



The population ecology of *Ecklonia maxima* in
relation to disturbance:
'stuck between a rock and a holdfast'.

Cosman Bolus, 2004, Seaweed Research Unit, Botany Department, UCT, South Africa



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KD Bolus
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Abstract

To investigate the ecological disturbance dynamics of *Ecklonia maxima* at different scales I looked at the influence of disturbance at the individual, population and biogeographical scale. The study was conducted on 8 sample sites of *E. maxima* populations on the south west coast of South Africa . It included sites from both the South/West transition and Benguela Province biogeographic regions. Nine beach wash-up samples of *E. maxima* were done to evaluate the removal of individuals from the population , as a result of disturbance. Measurements of individual stipe length, float diameter, basal diameter, breakage, present holdfast and which individuals shared a holdfast were done. *E. maxima* juveniles mostly recruit on rock or mature kelp holdfasts and the results support the hypothesis that holdfasts are not safe sites for recruitment of juveniles (< 50 cm). This was found to be the case because individuals ripped off the rocks from disturbance, with shared holdfasts (53 %), are commonly juveniles (56 %). This also shows that commonly large individuals are being removed by disturbance with juveniles attached to the holdfast. Percentage size class frequencies were done for the complete population samples and the beach wash-up sample. The entire population exhibited an inverse J-curve and a bimodal distribution for adults (>1 m). Also, shade tolerance was tested for juveniles by the presence/absence counts of individuals in the size classes <1 m, 1 – 2 m and > 2 m. This showed that juveniles (< 1m) commonly occurred with adult individuals (> 2m) showing that juveniles are shade tolerant. This suggests that the population demography is a result of juvenile shade tolerances and also the removal of large individuals by disturbance with juveniles attached to the holdfast. There are negative implications of these results for the re-colonization processes of *E. maxima* into 'gaps' formed in the canopy by disturbance, where grazers are abundant. These patterns are realized in the ecological differences across the two biogeographic regions as juvenile (> 1m) recruitment was found to be more successful in the Benguela Province (57 %) where there are less grazers , especially *Pareuchinus angulosus*, than in the South/West transition (26 %). Therefore there appear to be important underlying ecological processes in the kelp populations of these two regions at operating at different trophic levels with implications for kelp recovery from disturbance and commercial harvesting.

Key words: Kelp forests, *Ecklonia maxima*, 'Gap' disturbance, re-colonization

Introduction

The kelp species *Ecklonia maxima* is a dominant brown seaweed that is found on the shores of South Africa (Steegena et al., 1997). Brown algae forests are a major habitat for many marine organisms of the temperate regions of the world (Witman et al., 2001) and they are a major source of food for grazers and debris feeders (Mazure, 1977) as kelp can be the single largest source of fixed carbon (Graham, 2004) in these habitats. Consequently the structure and diversity of food-webs is reliant on kelp forests (Graham, 2004). The genus *Ecklonia* is also ecologically dominant in other warm-temperate regions of the world such as Australia, New Zealand and the north west Pacific (Steegena et al., 1997, Bolton et al., 1994) but *Ecklonia maxima* is only found in southern Africa with a few old records of it being noted in the sub-Antarctic (Steegena et al. 1997).

It is a fairly poorly studied species in terms of its population dynamics but has many present and potential commercial uses in South Africa. Concessionaries are being contracted to industry so that it can be supplied as abalone feed and therefore permits are already being issued for experimental harvesting (Levitt et al. 2002). It also has the potential to be used as an agricultural stimulant commercially, as a biosorbent for heavy metals and for it to be used medicinally (Stirk et al. 2004).

Central issues in community ecology involve the assessment of different scale dependant relationships in populations (Dayton et al., 1999). The scale at which this study is conducted is at the individual, population and biogeographical level. Firstly at the individual level, recruitment is considered the most fundamental process which may determine the structure and community composition of benthic marine algae (Anderson et al., 1997). One of the most important processes involved in the life history of benthic marine algae is also that of colonizing new substratum (Fletcher et al., 1992) and is especially pertinent to *Ecklonia maxima* sporophytes. The most commonly available substratum for *E. maxima* juveniles (young sporophytes) on the southwest coast of South Africa is rock, kelp holdfasts and sometimes the ascidian *Pyrura stolonifera* (Anderson et al., 1997). Anderson et al. (1997) has shown that mature kelp holdfasts are a preferred substratum for recruitment because they act as refugia for *E. maxima* juveniles from the grazers namely the urchin *Parechinus angulosus*, abalone *Haliotis midae*, limpets *Patella* species and gastropods *Turbo*

species. *E.maxima* sporophytes are an important source of food for these grazers especially the urchin *Parechinus angulosus* (Anderson et al., 1997). This theory therefore suggests that holdfasts are safer sites for recruitment rather than rock substratum in terms of grazer exposure.

Its distribution in South Africa extends from Cape Agulhas on the south coast all along the west coast to Luderitz in Namibia (Stegenga et al., 1997). Its distribution therefore lies within the western overlap region (South/West transition) and extends into the Benguela marine province (Bolton et al., 1997). The marine provinces of South Africa are divided by their temperature regimes with the west coast defined as temperate and the marine provinces becoming more tropical as you move east (Bolton et al., 1997). This is associated with floral species diversity changes that are evident across the different biogeographic marine provinces (Bolton et al. 2002) and which are also associated with different abundances of various marine fauna such as the invertebrate grazers namely the urchin *Parechinus angulosus*, abalone *Haliotis midae*, limpets *Patella* species and gastropods *Turbo* species (Anderson et al., 1997). This is consistent with the biogeographic marine provinces of for example Australia where large scale trends have also been found in grazer abundances that change between the East and West biogeographic regions (Fowler-Walker et al., 2002). And for the first time ecological differences have also been seen between biogeographic regions in South Africa through the evidence of higher grazer abundances in the South/West transition zone in comparison to the Benguela province. In general higher grazer abundance is associated with lower kelp recovery, lower over storey biomass, higher recruitment onto holdfasts and a lower abundance of the urchin predator, the rock lobster *Jasus lalandii* (Anderson et al., 1997).

The population ecology of kelp is influenced by the attributes of the plants and their interaction with the physical and biological environment. Kelp populations have been researched extensively in terms of the factors which influence their ecology. Some of the main influential factors are light intensity (Graham et al., 1997 a), herbivory (Anderson et al., 1997; Fowler-Walker et al., 2002; Duggins et al. 2001) and physical interference or disturbance (Graham et al. 1997 b; Tegner et al., 1997; Goodsell et al., 2004). In this study disturbance is defined as a form of interference that leads to the death and removal of individuals in the *E.maxima* population. These factors can be

influential on recruitment success. For example recruitment is influenced negatively by irradiance due to light requirements in *Macrocystis pyrifera* (Graham et al., 1997 a), herbivory is influential on recruitment substratum for *E. maxima* (Graham et al., 1997 b) and disturbance in monospecific *Ecklonia radiata* stands liberates substratum space for other macro algal recruitment (Goodsell et al., 2004). In kelp stands the physical factors of ecological significance such as light intensity (Kenelly, 1989), water motion (Eckman et al., 1989) and physical disturbance (Connell et al., 2003) can also be modified by dense forest canopies so that recruitment of canopy forming alga is inhibited, and consequently removing canopies can create opportunities for recruitment (Goodsell et al., 2004).

Much work has been done on the disturbance dynamics of terrestrial forests in comparison to kelp forests. The ecological characteristics of kelp forests can be analogous to terrestrial forest ecology in certain instances because of the striking similarities that exist. The gas filled float on the distal end of long stipe of *E. maxima* individuals allow the fronds to remain at the surface (Bolton et al., 1994) and consequently create a canopy similar to that of terrestrial forests. In the Knysna forest, South Africa, gap disturbances have an important ecological role in species succession. Shade tolerance is an important trait for plant juveniles because they need to establish under the canopy before gaps are created by disturbance from dead trees so that they can utilize the gap opportunity effectively (Midgley et al., 1995). Light is therefore an important factor as well as disturbance, for certain forest succession. Herbivory is also important in terrestrial forests, for example insect defoliation in oak trees can be an important factor as a form of disturbance (Pickett et al., 1985) or it can also have an ecological influence on recruitment through grazing or on the succession process of terrestrial plant communities (Pickett et al., 1985). Parallel dynamics appear to exist between terrestrial and kelp forests and therefore the ecological processes can be likened in certain instances to obtain a greater understanding of the ecological dynamics.

Ecklonia maxima is commonly found washed up on the beaches of its inshore distribution attached to other individuals on a shared holdfast after the notorious Cape winter storms. This is presumably as a result of disturbance impacts from oceanographic disturbance that remove individuals from kelp forests that exist nearby.

There has been little investigation into the population dynamics of *E. maxima* forests which are clearly being influenced by disturbance through the loss of individuals. However there has been research into the influence of grazers on the recruitment substratum of *E. maxima* juveniles by Anderson et al. (1997). The study showed that holdfast are preferred by juveniles to avoid herbivores which are more likely to graze juveniles on rock substratum (Anderson et al. 1997) suggesting holdfast are a safe place to recruit. The influence of disturbance on shared holdfasts and recruitment coupled with the known grazer affects allow for interesting dynamics in these populations especially because of the growing commercial and harvesting interest in *E. maxima*. This led me to investigating the implications of disturbance on *E. maxima* recruitment across the Benguela and South/West transition biogeographic regions to see if disturbance has an impact on recruitment and re-colonization after disturbance. The key questions which I attempt to answer at various scales of ecological interaction are:

- 1) Are holdfasts a safe place for *E. maxima* to recruit? In particular does *E. maxima* break or get dislodged off the rocks with its holdfast intact, consequently with a large proportion of recruits?
- 2) What is the impact of disturbance on the *E. maxima* population dynamics and its ability to re-colonize 'gaps'? Which sizes are dominant in the beach wash-up and what implications does this have for the population?
- 3) What is the population ecology of *E. maxima* forests in terms of their ability to decolonize 'gaps' across the Benguela and South/West transition biogeographic regions? Are there signs of recruitment limitation as expected from differences in urchin/lobster densities? And are there signs of biogeographic variation?

Materials and methods

Study site

The study focused on *E. maxima* was conducted on sites in and around Cape Town, the Cape Peninsula and the West coast. There was a focus on the beaches of Muizenberg, Fish Hoek and Moulle point and the kelp beds of the Cape Peninsula (Glencairn, Kommetjie, Soetwater, Olifantsbos 1, Olifantsbos 2, Bordjiesrif, Mullers point) and Jacobs baai (Kwaai baai, Mauritz baai and the Pump house) on the west coast. The Cape peninsula is in the western overlap region (South/West transition) between the biogeographical regions of the Benguela province (west coast) and the Agulhas province (south coast) (Bolton et al., 1997).

Species description

The focus of this study, *Ecklonia maxima*, is in the family *Alariaceae*. It has a sporophyte phase which can be up to 15m in length as an elongated stipe. The stipe is hollow and often inflated so that it commonly forms a gas bulb that narrows immediately at the juncture to the blade. The inshore specimens commonly have shorter stipes while the deeper water specimens are longer and more flexible. The blades are smooth and have a lightly dentate margin. They can be up to 1m long in juveniles or broadly triangular in adults or even ribbon shaped. The holdfast of the species is conical in shape and has many entwined branched haptera and can be up to 40 cm in diameter. (Stegenga et al.,1997)

In South Africa *Ecklonia maxima* dominates the inshore region of the west coast and forms large extending kelp beds. The kelp beds can be found in up to 10 meter deep water with the blades of individuals floating on the surface. Its distribution range extends from Papenkuilsfontein which is 10km west of Cape Agulhas to north of Luderitz in Namibia. (Stegenga et al.,1997)

Data collection

Scaling data

Two sets of data were acquired from Rob Anderson and Mark Rothman at the Seaweed Research Unit, Botany Department, University of Cape Town. The first data used was on the different lengths of the parts of *Ecklonia maxima* individuals so that scaling relationships could be determined. Scaling was needed to determine the stipe lengths of individuals from the beach wash-up that were broken. The data used for the scaling was from a site at Millers point and Romans Bay with 85 and 1292 individuals acquired respectively. The data had measurements of the length of the stipe, diameter of the base of the stipe and the diameter of the float.

Population data

The second data set acquired was of 1x1 meter quadrant samples of the stipe lengths of *E. maxima* individuals at various sites on the Cape Peninsula (Glencairn, Kommetjie, Soetwater, Olifantsbos 1, Olifantsbos2, Bordjiesrif) and Jacobs baai (Kwaai baai, Mauritz baai and the Pump house) on the west coast (see Fig 1). The data was collected by diving into the kelp beds and measuring *Ecklonia maxima* stipe lengths in the 1x1 meter quadrants. Two of the kelp bed samples had measurements of all individuals in the quadrants namely Olifantsbos 2 and Bordjiesrif while the other sites did not have the < 50 size class measurements done.

Millers point population sample

I then did an additional dive sample at Millers point, Cape Town, with the aid of the Seaweed Research Unit, Botany Department, University of Cape Town. Thirty 1x1 m quadrants were done measuring the size of all whole individuals (stipe length) and the number of broken individuals that were still attached to the substratum.

Beach wash-up sample

Beach wash-up sampling was also done on *Ecklonia maxima* with the assumption that individuals washed up are an accurate signal of individuals removed from kelp forests. Sampling was done on Sunrise beach in Muizenberg (False Bay), Fish Hoek beach (False Bay) and Moulle Point (Table Bay). The beaches were selected because

they are cleaned frequently of kelp and therefore did not have an accumulation of old and new kelp wash-up. The beaches were sampled immediately after a cold front winter storm had passed as this is usually associated with strong large swell and ocean disturbance. The beach wash-up samples consisted of approximately 100 individuals measured on random transects between the waters edge and the high water mark . A total of 916 individuals were measured from the 3 beaches. Measurements were of individual stipe length, float diameter, basal diameter, whether they were broken, whether they had a holdfast and which individuals shared a holdfast. A shared holdfast was defined as more than 1 individual having attached haptera which form a single holdfast conglomerate. The basal diameter was measured for individuals which were broken and had holdfasts. The float diameter was measured for individuals that were broken and had no holdfasts.

Data Analysis

Scaling correlations

Since some of the stipes were snapped I needed to obtain an accurate estimate of the stipe length and therefore did two correlations. First a correlation between the stipe length and the basal diameter was performed on 85 individuals collected from a site at Millers Point. However this had a very poor significance and therefore (Fig 5) the 73 individuals (8 %) with broken stipes and holdfasts present were not included in the analysis. The correlation of the log of the stipe length and the diameter of the float was also done from 1292 individuals collected from a site at Romans Bay, east of Cape Town. Both these data sets were acquired from the Seaweed Research Unit, Botany Department, University of Cape Town. The correlations were done so that the stipe length could be estimated for broken individuals found in the beach wash-up samples through scaling relationships.

Frequency size class distributions

Frequency size class distributions were then done for the beach wash-up samples using the measured stipe lengths and scaled stipe lengths of broken individuals. Frequency size class distributions were also constructed for the kelp bed sample data of Olifantsbos 2, Miller point and Bordjiesrif with all individuals measured in the 1x1

meter quadrants. The frequency size class distributions were constructed in 50 cm intervals so that the population dynamics of the kelp beds could be analysed.

Juveniles were defined as individuals $< 1\text{m}$ when analysing the sample sites with no individuals $< 50\text{ cm}$ as this is considered a representation of successful recruitment of juvenile individuals $< 50\text{ cm}$. For individuals with data of individuals $< 50\text{ cm}$ juveniles were defined as $< 50\text{ cm}$. An index of the ratio of individuals of juveniles $< 1\text{m}$ and adults $> 1\text{m}$ was done for the sample sites which had no individuals $< 50\text{ cm}$ namely; Glencairn, Kommetjie, Soetwater, Olifantsbos 1 and Kwaai baai, Mauritz baai and the Pump house. This was done so that sites could be compared in terms of the proportion of juveniles ($< 1\text{ m}$) to adults ($> 1\text{ m}$) across a wide geographical distribution of sites.

The beach wash-up data was also analysed in terms of the holdfasts to see what % frequency of the individuals in total, $< 50\text{ cm}$ and $> 50\text{ cm}$ were found on shared holdfasts. The % broken individuals were also noted so that they could be compared with the % of individuals that still had holdfasts.

Shade Tolerance

To investigate shade tolerance of juvenile *E. maxima* individuals a presence/absence count was done for the size classes $< 1\text{ m}$, $1 - 2\text{ m}$ and $> 2\text{ m}$ for $1 \times 1\text{ m}$ quadrants from the sample results with complete size class distributions. Therefore the sites looked at for this were Millers point, Olifantsbos 2 and Bordjiesrif.

Results

Geographical distribution of population sample sites

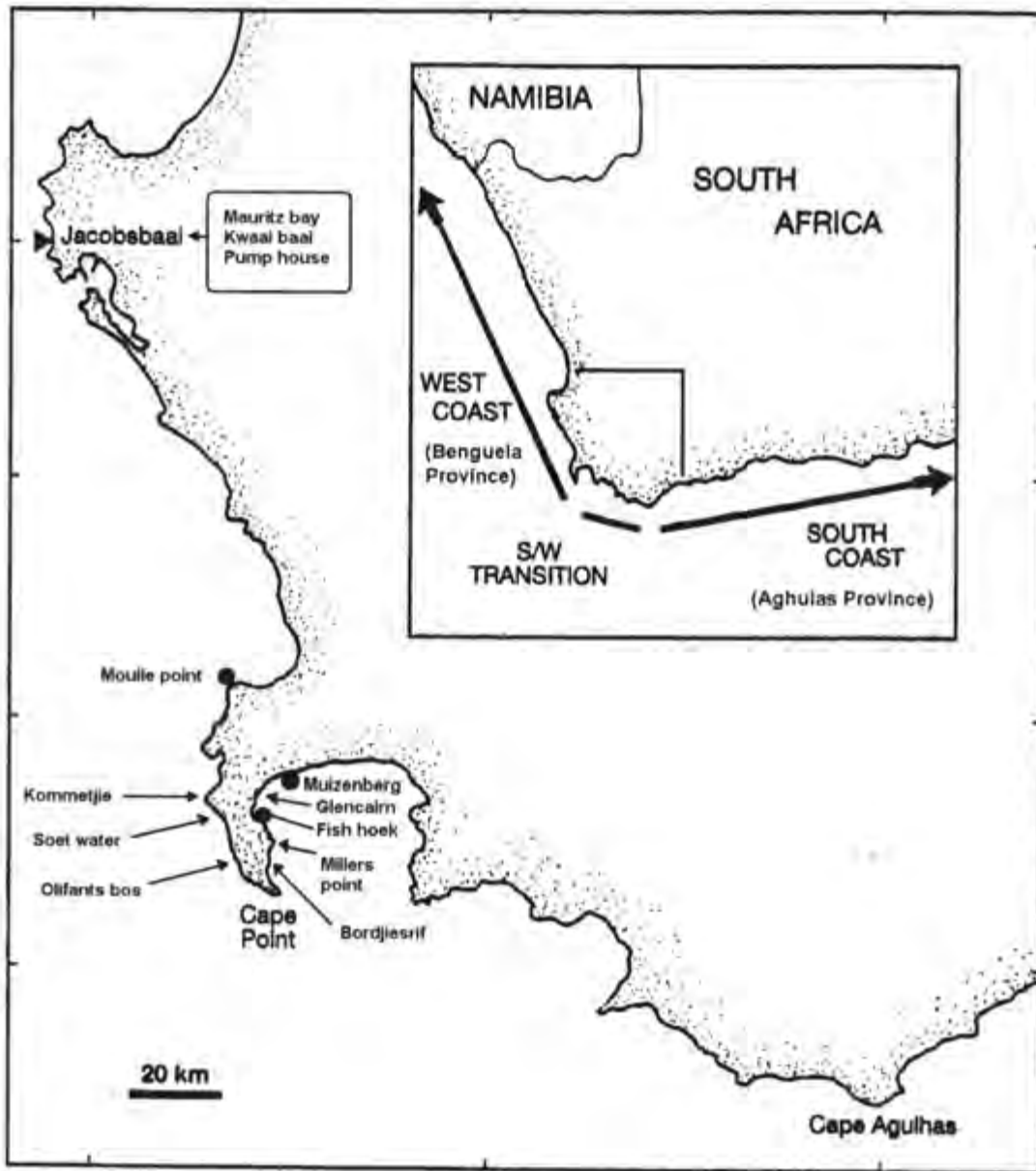


Fig 1. Distribution of *E. maxima* population sample sites from False bay to Jacobs baai shown with arrows. Beach wash-up sample sites shown with circles.

The *E. maxima* population sample sites extend from False bay , in the South/ West transition zone, to Jacobs baai along the west coast (Fig 1). The population index for the ratio of individuals <1 m to individuals > 1 m shows that there is a clear difference on average between the west coast sample sites and the South/ West Transition sites on the Cape Peninsula (Table 1). The west coast sites have a higher mean index of

57 which means there is a higher ratio of individuals < 1m to individuals > 1m. Individuals < 50 cm are not included in this sample because the data is not available. However there is still a marked difference between the west coast and S/W Transition sites evident from the population ratio of juveniles (<1m) to adults (>1m). This is evidence of differences in recruitment across the two biogeographic regions.

Table 1. Ratio of individuals < 1m to those > 1m for 9 *E. maxima* population samples from the Cape Peninsula to Jacobs baai. Samples did not include individuals < 50 cm.

Sample	Index value (<1/>1x100)
Glencairn (Cape Peninsula)	45
Kommetjie (Cape Peninsula)	23
Soetwater (Cape Peninsula)	27
Olifantsbos 1(Cape Peninsula)	14
Mauritz bay (Jacobs baai)	89
Kwaai baai (Jacobs baai)	34
Pump house (Jacobs baai)	49
Cape Peninsula mean	27
West coast mean	57

Population structure

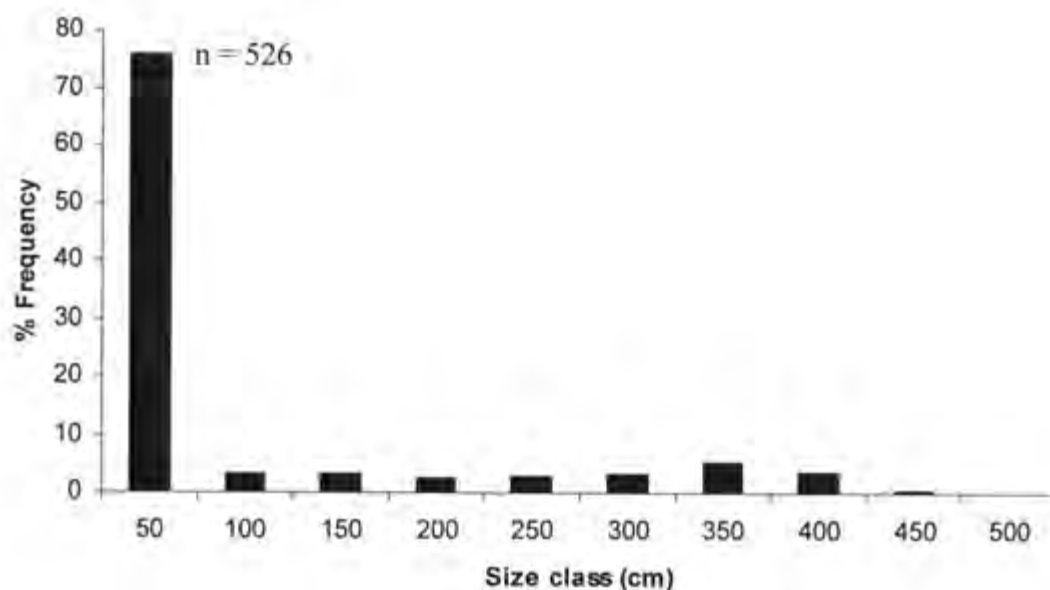


Fig 2. Percentage frequency size class distribution from 19 1x1 m quadrant samples done at Bordjiesrif, Cape Peninsula. n = number of individuals.

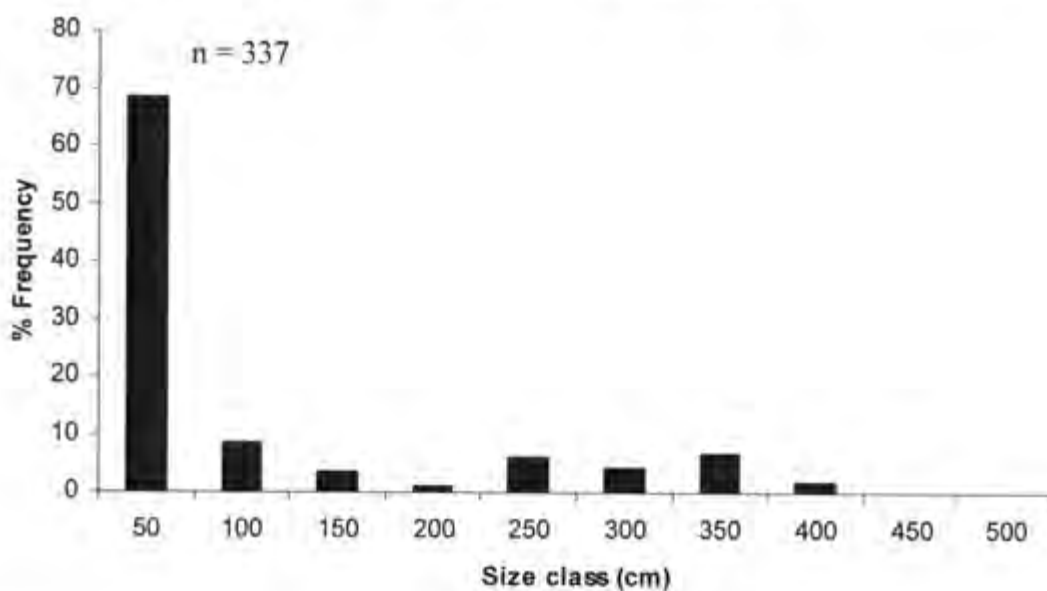


Fig 3. Percentage frequency size class distribution from 30 1x1 m quadrant samples done at Millers point, Cape Peninsula. n = number of individuals.

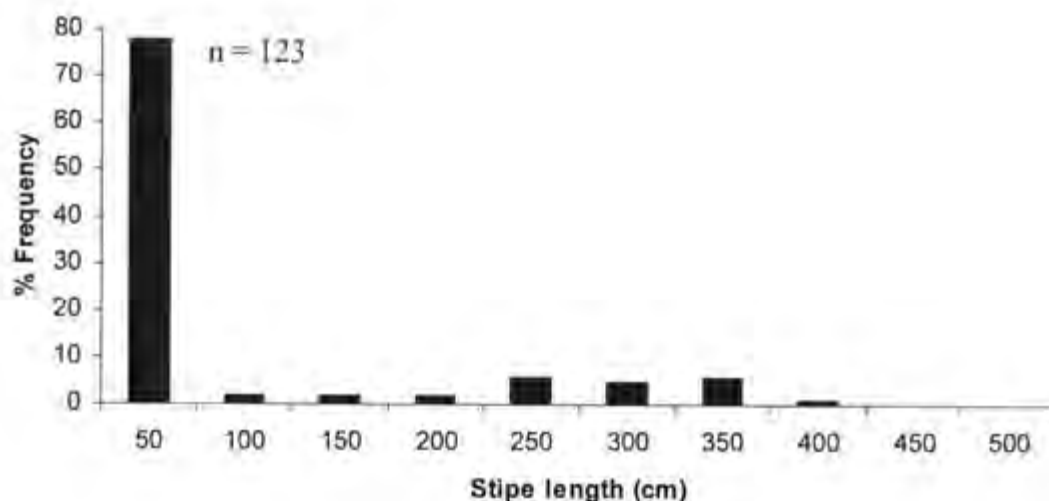


Fig 4. Percentage frequency size class distribution from 10 1x1 m quadrant samples done at Olifantsbos 2, Cape Peninsula. n = number of individuals.

The three population structures of Bordjiesrif, Millers point and Olifantsbos 2 are very similar in shape and in their % frequency of size class distributions. From these three sites the *E.maxima* population structure is dominated by a % frequency size class distribution that is an inverse J-curve shape with a large number of juveniles (<1 m) present and few adults (>1 m) (Fig 2, 3 & 4). The individuals < 50 cm alone make up 69 %, 76 % and 78 % of the Millers point, Bordjiesrif and Olifantsbos 2 population samples respectively. With individuals < 1m included, this goes up to 77 %, 79 % and 80 % respectively. The difference between the % juveniles (< 1m) for the three sites is marginal at 3 %. The adult (> 1m) individuals are fairly evenly distributed between the size classes > 1m to 4.5 m. There is however a bimodality in the distribution with individuals > 2m constituting the majority of all individuals > 1m. The individuals > 2m constitute 15 %, 19 % and 17 % for Bordjiesrif, Millers point and Olifantsbos 2 respectively. This leaves a remaining 6 %, 4 % and 3 % respectively of individuals in the size classes between 1 and 2 m. The size class with the lowest % individuals of the three sites was the 1.5 m – 2 m size class not including the 4 – 4.5 meter size class, with the lowest being shared between the size classes from 0.5 – 2 for Olifantsbos 2,. Individuals from the three samples had individuals with a maximum stipe length of up to 4.5 m.

Shade Tolerance

Presence and absence counts were done to test the occurrence of different size classes with each other as a simple measure of shade tolerance. The results show that commonly the size classes < 1 m, 1 – 2 m and > 2m all occur together (Table 2). The occurrence of individuals > 2m and > 1m only is rare. This suggests that juveniles (< 1m) have a high level of shade tolerance because they commonly exist with individuals (> 2m) or (> 1m) which can create a canopy cover and consequently limit light to the under storey. This was found to be the case at all three sites Bordjiesrif , Olifantsbos 2 and Millers point.

Table 2. The percentage of the presence and absence counts for the occurrence of a combination of the size classes < 1m, 1m – 2m and > 2m of the quadrants sampled at Bordjiesrif , Olifantsbos 2 and Millers point.

Presence/ Absence type	Bordjiesrif (%)	Olifantsbos 2 (%)	Millers Point (%)
all size classes present	58	30	40
only < 1m and 1m – 2m present	16	0	20
only < 1m present	11	30	13
only < 1m and > 2m present	11	40	23
only > 1m present	0	0	3
only > 2m present	5	0	0

Beach sample

The Log-log correlation of the stipe length and the float diameter was significant with an $r = 0.9068$ and a p value of 0.0025 , where significance is $p \leq 0.05$ (Fig 5).

Therefore it was used for scaling from the float diameter of broken individuals without holdfasts to obtain an approximate stipe length. The equation of the correlation , $y = 0.4079x + 0.0607$, was used to scale from the float diameter to the stipe length. Significance was determined at the $p \leq 0.05$ level.

However the best correlation found for the basal diameter and the stipe length was not a Log-log correlation but an un-transformed correlation which still had a poor significance with an $r = 0.1757$ and a p value of 0.1 , where significance is $p \leq 0.05$, (Fig 6) and therefore was not used for scaling up from basal diameter to stipe length.

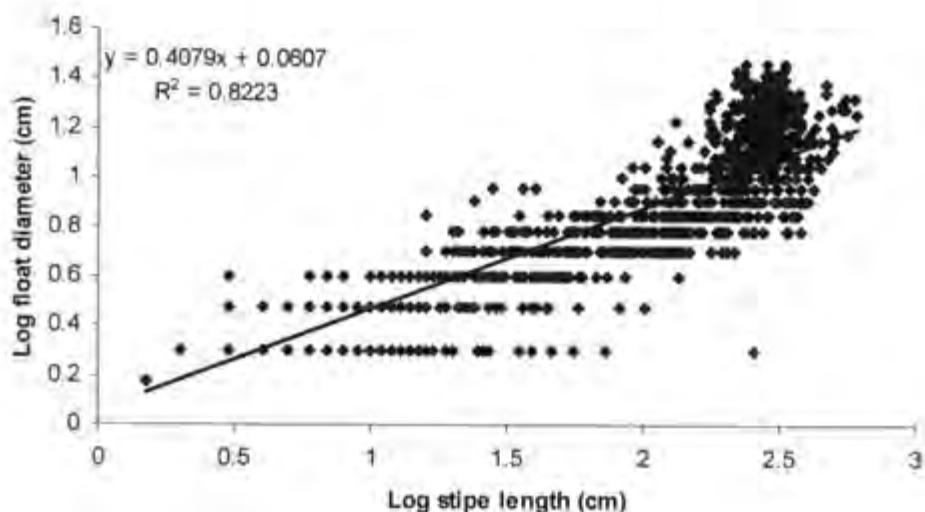


Fig 5. Log-log correlation of float diameter to stipe length for 1292 *E.maxima* individuals sampled at Romans Bay, Western Cape. R is 0.9068 with a significant value of $p = 0.0025$, where significance is $p \leq 0.05$.

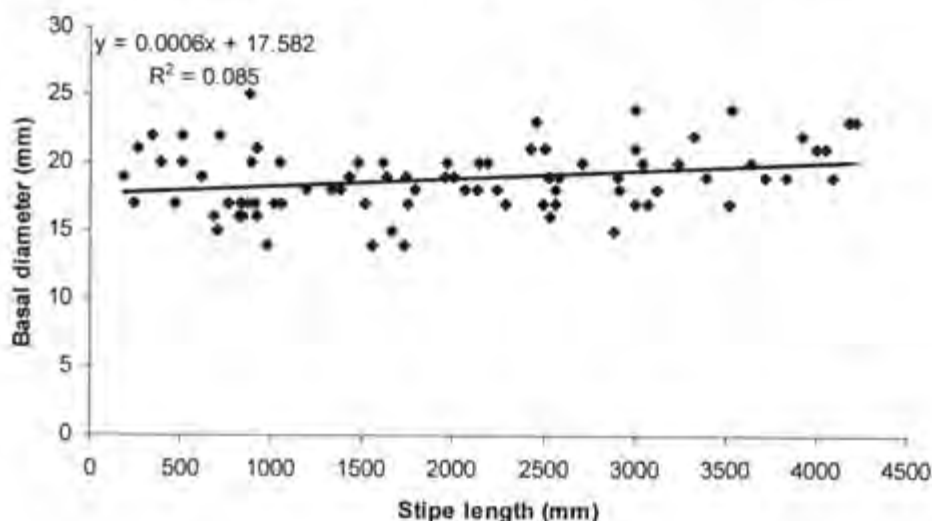


Fig 6. Correlation of basal diameter of stipe (mm) to stipe length (mm) for 85 *E.maxima* individuals sampled at Millers point, Cape Peninsula. R is 0.2915 with a significance value of $p = 0.1$, where significance is $p \leq 0.05$.

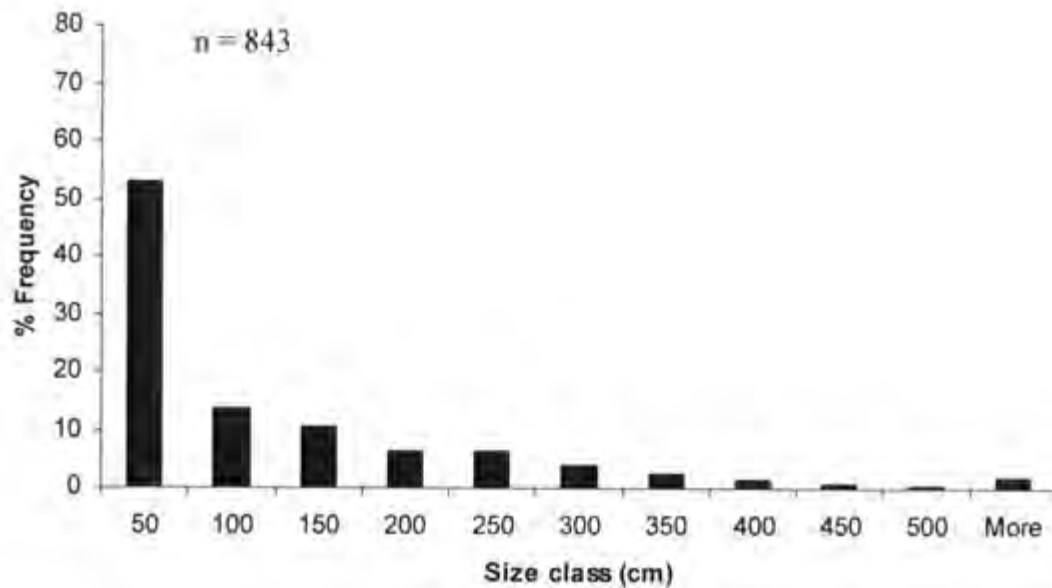


Fig 7. Percentage frequency size class distribution from 9 *E. maxima* beach-wash samples done at Muizenberg (False Bay), Fish Hoek beach (False Bay) and Moulle point (Table Bay) in Cape Town. n = number of individuals.

The total beach wash-up size class distribution has a distinct inverse J-curve shape with 53 % individuals < 0.5 m and a total of 66 % of the individuals < 1m (Fig 7). Therefore juveniles constitute well over 50 % of the individuals washed up on the three beaches. The adult individuals (> 1m) have a graduated decreasing distribution in the size classes from 1m to 5m. Almost 2 % of the adults washed up are > 5m. No individuals greater than 4.5 m were shown in the *E. maxima* population samples at Bordjiesrif, Millers point and Olifantbos 2(Fig 2,3 & 4).

Table 3. Beach sample results of *E.maxima* in Cape Town. (A) = % individuals on shared holdfast, (B) = % individuals on shared holdfast (<50 cm), (C) = % individuals on shared holdfast (>50 cm), (D) = % broken individuals, (E) = % individuals with holdfasts.

Beach		n	A (%)	B (%)	C (%)	D (%)	E (%)
Muizenberg	1	102	31	48	52	63	44
	2	78	26	70	30	71	44
	3	104	63	58	42	31	76
	4	109	83	59	41	9	96
Fish Hoek	1	106	44	28	72	53	56
	2	102	45	50	50	46	62
	3	108	71	55	45	16	88
Moulle Point	1	104	37	89	11	20	92
	2	103	80	49	51	15	87
Mean		102	53	56	44	36	72

The % of individuals on shared holdfasts are at a high mean of 53 % for all the samples (Table 3). This varies between samples from 26 % to 83 %. The size class of < 0.5 m constituted the highest % of the individuals on shared holdfast across the samples with a mean of 56 %. Individuals on shared holdfasts > 50 cm constituted only 44% showing that a shared holdfast is likely to have a few large adult individuals and high proportion of juvenile (< 50 cm) individuals on it. The % of individuals broken was low at 36 % in comparison to individuals which were washed onto the beach with their holdfast still intact which is at a mean of 72 % for all samples. This suggests that disturbance in general is removing individuals with their holdfasts intact rather than just breaking them.

Discussion

Are holdfasts safe sites for recruitment?

To begin at the individual scale, it is important to determine whether mature kelp holdfasts are safe sites for recruitment if they are facilitating as a refuge for juvenile *E.maxima* from grazers. There are two ways I measured how *E.maxima* individuals can be removed from the population namely by an individual being snapped or by being ripped off with the holdfast intact. The results of this study show that holdfasts are most commonly removed along with the whole *E.maxima* individual from disturbance, in comparison to individuals with broken stipes without holdfasts (Table 3). There is also evidence of grazers facilitating breaking of other algae (*Nereocystis luetkeana*) individuals by damaging the stipe and lowering the hydrodynamic energy required to snap the stipe (Duggins et al., 2001). This is not as important for *E.maxima*'s disturbance dynamics because broken individuals constitute a much lower portion of individuals removed from kelp beds in comparison to individuals removed with their holdfast intact (Table 3). In addition, the majority of individuals that are dislodged from *E.maxima* kelp beds are found on shared holdfasts and 53 % of these individuals are juveniles (< 0.5 m) (Table 3). Therefore this shows that holdfasts are actually not as safe as previously thought for recruiting as many juveniles are being removed on shared holdfasts (Table 3). While holdfasts may be a refuge for sporophyte juveniles from grazers (Anderson et al., 1997) they are not always the optimum substratum for recruitment because of the negative influence of disturbance on it. Therefore the two recruitment substratum, rock and mature holdfasts, are both potentially detrimental for juvenile *E.maxima* individuals because both can lead to significant mortality.

Population structure, gaps and re-colonization

What is the impact of disturbance?

“Large scale, low frequency oceanographic phenomena have been found to be important in kelp forest succession processes, population dynamics and competitive interactions among kelp guilds” (Tegner et al., 1997) pp 117

The consequences of this scenario are further realized in the population structure. The general population structure of *E.maxima* is that of an inverse J-curve distribution (Fig 2 ,3 & 4). This exhibits many juveniles and few adults (Everard, 1994). The beach wash-up sample (Fig 7) suggests there is a high mortality of juveniles and low mortality of adults in the population from disturbance because it exhibits a similar inverse J-curve distribution to that of the *E.maxima* populations (Fig 2 ,3 & 4). Assuming larger individuals have larger drag forces exerted on them (Sousa, 1985), juveniles are also being removed with larger individuals as they are being removed disproportionately from the population. Larger drag forces on larger thaluses have also been verified by Milligan et al., (2001), in the Laminariales species *Hedophyllum sessile*. This means that juveniles are essentially being dragged along on the holdfast of larger individuals that are more likely to be dislodged from disturbance.

The removal of the larger individuals (< 1 m) from the *E.maxima* forest canopy is similar to individuals in temperate forests that die and form a 'gap' in the canopy from disturbance (Runkle, 1985). A gap is therefore the death of a canopy individual from a form of disturbance (Runkle, 1985). Kelp populations can be almost destroyed by storm disturbance (Tegner et al., 2001) in some cases forming gaps that may be opportune for re-colonization. Consequently high recruitment can follow storm disturbance as found in the giant kelp *Macrosystis Pyrifera* in California, USA (Tegner et al., 1997). The bimodality of the *E.maxima* population from the size classes greater than > 1m cm (Fig 2 , 3 & 4) is also similar to that of plant species in forests where seedling survival is dependant on gaps from disturbance events (Everard, 1994). The population structure of *E.maxima* therefore has evident 'gap' disturbance characteristics and can be further analysed in terms of the processes involved in re-colonization after 'gap' disturbance.

What environment do gaps create?

Storms have different affects on communities which influence the rate at which they can recover to their original state, depending on what state the community was in before the disturbance occurred (Ebeling et al. 1985). 'Gap' disturbance creates an environment for re-colonization of terrestrial tree seedlings that is dependant on resource availability, physical structure defining the disturbed patch and herbivory

activity (Peterson et al., 2000). The *E.maxima* population is faced with similar challenges for re-colonization. In marine rocky intertidal habitats re-colonization of a patch formed within an occupied area commonly occurs via water borne propagules or vegetative encroachment (Sousa, 1985). In addition to this I will argue that *E.maxima* juveniles already occupying a patch or found on the fringes of a patch also have the opportunity to exploit the 'gap'. Also, excluding the effects of grazers and assuming that larger individuals have larger drag forces inflicted on them the juveniles which have a single holdfast recruiting on rock are more likely to survive a disturbance and exploit a 'gap' than those recruiting on a mature adult.

How can kelp exploit the gap?

Light resource

Light is an energy source for photosynthesis and is therefore very important for all plants that photosynthesize (Hellebust, 1970). Light is also an important resource in forest canopies because it is limited in the under storey by the canopy and increases radiance when gaps are formed so that seedlings with different shade tolerances adopt different strategies of exploiting 'gaps' (Midgley et al., 1995). Light exploitation levels also vary in kelp so that it is enhanced for kelp at higher canopies (Dayton et al 1984). *E.maxima* juveniles appear to have a high shade tolerance (Table 2) which suggests that they are employing a 'waiting' strategy for 'gaps'. This means that juveniles are able to maintain in the under storey until a 'gap' is formed. Rarely are shade tolerant species in terrestrial forests shown to grow steadily to the forest canopy but rather wait for 'gaps' where after they have a large growth spurt to reach the canopy (Runkle, 1985). Applied to *E.maxima* this implies that the juveniles can remain on mature kelp holdfasts or on rock until the light conditions are right for rapid growth to the canopy.

Substratum

The type of recruitment substratum is very important for *E.maxima*'s re-colonization as part of the physical structure or characteristic of a 'gap'. A patch surface which has large surface heterogeneity can influence settlement and enhance recruitment by for example supplying crevices and cracks that can protect juveniles from grazers (Sousa, 1985). This is especially pertinent to *E.maxima* because of the pressure of

grazers on sporophyte juveniles (Anderson et al., 1997). The pressure of grazers can lead to different kelp forest structures as shown by up to 75 % of *E. maxima* adults individuals found to have single stipes in grazer free areas in comparison to shared holdfasts (Anderson et al., 1997). This value went down to 45 % in areas where there were numerous grazers (Anderson et al., 1997). Consequently the dependence of *E. maxima* juveniles on substratum for recruitment may have knock-on affects for the population and its ability to re-colonize 'gaps'.

Re-colonization

In terms of exploiting the gap for re-colonization the ideal place for recruitment of *E. maxima* juveniles is likely to be on rock. Large scale, low frequency oceanographic phenomena have been found to be important in kelp forest succession processes and competitive interactions among kelp guilds (Tegner et al., 1997). The individuals on the rock substratum are able to minimize any characteristics of intra-specific competition that may exist between individuals found on holdfasts. This is in relation to light availability or space, which may occur when sharing a holdfast. Juveniles recruiting singly on a rock would also avoid the possibility of being removed with a large individual. However the rock substratum is clearly not always the ideal place for recruitment in general either, because of the pressures of grazers on sporophytes recruiting on rock (Anderson et al., 1997). For example re-colonization processes may be delayed if whole individuals are removed with their holdfasts in high-density grazer areas (Anderson et al. 1997). *E. maxima* individuals are therefore in essence 'stuck between a rock and a holdfast' when attempting to re-colonize 'gaps' where both options are either desirable or undesirable depending on the local grazer density or disturbance regime.

Biogeographical differences

Ecological differences

What are the implications of being 'stuck between a rock and a holdfast' at a biogeographical level? For the first time fundamental ecological differences between the biogeographical regions of the west coast and South/West Transition zone have been suggested (Anderson et al. 1997). At the biogeographical scale I also found significant differences between the *E. maxima* populations that occur in the different

biogeographic regions (Table 1). The two biogeographic regions compared are the Benguela Province and the Western Overlap (Bolton et al., 1997), also known as the South/West transition (Anderson et al., 1997) (Fig 1). The marine biogeographic regions are delineated by temperature differences of the inshore waters of South Africa (Bolton et al. 1997) and characterize different algae species diversity (Bolton et al, 2003), changes in grazer abundances and the abundance of the rock lobster *Jasus lalandii* which is considered a key stone species because it is a predator of the herbivore *Parechinus angulosus* (Anderson et al., 1997).

In general the grazer abundances of the urchin *Parechinus angulosus*, abalone *Haliotis midae*, limpets *Patella* species and gastropods *Turbo* species, decrease eastward of Cape point when compared with west coast sites (Anderson et al., 1997). In addition the rock lobster *Jasus lalandii*, a predator of the urchin *Parechinus angulosus*, is very abundant on the west coast and consequently associated with lower urchin abundance in this region (Anderson et al., 1997). Keystone species prevent resource monopolization by consuming prey species at lower trophic levels (Levinton, 1982) which is what the rock lobster *Jasus lalandii* serves as by preying on urchins.

Greater grazer abundance is also associated with reduced under storey algae biomasses when compared with west coast sites (Anderson et al., 1997) illustrating community structural differences due to ecological interactions. The results of juvenile (<1 m) proportions to adults (>1 m), when compared across the sites found at the South/West transition and the Benguela Province (Table 1), show that there are lower juveniles (<1 m) in proportion to adults (> 1m) in the Cape Peninsula sites. This is likely due to different ecological processes acting on the population structure and recruitment of *E.maxima* across this biogeographical range. This is in relation to the different ecological influences of grazers and disturbance on *E.maxima* recruitment.

Given the evident grazer abundance differences, especially the urchin *Parechinus angulosus*, between the Benguela biogeographic region and the South/West transition (Anderson et al., 1997) and assuming the disturbance regime is similar, certain inferences can be made from what is known about the influence of grazers and

disturbance on *E.maxima*. Adult individuals with single stipes rather than shared holdfasts would be expected to be more common in the Benguela biogeographic region as there are less grazers in this region. This is because grazer free areas can be associated with up to 75 % of adult individuals with single stipes whereas high grazer densities can drop this value to 45 % (Anderson et al., 1997). Also, more recruitment on rock substratum would be expected in the Benguela biogeographic region due to the absence of grazers as holdfasts are not needed as refugia from grazing. This would mean there is a higher likelihood of juveniles being removed on the holdfasts of mature adults, which exert greater drag (Sousa, 1985), in the South/West transition zone. This shows the possibility for different 'gap' dynamics in the Benguela province area because re-colonization can be more successful due to greater rock recruitment rather than holdfast recruitment consequently leading to decreased juvenile mortality and greater recruitment success. Holdfast recruitment leads to a high juvenile mortality from disturbance as shown from the results of this study while rock recruitment might not in the Benguela biogeographic region as grazers are less abundant. This has been found to be the case in harvesting experiments where west coast sites take 2.5 years to recover whereas recovery in transition zone sites can exceed 3 years (Anderson et al., 1997). Therefore disturbance may act as a more beneficial succession process on kelp beds of the Benguela biogeographic region in comparison to the South/West Transition zone because 'gaps' can be more effectively re-colonized with minimized affects on juvenile mortality.

Alternate stable states

Marine ecosystems have numerous examples of multiple stable states which may occur naturally (Knowlton, 2004). Phase changes are found commonly in kelp forests where ecological chain reactions are key factors in the process (Estes et al., 2004). The alternate stable state known as a kelp 'barren' is formed in the kelp beds of the Californian coastline in the North American Pacific (Dayton et al., 1984). This is because urchins are able to cause significant destruction on kelp forests when found in high densities, to the extent that all kelp is removed (Knowlton, 2004). This can also be triggered by storms which destroy parts of the kelp forest canopy (Dayton et al., 1984). A reverse transition is then also possible back to a kelp forest when grazer densities decrease again (Knowlton, 2004). The factors that lead to an increase in

urchin densities are poorly known (Knowlton, 2004) but are therefore critical to the formation of kelp barrens.

In South Africa 'barrens' do not commonly occur in sub tidal communities but occur along the west coast in deeper waters (Anderson et al., 1997) however they have the potential to be triggered in local kelp beds by two critical factors namely, the factors determining urchin abundance and the factors determining disturbance on kelp forests. Both are potentially negative forces on *E. maxima* recruitment and if working in conjunction together, by decreasing recruitment of *E. maxima*, have the potential to delay re-colonization and form 'barrens'. Specifically on grazer influences the South African rock lobster *Jasus lalandii* is an important predator on the urchin *Parechinus angulosus* and therefore acts as a keystone species in regulating urchin abundances (Anderson et al., 1997). It could therefore cause disastrous trophic cascade affects (Anderson et al., 1997) on *E. maxima* recruitment should rock lobster populations decrease and lead to higher urchin densities. Secondly, changes on the disturbance regime such as the severity or frequency of storms (Runckle, 1985) could potentially impact *E. maxima* recruitment negatively especially in the South/West biogeographic regions thereby leading to changes in the community composition and alternate stable states. Also, the influence of anthropogenic disturbance could become a factor if disturbance delays re-colonization through the removal of kelp holdfasts (Anderson et al., 1997) or through negative impacts from the frequency and severity of harvesting on kelp populations. As *Ecklonia maxima* is a commercially harvested kelp (Bolton et al., 1994) the methods of harvesting implored could act as a form of negative disturbance if it is unregulated. Studies are being carried out to determine the affects of harvesting on kelp recovery (Levitt et al., 2002).

Therefore the magnitude of influence of both top down forces on urchins and anthropogenic and natural disturbance regime impacts on *E. maxima* kelp populations are critical to maintaining either alternate stable states. This is because of their significant influence on *E. maxima*'s ability to re-colonize and recover to a previous state. Therefore the factors determining these two influences on kelp recruitment need to be monitored and better understood for a healthily balance of natural succession processes to occur in the *E. maxima* forests.

Conclusion

Kelp forests are important habitats for many other marine organisms (Witman et al., 2001) and are therefore a good place to investigate ecological processes. This study has shown how obtaining a better understanding of the ecological interactions involved in kelp re-colonization processes can be evaluated at different scales. It is useful to be able to investigate processes at the local level so that large-scale processes can also be understood too. The use of analogies also allows ecologists to utilize well realized processes to grasp a better understanding of those that are less understood and has been very useful in this study.

From the study crucial processes in the ecological succession of *E.maxima* have been realized at the small and large scale. Holdfasts are not good sites for recruitment as disturbance targets the holdfasts of *E.maxima* individuals. Also the inverse J- curve of the population appears to be a result of the shade tolerance of juveniles and the removal of large individuals from the population which are ripped off rocks with smaller individuals attached to the holdfast. These processes and their implications in different ecological environments reveal differences in the disturbance ecology of *E.maxima* across the biogeographic regions of the South/West transition zone and the Benguela Province. This has different implications for *E.maxima* re-colonization after natural disturbance or anthropogenic disturbance in these regions. Disturbance that removes holdfasts is likely to have a greater impact in the South/West transition zone and has the potential to form urchin barrens as succession in this region is more sensitive to ecological cascade effects from keystone species and the pressure of disturbance. In the Benguela Province recruitment is higher as juveniles can recruit on rock without the threat of grazers and therefore kelp populations are able to respond to disturbance by exploiting 'gaps' more effectively. Additional investigation into differences in the disturbance regimes and the relative influence of different trophic levels on grazers of the two biogeographic regions will be useful for a further understanding of the ecological disturbance dynamics of *E.maxima*. Therefore by extrapolating processes from the individual to the biogeographic scale much still can, and has already, been learned about the population ecology of *Ecklonia maxima*.

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Reference:

Anderson RJ, Carrick P, Levitt GJ, Share A, 1997. Holdfasts of adult kelp *Ecklonia maxima* provide refuges from grazing for recruitment of juvenile kelps. *MARINE ECOLOGY-PROGRESS SERIES* 159: 265-273

Bolton JJ, Anderson RJ, 1994. *Ecklonia*. In: *Biology of Economic Algae*. (Ed. by Akatsuka), pp 285-406. SPB Academic Publishing, Netherlands

Bolton JJ, Stegenga H. 2002. Seaweed species diversity, *South African Journal of Marine Science*, vol 4 pp 9-18

Bolton JJ, Anderson RJ. 1997. *Marine Vegetation, Vegetation of Southern Africa*, Cambridge University Press, pp 384-370

Connell SD, 2003. Negative effects overpower the positive of kelp to exclude invertebrates from the under storey community. published online, Springer Verlag

Dayton PK, Tegner MJ, Edwards PB, Riser KL. 1999. Temporal and spatial scales of kelp demography: The role of oceanographic climate. *ECOLOGICAL MONOGRAPHS* 69 (2): 219-250

Dayton PK, Currie V, Gerrodette T, Keller BD, Rosenthal R, Ven Tresca D, 1984. Patch dynamics and stability of some California kelp communities. *ECOLOGICAL MONOGRAPHS* 54: (3) 253 – 289

Duggins D, Eckman JE, Siddon CE, Klinger T, 2001. Interactive roles of mesograzers and current flow in survival of kelps. *MARINE ECOLOGY PROGRESS SERIES* 223: 143 – 155

Ebeling AW, Laur DR, Rowley RJ, 1985. Severe storm disturbances and reversal of community structure in a southern Californian kelp forest. *MARINE BIOLOGY* 84 : 287 - 294

Eckman JE, Duggins DO, Sewell AT, 1989. Ecology of under storey kelp environments. I. Effects of kelp on flow and particle transport near the bottom. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY* 129: 173 – 187

- Everard D.A, Van Wyk G.F, & Midgley J.J, 1994. Disturbance and the diversity of forests in Natal, South Africa: lessons for their utilization. *Strelizia* (1) p 275
- Estes JA, Danner EM, Doak DF, Konar B, Springer AM, Steinberg PD, Tinker MT, Williams TM, 2004. Complex trophic interactions in kelp forest ecosystems. *BULLETIN OF MARINE SCIENCE* 74 (3): 621-638
- Fletcher RL, Callow ME, 1992. The settlement, attachment and establishment of marine algal spores. *BRITISH PHCOLOGY* 27: 303 – 329
- Fowler-Walker MJ, Connell SD, 2002. Opposing states of sub tidal habitat across temperate Australia: consistency and predictability in kelp canopy-benthic associations. *MARINE ECOLOGICAL PROGRESS SERIES* 240 : 49 – 56
- Goodsell PJ, Connel SD, 2004. Disturbance initiates diversity in recruitment of canopy-forming algae: interactive effects of canopy-thinning and substratum availability. In Press
- Gordon R, Brawley SH, 2004. Effects of water motion on propagule release from algae with complex life histories. *MARINE BIOLOGY* 145 (1): 21-29
- Graham MH, Harrold C, Lisin S, Light K, Watanabe JM, Foster MS, 1997 (b). Population dynamics of Giant kelp *Macrocystis pyrifera* along a wave exposure gradient. *MARINE ECOLOGY-PROGRESS SERIES* 148 (1-3): 269-279
- Graham MH, 1997 (a). Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey Peninsula, central California, USA. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY* 218 (1): 127-149
- Graham MH, 2004. Effects of local deforestation on the diversity and structure of Southern California giant kelp forest food webs. *ECOSYSTEMS* 7 (4): 341-357
- Hellebust JA, 1970. Light; plants. In: *Marine Ecology*, (Ed. by Kinne O), pp 125-159. Wiley-Interscience, U.K
- Knowlton N, 2004. Multiple "stable" states and the conservation of marine ecosystems. *PROGRESS IN OCEANOGRAPHY* 60 (2-4): 387-396
- Levinton JS, 1982. *Marine Ecology*. Prentice-Hall, Inc, Englewood Cliffs, N.J
- Levitt GJ, Anderson RJ, Boothroyd CJT, Kemp FA, 2002. The effects of kelp harvesting on its regrowth and the under storey benthic community at Danger Point, South Africa, and a new method of harvesting kelp fronds. *SOUTH AFRICAN JOURNAL OF MARINE SCIENCE-SUID-AFRIKAANSE TYDSKRIF VIR SEEWETENSKAP* 24: 71-85
- Milligan KLD, DeWreede RE, 2004. Morphological variations do not effectively reduce drag forces at high wave-exposure for the macroalgal species, *Hedophyllum sessile* (Laminariales, Phaeophyta). *PHYCOLOGIA* 43 (3) 236-244

- Midgley JJ, Cameron MC, Bond WJ, 1995. Gap characteristics and replacement patterns in the Knysna Forest, South Africa. *JOURNAL OF VEGETATION SCIENCE* 6: 29 – 36
- Peterson CJ, Pickett STA, 2000. Patch type influences on regeneration in a western Pennsylvania, USA, catastrophic windthrow. *OIKOS* 90: 489 – 500
- Pickett STA, White PS, 1985. The ecology of natural disturbance and patch dynamics, Academic Press, U.K
- Stegenga H, Bolton JJ, Anderson RJ, 1997. Seaweeds of the South African West Coast. CREDA Press, Cape Town
- Stirk WA, van Staden J, 2004. Potential new applications for the southern African kelps. *SOUTH AFRICAN JOURNAL OF BOTANY* 70 (1): 145-151
- Tegner MJ, Haaker PL, Riser KL, Vilchis LI, 2001. Climate variability, kelp forests, and the Southern California red abalone fishery. *JOURNAL OF SHELLFISH RESEARCH* 20 (2): 755-763
- Tegner MJ, Dayton PK, Edwards PB, Riser KL, 1997. Large-scale, low-frequency oceanographic effects on kelp forest succession: A tale of two cohorts. *MARINE ECOLOGY-PROGRESS SERIES* 146 (1-3): 117-134
- Witman JD, Dayton PK, 2001. Rocky subtidal communities. In Marine community ecology (Ed. by Bertness M.D, Gaines S.D, Hay ME), pp 339-366. Sinauer Associates, Sunderland