Substrate dependant survivorship of *Ecklonia Maxima*, in southern African kelp communities.

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Abstract

Several south-western Cape *Ecklonia maxima* communities were examined to determine their basic demography and the effects of substrate selection. Overall percentage substrate composition, stipe lengths and substrate attachment for all kelps were recorded at four sites off the Cape Peninsula. Strength of attachment to different substrates was measured. Selection for substrate type was analysed using Jacobs' index. A substrate of *Pyura stolonifera* was the most common for juveniles, whereas substrates of rock and conspecific holdfasts were dominant in the larger individuals. No significant difference in strength of attachment was found for kelps less than 50 cm. An analysis of the frequency of single- and multi-stiped holdfasts indicates that survival on rock is greater than on that of holdfasts. Size-class distributions indicate that *E. maxima* is a shade-tolerant species showing advanced regeneration. Establishment on rock may occur through episodic recruitment escaping grazing pressure. In areas with low grazing intensity, recovery from catastrophic storms may be limited by competition with understorey algae.

at the
sites
selected
here!

Introduction

Kelp bed communities are the forests of the marine environment (Reed and Foster, 1984). Kelp beds can be found on shallow subtidal rocky habitats pan-globally in temperate environments and are dominated by large brown algae from the order Laminariales (Dayton, 1985). Although Dayton (1985) suggested that kelp communities share similar processes and keystone species, one must be careful of generalisations on the dynamics of different ecosystems. As Dean *et al.* (1989) point out, there may be many differences between giant kelp populations and shallow water kelp with simple morphology, such as *Ecklonia maxima*, in much the same way as occur in differing terrestrial forests.

Nevertheless, by far the most ecological research has been performed on the giant kelp, *Macrocystis pyrifera*, forests of Northern California (Reed and Foster, 1984; Harris *et al.*, 1984; Ebeling *et al.*, 1985; Dayton and Tegner, 1984; Dean *et al.*, 1989; Reed 1990 and others). These kelp beds have provided the standard by which to examine others.

The giant kelp forests are generally considered to be controlled by a strong interaction between grazers and macro-algae, which often lead to urchin-created barrens (Harrold and Reed, 1985). However, recent attention has turned to examining the demography of these kelp populations in a similar way to that of terrestrial forests (Dean *et al.*, 1989). This has lead to analysis of survivorship curves, density dependent survival and age and size dependent survival (Dean *et al.*, 1989) Thus, it has been realised that intraspecific competition is just as important as interspecific competition and physical processes in these kelp beds.

In fact, kelp systems can be regarded in terms of terrestrial forest dynamics. For all practical purposes, forest dynamics is centred around the complex interaction of three factors, namely the disturbance regime, the degree of shade-tolerance of constituent species and factors affecting regeneration (Midgley & Gobetz, 1993; Okitsu *et al.*, 1995; Hara *et al.*, 1995). All of these have relevance in the kelp system.

The disturbance regime can involve both small-scale and large-scale processes (Brokaw, 1985; Uhl *et al.*, 1995; van Wyk *et al.*, 1996; Veblen, 1992; Akashi & Mueller-Dombois, 1995; Okitsu, 1995). In kelp forests, small-scale disturbance would be caused by individual plant removal or mortality, whereas large scale disturbance would occur with heavy storm damage or the creation of urchin barrens (Dayton, 1985). The degree of shade-tolerance reflects a species' ability to thrive and regenerate under different grades of canopy closure. Shade-tolerant species are able to regenerate under a closed canopy and can fill small gaps created by individual mortality or dislodgement. Shade-intolerant species would only be able to establish after large-scale disturbances, such as catastrophic storms or urchin barrens. Recruitment bottlenecks, where recruitment is restricted past a certain level, are important factors affecting regeneration (Espelta, 1995). These are relevant to the kelp system as the causes behind these bottlenecks are of interest from a demographic and commercial point of view.

• Kelp communities in south-western Africa

The South-western kelp communities of southern Africa stretch from 15 km West of Cape Agulhas up to Rocky Point in northern Namibia (Stegenga *et al.*, in press). They are composed of two main species, *Ecklonia maxima* (Alariaceae: Laminariales) (see review on *Ecklonia*: Bolton and Anderson, 1994) and *Laminaria pallida* (Laminariaceae: Laminariales). *Macrocystis angustifolia* also occurs in sheltered areas. In the south-western Cape, *E. maxima* dominates the shallow subtidal down to about 8m deep, whereas *L. pallida* dominates deeper water from 8-10m (Velimirov and Griffiths, 1979). *E. maxima* has a hollow stipe at the distal end of which is a swollen, gas-filled bulb. This allows it to reach the surface, sometimes forming a dense canopy. *L. pallida*, which usually has a solid stipe, does not often reach the surface, and is smaller than *E. maxima*.

The main grazer in this system is the common sea-urchin, *Parechinus angulosus* (Echinoidea). Its diet consists principally of drift kelp, young kelp sporophytes and other seaweeds (Field *et al.*, 1977; Fricke, 1979) and it is estimated to consume between 14% and 20% of annual kelp production at some sites (Fricke, 1979; Buxton and Field, 1983). This species does not form the feeding fronts seen in the northern Californian genus, *Strongylocentrotus*, and is not known to sever adult plants (Carrick, unpub.).

Southern African kelp beds are subject to exposure to large swells (Field *et al.*, 1977; Velimirov *et al.*, 1977). These swells are a common cause of mortality in *E. maxima*.

Previous studies conducted in the south-western kelp communities have been general, energy flow investigations (Field *et al.*, 1977; Field *et al.*, 1980), or have examined the biogeography (Bolton and Anderson, 1987) and physiology of the component organisms (Fricke, 1979; Bolton and Levitt, 1985;). However, very little work has focused on species interactions and the population dynamics of the kelp itself.

In one such study, Carrick (unpub.) showed that grazers have a major effect on the recruitment of *E. maxima*. In areas of high grazing intensity, young kelp sporophytes required recruitment refuges in order to establish. These refuges took the form of holdfasts of adult *E. maxima* and, to a lesser extent, *Pyura stolonifera* pods. However, apart from this study, there is only a fragmentary knowledge of ecological processes in these kelp beds, particularly those controlling the recruitment and development of sporophytes of the dominant species. Certainly, no attempt has yet been made to interpret the population dynamics of *E. maxima* in terms of forest ecology.

Thus, the aims of this study were twofold. Firstly, to continue investigation into the survivorship of juvenile *E. maxima* sporophytes. The hypothesis was that the substrate of recruitment influences survival to reproductive maturity. Secondly, to examine basic demography of the *Ecklonia maxima* populations and attempt to relate this to some terrestrial models of forest dynamics. From these analyses it was hoped to achieve a clearer picture of ecological processes in the *E. maxima* communities.

Study sites

Four sites were sampled around the Cape Peninsula during the course of this study (see Figure 1). Three of these sites, Glencairn, Spaniard Rock and Miller's Point, were located in False Bay (see Carrick, unpub., for description), whereas the fourth site, Oudekraal, was located on the west coast of the Cape Peninsula.

Sites were selected on the basis of two characteristics. Firstly, the presence of extensive *Ecklonia maxima* beds in the depth range of roughly two to four metres. Secondly, a range of available substrata for kelp attachment was required. As both basement rock and holdfasts are associated with all kelp beds, this effectively meant looking for areas where *Pyura* was present. This range of substrata was essential for the analysis of substrate selection performed in this study.

~~As~~ the two coastlines are geographically adjacent and they are thus described under the west coast marine phytogeographic region of southern Africa (Bolton, 1986) as defined by sea water temperature regimes. For this entire region, the

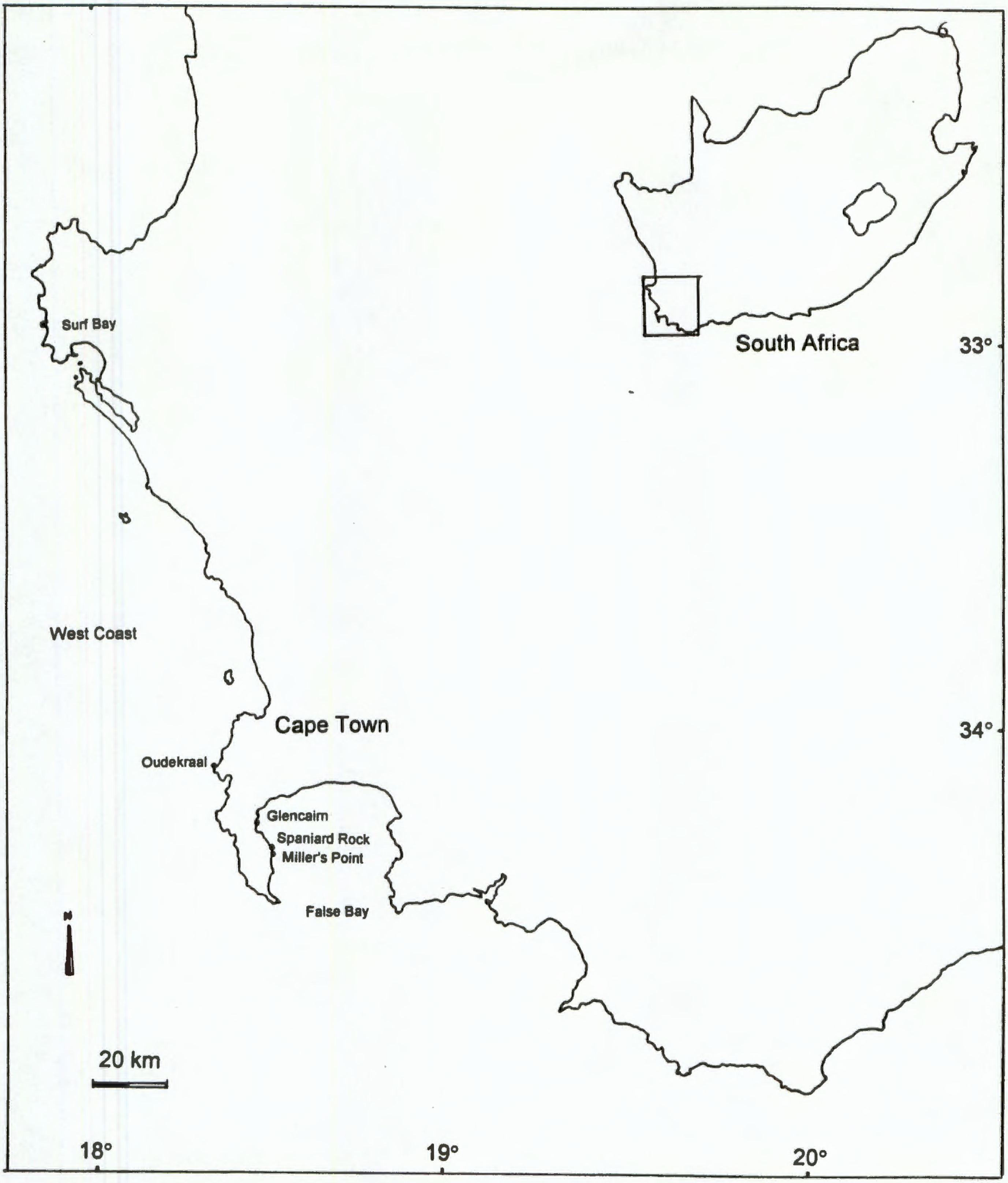


Figure 1: Map showing five subtidal sample sites off the coast of the western Cape Province, South Africa.

mean annual inshore sea water temperature is between 12° and 16° (Bolton, 1986). The mean for the coldest month is between 11.5° and 14.5° and for the warmest month, 13° to 19° (Bolton, 1986). It is important to note, however, that the water in False Bay is markedly warmer than that of the west coast (Bolton and Anderson, 1990). In fact, there are substantial differences between the west coast of the Peninsula and False Bay that are worth noting.

The different coasts are subject to almost directly opposite seasonal patterns. In the summer, the predominant south-easterly winds reduce swell and produce the seasonal upwelling on the west coast (Andrews and Hutchings, 1980). These same winds cause large swells in False Bay. In the winter, the predominant winds are north-westerly and these have exactly the opposite result, reducing swell in False Bay and causing storms on the west coast. In addition to this, there are also differences in the fauna between these coastlines. For the purposes of this study only two such differences are relevant. These are the reduced abundance of both the common sea urchin, *Parechinus angulosus*, (Carrick, unpub.) and of red-bait, *Pyura stolonifera*, from False Bay to the west coast.

Methods

- **Sampling methods**

Plot data were collected using between 5 and 10, 1 m^{-2} quadrats at each site. Data were collected by two divers operating on SCUBA and recorded on underwater slates. Due to time limits and the lengthy process of underwater data collection, it was not possible to collect sufficient data to make strictly random surveying a practical option. Thus data were only collected from the depth range of roughly 2 to 4 metres in areas with variable substrata including

Pyura. Vertical substrata and local barren patches were avoided. Within this subtype, quadrats were randomly positioned.

In each quadrat, all the *Ecklonia maxima* holdfasts were counted by one diver. Number of stipes, length of each stipe, reproductive maturity of each plant and substrate to which the holdfast was attached were recorded. This often necessitated prising the holdfast from the substrate. The second diver noted the depth (later converted to metres below mean low water spring, MLWS), the numbers and types of grazers and the percentage composition of the substrate, in each quadrat. Percentage composition of the substrate was estimated from markings on the quadrat. In order to keep estimations of substrate percentage consistent, the same diver recorded these data for all quadrats.

Strength of attachment of various sizes of *E. maxima* to its most common substrata, namely rock, holdfast and Pyura was measured at Glencairn and Miller's Point. This was achieved using a clamp and spring-scale method similar to that described by Shaughnessy *et al.* (1996). A clamp was attached to the base of a selected stipe. The clamp, consisting of a 5x5 cm hinge with a bolt welded to the open side, could be opened and positioned around the stipe and then screwed shut. In order to prevent the clamp cutting into the stipe, the hinge was lined with neoprene. This clamp was then connected to a 50 kg spring-scale which was pulled smoothly and quickly, at ninety degrees to the substrate. A sliding magnet on the spring-scale registered the maximum weight required to dislodge the kelp plant. In cases where the stipe broke without removing the holdfast, the maximum weight was still recorded, but it was noted that the holdfast had not been dislodged. Length of the stipe and the area of the holdfast were also recorded. Twenty-five plants on each of the three substrata were sampled.

This method of dislodging kelps was only suitable for the smaller size classes (<50 cm) as larger kelps a) would not fit the clamp and b) required in excess of 50 kg to remove them.

- **Data analysis**

Frequency distributions of *E. maxima* were created for each site by grouping the stipe measurements from the quadrat data into size classes and graphing these. From these size-class distributions one can see whether the population consists of only large individuals, or whether recruitment is occurring under the canopy. In terrestrial forest ecology an inverse-J shaped curve is indicative of a shade-tolerant species (Midgley *et al.*, 1990), whereas species with flat, unimodal or bimodal curves are shade-intolerant (Everard *et al.*, 1995). However, if competition for light is not the driving force, then one must look for other factors to explain these patterns.

"Selection" for substrate type by *E. maxima* was analysed using an index (1) proposed by Jacobs (1974) for selective feeding in animals. When transformed for substrate analysis, the degree of selection (log Q) is defined by *r*, the fraction of a given substrate type that plants are attached to, and *p*, the fraction of the same substrate in the environment:

$$\log Q = \log {}^{r(1-p)} / {}_{p(1-r)} \tag{1}$$

E. maxima is dispersed randomly and therefore cannot actively select substrate types. Thus, "selection" actually refers to "survivorship" and is the end result of several processes selecting for survival on that substrate. Negative values indicate decreased survivorship on that substrate, or "selection" against the particular substrate. Positive values indicate increased survivorship on that substrate, or positive "selection" for that substrate.

Jacobs' index was calculated separately for kelp plants of all sizes and for those less than 30 cm. This was performed for the three common substrata, Rock, *Pyura* and holdfast, at all four sites. The category of all plants greater than 30 cm was not used as there was insufficient data allow a meaningful analysis at this level.

Differences between the substrate composition of the sample plots were tested for. The plots were initially classified using the hierarchical classification program TWINSPAN (Hill, 1979). The program was run with defaults. The database consisted of the percentage cover of each substrate type at each plot for all sites. Each plot was given a code identifying the site of origin and the sample number at that site. This allowed individual plots from each site to be compared with one another.

As TWINSPAN is a polythetic divisive method (Kent and Coker, 1992), plots are separated on the basis of total substrata composition. Thus, the dendrogram produced by TWINSPAN provides an indication of which plots are similar in substrate composition to one another. This gives insight into possible community affiliations within the samples. The clustering produced by this analysis is then superimposed on to the ordination of the same database.

The ordination was performed as a detrended correspondence analyses (DCA) by the computer package CANOCO (ter Braak, 1988a, as cited by Kent & Coker, 1992; ter Braak, 1988). The programme was run with defaults. Percentage cover of substrata per plot served as the importance values. The output of this analysis was graphed, the similarity between samples being reflected by their proximity to one another.

Results

- **Site Characteristics**

Table 1 shows the general sample characteristics of each site, including mean depth of the sites, number of plots sampled, total plant sample size and various densities.

Table 1: **Mean depth (below MLWS), total number of plots and kelp plants and the density of all kelps, and those < 30 cm, at the sites sampled.**

Site	Mean depth (m)	Sample size		Density (m^{-2})	
		Plots	Plants	all plants	< 30 cm
Spaniard	2.63 ± 1.65	10	159	15.9	12.5
Glencaim	1.61 ± 0.75	8	183	22.9	17.1
Miller's Point	1.82 ± 0.50	5	73	14.9	6.20
Oudekraal	2.53 ± 1.25	10	111	11.1	3.50

The percentage composition of the substrata at each site is shown by Figure 2. Only the dominant three substrate types, *Pyura*, rock and *E. maxima* holdfasts, are shown. The rock category includes all bare rock and rock encrusted with coralline algae, as it is presumed that there is little difference between these substrata in terms of kelp sporophyte settlement.

Grazer densities at all False Bay sites were similar, with Glencairn recording the highest density of grazers, and Miller's Point the lowest (Figure 3). There was an absence of grazers recorded at the west coast site, Oudekraal. The grazer densities recorded in this study (Figure 3) are generally lower than those recorded by Carrick (unpub.). This is due to the fact that Carrick actively sought out areas with high grazer densities, a procedure not followed in this study.

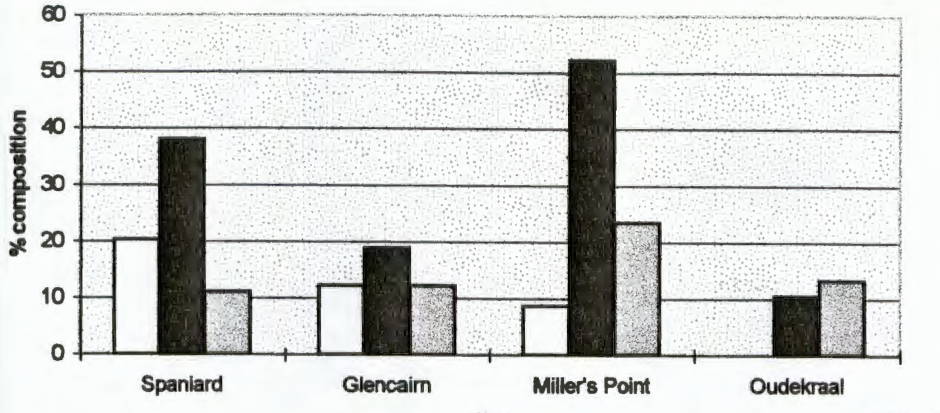


Figure 2: Percentage substrate composition of Pyura, Rock and Holdfast at each sample site

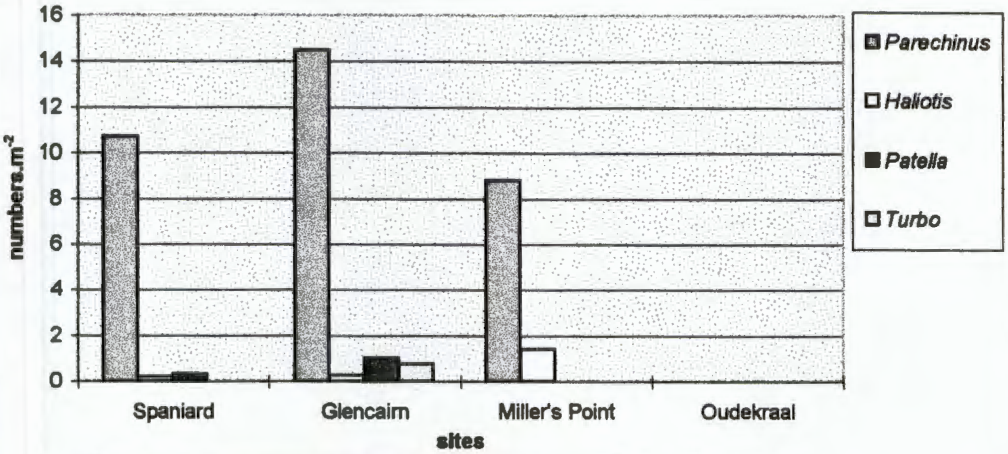


Figure 3: Average grazer densities (no.m^{-2}) for the various sample sites

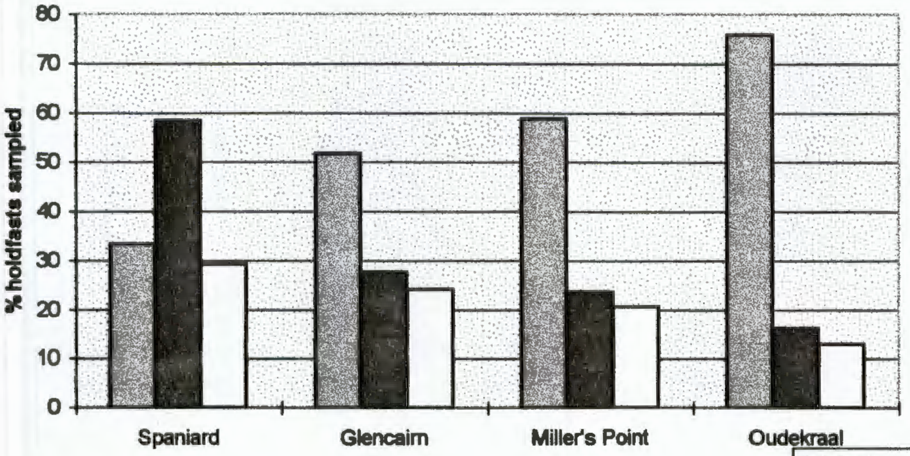


Figure 4: Percentage of holdfasts of single or multiple stipes and with recruits present

Figure 4 shows the percentage of single-stiped and multi-stiped holdfasts, and the percentage of holdfasts with juveniles recruiting on them, at the different sites. The categories were defined as follows. Single-stiped holdfasts included all holdfasts with a single stipe over 30 cm in length and with no juveniles (< 30 cm) recruiting upon it. Multi-stiped holdfasts included all holdfasts with more than one stipe of over 30 cm. Recruiting holdfasts included all holdfasts with one or more stipe/s of over 30 cm, with juveniles (< 30 cm) recruiting upon this holdfast. Thus, several holdfasts may have appeared in both the multiple-stiped and recruiting categories, hence the lack of unity in the proportions seen in Figure 4. In addition, all holdfasts without an individual of over 30 cm stipe length were excluded. For this reason, the sum of the percentages of single and multi-stiped holdfasts does not equal 100%.

Across all sites, one can observe an inverse relationship between the percentage of single holdfasts and the percentages of both multiple holdfasts and holdfasts with recruits. As the proportion of single-stiped holdfasts increases, so the proportion of multi-stiped and recruiting holdfasts decreases. At one extreme, Spaniard Rock has a proportion of holdfasts showing recruitment, which is greater than the proportion of single-stiped holdfasts. At the other extreme, Oudekraal has 76% single-stiped holdfasts, and the lowest proportion multi-stiped and recruiting holdfasts. At all sites, the percentage of holdfasts with recruits, was greater than the percentage of multiple holdfasts, indicating a less than complete survival of holdfast recruits.

From the TWINSPAN groupings and ordination (Figure 5) one can see that the substrate composition of the west coast site, Oudekraal, is distinct from the False Bay sites. At all the False Bay sites, the composition of the substrate was similar, and no significant distinction can be made between them. Certain plots, namely GC1, GC2 and M3, are regarded as anomalous outlies and do not significantly alter this finding. Thus, one can exclude intersite substrate variation

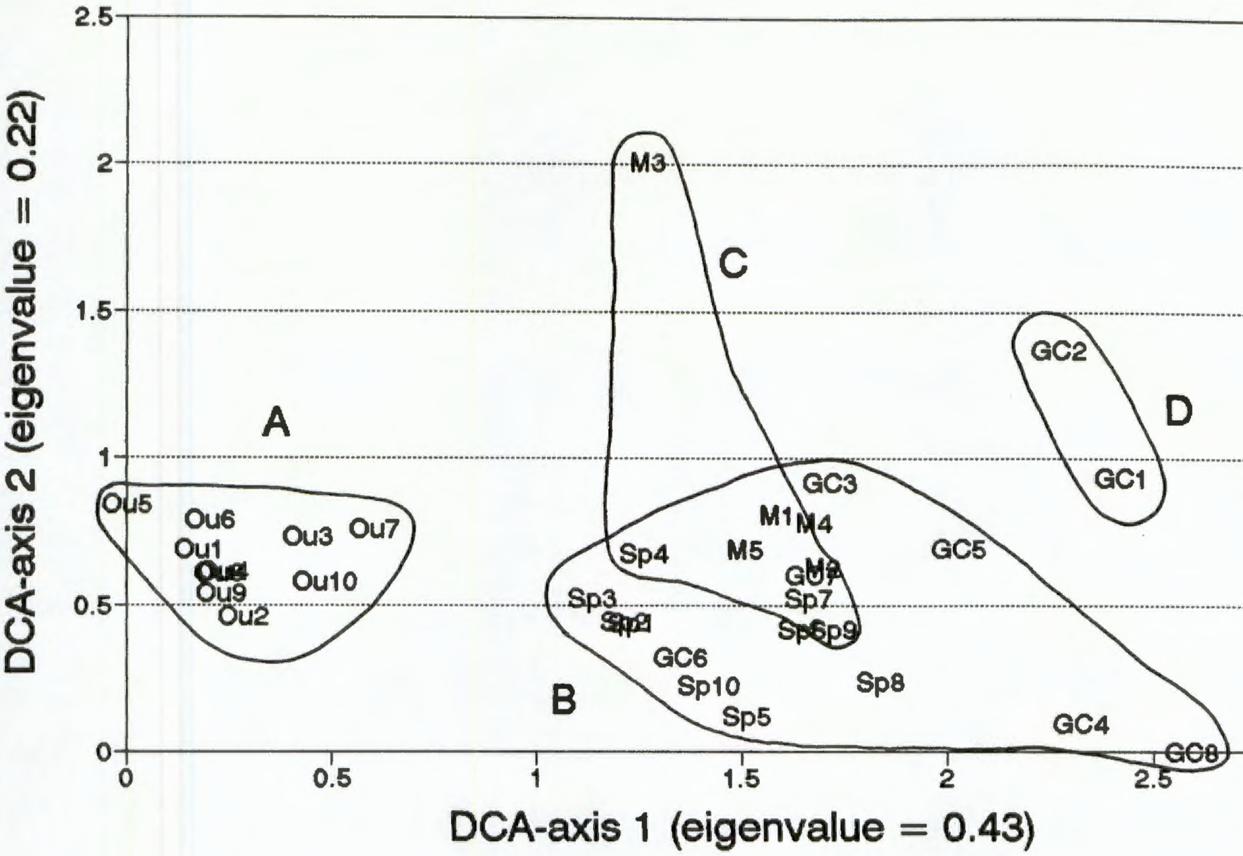
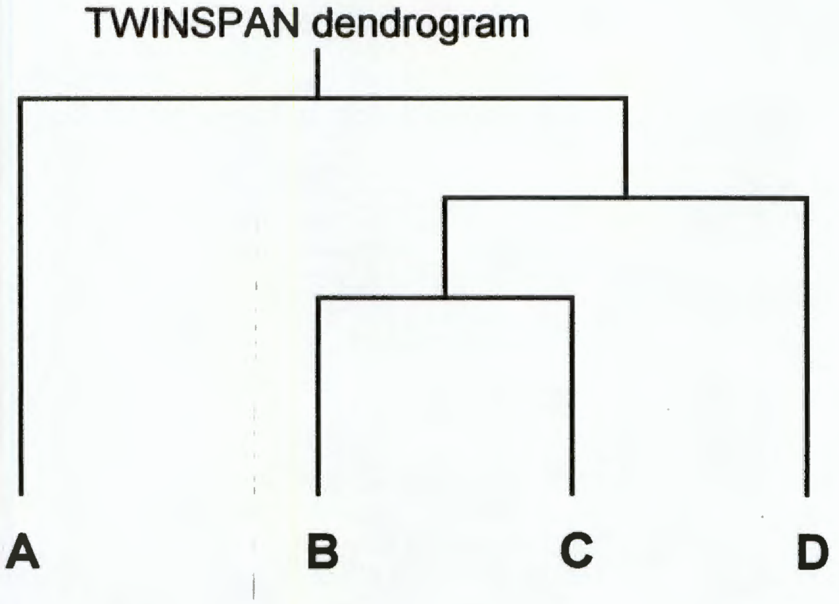


Figure 5: DCA ordination of sample sites, with % substrate composition as importance values. TWINSPAN grouping (shown below) are circled. Sites are represented by initials, numbers indicate plot number.



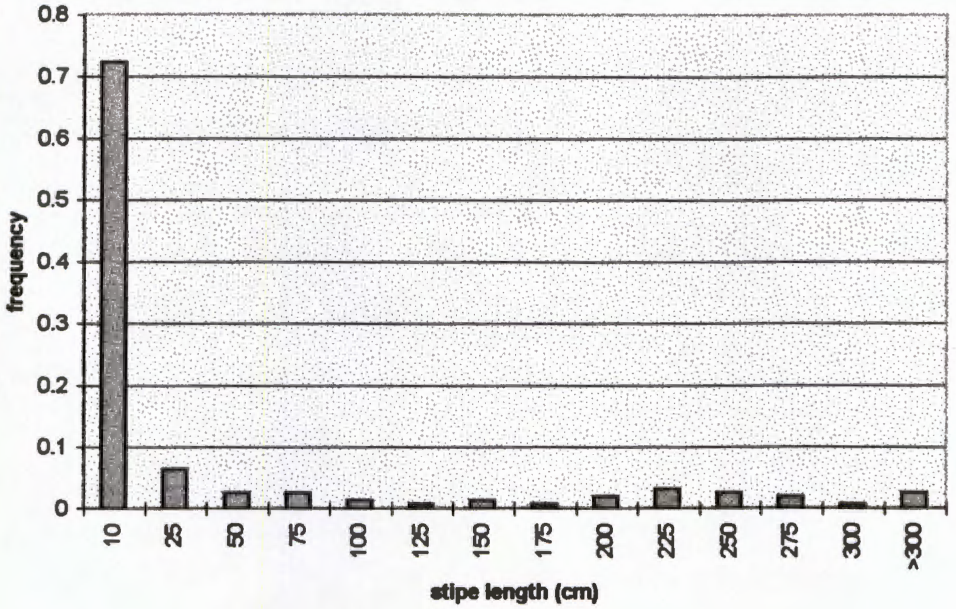


Figure 6: Size-class distribution of *Ecklonia maxima* at Spaniard Rock

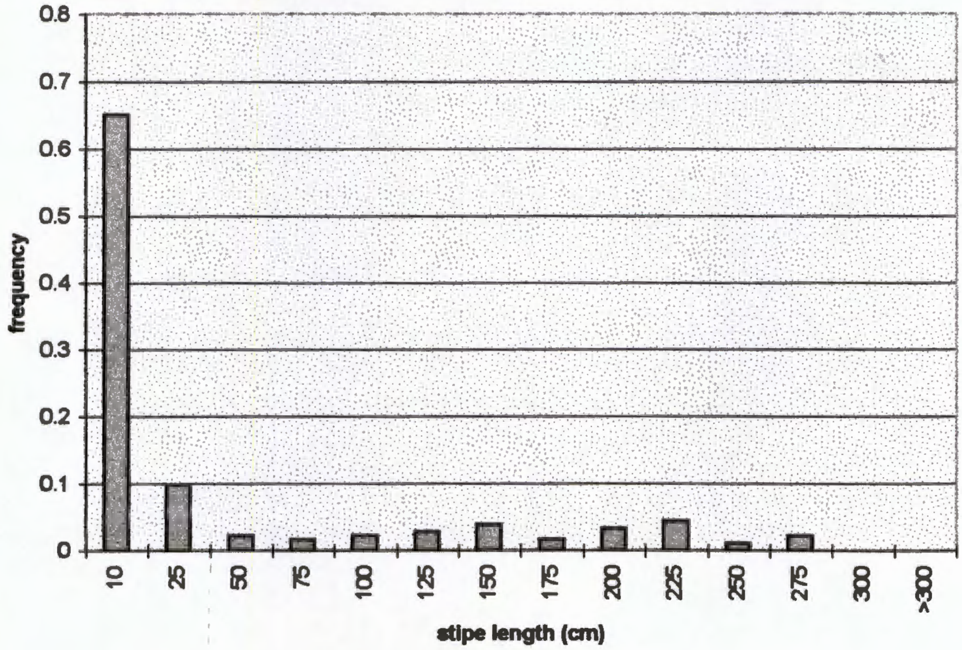


Figure 7: Size-class distribution of *Ecklonia maxima* at Glencairn

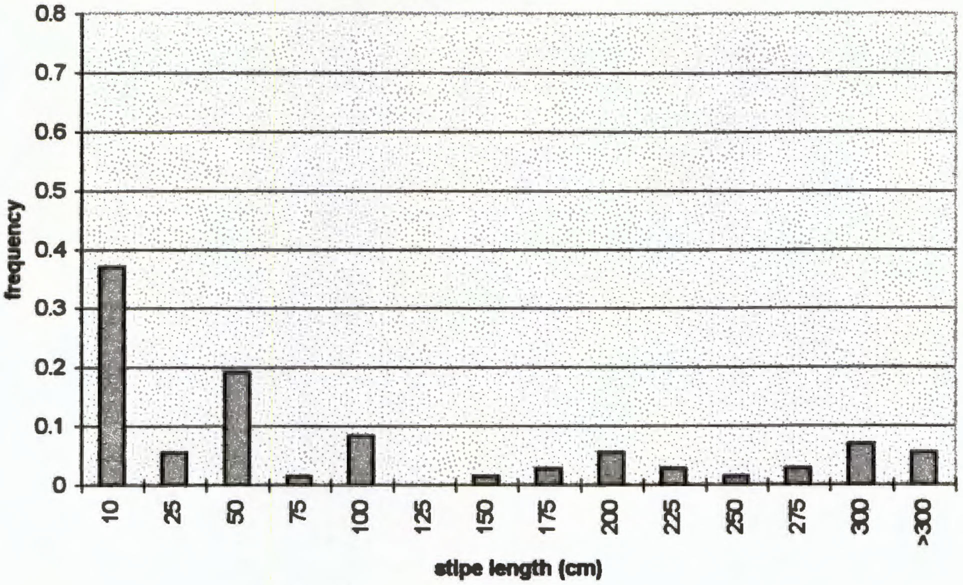


Figure 8: Size-class distribution of *Ecklonia maxima* at Miller's Point

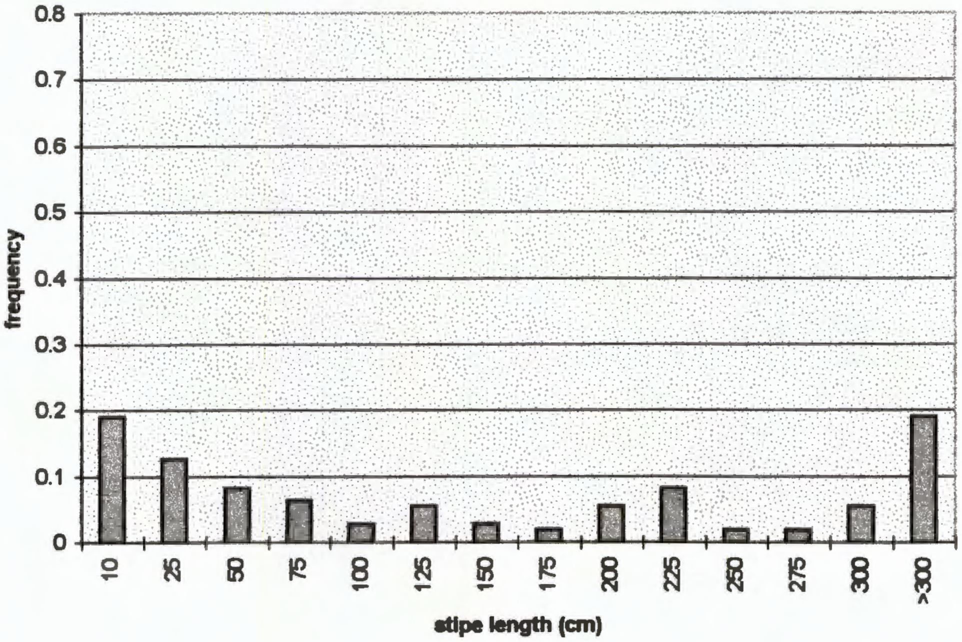


Figure 9: Size-class distribution of *Ecklonia maxima* at Oudekraal

as an explanation for any differences in dynamic processes that might occur across the False Bay sites.

- **Size-Class distributions**

Size-class distributions, at all sites, for *E. maxima* are shown in Figures 6-9. Spaniard Rock (Figure 6), Glencairn (Figure 7) and, to a lesser extent, Miller's Point (Figure 8) all exhibit inverse J-shaped curves. Spaniard Rock and Glencairn have extremely similar curves. These curves show high recruitment levels, with few of these recruits advancing beyond 10 cm stipe length. Miller's Point shows lower levels of recruitment but a greater number of individuals in the medium to small size classes (<100 cm). There is also a greater proportion of large plants present (>275 cm).

Oudekraal (Figure 9) exhibits a different shape of curve from the False Bay sites. At this site, recruitment seems to be the lowest of all four sites. There also seems to be a greater proportion of large plants (>275 cm) at this site.

- **Selection for substrate**

The percentage occurrence of different kelp size classes on particular substrata was found to vary (Figure 10). Smaller kelps were found attached to a variety of substrata, namely barnacles, perlemoen, sponges, limpets, mussels, corals and coralline turfs. However, these only made up 17% of the total number of plants. The remaining 83% were found on rock (including encrusting corallines) (28%), holdfasts (20%) and *Pyura* (35%). Reproductive and canopy kelps were found almost exclusively on rock (95%), with only 5% occurring on *Pyura*. No large plants were recorded on any other substrate.

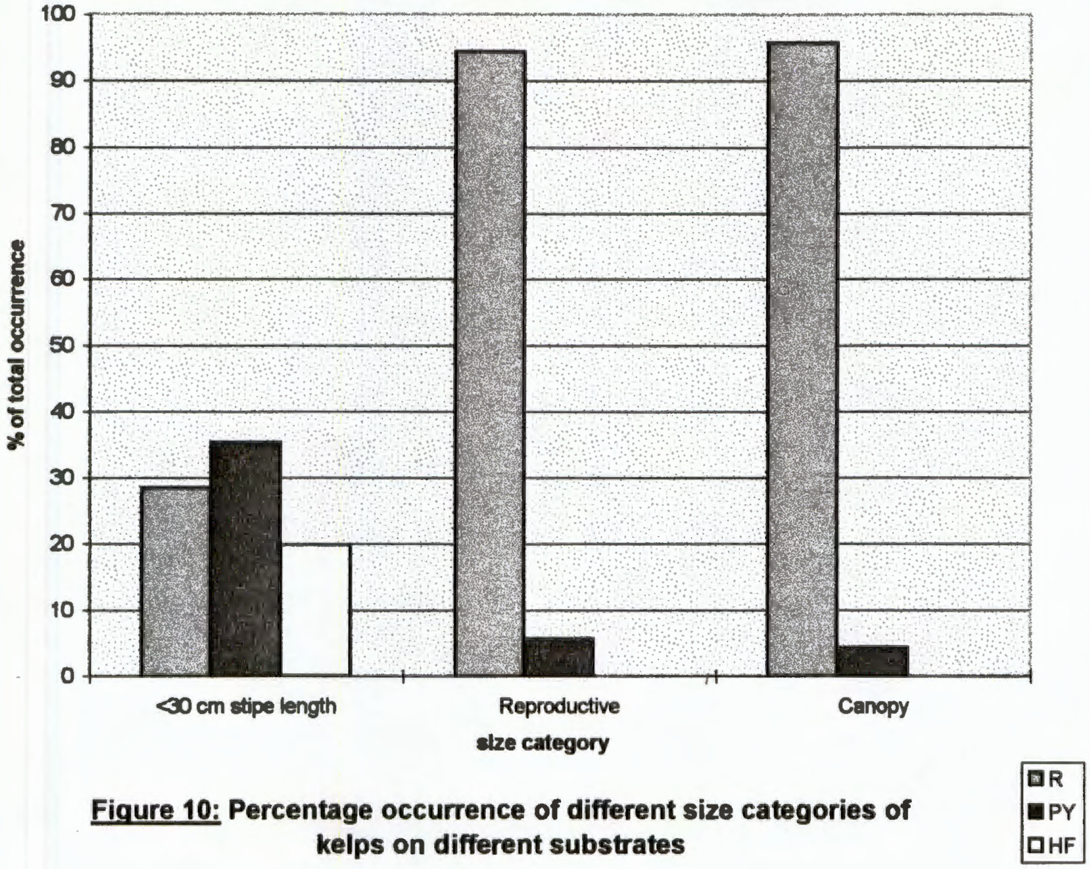


Figure 10: Percentage occurrence of different size categories of kelps on different substrates

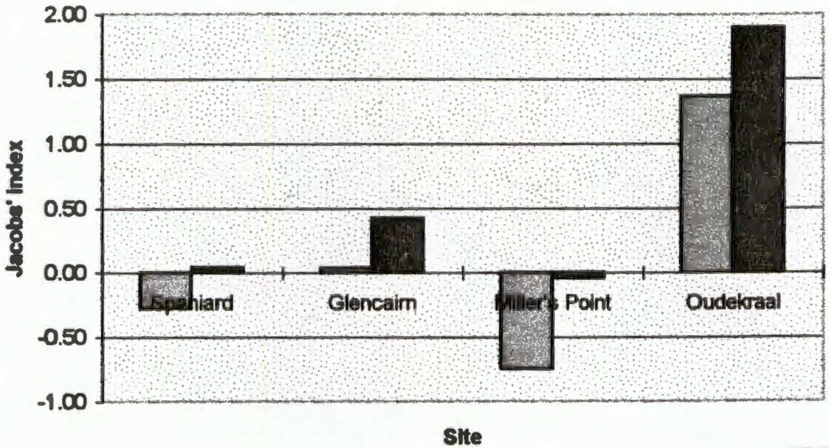


Figure 11: Jacobs' index for ROCK at all sites sampled

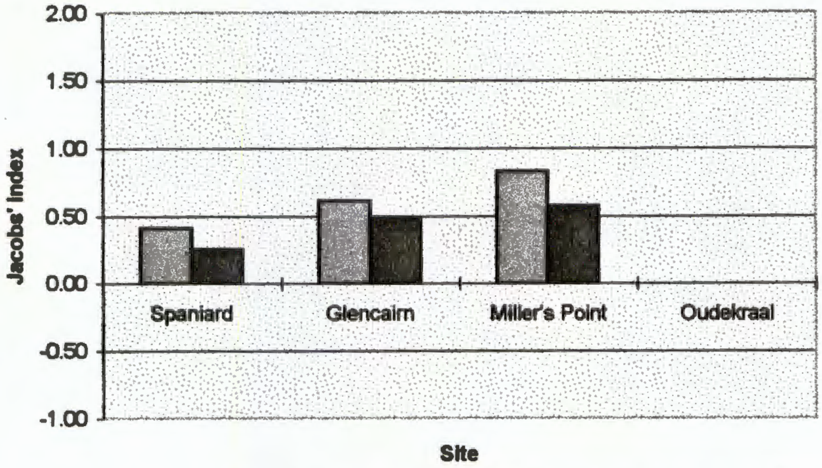


Figure 12: Jacobs' index for PYURA for all sites sampled

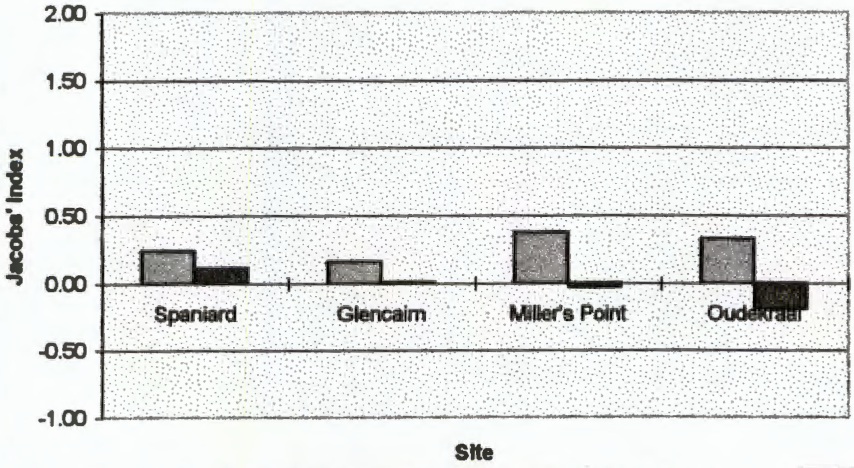


Figure 13: Jacob's index for HOLDFAST for all sites sampled

The apparent lack of any large plants on holdfasts was due to the inability to distinguish the order of appearance of adult plants in a holdfast mass. Thus, it is likely that a proportion of the large plants recorded on rock, may have recruited of holdfasts. This is an unfortunate situation, which is slightly remedied by the data presented in Figure 4, as the degree of multi-stipedness can be used to infer the success of holdfast recruitment.

The results of Jacobs' index are shown in Figures 11-13. If one compares the values obtained across all sites for a particular substrate type, a pattern emerges. On rock: There is weak selection for this substrate by plants <30 cm, except at Oudekraal. However, at every site, the selection for rock increases when one includes the larger size classes. Selection for rock in the largest plants can be inferred from Figure 10.

On *Pyura*: Selection for *Pyura* is stronger in the small size class. As one includes the larger plants, so the selection for *Pyura* decreases. The positive value obtained when examining all size classes is due to the swamping effect of the numerous juveniles. Once again, selection for *Pyura* in the largest plants can be inferred to be extremely low (Figure 10).

On holdfasts: This substrate follows the same pattern as *Pyura*. However, one must bear in mind the sampling problems elucidated above. These problems would have the effect of reducing the selection index for the larger size-classes.

- **Strength of attachment to substrata**

The scatter plots of the strength of attachment study are shown in Figures 14-17. All the data are similar and an analysis of variance showed no significant differences between the substrata. This was most likely due to small sample sizes and the limited size range that was sampled. Nevertheless, one can detect

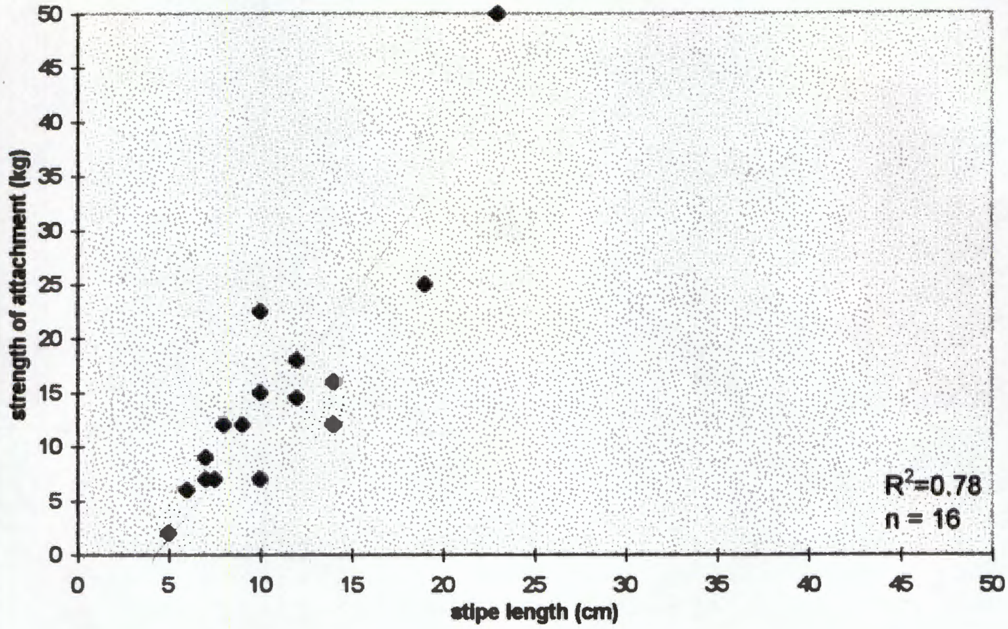


Figure 14: Length of stipe of *Ecklonia maxima* vs strength of attachment on HOLDFASTS

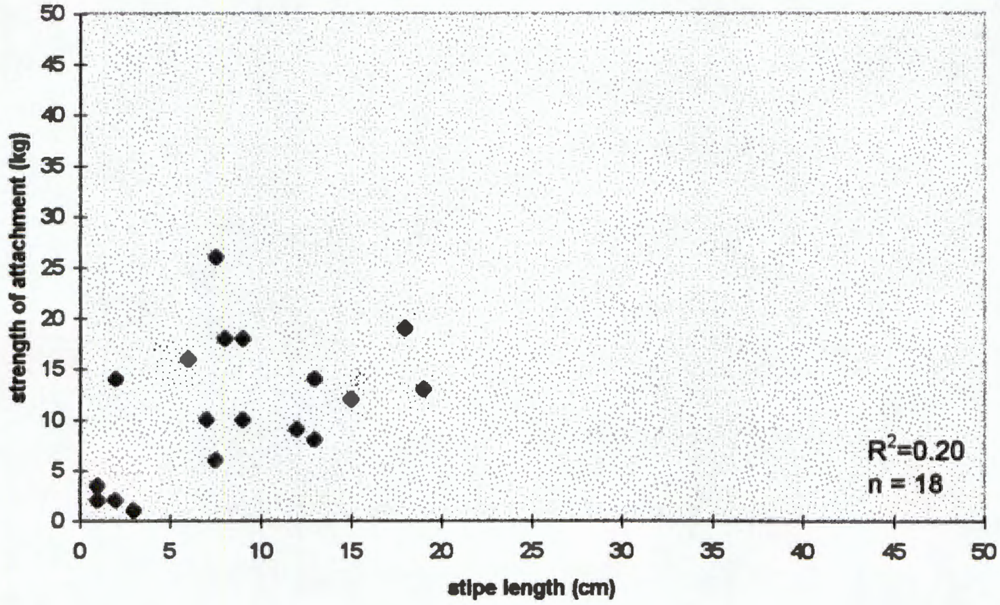


Figure 15: Length of stipe of *Ecklonia maxima* vs strength of attachment on ROCK

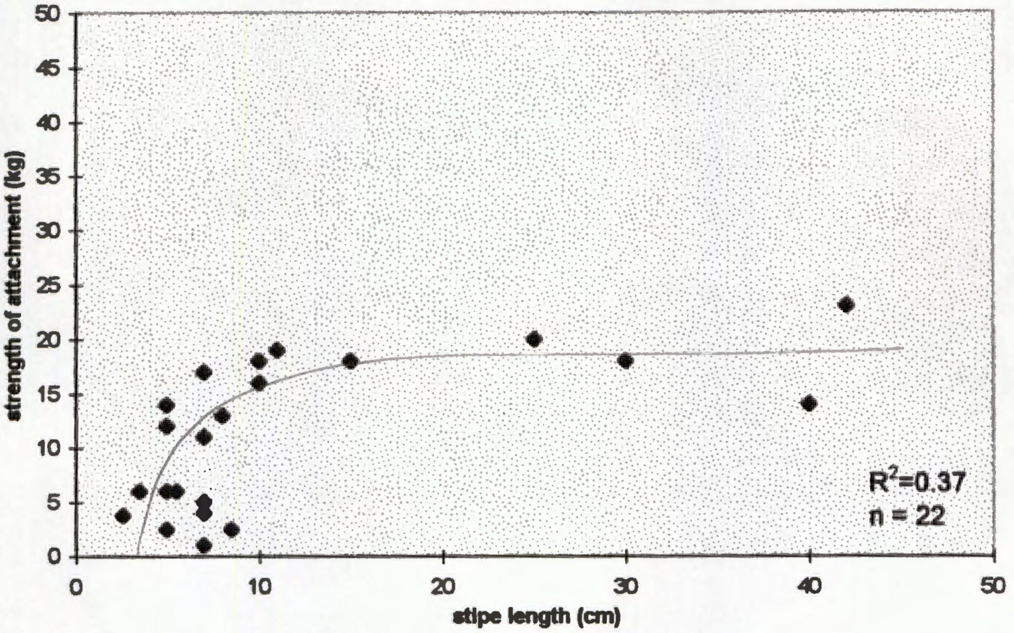


Figure 16: Length of stipe of *Ecklonia maxima* vs strength of attachment on *PYURA*

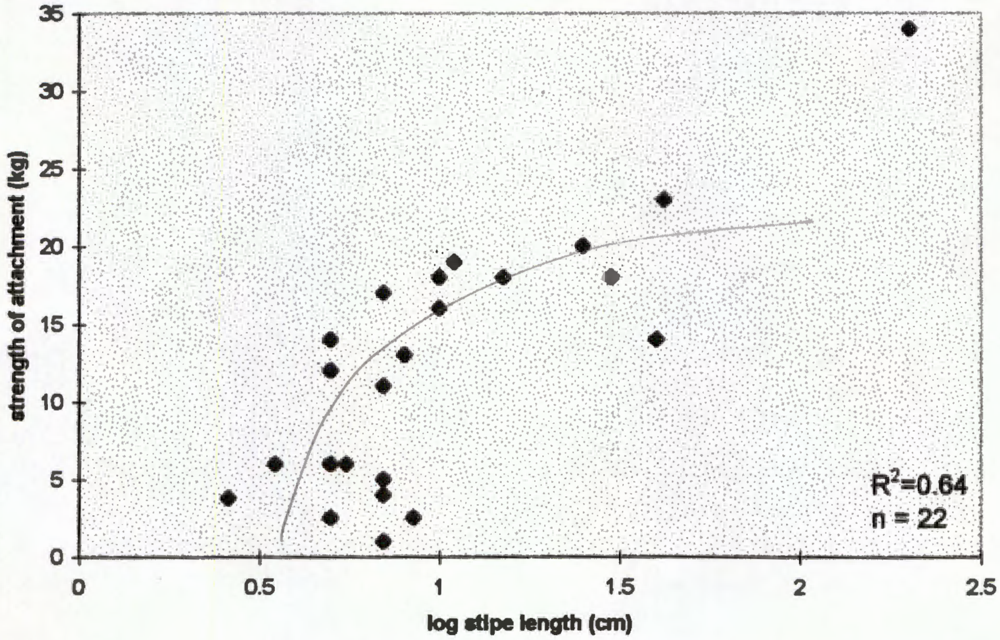


Figure 17: Log of length of stipe of *Ecklonia maxima* vs strength of attachment on *PYURA*

certain trends in the graphs themselves. In addition to this, the number of unsuccessful removals per substrate provides a measure of attachment strength. An unsuccessful removal occurred either when maximum force was exerted without result, or when the stipe in question snapped without its holdfast dislodging.

The holdfast data show a steep increase in strength of attachment with increasing size (Figure 14). Certainly, it proved impossible to remove many plants from the holdfasts without breaking their stipes. The high frequency of broken plants (38.4%) indicates strong attachment.

The rock data show no particular pattern in the smaller sizes (Figure 15). However, unsuccessful attempts were frequent (18.2%). Additionally, several large plants (200-325 cm) were tested and these were impossible to remove from the substrate, each recording a strain of in excess of 50 kg without dislodging.

The *Pyura* data show an increasing curve that flattens out logarithmically (Figure 16). When one plots strength with the logarithm of length (Figure 17), a linear relationship is found. There were relatively few unsuccessful removals (11.5%).

Discussion

Selection for substrate

The results from the Jacobs' index (Figures 10-13) can be interpreted in two ways. Firstly, at each site, the relative values between juveniles and all kelp sizes obtained on each substrate type can be examined, and it is here that the most meaningful result is obtained. Secondly, one can compare the absolute values obtained for different substrata in an attempt to infer degree of selection for substrata.

For all sites and all substrates, a single pattern emerges when examining the first of these interpretations. In all cases, there is an increase in selection for rock with an increase in kelp size. Similarly, there is a decrease in selection for both *Pyura* and holdfasts with an increase in kelp size. The fact that this trend is common across all sites, including both False Bay and the west coast, indicates its robustness. This finding is supported by the numbers of juvenile and reproductive kelps recorded on these substrata (Figure 10).

When comparing the absolute values obtained for each substrate, It would appear from the Jacobs' index that *Pyura* is the substrate most highly selected for *Ecklonia maxima* attachment. Holdfasts are also generally positively selected for whereas, in the False Bay sites, rock seems to be slightly negatively selected for. This could well be attributed to the dispersal biology of kelps. Spore settlement is not directed, and spores are at the mercy of the current. It has been shown that settlement in algae increases with increased substrate texture (Harlin and Lindbergh, 1977; Dudley and D'Antonio, 1991). At the dimension of a kelp spore (ca. 5 μm) no substrat~~a~~e is "smooth", however, it seems likely that spores would be more likely to collect and be trapped by the contoured surfaces of *Pyura* and holdfasts, whereas on flat rock there would be no aid to settlement. This could result in higher settlement on objects able to slow water movement and trap spores, such as *Pyura* and holdfasts. This does not necessarily mean that these plants will have increased survivorship, but merely that they will be able to establish there.

Those kelps that manage to find purchase on the flat rock may well be subject to grazing pressure as well, a factor which would be lower on *Pyura* and holdfasts (Carrick, unpub.).The strongly positive selection for rock at the west coast site, Oudekraal, may be due to a variety of circumstances, such as the lack of any other suitable substrate in the absence of *Pyura* and negligible levels of grazing. Thus, this positive selection for rock merely indicates increased survival rates on this substrate.

Thus, one can create the following scenario for substrate selection in *E. maxima*. Spores, dispersed randomly, settle on a variety of substrata, predominantly rock, holdfasts and *Pyura*. Establishment of young sporophytes depends on two factors, namely substrate texture and grazing pressure. Increased establishment is obtained on *Pyura* and holdfasts due to their contoured surfaces, which aid settlement. These substrata are also able to provide a refuge from grazing (Carrick, unpub.).

As the plants increase in size, so the proportion of those on *Pyura* and holdfasts decreases in favour of those on rock (Figure 10). As mentioned earlier, the inability to trace the origin of each mature stipe in a multi-stiped holdfast, led to the designation of a common substrate for all. This would naturally, diminish the amount of large kelps recorded on holdfasts. The fact that multi-stiped holdfasts do occur (Figure 4) indicates that recruitment on holdfasts is successful to some degree. The above statement must be heeded with this in mind. Equally, it must be noted that each additional kelp on a holdfast increases the drag force substantially. Thus, unless a holdfast recruit manages to attach at least some haptera to the basement rock, the entire holdfast mass is likely to be lost to wave action. For this reason, the relative proportions of kelps on *Pyura* and rock is of importance.

The shift in proportions from *Pyura* to rock with increasing plant size can only be due to the mortality of the *Pyura* based kelps. Thus, it would seem that only rock and, to a certain extent, holdfasts provide a suitable substrate for mature kelps. The possible explanations for this shall now be examined.

- **Strength of attachment**

The data collected on the strength of attachment of *E. maxima* to various substrata (Figures 14-17) is by no means comprehensive. The method of sampling used only enabled small plants to be tested. This creates two problems. Firstly, the soft tissue of young plants was generally cut through by the clamp at strains in excess of 20 kg. This biased the sampling towards weakly attached plants. Secondly, wave action is unlikely to affect the smaller size classes as much as the larger size classes. In fact, strength of attachment may not play such an important role in size range that was sampled (<50 cm). Due to this, detailed comparisons of the data obtained for each substrate is meaningless. Instead, the overall trends in these graphs should be evaluated together with the substrate data for adult plants (Figure 10). From this one can gain insight into the possible dynamics of this situation.

Pyura seems to offer initial refuge to young sporophytes. They can easily establish on the rough test of the pod. The first few haptera from these young kelps can obtain a firm grasp on the protuberant surface of these pods. Thus, the holdfast area to stipe length ratio would be high initially (pers. obs.). As these kelps increase in size, so this ratio decreases as the *Pyura* has only a limited area for attachment. As this stage, one of two things can happen. Either the kelp plant must reach basement rock with its haptera, or it will be dislodged by wave action. A similar pattern has been described for kelp growth on mussels in the Gulf of Maine (Witman, 1987).

Several kelps established on *Pyura* were observed to be sending haptera down to basement rock. However, the results from Figure 10 indicate that this cannot be successful, as very few canopy or reproductive kelps are attached to *Pyura*. This can be explained as follows. In the event of the kelp establishing a firm hold on rock, the *Pyura* will be smothered. The subsequent death of the *Pyura* will result in the dislodgement of the kelp, either through loss of substrate, or ✓ exposure of the holdfast to the rotting action of bacteria (Carrick, unpub.). Thus, it seems that recruitment on *Pyura* is extremely unlikely to result in a reproductive or canopy kelp.

Holdfasts show an increase in strength of attachment with an increase in stipe length. Certainly, holdfasts seem to provide a strong substrate for attachment as 38.4% of stipes tested broke without ~~out~~ being dislodged. A kelp sporophyte establishing on a holdfast can easily embed its haptera into the existing holdfast mass. This leads to a strong attachment for small kelp plants with no detrimental effect to the existing holdfast mass. However, as the recruit obtains sufficient size to incur the effects of wave action, this may shift from a facilitative relationship to a mutually harmful one. Unless, the holdfast mass is very securely attached, for example in a crevice, multiple stipes may provide too much drag and the holdfast may become dislodged.

This effect would account for the relatively low proportion of multiple-stiped holdfasts, as compared to single-stiped holdfasts and those with small recruits (Figure 4). In fact, one would predict that in areas with a smooth rock substrate ✓ and/or high wave action, one would find predominantly single-stiped holdfasts, whereas in areas with a more textured rock substrate and/or low wave action, more multi-stiped holdfasts would occur. This should prove readily testable.

The strength of attachment to rock seems very variable in the smaller sized kelps. This could be due to the variable texture of the substrate itself, as mentioned above. It seems unlikely that rock as a substrate is of major benefit to small sized kelps. However, with an increase in size of the kelp, rock is obviously a beneficial substrate to be attached to (Figure 4). Certainly, it proved impossible to dislodge canopy sized kelps attached to rock.

Thus, from a strength of attachment point of view, any kelps attached to *Pyura* are unlikely to survive to maturity. A kelp can only survive to maturity if attached to rock or other holdfasts. It also seems likely that certain rock patches will afford greater anchorage than others. Thus, the holdfast recruitment method may well optimise the search for a suitable rock patch by establishing on a successful plant. This is a classic example of facilitation (see Harris *et al.*, 1984) occurring intraspecifically.

- **Grazing pressure**

As the most prevalent grazer, *Parechinus*, has been documented to a~~e~~ffect only the juvenile sporophytes (Fricke, 1979; Buxton and Field, 1983), *E. maxima* can obtain a refuge in size from its predominant grazers. In effect, any kelp plant with a stipe length of greater than 10 cm is relatively safe from urchin grazing (R. Anderson and A. Share, pers. comm.). Smaller kelps are liable to be heavily grazed.

Carrick (unpub.) showed that *Pyura* and *E. maxima* holdfasts provide a refuge from grazing for these less than 10 cm sporophytes. This would account for the prevalence shown for these two substrata in the small size class (Figures 12 and 13). If this was the only selective force acting on kelps, one would expect to see this prevalence for substrata continued into the larger size classes, however this does not occur, due to the strength of attachment argument outlined above.

So in effect, the two selective forces acting on kelp sporophytes act at different stages in their development. Grazing pressure acts on kelps under 10 cm stipe length, whereas strength of attachment only has major implications for much larger kelp sizes. A scenario that would accommodate both of these pressures would be that kelps recruit on the refugia and then attach onto a rocky substrate by their extending haptera. As mentioned earlier, this seems likely to occur for holdfast recruits, but less so for those on *Pyura*.

This does not however, explain the prevalence of single-stiped holdfasts attached to rock. These kelps, by virtue of their single stipe, could not have recruited on holdfasts, nor are they partially attached to a *Pyura* pod. Thus, they must have recruited on rock. As one would expect, the proportion of single-stiped kelps on rock is much higher at Oudekraal than at any of the False Bay sites (Figure 4). As mentioned earlier, Oudekraal was found to have a far lower grazing pressure than that of the False Bay sites, an result supported by Carrick (unpub.). Thus, it would seem that rock recruitment is a factor of grazing pressure, an element that shall be alluded to later.

Demography

Generally, the frequency distributions obtained at all sites (Figures 6-9) show inverse J-shaped curves. This curve is indicative of a recruitment bottleneck, where many recruits establish, but fail to grow beyond a certain size. Spaniard Rock (Figure 6) and Glencairn (Figure 7) have the sharpest reduction from recruits to adults, whereas Miller's Point (Figure 8) shows a similar curve, but with a greater proportion of kelps in the larger size classes. Oudekraal (Figure 9) displays a curve with a similar proportion of individuals under 10 cm and over

300 cm stipe length. The variation in these curves indicates an increase in the survivorship of recruits from the Spaniard Rock and Glencairn data to those of Miller's Point and, ultimately, Oudekraal.

Thus, the question that arises is: what limits the survivorship of the recruits? Possible factors include intraspecific light competition, interspecific competition for space and the effects of grazing.

- **Intraspecific light competition**

According to terrestrial forest demography, an inverse J-shaped curve is indicative of a shade-tolerant species (Midgley *et al.*, 1990). These species are able to regenerate under a closed canopy. This is achieved by advanced regeneration, which is the maintenance of a seedling and sapling bank under the canopy. When gaps appear in the canopy, individuals from this advanced regeneration bank are able to fill them rapidly. Shade-intolerant species generally show a unimodal or bimodal curve (Everard *et al.*, 1995). These species require clearings in order to regenerate successfully. For shade-tolerant species, recruitment occurs close to the parents, whereas shade-intolerant species regenerate at a distance from their progenitors.

From this description it would seem that *E. maxima* fits into the shade-tolerant category, as there is certainly advanced regeneration occurring close to conspecific adults. There is evidence for this in other kelp communities. *Ecklonia radiata* juveniles are reported to persist under the canopy until a gap arises (Kirkman, 1981). Light limitation has also been shown to occur in *Macrocystis pyrifera* forests (Dean *et al.*, 1989). Due to the relatively complex morphology of the giant kelp and the depths to which they grow, light can be reduced by as much as 90% from the surface to the substrate (Reed and Foster, 1984; Santelices and Ojeda, 1984). This reduction can often drop light levels to

0.5-1% of surface irradiance (Reed and Foster, 1984), a level too low for Laminarian growth (Steemann Nielsen, 1975; Lüning, 1990). However, *Ecklonia maxima* has a relatively simple morphology and is not found below nine metres deep (Velimirov and Griffiths, 1979). In fact, for this study, the deepest sample was taken at 4.48 metres below MLWS. As Dean *et al.* (1989) explain, this would indicate that light is less likely to be limiting in *Ecklonia maxima* populations than in those of *Macrocystis pyrifera*. Certainly, the removal of canopy individuals of *Laminaria longicruris*, another shallow water kelp (Chapman, 1986), did not enhance recruitment (Chapman, 1984). Thus, unless light can be experimentally proven to be limiting, one cannot infer its effects on recruitment.

> Dean et al did not refer to E. maxima

Preliminary findings from a clearing study at Surf Bay (see Figure 1), indicate that *E. maxima* is a shade-tolerant species (Share, unpublished data). Moreover, it seems as if the lower subcanopy light levels do limit recruitment to a certain extent. In this ongoing study, all stipes over 50 cm were cleared from a 400 m^2 plot. A random subsample of ten separate 1 m^2 plots are sampled in the harvested area and in the control, an undisturbed adjacent area, every six months.

After the first six months post-harvest, there was a flush of juveniles under 25 cm stipe length, however this occurred in both the harvest and the control lanes. Closer examination of the data show that the control lane lost all of its canopy individuals over the same period. This is most likely attributable to heavy storm damage occurring over the winter of 1995. Thus, both the control and the harvest showed an increase in juveniles with the removal of the canopy. This would indicate that the juveniles, having been released from light limitation, are flourishing. However, over the next calendar year, there was no rapid growth up through the size classes from these juveniles, as one would expect for a shade-intolerant species. The control population maintained a normal balance of sizes, whereas the harvested lane contained only small individuals.

This lack of growth of the juveniles in the harvest lane indicates that although light limitation does occur, it is not the only limiting factor. Nevertheless, it is apparent that *E. maxima* is a shade-tolerant species. Furthermore, it shall be argued that canopy shading plays an important role in the demography of the kelp communities.

- **Interspecific competition and grazing**

The low survivorship of young kelp sporophytes could be caused by two factors. Firstly, the establishing kelps could be outcompeted by understorey algae. Secondly, intensive grazing of the recruits could reduce survivorship. It is likely that both of these have an effect in the kelp community.

-Competition for Space

Despite extremely low levels of grazing at Surf Bay (A. Share, pers. comm.), the development of kelp recruits was limited. Thus, in the absence of significant grazing pressure, the competition for space with shade-intolerant, colonising algae could be the main factor limiting the survivorship of young kelp sporophytes. In fact, the percentage of understorey algae is much higher in Surf Bay than in False Bay sites (Anderson, unpub. data)

Velimirov and Griffiths (1979) showed how *Laminaria pallida* swept the substrate clean of grazers. A similar sweeping action was seen to occur with understorey Rhodophytes, at the Oudekraal site of this study (pers. obs.). Actions such as this could possibly limit the success of young kelp sporophytes.

-Effects of grazing

The increase in recruit survivorship seen from Spaniard Rock and Glencairn (Figures 6 and 7) to Miller's Point (Figure 8) and Oudekraal (Figure 9) seems to be correlated with grazing pressure. For all the sites, Oudekraal was subject to the lowest grazing intensity. This site has the lowest density (Table 1) and lowest proportion of its individuals in the recruit stage, and a high proportion in the larger size classes. This implies that progression from recruits into the larger size classes (survivorship) is high. Of the False Bay sites, Miller's Point had the highest recruit survivorship and the lowest numbers of grazers. However, intersite comparisons within False Bay are dubious due to the homogeneity of the sites (Figures 3 and 5). Nevertheless, it seems as if low grazing pressure might allow increased survivorship of young kelps. Thus, grazing pressure might have a role in structuring these communities.

All of the above communities had full canopy cover and understorey algae were by no means dominant. Thus, it would seem as if, under a closed canopy, grazing is the more important determinant of community structure.

Survivorship dynamics

From the discussion above, one can construct a dynamic framework for the survivorship of developing kelp sporophytes. This framework includes the effects of strength of attachment, the demographic data obtained and the preliminary findings from the clearing experiment.

- **Stable kelp communities**

In light of the finding that continued survivorship largely depends on a substrate of rock (Figure 10), I suggest a possible model for establishment on this substrate. Since two of the major forces affecting survivorship of kelps in stable communities, namely strength of attachment and grazing pressure, act in opposition, there must be a mechanism for overcoming one of them. As it is obvious that the necessity of attachment to rock cannot be overcome, the answer must lie with escape from grazing pressure.

It can be shown that recruitment on rock is a function of grazing pressure, thus in order to increase recruitment, it is necessary to escape grazing pressure. This could well occur, through episodic recruitment, bearing in mind the feeding behaviour of urchins and the possible effect of storms.

Urchins are known to preferentially reside in crevices and feed on drift kelp (Ebeling *et al.*, 1985) as when out in the open, grazing sporophytes, they are subject to dislodgement by wave action. It has been shown that drift kelp forms a substantial part of the diet of *Parechinus* (Fricke, 1979). As Santelices and Ojeda (1984) point out, it has yet to be tested whether or not urchins select drift kelp over young sporophytes, however, if this is so, an increase in drift kelp could increase the survivorship of juvenile sporophytes by satiating the grazers. In the *Ecklonia maxima* communities, storms could provide this increase in drift fronds.

Spore production in *E. maxima* occurs all year round, although there is a distinct seasonal pattern (Joska and Bolton, 1987). If this pattern included an increased release after the stormy season, where there would presumably be increased amounts of drift kelp, recruitment on rock might well be aided. Dayton (1985) explains how the trapping of fertile fronds by urchins may increase settlement, by allowing the adjacent area to be inundated with spores. *E. maxima* sporophytes are capable of fast growth, reaching full size in 2 to 2.5 years (Bolton and Anderson, 1994). Thus, presumably, sporophytes establishing under these conditions would be capable of reaching sufficient size to escape urchin grazing before the urchins resumed active sporophyte grazing. In this manner, adult kelps could establish on rock despite the reported difficulty of doing so (Carrick, unpub.).

In sites with negligible grazing pressure, such as Oudekraal, this episodic recruitment would not play a role, as sporophytes should prove able to recruit on rock all year round. The results from this study support this. They show an increase in the number of single-stiped holdfasts (Figure 4) and a flatter size class distribution (Figure 9) resulting from increased juvenile survivorship, at this site.

- **Recovery from catastrophic storms**

Catastrophic storms are storms of above average intensity that can result in large areas denuded of kelp. The effects of catastrophic storms have been described in the *Macrocystis pyrifera* community (Harris *et al.*, 1984; Dayton and Tegner, 1984; Ebeling *et al.*, 1985). The clearing experiment (A. Share, unpublished data) serves as an example of recovery from the equivalent of a catastrophic storm.

Dayton and Tegner (1984) show how patches, dominated by understorey algae post-storm, are able to resist invasion by the canopy kelp species. Findings from Surf Bay indicate a similar pattern in *E. maxima* communities. Presumably, recovery from this situation is achieved by a slow restoration of the canopy. Due to the lack of replicate studies, it is not clear whether the presence of grazers would aid kelp recruitment, by reducing understorey algae, or be detrimental, by grazing the kelp sporophytes.

This lack of experimental work is surprising, as this sort of information is of vital importance to the creation of a sustainable kelp harvesting industry. Depending on whether grazing is shown to aid, or be detrimental to, kelp recovery, harvesting lanes should be set up with these dynamics in mind. Harvesting an inappropriate area would result in little or no recovery of the kelp community. As harvesting of *E. maxima* is a potentially large commercial venture in Southern Africa, studies of this nature should be conducted.

Conclusion

This study has shown that *Ecklonia maxima* survivorship is greatly influenced by the substrate on which sporophytes recruit. Generally, only kelps attached to rock or holdfasts survive to reproduce and reach the canopy. Recruitment on holdfasts provides a refuge from the grazing that limits recruitment on rock (Carrick, unpub.). Despite this, a large proportion of reproductive and canopy kelps are single-stiped, inferring recruitment on rock. It is hypothesised that this recruitment on rock is achieved by escaping grazing pressure during periods of grazer satiation. Post-storm periods, when drift kelp is abundant, might provide such situations.

The analysis of size-class structure indicates that *E. maxima* is a shade-tolerant species. Advanced regeneration is prevalent in the subcanopy of the kelp community. Shade-tolerant species require full canopy cover in order to be competitively superior. With canopy removal, shade-tolerant species can be outcompeted by subcanopy species. Preliminary evidence from a clearing experiment conducted in Surf Bay (A. Share, unpublished data) indicates that this could occur in *E. maxima* communities. However, the potential effects of high and low grazing pressure on post-storm recovery have not been examined and prove difficult to accurately predict. Knowledge of these is essential for the selection of sites suitable for sustainable harvesting of *E. maxima*.

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