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THE EFFECTS OF KELP HARVESTING ON ITS REGROWTH AND THE UNDERSTOREY BENTHIC COMMUNITY AT DANGER POINT, SOUTH AFRICA, AND A NEW METHOD OF HARVESTING KELP FRONDS

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At Danger Point, South Africa, mariculture of the abalone *Haliotis midae* has led to increased demand for freshly harvested kelp *Ecklonia maxima*. This study estimates the biomass of *E. maxima* available for harvesting, investigates the effects of harvesting on the recovery of kelp and on the benthic understorey biota, and tests an alternative method of harvesting kelp by cutting off only fronds rather than whole plants. Estimates from diver sampling between May 1992 and November 1994 and infra-red maps indicate an *E. maxima* biomass at Danger Point of 22 973 tons fresh mass in 336 ha of kelp beds, insufficient to sustain projected abalone feed requirements in the area if harvesting is done in the traditional manner of cutting the stipes. However, sufficient frond material may be harvested sustainably if only fronds are cut, at distances 20–30 cm from the bases of fronds. Cutting at 10 cm from the base significantly reduced regrowth rates, and there was little regrowth after cutting at 2 cm. Yield per unit effort was higher for a four-month interval between harvesting them for one-, two- and three-month intervals. Two years after harvesting whole plants (in two 100 × 20 m lanes), biomass and density of kelp had recovered (similar in control and harvested lanes), and there were no detectable differences in the understorey communities, as measured by detrended correspondence analysis. Although harvesting of whole kelp has a minimal effect on the understorey biota and kelp itself recovers within two years, selective cutting of fronds allows plants to remains alive and produce a higher yield. This method is likely to minimize damage to the kelp bed system.

Key words: *Ecklonia maxima*, harvesting, fronds, kelp, regrowth, South Africa, understorey biota

The steadily increasing demand for South African abalone *Haliotis midae* in both foreign and domestic markets has resulted in the development of a fledgling abalone mariculture industry. South African seaweed concessionaires have been contracted by industry to supply fresh and dried kelp as abalone feed. Predicted demand for kelp is 7% of animal body mass per day. On average, a facility that aims to produce 100 tons of abalone of "medallion" size (50–70 mm) would require about five tons of fresh kelp fronds per day (Levitt *et al.* 1992). Permits have been issued for the experimental harvesting of kelp, mainly *Ecklonia maxima*. One of the main harvesting sites is located near two of the largest abalone mariculture facilities, at Danger Point (Fig. 1).

The usual harvesting method is for a diver to cut all *Ecklonia* plants with stipes longer than about 50 cm at the stipe/holdfast junction. The gas-filled bladder at the top of the stipe carries the stipe with attached fronds to the surface, where they are collected. The holdfasts of harvested kelp subsequently die, and recovery depends on the growth of small sporophytes that are present at the time of harvesting, as well as recruitment of new plants. Plants are harvested from lanes 60-m wide, which are cropped at 2–3 year intervals. Kelp regrowth in similarly harvested kelp beds at Soetwater, near Kommetjie on the Cape Peninsula (Simons and Jarman 1981), followed a pattern of a sudden increase in density of juvenile *E. maxima* sporophytes, as a result of increased light availability, and grew to the surface to form a canopy about two years after harvesting.

Disturbance is defined as the total or partial loss of biomass from an area by causes other than senescence (Chapman and Johnson 1990). Commercial harvesting of whole kelp plants is therefore a form of disturbance that may alter the structure and dynamics of kelp beds, with potentially large ecological and commercial effects.

The aims of this investigation were to estimate the potential harvest (standing stock) of *E. maxima* at Danger Point and to assess the consequences of harvesting whole sporophytes on kelp recruitment, regrowth and the understorey community. Furthermore, because only the fronds of *E. maxima* are fed to abalone, methods were tested to harvest only fronds and to leave the rest of the plant alive.

MATERIAL AND METHODS

During May 1992, four experimental lanes 100 m long × 20 m wide were established in the kelp beds at Danger

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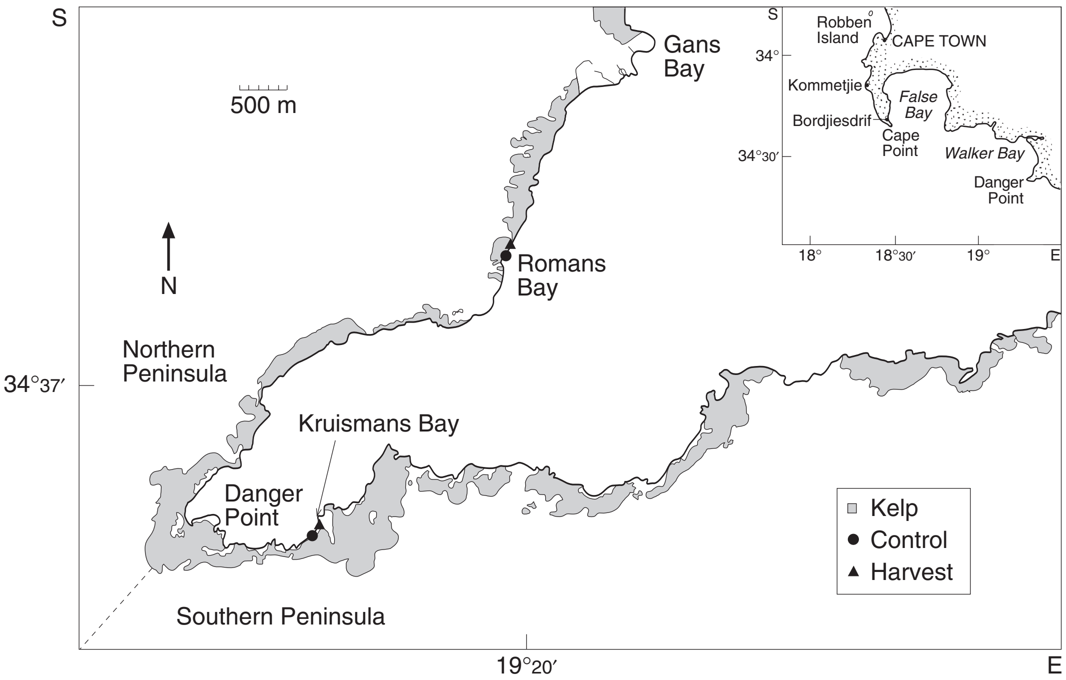

Fig. 1: Map of the Danger Point area showing the locations mentioned in the text and the study sites at Romans Bay and Kruismans Bay and the extent of the *E. maxima* surface canopy used to estimate standing stock

Point (34°40´S, 19°50´E; Fig. 1) by demarcation with chains of 100 m long laid along the substratum perpendicular to the shoreline. Various kelp parameters (biomass, density, mean plant mass, mean frond mass, stipe length) and understorey flora and fauna parameters were measured, then the kelp was cut from two of the lanes. This was done in Romans Bay in May 1992 and, because of weather and logistical limitations, in Kruismans Bay in November 1992. The effects of harvesting were then determined by re-sampling at six-month intervals and comparing the above parameters in harvested and control lanes, and following recovery to pre-harvest levels in the harvested lanes. Harvesting was done by the commercial method of removing all plants with a stipe length >50 cm, by cutting the stipes just above the junction of stipe and holdfast. One control and one experimental lane were located at Romans Bay on the northern side of the Danger Point Peninsula and a comparable pair of lanes was located at Kruismans Bay on the southern side, which is more exposed to the prevailing swells. The sites were sampled in May (autumn) and November (spring) each year from May 1992 to May 1997.

For the first five visits to each site (Romans Bay, May 1992–May 1994; Kruismans Bay, November 1992–1994), all kelp plants large enough to have stipes were harvested in 33 1-m^2 quadrats, located in groups of three at 10-m intervals along each chain. Each site was sampled before the harvesting treatment began, and at each subsequent sampling the position of quadrats was moved 1 m along the chain, and alternated from side to side, to avoid re-sampling the same quadrats. In each quadrat, kelp plants were removed by cutting at the stipe/holdfast junction. The plants were then carried to a boat, where they were counted and the stipe length, stipe mass and frond mass measured. Simultaneously, the benthic flora and fauna were subsampled by removing with an abalone lever all biota within a 0.5 × 0.5 m quadrat placed within the 1-m^2 quadrat. These samples were bagged and transported to the laboratory for identification and weighing. For this period, the benthic community structure in the control and harvested lanes was compared by detrended correspondence analysis (DCA), using the Canoco computer programme of Ter Braak (1986). For these analyses, wet mass of algae and animals (including shell) were used. Encrusting coralline algae were not collected. For the period November 1994

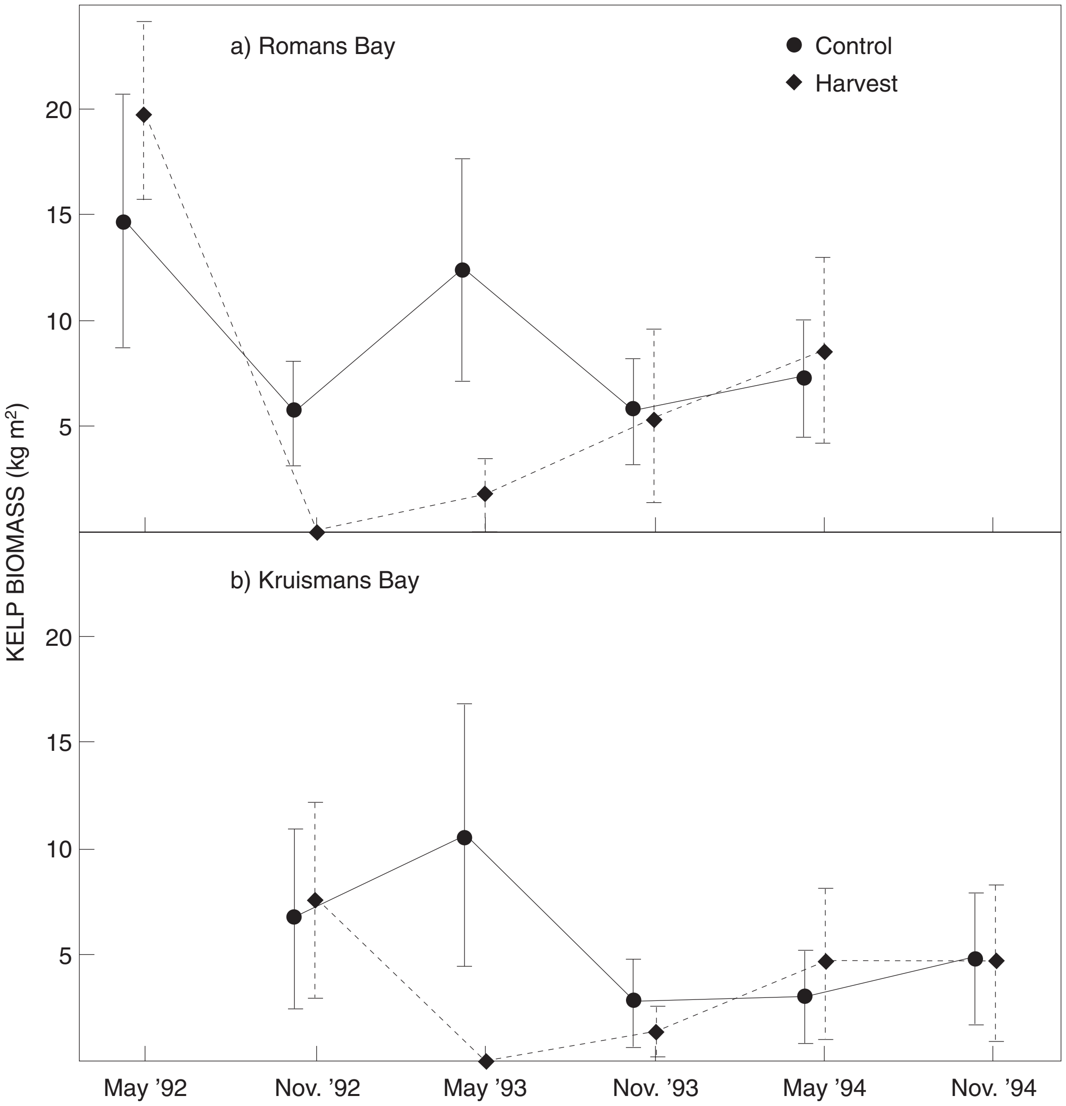

Fig. 2: Biomass (fresh mass) fluctuations of *E. maxima* for control and harvested lanes at (a) Romans Bay and (b) Kruismans Bay at six-month intervals (May 1992–November 1994). Bars denote 95% confidence limits. The first sample was obtained before harvesting began

–May 1995, kelp regrowth was monitored by means of counting and measuring, but not harvesting, the plants in quadrats placed as described above.

The biomass data obtained were used in conjunction with a determination of the Danger Point kelp bed area by Tarr (1993), who used infra-red aerial photography to estimate the standing stock of *E. maxima*. Although the kelp *Laminaria pallida* co-occurs with *E. maxima*, it is almost entirely subsurface (Dieckmann 1980) and far less abundant than *E. maxima*. The kelp surface canopy was therefore assumed to consist of *E. maxima* only, for the purposes of standing stock estimation. Kelp standing stocks were estimated separately for the northern and southern Peninsula, the division being located at Danger Point (Fig. 1).

A separate study to assess the effect of harvesting fronds (as opposed to whole plants) was undertaken at Bordjiesrif (34°19´S, 18°28´E), 81 km west of Danger Point. In June 1996, some 60 mature (but not senescent) individual canopy plants of *E. maxima* were tagged and numbered using cable ties. The sporophylls (secondary blades or fronds) were removed by cutting them off at various distances from their junction with the primary blade. Four experimental treatments were used, each with 15 replicate plants, blades being cut 2, 10, 20 and 30 cm from the base of the primary blade. Individual plants were re-harvested monthly in the same manner by SCUBA divers, and the net increase in sporophyll mass per plant was measured. Simultaneously, an additional 45 mature canopy plants of *E. maxima* were tagged and the sporophylls removed by excision 10 cm from their junction with the primary blade, in order to determine frond yield at harvest intervals of one, two, three and four months (four experimental treatments, 15 plants per treatment). At the appropriate interval, the individual plants were re-harvested in the same manner and the net increase in sporophyll mass per plant was measured. In both experiments, every plant in each treatment was individually examined each month and those that were dead, appeared unhealthy or were lost, were replaced with other mature canopy plants, and the sporophylls were harvested in the same manner. Throughout the study period, no more than three plants in any one treatment had to be replaced. All statistical analyses were performed using one-way analysis of variance and the Student Newman Keuls multiple range test to analyse the significance of difference between means.

RESULTS

Kelp biomass and standing stock

The biomass of non-harvested populations of *E. maxima* (Fig. 2) at both Romans Bay and Kruismans Bay showed marked fluctuations during the study, but were similar at the two sites. In the control lane at Romans Bay, the biomass was lower in November (spring) of the respective years, and higher in May 1992 and 1993 (autumn). The pattern was similar at Kruismans Bay (but note that sampling there started six months later).

At both sites, 99% of the kelp biomass was removed by harvesting, leaving only 0.1 kg m^{-2} (fresh mass) six months later. The kelp biomass in the harvested lanes 18 months later was statistically similar to that in the control lanes, although the latter was lower than at the start of the experiment. Furthermore, when viewed from the surface, the harvested lane at Romans Bay looked different from the control. The harvested lane had large bare patches where the kelp had not yet reached the surface, and these persisted for three years after harvesting, despite the biomass being statistically similar to the control. At Kruismans Bay, where the kelp was apparently more patchy, there was no visible difference in surface canopy cover, between the harvested and control lanes, two years after harvesting.

Table I: Estimate of standing stock of *E. maxima* at Danger Point, 1992–1994 (95% confidence limits are shown in parenthesis)

Parameter	Northern sector	Southern sector
Area (ha)	108	228
Kelp biomass (kg m^{-2})	9.22 (5.44–13.01)	5.71 (2.12–9.30)
Standing stock (tons fresh mass)	9 961 (5 874–14 048)	13 012 (4 822–21 201)

By averaging the biomass data for each sampling period, the standing stock of *E. maxima* kelp beds at Danger Point (Fig. 1) was estimated at 22 973 tons fresh mass (95% confidence limits = 10 696–35 249 tons; Table I), with a total kelp area of 336 ha, along about 16 km of coastline, for the period 1992–1994. Although the biomass of *E. maxima* at Kruismans Bay was 3.5 kg m^{-2} less than at Romans Bay, the larger area of the southern kelp beds resulted in their standing stock being some 3 000 tons greater than the northern kelp beds.

The mean plant mass in the control lane at Romans Bay (Fig. 3a) did not differ significantly ($F_{0.05(2),4,\infty} = 1.96 < 2.79$) between May 1992 and May 1994 (averaging 1.24 kg plant^{-1}). With the exception of the first measurement after harvesting (0.3 kg plant^{-1}, November 1992), plant mass in the harvested lane did not differ significantly ($F_{0.05(2),3,\infty} = 1.87 < 3.12$) during the same period, averaging 0.96 kg plant^{-1}. At Kruismans Bay, the mean plant mass (Fig. 3b) did not change significantly ($F_{0.05(2),4,\infty} = 8.96 > 2.79$) in the control lane after May 1993, averaging 0.63 kg plant^{-1} from November 1993 onwards, compared with 3.68 kg plant^{-1} until May 1993. In the harvested lane, the mean plant mass prior to harvesting (1.90 kg plant^{-1}, November 1992) was significantly greater ($F_{0.05(2),4,\infty} = 2.99 > 2.79$) than that after harvesting (mean = 0.72 kg plant^{-1}, May 1993–November 1994). After harvesting, there was no significant change ($F_{0.05(2),3,\infty}$ =

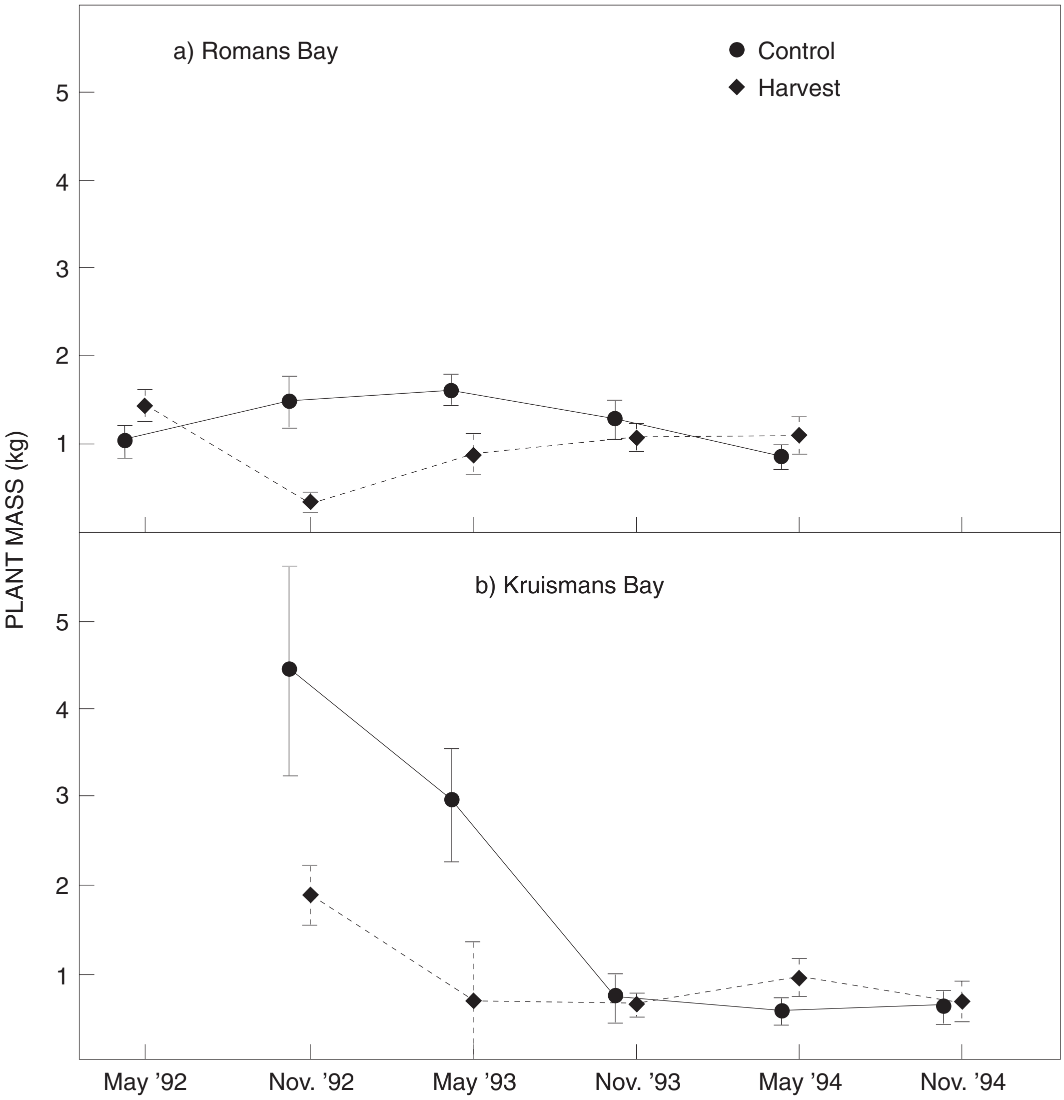

Fig. 3: Mean fresh plant mass of *E. maxima* for control and harvested lanes at (a) Romans Bay and (b) Kruismans Bay at six-month intervals (May 1992–November 1994). Bars denote 95% confidence limits. The first sample was obtained before harvesting began

2.62>3.12) in plant mass.

Variation in frond mass followed a similar trend to that of plant mass. There was no significant change ($F_{0.05(2),4,\infty}$ = 1.82<2.79) in the control lane at Romans Bay (Fig. 4a) between May 1992 and May 1994, averaging 0.56 kg plant^{-1}. In the harvested lane, there was a significant ($F_{0.05(2),4,\infty}$ = 3.51>2.79) decline in mass after harvesting between May and November 1992. Thereafter, frond mass increased gradually (no significant increase between successive samples), becoming similar to the pre-harvested mass some 18 months after harvesting (0.57 kg plant^{-1}, November 1993). At Kruismans Bay (Fig. 4b), there was a consistent, significant decline ($F_{0.05(2),4,\infty}$ = 3.26>2.79) in mean

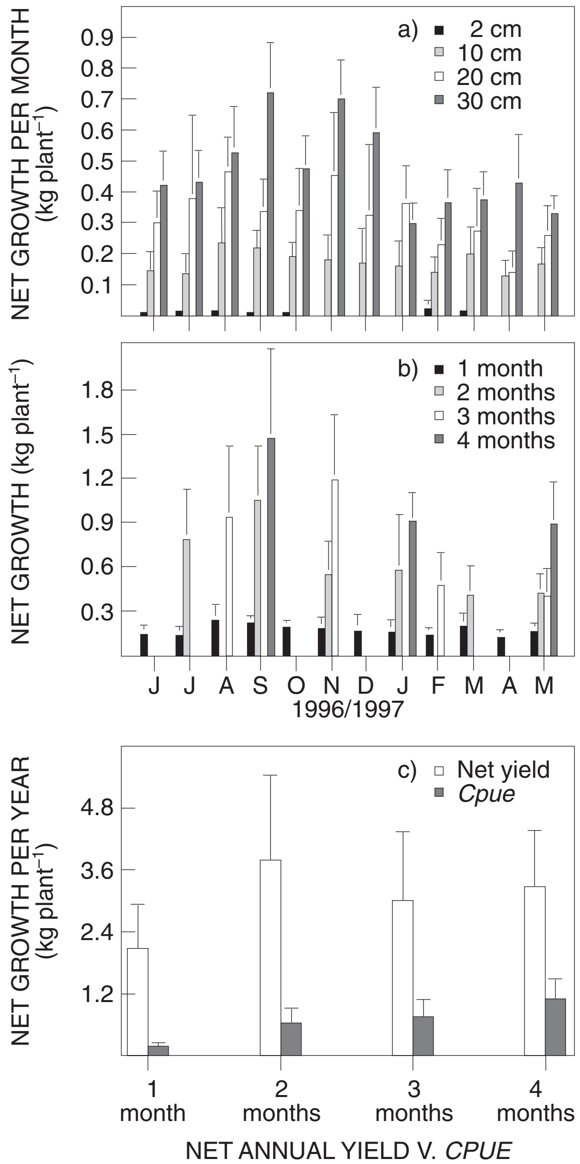

Fig. 4: Mean fresh frond mass of *E. maxima* for control and harvested lanes at (a) Romans Bay and (b) Kruismans Bay at six-month intervals (May 1992–November 1994). Bars denote 95% confidence limits. The first sample was obtained before harvesting began

frond mass in the control lane during the first year (November 1992–1993), but thereafter the mass remained relatively constant. In the harvested lane, there was no significant change ($F_{0.05(2),4,\infty}$ = 1.24<2.79) in frond mass throughout the study period, averaging 0.45 kg plant^{-1}. Between May 1992 and November 1994, frond mass of *E. maxima* averaged 45 and 31% of total plant mass in the control lanes at Romans Bay and Kruismans Bay respectively, and 51 and 47% in the harvested lanes.

The harvest yielded by cutting fronds from live plants increased with distance of the excision zone from the primary/secondary blade junction (Fig. 5a). The least re-growth (total = 0.75 kg plant^{-1} year^{-1}, June 1996–May 1997) occurred in sporophylls cut monthly 2 cm from the primary blade. Vegetative regrowth was significantly greater ($F_{0.05(2),3,\infty}$ = 28.46>3.12) in sporophylls cut 10 cm or more from the primary blade, with a total regrowth of 2.07 kg plant^{-1} year^{-1} being measured in plants cut at this distance. Similarly, significantly greater regrowth of 3.87 and 5.66 kg plant^{-1} year^{-1} was measured in sporophylls cut 20 and 30 cm from the primary blade respectively. Yield varied with harvest interval (Fig. 5b). In sporophylls cut 10 cm from the primary blade, the total net harvest yield was 2.07 kg plant^{-1} year^{-1} in plants harvested monthly, and 3.80, 3.00 and 3.27 kg plant^{-1} year^{-1} in plants harvested at two-, three- and four-month intervals respectively (Fig. 5b). Sporophylls harvested every month showed indications of a lower total net yield (Fig. 5c), but there were no significant differences ($F_{0.05(2),3,\infty}$ = 2.08<3.12) between the four harvest intervals. Mean yield per harvest (Fig. 5c) was inversely related to the time elapsed between harvests, being greatest in plants harvested at four-monthly intervals (1.09 kg plant^{-1} harvest^{-1}) and least in plants harvested at monthly intervals (0.17 kg plant^{-1} harvest^{-1}).

The mean stipe length of *E. maxima* was monitored from May 1992 to May 1997 (Fig. 6). In the control lane at Romans Bay (Fig. 6a), an initial mean stipe length of 0.82 m increased to 2.03 m by May 1993, declined to 0.8 m by May 1994 and thereafter maintained a mean length of 0.44 m between November 1994 and May 1997. The effect of harvesting was obvious in the harvested lane, stipe length declining significantly ($F_{0.05(2),10,\infty}$ = 2.94>2.05) from a pre-harvest mean of 1.55 m (May 1992) to 0.26 m (November 1992). Thereafter, the pattern was similar to the control lane. There was no apparent difference between the control and harvested lanes between November 1993 and May 1997.

In the control lane at Kruismans Bay (Fig. 6b), an initial (November 1992) mean stipe length of 3.92 m decreased to 0.82 m, and thereafter fluctuated between 0.53 and 0.80 m, with the exception of a marked decline to 0.19 m in May 1995. The harvested lane displayed a similar pattern, the effect of harvesting resulting in a decline in the mean stipe length from

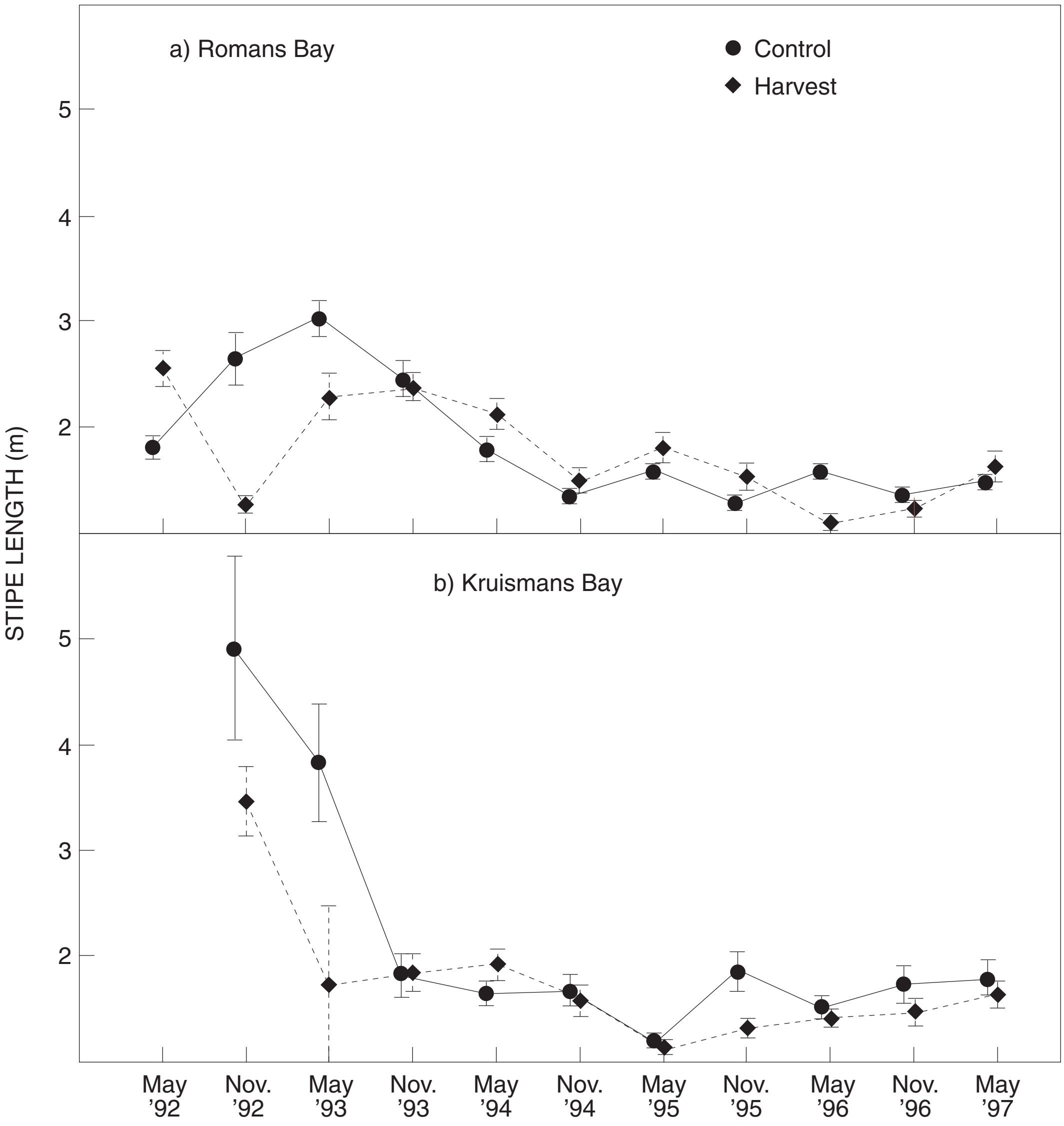

Fig. 5: Net growth of excised sporophylls of *E. maxima* at (a) different excision distances from the primary blade, (b) different harvest intervals and (c) net annual yield of 10 cm excision v. *cpue* (harvest; May 1992–November 1994). Bars denote 95% confidence limits

2.47 to 0.73 m between November 1992 and May 1993. Stipe length remained relatively constant between May 1993 and November 1994, with a mean stipe length of 0.77 m. A decline (to 0.11 m), concurrent with that noted in the control lane, was observed in May 1995. Thereafter, stipe length increased gradually to 0.64 m by May 1997.

Total plant density of *E. maxima* in the control lane at Romans Bay (Fig. 7a) fluctuated between 4 and 14 plants m^{-2} (mean = 11 plants m^{-2}), but it did not differ significantly ($F_{0.05(2),10,\infty} = 1.72 < 2.05$) between May 1992 and May 1997. The major pro-

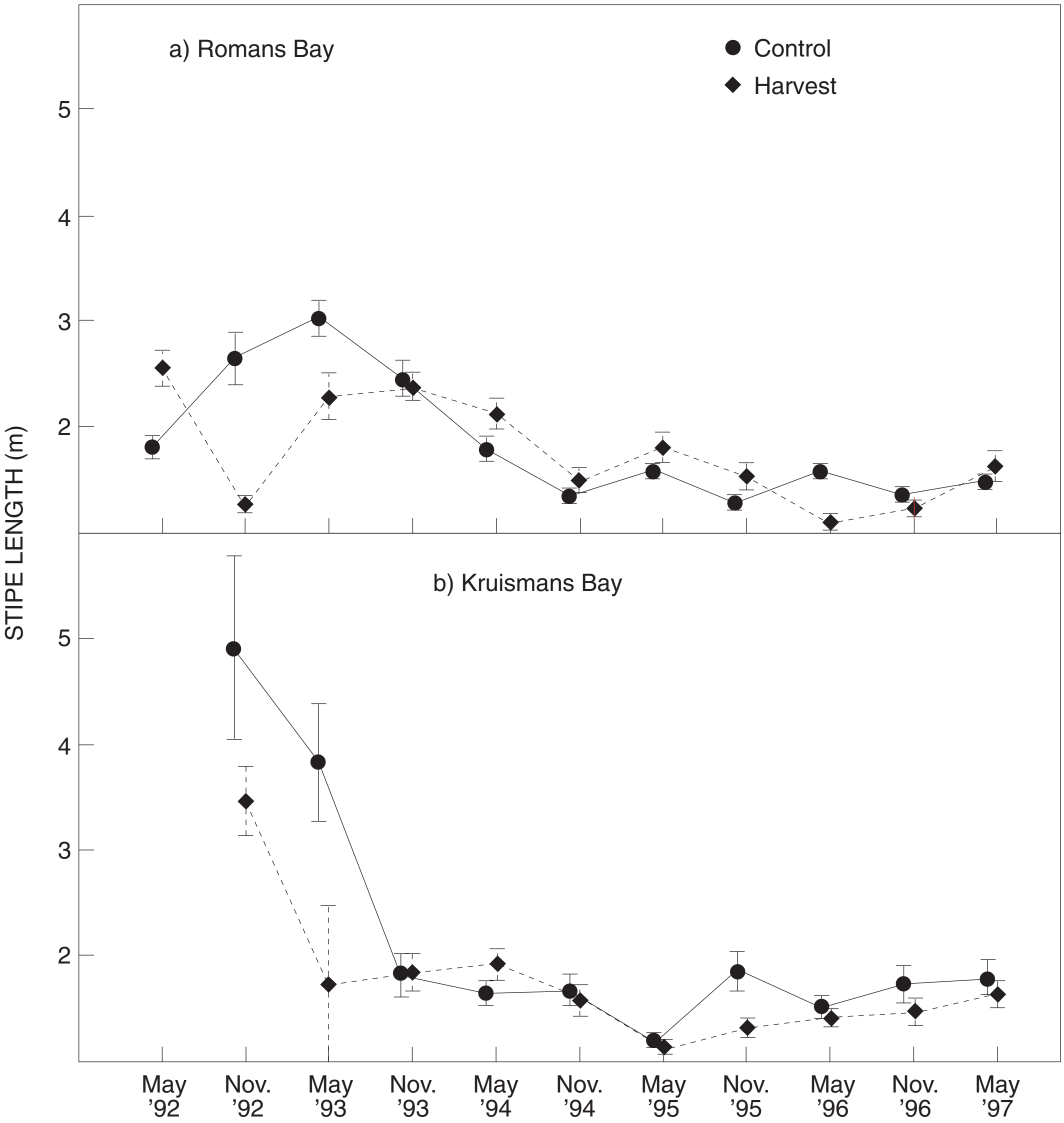

Fig. 6: Mean stipe length of *E. maxima* for control and harvested lanes at (a) Romans Bay and (b) Kruismans Bay at six-month intervals (May 1992–May 1997). Bars denote 95% confidence limits. The first sample was obtained before harvesting began

portion of plant density consisted of recruits (juvenile sporophytes with no stipe or a stipe <1 cm long), which accounted for an average of 63% of the total density, except for the period November 1992–November 1993 when recruits accounted for only 1% of the plant density. There was also considerable variation in plant density (4–14 plants m^{-2}) in the harvested lane at Romans Bay (Fig. 7b). Significant differences ($F_{0.05(2),10,\infty} = 2.43 > 2.05$) within the lanes were found only in the first year after harvesting, between November 1992 and May 1993. As in the control lane, total density was related to recruit density, with recruits accounting for an average of 54% of the total density, except for the period November 1992–

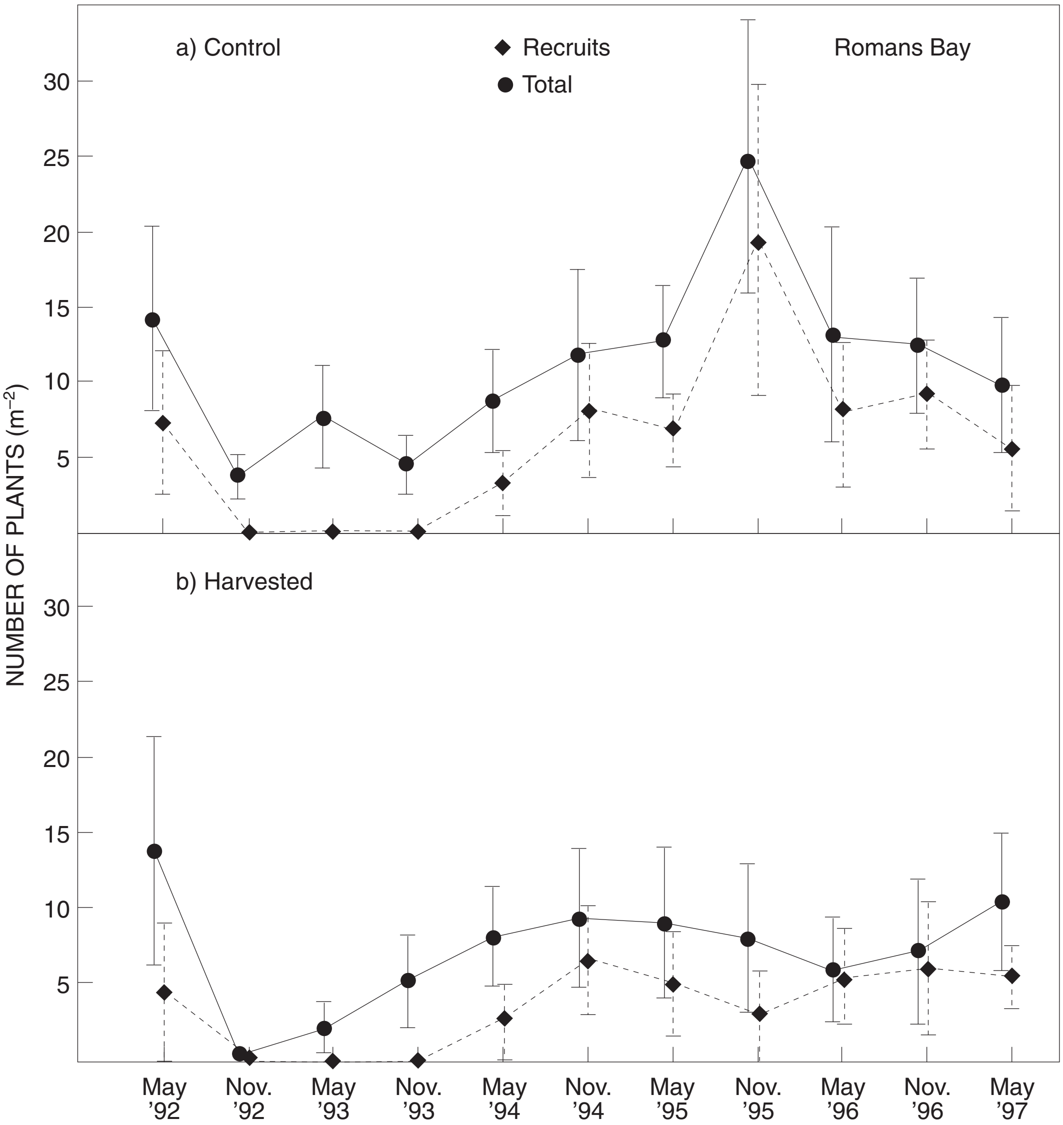

Fig. 7: Mean plant density (recruits and total) of *E. maxima* in Romans Bay for (a) control and (b) harvested lanes at six-month intervals (May 1992–May 1997). Bars denote 95% confidence limits. The first sample was obtained before harvesting began

November 1993 when few recruits were present.

In the control lane at Kruismans Bay (Fig. 8a), plant density increased from 2 to 8 plants m^{-2} (mean = 4.6 plants m^{-2}) and thereafter fluctuated between 11 and 19 plants m^{-2} (mean = 14.7 plants m^{-2}). The mean density over the study period was 10 plants m^{-2}. Until November 1994, the proportion of recruits was low (average = 10%), but thereafter it averaged 64% of the total population. In the harvested lane at Kruismans Bay (Fig. 8b), total plant density also displayed two distinct phases. During the period November 1992–November 1994, plant density ranged from 0

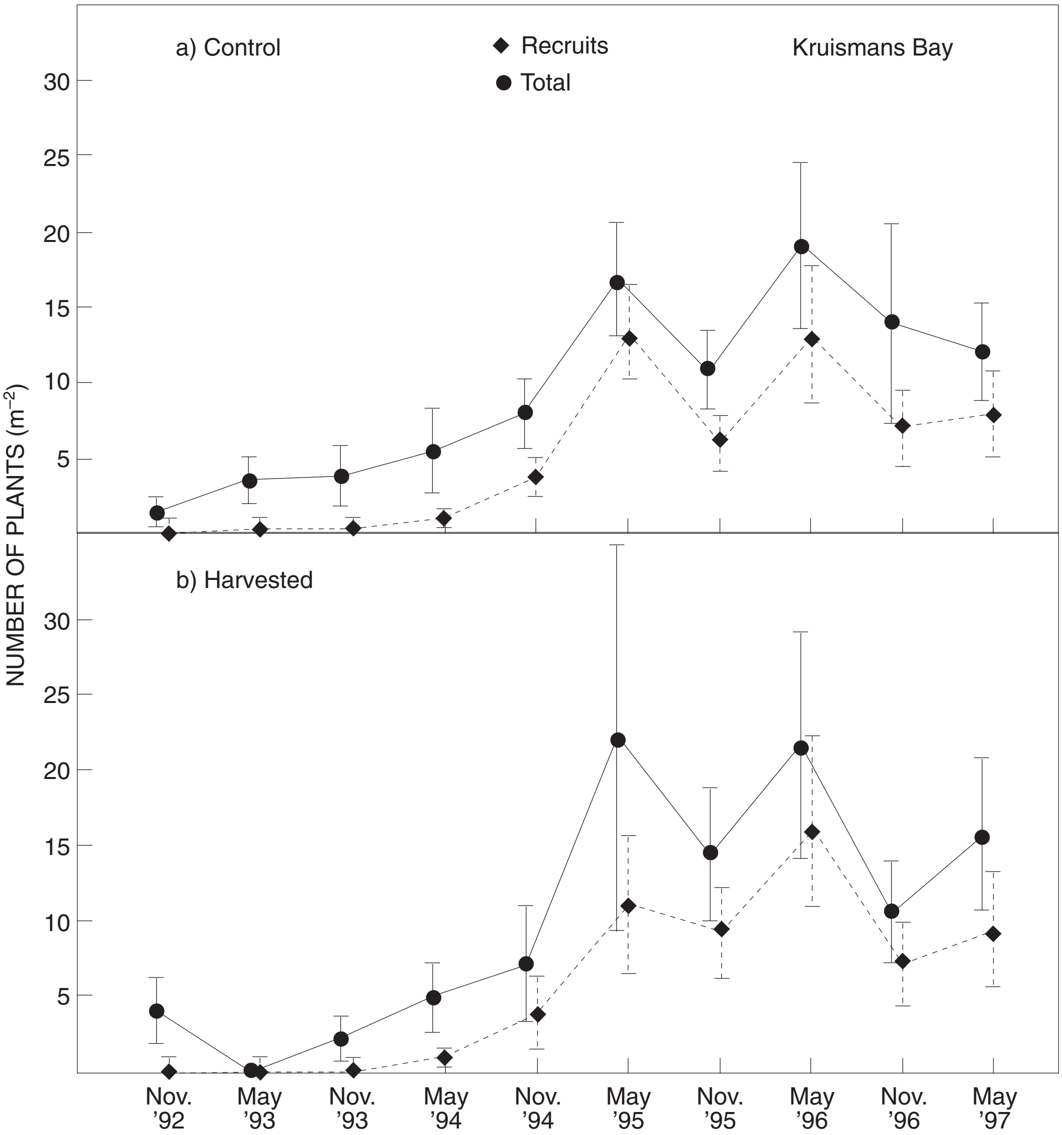

Fig. 8: Mean plant density of *E. maxima* in Kruismans Bay for (a) control and (b) harvested lanes at six-month intervals (November 1992–May 1997). Bars denote 95% confidence limits. The first sample was obtained before harvesting began

(after harvesting) to 7 plants m^{-2}, with a pre-harvesting density of 4 plants m^{-2}. Between May 1995 and May 1997, plant density ranged between 11 and 22 plants m^{-2}. The proportion of recruits at Kruismans Bay averaged 10% prior to November 1994 and increased thereafter to an average of 62%.

Associated benthic communities

At Romans Bay, the floral community structure changed little between May 1992 and May 1994 (Fig. 9). There was no observable difference in algal community structure (i.e. gross differences in distribution and

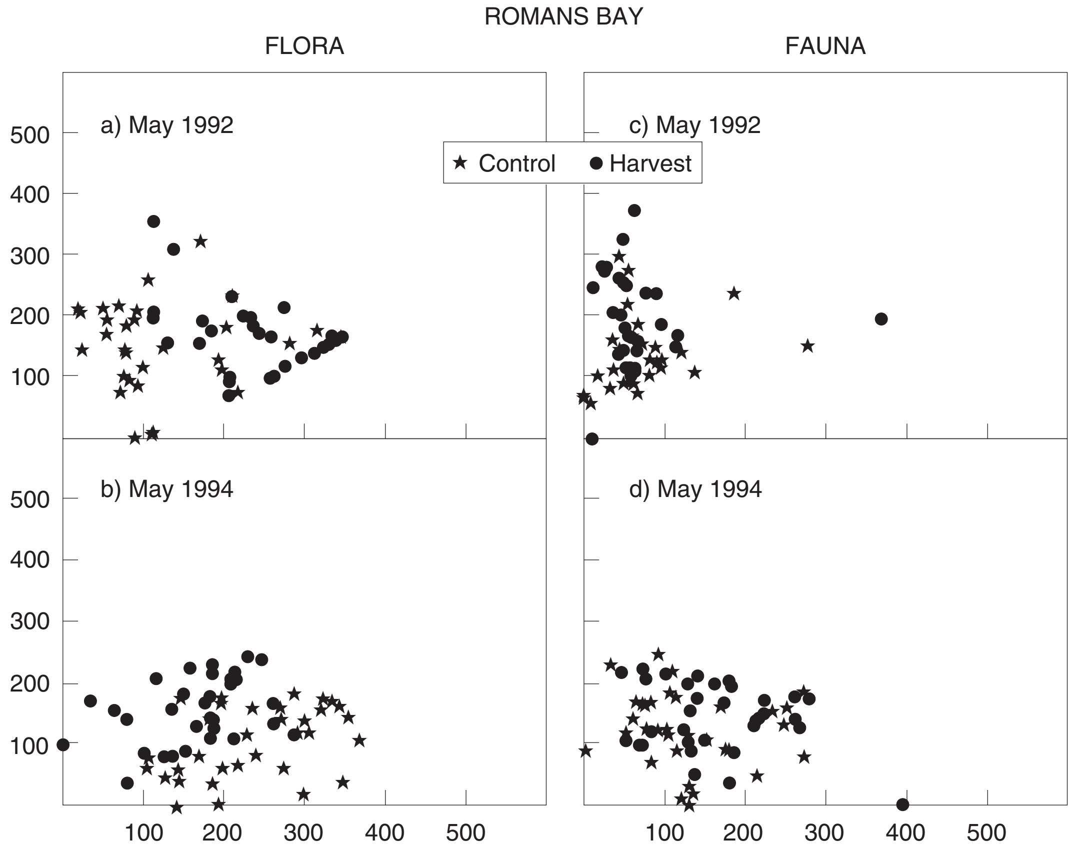

Fig. 9: Decorana ordination of the Romans Bay understorey benthos – (a) flora, May 1992; (b) flora, May 1994; (c) fauna May 1992; (d) fauna May 1994. Axis units are arbitrary. The first sample (May 1992) was obtained before harvesting began

spread of the individual quadrats in the ordination) in either the control or harvested lanes, based upon the ordination. Algal species richness (total number of species present in all quadrats during each sampling period) remained constant in the control lane (19 species), but it increased from 16 to 23 species in the harvested lane. Similarly, the faunal assemblages in May 1992 (Fig. 9c) differed little (control = 39 species, harvested = 40 species), with little spread over the ordination axes by the majority of quadrats sampled in both harvested and control lanes. By May 1994 (Fig. 9d), these faunal assemblages were slightly more evenly distributed, and richness had increased in the control lane (48 species) and was fairly constant in the harvested lane (41 species), although the overall spread across the ordination axes differed little from that observed in May 1992. The fauna did not differ in community structure between the control and harvested lanes and species richness remained fairly constant (November 1992, control = 40 species, harvested = 38 species; November 1994, control and harvested both 39 species).

At Kruismans Bay, there was also little change in floral community structure between May 1992 and May 1994 (Fig. 10), in either the control or harvested lanes. However, algal species richness declined in both control and harvested lanes, from 39 species in the control and harvested lanes in May 1992, to 25 and 26 species respectively by May 1994. At Kruismans Bay, the ordination of faunal data showed a greater spread (Fig. 10c) than at Romans Bay in May 1992, but by May 1994 (Fig. 10d) there was no difference between the two sites. Faunal species richness remained fairly constant at Kruismans Bay, 40 and 38

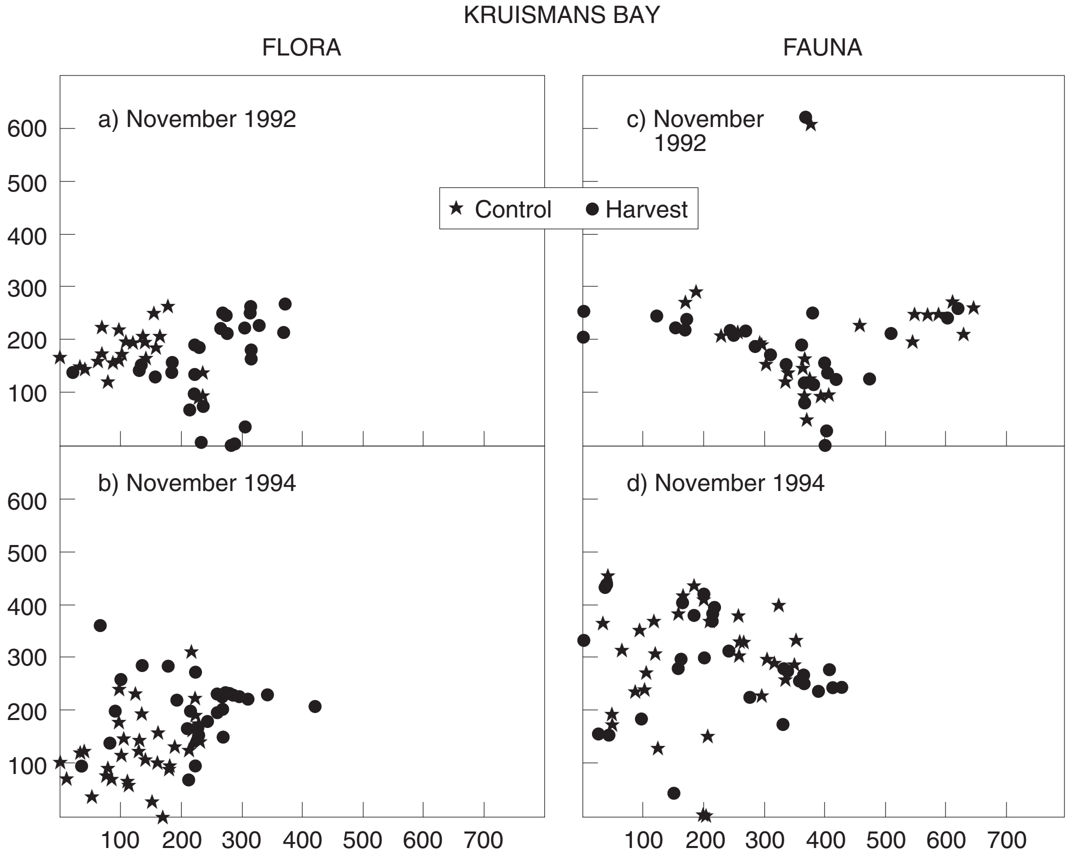

Fig. 10: Decorana ordination of the Kruismans Bay understorey benthos – (a) flora, November 1992; (b) flora, November 1994; (c) fauna, November 1992; (d) fauna, November 1994. Axis units are arbitrary. The first sample (November 1992) was obtained before harvesting began

species being recorded in the control and harvested lanes respectively in May 1992. By May 1994, 39 species were recorded in both lanes. As at Romans Bay, there were no differences in community structure between the control and harvested lanes at Kruismans Bay.

DISCUSSION

The standing stock of *E. maxima* estimated here (22 973 tons) is less than half that (46 398 tons) estimated for Danger Point by Levitt *et al*. (1992), using unpublished data by N. G. Jarman (formerly Sea Fisheries Research Institute). Because the present data were obtained from a total of 330 quadrats over a period of two years, compared with 16 quadrats used by Jarman over one year (1980), they are considered to be statistically more robust and a more reliable estimate of biomass. Using the control lane biomass data, the estimated frond standing stock of an unharvested *E. maxima* population at Danger Point is 8 535 tons fresh mass, comprising 4 480 and 4 055 tons in the northern and southern sectors respectively. Using the harvested lane biomass data, the estimated standing stock of *E. maxima* fronds at Danger Point, should the entire kelp bed have been previously harvested and allowed to recover for two years, is estimated to be 11 213 tons fresh mass (5 103 and 6 110 tons in the northern and southern sectors respectively). Average consumption of fronds at the largest Danger Point abalone farm is currently estimated at 6 tons per day, (N. Loubser, Irvin &

Johnson Ltd, pers. comm.). This is equivalent to 2 190 tons per year, or approximately 26% of the unharvested standing stock and 20% of the harvested and recovered standing stock. To maintain the yield required by the abalone industry, the entire kelp bed at Danger Point would have to be harvested every 4–5 years, which, irrespective of the questionable sustainability of such a harvest regime, is almost certainly impractical in terms of access to the kelp resource, bearing in mind problems of weather, geography and topography.

The processes that shape kelp bed structure and dynamics are of commercial as well as ecological importance. Given that disturbance is the primary process promoting diversity (Chapman and Johnson 1990), the likely consequence of removing the entire kelp biomass over a period of 3–4 years is increased benthic species diversity resulting from decreased interspecific competition, if new substratum space is available as a result of clearing. Therefore, disturbance may determine which species will compete, species diversity having been shown to increase in newly cleared *Laminaria* beds subject to primary succession (Christie *et al.* 1998). The fact that algal diversity increased in the Romans Bay harvested lane (from 16 to 23 species) may indicate a similar effect at this site. However, algal diversity declined at Kruismans Bay, so this change may be unrelated to harvesting. The comparatively constant faunal species diversity at both sites could indicate that the fauna is less susceptible to disturbance than the flora. It is possible that the increased light reaching the substratum after harvesting might promote algal diversity, by increasing algal colonization and succession, but have little effect on the benthic fauna, which likely would not respond to light.

The loss of kelp plants through mortality results in patchiness (Dayton *et al.* 1992), which, according to Keats *et al.* (1985), is a key factor promoting diversity. Therefore, species diversity is maintained by continued disturbance. According to Chapman and Johnson (1990), the highest levels of diversity are at intermediate levels of disturbance, which Christie *et al.* (1998), working in Norwegian *Laminaria* beds, suggest may be commensurate with regular harvesting.

The existence of a relationship between spore production, disturbance and recruitment in South African kelp beds has yet to be determined. Johnson and Mann (1988) found no evidence to suggest that re-establishment of the kelp *Laminaria longicruris* in Nova Scotia, Canada, is reduced by disturbance during periods of minimum spore production. Spore production in *E. maxima* has seasonal peaks, but it occurs throughout the year (Joska and Bolton 1987). Nevertheless, the overriding variations in the density of small sporophytes (which are here treated as recruits) are not seasonal at Danger Point. The general pattern there was of low recruitment between November 1992 and November 1993, followed by significantly higher but variable densities for the rest of the study period, indicating long-term or perhaps stochastic patterns. This is similar to conditions in California, where the episodic nature of kelp recruitment is well documented (Dayton 1985).

Nevertheless, the possible effects of disturbance on the benthos, together with the short lifespan of suspended kelp zoospores (Dayton 1985), may negatively affect *Ecklonia* recruitment, particularly if it is strongly episodic. *E. maxima* appears to be adapted to disturbances, because spore output is high (Joska and Bolton 1987), the gametophytes and juvenile sporophytes grow rapidly (Bolton and Levitt 1985), and the sporophytes tolerate low concentrations of nutrients (Probyn and McQuaid 1985), are resistant to wave action (Field *et al.* 1977) and have chemical anti-herbivore defences (Tugwell and Branch 1989). The competitive advantages that these qualities impart remain to be quantified, but they may contribute to the resilience of *E. maxima* in recovering from harvesting.

The rapid recovery of Norwegian *Laminaria hyperborea* depends on a reservoir of juvenile sporophytes that are unaffected by the harvesting (Christie *et al.* 1998). The lack of recruits at Danger Point in the year following harvesting indicates that recruitment during the year of harvesting and sporeling longevity are perhaps not such important factors in the case of *E. maxima*. Reed and Foster (1984) noted that the giant kelp *Macrocystis pyrifera* inhibits its recruitment by canopy shading. This does not appear to be the case in *E. maxima*, recruits being present in both shaded and open areas.

In Norway, intraspecific competition between *Laminaria* plants causes a reduction in density as the population matures after harvesting (Christie *et al.* 1998). However, there was no obvious reduction in the density of mature plants in the post-harvested *E. maxima* population in the two years following recovery to control levels. It therefore seems likely that these populations had matured fully, because densities were similar in the control lanes, and they looked typical of unharvested kelp beds in the area. It seems more likely that the density of *E. maxima* at this site is determined by factors other than intraspecific competition as the plants grow. The most likely determinants are grazing and the availability of primary space on the substratum. At Kommetjie (some 80 km west of Danger Point) there are few benthic grazers, and the harvesting of canopy plants is followed by dense recruitment of sporophytes, which have been observed to then thin out as they grow to the surface. Also, where benthic grazers are numerous, as at Danger Point, there is disproportionately high recruitment of *E. maxima* sporophytes on the holdfasts of mature kelps, compared to on the rock between holdfasts (Anderson *et al*. 1997). Therefore, grazers seem to have a controlling effect on the density of the young kelp sporophytes.

Periods of kelp recruitment at Danger Point appear to be interspersed with periods of poor or no recruitment (e.g. November 1992–November 1993), and may contribute toward slow regrowth where this coincides with natural mortalities or commercial harvesting. Recruitment was poor at Romans Bay from November 1992 to November 1993, coinciding with harvesting and a natural mortality event. However, no long-term negative effects of mortality on plant density were observed.

According to Chapman and Johnson (1990), control of herbivores is essential for the maintenance of kelp populations, and where herbivores predominate, kelp populations are restricted. There are numerous benthic grazers at Danger Point, including turbinid snails *Turbo sarmaticus* and *T. cidaris*, chitons and sea urchins (Anderson *et al*. 1997). The urchin *Parechinus angulosus* is particularly abundant at Romans Bay, possibly because there is less swell action there. The biological control of kelp by urchins has been documented in other regions (Chapman and Johnson 1990). In False Bay, South Africa, Fricke (1979) showed that urchin removal led to increased kelp recruitment. However, Day (1998) found that, in the same area, urchin removals had a negligible effect on algae, including kelp sporelings. In the present study, kelp recruitment was similar at the two sites, and most of the small sporophytes were in refugia provided by kelp holdfasts. Therefore, while it is not possible to distinguish the effects of urchins only, there is evidence that the suite of grazers present is an important determinant of kelp densities at Danger Point.

The harvesting of only fronds of *E. maxima* shows considerable promise, in that the required commercial yield can be achieved from much smaller areas than if whole plants are harvested. If harvest efficiency is maximized by harvesting every four months (annual net yield of 3.27 kg plant^{-1} year^{-1}), the gross annual yield resulting from harvesting the fronds of all plants, excluding those with stipes shorter than 50 cm, is estimated to be 17 939 and 31 678 tons fresh mass from Romans Bay and Kruismans Bay respectively. It is therefore estimated that a commercial frond requirement of 2 190 tons per year could be individually sustained by harvesting kelp beds of 13.2 and 15.8 ha respectively in those areas. It is not surprising that cutting the fronds too close to their junction with the primary blade inhibits regrowth, because the meristematic zone in *E. maxima* is somewhat diffusely spread at the base of secondary fronds (Mann *et al.* 1979). A further benefit of harvesting only frond material is that holdfasts are allowed to survive; these are important as "nursery areas" for kelp recruitment (Anderson *et al*. 1997).

Disturbance is reported as the main means of maintaining diversity in kelp bed systems (Chapman and Johnson 1990), and *E. maxima* beds are well adapted to stochastic and patchy biomass losses resulting from storms. Harvesting of larger plants is similar to storm losses, albeit on a potentially larger scale. However, the present study shows that, at Danger Point, the kelp bed recovered from harvesting in about two years, in terms of biomass and kelp density, although visual differences persisted for three years. Understorey communities were essentially unchanged two years after harvesting and showed no visual signs of change at any stage.

The projected commercial demand is for more than one-third of the local standing stock of *E. maxima* to be harvested per year. Given the apparent episodic nature of kelp recruitment, limited biomass and the practical difficulties imposed by restricted access, this level appears unsustainable. For this reason, harvesting of whole plants should, as far as possible, be avoided. However, the harvesting of fronds by excision shows promise, and appears to be the only possible means of maintaining a sustainable harvest from within the Danger Point region. Highest annual yield per plant is achieved by excision of the sporophylls 30 cm from the primary blades. However, the best catch per unit effort is obtained when cutting at four-month intervals (although this was only tested with a cut of 10 cm). This is proposed as the best management option.

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