportion of *L. pallida* increased steadily from inshore to offshore and with increasing depth.

The total standing crop at the mediate locality was as high as that of the inshore and offshore areas combined. The density of adult kelp in the mediate region (9/m^2) exceeded the highest value for the other localities (6/m^2 in the inshore 4–8 m range). The densities are based on holdfast counts (Table 3) and therefore include only adult plants, since juveniles have minute holdfasts which provide an insignificant habitat for the holdfast fauna. Total and mean standing crop decreased with increasing depth at the three deeper offshore zones, falling to 3,200 kJ m^{-2} or 0.3 kg dry mass m^{-2} at 16–20 m depth. Maximum standing crop values, however, were not reduced at greater depths because the deeper *L. pallida* occur at equal density but patchily, with areas of bare rock or rock colonized only by animals between patches of kelp. Therefore, although *L. pallida* extends much deeper than *E. maxima* it represents only 55 % of the total standing crop of kelp along the whole transect.

Frequency distributions of stipe lengths are given in Figure 4. Dieckmann (1975a) has shown that *E. maxima* plants can reach a stipe length of 20 cm after one year; all plants in their first year are referred to as juveniles. Juveniles form 27 % of the *E. maxima* plants in the 0–4 m range inshore, 40 % at 4–8 m inshore and 59 % in the mediate locality. The figures for juvenile *L. pallida* are 13 % at 0–4 m, 10 % at 4–8 inshore and 45 % in the mediate area. Offshore the percentage of juvenile *L. pallida* dropped from 74 % to 0 % with increasing depth.

The decreasing proportion of juvenile *L. pallida* with depth offshore, the smaller mean standing crop, and the virtual absence of *E. maxima* all suggest that the deeper kelp bed community offshore functions differently than its counterpart closer to land. Although light is an important factor which varies with depth, many other parameters are involved in structuring the community at different localities. One can speculate that wave action has less effect upon deeper kelps than it has in shallow areas where plants of large surface area may be torn loose more frequently. If this occurs, the removal of canopy plants is likely to result in faster development of both gametophyte and sporophyte generations. This may cause a higher turnover rate of plants in shallow water, while in deeper water the kelp canopy may be more stable, as indicated by the higher proportion of adult plants.

Young kelp are found all year round in the inshore and mediate areas but at 16–20 m depth young sporophytes have mainly been observed in September–October. Most of these disappear in early summer, leaving only the plants which settle at the edge of existing kelp patches or near holdfasts of isolated but established plants. Whether the disappearance is due to wave action, grazing or other factors is not yet clear.

Two other factors should be mentioned as affecting the community: grazing on newly settled plants by the urchin *Parechinus* (Greenwood, 1974) and sweeping of the substrate at the edge of kelp patches by *Laminaria pallida* fronds. The sweeping effect appears to keep marginal areas free of animals and thereby prevent predation by grazers, but it may also inhibit new kelp settlement.

Animals and understorey

Total dry mass and calorific content of the animals and understorey algae recovered by quadrat sampling are shown in Table 2. There is a distinct decline in algae as one passes from inshore to offshore and a corresponding increase, of between one and two orders of magnitude, in the faunal element, which dominates the offshore series.

Table 2

Mean animal and understorey plant standing crop obtained by quadrat samples expressed as kJ and grams dry mass per m^2 by locality, depth range and inclination of substrate (H = horizontal surface, V = vertical surface)

			Standing crop			
			Animals		Plants	
Locality	Depth (m)	Surface	g m^{-2}	kJ m^{-2}	g m^{-2}	kJ m^{-2}
Inshore	0–4	H	24.1	89.9	10.8	166.8
		V	23.0	66.8	5.7	69.4
	4–8	H	1.9	10.4	16.4	229.2
		V	12.2	41.5	9.8	108.3
Mediate	4–8	H	26.4	98.3	20.3	314.2
		V	99.0	354.5	4.4	53.4
Offshore	0–4	H	390.6	1,541.1	10.4	129.8
		V	171.6	996.5	3.5	30.9
	4–8	H	428.8	1,732.4	2.3	29.3
		V	70.5	208.1	3.7	42.8
	8–12	H	300.3	1,420.9	1.0	12.5
		V	720.5	2,014.4	0.1	0.1
	12–16	H	100.5	592.5	2.7	28.0
		V	90.6	316.0	0.5	5.5
	16–20	H	129.5	413.5	2.8	38.0
		V	117.7	231.0	0.2	0.3

Throughout the system algal values tend to be higher on horizontal, rather than vertical surfaces, but the difference is significant particularly inshore $t = 4.36$, df $= 6$, $p < 0.01$) and in the mediate locality ($t = 2.3$, df $= 6$, $p < 0.1$). Offshore the algae progressively decline with increasing depth, but even in the 0–8 m range the crop is considerably lower than at an equivalent depth inshore and in the mediate locality.

Within the offshore area animal standing crop is generally higher on horizontal, rather than vertical faces, although significant differences occur only between 4 and 8 m ($t = 4.29$, df $= 6$, $p<0.01$). The 8–12 m range is exceptional in having a higher biomass on the vertical surfaces, this value being the maximum recorded overall. Comparing this vertical surface with those of the other depth ranges offshore, significant differences can be found between its standing crop and those of the 12–16 m zone ($t = 2.81$, df $= 6$, $p<0.05$) and the 16–20 m zone ($t = 3.13$, df $= 6$, $p<0.05$). Below 12 m there is a distinct decline in standing crop, which falls to a minimum at 16–20 m, below which the rock-sand interface occurs.

Analysis of holdfast-infauna (Table 3) yielded comparable results with markedly higher animal values offshore. Within this locality, however, standing crop per holdfast rises with increasing depth. This is at least partially attributable to a comparable rise in mean holdfast size. (Plants in the deeper zones are generally older and taller, having a larger basal holdfast area). The free space between the haptera of the holdfast is greater and more living space is available for organisms. The sheltered environment within a holdfast appears to attract large numbers of juvenile kelp bed organisms and functions as a nursery. These share the habitat with a characteristic holdfast infauna (Shafir, pers. comm.) consisting of isopods, amphipods, polychaetes and tunicates. Few algae occur on holdfasts. Others than juveniles of the kelp themselves, the flora is dominated by four epiphytes – *Hymenena venosa*, *Codium stephensoni*, *Epimenia obtusa* and *Gigartina radula*.

Table 3

Holdfast density, mean basal area per holdfast and standing crop of infauna (expressed as grams dry mass and kJ per holdfast) by locality and depth range

Locality	Depth (m)	Holdfasts (adult only)		Associated fauna	
		(number/m^2)	mean basal area (cm^2)	dry mass (g)	value in kJ
Inshore	0–4	6.8	423.3	4.4	10.3
	4–8	5.3	368.0	7.6	12.1
Mediate	4–8	9.1	474.6	97.0	51.8
Offshore	0–4	(6.8)	247.5	503.1	357.2
	4–8	(5.3)	277.3	126.5	229.8
	8–12	7.5	309.5	173.4	335.3
	12–16	4.0	530.5	775.0	686.8
	16–20	1.0	418.8	492.0	383.1

Numerical analysis

The dendrogram obtained by analysis of quadrat data (Fig. 5) shows the biotic separation between offshore, mediate and inshore localities. Highest similarities are shown between the shallower offshore samples. In the inshore region, there is subdivision into clusters on vertical and horizontal surfaces and some similar grouping occurs in the offshore area.

The ordination also shows a good separation of the three localities (Fig. 6). Differentiation between horizontal and vertical surfaces is not clear but there is a definite trend from shallow to deep within the offshore group of samples.

Results of the information statistic tests used to reveal taxa characteristic of the three main clusters are given in Table 4. Only species which differ significantly between the clusters are listed. Each cluster differs significantly from the other in biotic composition and frequency. The offshore cluster is different from both the others in the significantly higher frequency of filter-feeding echinoderms such as the holothurians

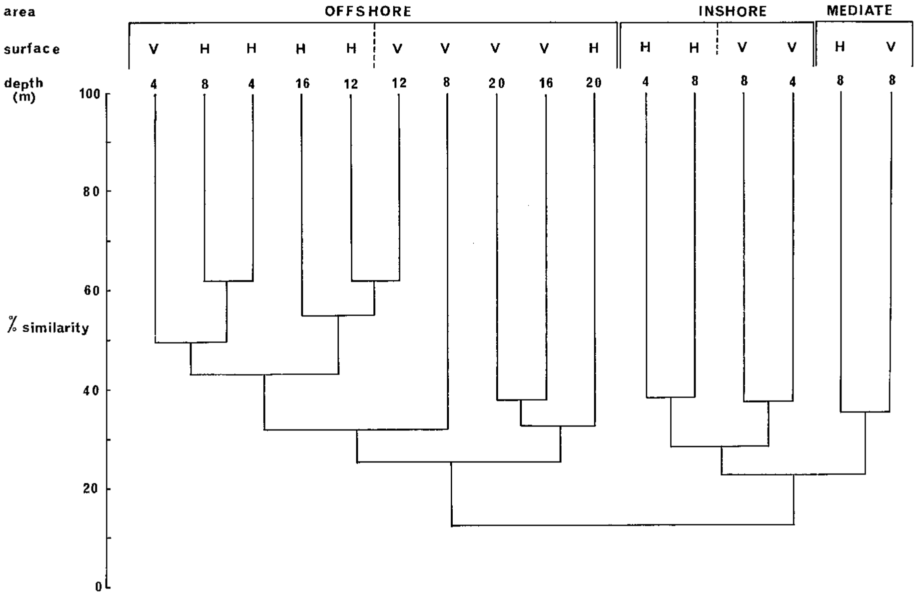

Fig. 5: Dendrogram showing the results of analysing log transformed pooled ash free dry mass data obtained by quadrat sampling, using Canberra metric with group average sorting. (H = horizontal surfaces, V = vertical surfaces)

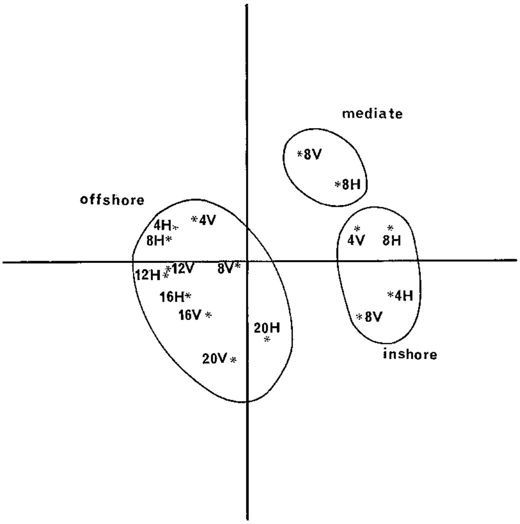

Fig. 6: Two dimensional ordination showing the results of analysing log transformed pooled ash free dry mass data obtained by quadrat sampling, using Canberra metric and multidimensional scaling. Samples coded as in Figure 5. Main associations of samples are demonstrated by boundary line. Stress = .296, rated as excellent (Kruskal, 1964)

Table 4

Information statistic results from quadrat sampling showing the frequency of occurrence of species which differ significantly between associations. * = significant difference in the frequency of occurrence at 5 % level, ** = at 1 % level in the association

Association	O	M	O	I	M	I	O (H)	O (V)	I (H)	I (V)
Number of quadrats: N	40	8	40	16	8	16	20	20	8	8
Porifera										
Chondrosia reniformis	3 **	6	3	0	6 **	0	1	2	0	0
Haliclona stilensis	1 **	3	1	1	3	1	0	1	0	1
Hymeniacedon sp.	1 **	4	1	0	4 **	0	1	0	0	0
Ircinia sp.	1 **	4	1	0	4 **	0	1	0	0	0
Lissodendoryx ternatensis	3	2	3	0	2 *	0	2	1	0	0
Sponge sp. 1	7	2	7	3	2	3	4	3	0 *	3
Sponge sp. 2	7	1	7 **	9	1 *	9	2	5	2 **	7
Sponge sp. 3	8	0	8	5	0 *	5	4	4	2	3
Cnidaria										
Hydrozoa	20	3	20	4	3	4	6 *	14	1	3
Acabaria capensis	3	0	3	0	0	0	0 *	3	0	0
Allopora nobilis	6	0	6 *	0	0	0	0 **	6	0	0
Eunicella papillosa	13	2	13 **	0	2 *	0	0 **	13	0	0
Melitodes dichotoma	3	0	3	0	0	0	0 *	3	0	0
Xenia sp.	0 **	2	0	1	2	1	0	0	1	0
Anthostella stephensoni	4	0	4	0	0	0	0 *	4	0	0
Ballanophyllia bonaspei	4 **	5	4 **	9	5	9	0 *	4	1 **	8
Bunodactis reynaudi	4	0	4	1	0	1	4 *	0	1	0
Corynactis annulata	11 *	0	11	1	0	1	7	4	1	0
Nematoda										
Nematoda	18 **	0	18 *	2	0	2	12	6	1	1
Annelida										
Polychaeta sedentaria	30 *	8	30 **	6	8 **	6	16	14	1 *	5
Arthropoda										
Cirripedia	5 *	1	5	1	1	1	5 **	0	0	1
Isopoda	26 *	8	26	10	8 *	10	12	14	7	3
Anomura	1 **	3	1	0	3 **	0	1	0	0	0
Pycnogonida	11 *	0	11	3	0	3	7	4	1	2
Bryozoa										
Bryozoa	17 *	7	17	7	7	7	4 **	13	3	4
Brachiopoda										
Kraussina rubra	10 *	0	10	4	0	4	1 **	9	0 **	4
Mollusca										
Chiton sp.	6	0	6 *	0	0	6	5	1	0	0
Aulacomya ater	37 **	2	27 **	0	2 *	0	19	18	0	0
Afrocominella sp.	1	0	1 *	3	0	3	1	0	1	2
Argobuccinum argus	16 **	0	16 **	0	0	0	7	9	0	0
Fissurellidea aperta	5	0	5	1	0	1	5 **	0	0	1
Thais cingulata	5	0	5	0	0	0	5 **	0	0	0
Thais squamosa	10 *	0	10 **	0	0	0	9 **	1	0	0

Table 4 (continued)

Association	O	M	O	I	M	I	O (H)	O (V)	I (H)	I (V)
Number of quadrats: N	40	8	40	16	8	16	20	20	8	8
Echinodermata										
Annametra occidentalis	3	2	3	0	2 *	0	2	1	0	0
Ophiothrix fragilis	24 **	0	24 *	5	0 *	5	14	10	2	3
Parechinus angulosus	10 *	0	10 **	0	0	0	8 *	2	0	0
Pentacta doliolum	21 **	0	21 **	0	0	0	13	8	0	0
Thyone aurea	10 *	0	10 **	0	0	0	8 *	2	0	0
Chordata										
Compound ascidian	3 **	5	3 *	5	5	5	1	2	2	3
Chlorophyta										
Bryopsis sp.	0 **	2	0 **	6	2	6	0	0	5 *	1
Codium papenfusii	0	0	0 **	2	0	2	0	0	1	1
Derbesia sp.	0	0	0 **	7	0 **	7	0	0	1 **	6
Phaeophyta										
Desmarestia firma	0	0	0 **	6	0 *	6	0	0	1 *	5
Rhodophyta										
Botryocarpa prolifera	6 **	5	6	6	5	6	3	3	4	2
Carpoblepharis flaccida	0	0	0 *	2	0	2	0	0	1	1
Dicurella scutellata	0 **	3	0	1	3	1	0	0	1	0
Epimenia obtusa	8 **	7	8	7	7 *	7	4	4	2	5
Gelidium sp.	0	0	0 **	4	0	4	0	0	1	3
Gigartina striata	3	0	3	0	0	0	3 *	0	0	0
Hymenena venosa	9	1	9	1	1	1	8 **	1	1	0
Kallymenia agardhii	0 **	3	0	1	3	1	0	0	1	0
Neuroglossum rinderianum	0	1	0 **	3	1	3	0	0	2	1
Pachymenia cornea	1	1	1 **	8	1	8	0	1	7 **	1
Polyopes constricta	2	1	2 *	4	1	4	0	2	3	2
Pterosiphonia cloiophylla	4	0	4	2	0	2	4 *	0	1	1
Tayloriella tenebrosa	0	0	0 *	2	0	2	0	0	1	1
Thamnophyllis discigera	4	1	4 *	6	1	6	2	2	3	3

Pentacta and *Thyone* and the ophiuroid *Ophiothrix*, and also the debris-feeder *Parechinus*. *Pentacta*, *Thyone* and *Parechinus* are completely absent from the inshore and mediate localities and can therefore be considered as indicators of the offshore cluster. The bivalve *Aulacomya* and whelks *Thais squamosa* and *Argobuccinum* are also rare or absent in the inshore and mediate clusters. Although some algae, such as *Epimenia* occur offshore, none of the algae are significantly more frequent there than elsewhere.

The mediate cluster is distinguished from the other two by the higher frequencies of sponges *(Chondrosia, Haliclona, Hymeniacedon* and *Ircinia)* and the red alga, *Epimenia.*

The inshore locality has most of its biota in common with the mediate area, with the dominance of understory algae such as *Bryopsis, Neuroglossum, Pachymenia, Polyopes* and *Thamnophyllis* which are shared by the two clusters. Only the echinoderm *Ophiothrix* and the green alga *Derbesia* are significantly more frequent in the inshore than the mediate area.

Comparing samples from the offshore horizontal and vertical surfaces, it is evi-

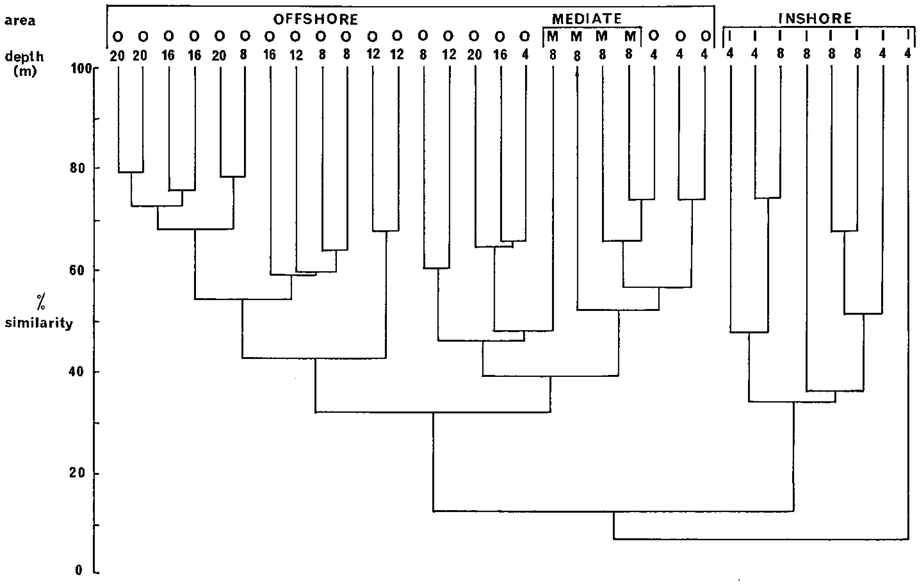

Fig. 7: Dendrogram showing the results of analysing log transformed ash free dry mass data obtained from holdfasts using Canberra metric with group average sorting

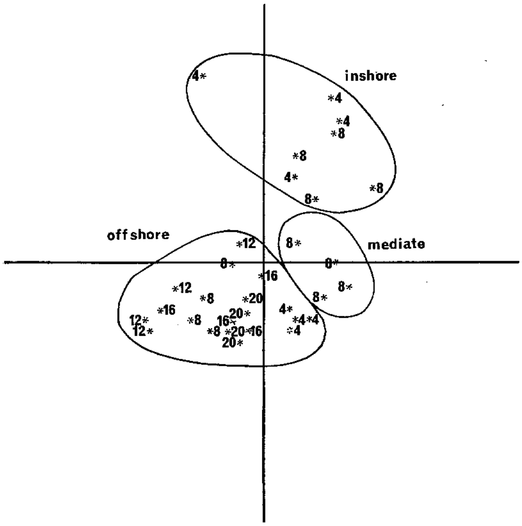

Fig. 8: Two dimensional ordination showing results of analysing log transformed ash free dry mass data obtained from holdfasts using Canberra metric and multidimensional scaling. Main associations demarkated by boundary lines. Stress = .244, rated as excellent (Kruskal, 1964)

Table 5

Information statistic results from holdfast sampling, showing the frequency of occurrence of species which differ significantly between associations, coded as in Table 4

Association	O		M	O		I	M		I
Number of holdfasts: N	20		4	20		8	4		8
Porifera									
Sponge sp. 3	9	*	4	9	*	7	4		7
Cnidaria									
Anthothoe stimpsoni	0	**	3	0		1	3	*	1
Bunodosoma capensis	0	**	2	0		0	2	*	0
Nematoda									
Nematoda	0	**	4	0		0	4	**	0
Arthropoda									
Plagusia chabrus	2		2	2	*	4	2		4
Pilumnoides perlatus	11		2	11	*	1	2		1
Synalpheus anisocheir	2	**	4	2		1	4	**	1
Bryozoa									
Bryozoa	0	**	4	0		0	4	**	0
Mollusca									
Anomia sp.	4	**	4	4		0	4	**	0
Gastropod sp.	10	*	4	10		7	4		7
Echinodermata									
Patiriella exigua	0	**	2	0		0	2	*	0
Ophiothrix fragilis	20		4	20	**	3	4	*	3
Parechinus angulosus	11	*	0	11	**	0	0		0
Pentacta doliolum	16	*	1	16	**	0	1		0
Thyone aurea	11		3	11	**	0	3	**	0

dent that vertical surfaces are characterized by a coelenterate association consisting of gorgonians *(Acabaria, Eunicella, Melitodes)*, hydroids, a hydracoral *(Allopora)*, a hexacoral *(Ballanophyllia)*, an anemone *(Anthostella)* and also Bryozoa. The brachiopod *Kraussina* is characteristic of vertical surfaces both inshore and offshore. Horizontal surfaces are distinguished by the anemone *Bunodactis* which occupies sandy crevices, by barnacles, several gastropods, the echinoderms *Parechinus* and *Thyone*, and the red alga *Hymenena*. Polychaetes, isopods, and the echinoderms *Ophiothrix* and *Pentacta* occur frequently on both horizontal and vertical surfaces (Fig. 11).

Analysis of holdfast biomass data gives a dendrogram with two main clusters (Fig. 7). The inshore holdfasts form one unit, and the offshore holdfasts another larger cluster, within which the mediate holdfasts are grouped. The low similarity between the two main clusters indicates a clear difference between the holdfast faunas of the inshore and other areas. The ordination (Fig. 8) is easier to interpret, with the mediate holdfasts forming a distinguishable group, closer to the offshore than the inshore clusters.

Information statistic tests (Table 5) reveal a complete absence of the holothurians *Pentacta* and *Thyone* from the inshore zone, although both are present in offshore and mediate holdfasts. *Parechinus* only occurs in offshore holdfasts. *Ophiothrix* although low in biomass, occurs significantly more frequently in offshore and mediate zones. No anemones were recovered from offshore holdfasts, but they and the small bivalve *Anomia* are characteristic of the mediate holdfasts.

CONCLUSIONS

Overall figures for standing crop per m^2 have been calculated by combining data from holdfast, quadrat and belt count samples (Table 6). Within each depth zone, the area covered by holdfasts was calculated from holdfast densities and mean basal area per holdfast. Since quadrats could not include holdfasts, the relative areas of rock surface represented by holdfast and quadrat samples were calculated and used to weight the standing crop figures obtained by each technique. Belt count readings were then superimposed on these results. If animals recorded in belt counts were also represented in an occasional quadrat, the belt count figure, being the mean of a much larger area (e.g. 50 m^2 compared to 0.1 m^2) was taken as being the more representative.

Considering the total standing crop figures in terms of trophic categories, the highest primary producer values were obtained in the inshore and mediate localities. Consumers were mainly represented in the inshore area by mobile carnivores, the rock lobster, *Jasus lalandii* and fish, *Pachymetopon blochii,* which move in and out of the area but may not necessarily feed there. The mediate locality showed an increase in filter-feeders (mainly sponges, mussels and ascidians) while grazers were insignificant and the lobster was the only important carnivore. The offshore locality had more grazers but was mainly characterized by patches of the urchin, *Parechinus* and filter- and detritus-feeders: the ribbed mussel, *Aulacomya,* holothurians *Pentacta* and *Thyone,* and sponges. The high standing crop of carnivores was mainly due to lobsters, large anemones and fish.

Using the term "community" in the broad sense as the biotic component of an ecosystem, we can subdivide the kelp bed community into subunits on the basis of numerical analysis. We propose to call the subunits associations, applying the definition of a community given by Mills (1969). Thus an association is briefly defined here as a group of organisms co-occurring in a particular environment and separable from other associations by ecological survey.

There are three main associations, inshore, mediate and offshore, the latter including a biotic gradient with depth which may have been obscured by random variation between individual holdfasts in one set of data. The offshore association is characterized by a large number of animal taxa (high species diversity). In addition to the depth gradient, there are differences between horizontal and vertical surfaces with horizontal surfaces characterized largely by carnivores and detritus feeders. Vertical surfaces have more filter-feeding animals which presumably would be smothered by settling detritus and movement of fine sand (Velimirov, 1971) had they been on horizontal surfaces.

The inshore and mediate associations are both conspicuous in the lack of animal life and in the density of the algal understory and two-layered kelp canopy, with

Table 6

Standing crop of principal kelp bed organisms by locality and depth range and according to trophic grouping. Figures obtained by integrating quadrat, belt count and holdfast data, expressed as kJ m^{-2}

Organisms		Inshore	Mediate			Offshore		
	Depth (m)	0–4 4–8	4–8	0–4	4–8	8–12	12–16	16–20
(a) Primary producers (mean values)								
Laminaria pallida		7,034.8	10,253.5			4,631.4		
Ecklonia maxima		12,097.8	9,766.8			2.1		
other algae		143.4	183.8			31.7		
Σ		19,276.0	20,204.1			4,665.3		
(b) Grazers								
Haliotis midae	—	25.6	34.2	126.0	8.4	15.2	—	0.2
Patella compressa		not counted		14.1	21.8	1.8	0.2	0.2
other *Patella* spp.	0.1	—	—	286.4	2.5	0.4	—	—
Turbo cidaris	1.4	1.1	15.5	0.3	4.4	0.8	4.7	3.0
Σ	1.5	26.7	49.7	302.1	36.9	18.2	4.9	3.4
(c) Debris feeders								
Parechinus angulosus	—	—	—	609.3	829.4	610.3	18.2	
Σ	—	—	—	609.3	829.4	610.3	18.2	
(d) Filter and detritus feeders								
Sponges	445.4	138.3	1,342.5	2,233.2	228.5	150.4	848.0	1,004.9
Hydrocorals	0.1	0.1	—	5.6	6.0	9.4	5.4	54.8
Hexocorals	19.7	9.4	0.7	—	1.6	—	6.3	21.6
Gorgonians	—	—	0.5	—	33.9	36.3	13.3	24.5
other octocorals	—	—	0.9	11.9	3.4	9.3	133.0	—
Bryozoa	0.6	0.2	0.5	0.1	0.2	3.6	0.9	18.9
Aulacomya ater	1.5	3.5	70.5	2,277.8	4,205.7	7,814.9	2,497.8	1,567.8
Ophiothrix fragilis	2.1	1.7	5.2	34.7	47.7	278.6	70.3	17.6

Table 6 (continued)

Organisms	Inshore		Mediate	Offshore				
Depth (m)	0–4	4–8	4–8	0–4	4–8	8–12	12–16	16–20
Pentacta doliolum	—	—	0.3	599.0	731.8	4,323.2	2,227.0	54.3
Thyone aurea	—	—	1.6	635.9	1,516.9	2,089.6	352.9	28.5
crinoids	—	1.2	1.2	10.8	3.1	11.5	7.3	0.8
Pyura stolonifera	—	—	198.0	1,225.0	1,037.0	117.0	—	—
other ascidians	0.1	4.4	11.3	16.3	—	66.8	85.6	2.5
Brachiopods	152.1	20.5	—	0.1	15.0	1.4	35.9	478.5
Σ	621.6	179.3	1,633.2	7,050.4	7,830.8	14,912.0	6,283.7	3,274.8
(e) Carnivores and scavengers								
Anemones	0.2	7.8	9.7	644.4	568.2	310.8	114.9	111.8
Argobuccinum argus	0.2	0.5	11.9	112.0	82.7	91.1	13.9	3.7
Burnupena papyracea	—	—	4.6	167.0	29.6	57.3	6.7	—
Thais squamosa	—	—	—	61.2	62.4	119.0	—	—
Jasus lalandii	506.0	303.0	507.0	758.0	946.0	539.0	1,621.0	1,118.0
Plagusia chabrus	77.9	20.9	66.9	13.3	7.2	14.5	2.2	—
Pilumnoides perlatus	3.0	—	27.8	64.4	30.4	35.3	16.3	7.9
other crustacea	40.8	26.8	35.5	43.8	50.4	61.5	71.7	26.9
Henricia ornata	3.4	3.9	4.1	1.5	0.6	2.8	7.9	4.5
Marthasterias glacialis	—	—	—	—	4.9	13.1	6.4	1.6
Patiria granifera	3.4	1.8	4.5	1.3	2.0	4.3	8.1	1.5
Pteraster capensis	—	10.3	2.6	—	—	—	—	—
Pachymetopon blochii	1,308.0	—	254.0	10.9	776.0	250.0	662.0	372.0
Σ	1,942.9	375.0	928.6	1,877.8	2,560.4	1,498.7	2,531.1	1,647.9
(f) Other unclassified organisms								
Polychaetes	11.9	13.4	125.2	87.5	95.8	90.8	33.4	31.2
small molluscs	14.3	23.0	10.2	6.9	3.3	47.8	6.3	12.8
Miscellaneous	0.7	0.5	27.8	1.3	12.1	21.3	4.2	1.2
Σ	26.9	36.9	163.2	95.7	111.2	159.9	43.9	45.2

Ecklonia at the surfaces and *Laminaria* several metres above the bottom. Small carnivores and detritus feeders are virtually absent, and filter feeders are only poorly represented.

A descriptive energy-flow model

An overview of the interactions between the different trophic categories and the main physical factors is presented as an energy-flow diagram (Fig. 9) using the circuitry symbols of Odum (1971, 1975). Where realistic values are available, estimates of production are given. Circles represent energy sources: the main one driving the ecosystem is solar radiation, with wind and waves as supplementary sources. Numbered workgates represent the action of energy subsidies in "opening the tap" to aid the main flow of energy. Thus work-gate (1) represents the action of south-easterly winds which cause upwelling of nutrients needed for photosynthesis, and hence promote faster trapping in the sun's energy. Similarly workgate (2) depicts the energy subsidy provided by waves which cause water movement over the kelp surfaces and thereby speed up growth. Indirect evidence of this has been given by Black (1950), while experimental work on aquatic macrophytes by Westlake (1967) has confirmed that increased growth occurs under conditions of water movement. Presumably this is caused by the maintenance of favourable concentration gradients for the supply of nutrients and removal of wastes at the kelp surfaces.

The bullet shaped module represents the primary producers: *Ecklonia maxima*, *Laminaria pallida* and the understorey plants. Energy flows in on the left and pro-

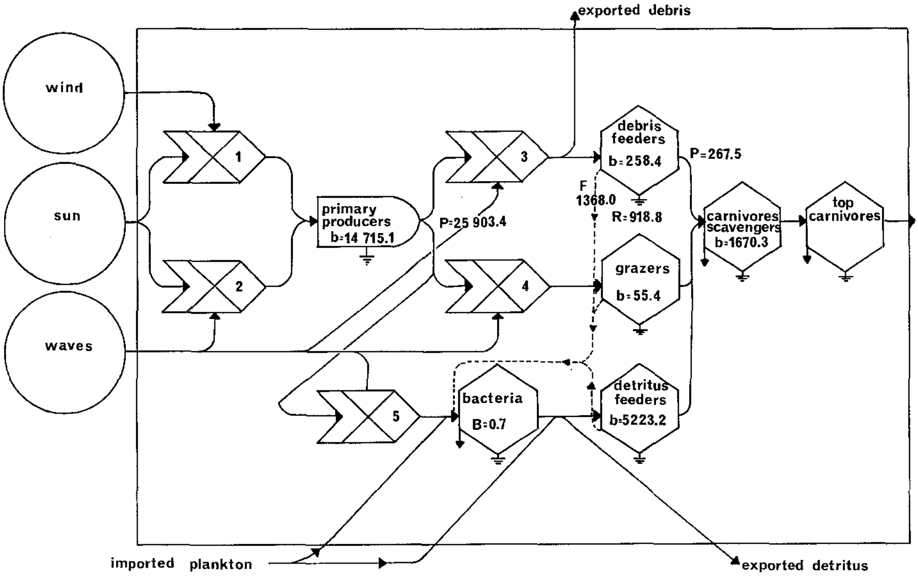

Fig. 9: Energy circuit diagram for the kelp community. b = standing crop in kJm^{-2} (P, R, F also in kJ). B = standing crop in grams in a water column under 1 m^{-2} sea surface

duction is passed on to the consumers to the right, while the dissipated energy of respiration is depicted as flowing downwards into the heat sink. Primary production is calculated as the sum of kelp frond growth plus an estimated mortality of 15 % of the total primary producer standing stock due to uprooting during storms. Kelp frond growth is estimated from the P/B ratio for fronds given by Dieckmann (1975) and Mann et al. (in press). The estimate obtained is 25,903.4 kJ m^{-2} $year^{-1}$ Work gate (3) depicts the action of waves in uprooting or breaking kelp plants. *Ecklonia maxima*, being buoyant, are exported from the kelp beds either to the open sea where they may decay and contribute to pelagic productivity or by being washed ashore. If not collected commercially on sandy beaches, this kelp is consumed by large populations of the intertidal amphipod *Talorchestia capensis*, while on rocky shores the main consumer is an isopod *Ligia dilatata*. Presumably the faeces of these populations are washed back to sea – along with kelp fragments – where they may contribute to the detritus consumed by filter-feeders. The fate of *Laminaria* broken free is different since these plants sink to the bottom and generally remain in the vicinity of the kelp beds. Sea urchins mainly consume this debris. By contrast, in the calmer Canadian conditions, urchins graze on attached *Laminaria* (Miller & Mann, 1973; Breen & Mann, 1976) whereas South African *Parechinus* is knocked off large plants swaying in prevailing swells, and probably only significantly affects kelp populations by grazing on newly settled plants.

Workgate (4) represents two different effects of waves on grazers, firstly by preventing them from climbing plants in rough weather, as in the case of the large winkle *Turbo cidaris*, and secondly by bending plants over so that the abalone *Haliotis midae* can trap fronds underfoot. Workgate (5) depicts a very important energy subsidy. Waves continually erode the tips of kelp fronds, breaking off small particles, the potential food of detritus- and filter-feeding animals, and releasing dissolved organic matter which provides a food source for bacteria.

Consumers are represented by hexagonal modules, with food energy consumed flowing in on the left and production passed on to other consumers on the right. Energy is lost as faeces (F), and is also dissipated to the heat sink as respiration (R). The only available consumer energy budget is that of the debris feeder, *Parechinus angulosus* which was studied in a similar kelp bed off Robben Island by Greenwood (1974). By assuming similar P/B ratios to prevail off Oudekraal, we have estimated the production of *Parechinus* to be 267.5 kJ m^{-2} y^{-1} at Oudekraal. Faeces and respiration figures have been estimated similarly. For simplicity, only the faeces of primary consumers are shown as contributing to the substrate for bacteria and as potential food for detritus feeders, although obviously the faeces of other consumers must be accounted for in the same way.

The main carnivore is the rock lobster *Jasus lalandii*. This in turn is preyed on (especially when young or moulting) by top carnivores such as dogfish, seals, octopus, bank cormorants and, outside fishing sanctuaries, by man.

The small standing crop of grazers (*Turbo*, *Haliotis* and the limpet *Patella compressa* – which lives on kelp stipes) indicates that very little kelp production can be passed on via this chain. Standing crop considerations also relegate the debris-feeding urchin to a minor pathway. Most of the animal standing crop is in the form of filter-and detritus-feeders which certainly provide the dominant energy pathway to carnivores, even if some of the species have slow turnover rates. Although holothurians *Pentacta* and *Thyone* form an important part of the standing crop, no predators have

Fig. 10: Dense *Laminaria pallida* forest in the mediate locality

Fig. 11: Offshore association showing faunal population on horizontal and vertical rock surface

been observed feeding on them, so the energy pathways are by no means completely known. The most important carnivore is the rock lobster *Jasus* whose main diet appears to be the mussel *Aulacomya* (Newman & Pollock, 1974; Pollock, 1976). The disproportionately low herbivore to carnivore ratio may be partly due to the exploitation of *Haliotis* by amateur divers at the study site, while lobsters are protected there by law. Comparative surveys at other sites (including Kreeftebaai, Melkbosstrand, Kommetjie and Olifantsbos; see Fig. 1) where lobsters are not protected gave a higher standing crop of *Haliotis*, but carnivores were still dominant. These surveys also confirmed the importance of filter- and detritus-feeders.

If the food of the filter- and detritus-feeders offshore is derived mainly from kelp (by no means certain since plankton has not yet been studied in the kelp bed), then the inshore, mediate, and offshore associations would appear to be complementary. The inshore and mediate associations (Fig. 10) provide most of the primary production while most of the consumers are offshore (Fig. 11). Together, the three associations may comprise a balanced community, but this needs to be confirmed by studies of the import-export of debris, detritus and plankton into and out of the kelp bed.

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