The extent of die-back of the kelp *Ecklonia radiata* in the Cape Rodney to Okakari Pt. Marine Reserve

Advice to the Department of Conservation
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Summary

The kelp *Ecklonia radiata* has undergone high rates of mortality in a region of north-eastern New Zealand stretching from Whangarei Heads south to Cape Rodney and east to Great Barrier Island. Die-back of this kelp began in late 1991 and continued up to May 1993, with mortathy of over 90% in many areas. The area most heavily affected by die-back appeared to be centered on the Cape Rodney to Okakari Pt. Marine Reserve where mature kelp plants are virtually absent below 15m, and densities overall are an order of magnitude lower than in 1991. Die-back was patchier in other areas such as Great Barrier Island where affected and unaffected areas may be separated by distances of less than 100m. High densities of recruits became established at the Marine Reserve between January and May 1993 and full re-establishment of kelp populations should proceed over the next year, unless recruiting kelp becomes more susceptible to die-back in the post-recruitment phase. The causes of mortality are not yet known but so far human influences are not implicated. Hypotheses put forward to date include the action of pathogens such as bacteria, fungi or viruses, environmental effects related to temperature and phytoplankton blooms, and episodic demographic processes associated with the longevity of *Ecklonia.*

Table of contents

Introduction

The kelp *Ecklonia radiata* is the dominant macroalga in the subtidal marine communities of north-eastern New Zealand (Choat & Schiel 1982) and is a major component of food webs in these habitats (Andrew 1986, Choat and Andrew 1986, Meekan 1986, Keestra 1987, Andrew & MacDiarmid 1991). This alga also provides a major structural component of the habitat, creating a dense canopy of fronds. The sporophyte thalli are fixed to the substratum by a holdfast of multiple haptera from which a robust cylindrical stipe up to 2m high arises. At the terminus of the stipe meristematic tissue gives rise to a blade-like primary lamina which supports multiple secondary laminae. Both primary and secondary laminae are commonly 20-30cm long and 5-10cm wide. The recent die-back of large areas of this kelp clearly has the potential to dramatically alter community structure, and the effects may be felt for a considerable period. The cause of mortality is still unknown. Affected plants are characterised in the early stages by light-coloured patches on the laminae, associated with increased rates of erosion of laminae. The erosion process reduces the size and number of laminae until only the stipe remains. The stipe then regresses irreversibly, having lost its meristematic region, until even the holdfast disappears.

At present we do not have a clear picture of the spatial scale of this die-back episode, what has caused it, or how long recovery will take. The current episode of die-back was first detected at the Cape Rodney to Okakari Point Marine Reserve in late 1991 and continued through 1992. Accordingly the Department of Conservation has commissioned this advice.

This report describes the results of preliminary investigations into the density of kelp populations and rates of recent kelp mortality, the local and regional geographic extent of die-back, and the depth and size distribution of affected plants. The suitability and performance of video survey techniques in relation to kelp surveys is also assessed. Finally, the likely biological effects and possible causes of the phenomenon are discussed.

Methods

Eight sites in the Cape Rodney to Okakari Pt. Marine Reserve were surveyed twice, in January and May 1993. A total of 19 additional sites were surveyed at eight locations along the north-east coast New Zealand between Cape Karikari and Great Barrier Island during May 1993.

Ecklonia populations were measured using two survey methods, one based on quadrats, and the other based on video transects. Each method was used simultaneously in surveys of the Marine Reserve allowing a direct comparison of the two techniques. Video transects alone were used elsewhere. Both quadrat and video sampling were conducted along transects perpendicular to the shore and were depth-stratified, data being recorded within 3m depth intervals, 0-3, 3-6 etc. The beginning and end of each transect were marked with plastic tags nailed into the substratum.

Data were recorded to the lower limit of kelp distribution, usually where rocky substratum met a soft sandy bottom, although at some sites (eg. Karikari) data collection was curtailed at around 27m because of time and depth constraints on SCUBA diving.

Plants in quadrats or in video surveys were scored as being in one of eight ontogenetic or pathological stages. These were:

recruit:	primary lamina with negligible stipe development
juvenile:	small plants in understorey but with fully developed stipe
intact:	undamaged adult plants
reduced:	adult plants with reduced area of primary and secondary laminae, often blotchy in appearance.
primary only:	adult plants with reduced primary lamina only present
stipe:	entire stipe present but without primary lamina
half stipe:	portion of original stipe remaining
holdfast:	holdfast only remaining, stipe less than lcm long.

Quadrats

Within each depth stratum five $1m^{-2}$ quadrats were deployed haphazardly over substratum occupied by *Ecklonia radiata*. Since the major objective of the exercise was to gather information on the proportion of healthy and moribund plants in the population at each depth, rather than to obtain estimates of absolute density, this often necessitated deliberate placement of the quadrat within areas of kelp rather than on bare patches where they might otherwise have fallen. Any density values obtained from this data are therefore overestimates of the true abundance.

Video transects

Continuous video recordings were made of transects at each site using a Panasonic MC10 VHS-C camera in a waterproof housing. Artificial lighting was provided using a battery powered system attached to the camera. A scale bar (20cm) was always present in the field of view and was supported by an aluminium rod mounted on the camera housing. This rod also acted as a range-finder so that the camera lens could be maintained at a fixed distance (lm) from the substratum. A depth gauge was fixed to the scale bar so that the depth could also be determined at all times from the video recording. The camera operator swam along the tape measure used to delineate the transect line, providing a constant record of distance travelled along the bottom.

Video recordings were analysed in the laboratory using a standard VCR with variable-shuttle playback control. This allowed the operator to stop the video precisely at any point in the recording. *Ecklonia* plants within the field of view $(0.17m^2)$ were counted and their stage recorded twice every 5m along the tape. For each measurement depth was noted and data were later apportioned into the correct depth strata for analysis. As with the quadrats, the objective was to obtain information on the proportion of affected and unaffected plants in the population. The tape was stopped accordingly, avoiding patches devoid of *Ecklonia* where possible, within each 5m section of transect. Due to features such as urchin dominated coralline flats data sets occasionally, and unavoidably, did contain a series of zero values however density estimates are still likely to be overestimates of real values.

Tagging

In order to document the rates at which die-back manifested itself in affected populations, *Ecklonia* sporophytes at four degenerative stages (intact, reduced, stipe, half-stipe) were tagged in January 1993 at the Marine Reserve, and re-censused 6 weeks later in March. Tags were numbered pieces of plastic dymo tape, attached to the haptera using cable ties. It was not possible to locate unaffected populations in the area which could be used as a basis for comparison with rates of mortality in unaffected populations.

Results

Mortality estimates

Kelp densities at two sites in the Marine Reserve varied greatly between 1991 and 1993 (Fig. 1). In depths greater than 10m, usually dominated by *Ecklonia radiata,* mortality related to the current die-back episode has been severe with a reduction of 90-100% in kelp density. For kelp between 9m and 15m at Lookout Point, densities decreased from over $70.m^{-2}$ to less than $5.m^{-2}$ and below 15m, mortality has been virtually total. This pattern of mortality is reflected in other parts of the reserve, with formerly dense forests of kelp now consisting of areas of coralline-encrusted rock sprinkled with stipes, holdfasts, and small thalli of *Carpophyllum flexuosum*. Both quantitative video surveys and quadrat counts at 8 sites encompassing the entire reserve (Fig. 2A,B; Fig 3A,B) indicate densities of kelp much lower than those reported in 1991 (Fig. 1).

Spatial patterns of mortality

Depth effects

The die-back of *Ecklonia* was first noticed in late 1991 (R. Cole and C. Syms *pers. comm.*) in about 15m depth. At this time it was localised in an area in front of the beach at Goat Island Bay. Extensive die-back of plants in other parts of the reserve was noticed in November 1992, initially at the bottom of the reef areas (15-20m), with plants in shallower water (9-12m) seemingly unaffected, and the worst effects visible in plants deeper than 15m. A similar pattern with the deepest plants dying first was also noted by workers diving in areas outside the reserve (F. Anthoni *pers. comm.*). Differential die-back with depth between 1991 and 1993 is apparent in Fig. 1, with little reduction in density at depths less than 6m, and variable reductions in density at 9m. Terminal die-back stages (holdfasts) were also most abundant in deeper areas (Fig. 4).

Later in the die-back episode, between January and May 1993, a similar depth related pattern was evident with proportionally greater decreases in the density of plants at mid-depths (9,12m) than for the deeper plants (15,18m) which had already undergone almost complete mortality (Fig 2B). A comparison of Figure 2 (intact and reduced plants) and Figure 3 (intact plants only) illustrates that most of this die-back is likely to have taken place in plants that were already in a "reduced" state.

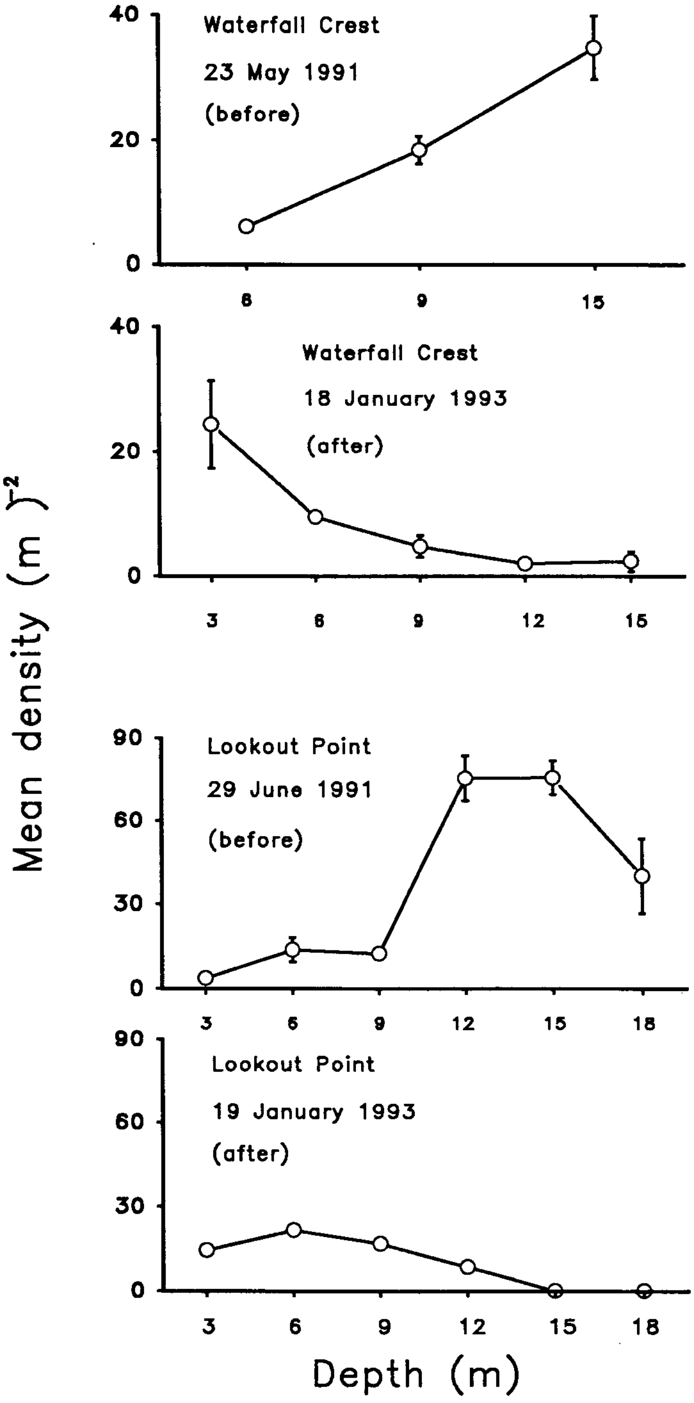

Figure 1. Kelp density before and after die-back. Mean density (± 95% C.I.) of *Ecklonia radiata* in the Marine Reserve based on 5 **1m^2** quadrats at each depth. Depths are maximum depths for each depth stratum (eg. 3-6m, 6-9m, 9-12m etc.). Seasonal variations in Ecklonia density are not significant (Schiel 1980).

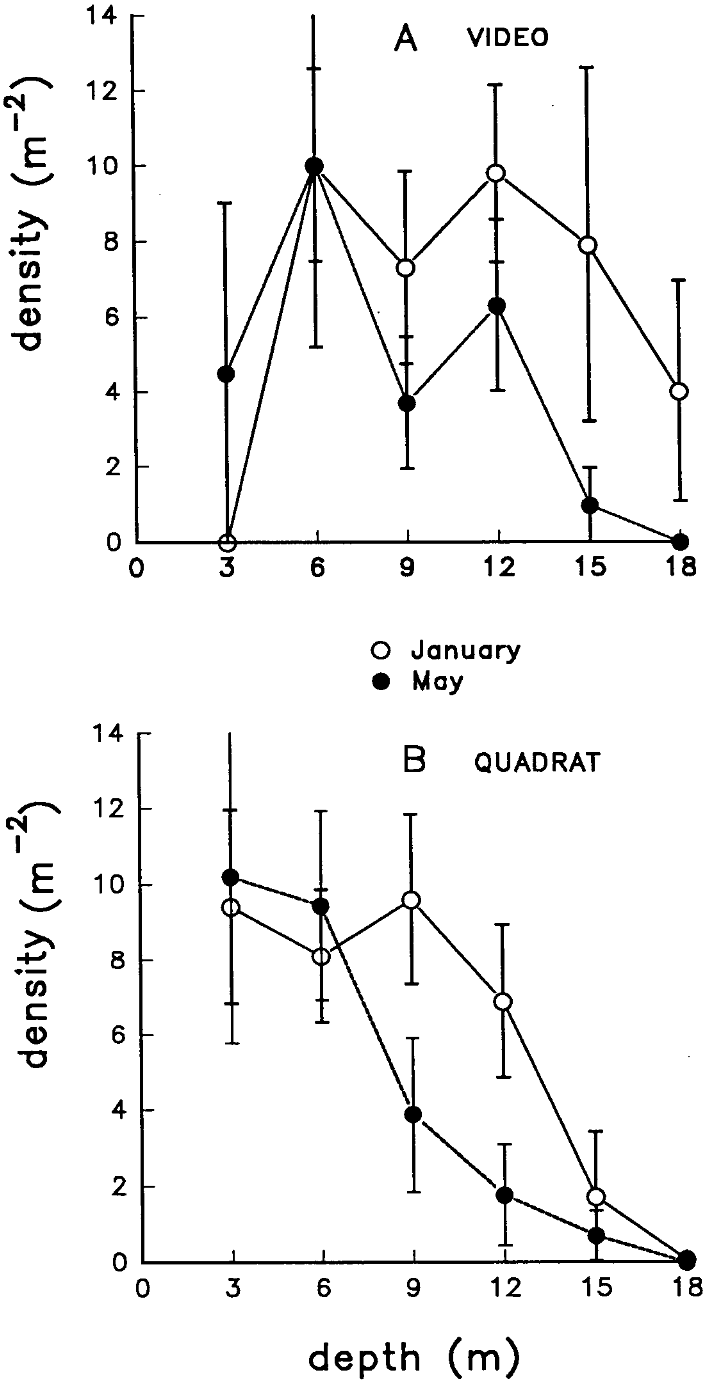

Figure 2. Density of *Ecklonia radiata* during the die-back event, 1993. Mean density (±95% C.I.) of plants (intact and reduced categories combined) at each depth stratum, based on surveys at eight sites in the Marine Reserve. A. Video data based on single video transects at each site with depth-stratified sub-sampling. B. Quadrat data based on 5 quadrats from each depth stratum.

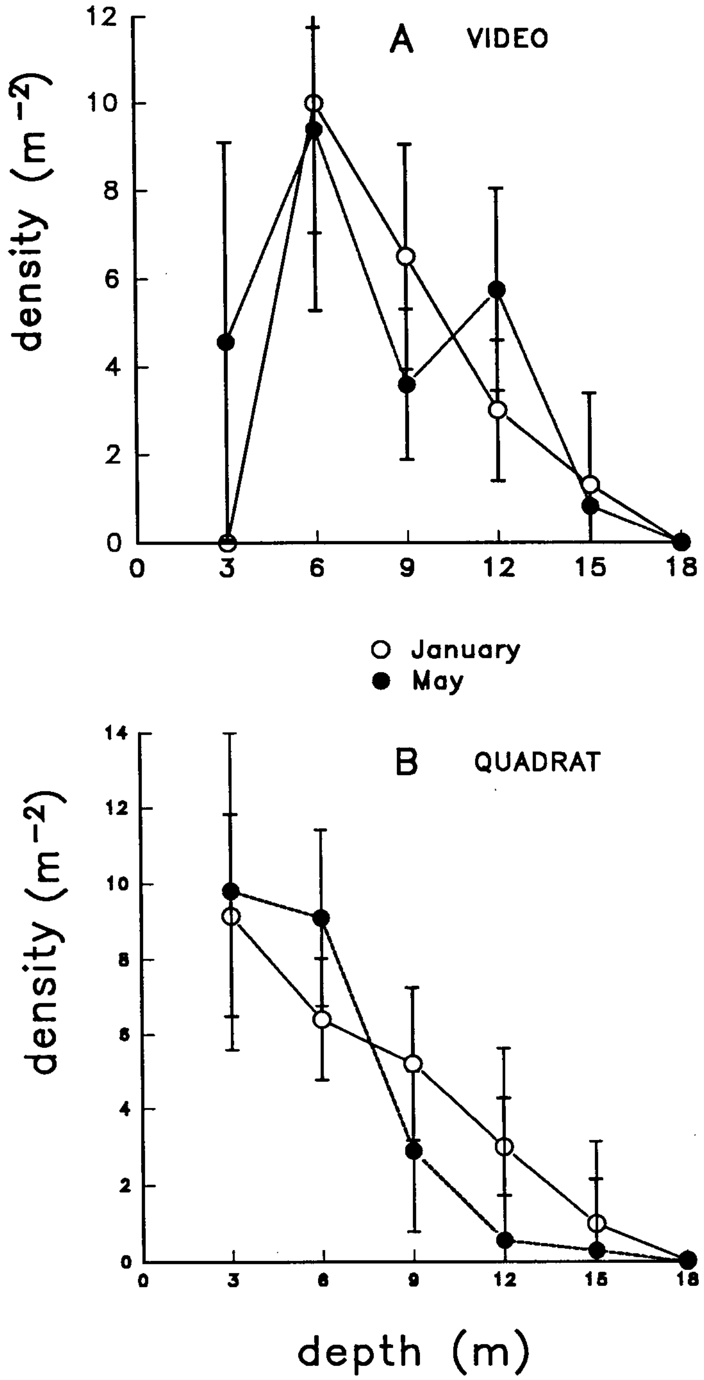

Figure 3. Density of *Ecklonia radiata* during the die-back event, 1993. Mean density (±95% C.I.) of intact plants at each depth stratum, based on surveys at eight sites in the Marine Reserve. A. Video data based on single video transects at each site with depth-stratified sub-sampling. B. Quadrat data based on 5 quadrats from each depth stratum.

Local die-back patterns

At each site within the Marine Reserve the proportion of *Ecklonia* affected by die-back, i.e. damaged or intact, varied considerably (Fig 5), though all sites had low densities of intact plants. The proportion of intact plants was relatively high (over 50%) at Marimo and Point, but was much lower elsewhere, for example Waterfall and "D", where degeneration appeared to be still active. The proportion of the populations composed of recruits was also variable, with North Reef and Lookout having the highest levels. Despite the overall variability, degeneration was consistently most severe at the deepest levels at each site (Fig. 4).

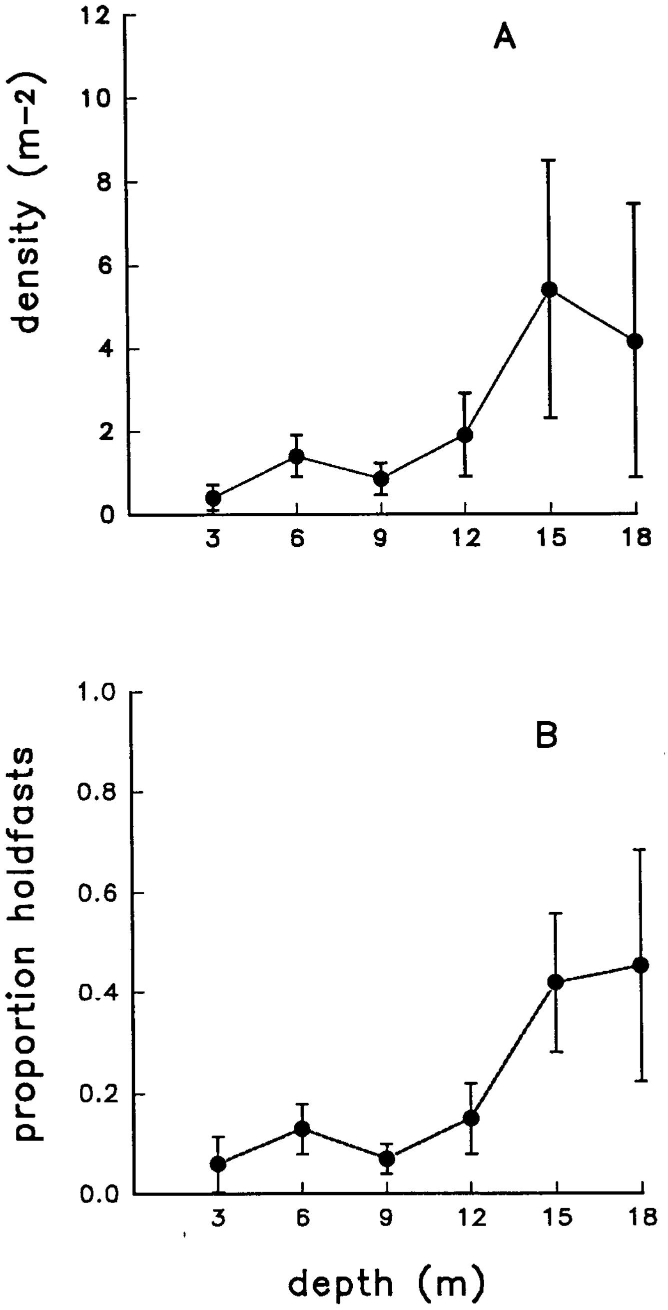

Figure 4. Density of *Ecklonia radiata* holdfasts during the die-back event, 1993. Mean values (±95% C.I.) for holdfasts at each depth stratum, based on surveys at eight sites in the Marine Reserve A. Density. B.Proportion of plants present as holdfasts only.

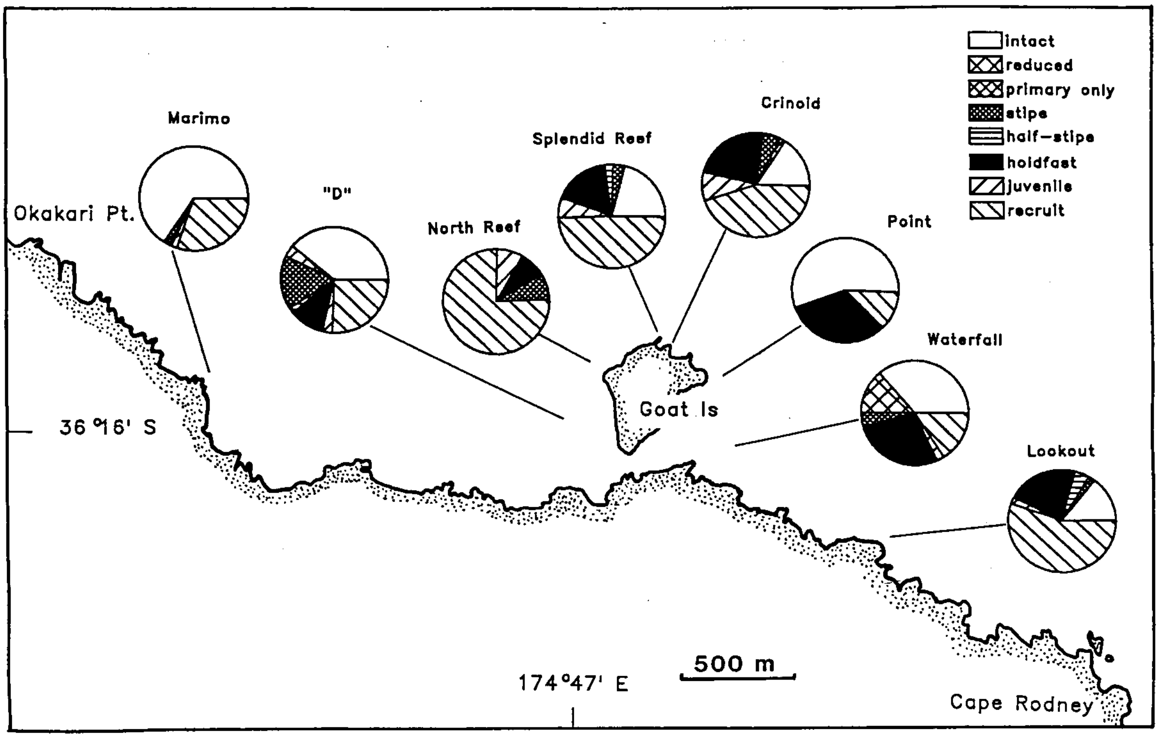

Figure 5. Local variation in proportion of *Ecklonia* affected and unaffected by die-back, Marine Reserve, May 1993. Data presented are proportions in each damage category based on video transects, and are totals of all depth categories.

Regional die-back patterns

A survey of locations between Cape Karikari in the north and Kawau Island in the south, and offshore to western Great Barrier Island, revealed that in this region kelp die-back was restricted to the outer Hauraki Gulf area (Fig. 6). All sites at Whangarei Heads, the Marine Reserve, Little Barrier Island were affected to some extent, however within the affected region there was again variation in the level of die-back among sites. For example Okakari Pt., adjacent to affected sites at the Marine Reserve, showed no sign of die-back. This local scale variability was evident over short distances with affected and unaffected sites at Great Barrier Island being separated by only 100m (Fig. 6).

The pattern of most severe die-back in deep water was not always seen outside the Marine Reserve. The affected site at Great Barrier Island had undergone high rates of die-back, with over 50% (excluding recruits) of plants present showing a total loss or reduction of laminae, yet the most seriously affected areas at this site were in shallow water.

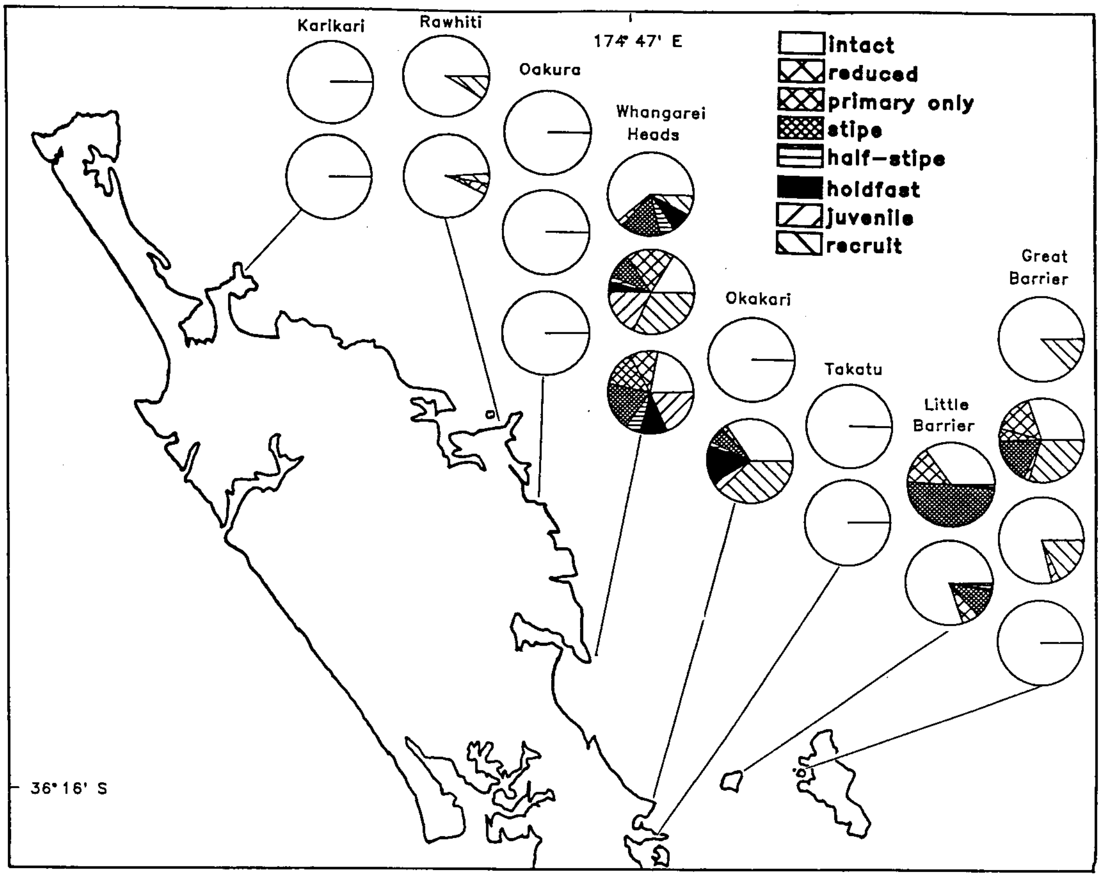

Figure 6. Regional variation in relative kelp die-back, Cape Karikari to Great Barrier Is., May 1993. Data presented are proportions of *Ecklonia* in each damage category based on video transects, and are totals of all depth categories. Several sites were surveyed at each location with the data for each displayed under the location name.

Temporal patterns of die-back

Tagged plants

Tagged plants of all degenerative stages underwent significant die-back, either regressing to a more moribund stage or disappearing altogether (Fig. 7). Only 25% of intact plants (at 9m) survived the 6 week period without damage, with approximately the same number of plants regressing to a reduced state or disappearing. Plants initially in the reduced category (12m) also suffered significant reductions, with 20% down one category. Degeneration in other stages (stipe and half-stipe, 15m) proceeded at various rates and since these plants had lost their meristematic tissue the process would be irreversible. Notably, plants at various stages of degeneration could only be readily found at specific depth strata, with the healthiest plants being in shallower water. This corroborates other data from the Marine Reserve which indicate the most severe die-back was in deep water first.

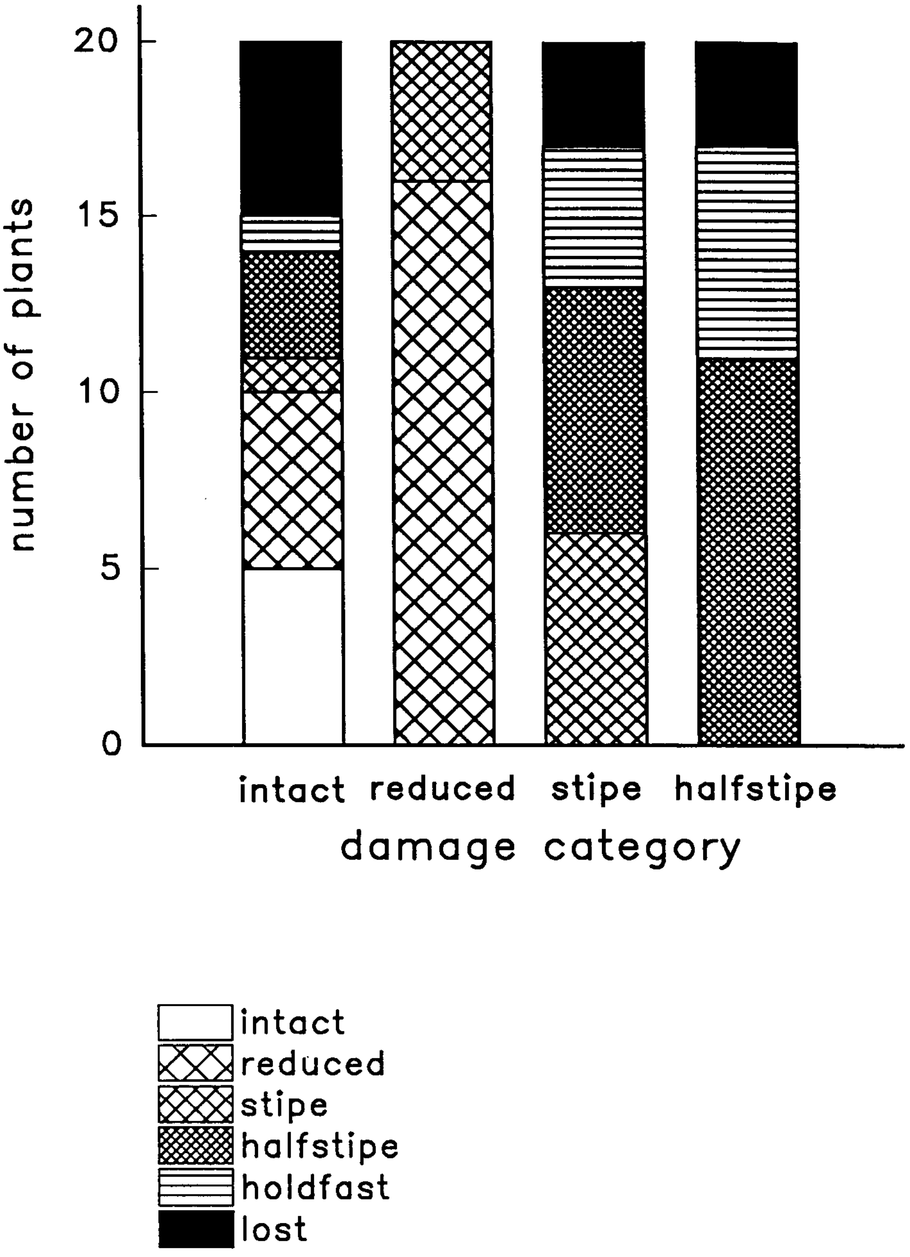

Figure 7. Fate of tagged *Ecklonia* plants. 20 plants from each of the categories intact, reduced, stipe and half-stipe were tagged and their fate (damage category) recorded after 6 weeks.

Recruitment

Very few recruits of *Ecklonia* were detected in surveys of the Marine Reserve during January 1993 (Fig 8). During March numerous recruits were noticed in parts of the reserve and by May high levels of recruitment were evident at most sites. The disappearance of degenerating plants during this period may have led to the apparent increase in the proportion of intact plants.

For the Marine Reserve as a whole, there was an average of 25 recruits m^{-2} (n=40) at 15m during a census in May (Fig 9a). These young plants would have become established while degeneration was still active at these sites, in the period October-December 1992 (Schiel 1980), and continued to grow through to May 1993. The gametes which give rise to the sporophyte thallus (kelp plants) of *Ecklonia* are produced by the diminutive gametophyte generation which can survive in the low-light conditions below an intact kelp canopy (Novacek 1984). Having been freed from the shading canopy of mature kelp plants the gametophytes have apparently produced enough gametes to establish a cohort of recruits at densities beginning to approach those found prior to the die-back episode.

Quantitative video survey techniques

The use of underwater video apparatus on SCUBA provides several logistic advantages over other survey techniques. Large areas of substratum can be covered in a short period of time, leaving a permanent record. Tapes can later be analysed in a variety of ways (% cover, densities, frequencies) and can also be directly compared with subsequent surveys. Negative aspects of video surveys, as opposed to direct *in situ* measurements, relate mainly to the accuracy of the data which can be derived from them. Video images can suffer from a lack of resolution and, when objects of widely varying sizes and relief are involved, the fixed camera angle usually employed can introduce bias. The result of these limitations is that single video records of sites cannot be employed to obtain useful information regarding all organisms present. In this respect it is not really different from other survey methods in that the technique used usually has to be tailored to the specific question and organism in question.

Video surveys proved to be an effective means of rapidly assessing and documenting kelp condition. Measurements from the Marine Reserve based on video recordings and on *in situ* quadrat measurements showed a high level agreement with one another (Fig 9, note overlap of confidence intervals) both in terms of absolute density and the proportion of intact plants. The exception, at 3m where agreement was low, was a result of the deliberate bias in the deployment of quadrats at this depth. Kelp in these shallow areas was more patchily distributed than in deeper water and quadrats were positioned over these patches in order to allow enough plants to be sampled. Measurements of density based on the video transect, which were recorded over a measuring tape laid perpendicular to the slope, were much less prone to this bias. The proportion of plants registered as intact at 3m varied little between the two methods (Fig. l OB).

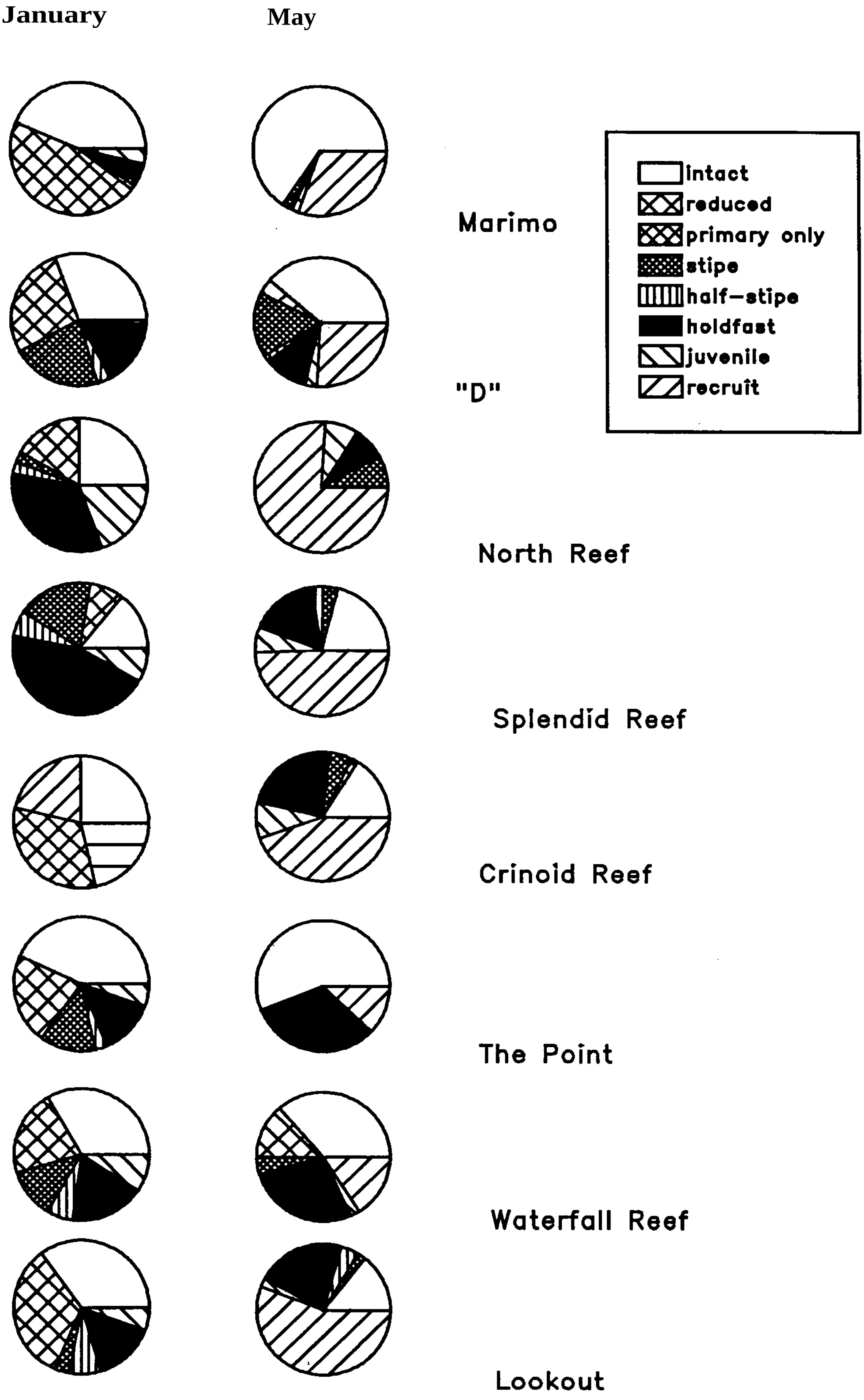

Figure 8. Variation in composition of *Ecklonia* sampled at sites within the Marine Reserve. Data were collected in January and May 1993 and are based on video transect data.

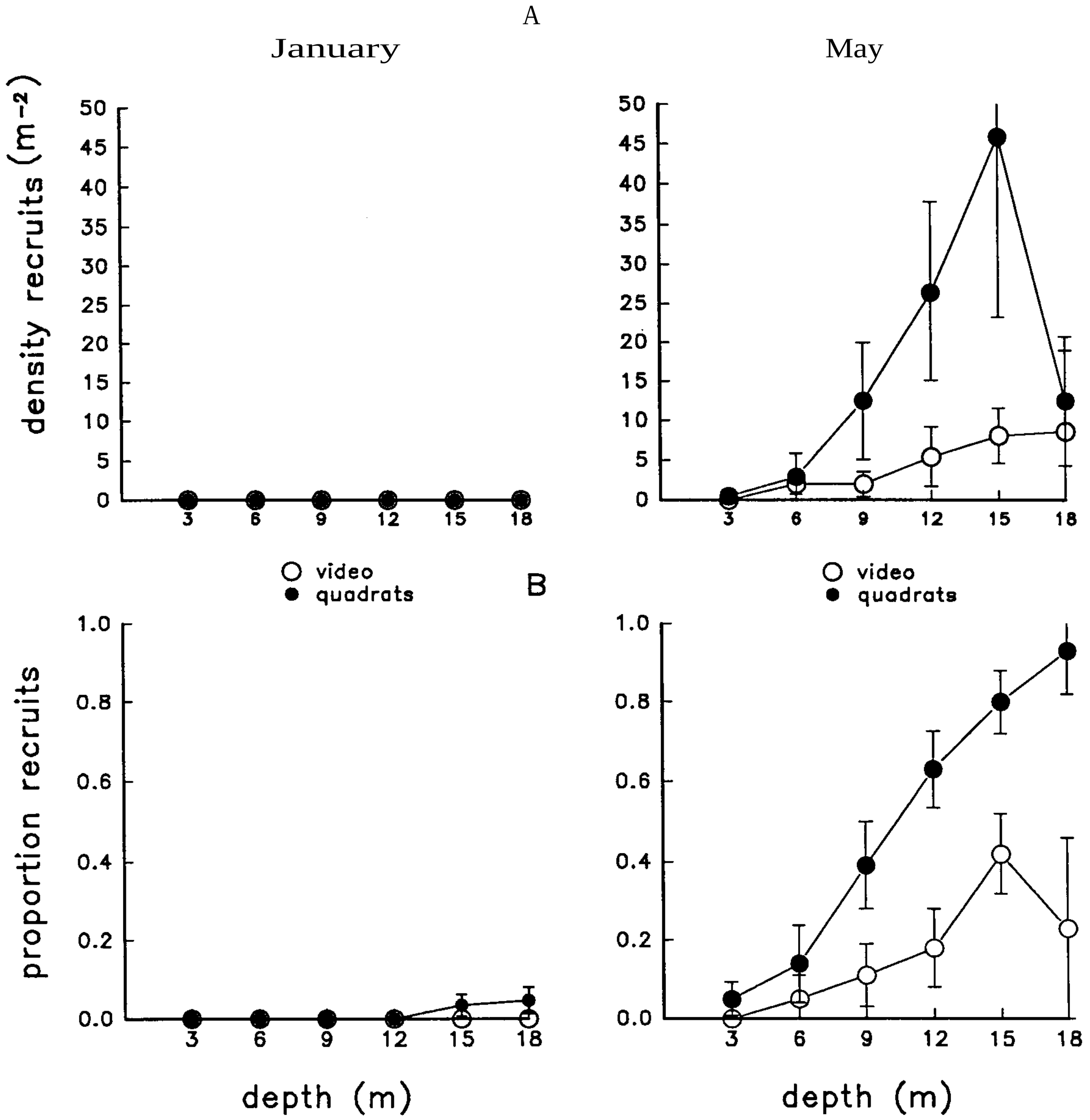

Figure 9. **A**. Density of recruits at each depth stratum (mean ±95% C.I.), as assessed by video and quadrat measures. **B**. Proportion of total plant numbers (mean ±95% C.I.) as assessed by both video and quadrat measures. Data for both A and B are means for eight sites at the Marine Reserve, and combine data from both January and May.

There was serious bias against recruits in the video transect method, due partly to the limited resolution of the camera system used, but also to larger plants obscuring them from view. Although resolution can be improved by better camera systems and more powerful lighting, it seems unlikely that video methodology will consistently be able to gather adequate data on both adult and recruiting plants. The laminae of adult *Ecklonia* may form a canopy 1-2m above the recruits on the substratum, and the focus and illumination settings required to record each adequately cannot easily be combined.

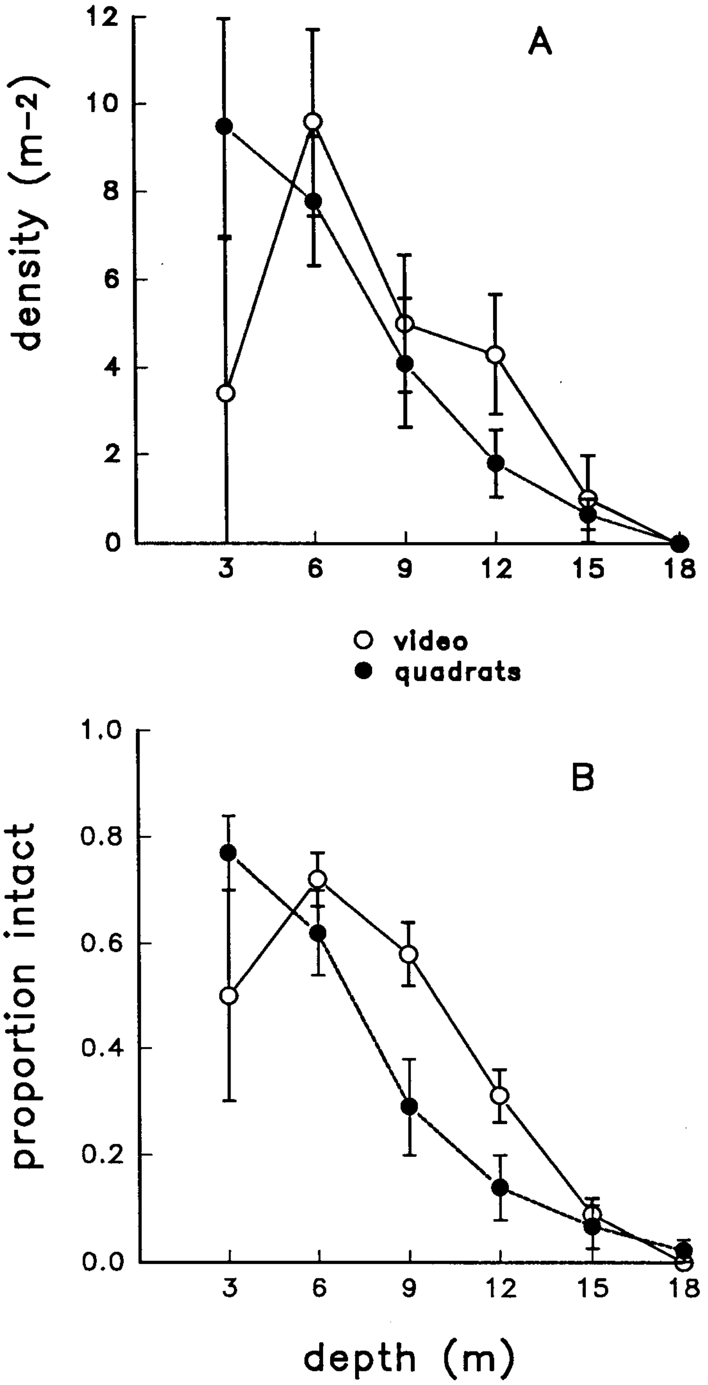

Figure 10. **A**. Density of intact kelp at each depth stratum (mean ±95% C.I.), as assessed by video and quadrat measures. **B**. Proportion of total plant numbers contributed by intact kelp (mean ±95% C.I.), as assessed by both video and quadrat measures. Data for both A and B are means for eight sites at the Marine Reserve, and combine data from both January and May.

It is concluded that the video surveys are a useful technique for recording the general density and status of stands of adult kelp, but that recruitment should be monitored using a separate strategy. This should either be quadrats or macro-video mini-transects nested within the main transects. Preliminary trials indicate that such mini-transects provide excellent resolution of *Ecklonia* recruits.

Possible causes of die-back

Three basic hypotheses to explain the degeneration of *Ecklonia* are the effects of pathogens, environmental factors or demographic cycles. None of these hypotheses is mutually exclusive and each can be considered equally likely at the present time.

Pathogens

The patchy nature of kelp degeneration at the time it was first detected in the Marine Reserve during late 1991, and at other locations such as Great Barrier Is., indicated the possible involvement of a pathogen, rather than a broad-scale physical phenomenon. Other laminarians are susceptible to a variety of diseases (Hay and Luckens 1987). Investigations underway at the University of Auckland's Department of Environmental Science (Dr. Gillian Lewis) have indicated the presence of viral particles in affected plants. Tests are now underway to determine whether these particles are restricted to sick plants, as well as to exclude the possibility of contamination. The possibility of viral involvement is still being actively pursued but the abundance of polysacharides in the plants tissues has hampered progress since it interferes with viral activity assay techniques (G. Lewis *pers. comm*.). Infectivity tests are planned which will give an indication of pathogen activity but these may not provide conclusive evidence as to the nature of the pathogen. The presence of numerous recruits among dead and dying plants is not consistent with the presence of a pathogen, unless large (or old) plants are differentially susceptible to the agent.

Environmental factors

The first general hypothesis is that *Ecklonia* die-back is simply and directly related to low temperatures. The current die-back episode began at the end of 1991, during a period of lower than average temperatures, and peaked during the summer of 1992-93 when seasonal sea surface temperatures were the lowest ever recorded at Leigh. In fact the sea temperatures during 1992 were more than 3 standard deviations below the 25 yr average (W. Ballantine *pers. comm*.). Temperature is known to affect the productivity of other laminarian populations, however adverse effects usually seem to be related to elevated, rather than reduced, temperatures. For example *Undaria pinnatifida,* experiences reduced growth during years of warmer sea-temperature (Sakai 1962), and the giant-kelp *Macrocystis pyrifera* has undergone large scale die-backs in the northeast Pacific which are also related to elevated temperatures (Dayton and Tegner 1990).

A simple relationship of die-back with temperature is not consistent with the observation that *Ecklonia* in shallow water remained healthy, since there was little if any temperature stratification around the Marine Reserve at this time (W. Ballantine *pers. comm.).* The absence of die-back at points further to the north of the Marine Reserve such as Karikari, Rawhiti and Oakura also tends to argue against such a relationship. Sea surface temperatures were reduced around the whole of New Zealand during the period in question. It is not known whether populations of *Ecklonia* in more southern waters were affected by die-back, however if they were not this would also have to be explained, perhaps on the basis of acclimation by these plants.

An intense algal bloom was present during September and October 1992, and persisted until December 1992, reducing light levels on the sea floor for extended periods of time. This phytoplankton bloom has also been suggested as a possible causative agent since it would have reduced light available to the kelp for photosynthesis. This may have been particularly critical to the P:R ratio of the plants if it took place at a time when rising spring sea temperatures were producing increased respiratory demands (C. Hay *pers. comm.*). The initial die-back of deep water kelp in the Marine Reserve is consistent with this hypothesis, as is the regional distribution of die-back, since the exceptionally strong and persistent phytoplankton bloom of late 1992 was most intense in the Hauraki Gulf between Whangarei Heads and Great Barrier Island (Ballantine 1993). During normal spring phytoplankton blooms in the Marine Reserve light transmission to 15m would be less than 2% of surface irradiance levels, while at 6m they would remain between 10-20% of surface irradiance (Novacek 1980,1984). Light levels at the bottom during the 1992 bloom could have been much lower than this (Haywood 1993), approaching the photosynthetic compensation point (Novacek 1984) for extended periods. Plants outside the worst affected bloom area or in shallow water are more likely to have experienced continuous adequate levels of light. Die-back of shallow-water kelp in some locations, as well as the continued progress of degeneration long after phytoplankton blooms had dispersed, may contradict this hypothesis. It is however possible that the energy debt incurred during the bloom may have been so great that plants could not catch up, despite improved conditions.

Demographic cycles

Die-back of stands of *Ecklonia radiata* have been reported in the past, originally in 1973-74 by Don (1975) around Little Barrier Island, and subsequently by C. Battershill and A. MacDiarmid at the Marine Reserve in 1983-84 (*pers. comm.*). The estimated longevity of *Ecklonia radiata* sporophytes can be over 10 years in water 14-20m deep (Novacek 1980), about the same order of time as the interval between previous die-backs. Since the presence of an intact kelp canopy inhibits the establishment of recruits in the understorey (Schiel 1988) it may be possible for one or two age classes of plants to dominate the benthos until they become senescent. The degeneration of a large proportion of kelp plants at this time would produce conspicuous levels of mortality and a marked change in population structure. The periodicity of such a phenomenon may have been enhanced over the past 20 years by low temperatures or other physical factors associated with ENSO events in 1972-73, 1982-83 and 1991-92. The demographic hypothesis is consistent with lower frequency of die-back in shallow waters since the age-structure of populations in these more frequently disturbed habitats (eg. storms) will be more evenly distributed among all age classes. Any mortality due to senescence would therefore be relatively constant.

Likely effects of die-back episodes

Detrital food webs.

Nothing is known about the size-distribution of *Ecklonia* fragments shed by degenerating plants. Large plant fragments are likely to be dispersed in a different manner and to different destinations than small particles. Regardless of this it is probable that the degeneration of large numbers of kelp sporophytes resulted in a large input of detrital matter to the reef environment. Although *Ecklonia radiata* normally loses material from the distal ends of the laminae, the accelerated erosion seen during die-back events is likely to have produced more material than usual. Further, the stipes and holdfasts also decay, contributing further material to detrital food webs. In areas where the topography of the reef is relatively flat, much of this material may be swept onto beaches, where it will likely be consumed by sand-burrowing invertebrates. Little is known of the organisms responsible for such processes in northeastern New Zealand (see Inglis 1989 for discussion of processes elsewhere). Otherwise the material will decay *in situ*, being localised in gutters by wave action.

Effects on other algae.
The sudden removal of the *Ecklonia radiata* canopy will obviously provide a chance for recruitment of other algal species. The areas affected by die-back are usually deeper on reefs, where few other algae occur (Choat & Schiel 1982, Schiel 1988, 1990). In the Marine Reserve there are frequently stands of *Carpophyllum flexuosum* adjacent to the deeper *Ecklonia radiata* forests. However, there do not appear to be high levels of recruitment of *Carpophyllum flexuosum* to the vacant areas of rock below 10 m in the reserve to date. Almost all of the recruitment of macroalgae in these areas appears to be of *Ecklonia radiata.* This is probably because *Ecklonia radiata* gametophytes are extremely abundant below the canopy. It therefore seems that this particular event may have little effect on the distribution of algal populations in the Marine Reserve.

If similar die-back episodes occur more frequently however, they may provide opportunities for other phaeophyte species to recruit to new areas of reef, for example by establishing their own "gametophyte banks" (Hoffman & Santelices 1991), from which recruitment may occur. Anecdotal accounts of long term changes in the inner Hauraki Gulf suggest that *Ecklonia radiata* stands may be replaced by *Carpophyllum flexuosum* after repeated die-back events of this nature (P. Barnes, *pers. comm.*). *C. flexuosum* is the most likely potential invader of the deeper areas of the Marine Reserve at present, being the species most abundant immediately adjacent to algal stands.

Effects on invertebrates

(i) **Gastropods**

Gastropods, especially *Cantharidus purpureus* and *Cookia sulcata*, live and graze on stands of *Ecklonia* (Andrew & MacDiarmid 1991, Cole, unpubl. data). The loss of habitat resulting from the recent kelp die-back suggests that the intensity of gastropod grazing on the substratum beneath the canopy may increase greatly following die-back events. One effect of this could be that kelp recruitment would be decreased due to gastropod grazing of spores or gametophytes (e.g. Lubchenco and Cubit 1980). Gastropod grazing could also lead to changes in the growth form of coralline algae present; intense grazing by gastropods may be sufficient to convert turfing forms of corallines into crustose forms (Keestra 1987). A change in coralline growth form may in turn have effects on the activity of fishes (Kingett & Choat 1981).

(ii) **Crustaceans**

Epifauna: There is a dense assemblage of small crustaceans which occupy algal canopies (see Jones 1984a, Jones, 1988 Sylvester 1986, Taylor 1991). The loss of habitat for these highly mobile organisms suggests that they will occupy other areas - either algal stands in shallow water, or perhaps turfing algae in deeper water. As most of the organisms are filter feeders (R. B. Taylor, unpubl.; Tegner & Dayton 1987, Robbins 1990), this need not necessarily pose an added grazing stress for shallow algal stands. It should be noted however that these organisms are probably short lived and such effects, if they occur, are likely to be temporary. Further, the abundances of most of these organisms decline with increasing depth below 6m (Taylor & Cole, unpubl.).

Macrocrustaceans: Andrew & MacDiarmid (1991) investigated the effects of kelp removals on the abundance patterns of the spiny lobster *Jasus edwardsii.* They could find no effects of kelp removal on the abundance of spiny lobsters for the 10 x 10 m clearances they conducted. Such conclusions might not necessarily apply to kelp clearances at the scale provided by the present phenomenon. There are no data at present to compare the abundances of *J. edwardsii* in areas without kelp with those in previous years, but they certainly occur on reefs without kelp at present (pers. obs.). There has been a trend of increasing spiny lobster abundances in the Marine Reserve for some time (MacDiarmid & Breen, unpubl.), and it is impossible to separate the effects of kelp die-back from other correlated changes such as water temperature.

(iii) **Echinoids**

The sea urchin *Evechinus chloroticus* is an important grazer on shallow rocky reefs in northeastern New Zealand, frequently maintaining areas clear of macroalgae adjacent to stands of *Ecklonia radiata,* at shallower depths (Andrew 1988). The local abundance of *Ecklonia* has well documented effects on the growth and behaviour of *Evechinus.* Choat & Schiel (1982) suggested that urchins near kelp forest borders were larger than those on nearby coralline flats. A continual supply of algal fragments from the adjacent kelp forests could produce these larger animals. A further characteristic of kelp forest - rock flat border areas is that they are often stable. Urchins near stable borders of kelp forests may also behave differently from those on barrens, moving little and seldom attacking intact plants (e.g. Mattison *et al.* 1977, Harrold & Reed 1985). Cole (unpubl.) found that *Evechinus chloroticus* moved little in *Ecklonia* forest at one site in the Marine Reserve, and experimentally demonstrated that feeding urchins fragments of *Ecklonia radiata* on rock flats led to a decrease in urchin movement rate. The sudden demise of kelp might have important implications for the stability of urchin-grazed coralline flats. The lack of drift algae, usually produced by the adjacent kelp forest, might result in the formation of grazing fronts of urchins which could expand the area of coralline flats either further down the reef, maintaining areas clear of recruits, or up into shallower water. The most likely time for this to occur is in late winter - early spring (July - September), when *Evechinus chloroticus* frequently forms temporary aggregations (A. M. Ayling, cited in Walker 1981, pers. obs.). The probability of feeding-front formation will depend on the availability of other food sources. Insufficient is known regarding the grazing biology of *Evechinus chloroticus* to comment further, however the depletion of *Macrocystis* beds on the coast of California has led to more intensive grazing of the remaining algae by urchins. This produced changes not only in other algal populations but also in associated grazers and detritivores (Ebeling et al. 1985).

Effects on fish

(i) **Algae as habitat**

Macro algae are an important habitat for many fishes (Jones 1988). The most important effect of the *Ecklonia radiata* die-back is likely to be on the availability of recruitment habitat for fishes such as leatherjackets *Parika scaber* (Poynter 1980, Milicich 1986, Ackley 1988) and spotties *Notolabrus celidotus* (Jones 1984b, Choat & Ayling 1987). Spotties recruit at highest densities into macro algal stands in shallow water (Jones 1984b), suggesting that their recruitment levels may be little affected by kelp die-back. Milicich (1986) found that greatest densities of leatherjackets settled into kelp border habitats, rather than the mid-forest. However, the area of forest available for recruitment is sufficiently reduced that some effect of habitat limitation might be expected. There is no available information on which to judge this possibility. As the juveniles grow larger they form schools and become less dependent on kelp (Ackley 1988), and it will probably be more difficult to assess the density of the population. Juvenile leatherjackets have been observed in the Marine Reserve this autumn (pers. obs.), but the densities are unknown. It is possible that this will have flow-on effects for year class strength of this species. Detailed monitoring of recruit densities over a number of years would be necessary to judge the uniqueness of this year, and as noted above, separating the effects of reduced juvenile recruitment habitat from reduced availability of presettlement individuals is still not possible. Syms (1992) found that the blenny *Parablennius laticlavius* and perhaps the triplefin *Ruanoho whero* recruited into patches of reef which had been cleared of *Ecklonia radiata* of a particular size (> $25m^2$).

During the early stages of *Ecklonia* die-back at Goat Island Bay in 1991, one of us (RGC) compared the number of visits by fish to areas of intact kelp, stipes only, and cleared areas. There were no significant differences among the different vegetation types, though the level of replication was low (R. Cole, unpubl. data).

(ii) **Algae as food**

Only one species of herbivorous fish, the odacid *Odax pullus*, is dependent on *Ecklonia radiata* as food (Clements 1985, Jones 1988). As this species mainly occupies stands of *Ecklonia* at shallower depths than those in which die-back occurred, it is unlikely that there will be any major effects on the abundance of this species, especially within the Marine Reserve. At more sheltered sites, where *Ecklonia* may form stands below urchin-grazed barrens to depths of only 10m, there is potential for a reduction of habitat for this species. The most likely consequence of this event would be for populations to move to adjacent unaffected localities. Meekan (1986) concluded that *Odax pullus* was unlikely to affect the abundance of *Ecklonia,* unlike the situation for another odacid in southeastern Australia (Andrew & Jones 1990).

One interesting feature of the kelp die-back was that the girellid *Girella tricuspidata* was frequently seen to direct bites at the decaying fronds of kelp plants. This fish does not usually feed on *Ecklonia radiata* at all (Jones 1988, Morrison 1990). Further, rather than removing frond material from the plant, the fish appeared to be scraping material from the surface of the lamina; when a particularly decayed portion of frond was removed from the plant, the fish appeared to hold it in the pharyngeal cavity for a short time, expanding the opercula to "swish" the portion of frond about, and then spat the plant material back out. The alga was not swallowed. The significance of this activity to the fish is unknown, but is noteworthy - some fish were directing most of their feeding bites toward these plants. The importance to the plants appears to be limited, except that in areas of high density of fish, erosion of laminae might be accelerated.

Conclusions

Kelp die-back was geographically limited to the outer Hauraki Gulf region. Within this area die-back was patchy, and was most common below 10m. Populations have been recruiting rapidly into affected areas and should recover over the next one to two years unless the cause of die-back (which has not yet been identified) persists. The effects of the kelp die-back on other organisms on the reef are not readily predictable, but potentially have considerable importance to energy flows, growth rates and behaviour of grazers, and the population characteristics of fishes. Insufficient long-term information exists to judge the magnitude of the effects which may derive from this event, or the significance of die-back to the reef environment.

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