Holdfasts of adult kelp *Ecklonia maxima* provide refuges from grazing for recruitment of juvenile kelps

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ABSTRACT: The distribution of young sporophytes (up to 0.25 m stipe length) of the kelp *Ecklonia maxima*, on various substrata, at depths of 2.5 to 5.0 m, was studied at 8 sites on the southwest coast of South Africa. The most common substratum available was rock (bare or covered with encrusting coralline algae), followed by kelp holdfasts, and the ascidian *Pyura stolonifera* at some sites. A disproportionately high ratio (relative to the available substrata) of young sporophytes grew on the holdfasts of mature kelps at most sites, but particularly where high densities of benthic invertebrate grazers were present (mainly the urchin *Parechinus angulosus*, also abalone *Haliotis midae*, limpets *Patella* spp. and gastropods *Turbo* spp. and *Oxystele* spp.). Jacobs' index of electivity was used an indicator of 'preference for' (interpreted as indicating survival on) the substratum type. This showed a statistically significant 'negative selection' of rock as a substratum at sites where grazers were numerous. The ratios of young sporophytes on holdfasts/young sporophytes on rock were directly proportional to grazer densities when sites were compared (r = −0.90, p = 0.002), supporting the hypothesis that mature holdfasts are an important refuge for recruitment of *E. maxima* sporophytes. There was an inverse relationship between percentage cover of understorey algae and grazer densities (r = 0.92, p = 0.001). In general, sites east of Cape Point (west coast/south coast transition zone) have far more grazers and reduced understorey algal biomasses compared to west coast sites. There thus appear to be fundamental differences in some of the major ecological processes in kelp beds in these 2 areas, with important implications for commercial kelp harvesting.

KEY WORDS: Kelp · Recruitment · Herbivores · Predation · Sea urchin · *Ecklonia maxima* · *Parechinus angulosus*

INTRODUCTION

Recruitment success is probably the most fundamental process determining the distribution and community structure of benthic marine organisms. Recruitment of kelps has been shown to depend on a variety of interacting factors. In California, *Macrocystis pyrifera* sporophytes recruited along large stretches of coast when the interrelated conditions of temperature, nutrients, light and water motion were optimal (Deysher & Dean 1986). Within such 'recruitment windows' these authors considered that biological interactions increased the variance in recruitment, but not the large-scale temporal and spatial patterns. Biological

interactions affecting recruitment in kelp systems include inter- and intraspecific competition (Kennelly 1987) and widespread examples of herbivory, where recruits may be completely eradicated, producing 'barrens' (see for example Chapman & Johnson 1990), or else reduced and spatially limited (Fletcher 1987, Santelices 1990, Dayton et al. 1992, Camus 1994).

Southern African kelp beds extend from just west of Cape Agulhas (the southern tip of Africa), around the southwest coast as far as northern Namibia. In the south the dominant species in shallow water (0 to 8 m) is *Ecklonia maxima* (Osbeck) Papenfuss. There is a sub-canopy of *Laminaria pallida* Greville ex J. Agardh which becomes the dominant species at depths from about 8 to 20 m and replaces *E. maxima* in inshore beds on the northern west coast and in Namibia. The dominant organisms in kelp beds of the southern west

coast of South Africa (see Fig 1) have
been fairly well studied from the point
of view of biomass (e.g. Velimirov et al.
1977, Field et al. 1980) and energy flow
(see review by Newell et al. 1982), and
the major trophic pathways identified.
The most abundant benthic herbivores
in 6 large beds surveyed by Field et al.
(1980) were the urchin *Parechinus an-
gulosus*, followed by the abalone *Halio-
tis midae* and the gastropod *Turbo
cidaris*. Energy-flow models indicate
that herbivores comprise a relatively
small trophic group (Newell et al. 1982).
However, interactions between grazers
and primary producers may move be-
yond the 'simple acquisition of energy'
(Fletcher 1987) and into the realm of
complex structuring processes, which
are almost unstudied in these kelp beds.

The above energy-flow models were
based on kelp beds west of Cape Point,
as typified by the system at Oudekraal,
on the west coast of the Cape Penin-
sula. There is a further 200 km of coast
between Cape Point and Cape Agulhas
which also supports extensive kelp
beds, but here the understorey (and
intertidal) seaweed flora is inter-
mediate between those of the cool west
coast and the warmer south coast. This
is termed the south/west coast transi-
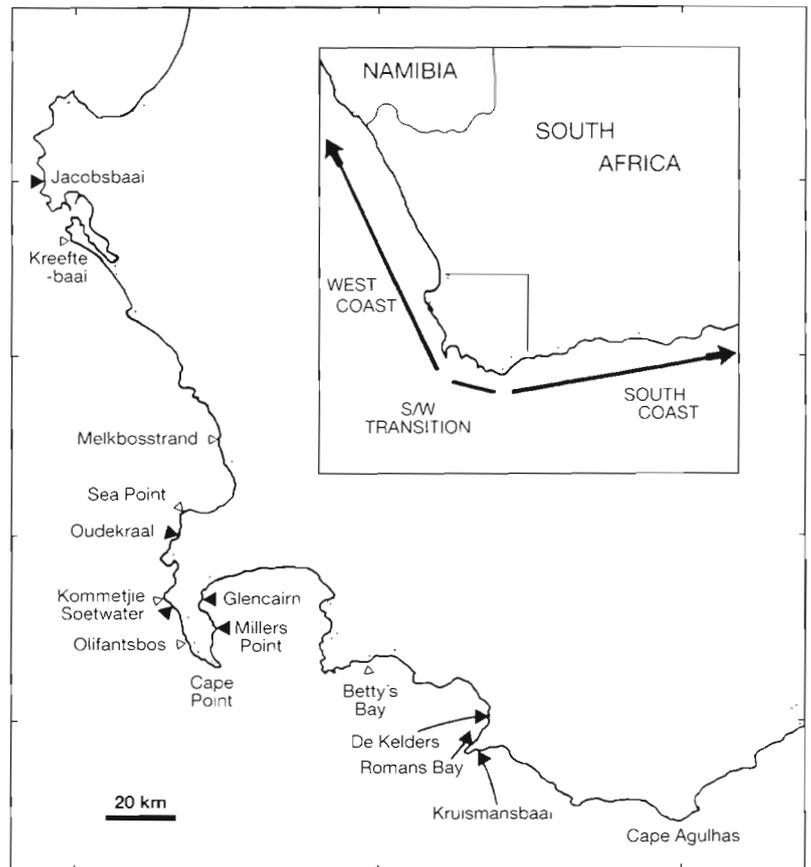tion zone by Bolton (1986), who studied

Fig. 1. The southwestern coast of South Africa, with inset showing location and
marine phytogeographical areas (after Bolton 1986). (▲) Sampling sites for this
study, (△) sites sampled by Field et al. (1980), whose data are used here

the phytogeography of the macroalgae. However, we
believe that the west coast and transition zone kelp
understorey communities also differ from each other in
structure and appearance. In the shallow water of west
coast kelp beds (1 to 8 m below MLWS, mean low
water spring tide), dense red algae cover most of the
substratum. In the transition zone there are numerous
benthic grazers (especially urchins), extensive pave-
ments of encrusting coralline red algae, and reduced
cover of foliose seaweeds.

Ecklonia maxima dominates the inshore areas of both
west coast and transition zone kelp beds. This species
has been harvested commercially at Soetwater (Fig. 1)
for many years, for the production of an agricultural
growth stimulant. In harvested areas, divers cut out all
plants with stipes longer than 0.5 m, but recruitment
into cut lanes is rapid at this west coast site. A dense
bottom cover of small sporophytes appears within a
year, and a surface canopy is re-established within 2 to
3 yr (Anderson et al. 1989). In the transition zone, at
Romans Bay and Kruismansbaai (Fig. 1), recovery of
harvested kelp beds is slower, and cleared lanes were

largely still visible more than 3 yr later. These areas
support numerous urchins, abalone, and *Turbo cidaris*.
During the course of harvesting experiments, we ob-
served that when benthic grazers are numerous, most
juvenile kelp sporophytes occur on the holdfasts of
adults, and few on rock. We therefore set out to test the
hypothesis that the holdfasts of adult kelp plants pro-
vide an important refuge for recruitment of juvenile
Ecklonia maxima sporophytes when benthic grazers
are abundant. In addition, we examined our own and
published information to see whether there are differ-
ences between the west coast and south/west coast
transition zone, with respect to biomass of benthic
grazers and understorey macroalgae, which might
indicate geographical differences in processes.

MATERIALS AND METHODS

Study sites. Eight sites were selected to represent
typical kelp beds on the southwestern coast of South
Africa (Fig. 1). Three sites (Soetwater, Oudekraal and

Jacobsbaai) are typical of the cool west coast (Benguela) phytogeographical region (sensu Bolton 1986). Five sites were placed in the somewhat warmer south/west coast transition zone (sensu Bolton 1986). De Kelders, Romans Bay and Kruismansbaai lie around the Danger Point peninsula, where temperatures are slightly warmer than the west coast and typical of the transition zone. The 2 remaining sites (Millers Point and Glencairn) are in False Bay, which lies in the transition zone but where summer temperatures are higher because of solar heating of entrained water Details of phytogeography and temperatures are provided by Bolton (1986). Data from Field et al. (1980) are referred to, from the 5 west coast and 1 transition zone site which they surveyed (Fig. 1).

Sampling. Diving was done over a 4 mo period from May to August 1994. All sampling employed SCUBA, and was limited to between 2 and 4.5 m below MLWS to reduce biotic differences due to depth. Only approximately horizontal surfaces with kelp plants were sampled. Between 10 and 20 replicate quadrats, each of 1 m², were placed haphazardly at each site. Within each quadrat all benthic macroinvertebrates were identified and counted. No attempt was made to count meso- or microherbivores (e.g. small crustaceans). The percentage cover of the following species or groups of organisms was visually estimated: rock (including encrusting coralline algae because these could often not be clearly differentiated when crusts were thin or patchy), *Pyura stolonifera* (Ascidiacea), understorey algae, holdfasts of *Ecklonia maxima* and *Laminaria pallida*, and sponges (Porifera). The stipe length of each kelp plant was measured, and its substratum recorded. The *E. maxima* and *L. pallida* sporophytes were initially separated into 8 size classes according to stipe length, but only 2 classes were retained for analysis: up to 0.25 m and larger than 0.25 m. This was because it was difficult to determine the substratum that plants larger than about 0.5 m were in fact growing on. Larger holdfasts were often fused together, and it was impossible to tell whether holdfasts may have grown off the initial site of recruitment and onto the rock. *Laminaria pallida* data were omitted from the analysis because this species occurred only in the 3 west coast sites, and even there was rare in this shallow water.

Analysis. Three broad substratum types were identified as common kelp recruitment sites: rock (including encrusting-coralline covered rock), holdfasts of larger kelps and tests of *Pyura stolonifera*. From percentage cover estimates, the mean proportion of each type of substratum at each site was calculated, as well as the mean number of young sporophytes occurring on each substratum type. To assess relative recruitment on the 3 main substrata, Jacobs' index of electivity (*Q*) was calculated, as follows:

$$Q = \log r(1 - p)/p(1 - r)$$

(Jacobs 1974) where p = fraction of given substratum type, and r = fraction of young sporophytes on that substratum.

Although we recognise that recruits may not be 'selecting' substrata, this index, which has been used in various studies (e.g. habitat selection in fish; Wilkins & Myers 1992), provides a useful measure of relative 'preference' for substrata which is interpreted here as an index of relative recruitment success of young sporophytes. Jacobs' indices were compared statistically using a 1-way ANOVA and Tukey HSD test (see Table 1). Because Jacobs' indices can be negative, all values were made positive by increasing the lowest value to a positive integer, and all others by a corresponding amount. The final results were then re-adjusted.

The mean densities of benthic grazers at each site were calculated. The ratio of young sporophytes on holdfasts/young sporophytes on rock and the mean percentage cover of understorey algae at the 8 sites were separately regressed against mean density of grazers. To determine whether there were geographical patterns in the biomass of algae and benthic grazers on west coast and transition zone shores, we re-analysed the following data from the appendices of Field et al. (1980), for depths from 0 to 10 m: total biomass of understorey algae, total biomass of kelps, biomass of *Parechinus angulosus*, *Turbo* spp., *Haliotis midae*, *Patella* spp. and total biomass of these 4 grazers. We converted their data from energy units to mass using the conversion values they provide. Further biomass data were obtained from a current study on the effects of kelp harvesting at Romans Bay and Kruismansbaai (G. J. Levitt unpubl.). Here several hundred 0.25 m² quadrats were placed in a series of transects from about 1.5 to 8 m depth, and all macroscopic benthic organisms collected and weighed. Data on benthic grazers and understorey algae are combined with re-calculations of data from Field et al. (1980) to examine the relationship between biomass of understorey algae and biomass of benthic grazers. Using the statistical package 'Fig P', the best fit was found using a logistic sigmoid curve.

RESULTS

At the 5 sites in the transition zone east of Cape Point (Millers Point, Glencairn, De Kelders, Romans Bay and Kruismansbaai), most of the available substratum (Fig. 2) was rock (bare rock and rock covered by encrusting corallines). Holdfasts of larger kelps were the next most abundant substratum, with *Pyura stolonifera* abundant at Glencairn. The 3 west coast sites
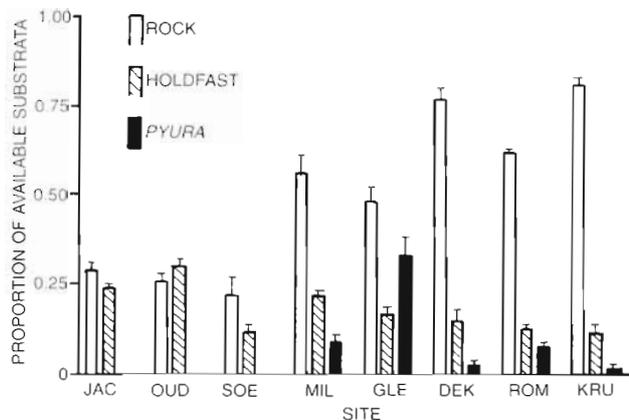
Fig. 2. Proportion of available substratum per area of sea bed at the 8 study sites, west (left) to east (right). JAC: Jacobsbaai; OUD: Oudekraal; SOE: Soetwater; MIL: Millers Point; GLE: Glencairn; DEK: De Kelders; ROM: Romans Bay; KRU: Kruismansbaai. Vertical lines show standard errors of means

Fig. 4. *Ecklonia maxima*. Jacobs' index of electivity for densities of kelp juveniles found on the 3 main substratum types (see text for explanation). Vertical lines show 95% confidence limits of means. Site names as in Fig. 2. See Table 1 for results of statistical tests

had considerably less rock, but similar holdfast abundance. There was no *P. stolonifera* at the west coast sites sampled, and the remainder of the bottom cover comprised dense understorey algae and sponges, which are not shown here as they are insignificant as a substratum for kelp recruitment.

At all sites except Soetwater, more juvenile *Ecklonia maxima* were attached to adult holdfasts than to any other substrata (Fig. 3), despite the general abundance of rock. Only at Millers Point and Glencairn, where the availability of *Pyura stolonifera* was high, were significant numbers of kelps growing on these ascidians.

When the density of kelp juveniles is related to available substrata using Jacobs' index of electivity (Fig. 4) a clear pattern emerges. At west coast sites, there is a

'positive preference' for holdfasts and rock as substrata, indicating a positive recruitment index. At the transition zone sites the index for rock is strongly negative. This is borne out by statistical comparisons of the results (Table 1). At all the transition zone sites the difference between recruitment indices ('preference') for rock and holdfast is significant. At Jacobsbaai this difference is significant, but the index for holdfasts is positive and that for rock weakly so or neutral. The position of *Pyura* is neutral.

There were striking differences in the densities of benthic grazers in the transition zone, compared to the west coast sites (Fig. 5). In the transition zone sites, there were 5 genera of grazers. *Parechinus angulosus* was by far the most abundant, with mean densities of 6 to 28 animals m^{-2}. *Patella* spp. were the next most
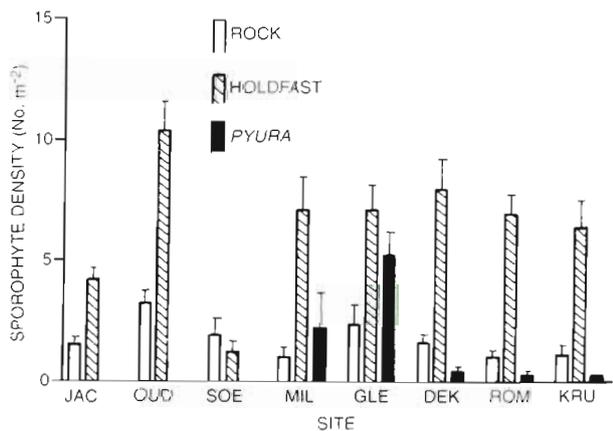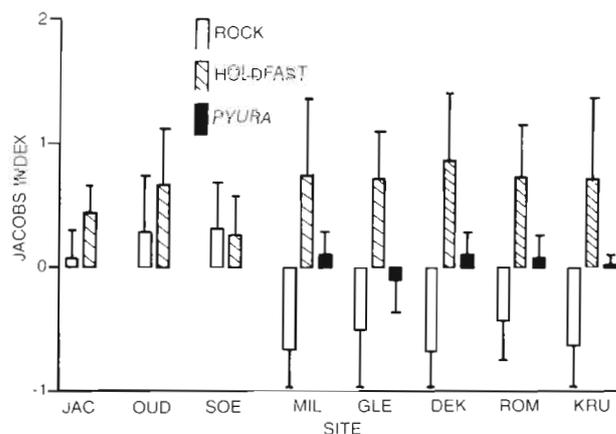

Fig. 3. *Ecklonia maxima*. Density (+SE) of juvenile sporophytes (up to 0.25 m) per area of seabed, on the 3 main substratum types. Site names as in Fig. 2

Table 1. Jacobs' index of electivity: results of ANOVA and Tukey HSD test carried out on the data presented in Fig. 4, comparing juvenile kelp densities on 3 substrata at each site, and for all sites combined. Different letters (within each line) denote differences at the 95% confidence level, and the same letters denote no statistical difference (see 'Materials and methods' for details)

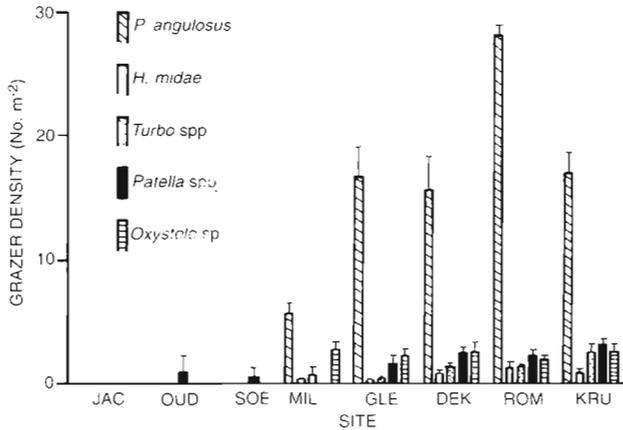| Site	Substrata		
	Rock	Holdfast	*Pyura*
Jacobsbaai	A	B	
Oudekraal	A	A	
Soetwater	A	A	
Millers Point	A	B	C
Glencairn	A	B	A
De Kelders	A	B	C
Romans Bay	A	B	A
Kruismansbaai	A	B	AB
All sites	A	B	C

Fig. 5. Density (+SE) of benthic macrograzers at the 8 study sites. Site names as in Fig. 2
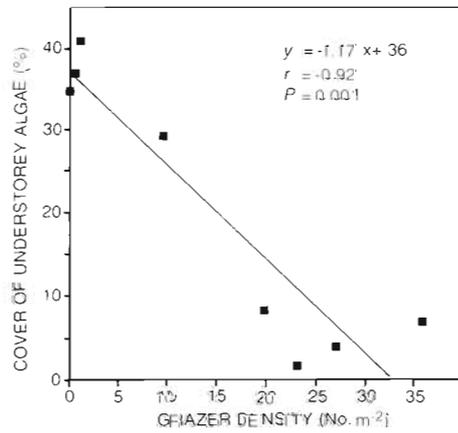

Fig. 7. Mean percentage cover of understorey algae regressed against the mean density of benthic macrograzers at the 8 study sites

abundant, followed by *Oxystele sinensis*, then *Turbo cidaris* (and the occasional *T. sarmaticus*), and the abalone *Haliotis midae*. The only benthic macro-herbivores found in the plots at the west coast sites were a few patellid limpets.

There was a direct relationship between the juvenile kelps on holdfast/juvenile kelps on rock ratio and the density of grazers, for the 8 sites (Fig. 6). The mean percentage cover of understorey algae was inversely related to the density of grazers at the 8 sites (Fig. 7). At Romans Bay, where *Parechinus angulosus* densities may exceed 40 animals m^{-2}, there were 27 to 38 times more young sporophytes on holdfasts than on rock, per unit available area.

In an attempt to generalise about differences between shallow subtidal communities on the west coast and those in the transition zone, we analysed data from the appendices in Field et al. (1980) for 5
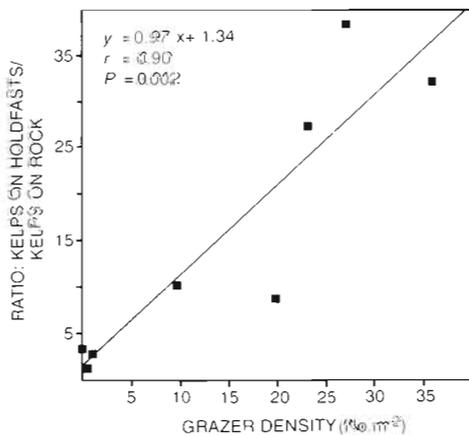
west coast and 1 transition zone site and data (G. J. Levitt unpubl.) from Romans Bay and Kruismansbaai. We tested for differences between these 5 west coast and 3 transition zone sites (listed under Fig. 8) with respect to total biomass of benthic macroherbivores, biomass of sea urchins, and biomass of abalone. None were significant. However, when the biomass of grazers from these sites is plotted against the understorey algal biomass, a classic 'log dose/effect' curve is obtained (Fig. 8). We inserted a vertical broken line (no statistical significance) to separate the transition zone
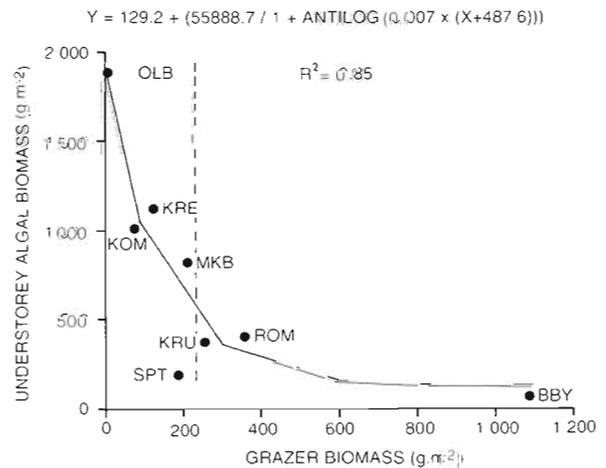

Fig. 6. *Ecklonia maxima*. Ratio of juvenile kelps on hold-fasts/juvenile kelps on rock regressed against the mean density of benthic macrograzers at the 8 study sites

$$Y = 129.2 + (55888.7 / 1 + ANTILOG (0.007 \times (X+487.6)))$$

Fig. 8. Relationship between biomass of understorey algae and biomass of benthic grazers at 8 sites in kelp beds of the south-western coast of South Africa. Vertical broken line separates west coast sites (on left) from south/west coast transition zone sites. Data calculated from Field et al. (1980) for sites OLB (Olifantsbos), KRE (Kreeftebaai), KOM (Kom-metjie), MKB (Melkbos), SPT (Sea Point) and BBY (Bettys Bay). Data for KRU (Kruismansbaai) and ROM (Romans Bay) from Levitt (unpubl.)

sites (on the right) from the west coast sites (on the left). These results indicate a broadly inverse relationship between understorey algal biomass and the biomass of these benthic grazers.

DISCUSSION

Holdfasts of large kelp plants bore a disproportionately high density of juvenile kelps, compared to rock and *Pyura stolonifera*. At all of the transition zone sites, where benthic grazers were numerous, juvenile kelp sporophytes showed a statistically significant 'negative selection' of rock, and 'positive selection' of holdfasts as substrata. This was borne out by the significant positive correlation between the ratio of sporophytes on holdfasts/sporophytes on rock and grazer densities (Fig. 6). Although the evidence is correlative, it supports the hypothesis that in heavily grazed areas the recruitment of kelp is strongly limited to holdfasts of large kelps. We measured up to 38 times higher rates of recruitment on holdfasts than on rock, where grazers were abundant. In such areas juvenile kelps are rare on rock, and tend to be restricted to crevices or pinnacles, where they are likely to be less accessible to grazers. Although we expected that the cylindrical tests of *P. stolonifera* would be an important refuge for kelp juveniles, this proved not to be the case, and they were 'neutrally' selected for. Further evidence that holdfasts are important refuges comes from a subsequent study which found that in a grazer-free area (Oudekraal), 75% of adult *Ecklonia maxima* clearly arose from single-stiped holdfasts, while at 3 sites with numerous grazers, this value fell to 45% (West & Anderson unpubl.).

Holdfasts of adult *Ecklonia maxima* plants are shallowly conical in shape and about 100 mm high at the apex (where the stipe originates). Single holdfasts may be 150 mm or more in diameter, whilst composite holdfasts, with several stipes, are larger. Holdfasts comprise a mass of intertwined haptera which become progressively thinner as they branch towards the substratum, with crevices and hollows between the haptera. Their effectiveness as refuges will depend on the size of crevices, herbivores, and sporelings. In addition, benthic grazers are probably easily dislodged from holdfasts, which provide an irregular surface for attachment. *Haliotis midae* was never seen on holdfasts, and *Parechinus angulosus* and *Turbo cidaris* were only found there during the calmest swell conditions, when they sometimes graze the haptera.

Various kelps recruit on a variety of 'temporary' substrata such as worm tubes and small algae, but their survival depends on attaching to the primary substratum (Dayton 1985). Small *Ecklonia maxima* sporo-

phytes can be found on corals, mollusc shells, and seaweeds such as geniculate corallines. However, unless their positively geotropic haptera reach a firmer substratum, they are likely to be torn off as they grow larger.

We assume that the recruitment we are measuring represents the sum of survival, on all available substrata, of all stages subsequent to the 'spore rain' (Chapman 1984), including the newly settled spores, the microscopic gametophytes and the young sporophytes. Demographic and recruitment studies indicate that mortality is highest among microscopic stages, followed by young sporophytes (e.g. Chapman 1984, Deysher & Dean 1986, Dayton et al. 1992). Survival of different stages is influenced by a variety of herbivores, from meoifauna to abalone, urchins and fish (Dayton 1985). According to Branch et al. (1994) microscopic algae and spores form the bulk of the diets of *Oxystele* and *Patella* spp., while *Haliotis midae*, *Turbo* spp. and *Parechinus angulosus* eat algal sporelings, drift and attached seaweeds (including small kelps): we have frequently seen them eat small sporophytes when the sea is very calm. It is likely that the vulnerability of kelp sporophytes to these benthic grazers decreases as their stipes grow. Their effect on understorey algae is shown by the negative correlation between percentage cover of understorey algae and grazer densities (Fig 7). We cannot rule out the possibility that hydrodynamic factors influence the sites that kelp spores (and thus gametophytes and ultimately sporophytes) settle on, as has been shown in some invertebrate larvae (Walters & Wethey 1996), but we do not know to what extent the motile *Ecklonia maxima* zoospores are capable of selecting a settlement site.

Parechinus angulosus is by far the most numerically abundant grazer in the shallow water (2 to 5 m) of transition zone kelp beds (Fig. 5). On the west coast it is generally uncommon in shallow water, but found in occasional but dense patches in deeper water (8 to 15 m), where it produces isolated barren areas of rock, from a few metres to tens of metres in diameter (Velimirov et al. 1977, Field et al. 1980). Buxton & Field (1983) estimated that *P. angulosus* consumed 14% of the annual production of *Ecklonia maxima* (mainly as drift) at Oudekraal on the west coast, while Fricke (1979) estimated a figure of 20% at Miller's Point in False Bay, and pointed out that grazing by *P. angulosus* appeared to regulate kelp densities to some extent. We suggest that *P. angulosus* has a greater effect than other grazers because it is more numerous and has a higher total biomass. *Haliotis midae* are much larger but far less numerous, and *Turbo cidaris* are a similar size to urchins, but less abundant. *Patella* spp. and *Oxystele* spp., are both less numerous and individually

smaller. Nevertheless, it is possible that *P. angulosus* is not the most functionally important grazer, and these animals may be affecting recruitment as a suite. Selective removals of the different species could test these ideas.

Factors which have been shown to inhibit kelp recruitment include the presence of red algae (northwest America; Sousa 1979), the presence of turf algae or a kelp canopy (Australia; Kennelly 1987), shedding of outer layers by coralline algae (Chile; Camus 1994) and adult interference and grazing by herbivores (in the *Lessonia/Durvillea* belt in central Chile), where recruitment fails if adult densities exceed 3 m^{-2} (Santelices 1990).

The phenomenon of facilitation of one species by another is well known in terrestrial ecology (Connell & Slatyer 1977). In a Californian kelp community, fast-growing brown algae colonised disturbed patches of reef, and facilitated the recruitment of kelps by providing a refuge from grazing fish (Harris et al. 1984). In Chile the intertidal kelp *Lessonia nigrescens* was shown by Camus (1994) to recruit effectively on *Corallina officinalis*, which provides a refuge from grazing by chitons. In the present study the enhanced densities of young sporophytes on the holdfasts of older plants show that self-facilitation is occurring in *Ecklonia maxima*. Velimirov & Griffiths (1979) described another of example of self-facilitation in the sweeping of the fronds of the deeper-water South African kelp *Laminaria pallida*. Once a few adults become established, their fronds, which are on the ends of the erect stipes, sweep the surrounding rock and prevent the establishment of other macro-organisms. New sporophytes establish under the adults, and so the patch of *Laminaria* slowly spreads. Adult *E. maxima* do not sweep the substratum, because the buoyant bladder at the top of the stipe suspends the fronds near the water surface. However, in both *L. pallida* and *E. maxima*, once a few sporophytes become established, survival is maximised closest to parent plants. Spore dispersal in kelps (Laminariales) is considered to occur only over short distances (Schiel & Foster 1986, Santelices 1990). This may have several advantages, including increasing the chance of fertilisation between dioecious gametophytes, and retaining spores within a localised habitat which is suitable for growth (Norton 1992). In *E. maxima* this may also serve to ensure recruitment on the holdfasts of adults, providing protection against herbivores.

If *Ecklonia maxima* sporophytes and their holdfasts were cleared from an area with numerous benthic grazers, the lack of refugia should prevent or delay re-colonisation. Whether this could lead to the 'alternative stable state' of an extensive 'urchin barren' similar to those reported in some northern hemisphere kelp beds

(Harrold & Reed 1985, Chapman & Johnson 1990) is not clear. The term 'barrens' as applied to South African kelp beds (Field & Griffiths 1991) is misleading, as these are no more than small, isolated patches of *Parechinus angulosus*, usually about 10 to 20 m in diameter, and limited to deeper water, invariably on the west coast. The absence of extensive urchin barrens in South African kelp beds, even in the transition zone where *P. angulosus* is very numerous, may relate to the behaviour of *P. angulosus*, which, unlike *Strongylocentrotus*, does not form feeding fronts, so that a mosaic of subtidal communities is maintained. Also, swells may be too strong for *P. angulosus* to form large aggregates in shallow water (down to 5 or 6 m), which would explain why the small aggregates that do occur are almost invariably limited to deeper water (8 to 15 m). Also, *P. angulosus* does not appear to destroy adult kelps, so that an alternative state would have to be induced by an external disturbance such as extreme storm damage or overharvesting.

On the North American Pacific coast, the development of an urchin-dominated alternative stable state is often triggered by storms removing kelp canopies (Dayton & Tegner 1984, Harris et al. 1984), and the resulting barren grounds may account for up to 20% of kelp habitats (Foster 1990). This does not occur in South African kelp beds, although they may be thinned out by storms. This difference may result from the morphology of *Ecklonia maxima*, which has a relatively short, thick smooth stipe (compared to *Macrocystis*), with far less potential for entangling with and removing other plants.

Whether an alternative stable state (barren) could be induced in the South African transition zone, by over-harvesting of adult kelps, is debatable. Nevertheless, our results predict that recruitment will be limited or delayed where benthic grazers are numerous: this is borne out by current kelp-harvesting experiments. At Soetwater and Jacobsbaai (west coast sites), recovery of the kelp canopy takes about 2.5 yr after harvesting of all kelps (almost entirely *Ecklonia maxima*) by cutting of stipes longer than 0.5 m. At Romans Bay and Kruismansbaai (transition zone sites), recruitment was severely delayed after similar harvesting, and after 3 yr there were still large gaps in harvested lanes (G. J. Levitt unpubl.). The numerous grazers (mainly urchins) not only severely limited recruitment on rock, but more important, the holdfasts of cut kelps rotted off the substratum within 4 to 6 mo, taking with them any small kelp sporophytes which were not also firmly attached to rock. Where there are few grazers and thus many small sporophytes on rock (typical of the west coast), the loss of holdfasts is not as serious, and rapid growth of these juveniles soon replaces the canopy. Our results suggest that if the major benthic grazers were

experimentally removed from areas such as Romans Bay, there would be a significant increase in kelp recruitment and understorey algal cover. Such urchin removals at Cape Banks, Australia, resulted in large increases in algal recruitment, growth and survival (Fletcher 1987).

Benthic understorey communities in shallow south/west coast transition zone kelp beds are different from those on the west coast, in terms of both seaweed biogeography (Bolton 1986) and densities of benthic grazers, especially *Parechinus angulosus*, as shown by diving observations and present results (Fig. 8). There are exceptional sites, such as Sea Point, which, of the 5 west coast sites cited by Field et al. (1980), was the only one with high densities of *P. angulosus*. These authors examined only 1 transition zone site (Betty's Bay) and noted that the herbivore biomass was very high, but from 1 site were unable to generalise about this zone.

There are other important differences between these coasts. On the west coast, recruitment of abalone is poor (R. Tarr pers. comm.) and rock lobsters *Jasus lalandii* are abundant (Field et al. 1980). Recently, increases in rock lobster abundance in parts of the transition zone have coincided with decreases in *Parechinus angulosus* (a favoured prey) and in juvenile abalone, which shelter under the urchins (Tarr et al. 1996). We predict that kelp recruitment and the cover of understorey algae will increase. In this system the rock lobsters are clearly a keystone species, as they are capable of causing a 'trophic cascade' effect (Menge et al. 1994).

The environmental reasons for biological differences between the transition zone and the west coast may be at least partly related to the average 2 or 3°C higher water temperature in the transition zone (Bolton 1986, Bolton & Anderson 1990). These authors explained phytogeographical differences between the zones on this basis, because the geographical distributions of seaweeds along continuous coastlines are almost completely controlled by temperature (Breeman 1988). However, patterns of abundance (rather than presence or absence) are not as easily explained. For example, temperatures in the transition zone are close to optimal for growth and reproduction of the gametophyte and growth of the young sporophyte of *Ecklonia maxima*, as measured in laboratory studies (Bolton & Levitt 1985, Bolton & Anderson 1987). Whatever the environmental causes, the present study suggests for the first time that there are fundamental differences between ecological processes in the kelp beds of the west coast and the transition zone that have important implications both for biological understanding and for the harvesting and management of commercial resource species such as *E. maxima*, abalone and rock lobsters.

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