EFFECTS OF GRAZING BY THE LIMPET *PATELLA COMPRESSA* ON THE STIPE EPIPHYTE FLORA OF *ECKLONIA MAXIMA* (ALARIACEAE, LAMINARIALES)

by

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Grazing marks of the limpet *Patella compressa* on the stipe of *Ecklonia maxima*. The seaweed growing on the shell of the limpet is *Suhria vittata*, a common epiphyte of *E. maxima* stipes. a = *Ralfsia* sp. b = *Clathromorphum* sp. The blackness of the stipe is a thin layer of *Sporocladopsis novae-zelandiae*, a filamentous green alga~~e~~ which may be an endophyte of the stipe.

ABSTRACT

The effect of host plant age and grazing by the limpet *Patella compressa* Linn. on the relative abundance of algal epiphytes on the stipe of *Ecklonia maxima* (Osbeck) Papenf. was investigated at Bakoven, Cape Peninsula. Vertical distribution patterns of epiphytes on the stipe were related to a vertical gradient in age of host tissue on the stipe. Maximum stipe circumference was used as an estimate of kelp plant age. The 121 kelp plants analysed were grouped into four circumference classes, which were found to differ significantly with respect to epiphytes and limpets. Large limpets occuring on older kelps significantly reduced the biomass of large epiphytes (eg. *Suhria vittata* (Linnaeus) J. Agardh. and *Polysiphonia virgata* (C. Agardh.) Sprengel) as well as a non-coralline crust, *Placophora monocarpa* (Montagne) Papenfuss. The coralline crust *Clathromorphum* spp. was unaffected by limpet grazing and *Ralfsia* sp. was more common on heavily grazed stipes. Blackened stipe, which is associated with a filamentous green algal epiphyte, *Sporocladopsis novae-zelandiae* Chapman, had a significantly higher percentage cover on plants with large limpets. The possibility that the limpet gardens filamentous epiphytes on the stipe is discussed, and a dynamic explanation for the distribution of epiphytes is proposed. Current ideas behind the evolution of limpet-laminarian relationships around the world are briefly discussed in the light of the results . Various suggestions are made for direction in future research in~~to~~ this field.

INTRODUCTION

Ecklonia maxima is a large kelp with a hollow stipe which attains lengths of over 10m. The stipe terminates in a broader 'hand' (primary blade) at the surface which bears lateral strap-shaped fronds (secondary blades).

The kelp limpet *Patella compressa* is almost entirely restricted to *Ecklonia maxima* and represents one of the four worldwide examples of an obligate limpet-laminarian relationship (Choat & Black, 1979). However, *P. compressa* is also occasionally found on *Laminaria pallida* Greville and *Laminaria schinzii* Foslie pers. obs.) which sometimes co-occur in *Ecklonia maxima* forests. Large adult kelp limpets usually occur singly on the kelp stipe, where they form a scar. Territorial behaviour has been reported ~~in~~ by larger limpets which apparently force conspecific intruders off from their plant host (Branch, 1975).

Kelp stipes differ in their degree of colonization by various species of epiphytes. It was my aim to identify the epiphytes and also the possible factors which could explain the differences in the extent of colonisation and relative abundance of epiphytes on kelp stipes. It is recognised that epiphyte species richness and percentage cover increases with the age of the host (Ballantine, 1979; Lüning, 1990; Markham, 1969). *Ecklonia maxima* is difficult to age, so to investigate the above pattern with respect to limpets and epiphytes, kelp plants were assigned to four 'age' classes on the basis of maximum stipe circumference. Vertical distribution patterns of the nine most common epiphyte species on the kelp stipe were also investigated.

Markham (1969) investigated the vertical distribution and species composition of algal epiphytes on the stipe of the kelp *Nereocystis luetkeana* (Mertens) Postels and Ruprecht in the North Pacific. However, this is an annual species with no associated limpet. Branch (1975) has studied some aspects of the population biology of *P. compressa*, and Allen and Griffiths (1980) described the fauna and flora of the kelp bed canopy. However, there is no published literature on the distribution of algal epiphytes on the stipe of *E. maxima*, or any information on the possible grazing effects of *P. compressa* on these epiphytes. This study, in addition to the above aims, investigates the hypothesis that the relative abundance of different epiphytes species found on the kelp stipe are controlled or restricted by kelp limpet grazing.

METHODS

Study Site

The study site was situated at Bakoven on the west coast of the Cape Peninsula (Fig. 1). Sampling was restricted to an area of about 50m^2 close to the shore ranging in depth from about 2 to 3.6m. This site was chosen for a number of reasons. Firstly, a small beach (Plate 1) facilitated the launching of a small fibreglass rowing boat, which was used for collecting kelp. Secondly, the beach and study site were in a fairly sheltered situation which allowed fieldwork to be carried out even while there was a small swell running. Thirdly, kelp stipes in the site showed varying degrees of epiphyte and limpet colonization.

The substratum in the area consisted of coarse sand with outcrops of granite. Large stable granite boulders supported dense beds of *Ecklonia maxima* and the occasional *Laminaria pallida*.

Fieldwork

Fieldwork was carried out using SCUBA and free diving (snorkeling). Twelve dives were carried out between April and September 1991. Fieldwork was divided into three different sections: (a) a general survey; (b) removal experiment; and (c) caging experiment.

(a) *General survey*

A total of 121 kelp plants were sampled for limpets and epiphytes. Plants were collected in three different ways. In the first method, 20 plants were collected by choosing 10 plants that were heavily colonised by epiphytes, and 10 plants with no foliose epiphytes*. In order to select older plants, and to reduce the variation in age, the plants chosen were of roughly similar length. In the second method, all the kelp plants longer than 0.6m were collected in a $1m^2$ quadrat laid down subjectively in a kelp bed. The quadrat was placed in a bed which had kelp plants of varying age and length, some with foliose epiphytes and some with large limpets. The aim was to include kelp plants showing all possible degrees of epiphyte colonization. A total of 79 kelp plants were collected from 3 separate quadrats. The data set at this stage did not include enough plants associated with large adult limpets (over 60mm in length) or plants heavily colonised by foliose epiphytes. Thus, in the third sampling method, 22 plants meeting the above criteria were collected.

Sampling procedure

The various epiphytic species found on the kelp stipes in the study site were identified and grouped into growth form classes. Species associated with these classes are provided in the results. The following data were collected on the 121 kelp plants:

(a) Maximum stipe circumference (mm)

(b) Length (cm) - measured from above the holdfast to the tip of the primary blade.

(c) Limpet length (mm) - all the limpets on each plant were measured. Limpets tend to let go of the plant as it floats to the surface. Thus, they were removed from the plant prior to cutting, and collected in numbered bags. The plant was given a similar numbered tag to its host limpets. Limpets less than 25mm in length tend to congregate on the primary and secondary blades of the kelp plant (Branch, 1975). Although I searched for them here, they are difficult to detect and were generally undersampled. This does not affect the interpretation of the results because their grazing effects are restricted to the primary and secondary blades of the plant, and are insignificant relative to adult limpets.

(d) Foliose epiphyte biomass (g) - the wet mass of all large and/or foliose epiphytes (i.e. not crustose or filamentous) on the stipe was measured.

(e) % cover crustose epiphytes

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* In this project the term 'foliose epiphytes' includes all epiphyte species that are not crustose or filamentous.

(f) % cover foliose epiphytes
(g) % cover blackened stipe
(h) % cover clear or uncolonised stipe

A more detailed sampling procedure was carried out for the 20 plants collected using the first method. The stipe of each plant was divided into 50cm sections. The percentage cover and biomass (for foliose epiphytes only) of each epiphyte species was estimated for each section. The primary blade was treated as a separate section. I tested my estimates by wrapping tracing paper around the stipe and tracing the outline of the various epiphyte species. The true percentage cover of the species was determined by weighing the different pieces of tracing paper that represented different species of epiphytes. The results of this test (Table 1) show that the estimates were not significantly different from the true percentage cover values except for in the estimates ranging from 10 to 50% cover. In the 0 to 10% estimate range the common error of overestimating was made, while in the 10 to 50% estimate range underestimates were more common. These discrepancies would not effect the general patterns which were investigated (see analysis section).

(b) *Removal experiment*

This experiment was aimed at determining whether the colonization of different epiphyte species was enhanced if the limpets were removed.

On 9 May 1991 20 kelp plants with adult limpets were tagged with cable ties. All the limpets were removed from these plants. The plants were all completely free of foliose epiphytes when the limpets were removed. On a separate dive, 20 plants were tagged and the limpets left untouched. Over four months later, on 24 September, 10 of the plants with removed limpets were found again, the remaining 10 were probably dislodged in storms. Observations were made on the status of the epiphytes as well as the presence or absence of limpets. Some of the control plants were chosen as part of the third method for the general survey.

(c) *Caging experiments*

The aim of these experiments was to find out whether limpets grazed on foliose epiphytes and crusts and whether they could clean the stipe free of epiphytes.

Orange fruit sacks approximately 60cm in length, were used to cage limpets on subjectively chosen portions of the stipe (see Plate 2). Limpets were caged on sections of the stipe which had a high percentage cover of foliose epiphytes. A total of 10 cages were tied on different kelp stipes and left for various lengths of time. Observations and photographs were taken to indicate the effect that the caged limpets had on the epiphytes.

Unfortunately, rough seas and a time limit underwater (due to approximately one hour of air in a tank and cold water) prevented real data from being collected for the removal and caging experiments. For example, it took about one hour to put six cages in place.

Analysis

Vertical distribution patterns of epiphytes and limpets were analysed by averaging the percentage cover of blackened and clear stipe and occurrence (presence or absence) of the other epiphyte variables on the different sections (Fig. 2; 3(a) and (b) and 4(a) and (b). The two groups of plants (A and B) were collected by the first method (see above). Group A had larger limpets and very few foliose epiphytes, while group B had smaller limpets and a high cover of larger and other epiphyte species. Two plants were excluded from both of these groups, because their lengths and circumferences deviated too widely from the mean. This was done to reduce the variation in age between and within the plants that were compared. This left 8 plants in each group. Sections 50cm in length were cut consecutively from the top of the stipe down, therefore, the bottom sections varied in length depending on the length of the plant. If the 'left over' section at the bottom was less than 25cm in length, then the data from the next section up was included in the bottom section, and the data from both were averaged. Thus the bottom section could vary in length from 25 to

75 cm. The middle section could vary between 50 and 100cm, depending on the length of the plant. The data for clear and blackened stipe were averaged when two sections (100cm) made up the middle section. This rather problematic analysis should be clarified by referring to Figure 2 ;3(a) and (b) and 4 (a) and (b). A more appropriate sampling procedure for displaying vertical distribution patterns should be planned in future research.

To show the effect of age of plants on the data collected, the 121 kelp plants were grouped into four circumference classes, and means and standard errors of limpet lengths and various epiphyte growth forms were displayed as histograms bargraphs (Figs. 6; 7(a) and (b)) Statistical tests for the significance of the difference between the means in each circumference class are displayed in Table 2.

To show the effects that the limpets were having on the epiphytes, the plants in each circumference class were divided into two groups on the basis of the total length of all limpets on each plant; one group with limpets shorter than 50mm, and the other with limpets longer than 51mm. The means and standard errors of the epiphyte data in these groups were also displayed as bargraphs (Figs 8; 9(a) - (d)), and the statistical tests are displayed in Table 3. The limpet lengths could not be divided into more than two groups because this would have made the sample sizes too small. The total limpet length per plant was used in the analysis because there were never more than three juvenile limpets (shorter than 25mm) found on a plant, and usually only one, so they never made a large contribution to the total limpet length, i.e. a large limpet length represents a large limpet not a lot of small ones. If they were displayed in numbers there would be a higher number of smaller limpets than larger ones on all kelp plants (Branch, 1975), which is why the average limpet length for each plant would have been an inappropriate measure.

RESULTS

Epiphyte Species

Foliose Epiphytes (see Plate 3)

The most common foliose epiphyte species was *Suhria vittata*. This species is also commonly found growing on the shells of *Patella compressa* and rarely on rocks in the subtidal zone (Anderson *et. al.*, 1989). Other epiphytes that are fairly common on kelp stipes include *Polysiphonia virgata* and *Cladophora capensis* (C. Agardh) De Toni. *Carpoblepharis flaccida* (C. Agardh) Kuetzing is usually restricted to the blades but it also occurs on the stipe. This species appears to have a holdfast that penetrates the host tissue, because it forms a bump on the stipe where the holdfast is attached. Other large and/or foliose species found growing on the stipe included *Ecklonia maxima, Laminaria pallida, Ulva* sp., *Gigartina stiriata* (Turner) J. Agardh., *Kallymenia* sp., *Botryocarpa prolifera* Greville and *Botryoglossum platycarpum* (Turner) Kuetzing.

Crustose Epiphytes

A crustose coralline alga of the genus *Clathromorphum* is well represented on kelp stipes (Plates 4 and 5). There may be several species of this genus occurring on the stipes (Stegenga, pers. comm.), but these were not identified. Two other crustose epiphytes identified on kelp stipes are *Ralfsia* sp. and *Placophora monocarpa*. The horizontal form of the latter species is two cells thick and produces uprights (Plate 6) which appear as a dense mat or turf on the stipe (Plates 4 and 5). Thus it can be filamentous as well.

Filamentous Epiphytes

Two prominent species of filamentous algae identified were *Colaconema nemalionis* (De Notaris) Stegenga, a red alga, and *Sporocladopis novae-zelandiae* a green alga (Plate 5). There are probably several other species of filamentous epiphytic algae, but these were not identified.

Blackened Stipe and Clear Stipe

? The black colour associated with all older stipes appears to be caused by a universal layer of *Sporocladopis novae-zelandiae* cells (see Plate 7) which absorbs most of the light. The attachment cells of this species appear to penetrate the cortex (Plates 7 and 8). The turf or fur that this filamentous algae forms (Plate 9) is relatively rare compared to the cover of the blackened stipe. Where the stipe is black the cortex shows extensive cell wall thickening (Plate 8). However, the cortex associated with clear stipe has no cell wall thickening (Plate 10) and epiphytes seldom grow on it, probably because of its young age. Cell wall thickening in the cortex appears to be a response to limpet grazing. This raises the interesting possibility that damage to the cortex caused by limpet grazing creates a suitable micro-environment for the establishment of *Sporocladopsis novae-zelandiae* and other algal epiphytes.

Vertical Distribution of Epiphytes in Relation to Limpet Grazing

Blackened stipe dominates over clear stipe on lower sections of the stipe (Fig. 2). Stipes possessing large limpets (group A) have a higher percentage cover of blackened stipe on the hand (H) and top section (1) than stipes with small or no limpets (group B). Clear stipe is most predominant, relative to the rest of the stipe, in the top section for both groups of plants. 'Other' epiphytes, made up mostly of the crustose coralline epiphyte are most abundant on the bottom and middle sections, being more abundant on plants with small limpets.

Figures 3(a) and (b) and 4(a) and (b) display results on the frequency of occurrence of epiphytic species for the same two groups of plants as in Figure 2. In the group of plants with only small limpets (Fig. 3(b)), the coralline crust, *Clathromorphum* sp., occurs on over 50% of the plants on all sections except the top section. *Placophora monocarpa* shows a similar trend. However, in the group of plants with large limpets (Fig. 3(a)), *Placophora monocarpa* is rare and only occurs on the bottom section on 50% of the plants. The coralline crust remains common on the bottom two sections but is relatively rare on the hand and top section in group A (Fig. 3(a)). The other encrusting epiphyte, *Ralfsia* sp., is absent from the lower sections in group B (Fig. 3(b)), and occurs on 30% of the plants in section 1 and on 40% of the plants on the hand. This species is apparently slightly more common than this on the hand and top two sections on plants with large limpets (Fig. 3(a)).

The two filamentous epiphytes *Colaconema nemalionis* and *Sporocladopsis novae-zelandiae* occur infrequently on plants with large limpets (Fig. 3(b)), being relatively more common on the bottom two sections. In Group A, the plants associated with large limpets, *S. novae-zelandiae* is apparently absent from the middle section, although Figure 2 indicates that its cortex layer of ? cells (blackened stipe) is common here. It occurs most frequently (50%) on the top section. *Colaconema nemalionis* is absent from the hand and top section but is relatively common (50 and 60%) on the bottom two sections in Group A (Fig. 3(a)).

The group of plants with large limpets (Fig 4(a)) have fewer epiphytes and a far higher percentage of grazing marks than those with small limpets (Fig 4(b)) *Suhria vittata, Polysiphonia* and *Carpoblepharis flaccida* occur more frequently on the bottom and middle sections in Group B (Fig. 4(b)). Foliose epiphytes (other) are relatively infrequent on the stipe, being most common (frequency (f) = 50%) on the hand. *Carpoblepharis flaccida*, is most common (f = 50%) on the top section in Group B (Fig 4(b)).

In Group A (Fig. 4(a)) *S. vittata, P. virgata* and *C. capensis* only occur on the bottom section, while foliose epiphytes and *C. flaccida* occur on the hand.

Distribution of Epiphytes and Limpets in Relation to Plant Age

There is a strong correlation (r = 0.8) between stipe length and maximum stipe circumference (Fig. 5). Plant length generally depends on water depth and kelp plants tend to grow to the surface rapidly, where light is optimal, and then the hollowness of the stipe (measured by maximum stipe circumference) increases with age. Plants were collected at depths ranging from 2 to 3.6m.

Therefore maximum stipe circumference was considered to provide a more accurate estimate of age than length, and was used to group the kelp plants into four 'age' classes. The circumference classes may be referred to as age classes or younger and older plants in the text.

Dangerous

Figure 6 shows that most of the plants in the two groups with smaller circumferences have no limpets while the two larger circumference classes have mostly larger limpets. The frequency of limpets of intermediate length (0<x<30) is highest on the third circumference class (200<x<250). Note that these limpet lengths are the sum of all limpet lengths on a single plant (see analysis section for explanation).

The statistical results for the data displayed in Figures 7(a) and (b) are given in Table 2.

Limpet length and percentage cover of limpet grazing marks show a significant increase with plant age for the first three younger age classes (Fig. 7(a)). There is no significant difference in the two limpet measures between the two largest age classes (Fig. 7(a); Table 2). There is a dramatic increase in foliose epiphyte biomass from 0.29 (x) ± 0.27 (S.D.) for the youngest plants, to 94.25 (x) ± 48.13 (S.D.) for the next circumference class and upwards (Fig. 7(a); Table 2). Foliose epiphyte biomass shows a decrease with increasing 'age' for the last three circumference classes. However, the large standard errors prevent them from being significantly different from each other (Fig. 7(a); Table 2).

The percentage covers of foliose epiphytes, crustose epiphytes, blackened stipe and clear stipe shown in Figure 7(b), account for the entire surface area of the kelp stipe. In other words, the means in each circumference class add up to 100 percent. Clear or uncolonised stipe makes up most of the percentage cover in the two younger age classes, while blackened stipe is the dominant cover in the two older age classes. The percentage cover of clear stipe decreases with increasing kelp plant age, while the percentage cover of blackened stipe and crustose epiphytes increases with kelp plant age (Fig. 7(b)). All cover estimates are significantly different across the four age classes, however, there is no significant difference in clear and blackened stipe between the last two age classes (M.R.A; Table 2). Crustose epiphytes are virtually absent from the younger plants and increase gradually with age of the host plants. The small holdfasts of foliose epiphytes contribute very little to the cover on the stipe, although their total wet biomass on a single stipe was often over 150g. The percentage cover of foliose epiphytes are not significantly different from each other in the last three age classes. However, the two older age classes did have a higher cover value which contrasts with the epiphyte biomass result in Figure 7(a).

Distribution of Epiphytes in Relation to Limpet Length

The statistical tests for the data in Figures 8 and 9(a)-(d) are shown in Table 3.

The foliose epiphyte biomass shows no difference between the last three circumference classes on plants with limpets shorter than 50mm (Fig. 8). However, on plants with limpets longer than 51mm the epiphyte biomass drops down to zero for the oldest age class.

Figure 9(a) shows that there are no limpets longer than 51mm on young plants and also that the kelp stipes are almost completely free of any epiphytes. In the second age class (Fig. 9(b)) the plants with limpets longer than 51mm have a significantly greater percentage cover of limpet grazing marks and blackened stipe. The percentage cover of clear stipe was significantly less on the stipes with larger limpets. There was no significant difference in the percentage cover of foliose epiphytes or crustose epiphytes.

A pattern similar to that in Figure 9(b) emerges in Figure 9(c), with regard to limpet grazing marks, blackened stipe and crustose epiphytes, although the difference in the percentage cover blackened stipe between the two limpet length classes is not as great as it was in the younger age class (Fig. 9(b). The graph is different from Figure 9(b) in that the percentage cover of foliose epiphytes is now significantly lower on kelp stipes with larger limpets. Also, the percentage cover of clear stipe is no longer significantly lower on kelp stipes with larger limpets.

In Figure 9(d), the oldest age class for kelp plants, a similar pattern is seen as for Figure 9(c), except that there is now no significant difference in the percentage cover of blackened stipe. Foliose epiphyte cover is completely absent from plants with larger limpets. The significance of difference in the percentage cover of limpet grazing marks is not as great as it was in yonger age classes. Crustose epiphytes, made up mostly by *Clathromorphum* spp., appear to be unaffected by limpet grazing.

Removal Experiment

The limpets on the control plants remained on their respective host plants during the four winter months of this study. Of the ten plants with removed limpets that were recovered, one of the plants had been reoccupied by a large limpet (>70mm), while on three of the others, younger limpets had moved down onto the stipe. Most of the plants showed signs of colonisation by foliose epiphytes, although these were still at a very early stage of development. (see Plate 11).

Caging Experiment

Limpets between 70 and 90mm in length caged on portions of the stipe with a high cover of foliose and crustose epiphytes cleaned the stipe of most epiphytes in 3 to 4 weeks (Plates 12a, 12b and 13). The crustose coralline epiphyte appeared to be the least affected by the limpet grazing. In some of the cages there were still unattached *Suhria vittata* plants, indicating that the limpets may dislodge foliose plants rather than actually grazing on them. Two caged limpets had broken through the thin cage material and escaped. In the one case, the limpet had disappeared, while in the other the limpet had remained on the upper portion of the stipe and 'cleared' that section of the stipe as well. One of the limpets was found in the process of trying to escape. It had

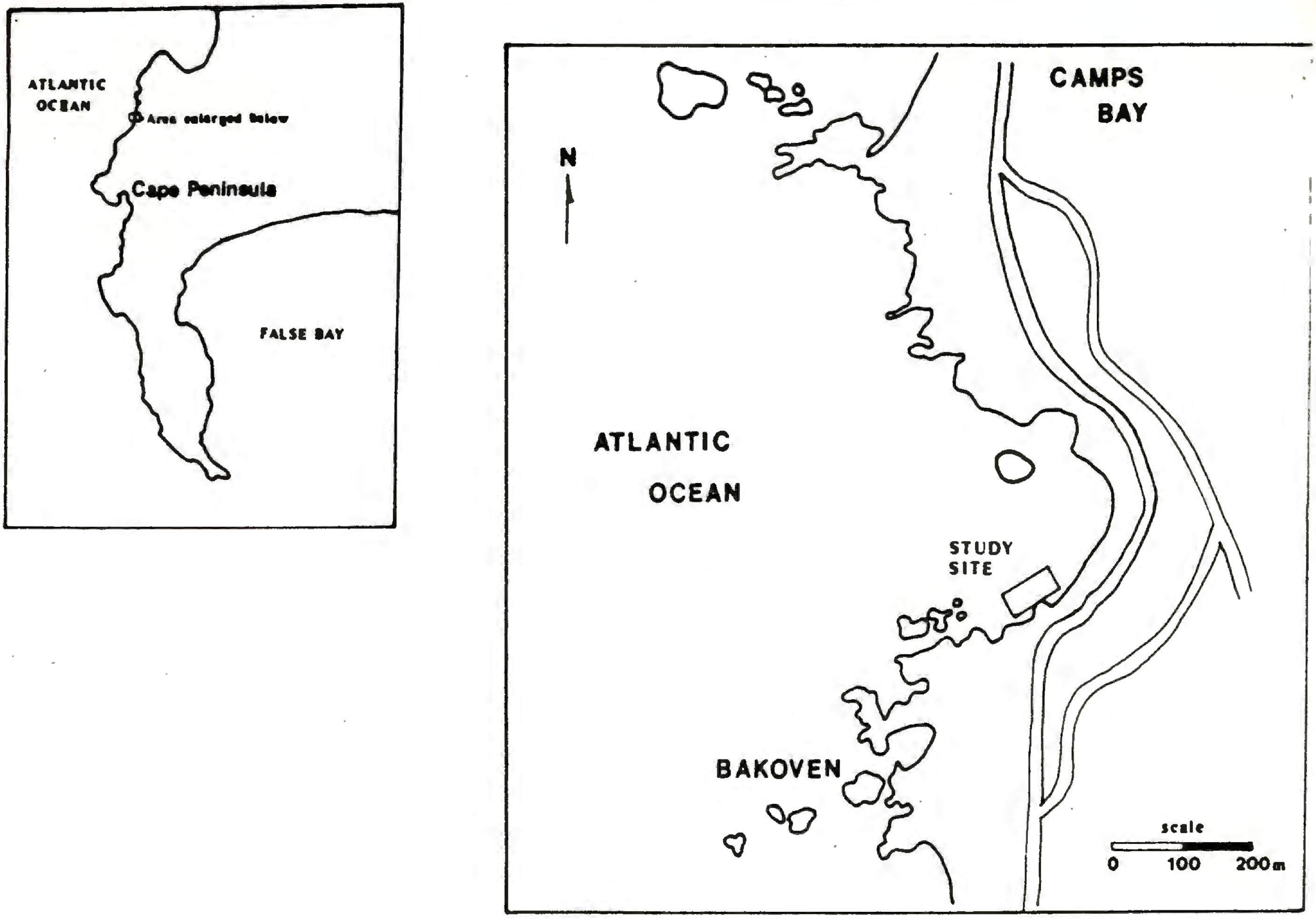

Figure 1: Map of Bakoven and the study site.

Plate 1: A = study site on an exceptionally calm and clear day at high tide.

worn a hole through the cage, but this was not big enough for it to escape. The limpet had caught onto a frond of a neighbouring kelp plant and appeared to be trying to break out of the cage with the help of the frond. Eating it?

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DISCUSSION

Epiphyte distribution patterns in relation to plant age

Hollowing of the kelp stipe is most pronounced at the top section of the stipe where the maximum stipe circumference is found. Expansion of the stipe, or growth in girth, requires continued growth of new cells at the epidermis, which is facilitated by a superficial meristem called the meristoderm (Bold & Wynne, 1985). Circumstantial evidence that this occurs can be found by observing the grazing marks left by limpets.. Where the stipe is a clear, light brown colour, the grazing marks become less obvious and eventually disappear. However, lower down on the stipe where it is black the grazing marks left by the limpet appear to last for much longer. From this we can infer that the external tissue of the top section of the stipe is growing and therefore much younger than that of the bottom section which stops growing and is generally older. Further, the difference in age between the top and bottom sections should increases with kelp age.

This age phenomenon on the kelp stipe can explain a large part of the vertical distribution patterns observed in Figures 2, 3(a) and (b), and 4(a) and (b), as well as differences in epiphyte colonisation between different circumference classes observed in Figures 7(a) and (b). For example, the coralline crust, *Clathromorphum* spp., and blackened stipe both show a clear tendency for being more common on the bottom and middle sections of the kelp stipe (Figs. 2; 3(a) and (b)), and also more abundant on older plants (Fig. 7(b)). In fact, the trend is so obvious, that I would predict that, in the absence of limpets, the distance that *Clathromorphum* spp. has colonised up the stipe will correlate better with age than any other measure. ✓ good idea

The hand provides circumstantial evidence supporting the above explanation. The intercalary meristem or the transition zone is located on the primary blade where the secondary blades are produced. The top end of the hand is the tip of the primary blade which does not expand, and represents the oldest portion of the hand. This portion of the hand is invariably black, and often has various species of epiphytes growing on it, depending on the presence and size of the kelp limpets (Figs 2; 3(a) and (b); 4(a) and (b)).

These vertical distribution patterns on the stipe support those of Ballantine (1979). He studied the distribution of algal epiphytes on macrophyte hosts offshore from Puerto Rico. He found that the older the plant the higher the percentage cover and species richness of epiphytes. He attributed vertical distribution patterns of epiphytes to a continuous gradient in the age of the host tissue, which became younger with proximity to the meristematic regions. However, vertical distribution patterns of epiphytes on the stipe of *Nereocystis luetkeana* were similar to those on false 'kelp plants' suggesting that the nature of the substratum is not as important in controlling epiphytic growth as is the vertical position of the substratum in relation to the environment (Markham, (1969). The annual nature of this species probably prevents differences in age of host tissue from having significant effects on the distribution of species on the stipe. However, a seasonal succession in the colonisation of epiphyte species was recorded, and a climax community had established by December, six months after the first epiphytes colonised the stipe in June(Markham, 1969).

Epiphyte distribution patterns in relation to limpet grazing

Figures 3(b) and 4(b) provide information on the susceptibility of the different epiphytes to limpet grazing, and possibly which portions of the stipe are most heavily grazed. The species that are apparently susceptible to grazing include all the foliose epiphytes, *Placophora monocarpa* and *Colaconema* spp. The presence of some of these species on the hand and bottom section of the plant in Figures 3(b) and 4(b) would suggest that these portions of the stipe are not often grazed by limpets. This may be true for the bottom section because the stipe is thinner here (smaller circumference), making it difficult for the limpet to attach firmly onto the stipe, thus rendering it more prone to predation. Kelp limpets are preyed on by octopus (pers. obs.) and possibly the rock lobster (*Jasus lalandii*). Kelp limpets may escape predation by their large size, which makes them more difficult to remove from the stipe (pers. obs.). Thus, it may be that the limpets have evolved a predator avoidance behaviour and only the much larger limpets venture down to the bottom of the stipe. Markham (1969) found that the lower sections of the stipe of *N. luetkeana* were mostly free of epiphytes which he suggested was due to grazing by snails, although this was not investigated.

The hand is usually the most heavily grazed because this is where younger limpets aggregate. However, on some plants the recruitment of new limpets may be poor and the adult limpet on the stipe may not be able to graze into the notches and bumps of the hand as well as juvenile limpets can.

NA good fig. 11

Crustose corallines are well known for the~~re~~eir resistance to grazing (Lubchenco & Cubit, 1980; Paine, 1984; Branch, 1976). The results indicate that *Ralfsia sp.* is positively affected by limpet grazing, being more common on plants exposed to intense grazing than on those that are not. *Clathromorphum* spp., appears to be unaffected by limpet grazing (Figs. 9(b), (c) and (d). However, the limpet does appear to hinder the spread of the crust and fragments have been observed in the stomach contents. It is likely to be of low nutritional value to the limpet and its competitive superiority over the filamentous forms may be the biggest threat to the limpets optimal food resource on the stipe. Cross sections of the crust on the stipe viewed under the microscope revealed that the filamentous species were still alive after having been overgrown by the crust. This may increase the limpets 'incentive' to graze on or 'chisel' ? the crust off.

What about plate 12b?

The growth rates and maximum age of limpets are unknown. Figures 6 and 7(a) suggest that the kelp limpets mature with the kelp plant. They also indicate that large limpets never move onto young plants with clear stipes. The removal experiment suggested that they may move onto old plants previously occupied by a large limpet. There are plants in all age classes with no limpets, but the frequency of these apparently decreases with increasing plant age. This can be explained simply in terms of the time the kelp plant has been available for colonisation. The greater the length of time the substrate has been available, the greater the chance of colonisation. The distribution of epiphytes can be interpreted the same way except that the size of the limpet occurring on the stipe can play an overriding role in the establishment of epiphytes.

The results clearly show that on older plants with large limpets, foliose epiphytes are entirely absent (Fig.8). This is illustrated in Plate 14. This can be attributed to kelp limpet grazing on the stipe. The caging experiment indicated that large limpets are capable of clearing the stipe of foliose epiphytes and eventually crustose epiphytes as well. The presence of foliose epiphytes on the two younger age classes with large limpets are represented by only one individual in both cases. These can probably be explained in terms of time lapses between when a limpet is lost from the stipe and a new one recolonises it or a juvenile grows up (see below).

Is the limpet gardening?

This study did not determine whether the kelp limpet induces cell wall thickening or whether this was merely an artifact of age of the cortex. It seems likely from the slide material that it is induced by limpet grazing (Plate 15). The grazing marks caused by the radula roughen and damage the cortex and this may provide the ideal microenvironment for the settlement and establishment of *Sporocladopsis novae-zelandiae* and other epiphytes (Plate 16). The cellular difference between black and clear stipe is profound, and *S. novae-zelandiae* is always associated with blackened stipe.

? not in Fig.(Plate) 8 !

An important and unanswered question is, how does *S. novae-zelandiae* (blackened stipe) colonise the stipes so uniformly and extensively? It would seem unlikely that they should colonise via

Why?

spores because this should result in a clumped distribution. Further, reproductive material is generally rare. One possible mechanism is that the cells of this species are extremely hardy and can vegetatively reproduce from very small fragments. If this is true, then it may be possible that the limpet actually spreads and 'plants' the cells into the cortex with its radula. Stomach contents of the limpet consist mostly of the thickened cell wall material which appears to be indigestible and possibly of no nutritional value. However, *S. novae-zelandiae* may be the primary food source of the limpet. It therefore seems possible that the kelp limpet is a highly specialised 'gardener'.

The other explanation for the uniform distribution of *S. novae-zelandiae* is that it may be an endophytic alga that could be ? symbiotically related to the kelp plant (Simons, pers. comm.). Whatever the explanation, the large kelp limpets appear to maintain the epiphyte community on the kelp stipe in an early successional stage which may provide them with a continuous and reliable source of food.

Algal 'gardening' by grazers is defined by Branch *et al.* (1990) as a modification of plant assemblages, caused by the activities of an individual grazer within a fixed site, which selectively enhances a particular plant species and increases the food value of the plants for the grazer. The results by no means prove that the kelp limpet is gardening *S. novae-zelandiae*, but they do suggest this to be highly likely.

Turfs of fine filamentous algae tend to comprise species which are small, short-lived, opportunistic, fast-growing and highly productive (Branch *et al.*, 1990). They also have minimal structural tissue, a high energy content and nitrogen intake and few anti-herbivore defences. Their value to grazers is apparently high (Branch *et al.*, 1990). *Colaconema spp.* (there may be more than one species (Stegenga, pers. com..) and *S. novae-zelandiae* may well represent classic examples of the above description. Conversely, coralline crusts (e.g. *Clathromorphum* spp.) and foliose algae often have properties which diminish their yield to herbivores (Branch *et al.*, 1990). The foliose epiphytes on the stipe (e.g. *Suhria vittata* and *Polysiphonia virgata*) could be of little value to the limpets as well as overgrowing and outcompeting the filamentous forms.

Kelp limpets may keep the kelp stipe in the very early stage of epiphyte colonisation. This would favour the continued existence of *S. novae-zelandiae*. That some algae benefit where grazing pressure is high is well documented (e.g. Lubchenco, 1978; Westoby, 1989; Branch *et al.*, 1990). However, once the limpets are lost or removed from the kelp stipe it becomes especially susceptible to colonisation by various other epiphytes. This is because the settlement, attachment and establishment of various epiphyte species may be enhanced by the grazing marks left by the limpet. Also, the micro-environment inside the filamentous turfs which proliferate in the absence of limpet grazing (pers. obs., and see Plate 17), may also be favourable for the settlement and establishment of some foliose epiphyte species.

A possible explanation for the patterns observed

Bearing the above in mind and speculating on the life span of kelp limpets compared with that of their hosts can lead to a plausible explanation for the distribution of heavily epiphytised kelp stipes at the study site. It is proposed that, in the study site, the limpets do not live as long as the kelp plants or they are removed by predators. The recruitment and growth of a juvenile limpet onto the stipe may or may not be fast enough or keep up with epiphyte colonisation. The kelp stipe may reach a stage of foliose epiphyte colonisation where it is no longer feasible for the limpet to try and re-establish a *S. novae-zelandiae* garden. In this case a maturing limpet may travel via the fronds to another more favourable host.

The recruitment of new kelp limpets may be low in the study site because of the isolation of kelp plants and discontinuity of the kelp forest as a result of the patchy granite boulder substrate. Black (1976) found that settlement of the limpet, *Notoacmea insessa* Hinds, was greater on crowded populations of the infratidal kelp, *Egregria laevigata* Setchell, than on isolated plants. An *E. maxima* forest of greater density may facilitate the dispersal of juvenile and adult limpets from one plant to the other via the fronds. Further, the availability of settlement sites will be greater, increasing the chance of successful settlement of limpet larvae. Thus, I would predict that the density and continuity of a kelp bed can have an effect on the recruitment and age structure of kelp limpet populations with subsequent effects on the abundance and distribution of epiphytes that are susceptible to limpet grazing.

In Nuwebaai near Hawston, Hermanus, epiphytes appear to be more common in wave exposed than in sheltered sites (Euston-Brown, unpublished) and this distribution pattern appears to be widespread (pers. obs.) This may be due to differences in the age structure and dynamics of the different kelp beds. Kelp plants heavily colonised with epiphytes are often isolated (pers. obs.). This isolation can either be a result of the substrate in the area or the dynamics of the kelp bed. Many plants in a particular site may be ripped up by the same winter storm. Some individuals with strong holdfasts that are not interlinked with other holdfasts may survive the storm. The increased light availability on the stipes of isolated kelp plants may effect the growth rate of the epiphytes. In the removal experiment the kelp stipes that were on the north or sunny side of a kelp bed, showed the most signs of foliose epiphyte colonisation and growth. If a large limpet is lost from its host under these isolated conditions, the host is unlikely to be recolonised by a limpet of comparable size before the stipe has been colonised by a dense bed of foliose epiphytes. Whether a maturing juvenile limpet or dispersed limpet can bring the kelp stipe back to its former, early successional state, has been shown to be possible by the caging experiments. Whether this happens in nature remains to be tested.

The above ideas could be easily tested by manually isolating kelp plants, removing their limpets and then monitoring the colonisation and growth of epiphytes and limpets on them over a period of time (probably 1 to 2 years). This could also provide information on the seasonal growth and abundance of the different epiphyte species. To verify the speculations on limpet gardening on the stipe, energy and nitrogen contents of the different epiphytes should be analysed. Carefully designed caging and removal experiments are also needed and the results must be quantified. Experiments must be done at a variety of different sites to establish how general the observed patterns are.

Evolutionary Origin of Obligate Kelp-Limpet Associations

There are three other documented examples of obligate kelp-limpet associations from different parts of the world. In Central Chile, the limpet *Scurria scurra* Lesson, lives in open cavities on the stipe of *Lessonia nigrescens* Bory (Munoz & Santelices, 1989). In England, the limpet *Helcion pellucidus* lives on fronds or holdfasts of *Laminaria hyperborea* (Gunn.) Foslie or *Saccorhiza polyschides* (Lightf.) Batt.(Graham & Fretter, 1947, in Munoz & Santelices, 1989). In California, *Notoacmea insessa*, inhabits the fronds of *Egregia laevigata* (Black, 1976; Choat & Black, 1979).

Munoz and Santelices (1989) found that several generalizations could be made about these kelp-limpet associations. These were that the limpets do not damage the meristematic or reproductive algal tissues; the older stipes in the algae are most affected by the limpets' activities; limpet reproduction starts at an early age and is generally continuous throughout the year; and lastly, limpet longevity generally matches algal longevity. With respect to *P. compressa*, I would agree with the first two points but there is as yet no evidence to support or to contradict the last two.

Choat and Black (1979) did not mention the possible role of epiphytes in their speculations on the evolutionary origin of obligate kelp-limpet relationships around the world. I believe that considering the role that epiphytes play in the life of *P. compressa* and their hosts, may provide a much deeper insight into the evolution of the association. Algal epiphytes may also be important in the other kelp-limpet associations and they appear to have been completely overlooked. Good

That the grazer must be 'prudent' (i.e. its grazing activities on the host should not ~~e~~affect the survival of the host and possibly even enhance the hosts survival) has been illustrated by Black (1976) for the association between the limpet *Notoacmea insessa* and the infratidal kelp *Egregia laevigata*. I do not think that *Patella compressa* could be prudent if it were not for the epiphytes, especially *Sporocladopsis novae-zelandiae*. The cell wall thickening of the epidermis and cortex of the stipe almost definitely reduces the value of this food source to the limpet. If it were not for the epiphytes the limpets would have to eat more of the kelp cortex which could damage the plant to the extent that it would be severely weakened. The territorial nature of the limpets may ensure that the cortex and *Sporocladopsis novae-zelandiae* are never overgrazed.

A complication here is that *P. compressa*, unlike other kelp limpets, tends to drop off the kelp plant if the plant is dislodged (pers. obs.), apparently in response to pressure changes as the stipe floats to the surface. Whether or not these limpets re-establish themselves on another host is not known. If they do so successfully, why should they be affected by the survival of their hosts? The answer would probably lie in kin selection because young limpets do not appear to have developed the rapid escape response (pers. obs.). Further, it may be that a dense kelp bed favours the colonisation and dispersal of limpet populations, as well as increasing the chance of a dislodged limpet re-establising itself on another plant before being taken by a predator.

Choat and Black (1976) tried to explain why the kelp-limpet associations had evolved in some parts of the world and not in others, by referring to competition theory. They suggested that interspecific competition between ecologically similar co-occurring limpet species in California had resulted in niche divergence and habitat specialisation. Although this may be true for the genus *Patella* in South Africa (Branch, 1976), it does not seem to apply in other parts of the world. For example, in northern New Zealand there is a more diverse fauna of limpets and herbivorous gastropods than northern Europe (where *Helcion pellucidus* lives on algae of the genus *Laminaria*), but has no algal associated limpets despite the presence of suitable hosts (Choat & Black, 1976).

It may be worth investigating the prediction that kelp-limpet associations only develop when obligate algal epiphytes of the host are present and they form part of the limpets' diet. The kelp plant can actually benefit from the association with the limpet, if it prevents the stipe from being heavily colonised by foliose epiphytes. To prove this benefit, one would have to show that the increased drag associated with heavily colonised stipes causes them to be more prone to dislodgement than clean stipes. Some *E. maxima* plants are hosts to *Laminaria pallida* plants which is very likely to be to the detriment of the host.

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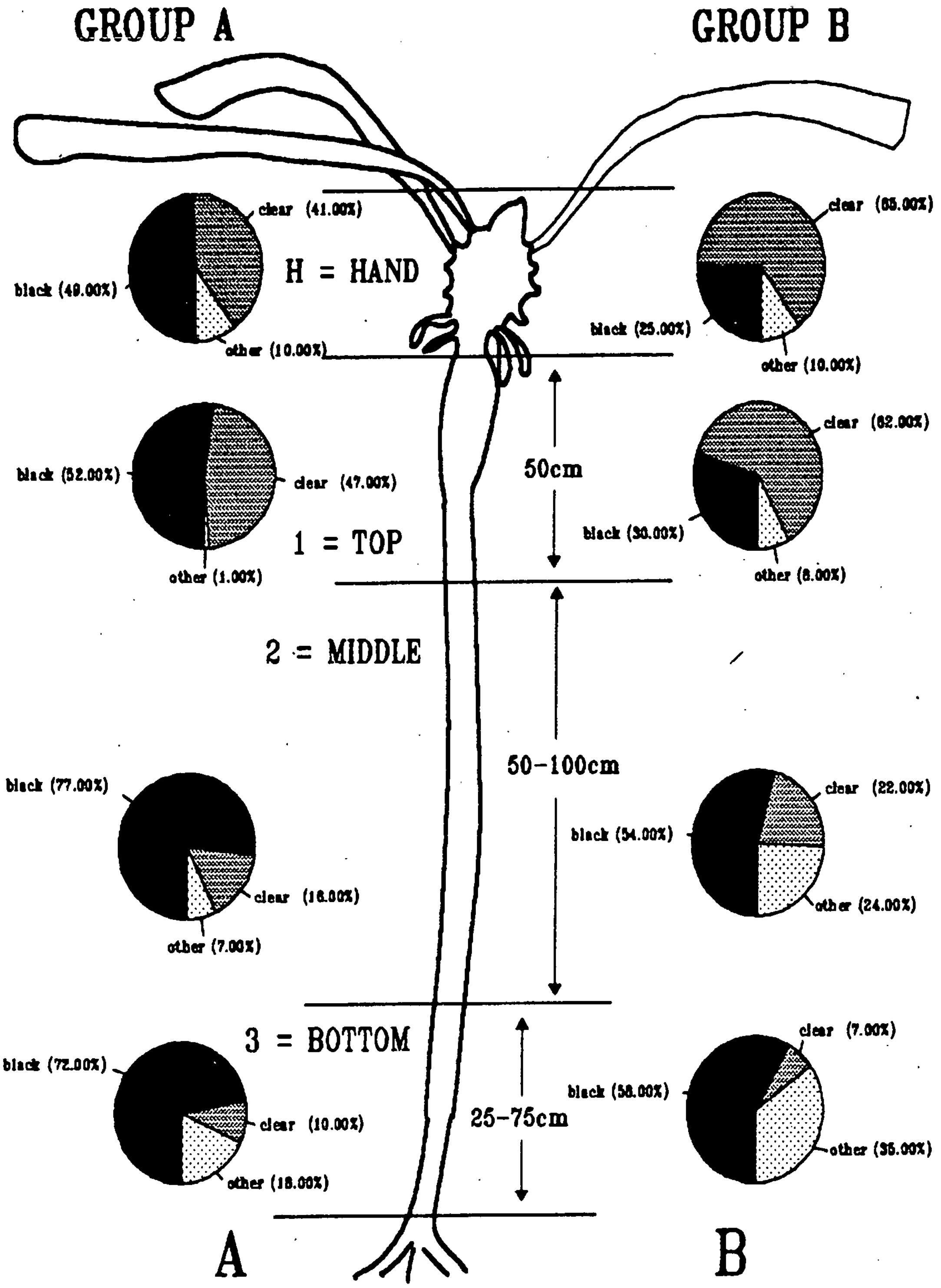
Table 1: The mean and standard deviation of true and estimated percentage covers grouped into three classes on the basis of estimated percentage covers. The significance levels for the difference between the two percentage covers is derived from the Student's t-test.

Classes	Stats.	True % cover	Estimated % cover
0-10 n=4	Mean	2.9	6
	S.D.	2.6	6.1
	p=0.383		
10-50 n=6	Mean	25	16.7
	S.D.	7.9	4.1
	p=0.046		
50-100 n=7	Mean	76.2	83
	S.D.	10.8	9.7
	p=0.239		
All n=17	Mean	40.88	41.47
	S.D.	32.65	36.71
	p=0.96		



CIRCUMFERENCE (mm)

mean=23.3 std.dev.=2.5
n=8

LIMPET LENGTHS (mm)

>31 mean=81.4 std.dev.=10.4
n=12
<30 mean=7 std.dev.=1.5
n=7

CIRCUMFERENCE (mm)

mean=22.2 std.dev.=4.2
n=8

LIMPET LENGTHS (mm)

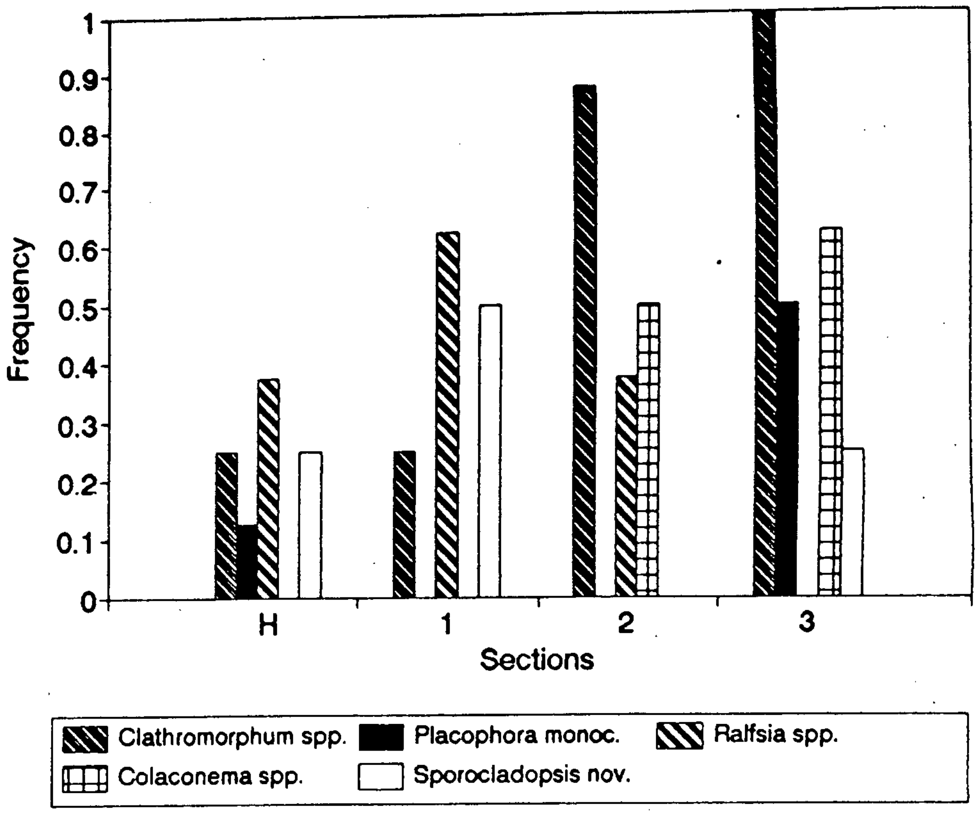
>31 mean=0

<30 mean=6.8 std.dev.=9.5
n=10

Figure 2: Limpet and circumference data (in boxes) for the two groups (A & B) of eight plants each that were chosen in the first sampling method of the general survey. Limpets are grouped into two classes, those less than 30mm in length, and those greater than 31mm in length. Mean of the percentage cover of blackened and clear stipe on four sections of the stipe, are given for the two groups (pie graphs). The mean percentage cover of 'other' epiphytes is also given, which is mostly made up of the coralline crust. H = hand (primary blade); 1 = top section; 2 = middle section; 3 = bottom section.

Group A

3(a)



Group B

3(b)

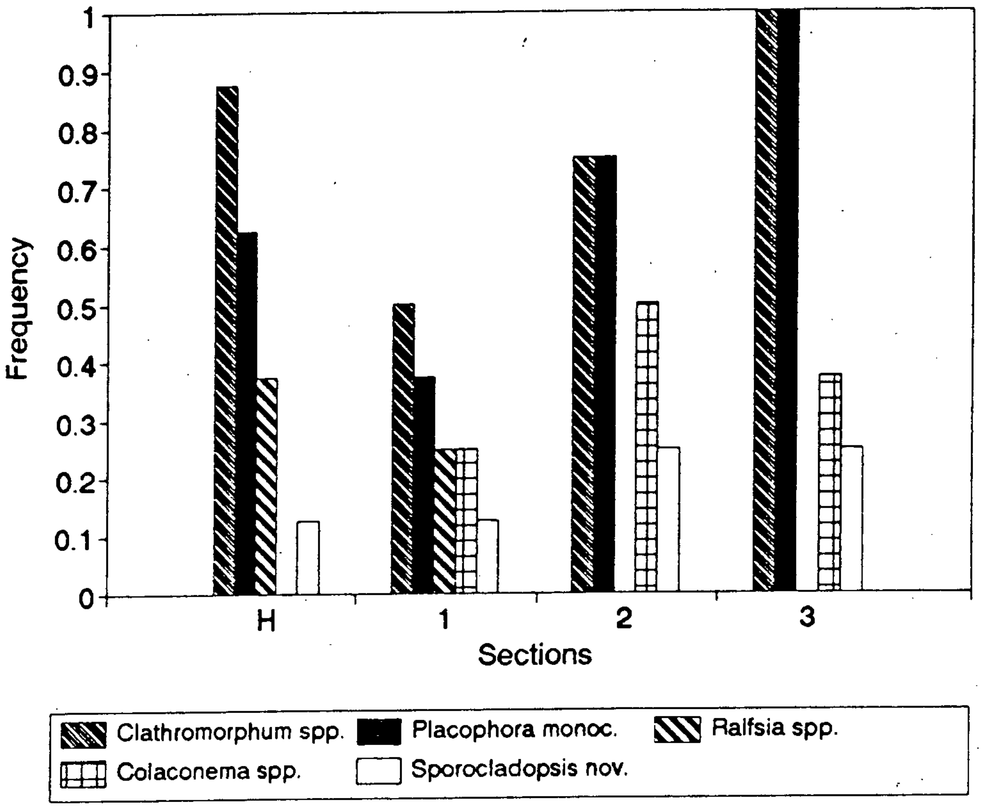
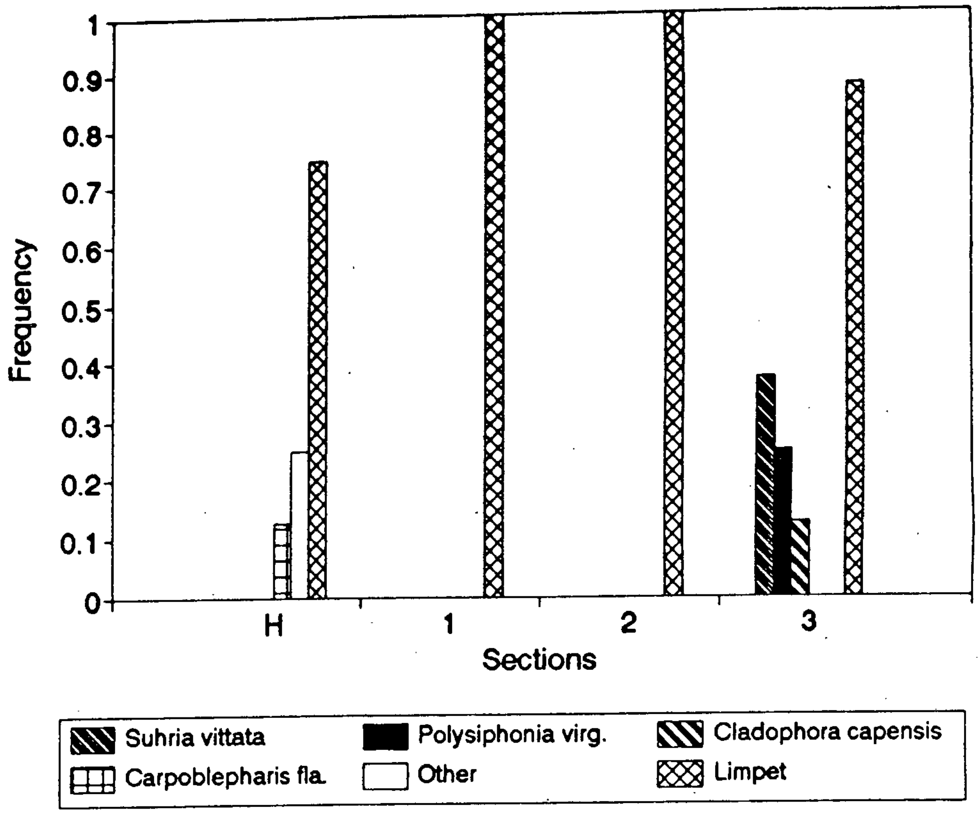


Figure 3(a) and (b): Frequency of occurrence on each section of the kelp stipes of five epiphyte species for the same two groups of kelp plants as in Figure 2. The horizontal axis represents the four different sections on the kelp stipe. Groups A and B show frequency of occurrence of crustose and filamentous epiphytes on plants with large limpets ((a), group A) as opposed to plants with smaller limpets ((b), group B).

Group A

4 (a)



Group B

4(b)

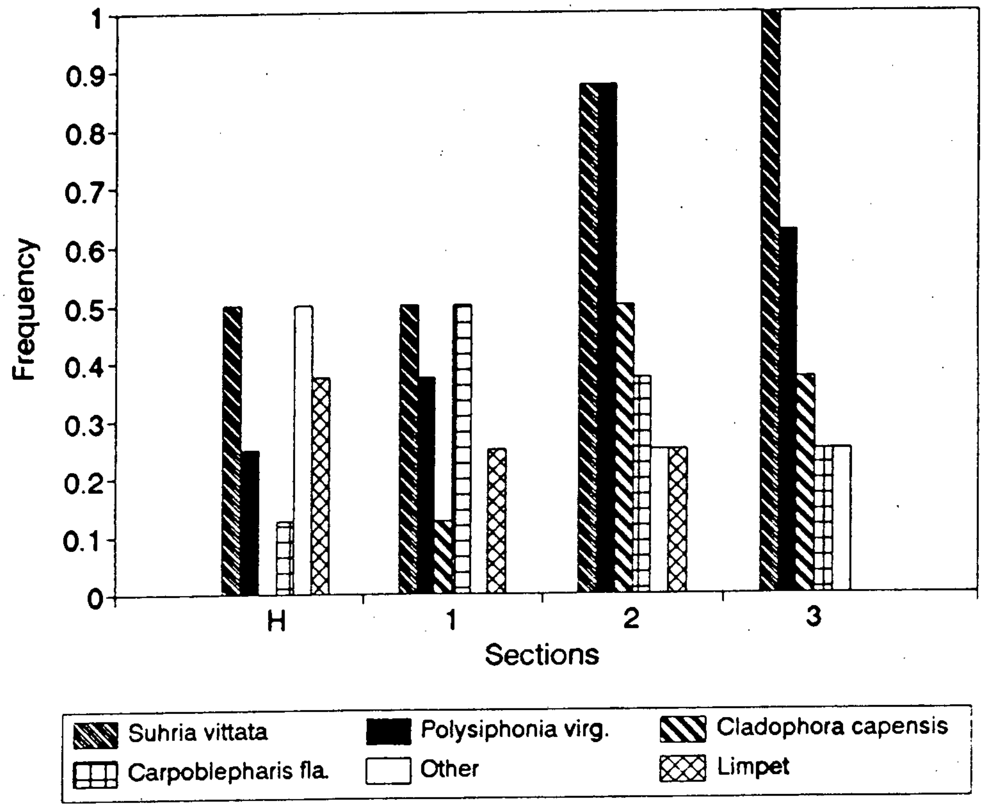


Figure 4(a) and (b): The same as for Figures 3(a) and (b), except now the frequency of occurrence of larger epiphyte species and limpet grazing marks is shown for group A (a) and group B (b). 'Other' = other large epiphyte species. Limpet = limpet grazing marks.

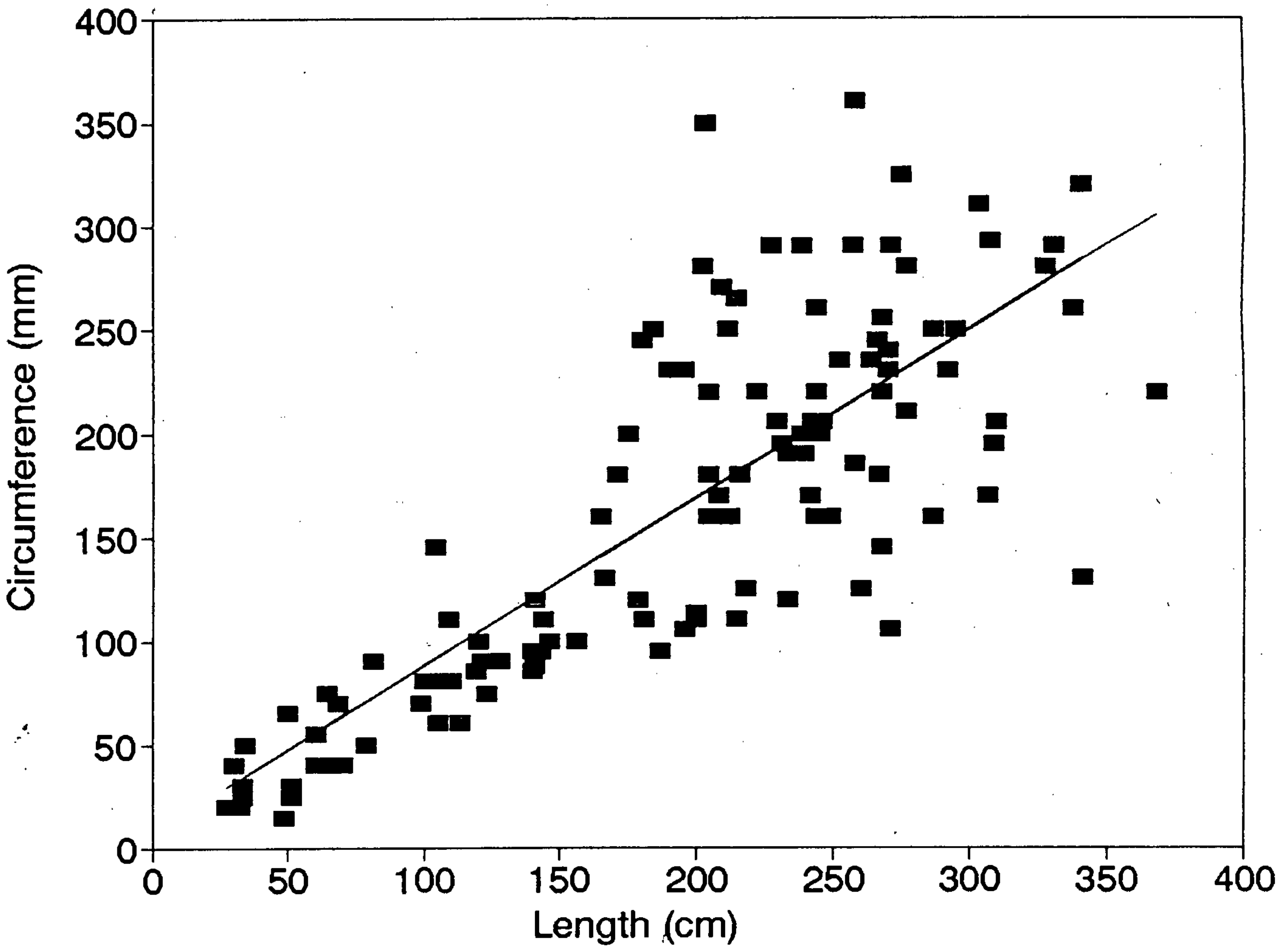


Figure 5: The maximum stipe circumference versus stipe length for the 121 kelp plants collected at Bakoven. $r^2 = 0.644$.

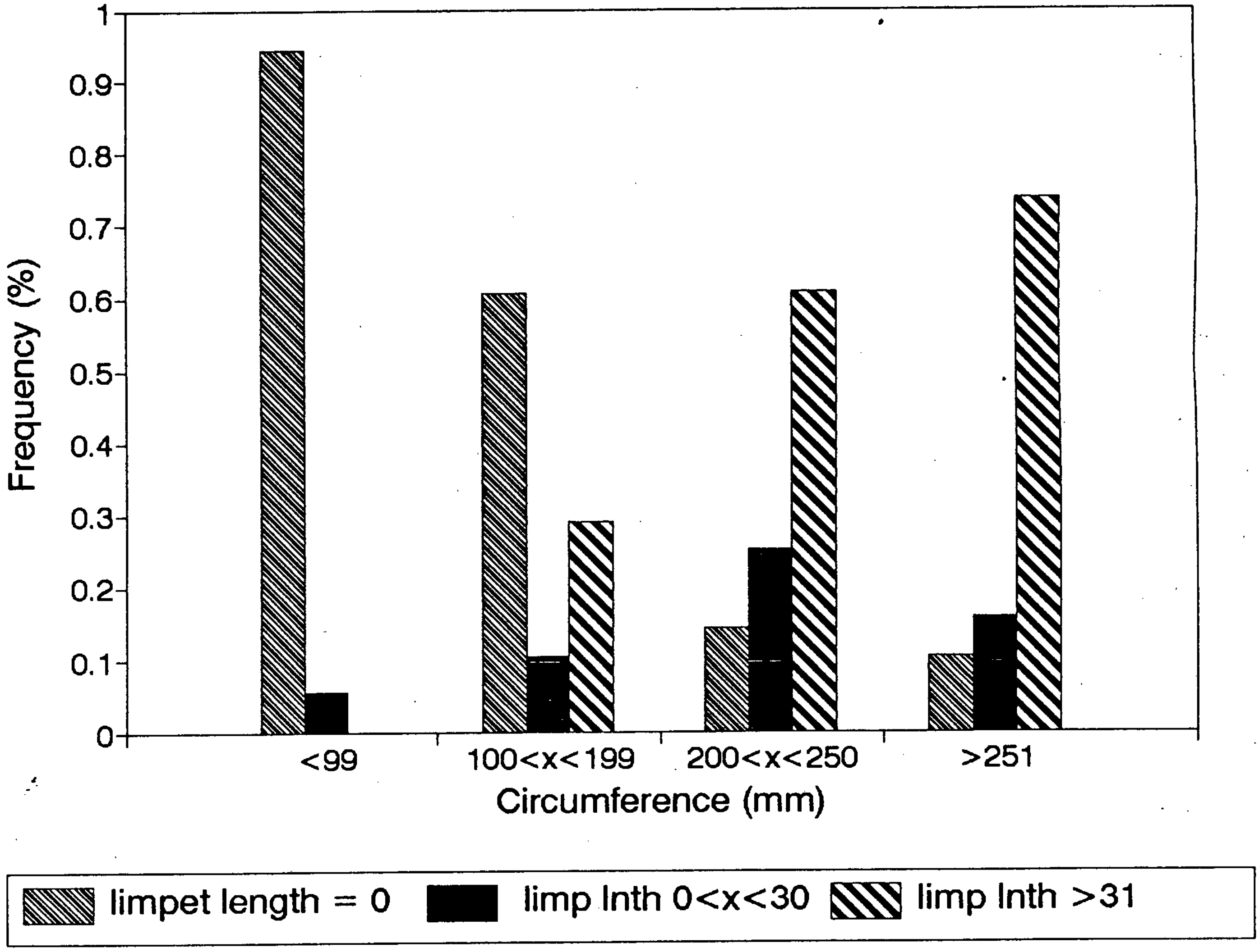


Figure 6: The frequency of plants in each circumference class with (a) no limpets, (b) limpets less than 30mm in length, and (c) limpets greater than 31mm in length. Summed limpet lengths for each kelp plant are used.

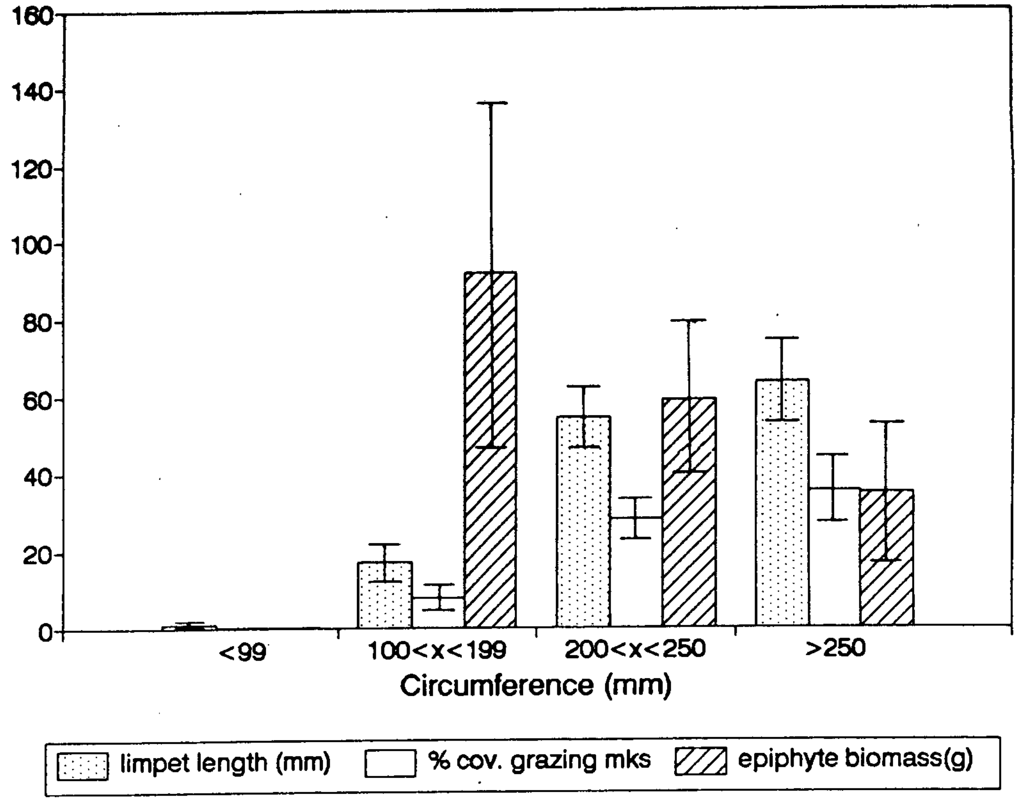


Figure 7(a): The mean (bar) and standard error (line) for limpet lengths (mm), percentage cover limpet grazing marks and foliose epiphyte biomass (g) for four circumference classes: plants less than 99mm (n = 36); plants between 100 and 199mm (n= 38); plants between 200 and 250mm (n = 28); plants geater than 251mm (n = 19).

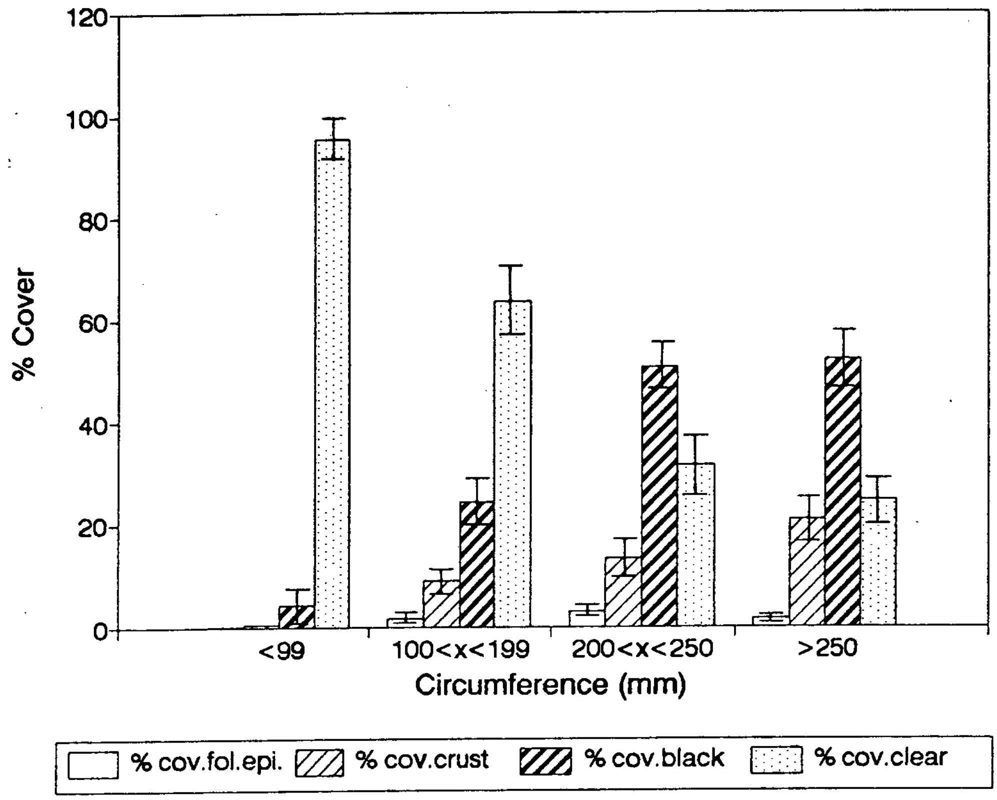


Figure 7(b): The percentage cover of foliose epiphytes, crustose epiphytes, blackened stipe and uncolonised or clear stipe for the same four circumference classes used in Figures 6 and 7(a).

Table 2: Statistical tests on data displayed in Figures 6(a) and (b). For each data set the first two rows give the mean and standard errors for the four circumference classes. M.R.A. (third row) = Multiple Range Analysis. ANOVA (LSD) is the 'least significant difference test' for which the F-ratio and the significance level are shown. The homogeneity test tells us whether the data pass or fail the assumptions that should be met in order for the statistical results to be meaningful. If the homogeneity test failed then the Kruskal-Wallis test, a non-parametric analysis of variance, was used.

Variables	Tests	Circumference classes (mm)			
		<99	100-199	200-250	>251
Limpet length (mm)	Mean	1.14	16.93	54.68	63.42
	S.E.	0.81	4.34	8.77	9.33
	M.R.A	a	b	c	c
	ANOVA (LSD)	p=0.0000		F=24.23	
	Homogeneity test	pass			
	K-W.A	-			
Foliose epiphyte biomass (g) *	Mean	0.29	94.25	58.88	35.12
	S.E.	0.27	48.13	19.27	18.69
	M.R.A	a	b	b	b
	ANOVA (LSD)	p=0.0002		F=7.24	
	Homogeneity test	pass			
	K-W.A	-			
% cover limpet grazing marks *	Mean	0.10	8.16	28.18	35.55
	S.E.	0.04	2.81	5.37	6.59
	M.R.A	a	b	c	c
	ANOVA (LSD)	p=0.0000		F=23.81	
	Homogeneity test	fail			
	K-W.A	p=0.000000001			
% cover foliose epiphytes *	Mean	0.03	1.74	2.90	1.71
	S.E.	0.02	0.46	0.83	0.73
	M.R.A	a	b	b	b
	ANOVA (LSD)	p=0.0002		F=7.18	
	Homogeneity test	fail			
	K-W.A	p=0.00006			
% cover crustose epiphytes	Mean	0.47	9.32	13.34	21.06
	S.E.	0.30	2.35	3.13	4.12
	M.R.A	a	b	bc	c
	ANOVA (LSD)	p=0.0000		F=10.46	
	Homogeneity test	fail			
	K-W.A	p=0.0000000000004			
% cover blackened stipe	Mean	4.33	25.03	50.79	52.26
	S.E.	2.78	3.95	4.33	4.57
	M.R.A	a	b	c	c
	ANOVA (LSD)	p=0.0000		F=32.79	
	Homogeneity test	pass			
	K-W.A	-			
% cover clear stipe	Mean	95.19	62.55	31.59	24.79
	S.E.	3.07	5.77	4.83	4.03
	M.R.A	a	b	c	c
	ANOVA (LSD)	p=0.000		F=41.93	
	Homogeneity test	fail			
	K-W.A	p=0.00000000000002			

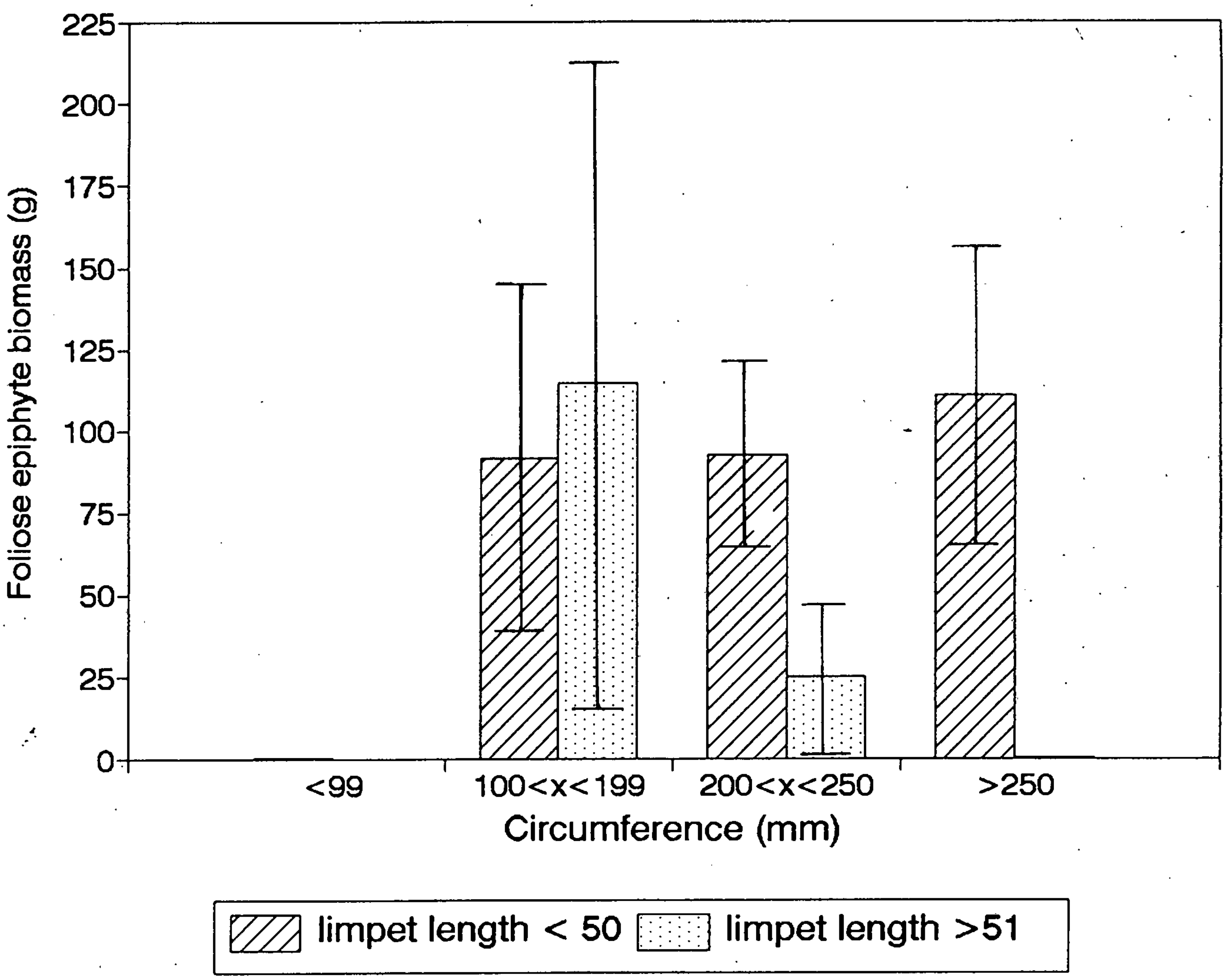
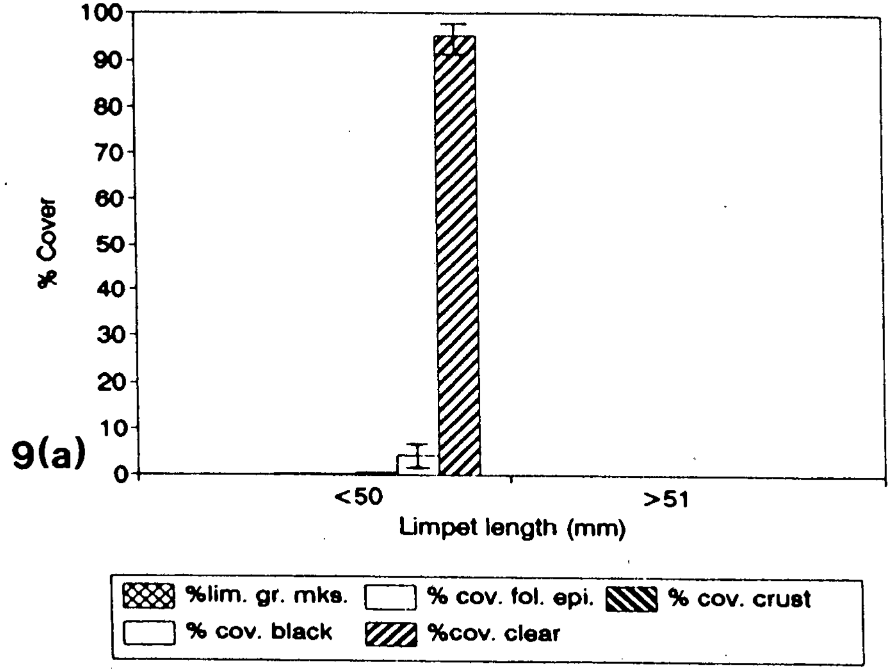
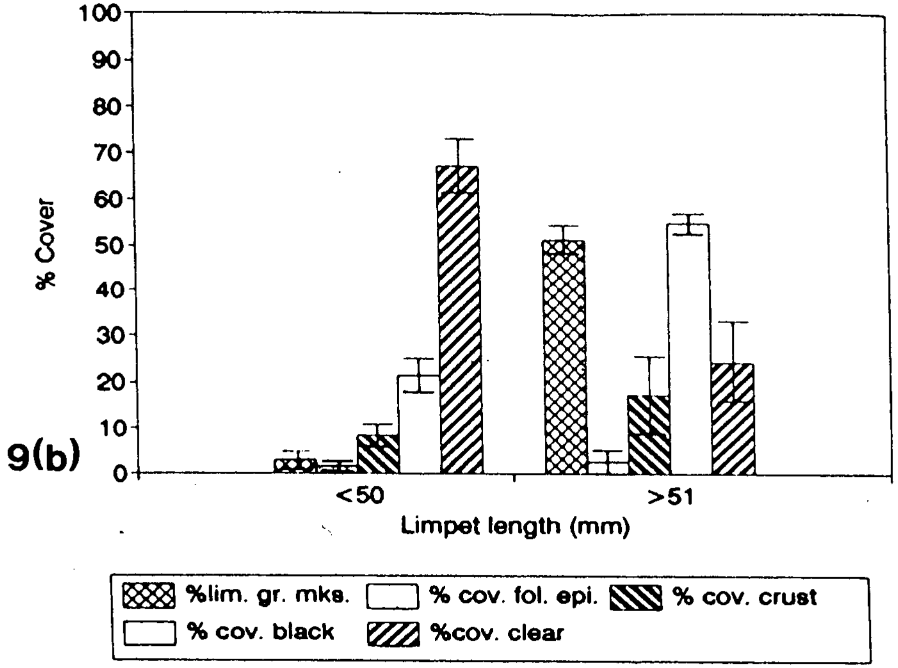


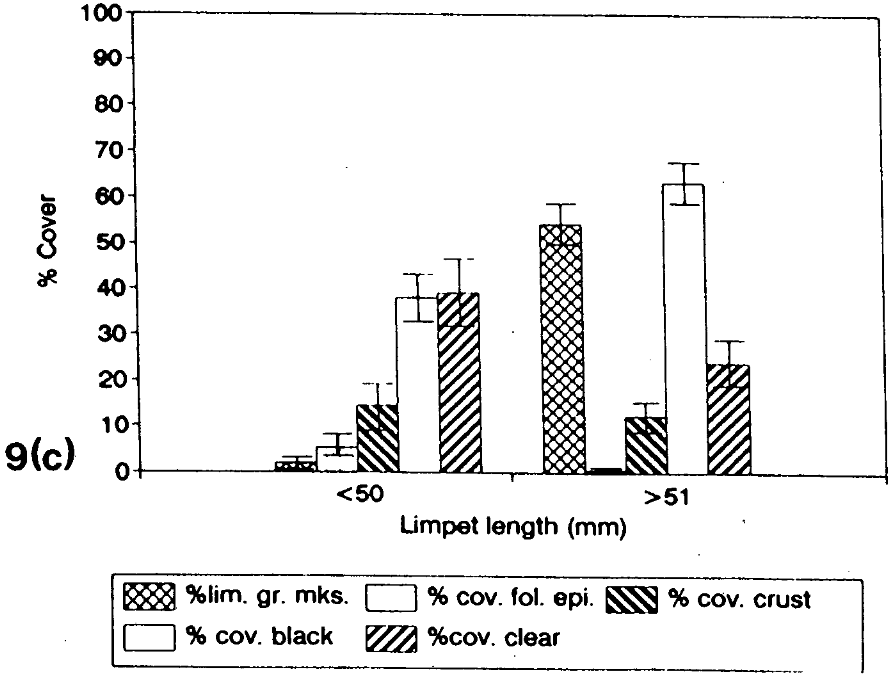
Figure 8: The foliose epiphyte biomass (g) between stipes with limpets less than 50mm in length, and those with limpets greater than 51mm in length, across the same four circumference classes, used in Figures 6 and 7(a) and (b).

● Legend for Figures overleaf:

Figure 9(a) - (d): Each of this series of graphs represents a circumference class used in the previous figures. (a) Less than 99mm; (b) between 100 and 199mm; (c) between 200 and 250mm; (d) greater than 251mm. In each graph the percentage cover (see key in boxes below graphs) of limpet grazing marks, large epiphytes, crustose epiphytes, blackened stipe and clear stipe are given for plants with limpets of lengths less than 50mm, and plants with limpets of lengths greater than 51mm.


9(a)
100
90
80
70
60
50
40
30
20
10
0
% Cover
<50
>51
Limpet length (mm)
%lim. gr. mks.
% cov. fol. epi.
% cov. crust
% cov. black
%cov. clear


9(b)
100
90
80
70
60
50
40
30
20
10
0
% Cover
<50
>51
Limpet length (mm)
%lim. gr. mks.
% cov. fol. epi.
% cov. crust
% cov. black
%cov. clear


9(c)
100
90
80
70
60
50
40
30
20
10
0
% Cover
<50
>51
Limpet length (mm)
%lim. gr. mks.
% cov. fol. epi.
% cov. crust
% cov. black
%cov. clear

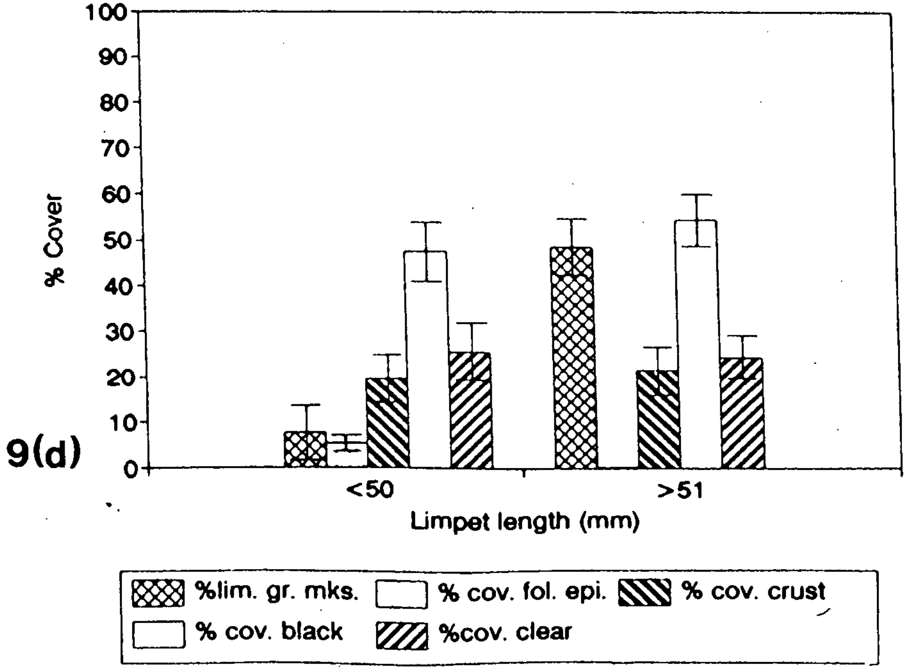

9(d)
100
90
80
70
60
50
40
30
20
10
0
% Cover
<50
>51
Limpet length (mm)
%lim. gr. mks.
% cov. fol. epi.
% cov. crust
% cov. black
%cov. clear

Table 3: The results of Student's t-test for the significance of difference of various limpet and epiphyte data between plants with limpets less than 50mm in length and plants with limpets greater than 51mm in length.

Variables	Circumference classes (mm)		
	100-199	200-250	>250
Epiphyte biomass (g)	-	t=4.95 p=0.00003	t=3.35 p=0.0038
% cover grazing marks	t=-9,8 p=0.00000	t=-11.9 p=0.00000	t=-3.63 p=0.002
% cover foliose epiphytes	-	t=3.29 p=0.0028	t=5.09 p=0.00009
% cover crustose epiphytes	-	-	-
% cover black	t=-2.8 p=0.0083	t=-3.37 p=0.0023	-
%cover clear	t=2.36 p=0.024	-	-

Plate 2: Orange fruit sacks used as limpet cages on the kelp stipe.

Plate 3: Epiphytes on the stipe: a = *Cladophora capensis*; b = *Suhria vittata*; c = *Polysiphonia virgata*; d = *Placophora monocarpa*.

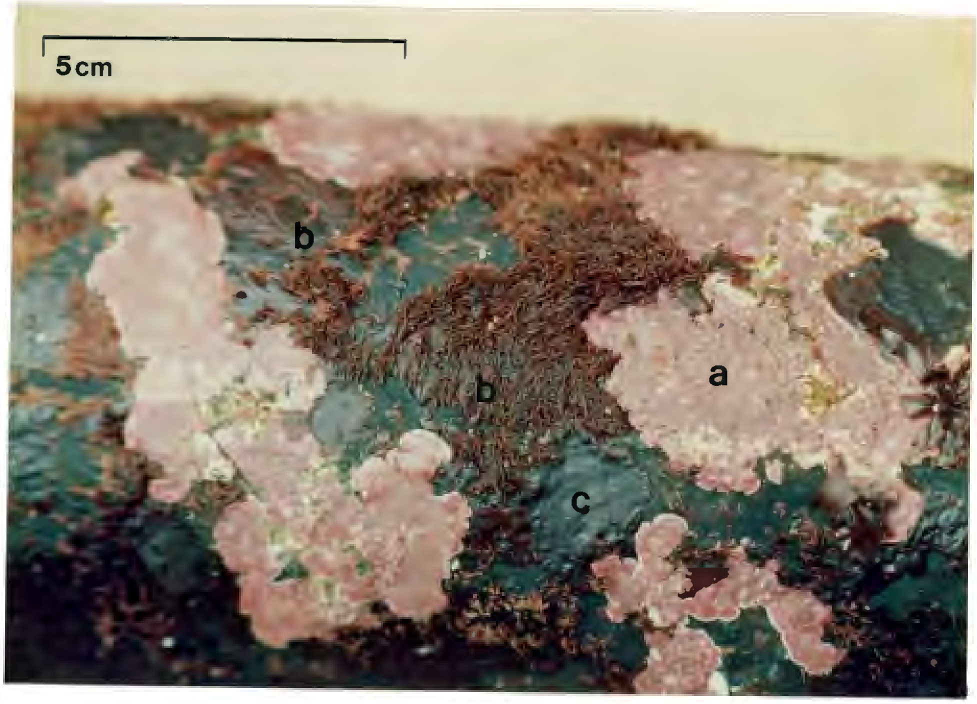


Plate 4: Crustose epiphytes: a = *Clathromorphum* spp.; b = *Placophora monocarpa*; c = *Ralfsia* sp.

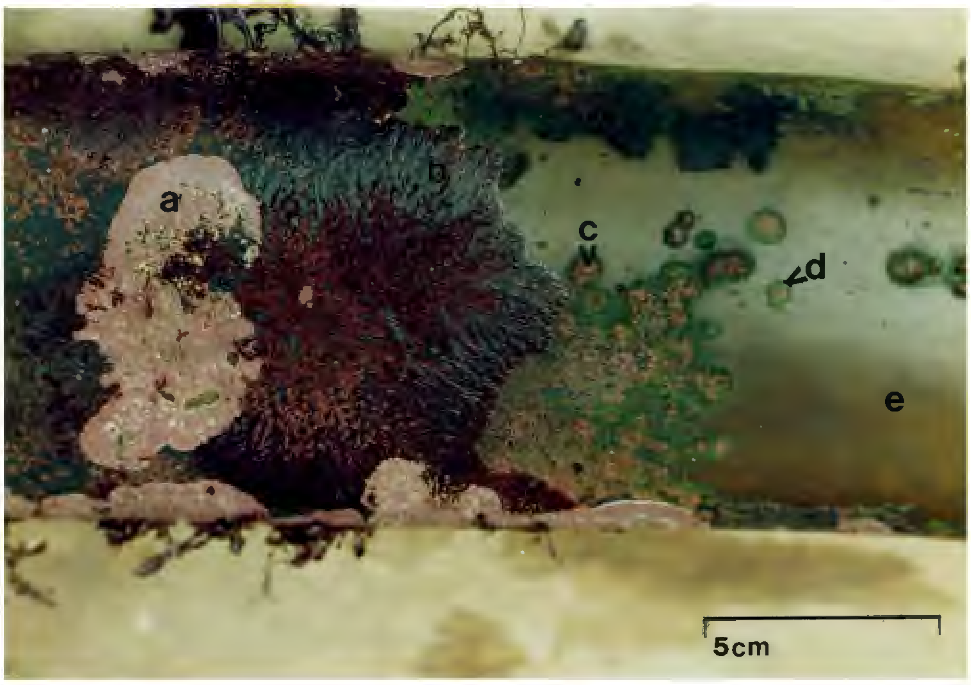


Plate 5: Crustose and filamentous stipe epiphytes: a = *Clathromorphum* spp.; b = *Placophora monocarpa*; c = *Colaconema nemalionis* (red); d = *Sporocladopsis novae-zelandiae* (green); e = clear stipe.

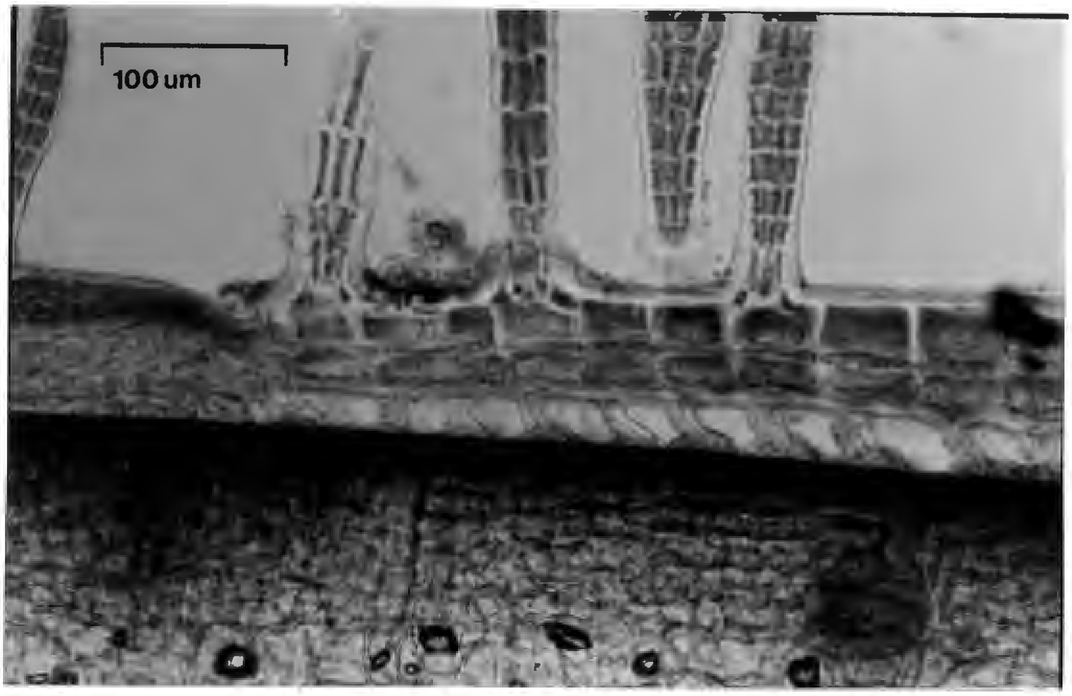


Plate 6: *Placophora monocarpa*:- cross-section of upright and horizontal form attached by special structures to the stipe surface.

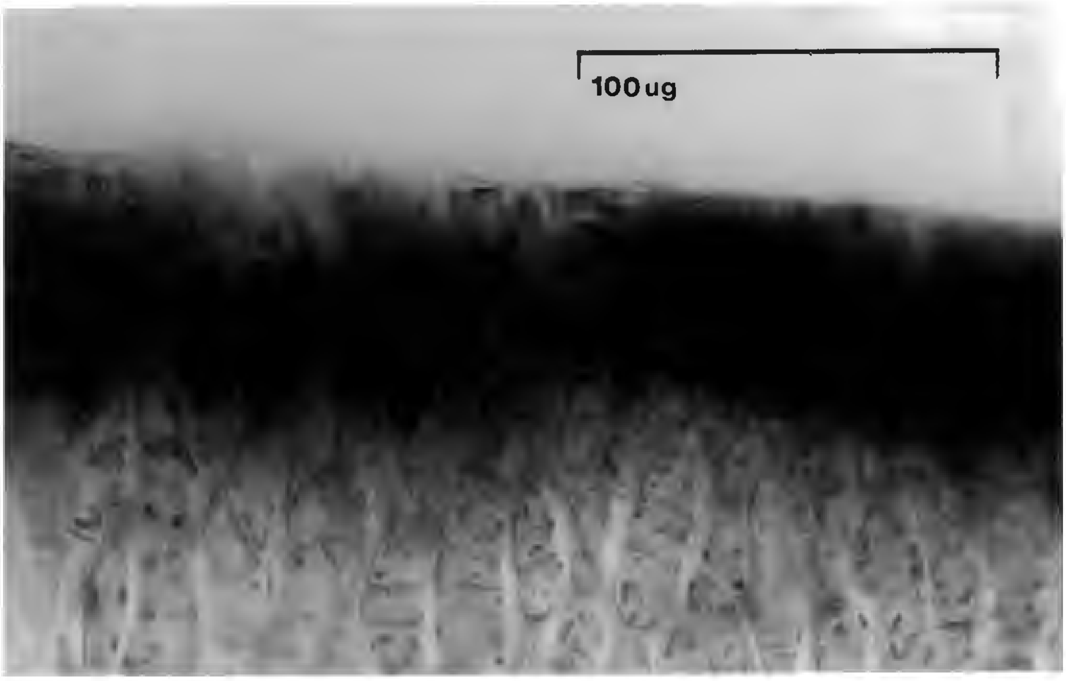


Plate 7: Cross-section of black stipe showing layer of *Sporocladopsis novae-zelandiae* on top of the kelp stipe cortex. Note cell wall thickening of cortex and chloroplasts.

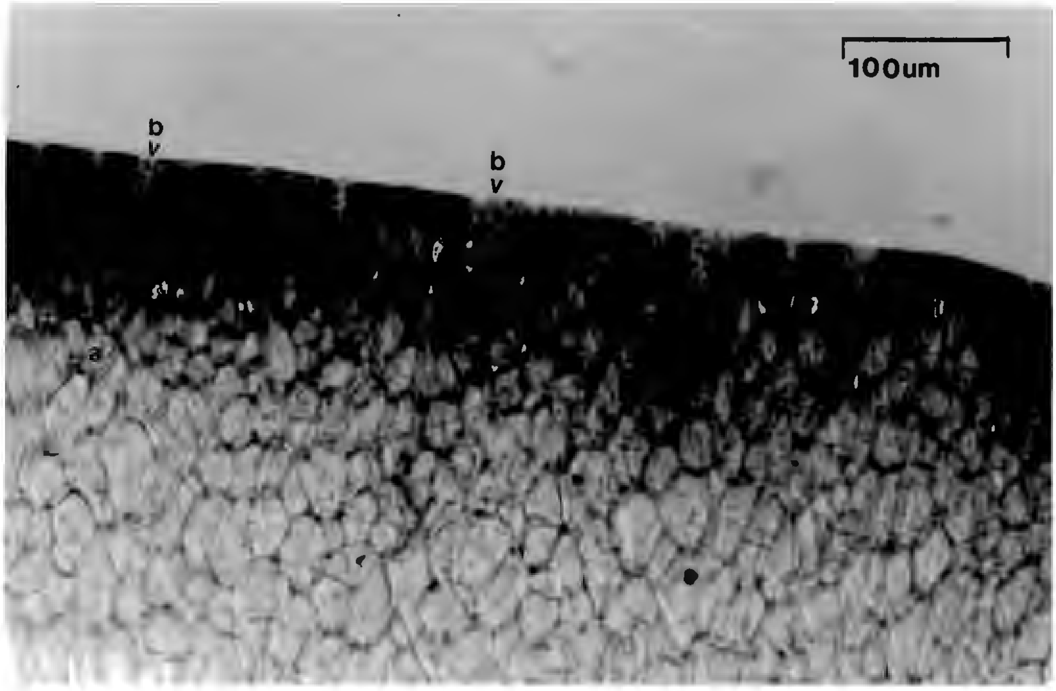


Plate 8: Cross-section of black stipe showing cell wall thickening of stipe cortex (a) and *Sporocladopsis novae-zelandiae* cells penetrating the cortex in places (b).

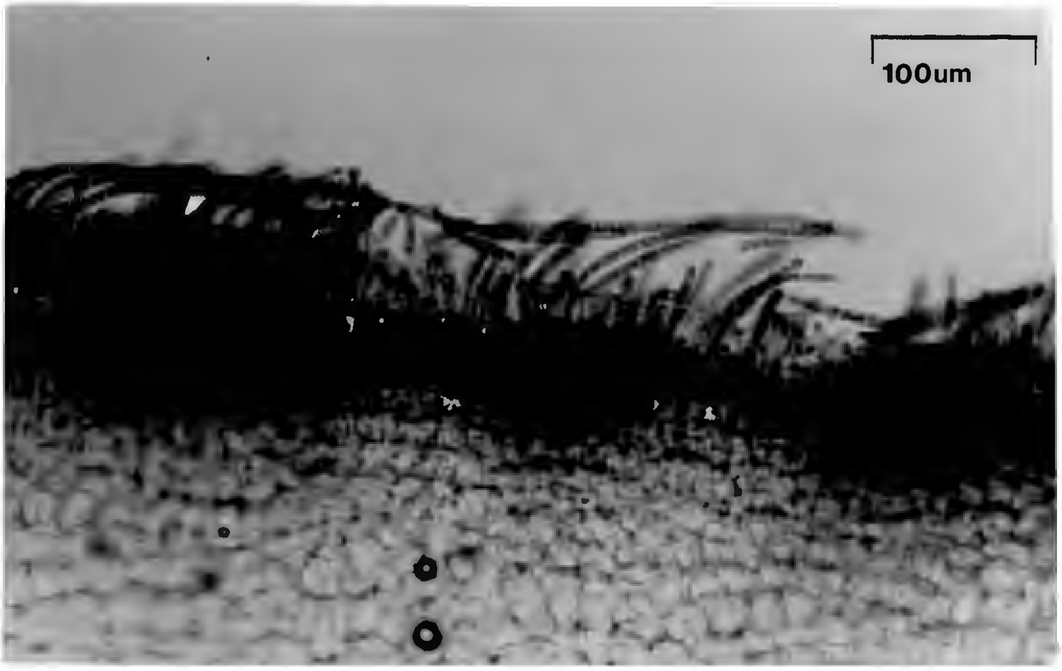


Plate 9: Cross-section of filamentous form of *Sporocladopsis novae-zelandiae*. Note cell wall thickening in stipe cortex.

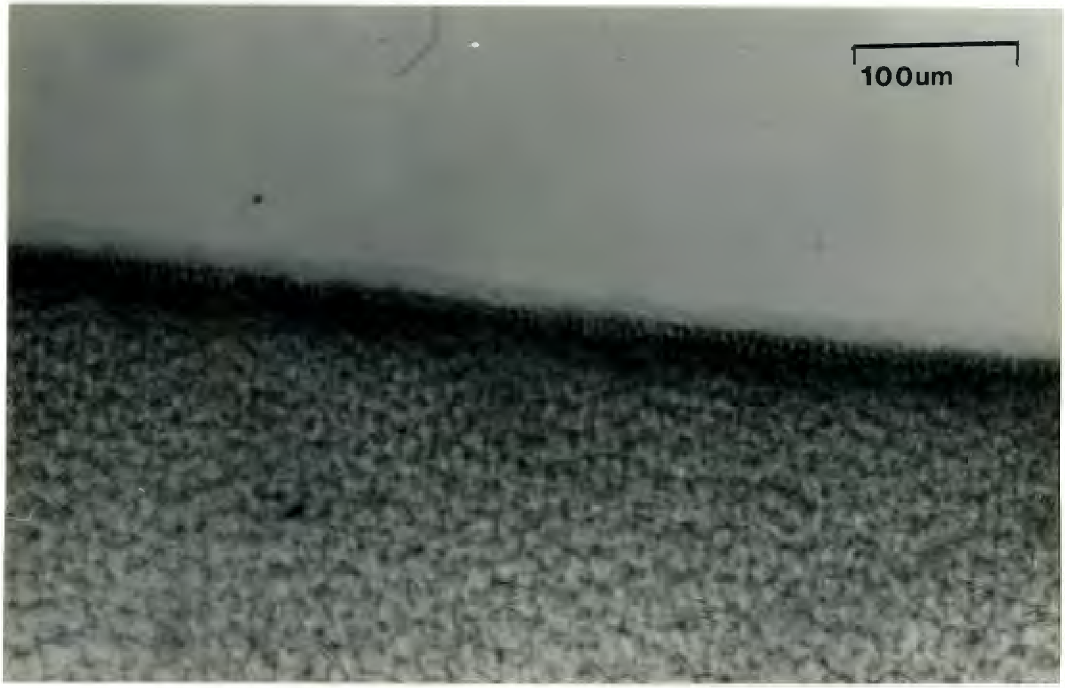


Plate 10: Cross-section of clear stipe showing no cell wall thickening and absence of *Sporocladopsis novae-zelandiae* cells.

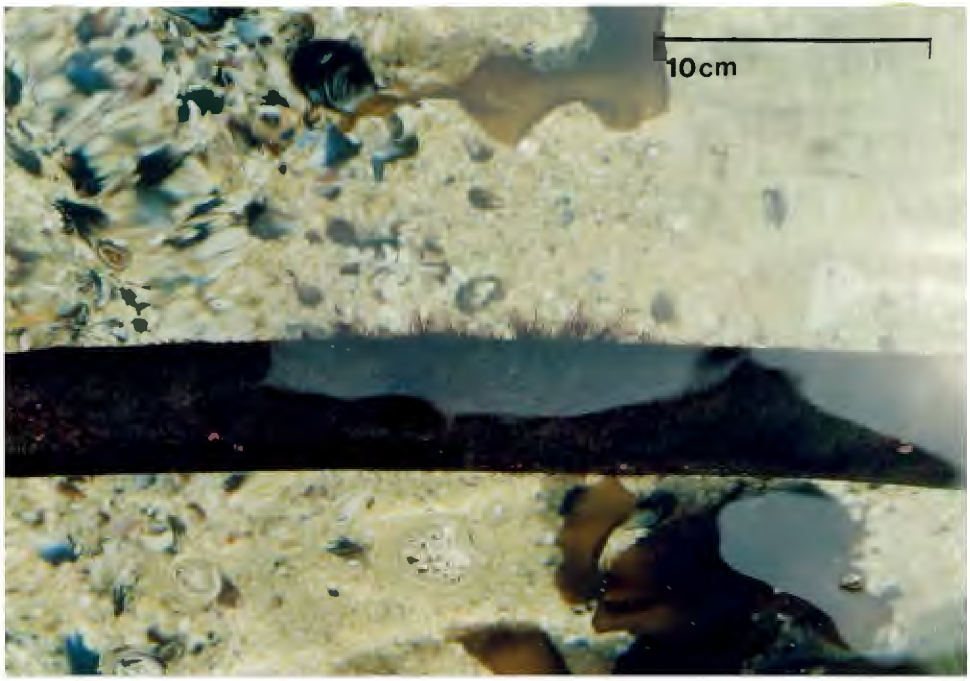


Plate 11: Removal experiment: early stages of colonisation of *Polysiphonia virgata* on a kelp stipe that had been free of limpets for four months.

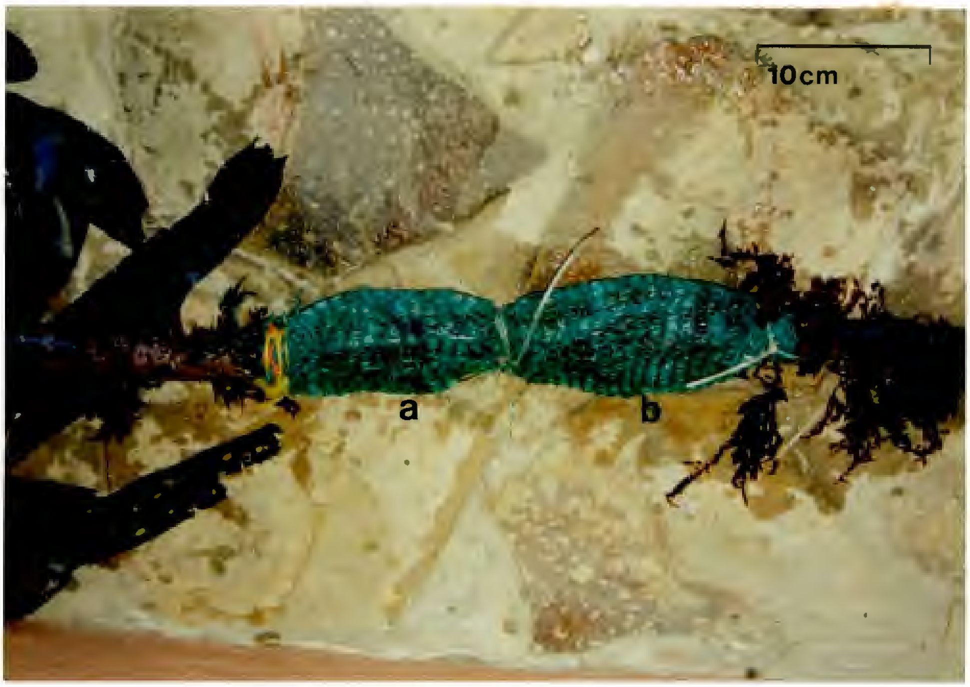


Plate 12(a): A limpet cage divided into two halves, one with a limpet inside (a) and one without (b, the control).

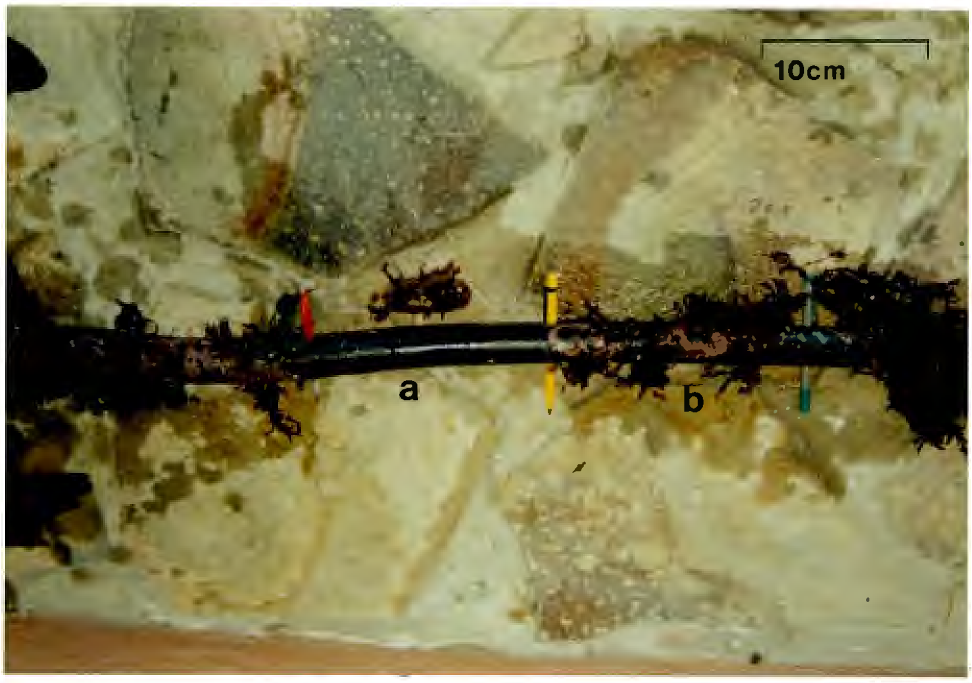


Plate 12(b): Result after four weeks: the limpet has cleared the portion of the stipe to which it was restricted (a) while b remains covered with various species of epiphytes.

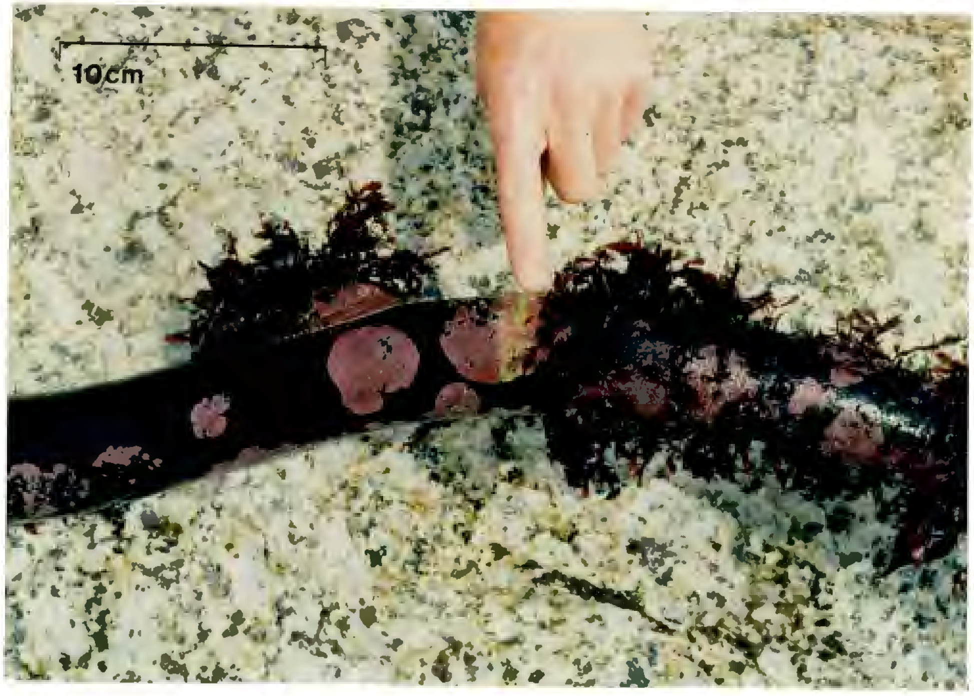


Plate 13: Caging experiment result after two weeks: the finger points to where the cage ended. Note the presence of *Clathromorphum* sp. in the caged portion.

Plate 14: The stipes of the three plants free of foliose epiphytes are hosts to large limpets while the three plants with a high cover of foliose epiphytes are free of kelp limpets.

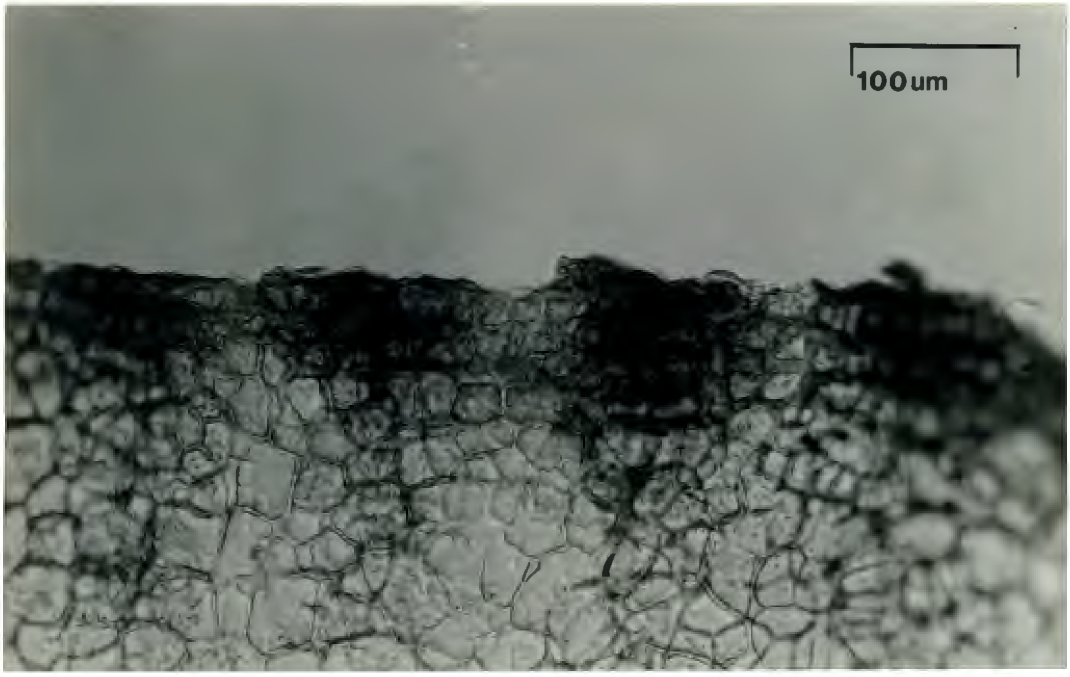


Plate 15: Kelp limpet grazing marks on the surface of the stipe showing extensive cell wall thickening of the cortex (pointers).

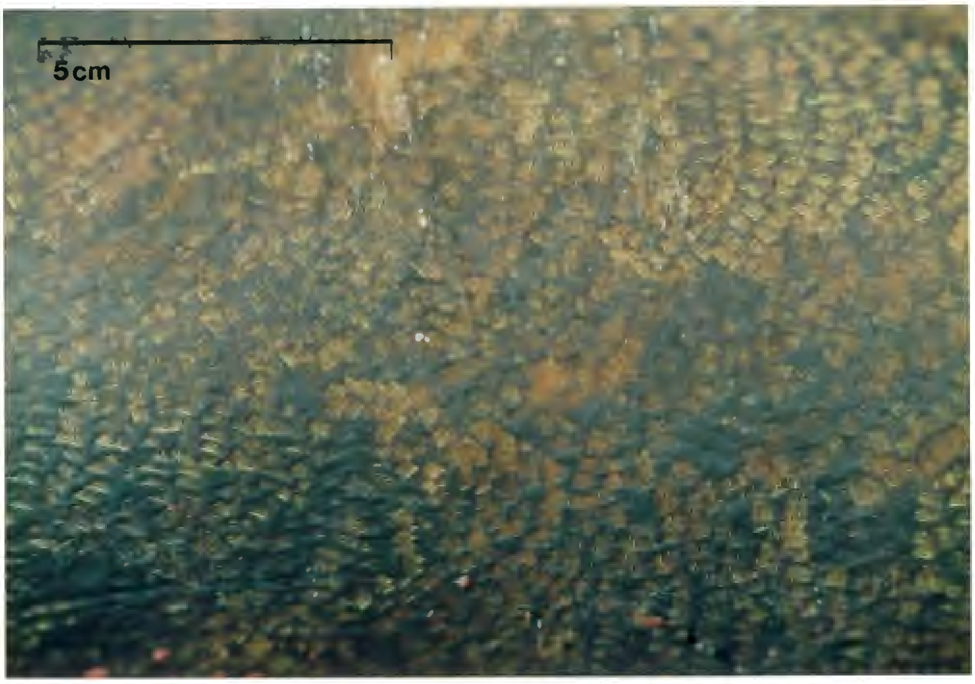


Plate 16: The grazing marks left by the kelp limpet on the surface of the stipe.

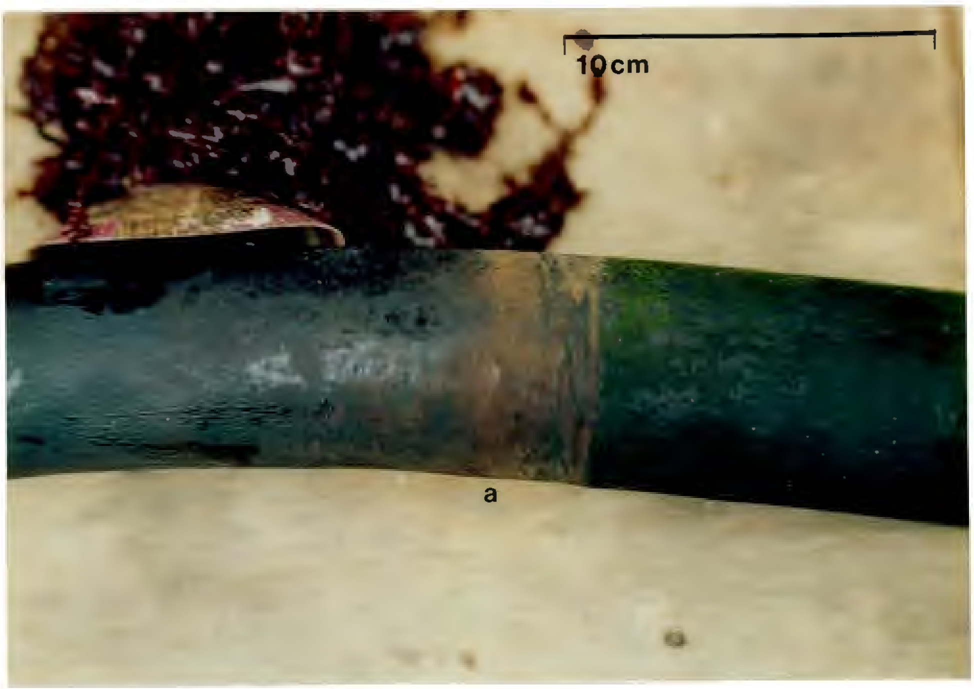


Plate 17: Proliferation of Sporocladopsis novae-zelandiae in the absence of limpet grazing. a=where the cage ended.