The fauna and flora of a kelp bed canopy

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The fauna and flora of the canopy of a kelp bed off Oudekraal, on the Cape Peninsula, is surveyed. Four species of epiphytic algae occur in the kelp canopy, three restricted to *Ecklonia maxima* and the fourth to *Laminaria pallida*. Epiphyte biomass is equivalent to 4 – 9% of host standing crop amongst *E. maxima*, but less than 1% in stands of *L. pallida*. Wherever *E. maxima* is common, epiphyte standing crop considerably exceeds that of benthic understorey algae. The canopy fauna comprises at least 27 species and is composed largely of small Crustacea, molluscs and polychaetes. Since these organisms are mainly associated with the epiphytic algae they are most abundant amongst *E. maxima* in the shallower regions of the kelp bed. In such areas the biomass of the canopy fauna may exceed that of the relatively impoverished benthos, but further offshore the canopy fauna is insignificant in relation to a rich benthic community. Indications are that canopy organisms are an important source of food for the fish of the kelp bed system.

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'n Opname van die flora en fauna in 'n seebamboesblaredak naby Oudekraal aan die Kaapse Skiereiland is gemaak. Vier spesies van epifitiese seewiere is in die blaredak van die seebamboesgemeenskap gevind, drie hiervan is beperk tot *Ecklonia maxima* en die vierde tot *Laminaria pallida*. Epifietbiomassa is gelyk aan 4 – 9% van die gasheer se biomassa in *E. maxima*, terwyl dit minder as 1% is in die geval van *L. pallida*. Waar *E. maxima* volop is, is die biomassa van die epifiete heelwat groter as die van die bentiese seewiere. Die blaredak-fauna bestaan uit minstens 27 spesies, meestal klein Crustacea, Mollusca en Polychaeta. Aangesien hierdie organismes hoofsaaklik met die epifitiese seewiere verbonde is, kom hulle hoofsaaklik tussen *E. maxima* in die vlakker gebiede van die seebamboesgemeenskap voor. In sulke gebiede kan die biomassa van die blaredak-fauna die relatief verarmde bentos oorskry, maar verder van die kus is die blaredak-fauna onbelangrik in vergelyking met die ryk bentosgemeenskap. Daar is ook aanduidings dat die blaredak-fauna as 'n belangrike voedselbron vir die visse in die seebamboesgemeenskap dien.

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The distribution patterns and standing crops of plants and animals associated with kelp beds off the west coast of South Africa have been investigated in some detail by Velimirov, Field, Griffiths & Zoutendyk (1977), Field, Jarman, Dieckmann, Griffiths, Velimirov & Zoutendyk (1977) and Field, Griffiths, Griffiths, Jarman, Zoutendyk, Velimirov & Bowes (1980). These papers mainly considered bottom dwelling organisms, although attempts were made to count Hottentot fish and the large gastropod *Patella compressa*, which lives in the kelp canopy. The epiphytic algae which occur on both the major kelp species, *Ecklonia maxima* and *Laminaria pallida* were, however, removed and discarded before the kelps were weighed and no attempt was made to recover the smaller animals which live in the canopy. Although these omissions appeared insignificant at the time subsequent observations suggest that epiphytic algae may contribute significantly to overall standing crop of algae, at least in certain areas. The canopy fauna may also be of disproportionate significance, since it is rich in small invertebrates which may be more readily available to predators than the large biomass of mussels, ascidians, sponges and holothurians which dominate the benthos (Velimirov *et al.* 1977, Field *et al.* 1980). A preliminary survey of the canopy fauna and flora was thus undertaken in an attempt to assess the significance of this element of the community to the economy of the kelp beds as a whole.

Methods

All samples were collected from the kelp bed at Oudekraal, on the Cape Peninsula. Velimirov *et al.* (1977) describe this site in detail and consider it to be composed of three relatively distinct habitats — a shallow inshore zone (0 – 8 m depth), a boulder-strewn mediate zone (4 – 8 m depth), and an offshore zone (0 – 20 m depth) abutting a large granite outcrop. Duplicate canopy samples were thus collected from the centre of each of these zones, at 4 m, 6 m and 10 m depth respectively.

Each sample consisted of kelp plants attached within a three-sided 0,25-m^2 quadrat placed at random within a kelp patch in the appropriate area. A pair of SCUBA divers would descend to the quadrat and cut the kelp plants immediately above their holdfasts. One diver then held the cut stipes within the cod-end of a gathered Indian Ocean Standard plankton net (330-μm aperture mesh) while his partner swam the mouth of the net up

over the plants and closed off the opening with a drawstring. The whole net was then pulled to a nearby boat, from which it was suspended with the mouth above the water surface. Individual plants were then removed from the net and cut into stipe and frond (*Laminaria pallida*), or stipe, primary frond and secondary frond (*Ecklonia maxima*) portions. Each portion was washed in a separate bath of dilute formalin, to dislodge motile elements of the fauna and then transferred to a large sorting dish where the epiphytes and sessile animals were scraped off. The remaining kelp portions were finally weighed and discarded. When all the plants from each quadrat had been processed the contents of the sorting dishes and formalin baths were poured through a 0,2-mm sieve and the resulting organisms preserved. Any organisms left in the plankton net after all the plants had been removed were also preserved separately.

In the laboratory epiphytic algae were searched for any remaining fauna before being identified, dried at 60 °C for three days and weighed. The fauna was sorted to species and similarly dried and weighed. Biomass measurements were subsequently converted to energy equivalents by burning subsamples of each species in a Phillipson Microbomb Calorimeter.

Results

Since they are resistant to swell action, few organisms were dislodged from the kelp plants by the collection procedure, and these could invariably be allocated to a specific portion and species of host plant on the basis of other records. The distribution and abundance of canopy organisms in relation to host species, location on the host, and collection site could thus be determined and these results are displayed in Table 1.

Four different epiphytic algae and 27 animal species were recorded in the canopy samples. Of the epiphytic algae one species, *Carpoblepharis minimum*, occurred exclusively on *Laminaria pallida*, while *Ecklonia maxima* was the host for the remaining three forms, *C. flaccida, Carradoria virgata* and *Suhria vittata*. All three *Ecklonia* epiphytes were found on both stipes and primary fronds, but only *C. flaccida* extended onto the secondary fronds (where it accounted for up to 5% of frond mass).

The fauna of the canopy was composed largely of Crustacea and molluscs, with polychaetes, fish and Bryozoa making up the balance. Amongst the Crustacea the most abundant species were the amphipods *Hyale grandicornis* and *Paramoera capensis* and the isopod *Dynamenella huttoni*, all of which appeared to be closely associated with epiphytic algae. Also significant were the larger kelp-grazing forms *Ampithoe humeralis* (Amphipoda), *Paridotea reticulata* and *P. rubra* (Isopoda). Of the molluscs the tiny gastropod *Eatoniella nigra* reached immense population densities and newly settled *Choromytilus meridionalis* were locally abundant. In terms of biomass the large limpet *Patella compressa*, which is restricted to kelp plants, was also important. A distinct zonation pattern was evident in this limpet, small individuals being found on the fronds and larger ones on the stipes. Other species of note included the polychaetes *Platynereis dumerilii*, which colonized thick bunches of epiphytic algae, and *Paralaeospira patagonicus*, which attached its calcareous tubes within the folded primary fronds of *E. maxima*.

The encrusting *Membranipora membranacea* was recorded from fronds of both *E. maxima* and *L. pallida*, but was not assessed quantitatively. Five species of fish were found on *E. maxima* plants, the most common being the tiny cryptic suckerfish *Eckloniaichthys scylliorhiniceps*, which occurs only on algal surfaces. The remaining fish were typically benthic forms which had probably ventured into the canopy in search of food. Similarly, the large Crustacea *Jasus lalandii* and *Plagusia chabrus*, and gastropods *Burnupena papyracea* and *Argobuccinum argus*, are typically benthic species, and cannot be considered as normal residents of the canopy.

Considerable differences are evident between the canopy communities associated with *E. maxima* and *L. pallida*, as well as between the inshore, mediate and offshore zones of the kelp bed. In order to determine the significance of site, relative to host species, on the composition of the canopy fauna the animals associated with the two kelp species at the three sites were compared numerically by subjecting log-transformed numerical data to a Bray-Curtis similarity analysis, using group average sorting (Bray & Curtis 1957). The results (Figure 1) clearly indicate kelp species to be the most important variable, with only 37% similarity being recorded between the communities colonizing the two host algae.

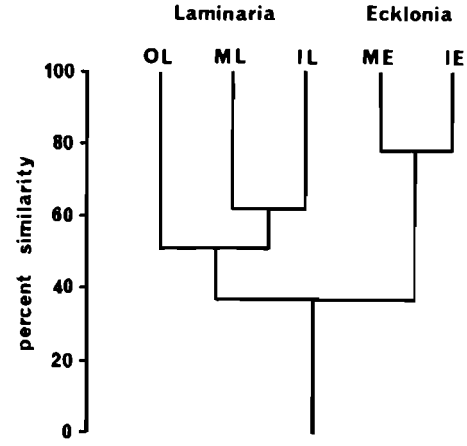

Fig. 1 Dendrogram showing percentage similarity of canopy flora and fauna according to site and host species (O, M, I = Offshore, Mediate, Inshore respectively: L = *Laminaria*, E = *Ecklonia*). Log transformed numerical data used throughout.

The importance of each animal group to the community as a whole is best judged by converting the numerical data in Table 1 to units of biomass or energy. A summarized version of such an analysis is shown in Table 2. Certain of the figures are elevated by the presence of large benthic organisms making incursions into the canopy and are probably atypical. Excluding these forms (which are indicated on the table) it would appear that the most important resident groups, in terms of biomass, are small molluscs, followed by isopods, amphipods and polychaetes. In terms of energy, however, the molluscs, whose mass is largely in the form of shell, rate considerably below the other three groups, which maintain their previous order of importance.

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Table 1 Distribution and abundance of kelp canopy organisms in relation to host species, location on host and position within kelp bed. Abundance expressed as numbers m^{-2} for animals, g dry mass m^{-2} for algae. *Ecklonia maxima* was absent from the offshore zone of the kelp bed

	Inshore zone					Mediate zone					Offshore zone	
	Ecklonia maxima			*Laminaria pallida*		*E. maxima*			*L. pallida*		*L. pallida*	
	Stipe	Primary frond	Secondary frond	Stipe	Frond	Stipe	Primary frond	Secondary frond	Stipe	Frond	Stipe	Frond
Kelp biomass	9 322,5	363,0	4 505,2	2 249,5	3 197,5	7 671,7	469,7	7 723,6	562,9	674,2	2 342,3	1 711,1
Epiphytic algae												
Carpoblepharus flaccida	27,2	21,6	104,8	–	–	496,0	14,0	322,0	–	–	–	0,8
Carpoblepharus minimum	–	–	–	15,6	10,0	–	–	–	14,8	–	–	–
Carradoria virgata	247,6	0,8	–	–	–	442,0	26,8	–	–	–	–	–
Suhria vittata	165,2	0,8	–	–	–	102,0	–	–	–	–	–	–
Polychaeta												
Paralaeospira patagonicus	–	3 444	–	–	–	–	592	–	–	–	–	–
Platynereis dumerilii	52	12	28	–	4	84	12	4	4	–	–	–
Cirripedia												
Balanus algicola	–	–	–	–	–	–	36	–	–	–	–	–
Isopoda												
Dynamenella huttoni	64	4	16	–	–	104	96	232	12	–	–	–
Paridotea reticulata	8	–	36	168	12	8	32	524	8	–	–	20
Paridotea rubra	4	–	–	4	4	8	8	108	4	–	–	4
Parisocladus stimpsoni	–	–	–	4	–	–	–	4	–	–	–	
Amphipoda												
Ampithoe humeralis	20	–	52	–	20	4	–	56	–	16	–	48
Caprella spp.	4	–	4	4	–	12	–	4	–	–	–	16
Hyale grandicornis	68	16	112	16	72	364	500	2 376	32	–	–	
Maera inaequipes	–	–	–	–	–	4	–	–	–	–	–	–
Paramoera capensis	2 508	24	696	108	140	7 600	400	10 392	152	–	–	8
Decapoda												
Jasus lalandii	–	–	–	–	–	–	–	4	–	–	–	–
Plagusia chabrus	–	–	4	–	–	–	–	8	–	–	–	–
Mollusca												
Argobuccinum argus	–	–	–	–	–	–	–	–	–	–	–	4
Burnupena papyracea	–	–	–	–	–	–	–	–	–	–	–	4
Choromytilus meridionalis	200	–	–	–	–	7 400	–	2 800	20	–	–	
Eatoniella nigra	43 560	–	–	–	–	16 712	–	2 780	376	–	–	52
Gibbula capensis	–	–	4	–	–	–	–	–	–	–	–	–
Lasaea rubra	–	–	–	–	–	296	–	100	32	–	–	–
Patella compressa	4	4	4	–	–	36	–	16	–	–	4	12
Tricolia neritina	172	–	–	–	–	296	–	56	–	–	–	8
Bryozoa												
Membranipora membranecea		++	++		+		++	++		+		+
Pisces												
Chorisochismus dentex	–	–	–	–	–	4	–	–	–	–	–	–
Clinus superciliosus	–	–	–	–	–	–	–	4	–	–	–	–
Eckloniaichthys schylliorhiniceps	–	–	8	–	–	4	–	16	–	–	–	–
Gynutoclinus rotundifrons	–	–	–	–	–	–	–	4	–	–	–	–
Peroclinus laurentii	–	–	–	–	–	4	–	–	–	–	–	–

Discussion

Our results show the kelp canopy to be richly colonized by epiphytic algae and both sessile and motile animals. Similarly structured communities have been described from the canopies of kelp beds in both California (Wing & Clendenning 1971) and Eire (Ebling, Kitching, Purchon & Bassindale 1948), although in both these areas the canopy community appears to be based on Bryozoa or Hydrozoa, rather than algae. Most of the motile invertebrates in these systems appear to utilize encrusting forms (whether these are animals or plants) as food or shelter, so that they are most abundant where the host plants are heavily encrusted. The sessile forms in turn appear to utilize the canopy in order to expose themselves to

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Table 2 Dry mass (g m^{-2}) and energy value (kJ m^{-2}) of canopy epiphytes and epifauna, with comparable figures for understorey algae and benthos, taken from Velimirov *et al* (1977)

	Inshore zone		Mediate zone		Offshore zone	
	g m^{-2}	kJ m^{-2}	g m^{-2}	kJ m^{-2}	g m^{-2}	kJ m^{-2}
Canopy						
Total epiphytes	563,6	8 452,1	1 417,6	21 785,1	0,8	12,0
Polychaeta	3,6	70,8	1,8	35,8	–	–
Isopoda	7,8	77,6	28,2	281,6	0,1	1,0
Amphipoda	1,6	24,6	11,5	174,6	0,1	1,6
Other Crustacea	36,6*	532,3*	272,8*	3 963,7*	–	–
Mollusca	15,3	27,1	12,7	22,5	144,1*	255,1*
Pisces	0,1	0,6	70,3*	1 122,5*		
Total animals	65,0	733,0	397,3	5 600,7	144,3	257,7
Benthos						
Total understorey	–	143,4	–	183,6	–	31,7
Total benthos	–	1 286,0	–	2 521,0	–	16 949,0

*Indicates presence of normally benthic forms in canopy samples.

favourable nutrient or feeding regimes and their distribution patterns are hence largely determined by current patterns (Ebling *et al.* 1948). While the composition of the fauna is comparable to those of other kelp canopies it differs from that of algal turfs on the South African intertidal (Beckley & McLachlan 1980). This is probably because the short intertidal turfs tend to trap sediment and detritus and are therefore rich in interstitial forms, such as nematodes, copepods, ostracods and mites, which were not recorded during the present study.

Considering the vastly greater standing crop of algae in the kelp bed, however, epifaunal biomass in the two systems is surprisingly similar (11,4 g epifauna in 227,2 g m^{-2} algae in the rocky intertidal as compared to 1,0 – 54,2 + g epifauna on 4,1 – 20,2 kg m^{-2} kelp plus epiphytes in the kelp bed, when temporary immigrants are excluded). Within the kelp bed the canopy fauna of *E. maxima* is far richer and more diverse than that of *L. pallida*, probably because the densely tufted epiphytic algae so abundant on this species provide favourable microhabitats for a wide variety of organisms (cf. Beckley & McLachlan 1980). Since *E. maxima* grows to approximately 8 m depth, epiphyte biomass was low in our offshore samples, which were taken from an area of pure *L. pallida* at 10 m. The richest canopy community occurred in the mediate zone, at 6 m, where the highest standing crop of mature *E. maxima* plants was recorded.

The importance of the canopy community to the kelp bed as a whole can be assessed by comparing the standing stocks of canopy organisms recorded here with figures given for the benthos of the same area by Velimirov *et al.* (1977). Appropriate results taken from that work (and adjusted by exclusion of Hottentot fish, and *Patella compressa*, which occur off the bottom), are reproduced in Table 2. On direct comparison these indicate that the standing crops of epiphytic algae greatly exceed those of understorey species in both inshore and mediate zones; while the canopy fauna accounts for 0,6 and 2,2 times the benthic fauna respectively. In the offshore part of the beds both canopy and understorey algae are very poorly represented and the rich benthic fauna greatly overshadows that of the canopy.

It should be recalled, however, that in the present study samples were collected specifically from kelp stands, whereas Velimirov *et al.* (1977) values are means over a much wider area, which included sand patches and considerable expanses of rock bare of kelp. This is clearly demonstrated by comparing the standing stock figures for kelp, which are 8 – 10 times higher here than in Velimirov *et al.* We may, however, reasonably assume the biomass of canopy organisms to be proportional to that of the kelp itself and adjust our figures downwards to equate with the more general ones of Velimirov *et al.* (1977). If this is done we still find that epiphyte standing stocks exceed those of understorey algae in both the inshore zone (1,7:1) and mediate zone (13,2:1), although benthic algae are more important offshore, where very few epiphytes occur.

Velimirov *et al.* (1977) found the benthic fauna to be relatively impoverished inshore and in the mediate zone, but extremely rich in the offshore region of the kelp bed. Conversely, few animals are found in the canopy of *L. pallida* stands in deeper waters while the canopy fauna amongst *E. maxima* is rich, especially in the mediate zone. Standing crop of the canopy fauna as a whole is in fact 5,6% of benthic standing crop inshore, 21,3% in the mediate zone but only 0,3% offshore. Although on this basis the benthos may appear to be by far the more significant, it should be recalled that the canopy is colonized by small, readily-digestible organisms such as isopods, amphipods and polychaetes. By contrast the benthos consists largely of sponges in the inshore and mediate zones and of large mussels, echinoderms and ascidians offshore. Few of these appear to be available as food for the fish in the system (primarily the commercially important Hottentot, *Pachymetopon blochii*, a variety of clinids, principally *Clinus superciliosus* and the suckerfish *Chorisochismus dentex* and *Ecklonia ichthys schylliorhiniceps*). Stomach contents studies confirm that epiphytic algae or canopy animals form important components in the diets of most of these fish. Nepgen (1977), for example, gives the epiphyte *Carpoblepharis flaccida* as the most common element in the diet of Hottentot from the Cape Peninsula (although this, and a variety of other canopy invertebrates, are undoubtably supplemented by both benthic species such as echinoderms, and pelagic forms, including copepods and hyperiid amphipods). Penrith (1965) shows the most important items in the diets of most clinids to be amphipods, isopods, polychaetes and small molluscs, particularly species recorded here as being most common in the canopy. Similarly Stobbs (1980) shows that young *C. dentex* feed mainly on small Crustacea, while the principal food items of adults are patellid molluscs (juvenile *Patella compressa* in the case of fish caught during this study).

In conclusion it appears that, at least in the shallow regions of kelp beds, epiphytic algae may contribute significantly to primary production and that they and their associated fauna may be of disproportionate significance in the food chains leading to important fish species in the system.

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