STRUCTURE AND DYNAMICS OF THE ALGAL UNDERSTOREY IN A KELP COMMUNITY AT CAPE HANGKLIP, WESTERN CAPE, SOUTH AFRICA

by

JAMES JACKELMAN

THESIS

Submitted in fulfilment of the
requirements for the degree of
MASTER OF SCIENCE (Botany)
University of Cape Town
August 1996

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

"*Then said a rich man, Speak to us of giving:*
And he answered:
You give but little when you give of your possessions.
It is when you give of yourself that you truly give. (Kahlil Gibran)

It is those people, who have given of themselves during the course of this thesis, to whom I am gratefully indebted. In my dark hours - and there were many - some very special people lifted my spirits. In my times of technical and scientific naivete - and there were many - a number of people gave freely of their time and expertise. Thank you.

The diving, particularly during the stormy winter months, was particularly energy sapping. To my hardy diving partners, Tim, Garrick, Jeff, Derek, Graham, Rob and many other transient friends en route through Betty's Bay, I value the special times spent underwater with you. Without you I could not have completed the field work safely.
Like a seal out of water, I floundered many times on dry land. Without Herre, Rob, Graham and Podge to guide me through species identifications, laboratory techniques, statistical analyses and rigorous scientific writing I may not have reached this point. I value your guidance and assistance. My thanks also to Clare, who in hand drawing the figures, added a personal touch in this day of high-tech computers. To the omnipresent Linda, my special thanks for typing Chapter 2 and putting the finishing touches to the final product.
During the entire course of this project, my employers have provided the space and support to enable me to complete this thesis. My special thanks to Sea Farm Private Nature Reserve, notably Peter Cloete, and Cape Town City Council, notably Paul Britton.

Financial support from the Foundation for Research and Development and the Cape Tercentenary Foundation is gratefully acknowledged.

All would have been in vain if it were not for the people who truly believed in me. You may never know how deeply you touched me through your continuous, sometimes aggressive, emotional support. To Dave and Melody, Carol, Paul and my supervisors Rob and John, thank you.

There are however three very special people who have stood by me through the many years required to complete this project. To my wife, Susan and to my Mom and Dad, words are not sufficient to express my gratitude. I am blessed to have you so close to me during my good and bad times.

ABSTRACT

The objective of this thesis is to describe the composition and distributional variation of, and environmental factors influencing, the bottom canopy assemblages in a southern African kelp community at **Cape Hangklip**, Western Cape, South Africa.

A detailed collection of intertidal and subtidal marine macroalgal species from the Cape Hangklip area, a site centrally located in the south coast/west coast overlap, yielded a list of 201 species (26 Chlorophyta, 24 Phaeophyta, 150 Rhodophyta). The list of taxa included four new records for southern Africa (*Aphanocladia cf. skottsbergii*, *Audouinella endophytica*, *Centroceras distichum* and *Grateloupia doryphora*), five undescribed species (*Antithamnion* sp., *Colaconema* sp.,, *Erythrocladia* sp., *Erythroglossum* sp. and *Pterosiphonia* sp.) and one rhodophyte of uncertain affinity (*cf.* Ceramiaceae *indet.*), probably representing a new genus in the Ceramiaceae.
A summary of the distribution of 170 of the macroalgal species with adequate distribution records indicated that there is no dominance of species with warm-water or cold-water affinities. It is demonstrated that the south coast/west coast overlap area contains many west and south coast macroalgal species which reach the limit of their ranges here.

Quantitative data on the distribution and biomass of the benthic bottom canopy assemblages of four transects (subjectively selected to represent a range of wave exposure - from sheltered to exposed) at a study site within the kelp forests of the Cape Hangklip area, are analysed with ordination and numerical classification techniques (TWINSPAN, PCA, DCA and CCA). Discrete combinations of benthic organisms and their respective environmental settings are identified. The effect that these environmental factors have on the distribution of the sessile bottom canopy plants and animals, as well as inter-correlations between these environmental factors, at different scales of investigation, is assessed.

Though the species composition, projected canopy cover and biomass of plants and animals changes fairly gradually with depth, two distinctive bathometric zones are identified - shallow (0.5 - 6m) and deep water (6 - >10m) zones, with an indistinct intermediate depth zone (approximately 4 -8m) which has components of both the shallow and deep water communities. Generally the algal community in the shallow water zone is dominated by a mixture of fleshy and foliose algae and articulated corallines. The shallow water supports a few large mobile and sessile indicator filter feeders (*Pyura* and *Austromegabalanus*), grazers/debris feeders (*Parechinus*, *Haliotis*, *Turbo* and *Dinoplax*) and carnivores (Actiniaria and *Thyone*). At the intermediate depths the algal community is a heterogenous complex of species with high biomass and alpha diversity. Animals are poorly represented at this intermediate depth. As the kelp plants thin out at the seaward margin of the beds, they give way to a dense animal-dominated community. Most of the animal biomass and substratum-cover in this deep water zone are represented by filter-feeding species, notably Porifera. The algal community in this deep water zone has a more homogenous distribution and comprises predominantly large foliose Phaeophyta and Rhodophyta and articulated corallines. The sheltered transect did not fit this generalized bathometric zonation.. Except for a few psammophilic animal species (*Dinoplax gigas* and *Thyone aurea*), macroinvertebrate species are generally inconspicuous. This transect is represented by high alpha and beta algal species diversity and supports a number of algal species not found elsewhere in the kelp forest.

Six main community cluster groups are derived from the Two-Way-Indicator-Species-Analysis (TWINSPAN) of all transect data - (A) Algae-poor group, (B) *Zonaria - Sargassum - Phloiocaulon* group, (C) *Pterosiphonia - Codium* group, (D) *Halopteris - Botryocarpa - Jania* group, (E) *Jania - Plocamium* group and (F) *Bifurcariopsis - Iridaea* group. The coherence of these cluster groups with the main environmental factors in the study is shown. The clearest differentiation of these cluster groups is brought about by depth and sand cover. Sand is considered to be highly correlated with depth and wave exposure. Within the groups, urchin and abalone density and slope are environmental factors which differentiate between clusters. These classified cluster groups were superimposed onto the ordination analyses.

The ordination of all the transect data using Canonical Correspondence Analysis (CCA) identified two major environmental complex-gradients considered to explain the compositional variation - (i) a depth complex-gradient strongly correlated with axis 1, and (ii) a sand cover complex-gradient strongly correlated with axis 2. Species combinations (reflected in results from quadrats) are shown to be a good indicator of community structure and correlate strongly with the environmental variables. Environmental factors considered in this study were shown to be strongly inter-correlated. A within-transect CCA analysis showed significant small-scale heterogeneity, with highly variable environmental parameters, which appear to cause multiple solutions of species composition. Even at this small scale of investigation, depth was still strongly correlated with axis 1 for all transects.

Plant and animal species are in many instances diagnostic of particular environmental conditions. The effects of independent biotic (grazer/debris feeders, shading, competition for space) and abiotic (depth, sand cover, substrate, slope/aspect) factors on individual species distribution are discussed. Despite these single-factor associations, the bottom canopy understorey of the kelp forest in this study is an expression of the effects of a variety of biological processes which are moderated by a complex of physical disturbances. It is suggested that the patterns of community structure identified in this study are, at the local scale, generally determined to a large extent by abiotic factors, and, at a smaller scale, by biotic factors.

A model is presented which shows the inter-correlation between the primary, secondary and tertiary environmental variables measured in this study and the effect of the extremes of these environmental variables on algal alpha diversity. The model is discussed in the context of the "intermediate disturbance hypothesis". The model shows that, irrespective of the regulatory pathway, all combinations of environmental extremes results in low algal diversity. High algal diversity occurs when disturbance is at intermediate levels of frequency, intensity and spatial scale, and is patchy in time and space.

The effect of one of these environmental variables - sand burial and scour - on the settlement and early post-settlement (EPS) phases of three red algae, *Aeodes orbitosa*, *Gigartina radula* and *Iridaea capensis*, was experimentally tested. All three species are found in the shallow sublittoral along the sheltered, sand-inundated transect (transect 1) at the study site. The species were subjectively selected to represent a gradient of tolerance to sand inundation (*Aeodes orbitosa* < *Gigartina radula* < *Iridaea capensis*). The effects of four mechanisms of sediment damage are tested: (i) prevention of tetraspore/carpospore attachment by sand burial; (ii) prevention of tetraspore/carpospore attachment by sand in suspension; (iii) damage to attached sporophyte/gametophyte sporeling by sand burial; and (iv) damage to attached sporophyte/gametophyte sporeling by sand in suspension.

Where sediment was present before spore release, high concentrations of sediment led to poor survival of all spores. Where sand was kept in suspension before spore release, spore survival was extremely low at high sand concentrations. When spores were allowed to settle and attach, prior to sediment burial, the *Gigartina* and *Iridaea* sporelings were considerably more resistant to damage. Survival was relatively high for these species with less than 100mg cm^{-2} sand cover (>15% relative survival). Where spores were allowed to attach, prior to treatment with sand in moving water, the effects on relative survival was extreme at high concentrations of sand (>80mg cm^{-2}). *Iridaea* consistently showed significantly higher relative survival than *Gigartina* and *Aeodes*.

The results of the experimental manipulations indicate that: (i) All spores and germlings of the test species suffered considerable stress and mortality from sand burial and sand scour. It is suggested that these species have rather evolved vegetative and intrinsic (seasonal spore dispersal) mechanisms to survive and persist in seasonally sand-covered habitats; (ii) *Aeodes* spores and germlings are highly susceptible to sand burial and scour; (iii) *Gigartina* and *Iridaea* germlings are moderately resistant to sand burial for short periods; (iv) *Iridaea* germlings are moderately more persistent under conditions of sand scour than the other two species; and (v) No significant difference was noted in relative survival of carpospores and tetraspores or gametophyte and sporophyte germlings. Alternative intrinsic and vegetative mechanisms which may enable *Aeodes*, *Gigartina* and *Iridaea* to persist, or even thrive, under conditions of seasonal sand burial and scour, are discussed.

CHAPTER 1

OVERVIEW - STRUCTURE AND DYNAMICS OF KELP COMMUNITIES

INTRODUCTION

The focus of this thesis is on the distributional variation of, and factors influencing, the algal understorey in a South African south coast/west coast overlap kelp community.

The huge and often rather diffuse literature relating to the structure and dynamics of kelp communities has received excellent consolidated reviews (eg. Chapman 1979, Kain 1979, Mann 1982, North 1971, Vadas & Norton 1982, Dayton and Tegner 1984a, Dayton 1985a, Foster & Schiel 1985, Schiel and Foster 1986, Schiel 1990, Foster 1990, Chapman and Johnson 1990, Underwood and Kenelly 1990). It is thus not the objective of this introductory chapter to exhaustively review the existing literature on kelp communities.

This chapter will however provide a succinct overview of:

- **The distribution and structure of kelp communities** - the dominant overstorey laminarian species typical of kelp forests, the geographical distribution of these kelp communities and the basic vertical structure of kelp communities
- **The depth zonation and local organizing processes of kelp communities** - the depth zonation of the dominant kelp species and the abiotic and biotic factors known to influence the structure of kelp communities around the world.
- **The algal understorey component of kelp communities** - a short review of the literature documenting kelp understorey algal associations and physical and biotic factors considered to affect their local and regional distributional patterns.
- **South African kelp communities** - a short review of the information known about South African kelp beds.

DISTRIBUTION AND STRUCTURE OF KELP COMMUNITIES

The term kelp refers to the genera of larger brown algae (primarily of the Order: Laminariales). Mann (1982) has characterised the worlds kelp forests by their dominant genera. *Laminaria* species dominate both sides of the North Atlantic and the coasts of China and Japan. *Ecklonia* dominates kelp forests in Australia, New Zealand, South Africa and some other southern hemisphere localities. *Macrocystis* forms dense forests in the northeast Pacific, the southern shores of South America, many Southern Ocean islands, and isolated areas of Australia and New Zealand.

The large-scale distributional patterns of these taxa are well known, as are many physical (light, substrata and sedimentation, nutrients, water motion, salinity and temperature) and biological influences (dispersal, grazing, indirect effects of predators and herbivores, interactions among plants and interaction within species) that determine large- and small-scale distributional patterns for the more common forms within kelp beds (see Dayton 1985a, Schiel and Foster 1986, Estes and Steinberg 1988). Species composition, distribution and abundance of the benthic fauna and flora change both geographically and between and within local areas in response to broad environmental conditions and local site characteristics (see later discussion).

Worldwide, the distribution of structured kelp communities (Figure 1.1) is confined to shallow rocky coastal regions of temperate latitudes (Lüning 1990). Kelps are generally absent from the tropics (however see Hatcher *et al* 1987) and Antarctica. Temperature is most often correlated with this geographic distribution, although its direct influence is difficult to test in the field. For the purposes of reference in this chapter to geographical regions of kelp distribution, I have divided the worldwide distribution into 9 regions: **northeast Pacific** (Gulf of California, Mexico to Alaska); **northwest Atlantic** (North Carolina, U.S.A. to Greenland); **southeast Pacific** (Peru to the southern tip of Argentina); **southwest Atlantic** (east coast of Argentina); **northeast Atlantic** (Morocco to Norway); **southern Australia** (NSW, Victoria, Tasmania, South Australia, and Western Australia); **eastern New Zealand**; **northwest Pacific** (Japan to eastern Russia) and **southwestern Africa** (Namibia to the south coast of South Africa).

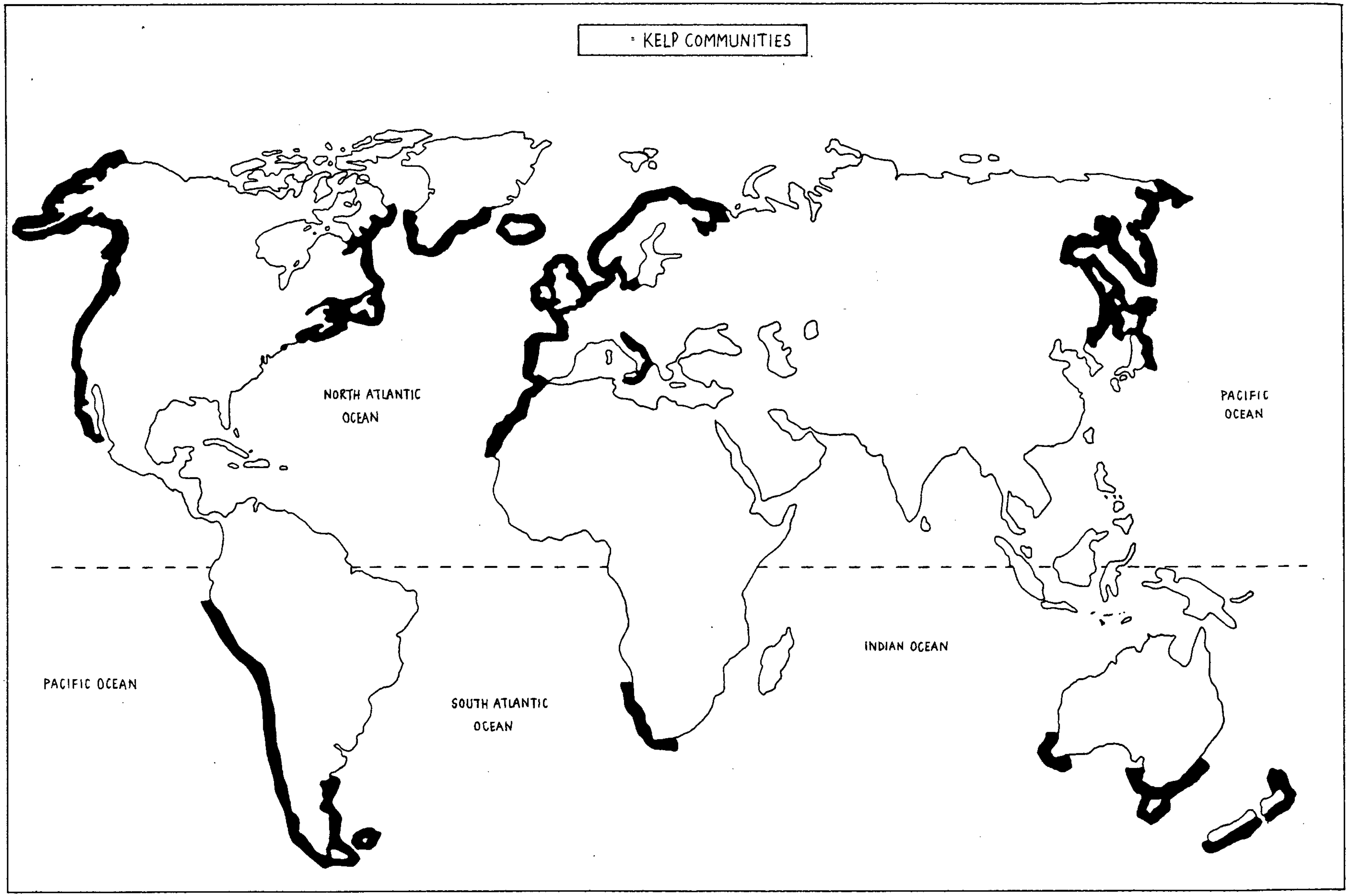


Figure 1.1 The worldwide distribution of structured kelp communities.

In general kelps inhabit the sublittoral fringe and midsublittoral zone due to their relatively high light requirements (Lüning 1990). Kelps in the sublittoral fringe (low intertidal to a few metres below mean low water) are mechanically adapted to high wave action, generally through flexible stipes and resistant thalli. The midsublittoral zone is populated by a dense vegetation of large growth forms. Competition for light is the main problem in this zone and each algal species must find a way to spread a maximum of photosynthesizing thallus surface area to intercept light and hence have a competitive advantage over other species. For this purpose blade-like thalli are carried by stiff stipes or held upright by air bladders in kelp species. Kelp species hence typically form the canopy overstorey. However the kelp species do not completely dominate the substrate and kelp canopies enclose complex assemblages of algae and animals in the understorey of these kelp forests. In general, the literature indicates that a maximum of five canopy layers may be identified (these may occur in different combinations at different places): (a) a floating canopy with fronds at or near the surface, (b) a stipitate, erect understorey in which the fronds are supported above the substratum, (c) a prostrate canopy in which the fronds lie on or immediately above the substratum, (d) various turf-forming associations, usually composed of articulated coralline algae or foliose and filamentous red algae, and (e) encrusting coralline algae. With increasing water depth and decreasing light intensity, one vegetation layer after another disappears. The focus of this thesis is on the bottom canopy species of canopies (c) and (d).

The algal benthic communities inhabiting the substrate beneath the canopy overstorey of kelp plants have been neglected in the literature with much of the emphasis being placed on the large kelp species and their direct and indirect interaction with dominant herbivores and predators. This thesis will focus on the composition, biogeography, structure and dynamics of the kelp understorey (with an emphasis on the benthic macroalgae) in a southern African south coast/west coast overlap kelp community.

DEPTH ZONATION AND LOCAL ORGANIZING PROCESSES OF KELP COMMUNITIES

One of the major functional differences between algal stands on a geographical scale is the canopy layering of vegetation (Schiel and Foster, 1986). Virtually all descriptive studies from kelp beds around the world also centre on the observation that subtidal benthic communities are broadly zoned along a depth gradient (Schiel & Foster 1986). Much of this depth zonation has been identified by qualitative descriptions of the change in overstorey canopy species and the associated understorey. Few published surveys however discuss the local distributional variation of plants or animals between and within depth strata, but qualitative observations and the high variances associated with abundance estimates (eg. Choat and Schiel 1982, Dayton *et al* 1984) suggest that distributions may be clumped at fairly small scales. This variability can result from a number of organizing processes. These processes may include variation in the distribution of many abiotic factors (Schiel and Foster 1986), physical disturbances (eg. Cowen *et al* 1982), grazers (eg. John and Lawson 1990) and shifts in their behaviour (eg. Harrold and Reed 1985), predator -prey interactions (eg. Bernstein and Jung 1979), territorial behaviour and interactions among fish (eg. Choat 1982), changes created by the organisms themselves (Schiel and Foster 1986), limitations in spore dispersal (Dayton *et al* 1984, Schiel 1985) and stochastic events (Schiel and Foster 1986).

In diverse and structurally complex subtidal benthic algal communities, most of the patterns of distribution remain undescribed, and the mechanisms producing local patchiness are only beginning to be explored. It appears that there may even be, within local patches, an element of randomness superimposed on some of the more deterministic processes. Dayton (1984) summarizes the non-exclusive hypotheses relating to the existence of distinct patches of varying size, and suggests that alternate mechanistic processes may be complementarily responsible for the spatially distinct patches observed. These hypotheses include the following:

(1) Patches are maintained by local physical characteristics tolerable to some species but not to others;

(2) other species have not had the opportunity to colonize and patches are hence ephemeral entities defined by relative dispersal patterns;

(3) all species colonize together, but different life history phenomena alone determine the composition of the patch; and

(4) beneficial biological interactions such as mutualism enhance the successful colonization of certain species into patches, and deleterious interactions such as competition or predation prevent colonization.

Dayton *et al* (1992) later postulate that at a large scale, abiotic factors appear to define broad distributional patterns. However, within these coarse distributional patterns, a complex interaction between a number of abiotic and biotic processes define the small patterns of distribution of benthic species.

In this section, I have provided a short overview of the canopy layering and depth zonation patterns observed from kelp beds around the world and summarized the major organizational processes considered to influence kelp community structure in the different geographical regions.

In the **northeast Pacific**, considered to be the centre of origin of Laminariales (Estes and Steinberg 1988), three broad subtidal zones have been recognized in localities where hard substrata are available (eg. McLean 1962, Neushul 1967, Druehl 1967, Foster 1975a, Foster & Schiel 1985, Foster 1990). In shallow water, species of kelp such as *Egregia menziesii* and *Eisenia arborea* usually occur inshore with fucalean algae. Kelps that form surface canopies, such as *Macrocystis* and *Nereocystis*, are prominent at middle depths, with an understorey of stipitate laminarians (eg. *Pterygophora californica*, *Laminaria setchelli*). The zone in deepest water, seaward of kelp surface canopies, is inhabited by sparse stands of understorey kelps such as *Agarum fimbriatum* and *Laminaria farlowii*, encrusting corallines and small foliose red algae. Another kelp, *Alaria fistulosa* can also form surface canopies with *Laminaria longipes* in shallow waters in Alaska (Druehl 1970).

All but one of the 27 presently recognized kelp genera occur in the North Pacific, 19 of these exclusively. In contrast, the North Atlantic and the cool seas of the southern hemisphere contain only five and four kelp genera, respectively (Estes and Steinberg 1988).

In these species-rich kelp forests of the northeast Pacific it has been shown that sea urchins form active feeding fronts and overgraze macroalgal assemblages in kelp beds in some areas (Lawrence 1975, Pearse and Hines 1979) resulting in distinct persistent alternate community types; ie. "kelp-dominated" areas and "barren" areas (coralline dominated). Transitions from one state to the other occur on a time-scale of decades and over large spatial scales (Simenstad *et al* 1978, Tegner and Dayton 1987). These transitions are generally attributed to changes in the abundance of sea urchin grazers as a result of "stabilizing predatory relationships" (Dayton 1985a) by sea otters (Estes *et al* 1978, Duggins 1980, Estes and Harrold 1988), fishes (Bernstein *et al* 1981, Tegner and Dayton 1981, Cowen 1983), crabs and lobsters (Bernstein *et al* 1981, Tegner and Levin 1983), man (McLean 1962, Druehl and Breen 1986), storms, wave-stress and large-scale oceanographic processes (Cowen *et al* 1982, Dayton and Tegner 1984b, Harris *et al* 1984, Ebeling *et al* 1985) or disease (Pearse and Hines 1979, Miller and Colodey 1983). In the northeast Pacific, the emphasis has been on a particular predator, the sea otter. This interaction has been generalized as 'extremely' or 'most' important in organizing kelp assemblages in this region (Estes and Palmisano 1974, Dayton 1975, Duggins 1980) and appears to have achieved the status of a paradigm (Estes and Harrold 1988, Levin 1988).

Manipulative and 'natural' experiments in the northeast Pacific (eg. Pearse and Hines 1979, Duggins 1980, Ebeling *et al* 1985), and northwest Atlantic (eg. Breen and Mann 1976, Himmelman 1980, Witman 1985, Scheibling 1986) have demonstrated unequivocally that if urchins are removed from the system, seaweeds establish rapidly. Conversely, adding urchins to seaweed beds can result in rapid destruction of all fleshy macroalgae (Johnson 1984). Clearly the factors that influence the urchins distribution, abundance and behaviour are pivotal in determining community state.

Extensive parts of the California coastline however suffer no large-scale effects (Foster and Schiel 1988) and organizational processes may occur on smaller spatial scales. Harrold and Reed (1985) documented a kelp forest in which barren or kelp-dominated patches are unstable, appearing and disappearing over small spatial and temporal scales. In this kelp bed, the transformation from one configuration to the next is triggered by a behavioural switch in the mode of urchin feeding initiated by hydrographic conditions extrinsic to the kelp forest community. Where patchiness in the algal assemblages is not accounted for by the effects of grazers, which Foster (1990) asserts might be the case for most kelp communities, competitive interactions among species have been shown to affect the local-scale distribution and abundance of individual species (eg. Dayton 1975, Foster 1975b, Reed and Foster 1984, Miles and Meslow

1990) and these competitive interactions may be regulated by physical disturbances such as extreme storms precipitated by El Niño (Dayton and Tegner 1984b).

In the **northwest Atlantic**, rocky subtidal habitats are dominated largely by crustose coralline communities (Steneck 1986), dense populations of green sea urchins *Strongylocentrotus droebachiensis* and a diverse fauna both of sessile and mobile forms (Witman 1985, Ojeda & Dearborn 1989). In these environments, kelp species (mainly *Laminaria*, *Alaria* and *Agarum*) and other macroalgal associations are in general less common, usually occupying a narrow zone in shallow waters or a more extensive band (to a depth of 15-20m) in some protected habitats where urchins are absent or rare (Sebens 1986, Johnson and Mann 1988, Chapman and Johnson 1990). In the absence of dominant effects of sea urchins, the biological and physical structure of the seaweed communities is three-tiered and relatively simple. Typically *Laminaria* forms a closed canopy over perennial and ephemeral algae, and there is a basal layer of encrusting coralline algae (Novaczek and McLachlan 1986) although different kelp species may dominate the overstorey depending on wave exposure, depth and geographical location (Chapman and Johnson 1990). For example, on the Atlantic coast of Nova Scotia *L. longicruris* dominates the subtidal in sheltered and exposed sites to a depth of ca. 15-20m, growing in a more or less continuous band where there is suitable substratum (see Johnson and Mann 1988). However with increasing exposure *L. longicruris* may co-exist with *L. digitata* in shallow water and, in shallow areas of extreme exposure, *L. digitata* may replace its congener entirely (Smith 1986). A similar pattern occurs in New England (Witman 1987). However Chapman (1984) noted that at some moderately exposed sites on the southwest coast of Nova Scotia, *L. digitata* is roughly twice as abundant as *L. longicruris*. *Alaria* occurs only at very exposed sites, usually as a narrow band above *Laminaria* in the high subtidal. In Nova Scotia, *Agarum* usually replaces *L. longicruris* in deeper water (Gerard and Mann 1979).

In the northwest Atlantic subtidal communities, kelps are dominant space competitors in the absence of strong grazing interactions (Chapman and Johnson 1990). However, where sea urchins are the major algal herbivores, destructive grazing by urchins cause the transition from seaweed bed to urchin/coralline barren (Witman 1985, 1987, Breen and Mann 1976, Chapman 1981, Johnson 1984, Miller 1985, Scheibling 1986, Himmelman 1984, Hooper 1980, Johnson and Mann 1988) and conversely disease is effective in removing urchins from the system and facilitating recovery of kelp beds.

Parasitic amoebae have been shown to decimate sea urchin populations (Jones 1985, Jones and Scheibling 1985) so that a switch back to kelp forest dominance occurs (Miller and Calodey 1983, Moore and Miller 1983, Scheibling 1986, Johnson and Mann 1986). The importance of carnivory of urchins by decapods and fin fish (Breen and Mann 1976, Breen 1980, Wharton and Mann 1981, Bernstein *et al* 1983) is still unclear (*cf.* Elner and Campbell 1987, Chapman and Johnson 1990) although it has been demonstrated that physical disturbances such as wave action (Himmelman 1984, Witman 1985, Sebens 1986), abrasion from algal fronds (Himmelman 1984), shifting sediments and sand scouring (Himmelman 1980) and salinity (Himmelman *et al* 1983) control or reduce sea urchin densities. At a more localized scale in the seaweed dominated state, demographic processes of algal species (Chapman 1984), wave exposure (Gerard and Mann 1979, Cousens 1981, Davis and Wilce 1987, Chapman and Johnson 1990), ice scour (Keats *et al* 1985), intraspecific competition (Johnson and Mann 1988, Duggins *et al* 1990), mutualistic relationships between mussels and several invertebrate species (Witman 1987), gastropod grazers (Fralick *et al* 1974), depth (Ojeda and Dearborn 1989) and aspect of the hard substratum (Sebens 1985a, 1986) have been shown to affect the structure of subtidal assemblages.

In the **northeast Atlantic** laminarian species are broadly zoned with depth, with *Laminaria digitata* and *Alaria esculenta* occurring in the wave-exposed shallow subtidal (although they may extend to depths of 20 and 35m respectively - Lüning 1990), followed by *L. saccharina*, *L. hyperborea*, and/or *Saccorhiza polyschides* along progressively deeper areas of reef - to a depth of 35m (Norton 1978, Kain 1975, 1979). Kain (1975, 1976) found that *L. digitata* was more tolerant to wave action than was *L. hyperborea.* In calmer subtidal sites however, *L. hyperborea* eventually appeared to become dominant where both species had recruited.

In the **southeast Pacific**, results from the southern and northern regions of the *Macrocystis pyrifera* range in Chile have indicated that the kelp-sea urchin parallels from the northeast Pacific and northwest Atlantic do not exist (Castilla and Moreno 1982, Moreno and Sutherland 1982). The Chilean *Macrocystis pyrifera* communities are simpler than their northeastern Pacific counterparts, with less algal and animal diversity (Dayton 1985b). The presence of two distinct depth zones and one indistinct zone have been described for southeast Pacific kelp beds. In shallow water a narrow belt (1-2m) of *Lessonia vadosa* or *Lessonia nigrescens* abuts a bed of small-sized, densely packed individuals of *Macrocystis pyrifera*. Individuals of *M. pyrifera* and their inter-plant distances become increasingly larger with increasing depth and here *Lessonia flavicans* and *Gigartina skottsbergii* form a second and third stratum (Santelices & Ojeda 1984a, 1984b, Dayton 1985b). The midsublittoral zone is hence dominated by *M. pyrifera* in localities that are not too wave-exposed, while deep water kelps are represented by *Lessonia trabeculata*.

In kelp communities of the southeast Pacific, sea urchins do not seem to graze extensively on attached plants and were observed to eat only drift algae (Moreno and Sutherland 1982, Castilla and Moreno 1982, Dayton 1985b). It has been hypothesised by Dayton (1985b) that low urchin densities may be attributed to limitations to larval availability in the Westwind Drift, harvesting by humans or wave exposure. No clear idea has emerged concerning grazers, storms and competition as structuring agents of kelp forest communities in the southeast Pacific, but it is apparent that inter-algal interactions may strongly influence the structure of algal stands (Santelices and Ojeda 1984a, 1984b).

In **eastern New Zealand**, fucalean species are abundant in shallow water to several metres depth and laminarian species dominate areas of deeper reefs. Choat and Schiel (1982) identified five depth-related zones; (i) shallow areas dominated by fucalean algae (eg. *Carpophyllum* spp.) - however in the southern areas this zone is dominated by *Durvillaea antartica*, (ii) mixed stands of fucalean (eg. *Carpophyllum* or *Landsburgia*) and laminarian (*Ecklonia radiata* or *Lessonia virgata*) algae (3-6m depth), (iii) areas dominated by sea urchins and encrusting red algae (5-10m depth), (iv) sea urchin-laminarian borders (10m depth) and (v) deep algal stands (including *Macrocystis* in some areas). A major difference between northern and southern localities is the distribution of sea urchins. Many northern sites have characteristic and extensive areas dominated by echinoids. These are reduced to small patches in most southern sites (Schiel 1990).

In the kelp forests of eastern New Zealand, the small-scale effects of large invertebrate grazers (sea urchins, turbinids and limpets), and the interaction between them, on algal assemblage structure, has been shown to be significant only in some localities (Ayling 1981, Schiel 1981, Andrew and Choat 1982, Choat and Andrew 1986). Sea urchins clearly have a depth-related density-dependent impact in northern New Zealand (Andrew

1988, Schiel 1990) but the alternate community state observed in the northeast Pacific and northwest Atlantic has not been documented in New Zealand. In northeastern New Zealand, Andrew and Choat (1982) found that, though fish have a significant impact on urchin abundance, juvenile urchin survival was still great enough to sustain an urchin dominated area. Experiments from northern New Zealand show strong interspecific effects among algal species, particularly due to canopy shading (Schiel 1981, 1988, 1990).

In **southern Australia**, Sheperd and Womersley (1970, 1971, 1976, 1981) concluded that there was a consistent pattern of sublittoral zonation on south Australian coasts. On wave-exposed coasts the upper zone (3-5m depth) was characterized by a dense algal community where fucalean species may be abundant, the mid-zone (5-50m) was dominated by the kelp *Ecklonia radiata* and the lower zone (17-60m) by a dense cover of diverse red algae. In sheltered waters the upper zone may be absent (May & Larkum 1981) or in other parts of Australia, differ substantially in species composition (eg. Sanderson and Thomas 1987). Sheperd and Womersley (1976) stress the substantial variability in particular species present in these zones at different sites, notably the high diversity of fucoids. Such variability in species composition was considered to be influenced by the wave exposure of the sites.

In southern Australian kelp beds field experimentation has suggested that grazing by invertebrates (chitons, gastropods and sea urchins primarily) is a major organizer of structure, composition, diversity and patchiness of assemblages (Kenelly 1983, Hatcher and Rimmer 1985, Fletcher 1987, Underwood and Kennelly 1990). Fish (Kennelly 1983) and storms (Underwood and Kennelly 1990) are thought to control the abundances of some of these grazing invertebrates. Storms and wave action are strongly implicated as having important effects on the patterns of distribution in the subtidal forests (Kennelly 1983, 1987a, 1987b) but there have been few attempts to integrate the role of disturbance and grazing in any area of Australia (Underwood and Kennelly 1990). On a local scale, intraspecific (Sheperd 1981, Kennelly 1983, Kennelly 1987b, Kennelly 1989) and interspecific (Kirkman 1981) competition have been shown to influence spatial and temporal variability in the structure of algal assemblages.

In the **northwest Pacific** some of the longer-bladed Laminariales[1] from Japan (eg. *Laminaria japonica*, *L. angustata* and *L. longissima*) form surface canopies in shallow water. Other dominants in the sublittoral zone are representatives of the Alariaceae, *Undaria pinnatifida*, *Eisenia bicyclis* and *Ecklonia cava*. The last two species form dense marine forests in the sublittoral zone, with *E. bicyclis* dominating in the upper sublittoral down to 5m deep, and *E. cava* in the midsublittoral from 3m to 25m or more (Chihara 1975, Hayashida 1983, Maegawa *et al* 1987).

It must be emphasized that these depth zones for the geographical regions are not coherent non-overlapping zones. Different zones often comprise different species in different places.

There also appears to be enormous temporal and spatial variability in subtidal habitats from around the world, and Underwood and Kennelly's (1990) assertion that zones may not actually exist as discrete non-overlapping sub-assemblages of algae may be true. If they do not, or if they cannot be simply demonstrated, it would be more sensible to accept that differences exist from place to place and time to time and to describe what is found in its own terms rather than attempting to force observations into a simplified zonation scheme.

Of apparent importance to algal distribution is the co-occurrence of grazers, particularly sea urchins. Although echinoids in Alaskan kelp beds form dense aggregations at all depths, the majority of studies have recorded the dominance of sea urchins at particular depths, rather than being densely aggregated along an entire depth gradient (eg. California, Washington, Britain, southern Chile, Australia and New Zealand). I believe that it is only with substantially more quantitative assessments along an entire depth gradient at a large number of sites and a record of the variation over this gradient with time, that generalizations of organizing processes for all kelp communities may be made. The general conclusion from studies conducted in kelp beds around the world appears to be that, for most areas of the world, too few localities have been described quantitatively for their patterns of distribution and abundance of algae and macrofauna to assess the relative importance of different environmental factors on the structure of kelp communities. As more sites are examined, it seems that even fewer generalizations

---

[1] *Within the genus Laminaria about 13 species with an undivided blade are reported to occur on Hokkaido (Tokida et al 1980) although not all of these represent truly distinct species (Kain 1979).*

are appropriate. For example, even in southern California where research in kelp forests led to the generalized postulation of hierarchical interactions between predators on sea urchins, sea urchins and the abundance of macroalgal assemblages, Foster and Schiel (1988) found that sites dominated by echinoids comprised only 8.5% of those examined over a wide geographic region. Less than 20% of these were entirely deforested or composed of large (20-50m diam.) deforested patches of kelp and associated algal species. This relatively small occurrence of dominant effects diminishes any arguments for generality.

THE ALGAL UNDERSTOREY COMPONENT OF KELP COMMUNITIES

There are hundreds of species of fleshy, filamentous and articulated coralline algae found in kelp communities. Many of these have been adequately described for kelp forest communities in parts of the northeast Pacific (eg. Dawson *et al* 1960, North 1971, Devinny and Kirkwood 1974, Pearse and Lowry 1974, Foster *et al* 1979, Abbott and Hollenberg 1976), southern Australia (eg. Sheperd and Womersley 1970, 1971, May and Larkum 1981, Womersley 1981, Fletcher 1987), southeast Pacific (eg. Santelices and Ojeda 1984b, Dayton 1985b, Santelices 1989, 1990), northeast Atlantic (eg. Kitching 1941, Kain 1979) and the northwest Atlantic (eg. Bird *et al* 1983, Witman 1985). The bottom canopy species from kelp communities found in many other parts of the world however have generally been poorly documented.

Several studies by Foster and his co-workers in California have paid particular attention to bottom canopy species as important members of kelp communities (Foster 1982). Foster (1975a) placed these species into three groups in a study at Santa Cruz Island:

- Ephemerals - include species such as *Colpomenia* that rapidly colonized free space, but were seasonal in their appearance and disappearance.
- Perennials (rapid growth) - include species such as the reds *Pterosiphonia dendroidea* and *Rhodymenia californica*, which were seasonal in their colonization of space, but could persist through time.
- Perennials (slow growth) - include species such as *Gigartina* spp. and the corallines which were very slow to colonize free space,but could persist for several years.

Colonization by these species varied with season, with most having either a spring-summer or autumn-winter period of maximum reproduction.

In an observation of succession in a kelp community in Fortaleza Cove, Sao Paulo (Brazil), de Eston and Bussab (1990) found that the bottom canopy algal species comprised the same groups as those defined by Foster (1975a). Three distinct periods of colonization were observed in this kelp bed, relative to competitive interactions among species: (1) an initial period of succession, with increased abundance of ephemerals, (2) an intermediate period, with maintenance of *Dictyopteris* spp. cover and (3) the re-establishment of closed canopies of *Sargassum stenophyllum*, an opportunist colonist.

A few studies have shown the effects of overstorey plants on the bottom canopy algal species, and also the effect of these bottom canopy species on the recruitment of other species. Kastendiek (1982) found at Santa Catalina Island, California that the red alga *Pterocladia capillacea* was abundant under a canopy of *Eisenia*. With the removal of this canopy, the fucoid *Halidrys dioica* was able to spread adventitiously and exclude *Pterocladia*. *Pterocladia* could flourish outside of canopies if *Halidrys* was prevented from pre-empting space. *Pterocladia* appeared in this case to act as refuge species, occupying space under canopies of *Eisenia* where *Halidrys* could not flourish. Druehl and Breen (1986) found that the harvesting of the kelp *Macrocystis integrifolia* in Barkley Sound, British Columbia significantly altered the abundance of the bottom canopy algal species. In harvested plots, the relative abundance of the brown alga *Desmarestia ligulata* and the green alga *Ulva* sp. increased relative to the control plot. Similarly Cowen *et al* (1982) and Foster (1982) found that following removal of *Macrocystis* canopies near Santa Cruz, California, the annual brown alga *Desmarestia ligulata* var. *ligulata* became locally abundant during spring and summer. Reed and Foster (1984) also found that this species became abundant when *Macrocystis* and *Pterygophora* canopies were removed. Reed and Foster (1984) further assessed the effects of *Calliarthron* (an articulated coralline) on the recruitment of other species. In a site where *Macrocystis* and *Pterygophora* canopies were removed, they found that the greatest recruitment of *Desmarestia* spp. and Laminariales were in treatments from which the branches of articulated corallines were also removed. Clearance to bare rock did not increase recruitment of other species, suggesting that it is the branches themselves that inhibit recruitment. This could be caused by shading, by abrasion, by the presence of sediment which may be trapped in the articulated algae, or by small grazers concealed in the branches.

Kennelly (1987a) found that clearing kelps in any season in a kelp forest at Fairlight, NSW, Australia, led to encrusting algae, sponges and ascidians being overgrown by filamentous algae (eg. *Enteromorpha*, *Giffordia*), then by turf algae (eg. *Zonaria*, *Lobophora*), which occupied the clearing for up to 14 months until individual *Ecklonia radiata* gradually re-invaded the edges of the experimental plots. In winter, juvenile *E. radiata* rapidly colonized the substratum. Kennelly (1987b) showed that although kelp recruited very quickly from areas from which the overlying canopy was removed, few recruits appeared under a natural canopy, or in areas with turf algae. Turf species

(*Zonaria*, *Lobophora* and *Dictyota*) returned and dominated the substratum in clearings where turf had been experimentally removed. Kennelly (1989) further examined the effects of shading and scouring by kelp plants on understorey species. Scour by kelp plants did not affect most species, but the amount of sediment and microscopic silt were enhanced where scouring was prevented.

Kennelly (1983) experimentally investigated factors influencing the early colonization by benthic macroalgae in a subtidal *Ecklonia radiata* forest in Port Jackson, NSW, Australia. He found that the effect of grazers, and competition between different algal types were important. The results suggested that the amount of algae initially present was affected by invertebrate grazers, the abundances of which were, in turn, affected by predation. Grazing was important in determining the temporal variability of early growth of individual species. Siltation was also positively correlated with early algal growth. Quantitative surveys of percentage covers of encrusting, filamentous and foliose algae, with densities of grazing urchins and gastropods were presented by Fletcher (1987) at Cape Banks, NSW, Australia. The cover of encrusting algae decreased with increasing distance from crevices containing sea urchins, which move out at night to feed. Foliose algae increased in cover over the same area, but filamentous algae first increased and then decreased in cover with increasing distances from crevices. Cover of encrusting algae showed positive correlations with densities of limpets, turbinid gastropods and urchins; in contrast, the densities of these grazing animals were negatively correlated with the percentage of foliose plants.

Overall, there appears to be a general negative correlation between the percentage cover of *Macrocystis* canopies and the cover of understorey species in kelp forests in California (Foster & Schiel 1985). For example Foster (1975b) found that the presence of an overstorey reduces algal diversity and the percentage cover of species below. This may be the direct result of shading on recruitment and growth, and/or an indirect result of overgrowth of these plants by sessile invertebrates when light is low (Breda 1982).

SOUTH AFRICAN KELP COMMUNITIES

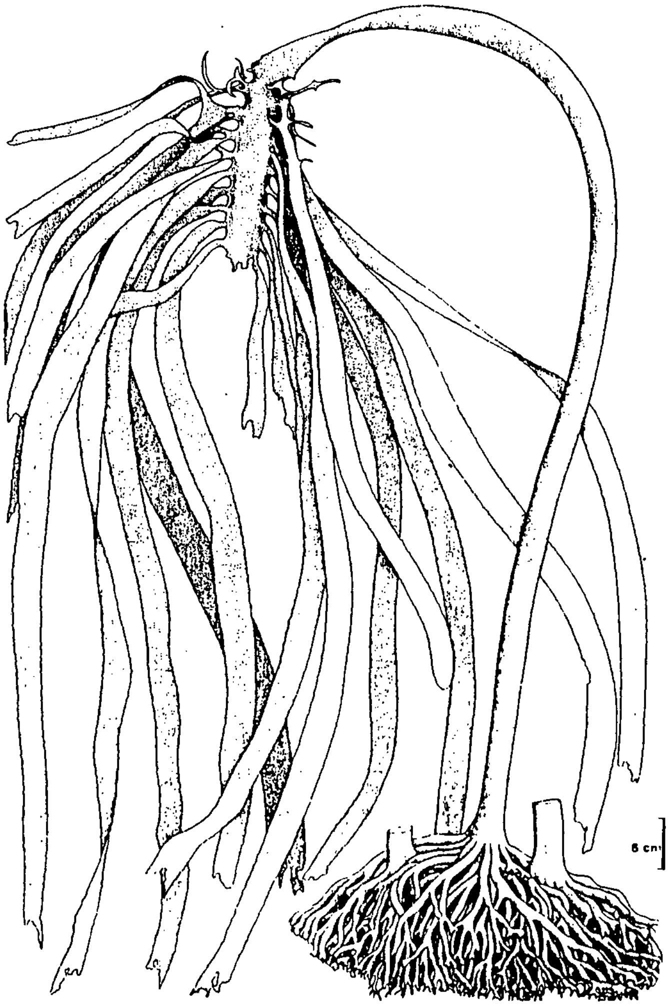
On the coast of southern Africa, from Cape Agulhas, South Africa to Rocky Point, Namibia (Wynne 1986, H. Engledow pers. comm.) - generally in the region of upwelling - there are three genera of true kelp: *Ecklonia*, *Laminaria* and *Macrocystis*.

Belonging to the family Alariaceae, *Ecklonia maxima* is the prominent kelp in southwestern Africa. It is abundant between Cape Agulhas and Luderitz (Field *et al* 1980, Bolton 1987, Bolton and Levitt 1987, F. Molloy, pers. comm.) and forms dense overstories in rough water to a depth of some 10-12m. This species is characterized by a long, hollow terminally-inflated stipe that buoys the short spear-shaped primary blade and its lateral secondaries near the water surface (Figure 1.2). The second *Ecklonia* species *Ecklonia biruncinata*, is less than 50cm long and represents the only member of the Laminariales on the warmer south coast, that is, in the Agulhas province. The species occurs from 60km west of Cape Agulhas to the border of the Indo-West Pacific tropical region at Port Edward, although in deeper water it's range extends further northeast (Lüning 1990). *E. biruncinata* often has spiny growths on the sporophylls and usually also the primary blade, and a short and solid stipe.

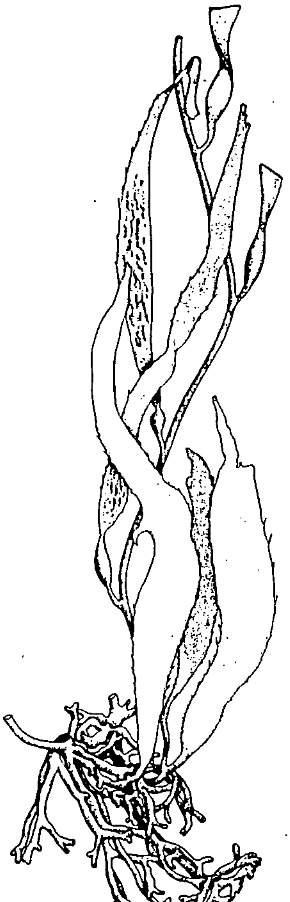
Laminaria pallida forms an understorey beneath the *Ecklonia* canopy to a maximum depth of 15m. Beyond this it forms a dense, dominant community to a depth of 20m. The species ranges from Cape Agulhas to Namibia (30^{0}S). *Laminaria pallida* has a stiff, solid tapering stipe, 2-2.5m long supporting a single palmate frond (Figure 1.2). North of St. Helena Bay, the kelp beds are co-dominated by *Ecklonia maxima* and *Laminaria schinzii*. *Laminaria schinzii* has a similar appearance to *L. pallida* but the stipe, apart from being longer (2.5-3m), has a hollow swelling in the middle which makes it buoyant, and it has a proportionally larger frond (Dieckmann 1980). *Laminaria pallida* possibly represents the southern African descendant of the warm-temperate Mediterranean and Atlantic species *L. ochroleuca* (Lüning 1990).

The more delicate rope-like *Macrocystis angustifolia* (Figure 1.2), occurring from Cape Hangklip to Cape Columbine (J.J. Bolton, pers. comm.), is generally only found in more sheltered localities, typically with a patchy distribution. *M. angustifolia* often forms an understorey in *Ecklonia* forests and may occasionally dominate the canopy shorewards of *Ecklonia* beds.

a. *Ecklonia maxima*



b. *Laminaria pallida*



c. *Macrocystis angustifolia*

Figure 1.2 The kelp species occurring in the Cape Hangklip area
a. *Ecklonia maxima*, b. *Laminaria pallida* and c. *Macrocystis angustifolia*
(from Stegenga *et al* ,in press)

Underneath the kelp is an understorey of primarily red and brown algae, only a few of which have been studied ecologically. The life history of *Desmarestia firma* and it's seasonal pattern of population structure, energy content, growth rate and standing crop have been studied by Anderson (1982). *Desmarestia firma* is an annual species, sporophytes first appearing in spring, growing rapidly during summer and declining in density by the following winter. Annual net production is estimated at 23.4 g dry wt/m^2 of which 22% were accounted for by mortality, 54% by grazing and decay losses and 24% by end of season biomass. As grazing accounts for a substantial proportion of annual net production loss, Anderson and Velimirov (1982) considered the relative palatibility of 13 understorey algae common to kelp beds of the west coast of the Cape Peninsula, South Africa with respect to sea urchin (*Parechinus angulosus*) feeding. It was found that the feeding rate of sea urchins on single species of algae is negatively correlated with the relative astringencies of the algae. Because of the high relative astringency of *D. firma*, Anderson and Velimirov (1982) considered it to be a "non-preferred" species.

Although benthic light levels show pronounced short term fluctuations bought about by turbidity during upwelling and downwelling, rates of photosynthesis still show a pronounced annual cyclical pattern in at least three kelp understorey species, *Botryocarpa prolifera*, *Gigartina radula* and *Epymenia obtusa* (Bolton and Levitt 1987, Levitt and Bolton 1990).

The animals in the understorey are dominated by suspension feeders (eg. the ribbed mussel *Aulocomya ater*, sponges, holothurians *Pentacta doliolum* and *Thyone aurea*, the ascidian *Pyura stolonifera* and the barnacle *Notomegabalanus algicola*). These suspension feeders vary in relative abundance from place to place and tend to form a dynamically changing mosaic of patches (Field and Griffiths, 1991). The dynamics of patches is believed to be caused by a combination of storms uprooting kelp plants, patchy stochastic recruitment of animals and plants, and the sweeping effect of kelp fronds keeping areas of rock clear of competing animals and plants (Velimirov and Griffiths 1977, Velimirov 1983). It is characteristic of kelp beds in this region that the attached macrophytes are subject to little grazing pressure (Newell *et al* 1982) and grazers/debris feeders are thus less common in kelp beds. Common species include the specialized limpet *Patella compressa* which occurs exclusively on the stipes of *Ecklonia maxima* (Branch 1975), the gastropod *Turbo cidaris*, the isopod *Paridotea reticulata*, the amphipod *Ampithoe humeralis*, the abalone *Haliotis midae* and the sea urchin *Parechinus angulosus*. The most important herbivores, sea urchin and abalone, both probably subsist mainly on drift weed or on sporelings and microalgae (Fricke 1979, Field and Griffiths 1988). Sea urchins less than about 10mm in diameter are believed to feed on detritus or microalgae (Greenwood 1980) while larger individuals take small sporophytes of *Ecklonia maxima* as well as detached pieces of kelp stipe and fronds. The diet of abalone varies somewhat with body size, season and geographical location, but the most important components are kelp, *Ecklonia maxima* and *Plocamium* spp.which together comprise 77% of the food eaten by volume (Barkai and Griffiths 1986). Several fish (eg. large individuals of *Pachymetopon blochii*) may consume significant quantities of algae, but are primarily carnivorous (Branch and Griffiths 1988). The carnivores are dominated in biomass by the spiny lobster *Jasus lalandii* who typically feed on the ribbed mussel *Aulocomya ater* (Velimirov *et al* 1977)[2]. Other carnivores include various polychaete worms, the isopod *Cirolana imposita* and the omnivorous hottentot fish *Pachymetopon blochii*.

Other components of the kelp bed community that have been studied to a greater or lesser extent are the canopy fauna and epiflora (eg. Allen and Griffiths 1981), the phytoplankton (eg. Carter 1982) and the microrganisms such as the bacterial and protozoan community (eg. Mazure 1978, Mazure and Field 1980, Linley and Newell 1981, Koop *et al* 1982) but these will not be discussed in this short overview as they are not considered in the research data in this thesis.

Newell *et al* (1982) and Wulff and Field (1983) have attempted to model west coast kelp beds as a closed and open ecosystem respectively by assembling an energy budget for the system, incorporating energy budgets for the dominant organisms, modelling transfers of energy to the primary and secondary consumers, and modelling energy fluxes through the microorganisms. The results in the form of energy flow diagrams and simulation models respectively are effectively summarized in Branch and Griffith (1988). I believe that a major shortcoming of these models is the limited quantitative data used. The only adequate survey of a kelp bed in any detail in South Africa is that at Oudekraal on the west coast of the Cape Peninsula, although the bottom canopy algal component

---

[2] *Personal observation from the study site indicates that sea urchins form the most common dietary component of the rock-lobsters in this west coast/south coast overlap kelp bed.*

of this kelp community was inadequately assessed. Preliminary surveys of the overlap zone (see Chapter 2) site selected for this thesis indicate that generalization made from this "typical" kelp bed at Oudekraal are not appropriate for kelp communities east of the Cape Peninsula.

What little is known of subtidal algal distribution patterns in the southwestern Cape has been described by Field *et al* (1977), Velimirov *et al* (1977) and Field *et al* (1980). Generally, the inshore zone is dominated by small *Ecklonia* plants and supports a few animals. Intermediate depths support maximal algal biomass with the larger *Ecklonia* plants forming a canopy, beneath which *Laminaria* and understorey algae thrive, but where animals are poorly represented. As the kelp beds thin out at the seaward margin of the beds they give way to a dense animal community dominated by sea-urchins and filter-feeding mussels, sponges and holothurians. Field *et al* (1980) compared the standing stocks of benthic animals and plants across six kelp bed transects located between Cape Agulhas and Saldanha Bay. The more southerly transects tend to have higher overall standing stocks of kelp and sponges and lower overall standing stocks of mussels and rock lobsters. The fluctuation in standing stocks have been attributed to the greater water clarity in the south, as well as the generally shallower profile of the shore, which increases the width of the beds.

At a more local level Field *et al* (1980) showed that the transect sited at Bettys Bay (approximately 5km east of the study site researched in this thesis) reflects an unusual kelp community compared to transects from the west coast. In the Bettys Bay transect, ribbed mussel, holothurians and sea urchins together with rock lobster do not comprise the main biomass offshore or form characteristic associations as they do along the west coast. Rather, the inshore zone is dominated by a canopy of *Ecklonia maxima* with a sub-canopy of *Laminaria pallida* and a good representation of animals, with the greatest abundance of the abalone, *Haliotis midae*. The intermediate zone is indistinct and comprises a large variety of inconspicuous taxa. The offshore zone is dominated by *Laminaria pallida* and most of the animal biomass is represented by filter-feeders (sponges and *Aulocomya ater*).

As in the south-east Pacific, it is characteristic of kelp beds in southwestern Africa that attached macrophytes are subject to little grazing pressure (Newell *et al*, 1982) and it is considered that grazers are unlikely to significantly influence the structure of kelp forests at the scale encountered in kelp forests in the northeast Pacific and northwest Atlantic. Consumption of live attached macroalgae by grazers was estimated to account for less than 1% of the primary production in South African kelp forests (Branch and Griffiths 1988).

At the large spatial scale, coarse distributional patterns of kelp forests of the southern African Benguela ecosystem have been attributed to temperature and water clarity (Field *et al* 1980). At the more localized scale, inter-species interactions (Velimirov and Griffiths 1979, Fricke 1979) and depth and distance from the shore (Velimirov *et al* 1977, Field *et al* 1980) were mechanisms considered to regulate the kelp bed structure.

A number of interactions between species which have a profound influence on the structure and functioning of southern African kelp systems have been identified. Velimirov and Griffiths (1979) suggest that the sweeping action of adult *Laminaria pallida* performs a vital function by maintaining a grazer-free swathe around the plants, where fresh recruitment of sporophytes can occur. In a False Bay kelp community, Fricke (1979) showed that experimental removal of sea urchins more than doubles the recruitment of *Ecklonia maxima*. The effect of sea urchins on the dynamics of the kelp bed may thus be substantial, even though sea urchins account for only a small fraction of the kelp production if their role is assessed in terms of the energy flow model for west coast kelp communities presented by Branch and Griffiths (1988).

At a localized scale, Barkai (1987) has postulated the existence of an "alternative community state" from an investigation of the subtidal fauna and flora of two islands in Saldanha Bay having similar topographies and physical conditions. The community present at Malgas Island is almost entirely controlled by intense predation by rock lobsters. The rock lobsters prevent most benthic animal species from colonizing the substratum at Malgas, and in the absence of grazers and spatial competitors, algae can grow prolifically. At nearby (4km away) Marcus Island however, in the near absence of rock lobsters, the black mussel *Choromytilus meridionalis* covers almost all the substratum in multiple layers. Sea urchins are abundant at Marcus Island and almost completely prevent algal colonization. The critical question however is why there are virtually no rock lobsters at Marcus Island, especially in view of the abundant food there?

In an experimental manipulation, Barkai (1987) found that the whelk *Burnupena* spp. killed any translocated rock lobsters released at Marcus Island. It appears that once the *Burnupena* spp have established a sufficiently large population, they are capable of preventing colonization by rock lobsters. Theoretically, if the *Burnupena* population crashes, the dynamics of the community will change and rock lobsters will dominate. Clearly the population dynamics and roles of several important groups of organisms in the kelp bed are strongly influenced by biological interactions between species, in addition to physical factors and restrictions imposed by energy flow.

The emphasis in this thesis is on the algal understorey of a South African kelp community, in which the overstorey canopy is composed of *Ecklonia maxima* and *Laminaria pallida*. The zonation with depth, of the understorey, in a local west coast/south coast overlap kelp bed will be investigated. An assessment of whether this study can contribute to generalizations made about the depth zonation of South African kelp communities will be made.

It will be established to what extent discrete combinations of benthic organisms in the understorey of the kelp community can be identified and what environmental setting these communities have. The effect that these environmental factors have on the distribution of the sessile understorey plants and animals at different scales, as well as the inter-correlations between these environmental factors, will be evaluated. The effect of an environmental factor (sand cover and abrasion) on selected understorey species (*Gigartina radula*, *Aeodes orbitosa* and *Iridaea capensis*) spore settlement and germination will be experimentally tested.

CHAPTER 2

PHYCOGEOGRAPHIC AFFINITIES OF THE STUDY AREA

INTRODUCTION

Along the southern African coastline, the contrast between the strong-flowing warm Agulhas current down the east coast and the weak cool Benguela current up the west coast has manifested itself in the different marine algal species found on the west and south coasts of South Africa. Where these currents meet, Stephenson (1944) defined, on the basis of determining intertidal faunal and flora species change around the coast, the south coast/west coast overlap region, a transitional area between the cool-temperate west coast and the warm-temperate south coast. Lüning (1990), following Briggs (1974), identified two provinces within the warm temperate southern African region, namely the south-western Africa province (including the South African west coast) and the Agulhas province (south coast). The boundaries of the overlap between these two provinces are not yet clear, but biogeographers generally agree that they fall in the region between Kommetjie and Cape Agulhas (Figure 2.1), although Bolton and Anderson (1990) have suggested that the change from an overlap to a true west coast flora may be in the vicinity of Cape Columbine. The reasons for this well-defined overlap between the west and south coast floras are poorly understood. It is, however, apparent that a complex interplay of related physical and chemical factors, characteristic of both the west and south coasts, occurs in this region. These include patterns of oceanic circulation (Isaac, 1938), periodicity and seasonality of ambient temperatures (Isaac, 1938; Bolton, 1986; Hommersand 1986; Bolton & Stegenga, 1990; Bolton & Anderson, 1990) and levels of nutrients (Bolton, 1986; Hommersand, 1986).

It is only recently (e.g. Bolton, 1986; Bolton & Stegenga, 1987; Bolton & Stegenga, 1990; Bolton & Anderson, 1990; Stegenga & Bolton, 1995) that South African phycogeographers have evaluated detailed regional floristic composition with respect to the existing concepts of floristic regions and overlap zones of seaweed floras pioneered by Stephenson and his co-workers (summarised in Stephenson, 1944, 1948). These detailed collections of macroalgae have, however, taken place primarily in the intertidal with only incidental beach cast macroalgae being considered. There is a paucity of detailed floristic information on the subtidal algal communities. Though Field *et al* (1980) and Velimirov *et al* (1977) have quantified the major algal species (55 species) along the south-west Cape coast, they provide little detailed floristic information. In the only comprehensive published account of local subtidal algal communities, Anderson and Stegenga (1989) described the major communities at Bird Island near Port Elizabeth and listed 122 species, but the biogeographic affinities of the flora were not analysed. The aim of this chapter is to provide a descriptive record of the intertidal and subtidal floristic composition of a site centrally located in the overlap region between the west and south Cape coasts. The phycogeographic affinities of the macroalgal species recorded will be discussed.

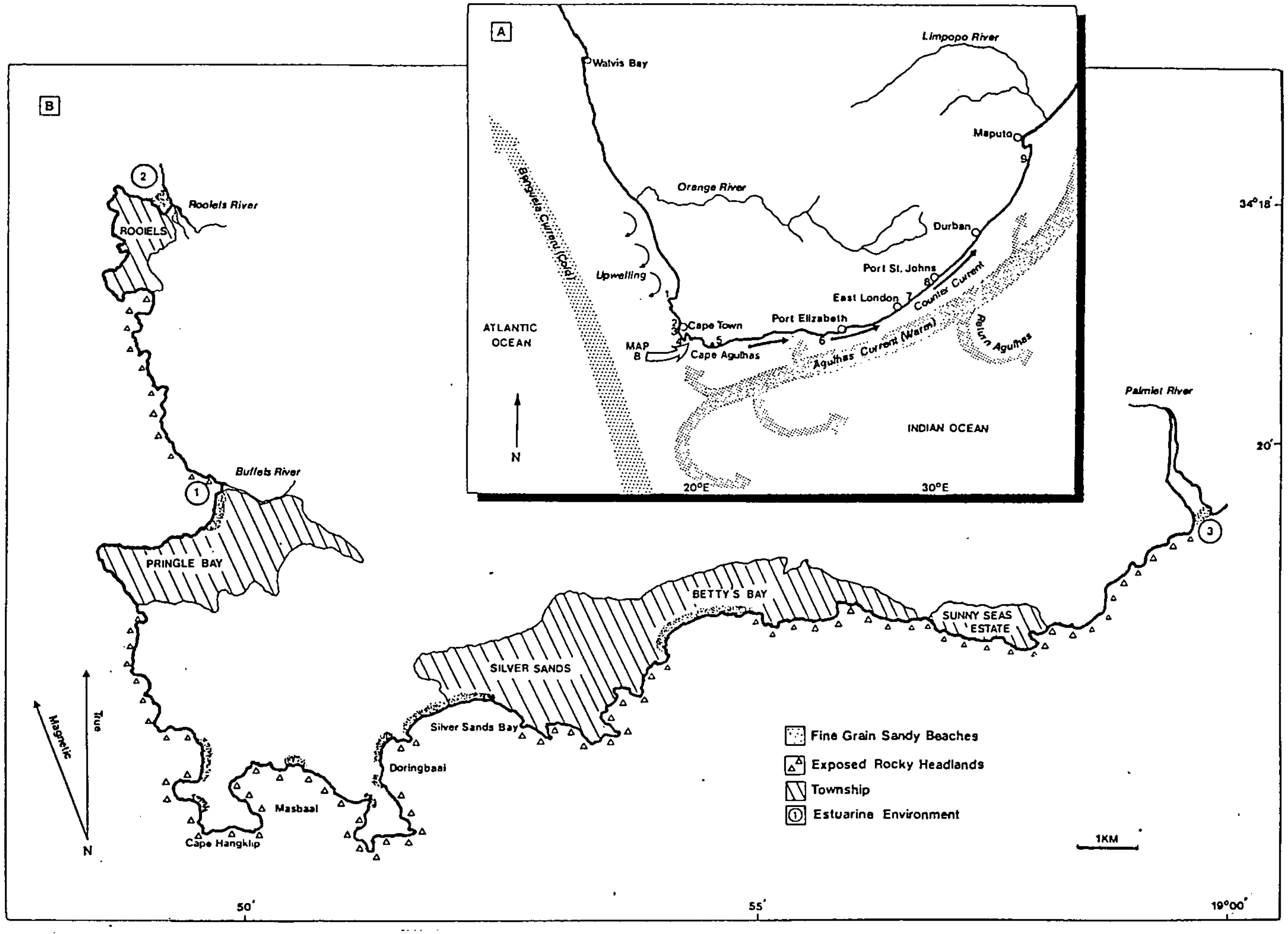


Figure 2.1 Map of the Cape Hangklip area (Map B) and inset (Map A) showing the South African coastline with the prevailing currents and sites mentioned in the text: Cape Columbine (1), Sea Point (2), Kommetjie (3), Cape Point (4), De Hoop (5), Cape St. Francis (6), Kei Mouth (7), Hluleka (8) and Ponto do Ouro (9).

STUDY SITE AND COLLECTION METHODS

The Hangklip area, forming the south-western limit of False Bay in the south-western Cape, South Africa, is located approximately 30 km due east of Cape point and is bounded by the Rooiels and Palmiet rivers (Figure 2.1). The coastline in general is rugged, with rocky outcrops. The substratum belongs to the Peninsula formation of the Table Mountain group and consists of medium- to large-grained quartzitic sandstone. The intertidal coastal area exhibits variable topography which includes vertical rock faces of exposed rocky headlands; unstable boulder fields; sheltered medium-grained sandy beaches; broad, gently sloping beaches of medium-grain Table Mountain sandstone (TMS) and highly irregular and unevenly weathered pinnacles of large-grain TMS.

The substratum of the shallow subtidal is generally composed of a well-structured rocky substrate of TMS interspersed with patches of loose cobbles, boulders and sand. In sheltered areas, loose boulders in shallow water give way to rocky shelves which are seasonally covered by sand during the late spring and summer months. In exposed areas, weathered sandstone often forms jagged, submerged pinnacles running parallel to the shore with troughs typically filled with sand and cobbles.

The sublittoral fringe and subtidal are dominated by an extensive laminarian overstorey (*Ecklonia maxima* - species authorities can be found in Appendix 2.1) and sub-canopy (*Laminaria pallida*). Winter storms and exposure to the prevailing summer wind (south-east) and swell direction (south to south-west) result in conditions of high wave energy prevailing along most of the coastline through much of the year, though Masbaai and to a lesser extent Holbaai provide a degree of shelter. Both the Agulhas current and the cool Benguela upwelling system are influential in determining the chemical, physical and biological status of the area. Temperature conditions, considered to be an overriding factor regulating the geographical distribution of seaweeds (Lüning, 1990) are, at about 8 m depth, intermediate between False Bay and the west coast of the Cape Peninsula (Anderson & Bolton, 1989 and unpublished Sea Fisheries Research Institute data). Average minimum and maximum monthly mean temperatures for Betty's Bay for the period from 1986 to 1989 (11.4° and 15.6°C) are higher than for Oudekraal (9.7° and 14.6°C) on the west coast, but lower than for Buffelsbaai (11.5° and 17.4°C) in False Bay (Anderson & Bolton, 1989, and unpublished Sea Fisheries Research Institute data).

Low average monthly temperatures for Betty's Bay during the summer months are a result of wind-induced coastal upwelling.

Collections of intertidal and subtidal plants were made from June 1989 to July 1990. Samples preserved in 5% formalin in seawater were identified and mounted on herbarium sheets or permanent slides. Pressed or slide-mounted voucher specimens of species not previously recorded for the area were deposited in the Bolus Herbarium of the University of Cape Town (BOL). Species of crustose coralline Rhodophyta are not identified in this paper, as South African representatives of this group,. including specimens from the Cape Hangklip area, are currently under review by Y.M. Chamberlain (University of Portsmouth, U.K.) and D.W. Keats (University of the Western Cape, South Africa).

DESCRIPTION OF INTERTIDAL AND SUBTIDAL COMMUNITIES FROM THE CAPE HANGKLIP AREA

A general account of the algal "associations" and "consociations" in the intertidal and sub-littoral fringe of the coast between Rooiels and Gansbaai has been documented by Isaac (1949). Despite the poorly defined term "mixed algal vegetation", the generalisations are still relevant today. With the exception of the presence of *Ecklonia maxima*, the shore zonation generally concurs with the "south coast zonation" of Branch and Branch (1981, p. 28). However, the validity of this zonation pattern being indicative of a true south coast zonation is questionable since algal species such as *Gigartina stiriata*, *Gigartina radula* and *Bifurcaria brassicaeformis* are rare or absent east of Cape Agulhas. This zonation pattern is more representative of the west coast/south coast overlap region than the south coast.

Truly intertidal algae (i.e. those algae occurring on open rock) are low in abundance and diversity (e.g. *Splachnidium rugosum*, *Gelidium pristoides*, *Gigartina* spp. and *Porphyra capensis*). It is apparent that, as for rocky intertidal communities on the Cape Peninsula (*cf.* McQuaid & Branch, 1984; McQuaid *et al*, 1985), wave exposure may be the primary factor influencing the intertidal community structure in this area. In wave-exposed areas, the sublittoral fringe is dominated by *Bifurcaria brassicaeformis*, whereas there is no truly dominant species in the sheltered areas. Predominant sublittoral fringe flora generally include *Plocamium corallorhiza*, *Sargassum heterophyllum*, *Anthophycus longifolius*, *Hypnea spicifera*, *Pterosiphonia cloiophylla*, *Dictyota dichotoma* and *Laurencia flexuosa*. In sheltered areas, rockpools in the lower and middle eulittoral zone have high biomass and species diversity and are dominated by a wide variety of seaweeds, including *Ulva rigida*, *Chordariopsis capensis*, *Codium fragile* subsp. *capense*, *Aeodes orbitosa*, *Codium stephensiae*, *Gelidium capense*, *Jania crassa*, *Scinaia capensis* and *Pterosiphonia cloiophylla*. In rockpools in the upper eulittoral, *Enteromorpha intestinalis* predominates. The rockpool flora in the exposed areas, however, comprises different dominant species such as *Cladophora prolifera*, *Bifurcariopsis capensis*, *Centroceras clavulatum*, *Ceramium centroceratiforme*, *Champia lumbricalis*, *Arthrocardia* spp. and *Rhodymenia natalensis*.

In a paper describing the shallow subtidal spatial variability of plant-animal communities at a number of localities, Field *et al* (1980) recorded 14 large, common macroalgal species along a single 1 300 m transect line at Betty's Bay but, to date, no detailed survey has been carried out in this area.

In the present study, five subtidal algal strata were recognised:

- A floating canopy of *Ecklonia maxima*.
- A 0.25 - 2 m stipitate erect sub-canopy in which the fronds are supported well above the substratum (e.g. *Laminaria pallida*, *Sargassum heterophyllum*, *Anthophycus longifolius*).
- A fleshy, foliose and articulate stratum in which fronds lie immediately above the substratum (e.g. *Codium stephensiae*, *Aeodes orbitosa*, *Gigartina radula*, *Amphiroa ephedraea*).
- A short, entwined, tightly adherent turf stratum (e.g. *Polysiphonia virgata*, *Griffithsia confervoides*).
- A fleshy and coralline encrusting stratum (e.g. *Ralfsia verrucosa* and crustose corallines).

In the shallow (< 3m depth) sheltered waters, large foliose macroalgae such as *Pachymenia carnosa*, *P. cornea*, *Nemastoma lanceolata*, *Gigartina radula* and *Aeodes orbitosa*, dominate the kelp understorey. In the deeper water (to 10 m), where seasonal sand deposition takes place, algae such as *Gigartina insignis*, *G. pistillata*, *G. scutellata*, *G. bracteata*, *Chondria capensis*, *Jania natalensis* and turf species persist on the flat rocky shelves while species such as *Botryocarpa prolifera*, *Trematocarpus flabellatus*, *Bartoniella crenata*, *Laminaria pallida*, *Plocamium corallorhiza* and *P. cornutum* are abundant on the vertical rock faces or substrates not seasonally inundated with sand. In areas of high sand deposition and low water movement, the sea cucumber (*Henricia ornata* Perrier), Pelecypoda and the giant chiton (*Dinoplax gigas* Gmelin) were abundant, whereas urchins (*Parechinus angulosus* Leske), tunicates (*Pyura stolonifera* Heller), *Turbo sarmaticus* L. and *Austromegabalanus cylindricus* Gmelin occurred in low numbers or were absent.

In the shallow water of wave-exposed sites, articulated corallines, *Halopteris funicularis*, *Gelidum pteridifolium*, *Codium stephensiae*, *Plocamium cornutum*, *Laurencia flexuosa*, *Bifurcariopsis capensis*, *Sargassum heterophyllum* and *Anthophycus longifolius* were common beneath the kelp canopy. In the deeper water, *Desmarestia firma*, *Laminaria pallida*, *Zonaria subarticulata*, *Plocamium suhrii*, *Gymnogongrus glomeratus*, *Amphiroa capensis* and *Cheilosporum cultratum* dominated the understorey.

Certain species such as *Plocamium rigidum*, *Caulerpa holmesiana*, *Halopteris funicularis* and *Pterosiphonia cloiophylla* were ubiquitous throughout the depth and exposure range. Major species composition and local dominants remained constant through the year of collection.

RESULTS

A total of 200 taxa (see Appendix 2.1) were collected of which four [*Aphanocladia cf. skottsbergii* (Figures 2.2B, 2.2C), *Audouinella endophytica* (Figures 2.2D, 2.2E), *Centroceras distichum* (Figure 2.2F) and *Grateloupia doryphora*)] are new records for southern Africa. Five taxa [*Antithamnion* sp. (Figure 2.2A), *Colaconema* sp., *Erythrocladia* sp. (Figure 2.3B), *Erythroglossum* sp., and *Pterosiphonia* sp. (Figure 2.3C)] are currently undescribed and two [*Pterosiphonia spinifera* and *Symphocladia cf. marchantioides* (Figures 2.3D, 2.3E)] represent considerable extensions of the known range of distributions. One species, *cf.* Ceramiaceae *indet.* (Figure 2.3A) of as yet uncertain affinity, probably represents a new genus in the Ceramiaceae. The list comprises 10 genera of Chlorophyta (27 taxa), 23 genera of Phaeophyta (25 taxa) and 86 genera of Rhodophyta (148 taxa). A floristic ratio of Rhodophyta and Chlorophyta divided by Phaeophyta (Cheney, 1977) commonly used to describe correlations between sea temperature and ratios of red, green and brown algal species numbers in the North Atlantic, yields a value of 6.96 which is characteristic of a tropical flora. However, as Bolton (1986) has emphasised and is borne out here, this floristic ratio appears not to be applicable in southern Africa due to the depauperate brown algal flora in this region.

Figure 2.4 summarises the distribution of 170 species for which adequate published and unpublished distribution records exist. Those species whose distribution data or taxonomy are poorly known have been omitted from the analysis. It is apparent that there is no overwhelming dominance of either west coast (occurring west of Cape Agulhas) or south coast (occurring east of Kommetjie and west of Port St. Johns) species, these numbering 38 (22%) and 43 (25%), respectively. Temperate species, defined as those species only occurring west of Port St. John's, number 31 (18%), while species occurring east to the Mozambique border but not recorded west of Kommetjie number 34 (20%). Ubiquitous species which occur along the whole South African coastline total 16 (9%) species, and 8 (5%) species have, to date, not been recorded outside the west coast/south coast overlap region.

In this survey, based on current distribution records, 31 warm-water species have their western limit at Cape Hangklip (Table 2.1).

Table 2.1: List of species reaching the eastern and western limit of their distribution in the Cape Hangklip area.

Warm-water species	Cold-water species
Amphiroa cf. beauvoisii	*Botryocarpa prolifera*
Amphiroa capensis	*Ceramium capense*
Amphiroa ephedraea	*Colaconema plumosum*
Arthrocardia duthiae	*Gigartina bracteata*
Bartoniella crenata	*Gigartina scutellata*
Bryopsis cf. setacea	*Lomathamnion humile*
Callithamnion cordatum	*Macrocystis angustifolia*
Ceramium centroceratiforme	*Microcladia gloria-spei*
Chaetomorpha antennina	*Nemastoma lanceolatum*
Cladophora prolifera	*Phyllymenia belangeri*
Compsothamnionella sciadophila	*Schizymenia obovata*
Delisea flaccida	*Streblocladia corymbifera*
Gelidium pteridifolium	
Gelidium cf. reptans	
Gigartina insignis	
Gigartina paxillata	
Gracilaria capensis	
Halicystis sp.	
Herposiphonia prorepens	
Jania adhaerens	
Jania capillacea	
Jania verrucosa	
Laurencia cf. obtusa	
Nienburgia serrata	
Pachychaeta cryptoclada	
Peyssonnelia capensis	
Placophora binderi	
Pollexfenia minuta	
Pterosiphonia spinifera	
Sargassum elegans	
Symphocladia cf. marchantioides	

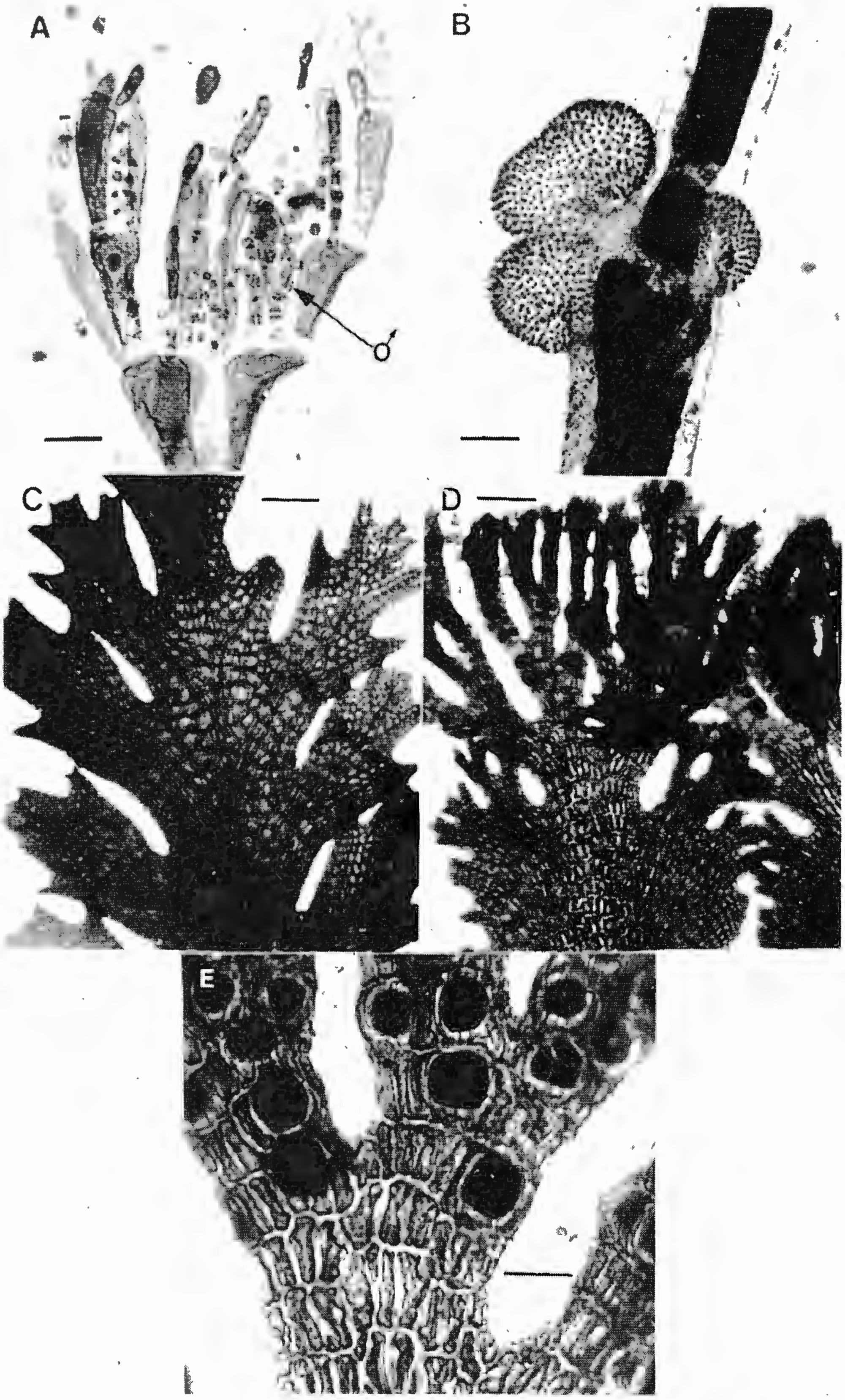


Figure 2.3 (a) Ceramiaceae *indet.* Fascicle of branchlets at apex bearing male capitula (scale = 100µm); (b) *Erythrocladia* sp., semi-globose cushions epiphytic on *Cladophora* sp. (scale = 100µm); (c) *Pterosiphonia* sp., compressed pinnate thallus (scale = 1mm); (d) *Symphocladia cf. marchantioides*, thallus (scale = 0.5mm); (e) *Symphocladia cf. marchantioides*, one tetrasporangium per segment (scale = 100µm).

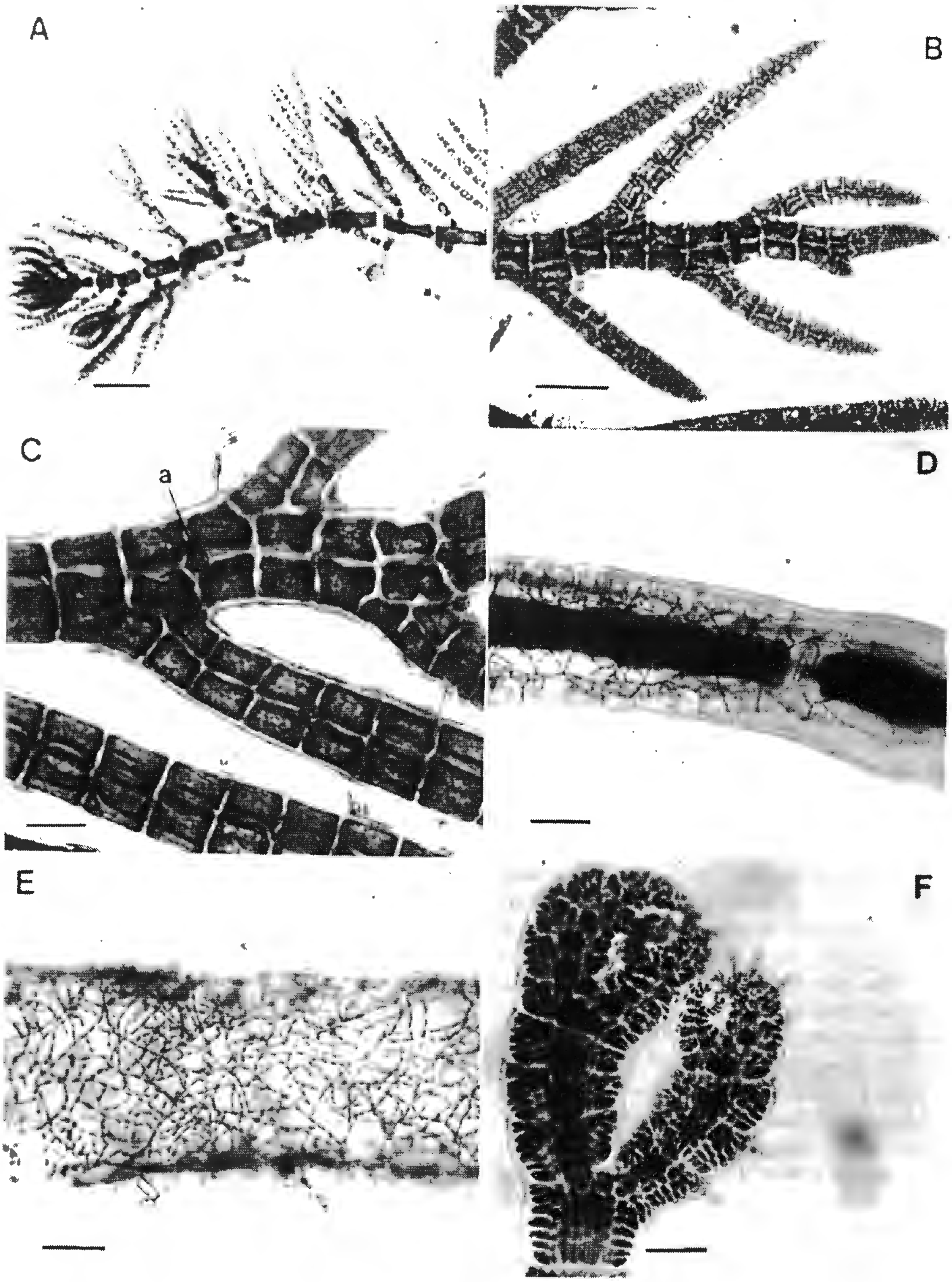


Figure 2.2 (a) *Antithamnion* sp., main (prostrate) axis, multicellular haptera and opposite branchlets (scale = 100 µm); (b) *Aphanocladia cf. skottsbergii*, erect axis with alternating laterals (scale = 100µm); (c) *Aphanocladia cf. skottsbergii*, non-lateral bearing segment with 'scar cell' (scale = 50µm); (d) & (e) *Audouinella endophytica*, growing in the cell wall of an unidentified member of the Ceramiaceae (scale = 50µm); (f) *Centroceras distichum*, thallus apex with embedded tetrasporangia (scale = 100µm).

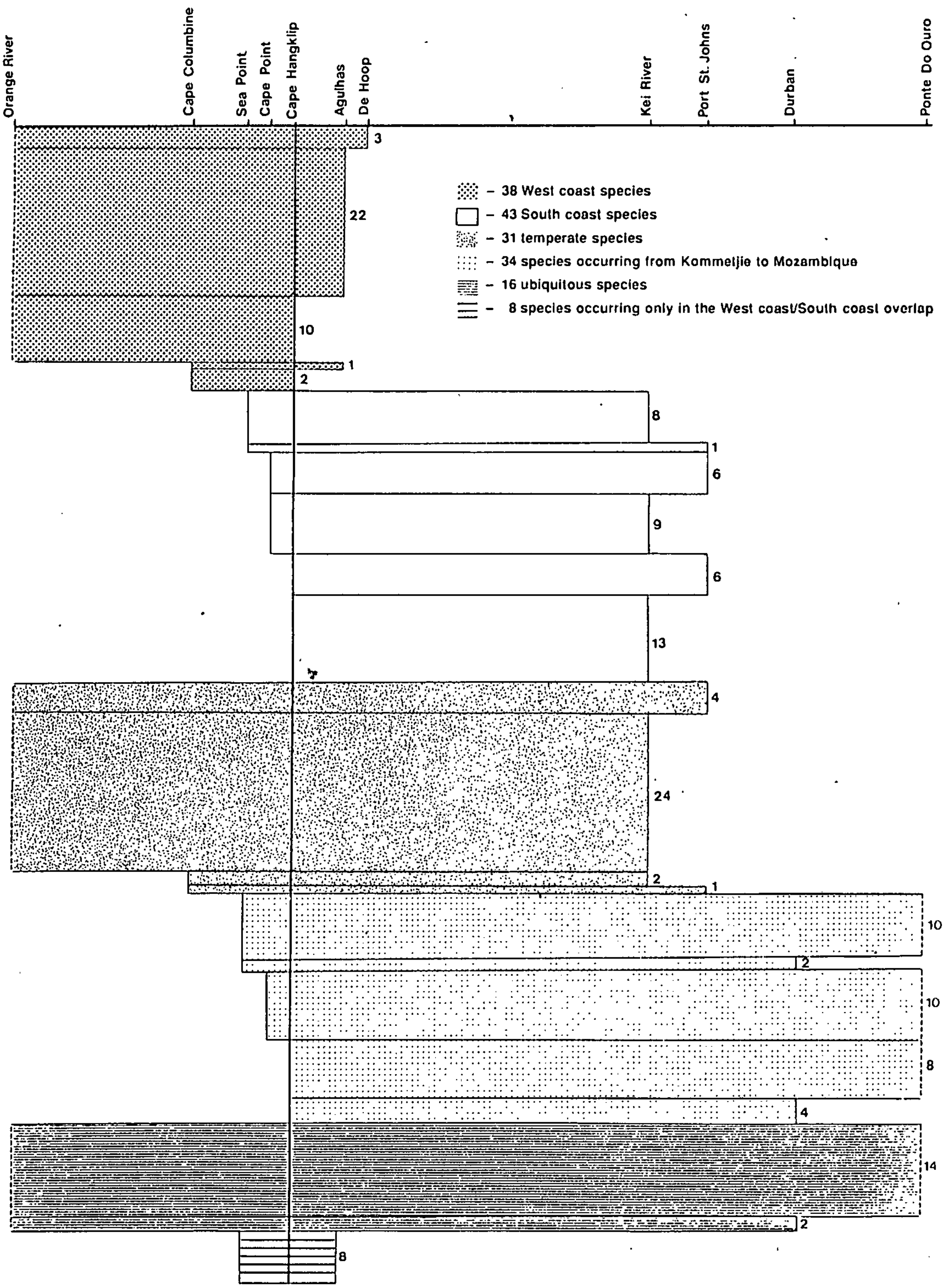


Figure 2.4 Distributional analysis of 170 species with adequate distributional records, represented as proportional bar charts of number of species. Biogeographical groups with similar distributions and affinities are clustered. Solid vertical line depicts the study site.

DISCUSSION

The seaweed flora of the Cape Hangklip area has neither a predominance of west nor south coast species. This suggests that the overlap region can be described as an area demarcated by two boundaries where major floral compositional changes take place, but within which an intermixing of primarily south and west coast species that reach the extent of their distributional ranges, occurs.

It is evident from recent literature (Bolton & Anderson ,1990; Bolton & Stegenga, 1990) that at the eastern boundary of the overlap region there is a rapid change in community composition over a relatively short length of coastline in the area immediately west of Cape Agulhas. This apparent discontinuity is characterised by a rapid gain of species with warm-water distributions and a simultaneous, but less rapid, loss of species with cold-water distributions. The western boundary of the overlap area is, however, not as well-defined, as a number of common south coast and overlap species have been recorded west of Kommetjie (Bolton & Anderson, 1990), the suggested junction between the overlap and the west coast (see Brown & Jarman, 1978 for discussion).

In the vicinity of Cape Agulhas, many species with warm-water affinities do reach their western distribution limits, but as is evident from the list of species from Cape Hangklip, a large number (77 species) extend beyond this boundary. These species are then likely to reach the limits of their distribution at different localities along the length of the overlap zone. For example, 43 (25%) of 170 species with sufficient distribution data, reach their eastern or western boundary in the Cape Hangklip area (Figure 2.4 and Table 2.1), although more detailed subtidal collections in other regions of the overlap may extend the range of many species. The location of the western boundary of the overlap zone is currently uncertain, but it may be speculated that the Cape Peninsula acts as a significant topographical or physical barrier to the westward spread of warm-water species. In an analysis of individual distributions of species of Ceramiaceae, Stegenga and Bolton (1995) found that the most dramatic change in floristic composition occurs in the area between the Cape Peninsula and Cape Agulhas.

Temperature conditions at the study site show strong similarities to those of the west coast. The lack of dominance by west coast species in the Hangklip area however indicates that a gradual or drastic loss of cold-water species occurs west of Cape Hangklip. The significantly higher temperatures of False Bay (sites 8, 9 and 10, Bolton, 1986) may be instrumental in limiting the eastward spread of many west coast species. A re-evaluation of seaweed distributional information may reveal that the western boundary of the overlap is in the vicinity of Cape Point. More detailed collection in other sectors of the overlap region and subsequent mapping of the intermixing of species is needed to elucidate more clearly the factors limiting distribution of many south and west coast species.

Detailed reports of local seaweed diversity include: the region west of Cape Agulhas to the Namibia/Angola border (268 taxa, Bolton, 1986); De Hoop Nature Reserve (126 taxa, Bolton & Stegenga, 1990); East Cape coast (Cape St. Francis to Kei mouth) (276 taxa, Seagrief, 1988); False Bay (217 taxa, Bolton *et al*, 1991); Bird Island (122 taxa, Anderson & Stegenga, 1989); and Hluleka, Transkei (178 taxa, Bolton & Stegenga, 1987). The seaweed species diversity of Cape Hangklip compares favourably with data from other parts of the temperate southern African region. The floristic richness of this region may be attributed to a wide variety of microhabitats for growth, the nature of the overlap of two distinct floras, and infrequent summer upwelling with consequent relatively stable temperature conditions.

APPENDIX 2.1: List of algae from the Cape Hangklip area. The species nomenclature follows Seagrief (1984), and those species not catalogued by Seagrief are marked with an asterisk. Brief descriptions and taxonomic notes on noteworthy records are included. Animal groupings (Phyla, Sub-Phyla, Class or Order) used during data collection in Chapter 3 are included. Plant species numbers and animal group numbers are used in the data analyses in Chapter 3.

ALGAE

Chlorophyta

51 **Acrochaete viridis* (Reinke) R. Nielsen
1 *Bryopsis cf. setacea* Her.
2 *Bryopsis* sp.
3 *Caulerpa bartoniae* Murray
4 *Caulerpa filiformis* (Suhr) Her.
5 *Caulerpa holmesiana* Murray
6 *Chaetomorpha aerea* (Dillw.) Kuetz.
7 *Chaetomorpha antennina* (Bory) Kuetz.
8 *Chaetomorpha robusta* (Aresch.) Papenf.
9 **Chloropelta caespitosa* Tanner
10 *Cladophora capensis* (C. Ag.) De Toni
11 *Cladophora flagelliformis* (Suhr) Kuetz.
12 *Cladophora mirabilis* (C. Ag.) Rabenh. in Hohenack.
13 *Cladophora prolifera* (Roth) Kuetz.
14 *Cladophora radiosa* (Suhr) Kuetz.
15 *Cladophora* sp.
16 *Codium duthieae* Silva
17 *Codium fragile* (Suring.) Hariot subsp. *capense* Silva
18 *Codium papenfussii* Silva
19 *Codium platylobium* Aresch.
20 *Codium stephensiae* Dickinson
21 *Enteromorpha intestinalis* (L.) Link in Nees
22 *Enteromorpha cf. prolifera* (O.F. Muell.) J. Ag.
23 **Halicystis* sp.
24 *Ulva capensis* Aresch.

25 *Ulva rigida* C. Ag.
26 *Ulva* sp.

Phaeophyta

27 *Anthophycus longifolius* (Turner) Kuetz.
28 *Axillariella constricta* (J. Ag.) Silva
29 *Bifurcaria brassicaeformis* (Kuetz.) Barton
30 *Bifurcariopsis capensis* (Aresch.) Papenf.
31 *Carpomitra* sp.
32 *Chordariopsis capensis* (Kuetz.) Kylin
33 *Colpomenia sinuosa* (Roth) Derbés et Solier in Castagne
34 *Desmarestia firma* Skottsberg in Nordenskjöld
35 *Dictyota dichotoma* (Huds.) Lamour.
36 *Ecklonia maxima* (Osbeck) Papenf.
37 *Ectocarpus siliculosus* (Dillw.) Lyngb.
110 *Feldmannia irregularis* (Kuetz.) Hamel
38 *Halopteris funicularis* (Montagne) Sauvageau
39 *Iyengaria stellata* (Boerg.) Boerg.
40 *Laminaria pallida* Greville ex J. Agardh
41 *Leathesia difformis* (L.) Aresch.
42 *Macrocystis angustifolia* Bory
43 *Phloiocaulon squamulosum* (Suhr) Geyler
44 *Ralfsia verrucosa* (Aresch.) J. Ag.
46 *Sargassum elegans* Suhr
45 *Sargassum heterophyllum* (Turner) C. Ag.
47 *Sphacelaria* sp.
48 *Splachnidium rugosum* (L.) Grev.
49 *Zonaria harveyana* (Pappe ex Kuetz.) Aresch.
50 *Zonaria subarticulata* (Lamour.) Papenf.

Rhodophyta

52 **Acrochaetium catenulatum* Howe

53 *Acrosorium acrospermum* (J. Ag.) Kylin

54 *Acrosorium maculatum* (Kuetz.) Papenf.

55 *Acrosorium uncinatum* (Turner) Kylin

56 *Aeodes orbitosa* (Suhr) Schmitz

57 *Amphiroa cf. beauvoisii* Lamour.

58 *Amphiroa capensis* Aresch. in J. Ag.

59 *Amphiroa ephedraea* (Lamarck) Decaisne

60 **Anotrichium tenue* (C. Ag.) Naegeli

61 **Antithamnion cf. diminuatum* Wollaston

62 *Antitamnion* sp.: Only a small sterile fragment was found of an *Antithamnion* species which is different from South African species described so far. Plants attach by multicellular haptera originating from basal cells of opposite branchlets. The main (prostrate) axis is 40 - 50 μm in diameter and cells about three times longer than broad. Branchlets are opposite, decussate in successive segments, up to 300 μm long, *ca.* 20 μm in diameter basally, tapering towards the apex and with a deciduous acute apical cell. Opposite branchlets are sometimes simple, but usually with a pectinate series of 3 - 5 ramuli. Gland cells are rare, occurring on a four-celled branchlet in the position of an ordinary ramulus. Indeterminate laterals replacing a determinate branchlet are adventitious and originate frm the basal cell of a determinate branchlet. To date three species of *Antithamnion* are known from the Southern African coast outside of Natal; *A. diminuatum* Wollaston, *A. pseudoarmatum* Stegenga and the Namibian species *A. leptocladum* (Montagne) Wynne. Both *A. pseudoarmatum* and *A. leptocladum* have pectinate opposite branchlets, but differ from this material in the distichous arrangement of the branchlets. The same applies to *A. secundum* Itono, the only one of several Natalian species that shows a superficial similarity with our species (*cf.* Norris, 1987).

63 **Aphanocladia cf. skottsbergii* (Levring) Ardré: Plants with prostrate filaments, erect axes at frequent intervals and about 7 mm tall. Four pericentrals and no secondary cortication. Erect axes, once pinnately branched, have alternating laterals every other segment. The non-lateral bearing segments with a prominent 'scar cell' (= reduced lateral initial). No reproductive structures were found.

Comparing this specimen with the literature, it shared with *A. skottsbergii* the once pinnately branched erect axes and the regular distribution of laterals (*cf.* Ardré, 1970). *A. skottsbergii* is known from the eastern South Pacific. The genus *Aphanocladia* appears to be a new record for South Africa.

64 *Apoglossum ruscifolium* (Turner) J. Ag.

65 *Aristothamnion collabens* (Rudolphi) Papenf.

66 *Arthrocardia duthiae* Johansen

67 *Arthrocardia flabellata* (Kuetz.) Manza

68 *Arthrocardia cf. palmata* (Ellis et Solander) Aresch. in J. Ag.

69 *Arthrocardia* sp.

70 **Audouinella endophytica* (Batters) Dixon: New to South Africa and found growing in the cell wall of an unidentified member of the Ceramiaceae (see below). *A. endophytica* is known from the European Atlantic as well as the eastern North Pacific (Garbary, 1987).

71 **Ballia callitricha* (C. Ag.) Kuetz.

72 *Bartoniella crenata* (J. Ag. ex Mazza) Kylin

73 **Bornetia repens* Stegenga

74 **Bostrychia intricata* (Bory) Montagne

75 *Botryocarpa prolifera* Grev.

76 **Callithamnion cordatum* Boerg.

77 *Callophycus densus* (Sonder) Kraft

78 *Carpoblepharis flaccida* (C. Ag.) Kuetz.

79 *Caulacanthus ustulatus* (Turner) Kuetz.

80 *Centroceras clavulatum* (C. Ag. in Kunth) Montagne

81 **Centroceras distichum* Okamura: This species, known from southern Japan (Itono, 1977), was found growing epiphytically on *Amphiroa* sp. and on crustose corallines. It differs from *C. clavulatum* (the only other species of *Centroceras* known from South Africa) in: (i) the prostrate rather than erect habitat; (ii) the alternate rather than dichotomous branching, laterals being formed at intervals of 4 - 6 segments; (iii) the slightly fewer periaxial cells, viz. 8 - 14 rather than the 16 - 20 in South African *C. clavulatum*; (iv) the tetrasporangia being embedded, as opposed to exserted in *C. clavulatum* (*cf.* Stegenga, 1986).

82 Ceramiaceae indet.: A species of as yet uncertain affinities, probably representing a new genus. Thus far only male and tetrasporangial specimens have been found. In external appearance it resembles small species of *Griffithsia* or *Bornetia*, with several erect filaments arising from a prostrate filamentous part. Erect filaments up to 10 mm high, *ca.* 300 μm in diameter and virtually unbranched, though a fascicle of branchlets bearing the reproductive structures is provided at the apex. Tetrasporangia and globose spermatangial heads (on separate plants) in adaxial double rows on the cells of the terminal fascicle, and up to 8 or 10 sporangia or male capitula per cell. No other member of the Ceramiaceae appears to show a similar arrangement of reproductive structures, and its taxonomic affinities can only be established after the study of female reproductive material.

83 *Ceramium capense* Kuetz.

84 *Ceramium centroceratiforme* Simons

85 *Ceramium glanduliferum* Kylin

86 *Ceramium papenfussianum* Simons

87 *Ceramium planum* Kuetz.

88 *Ceramium tenerrimum* (Martens) Okamura

89 *Champia compressa* Harv.

90 *Champia lumbricalis* (Roth) Desvaux

91 *Cheilosporum cultratum* (Harv.) Aresch. in J. Ag.

92 *Cheilosporum sagittatum* (Lamour.) Aresch.

93 *Chondria capensis* (Harv.) Falkenb.

94 *Chylocladia capensis* Harv.

95 **Colaconema caespitosum* (J. Ag.) comb. nov. Jackelman *et al* 1991.

96 **Colaconema daviesii* (Dillw.) Stegenga

97 **Colaconema nemalionis* (De Notaris) Stegenga

98 **Colaconema plumosum* (Drew) Woelkering

99 *Colaconema* sp.: A semi-endophytic species on/in *Anthophycus longifolius.* Plants with a large basal cell immersed in the epidermis of the host, a rhizoidal multicellular endophytic part and two or three short erect filaments that bear the reproductive structures (i.e. monosporangia). The basal cell measures up to 20 x 15 μm, emergent filaments rarely measure longer than 150 μm and 5 - 6 μm in diameter often tapering towards the apex, and the monosporangia (terminal or lateral) measure 13 - 15 x 8 - 10 μm. The endophytic system gives rise to

secondary emergent axes that can be distinguished by the absence of a much enlarged basal cell. The presence of a large basal cell (apparently the persistent original spore) suggests that this species belongs to the gametophytic part of the genus *Colaconema*.

100 **Compsothamnionella sciadophila* Stegenga

101 *Corallina officinalis* L.

102 *Corallina* sp.

201 *Dasya scoparia* Harv. ex J. Ag.

103 *Dasya* sp.

104 **Delesseria papenfussii* Wynne

105 *Delisea flaccida* (Suhr) Papenf.

106 *Epymenia capensis* (J. Ag.) Papenf.

107 *Erythrocladia* sp.: Plants epiphytic on *Cladophora* sp., at first flat discoid becoming pulvinate and forming semiglobose cushions up to 0.5 mm in diameter. In a cross-section of the thallus, the cells are arranged in a monostromatic layer on the periphery of the cushion, the centre of the thallus being mucilaginous and devoid of cells. Cells are radially elongate, 5 - 10 μm in diameter and up to 50 μm long and with a stellate chloroplast. Reproduction is via monospores cut off towards the exterior of the plant by unequal division of vegetative cells. This species is reminiscent of pulvinate species of the genus *Erythrotrichia* (e.g. *E. pulvinata* Gardner and *E. tristanensis* Baardseth), but erect filaments were not observed in this material. It differs from *Erythrocladia polystromatica* Dangeard in being strictly monostromatic.

108 *Erythroglossum* sp.: An as yet undescribed species, also known from the East Cape (Seagrief, 1988).

109 *Falkenbergia rufolanosa* (Harv.) Schmitz in Engler et Prantl

111 *Gelidium abbottiorum* R.E. Norris

112 *Gelidium capense* (Gmelin) Silva

113 *Gelidium pristoides* (Turner) Kuetz.

114 **Gelidium pteridifolium* Norris, Hommersand et Fredericq

115 *Gelidium cf. reptans* (Suhr) Kylin

116 *Gigartina bracteata* (Gmelin) Setch. et Gard.

117 *Gigartina insignis* (Endlicher et Diesing) Schmitz in Barton

118 *Gigartina paxillata* Papenf.

119 *Gigartina pistillata* (S.G. Gmelin) Stackhouse

120 *Gigartina radula* (Esper) J. Ag.

121 *Gigartina scutellata* (Her.) Simons

122 *Gigartina stiriata* (Turner) J. Ag.

123 *Gracilaria capensis* Schmitz ex Mazza

124 *Gracilaria verrucosa* (Huds.) Papenf.

125 **Grateloupia doryphora* (Montagne) Howe: A large foliaceous species with proliferations from the margins, apparently not recognised from South Africa before. Irvine (1983) states that '... foliose plants belonging to the genus *Grateloupia* ... are probably all conspecific with *G. doryphora*.' The morphological variation of the South African material is in actual fact very large and might well include the more familiar *G. longifolia* Kylin.

126 *Grateloupia filicina* (Lamour.) C. Ag.

127 *Grateloupia longifolia* Kylin

128 *Griffithsia confervoides* Suhr

129 **Griffithsia subbiconica* Stegenga

130 *Gymnogongrus glomeratus* J. Ag.

131 *Gymnogongrus polycladus* (Kuetz.) J. Ag.

132 *Helminthocladia papenfussii* Kylin

133 *Helminthora furcellata* (Reinbold apud Tyson) Martin

134 *Heringia mirabilis* (C. Ag.) J. Ag.

135 *Herposiphonia prorepens* (Harv.) Schmitz in Engler

136 *Heterosiphonia crispa* (Suhr) Falkenb.

137 *Heterosiphonia dubia* (Suhr) Falkenb.

138 *Hildenbrandia pachythallos* Dickonson

139 *Hildenbrandia rosea* Kuetz.

140 *Hypnea ecklonii* Suhr

141 *Hypnea spicifera* (Suhr) Harv. in J. Ag.

142 *Iridaea capensis* J. Ag.

143 *Jania adhaerens* Lamour.

144 **Jania capillacea* Harv.

145 *Jania crassa* Lamour.

146 *Jania verrucosa* Lamour.

200 *Jania* sp.

147 *Kallymenia agardhii* R.E. Norris
148 *Kallymenia schizophylla* J. Ag.
149 *Laurencia flexuosa* Kuetz.
150 *Laurencia glomerata* Kuetz.
151 *Laurencia cf. obtusa* (Huds). Lamour.
152 **Lomathamnion capense* Stegenga
153 **Lomathamnion humile* (Kuetz.) Stegenga
154 **Microcladia gloria-spei* Stegenga
155 *Nemastoma lanceolata* J. Ag.
156 *Nienburgia serrata* (Suhr) Papenf.
157 *Nothogenia erinacea* (Turner) Parkinson
158 *Ophidocladus simpliciusculus* (Crouan) Falkenb.
159 *Pachychaeta cryptoclada* Falkenb.
160 *Pachymenia carnosa* (J. Ag.) J. Ag.
161 *Pachymenia cornea* (Kuetz.) Chiang
163 *Peyssonnelia capensis* Montagne
164 *Phyllymenia belangeri* (Bory) Setchell et Gardner
165 *Placophora binderi* (J. Ag.) J. Ag.
166 **Platythamnion cf. capense* Stegenga
167 *Pleonosporium harveyanum* (J. Ag.) De Toni
168 *Plocamium beckeri* Simons
169 *Plocamium corallorhiza* (Turner) Harv. in Hooker et Harv.
170 *Plocamium cornutum* (Turner) Harv.
171 *Plocamium maxillosum* (Poiret) Lamour.
172 *Plocamium rigidum* Bory in Bélanger
173 *Plocamium suhrii* Kuetz.
174 *Pollexfenia laciniata* Harv.
175 *Pollexfenia cf. minuta* (Kylin) Papenf.
176 *Polyopes constrictus* (Turner) J. Ag.
177 *Polysiphonia incompta* Harv.
178 *Polysiphonia urbana* Harv.
179 *Polysiphonia virgata* (C. Ag.) Sprengel
180 *Porphyra capensis* Kuetz.
181 *Pterosiphonia cloiophylla* (C. Ag.) Falkenb. in Schmitz

182 **Pterosiphonia spinifera* (Kuetz.) Norris et Aken: Earlier recognised in Natal (Norris & Aken, 1985), the present record presents a considerable extension of the known range of distribution.

183 *Pterosiphonia* sp.: Thallus compressed and pinnate. Segments with five pericentral cells, developing complete cortication. Material not fertile. Differs from other compressed South African species [*P. cloiophylla* and *P. stangeri* (J. Ag.) Falkenb.] by the laterals being confluent with the main axis for the proximal 6 - 8 segments (2 - 4 segments in the other species). Cortication is more developed than in *P. stangeri*, but only one layer thick, not several as in *P. cloiophylla*.

184 *Rhodophyllis reptans* (Suhr) Papenf.

185 *Rhodomenia natalensis* Kylin

186 **Rhodymenia linearis* J. Ag.

188 *Schizymenia obovata* (J. Ag.) J. Ag.

187 **Scinaia capensis* (Setchell) Huisman

190 *Streblocladia corymbifera* (C. Ag.) Kylin

191 *Stromatocarpus parasiticus* Falkenb. in Engler et Prantl

189 *Suhria vittata* (L.) J. Ag.

192 **Symphyocladia cf. marchantioides* (Harv.) Falkenb.: Sterile material of *S. marchantioides* was earlier reported from Natal (Norris & Aken, 1985). The Hangklip material is of similar habit, but differs from earlier descriptions by the possession of only 5 pericentral cells per segment (6 - 8 in *S. marchantioides* Ardré, 1974). A light cortication is present, developing laterally between adjacent segments, especially on the dorsal side of the thallus. The sample specimen was a fertile tetrasporophyte, showing the typically decoalesced thallus margin and one tetrasporangium per segment.

193 *Tayloriella tenebrosa* (Harv.) Kylin

194 *Thamnophyllis discigera* (J. Ag.) Norris

195 *Trematocarpus flabellatus* (J. Ag.) De Toni

196 *Trematocarpus fragilis* (C. Ag.) De Toni

197 *Wrangelia purpurifera* (Harv.) J. Ag.

INVERTEBRATES

Phylum: Porifera

203 Porifera - sponges

Phylum: Cnidaria

204 Order: Actiniaria - sea anemones

205 Cnidaria (excluding Actiniaria) - soft corals, sea fans, sea fans, etc.

Phylum: Nemertea

221 Nemertea - ribbon worms

Phylum: Sipunculida

206 Sipunculida - peanut worms

Phylum: Annelida

207 Class: Polychaeta - bristle worms

Phylum: Arthropoda

208 Class: Cirripedia - barnacles

209 Orders: Isopoda/Amphipoda - isopods, amphipods

210 Order: Decapoda - prawns, crayfish, crabs

211 Arthropoda (excluding 208, 209 & 210) - sea spiders, tanaids

Phylum: Bryozoa

212 Bryozoa - moss or lace animals

Phylum: Mollusca

213 Class: Polyplacophora - chitons

214 Class: Bivalvia - bivalve molluscs

215 Class: Gastropoda - limpets, sea slugs

Phylum: Echinodermata

216 Class: Asteroidea - starfish

217 Class: Ophiuroidea - brittlestars

218 Class: Crinoidea - feather stars

219 Class: Holothuroidea - sea cucumbers

222 Class: Echinoidea - sea urchins

Phylum: Chordata

220 Subphylum: Tunicata - sea squirts

CHAPTER 3

A MULTIVARIATE ANALYSIS OF THE VARIATION IN PHYTOBENTHIC COMMUNITIES AND ENVIRONMENTAL VECTORS IN A KELP COMMUNITY AT CAPE HANGKLIP

INTRODUCTION

Community ecologists have devoted considerable effort to quantitative analyses of local variation in marine communities and there is substantial literature documenting variability in species composition and structure of kelp forests on small spatial scales, both within and between localities. This variability has been shown to be the result of biological and physical disturbance, competition, and differential recruitment into the constituent populations[3] (see reviews by Dayton 1985a and Schiel & Foster 1986 and regional overviews by Foster 1982, Dayton & Tegner 1984a, Foster & Schiel 1985, Dayton 1985b, Johnson & Mann 1988, Chapman & Johnson 1990, Foster 1990, Underwood & Kennelly 1990).

Despite a considerable volume of literature, the specific *processes* that structure many macroalgal assemblages, and more importantly the interaction between these abiotic and biotic processes, are generally poorly understood in the subtidal zone. This is because of the complexity of the interactions, the lack of suitable numerical techniques to elucidate this complexity and the general inaccessibility of the habitat.

Studies from kelp beds around the world highlight the large variability in the structure of sublittoral algal assemblages but reveal a considerable discrepancy in views concerning organizational processes and conditions under which they operate (see Chapter 1). Foster (1990) suggests that there are still too few studies that have quantitatively assessed the abundance of kelps and associated species along the complete depth gradient over which they occur to adequately understand the interaction between organizational processes.

---

[3] *The term* ***physical and biological disturbance*** *is generally considered in the reviewed literature as an event - extrinsic or intrinsic - which results in the removal of biomass or individuals and consequently directly or indirectly creates opportunities for the establishment of new individuals (Sousa 1984).* ***Competition*** *is generally defined as the simultaneous use by two or more individuals or species of some limiting resource in short supply (Paine 1990). The term* ***recruitment*** *is generally considered for all transitions in the life history of an organism (see Vadas et al, 1992).*

With a few exceptions, most of the quantitative and qualitative research in kelp beds has suggested that grazing in subtidal habitats is a major organizer of structure, composition, diversity and patchiness of assemblages. This, as suggested by Underwood and Fairweather (1986), probably reflects the "predilections and preoccupations" of current ecologists rather than the ecologies of the plant communities. More recent research findings indicate that the generalization that grazing is the be-all and end-all of relevant processes, is unfounded. Several abiotic and biotic factors have been shown to shape the local distribution of benthic seaweeds, with light generally considered as having the most important direct effect (Lobban *et al* 1985, Lüning 1990). The complex fluid dynamics resulting from the interaction of water motion with depth and the topographic characteristics of substratum also have an important effect on the physical stress acting on plants (Vogel 1981, Koehl 1986), on the assimilation of nutrients and on the settling and development of algal spores (Lobban *et al* 1985, Lüning 1990). Another major process considered to determine the patterns of distribution and abundance of algal species is intra- and interspecific competition (Paine 1990). Physical processes such as sand scour and burial have generally been ignored as factors likely to affect the structure of subtidal benthic communities.

A synthesis of contemporary research in kelp beds around the world emphasizes the multi-dimensional nature of the disturbance phenomenon. As Ricklefs (1987) demonstrated in the terrestrial environment, community structure and patterns of species diversity in kelp beds probably represent large-scale specific histories, local and geographical dispersal patterns and dispersal history, and local processes such as predation, competitive exclusion, and stochastic variation. This mosaic is superimposed over physical processes that influence the biota in many ways. The implication of this dynamic nature of community structure is that most natural communities exist in a non-equilibrium condition and that their structure is determined by an array of historical events as well as changing physical and biological processes (Dayton *et al* 1992).

The causal mechanisms that determine patterns of species distribution will only be detected by experimentation (Underwood 1986) but efficient design of experiments will require extensive preliminary analyses of observational data. Numerical descriptive studies play an important role in determining which hypotheses to test experimentally (James and McCulloch 1990, Santos 1993). To date, field correlations and laboratory studies have typically provided single factor explanations outlining the general relationships between abiotic and biotic environment and stand abundance, but the effects of interactions between these are largely unknown. Multivariate methods have been widely used in vegetation science to expose trends and patterns of co-distribution of species and environmental factors, and to generate hypotheses of community-environment interactions (Gauch 1982, Greig-Smith 1983, Ter Braak 1987), but marine ecologists have not used these numerical methods very extensively (Kautsky and van der Maarel 1990, Santos 1993). Various programs developed and applied with success by terrestrial ecologists have hardly been tried on marine benthos, notably canonical correspondence analysis (Ter Braak 1986, 1987). Applications of numerical methods to the study of biotic and environmental relationships in phytobenthic communities were carried out early by Neushul (1967) who related clusters of similar seaweed species to depth and substrate type along transects. Lindstrom and Foreman (1978) analysed the seaweed communities of British Columbia, Canada to determine major environmental factors related with species composition. Kautsky and van der Maarel (1990) correlated environmental factors of the Baltic sea, such as depth, bottom type, slope, wave exposure and amount of sediment on the bottom, with the patterns of species distribution. More recently Santos (1993) investigated distribution patterns of dominant macrophytes from a commercial stand of *Gelidium sesquipedale* in Portugal, in relation to local abiotic conditions such as depth, sediment loading and substrate topography.

Much of the quantitative and experimental work in kelp beds has concentrated on the large laminarian and fucoid species and the dominant animal herbivores and predators. There is a paucity of information on the structure of the sub-canopy algal and invertebrate components and the physical and biotic factors affecting this community structure. Only a few studies have investigated the nature and dynamics of this sorely neglected habitat (eg. Foster 1982, Dayton et al 1984, Santelices & Ojeda 1984b, Kennelly 1987a, Miles & Meslow 1990, Duggins *et al* 1990).

It is also evident that different research scales result in different ecological patterns being identified (Menge and Olson 1990). Terrestrial biogeographers have long stressed that plants and animals are not distributed evenly or randomly in nature, but are aggregated in patches of varying size, or form gradients or other kinds of functional spatial structures (Wiens 1976, Myers and Giller 1988, Legendre and Fortrin 1989, Kitching and Beaver 1990). Natural communities are generally considered as an aggregate of patches and guilds within which there are strong biological interactions. The nature of these biological interactions varies considerably, and within a patch or guild the interactions often determine the local structure. The large-scale or community structure however is determined by the aggregate of the seperate patch dynamics, by the types of interactions between the patches and especially by the physical regimes that strongly influence so many of these relationships. Because of the apparent unpredictability at the smaller scale, researchers in the subtidal benthic environment have concentrated on the more robust general pattern at a larger scale. In a recent review, Dayton *et al* (1992) consider large-scale (both spatial and temporal) abiotic factors as defining broad patterns of distribution. They suggest that, within these coarse distributional patterns, other processes, operating at smaller temporal and spatial scales, modify distributions and abundances of plant and animal species. At these smaller scales organizational processes may be biotic, abiotic or involve interactions between the two. Many of these organizational processes will operate at a range of scales but have different influences at each scale.

My main questions in this chapter are:

1) To what extent can benthic communities (i.e. discrete combinations of benthic organisms) in a kelp bed at Cape Hangklip, be distinguished and which environmental settings do such communities have?
2) To what extent and in what combinations do these environmental factors affect the distribution of kelp understorey phyto- and zoobenthos?
3) Are these discrete combinations of benthic organisms still distinguishable at a very localized level and are the organizing processes the same?

Based on the assumption that the structure of the biota of the kelp understorey is an indication of the community organizational procedures and that estimates of relative distribution and abundance of species define among-area patterns, this chapter quantifies seasonally, and along a depth and wave action gradient;

- the diversity, abundance and biomass of the macroalgal understorey;
- the biomass and abundance of associated animals;
- sand cover, substrate topography, turbidity, water movement and temperature.

Using ordination and numerical classification techniques spatial patterns at different patch sizes are identified and correlated with environmental factors.

METHODS

Study site

The study site was located along a five kilometre stretch of coastline in the Cape Hangklip area, an area forming the south-eastern limit of False Bay in the Western Cape, South Africa (see Figure 2.1 and Figure 3.1). A general description of the intertidal and subtidal communities in the Hangklip area and a detailed list of the intertidal and subtidal macroalgal species and their phytogeographical affinities is found in Chapter 2. Four study transects around the outlying promontory were subjectively selected (see Figure 3.1), each having different combinations of environmental factors (ie. combinations of wave action, temperature, turbidity, kelp density, sand cover, substrate, human impacts, sessile invertebrate cover and density and aspect). Table 3.1 summarizes preliminary observations of the physical features of the respective study transects (transects 1-4).

For the purpose of this study, the kelp understorey was defined as the plant and invertebrate animal community occupying available space immediately below the primary blade canopy of *Ecklonia maxima* and sub-canopy of *Laminaria pallida*. Young plants of *E. maxima* and *L. pallida* below the sub-canopy layer were considered as understorey plants. Although holdfasts of adult laminarians were cleared of attached plant and animal species, the holdfasts were left intact and not considered part of the understorey.

Table 3.1 Preliminary observations of the physical characteristics of the survey transects (Transects 1-4).

Exposure	
1	Relatively protected from prevailing south to south-west swell direction. Large swells of 1-2m only intermittently observed during winter storms.
2	Full exposure to wave action throughout the year. Swells frequently exceed 3m.
3	Exposed to prevailing south to south-west swell during the winter months. Large swells of up to 3m common during winter storms.
4	Large swells of 1-2 metres common during winter storms.

Turbidity

1 High water motion disturbs both the nearshore sediments and drift algal material which collects in the bay and produces generally turbid water during much of winter and occasionally in summer.
2 Diver observations indicate long periods of relatively clean water, though high water motion occasionally produces turbid conditions.
3 & 4 Winter storms may cause turbid conditions to prevail for anything up to three weeks. Relatively clear conditions persist during summer.

***Sand* deposition and scour**

1 A striking feature of the site is the high sand deposition during the summer months from a depth of 3.5m down, with the understorey incapable of persisting beyond 9.5m depth. During winter storms, much of this sand is suspended in the water column and contributes to a "scouring effect".
2 Generally free of sand throughout the year although gulleys running parallel to the shore may intermittently collect sand.
3 Low sand deposition during summer months. Transect is generally free of sand during the winter months.
4 No sand in shallow water but moderate sand deposition in the deeper water during the summer months. Transect is generally free of sand during the winter months.

Substrate

1 Loose boulders in shallow water give way to rocky shelves of Table Mountain Sandstone which are seasonally covered in sand.
2 Weathered sandstone often forms jagged, submerged pinnacles running parallel to the shore with troughs typically filled with large and small boulders and cobbles. Large boulders in deep water.
3 Relatively flat Table Mountain Sandstone (TMS) in shallow water. Rocky shelves in deeper water.
4 Rocky shelves interspersed with loose cobbles, boulders and sand.

Nature of the *E. maxima* overstorey (see Figure 3.1)

1 A relatively narrow coastal belt, homogenous in cover and regular in size and distribution pattern.
2 Dense, large, homogenous stand often having an apparent dampening effect on large winter swells.
3 & 4 Patchy but dense distribution.

Human impact

1 None
2 Non-commercial harvesting of abalone, Cape turban shell and crayfish.
3 Commercial harvesting of abalone and non-commercial harvesting of abalone and crayfish.
4 Commercial harvesting of abalone and non-commercial harvesting of abalone, mussels and crayfish.

Figure 3.1 An aerial view of the study site at Cape Hangklip showing the locality of the four transects (1-4).

Transect Descriptions

Physical parameters

To estimate water movement near the substrate, the dissolution rates of uniform, pre-weighed gypsum blocks measuring 200 x 70 x 30mm, attached by stainless steel bolts to the substrate, were measured. Eckman *et al* (1989) suggests that dissolution of gypsum ($CaSo_4$ $2H_2O$) in seawater is a transport-limited process and showed that gypsum flux closely mirrored results of current speed (measured with a current-meter). Gypsum flux has been shown to provide a reasonable analog measure of shear and fluid transport near the bottom. The dissolution rate of each slab was converted to an estimate of gypsum flux using a model proposed by Eckman *et al* (1989) that accounts for the time-dependent surface area of slabs:

$$\Delta M_t = 2F_m c_4 t(x_{li}^2 + \frac{2F_m c_4 t x_{li}}{3pc_2c_3} + \frac{4F_m^2 c_4^2 t^2}{27p^2 c_2^2 c_3^2})$$

ΔM_t = observed change in mass over time

F_m = time and area averaged gypsum flux during dissolution period = weight loss (area x $time^{-1}$)

t = time interval (time of immersion)

c_2, c_3 & c_4 = constants ($c_2 = x_2/x_1$; $c_3 = x_3/x_1$; $c_4 = c_2+c_3+c_2c_3$)

x_1 = length of gypsum block

x_2 = breadth of gypsum block

x_3 = height of gypsum block

p = density of gypsum

X_{li} = initial length of gypsum block

Four replicates at each depth range (shallow, intermediate and deep) at the study transects were placed in winter of 1989 (June 1989, July 1989, August 1989) and summer of 1989/1990 (December 1989, January 1990 and February 1990) for 2-5 days of each month. The gypsum blocks were placed on topographically similar substrate (flat Table Mountain Sandstone) at all transects and depth zones. Methods of sampling closely followed those of Eckman *et al* (1989).

Daily surface temperature recordings and subjective estimates of turbidity and swell height were made at each transect through the six months during which water movement was measured.

Turbidity was subjectively assessed on a scale of 1-10 (turbid-clear). Extreme turbid conditions were subjectively considered to be < 1m visibility and extreme clear conditions to be > 30m visibility.

Surface temperature was measured at 1m depth adjacent to the line transects using a hand-held mercury thermometer. Temperature measurements at 8m depth, were provided by the Sea Fisheries Research Institute, from continuous mechanical temperature recorders (Thermoscript by Goerz) bolted to concrete anchors placed on the sea bottom at Bettys Bay.

Line Transects

Line transects were used to determine the distribution, abundance and size classes of large plants and animals down depth gradients, using SCUBA. Line transects, running perpendicular to the shore, were marked by a 30m long leaded orange polyethylene rope which acted as a reference line and was moved as required. The substratum profile, type and depth, at 20m intervals along the leaded line, was recorded on a plastic underwater writing sheet. Numbers and size categories (large = adult plants; medium = sub-adult plants and small = juveniles) of canopy (*Ecklonia maxima*) and sub-canopy (*Laminaria pallida*) kelp plants in a 5 x 5 m quadrat, centred on the transect line at 50m increments, were measured. Along each 20m interval of the line transect, mean density of *Parechinus angulosus* and *Haliotis midae* in ten randomly distributed 1m^2 quadrats was measured. Line transects ran from the immediate subtidal to the seaward edge of the *Ecklonia maxima* overstorey (generally 10-12m depth and 180-570m from the shore, depending on the depth profile). One line transect was placed at each locality (see Figure 3.1). Attempts were made to site line transects objectively, but local conditions of surge and exposure often controlled the selection. Line transects were removed after each working dive as large swells ripped the line up and caused considerable damage to large kelp plants if lines were left *in situ*. Each transect line was marked by three sub-surface buoys secured to stainless steel concrete bolts drilled into the substrate. Stainless steel bolts with luminescent marker ties at 10m intervals along the transect line were attached with quick set epoxy putty for more accurate relocation of the line.

Depth Stratified Quadrat Sampling

To identify bathymetric, seasonal and spatial variation in understorey macroalgal and sessile invertebrate species distribution, stratified random quadrats, along the length of the line transects, were used. Twenty random quadrat samples (10 summer, 10 winter) of 0.5m x 0.5m were collected within each of three depth ranges (subjectively divided into 0.5 - 4m = shallow; 4 - 8m = mid-depth; 8 - 12m = deep) at the four localities, to give a replicated measure of wet biomass and canopy cover. It was decided to measure projected canopy cover as a measure of abundance since many of the subtidal species in this study were difficult to identify as separate individuals (eg. *Caulerpa holmesiana*, *Hypnea spicifera, Jania* spp.) and past demographic studies have commonly failed to emphasize the importance of species which persist by clonal expansion. All macroinvertebrates and macroalgae found within the quadrat were removed from the substrate with the aid of a scraper and manually collected and deposited in mesh bags of 1-2mm mesh size. Prior to removal, percentage canopy cover of the visible macroalgae and invertebrate species was estimated by recording projected canopy cover (PCC) of taxa from the different vegetational strata. Water motion occasionally moved the blades of a number of algal species back and forth over a point. These species were noted as being over the point, even if their presence was intermittent. In a few instances (17 quadrat samples) rough conditions prevented accurate estimation of PCC. For these samples a grid was placed over individual species in a 0.25m^2 plastic tray *ex situ* and a rough estimate made of projected canopy cover (+ indicates presence; 1-5%; 6-10%; 11-25%; 26-50%; 51-75%; >76% for both *in* and *ex situ* estimation). All sampled organisms were placed in labelled plastic bags, fixed in a 5% formalin-seawater mixture or deep-frozen (-25^0 C), and transported to the laboratory for analysis. In the laboratory, the macroalgae were sorted, identified to the lowest taxon possible, usually to species, and weighed to the nearest 0.1g. Sessile invertebrates were identified to phylum, sub-phylum, class or order where feasible. Common large invertebrates were identified to species.

For each destructive quadrat, the following observations were thus made ; (i) number and biomass of urchins (URC), (ii) number and biomass of abalone (ABA), (iii) nature of substrate (sand, gravel, cobble, small boulders, large boulders, consolidated Table Mountain Sandstone and combinations thereof) (SUB), (iv) depth (in metres corrected for tidal state) (DEP), (v) sand cover as a percentage of quadrat area (SAN), (vi) projected canopy cover of kelp overstorey (KCC) (vii) percentage cover of crustose corallines covering occupiable substrate (%CC), (viii) slope angle of the face of the substrate (ie. aspect) ranging from 0^0 horizontal to 90^0 (SLO) (ix) projected canopy cover (phylum, sub-phylum, class or order), biomass (phyla, sub-phylum, class or order), trophic category (phyla, sub-phylum, class, order or species) and number (species) of benthic macroinvertebrates and (x) projected canopy cover and biomass of macroalgal species.

Data analysis

The most accurate and objective data were the biomass values for each of the 240 quadrats, which varied from 55g to 1.6kg wet weight/0.25m^2. All these real data were initially $\log_{10}$ (x +1) transformed before further analysis to compensate for the large variation in biomass and the skewed distribution of data. Despite this transformation, results of the F_{max} test (Sokal and Rohlf 1981) showed that variances of macroalgal and macroinvertebrate biomass were non-homogenous over the spatial, bathymetric and seasonal gradients studied. Van der Maarel (1979) suggests that if the highest scores in a matrix are much higher than the lowest ones, results of any multivariate treatment will be entirely determined by the variation in scores for the one or two dominant species. Jensen and van der Maarel (1980) recommend the use of roughly geometrical scales. A scale with median classes from 1 to 6 with the next upper limit two times the former provided a satisfactory transformation (ie Class 1 = 0 - 60g; Class 2 = 61 - 120g; Class 3 = 121 - 240g; Class 4 = 241 - 480g etc.). Using this transformation, results from the ordination and classification programs were remarkably similar to those where projected canopy cover for species was used in place of biomass. I consider the median classes for projected canopy cover to be a better indicator of plant and community structure, and for ease of interpretation and presentation only projected canopy cover has been presented in the statistical analyses.

The objective of the statistical analysis was three-fold:-

- to summarise plant and animal community data and provide an indication of the true nature of variation within the kelp understorey;
- to provide summaries of variation within sets of vegetation samples which can then be correlated with environmental variables to determine environmental gradients; and
- to formulate ideas about plant community structure as well as possible **causal** relationships between variation in the biotic composition and it's environment.

Figure 3.2 summarises the hierarchical approach of this study to the statistical classification and ordering of the species and environmental data collected. Statistical techniques have been selected to first analyse the species and environmental data independently. This then facilitates interpretation of the ordination and correlation analysis of the direct relationship between species and the environmental variables.

Invariably a variety of techniques for statistical classification and ordering will yield similar results. Where results appear to be of no additional help in further explaining community structure, these will not be presented or discussed further in the results section.

For ease of data presentation the depth gradient was subjectively divided into approximately three equal depth ranges - shallow (0.4m - 4m), intermediate (4 - 8m) and deep water (8 - 12m). The existence of different depth zones based on the community structure is discussed later.

Classification:

Methods of numerical classification, like methods of ordination, are techniques for data reduction and data exploration. A classification analysis TWINSPAN (Two-way-indicator-species-analysis; Cornell Ecological Programs 41; Hill 1979) was used to group a set of quadrats into classes on the basis of their floristic composition. TWINSPAN employs the idea of the pseudospecies, whereby the presence of a species at different predetermined levels of abundance is used (Hill 1979). The abundance of a species is then used in presence/absence form to make the classification. The explanations of the workings of TWINSPAN are fairly complex (see Kent & Coker 1992). However, the final sorted two-way table is relatively straightforward and is very easily understood. In this analysis, rarer pseudospecies are downweighted in the reciprocal averaging ordination. This is done to avoid sets of similar rare species splitting off small groups of quadrats at an early stage of the classification. One of the major shortcomings of TWINSPAN is that species which are rare and moreover occur in species-poor samples, will determine the arrangement of samples. The program's default options were otherwise used.

Ordination

For the **environmental data** an indirect ordination method, principal component analysis (PCA), was used to produce an ordination of quadrats based on environmental variables alone. The basic idea of PCA is that if data are collected to form a matrix of n quadrats and m environmental variables, there will be a large amount of duplication or correlation in the variability of the environmental variables across the quadrats. Thus an original data matrix of, for example, 100 quadrats and 50 variables can be reduced to 100 quadrats and 5 or even fewer components. These components can be regarded as "super variables", made up of highly correlated combinations of the original 50 environmental variables (Kent & Coker, 1992). These components are however unrelated. In the new component matrix each quadrat has a score for each component which taken together are known as the component scores. The core of any PCA are the eigenvectors (represents the weighting of each of the original variables on each component and are ranged from +1 to -1; the furthest away from zero, the more important the variable in terms of weighting that component) and eigenvalues (values that represent the relative contribution of each component to the explanation of the total variation in the data). In most ecological applications, data are analysed using centred and standardized PCA. This option was employed using the FORTRAN program CANOCO (Ter Braak, 1987) to provide a correlation coefficient between samples. Great care however should be taken in the interpretation of correlation coefficients (see also for Spearmans Rank Correlation referred to later). A significant result does not mean that there is a causal relationship between the variables. Rather than one causing variation in the other, it is more realistic to talk of these variables "varying together" rather than a one-way causal relationship (see Legendre & Fortin 1989).

For the **species data**, an indirect ordination of the quadrats (Detrended Correspondence Analysis - DCA) was used to analyse the floristic data independently of any preconceived notions of controlling environmental factors. The DCA is used on the same set of data in order to examine patterns and to search for group structure. The concern here is with the internal variability of the data and the assumption is made that examination of variability in floristics will inevitably reflect variation in environment.

Using the indirect ordination method of DCA, the similarity or dissimilarity of floristic composition of the quadrats was examined. In simple terms, the similarity or dissimilarity is expressed in graph form with plots of points in n dimensions, where each point represents a quadrat. The distances between the points on the graph are taken as a measure of their degree of similarity or difference. Points which are close together will represent quadrats that are similar in species composition; the further apart any two points are, the more dissimilar or different the quadrats will be. As a general rule, the axes of the ordination come out in descending order of importance. In this analysis, outliers (individual quadrats that are well separated from the rest of the points on the ordination diagram - hence very different in species composition) are removed for easier interpretation. Removal of the "arch effect" by DCA involves what is known as detrending. Detrending-by-polynomials is a more stable method of detrending (Ter Braak 1987) and, because initial data investigation revealed a strong dominant first gradient, the axes were detrended by fourth-order polynomials. The DCA analysis was done using the FORTRAN computer program CANOCO (Ter Braak 1987)

Since the results of PCA and DCA appeared to be of no additional help in further examining the groupings identified by TWINSPAN and CCA (see below), these programs will not be further discussed in the main results.

To **jointly analyse directly the species data table and the environmental data matrix**, canonical correspondence analysis (CCA), using the computer program CANOCO (Ver. 2.1; ter Braak 1987), was applied. Instead of relying on *a posteriori* correlations to associate environmental characteristics to species ordination axes ("indirect gradient analysis" - ter Braak 1987), there are ways of jointly analysing directly a species abundance data table and an environmental data matrix ("direct gradient analysis" - ter Braak 1987). These methods are called canonical ordination and pertain to two families; (a) canonical correlation analysis which preserves the Euclidean distance among points and; (b) Canonical correspondence analysis (CCA) which preserves the Chi-square distance. CCA is used to provide an integrated description of species-environment relationships (ter Braak 1986). Many recent papers on the relationship between species distributions and environmental variables in terrestrial environments have used CCA (eg. Franklin & Merlin 1992, Veblen *et al* 1992). Assuming that species tend to have single-peaked response functions (Gaussian response surfaces) to compound environmental gradients and that these gradients are linear combinations of the environmental variables, restricted CCA selects ordination axes in the light of known environmental variables by imposing the restriction that the axes be linear combinations of environmental variables (Legendre 1990). The ordination diagram of CCA displays points representing species and transects, and vectors representing environmental variables. The biplot summarises the main patterns of variation in community composition as accounted for by the environmental variables and also shows, in an approximate way, the distributions of the species along each environmental variable (ter Braak 1986). The "arch effect" of Hill and Gauch (1980) was not evident in the ordination diagrams generated by CCA and the axes were not detrended. Furthermore, detrending is known to impose a homogenous distribution of scores (of the first two axes) where none exists (Ter Braak 1986). CCA cannot directly cope with nominal variables, so in this analysis the two nominal variables were treated as quantitative (substrate) and ordinal (season - summer = 0/winter = 1). Substrate should ideally have been treated as an ordinal variable, and accordingly transformed into "dummy variables" (ter Braak 1986, 1987) but in this instance, to prevent multicolinearity problems (see Ter Braak 1986) substrate categories were treated as intermediaries between 100% Table Mountain Sandstone (TMS) and 100% sand.

TABLE 3.2 Variable conversion for Cornell Condensed Format in CANOCO

Environmental variable	Measurement scale*	Value
Depth (DEP)	Interval	in metres corrected for tidal state
Urchin (URC)	Ratio	number
Abalone (ABA)	Ratio	number
Substrate (SUB)	Nominal	complex of substrate type
Kelp canopy cover (KCC)	Ordinal	Braun-Blanquet cover scale
Angle of slope (SLO)	Ordinal	Scale of 1 - 10 where 0° - 10° = 1; 11° - 20° = 2 etc
Sand cover (SAN)	Ordinal	Braun-Blanquet cover scale
Cover of crustose corallines (%CC)	Ordinal	Braun-Blanquet cover scale
Season (SEA)	Nominal	Summer(1) \ Winter(2)

* Nominal scale = values which have no relation to each other; Ordinal scale = rank order between the values or classes; Interval scale = constant unit of measurement but position of zero point is arbitrary; Ratio scale = like an interval scale but with a fixed zero point.

In the analysis weighted mean species scores were used, crustose coralline canopy cover and season were covariables, six anomalous samples were omitted, 17 rare species were made passive and preferential species identified by the TWINSPAN analysis were made active species (weight=2).

CCA in CANOCO assumes that the species distributions are either unimodal or linear with respect to the environmental variables but in a complex community such as this there is probably a wide range of species responses and any assumption is unlikely to be true for all species. In the ordination diagram of CCA;

(a) the joint plot of species points, quadrats and environmental arrows is a biplot that approximates the weighted averages of each of the species and quadrats with respect to each of the environmental variables;

(b) vectors indicate the direction of maximum change of a transect variable;

(c) the length of the vector indicates the strength of correlation with ordination axes;
(d) each arrow representing an environmental variable determines a direction or axis in the diagram and species points can be projected on to this axis ;
(e) small angles between arrows indicate a positive correlation between those variables, arrows pointing in opposite directions reflect a high negative correlation and arrows meeting at right angles suggest a correlation near to zero and;
(f) projection of the species position in the biplot onto the arrow of an environmental variable using a line perpendicular to the arrow allows an assessment of the relation between a species and the environmental variable.
(see ter Braak 1986)

The Monte Carlo permutation test was carried out using CANOCO. The sample numbers in the environmental data were randomly permutated (in this analysis 20 permutations were used) and the environmental data are then randomly linked to the species data giving rise to a "random data set". For each random data set, CANOCO calculates one or two test statistics, namely for the first eigenvalue and/or the sum of all eigenvalues (= the trace). If the species react to the current environmental variables, then the test statistic calculated from the data-as-observed will be larger than most of the test statistics calculated from the random data. The test of significance ($p<0.05$) was calculated for the first two ordination axes.

To examine the within-transect spatial patterns and their correlated environmental factors, CCA was applied to the sub-sets of the larger database relating to each transect. The objective was thus to see if the species and sample correlations with the environmental variables were transect-specific or reflected similar variation to that indicated at the between-transect scale of investigation.

An important practical shortcoming of CCA is that species that are unrelated to the ordination axes tend to be placed in the center of the ordination diagram and are not distinguished from species that have true optima there. Ordination can be used in conjunction with clustering, and in particular with hierarchical clustering, to help divide what is the most informative partition (cutting level) in a dendrogram. The CCA ordination diagram was thus plotted in conjunction with results of the TWINSPAN output.

Species richness and correlation analysis

Species richness is an appropriate measure of **alpha diversity** (Peet 1974; Whittaker 1977) and in this chapter is defined simply as the number of species per quadrat. Species diversity consists of two components, viz. species richness (ie. the number of species per unit area) and equitability (or evenness of composition). In this study equitability was however not a given, due to occasional small-scale heterogeneity within a quadrat. Richness was compared at the 0.25m^2 scale (quadrat) and at the local scale (=study area). The former describes point diversity (Whittaker 1977) where species numbers are presumably controlled by biological interactions such as competition. Though the latter is also regarded as a measure of alpha diversity, significant turnover or internal beta diversity (Whittaker 1977) is likely to be associated with habitat heterogeneity at this scale. Species richness data were correlated with a range of abiotic and biotic variables by using Spearmans rank correlation, r_s. Wilson and Schmida's (1984) measure was used to quantify beta diversity along a depth gradient at each transect. Diversity, B, is defined as:

$B = (g_E + 1_E)/2s$

g_E is the number of species gained along the gradient E;

1_E is the number of species lost along E; and

s is the mean sample richness of all samples along the gradient (Wilson and Schmida 1984).

The value of B equals exactly the the number of community changes, or B + 1 distinct communities, along a habitat gradient and thus conforms adequately with the notion of community turnover.

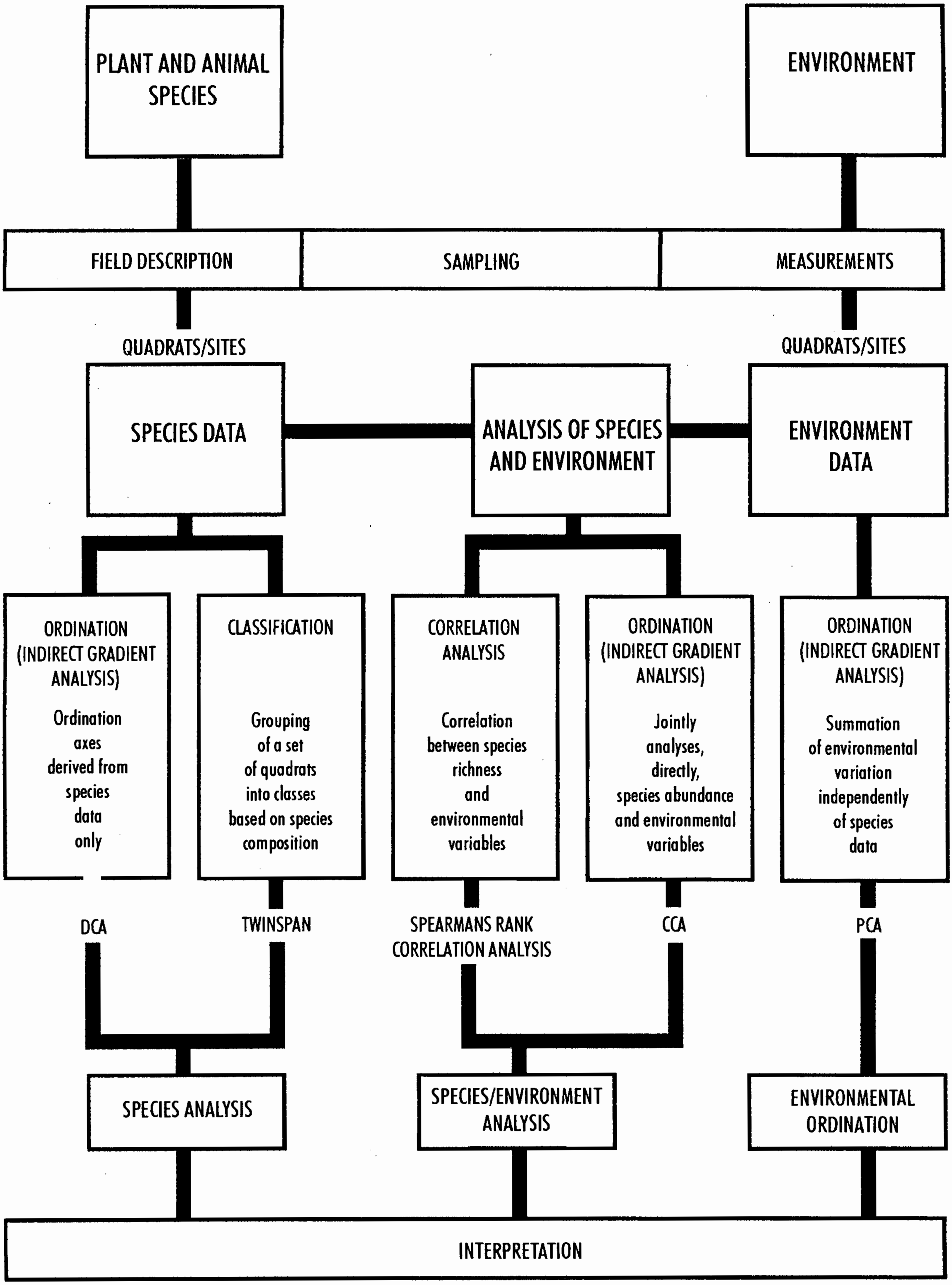


Figure 3.2 Summary of the statistical classification and ordering of the environmental and species data (adapted from Kent & Coker, 1992).

RESULTS

Physical characteristics

Ranking of mean gypsum flux for the four transects corresponded to the subjective wave exposure ranking of the transects (Transect 1 < Transect 4 < Transect 3 < Transect 2). Transect 1 was however the only transect significantly different (one-way ANOVA: $P = 0.03$) from the other transects (Figure 3.3). Mean gypsum flux was in some cases (site 4 shallow, site 2 intermediate) twice as high during winter when compared to the summer results but generally of the order of 1.5. Mean gypsum flux in the shallow water was generally marginally higher than those recorded for the intermediate and deep water zones.

Thermoscript temperature readings (at 8m depth) from Bettys Bay, an area adjacent to the study site, showed a narrow temperature range in winter (June -September) with temperatures generally not exceeding a maximum of 17°C and a minimum of 12°C (Figure 3.4). Temperatures in summer, the peak of the upwelling season, showed greater temperature fluctuations with temperatures ranging from a maximum of 22°C to a minimum of 8°C. The highest maximum temperatures were generally recorded in December-January and the lowest minimum temperatures in March-May.
Local transect-specific surface temperature readings were taken daily over the three months of summer and three months of winter in the vicinity of the line transects to complement the thermoscript readings from Bettys Bay (see Figure 3.5). These results show that the sheltered transect 1 was marginally warmer than all other transects by 0.5° - 3°. Conversely transect 2, the wave exposed transect, was marginally colder than the other transects by the same order of magnitude. Transects 3 and 4, in closer proximity to one another, had similar temperature readings. Transect-specific surface temperature readings showed similar trends to the thermoscript records for Bettys Bay but were generally 1-3°C higher.

Daily subjective assessments of turbidity (on a scale of 1 = turbid to 10 = clear) during the three months of summer and three months of winter indicated that the most turbid conditions generally occurred during winter, most notably at transects 1, 3 and 4 (Figure 3.6).

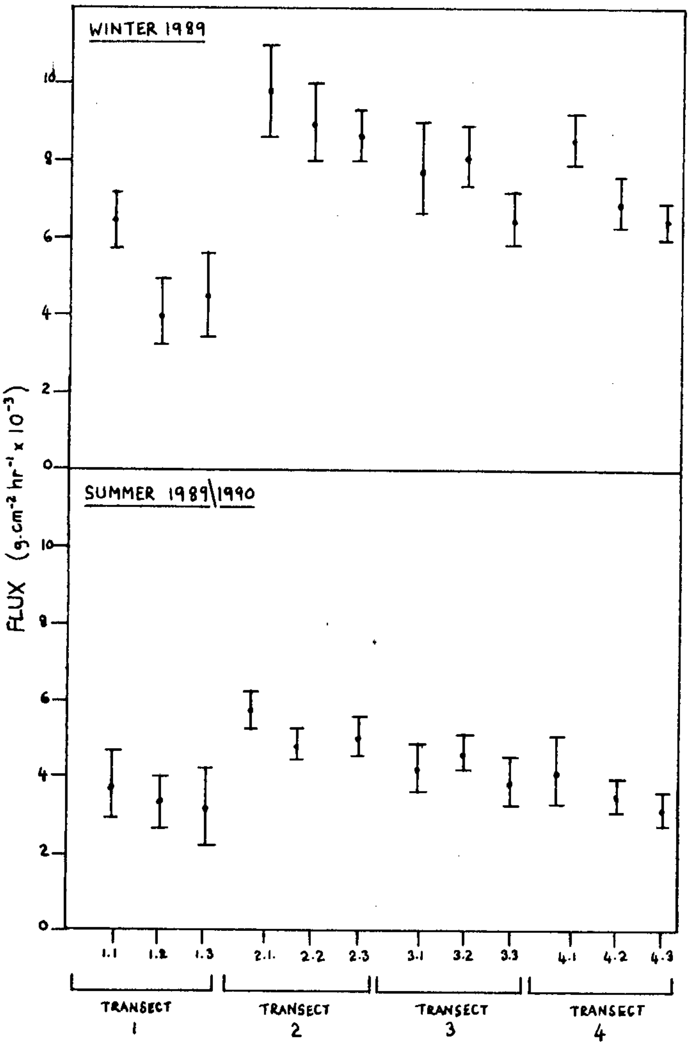


Figure 3.3 Mean gypsum flux at the three depth zones for transects 1-4 in winter and summer. Error bars show ± 2 S.E. from x (n= 12 /depth zone/ season) and x.1 = 0.5 - 4m; x.2 = 4 - 8m and x.3 = 8 - >10m.

Figure 3.4 Thermoscript temperature measurements, from mechanical temperature recorders, for an adjacent site at Bettys Bay for 1986-1989 (data provided by the Sea Fisheries Research Institute).

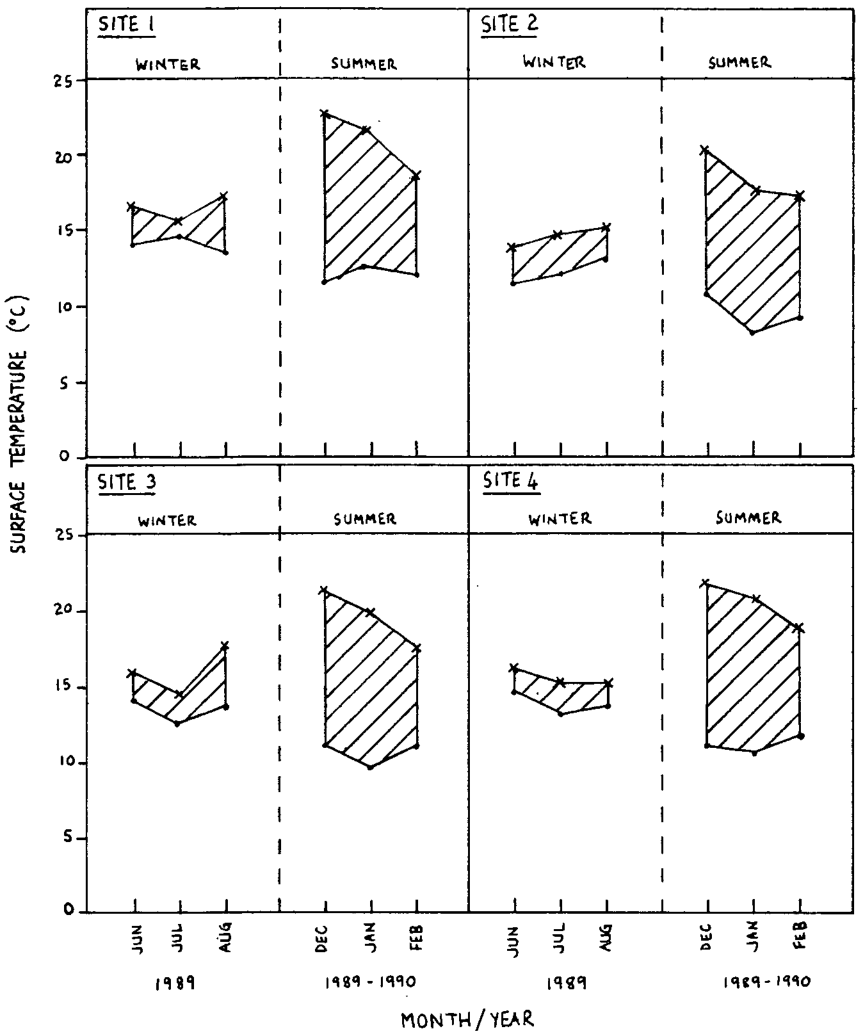


Figure 3.5 Transect-specific surface temperature readings for the three months of winter 1989 (Jun-Aug) and three months of summer 1989/1990 (Dec-Feb).
(· = minimum temperature and x = maximum temperature)

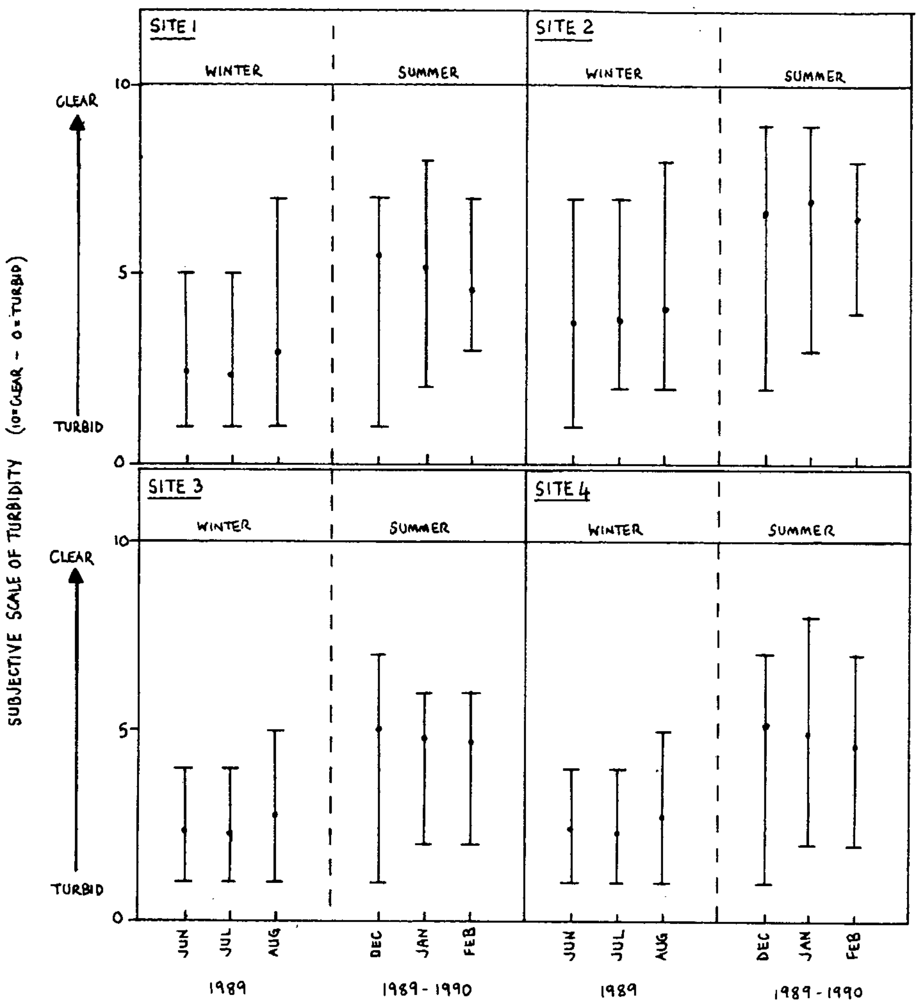


Figure 3.6 Transect-specific turbidity estimates (on a scale of 1 = turbid to 10 = clear) for the three months of winter 1989 (Jun-Aug) and three months of summer (Dec-Feb). Maximum, minimum and mean values are shown.

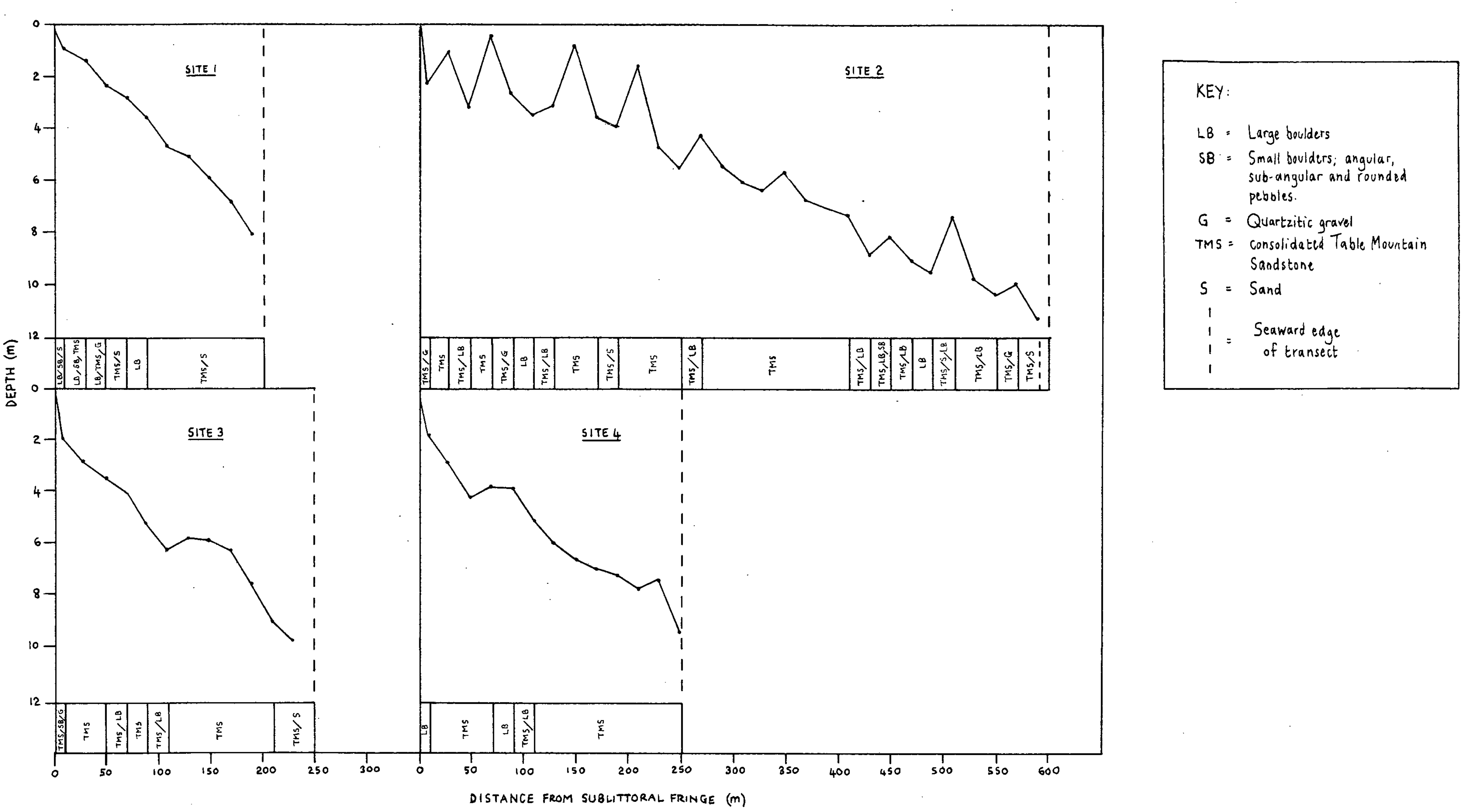


Figure 3.7 Transect-specific changes in substrate with distance from the sublittoral fringe. The associated depth, at 20m intervals, for the four transects is shown.

The clearest conditions generally prevailed during the summer periods, most notably at the exposed transects 1, 2 and 4 during early summer. Transect 3 was generally the most turbid transect throughout both the summer and winter and transect 2 the clearest.

Changes in substrate were transect-specific (Figure 3.7). In the sheltered transect, transect 1, the shallow water (<4m depth) was typified by a composite of stable angular or rounded large boulders, unstable angular, subangular or rounded small boulders and cobbles and quarzitic gravel fragments and consolidated sandstone. The deeper waters were characterised by flat consolidated sandstone overlain with sand. The exposed transect, transect 2, was predominantly consolidated sandstone forming jagged pinnacles with troughs filled with large boulders and quartzitic gravel. Large boulders generally became more prolific in the deeper water (>8m). Transects 3 and 4, the moderately exposed transects, had a typically more homogenous substrate with large patches of well-structured flat and shelved sandstone interspersed with large boulders, quartzitic cobbles and sand.

Floristic and faunistic structure

Major grazers and kelp overstorey

Line transects at the four localities showed a number of features related to distance from the sublittoral fringe (and by association, depth - see Figure 3.7).

Sea urchins (*Parechinus angulosus*) were generally absent beyond 100m from the sublittoral fringe reaching the highest densities at 10 - 40m from the sublittoral fringe, generally 1 - 3m depth (Figure 3.8).

Abalone (*Haliotis midae*) generally persisted, albeit at lower densities, through the whole kelp bed (Figure 3.8). The highest densities of abalone were generally found close to the sublittoral fringe. In the case of the exposed transect, transect 2, abalone occur in moderate numbers on shallow to moderately deep (0.5-5m), exposed, seaward-facing, consolidated rocky substrate considerable distances from the sublittoral fringe.

Urchins in the nearshore zone were generally associated with horizontal flats in the moderately sheltered transects (transects 3 & 4) or boulders in the wave-exposed or sand-scoured transects. Conversely, abalone were strongly associated with vertical or shallow, wave- or swell-exposed consolidated Table Mountain Sandstone (see also Figure 3.7).

Both Laminarian species occurred along the whole profile of the transects (Figure 3.9), but *E. maxima* reached its highest density at intermediate distances from the sublittoral fringe (generally 4-8m depth) whereas *L. pallida* tended to have the highest density at the seaward edge of the kelp bed (generally 7 - >12m depth). At the time of sampling (May/June 1989) Laminarian recruitment was poor and a high proportion (generally > 50-70%) of individuals encountered were adult plants dominating the canopy and sub-canopy (Figure 3.9). Sub-adult and juvenile laminarians were virtually absent in the nearshore transect (generally 0.5-4m depth). The highest number of sub-adult and juvenile *E. maxima* plants were found in the intermediate zone, but a total of only two identifiable[4] juveniles of *L. pallida* were observed along all four line transects. Diver observations indicate that beyond the seaward edge of the kelp beds (>12m depth), numbers of *E. maxima* decrease markedly. In a transect at an adjacent kelp bed at Bettys Bay, Field *et al* (1980) recorded a maximum depth of 15m for *E. maxima*. Concommitant with the decrease of *E. maxima* at the seaward edge of the kelp bed was an increase in the standing crop of *L. pallida*, reaching a maximum depth of 20m (Field *et al*, 1980).

Plant and animal species occurrence and richness, and plant species turnover

Among the 131 seaweed taxa in the data set, 4 species occurred in more than 50% of the quadrat samples - *Plocamium rigidum* (65%), *Amphiroa ephedraea* (> 60%), *Ecklonia maxima* and *Arthrocardia* sp. (> 50%) (Figure 3.10a). Eighteen seaweed taxa occurred in more than 20% of these samples.

The most abundant macroinvertebrates were Gastropoda, Isopoda/Amphipoda and Polychaeta, occurring in more than 75% of the samples, and Porifera occurring in more than 50% of the samples (Figure 3.10b). Of the 20 Phyla, sub-phyla, classes and orders, 14 occurred in more than 10% of the samples.

---

[4] *Very young (< 1 month old) juveniles of E. maxima and L. pallida were difficult to tell apart*

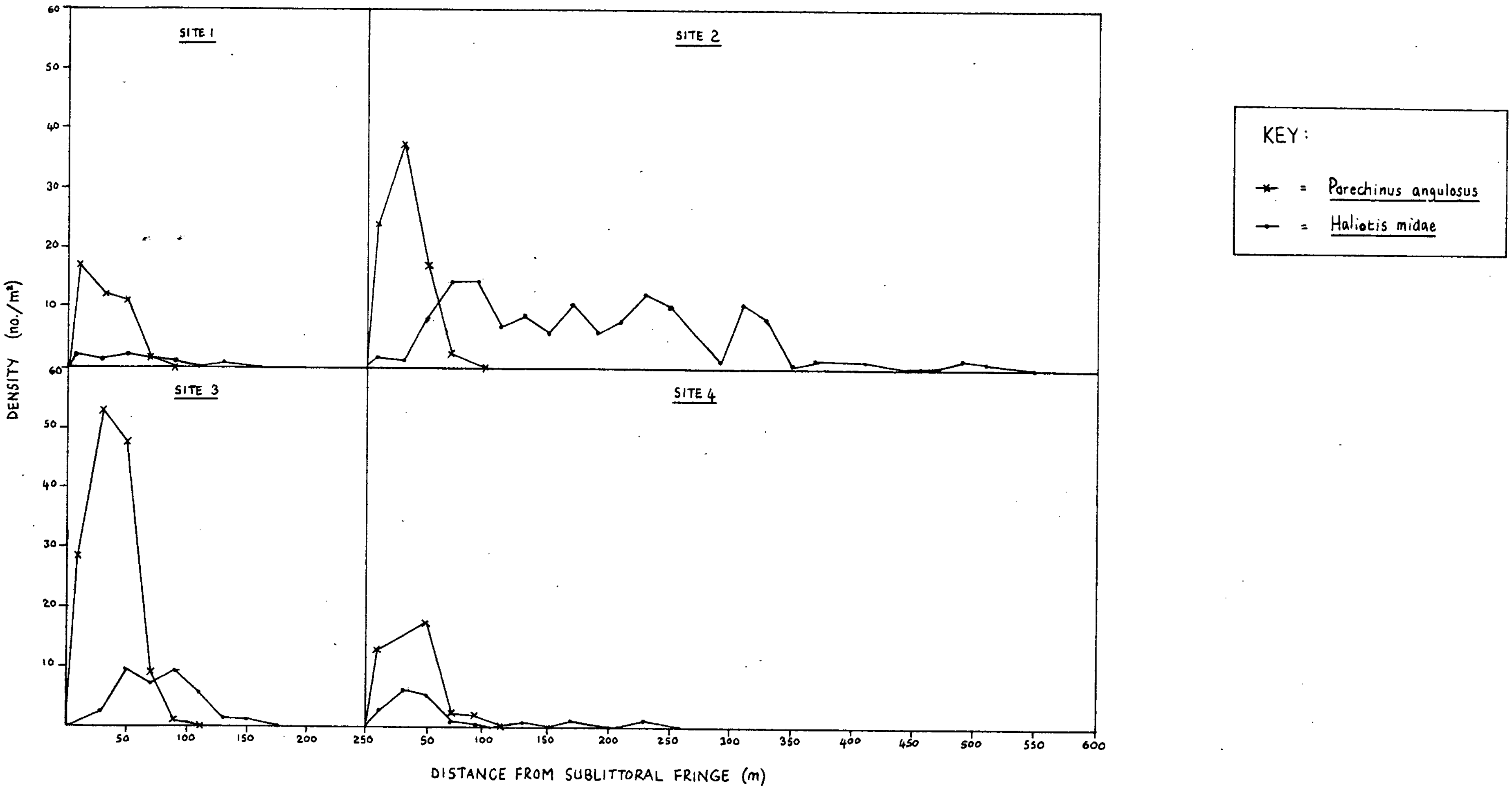


Figure 3.8 Transect-specific distribution and density of sea urchins (*Parechinus angulosus*) and abalone (*Haliotis midae*) at 20m increments.

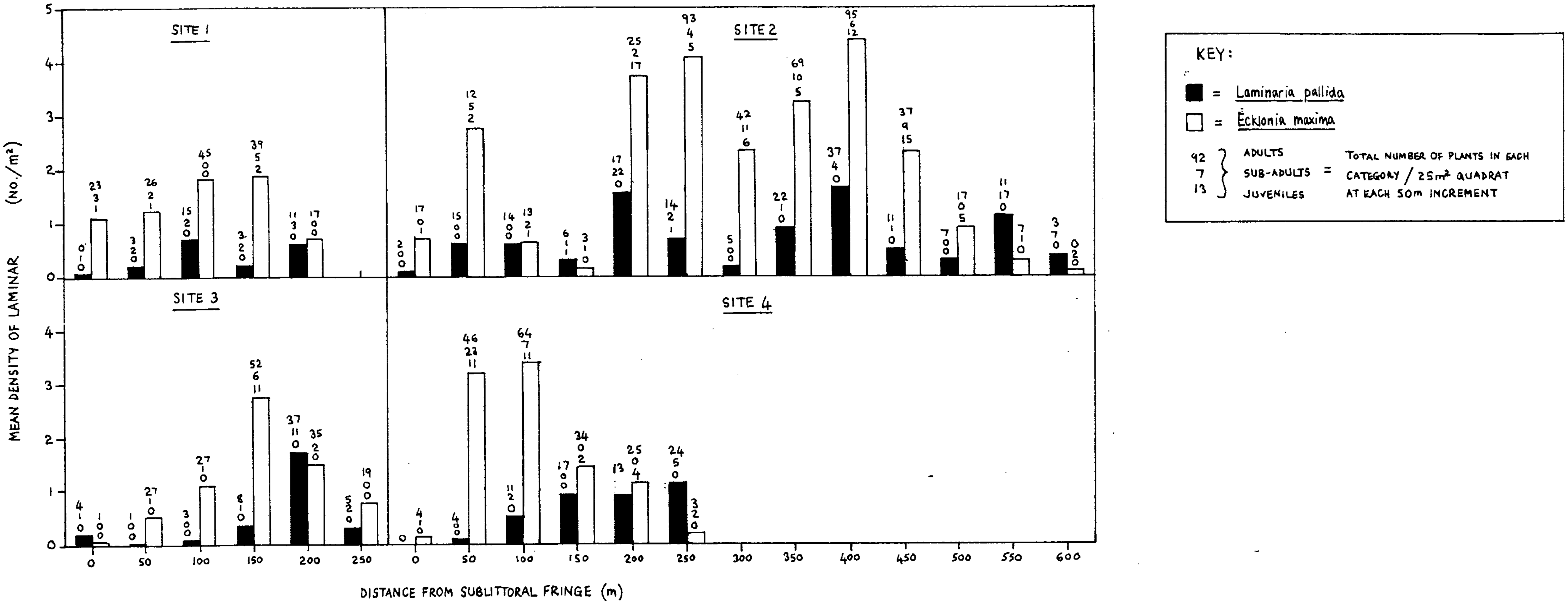


Figure 3.9 Transect-specific distribution and density of the laminarian overstorey (*Ecklonia maxima*) and understorey (*Laminaria pallida*) at 50m increments.

Plant species diversity was substantially higher in the sheltered transect (97 species), transect 1, when compared to the intermediate exposure transects (67 and 57 species) at transects 3 and 4 and the exposed transect (71 species), transect 2. Plant species diversity was extremely high at depths exceeding 4m at the sheltered transect (>64 species at each depth range, up to 28 species/0.25m^2 and a mean of >17 species/0.25m^2 - Table 3.3). The shallow water (<4m depth) in all transects supported the lowest average number of plant species (<9.5 species/0.25m^2).

The average number of animal species was highest in the deep water zone in each respective transect (9.4 - 29.65 species/0.25m^2).

TABLE 3.3 Point diversity at the 0.25m² scale for plant and animal species richness at transects 1-4 and within the three depth ranges (shallow, intermediate and deep).

Transect	PLANT SPECIES			ANIMAL SPECIES	
	TOTAL SPP AT DEPTH ZONE	RANGE/0.25m^2	X (±S.E)/0.25m^2	RANGE/0.25m^2	X(±SE)/0.25m^2
Transect 1.1	38	4 - 18	8.93 (3.49)	4-18	9.3 (3.1)
Transect 1.2	64	12 - 27	18.31 (5.25)	1-22	7.8 (5.2)
Transect 1.3	66	7 - 28	17.08 (6.57)	2-16	9.4 (3.7)
Transect 2.1	41	0 - 16	8.66 (5.00)	3-22	9.3 (3.7)
Transect 2.2	41	11 - 23	16.50 (4.32)	5-18	10.1 (3.2)
Transect 2.3	39	5 - 14	9.53 (2.72)	6-21	11.6 (3.5)
Transect 3.1	44	3 - 18	9.50 (4.36)	4-35	10.3 (7.1)
Transect 3.2	41	3 - 19	11.36 (4.12)	5-16	9.1 (2.9)
Transect 3.3	31	7 - 16	11.06 (2.66)	12-49	29.65 (9.1)
Transect 4.1	28	5 - 11	8.06 (2.08)	4-15	9.5 (2.8)
Transect 4.2	38	5 - 16	11.23 (3.74)	5-21	12.5 (4)
Transect 4.3	38	7 - 20	12.40 (4.38)	4-22	13.8 (6.3)

where: x.1 = 0.5-4m (shallow); x.2 = 4-8m (intermediate); x.3 = >8m (deep)

Turnover between adjacent depths along the entire depth transect for each transect (Table 3.4) were high (0.785 - 0.934) but, because of the nature of the mid-depth range as an intermediary between the shallow and deep water transects, the B values for turnover between individual depth ranges along the depth transect were significantly lower (0.364 - 0.534). There were a large number of species which persisted down the depth gradient.

Table 3.4 Beta turnover both along the entire transects (S-D) and between adjacent depths (S-M/M-D)

Transect	S-D				S-M				M-D			
	CS	SG	SL	BT	CS	SG	SL	BT	CS	SG	SL	BT
Transect 1	42	66	37	0.904	24	40	15	0.534	42	26	22	0.364
Transect 2	21	34	35	0.862	25	16	15	0.383	21	18	20	0.475
Transect 3	22	30	41	0.934	20	21	22	0.518	9	9	19	0.389
Transect 4	25	33	23	0.785	20	19	9	0.412	14	14	14	0.359

Key: S-D = shallow - intermediate depth - deep transect
S-M = adjacent shallow - intermediate depth
M-D = adjacent intermediate depth - deep
CS (common species); SG (species gained); SL (species lost); BT (Wilson & Shmida's [1984] β diversity measure)

Spearmans rank correlation analysis indicated that plant species richness had a strong negative correlation with urchin and abalone density and invertebrate canopy cover (ie. less plant species in areas of high abalone and urchin density and high invertebrate cover) and a strong positive correlation with sand cover (ie. high plant diversity with high sand cover) (Table 3.5). A weak negative correlation between species richness and depth and a weak positive correlation with slope (aspect) was also indicated (ie. low plant species diversity in deeper water and high plant species richness on some steep slopes).

Table 3.5 Rank correlation analysis (Spearmans r_s) between plant species richness $\underline{S}$ and selected variables for all transects (n=240 X 0.25m^2 quadrats)

Variable	S/0.25m^2 r^a	Significance^b
Depth	-0.126	*
No. of urchins	-0.231	**
No. of abalone	-0.215	**
Substrate	-0.021	NS
Sand cover	0.272	**
Projected kelp canopy cover	0.052	NS
Cover of crustose corallines	-0.003	NS
Aspect	0.137	*
Invertebrate canopy cover	-0.216	**

a Read from table B.16 (Zar 1984) using linear interpolation
b NS = P>0.05; * = P<0.05; ** = P<0.01

Biomass

For all transects and quadrat samples, the biomass recorded for the understorey algae and benthic invertebrates was in the range 0.05 - 1.6 kg wet weight/0.25m^2 and 0.06 - 2 kg wet weight/0.25m^2 respectively.

No clear pattern emerged from the data. At a local scale (transects and depth zones), average plant biomass was high in the shallow and intermediate depth zones (<7m) of the sheltered transect, transect 1, and the intermediate depth zone (4-8m) of the exposed transect, transect 2 (Figure 3.11). Conversely average plant biomass was lowest in the deep water (>8m) of transects 2 and 4.

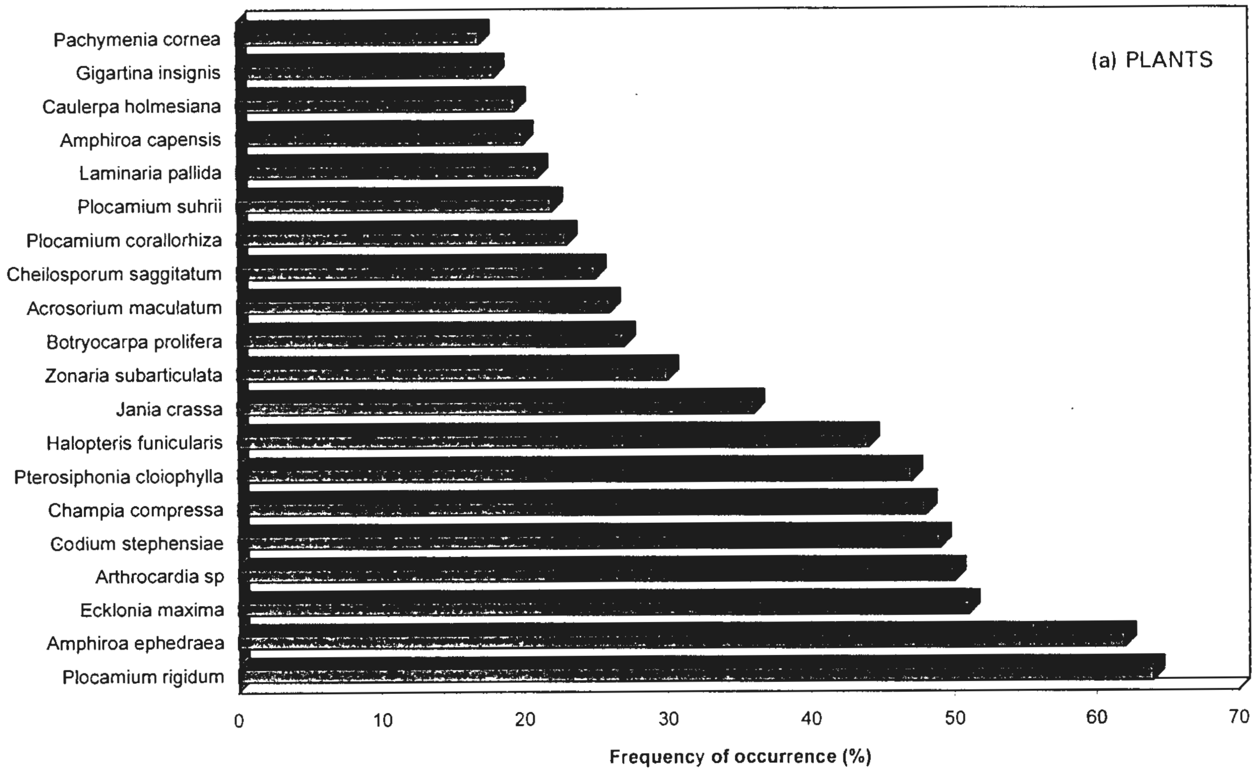
Average animal biomass was highest in the shallow and deep water of transect 3, whereas the intermediate and deep water of the sheltered transect (transect 1), where sand deposition was high, yielded the lowest average animal biomass.

The plant:animal biomass ratio tended towards 1 in the shallow water (0.5-4m) of all transects, 1.4 in the intermediate depths and 0.9 in the deep water.

Community structure

Classification of data

A TWINSPAN run with the option of downweighting rare pseudospecies (17 in this analysis) and six levels of division resulted in a cluster structure with 42 clusters, 6 of which are outlier 1-sample clusters and 7 heterogenous small clusters with 3 or less samples. Most of these outlier and heterogenous clusters are generally compositionally isolated both towards the bigger groupings and towards each other. These outliers and small clusters may reflect the fact that the small-scale heterogeneity of the study area, with it's highly variable and unpredictable environmental parameters, causes multiple solutions of species composition due to chance effects. The remaining 29 clusters however appeared to be optimal in terms of identifying and differentiating taxa and these are presented in Figure 3.12. Six main groups of clusters can be derived from Figure 3.12. These groups can be interpreted in terms of their pseudo-species (note: in the TWINSPAN analysis, an absolute preference score of 1 is assigned to each pseudo-species that is at least three times more frequent on one side of the dichotomy as on the other side):



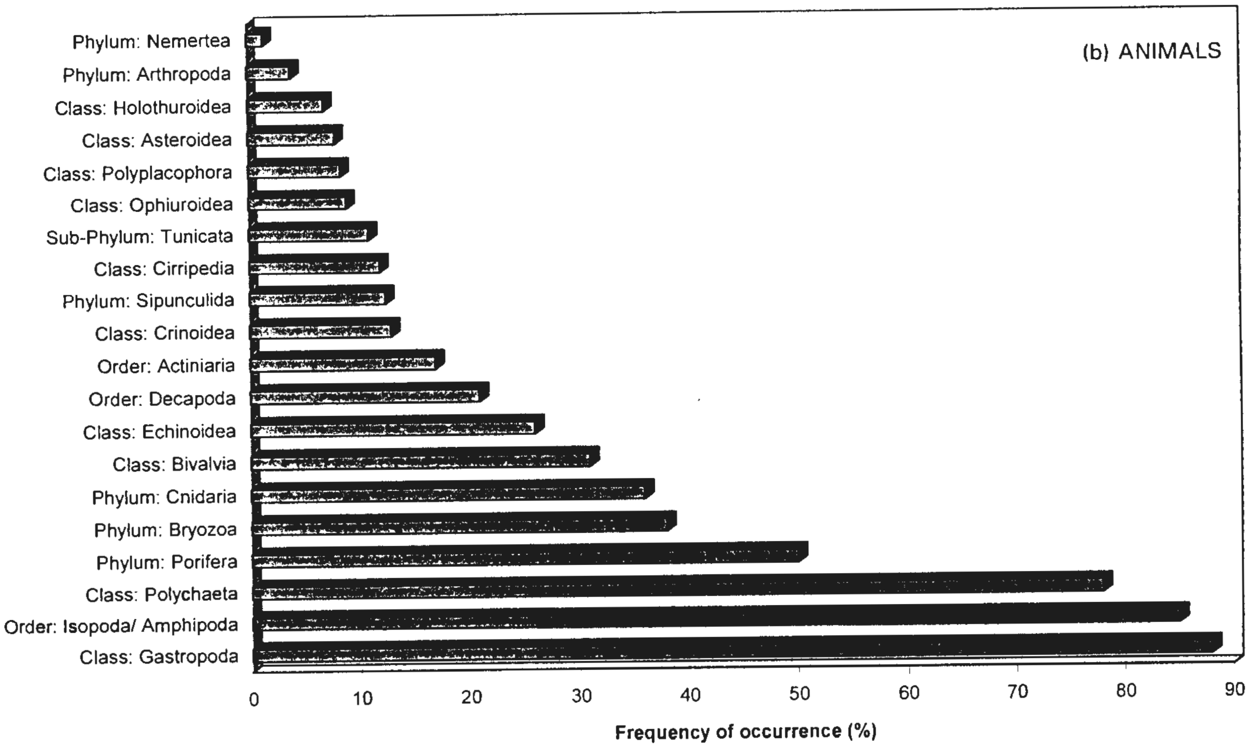


Figure 3.10 Rank order of; (a) 20 plant taxa occurring most frequently; and (b) all animal phyla, sub phyla, class or order, in the 240 0.25m^2 descriptive quadrats sampled in the kelp understorey.

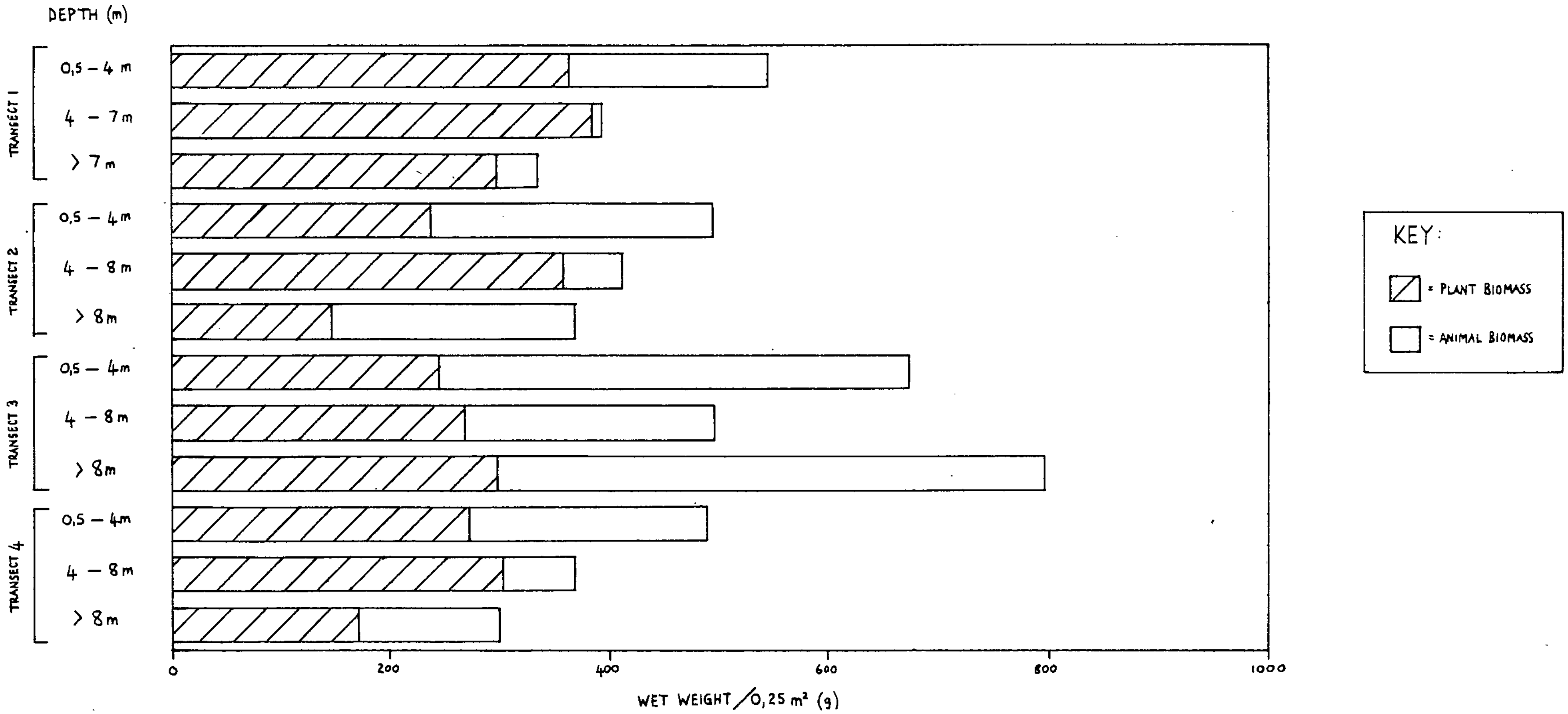


Figure 3.11 Transect- and depth-specific average wet weight/ 0.25m^2 at the study site.

(A) Algae-poor group (very poor in taxa): characterised by dominance of *Zonaria subarticulata* and *Caulerpa holmesiana* and a very high cover of sessile invertebrates (notably Porifera, Byrozoa and Tunicata).

(B) *Zonaria subarticulata* - *Sargassum heterophyllum* - *Phloiocaulon squamulosum* group: generally a heterogenous group with low sessile invertebrate cover and typified by abundance of the above algal taxa.

(C) *Pterosiphonia cloiophylla* - *Codium stephensiae* group: a group poor in constant taxa with low within-group similarity and low to moderate sessile invertebrate cover.

(D) *Halopteris funicularis* - *Botryocarpa prolifera* - *Jania crassa* group: very high diversity of algal taxa (notably red algae) and a low to moderate cover of sessile invertebrates. Generally comprises species able to persist in seasonally sand-inundated habitats.

(E) *Jania crassa* - *Plocamium suhrii* group: compositionally a very heterogenous group characterized by samples from the intermediate depth zone.

(F) *Bifurcariopsis capensis* - *Iridaea capensis* group: low cover of sessile invertebrates and compositionally homogenous (high within-group similarity). Characterised by samples from the shallow depth zone.

Ecological structure

Classification of data

Figure 3.12 shows the coherence of the clusters and cluster groups with the main environmental factors involved in the study. With the exception of cluster 23 the cluster coherence in groups reflects the observed *in situ* community structure. The clearest differentiation is brought about by depth and sand cover (highly correlated with depth and wave exposure ie. deep water and low water movement = high sand cover). Within the groups, urchin and abalone density and slope are environmental factors which differentiate clusters.

Group A occurs in deep water at moderately-exposed and exposed transects (2-4) and has very low sand cover. Group B occurs exclusively at the moderately sheltered transect 4 and typically on steep slopes. Group C generally occurs in the shallow waters of the moderately exposed and exposed transects (2-4) and the clusters within this group have a low sand cover. Urchin and abalone density have a strong influence on internal cluster classification. Group D generally reflects the intermediate and deep zones of the sheltered transect 1 and have a high sand cover. Cluster 23 (deep water zone from transect 2) appears to have strong floristic affinities with other clusters in group D but this is not adequately explained by the environmental factors considered here. Group E occurs in the shallow and intermediate depth zones of the exposed transects and typically on moderately steep slopes. Group F occurs in the shallow water of the sheltered transect, transect 1. Slope and sand cover are strong factors distinguishing internal cluster classification within this group.

Ordination of data

Between-transect analysis:-

The first three axes of the CCA analysis accounted for 77% of the variance in the weighted averages of the species with respect to each of the environmental variables. The Monte Carlo permutation test indicated that canonical axes 1 and 2 are significant at the 5% level (test statistics range 0.037-0.080 for the first axis and 0.046-0.066 for the second axis).

The correlation between the main axis of compositional variation and the environmental factors involved, as elaborated by the CCA, is shown in Figures 3.13 and 3.14. The axis values in the CCA output have no ecological meaning but are more or less correlated to various environmental factors (illustrated as vectors in Figure 3.14). Figure 3.13a shows the configuration of samples in the diagram of CCA axes 1 and 2. Each sample is numbered with it's group classification position from the TWINSPAN analysis (A-E) and isolines drawn to show their position in two-dimensional space. There is a clear compositional gradient from the algae-poor group (A) at the left side of axis 1, via the *Jania-Plocamium* group E, and part of group B (clusters 8,9 and 10) to the *Bifurcariopsis-Iridaea* group F. A second distinct compositional gradient runs from the *Pterosiphonia-Codium* group C, via the *Zonaria-Sargassum-Phloiocaulon* group B, and part of group E (cluster 26 and part of cluster 25), to the *Halopteris-Botryocarpa-Jania* group D. The patterns generally follow the depth gradient (deep to shallow) for the first compositional gradient and urchin density (high to low) and sand cover (low to high) gradient for the second compositional gradient.

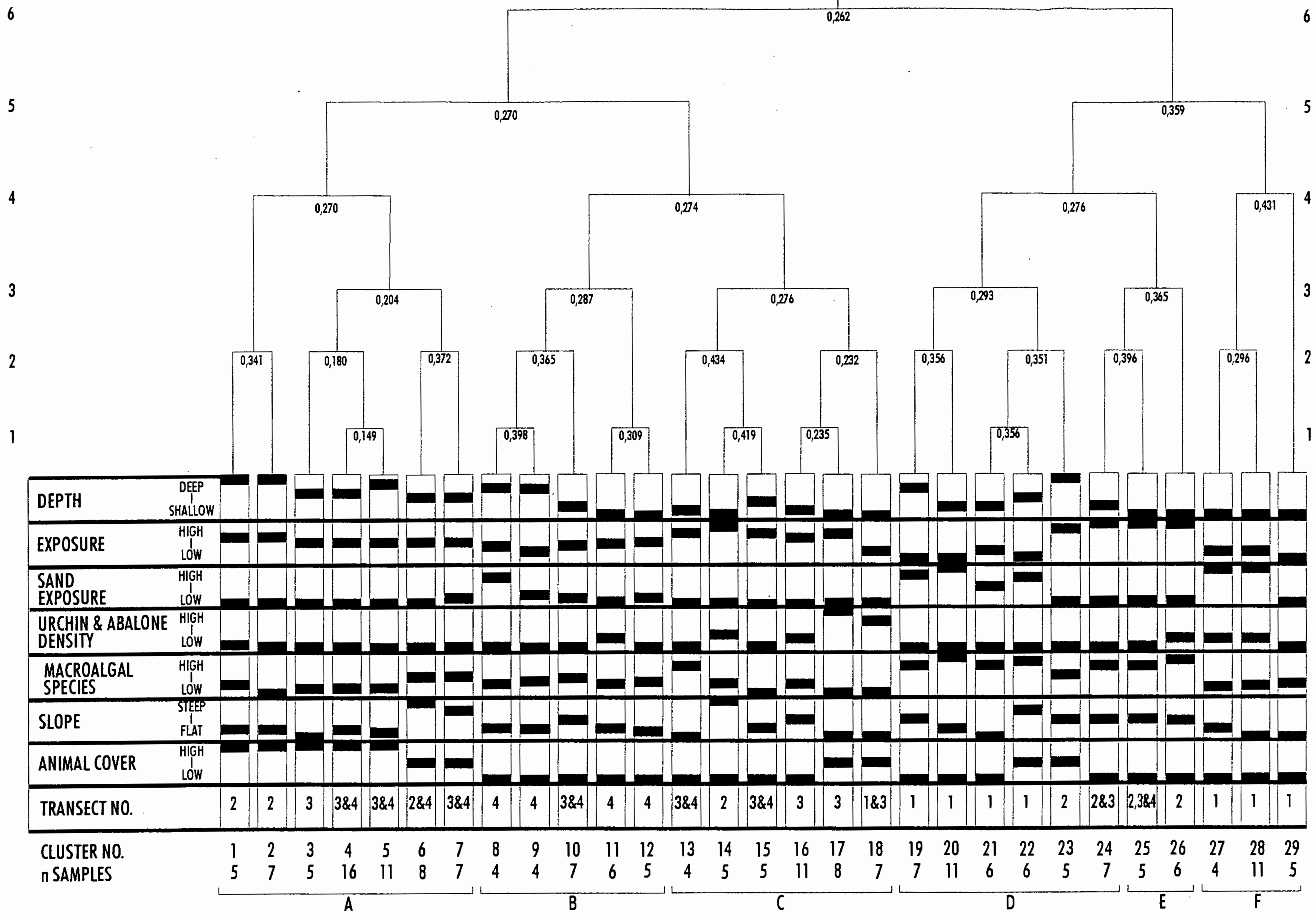


Figure 3.12 Classification dendrogram of the 29 remaining clusters from the TWINSPAN analysis. Status of environmental and biotic factors indicated with dark fields. Cluster number, number of samples for each branch (n), transect number relating to clusters and a subjective grouping (A-F) is given. Eigenvalues for each level of division are indicated.

Some isolines for the main environmental variables based on the values for these variables in the various samples are shown in Figure 3.13b-d. The patterns for depth (scale of 1 = shallow to 3 =deep), sand cover (scale of 1 = <1% sand cover to 4 = >75% sand cover) and urchin density (1 = 0/0.25m^2 to 4 = >6/0.25m^2) are clear. Samples from shallow depths are gathered in the top right corner getting increasingly deeper along the diagonal of the axes (Figure 3.13b). Samples with low sand cover are gathered at the top and upper left sector of the figure and sand cover becomes increasingly higher along the diagonal of the axes to the bottom right corner (Figure 3.13c). Samples with a high density of urchins are clustered at the top of the figure and get increasingly lower to the bottom half of the figure (Figure 3.13d).

In general two major environmental complex-gradients were identified and considered to explain the compositional variation:

(1) A depth complex-gradient strongly correlated with axis 1. Urchin density, substrate, kelp cover and canopy cover of crustose corallines point in an approximate opposite direction and suggest a high negative correlation with deeper water (Figure 3.14). The arrows for urchin density and crustose corallines do not run quite parallel with the depth arrow and it is apparent that factors other than depth may also influence these variables (Figure 3.14).

(2) A sand cover complex-gradient, though in most instances at approximately 90^0 to the depth complex-gradient (Figure 3.14), is weakly correlated with these variables. Low sand deposition tends to occur on steep slopes and in shallow water, and hence aspect and depth show a weak negative correlation with sand deposition (Figure 3.15).

A weighted correlation matrix for the different axes and environmental factors used in the analysis is presented in Figure 3.15. The first two species axes in the CCA run are highly correlated to depth (81 and 52%), urchin density (75% and 38%) and sand cover (65% and 58%). The first species axis is also weakly correlated to aspect (31%) and substrate (29%). The second species axis is also moderately correlated to abalone density (57%). The first and second environmental axis have the same pattern of correlations to the environmental vectors as the species axis although the correlation values are higher. The third axis was strongly correlated with projected kelp canopy cover (72%).

The weighted correlation matrix indicated that the environmental variables are strongly inter-correlated. Though the strength of significance varies; (a) depth is negatively correlated with number of urchins, number of abalone, substrate and cover of crustose corallines and positively correlated with sand cover; (b) kelp canopy cover is positively correlated with slope angle (aspect) and negatively correlated with urchins and substrate; (c) slope angle is positively correlated with number of abalone and negatively correlated with sand and; (d) cover of crustose corallines is negatively correlated with sand and positively correlated with density of urchins and abalone. It is thus apparent that few or none of the measured environmental variables represent simple environmental gradients as each covaries or directly interacts with different primary determinants of species composition.

Figure 3.14 shows the distribution of the taxa in the same space as that of Figure 3.13, as well as the length and direction of the environmental vectors. The taxa with positions near the end of environmental vectors are highly correlated with the corresponding variables (Figure 3.14). Obviously taxa with such high correlations are rare taxa, which had little influence on the result of the classification. Along the sand cover vector some highly correlated, more frequent taxa which characterise group D are *Gigartina insignis* (117), *Tayloriella tenebrosa* (193), *Halopteris funicularis* (38), *Gracilaria verrucosa* (124), the giant chiton *Dinoplax gigas* (213) and *Jania capillacea* (144). Along the urchin and abalone density vectors there are highly correlated frequent taxa associated with group C, and parts of F (eg. *Amphiroa ephedraea* [59], *Arthrocardia* spp. [67 & 69], *Cheilosporum* spp. [91 & 92], *Corallina officinalis* [101], *Plocamium cornutum* [170] and *Codium stephensiae* [20]). At the negative end of the depth vector are the typical shallow water taxa such as *Aeodes orbitosa* (56), *Bifurcariopsis capensis* (30), *Iridaea capensis* (142) and *Colpomenia sinuosa* (33).

The taxa with low correlation with any of the environmental variables are situated near the centroid of the diagram. Here the common taxa which hardly differentiate between community types such as *Laminaria pallida* (40), *Ecklonia maxima* (36), *Plocamium corallorhiza* (169), *Champia compressa* (89) and Isopoda/Amphipoda (209), are found. The individual configuration of species positions in the CCA is however generally difficult to interpret and species combinations (reflected in results from quadrats) is a better indicator of community structure and correlation with environmental variables.

Within-transect analysis:-

Correlations with the environmental variables and the main axis of compositional variation within individual transects, as elaborated by the CCA biplots is presented in Figure 3.16. In all transects the first axis of CCA is strongly correlated with depth and urchin density ($r > 0.8$). The correlation of environmental variables with ordination axis 2 was transect-specific. In the sheltered and moderately sheltered transects, transect 1 and 4, axis 2 was strongly correlated with aspect and sand cover ($r > 0.8$). In the exposed transect, axis 2 was strongly correlated with abalone density and substrate ($r > 0.75$). In the moderately exposed transect 3, the second axis was weakly correlated with projected kelp canopy cover ($r = 0.62$). Ordination axis 3 showed a moderate to strong correlation with projected kelp canopy and aspect from all transects. The weighted correlation matrices for each analysis showed a similar inter-correlation to that shown by the analysis for all samples and is not discussed further. Analyses of the first three axes accounts for 64.1%, 65.2%, 74%, and 68.9% of the variance in transects 1,2,3 and 4 respectively. The Monte Carlo permutation test indicated that canonical axes 1 and 2 are significant at the 5% level for all CCA analyses.

Isolines for the main environmental variables were, except for depth (Figure 3.16), generally unclear. At this scale of analysis there is, within a depth range, significant small-scale heterogeneity with highly variable environmental parameters which may cause multiple solutions of species composition. More intensive sub-sampling within a depth range may elucidate this small-scale heterogeneity and the biotic and abiotic factors influencing the community structure. This study however fails to clarify further the trends identified from the between-transect analysis.

The only significant seasonal separation of samples in the biplots was in the deeper water of transect 4, the intermediate depths of transect 3 and the shallow water of site 1 (Figure 3.16). Community structure and local dominant species however generally remained consistent throughout the year in most areas and seasonal changes are not strongly pronounced. The effect of sand deposition (more strongly pronounced in summer when water motion is lower) is essentially limited to localized effects on individual quadrat samples causing those quadrats to seperate out in the CCA biplot. In general however the season of data collection was poorly reflected in the spatial distribution of samples in the CCA biplots. It is hence considered that, in the context of this study, seasonality is not a major factor causing variation in the community structure of the kelp understorey sessile plants and animals.

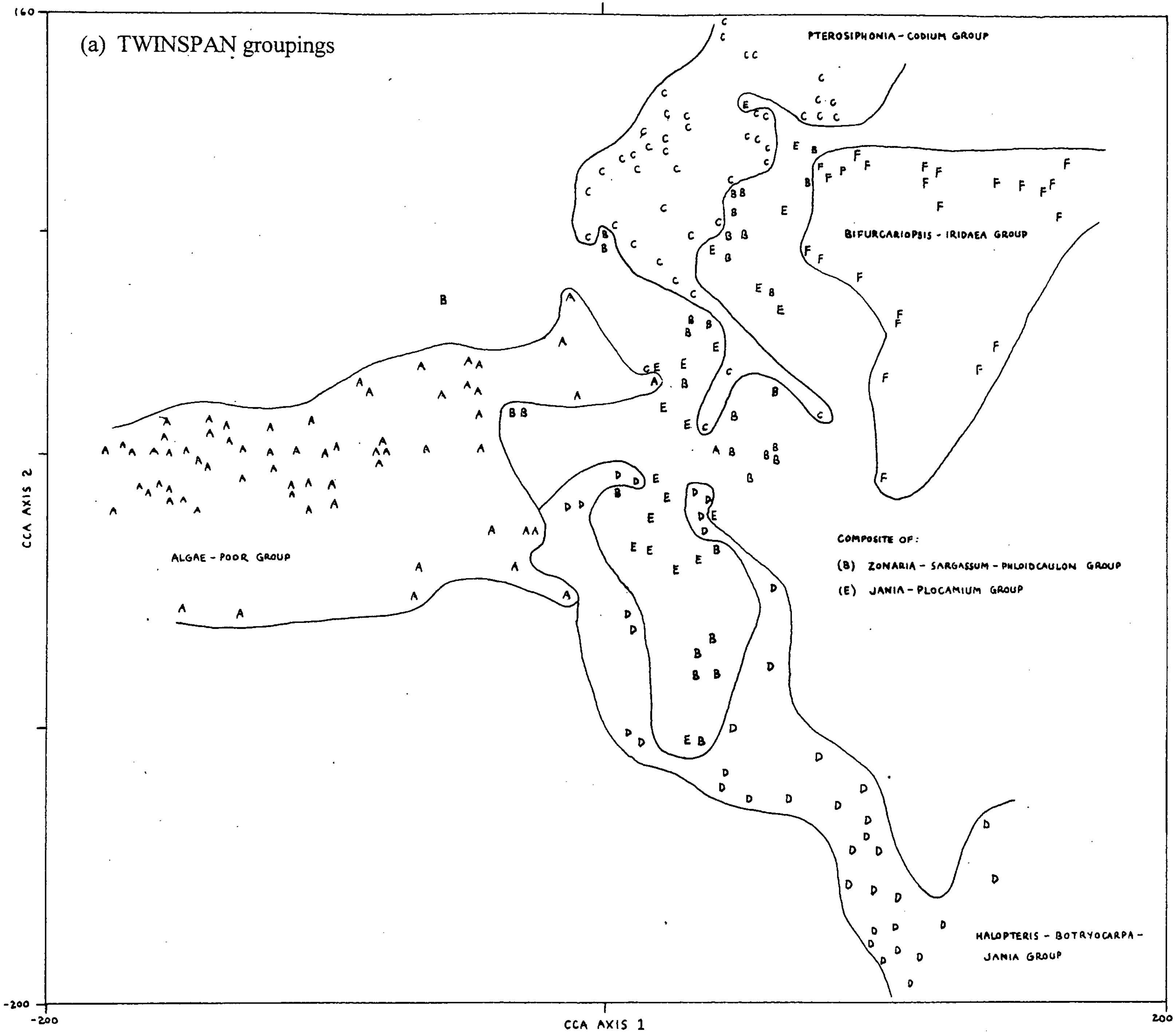
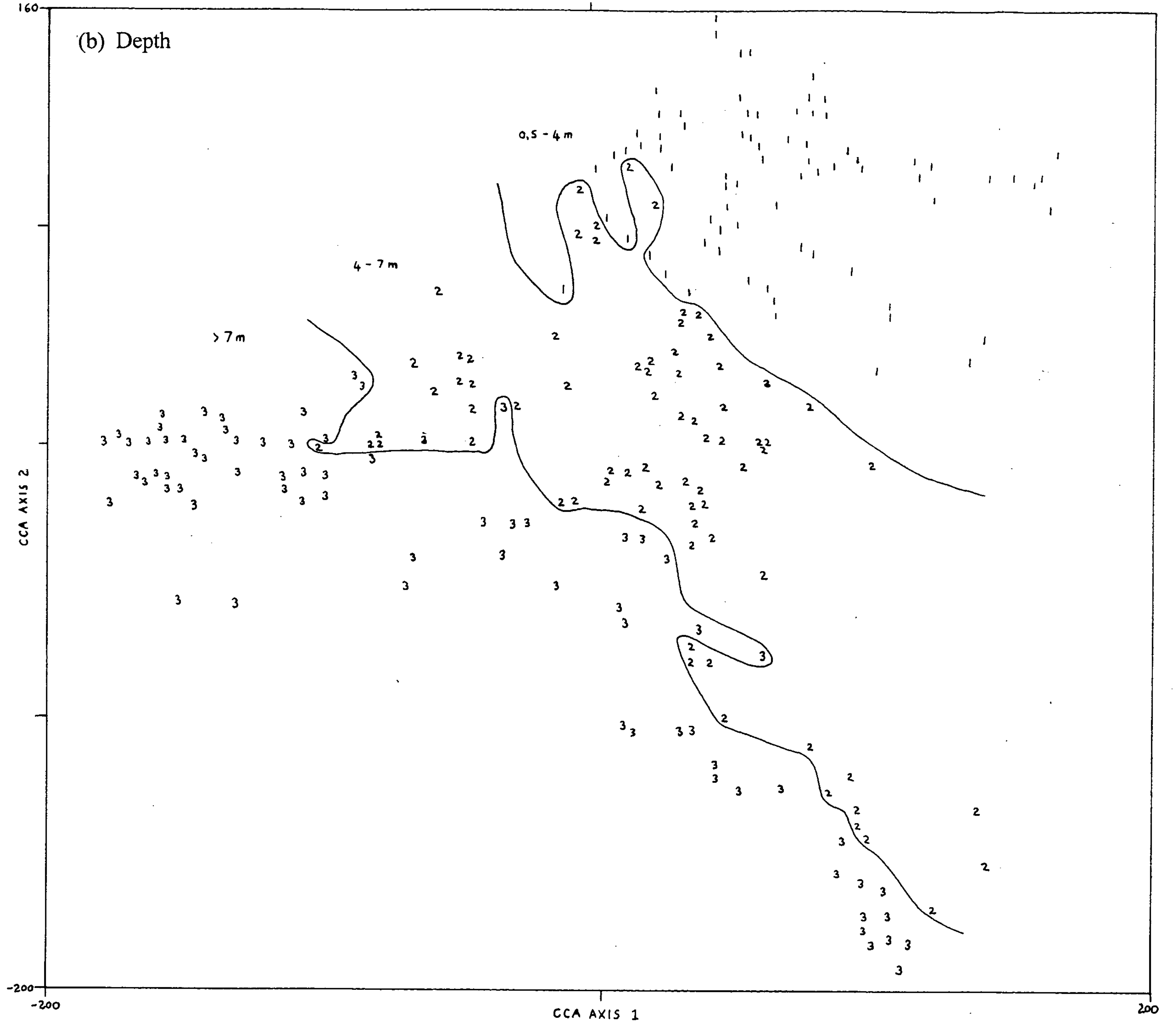
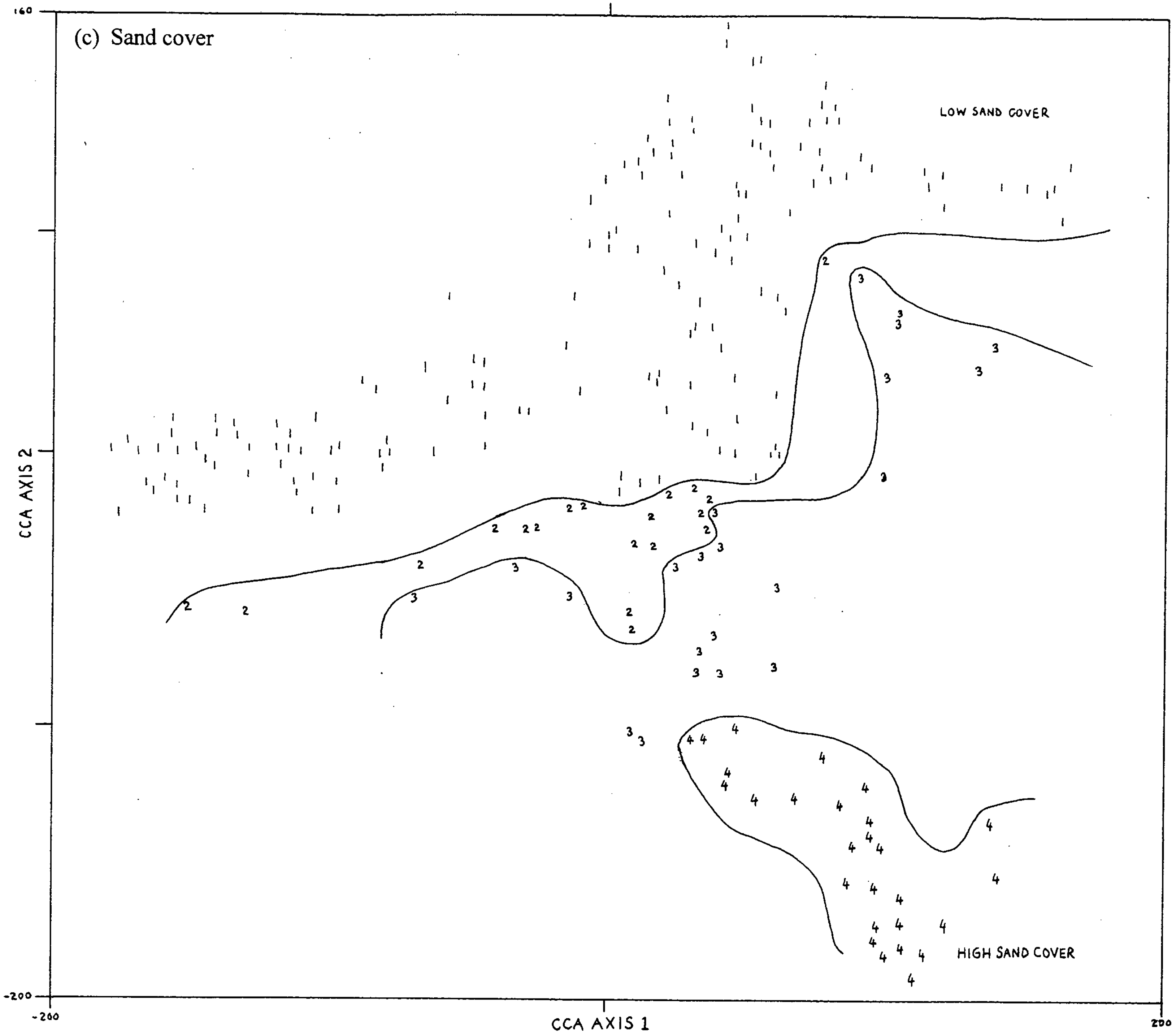


Figure 3.13 Sample distributions along the first and second axis of the CCA analysis. Equal (a) group numbers from the TWINSPAN analysis (A-F, see Figure 12), (b) depth (shallow - deep), (c) sand cover (low - high) and (d) density of urchins (low - high) are indicated with isolines.

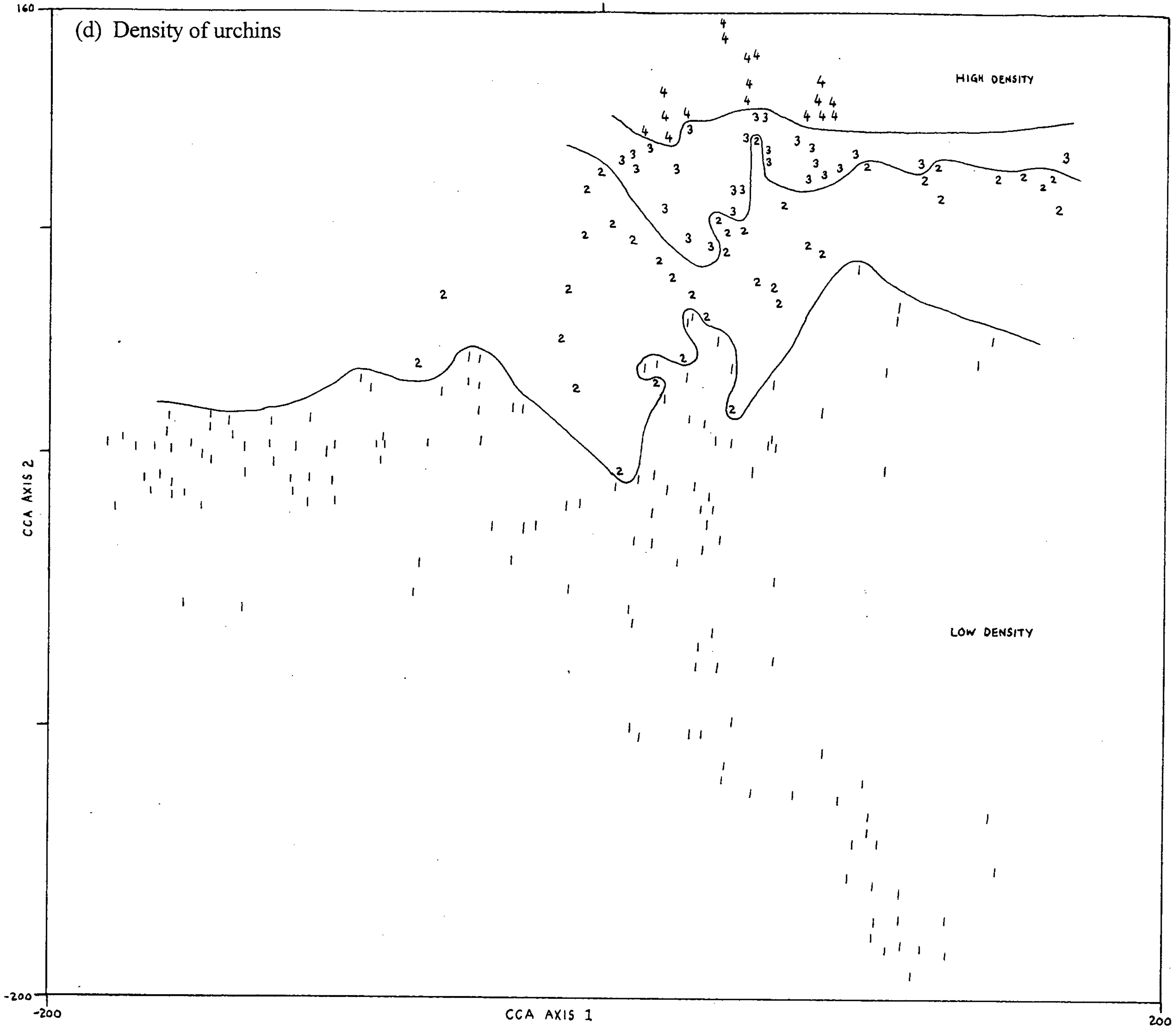


(b) Depth



(c) Sand cover

LOW SAND COVER
HIGH SAND COVER
CCA AXIS 1
CCA AXIS 2
160
-200
-200
200



(d) Density of urchins

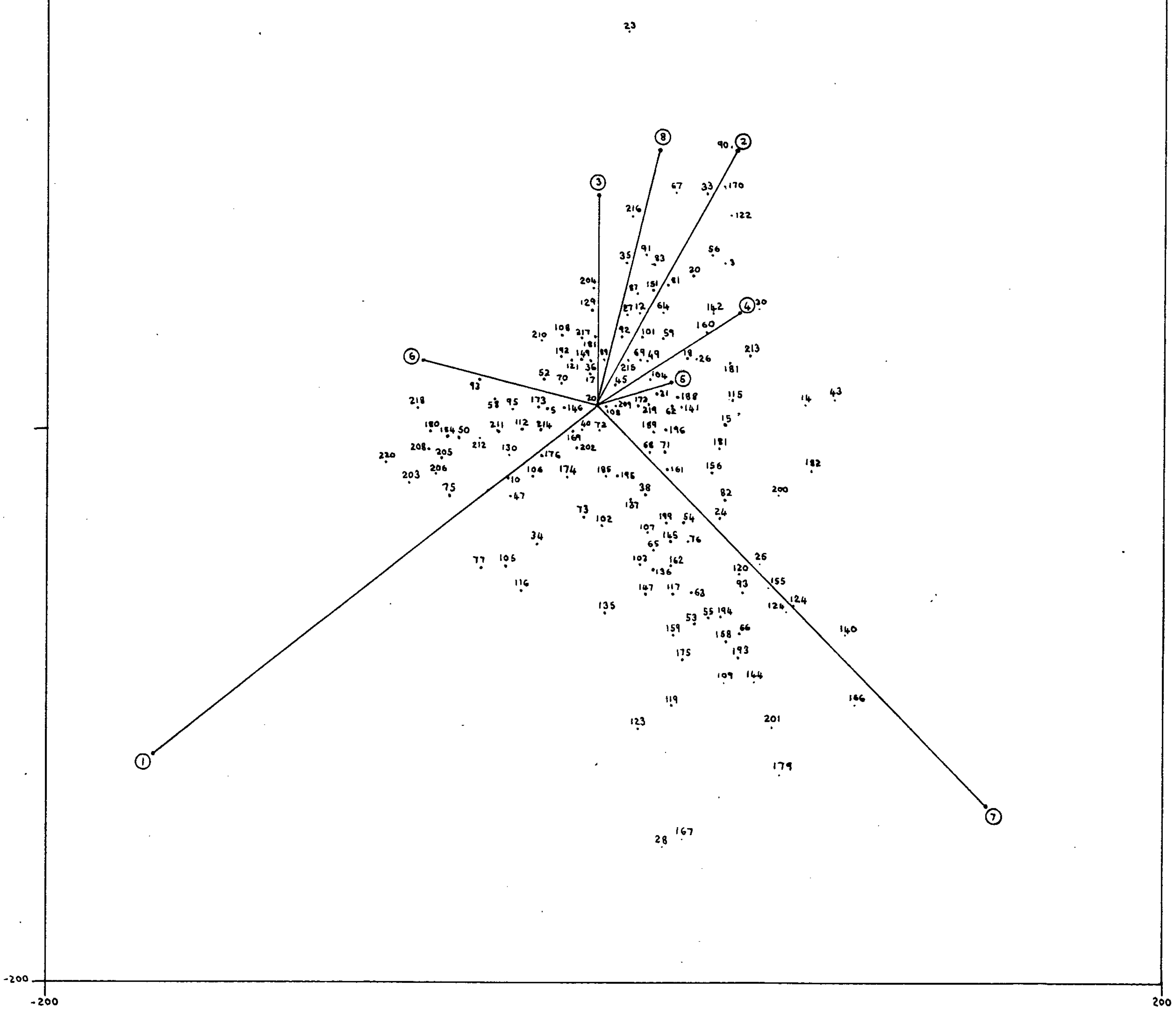


Figure 3.14 Species distribution along the first and second axis of the CCA analysis. Species code numbers up to 230 are plant taxa, higher numbers are animals (see code list in Chapter 2). Environmental vectors are indicated originating from the centroid of the cluster. Encircled are the numbers of the environmental variables (1 = depth; 2 = urchin density; 3 = abalone density; 4 = substrate; 5 = kelp canopy cover; 6 = aspect; 7 = sand cover; and 8 = cover of crustose corallines.

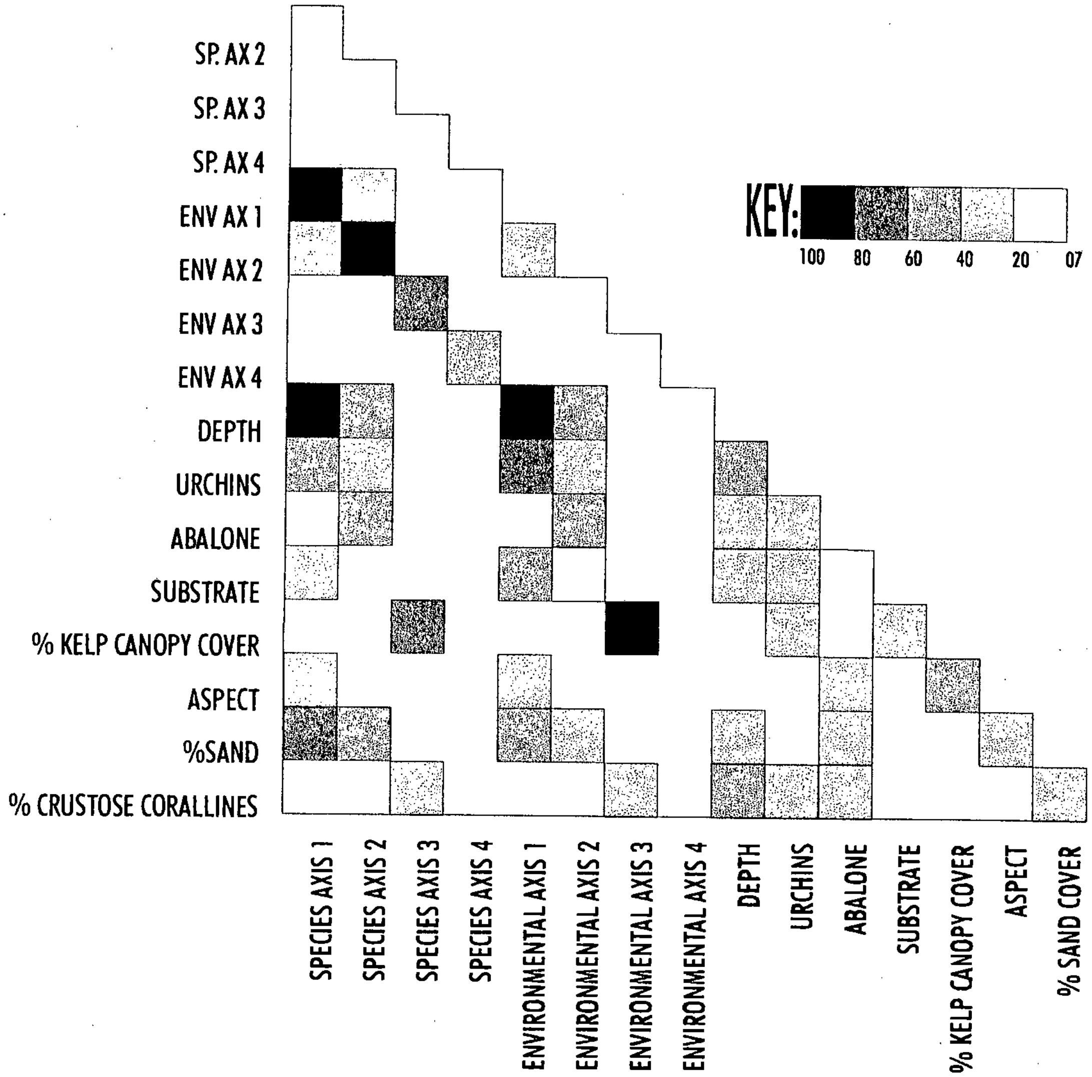


Figure 3.15 Correlation matrix for axes and environmental factors for the CCA run.

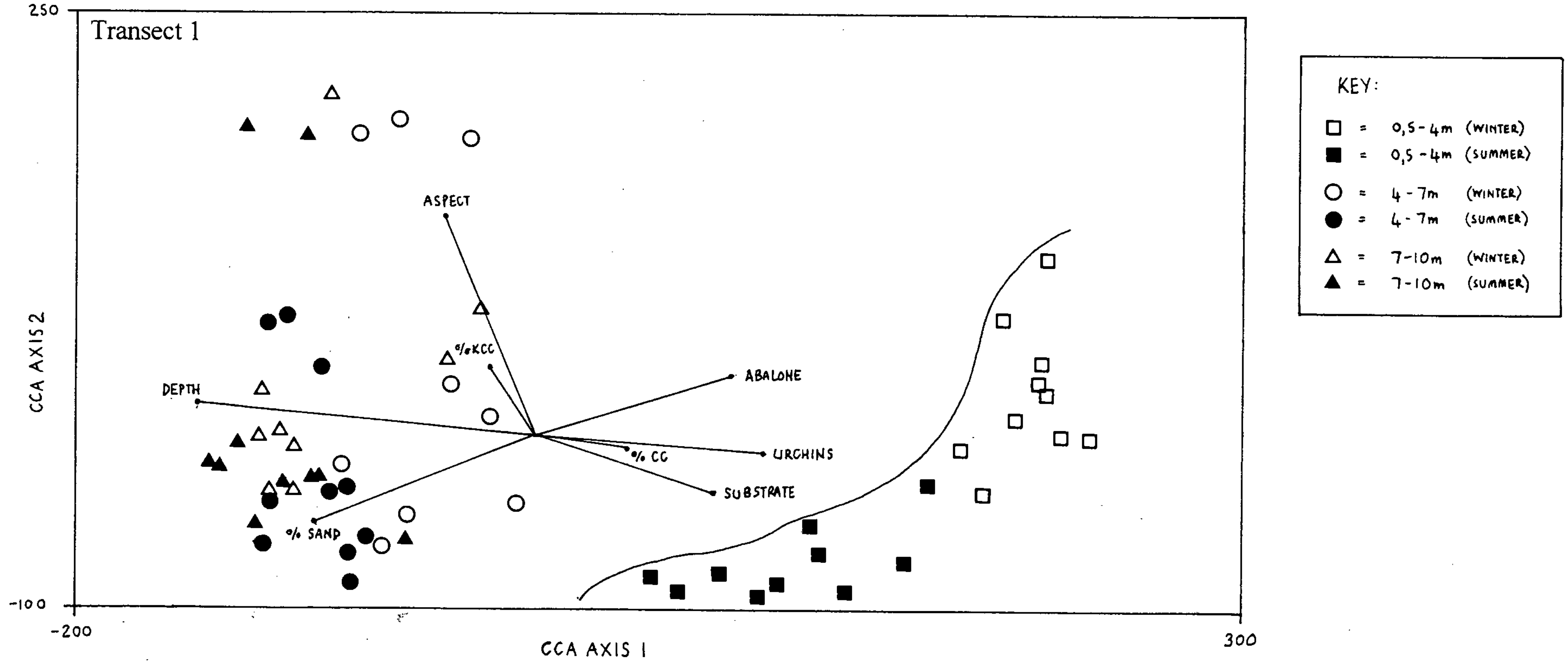
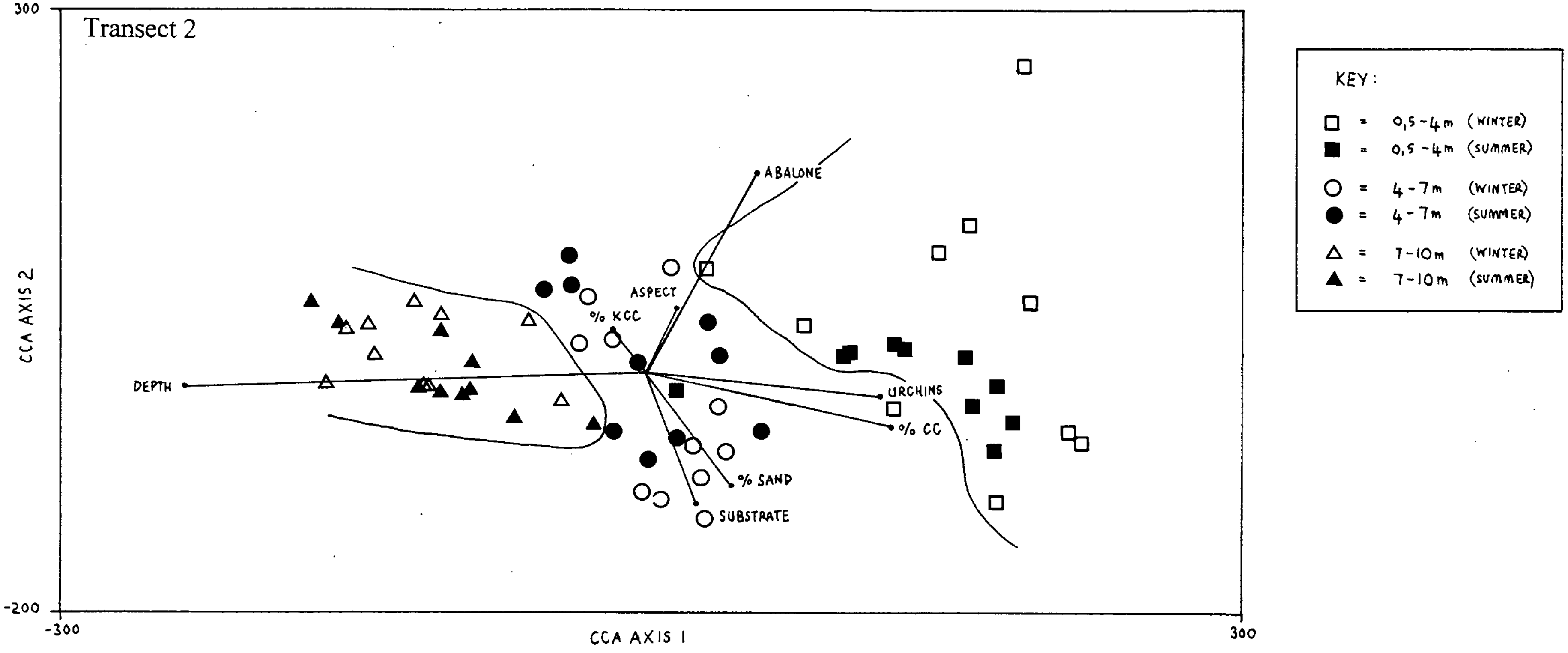
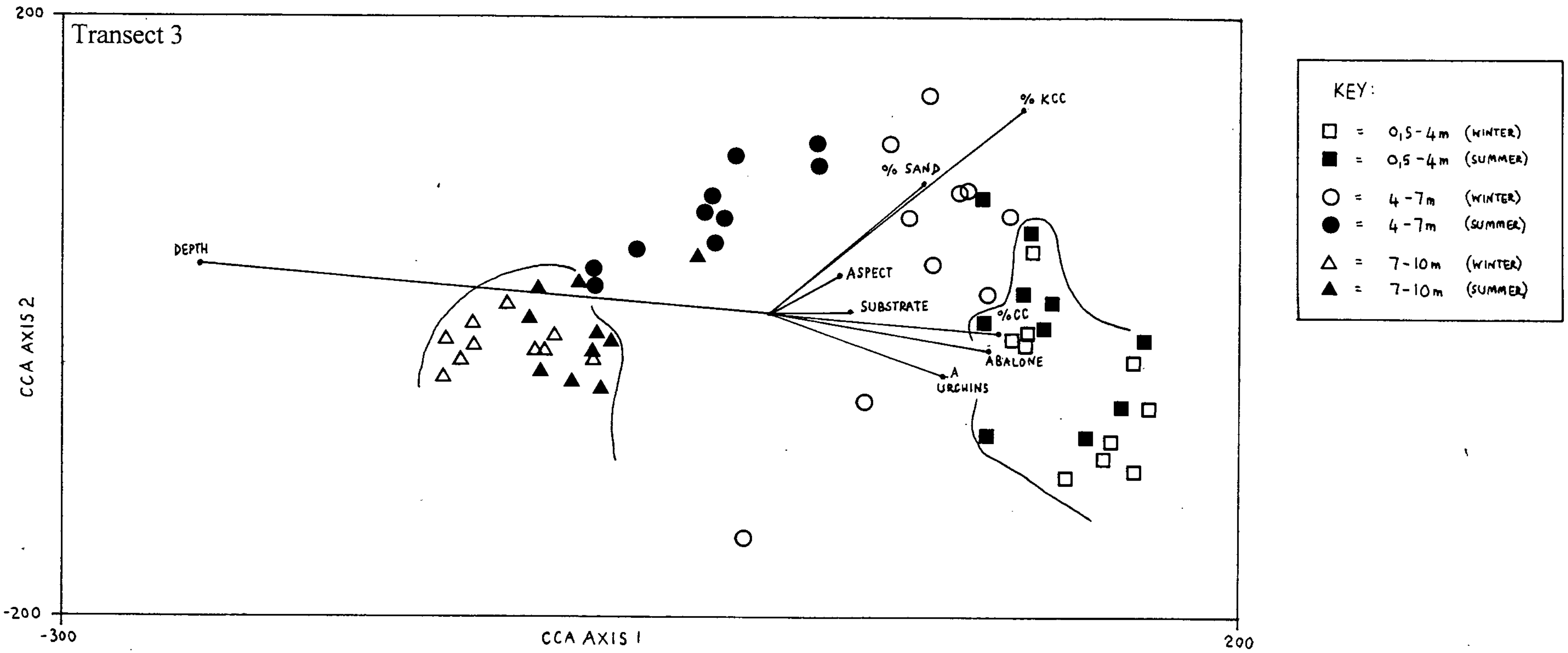
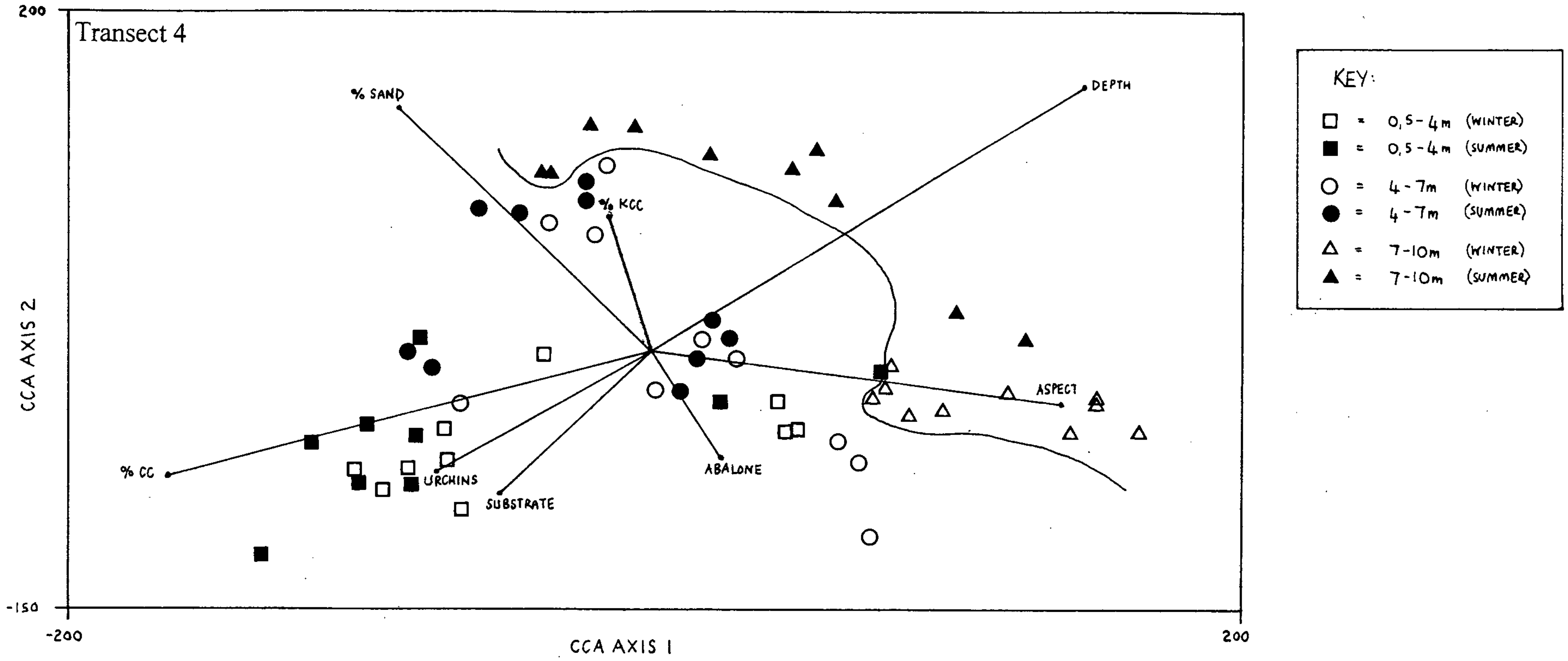


Figure 3.16 Transect-specific (transects 1-4) sample distributions along the first and second axis of the CCA analysis. Environmental vectors are indicated originating from the centroid of the cluster. Isolines indicate the separation of quadrats.


Transect 2
KEY:
□ = 0,5 - 4m (WINTER)
■ = 0,5 - 4m (SUMMER)
○ = 4 - 7m (WINTER)
● = 4 - 7m (SUMMER)
△ = 7 - 10m (WINTER)
▲ = 7 - 10m (SUMMER)
ABALONE
ASPECT
% KCC
DEPTH
URCHINS
% CC
% SAND
SUBSTRATE
CCA AXIS 1
CCA AXIS 2
300
-200
-300
300


Transect 3
CCA AXIS 1
CCA AXIS 2
-300
200
200
-200
DEPTH
% KCC
% SAND
ASPECT
SUBSTRATE
%CC
ABALONE
A URCHINS
KEY:
□ = 0,5-4m (WINTER)
■ = 0,5-4m (SUMMER)
○ = 4-7m (WINTER)
● = 4-7m (SUMMER)
△ = 7-10m (WINTER)
▲ = 7-10m (SUMMER)


Transect 4
% SAND
DEPTH
% KCC
ASPECT
% CC
URCHINS
SUBSTRATE
ABALONE
200
-150
-200
200
CCA AXIS 2
CCA AXIS 1
KEY:
□ = 0,5 - 4m (WINTER)
■ = 0,5 - 4m (SUMMER)
○ = 4 - 7m (WINTER)
● = 4 - 7m (SUMMER)
△ = 7-10m (WINTER)
▲ = 7-10m (SUMMER)

DISCUSSION

A subjective interpretation of the line transects, the random depth-stratified quadrats, a synthesis of plant and animal occurrence for each transect and depth range (appendix 1) and diver observations from the study area in Cape Hangklip reveals a similar depth-related zonation to those described by Field *et al* (1977), Velimirov *et al* (1977) and Field *et al* (1980). Generally the shallow inshore zone (<4m depth) is dominated by small *Ecklonia* plants and a composite of shallow water algae, and supports a few large mobile and sessile indicator filter-feeders, grazers/debris feeders and carnivores. Intermediate depths (4 - 8m depth) support maximal algal biomass, with the larger *Ecklonia* plants forming a canopy, beneath which *Laminaria* and understorey algae thrive, but where animals are poorly represented. As the kelp plants thin out at the seaward margin of the beds (<12m depth) they give way to a dense animal community dominated by filter-feeding sessile invertebrates.
In this study both *E. maxima* and *L. pallida* persist from the sublittoral fringe to 12m depth with *L.pallida* replacing *E. maxima* as the dominant overstorey in deeper water (generally in >12m depth). Though the species composition, projected canopy cover and biomass of plants and animals changes fairly gradually with depth, the line transects established that there were two distinctive community zones - shallow (0.5 - 6m) and deep water (6 - >10m) communities - with an indistinct intermediate depth (at approximately 4 - 8m) community which has components of both the shallow and deep water communities.

In the shallow water (<4m depth) the faunal complement is dominated by the carnivores *Thyone aurea* (golden sea cucumber) and Actiniaria (eg. *Corynactis annulata* - strawberry anemone), the grazer/debris feeders *Parechinus angulosus* (Cape urchin), *Haliotis midae* (abalone), *Turbo sarmaticus* (giant periwinkle) and *Dinoplax gigas* (giant chiton) and the filter feeders *Pyura stolonifera* (red-bait) and *Austromegabalanus cylindricus* (giant barnacle). The understorey algal community in this shallow water zone is dominated by fleshy and foliose algae and articulated corallines. Unlike the animal community in the shallow water zone, the plant community is not readily defined by dominant species, but rather by a complex of species occuring at each transect.

Animal species diversity is low in the ill-defined intermediate depth zone (4-8m) whereas it is generally in this zone that the understorey plant communities show both their highest alpha diversity and biomass (see Table 3.3 and Figure 3.11). The algal community at this intermediate depth, as in the shallow water, exhibit a heterogeneous complex of species composition and distribution.

At the seaward limits of the transects (>8m) the community structure changes noticeably, generally comprising a dense animal community where a number of animal taxa are represented, but only a few dominate the understorey in terms of biomass (see Figure 3.11) and canopy cover. Most of the animal biomass is represented by filter- feeding species, notably sponges (Porifera). The understorey algal community is represented by fewer species than those recorded from shallower waters (see Table 3.3), exhibits a more homogenous distribution, and comprises predominantly large foliose Phaeophyta (eg. *Desmarestia firma*, *Zonaria subarticulata*) and Rhodophyta (eg. *Botryocarpa prolifera*, *Rhodymenia natalensis*) including articulated corallines (eg. *Amphiroa ephedraea*, *A. capensis*).

Thirty plant species and eleven animal phyla, sub-phyla, classes or orders occcur at all transects and through the three depth ranges (see Appendix 3.1).

In general, results from the line transects and depth-stratified quadrats in exposed and moderately wave-exposed transects at Cape Hangklip indicate that neither the algal overstorey or understorey satisfactorily define the bathymetric zonation pattern. Rather the presence, or absence, of large indicator macroinvertebrates broadly define the respective depth-related zones.

However in the sheltered transect, transect 1, this zonation pattern was not readily recognizable. Here, a marked feature was the presence in the shallow water of a significant number of typically intertidal species which defined the shallow water zone. It appears that many of these species persist into the shallow subtidal because of the absence of a disturbance factor prevalent in the other transects (see later discussion). Many of the algal species present in the shallow waters of the sheltered transect persisted to the seaward edge of the kelp bed. Macroinvertebrate species were generally inconspicuous (except for a few psammophilic species such as *Dinoplax gigas* and *Thyone aurea*) in the sheltered transect and the seaward side of this kelp bed was decisively defined by sand.

My main question in this chapter however, was: do patterns of variation in phyto- and zoobenthic community composition occur in a kelp bed understorey at Cape Hangklip and can these patterns be related to environmental variation? This chapter has demonstrated that patterns of variation do exist, that they show good correlations with environmental variables, and that this variation may be continous or discontinuous. Discontinuous variation is expressed in the cluster and group structure of the TWINSPAN classification showing clear patterns of co-occurrence of certain taxa (Figure 3.12) and moderately sharp contours between adjacent groups in the CCA (Figure 3.13a). Such patterns may be determined by (1) sharp transitions between environmental zones and correlations of certain species to a particular zone, (2) positive interactions between species co-occurring under certain environmental conditions and (3) negative interactions between species occurring at different intervals along environmental gradients and showing competitive exclusion in zones of overlap (Kautsky and van der Maarel, 1990).

Apart from the local discontinuities brought about by topographic elevations and depressions and associated substrate changes, the main gradient, water depth (light), appears to be relatively steep. Depth is the major environmental vector in this study shown to determine plant and animal species distribution and was strongly correlated with axis 1 in the CCA analyses (Figure 3.13, 3.14 and 3.15). This is in accordance with the findings of Velimirov *et al* (1977), Shepherd and Womersley (1981), Choat and Schiel (1982), Hiscock (1985) and Kautsky and van der Maarel (1990) who found similar evidence from other marine benthic communities. Urchin density had a strong negative correlation with depth (Figure 3.14 and 3.15) and where urchins occurred in high densities this resulted in strong localized discontinuities in species composition. The large-scale effects of grazing by sea urchins in California and elsewhere which results in the wholesale removal of most macroalgae, including the dominants (see Chapter 1) was not observed in this study. A second complex gradient resulting in discontinuous variation of benthic kelp understorey communities, and strongly correlated with axis 2 in the CCA analyses (Figure 3.15), was sand cover. This is generally an environmental variable that has been neglected in the literature, but in this study was shown to have a strong localized effect on species composition of patches where sand cover is high.

Contrary to expectations, although a minor gradient of wave exposure did exist between the transects (Figure 3.3), wave exposure was not shown to be a major direct environmental factor affecting the local distribution of the kelp understorey phyto- and zoobenthos. Seasonal sand cover may however be correlated in part to low wave exposure. Local variation in temperature and turbidity, because of their temporal heterogeneity, showed no relationship with community structure. The season of sampling was poorly reflected by the benthic community structure of the understorey and it is likely that the effect of seasonality will only be elucidated with replicate sampling over a longer sampling period.

This chapter concentrated on two scales of investigation - the local site represented by the four transects (4 levels of exposure, turbidity and temperature) and the individual transect (3 depth ranges).

At the larger regional biogeographic scale, ocean current patterns and the corresponding temperature regimes (see Chapter 2) have been postulated as the primary factor influencing the distributional variation of plant and animal communities in the marine benthic habitats of the southern African coast (Isaac 1938, Stephenson 1944, 1948, 1972, Brown and Jarman 1978, Lüning 1985, 1990, Bolton and Anderson 1990).

Within the kelp beds of the southern Benguela system it has been suggested that water motion, temperature (associated with upwelling events) and water clarity may influence the structure of kelp communities (Field *et al* 1980).

At a local scale, Velimirov *et al* (1977) suggest that distance from the sublittoral fringe, depth and aspect correlate most closely with community structure in a west coast kelp bed. In this study of a local "west coast/south coast overlap" (see Chapter 2) kelp bed, physical factors were identified as the overriding organizational processes determining the structure of the kelp understorey community.

Between transects, a depth complex gradient and a sand cover gradient accounted for the broad patterns of plant and animal distribution.

Within transects the primary factor considered to determine the local community structure was depth. Secondary factors tended to be transect-specific and included an aspect-sand cover association and abalone density. The density and distribution of sessile invertebrates, herbivorous grazers (urchin density-depth gradient, abalone density-substrate gradient) and projected kelp canopy cover correlated strongly with the physical factors, sand and depth. The roles of these factors are difficult to evaluate because they may never be entirely independent of each other and because they have highly variable distributions in nature.

Plant and animal species were in many instances diagnostic of particular environmental conditions. Considering the effects of independent abiotic factors and their effects on species distribution, the following generalizations can be interpreted from the results:

(a) **Depth** was consistently the most influential environmental factor causing separation of plots and species in the CCA biplots. Though many species persisted through the depth range it was evident that, in terms of biomass or projected canopy cover, a number of indicator plant species and animal phyla were notably dominant at specific depths. In the shallow water (generally < 6m depth) *Bifurcariopsis capensis*, *Aeodes orbitosa*, *Iridaea capensis*, *Pachymenia spp.*, *Cladophora mirabilis*, *Ulva rigida*, *Scinaia capensis*, *Nemastoma lanceolata*, *Codium stephensiae*, Holothuroidea and Gastropoda are commonly abundant (Appendix 3.1). In the deeper water (generally >6m depths) Tunicata, Porifera, Cirripedia, Cnidaria, *Botryocarpa prolifera*, *Desmarestia firma*, *Zonaria subarticulata* and *Plocamium corallorhiza* are locally dominant (Appendix 3.1). Plant species that commonly occur through the depth range include *Laminaria pallida*, *Ecklonia maxima*, *Pterosiphonia cloiophylla*, *Anthophycus longifolius*, *Plocamium rigidum*, *Halopteris funicularis*, *Amphiroa ephedraea*, and *Champia compressa* (Appendix 3.1).

(b) **Urchin and abalone density** generally appeared to have a significant local impact on community structure and, although they occupy different niches in the shallow water (ie. urchins in crevices, behind boulders or protected from direct wave action, and abalone on consolidated rock surfaces directly exposed to water movement), it is evident that their presence in high densities results in similar community composition. Articulated corallines (*Amphiroa ephedraea*, *Arthrocardia spp.*, *Cheilosporum spp.*, and *Corallina spp.*), *Plocamium rigidum* and *Codium stephensiae* are species commonly associated with urchins and abalone (Figure 3.14) or other areas of high grazing pressure (eg. herbivorous gastropods - notably *Turbo cidaris*). There was a strong positive correlation of cover of crustose corallines with density of urchins (Figures 3.14 and 3.15). The impact of urchins is restricted solely to shallow water (< 4m) whereas the abalone persist, at lower densities, into deeper water (>10m) (Figure 3.8). High densities of urchins are negatively correlated with kelp canopy cover (Figure 3.15) and it appears that high urchin densities may have a localized impact on the recruitment and survivability of kelp spores and sporelings. It is suggested that high water motion allied with a localized concentrated availability of drift material in the shallow water, limit both the spread and impacts of urchins in these kelp beds. Fricke (1980) in a study of the population structure of *P. angulosus* showed that urchins inhabit a range of substrates, adjusting their population structure mainly in response to substrate quality, turbulence and food availability. Movement of urchins was shown to occur on a small scale in response to sea state and proximity of food. The results from this study generally agreed with Fricke's conclusions. Fricke (1980) however indicated that distance from shore and depth did not appear to influence urchin distribution where food was readily available. This study showed that depth, distance from shore and high sand cover had a strong negative correlation with urchin distribution, despite readily available drift material.

(c) **Sand burial** and, though not measured in this study, by implication sand scour, have a marked effect on community structure. There were few truly "psammophilic" (Daly and Mathieson 1977) species, but a number of plant and animal species such as *Gigartina insignis*, *Botryocarpa prolifera*, *Gigartina radula*, *Desmarestia firma, Dasya scoparia*, *Tayloriella tenebrosa*, *Jania crassa*, *Halopteris funicularis*, *Phloiocaulon squamulosum* and the giant chiton *Dinoplax gigas* are abundant in areas where seasonal sand deposition takes place (Figure 3.14 and Appendix 3.1). The mid-depth and deep water at transect 1 and to a lesser extent the deep transect at transect 4 are areas of high sand deposition during the summer months. Species occurring on flat, sand-covered sandstone at these transects are mainly turf-forming algae including *Ophidocladus simpliciusculus*, *Antithamnion sp.*, *Pachychaeta cryptoclada*, Ceramiaceae *indet.*, *Jania capillacea*, and *Ballia callitricha* (Figure 3.14). In terms of biomass and canopy cover, this study recognized only *Jania capillacea* as a dominant indicator species in heavily sand-inundated transects. Species such as *Desmarestia firma* appear to have evolved to rapidly colonize patches in deeper water disturbed by sand scour and burial. Anderson and Hay (1986) have shown that *D. firma* sporophytes appear in spring, grow rapidly throughout summer - a period of low sand scour but high deposition in sheltered areas - and show declining growth rates in winter. In the Point Loma kelp forest in California, Dayton *et al* (1992) show that *Desmarestia* is restricted to isolated patches cleared by storms or where sea urchins had been removed. Thus, species of this genus respond to disturbance similarly in both this study and in California, only the disturbance factors differ. Foster (1982) documents a similar response in *Desmarestia* after experimental removal of *Pterygophora californica.*

Seasonally sand-covered areas exhibited significantly higher plant species alpha diversity (Table 3.3). This may be attributable to a greater habitat heterogeneity both spatially and temporally. Engledow and Bolton (1994) found that alpha diversity (defined as the number of species in a small homogenous area) of seaweeds in the lower sublittoral along the Namibian coast was also strongly related to sand inundation (where sand exceeded 5.6kg. m^{-2}). The nature of the effect of sand inundation in combination with wave exposure was however to decrease species diversity. In this study sand inundation never reached the extent of that recorded by Engledow and Bolton (1994) and the habitats surveyed were generally considerably more heterogenous (both spatially and temporally) even at a very localized scale.

There were a number of plant species and animal phyla intolerant of sand inundation. These were generally found only in areas of high water motion or on steep aspects where sand cover is negligible or less likely to settle. They included *Laurencia flexuosa*, *Gelidium capense*, Porifera, Cnidaria, Cirripedia, *Haliotis midae*, and *Parechinus angulosus* (Figure 3.14).

Where sand had an overriding influence on plant and animal species composition, there was a strong negative correlation between sand and slope angle (Figure 3.15). Steep slopes in sandy areas enabled persistence of species tolerant to sand abrasion but susceptible to sand covering. In deep water transects where high sand deposition occurred, large filter-feeding invertebrates generally predominated on steep slopes (eg. Porifera) and many macroalgal species such as *Zonaria subarticulata*, *Caulerpa* *holmesiana*, *Champia compressa*, *Plocamium corallorhiza*, *Trematocarpus flabellatus* and *Acrosorium spp.* often used these sessile persistent invertebrates as an alternative substrate or to escape sand burial.

(d) The influence of **substrate** on the understorey community was varied and difficult to generalize. It was however evident that substrate type had a strong negative or positive impact on the kelp overstorey (Figure 3.15) with high canopy cover of the overstorey correlated to consolidated Table Mountain Sandstone and low projected canopy cover correlated with small unstable boulders.

In the shallow water, and to a lesser extent the intermediate depth range, the substrate is variable and comprises gravel, angular/subangular cobbles, quartzite fragments, rounded pebbles, angular/rounded small and large boulders and consolidated quartzite of the Table Mountain Group (Figure 3.7). At a within-transect level of investigation the composite of substrate types appears to strongly influence the species composition, biomass and projected canopy cover within and betweeen quadrats, notably in the shallow water. The deeper transects are primarily composed of large stable boulders and consolidated Table Mountain Sandstone (Figure 3.7), and substrate here appears to have a limited effect on species composition, biomass and canopy cover of the understorey at these transects. Substrate is generally strongly positively or negatively correlated with season in the shallow and intermediate depths (Figure 3.15), and it was apparent that during the present study, strong surge of extreme winter storms was responsible for shifting sand, gravel, cobbles, quartzite fragments, pebbles and small boulders. This seasonally unstable substratum in the shallow subtidal appears to support a different complex of plant and animal species, lower species numbers and lower biomass when compared to those adjacent deeper areas where the substrate is more temporally stable (Figure 3.7).

(e) Although vertical rock walls (**slope/aspect**) comprise a relatively small portion of the total hard substrata, these supported a diverse assemblage of sessile invertebrates. It is supposed that the low light levels on steep slopes may preclude colonization by algae (see Chapman and Johnson 1990), but competition for space is intense and strong competitive hierarchies probably exist. Generally foliose macroalgal species which use sessile invertebrates as an alternative substrate were able to persist on the vertical walls typically dominated by invertebrates. Species such as *Champia compressa*, *Acrosorium spp.*, *Zonaria subarticulata* and *Caulerpa holmesiana* were typical indicator species in these habitats (Figure 3.14).

(f) The effect of **projected kelp canopy** cover was difficult to interpret, although this investigation revealed a strong correlation with ordination axis 3 (Figure 3.15). This may be a result of interactive effects with other environmental variables such as negative correlations with sand in transect 1, substrate in transect 2 and aspect in transects 3 and 4 (Figure 3.16). In the shallow water, the kelp canopy cover was negatively correlated with season (Figure 3.16), and it was noted that the winter storms have a significant impact on the blade overstorey of *Ecklonia maxima* by shearing the primary blades from the adult plants. Late spring/early summer has been observed to be a period of rapid growth of the primary blades of the overstorey (*see* Joska and Bolton 1987).

(g) There is a strong positive correlation of cover of **crustose corallines** with urchin density evident in the between-transect and within-transect analyses (Figures 3.14 and 3.16). Urchins are relatively mobile in response to environmental cues such as an increase in bottom surge during data collection and urchins may not be encountered in the immediate area where they are having a direct effect on the community structure. However the results indicate that the presence of sea urchins results in clearing of foliose algae and the subsequent dominance by crustose and articulated corallines.

Despite these single-factor algal associations, many researchers suggest that the associations in kelp forests are an expression of the effects of a variety of biological processes, and that these are moderated by a complex of physical disturbances. The organization of each community can thus be described in terms of a small number of mechanisms involving both biological interactions and physical disturbance (albeit of very different outcomes in each community or sub-community at different temporal and spatial scales). This study suggests that the patterns of community structure are, at the local scale generally ruled to a large extent by abiotic factors and, at a smaller scale, by biotic factors.

Figure 3.17 simplifies the postulated inter-correlation between the primary, secondary and tertiary environmental variables measured in this study and the combination of the extremes of these environmental variables on algal alpha diversity. The direction of the arrows indicate the regulatory pathways and point from postulated cause to effect. The diagram was simplified by considering only the extremes of each environmental variable. What is strongly evident is that, irrespective of the regulatory pathway, all combinations of environmental extremes results in low algal alpha diversity. This supports the basic tenet of the 'intermediate disturbance hypothesis'. This hypothesis proposes that disturbances can maintain species diversity by preventing a small number of species from monopolizing limiting resources to the exclusion of poorer competitors, by interrupting succession to competitive exclusion at an equilibrium state in which co-existence is maintained by niche diversification (see Connell 1978). In this non-equilibrium view, highest diversity occurs when disturbance is at intermediate levels of frequency, intensity and spatial scale, and is patchy in time and space. If disturbance does not occur, then competitive exclusion by late successional species reduces diversity. Diversity is also low when the frequency and intensity of disturbance is high because time for colonization is short. It is interesting to note that, in a regulatory pathway for the faunal component (not shown here), alpha diversity is highest when frequency and intensity of disturbance is low (deeper water). The sessile invertebrate component is postulated here to be a late successional stage in the subtidal. The intermediate disturbance hypothesis thus does not hold true for the sessile invertebrates. It appears that, where both sessile invertebrates and macroalgae compete for the same resource, space, the macroalgae are competitively dominant in areas of intermediate disturbance (see Table 3.3 and Figure 3.11) and sessile invertebrates dominate in areas of low disturbance.

It appears that processes that regulate local spatial and temporal patterns in the kelp understorey at Cape Hangklip can only be understood when mechanistic causes are revealed. Mosteller and Tukey (1977) indicate that three types of information are required to support causality: **consistency**, **responsiveness** and a **mechanism**. There is not sufficient information in this study to satisfactorily demonstrate any of these.

The results show that the statistical analyses used in this chapter (TWINSPAN and CCA) are useful in interpreting complex data from the phytobenthic zone, giving ecologically relevant results. Such analysis helps reveal species assemblages and highlights environmental factors which may cause the observed patterns. Numerical analyses in this chapter indicates that the broad patterns of species distribution in the understorey of a kelp bed at Cape Hangklip are primarily defined by abiotic factors such as depth and to a lesser extent sand cover. Biotic interactions, such as grazing, competition for light and competition for space, and abiotic factors such as aspect and substrate become more important at a smaller temporal and spatial scale. Many of these organizational processes however do operate at both scales and not necessarily by the same process, or of equal influence, at each scale.

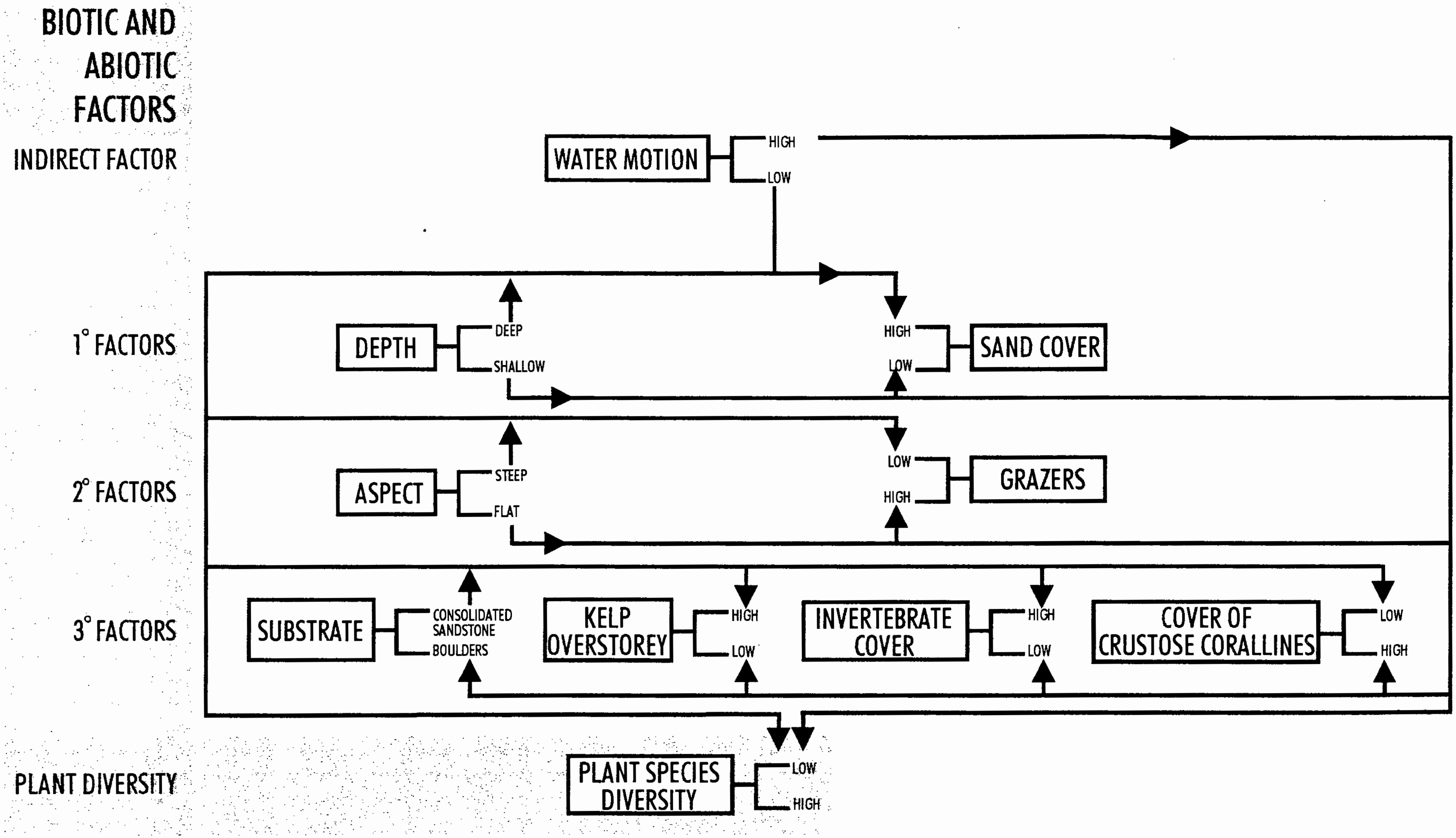


Figure 3.17 A hierarchy of biotic factors measured in this study and their inter-correlation. The effects of the extremes of each variable on other variables and plant species diversity is shown. The direction of the arrows indicate the regulatory pathways and point from postulated cause to effect.

APPENDIX 3.1: Depth distribution of subtidal algal species documented from the depth-stratified quadrats at the four study transects at Cape Hangklip.

SPECIES	DEPTH RANGE (m)			
	Transect 1	Transect 2	Transect 3	Transect 4
Caulerpa holmesiana	4.2 - 7.6	2.5 - 9.9	3.8 - 9.9	3.4 - 9.9
Cladophora mirabilis	2.8 - 5.1	2.1 - 5.1	3.0 - 9.9	1.9 - 6.4
Codium stephensiae	2.8 - 3.2	1.5 - 4.6	1.4 - 9.9	1.8 - 9.8
Ecklonia maxima	1.5 - 7.3	1.5 - 11.0	1.4 -9.8	3.2 - 9.8
Halopteris funicularis	2.2 - 7.6	7.0 - 11.0	4.8 - 9.9	2.7 - 8.9
Laminaria pallida	5.1 - 6.1	2.1 - 11.0	4.8 -9.9	3.4 - 9.1
Amphiroa capensis	3.7 - 4.6	2.1 - 8.9	2.3 - 9.9	2.2 - 9.8
A. ephedraea	1.5 - 7.2	1.5 -5.4	1.4 - 9.9	1.8 - 9.8
Arthrocardia sp.	1.5 - 7.2	1.2 - 9.1	1.4 - 9.9	1.8 - 9.1
Bartoniella crenata	3.9 - 7.3	2.7 - 11.0	4.5 - 7.0	6.8 - 8.9
Champia compressa	3.2 - 7.6	1.5 - 10.9	1.4 - 9.8	1.9 - 9.8
Cheilosporum sagitatum	1.8 - 7.6	1.2 - 7.0	1.4 - 9.9	2.1 - 7.5
Corallina sp.	4.7 - 7.2	5.4 - 8.9	2.5 - 8.9	3.4 - 8.8
Gymnogongrus glomeratus	3.2 - 7.6	7.0 - 11.0	3.8 - 9.9	8.6 - 8.9
Jania crassa	3.7 - 7.6	1.2 - 7.0	1.4 - 9.9	7.1 -9.8
Laurencia flexuosa	2.8 - 3.1	2.1 - 4.6	1.9 - 9.8	4.2 - 8.4
L. obtusa	6.8 - 7.1	1.9 - 2.4	4.1 -6.4	2.7 - 5.6
Pachymenia cornea	3.9 - 6.5	5.1 -11.0	5.3 - 7.3	4.5 - 9.2
Phloiocaulon squamulosum	2.0 -5.1	9.5 - 11.0	5.1 - 5.3	3.9 - 9.2
Plocamium corallorhiza	3.1 - 6.1	1.9 - 10.9	1.4 - 9.9	4.1 - 8.9
P. cornutum	6.7 - 6.9	1.2 - 7.0	3.8 - 4.1	1.8 - 3.7
P. rigidum	2.2 - 7.6	1.2 - 9.3	1.4 - 9.8	1.8 - 9.2

SPECIES	DEPTH RANGE (m)			
	Transect 1	Transect 2	Transect 3	Transect 4
P. suhrii	2.3 - 7.3	1.2 - 11.0	3.0 - 9.9	4.5 - 9.8
Polyopes constrictus	4.9 - 6.7	1.2 - 11.0	3.0 - 3.4	5.9 - 8.9
Pterosiphonia cloiophylla	1.5 - 7.6	1.2 - 11.0	1.9 - 9.9	2.1 - 9.8
Rhodymenia natalensis	4.6 -6.7	1.2 - 5.1	4.8 - 7.0	5.9 - 6.2
Cheilosporum multifidum	2.2 - 5.1	1.2 - 2.1	4.9 -5.9	6.2 - 6.4
Corallina officianalis	4.2 - 6.5	2.3 - 2.5	1.9 - 9.9	6.9 - 7.1
Botryocarpa prolifera	3.7 - 7.6	5.2 - 11.0	4.8 - 9.9	4.1 - 8.1
Thamnophyllis discigera	4.2 - 7.8	8.9 - 11.0	6.5 - 7.0	9.0 - 9.8
Caulerpa bartoniae	3.7 - 3.9	1.8 - 1.9	3.4 - 3.7	
Anthophycus longifolius	2.2 - 4.2	3.5 - 9.8	1.4 - 3.4	
Acrosorium maculatum	2.5 - 7.6	1.5 - 9.8	3.2 - 9.8	
Ceramium planum	2.5 - 3.2	1.2 - 7.0	2.8 - 3.4	
Cheilosporum cultratum	6.3 -6.5	1.2 - 5.2	3.4 - 5.1	
Gelidium capense	6.2 - 6.4	8.7 - 11.0	3.4 - 5.0	
Hypnea spicifera	2.2 - 5.0	2.3 - 2.5	3.2 - 3.5	
Jania verrucosa	6.5 - 7.1	4.6 - 6.9	5.0 - 6.9	
Centroceras distichum	3.0 - 3.2	4.9 - 5.2	3.0 - 3.8	
Cladophora sp.	4.7 - 7.2	5.0 - 7.0	3.5 - 3.7	
Erythroglossum sp.	3.9 - 7.3	5.2 - 7.0	3.5 - 3.8	
Acrosorium maculatum	6.8 - 7.2	1.2 - 5.1		
Gigartina insignis	3.7 - 7.6	4.6 - 11.0		
G. radula	1.5 - 7.1	2.3 - 2.6		
Gymnogongrus polycladus	6.7 - 6.9	5.2 - 5.7		
Pterosiphonia spinifera	3.9 - 7.6	1.8 - 2.1		

SPECIES	DEPTH RANGE (m)			
	Transect 1	Transect 2	Transect 3	Transect 4
Aristothamnion collabens	6.5 - 6.7	6.6 - 6.9		
Callithamnion cordatum	6.3 - 6.5	5.2 - 5.7		
Arthrocardia duthiae	6.2 - 6.8	2.1 - 2.5		
Sargassum heterophyllum		2.5 -11.0	6.8 - 7.0	1.8 - 9.2
Zonaria subarticulata		7.0 - 11.0	2.5 - 9.9	2.1 - 9.8
Epymenia capensis		9.7 - 11.0	3.5 - 3.7	8.7 - 8.9
Plocamium maxillosum		9.6 - 9.8	3.2 - 3.5	3.7 - 6.4
Ceramium capense		1.5 - 1.7	3.2 - 3.8	
Rhodophyllis reptans		8.9 - 9.9	6.5 - 7.7	
Pollexfenia laciniata		9.4 - 10.6	4.8 - 5.3	
Zonaria harveyana			3.9 - 6.8	2.7 - 6.2
Ulva capensis	4.2 - 5.4		3.2 - 4.1	6.0 - 6.4
Bifurcariopsis capensis	1.1 - 3.1		1.7 - 3.5	1.6 - 4.1
Heterosiphonia dubia	3.7 - 7.6		3.4 - 9.1	5.7 - 9.2
Desmarestia firma	5.0 - 5.4	8.7 - 11.0		8.2 - 8.4
Acrosorium uncinatum	3.9 - 7.6	4.6 - 4.9		8.6 - 8.9
Aphanocladia skottsbergii	3.2 - 7.6	9.5 - 10.6		6.2 - 6.7
Trematocarpus flabellatus	3.2 - 7.3	5.2 - 11.0		4.5 - 6.3
Cladophora virgata	2.5 - 7.6	1.5 - 11.0		8.2 - 8.8
C. capensis	5.1 - 6.7		9.6 - 9.9	
Iridaea capensis	1.4 - 3.2		3.2 - 4.1	
Kallymenia agardhii	7.3 - 7.6		4.8 - 7.0	
Pachymenia carnosa	1.3 - 6.9		3.4 - 6.1	
Scinaia capensis	1.9 - 5.1		5.8 - 6.4	

SPECIES	DEPTH RANGE (m)			
	Transect 1	Transect 2	Transect 3	Transect 4
Antithamnion sp.	5.0 - 5.4		3.2 - 3.8	
Sphacelaria sp.	6.5 - 6.8		6.9 - 9.8	
Codium papenfussii	1.5 - 6.5			8.9 - 9.2
Aeodes orbitosa	1.1 - 3.9			1.5 - 2.1
Chondria capensis	4.6 - 7.1			5.0 - 5.7
Herposiphonia prorepens	6.5 - 6.8			8.9 - 9.2
Arthrocardia palmata		1.9		8.8 - 9.2
Gelidium pteridifolium		3.5 - 5.4		1.8 - 5.9
Cladophora rugulosa	2.1 - 2.4			
Ulva rigida	1.4 - 7.6			
Colpomenia sinuosa	1.1 - 1.6			
Ceramiaceae indet.	2.5 - 7.2			
Gigartina pistillata	6.9 - 7.1			
G. scutellata	4.7 - 5.1			
Jania capillacea	2.7 - 7.6			
Gelidium reptans	2.5 - 6.8			
Nemastoma lanceolata	3.7 - 7.6			
Nienburgia serrata	3.7 - 6.1			
Pachychaeta cryptoclada	6.8 - 7.3			
Schizymenia obovata	4.7 - 5.0			
Tayloriella tenebrosa	5.4 - 7.6			
Trematocarpus fragilis	4.5 - 4.7			
Ulva sp.	1.8 - 5.1			
Gigartina stiriata	2.3 - 2.5			

SPECIES	DEPTH RANGE (m)			
	Transect 1	Transect 2	Transect 3	Transect 4
Ballia callitricha	4.2 - 5.1			
Jania sp.	3.9 - 4.2			
Gracilaria verrucosa	3.9 - 6.5			
Heterosiphonia crispa	4.2 - 6.9			
Hypnea ecklonii	3.7 - 5.1			
Ophidocladus simpliciusculus	3.9 - 7.3			
Platythamnion capense	3.9 - 6.5			
Dasya sp.	5.4 - 6.9			
D. scoparia	5.4 - 6.5			
Bornetia repens	6.7 - 6.9			
Falkenbergia rufulonosa	6.5 - 7.2			
Pollexfenia minuta	7.0 - 7.2			
Polysiphonia virgata	7.6			
Axillariella constricta		9.6 - 11.0		
Arthrocardia flabellata		1.6 - 2.5		
Champia lumbricalis		1.2 - 2.3		
Gigartina bracteata		9.5 - 11.0		
Griffithsia subbiconica		4.9 - 5.2		
Pleonosporum harveyanum		9.6 - 11.0		
Callophycus densus		9.7 - 9.8		
Dictyota dichotoma			2.3 - 3.0	
Suhria vittata			5.0 - 5.3	
Delesseria papenfussii			6.2 - 6.4	
Halicystis sp.			1.8 - 2.1	

SPECIES	DEPTH RANGE (m)			
	Transect 1	Transect 2	Transect 3	Transect 4
Compsothamnionella sciadophila			3.2 - 9.1	
Colaconema caespitosum			7.0 - 7.5	
Symphocladia marchantioides			4.8	
Acrochaetium catenulatum			6.6 - 6.8	
Audouinella endophytica			6.5 - 6.8	
Apoglossum ruscifolium				3.7 - 3.9
Carpomitra sp.				4.1
Chordariopsis capensis				6.9
Delisea flaccida				8.6 - 8.9
Gracilaria capensis				8.7 - 8.8

CHAPTER 4

EFFECTS OF SEDIMENTATION ON THE COLONIZATION AND EARLY POST-SETTLEMENT STAGES OF THREE RED ALGAL SPECIES

INTRODUCTION

One of the most fundamental and precarious stages in the life history of a marine benthic alga is colonization of new substratum. The colonization and survival of early post-settlement (EPS) phases of spores of marine macroalgae is considered critical to the successful establishment of benthic populations. The first cell divisions that lead to holdfast differentiation are particularly important because the holdfast determines the tenacity of a plant and fixes its place in life (Fletcher & Callow 1992). A number of studies on algae suggest that high mortality occurs during EPS phases (Gunnill 1986, Pearson and Evans 1990, Vadas *et al* 1990). It is possible that processes influencing EPS stages may affect not only the ecology of a species but also its evolution and role in communities. Past studies on the ecology of EPS stages have highlighted the variability in, and multiplicity of, factors preventing successful recruitment of early stages of benthic algae. Vadas *et al* (1992) have broadly categorized the processes influencing EPS stages as **intrinsic** (polyspermy; age-specific survival; growth rate and size; mast year effects; germination and spore viability; and attachment setting time) and **extrinsic** (substratum; sediment, silt and scour; water motion; dessication; temperature, nutrients and insolation; canopy effects; turf and invertebrate covers; density and competition; grazing; and spatial and temporal refuges).

One of these extrinsic factors, sand deposition and movement, has begun to receive empirical attention in the literature (eg. Daly and Mathieson 1977, Robles 1982, Taylor and Littler 1982, Littler *et al* 1983, Stewart 1983, Bally *et al* 1984, D'Antonio 1986, McQuaid and Dower 1989, Kendrick 1991, Dexter 1992). Several authors have noted the decreased diversity (Stephenson and Stephenson 1972, Phinney 1977, Engledow and Bolton 1994) or increased diversity (Foster 1975b, Taylor and Littler 1982, Dower 1989, this thesis) of organisms associated with sand-influenced intertidal and subtidal rocky habitats. Many investigators have also described species characteristically associated with sandswept habitats (eg. Markham and Newroth 1972, Markam 1973, Daly and Mathieson 1977, Phinney 1977, D'Antonio 1986, Chapter 3). Markham and Newroth (1972) suggest that several of these species may be dependent upon sandy conditions for survival[5]. Stewart (1983) suggests that seasonal variations in relative abundance of algal species and the persistence of the several perennial species that dominate the vegetation may be consequences of adaptations to the presence and movement of sediment in the habitat. For example, several of the perennial, psammophytic (sand-dwelling) and silt-tolerating species exhibit incomplete or asexual life histories, usually allied to remarkable powers of regeneration (Markham 1969, Newroth and Markham 1972, Lewis and Kraft 1979, Stewart 1983, D'Antonio 1986). Norton *et al* (1982) suggest that such asexual life histories are functionally equivalent to vegetative reproduction as they may be advantageous in such habitats and ensure continued genetic stability. In addition, vegetative propagation (eg. by stolons) may allow a plant to withstand periods of heavy siltation (eg. *Caulerpa filiformis* at the study site). In some instances, sand burial and abrasion stimulates branching and influences thallus width (e.g. *Zonaria farlowii* - Dahl, 1971). The effects of moving sand as a disturbance agent include removing plant tissue, epiphytes or invertebrates with poor attachment to the rock surface (scouring), and decreasing light, oxygen and substratum available to organisms (burial). The depth and duration of burial or degree of water movement will be important in determining the intensity of the disturbance.

The effects of sand deposition and sand scour on EPS stages of benthic marine algae have however not received much attention. In the limited literature available, algal propagules and EPS stages have been shown to suffer considerable stress and mortality from silt and sediments. Devinny and Volse (1978) postulated at least 4 mechanisms of sediment damage to germlings; (i) if sediment is on the substrate when the spore settles, attachment to the surface may be prevented; (ii) once the spore is settled, an ensuing episode of sedimentation could smother it, cutting off light and nutrients; (iii) if sediment is present in turbulent water, spores may be damaged by scouring action; and (iv)

---

[5] *For example, Chapter 3 found one species, Jania capillacea, to be strongly correlated to, and perhaps dependent on, sand cover.*

sediments could change the chemical and biological nature of the microenvironment surrounding the spore. These effects have been experimentally tested in only a few cases (eg. Neushul *et al* 1976, Norton 1978, Devinny an Volse 1978, Dean *et al* 1983, Kendrick 1991) but disturbance by sand appear to have important effects on composition and diversity within certain kelp forests (eg. Markham 1973, Rosenthal *et al* 1974, Dayton 1975, Foster 1975a, Grigg 1975, Foster *et al* 1983, Chapter 3) and other intertidal and subtidal communities (eg. Daly and Mathieson 1977, Stewart 1983, Littler *et al* 1983 D'Antonio 1986, Dower 1989).

In this chapter, I experimentally test the influence of sand burial and sand movement in suspension (scour) on the settlement and early post-settlement (EPS) stage of three sublittoral fringe red algae, *Aeodes orbitosa* (Family: Halymeniaceae), *Gigartina radula* and *Iridaea capensis* (both Family: Gigartinaceae). All three species were found in the intertidal and shallow sublittoral along the research transects at the study site, the results of which are presented in Chapters 2 & 3. These three carrageenophytes, recorded from the shallow subtidal (0.5 - 3m depth) of the sheltered transect (Transect 1) at the Cape Hangklip site, were subjectively selected to represent a gradient of tolerance to sand inundation (*Aeodes orbitosa* < *Gigartina radula* < *Iridaea capensis*).

A. orbitosa grows in the intertidal and shallow subtidal (to 3m depth) of the sheltered transect, transect 1. The broadly lobed olive-brown or yellowish blade is tough and extremely slippery with simple to finely toothed margins (in older specimens). A stipe is absent and the holdfast is generally a thickened disc. The blade may exceptionally reach a length of 1.5m and almost the same width, but in general, this broadly elliptical lamina reaches a breadth of about 30cm (Simons and Hewitt 1976). Under exposed conditions, thalli are small and stunted (Molloy 1990). Although occurring in areas subject to sand movement at the study site, *A. orbitosa* appeared to be sensitive to sand burial and consequently was recorded on rocks where sand failed to settle and where water motion appeared to be higher. Both *A. orbitosa* and *I. capensis* have isomorphic gametophytes and tetrasporophytes. Chiang (1970) has suggested that *A. orbitosa* be seperated from *Aeodes* as an autonomous genus on the basis of vegetative structure.

G. radula is common in the low intertidal zone, especially in sheltered areas. Although recorded subtidally at a depth of 7m in the sheltered transect, *G. radula* is typically scattered in the shallow subtidal (to 3m depth). *G. radula* has tough, fleshy, oval blades with a small disc holdfast and a short stem with lateral blades. Blades (15cm long and 20-30mm wide) are rubbery and dark reddish-brown. The female gametophyte is covered with knobbled papillae (cystocarps) reminiscent of a rough tongue. The male plant has many fleshy protuberances. The tetrasporophyte is more ear-like with a pointed tip, a smooth marginal region, and the surface has a network of ridges and grooves. *G. radula* appears to tolerate low to moderate occasional sand burial in sheltered areas, but appears to be susceptible to sand scour in areas of moderate to high water motion. The applicability of the name *G. radula* to the southern African species may be questionable, because the type specimen of this species is of a subtidal species from Australia (Bolton pers. comm.). The species has been given the name *Gigartina polycarpa* by Hommersand *et al* (1994), although there is currently no full consensus over this nomenclature.

I. capensis is common intertidally, often forming a narrow zone above the more abundant *Aeodes* (Bolton pers. comm.), and persists subtidally to a depth of 4m. *I. capensis* has, characteristically, an insignificant holdfast producing one or two thin, rubbery and strap-shaped blades. The blades narrow proximally into chanelled stipes with turned up thallus margins. The distribution of *I. capensis* is almost entirely confined to areas of rocky shore directly affected by sand action and periodic inundation, from the mid eulittoral zone into the immediate subtidal (Bolton and Levitt 1992). *I. capensis* appears to be the only species of this trio which may be tolerant to high levels of sand inundation in bays sheltered from direct wave action. Bolton and Joska (1993) note that the epilithic crustose phase of *Iridaea* can survive for months under sand and, when the sand clears, produces many individual juveniles. *Iridaea capensis* has been transferred to *Mazaella* by Hommersand *et al* (1994).

The size of carpospores and tetraspores of these species is generally similar, falling in the range 10 - 16μm in diameter. Tetraspores of *Aeodes* were significantly larger (20-25μm). However, during the course of this experiment, although fertile *Aeodes* sporophyte plants were located, tetraspore release was infrequent and in extremely low densities. Survival rates of tetraspores of *Aeodes* have consequently not been included in the results.

Iridaea and *Gigartina* exhibited two distinct developmental sequences. One sequence, the most common, produces a discoid, radially symmetrical holdfast. The other sequence, which is infrequent and occurs where spore density is significantly lower (ie. at edges of spore mass), produces a filamentous mat with a rhizoidal base. It has been speculated that the two patterns of development may be influenced by substratum contact (West 1972, West and Crump 1974), mucilage differences (Chen and Taylor 1976), differences in individual spore densities (Ring 1970) or a complex of these (Sylvester and Waaland 1984). The first few cell divisions of the discoid sequence were not accompanied by cell enlargement, and the sporelings remained approximately the same size as the original spore. SEM showed a strong polysacharide connection of the sporeling to the substrate. At first young discs are monostromatic throughout, and later became polystromatic in the centre. Erect fronds were issued from a basal disc 3 weeks to 1 month after settlement.

In *Aeodes*, the carpospores begin to germinate by pushing out a germ tube from one side, one or two days after the start of germination. Then the contents of the spore cells migrate into the tube. The germ tube is then separated from the empty mother spore body by a cross wall, forming the initial cell of the germling. The initial cell is divided into two daughter cells by a transverse cleavage at the centre. Successive parallel division takes place to result in a multicellular disc-shaped sporeling.

The effects of four mechanisms of sediment damage on the carpospores and tetraspores of *Aeodes*, *Gigartina* and *Iridaea* were tested: (i) prevention of tetraspore/carpospore attachment by sand burial; (ii) prevention of tetraspore/carpospore attachment by sand in suspension (water movement); (iii) damage to attached spore by burial; and (iv) damage to attached spore by sand in suspension (water movement).

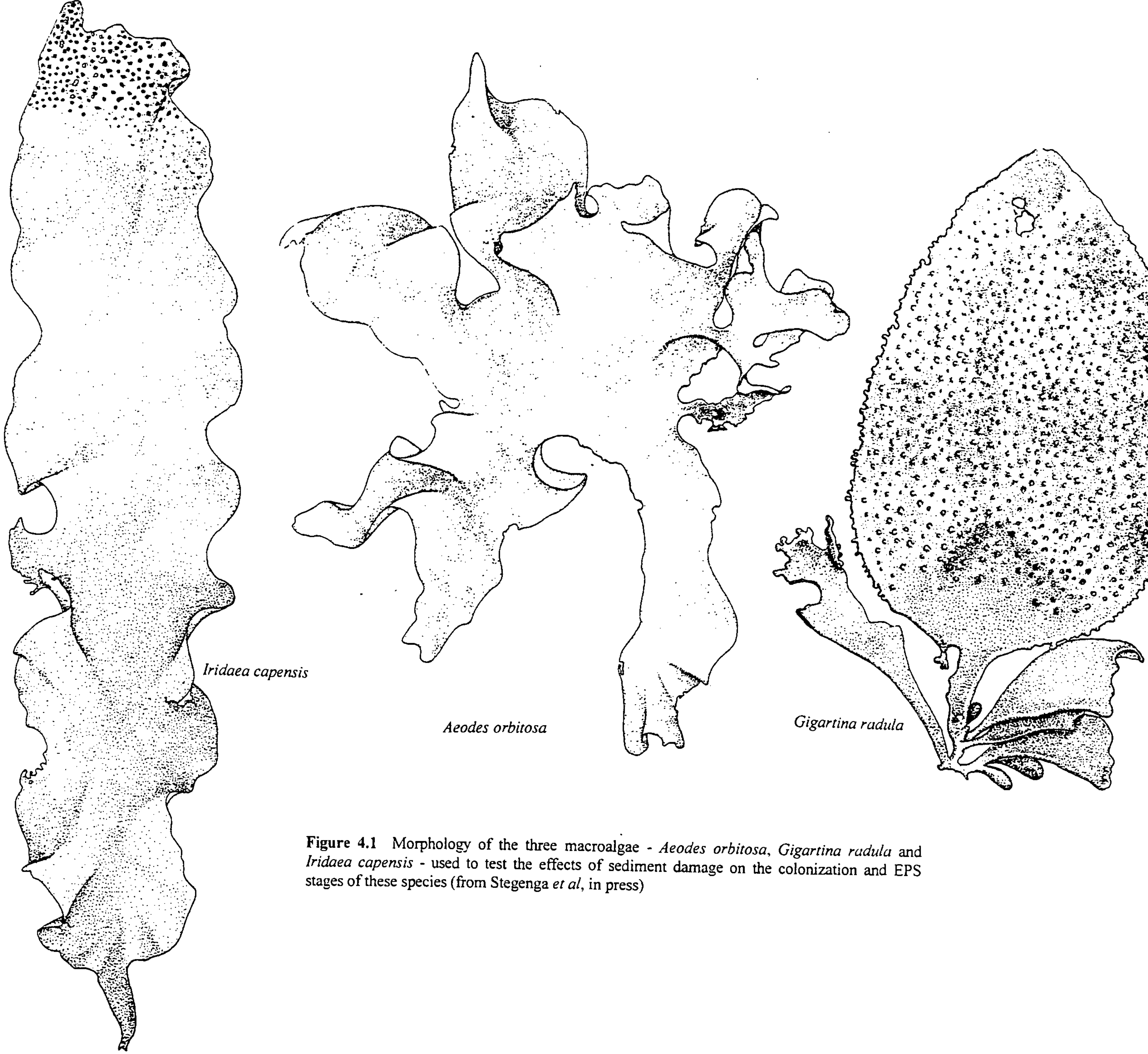


Figure 4.1 Morphology of the three macroalgae - *Aeodes orbitosa*, *Gigartina radula* and *Iridaea capensis* - used to test the effects of sediment damage on the colonization and EPS stages of these species (from Stegenga *et al*, in press)

METHODS

Culturing

Fertile sporophyte and gametophyte specimens of *Aeodes orbitosa*, *Gigartina radula* and *Iridaea capensis* were collected from the sublittoral fringe of a stretch of sand-affected shore at Kommetjie (34^0 08'S, 18^0 20'E), on the west coast of the Cape Peninsula, South Africa during the summer months of 1991. *Iridaea* plants were subjected to the resorcinol test to separate gametophytes and sporophytes (Garbary and de Wreede 1988). Sections were made of fertile *Aeodes* to identify the sporophyte and gametophyte plants, as tetrasporangia occur singly in this species. *Gigartina* life history phases were identified morphologically. Fertile, epiphyte-free fronds from sporophytes and gametophytes of all species were cut into a number of strips (approx 5mm x 20mm) and placed above glass slides in crystallizing dishes with 200ml of enriched sea-water medium (30% strength PES: Provasoli 1968) to which 0.1ml l^{-1} of a saturated solution of germanium dioxide had been added to inhibit diatom growth. Frond portions were removed the following morning. The liberated spores were used for the experimental manipulations. All cultures were maintained at 15^{0}C under cool white fluorescent lamps with a daily cycle of 16h light: 8h dark and at an irradiance of 5-10 μmol m^{-2} s^{-1}. Germinating spores in control dishes (no sand) were counted to determine the density of each set of cultures.

Test sediment

The test sediment was collected from Kommetjie and oven-dried at 150^{0}C for 24h to ensure that it would be biologically inert. The sediment was spread in petri dishes by mixing it with a measured amount of enriched sea-water medium and pouring the mixture into the plate. To ensure comparative results with similar experimental manipulations by Devinny and Volse (1978), amounts of sediment are reported as mg cm^{-2} (dry weight). Four sand concentrations were used in the experimental manipulations - 40, 60, 80 and 100mg cm^{-2}. Amounts of sediment greater than about 60mg cm^{-2} formed a layer which completely covered the slide surface. During experiments where flasks (in place of petri dishes) were agitated, the sediment typically formed uneven, shifting deposits.

Counting

The success of the experimental cultures was assessed by counting the number of attached, normally developing germlings after 4 days. Devinny and Volse (1978) suggested that harmful effects of sediment burial or scour occur almost immediately, and longer experiments (8 and 16 days) show no significant difference to those results shown at 4 days. For each count, the slide was removed from the petri dish/flask, rinsed gently to remove the sediment, and protected with a cover slip. Spores were counted as surviving if germination had occurred. Five random microscope fields (400X magnification) were examined and the number of germlings within each counted. Mean spore counts in experimental cultures were divided by those for control plates (standard) to determine "relative survival" rates expressed in percent. For each species and treatment three replicates were done.

Experimental cultures

Interference with spore attachment

(i) The effects of *in situ* sediment on spore attachment was tested by pipetting an inoculum[6] into plastic petri dishes (20ml seawater) with varying concentrations of sediments already in place.

(ii) The effects of sand in suspension, on the settlement and attachment of spores, was tested by pipetting an inoculum into a flask (200ml) mounted on a shaker (Derrick Manufacturing Company, Model 150) with varying concentrations of sand already in partial suspension. An oscillatory motion with an amplitude of 5mm and a frequency of 5 cycles per second was produced. Average water velocity was thus approximately 5cm sec^{-1}.

---

[6] *Inoculum was prepared from spores liberated less than 6h previously because spores liberated 24h or more showed greater developmental abnormalities than freshly liberated spores. Many did not attach to the substrate, developing as irregular spheres or rhizoidal types in the Gigartinaceae.*

Damage to spores by burial

Spores were allowed 24h to attach to the slide before sediment was added. The cultures were initiated in 200ml of seawater and slides were transferred to petri dishes with 20ml of seawater. The sediment was suspended in 10ml and added to the petri dishes.

Damage to spores by moving sand

Spores were allowed 24h to attach to the slide before sediment was added. Effects in moving waters were tested by placing the experimental culture in flasks with seawater, adding varying concentrations of sediment, and mounting these on the shaker (see above for details of setting).

RESULTS

For all treatments and at all sediment concentrations, *Iridaea* carpospores and tetraspores showed the highest relative survival (Figure 4.1). *Gigartina* spore survival however was still comparatively high and not significantly different (one-way ANOVA) to that of *Iridaea*. *Aeodes* spore survival was consistently significantly lower than that of *Iridaea* and *Gigartina* for all treatments and sediment concentrations (one-way ANOVA; $P<0.05$).

Interference with spore attachment

(i) The effects of *in situ* sand on the relative survival of the spore inocula was marked for all species (Figure 4.1A). No germinating spores were found at *in situ* sediment concentrations of 100 mg cm^{-2}. Sand tended to settle in clumps and, at sediment concentrations of 60 mg cm^{-2} or less, parts of the substrate (slide) were partially visible. It was in these areas that high germination of spores occurred. *Aeodes* typically showed the poorest relative survival at all sediment concentrations.

(ii) The relative survival of spores, when added to sand in suspension, was generally 3-10% lower (Figure 4.1C) than in (i) above, notably at concentrations of 60 mg cm^{-2} or less. The general trends of spore germination at different concentrations of sediment in suspension was generally the same as the trends for *in situ* sand. No germinating *Aeodes* were found at sediment concentrations greater than 60 mg cm^{-2}. This treatment appeared to have the strongest negative impact on relative survival of all spores.

Damage to spores by burial

Spores given an initial 24h to attach before addition of sediment were considerably more resistant to damage (Figure 4.1B) than those where sediment was introduced prior to spore release and settlement (Figure 4.1A). For *Gigartina* and *Iridaea* spores, relative survival stayed reasonably constant at sediment concentrations of 60 mg cm^{-2} or more.

Damage to spores by moving sand

Spores given an initial 24h to attach were subjected to movement of sand in suspension. Mean relative survival of *Iridaea* carpospores and tetraspores was significantly higher (one-way ANOVA; $P<0.05$) than *Gigartina* and *Aeodes* (Figure 4.1D). In general, allowing a day for the spores to settle only marginally alleviated spore damage. At a sediment density of 100 mg cm^{-2}, allowing spores to settle or releasing them into moving sediment made no significant difference (2-way ANOVA) to the impact on spore survival.

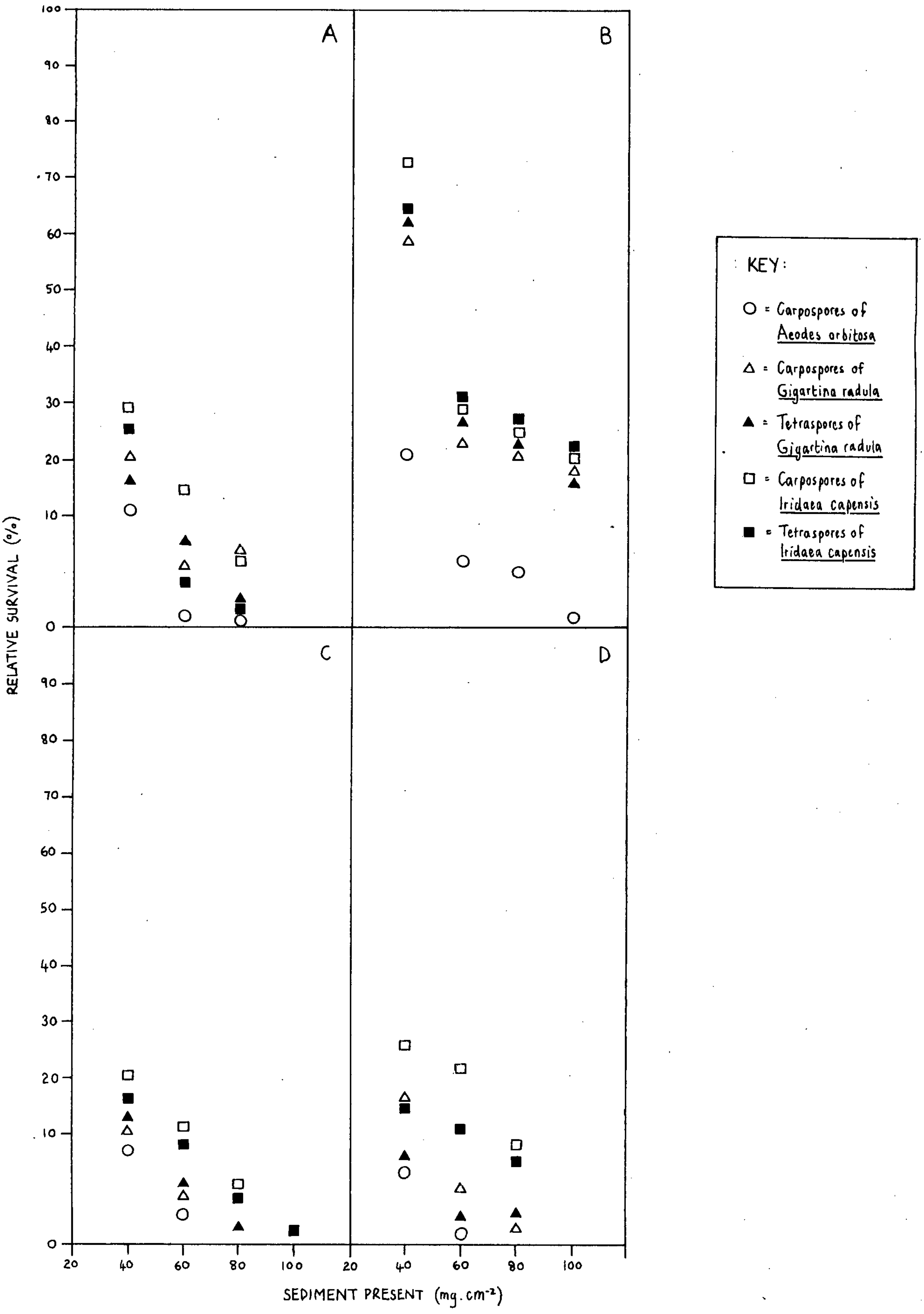


Figure 4.2 Relative mean survival of carpospores (○) of *Aeodes orbitosa*, carpospores (△) and tetraspores (▲) of *Gigartina radula* and carpospores (❑) and tetraspores (■) of *Iridaea capensis* when subjected to different treatments; (a) sediment applied before spore attachment, (b) sediment applied after spore attachment, (c) sediment and water motion applied before spore attachment, (d) sediment and water motion applied after spore attachment.

DISCUSSION

The results of the experimental treatments reported here are generally consistent with other experimental and field observations reported elsewhere.

Prevention of attachment by sand burial

Where sediment is present before spore release, the proportion of spores attaching to the glass slide substrate was roughly equivalent to that amount of substrate not covered by sediment. High concentrations of sediment led to poor survival of all spores. Norton (1978) similarly showed that, in culture, an underlying layer of silt prevented attachment of young kelp sporophytes. In similar experiments to those carried out in this chapter, Devinny and Volse (1978) postulated that spores of *Macrocystis* may have attached to the sand grains and are lost when the slide is washed. This postulation was based on the fact that Neushul (1971) and North (1971) had showed that *Macrocystis* commonly grows attached to sediment. However, a test of sand grains and seawater washed away during preparation for counting in these experiments revealed a large number of abnormally-developing or undeveloped, unattached spores of *Gigartina*, *Iridaea* and *Aeodes*. *Gigartina* and *Iridaea* also secondarily attached to sand grains, but generally in small numbers. An alternative explanation may be that germination is delayed or staggered because of unfavourable "recruitment windows" (Reed *et al* 1988). Dayton (1975) suggests that for some species propagule longevity may provide a "dormancy strategy" until conditions favour growth. However, in the majority of red macroalgae investigated to date, spore germination proceeds soon after attachment with no obvious resting stages apparent (Fletcher and Callow 1992). It is suggested that in natural conditions these undeveloped or abnormally developing spores of the test species will probably not survive.

Prevention of attachment by sand in suspension

The effects of flow and turbulence on spore settlement and attachment have been previously documented. For example, North (1969) reported experiments in which significantly reduced spore attachment success was recorded in moving water. Charters *et al* (1972) tested the effects of water motion on the adhesion of algal spores to submerged substrates and showed that the fraction of carpospores of *Agardhiella tenera*, *Cryptopleura violacea* and *Gracilariopsis sjoestedtii* remaining attached after exposure to simulated wave surge depended on the time that the spores had been in contact with the surface. Devinny and Volse (1979) also experimentally showed lower mean survival rates of spores in moving water. However, in nature water movement may not act independently of scour and, in the treatment where sand was kept in suspension before spore release, spore survival was extremely low at high sand concentrations. This is comparable with the results of Devinny and Volse (1978) who reported that, at only 7.1 mg cm $^{-2}$ sediment concentration, the difference in relative survival of spores of *Macrocystis pyrifera* between the still and agitated plates was highly statistically significant. Thus, the effect of water motion and sediment were found to both be detrimental to spore survival, but the effects in combination were significantly more harmful than either alone (Devinny and Volse 1978). In this study, this treatment had the most detrimental impact on relative survival of all spores.

Damage to attached spores by burial

If the spores were allowed to settle and attach, prior to sediment burial, the *Gigartina* and *Iridaea* spores were considerably more resistant to damage. Survival was relatively high for these species with less than 100 mg cm^{-2} sand cover (>15%). Devinny and Volse (1978) found that about 10% of *Macrocystis pyrifera* spores developed even under 108 mg cm^{-2}. North (1970) however found that even small amounts of sediment had significant deleterious effects on recruitment of *Macrocystis.* In an experimental manipulation, North (1970) seeded slides with embryo sporophytes and these were suspended in Newport Bay. When portions of the slide were covered with sediment, sporophytes in those portions did not develop. Adjacent, uncovered areas of the slide supported normal growth. Neushul *et al* (1976) observed high settlement, early recruitment and high mortality on subtidal settling plates. They found it difficult to quantify sediment effects, but differences between naturally swept-free and sedimented areas of their test apparatus showed marked differences in species composition. They concluded that sedimentation was an important source of mortality to EPS stages, especially in winter. Dayton (1975) suggests that the total absence of *Hedophyllum* plants from a site where transplanted adults survived was likely due to siltation on EPS stages. Moss *et al* (1973) noted that silt was a major factor inhibiting colonization of *Himanthalia*, and suggested that reduced light prevented germination. There has however been no assessment of the long-term survival of germlings which have been buried under sand after initial settlement and attachment. Results from Devinny and Volse (1978) and this study indicate that persistence of these germlings under periodic sand burial may be ecologically significant. Devinny and Volse (1978) suggest that the effects of burial probably arise from alteration of the chemical or physical characteristics of the microenvironment of the germling. It is postulated here that germlings may not survive for long periods buried under sand. Foster's (1975b) assertion that occasional burial of germlings (and adult plants) by shifting sand may be an important factor in maintaining subtidal diversity because it clears substrate for further colonization, is supported.

Damage to attached spores by sand in suspension

Although water movement has long been suspected of influencing settlement, attachment and survival of algal propagules (Lewis 1968), the effects of moving sand on spore survival after attachment is generally unknown. In the experiment where spores were allowed to settle and attach, prior to treatment with sand in moving water, the effects on relative survival were extreme at high concentrations of sand (>80mg cm^{-2}). At lower sand concentrations (<80 mg cm^{-2}), *Iridaea* consistently showed significantly higher relative survival than *Gigartina* and *Aeodes*. This treatment perhaps simulates most closely the natural conditions prevailing in the study site at Cape Hangklip where all three species co-occurred. Sediment carried in moving water may induce high mortality of EPS stages (see Neushul *et al* 1976, Emerson and Zedler 1978) or prevent the settlement of propagules (see Vadas *et al* 1992). Scour caused high mortality to spores and gametophytes of *Macrocystis* in culture (Devinny and Volse 1978) and was important in substratum-associated mortality to gametophytes and EPS stages in nature (Dayton *et al* 1984, Neushul *et al* 1976). Underwood and Jernakoff (1981) found that despite a reduction in molluscan grazers at one site, sand scour prevented macroalgae from colonizing. Although ecological effects of sand scour have been hypothesised (eg. Neushul *et al* 1976, Underwood and Jernakoff 1981, Dayton *et al* 1984, Gunnill 1986) only Devinny and Volse (1978) and Kendrick (1991) have experimentally addressed the relationship between algal recruitment and sediment movement. Devinny and Volse (1978) showed that sediment reduced survival of *Macrocystis* germlings in both still and moving water. The effects were shown to be more severe in moving water, however. At

7.1 mg cm^{-2} sediment concentration the difference between still and agitated plates was highly statistically significant. Kendrick (1991), in studies of crustose coralline and filamentous turf algae in the Galapagos archipelago (Ecuador), found that crustose corallines were associated with environments of scour whereas filamentous turf-forming species were more common in environments of sediment accretion and sedimentation.

Ecological interpretation

A few reports suggest that sediment can also have a positive influence on EPS stages. For example, Kennelly (1983) suggested that sedimentation provided nutrients for early development of EPS stages or protection of these EPS stages from disturbance (eg. grazing). D'Antonio (1986) proposed a number of mechanisms, none of which are mutually exclusive, which benefit the EPS and adult stages of the psammophilic *Rhodomela larix*: (1) sandy areas may serve as refuges for *R. larix* from the potentially detrimental effects of large herbivores such as chitons and sea urchins; (2) seasonal sand coverage may eliminate many of the smaller herbivores, which are able to colonize and consume the plant; (3) sand cover may eliminate detrimental epiphytes, while protecting the lower portions of the plant from exposure stress during the summer months; (4) sand may eliminate some of the potential competitors which cannot stand anoxic burial or sand scour. These were not tested in this chapter, but chapter 3 suggests that these may be important considerations when evaluating the spatial distribution of these species. It is considered that these positive influences may be beneficial to the juvenile and adult plants, but the negative influences of sand burial and scour on the EPS stages of the test species probably outweigh any beneficial effects.

Although the three test species are associated with areas of low to moderate water movement and moderate to high seasonal sand deposition (see Chapter 3), it is apparent from the experimental manipulations that the spores and EPS stages of these species suffer considerable stress and mortality from sand burial and sand movement. *Iridaea* and *Gigartina* sporelings (1 day old) displayed an ability to persist, buried under sand, for a short time (4 days), but *Aeodes* mortality was high for all treatments. It is unlikely that *Iridaea* and *Gigartina* sporelings are able to survive prolonged periods of sand burial. Hence, it is suggested the adult or juvenile plants of these species have alternatively developed vegetative mechanisms to enable them to persist the seasonal sand burial and scour, as opposed to evolving a resistance of the spore and EPS stages to sand effects. Many other species which appear particularly adapted to survival and growth within sand appear to have been released from dependence on spore attachment to substrata that are mostly buried, by evolving mechanisms for vegetative propagation. For example, Dahl (1971) detailed the resistance of *Zonaria farlowii* to complete long-term burial by cessation of apical meristem growth and initiation of a resting configuration. Stewart (1983) identifies a host of morphological attributes that might give thalli of anchor species advantages in environments with moving sand. These include apical meristems that maintain dividing cells above sediment and basal thallus parts that can physically resist or tolerate burial and abrasion and that can initiate erect axes in the appropriate temporal cycle. Santelices *et al* (1989) showed that the crustose base of *Gymnogongrus furcellatus* can survive sand burial for several months. Individual *Rhodomela larix* axes have been shown to have the ability to perennate and can regenerate from a minimal number of basal cells (D'Antonio 1986). Field observations by Santelices *et al* (1989) indicated that the crustose base is the most resistant part of the plant, often regenerating new axes after being uncovered by sand. It appears that the three test species have developed similar vegetative mechanisms to those elucidated above. *Aeodes orbitosa* has internal reinforcing filaments (Simons and Hewitt 1976) and may have a basal crust that is moderately resistant to sand burial and scour (Bolton pers. comm.). *Gigartina radula* has basal thallus parts that can physically resist or tolerate sand burial and apical meristems that maintain dividing cells above the sediment (pers. obs.). *Iridaea capensis* has an epilithic crustose base which can survive for months under sand and, when exposed, produce many juveniles, with each subsequently producing it's own holdfast (Bolton and Joska, 1993).

The asynchrony between algal recruitment and sand deposition and scour suggests that temporal variation of spore release may account for algal survival at these sites. For example, Bolton and Joska (1993) report a massive recruitment of *Iridaea* plants into an intertidal population at the collection site (Kommetjie) over a two month period which coincided with a relatively sand-free period. The rapid alternation from a sporophyte- to a gametophyte-dominated population over a two month period suggests that when most of the macroscopic plants were sporophytes, the crustose biomass in the population was dominated by haploid tissue, which produced the burst of recruitment. Assuming that the

EPS stages are equally, or more vulnerable to, sand burial and scour than juveniles or adults, then it would be advantageous for algae to grow through the germling phase as quickly as possible (see De Wreede and Klinger 1988). It was observed in light microscopy and SEM that all three species dispersed spores in dense mucilagenous masses which enhanced the sinking and coalescence of spores. This is consistent with the results of Boney (1978) and Pacheco-Ruiz *et al* (1989) for *Rhodymenia pertusa* and *Gigartina canaliculata* respectively. Cohesion via mucilage would increase the sedimentation rate and reduce drift from the parental habitat. It would also permit a greater residence time on the settling substratum for fixation (Charters *et al* 1973). Coalesced sporelings appear to initiate upright fronds faster and are more robust than single sporelings (Norton *et al* 1982). Earlier initiation and faster growth of uprights are promoted by coalescence of sporelings in *Gracilaria verrucosa* (Jones 1956), *Chondrus crispus* and *Mastocarpus stellatus* (Tveter and Mathieson 1976). Jones (1956) pointed out that *G. verrucosa* grows in habitats subject to sand inundation, so that rapid formation and growth of fronds would be particularly advantageous. Maggs and Cheney (1990) suggest that, besides enhancing the colonization by, and establishment of, a group of plants, sporeling coalescence also contributes to longevity by forming a large basal holdfast. The capability of such a holdfast to persist and propogate new fronds vegetatively over a long time period offers a significant competitive advantage over plants without such a system.

In assessing the relative competitive advantage of the three test species in sand-inundated habitats, I believe that the focus of future research should lie in evaluating the vegetative strategies of the adult plants in surviving seasonal sand scour and burial. The strategies for rapid colonization of the hard substrate during periods of low sand scour and burial should be investigated to complement this information.

CONCLUSIONS

The results of this chapter indicate that: (i) All spores and germlings of the test species suffered considerable stress and mortality from sand burial and sand scour. It is suggested that these species may have rather evolved vegetative and intrinsic (seasonal spore dispersal) mechanisms to survive and persist in seasonally sand-covered habitats; (ii) *Aeodes* spores and germlings are highly susceptible to sand burial and scour; (iii) *Gigartina* and *Iridaea* germlings are moderately resistant to sand burial for short periods; (iv) *Iridaea* germlings are moderately more persistent under conditions of sand scour than the other two species; and (v) No significant difference was noted in relative survival of carpospores and tetraspores or gametophyte or sporophyte germlings.

CONCLUSION

The detailed collections of intertidal and subtidal marine algae from the Cape Hangklip area represents the most comprehensive floristic database collected to date for this area. Of the 201 algal species identified, four are new records for southern Africa, five are undescribed species and one is a rhodophyte of uncertain affinity (*cf* Ceramiaceae *indet.*), probably representing a new genus in the Ceramiaceae. An analysis of the phytogeographic affinities of 170 of the macroalgal species with adequate distribution records contributes to the understanding of the nature of the transitional area (the south coast/west coast overlap region) between the cool-temperate west coast and the warm-temperate south coast. The distributional analysis shows that, in the Cape Hangklip area, there is no dominance of species with warm-water or cold-water affinities. Many west coast and south coast macroalgal species reach the limit of their ranges in the Cape Hangklip area. More detailed floristic studies of the intertidal and subtidal flora from other areas within the south coast/ west coast overlap region are required to more conclusively define the extent of the overlap region.

In the diverse and structurally complex algal communities within South African kelp forests, most of the patterns of distribution are undescribed. Very few studies have explored the mechanisms producing local patchiness in kelp communities in southern Africa. This thesis provides the first detailed quantitative analysis of the floristic component of the understorey of a South African kelp community. Using TWINSPAN and CCA, as interpretive tools for a complex dataset, species assemblages in the phytobenthic zone of a kelp community at Cape Hangklip, are revealed, and environmental factors which may cause the observed spatial patterns are highlighted. Two major environmental complex-gradients explain the compositional variation in the study area - (i) a depth complex-gradient and (ii) a sand cover complex-gradient. Although the numerical analyses indicate that the broad patterns of species distribution in the understorey are primarily defined by these abiotic factors (depth and sand), biotic interactions such as grazing, competition for light and competition for space, and abiotic factors such as aspect and substrate become more important at a smaller temporal and spatial scale. Many of these organizational processes do not operate at both scales and not necessarily by the same process, or of equal influence, at each scale. The processes that regulate the spatial and temporal patterns in the study area will however only be understood when mechanistic causes are elucidated. The observed patterns in this study may thus be used to postulate testable hypotheses.

Based on the results of Chapter 3, the following question is posed: Is the distribution of three sublittoral fringe red algae directly related to the effects of sand inundation and scour on the colonization and early post-settlement life history stages? Although it has often been suggested that sand scour and sand deposition may have a significant effect on the survival of algal spores, few species worldwide have been tested to qualify this effect. Although using techniques established elsewhere, the experimental study in this thesis is to my knowledge the first study of this nature to have been initiated in South Africa. The experimental treatments employed suggest that spores and germlings from all three species suffer considerable stress and mortality from sand burial and scour. Although not tested here, it appears that seasonality of spore dispersal and morphological adaptations of the adult plants may more adequately explain the distributional variation of these three algal species.

REFERENCES

ABBOTT, I A & HOLLENBERG, G J. 1976. Marine algae of California. Stanford University Press, Stanford, Calif. 827 pp.

AGARDH, J G. 1851. Species, genera et ordines algarum, Vol. 2. Floridearum Part 1. Lund, pp. pp. 1 - 351.

ALLEN, J C & GRIFFITHS, C L. 1981. The fauna and flora of a kelp bed canopy. *S. Afr. J. Zool.* 16:80-84.

ANDERSON, R J. 1982. A biological study of *Desmarestia firma* (C.Ag.) Skottsb. Phaeophyceae, Desmarestiales. PhD Thesis, University of Cape Town, South Africa. 246pp.

ANDERSON, R J & VELIMIROV, B. 1982. An experimental investigation of the palatability of the kelp bed algae to the sea urchin *Parechinus angulosus* Leske. *Mar. Ecol.* 3(4):357-373.

ANDERSON, R J & HAY C H. 1986. Seasonal production of *Desmarestia firma* (C. Ag.) Skottsb. (Phaeophyceae, Desmarestiales) in a kelp bed on the west coast of the Cape Peninsula, South Africa. *Bot. Mar.* 29:523-531.

ANDERSON, R J & BOLTON, J J. 1989. Growth and fertility, in relation to temperature and photoperiod, in South African *Desmarestia firma* (Phaeophyceae), *Bot. Mar.* 32:149-158.

ANDERSON, R J & STEGENGA, H. 1989. Subtidal algal communities at Bird Island, Eastern Cape, South Africa. *Bot. Mar.* 32:299-311.

ANDERSON, R J, SIMONS, R H & JARMAN, N G. 1989. Commercial seaweeds in Southern Africa: A review of utilization and research. *S. Afr. J. Mar. Sci.* 8:277-299.

ANDREW, N L. 1988. The ecology of the common sea urchin *Evechinus chloroticus* in northern New Zealand. *N. Z. J. Mar. Freshwat. Res.* 22

ANDREW, N L & CHOAT, J H. 1982. The influence of predation and conspecific adults on the abundance of juvenile *Evechinus chloroticus* (Echinoides: Echinometridae). *Oecologia* 54:80-87.

ARDRÉ, F. 1970. Observations sur le genre *Aphanocladia* Falkenberg (Rhodomélacées) et sur ses affinités. *Rev. Algol. N. S.* 10:37-55.

ARDRÉ, F. 1974. Remarques sur la structure et les affinités des *Symphyocladia* (Rhodomélacées, Céramiales). *Botaniste*, ser. 56:19-54.

AYLING, A M. 1981. The role of biological disturbance in temperate subtidal encrusting communities. *Ecology* 62:830-900.

BALLY, R, McQUAID, C D & BROWN, A C. 1984. Shores of mixed sand and rock: an unexplored marine ecosystem. *S. Afr. J. Sci.* 80:500-503.

BARKAI, A. 1987. Biologically induced alternative states in two rocky subtidal benthic communities. PhD. Thesis, Zoology Dept., University of Cape Town, South Africa. 231 pp.

BARKAI, R & GRIFFITHS, C L. 1986. Diet of the South African abalone *Haliotis midae*. *S. Afr. J. Mar. Sci.* 4:37-44.

BERNSTEIN, B B & JUNG, G. 1979. Selective pressures and coevolution in a kelp canopy community in southern California. *Ecol. Monogr.* 49:335-355.

BERNSTEIN, BB, WILLIAMS, B E & MANN, K H. 1981. The role of behavioural responses to predators in modifying urchins (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterms. *Mar. Biol.* 63:39-49.

BERNSTEIN, B B, SCHROEDER, S C & MANN, K H. 1983. Sea urchin (*Strongylocentrotus droebachiensis*) aggregating behaviour investigated by a subtidal multifactorial experiment. *Can. J. Fish. Aquat. Sci.* 40:1975-1986.

BIDOUX, C & MAGNE, F. 1989. Etude de quelques Acrochaetiales (Rhodophyta) devat être rapportées au genre *Rhodothamniella*. *Cryptogamie Algol.* 10:33-55.

BIRD, C J, GREENWELL, M & MCLACHLAN, J. 1983. Benthic marine algal flora of the north shore of Prince Edward Island (Gulf of St. Lawrence), Canada. *Aquat. Bot.* 16:315-335.

BOLTON, J J. 1986. Marine phytogeography of the Benguela upwelling region on the west coast of southern Africa: A temperature dependent approach. *Bot. Mar.* 29:251-256.

BOLTON, J J. 1987. Where did our kelps come from? *Veld & Flora* (April):21-22.

BOLTON, J J & ANDERSON, R J. 1990. Correlation between intertidal seaweed community composition and sea water temperature patterns on a geographical scale. *Bot. Mar.* 33:447-457.

BOLTON, J J & ANDERSON, R J, 1994. *Ecklonia*. In: I Akatsuka (ed.) Biology of economic algae. SPB Academic Publishing, The Hague, Netherlands, pp 385-406.

BOLTON, J J & JOSKA, M A P. 1993. Population studies on a South African carragenophyte: *Iridaea capensis* (Gigartinaceae, Rhodophyta). *Hydrobiologia*, 260/261:191-195.

BOLTON, J J & LEVITT, G J. 1987. The influence of upwelling on South African west coast seaweeds. *S. Afr. J. Mar. Sci.* 5:319-325.

BOLTON, J J & STEGENGA, H. 1987. The marine algae of Hluleka (Transkei) and the warm temperate/subtropical transition on the east coast of southern Africa. *Helgolander Meeresunters.* 41:165-183.

BOLTON, J J & STEGENGA, H. 1990. The seaweeds of De Hoop Nature Reserve and their phytogeographical significance. *S. Afr. J. Bot.* 56:233-238.

BOLTON, J J & LEVITT, G J. 1992. South African west coast carrageenophytes. In: K.E. Mshigeni, J. J. Bolton, A. T. Critchley & G. Kiangi (eds), Proceedings of the First International Workshop on Sustainable Seaweed Rescource Development in Sub-Saharan Africa. Published by K. Mshigeni, pp 37-50.

BOLTON, J J & STEGENGA, H. 1994. Patterns of seaweed distribution in the Cape Province, South Africa, with particular reference to the Phaeophyta and Ceramiaceae (Rhodophyta). In: J H. Seyani & A C Chikuni (eds), Proc. XIIIth Plenary Meeting AETFAT, Malawi, 2:849-854.

BOLTON, J J, STEGENGA, H & ANDERSON R J. 1991. The seaweeds of False Bay. *Trans. Roy Soc. S. Afr.* 47(4&5):605-609.

BONEY, A D. 1978. The liberation and dispersal of carpospores of the red alga *Rhodymenia pertusa* (Postels et Rupr.) J. Ag. *J. Exp. Mar. Biol. Ecol.* 32:1-6.

BRANCH, G M. 1975. Intraspecific competition in *Patella cochlear* (Born). *J. Animal Ecol.* 44:263-282.

BRANCH, G & BRANCH, M. 1981. The living shores of Southern Africa. Struik, Cape Town, 272 pp.

BRANCH, G M & GRIFFITHS, C L. 1988. The Benguela ecosystem part V. The coastal zone. *Oceonogr. Mar. Biol. Annu. Rev.* 26:395-486.

BREDA, V A. 1982. Composition, abundance and phenology of foliose red algae associated with two *Macrocystis pyrifera* forests in Monterey Bay, California. Master's Thesis, San Jose State University, California. 67 pp.

BREEN, P A. 1980. Relations among lobster, sea urchins and kelp in Nova Scotia. *Can. Tech. Rep. Fish. Aquat. Sci.* 954:24-47.

BREEN, P A & MANN, K H . 1976. Destructive grazing of kelp by sea urchins in eastern Canada. *J. Fish. Res. Board Can.* 33:1278-1283.

BRIGGS, J G. 1974. Marine Zoogeography. McGraw-Hill, New York. 475 pp.

BROWN, A C & JARMAN, N G. 1978. Coastal marine habitats. In: M Werger (ed), Biogeography and ecology of Southern Africa. Junk, The Hague, pp. 1239-1277.

CARTER, R A. 1982. Phytoplankton biomass and production in a southern Benguela kelp bed system. *Mar. Ecol. Prog. Ser.* 8:9-14.

CASTILLA, J C & MORENO, C A. 1982. Sea urchins and *Macrocystis pyrifera:* experimental test of their ecological relations in southern Chile. In: J M Lawrence, Echinoderms: proceedings of the International Conference,Tampa Bay. A.A. Balkema, Rotterdam. pp. 257-263.

CHAPMAN, A R O. 1979. Biology of Seaweeds. University Park Press, Baltimore, Maryland, USA.

CHAPMAN, A R O. 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, eastern Canada. *Mar. Biol.* 62:307-311.

CHAPMAN, A R O. 1984. Reproduction, recruitment and mortality in two species of *Laminaria* in southwest Nova Scotia. *J. Exp. Mar. Biol. Ecol.* 78:99-109.

CHAPMAN, A R O & UNDERWOOD, A J. (eds.) 1990. Determinants of structure in intertidal and subtidal macroalgal assemblages. Kluwer Academic Publishers, Belgium.

CHAPMAN, A R O & JOHNSON, C R. 1990. Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. *Hydrobiologia*, 192:77-121.

CHARTERS, A C, NEUSHUL, M & COON, D A. 1972. Effects of water motion on algal spore attachment. *Proc. Int. Seaweed. Symp.* 7:243-247.

CHARTERS, A C, NEUSHUL, M & COON, D. 1973. The effect of water motion on algal spore adhesion. *Limnol. Oceanogr.* 18:884-896.

CHEN, L C-M, & TAYLOR, A R A. 1976. Scanning electron microscopy of early sporeling ontogeny of *Chondrus crispus*. *Can. J. Bot.* 54:672-678.

CHENEY, D F. 1977. R and C/P, a new and improved ratio for comparing seaweed floras. *J. Phycol.* 13 (suppl.):12.

CHIANG, Y-M. 1970. Morphological studies of red algae of the family Cryptonemiaceae. University of California Press, Los Angeles, pp 15-17.

CHIHARA, M. 1975. Geographic distribution of marine algae in Japan. In: Tokida, J A & Hirose, H. (eds.), Advance of phycology in Japan. VEB Gustav Fischer, Jena, pp. 241-253.

CHOAT, J H. 1982. Fish feeding and the structure of benthic communities in temperate waters. *Ann. Rev. Ecol. Syst.* 13: 423-449.

CHOAT, J H & ANDREW, N L. 1986. Interactions amongst species in a guild of subtidal benthic herbivores. *Oecologia* 68:387-394.

CHOAT, J H & SCHIEL, D R. 1982. Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *J. Exp. Mar. Biol. Ecol.* 60: 129-162.

CONNELL, J H. 1978. Diversity in tropical rain forests and tropical reefs. *Science* 199:1302-1309.

COUSENS, R. 1981. Variation in annual production by *Ascophyllum nodosum* (L.) Le Jolis with degree of exposure to wave action. Xth Int. Seaweed Symp, pp. 253-258.

COWEN, R K. 1983. The effect of sheepshead (*Semicossyphus pulcher*) predation on red sea urchin (*Strongylocentrotus franciscanus*) populations: an experimental analysis. *Oecologia* 58:249-255.

COWEN, R K, AGEGIAN, C R & FOSTER, M S. 1982. The maintenance of community structure in a central California giant kelp forest. *J. Exp. Mar. Biol. Ecol.* 64:189-201.

DAHL, A L. 1971. Development, form and environment in the brown alga *Zonaria farlowii* (Dictotales). *Bot. Mar.* 14:76-112.

DALY, M A & MATHIESON, A C. 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, U S A. *Mar. Biol.* 43:45-55.

D'ANTONIO, C M. 1986. Role of sand in the domination of hard substrata by the intertidal alga *Rhodomela larix*. *Mar. Ecol. Prog. Ser.* 27:263-275.

DAVIS, A N. & WILCE, R T. 1987. Floristics, phenology, and ecology of the sublittoral marine algae in an unstable habitat (Plum Cove, Cape Ann, Massachusetts, USA). *Phycologia* 26:23-34.

DAWSON E Y, NEUSHUL M & WILDMAN R D. 1960. Seaweeds associated with kelp beds along southern California and northwestern Mexico. *Pac. Nat.* 1:1-81.

DAYTON, P K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45:137-159.

DAYTON, P K. 1984. Processes structuring some marine communities: are they general? In: Strong, D R, Simberloff, D, Abele, L G & Thistle, A B. (eds.), Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, pp. 179-197.

DAYTON, P K. 1985a. Ecology of kelp communities. *Ann. Rev. Ecol. Syst.* 16:215-245.

DAYTON, P K. 1985b. The structure and regulation of some South American kelp communities. *Ecol. Monogr.* 55(4):447-468.

DAYTON, P K & TEGNER, M J. 1984a. The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: Prince, P W, Slobodchikoff, C N & Gand, W S (eds), Novel approaches to interactive systems. J. Wiley and Sons, New York, pp 457-481

DAYTON, P K & TEGNER, M J. 1984b. Catastrophic storms, El Nino, and patch stability in a Southern California kelp community. *Science* 224:283-285.

DAYTON, P K, CURRIE, V, GERRODETTE, T, KELLER, B D, ROSENTHAL, R & VEN TRESCA, D. 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.* 54:253-289.

DAYTON, P K, TEGNER, M J, PARNELL, P E & EDWARDS, P B. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* 62(3):421-445.

DEAN, T A, DEYSHER, K, THIES, K, LAGOS, S, JACOBSEN, F & BOST, L. 1983. The effects of the San Onofre Nuclear Generating Station (SONGS) on the giant kelp *Macrocystis pyrifera*: final pre-operational monitoring report. *Mar. Rev. Comm.* California.

DEAN, T A, THIES K & LAGOS, S. 1989. Survival of juvenile giant kelp: the effects of demographic factors, competitors and grazers. *Ecology* 70(2):483-495.

DEVINNY, J S, & KIRKWOOD, P D. 1974. Algae associated with kelp beds of the Monterey Peninsula, California. *Bot. Mar.* 17:100-106.

DEVINNY, J S & VOLSE, L A. 1978. Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. *Mar. Biol.* 48:343-348.

DEWREEDE, R E & KLINGER, T. 1988. Reproductive strategies in algae. In: Doust, J L & Doust, L L (eds) Plant Reproductive Ecology: patterns and strategies. Oxford Univ. Press, New York, pp 267-284.

DEXTER, D M. 1992. Sandy beach community structure: the role of exposure and latitude. *J. Biogeog.* 19:59-66.

DIECKMANN, G S. 1980. Aspects of the ecology of *Laminaria pallida* (Grev.) off the Cape Peninsula (South Africa). I. Seasonal growth. *Bot. Mar.* 23:579-585.

DOWER, K M. 1989. Sand inundation on rocky shores: its effects on species richness and the structure of species assemblages. Msc thesis, Rhodes University, South Africa. 121 pp.

DRUEHL, L D. 1967. Distribution of two species of *Laminaria* as related to some environmental factors. *J. Phycol.* 3:103-108.

DRUEHL, L D. 1970. The pattern of Laminariales distribution in the northeast Pacific. *Phycologia* 9:237-247.

DRUEHL, L D & BREEN, P A. 1986. Some ecological effects of harvesting *Macrocystis integrifolia*. *Bot. Mar.* 29:97-103.

DUGGINS, D O. 1980. Kelp beds and sea otters: an experimental approach. *Ecology* 61(3):447-453.

DUGGINS, D O, ECKMAN, J E & SEWELL, A T. 1990. Ecology of understory kelp environments. II. Effects of kelps on recruitment of benthic invertebrates. *J. Exp. Mar. Biol. Ecol.* 143:27-45.

EBELING, A W, LAUR, D R & ROWLEY, R J. 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Mar. Biol.* 84:287-294.

ECKMAN, J E, DUGGINS, D O & SEWELL A T. 1989. Ecology of understorey kelp environments. I. Effects of kelps on flow and particle transport near the bottom. *J. Exp. Mar. Biol. Ecol.* 129:173-187.

ELNER, R W & CAMPBELL, A. 1987. Natural diets of lobster *Homarus americanus* from barren ground and macroalgal habitats off southwestern Nova Scotia, Canada. *Mar. Ecol. Prog. Ser.* 37:131-140.

EMERSON, S E & ZEDLER, J B. 1978. Recolonization of intertidal algae: an experimental study. *Mar. Biol.* 44:315-324.

ENGLEDOW, H R & BOLTON, J J. 1994. Seaweed alpha-diversity within the lower eulittoral zone in Namibia: the effects of wave action, sand inundation, mussels and limpets. *Bot. Mar.* 37:267-276.

ESTES, J A & HARROLD, C. 1988. Sea otters, sea urchins and kelp beds: some questions of scale. In: VanBlaricom, G R & Estes, J A (eds), The community ecology of sea otters. Springer-Verlag, Berlin, pp. 116 - 150.

ESTES, J A & PALMISANO, J F. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185:1058-1060.

ESTES, J A, SMITH, N S & PALMISANO, J F. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* 59:822-833.

ESTES, J A & STEINBERG, P D. 1988. Predation, herbivory, and kelp evolution. *Paleobiology* 14(1):19-36.

de ESTON, V R & BUSSAB, W O. 1990. An experimental analysis of ecological dominance in a rocky subtidal macroalgal community. *J. Exp. Mar. Biol. Ecol.* 136:170-195.

FIELD J G & GRIFFITHS, C L. 1991. Littoral and sublittoral ecosystems of Southern Africa. In: Mathieson, A C & Nienhuis, P H (eds), Ecosystems of the world 24: Intertidal and littoral ecosystems. Elsevier, Amstersdam, pp 323-346.

FIELD, J G, JARMAN, N G, DIECKMANN, G S, GRIFFITHS, C L, VELIMIROV, B & ZOUTENDYK, P. 1977. Sun, waves, seaweed and lobsters: The dynamics of a west coast kelp-bed. *S.Afr. J. Sci.* 73:7-10.

FIELD, J G, GRIFFITHS, C L, GRIFFITHS, R J, JARMAN, N, ZOUTENDYK, P, VELIMIROV, B & BOWES, A. 1980. Variation in structure and biomass of kelp communities along the South-West Cape coast. *Trans. R. Soc. Afr.* 44:145-203.

FLETCHER, W J. 1987. Interactions among subtidal Australian sea urchins, gastropods and algae: effects of experimental removals. *Ecol. Monogr.* 57(1):89-109.

FLETCHER, R L & CALLOW, M E. 1992. The settlement, attachment and establishment of marine algal spores. *Br. Phycol. J.* 27: 303 - 329.

FOSTER, M S. 1975a. Algal succession in a *Macrocystis pyrifera* forest. *Mar. Biol.* 32:313-329.

FOSTER, M S. 1975b. Regulation of algal community development in a *Macrocystis pyrifera* forest. *Mar. Biol.* 32:331-342.

FOSTER, M S. 1982. The regulation of macroalgal associations in kelp forests. In: L Srivastava (ed.), Synthetic and degradative processes in marine macrophytes. Walter de Gruyter & Co., Berlin.

FOSTER, M S. 1990. Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia.* 192:21-33.

FOSTER, M S & SCHIEL, D R. 1985. The ecology of giant kelp forests in California: a community profile. Biological Report 85 (7.2), Fish & Wildlife Service, U.S. Dept. of the Interior, 152 pp.

FOSTER, M S & SCHIEL, D.R. 1988. Kelp communities and sea otters: keystone species or just another brick in the wall? In: VanBlaricom, G R & Estes, J A. (eds), The community ecology of sea otters, Springer-Verlag, Berlin, pp 92 - 115.

FOSTER M.S, AGEGIAN C, COWEN R, VAN WAGENAN R, ROSE D & HURLEY A. 1979. Toward an understanding of the effects of sea otter foraging on kelp forest communities in central California. Final Rep. to U.S. Marine Mammal Commission, Contract No. MM7AC023. National Technical Information Service, Springfield, Va. Publ. Pb293891. 60 pp.

FOSTER, M S, CARTER, J & SCHIEL, D R. 1983. Ecology of kelp communities. In: W. Bascom (ed.), The effects of waste disposal on kelp communities. Southern California Coastal Water Research Project, Long Beach, pp 53-69.

FRALICK, R A, TURGEON, K W, & MATHIESON, A C. 1974. Destruction of kelp populations by *Lacuna vincta* (Montagu). *Nautilus* 88:112-114.

FRANKLIN, J & MERLIN, M. 1992. Species-environment patterns of forest vegetation on the uplifted reef limestone of Atiu, Mangaia, Ma'uke and Miti'aro, Cook Islands. *J. Veg. Sci.* 3(1):3-14.

FRICKE, J G. 1979. Kelp grazing by the common sea urchin *Parenchinus angulosus* Leske in False Bay, Cape. *S. Afr. J. Zool.* 14:143-148.

FRICKE, A H. 1980. Aspects of population structure of *Parenchinus angulosus* Leske, around the Cape Peninsula. *S.-Afr. Tydskr. Dierk.* 15(3):177-185.

GARBARY, D J. 1987. The Acrochaetiaceae (Rhodophyta): an annotated bibliography. *Bibl. Phycol.* 77:267 pp.

GARBARY, D J & DE WREEDE, R E. 1988. Life history phases in natural populations of Gigartinaceae (Rhodophyta): quantification using resorcinol. In: C.S. Lobban, D. J. Chapman & B. P. Kremer (eds), Experimental phycology: a laboratory manual. Cambridge Univ. Press, pp 174-178.

GAUCH, H G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge.

GERARD, V A & MANN, K H. 1979. Growth and production of *Laminaria longicruris* (Phaeophyta) populations exposed to different intensities of water movement. *J. Phycol.* 15:33-41.

GREENWOOD, P G. 1980. Growth, respiration and tentative energy budgets for two poulations of the sea urchin *Parechinus angulosus* (Leske). *Est. Cstl. Mar. Sci.* 10:347-367.

GREIG-SMITH P. 1983. Quantitative plant ecology. Butterworths, London.

GRIGG, R. 1975. Age structure of a longevous coral: a relative index of habitat suitability and stability. *Am. Nat.* 109:647-657.

GUNNIL, F C. 1986. Demography of *Cystoseira osmundacea* and *Halidrys diocia* (Phaeophyta, Cystoseiraceae) at La Jolla, California, USA. *Bot. Mar.* 29:137-146.

HARRIS, L G, EBELING, A W, LAUR, D R & RAWLEY, R J. 1984 Community recovery following storm damage: a case of facilitation in primary succession. *Science* 224:1336-1338.

HARROLD, C & REED, D C. 1985. Food availability, sea urchin grazing and kelp forest community structure. *Ecology.* 66(4):1160-1169.

HATCHER, B G & RIMMER D W. 1985. The role of grazing in controlling community structure on a high latitude coral reef: measurements of grazing intensity. In: Moorea & Gabrie (eds.), Proc. 5th Int. Coral Reef Congr. 6: 229-236.

HATCHER, B G, KIRKMAN, H & WOOD, W F. 1987. Growth of the kelp *Ecklonia radiata* near the northern limit of its range in Western Australia. *Mar. Biol.* 95:63-73.

HAYASHIDA, F. 1983. Synecological studies of a brown alga, *Ecklonia cava* Kjellmann, forming aquatic forest. I. Benthic marine algal vegetation at survey area. *J. Fac. Mar. Sci. Technol. Tokai University.* 16:207-212.

HILL, M O. 1979. TWINSPAN. A fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Microcomputer Power, New York, 47pp.

HILL, M O & GAUCH H G. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42:47-58.

HIMMELMAN, J H. 1980. The role of the green sea urchin, *Strongylocentrotus droebachiensis*, in the rocky subtidal region of Newfoundland. *Can. Tech. Rep. Fish. Aquat. Sci.* 954:92-119.

HIMMELMAN, J H, CARDINAL, A & BOURGET, E. 1983. Community development following removal of urchins, *Strongylocentrotus droebachiensis*, from the rocky subtidal zone of the St. Lawrence Estuary, eastern Canada. *Oecologia* 59:27-39.

HIMMELMAN, J H. 1984. Urchin feeding and macroalgal distribution in Newfoundland, eastern Canada. *Naturaliste Can. (Rev. Ecol. Syst.)* 111:337-348.

HISCOCK, K. 1985. Aspects of the ecology of rocky sublittoral areas. In: Moore, P G & Seed, R. (eds.), The ecology of rocky coasts. Hodder and Stougton, London, pp 290-328.

HOMMERSAND, M H. 1986. The biogeography of the South African marine red algae: a model. *Bot. Mar.* 29:257-270.

HOMMERSAND, M H, FREDERICQ, S & FRESHWATER, D W. 1994. Phylogenetic systematics and biogeography of the Gigartinaceae (Gigartinales, Rhodophyta) based on sequence analysis of *rbc*L. *Bot. Mar.* 37:193-203.

HOOPER, R. 1980. Observations on algal-grazer interactions in Newfoundland and Labrador. *Can. Tech. Rep. Fish. Aquat. Sci.* 954:120-124.

IRVINE, L M. 1983. Seaweeds of the British Isles Vol. 1. Rhodophyta Pt. 2A: Cryptonemiales (*sensu stricto*), Palmariales, Rhodymeniales. British Museum (N.H.), XII + 115 pp.

ISAAC, W E. 1938. The geographical relationship of seaweed vegetation in relation to temperature and other factors, with special reference to South Africa. *C. R. Congr. Int. Geogr. Amsterdam* 2:12-28.

ISAAC, W E. 1949. Studies of South African seaweed vegetation II. Rooi Els to Gansbaai, with special reference to Gansbaai. *Trans. R. Soc. S. Afr.* 32:125-160.

ITONO, H. 1977. Studies on the ceramiaceous algae (Rhodophyta) from southern parts of Japan. *Bibl. Phycol.* 35:499 pp.

JACKELMAN J J, STEGENGA, H S & BOLTON J J. 1991. The marine benthic flora of the Cape Hangklip area and its phytogeographical affinities. *S. Afr. J. Bot.* 57(6):295-304.

JAMES, F C & McCULLOCH C E. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? *A. Rev. Ecol. Syst.* 21:129-166.

JENSEN, S & VAN DER MAAREL, E. 1980. Numerical approaches to lake classification with special reference to macrophyte communities. *Vegetatio* 42:117-128.

JOHN, D M & LAWSON, G W. 1990. The effects of grazing animals on algal vegetation. In: I Akatsuka (ed.), Introduction to applied phycology. SPB Academic Publishing, The Hague, Netherlands, pp. 307-345.

JOHNSON, C R. 1984. Ecology of the kelp *Laminaria longicruris* and its principal grazers in the rocky subtidal of Nova Scotia. PhD Dissertation, Dalhousie University, Halifax, N.S., 280pp.

JOHNSON, C R. & MANN, K H. 1986. The importance of plant defence abilities to the structure of subtidal seaweed communities: the kelp *Laminaria longicruris* de la Pylaie survives grazing by the snail *Lacuna vincta* (Montagu) at high population densities. *J. Exp. Mar. Biol. Ecol.* 97:231-267.

JOHNSON, C R & MANN, K H. 1988. Diversity, patterns of adaptation and stability of Nova Scotia kelp beds. *Ecol. Monogr.* 58:129-154.

JONES, W E. 1956. Effect of spore coalescence on the early development of *Gracilaria verrucosa* (Hudson) Papenfuss. *Nature* 178:426-427.

JONES, G M. 1985. *Paramoeba invadens* n. sp. (Amoebida, Paramoebidae), a pathogenic amoeba from the sea urchin *Strongylocentrotus droebachiensis*, in eastern Canada. *J. Protozool.* 32:564-569.

JONES, G M. & SCHEIBLING, R E. 1985. *Paramoeba* sp. (Amoebida, Paramoebidae) as the possible causative agent of sea urchin mass mortality in Nova Scotia. *J. Parasitol.* 71:559-565.

JONGMAN, R H, TER BRAAK, C J F & VAN TONGEREN, O F R. 1987. Data analysis in community and landscape ecology. Pudoc Wageningen.

JOSKA, M A P & BOLTON, J J. 1987. *In situ* measurement of zoospore release and seasonality of reproduction in *Ecklonia maxima* (Alariaceae, Laminariales). *Br. Phycol. J.* 22:209-214.

KAIN, J M. 1975. The biology of *Laminaria hyperborea.* VII. Reproduction of the sporophyte. *J. Mar. Biol. Assoc. U.K.* 55:567-582.

KAIN, J M. 1976. The biology of *Laminaria hyperborea.* IX. Growth patterns of fronds. *J. Mar. Biol. Assoc. U.K.* 56:603-628.

KAIN, J M. 1979. A view of the genus *Laminaria. Oceanogr. Mar. Biol. Ann. Rev.* 17:101-161.

KAIN, J M. 1989. The seasons in the subtidal. *Br. J. Phycol.* 24:203-215.

KASTENDIEK, J. 1982. Competitor-mediated coexistence: interactions among three species of benthic macroalgae. *J. Exp. Mar. Biol. Ecol.* 62:201-210.

KAUTSKY, H & VAN DER MAAREL E. 1990. Multivariate approaches to the variation in phytobenthic communities and environmental vectors in the Baltic Sea. *Mar. Ecol. Prog. Ser.* 60:169-184.

KEATS, D W, SOUTH, G R & STEELE, D H. 1985. Algal biomass and diversity in the upper subtidal at a pack-ice disturbed site in eastern Newfoundland. *Mar. Ecol. Prog. Ser.* 25:151-158.

KENDRICK, G A. 1991. Recruitment of coralline crusts and filamentous algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion. *J. Exp. Mar. Biol. Ecol.* 147:47-63.

KENNELLY, S J. 1983. An experimental approach to the study of factors affecting algal colonization in a sublittoral kelp forest. *J. Exp. Mar. Biol. Ecol.* 68:257-276.

KENNELLY, S J. 1987a. Physical disturbances in an Australian kelp community. 2. Effects on understorey species due to differences in kelp cover. *Mar. Ecol. Progr. Ser.* 40:155-165.

KENNELLY, S J. 1987b. Inhibition of kelp recruitment by turfing algae and consequences for an Australian kelp community. *J. Exp. Mar. Biol. Ecol.* 112:49-60.

KENNELLY, S J. 1989. Effects of kelp canopies on understorey species due to shade and scour. *Mar. Ecol. Progr. Ser.* 50:215-224.

KENT, M & COKER, P. 1992. Vegetation description and analysis. A practical approach. Belhaven Press, London.

KIRKMAN, H. 1981. The first year in the life history and the survival of the juvenile marine macrophyte, *Ecklonia radiata* (Turn.) J. Ag. *J. Exp. Mar. Biol. Ecol.* 55:243-254.

KITCHING, R L & BEAVER, R A. 1990. Patchiness and community structure. In: Shorrocks, B & Swingland, I R. (eds.), Living in a patchy environment. Oxford University Press, Oxford.

KOEHL, M A R. 1986. Seaweeds in moving water: form and mechanical function. In: Givnish, T J. (ed.), On the economy of plant form and function. Cambridge University Press, Cambridge.

KOOP, K, NEWELL R C. & LUCAS M I. 1982. Biodegradation and carbon flow based on kelp (*Ecklonia maxima*) debris in a sandy beach microcosm. *Mar. Ecol. Prog. Ser.* 7:315-326.

LAWRENCE, J M. 1975. On the relationships between marine plants and sea urchins. *Oceanogr. Mar. Biol. Ann.* [illegible] 13:213-286.

LEGENDRE, P & FORTIN, M J. 1989. Spatial patterns and ecological analysis. *Vegetatio* 80:107-138.

LEVIN, S A. 1988. Sea otters and nearshore benthic communities: a theoretical perspective. In: G R VanBlericom & J E Estes (eds), The community of sea otters. Springer-Verlag, Berlin, pp 202-209.

LEVITT, G J & BOLTON, J J. 1990. Seasonal primary production of understorey Rhodophyta in an upwelling system. *J. Phycol.* 26:214-220.

LEVITT, G J & BOLTON, J J. 1991. Seasonal patterns of photosynthesis and physiological parameters and the effects of emersion in littoral seaweeds. *Bot. Mar.* 34:403-410.

LEWIS, J R. 1968 Water movements and their role in rocky shore ecology. *Sarsia* 34:13-36.

LEWIS, J A & KRAFT, G T. 1979. Occurrence of a European red alga (*Schottera nicaeensis*) in southern Australian waters. *J. Phycol.* 15:226-230.

LINDSTROM, S C & FOREMAN R E. 1978. Seaweed associations of the Flat Top Islands, British Columbia: a comparison of community methods. *Sycsis* 11:171-185.

LINLEY, E A S & NEWELL, R C. 1981. Microheterotrophic communities associated with the degradation of kelp debris. *Kieler Meeresforsch., Sonderh.* 5:345-355.

LITTLER, M M, MARTZ, D R & LITTLER, D S. 1983. Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. *Mar. Ecol. Prog. Ser.* 11:129-139.

LOBBAN, C S, HARRISON, P J & DUNCAN, M J. 1985. The physiological ecology of seaweeds. Cambridge University Press, Cambridge.

LUNING, K. 1985. Meeresbotanik: Verbreitung, okophysiologie und nutzung der marinen Makroalgen. Thieme, Stuttgart, 375pp.

LÜNING, K. 1990. Seaweeds: Their environment, biogeography and ecophysiology. Biologische Anstalt Helgoland. Hamburg, F.R.G., 527 pp.

MAEGAWA, M, YOKOHAMA, Y & ARUGA Y. 1987. Critical light conditions for young *Ecklonia cava* and *Eisenia bicyclis* with reference to photosynthesis. *Hydrobiologia* 151/152:447-455.

MAGGS, C A & CHENEY, D P. 1990. Competition studies of marine macroalgae in laboratory culture. *J. Phycol.* 26:18-24.

MANN, K H. 1982. Ecology of coastal waters. University of California Press, Berkeley, 322 pp.

MARKHAM, J W. 1969. An ecological study of *Laminaria sinclairii* and *Laminaria longipes*. Ph.D. thesis, Univ. Of British Columbia, Vancouver, Canada.

MARKHAM, J W. 1973. Observations on the ecology of *Laminaria sinclairii* on three northern Oregon beaches. *J. Phycol.* 9:336-341.

MARKHAM, J W & NEWROTH, P R. 1972. Observation on the ecology of *Gymnogongrus linearis* and related species. *Proc. Int. Seaweed. Symp.* 7:127-130.

MAY, V & LARKUM, A W D. 1981. A subtidal transect in Jervis Bay, N.S.W. *Aust. J. Ecol.* 6:439-457.

MAZURE, H G F. 1978. Bacteria associated with the surface of kelp fronds. PhD Thesis, University of Cape Town, 157pp.

MAZURE, H G & FIELD, J G. 1980 Density and ecological importance of bacteria on kelp fronds in an upwelling region. *J. Exp. Mar. Biol. Ecol.* 43:173-182.

McLEAN, J H. 1962. Sublittoral ecology of kelp beds of the open coast area near Carmel, California. *Biol. Bull.* (Woods Hole) 122:95-114.

McQUAID, C D & BRANCH, G M. 1984. Influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Mar. Ecol. Prog. Ser.* 19:145-151.

McQUAID, C D, BRANCH, G M & CROWE A A. 1985. Biotic and abiotic influences on rocky intertidal biomass and richness in the southern Benguela region. *S. Afr. J. Zool.* 20:115-122.

McQUAID, C D & DOWER, K M. 1990. Enhancement of habitat heterogeneity and species richness on rocky shores inundated by sand. *Oecologia* 84:142-144.

MENGE, B A & OLSON, M A. 1990. Role of Scale and environmental factors in regulation of community structure. *Tree* 5(2):52-57.

MILES, A K & MESLOW, E C. 1990. Effects of experimental overgrowth on survival and change in the turf assemblage of a giant kelp forest. *J. Exp. Mar. Biol. Ecol.* 135:229-242.

MILLER, R J. 1985. Succession in sea urchin and seaweed abundance in Nova Scotia, Canada. *Mar. Biol.* 84:275-286.

MILLER, R J & COLODEY, A G. 1983. Widespread mass mortality of the green sea urchin in Nova Scotia, Canada. *Mar. Biol.* 73:263-267.

MOLLOY, F J. 1990. Utilized and potentially utilizable seaweeds on the Namibian coast: biogeography and accessibility. *Hydrobiologia* 204/204:293-299.

MOSTELLER, F & TUKEY, J W. 1977. Data analysis and regression. A second course in statistics. Addison-Wesley, Reading, MA.

MOORE, D S & MILLER, R J. 1983 Recovery of macroalgae following widespread sea urchin mortality with a description of the nearshore hard-bottom habitat on the Atlantic coast of Nova Scotia. *Can. Tech. Rep. Fish. Aquat. Sci.* 1230.

MORENO, C A. & SUTHERLAND J P. 1982. Physical and biological processes in a *Macrocystis pyrifera* community near Valdivia, Chile. *Oecologia* 55:1-6.

MOSS, B L, MERCER, S & SHEADER, A. 1973. Factors affecting the distribution of *Himanthalia elongata* (L) S.F. Gray on the North-East coast of England. *Estuar. & Coast. Mar. Sci.* 1:233-243.

MYERS, A A & GILLER, P S. (Eds.) 1988. Analytical Biogeography. An integrated approach to the study of plant and animal distributions. Chapman and Hall, London.

NEUSHUL, M. 1967. Studies of subtidal marine vegetation in western Washington. *Ecology* 48:83-94.

NEUSHUL, M. 1971. The species of *Macrocystis* with particular reference to those of North and South America. *Nova Hedwigia* 32:211-228.

NEUSHUL, M, FOSTER, M S, COON, D A, WOESSNER, J W & HARGER, B W. 1976. An *in situ* study of recruitment, growth and survival of subtidal marine algae: techniques and preliminary results. *J. Phycol.* 12:397-408.

NEWELL, R C, FIELD, J G & GRIFFITHS, C L. 1982. Energy balance and significance of micro-organisims in a kelp bed community. *Mar. Ecol. Prog. Ser.* 8:103-113.

NEWROTH, P R & MARKHAM, J W. 1972. Observations on the distribution, morphology and life histories of some Phyllophoraceae. *Proc. Int. Seaweed Symp.* 7:120-126.

NORRIS, R E. 1987. Species of *Antithamnion* (Rhodophyceae, Ceramiaceae) occurring on the southeast African coast (Natal). *J. Phycol.* 16:128-137.

NORRIS, R E & AKEN, M E. 1985. Marine benthic algae new to South Africa. *S. Afr. J. Bot.* 51:55-65.

NORTH, W J. 1969. Kelp habitat improvement project: annual report 1968-1969. W.M. Keck Laboratory of Environmental Health Engineering. California Institute of Technology, Pasadena. 142 pp.

NORTH, W J. 1970. Culturing and "seeding" *Macrocystis*. In: Kelp habitat improvement project. Annual Report, 1969-1970, California Institute of Technology, Pasadena, California. pp 36-52.

NORTH, W J. 1971. The biology of giant kelp beds (*Macrocystis)* in California. *Nova Hedwigia*, 32:1-600.

NORTON, T A. 1978. The factors influencing the distribution of *Saccorhiza polyschides* in the region of Lough Ine. *J. Mar. Biol. Assoc. U.K.*, 58:527-536.

NORTON, T A, MATHIESON, A C & NEUSHUL, M. 1982. A review of some aspects of form and function in seaweeds. *Bot. Mar.* 25:501-510.

NOVACZEK, I & McLACHLAN, J. 1986. Recolonization by algae of the sublittoral habitat of Halifax county, Nova Scotia, following the demise of sea urchins. *Bot. Mar.* 29:69-73.

OJEDA, P F & DEARBORN, J H. 1989. community structure of macroinvertebrates inhabiting the rocky subtidal zone in the Gulf of Maine: seasonal and bathymetric distribution. *Mar. Ecol. Prog. Ser.* 57:147-161.

PACHECO-RUIZ, I, GARCIA-ESQUIVEL, Z & AGUILAR-ROSAS, L E. 1989. Spore discharge in the carrageenophyte *Gigartina canaliculata* Harvey (Rhodophyta, Gigartinales). *J. Exp. Mar. Biol. Ecol.* 126:293-299.

PAINE, R T. 1990. Benthic macroalgal competition: complications and consequences. *J. Phycol.* 26:12-17.

PAPENFUSS, G F. 1942. Studies on South African Phaeophyceae. 1. *Ecklonia maxima, Laminaria pallida, Macrocystis pyrifera.* *Am. J. Bot.* 29(1):15-24.

PEARSE, J S. & HINES, A H. 1979. Expansion of a central California kelp forest following the mass mortality of sea urchins. *Mar. Biol.* 51:83-91.

PEARSE, J S & HINES, A H. 1987. Long-term population dynamics of sea urchins in a central California kelp forest: rare recruitment and rapid decline. *Mar. Ecol. Prog. Ser.* 39:275-283.

PEARSE, J S & LOWRY, L F. 1974. An annotated species list of the benthic algae and invertebrates in the kelp forest community at Point Cabrillo, Pacific Grove, California. Coastal Marine Laboratory, University of California, Santa Cruz. *Tech. Rep.* 1, 73 pp.

PEARSON, G A & EVANS, L V. 1990. Settlement and survival of *Polysiphonia lanosa* (Ceramiales) spores on *Ascophyllum nodosum* and *Fucus vesiculosus* (Fucales). *J. Phycol.* 26:597-603.

PEET, R K. 1974. The measurement of species diversity. *Ann. Rev. Ecol. Syst.* 5:285-307.

PHINNEY, H K. 1977. The macrophytic marine algae of Oregon. In: Krauss, R W. (ed.), The marine plant biomass of the pacific Northwest coast. Oregon State Univ. Press, Corvallis, pp 93-116.

PROVOSOLI, L. 1968. Media and prospects for the cultivation of marine algae. In: Watanabe, A & Hattori, A. (eds.), Cultures and collection of algae. Proceedings of the United States-Japan Conference, Hakone, Japanese Society of Plant Physiologists, Kyoto, Japan, pp 63-75.

REED, D C & FOSTER, M S. 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65(3): 937-948.

REED, D C, LAUR, D R & EBELING, A W. 1988. Variation in algal dispersal and recruitment: the importance of episodic events. *Ecol. Monogr.* 58: 321 - 335.

RICKLEFS, R E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:1009-1014.

RILEY, F R. 1978. Seaweed: South Africa's under-exploited resource. *S. Afr. Food Rev.* (April): pp 23,24,26,28,41,55.

RING, P D. 1970. Development and ecophysiological studies of *Chondrus crispus*. MS thesis, University of Maine.

ROBLES, C. 1982. Disturbance and predation in an assemblage of herbivorous diptera and algae on rocky shores. *Oecologia* 54:23-31.

ROSENTHAL, R J, CLARKE, W D & DAYTON, P K. 1974. Ecology and natural history of a stand of giant kelp, *Macrocystis pyrifera*, off Del Mar, California. *Fish. Bull.* 72: 670 - 684.

RUSSELL, G. 1973. Phytosociological studies on a two-zone shore. II. Community structure. *J. Ecol.* 61:525-536.

RUSSELL, G. 1986. Variation and natural selection in marine macroalgae. *Oceanogr. Mar. Biol. Rev.* 24:309-377.

SAITO, Y. 1972. On the effects of environmental factors on morphological characteristics of *Undaria pinnatifida* and the breeding of hybrids in the genus *Undaria*. In: Abbott, I A & Kurogi, M (eds), Contributions to the systematics of benthic marine algae of the North Pacific. Japanese Society of Phycology, Kobe, pp 117 - 132.

SANDERSON, J C & THOMAS, D P. 1987. Subtidal macroalgal communities in thè D'Entrecasteaux Channel, Tasmania. *J. Ecol.* 12:41-51.

SANTELICES, B. 1981. Perspectivas de investigacion en estructura y dinamica intermareales rocasas de Chile Central. I. Cinturones de macroalgas. *Medio Ambiente* 5:175-189.

SANTELICES, B. 1989. Coastal ecosystems of mainland Chile. In: Nienhuis, P & Mathieson, A. (eds.), Intertidal and littoral ecosystems of the world. Elsevier Scientific Publishing Company.

SANTELICES, B. 1990. Patterns of organizations of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile. *Hydrobiologia* 192:35-57.

SANTELICES, B, CAMUS, P & HOFFMANN, A J. 1989. Ecological studies for harvesting and culturing *Gymnogongrus furcellatus* (Rhodophyta, Gigartinales) in central Chile. *J. Appl. Phycol.* 1:171-181.

SANTELICES, B & OJEDA, F P. 1984a. Effects of canopy removal on the understory algal community of coastal forests of *Macrocystis pyrifera* from southern South America. *Mar. Ecol. Prog. Ser.* 14:165-173.

SANTELICES, B & OJEDA, F P. 1984b. Population dynamics of coastal forests of *Macrocystis pyrifera* in Puerto Toro, Isla Navarino, Southern Chile. *Mar. Ecol. Prog. Ser.* 14: 175-183.

SANTOS, R. 1993. A multivariate study of biotic and abiotic relationships in a subtidal algal stand. *Mar. Ecol. Prog. Ser.* 94:181-190.

SCHEIBLING, R E. 1986. Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia. *Oecologia* 68:186-198.

SCHIEL, D R. 1981. A demographic and experimental evaluation of plant and herbivore interaction in subtidal algal stands. Ph.D. Thesis, University of Auckland, 166 pp.

SCHIEL, D R. 1985. Growth , survival and reproduction of two species of marine algae at different densities in natural stands. *J. Ecol.* 73:199-217.

SCHIEL, D R. 1988. Algal interactions on shallow subtidal reefs in northern New Zealand: A review. *N. Z. J. Mar. Freshwat. Res.* 22.

SCHIEL, D R. 1990. Macroalgal assemblages in New Zealand: structure, interactions and demography. *Hydrobiologia* 192:59-76.

SCHIEL, D R & FOSTER, M S. 1986. The structure of subtidal algal stands in temperate waters. *Oceanogr. Mar. Biol. Ann. Rev.* 24:265-307.

SEAGRIEF, S C. 1984. A catalogue of South African green, brown and red marine algae. *Mem. Bot. Surv. S. Afr.* 47:1-72.

SEAGRIEF, S C. 1988. Marine Algae. In: Lubke, R A, Gess, F W & Bruton, M N, A field guide to the eastern Cape coast. Wildlife Society of Southern Africa, pp 35-72.

SEBENS, K P. 1985a. Community ecology of vertical rock walls in the Gulf of Maine, U.S.A.: a small scale processes and alternative community states. In: Moore, P G & Seed, R. (eds.), The ecology of rocky coasts. Hodder & Stoughton, London, pp 346-371.

SEBENS, K P. 1985b. The ecology of the rocky subtidal zone. *Am. Sci.* 73:458-557.

SEBENS, K P. 1986. Spatial relations among encrusting marine organisms in the New Zealand subtidal zone. *Ecol. Monogr.* 56:73-96.

SHEPHERD, S A. 1981. Ecological strategies in a deep water algal community. *Bot. Mar.* 24:457-463.

SHEPHERD, S A & WOMERSLEY, H B S. 1970. The sublittoral ecology of West Island, South Australia. I. Environmental features and the algal ecology. *Trans. R. Soc. S. Aust.* 94:105-137.

SHEPHERD, S A & WOMERSLEY, H B S. 1971. Pearson Island expedition 1969. - 7. The subtidal ecology of benthic algae. *Trans. Roy. Soc. S. Aust.* 95(3):155-167.

SHEPHERD, S A & WOMERSLEY, H B S. 1976. The subtidal algal and seagrass ecology of St. Francis Island, South Australia. *Trans. R. Soc. S. Aust.* 100:177-191.

SHEPHERD, S A & WOMERSLEY, H B S. 1981. The algal and seagrass ecology of Waterloo Bay, South Australia. *Aquat. Bot.* 11:305-371.

SIMENSTAD, C A, ESTES, J A & KENYON K W. 1978. Aleuts, sea otters, and alternate stable-state communities. *Science* 200:403-411.

SIMONS, R H & HEWITT. 1976. Marine algae from Southern Africa. II. Morphology and taxonomy of five foliaceous Florideophyceae (Rhodophyta). *Sea Fisheries Branch Investigational Report no. 110.*:46 pp.

SMITH, B D. 1986. Implications of population dynamics and interspecific competition for harvest management of the seaweed *Laminaria. Mar. Ecol. Prog. Ser.* 33:7-18.

SOKAL R R & RHOLF F J. 1981. Biometry. W.H. Freeman & Co., San Francisco, California (2nd edition), 859pp.

SOUSA, W P. 1984. The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.* 15:353-391.

STEGENGA, H. 1985. The marine Acrochaetiaceae (Rhodophyta) of southern Africa. *S. Afr. J. Bot.* 51:291-330.

STEGENGA, H. 1986. The Ceramiaceae (excl. *Ceramium*) (Rhodophyta) of the south west Cape Province, South Africa. *Bibl. Phycol.* 74:149 pp.

STEGENGA, H & BOLTON, J J. 1995 The Ceramiaceae (Rhodophyta) of the Cape Province, South Africa and their distribution in relation to concepts of marine provinces. In: Proceedings of the XIIIth AETFAT Congress, Zomba, Malawi.

STENECK, R S. 1986. The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Ann. Rev. Ecol. Syst.* 17:273-303.

STEPHENSON, T A. 1944. The constitution of the intertidal flora and fauna of South Africa II. *Ann. Natal Mus.* 10:261-358.

STEPHENSON, T A. 1948. The constitution of the intertidal flora and fauna of South Africa III. *Ann. Natal Mus.* 11:207-324.

STEPHENSON, T A & STEPHENSON, A. 1972. Life between tidemarks on rocky shores. W H Freeman and Co., San Francisco, 425 pp.

STEWART, J G. 1983. Fluctuations in the quantity of sediments trapped among algal thalli on intertidal rock platforms in southern California. *J. Exp. Mar. Biol. Ecol.* 73:205-211.

SYLVESTER, A W & WAALAND, J R. 1984. Sporeling dimorphism in the red alga *Gigartina exasperata* Harvey & Bailey. *Phycologia* 23:427-432.

TAYLOR, P R & LITTLER, M M. 1982. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced, rocky-intertidal community. *Ecology* 63(1):135-146.

TEGNER, M J & DAYTON, P K. 1981. Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* & *S. purpuratus.*) in a kelp forest. *Mar. Ecol. Prog. Ser.* 5:255-268.

TEGNER, M J & LEVIN, L A. 1983. Spiny lobsters and sea urchins: analysis of a predator-prey interaction. *J. Exp. Mar. Biol. Ecol.* 73:125-150.

TEGNER, M J & DAYTON, P K. 1987. El nino effects on southern California kelp forest communities. *Advances in Ecological Research* 17:243-279.

TER BRAAK, C J F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67(5):1167-1179.

TER BRAAK, C J F. 1987. The analysis of vegetation-environment relationship by canonical correspondence analysis. *Vegetatio* 69:69-77.

TOKIDA, J, NAKAMURA, Y & DRUEHL, L D. 1980. Typification of species of *Laminaria* (Phaeophyta, Laminariales) described by Miyabe, and taxonomic notes on the genus in Japan. *Phycologia* 19:317-328.

TVETER, E & MATHIESON, A C. 1976. Sporeling coalescence in *Chondrus crispus* (Rhodophyceae). *J. Phycol.* 12:110-118.

UNDERWOOD, A J. 1986. The analysis of competition by field experiments. In: Kikkawa, J & Anderson, D J. (eds.), Community ecology: patterns and process. Blackwell Scientific Press, pp 240-268.

UNDERWOOD, A J & JERNAKOFF, P. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia* 48:221-233.

UNDERWOOD, A J & FAIRWEATHER P G. 1986. Intertidal communities: do they have different ecologies or different ecologists? *Proc. Ecol. Soc. Austr.* 14:7-16

UNDERWOOD, A J & KENNELLY, S J. 1990. Ecology of marine algae on rocky shores and subtidal reefs in temperate Australia. *Hydrobiologia* 192:3-20.

VADAS, R L & NORTON, T A. 1982. Ecology of benthic marine algae: introduction and bibliography. In: Rosowski, J R & Parker, B B (eds.), Selected papers on Phycology II. Lawrence, Kan: Phycol. Soc. Am., pp 549-556.

VADAS, S R, WRIGHT, W A & MILLER, S L. 1990. Recruitment of *Ascophyylum nodosun:* wave action as a source of mortality. *Mar. Ecol. Prog. Ser.* 61:263-272.

VADAS, S R, JOHNSON, S & NORTON, T A. 1992. Recruitment and mortality of early post-settlement stages of benthic algae. *Br. Phycol. J.* 27:331-351.

VAN DER MAAREL, E. 1979. Transformation of cover-abundance values in phytosociology and its effect on community similarity. *Vegetatio* 39:97-114.

VEBLEN, T T, KITZBERGER, T & ANTONIO, L. 1992. Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. *J. Veg. Sci.* 3:507-520.

VELIMIROV, B. 1983. Succession in a kelp bed ecosystem: clearing of primary substrate by wave-induced kelp sweeping. In: *Proc. 17th Europ. Mar. Biol. Symp., Brest. Oceanologia Acta*, pp 201-206.

VELIMIROV, B & GRIFFITHS, C L. 1977. Wave-Induced kelp movement and its importance for community structure. *Bot. Mar.* 22:169-172.

VELIMIROV, B, FIELD, J G, GRIFFITHS, C L & ZOUTENDYK, P. 1977. The ecology of kelp bed communities in the Benguela upwelling system: analysis of biomass and spatial distribution. *Helgol. Wiss. Meeresunters* 30:495-518.

WEST, J A. 1972. The life history of *Petrocelis franciscana. Br. phycol. J.* 7:299-308.

WEST, J A & CRUMP, E. 1974. The influence of substrate and spore concentration on spore survival and germination in *Gigartina* and *Petrocelis* (Rhodophyta). *J.Phycol. 10 (suppl) June*: pg 12

WHARTON, W G & MANN, K H. 1981. Relationship between destructive grazing by the sea urchin *Strongylocentrotus droebachienis*, and the abundance of american lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia. *Can. J. Fish. Aquat. Sci.* 38:1339-1349.

WHITTAKER, R H. 1977. Evolution of species diversity in land communities. *Evol. Biol.* 10:1-67.

WIENS, J A. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7:81-120.

WILSON, M V & SHMIDA, A. 1984. Measuring beta diversity with presence-absence data. *J. Ecol.* 72:1055-1064.

WITMAN, J D. 1985. Refuges, biological disturbance and rocky subtidal community structure in New England. *Ecol. Monogr.* 55:421-445.

WITMAN, J D. 1987. Subtidal coexistence: storms, grazing, mutualism and the zonation of kelps and mussels. *Ecol. Monogr.* 57(2):167-187.

WOMERSLEY, H B S. 1981. Marine ecology and zonation of temperate coasts. In: M.N. Clayton & R.J. King (eds), Marine Botany: an Australasian Perspective. Longman - Cheshire, Melbourne, pp 211-240.

WULFF, F V & FIELD, J G. 1983. Importance of different trophic pathways in a nearshore benthic community under upwelling and downwelling conditions. *Mar. Ecol. Prog. Ser.* 12:217-228.

WYNNE, M J. 1986. Report on the collection of benthic marine algae from the Namibian coast (southwestern Africa). *Nova Hedwigia* 43:311-355.

ZAR, J H. 1984. Biostatistical analysis. 2nd Ed. Prentice Hill, Englewood Cliffs, N.J.