INVESTIGATIONS INTO THE HARVESTING ECOLOGY OF THE SOUTH AFRICAN KELP *ECKLONIA MAXIMA* (ALARIACEAE, LAMINARIALES).

BY

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DEDICATION

This thesis is dedicated to the memory of my father, Leslie Brian Rothman, who always fills my mind with fond memories.

DECLARATION

I declare that "Investigations into the harvesting ecology of the South African kelp *Ecklonia maxima* (Alariaceae, Laminariales)" is my own work and that all the sources I have used or quoted have been indicated and acknowledged by means of complete reference.

Name: Mark D. Rothman

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Abstract

Kelp (*Ecklonia maxima*) exploitation in South Africa has increased exponentially over the last decade. This increase is fuelled by the ever-increasing demand for freshly harvested kelp fronds for cultured abalone (*Haliotis midae*). This increase in harvesting has raised some concerns about its effects on the kelp beds in South Africa. This present study examines several questions that were not addressed by previous studies of South African *Ecklonia maxima* beds.

Firstly, this thesis examined the distribution of kelp biomass, at various sites around the Cape Peninsula and on the west coast, and at different depths within sites. An attempt was made to calculate a single figure that could be used in determining the biomass of kelp beds. Divers, using SCUBA, collected the data, at each site, by cutting kelp from a series of 1 m^2 quadrats that were placed on the substratum and from which all the plants were cut just above the holdfast. The plants were brought to shore where the stipes and fronds were weighed separately.

The average kelp biomass over all the sites was 14.4 kg wet wt m^{-2} and the average frond biomass was 8.6 kg wet wt m^{-2}. Sixty two percent of the kelp biomass comprised surface-reaching plants while 38% was subsurface kelp. Sites differed statistically in the average biomass m^{-2}. The lowest average biomass was 10.5 kg wet wt m^{-2} and the highest 21.3 kg wet wt m^{-2}. It was suggested that a conservative figure 10 kg wt m^{-2} be used to estimate standing kelp stock. This conservative figure would eliminate the possibility of kelp beds being over harvested. Kelp densities, at different sites, were also variable ranging from 2.8 – 5.7 plants m^{-2}.

Secondly, the method, described above is fairly accurate but it is very labour intensive and time consuming. Thus a new, quick method for estimating biomass from measurements of the density of kelp heads at the surface was tested. Two snorkel

divers worked along a transect, at 2 m intervals, from the seaward edge of the kelp bed towards the shore. The number of kelp heads in 1 m^2 quadrats, at the surface, was counted. The surface-reaching plants were followed down to the substratum and then cut, just above the holdfast, and brought to shore and weighed.

A relationship was established between the number of heads at the surface and the kelp biomass. This method was tested by comparing the data from the 'surface method' to data from the 'bottom quadrate method' (see above). A direct correlation was established between the number of heads at the surface and the kelp biomass. This method provides a quick estimate of *E. maxima* biomass, and can be used together with a limited number of 'bottom quadrats' to obtain accurate biomass data.

Thirdly, although studies have examined the effects of kelp harvesting on understorey seaweeds, effect on subsurface kelp have not been studied. This thesis examined the effect of canopy harvesting on the stipe growth, recruitment and population structure of *E. maxima*. Two 30x10 m sites were demarcated and subdivided in to three 10x10 m plot, each with a different treatment. The treatments mimicked the harvesting methods commercially employed. In treatment 1 (T1) the whole kelp 'head' was removed (killing the plants: 'lethal' harvesting). In treatment 2 (T2) only the fronds were harvested leaving 20-30 cm of frond on the primary blade and thus not killing the plants ('non-lethal' harvesting). The third treatment was the control (C).

The data showed that harvesting had no effect on rates of stipe elongation, recruitment or the population structure of the subsurface kelp. It is concluded that factors other than irradiance levels drive these processes. However, the data showed that the stipes of long plants had a higher relative growth rate than medium and short plants. Furthermore, once sporophytes attain a stipe length of between 11-25 cm they have a 70% chance of becoming a surface-reaching plant.

Fourthly, *E. maxima* is a canopy forming kelp and a high proportion of the kelp biomass is situated at the surface. The fertile material of this plant is borne on the fronds, which are harvested for abalone feed. This study investigated the effect that harvesting would have on the potential spore output in a kelp bed. Thirty surface-reaching plants and thirty subsurface plants were harvested in a deep and shallow zone of a typical kelp bed. The length of fertile material on each frond was related to the total frond length as well as the stipe length of the plants. Surface-reaching plants in the deep zone had the highest amount of fertile material. The surface-reaching plants, in the shallow zone, had less fertile material, than those in the deep zone, but more than the subsurface plants in the deep and shallow zones. The subsurface kelp from both zones, however, had similar amounts of fertile frond material. Using the results and data from Chapter 2, it is estimated that plants in a 1 m^2 area will produce 1.35×10^{11} spores annually. If the whole canopy should be removed the subcanopy would still be able to produce 5.4×10^{10} spores annually. It is calculated that current levels of frond-harvesting (limited to 10% of the estimated biomass of kelp beds) is unlikely to have significant effects on recruitment of gametophytes and ultimately on the population structure and biomass of sporophytes populations.

The result of this study indicate that current methods of harvesting *E. maxima*, and current management controls, should ensure that harvesting has minimal effects on kelp population structure, recruitment and reproductive output.

Chapter 1

General Introduction

Kelps are brown algae of the order Laminariales (Stegenga *et al.*, 1997) with a world wide distribution. Although taxonomically not very diverse (Steneck *et al.*, 2002) they inhabit sub- and intertidal rocky substrates mainly in warm to cold temperate waters (Dayton, 1994) as well as in the Arctic and sub-Antarctic regions (Lüning, 1990).

Kelp bed communities are highly productive (Field *et al.* 1980) and have a fairly complex structure (Dayton, 1985). Ecologically kelp is very important because it supports and shelters a number of herbivorous fish and many different species of invertebrates (Field *et al.*, 1980; Dayton, 1994).

Kelps have a heteromorphic life cycle with an alternation of generations with microscopic haploid gametophytes and macroscopic diploid sporophytes (Dayton, 1985). The sporophytes (the large kelp plants) produce sporangia from which motile zoospores are released into the water to settle on the bottom. There they develop into male and female gametophytes. The male produces sperm which is released to fertilise the egg produced by the female. The result is a diploid zygote which develops into the sporophyte which is usually restricted to growing on hard substrata.

Kelps and kelp beds are shaped or influenced by different factors (Dayton, 1985) and although these factors influence kelp communities in similar ways, individual kelp beds differ in different ecosysytems (Dayton, 1985) due to the variability of the factors. These factors include temperature, wave action (Field and Griffiths, 1991), nutrients, photoperiod, salinity, tides, availability and topography of substrata for settlement, disturbance (Odum, 1963; Dayton, 1994), patch dynamics, dispersal and grazing (Dayton, 1985). The role each factor plays is difficult to determine as there is usually a combination of these factors at work in a kelp bed (Dayton, 1985).

A major limiting factor for kelp growth and distribution is light. It can be assumed that light influences all stages of development of *Macrocystis* plants, but their response to light is dependent on life-history phase (Fei & Neushul, 1984). The fronds of *Macrocystis* are even designed to be suspended by gas bladders, in the water column for maximum exposure of photosynthetic tissue to light, to enable it to out-compete other seaweeds (Lüning, 1990). Many kelp species form a canopy which greatly decreases the amount of light that reaches the substrate (Norton *et al.*, 1982; Fei & Neushul, 1984; Kimura & Foster, 1984; Edwards, 1998; Schroeter *et al.*, 1995; Levitt *et al.*, 2002) and limits recruitment and growth of turf forming algae (Dayton *et al.*, 1984; Reed & Foster, 1984). Thus, by removing the canopy the bottom irradiance would be increased and increase the production of understorey seaweeds (Edwards, 1998). Kimura & Foster (1984) suggest that understorey algae decrease in conditions of low light due to a dense canopy formed by adult stands of *Macrocystis pyrifera* (Linnaeus) C. Agardh. In some instances light levels under the canopy can be less than 1% of those at the surface (Reed & Foster, 1984). Removing the canopy of *M. pyrifera* has greatly affected recruitment by increasing the amount of light that reaches the bottom (Kimura & Foster, 1984). This was also found by Johnson & Mann (1988) in a *Laminaria* bed in Nova Scotia although these recruits were smaller than the ones growing more sparsely beneath the canopy. Schroeter *et al.* (1995) have shown that fronds of *Macrocystis pyrifera* grew up to 77% slower under the canopy compared to kelps growing in a canopy gap caused by an El Niño event between 1982 and 1984.

Wave action can have a profound effect on shaping seaweed communities (Norton, 1994). Because kelps need to give way as waves sweep over them, they have strong, flexible thalli (Norton *et al.*, 1982). Norton *et al.* (1982) also found that *Laminaria longicruris* Bachelot de la Pylaie growing in sheltered areas has three times the surface area/mass ratio of populations growing in exposed areas. They further state that plants in wave-exposed areas are sturdier, tougher and more securely attached than those in sheltered areas.

The microscopic gametophytes of kelps can generally survive a wide range of temperatures. Bolton & Levitt (1985) also Bolton & Lüning (1983) showed that gametophytes of *E. maxima* survived temperatures of up to 26°C in laboratory cultures, but *E. maxima* sporophytes are not found where monthly mean temperatures exceed 20°C (Bolton, 1986; Bolton and Anderson, 1987). Kelp sporophytes appear to have limited temperature tolerances. During El Niño, entire kelp beds can be lost due to prolonged periods of increased water temperatures and low nutrients (Dayton and Tegner, 1984; Ladah *et al.*, 1999). After an El Niño event notable changes in the canopy can be observed (North *et al.*, 1993).

Temperature can be used as an indicator of nutrient levels in the water column; high water temperatures often indicate low nutrient levels and low temperatures often indicate high nutrient levels (Jackson, 1977; Schroeter *et al.*, 1995). This is certainly the case in the Benguela upwelling system on the South African west coast (Chapman & Shannon, 1985). Kelps, like other seaweeds, lack roots to absorb nutrients but rather take up nutrients over their entire surface (Norton *et al.*, 1982). Surface area to mass ratio is thus of great importance to seaweeds as the greater their surface area the more nutrients that can be taken up. Some kelps, including *Ecklonia maxima* (Osbeck) Papenfuss, have the ability to store nutrients for periods of low nutrient conditions (Probyn & McQuaid, 1985). They tested this by enclosing the fronds in large plastic bags fastened around the stipes and monitoring the nutrient depletion. Their results indicated that growth rate for *E. maxima* do not reach their potential based on its nutrient absorption. It is thus likely that the plant stores the nutrients for periods when nutrients are limited. *Macrocystis pyrifera* plants are able to translocate nutrients from parts of the plants, which are bathed in higher nutrients, to parts which are nutrient-limited (Jackson, 1977). North *et al.* (1993) noted the largest total *Macrocystis* areas develop during periods of low temperatures and high nutrients.

The monitoring of kelp beds is important because of their economic importance and the economically important organisms they support. Changes in the kelp populations can be detected by studying the demography of the beds. The parameters governing the population demography can be sub-divided into three classes: the size or the density of the population, the age distribution, and how these individuals are spaced within the population (Chapman, 1979).

World wide the total annual value of commercially exploited seaweeds is US$ 5.5 – 6 billion of which more than 90% is contributed from seaweeds used as food for human consumption (McHugh, 2003). In 1993 kelp accounted for 75% of the total revenue made from seaweeds worldwide (Guiry, 1997). In many countries (Argentina, Canada, Chile, China, France, Japan, Ireland, Morocco, New Zealand, Norway, Scotland, South Africa, Republic of Korea, UK and the USA) kelp is harvested, mainly for extraction of the hydrocolloid, alginate, an emulsion stabilizer (Isaac, 1942; Chapman, 1970; Chapman, 1984, Anderson *et al.*, 1989; Soegiarto & Sulustijo, 1990; Kang, 1990; Ohno & Critchley, 1993). Uses for alginate include: dressing and polishing materials, thickening material for colours in printing, hardener and adhesive in weaving, emulsifier, suspension agent in pigments, smoothing agent in ice-cream, stabilising agent in icing, sherbets and beer (Chapman, 1970).

The commercial use of seaweeds in South Africa began during the Second World War when agar from Japan became unavailable in Britain (Chapman, 1970; Anderson *et al.*, 1989). Since then a number of seaweeds have been harvested for commercial use in South Africa (Anderson *et al.*, 1989; Levitt *et al.*, 1992; Anderson *et al.*, 2003) especially the harvesting of fresh kelp fronds for abalone (*Haliotis midae*) feed. Only recently has seaweed culturing taken off at abalone farms as a supplement to the abalone's diet. Due to the unpredictable weather conditions in South Africa kelp harvesters are sometimes limited by inclement weather and are thus unable to harvest kelp for the abalone farms. This has led some abalone farmers to start experimenting with culturing their own seaweeds on their farms. These seaweeds can be fed as a supplement to the abalone's diet or as a staple diet when kelp is unavailable (Troell *et al.*, in press). This relieves the harvesting pressure on the kelp beds but also benefits the abalone farmers as they are not as dependent on the kelp supplied by harvesters. On the South African east coast, where *E. maxima* does not occur, one abalone farm is entirely dependant on cultured seaweeds producing 5 t (wet wt) of *Ulva* per working day (Richard Clark, pers.comm.). This is the largest seaweed culturing enterprise in South Africa. Apart from a few abalone farms culturing seaweeds, there is no large-scale commercial cultivation of seaweeds.

Worldwide, most kelps are harvested from the wild with the exception of *Laminaria japonica* Areschong which is cultivated in China for food (McHugh, 2003). In South Africa kelp is the most commonly harvested seaweed and occurs along the west coast. *Ecklonia maxima* , *E. radiata* (C. Agardh) J. Agardh, *Laminaria pallida* Greville ex J. Agardh and *Macrocystis angustifolia* Bory are the four species of kelp found in South Africa (Bolton & Anderson, 1997; Stegenga *et al.*, 1997). *E. maxima* is of greatest importance in the South African context as this is the dominant and most abundant kelp, forming near-homogeneous stands between Cape Agulhas and Cape Columbine (Simons & Jarman, 1981; Bolton & Anderson, 1997). *Ecklonia maxima* usually makes up 50% of the total plant biomass (Velimirov & Griffiths, 1979; Field *et al.*, 1980) even though it only occurs down to a depth of about 9 m (Anderson *et al.*, 1989). *Laminaria pallida* is mostly a subsurface kelp in this area, but progressively becomes the dominant and canopy-forming kelp north of Cape Columbine (Stegenga *et al.*, 1997)(see Fig. 2). *Macrocystis angustifolia* only occurs in patches in a few localities along the west coast (Field *et al.*, 1980) while *Ecklonia radiata* is only found in the intertidal and shallow subtidal zones of the warm temperate south and east coasts, extending from East of Cape Agulhas to southern Kwa-Zulu Natal (Stegenga *et al.*, 1997). The South African west coast with its high-energy waves and cool nutrient-rich upwelled water provides favourable conditions for the growth of *E. maxima* (Field *et al.*, 1980, Field & Griffiths, 1991, Levitt *et al.*, 1992; Bolton & Anderson, 1994).

The southwest coast (area between Cape Agulhas and the Cape Peninsula) is regarded as an overlap zone between the warm-temperate south coast (influenced by the Agulhas Current) and the cool-temperate Benguela region (characterised by upwelling) (Field & Griffiths, 1991; Bolton & Anderson, 1997; Stegenga *et al.*, 1997). This is the region where many seaweed species, occurring on the east coast, reach their western limit (Stegenga *et al.*, 1997). The understorey seaweeds here are thus a combination of east and west coast species making this area very species rich with around two thirds of the entire west coast flora in False Bay (Stegenga *et al.*, 1997). The large *E. maxima* sporophytes are dark brown and consist of a holdfast,

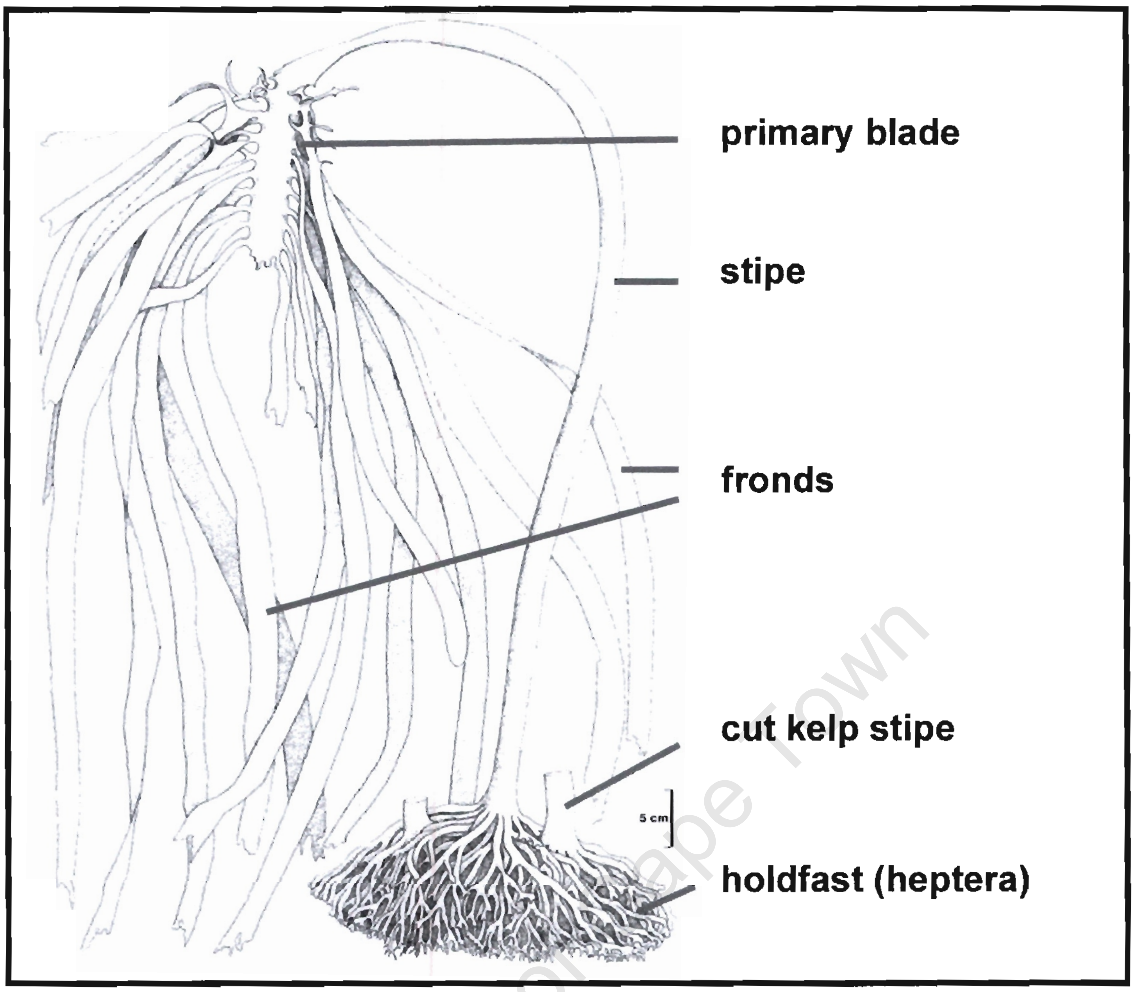

Figure 1. A young *Ecklonia maxima* sporophyte. (After Stegenga *et al.*, 1997)

stipe and blades (Stegenga *et al.*, 1997) (Fig 1). *E. maxima* beds forms a forest-like stand with a dominating dense canopy (Borchers & Field, 1981). The single large, but simple stipe is narrow near the substratum and increases in diameter upwards and can grow up to 10 m long (Papenfuss, 1940; Simons, 1976; Anderson *et al.*, 1989). Near the apex of the stipe the thallus forms a gas-filled bulb, to assist with flotation, then it narrows and flattens to a tough, often spearhead-like, primary blade. The meristematic region, where primary growth takes place, is located between the junction of the stipe and the primary blade just above the bulb. Laterally, from the primary blade, grow the belt-like secondary fronds which, when mature, bear the spores in sori (dark, raised patches) where spore production takes place throughout the year (Joska & Bolton 1987). They found that spore release in *E. maxima* takes place seasonally with the maximum values being observed in spring and summer (September to January). Furthermore, although there are large areas of reproductive sori present on the fronds, they do not release spores continuously even from healthy, mature fertile tissue.

Stipe growth takes place incrementally during the course of the plants life (until it reaches the surface) while the fronds grows like belts from the meristem (Mann *et al.* 1979). Fricke (1978) in his study of kelp grazing by urchins concluded *E. maxima* has a seasonal growth pattern. He concluded that young *E. maxima* sporophytes started active growth in early summer and continues into autumn. This is the only literature which make mention of the seasonal growth of *E. maxima* even though his findings were based on peak number of kelps harvested between January and March and low values between June and September. Furthermore, one can expect that periods of high carbon production of *E, maxima* to coincide with periods of growth. It would thus be reasonable to assume that the seasonal growth pattern of *E. maxima* is related the seasonal variation in alginate content as found by von Holdt *et al.* (1955), Hay *et al.* (1983) and Stacey (1984). Von Holdt *et al.* (1955) and Stacey (1983) showed that maximum alginate content in summer while Hey *et al.* (1983) observed a maximum in winter. Dieckman (1980) however, recorded seasonality in the growth rates of *Laminaria pallida*. He observed highest growth rates during spring and early summer and lowest rates in winter. This might be the same for *E. maxima* considering what von Holt *et al.* (1955) and Stacey (1983) found which will also agree with the findings of Fricke (1978). But more data needs to be collected on the seasonal growth of *E. maxima* because reliable seasonal data is lacking.

On older kelp fronds and stipes, epiphytes can be found (Stegenga *et al.*, 1997; Anderson *et al.*, in press) as it occurs on other kelps e.g. *Laminaria hyperborea* (Gunnerus) Foslie (Christie *et al.*, 1998). The typical *E. maxima* epiphytes *Carpoblepharis flaccida* (Lamouroux) Kützing, *Polysiphonia virgata* (C. Agardh) Sprengel (both of which occur on the stipes as well as fronds) and *Gelidium vittatum* (Linnaeus) Kützing are important as they sustain many herbivorous fish, amphipods and isopods (Allen & Giffiths, 1981; Field & Giffiths, 1991; Anderson *et al.*, in press).

According to Field & Giffiths (1991) the most important grazers found in these kelp beds are sea urchins, *Parenchinus angulosus*: urchins are known to cause major damage in a kelp beds (Fricke, 1979; Dayton, 1994; Fletcher, 1987). Fricke (1979) observed an increase in the survival of juvenile *E. maxima* with the exclusion of sea urchins. However, a study by Day & Branch (2002) questioned this generalization because drift kelp forms an important food source for sea urchins and their study indicated no change in algal communities after urchin removal. In South Africa, it is estimated that urchins consume about 14% of the kelp production, as debris, annually (Buxton & Field, 1983). Abalone, *Haliotis midae* and crayfish (lobster), *Jasus lalandii*, are two of the economically important animals associated with *E. maxima* beds (Field *et al.*, 1980, Field & Giffiths, 1991). Apart from these invertebrates, kelp beds are a habitat for numerous molluscs, crustaceans, teleosts, chondrichthyans, etc.

Ecklonia maxima is attached to the substratum by a network of terete haptera, forming a holdfast, which is a habitat for many invertebrates as well as a refuge for *E. maxima* recruits (Anderson *et al.*, 1997). Simons & Jarman (1981) reported that about 10% of kelp biomass at Kommetjie, on the Cape Peninsula, is cast ashore annually through storms and natural deaths.

In South Africa, prior to about 1980, kelp was collected mainly as beach cast, then dried and exported for extraction of alginate (Field *et al.*, 1980). Since the 1970's limited quantities of *E. maxima* have been harvested for the production of an agricultural plant-growth stimulant through a patented process and exported under the name Kelpak. However, since about 1990 a kelp-harvesting industry has developed in South Africa to supply fresh *E. maxima* fronds to the rapidly growing land-based abalone aquaculture sector (Anderson *et al.*, 2003). The harvesting is mostly done by hand from boats at low tide when more kelp heads are exposed at the surface. The harvesters simply reach over the side of the boat, lift the kelp head out of the water and cut it off, with a sickle, just above the bulb, thus killing the plant. The bulb with the kelp fronds is then tossed into the boat (see Anderson & Rothman, unpublished). Some harvesters do not remove the whole kelp head but only the fronds 20 – 30 cm from the primary blade. Although this method is more labour intensive and requires more precision, the plants are not killed and can be re-harvested four months later (Levitt *et al.*, 2002).

During the last decade the amount of fresh kelp fronds, harvested for abalone feed, in South Africa has increased exponentially from less than one ton (wet) in 1992 to more than 6000 tons (wet) in 2003 (Troell *et al.*, in press). This increase is mainly due to the increase in the number of abalone farms along the South African west coast.

The commercial exploitation of seaweed resources in South Africa is regulated by the Marine Living Resources Act of 1998 (Act No. 18 of 1998). In this Act clear objectives are laid out and the government department, responsible for these objectives, is Marine and Coastal Management (M&CM). The South African coastline is divided into 23 concession areas for which prospective applicants apply, with a motivation, for the functional seaweed group in a specific area (Fig. 2). A committee reviews the applications and awards the area, applied for, to the most suitable applicant. Each area can only have one right holder per functional group and in the case of kelps, the harvestable limit is set by a Maximum Sustainable Yield (MSY) which is determined by M&CM through monitoring and research projects.

Monitoring is necessary to ensure the sustainability of the resource. As previously mentioned we have seen a massive increase in the amount of *E. maxima* harvested. This has raised concerns about the effects this might have on the kelp beds. While previous studies showed that harvested *E. maxima* beds recover to their previous biomass within 2.5-3 years and that controlled harvesting has a negligible effect on understorey biota (Levitt *et al.*, 2002), many questions remain unanswered. One such question is: is it possible to use a single biomass figure per m^2 of kelp bed to determine the total standing stock of kelp in that bed? If this is possible it would speed up the process of determining the biomass of kelp beds.

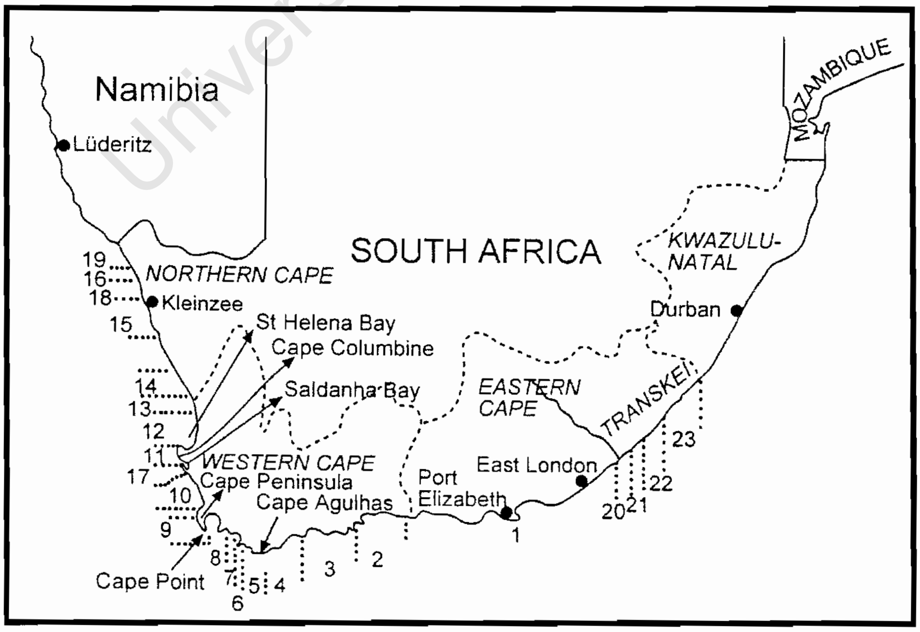

Figure 2. South Africa. Map indicating boundaries of the 23 concession areas.

The traditional method for estimating kelp biomass is a labour intensive and often long process. This involved a diver (on SCUBA) cutting kelp from one 1 m^2 quadrat at a time on the substratum and two more divers (on snorkel) to swim the kelp to shore. This led me to test a rapid method of assessing the biomass in order to monitor the state of harvested areas. The aim was to establish a relationship between the number of kelp heads present at the water surface, at low water spring tide, and the biomass of the kelp bed.

Levitt *et al.*, (2002) showed that harvesting had a negligible effect on the understorey biota, but the effect that canopy harvesting had on the subcanopy kelp was not studied. It has been mentioned that a kelp canopy can drastically decrease the amount of light that reaches the substratum (Norton *et al.*, 1982; Fei & Neushul, 1984; Kimura & Foster, 1984; Edwards, 1998; Schroeter *et al.*, 1995; Levitt *et al.*, 2002). I investigated the effect harvesting the canopy would have on kelp population structure, growth and recruitment. I tested the hypothesis that harvesting of the canopy would increase the irradiance reaching the bottom and hence, increase recruitment of sporophytes, increase growth of subcanopy sporophytes and change the population structure.

The sori of *E. maxima* are borne on the fronds and thus harvesting of the fronds would remove the sporangia. Although Joska & Bolton (1987) studied the spore production of individual *E. maxima* plants, the amount of fertile material available in a kelp bed has not yet been studied. I investigated the amount of fertile frond material present below, as well as at the surface, to determine the extent to which harvesting will have a negative effect on spore production.

Work in this thesis was done in the part of the kelp bed where the kelp reaches the surface, which is usually the inshore part of the kelp bed (0-4 m depth at low water of spring tide). In the inshore, *E. maxima* forms about 70% of the kelp standing stock (Velimirov *et al.*, 1977) on the South African west coast. Velimirov *et al.* (1977) also state that standing stock of *E. maxima* drops to 50% between 4-8 m depth range (where it gets partially replaced by *Laminaria*). However, beds vary in size and some are larger and extend into deep water. *Ecklonia maxima* may reach surface in areas as deep as 9 to 10 m but the bulk of the biomass is found in shallower water < 6 m deep (Field *et al.* 1980., Velimirov *et al.*, 1977).

Chapter 2

Structure of South African west coast kelp beds at different depths and sites.

Introduction

While the production of *E. maxima* in South Africa has been studied, there is little information on the structure of these kelp beds. Dayton (1985) compared productivity ranges of some *Laminaria* kelp populations to the productivity of *Macrocystis* and *Ecklonia* kelp populations. The ranges are between 120 – 1900 grams of carbon per square meter per year (g C $m^{-2}yr^{-1}$) for *Laminaria*, 600 – 1300 g C $m^{-2}yr^{-1}$ for *Macrocystis* and 350 – 1500 g C $m^{-2}yr^{-1}$ for *Ecklonia* populations. Mann *et al.* (1979) however, estimate this figure for *E. maxima* at over 2000 g C $m^{-2}yr^{-1}$. About 16% of the energy produced by *E. maxima* and 34% produced by *Laminaria pallida* enters the system as dissolved organic matter (Newell *et al.*, 1980) which is quickly utilised by mircoheterotrophs (Newell *et al.*, 1988). It is evident that kelp beds are very productive systems (Field *et al.*, 1980) supporting and providing shelter for many fish species, crustaceans and molluscs (Field & Griffiths, 1991).

In South Africa the kelp *Ecklonia maxima* has been exploited since about 1953 (Levitt *et al.*, 1992). Stipe elongation of this species is relatively slow and it can increase its biomass by 1% per day (Mann *et al.*, 1979). Although it has been reported that a single plant can produce seven times its own weight per year, the biomass of an entire kelp bed will turn over about twice a year (Simons & Jarman, 1981). Jarman & Carter (1981) estimated the biomass of *E. maxima*, from Cape Point to Cape Columbine, at 336 370 tons fresh fronds while between Cape Agulhas and Cape Point these estimates are 114 000 tons fresh fronds (Levitt *et al.*, 1992). Although surface kelp occur to a maximum of 9 m, *Ecklonia maxima* have been reported to occur to depths of up to 20 m (Velimirov *et al.* 1977; Jarman *et al.* 1981). Velimirov *et al.* (1977) estimated that almost 52% of the *E. maxima* standing stock occurs in the 0-4 m depth range.

Biomass measurements are important especially for Marine and Coastal Management who are responsible for allocating Concession Areas and harvesting permits. Previously, Concession Areas were allocated only for one year but since 2006 this has been extended to ten years. To make these kinds of decisions it is important to limit the amount of kelp available to harvesters so that there are no detrimental effects on the kelp beds. To ensure the sustainability of the resource, concessionaires are thus limited by a maximum sustainable yield (MSY). The current management practice is to allow the annual amount harvested to equal natural mortality as estimated by Simons & Jarman (1981), i.e. about 10% of the biomass. Levitt *et al.*, (2002) estimated *E. maxima* biomass at Danger Point, ± 60 km from Cape Town, to be 22 973 tons fresh mass. This would mean that at Danger Point harvesters are allowed to harvest 2 298 tones of total fresh kelp per year. Levitt *et al.*, (2002) showed that by harvesting only the distal parts of fronds, and leaving 20-30 cm of the basal fronds (and meristems) undamaged, the yield over time is increased 5-fold. This non-lethal harvesting method is currently being tested in one kelp concession area where the commercial operators are allowed to double the frond MSY that would be allowed if the whole kelp heads (with the primary frond and all secondary fronds) were harvested.

The biomass of kelp in various kelp concession areas is currently being estimated using a combination of Geographical Information Systems (GIS) mapping, infra-red aerial photography and diver-based (SCUBA) biomass determination (Rand, unpublished). One of the problems to emerge from this study is whether the surface canopy (as determined from aerial photographs) varies with the depth at which the kelp is growing. I therefore set out to determine the relationship between depth and stipe length, stipe weight, frond weight and total plant weight. My aim was to describe the structure of selected inshore kelp beds, and compare structure and biomass within and between kelp beds to decide if kelp beds are sufficiently homogeneous to warrant a minor, rapid sampling programme when determining kelp standing stock.

Materials and Methods

Biomass estimations

The quantification of biomass of stands of kelp was done in apparently dense, near homogenous stands of kelp (*Ecklonia maxima*) beds (See Fig. 1 for sites). The beds, on the Cape Peninsula, ranged between 70-200 m wide and between 400-500m long. At Jacobsbaai the beds were narrower and ranged between 50-80 m wide. The sites were Glencairn (34°09'57"S 18°25'54"E), Olifantsbos (34°16'15"S 18°22'50"E), Soetwater (34°10'00"S 18°19'54"E), Kommetjie (34°08'30"S 18°19'16"E), and three sites close to Jacobsbaai on the West Coast namely Kwaai Bay (32°58'36"S 17°52'55"E), Mauritz Bay (32°58'42"S 17°52'55"E) and 'Pump House' (32°57'57"S 17°53'04"E). Sites were chosen on the basis that they must be a typical kelp bed and that no previous harvesting had taken place there. The sites should also be easily accessible from the shore. There should be a degree of sheltering to allow access even if weather conditions are not favourable. The substrata are mostly Table Mountain sandstone on the Cape Peninsula and granite at Jacobsbaai. The substratum had a medium relief with 1-1.5 m deep gullies with mixed vertical/horizontal aspect. The sites I selected were unharvested, had near homogeneous kelp beds and were the largest in the vicinity. The sites near Jacobsbaai however, although the largest in the area, lacked sites deeper than three meters.

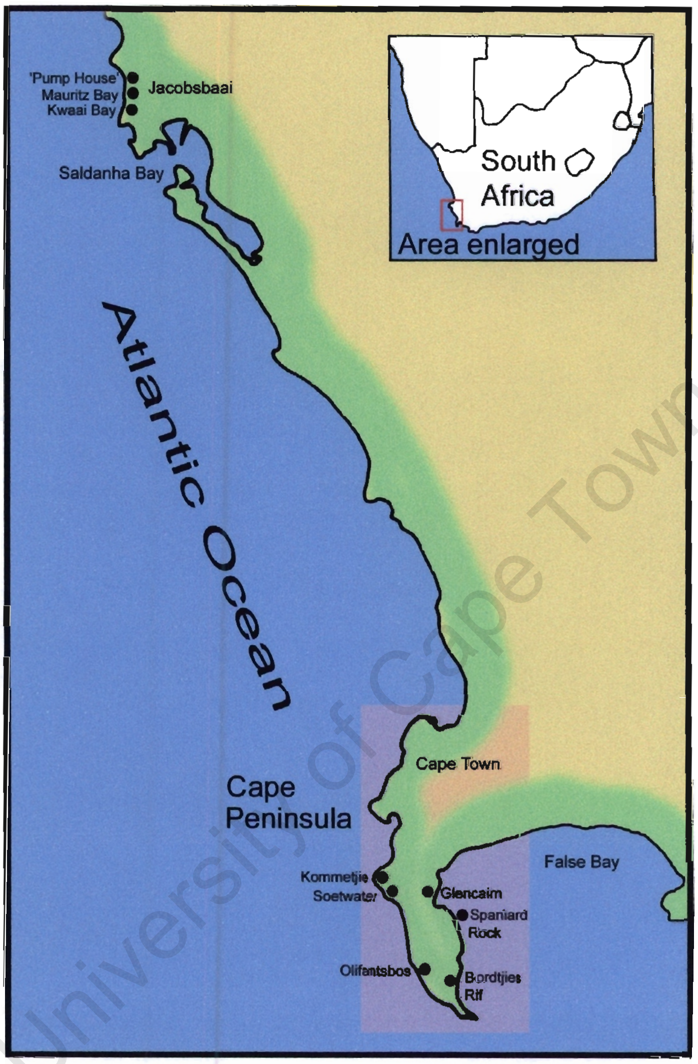

Figure 1. South Africa: Cape Peninsula (coloured area) and the west coast and the vicinity of the study sites mentioned in this thesis.

A diver, using SCUBA, cut the kelp from a 1 m^2 quadrat, just above the holdfast, and passed it on to two more divers on snorkel who then swam the cut kelp to an assistant on the shore. Only kelps with a stipe length of more than 50 cm were cut because smaller plants are not used commercially and the biomass is negligible. Kelp harvesters only harvest kelp that reaches the surface but the data are not limited to surface reaching kelp. Sampling took place only to the depth where surface kelp occurred. Quadrats were sampled, at 4m intervals, along a transect spanning the width of the bed. The diver, on SCUBA, sampled from the shore to the furthest extent of the surface canopy. The width of the kelp bed determined the number of quadrats sampled, with a minimum of ten quadrats per bed.

On shore the fronds were separated from the stipe by cutting at the junction between the primary and secondary blades. The stipe was then measured, using a tape measure, from just above the holdfast to just above the bulb. The fronds were place in a bag and weighed with a spring balance. The weighed plants were discarded.

Kolmogorov-Smirnov (KS) shows that the data was normal ($p > 0.05$) (Zar, 1984). A two-way ANOVA and Tukey post-hoc analysis were done to determine variations in biomass of different kelp beds and different depths by using STATISTICA (version 7). Three depth classes were used: shallow (0-2 m), intermediate (2.1-3 m) and deep (deeper than 3.1 m) Depth was in relation to mean low water of spring tides (MLWS). Furthermore, regression correlations were done to determine the relationship of the weight and size of the various components of the kelp plants with depth (in the three depth classes).

Results

There is a general pattern in the mean total stipe length of surface-reaching plants (Fig 2), mean total stipe weight (Fig 3), mean total frond weight (Fig 4) and mean total plant weight (Fig 5), over the three depths. Generally the deeper sites had higher values compared to those of the shallow sites.

A series of regression correlations indicates a direct relationship between the depth at which the kelp plants occurred and the mean stipe length ($r^2 = 0.5929$; $p <$

0.00005) (Fig. 6), mean stipe weight ($r^2 = 0.4965; p < 0.00005$) (Fig. 7), mean frond weight ($r^2 = 0.2282; p < 0.00005$) (Fig 8) and mean total weight of a kelp plant ($r^2 = 0.3825; p < 0.00005$) (Fig. 9). Generally plants in deep water had longer, heavier stipes with more frond biomass compared to plants occurring at shallower depths. This is substantiated by the direct relationship between the stipe weight and stipe length ($r^2 = 0.5594; p < 0.00005$) (Fig 10) and the direct relationship between stipe length and frond weight ($r^2 = 0.2330; p < 0.00005$) (Fig. 11) and the total plant weight and the stipe length ($r^2 = 0.4105; p < 0.00005$) (Fig 12).

Figure 13 shows the inverse relationship that exists between plant density and depth ($r^2 = 0.2436; p = 0.00003$) with a significant decrease in density of surface plants with depth. Table 1 shows the contribution the different parts of a kelp plant make to the biomass as well as the total contribution the plants make at three different depth classes as well as the average biomass m^{-2}. In the deep zone the contribution to the biomass of the stipes of surface reaching plants is less than half of that of the subsurface kelp. This is the same trend for the contribution of the total biomass of fronds. However the total contributions of stipe and frond biomass in the deep zone is nearly the same (49% for stipe to 51% for fronds). At the intermediate depth, fronds contributed more to the total biomass compared to the contribution of the stipe biomass. Also the frond biomass at the surface is higher than the fronds in the subsurface. Generally in the shallow zone the frond biomass contributes most of the total biomass. More than half the total biomass is contributed by the fronds at the surface. In total, surface kelp contribute 62% while the contribution of the subsurface kelp is 38% of the total biomass in the kelp bed. The last column of table 1 shows the average biomass (kg m^{-2}). There was no significant difference between the mean biomass of *E. maxima* at deep, intermediate and shallow depths as indicated by the matrix supplemented to table 1.

Table 2 compares the total biomass as well as the frond biomass, of all the harvestable plants (surface and subsurface) and the plants which reach the surface, at all the sampled sites. The mean total biomass across all the sites is 14.5 kg wet wt m^{-2} for harvestable plants (i.e. plants with a stipe longer than 50cm); mean frond biomass is 8.6 kg wet wt m^{-2} with an average density of 4.4 plants m^{-2}. When only plants that reach the surface are considered, the mean biomass is 8.8 kg wet wt m^{-2} with 5.3 kg wet wt m^{-2} frond biomass (table 2). The supplement to table 1 indicates the statistical difference between the various sites (ANOVA, $p < 0.05$).

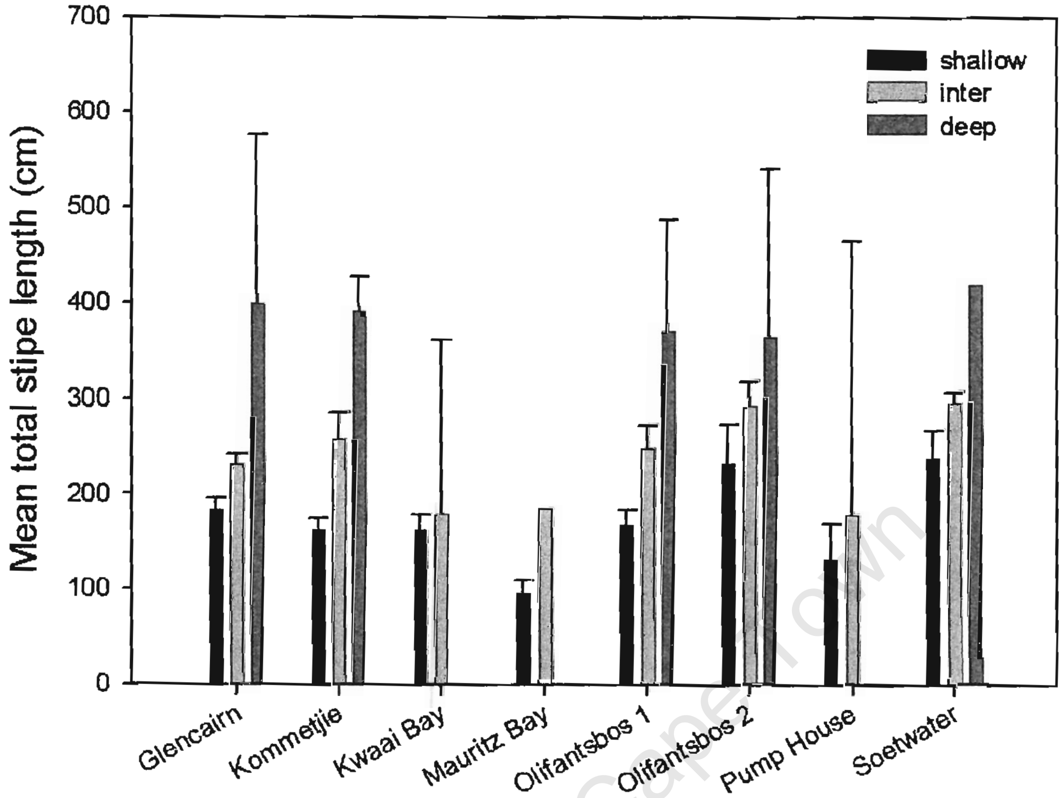

Figure 2. Mean total stipe length (cm) over a range of depths at different sites on the Cape Peninsula and the West Coast. Bars denote 95% confidence limit.

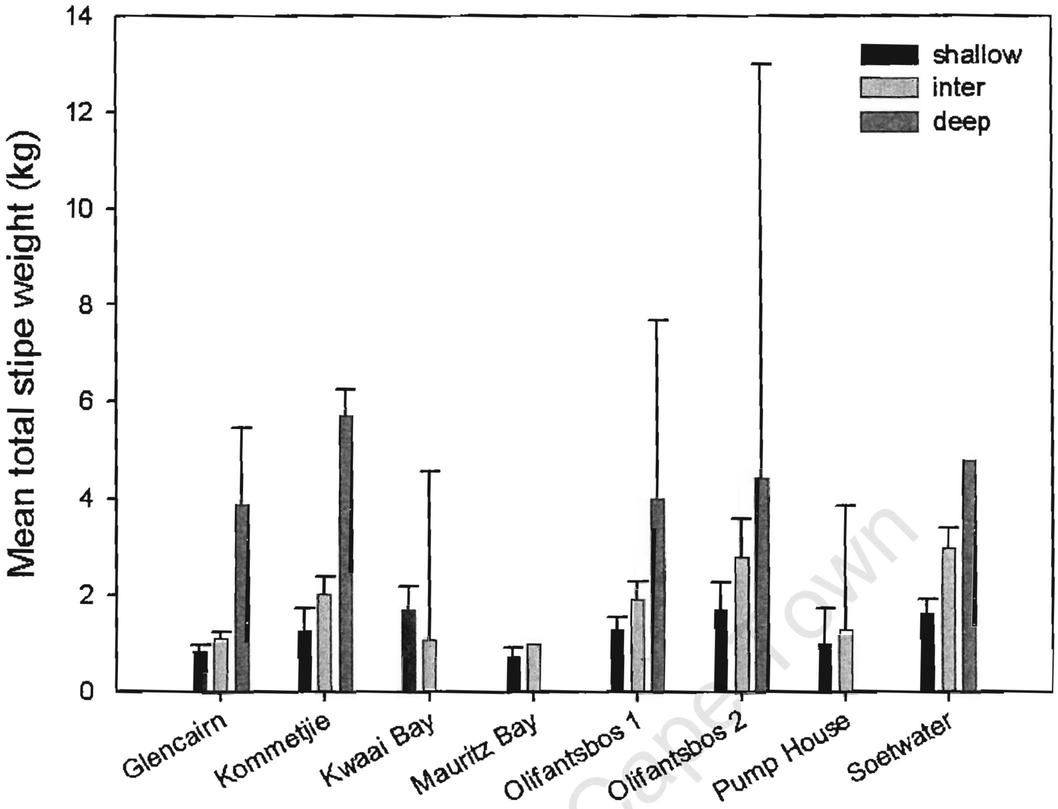

Figure 3. Mean total stipe weight (kg) over a range of depths at different sites on the Cape Peninsula and the West Coast. Bars denote 95% confidence limit.

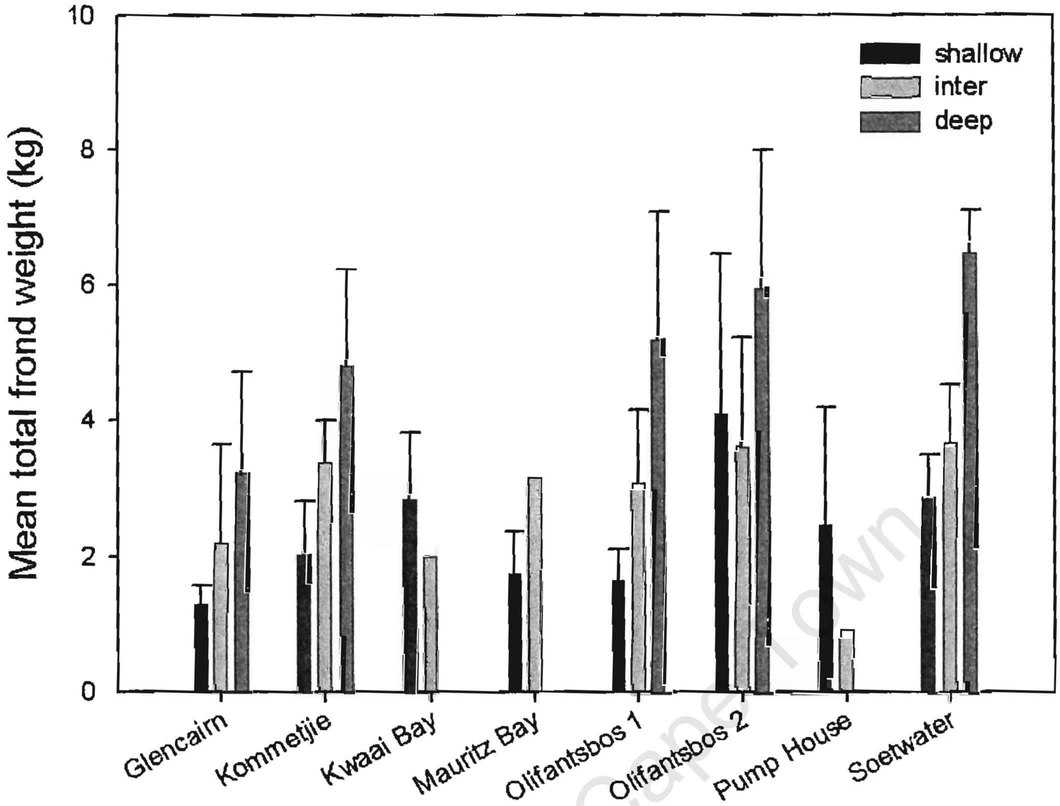

Figure 4. Mean total frond weight (kg) over a range of depths at different sites on the Cape Peninsula and the West Coast. Bars denote 95% confidence limit.

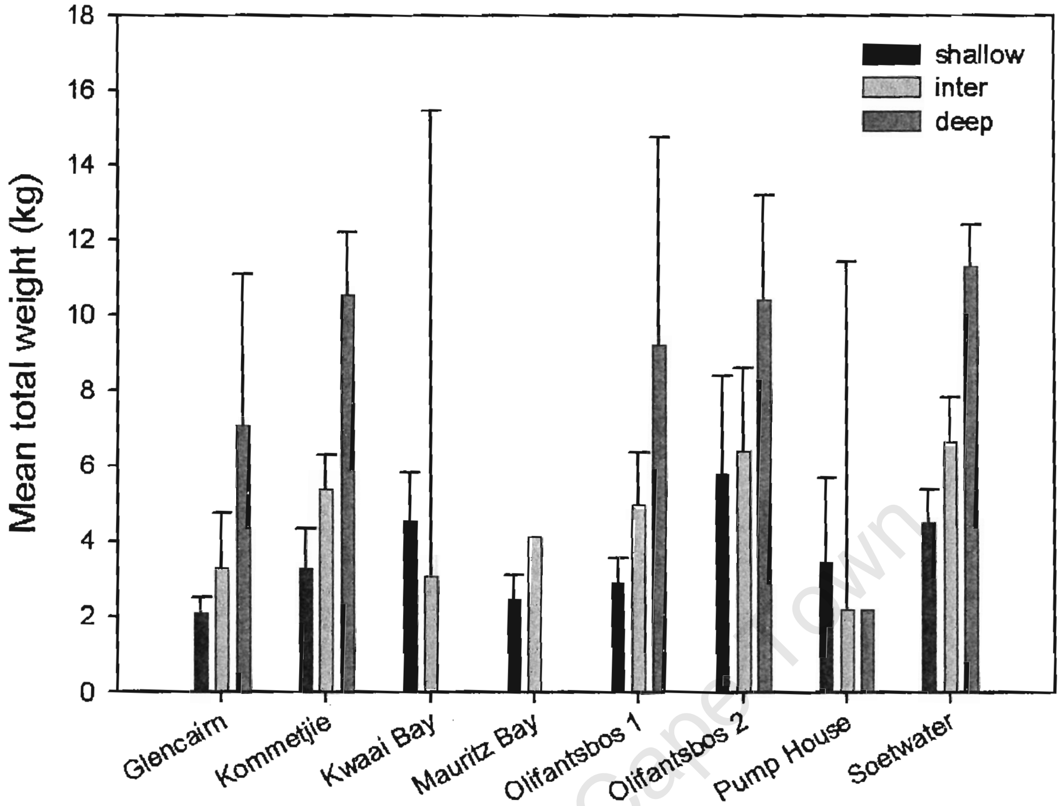

Figure 5. Mean total plant weight (kg wet wt) over a range of depths at different sites on the Cape Peninsula and the West Coast. Bars denote 95% confidence limit.

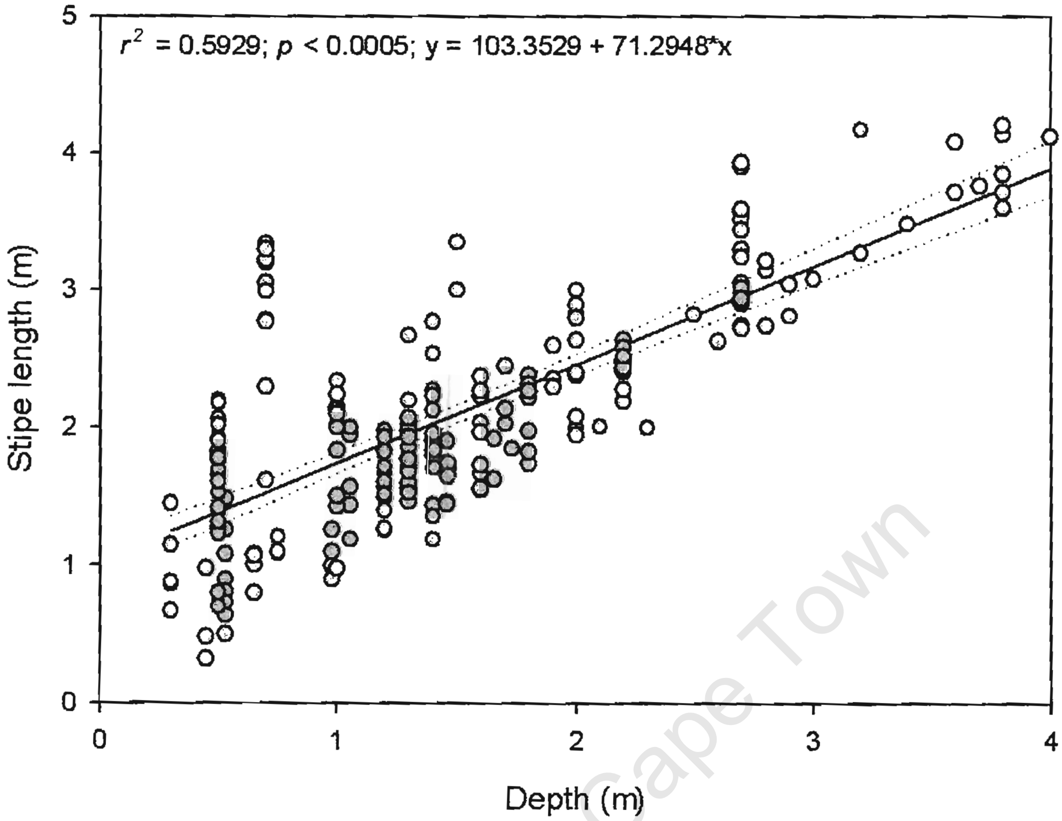

Figure 6. Total stipe length (cm) of *E. maxima* with depth. Dotted lines indicate the 95% confidence interval.

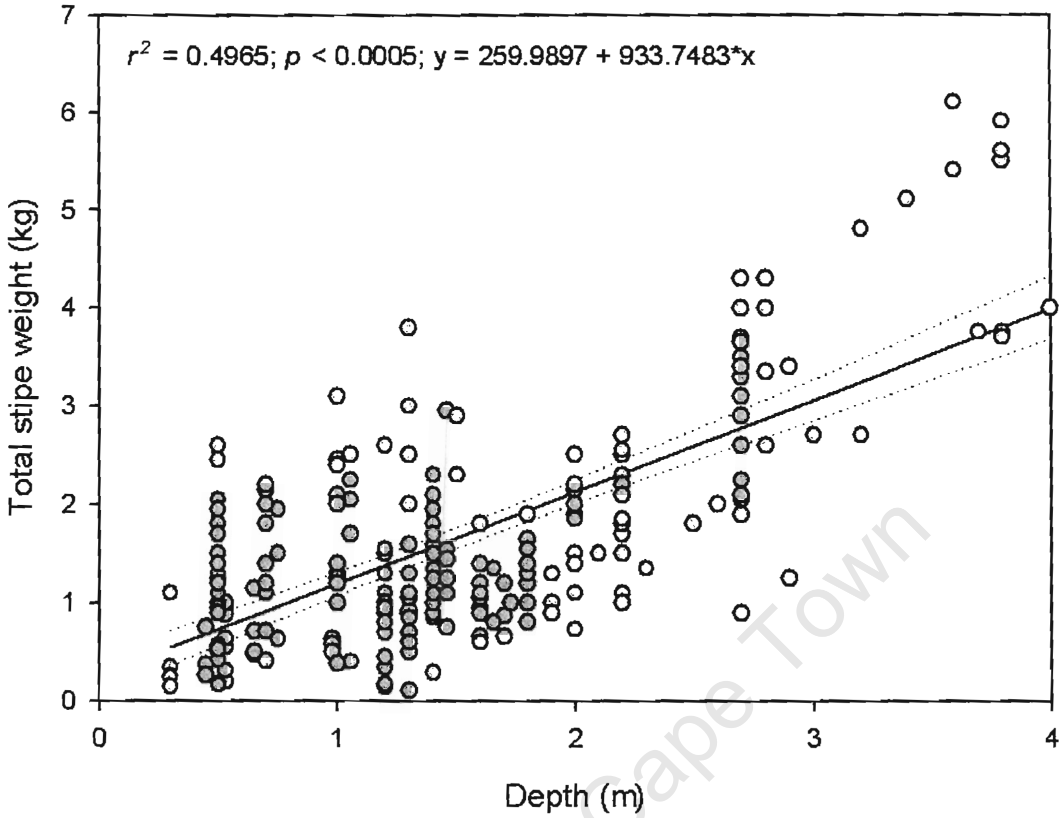

Figure 7. Total stipe stipe weight (kg wet wt) of *E. maxima* with depth. Dotted lines indicate the 95% confidence interval.

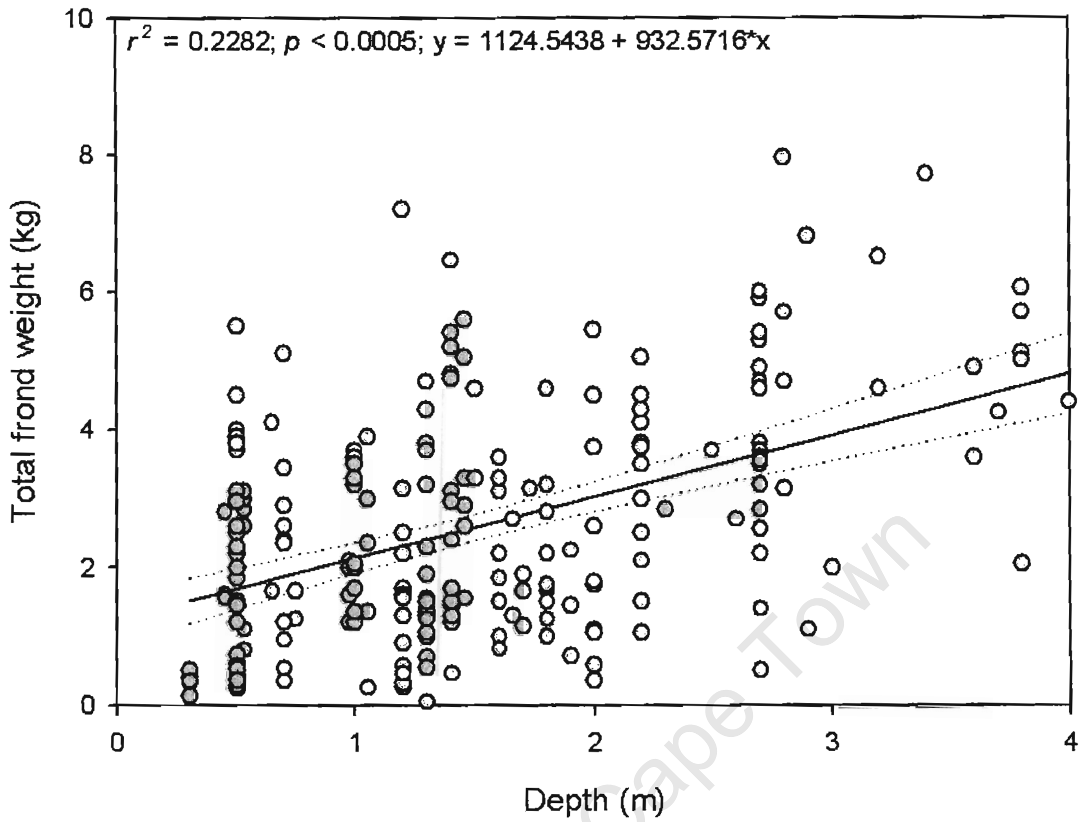

Figure 8. Total frond weight (kg wet wt) of *E. maxima* with depth. Dotted lines indicate the 95% confidence interval.

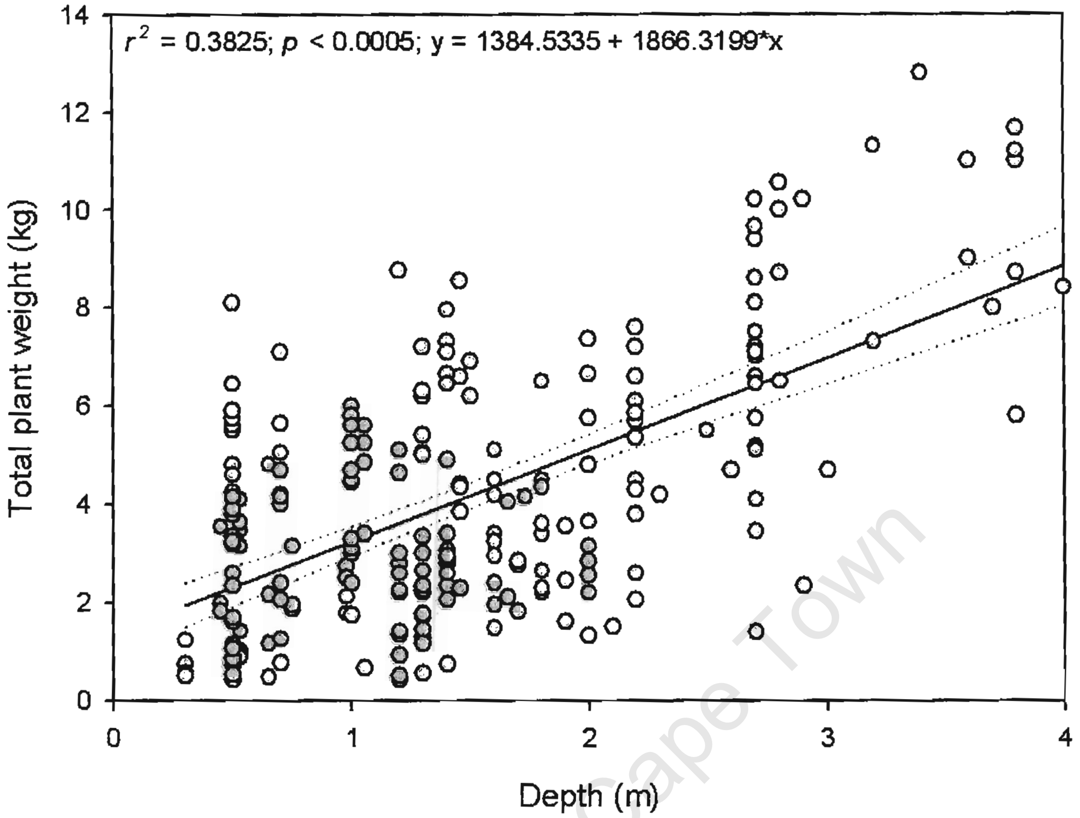

Figure 9. Total plant weight (kg wet wt) of *E. maxima* with depth. Dotted lines indicate the 95% confidence interval.

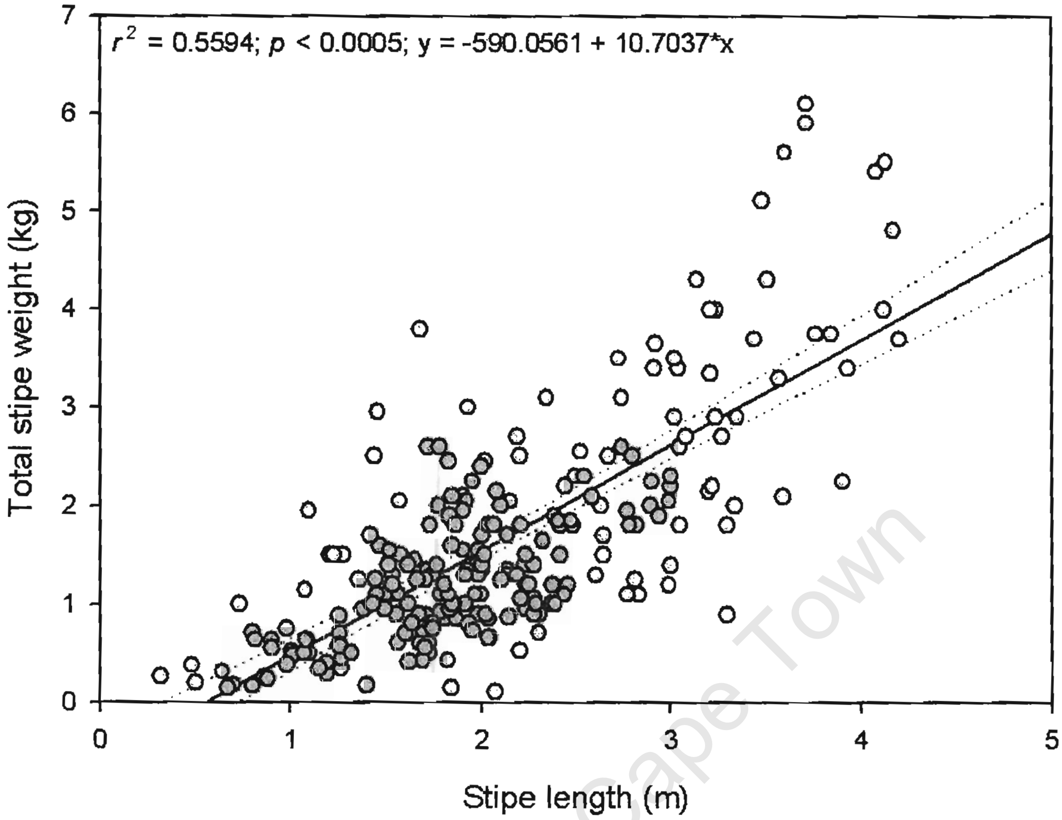

Figure 10. Total stipe weight (kg wet wt) of *E. maxima* with an increase in total stipe length (cm). Dotted lines indicate the 95% confidence interval.

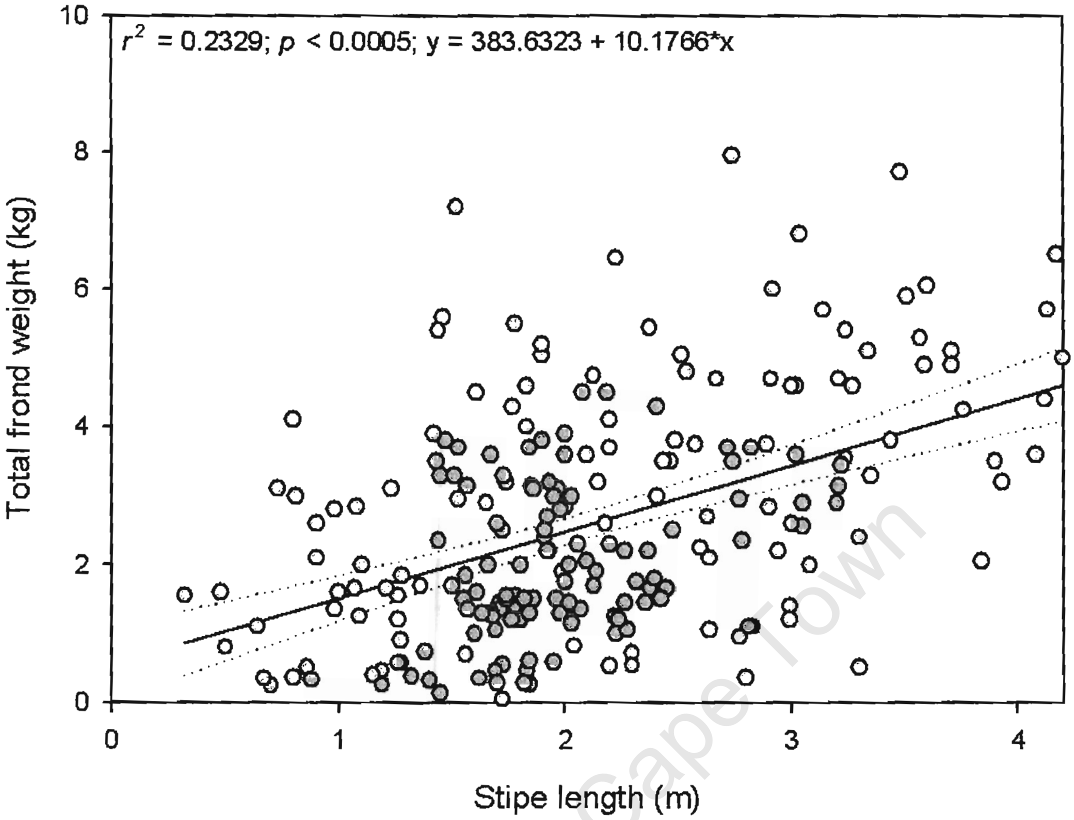

Figure 11. Total frond weight (kg wet wt) of *E. maxima* with an increase in total stipe length (cm). Dotted lines indicate the 95% confidence interval.

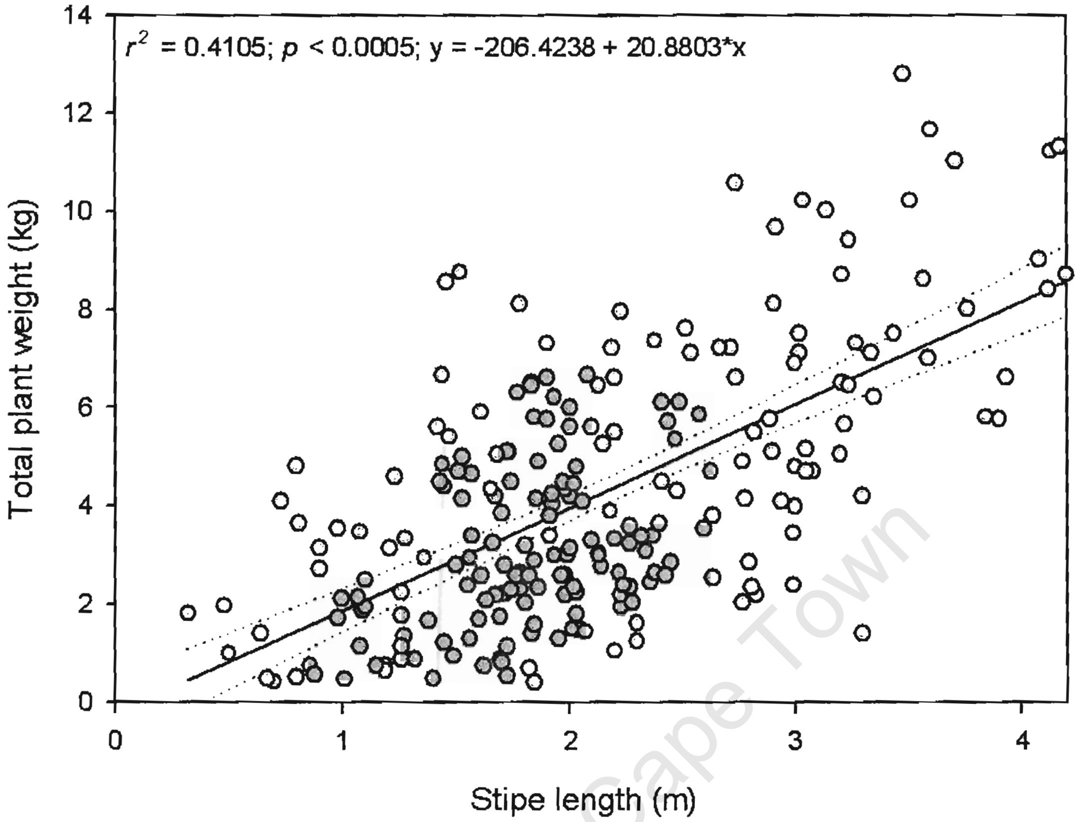

Figure 12. Total plant weight (kg wet wt) of *E. maxima* with an increase in total stipe length (cm). Dotted lines indicate the 95% confidence interval.

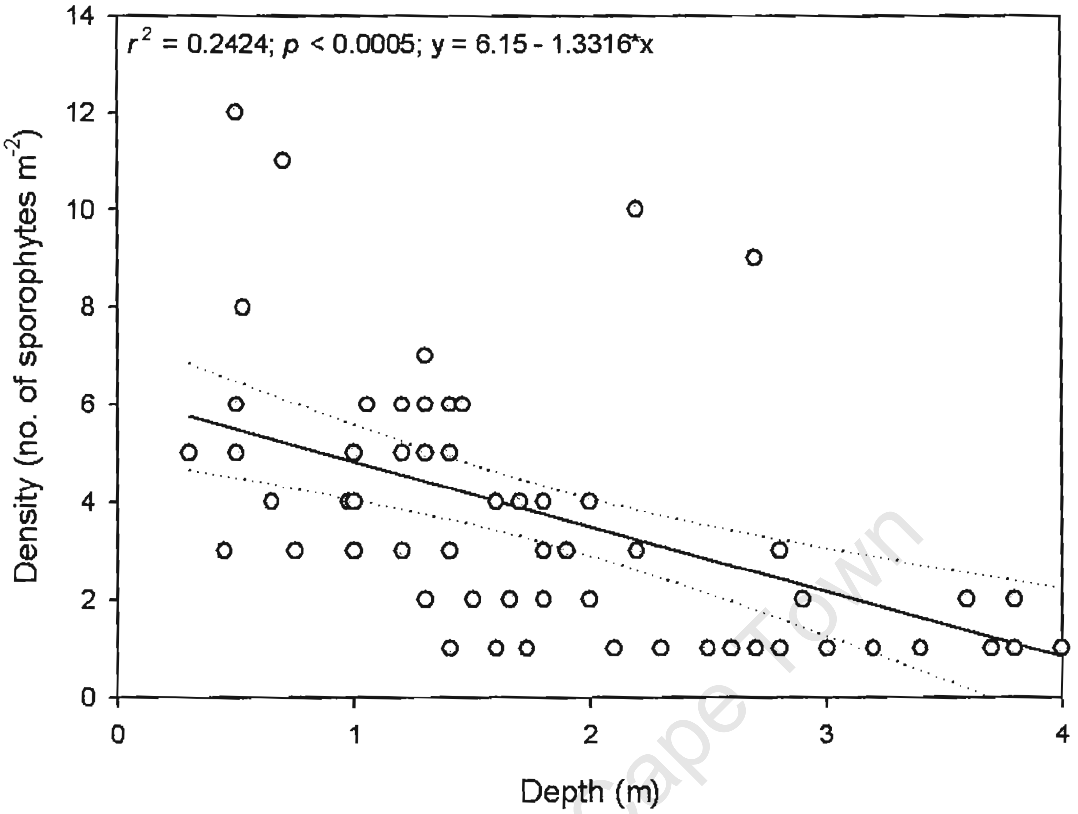

Figure 13. Density of *E. maxima* with depth. Dotted lines indicate the 95% confidence interval.

Table 1: Shows the contribution to total biomass of the different parts of a kelp sporophyte at different depths. The average biomass (kg wet wt m^{-2}) is also indicated with Standard Errors. The supplement table indicates the significant values (*p*) between the different depth classes (AVOVA, Tukey *post-hoc* HSD test).

		Surface kelp (%)	Subsurface kelp (%)	total contribution (%)	Average biomass (kg m^{-2}) with Standard Errors
deep n=91	stipe	15	34	49	16.1 ± 2.56
	fronds	16	35	51	
intermediate n=218	stipe	22.5	16.5	39	12.3 ± 1.75
	fronds	35	26	61	
shallow n=193	stipe	32	3	35	14.2 ± 1.30
	fronds	55	10	65	
	Total	**62**	**38**		

Depth class	**Intermediate**	**Shallow**
Deep	0.4433	0.9322
Intermediate		0.6803

Table 2. Comparison between the biomass at different study sites. Comparison is made between the average biomass of all plants and only surface-reaching plants as well as the biomass of the fronds of all the plants and of those of surface-reaching plants with Standard Errors. The supplement table indicate significant values (*p*) for total biomass between sites (ANOVA, Tukey *post-hoc* HSD test).

Place	Average biomass of all plants per m^2 (kg wet)	Average biomass of fronds of all plants per m^2 (kg wet)	Average biomass of all surface reaching plants per m^2 (kg wet)	Average biomass of fronds of all surface reaching plants per m^2 (kg wet)	Density of plants per m^2
Glencairn	10.0 ± 1.53	6.0 ± 1.19	7.6 ± 1.66	4.7 ± 1.25	5.7 ± 0.66
Kommetjie	21.3 ± 4.26	12.7 ± 2.40	13.1 ± 3.68	7.8 ± 2.14	5.7 ± 0.93
Kwaai Bay	10.7 ± 3.52	6.8 ± 2.32	5.1 ± 3.06	3.2 ± 1.96	2.8 ± 0.87
Mauritz Bay	10.5 ± 1.73	7.6 ± 1.37	6.1 ± 1.79	4.4 ± 1.31	4.3 ± 0.87
Olifantsbos 1	15.1 ± 3.05	8.7 ± 1.79	8.6 ± 2.01	5.0 ± 1.17	4.1 ± 0.75
Olifantsbos 2	14.4 ± 3.79	8.4 ± 2.34	10.8 ± 3.51	6.5 ± 2.22	2.8 ± 0.73
'Pump House'	11.1 ± 2.68	6.9 ± 1.54	1.8 ± 1.08	1.2 ± 0.81	4.5 ± 1.14
Soetwater	17.0 ± 4.97	9.0 ± 2.60	12.2 ± 4.51	7.4 ± 2.65	3.9 ± 0.92
Average	**14.5 ± 1.33**	**8.6 ± 0.77**	**8.8 ± 1.13**	**5.3 ± 0.68**	**4.4 ± 0.32**

Place	Glencairn	Kommetjie	Kwaai Bay	Maurits Bay	Olifantsbos 1	Olifantsbos 2	'Pump House'
Kommetjie	0.0001						
Kwaai Bay	0.2630	0.9792					
Maurits Bay	1.0000	0.0006	0.3137				
Olifantsbos 1	0.3335	0.1181	0.9914	0.4579			
Olifantsbos 2	0.0001	0.1779	0.1000	0.0001	0.0003		
'Pump House'	0.9999	0.5162	0.9510	0.9998	0.9974	0.0236	
Soetwater	0.0001	0.9997	0.9129	0.0003	0.0607	0.4296	0.3832

Discussion

Kelp harvesting is a labour intensive process so ideally harvesters would want to harvest in areas where they can get the most kelp for the least amount of work. Currently, harvesting in South Africa is done by hand from a boat by lifting the head of the kelp plant out of the water, cutting it off using a sickle and tossing it into the boat. The present study shows that stipe length (Fig. 2), stipe weight (Fig. 3), frond weight (Fig.4) and average total plant weight (Fig.5) over a range of depths and at different sites, is higher in deep than shallow zones. This means that generally the deeper plants were longer, heavier and had more frond biomass.

The variation between sites could be due to differences in the different environmental factors at these sites (see for example Odum, 1963; Field & Giffiths, 1991; Dayton, 1985) but it was beyond the scope of this study to measure such factors. It would be possible that maximum depth of the site would affect some environmental factors which in turn affect the kelp. The three Jacobsbaai sites did not have kelp deeper than 3 m at these sites. Here the kelp beds are narrow (± 80 m wide) and bordered offshore by sand or sand-covered rock. Taylor & Littler (1982) showed that sand can control community structure and I have observed that often kelp does not occur on sand-covered rock.

The effect of depth becomes more apparent when studying Figures 6-9 which show the direct relationship that exists between depth and stipe length (Fig. 6), stipe weight (Fig. 7), frond weight (Fig. 8) and total plant weigh (Fig. 9). Allen & Griffiths (1981) also found an increase in the stipe weight, frond weight and total weight with an increase in depth. Since kelp harvesting is a labour intensive process and often the time spent harvesting is limited by the low tide (more kelps are exposed at the surface during this time) they would want to harvest the largest plants to gather the most amount of frond material in the shortest amount of time. The individual sporophytes in the deep have the highest frond biomass and thus it would be advantageous to harvest these plants. Figures 11-13 confirm this and the plants with the longest stipes have the highest stipe weight, frond weight and total weight. A similar relationship was found by Mann *et al.* (1979) when he compared the stipe weight to the stipe length of *E. maxima* sporophytes.

In the deep zone, half of the biomass of surface-reaching plants comprises fronds while the other half comprises stipe (Table 1) with a total biomass of 16.1 kg m^{-2} (wet wt). This figure is similar to what North (1971) and Mann (1972, 1973) found for *Laminaria* beds and what Aleem found (1973) for *Macrocystis* beds. This pattern of frond biomass to stipe ratio is also observed for the subsurface kelp although there is a greater total kelp biomass in the subsurface component of the population. In *Laminaria hyperborea* beds it was found that the understorey is 'ready to take over' when adults are removed (Christie *et al.*, 1998). The same process might be at work in these kelp beds.

In the intermediate depth zone the frond biomass contributed more to the overall biomass of the population than the stipe biomass. The frond biomass of the surface kelp is also higher than the frond biomass of the subsurface kelp and this is the same for the stipe biomass. Because the water is shallower we can expect sporophytes to reach the surface more rapidly, so that there are more young plants at the surface. Young plants as well as old plants are able to reach the surface. The total biomass in the intermediate depth was estimated at 12.3 kg m^{-2} (wet wt), a value intermediate between those in the shallow and deep zones.

It was not surprising that in the shallow zone, a large percentage of the overall kelp biomass comprised surface-reaching kelp, because young sporophytes can reach the surface rapidly, and the vigorous wave action ensures a good supply of light and nutrients to a high frond biomass. Furthermore, although the density of kelp sporophytes is limited by the two-dimensional space available for attachment (substratum area), in the sub-canopy, it may also be limited to some extent by the three-dimensional space (volume) available to be occupied by the stipe and canopy: this is clearly proportional to the depth of the water. In other words, the deeper the water, the more sub-canopy can fit in under the water surface. The shallow zone contained the highest percentage of the fronds relative to stipes, as might be expected, because shorter stipes are necessary in shallow water. However, the lack of any statistical difference between the overall biomass of *E. maxima* in the three depth zones tested, results from the relationship between sporophytes sizes (length and weight) and densities: the individual plants in the deep water are on average larger and heavier compared to those in the shallower depths. Kelps in deeper water tend to have longer stripes so that they can reach the surface to expose the maximum amount of photosynthetic material to light, as was reported for *Macrocystis* by Lüning (1990). The higher densities in the shallow and intermediate sites compensate for the lower per plant biomass. Although the densities of the sporophytes are lower in the deep zone, compared to the intermediate and shallow zones, per plant a harvester would be able to harvest more kelp fronds from a plant in this zone. Shallower areas also pose the problems of sub-surface rocks and blinders which could cause major damage to the hull of a boat as well as the danger of 'freak waves' which could capsize the vessel. It is also more difficult to manoeuvre boats in shallower water because of the dense canopies of kelp.

Allen & Griffiths (1981) worked out a total biomass of *Ecklonia maxima* at 17 kg m^{-2} (wet wt), compared to our 14.5 kg m^{-2} (wet wt), but their study was done over a depth range of 0-8 m while this study had a maximum depth of 4 m. However, they used only one 0.25 m^2 quadrate, with no replication, compared to the multi replicated 1 m^2 used in this study. Their lack of replication raises doubts to the reliability of their data. Mann *et al.* (1979), on the other hand estimated the biomass at 12 kg m^{-2} for this species at Miller's Point in False Bay. Considering only plants that reach the surface, the present study calculated a mean biomass of 8.8 kg m^{-2} (wet wt), with a mean frond biomass of 5.3 kg m^{-2} (wet wt). These figures compare well with those obtained for *Laminaria hyperborea* beds by Sjøtun *et al.* (1993) in Norway. They estimated *L. hyperborea* biomass at between 6-16 kg m^{-2} (wet wt) while Kain (1977) estimated it at 14 kg m^{-2} (wet wt) at the Isle of Man for the same species. Chapman & Lindley (1981) estimated the biomass of *Laminaria solidungula* at 0.9 kg m^{-2} (wet wt) in Canada. Mann (1972, 1973) estimated the biomass of *L. lonicruris* at 11.5 kg m^{-2} (wet wt) and for *L. digitata* and *L. longicruris* at 16 kg m^{-2} (wet wt), also in Canada. These figures gives an indication of the enormous regional and geographical variability in kelp biomass.

Glencairn and the three Jacobsbaai sites (Kwaai Bay, Mauritz Bay and 'Pump House') had the lowest biomasses of 10.0; 10.7; 10.5 and 11.1 kg m^{-2} (wet wt) respectively. These four sites are also where the kelp beds are very narrow (50-80 m), and perhaps more influenced by sand movement, since their outer boundaries are sandy. However, these sites are also topographically rather different from the others in this study. The three Jacobsbaai sites are on granite, with substrata of broken rocks and boulders, and large ledges. The Glencairn site, although on a substratum of Table Mountain Sandstone, also is broken and topographically varied. All the other sites comprise gentle-sloping, wide, wave-cut platforms of Table Mountain Sandstone, with wider, more uniform kelp beds. The rest of the sites, Kommetjie, Olifantsbos 1 and 2, and Soetwater had biomasses of 21.3; 15.1; 14.4 and 17.0 kg m^{-2} (wet wt) respectively and these sites have kelp beds of up to 200 m wide.

Apart from the variability in biomass there was also variability in the density of plants. The average density was 4.4 plants m^{-2} with the highest being 5.7 and the lowest 2.8 plants m^{-2}. This is lower than what was found by Velimirov *et al.* (1977), who reported a density of 6 plants m^{-2} in a depth range of 4-8 m. The point is that densities are highly variable, and can range from zero to 9 plants m^{-2} (Velimirov *et al.* (1977). All the sites from this study had fairly consistent densities ranging from 2.8 – 5.7 plants m^{-2}, but the average across the sites was 4.4 plants m^{-2}.

Once the average total biomass per m^2 and the size of the kelp bed is known, the biomass of the entire kelp bed cab be calculated:

$$b = w \times a$$

where b is the biomass of the entire kelp bed, w is the average biomass per m^2 (kg.m^{-2}) and a is the area of the kelp bed (m^2). This is an essential step for the South African Marine and Coastal Management to use in establishing Maximum Sustainable Yields (MSY), kelp reserves and concession boundaries. Can a universal average biomass weight (kg m^{-2}) be used to determine the biomass of kelp beds?

The average biomass over all sites (Table 2) suggest the use of a mean of 14.5 kg m^{-2} but this figure is considerably higher than data for some of the areas. Using this data it would be more realistic to use a figure of 10 kg m^{-2}. This would ensure, when calculating the total biomass of kelp beds, a degree of conservatism that would decrease the possibility of over-harvesting of areas. Nevertheless, caution must be exercised in assuming that particular kelp beds have a particular biomass, and where possible, *in situ* measurements should be done, at least to estimate the density of sporophytes.

Conclusions

The biomass at different sites varies but a general pattern shows that plants in deeper water are larger and heavier. However, whether you harvest in deep water, intermediate depth or shallow water makes no difference to the amount of kelp biomass that is available to harvesters. The average biomass of plants increase with depth but at the same time the density of plants decreases. Thus, although plants in the deep are bigger and heavier, the average biomass across a kelp bed (from deep to shallow) is similar. Because the average biomass for all the sites was 14.5 kg per m^2, and there were no significant difference between depths, this value can be used as a general biomass estimate. But the area with the lowest biomass has a biomass of 10.7 kg m^2 (wet) and thus I propose the use of a conservative figure of 10 kg m^2 (wet) to ensure that no areas are over-harvested. However, it is recommended that for greater accuracy, at least densities should be measured *in situ*.

Chapter 3

A simple, new method for rapid estimation of *Ecklonia maxima* biomass.

Introduction

The amount of fresh kelp fronds (*Ecklonia maxima*) harvested in South Africa increased exponentially from less than one ton (wet) in 1992 to more than 6000 tons (wet) in 2003 (Troell *et al.*, in press). This increase is due to the increase in the number of abalone farms along the South African west coast that use the kelp fronds as feed for the delicacy, *Haliotis midae* (abalone). Demand for kelp is about 7% of the animals' body mass per day. This means that to produce 100 tons of abalone, to a size between 50-70mm in diameter, would require five tons of freshly harvested kelp daily (Levitt *et al.,* 1992). As more abalone farms are built along the South African west coast we will see the harvesting pressure on kelp beds increase.

As this pressure on the resource increases, it is imperative to know the biomass of kelp beds to be able to set maximum sustainable yields (MSY) for the harvesters. Currently the determination of the biomass of kelp beds is a labour intensive and time-consuming exercise. To obtain biomass data from ten – twelve 1 m^2 quadrats, at one site, requires six people working for a period of between four to five hours.

In South Africa biomass estimates have traditionally been done by laying a transect line, from the shore to the end of the kelp bed, and sampling, at intervals, 1 m^2 quadrats along that transect. Every second quadrat was taken as a sample and the kelp weighed (Velimirov *et al.*, 1977; Field *et al.*, 1980; Levitt *et al.*, 2002). This was the same method employed by Mann (1972) in a *Laminaria* bed in Canada but he used a 0.5 m^2 quadrat. The sampling of kelp biomass is normally done by placing quadrats on the substratum and harvesting all the kelp contained in them. This has been used successfully by Aleem (1973) in California in a *Macrocystis* bed, by Schiel & Nelson (1990) sampling *Macrocystis pyrifera* and *Ecklonia radiata* in New Zealand and also Christie *et al.* (1998) in a *Laminaria hyperborea* bed in Norway. Others have also used this method but with 0.25 m^2 quadrats (Chapman & Lindley, 1981; Kendrick *et al.*, 1999).

Since *E. maxima* is a canopy-forming kelp, and abalone-feed harvesters cut surface fronds, the most efficient method to determine the biomass of a kelp bed would be to establish a relationship between the number of kelp heads floating at the surface and the kelp biomass.

Materials and Method

The method compares densities of kelp heads at the water surface, obtained from a floating 1m^2 quadrat, with the biomass (kg m^{-2}) of the kelp bed. The 1 m^2 quadrat is made of white, 40 mm PVC pipe with a screw top at the one corner to get rid of water if there is a leak in one of the pipes.

The kelp bed, at Olifantsbos (34°16’15”S 18°22’50”E) (see Fig. 1 in Chapter 2) that was selected, consisted entirely of *Ecklonia maxima*. It is a typical kelp bed, exceeding 150 m in width and is about 500m long but is accessible only at certain times of the year as most of the time there is a large swell making it virtually impossible to sample. On the day of sampling conditions were near perfect with little to no wind or swell and 20 – 25 m underwater visibility.

The quantification of surface kelp density (number of heads at the water surface within 1 m^2) was done within 30 minutes either side of low spring tide (because the density of kelp heads reaching the surface is the highest at low spring tide and this is when harvesters operate). The procedure required two divers; one to position the buoyant quadrat (1 m^2), and another to record the number of heads reaching the surface. The diver then followed the surface kelp to the substratum and cut the plant just above the holdfast. The second diver then swam the cut kelp to the shore where it was weighed. The density–biomass relationship was established by setting biomass of surface-reaching kelp as a linear function of the number of surface heads. Quadrats were haphazardly sampled at equal intervals along a transect spanning the width of the kelp bed, starting at the outer extreme of the kelp bed and working toward the shore. Quadrats were placed at a maximum of 5 m intervals with a minimum of 10 quadrats being done over a depth range of between 1.5-7 m.

Further comparisons between surface density and biomass were obtained at a number of sites; Glencairn (34°09'57"S 18°25'54"E), Olifantsbos (34°16'15"S 18°22'50"E), Soetwater (34°10'00"S 18°19'54"E), Kommetjie (34°08'30"S 18°19'16"E), and one site close to Jacobsbaai on the West Coast, Mauritzbaai (32°58'42"S 17°52'55"E) (see Fig. 1 in Chapter 2). At these sites the method differed from the first test at Olifantsbos, in that only bottom quadrats were used, but a simple linear regression was performed using STATSTICA (version 7) to determine the relationship between the biomass of surface-reaching kelp and the number of heads at the surface, at these sites. The number of heads reaching the surface in each 1 m^2 quadrat calculated from the depth at which the plant occurred and the stipe length of that plant. If a plant had a stipe length longer or equal to the depth it was assumed that it would be a surface-reaching plant.

Results

The density-biomass relationship at Olifantsbos showed a linear relationship between the density of surface reaching kelp, as measured by counting the exposed kelp heads, and kelp biomass of surface reaching kelp ($r^2 = 0.5973$; $p = 0.0007$) (Fig. 1). A similar relationship exists between surface density and frond biomass of surface reaching kelp ($r^2 = 0.4767$; $p = 0.0044$) (Fig 2).

Figures 3 – 7 shows the correlation between the total biomass of surface-reaching kelp and the number of heads reaching the surface, obtained by the second method. A very good direct relationship exists at all the sites: Glencairn ($r^2 = 0.4284$; $p = 0.0289$) (Fig. 3); Olifantsbos ($r^2 = 0.4611$; $p = 0.0107$) (Fig. 4); Kommetjie ($r^2 = 0.6620$, $p = 0.0013$) (Fig. 5); Soetwater ($r^2 = 0.7977$; $p = 0.0028$) (Fig. 6) and Mauritz Bay ($r^2 = 0.9142$; $p = 0.0008$) (Fig. 7). Furthermore, when combining the data from all the different sites (only sites where data was collected using the second method), for the surface-reaching kelp, there was a direct relationship between both the total biomass and total frond biomass (kg m^{-2}) of surface kelp and the density of kelp heads at the surface ($r^2 = 0.5607$; $p < 0.0005$) (Fig. 8); ($r^2 = 0.5736$; $p < 0.0005$) (Fig. 9). The same trend was observed when the total biomass (kg m^{-2}) (all plants: surface and subsurface kelp) was correlated with the density of kelp heads at the surface ($r^2 = 0.3262$; $p < 0.0005$) (Fig. 10) although a big variation around the regression line was observed.

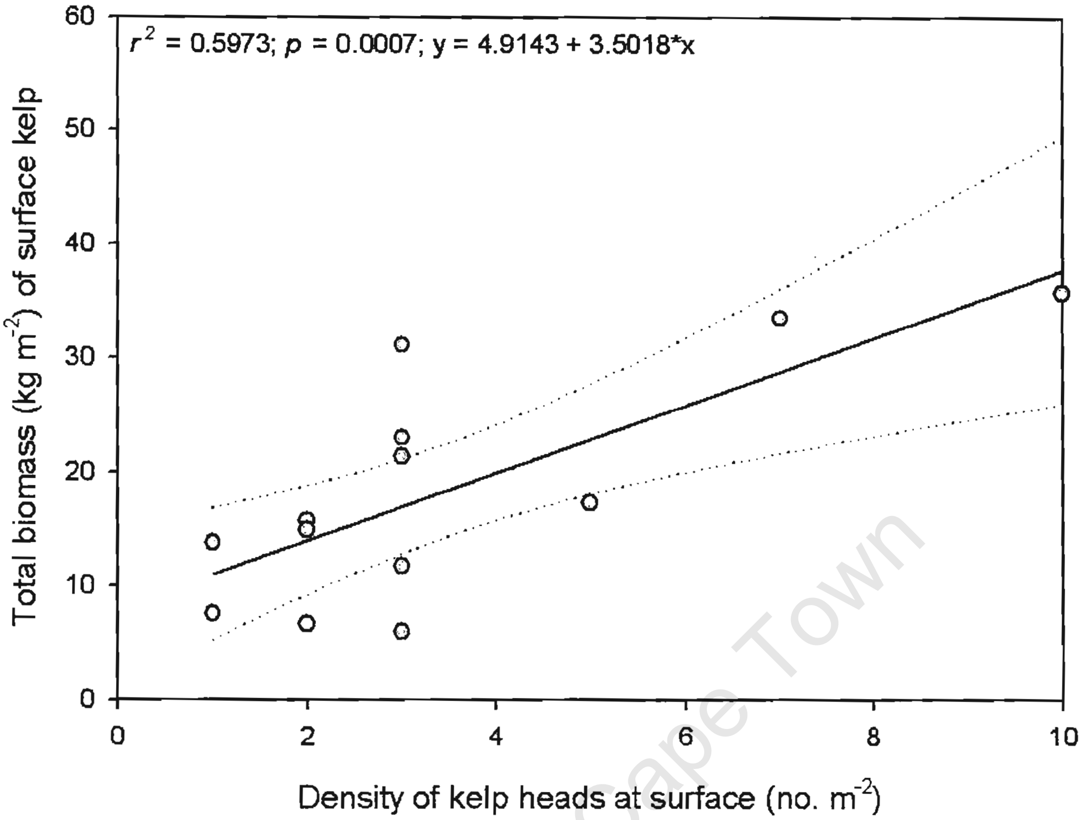

Figure 1. The relationship between the total biomass of surface-reaching kelp and the density of kelp heads present at the surface at Olifantsbos. Dotted lines indicate the 95% confidence limit.

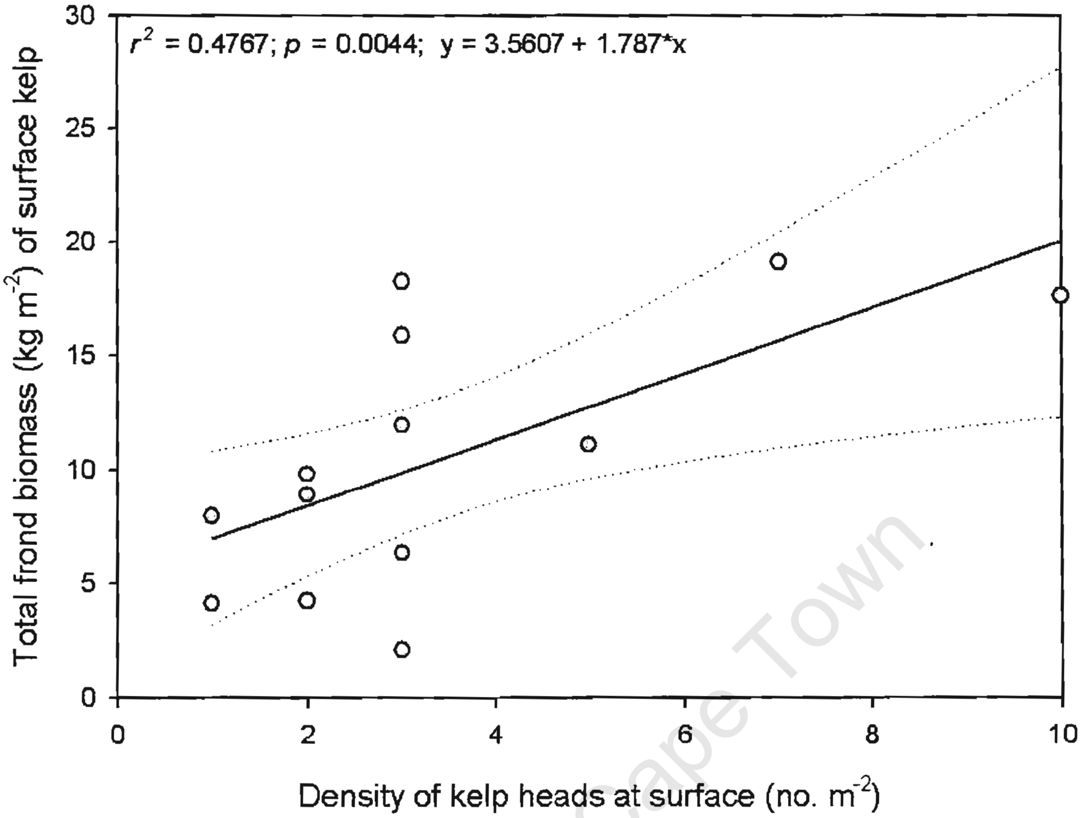

Figure 2. The relationship between the total frond biomass of surface-reaching kelp and the density of kelp heads present at the surface at Olifantsbos. Dotted lines indicate the 95% confidence limit.

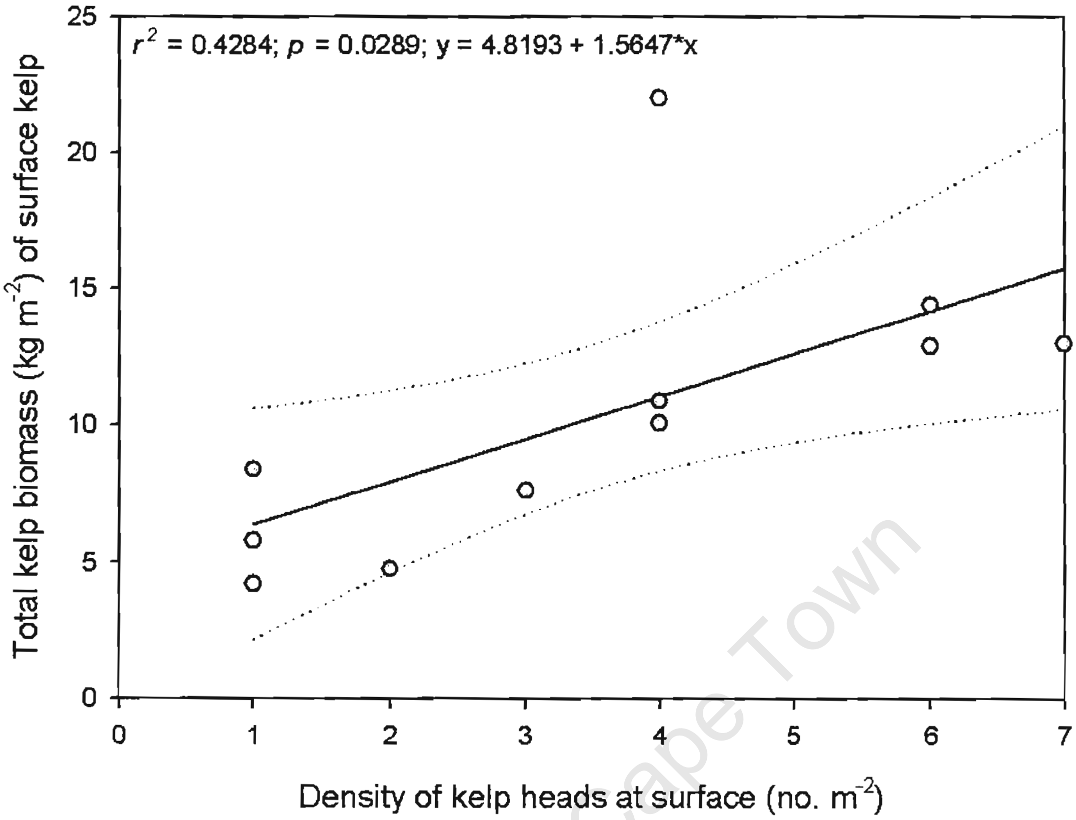

Figure 3. The relationship between the total biomass of surface-reaching kelp and the density of kelp heads present at the surface at Glencairn using the traditional (bottom quadrat) biomass estimation method. Dotted lines indicate the 95% confidence limit.

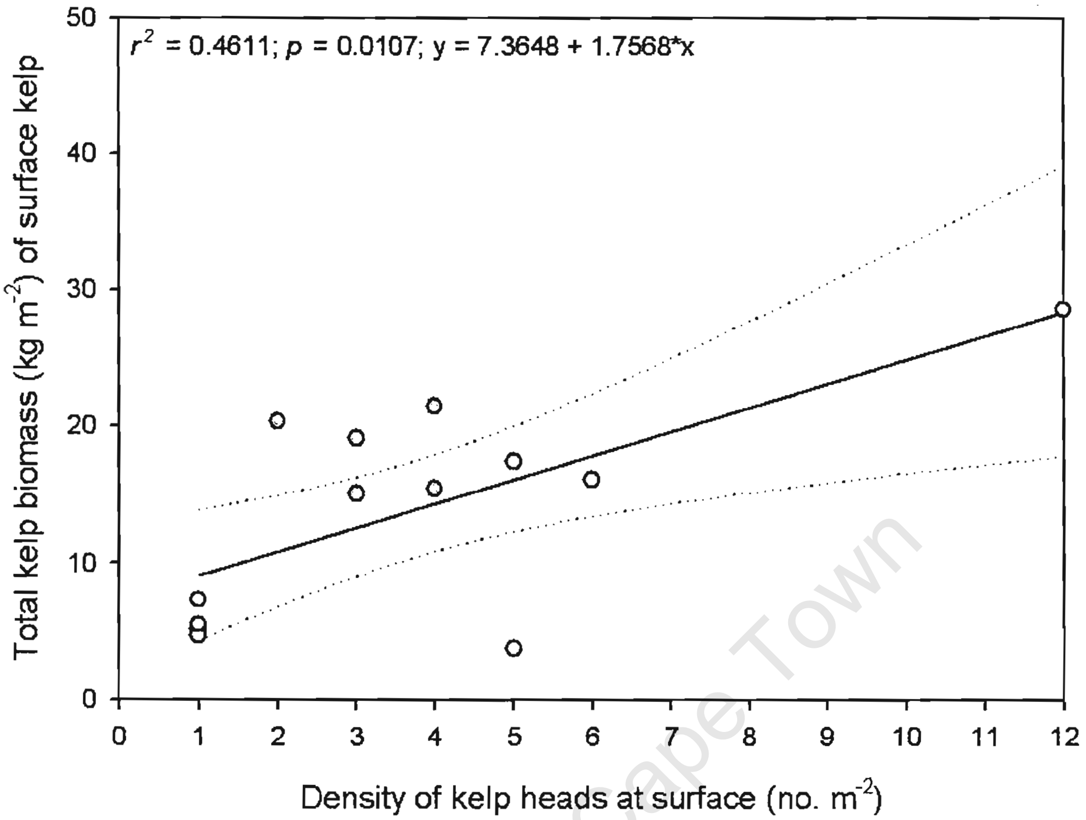

Figure 4. The relationship between the total biomass of surface-reaching kelp and the density of kelp heads present at the surface at Olifantsbos using the traditional (bottom quadrat) biomass estimation method. Dotted lines indicate the 95% confidence limit.

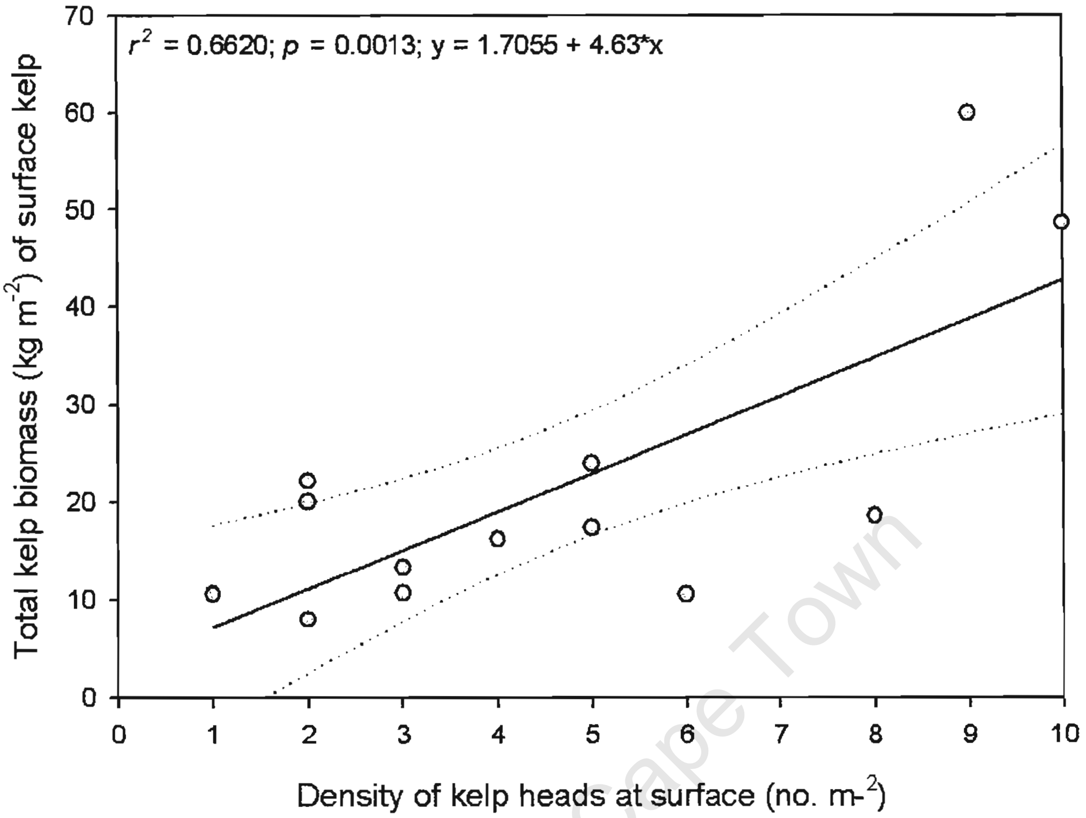

Figure 5. The relationship between the total biomass of surface-reaching kelp and the density of kelp heads present at the surface at Kommetjie using the traditional (bottom quadrat) biomass estimation method. Dotted lines indicate the 95% confidence limit.

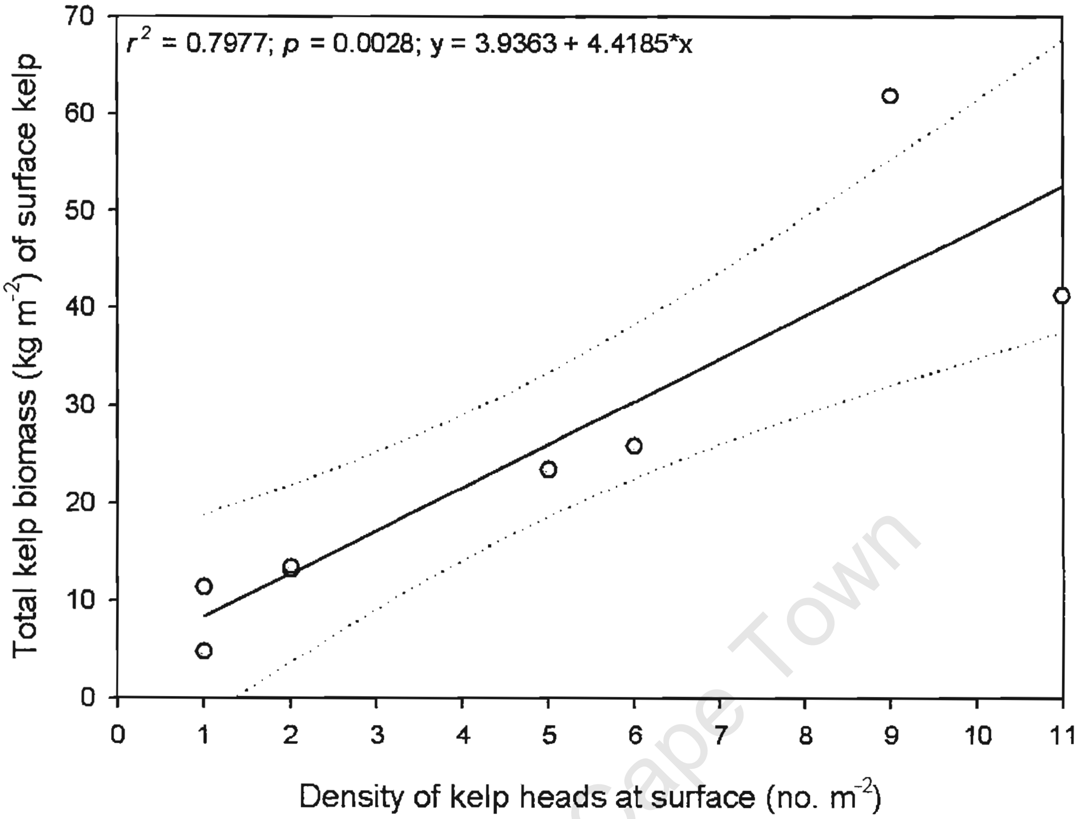

Figure 6. The relationship between the total biomass of surface-reaching kelp and the density of kelp heads present at the surface at Soetwater using the traditional (bottom quadrat) biomass estimation method. Dotted lines indicate the 95% confidence limit.

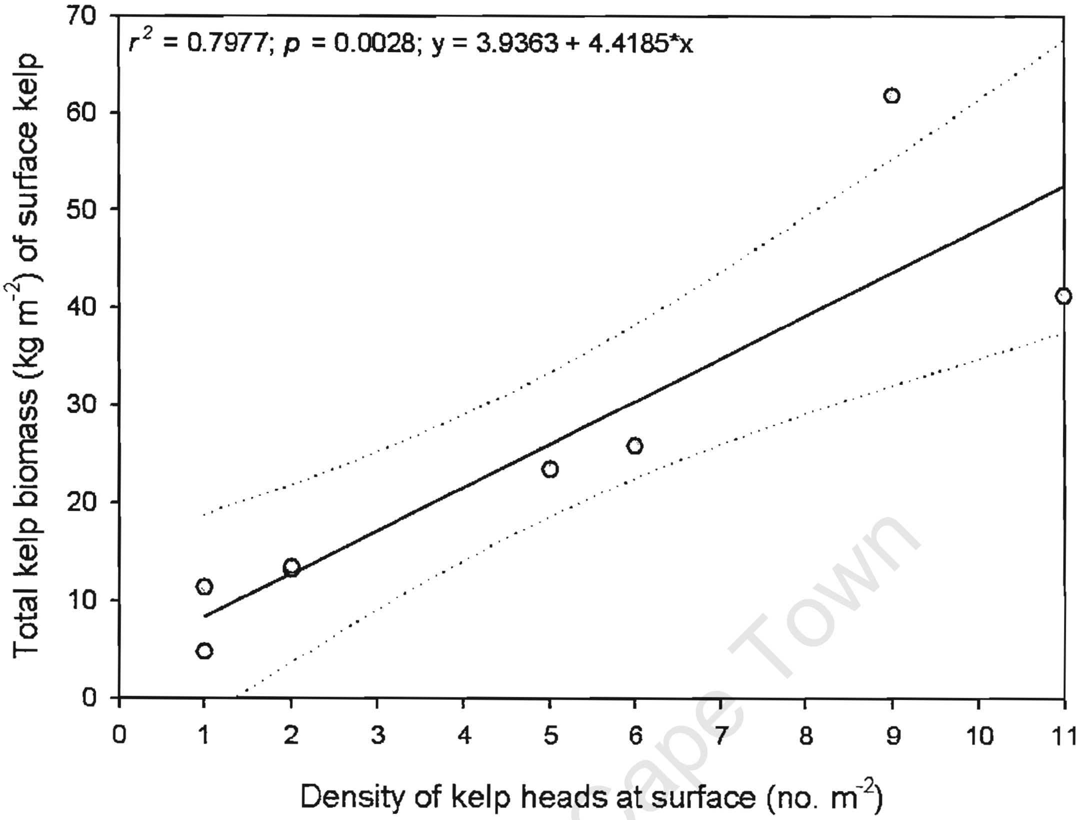

Figure 7. The relationship between the total biomass of surface-reaching kelp and the density of kelp heads present at the surface at Mauritz Bay using the traditional (bottom quadrat) biomass estimation method. Dotted lines indicate the 95% confidence limit.

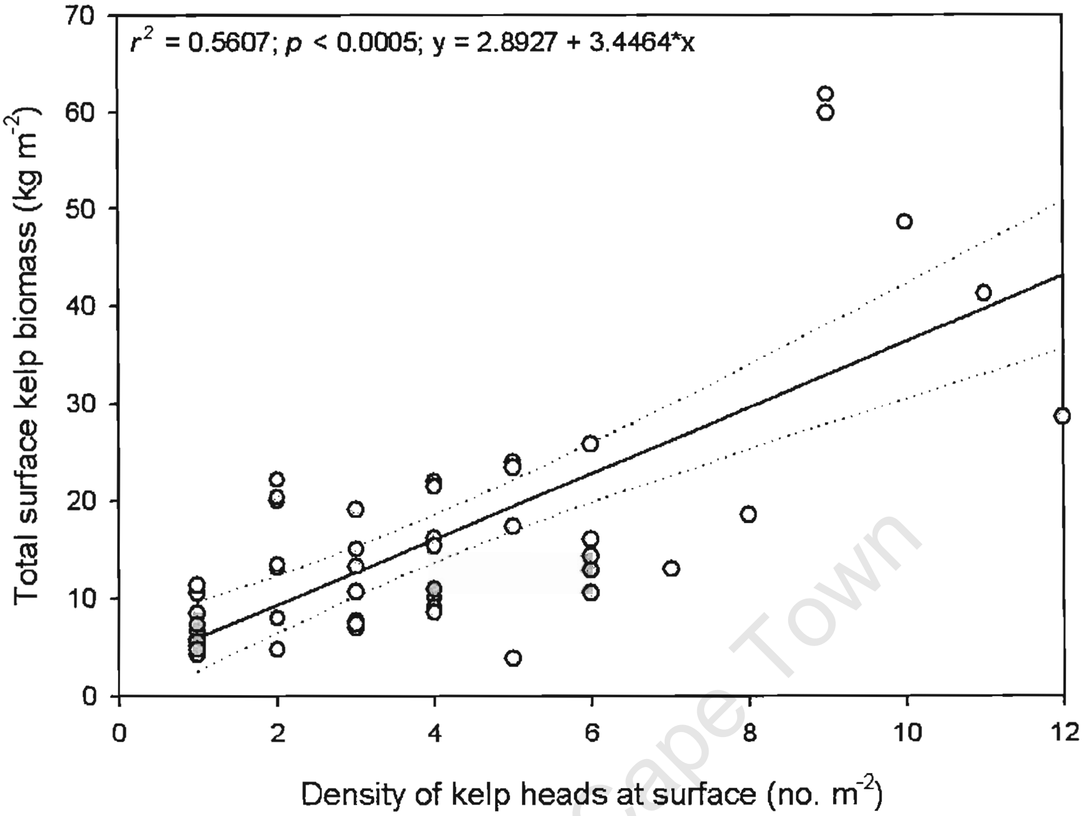

Figure 8. The relationship between the total biomass of surface-reaching kelp (kg m^{-2}) and the density of heads at the surface (m^{-2}). The data from all the sites where the traditional (bottom quadrat) biomass estimation process was used, were combined. The dotted lines indicate the 95% confidence limit.

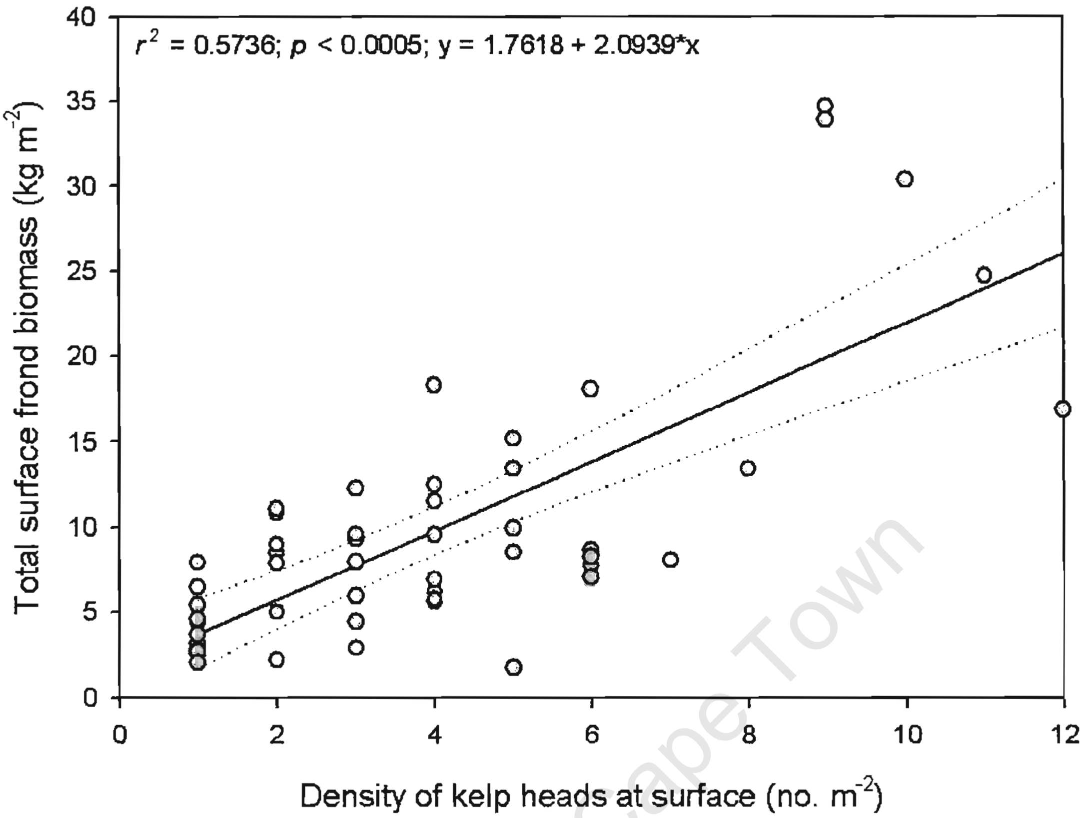

Figure 9. The relationship between the frond biomass of surface-reaching kelp (kg m^{-2}) and the density of heads at the surface (m^{-2}). The data from all the sites where the traditional (bottom quadrat) biomass estimation process was used, were combined. The dotted lines indicate the 95% confidence limit.

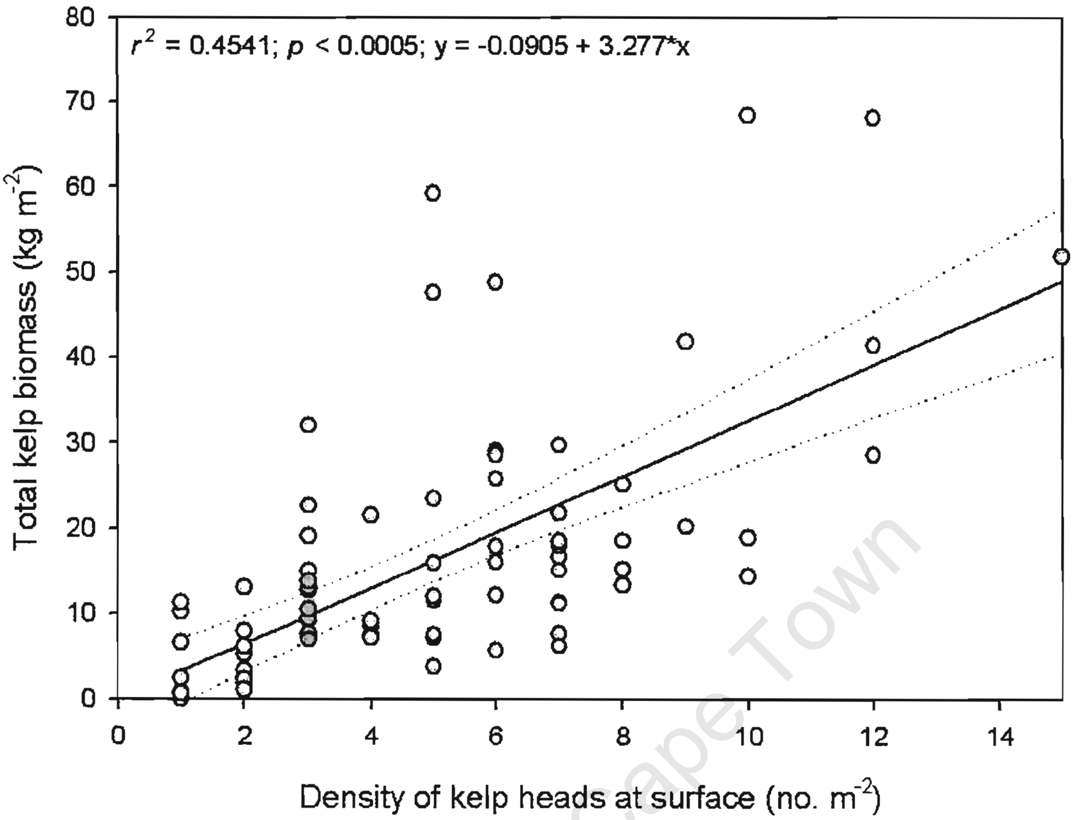

Figure 10. The relationship between the total biomass of kelp (kg m^{-2}) (surface and subsurface kelp) and the density of heads at the surface (m^{-2}). The data from all the sites where the traditional (bottom quadrat) biomass estimation process was used, were combined. The dotted lines indicate the 95% confidence limit.

Discussion

Previous methods of determining *E. maxima* biomass involved long diving hours and physically demanding methods. This made kelp monitoring and biomass assessment very difficult and time consuming. Previously all kelp in 1 m^2 area was harvested and carried ashore by divers. Once these quadrats have been harvested and brought to shore the measuring and weighing would start.

This new method will make biomass estimation quicker and easier, so that the biomass of more kelp beds can be established and information can be relayed to management quicker for better decision making.

The relatively good r^2 and small *p*-values show that the density of surface-reaching kelp can reliably be used as a proxy measure of kelp biomass, and that it can, to a large degree, be used to replace the current diver-based method in future.

Many studies of kelp biomass have used the bottom quadrat approach (Mann, 1972; Allen, 1973; Velimirov *et al.*, 1977; Field *et al.*, 1980; Chapman & Lindley, 1981; Schiel & Nelson, 1990; Christie *et al.*, 1998; Kendrick *et al.*, 1999; Levitt *et al.*, 2002;), but this is the first time an attempt has been made to estimate the biomass (either surface biomass or overall biomass) from floating quadrats. Questions might arise as to why remote sensing (e.g. aerial photos) were not used to determine the kelp biomass. A separate study is in progress (Andrew Rand, M.Sc. thesis *in prep.*) involving assessment of various methods of remote sensing of kelp bed area, but to use this method for regular monitoring is both impractical and very expensive. Also, previous attempts to establish a relationship between the diameter of the bulb and the diameter of the stipe to determine the biomass of the kelp have been unsuccessful (*pers com.* R.J. Anderson). The floating quadrat is the first method, other than the bottom sampling method, to show reliable results.

The increased efficiency of the new method can be expressed by comparing the number of man-hours needed for the traditional method of cutting the kelp and swimming it to the shore. The traditional method requires 0.18 man-hours per quadrat compared to the 0.07 man-hours required for the floating quadrat method. The new method is thus 2.6 times faster and equates to a time saving of about 61%.

The data suggest that the new method relates well to the traditional method of establishing kelp biomass (Fig 3-7) which requires the use of SCUBA diving and physically collecting the data. Both methods, as expected, indicated a direct relationship between the biomass of the surface-reaching kelp and number of heads that were present at the surface (Fig. 1-7). This is further supported by the relationship between the density of kelp heads at the surface and the total biomass of surface-reaching kelp as well as the total frond biomass of surface-reaching kelp (Fig. 8-9). Although a weaker relationship than what exists between the surface density and surface biomass, a direct correlation still exists between the density of kelp heads at the surface and the total biomass of kelp (Fig. 10). However, there is a big scattering around the regression line (Fig. 10) and that is why it is recommended that a large number of surface quadrats be done, at a site, to minimize this scatter. Because this floating quadrat method is so quick and easy to do it is realistic to sample 50 quadrats at a time. This would greatly improve the reliability of the results. The best approach would probably be to use the new 'floating quadrat method', to estimate total kelp biomass of an entire bed, provided that, first, a limited traditional biomass estimation is done at the site. This is because different sites appear have somewhat different biomasses, because the differences in local environmental factors. From the findings in Chapter 2 it could be assumed that *E. maxima* beds with similar depth profiles and similar bottom topography could be regarded as being similar and thus data from one site could be extrapolated to another kelp bed.

The main reason this technique is successful in *E. maxima* beds is because this is a canopy-forming kelp and a substantial part of the biomass is concentrated at the surface. Another key to this technique is that it must be possible to estimate the density of sporophytes at the surface; *i.e.* individual plants must be distinguishable from the surface. This would not work for *Macrocystis*, where a singe sporophytes have multiple terete stipes and may tail over many m^2 of water surface, making it almost impossible to distinguish individual plants. Also, obviously, this 'surface method' cannot be employed in subtidal kelp. In these kelp communities the 'bottom quadrate' method must be used.

Conclusion

The method of biomass estimation using surface plant densities is feasible for future use as it enables managers to assess kelp beds more rapidly. Less man-power is needed: even two snorkellers can make the required measurements. This technique allows for teams of two to operate simultaneously in different kelp beds, greatly increasing work efficiency. The fact that limited SCUBA is needed also allows the use of people with no formal dive training which is an added benefit as it will reduce the cost involved in such an operation. However, because a wide variation could be observed around the mean when correlating total biomass with surface kelp head density, it is recommended that a minimum of 50 quadrats be sampled per site. Further studies are needed to continue to refine this promising method of rapid biomass estimation.

Chapter 4

The effect of harvesting on *Ecklonia maxima* population structure, growth and recruitment.

Introduction

South Africa's coast is divided into 23 concession areas and fourteen of these areas have kelp in them, the main species being *Ecklonia maxima*. Levitt *et al.* (2002) studied the regrowth of *Ecklonia maxima* and the understorey biota after harvesting, but knowledge of the effects of harvesting on the subcanopy kelp and kelp recruitment is still very limited. In South Africa kelp is harvested by various methods. When stipe and fronds are required divers cut the stipe at the bottom just above the holdfast, thus killing the plant. The kelp harvested in this manner is used in a patented process to extract growth hormone to be used in the agricultural industry marketed as Kelpak. However, this method is not used for abalone feed and is not considered further here. Only fronds (blades) are used for abalone feed, and there are two methods of frond-harvesting. In the first method the whole 'head' of the kelp sporophyte is cut off between the bulb at the top of the stipe and the primary blade (Fig. 1). This is an easy way of harvesting and most harvesters employ this method, but it kills the plant. In the second method, the secondary fronds are cut 20-30 cm from the junction with the primary blade (Fig. 1). This method is currently used on an experimental basis in one of the concession areas. Levitt *et al.* (2002) showed that the latter type of harvesting does not kill the plant, because the meristematic zone at the base of the secondary fronds is unharmed. The fronds continue to grow, and Levitt *et al.* (2002) calculated that this non-lethal harvesting method ultimately give yields that are 4-5 times higher than the 'lethal' method. Both of these frond-harvesting methods alter the state of the canopy in a kelp bed.

Reports from other countries indicate that dense kelp canopy can decrease the amount of light that penetrates to the bottom by more than 90% (Norton *et al.*, 1982; Kimura & Foster, 1984; Schiel & Nelson, 1990). A study done by Schroeter *et al.* (1995) in a *M. pyrifera* bed indicated a slower growth rate for juvenile kelp under the canopy. Anderson & North (1969) also found that gametophyte development is prevented by dense canopies in *Macrocystis* beds. However, Chapman (1984), in a *Laminaria* bed in Nova Scotia, showed that the removal of large kelp sporophytes had no effect on recruitment of the visible stages. He observed high survival rates for the survival of *Laminaria longicruris* and *Laminaria digitata*, for one year, of 25% and just under 50% respectively. Removing kelp canopies can increase the abundance of understorey seaweeds (Kimura & Foster, 1984; Sharp & Pringle, 1990) because light is one of the factors affecting their growth (Schroeter *et al.*, 1995). I therefore hypothesized that removal or thinning (by cutting the distal fronds) of the surface canopy of *E. maxima*, would, through its effect on light penetration, result in an increase in the relative growth rate of the subcanopy kelp plants. Furthermore, I expected an increase in kelp recruits (juvenile sporophytes) and ultimately in the number of subcanopy kelp plants, which would alter the population structure of harvested beds. This study investigated the effects of these two methods of frond-harvesting (of the canopy) on the growth (stipe elongation) rate, recruitment, and population structure of the sub-canopy of the kelp *E. maxima*.

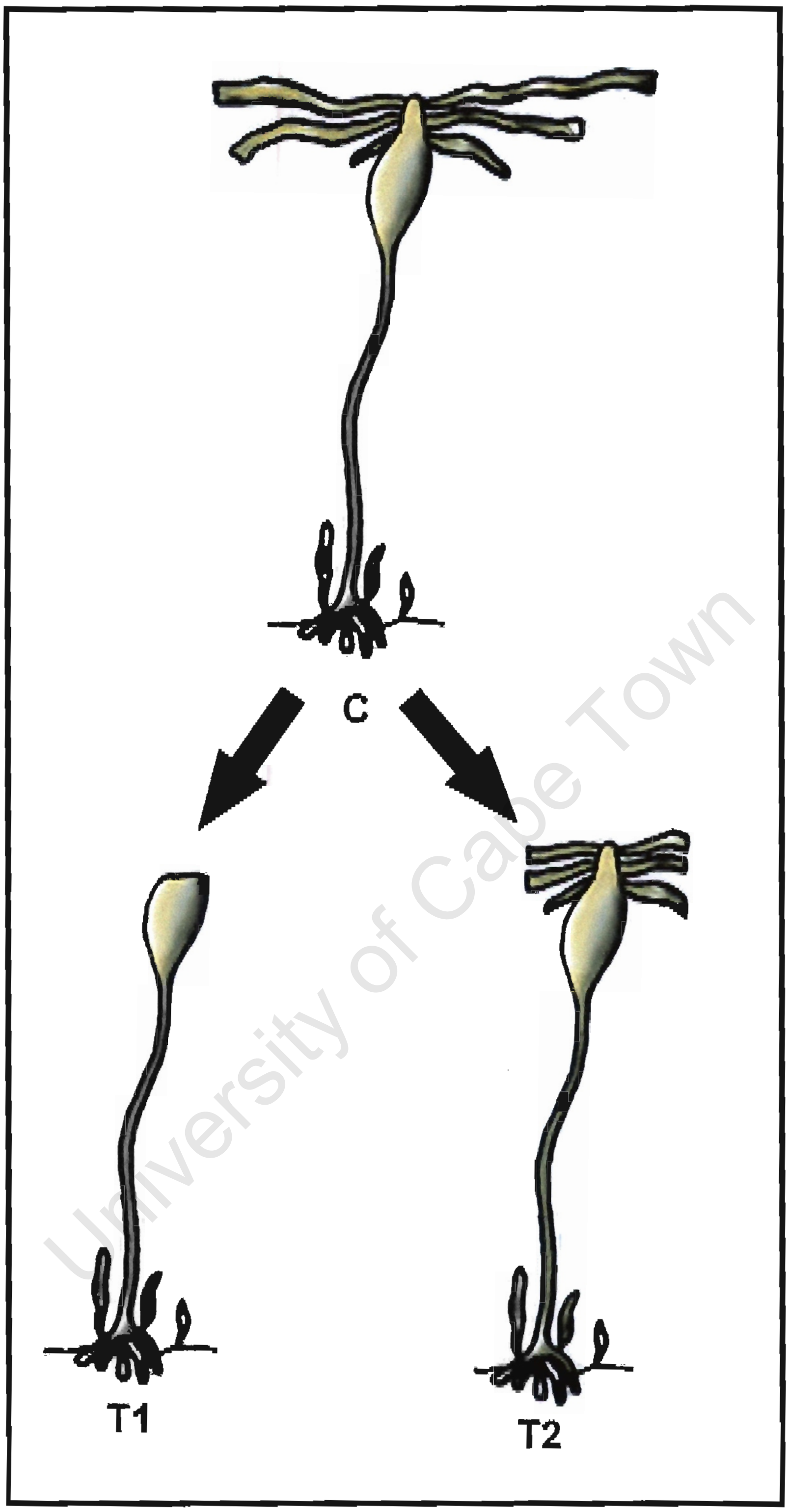

Figure 1. Different harvesting methods employed in South Africa. C = un-harvested kelp; T1 = 'lethal harvesting' where the whole kelp 'head' is cut off; T2 = 'non-lethal' harvesting where only the fronds are harvested 20-30 cm from the primary blade.

Materials and Methods

Study Site

A site was selected on the Cape Peninsula, about 60 km south of Cape Town, at Bordjies Rif (34°18'54"S 18°27'48"E) (see Fig. 1 in Chapter 2), where no previous harvesting had taken place. The substratum is of Table Mountain Sandstone, with gentle slope, with 1-1.5 m gullies and mixed vertical/horizontal aspect. The homogeneous stand of kelp (*Ecklonia maxima*) is fairly dense (~ 8 plants m^{-2}) and the bed is between 70-100 m wide and 300-400 m long. The study site is in a bay that is partially sheltered from the prevailing wind and allows for favourable working conditions most of the time.

Experimental design

Two areas, each 30x10 m, were marked out parallel to the shore (Fig. 2; ABCD) with weights and stainless steel eyebolts fixed to the rock with epoxy putty. The corners were marked with small sub-surface buoys. Each 30x10 m area was then subdivided into three 10x10 m plots and marked with eyebolts (Fig. 2; efgh). The two replicate, 30x10 m areas were approximately 100 m apart, and both were between 2-5 m deep. Depth as measured at MLWS.

Each 30x10 m area was subdivided into three treatments. In treatment 1 (T1) the whole 'head' of each kelp sporophyte that reached the surface was cut off between the bulb and the primary blade, and the primary blade and the secondary fronds were removed ('lethal' method). In treatment 2 (T2) ('non-lethal' method), the secondary fronds of all sporophytes that reached the surface were cut 20-30 cm from their junction with the primary blade, and removed. In the control plot, the kelp plants were not harvested. Harvesting treatments were done approximately every four months, at low spring tide, from 03 March 2003 till 03 November 2003 (three treatments). These treatments mimicked the two frond-harvesting methods used commercially. Edge effects, during harvesting, were minimized by tying 8 surface buoys to the eyebolts (ABCDefgh), demarcating the plots on the bottom. All subsequent sampling was done on sub-canopy kelps (see below).

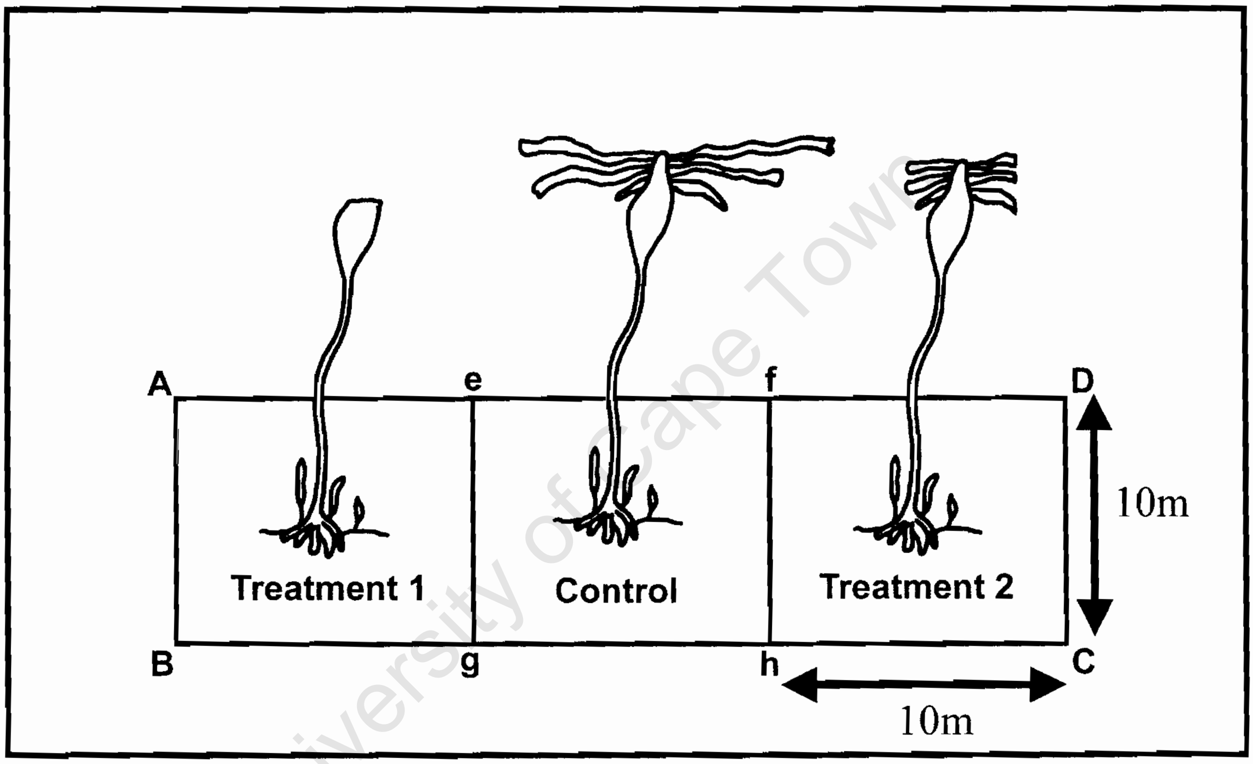

Figure 2. Treatments done on the site. Treatments 1 (T1), where the whole head was harvested just above the bulb (lethal). Treatment 2 (T2), where only the fronds were harvested 20-30cm from the primary blade (non-lethal). The centre plot was the control (no treatment).

Stipe Growth Rates

Divers using SCUBA made measurements once every two months as far possible but often inclement weather prevented this from happening, especially during the winter months. Our initial measurements were made on 9 April 2003. Two weeks later we returned to re-measure the plants because from past experiences I knew it might be difficult to re-measure as the period for 'bad weather' was approaching. Re-measuring took place during periods of very little to no swell. In each 10x10 m plot (in each treatment, in three different size classes, 10 in each) 30 plants were marked, each with an unique number. The first group of plants, with stipe lengths ranging from 0-10 cm (small plants), were numbered 1-10. The second group, with stipe lengths ranging from 11-50 cm (medium plants), were numbered 11-20. The third group, with stipe lengths of 51-100 cm (long plants), were numbered 21-30. In total, 180 plants (in six plots at two sites) were marked.

Divers measured the stipe length of each marked plant and recorded it on an underwater slate. During re-measuring, the tags were then removed and new sets of plants in each size class were marked and measured to keep the samples independent. It is important to note that growth rate was measured as stipe elongation. The relative growth rates (RGR, %day^{-1}) were determined using the formula

$$RGR = \frac{\ln(L_2 / L_1)}{n} \times 100$$

where L_2 and L_1 are the final and initial mass, respectively, and n is the number of days. Kolmogorov-Smirnov (KS) shows that the data was normal ($p > 0.05$) (Zar, 1984). An ANOVA and a Tukey post-hoc comparison were done (STATISTICA, version 7) to determine the effect that the different treatments had on growth. By using a 3-way analysis of variance, the growth rates were compared over time, treatment and between the different size classes.

Plant density, recruitment and population structure

Divers haphazardly placed ten 1 m^2 quadrats within each of the six blocks. The number of plants within six size classes (0-1 cm, 2-10 cm, 11-25 cm, 25-50 cm, 50-100 cm and >100 cm) was recorded in each 1m^2 quadrat. For this study kelp plants with a stipe length of $\leq$ 10 cm were regarded as recruits.

Water Temperature

Water temperature was measured using a Starmon-mini temperature recorder with a Hart 1504 thermometer at 8 m depth placed on a concrete block approximately 300 m from the site at Bordjies Rif. Temperatures were recorded every 10 minutes and daily means calculated.

Light Measurements

Light was measured using a LI-COR LI-1000 Data Logger and SA: LI-193SA Underwater Type Spherical Quantum Sensor. Eight to twelve readings were made at each of the following depths: above the surface, 10 cm under the surface, 1 m, 2 m, 3 m, and at the bottom and between 10h00 and 12h00, with good visibility (about 15 m) on a cloudless day in November. Mean values were calculated for each depth and expressed relative to the surface value (1). The light measurements were taken before and after experimental harvesting in a treatment 1 plot, a treatment 2 plot, and once in a control.

Results

Stipe Growth Rate

Treatment had no significant effect on growth rate in all three size classes of sub-canopy kelp (Fig.3). Long plants (50-100 cm) grew faster than short plants (0-10 cm) in all treatments (Fig. 3 and Fig. 4). Growth rates of medium plants (11-50 cm) were intermediate between those of long and short plants (Fig. 3 and Fig. 4) and were often significantly different from one or both (Fig. 3). A peak in growth rate of all three size classes of sporophytes was observed in April 2003 (Fig. 4).

Plant density and recruitment

Treatment had no effect on density of recruits (n=960, *p*=0.8796) although the density of the recruits varied significantly between sampling periods (n=960, *p*<0.0001: Fig. 5). The density of sporophytes with stipe lengths between 11 and >100 cm (Fig. 6) differed between treatments and size classes (n=5280, *p*<0.0001) but densities at each sampling were variable and showed no consistent pattern. Note that densities of recruits (plants with stipe <10cm: Fig. 5) were consistently higher than those of the longer sporophytes (Fig. 6), but showed similar patterns of temporal fluctuation.

Population Structure

Recruits (plants with stipe length <10 cm) constituted the largest proportion of the kelp bed population (Fig. 7). Once sporophytes reached the 11-25 cm size class, decline in density (mortality) was relatively gradual over the rest of the size classes (Fig. 7). The three treatments followed a similar trend. However, in the 201-250 cm size class internal a 50 % increase in the density has been observed.

Water Temperature

A seasonal pattern in the mean daily seawater temperature was observed, with the winter monthly temperatures (mid-May 2003 to end August 2003) being low, and less variable while the summer water temperatures (September 2003 to May 2003) are 2-5°C higher but a lot more variable (Fig. 8). In February 2003 to March 2003 and November 2003 to March 2003 water temperatures were above 17°C for long periods but also occasionally fell to below 14°C but only for short periods (Fig. 8). In April 2003 temperatures fluctuated regularly (every 5-7 days) between about 14 and 16°C, but were on average about 2°C lower than during the previous 2 months.

Light Measurements

In the control and before harvesting in both treatments, 60-80% of light incident on the surface was lost in the first 10 cm (in the kelp canopy) (Fig. 9). At 1 m depth, over 90% of the light was lost and light remained low down to the bottom at 3-3.4 m (between 27.5 and 54 μmol m^{-2} s^{-1}). Harvesting treatment 1 (removal of entire kelp heads), increased light penetration at all depths: the mean amount of light at the bottom (about 3-3.4 m depth) increased 12 times from 27.5 μmol m^{-2} s^{-1} to 330.8 μmol m^{-2} s^{-1} (Fig. 9).

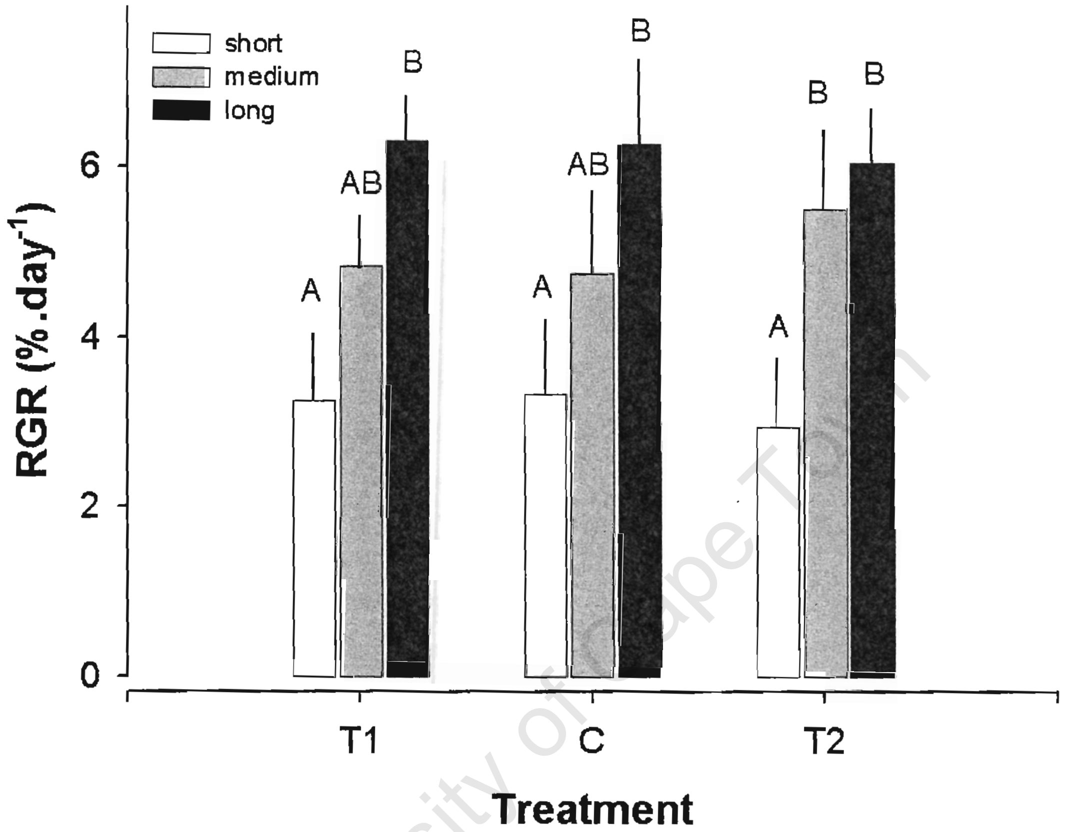

Figure 3. Relative Growth Rate (stipe elongation) of the different size classes of *Ecklonia maxima* under different harvesting conditions. Bars denote 95% confidence intervals. Letters denote statistical grouping (ANOVA and Tukey post-hoc test). Treatments 1 (T1), where the whole head was harvested (lethal). Treatment 2 (T2), where only the fronds were harvested (non-lethal), Control (C) (no treatment).

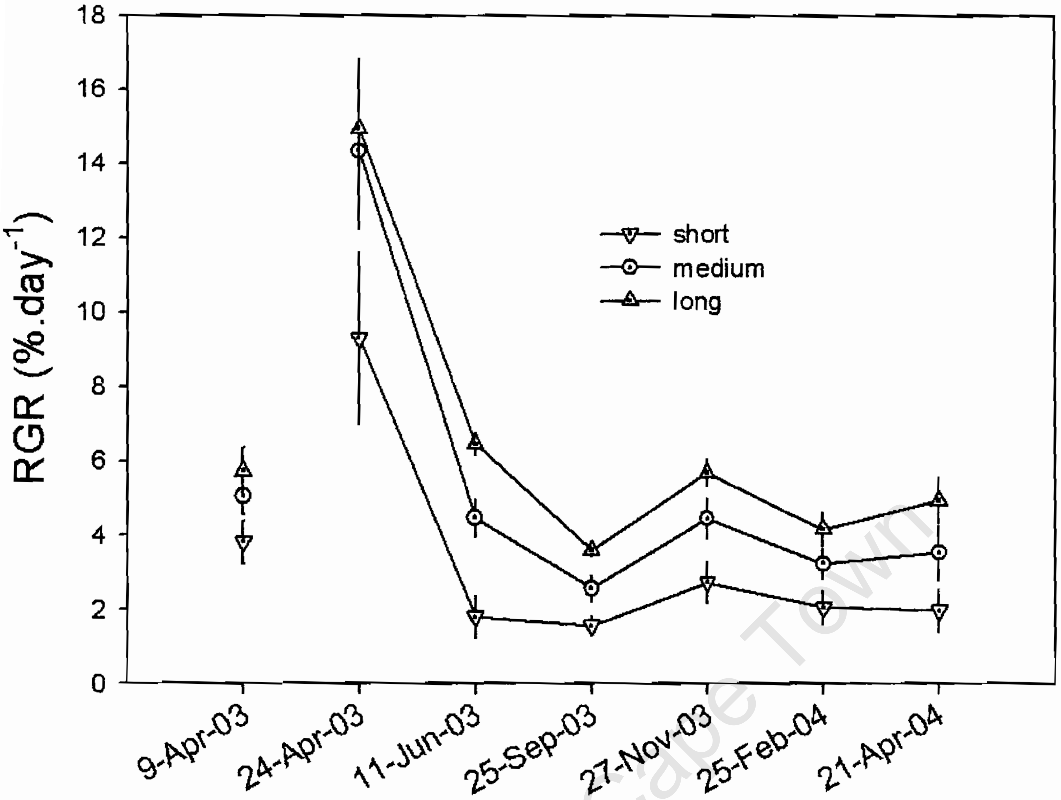

Figure 4. Relative Growth Rate (stipe elongation) of the different size classes of *Ecklonia maxima* over time. Bars denote 95% confidence intervals.

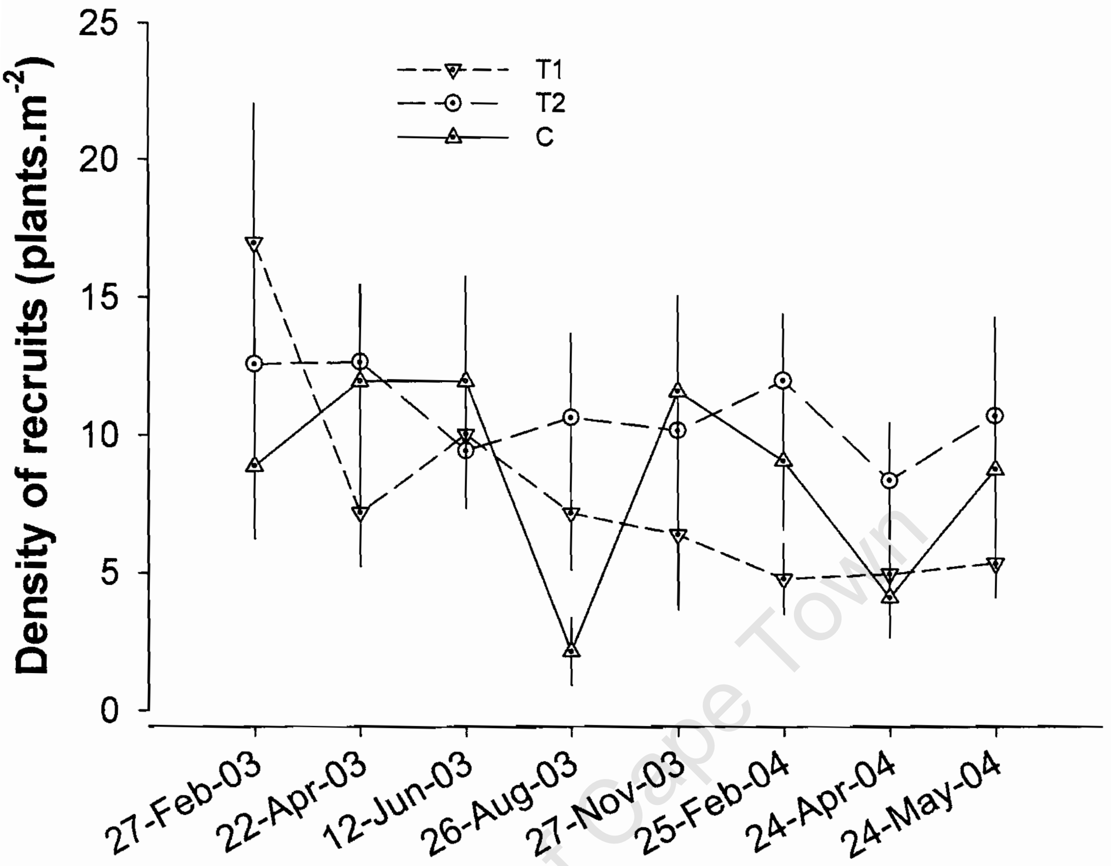

Figure 5. Mean densities of recruits (sporophytes with stipe length under 10cm) over time under different harvesting conditions. Bars denote 95% confidence intervals. Treatments 1 (T1), where the whole head was harvested (lethal). Treatment 2 (T2), where only the fronds were harvested (non-lethal), Control (C) (no treatment).

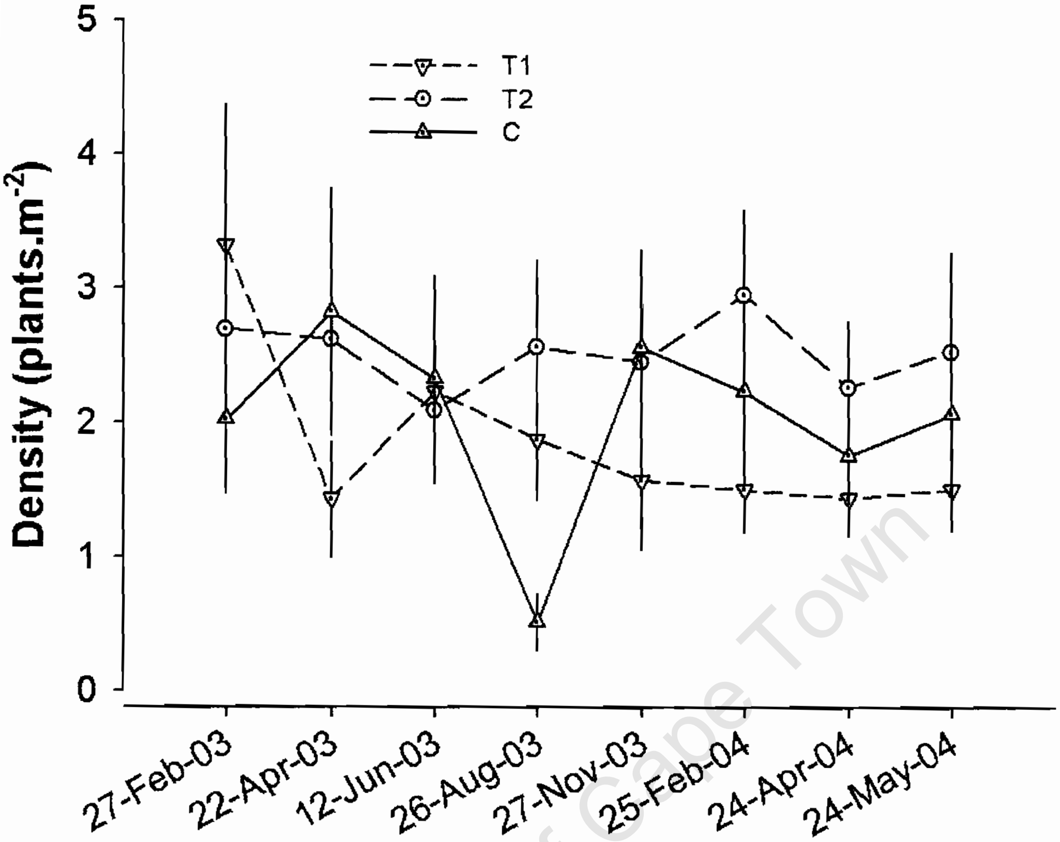

Figure 6. Mean densities of sporophytes (sporophytes with stipe length >10cm) over time under different harvesting conditions. Bars denote 95% confidence intervals. Treatments 1 (T1), where the whole head was harvested (lethal). Treatment 2 (T2), where only the fronds were harvested (non-lethal), Control (C) (no treatment).

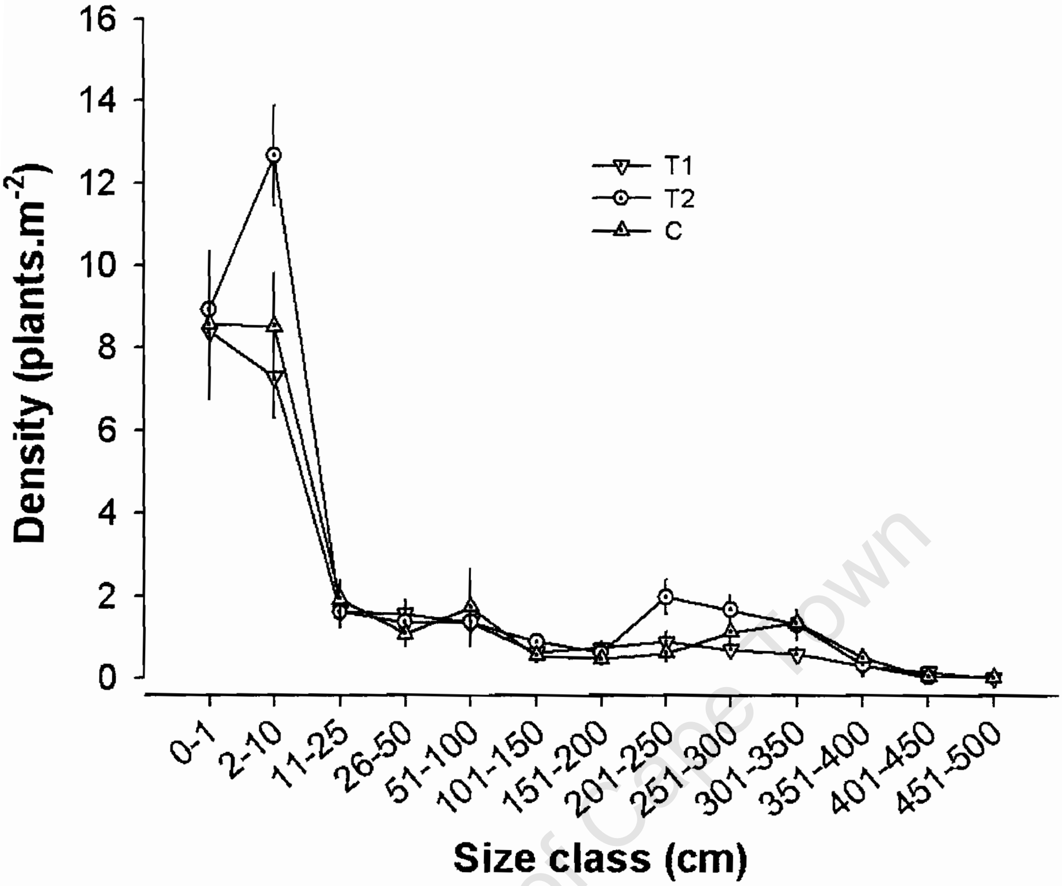

Figure 7. Mean densities of sporophytes of different size classes under different harvesting conditions, after harvesting (21 April 2004), at the end of the experiment. Bars denote 95% confidence intervals. Treatments 1 (T1), where the whole head was harvested (lethal). Treatment 2 (T2), where only the fronds were harvested (non-lethal), Control (C) (no treatment).

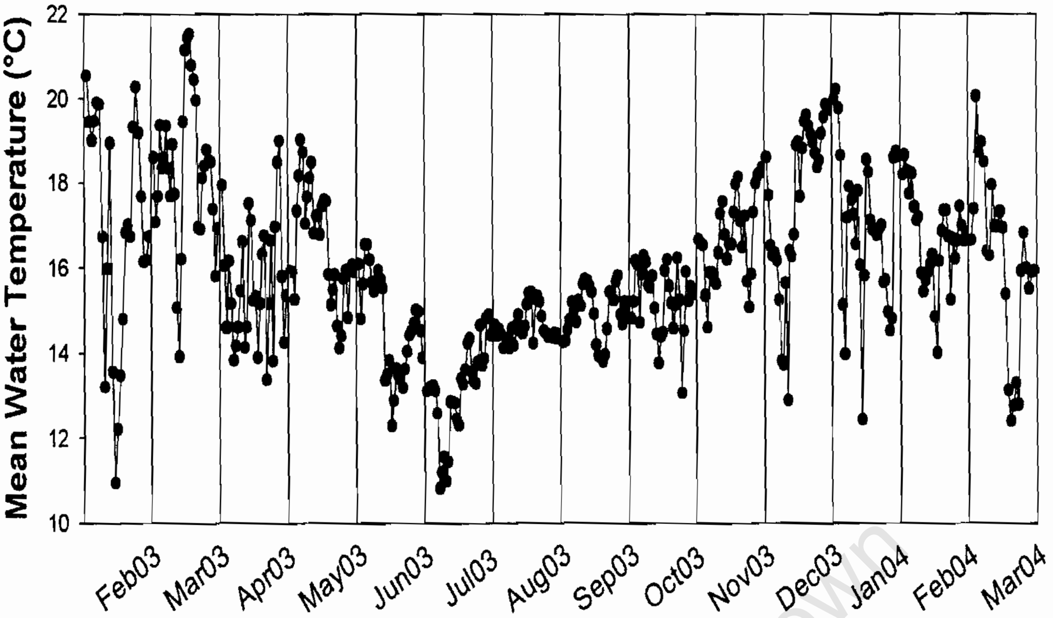

Figure 8. Mean daily water temperatures (°C) at Bordjies Rif, 8m depth.

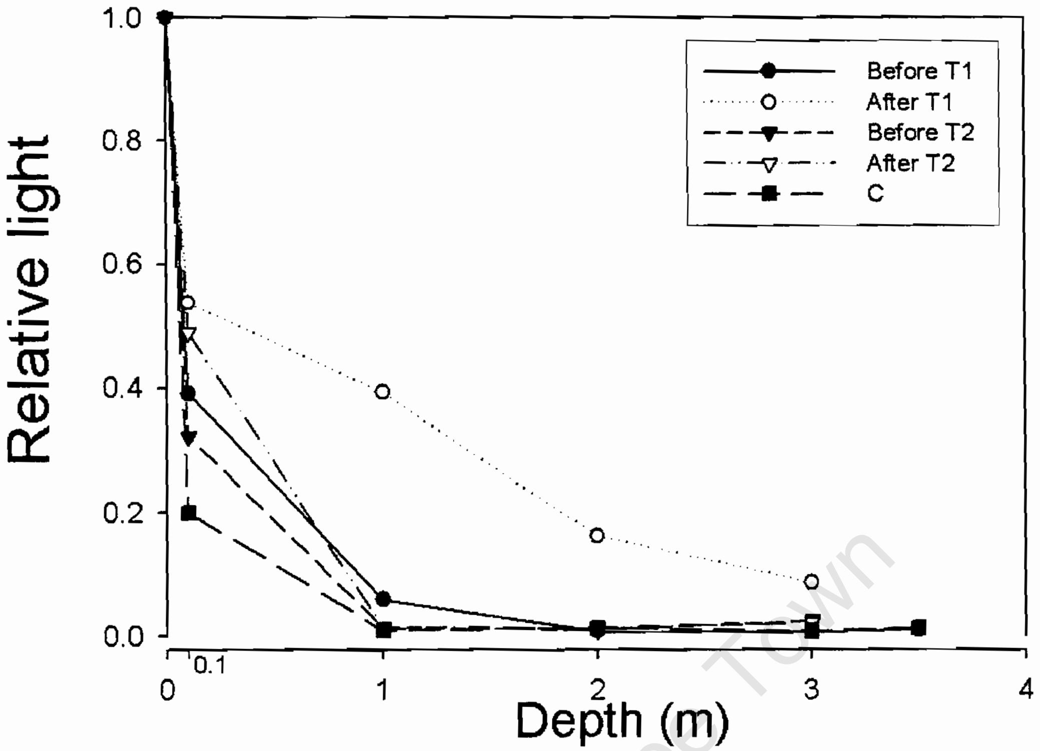

Figure 9. Relative light, before and after harvesting, with increase in depth in the kelp bed at Bordjies Rif. 60-80% of incident light was lost in the first 10 cm under the water surface. Mean values were calculated for each depth and expressed relative to the surface value (1).

Discussion

Growth Rates

Contrary to my hypothesis, removal of either the whole surface canopy (T1) or only distal portions of the secondary fronds (T2) had no effect on rate of stipe elongation of sub-canopy kelps despite a 12 times increase in bottom light after harvesting in T1. Treatment 2 left a considerable biomass of fronds intact and shading at depths below 1 m remained similar to the control. In treatment 1 (after harvesting) the bulbs protruded above the surface of the water and light penetration on the bottom increased visibly. I considered this result to show that growth (measured as stipe elongation), in this kelp bed, is limited by a factor other than light.

In the South African west coast upwelling system, water temperature is inversely related to nutrient levels, with temperatures below 14°C generally associated with nutrient-rich conditions (Andrews, 1974). Bolton & Anderson (1987) showed that, under nutrient-sufficient culture conditions, small sporophytes grew well over a range of temperatures of between 8-18°C with the best growth achieved at 12°C. It is thus likely that kelp growth may be faster when there is frequent import of cold, nutrient-rich water interspersed with short periods of warmer water, such as occurred in April 2003 when very high growth was recorded. Long periods (up to 2 weeks) of high temperatures (>17°C) may have indicated poor nutrient conditions: this response was corroborated by the presence of pale, unhealthy looking fronds in February 2003. However, there must be a balance between available light and nutrients: although the water was cold and nutrient-rich in June, this is midwinter, when rainfall is high and irradiance levels low. The slow relative growth rate of short (0-10 cm) compared to long (51-100 cm) sporophytes may be a result of the former expending more growth effort in frond production rather than stipe elongation, although I did not measure frond growth. This is consistent with what Sjøtun *et al.* (1998) found in *Laminaria hyperborea* beds. This growth strategy might be part of the developmental stage of the sporophytes although environmental factors might also act as a 'trigger' for stipe elongation. As the small plants invest in their frond growth, the resulting imbalance between surface area/mass ratio might act as a 'trigger' to stimulate stipe growth to expose the newly developed photosynthetic tissue to higher levels of irradiance. The maximum rate of stipe elongation of subcanopy *E. maxima* appears to be greater (57mm/week or 32% day^{-1}) than the maximum rate of stipe elongation in *Laminaria hyperborea* (13mm/week: Kain, 1979). This is perhaps not surprising for a sporophyte with a gas-filled bulb that suspends its fronds at the surface, such as *E. maxima*.

Density and Recruitment

The absence of a treatment effect on the density of *E. maxima* recruits, despite a large increase in light penetration after treatment 1 has been harvested, suggests that at least in this kelp bed, which is only 3-5 m deep at low tide, density is controlled by a factor other than irradiance. Additionally, the absence of a clear seasonal pattern in recruit density suggests that recruitment here may be stochastic, as has been shown in the study on *E. maxima* done by Levitt *et al.* (2002) and in California *Macrocystis* beds (Deysher & Dean, 1986). In the latter study recruitment was shown to be episodic rather than seasonal, and resulted from a combination of several factors creating an 'environmental window' (Deysher & Dean, 1986). Factors which may control the density of recruits in South African kelp beds include grazers (Fricke, 1979), and the availability of substratum (Anderson *et al.,* 1997). The fecundity of the kelp population also plays a role as well as suitable environmental conditions and the time it takes for the propagules to settle and to become established (Reed *et al.*, 2004). It appears likely, therefore, that the availability of primary space may be the most important factor for recruitment in *E. maxima* beds where light does not appear to be limiting.

Population Structure

The population structure of *E. maxima* sporophytes at all sites (Fig 7) is typical of many plant populations where most of the mortality is among the juveniles (Everard *et al.*, 1995). Juvenile sporophytes are easily accessible to a suite of benthic grazers in the kelp beds of False Bay, including abalone, sea urchins, and two turbinid snails: *Turbo sarmaticus* and *T. cidaris* (Anderson *et al.*, 1997). We frequently observed grazing damage to the stipes of juvenile *E. maxima*. These results show that, in this kelp bed, once sporophytes attain a stipe length of between 11 and 25 cm, they have approximately a 70% chance of growing to reach the canopy. This might be the range where *E. maxima* is not as vulnerable to grazing as suggested by Fricke (1979). Fricke found that once sporophytes reached a certain size (stipe length), they are less vulnerable to grazing by urchins. At the end of this experiment we did however observe an 50% increase in the density of the 201-250 cm class size.

Conclusions

Current frond-harvesting methods (lethal and non-lethal) do not affect the growth (stipe elongation) rate of sub-canopy *E. maxima* plants, their density or recruitment of juveniles in a shallow-water, dense kelp bed in False Bay over the course of this short-term experiment. Management should thus continue to allow both methods of harvesting to be used when ease of harvesting is more important than obtaining maximum yields. Future research should investigate the effects of canopy clearing on deeper and/or denser kelp beds, as well as trying to determine what factors may affect kelp recruitment.

Chapter 5

The effect of depth and plant size on blade fertility in *Ecklonia maxima* (Alariaceae, Laminariales).

Introduction

Kelp belong to the order Laminariales in the division Phaeophyta. Kelp has a heteromorphic life cycle with a large sporophyte stage and a microscopic gametophyte stage. The sporophyte bears the microscopic unilocular sporangia in sori, which are borne predominantly on the secondary blades although it has been observed on the primary blades (Bolton & Anderson, 1994). The sori appear as large, dark, raised patches on both surfaces of the secondary blades. Motile zoospores are released from the sporangia. These settle and germinate to produce dioecious microscopic filamentous male and female gametophyes. The female gametophytes have fewer cells and are less branched than the male gametophytes. The antheridia produce motile, biflagellate sperm while the females produce a single, non-motile egg in the oogonium. A zygote results from fertilization, and grows to produce a sporophyte.

The interactions between the organisms and the physical environment in which they occur, have a great effect on the structure of that community (Reed & Foster, 1984). There are many processes at work within these communities but the process controlling the distribution and the abundance of marine populations is recruitment (Deysher & Dean, 1986, Anderson *et al.*, 1997). Deysher & Dean (1986) coined the phrase 'recruitment window', to refer to an episode or period when environmental conditions (e.g. temperature and irradiance levels) are favourable for large-scale recruitment to take place.

Studies on the recruitment of different kelp species, under different conditions, have been performed around the world but most of these studies focussed on the giant kelp *Macrocystis pyrifera* (Anderson & North, 1966; Reed & Foster, 1984; Deysher & Dean, 1986; Kinlan *et al.*, 2003; Reed *et al.*, 2004).

In *Macrocystis pyrifera*, like in many other kelps, recruitment is dispersal limited (Reed *et al.*, 2004) because spores, once released in the water, are only able to move a few meters from the parent plant (Anderson & North, 1966, Schiel & Foster, 1986; Ladah *et al.*, 1999). In California entire *Macrocystis* kelp beds were lost due to an El Niño event, but new recruits were visible only 8 months later. Ladah *et al.* (1999) first hypothesised that the spores were imported from somewhere else, but the great distances to the closest spore source (more than 100 km away) ruled out this possibility. They, just like Bolton & Lüning (1983), observed that the gametophytes were able to survive higher temperatures than the sporophytes. Ladah *et al.* (1999) found that 'banks' of *Macrocystis* gametophytes survived the unfavourable conditions and developed into sporophytes when conditions improved. The small size of gametophytes makes it difficult to study this phase *in situ*, and this is why many studies of gametophytes are conducted in laboratories under controlled conditions (Anderson & North, 1969; Bolton & Lüning, 1983; Chapman, 1984; Bolton & Levitt, 1985; Kinlan *et al.*, 2003). Although the study by Ladah *et al.* (1999) found that 'banks' of spores, unaffected by El Niño, were responsible for recruitment, Reed *et al.* (2004) suggest that colonization to 'new' areas can happen through 'drifters'. They define 'drifters' as kelps from neighbouring kelp beds that become dislodged, drift to another area and release their spores there. This almost certainly occurs in *Ecklonia maxima* (Osbeck) Papenfuss because dislodged plants often get entangled and form 'kelp rafts' that float to other areas and can release their spores there. Furthermore, because this kelp is able to store nutrients (Probyn & McQuaid, 1985) the sporophytes will be able to survive for long periods after dislodgement.

Harvesting of the kelp fronds might pose a problem as the sporangia of *E. maxima* are borne on the fronds. Harvesters cut kelp by leaning over the side of the boat, lifting the kelp head out of the water, and with the aid of a sickle, removing the kelp head (with the fronds) and tossing it into the boat. By removing the fronds the fertile material of the plant is also removed. However, harvesters do not harvest the entire canopy at any one time but choose small areas and leave others.

However, there are several reasons why this method of harvesting does not remove all the fertile sporophylls from the kelp bed. First, many sporophytes do not reach the surface, and hence are not harvested. What proportion of the fertile fronds do they comprise? Other factors that ameliorate the effect of harvesting on kelp bed spore output are more difficult to measure. These include accessibility to harvesters (are certain areas too shallow or otherwise inaccessible?) and overall harvesting efficiency. Furthermore, a seasonal variation in spore production and release must be considered in predicting harvesting effects. Joska & Bolton (1987) showed that although there are fertile sporophytes throughout the year, the overall amount of soral tissue is highest in autumn, spore release per unit fertile area peaks in mid-summer. New Zealand *E, radiata* also shows seasonal patterns of fertility, but these vary with depth (Novaczek, 1984). Seasonal patterns of fertility are also reported in *Laminaria longicruris* and *L. digitata* (Chapman, 1984), but these are more arctic and are not fertile for most of the year.

The aim of this study was to quantify the potential effect of the harvesting of surface fronds on the amount of fertile sporophytes material in a kelp bed, and in the light of other factors mentioned above, to predict the effect harvesting might have on spore production.

Methods and Materials

Thirty subsurface plants and thirty surface plants were collected in June 2002. Plants were collected at two depths (4-5m, which we called 'deep' zone and 2-3m, which was called 'shallow' zone) by a diver using SCUBA at Spaniard Rock (34°13'S; 18°28'E) near Simonstown (see Fig. 1 of Chapter 2). Plants were cut just above the holdfast and handed to another diver (on snorkel) at the surface who carried the kelp to shore. Once all the kelp was collected the plants' fronds were separated from the stipe and each part weighed separately.

The stipe lengths ranged in length from 10cm to about 5 m. The stipe length was measured, with a measuring tape, from where it was cut just above the holdfast to the junction between the bulb and the primary blade. The whole stipe was weighed using a spring balance. The fronds were removed from the primary blade, placed in a bag and weighed. The primary blade was also weighed and its length measured separately. Each individual frond's length was measured as well as the length of the patch of fertile material (sorus) on the frond. Correlations were plotted of stipe length verses total frond length and stipe length versus total fertile frond length as well a between the total frond length and total fertile material using a linear regression with STATISTICA, version 7. Kolmogorov-Smirnov (KS) shows that the data was normal ($p > 0.05$) (Zar, 1984). Statistical differences were tested by an ANOVA, *post hoc* Tukey test.

Results

The plants that reached the surface had considerably more fertile frond material (total length of fertile frond per plant) than the subsurface plants (Fig. 1). Also the surface-reaching plants in the deep zone had more fertile frond material than the surface-reaching plants in the shallow zone. This becomes more apparent when correlating the percent fertile material per meter of frond with the total stipe length (Fig 2). The plants reaching the surface, in deep water, have the highest percentage of fertile frond material per meter of frond followed by the surface-reaching plants in the shallow zone. Again the subsurface plants in deep and shallow zones are statistically similar. A direct relationship exists between the stipe length and the total frond length of a plant (Fig 3). It is therefore not surprising to find the same trend between stipe length and the total fertile frond material per plant have (Fig 4), and the total frond material and the total fertile frond material of a plant (Fig 5). Table 1 shows the percentage of fertile material which occurred on the surface compared to the subsurface kelps.

Discussion

Most kelp harvesting is done from a boat at the surface and usually in the deeper part of the kelp bed. The harvesters reach over the side of the boat, grab the kelp head and cut the head of the kelp off with a sickle. This is the easiest method of harvesting and the majority of harvesters employ this method of 'lethal' harvesting. The result is that areas of the kelp canopy are removed and with them all the fertile material associated with these plants. Figures 1 and 2 show where most of the fertile frond material is found in a kelp bed. Joska & Bolton (1987) showed that although the area of fertile area per plant occurs all year round, maximum production is during winter. The

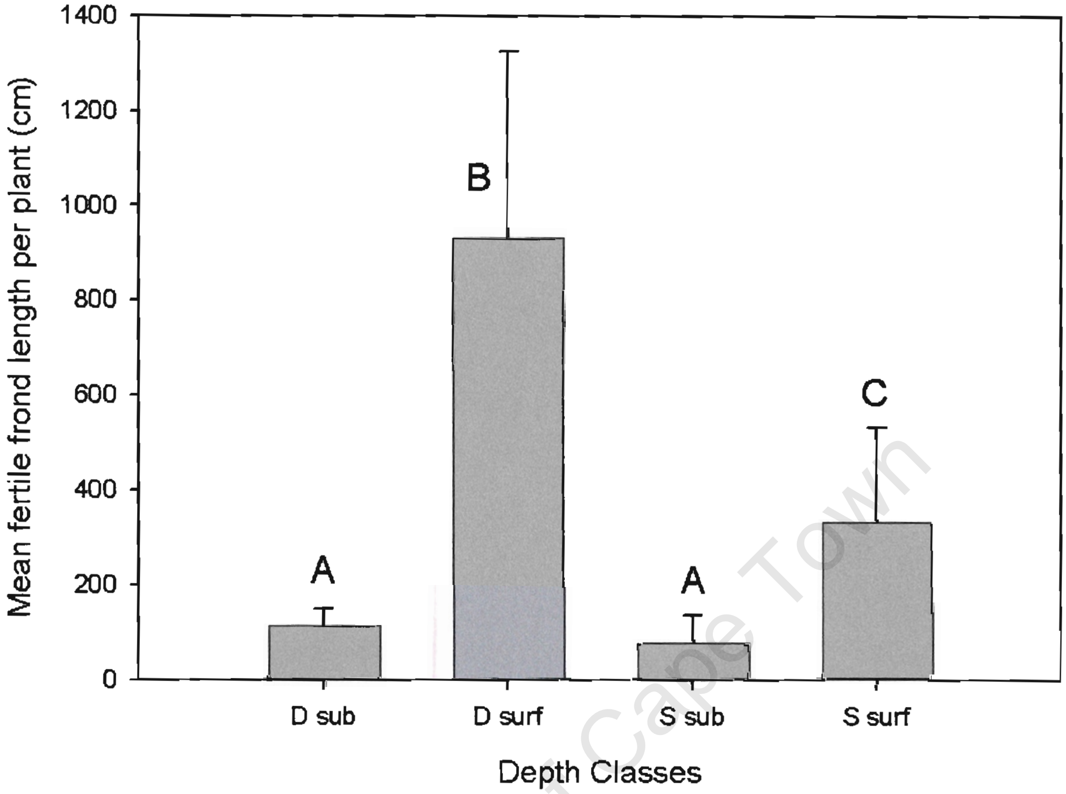

Figure 1. Bar graph indicating the mean fertile frond length per plant (cm) at a deep and a shallow site. D sub = deep site, subsurface plants; D surf = deep site surface plants; S sub = shallow site, subsurface plants; S surf = shallow site surface plants. Bars denote 95% confidence limit. The matrix at the bottom gives significance values for the different depth classes (ANOVA, $p = 0.5$).

	D sub	D surf	S sub
D surf	0.0002		
S sub	0.9096	0.0002	
S surf	0.0269	0.0002	0.0073

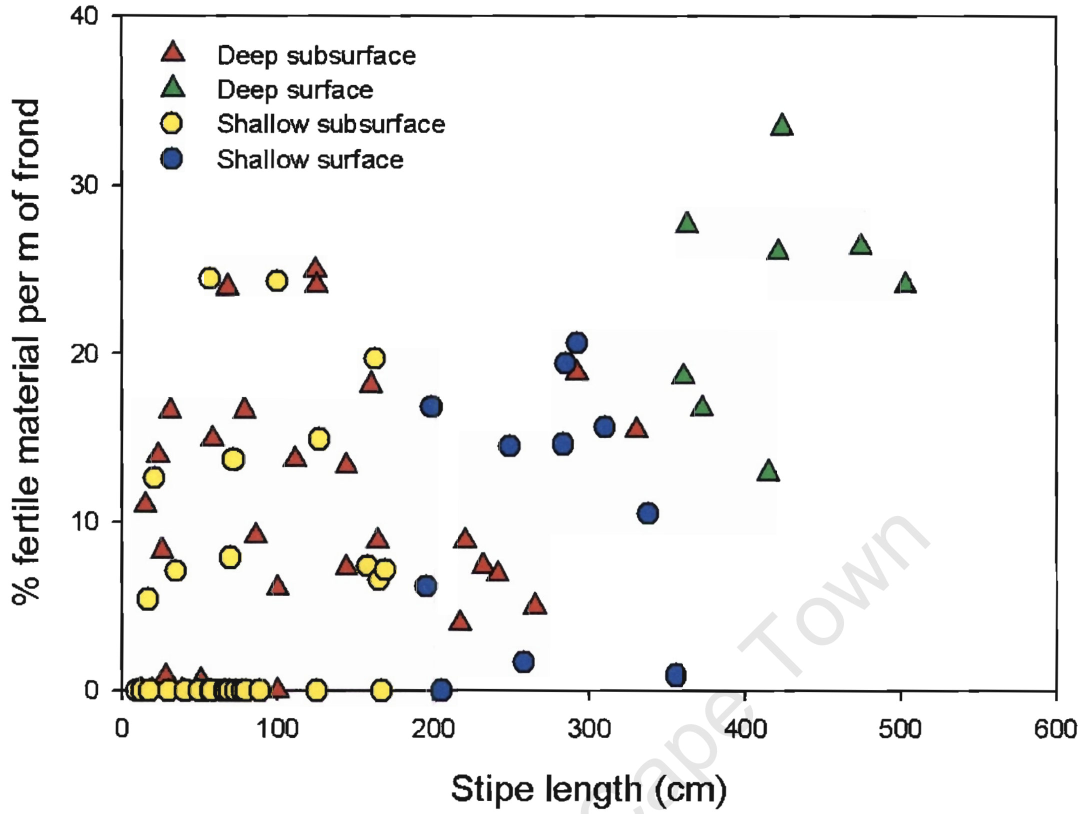

Figure 2. Percent fertile material per meter of frond with an increase of stipe length. The triangles (Δ) are the plants in the deep water and the circles (O) are the plants in the shallow water. The matrix at the bottom indicates significant values for the different depth classes (ANOVA, $p = 0.5$).

	D sub	D surf	S sub
D surf	0.0003		0.0002
S sub	0.9562	0.0002	
S surf	0.1203	0.0050	0.1483

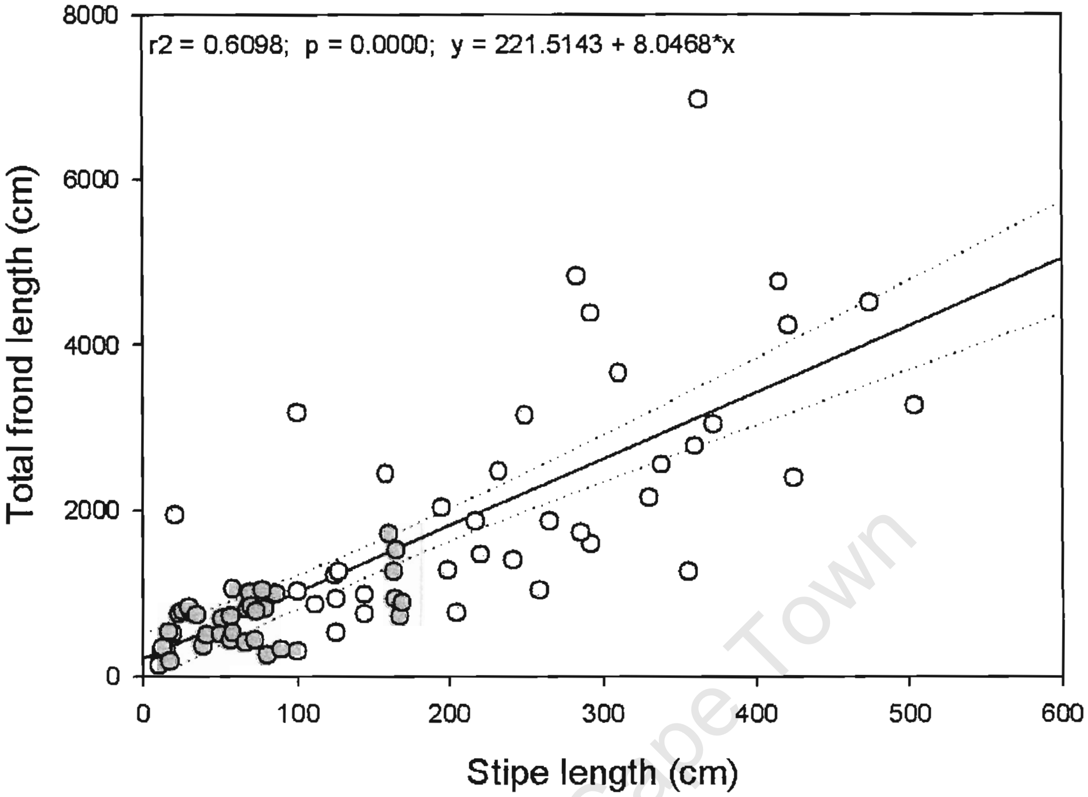

Figure 3. Total frond length (cm) with an increase in stipe length (cm). The dotted lines indicate 95% confidence limits.

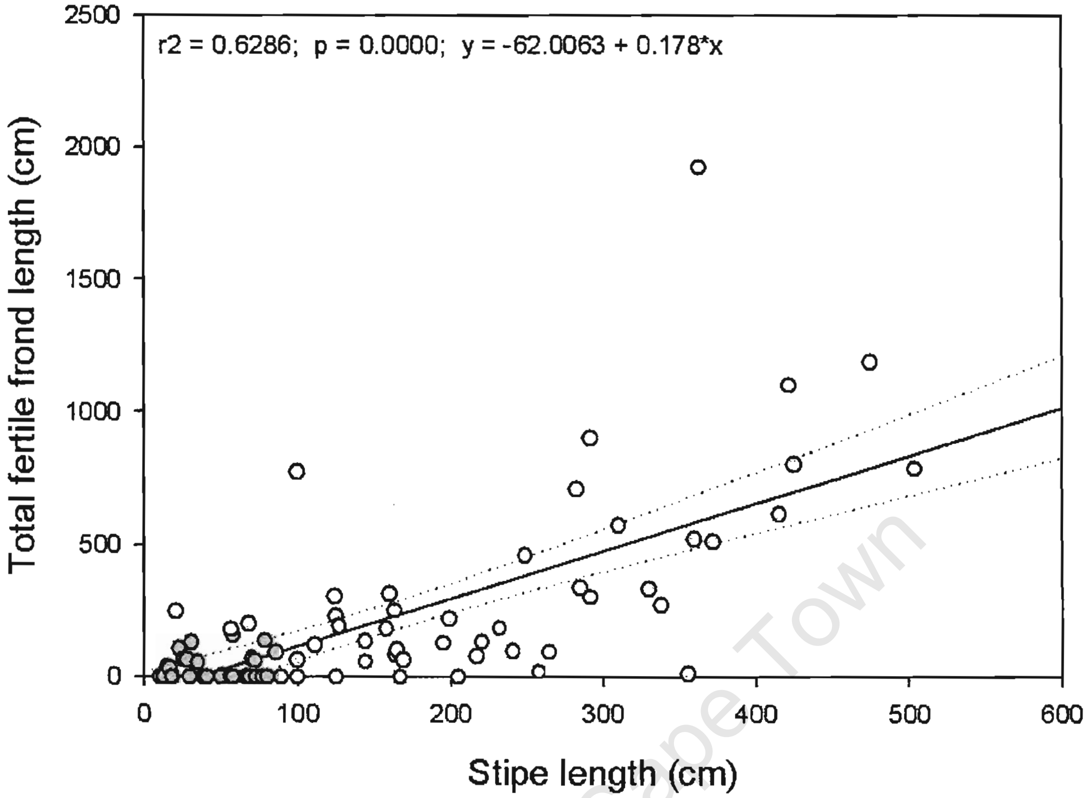

Figure 4. Total fertile frond length (cm) with an increase in stipe length (cm). The dotted lines indicate 95% confidence limits.

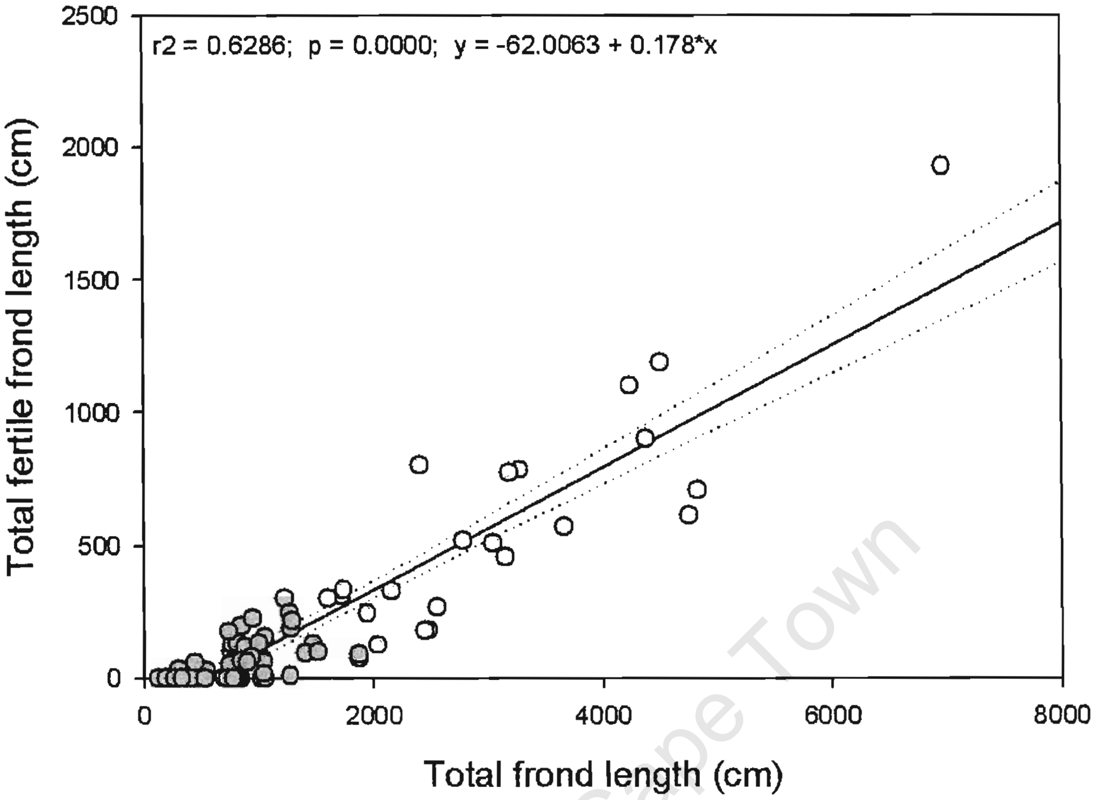

Figure 5. Total fertile frond length (cm) with an increase in the total frond length (cm). The dotted lines indicate 95% confidence limits.

Table 1. Contribution of fertile material of surface and subsurface kelp to total fertile material. Total sub = subsurface fronds in the deep and shallow zones; Total surf = surface fronds in the deep and shallow zones.

Total sub (%)	Total surf (%)
40	60

winter months will thus have the highest total fertile area per plant during this period. This study was done during the winter so the figures observed correspond to the period of maximum fertile area per plant. Joska & Bolton (1987) further showed that the presence of sori on a plant does not indicate that the plant is able to release spores. This was also found in *Macrocystis pyrifera* (Anderson & North, 1966).

The surface kelp in the deep water, where most harvesting occurs, had most of the fertile frond material. It is thus not surprising to find that the longer the plant stipes are, the more frond material and hence the more fertile material the plant has (Figures 3 and 4). This correlation results from the relationship between the total frond length per plant and the total fertile frond length per plant (Fig 5). In essence, larger plants have more frond material and thus more fertile frond material. Mann *et al.* (1979) showed a direct relationship between stipe length and stipe weight as well as frond length and frond weight in *E. maxima*. Although most of the fertile material is situated in the fronds that are likely to be harvested, we do not foresee this to have a detrimental effect on whole kelp beds. Table 1 shows that 40% of fertile frond material was present in the subcanopy. Furthermore, there are 'natural reserves' where harvesters are unable to harvest because the area is very rocky, very exposed to swell, or too far from a launching. Moreover, Marine and Coastal management demarcated 10% of all heavily-exploited kelp concession areas as reserves in which no harvesting is allowed. Most of the fertile frond material is concentrated in the surface plants where harvesting takes place. Considering how much fertile material occurs in the subsurface plants, however, it is reasonable to expect that harvesting, as it is currently practised, should be sustainable. Subsurface plants produce enough spores to ensure proper recruitment. Joska & Bolton (1987) showed that an *Ecklonia maxima* sporophyte releases 3.07 x 10^{10} spores m^{-2} annually. If we extrapolate data from Chapter 2 (Table 2) and assume the kelp density to be 4.4 plants m^{-2} it would mean that per m^2 the plants should produce 1.35 x 10^{11} spores annually m^{-2}. If 60% of the fertile frond material is removed (Table 1), i.e. the whole canopy is harvested, the subcanopy would still produce 5.4 x 10^{10} spores annually m^{-2}. It may well be that this large amount of spore production is sufficient to perpetuate the kelp beds. However this might be an over estimate as this study was done in winter when sporophytes have the maximum amount of fertile material, according to Joska & Bolton (1987). Harvesting is a year-round exercise so it is to be expected that during the winter period, when we observe most fertile material, that also most of the fertile material would be removed by the harvesters. It must be borne in mind that it is extremely difficult to estimate how many spores a kelp bed needs to produce to continue to recruit sporophytes maximally. It is possible that there is a threshold of spore numbers below which recruitment of sporophytes could be reduced. Much further work would be needed to investigate this possibility.

Chapman (1984) showed that *L. longicruris* at a density of 1.2 plants m^{-2} produced an average of 8.9 x 10^9 spores m^{-2} yr^{-1} while *L.digitata* with a density of 3.2 plants m^{-2} produced 20.02 x 10^9 spores m^{-2} yr^{-1}. These figures are about two orders of magnitude smaller than those estimated for *E. maxima*. This is not surprising considering that the density of *E. maxima* plants is much higher than the density of *Laminaria*. Furthermore, *E. maxima* is fertile all year round while *Laminaria* plants are only fertile part of the year.

However, to be able to draw better conclusions on the effect that removing kelp might have on the fertility of the kelp bed requires more research. Furthermore, these figures presented here do not consider the effects of 'drifters' in importing of spores, as discussed by Reed *et al.* (2004). It is likely that other factors e.g. grazers, adverse weather conditions, high water temperature and low nutrients are much more important factors influencing recruitment, than the numbers of spores released from sporophytes.

Conclusion

Harvesters harvest the kelp plants indiscriminately but usually target the larger plants. Harvesting is a labour intensive process and harvesters try to collect the most kelp in the shortest time and hence they prefer the larger plants. The larger plants are usually the ones with the most fertile material per plant. However, this study shows that when the entire surface canopy of fronds is removed, 40% of the sub-surface fertile material remains to supply high numbers of spores. With the limited data available it cannot be accurately predicted what effects this reduction in spore production may have in a particular kelp bed. It must, however, be considered that other mitigating factors (reserve areas, inaccessible areas) will reduce any possible impact on the kelp resource as a whole. It is perhaps unlikely that harvesting, at the levels that it is generally carried out, reduces spore output to a level where this would significantly decrease recruitment of gametophytes, and ultimately of new sporophytes, but more research is required to confirm this hypothesis.

Chapter 6

General Discussion

The exploitation of kelp (*Ecklonia maxima*) in South Africa is increasing (Troell *et al.*, in press). Levitt *et al.* (2002) have attempted to provide some answers to the question of the impact the harvesting of kelp will have on these natural populations, they left some questions unanswered. This study attempted to provide answers to some of these questions.

Many studies have attempted to quantify the amount of kelp in South Africa (Field *et al.*, 1980; Allen & Griffiths, 1981; Jarman & Carter, 1981; Simons & Jarman, 1981; Levitt *et al.*, 2002) but these studies did not attempt to calculate a single figure that could be used as an average biomass m^{-2} of kelp beds. If the average biomass of kelp were known it would greatly accelerate the process of biomass determination of kelp beds.

The data indicated that the kelp biomass at different sites varies and that the depth profile and bottom topography play a role in these differences. The average biomass varied between 10 - 20 kg wet wt m^{-2}. However, between shallow, intermediate and deep zones, in a kelp bed, there was no difference in the amount of kelp biomass. This can be explained by the inverse relationship that exists between the density of plants and their depth. With an increase in depth, an increase in plant size and weight was observed. However, although the plants became larger and heavier, with an increase in depth, there were fewer plants. In the shallow and intermediate zone plants were smaller and lighter but there were more plants per m^2 that contributed to the total biomass in these zones.

This study gave an indication of the distribution of the biomass of kelp in an *Ecklonia maxima* kelp bed. In the deep zone most of the kelp biomass was concentrated in the subsurface but overall, stipes contributed nearly half the total biomass (49%) while the fronds contributed the other 51%. In the intermediate depth zone most (61%) of the biomass consists of fronds at the surface. About 55% of the total biomass in the shallow zone was surface frond biomass. In this zone subsurface kelp, in total, made a total biomass contribution of only 13%. Over all, surface kelp contributed 62% of the total kelp biomass while the other 38% was subsurface kelp.

Kelp harvesting is usually a tide-bound operation because more of the kelp would be visible at the surface during low spring tide. This also means that the period in which harvesting can take place is limited by the time that the tide is low. Although the kelp density is higher in the shallow zone, harvesters would be able to harvest more kelp, per unit effort, by harvesting the larger, heavier plants in the deep zone.

It was found that the average biomass for all sites were 14.4 kg wet wt m^{-2}, but this estimate disregarded depth and substratum topography of the kelp bed. I thus suggest classifying kelp beds as being 'shallow' or 'deep'. 'Shallow' kelp beds would be those narrower than 80 m and with a depth of less than 3 m. In these cases a biomass of 10 kg m^{-2} of kelp bed could be used while for 'deep' kelp beds an average of 14.4 kg m^{-2} could be used. The logic is that these are conservative figures that will ensure that over-harvesting is prevented. For greater accuracy, however, densities of the kelp bed should first be measured.

To further assist in this process of assessing kelp bed biomass, a new method was developed and tested. This method attempted to determine a relationship between the number of kelp heads visible at the water surface, during low spring tide, and the kelp biomass. Good correlations were observed between the number of heads at the surface and the kelp biomass. This new method also compared well to the results obtained from the traditional 'bottom quadrat' method. This means that this method could be used to replace the traditional 'bottom quadrat' method. However, this study only investigated this relationship in *E. maxima*, and so further studies should be conducted to determine if this relationship also pertains to in *Laminaria pallida* beds, since they are also harvested in parts of the Northern Cape.

This study also investigated the effect that different harvesting methods might have on kelp growth, recruitment and population structure of subcanopy kelp. Although three methods of kelp harvesting are employed in South Africa, this study only looked at the 'lethal' and 'non-lethal' harvesting methods because the third method of 'whole' kelp harvesting is only used on a small-scale basis (for the production of Kelpak). The results indicate that harvesting had no effect on growth (as stipe elongation), recruitment or population structure of subcanopy kelp, irrespective of the harvesting method used. In this study growth was measured as stipe elongation. It was found that the long plants had a higher relative growth rate than medium and short plants. One explanation could be that plants invest a great proportion of their energy in stipe elongation to escape low irradiance levels close to the bottom. Long plants had a higher relative growth rate (stipe elongation rate) than medium and short plants. An explanation could be that smaller plants are investing more energy in frond growth, and that they 'wait' until some endogenous or environmental factor triggers a burst of stipe elongation, when they then rapidly reach the canopy. Although I expected the increased light levels resulting from harvesting to trigger growth of sub-canopy sporophytes, it did no do so. It seems unlikely, therefore, that light is triggering the rapid growth of long plants. Further studies could test whether endogenous factors are involved by transplanting sporophytes of different lengths vertically to several depths within the kelp bed. If small plants moved to near the surface continued to show low stipe elongation rates, and long plants transplanted deeper (to lower light) continued to grow fast, this would indicate that light is not a controlling factor, and that an endogenous control may be operating.

This study showed that harvesting all of the canopy fronds from a kelp bed reduced potential spore output by about 54%. While the reduction is large, I considered it unlikely to notably affect recruitment rate of sporophytes, given the estimate of 1.13 x 1011 spores m^{-2} annually that will still be produced by the subcanopy sporophytes, and probably overwhelming effects that other factors (e.g. primary space, herb ivory, and "environmental windows") have on kelp recruitment.

From a management perspective this study showed that the sub-canopy component of an *Ecklonia maxima* bed serves both as a source of future canopy, and an important source for zoospores to provide future gametophytes and, ultimately, sporophytes recruits. Current management practices (maximum sustainable yields, harvesting of surface fronds) should ensure that growth and recruitment are sufficient to maintain *E. maxima* beds and the ecosystem they are part of.

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