Effects of sedimentation on the structure of a phaeophycean dominated macroalgal community

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Declaration

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Abstract

Macroalgae are abundant on shallow temperate reef environments, often forming complex communities that comprise several strata. In southern Australia, these assemblages are dominated by large canopy forming taxa from the Orders Laminariales and Fucales. The presence of subtidal fucoid macroalgae differentiates these communities from that elsewhere, and emphasises the need for local studies rather than relying on generalisations made elsewhere.

Like most natural systems, temperate reefs are often threatened by human activity with degradation reported from many locations in close proximity to urban settlements. The work presented in this thesis involves an examination of the temporal and spatial variability in the structure of macroalgal communities from reefs along the Adelaide (South Australia) metropolitan coast. The work looked specifically at the effects of a dispersed sediment plume, resulting from the 1997 beach sand-replenishment dredging program, on shallow sub-tidal reef systems.

An examination of the structure of canopy forming phaeophycean macroalgae in Gulf St Vincent (South Australia), noted large amounts of both spatial and temporal heterogeneity. Notwithstanding, this variation was not random, but demonstrated considerable structure that could be linked to a number of important underlying processes. In particular, macroalgal assemblages appeared as a mosaic of patches, each of which comprised a high-density state clearly dominated by a single genus (*Cystophora*, *Sargassum*, or *Ecklonia*), or alternatively a lower density mixed assemblage (Variable Low Abundance, VLA).

Macroalgal community structure appeared to be driven by biotic interactions at small scales (metres), such that patches comprised of different species of algae in high density states rarely abutted one another. Instead, VLA assemblages frequently formed a buffer being situated between these mono generic patches. In terms of successional processes, the high-density states appeared to be relatively stable whereas the VLA state, at least in some systems, was transitory. This finding was supported by the absence of intermediary high-density states (e.g. a mix of *Cystophora* and *Ecklonia*) implying that state changes must occur via the VLA state following some form of disturbance.

Larger scale patterns appeared to be driven by environmental variation, with factors such as wave exposure influencing habitat suitability for individual species and thereby

affecting community composition. These phenomena were examined in terms of life history strategies that tend to promote stability, and which are common in late successional taxa.

The importance of properties enhancing stability and the role of disturbance was investigated experimentally using a dispersed sediment plume, which entirely engulfed two reefs[1], as a pulse impact. This disturbance was of particular relevance given that degradation of macroalgal communities in close proximity to the City of Adelaide has been, at least in part, attributed to the effects of elevated levels of sediment. Follow up surveys revealed that the sedimentation from the plume had primarily affected newly recruiting individuals, with few juveniles surviving to one year of age. Over the following few years, the effect of this recruitment failure cascaded into the adult stand.

In broader terms, unfavourable climatic conditions prior to the start of the study, including a particularly severe El Niño event, had a widespread effect on local assemblages, causing high levels of both adult and juvenile mortality. As such, at the commencement of the study, macroalgal communities across the study area were in the process of recovery. This was observed at control sites over the duration of the study. In contrast, recruitment failure at the sediment-affected sites retarded the recovery process, exacerbating the problems associated with prior unfavourable climatic events and leaving them in a degraded state.

This study demonstrated that macroalgal assemblages are equipped (under natural conditions) to handle 'normal' environmental fluctuations (such as inter-annual variability). However, the additional stress associated with certain anthropogenic impacts has the potential to push them over the limit, causing degradation. The loss of canopy macroalgae reduces the structural complexity of the system, leading to a concomitant reduction in their ability to recover. As such, these findings are of particular relevance to those charged with the responsibility for managing near-shore marine environments.

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[1] The plume was created accidentally during a dredging operation for beach sand replenishment of Adelaide's eroding shoreline.

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Preface

Macroalgal communities are prominent inhabitants of the near-shore marine environment at temperate latitudes. In southern Australia, assemblages are often dominated by large canopy forming phaeophycean taxa from the orders Laminariales and Fucales. Together they are major primary producers and create important habitat complexity. Yet the ecology and sensitivities of these communities' remain poorly understood.

Recent surveys of macroalgal-dominated reefs have identified a loss of canopy forming species from the northern part of Adelaide's metropolitan coastline. This impact has been attributed to declining water quality in the region; a stance supported by the more voluminous work on local seagrass communities. However, while seagrass decline has primarily been linked to eutrophication and stormwater discharge, macroalgal communities are also likely to have been affected by increased levels of sediment.

Pretext for this work

During November 1997, offshore dredging for beach sand replenishment led to the creation of a large sediment plume that was observed in close proximity to a number of metropolitan reefs, south of Adelaide. The scale of this event presented a unique opportunity to examine the effect of this disturbance on the resident macroalgal communities. In particular, the most likely impact of the sediment plume would be to affect recruiting individuals through a reduction in suitable hard substrate and by smothering propagules. However, in order to address this issue, it was first necessary to develop an understanding of the inherent structure of the system.

This thesis represents an attempt to understand some of the important structural components of brown algal dominated macroalgal communities. The dynamic nature of the system is considered and used as a framework for investigating spatial and temporal changes in structure under natural conditions and in response to environmental perturbation.

Specific aims of the research

The first objective of this study was to examine of local assemblages in order to create a framework that will enable a degree of prediction. Furthermore, it will address the dynamic processes that give rise to assemblage structure, thereby providing a level of explanation. The use of this procedure will allow for the subsequent testing of a specific disturbance in a robust manner. Specific aims are:

AIM: *To build an understanding of how local canopy dominated macroalgal systems are structured, and whether knowledge of the current state of a patch can be used to determine past or future states.*

AIM: *To quantify the relationship between adult canopy structure and the underlying juvenile assemblage.*

AIM: *To construct a model that effectively describes assemblage structure.*

AIM: *To determine how the reefs in the study area change through time.*

The second objective of this study was to distinguish the effect of the sediment plume as the signal of interest from the influence of other environmental phenomena.

AIM: *To investigate the impact of elevated sediment levels as a pulse disturbance on the recruitment of canopy forming genera of macroalgae.*

AIM: *To identify the longer term effects of the sediment impact.*

Thesis structure and layout

This thesis attempts to embrace some of the complexity displayed by canopy dominated macroalgal systems and explain some of the important components of structure. Using a sediment plume as a case study, the effect of a pulse disturbance is tracked as it propagates through time.

Chapter 1 provides a background and literature review of current knowledge on macroalgal communities. Included here is a description of the uniqueness of South Australia's marine biota and life history treatises for each of the dominant canopy forming genera present in the study area.

Chapter 2 introduces the Gulf St Vincent environment and discusses some of the threats to ecosystem health. Following this, a description of a sediment plume resulting from sand dredging for beach replenishment is used as the basis for a natural experiment into macroalgal dynamics.

Chapter 3 describes local reef structure based on 4 selected reefs within Gulf St Vincent and explores some of the patterns observed.

Chapter 4 specifically addresses the impact of the sediment plume on algal recruitment dynamics. This is done through a spatial investigation comparing a number of control and impact sites.

Chapter 5 broadens the study, places the state of macroalgal communities in context with other environmental perturbations, and introduces a temporal component. The longer-term effects of the initial disturbance are then placed in the context of the overall state of macroalgal communities.

Chapter 6 summarises the major findings of this research and provides a synthesis of the results in the context of the relevant literature. It also serves to highlight future research initiatives, which would greatly improve knowledge of macroalgal dynamics.

Chapter 1

Aspects of macroalgal biology

This chapter reviews our understanding of the ecology of macroalgal systems. Included is a discussion on how varying life history strategies allow the larger macroalgae to maintain dominance within a stand.

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1.1 An introduction to macroalgae

Macroalgae dominate shallow reef environments throughout the temperate regions of southern Australia. Evolving in isolation, macroalgal communities in this region have a number of unique features including high levels of diversity (>1155 species) and endemism (~60%, Womersley 1990) that differentiates them from similar systems elsewhere in the world. The significance of these features has long been recognised (Womersley 1984) but until recently the comparative ecology of these systems was still poorly understood (Underwood and Kennelly 1990). Notwithstanding, there have been a number of studies over the last decade that have attempted to address this issue (e.g. Walker and Kendrick 1998; Phillips 1998; Huisman *et al.* 1998; Nelson 1994; Womersley 1990; Collings 1996; Turner and Cheshire 2003; Irving *et al.* 2004; King 1995; Collings and Cheshire 1998).

As a group, macroalgae are the dominant photosynthetic organisms present in great abundance on hard substrates in shallow marine environments. Their morphological organisation is superficially similar to that of land plants despite a number of important differences (Price 1990).

Seaweeds are ideally suited to growth on hard surfaces by way of a specialised holdfast that effectively glues the organism in place. They range in size from tiny encrusting and turfing forms up to giant kelps that can be thirty or more metres in length. The larger taxa display complex differentiation of tissues into a number of specialised structures (Price 1990).

Macroalgae often dominate reef systems producing structurally complex communities generally comprised of many separate layers. This structure not only greatly increases the total productivity of the system but also defines the habitat that in turn supports a vast range of other organisms (Shepherd and Sprigg 1976).

The largest and most visually dominant macroalgae belong to the orders Laminariales Kylin, Durvillaeales Petrov and Fucales Kylin. On global scales, kelps such as *Macrocystis spp.* C.Agardh, *Laminaria spp.* Lamouroux, and *Ecklonia spp.* Hornemann dominate the subtidal zone of temperate regions (Mann 1982). In the southern hemisphere, Fucalean species often coexist with or replace the Laminarian taxa; while in the northern hemisphere they mainly occur in the intertidal (e.g. *Fucus spp.* Linnaeus and *Cystoseira* *spp.* C.Agardh). Fucalean algae including *Sargassum spp.* C.Agardh and *Turbinaria spp.* Lamouroux are also common in the subtidal in tropical regions (Womersley and King 1990).

1.2 Biogeography on a world scale

Few macroalgae are cosmopolitan. More usually, species are confined to narrower distributional range (e.g. temperate, tropical, or polar). This phenomenon is linked primarily to water temperature with most species being limited to a 5^{o}C range based on either the summer or winter isotherm (Van Den Hoek 1982) although intra-annual variation is often greater than this. Furthermore species common in temperate regions of the southern hemisphere are rarely found to exist in the northern hemisphere under similar conditions (Womersley 1990), although a notable exception is the genus *Caulerpa* Lamouroux (Womersley 1984).

1.2.1 Diversity in context

Algal diversity is greatest in the world's temperate regions with notable floras occurring off the coasts of Southern Australia, Japan, South Africa, Pacific North America and the Mediterranean (Womersley 1990).

Temperate regions are generally divided into cold (10-15^{o}C) and warm (15-20^{o}C), with the cold regions offering the richest and most diverse array of species. These regions tend to be characterised by the presence of large brown (phaeophycean) algae (Womersley 1990). In contrast, tropical and subtropical areas (>20^{o}C) support fewer phaeophycean algae but are still rich in the smaller coralline species (Rhodophyta). The polar regions (<10^{o}C) have limited diversity but nevertheless support a number of larger taxa (Womersley 1990).

In terms of macroalgal diversity, southern Australia is one of only a few areas with more than 1000 species (Table 1.1). Southern Australia is the only region contained within a limited climatic region to support such diversity (Womersley 1990).

Table 1.1 World comparison of algal biodiversity (based on Womersley 1990).

Geographic region	Climatic zones	Coastline length (km)	Total taxa Genera	Species
Britain	Cold temperate	5000	261	604
Northern north Atlantic	Cold temperate to arctic	>25,000	387	1,170
North eastern north America	Arctic to warm temperate	8,000	170	392
Tropical eastern America	Tropical	16,000	237	752
Pacific north America	Arctic to tropical	12,000	366	1,254
California	Cold temperate	1,400	282	666
Malaysia / Indonesia	Tropical		189	629
Japan	Subarctic to subtropical	6,500	411	1,452
South Africa	Cold temperate to subtropical	2,500	254	539
Southern Australia	Cold temperate to warm temperate	5,500	427	1,155
New Zealand	Subantarctic to warm temperate	6,970	288	835

1.3 Biogeography in Southern Australia

1.3.1 Biodiversity and Endemicity

The southern Australian coast spans 5500 km and represents the longest east west stretch of coastline in a temperate location in the world. The area comprises both cool and warm temperate regions with water temperatures ranging 10-19^{0}C. While there is typically only a 5^{0}C annual variation in any location, sheltered areas including the South Australian Gulfs tend to experience larger fluctuations (12 – 25^{0}C, Womersley 1984).

Along this coastline are many geographic features including bays and inlets, gulfs, offshore islands, as well as long stretches of more exposed rocky shoreline. These structures give rise to a large range of different habitats which in turn support some of the most diverse macroalgal communities in the world (Table 1.1, Womersley 1990).

A number of major currents influence the southern Australian coastline, moderating temperature and nutrient levels, and restricting species migration to and from other temperate areas (Figure 1.1).

The Eastern Australian Current and Leeuwin Current dominate water movement along Australia's eastern and western coastlines respectively. Both currents move warm, nutrient poor water from north to south (Jeffrey *et al.* 1990).

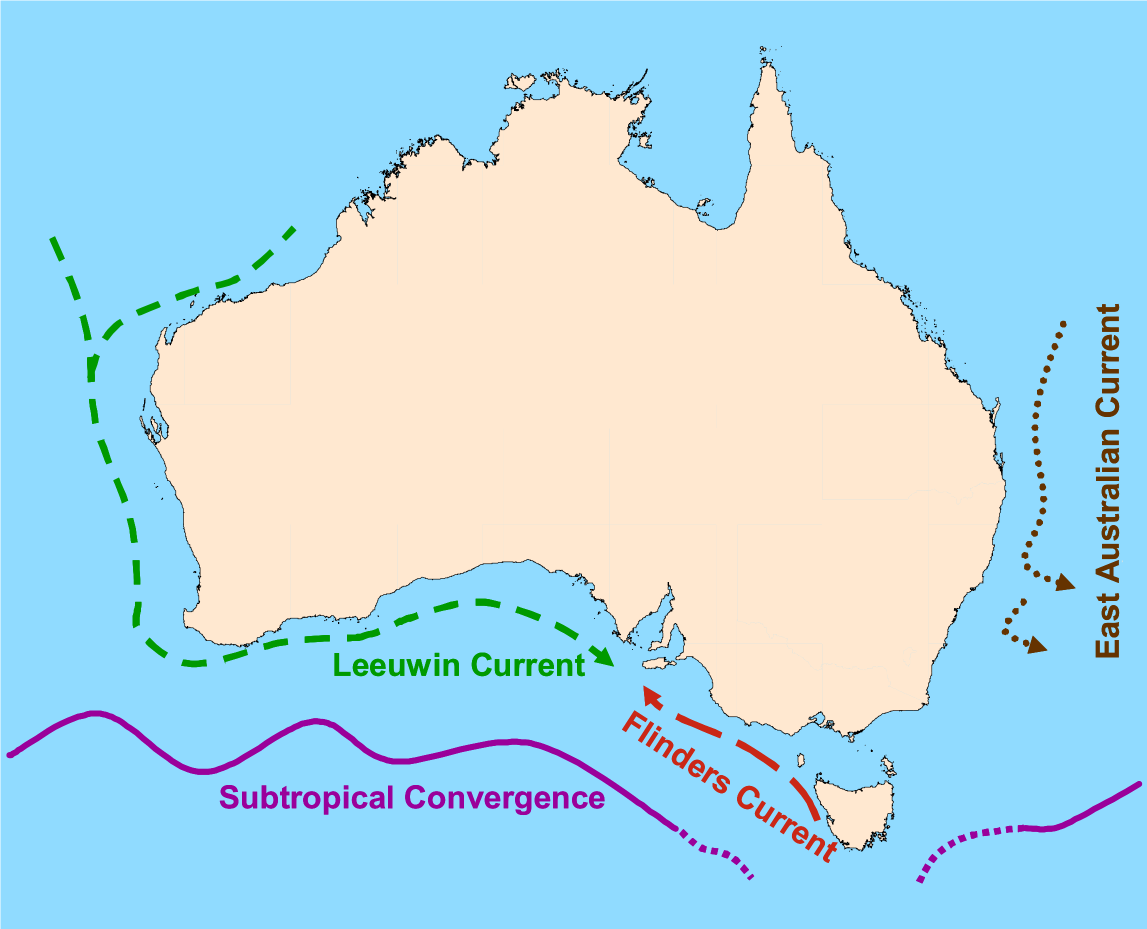

Figure 1.1 Major currents around southern Australia (after Jeffrey *et al.* 1990)[2].

In the east, the influence of the East Australian Current and its eddies has a significant effect on continental shelf waters modifying currents and nutrient dynamics (Jeffrey *et al.* 1990). Further south, the Flinders Current flows northward along the western Tasmanian coastline then crosses Bass Strait before heading westward along the Victorian and South Australian coastlines towards the Great Australian Bight. Associated with this current,

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[2] This figure incorporates data that is © Commonwealth of Australia (Geoscience Australia 2003).

which flows in summer, is a small upwelling bringing cooler nutrient rich water to the surface off Pt. MacDonnell, SA (Jeffrey *et al.* 1990).

On the western coastline, the Leeuwin Current continues around the southwest corner of Australia, and then travels east into the Great Australian Bight. This leads to an interaction between it and the Flinders current (Jeffrey *et al.* 1990).

Most tropical species travelling on the Leeuwin and Eastern Australian Currents are unable to survive in the cooler waters of southern Australia. Furthermore, the Southern Polar Current is kept offshore by the presence of the Leeuwin Current. As a result, Australia's southern coastline is effectively isolated from the other major southern landmasses (Jeffrey *et al.* 1990).

Isolation has in turn led to local evolution and resulted in a highly endemic algal flora (Table 1.2) with an especially high proportion of the Phaeophycean and Rhodophycean taxa (Womersley 1990).

Table 1.2 Endemicity in southern Australian macroalgae (based on Womersley 1990).

	Total numbers		Level of endemicity	
Taxonomic division	Genera	Species	Genera	Species
Chlorophyta	39	124	2 (5%)	43 (30%)
Phaeophyta	104	231	20 (19%)	131 (57%)
Rhodophyta	284	>800	72 (30%)	538 (75%)
Totals	427	>1155	94 (22%)	712 (62%)

While the Chlorophyta are less prominent than the other two divisions (Table 1.2), there are a couple of noteworthy genera (in terms of species diversity) including *Codium* Stackhouse and *Caulerpa* (Womersley 1990).

High diversity orders within the Phaeophyta include the Dictyotales Kjellman, Ectocarpales Setchell & Gardner, Sphacelariales Oltmanns, Chordariales Setchell & Gardner, and Fucales. Interestingly both the Dictyotales and Fucales are commonly referred to as tropical orders (Womersley 1987). However, the Dictyotales are better represented in southern Australia than anywhere else, while local Fucales differ from their northern hemisphere counterparts in that most are subtidal (Womersley 1990).

There are also large numbers of Rhodophycean macroalgae in southern Australia with prominent orders including the Nemaliales Schmitz, Gelidiales Kylin, Gigartinales Schmitz, Rhodymeniales Schmitz, and Ceramiales Oltmanns, of which roughly 50% of genera are present locally (Womersley 1990).

1.3.2 Trends across the continent

A number of biogeographic provinces have been identified around the Australian coastline by Womersley (1984; 1990). These were based largely on the resident macroalgal flora (Figure 1.2). The majority of the southern Australian coastline is contained within the Flindersian Province, which is characterised as being transitional between cool and warm temperate. To the north of this province are the warm temperate Peronian and southern extent of the Dampierian Provinces that extend up the east and west coasts respectively.

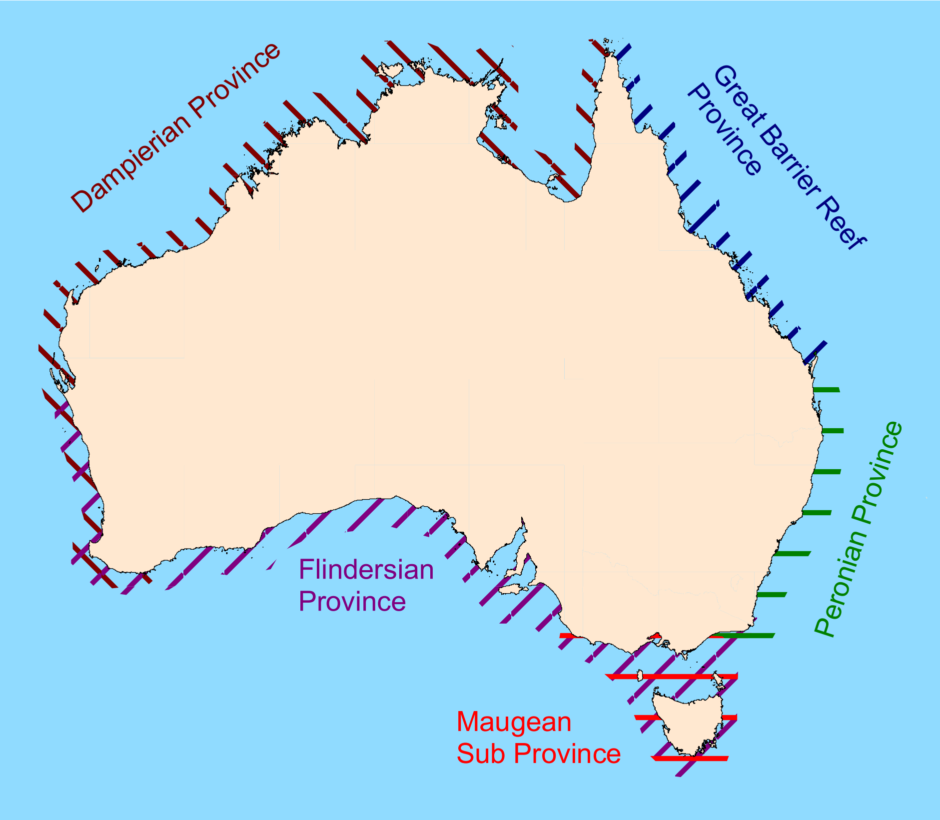

Figure 1.2 Marine biogeographic provinces of Australia (based on Womersley 1984)[3].

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[3] This figure incorporates data that is © Commonwealth of Australia (Geoscience Australia 2003).

Within the eastern part of the Flindersian province is the Maugean subprovince that encompasses Victoria, Tasmania, and extends into South Australia as far as Robe. This area is cold temperate due to the presence of a cold water upwelling (Womersley 1990) and is differentiated from the rest of the Flindersian Province by the presence of massive taxa such as *Durvillaea* Bory, *Macrocystis* and *Lessonia* Bory, that are not found elsewhere in southern Australia (Womersley 1987).

Although the southern Australian coastline is mainly temperate, a slight subantarctic element exists in South East Tasmania while parts of the South Australian gulfs have a subtropical element (Womersley 1984).

Species present along the southern Australian coastline can be grouped according to distributional range, using the definitions in Table 1.3.

Table 1.3 Definitions of distributional range (Womersley 1959).

Cosmopolitan	Widely distributed in the worlds temperate oceans
Southern Australian	Found in suitable habitats across southern Australia
Eastern element	Victoria, Tasmania and parts of South Australia
Western element	Western Australia and parts of South Australia
Restricted	Known only from isolated samples

Only thirteen percent of local taxa have a cosmopolitan distribution, and most of these belong to the Chlorophyta or Phaeophyta (Table 1.4). At the other end of the scale, only a fraction of the taxa (approximately two percent), are restricted to a small geographical area within the region. The rest are either broadly distributed along the length of the coastline (within the Flindersian Province) or confined to the eastern or western halves (i.e. inside or outside the Maugean Sub Province, Table 1.4). Of these, the eastern area contains the greatest diversity.

Table 1.4 Distribution of algal flora in southern Australia (based on Womersley 1990).

	Chlorophyta	Phaeophyta	Rhodophyta	Total
Number of Species	124	231	>800	>1155
Cosmopolitan	41 (33%)	69 (30%)	40 (5%)	150 (13%)
Southern Australian	37 (30%)	59 (25%)	272 (34%)	368 (32%)
Eastern Element	25 (20%)	67 (29%)	344 (43%)	436 (38%)
Western Element	12 (10%)	20 (9%)	144 (18%)	176 (15%)
Restricted	9 (7%)	16 (7%)	unknown	>25 (>2%)

1.4 Algal domination of southern Australia's rocky shores

Marine environments are conveniently divided into intertidal and subtidal regions, each of which is often further divided into a number of zones. Recently there has been debate over whether there is indeed any biological relevance for assigning zones based on the dominant biota (e.g. Underwood 1998). However the concept is used here as a convenient way of describing the upper and lower limits of algal distributions as first described by Shepherd and Womersley (1970).

In South Australia, macroalgae are generally confined to the lowest parts of the intertidal and into the subtidal, with the exception of a few encrusting brown and red taxa (Womersley 1984). However frequent examples higher in the intertidal do occur in Victoria and Tasmania (Bennett and Pope 1953; Bennett and Pope 1960). Additionally macroalgae are mostly absent from sandy environments (Womersley 1984). Animals including mussels and barnacles generally dominate the mid-eulittoral, although several macroalgae appear seasonally including *Ulva* spp. Linnaeus, *Enteromorpha* spp. Link[4], and *Porphyra* spp. C.Agardh. Lower zones within the intertidal often play host to coralline algae and red foliaceous species on steeply sloping shores, whereas the conspicuous *Hormosira banksii* (Turner) Decaisne often dominates rocky platforms (Womersley 1984).

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[4] The genus *Enteromorpha* was recently incorporated into the genus *Ulva* (see Hayden *et al.* 2003).

Both water movement and depth are known to influence the structure of macroalgal communities, with depth having a dual role, reducing both wave energy and light levels (Lobban and Harrison 1994). While overall community structure may vary, rocky subtidal regions in southern Australia tend to be dominated by large brown macroalgae wherever sufficient light is available. Shepherd and Womersley (1970), identified three zones (upper, mid, and lower) within the sublittoral based on the community dominants, although they acknowledge the presence of considerable gradation (Womersley 1984).

Along most parts of the southern Australian coastline, dominants of the upper sublittoral zone extend from the mean low water mark down several metres (Shepherd and Womersley 1970, 1971, 1976, 1981). In the east and extending to Cape Jaffa in South Australia, dominants include the massive genera *Durvillaea potatorum* (Labillardière) Areschoug and *Macrocystis* spp. on rough water coasts, while fucoids such as *Phyllospora comosa* (Labillardière) C.Agardh occur where wave force is less (Womersley 1984).

West of Cape Jaffa, the upper zone tends to be dominated by *Ecklonia radiata* (C.Agardh) J.Agardh along with numerous species of fucoids including *Cystophora* J.Agardh, *Sargassum*, and *Scytothalia* Greville (Womersley 1984). Additionally, low energy environments may also contain patches of *Caulocystis* spp. Areschoug and *Cystoseira trinodis* (Forsskål) C.Agardh while in very high wave force environments there may also be a fringe zone dominated by fucoids such as *Cystophora intermedia* J.Agardh (Shepherd and Womersley 1970; Womersley 1984).

The mid-sublittoral zone (identified by Shepherd and Womersley 1970), occupies the largest depth range, and is generally dominated by large brown macroalgae. Notable taxa once again include the kelp *Ecklonia radiata* along with a host of fucoids such as *Cystophora* spp., *Sargassum* spp., *Scytothalia dorycarpa* (Turner) Greville, *Acrocarpia paniculata* (Turner) Areschoug and *Myriodesma* spp. Decaisne (Womersley 1984).

Below the mid-sublittoral is the lower sublittoral zone, which extends until insufficient light is available for photosynthesis (Shepherd and Womersley 1970). This zone is dominated by a diverse range of red algae including *Plocamium* Lamouroux and various encrusting coralline species (Womersley 1984).

Macroalgal communities tend to comprise a number of separately identifiable layers (based on size) that may or may not coexist within a single assemblage depending on local factors

(Shepherd and Sprigg 1976; Turner 1995; Turner and Cheshire 2003). Across much of Australia, the upper stratum is comprised of large brown canopy forming taxa (Fucales and Laminariales, Shepherd and Sprigg 1976), although in colder areas (generally within the Maugean Sub-province), there may additionally be a floating canopy containing massive species such as *Macrocystis* (Womersley 1984).

Foliaceous representatives of all three macroalgal divisions often form a stipitate (sub) canopy that may be observed below the main canopy, or alternatively as dominant in areas unsuitable for the larger phaeophycean taxa (Shepherd and Sprigg 1976; Turner and Cheshire 2003). Similarly, smaller specimens (a few centimetres tall) may exist below the larger canopy, but are also capable of forming dense stands of 'turf'. Once established, turf beds have the ability to exclude larger taxa and thereby dominate patches of reef (Kennelly 1987; Shepherd and Sprigg 1976).

The smallest of the macroalgae may only be a few millimetres tall and are often observed as an encrusting layer on the substrate (Shepherd and Sprigg 1976). Encrusting species are also able to dominate substrate in areas less suitable for larger taxa (Dethier 1994). Alternatively, many can adapt to lower light conditions and survive even when overgrown by larger taxa (Cheshire 1985).

1.5 Factors shaping a macroalgal community

The following presents a brief overview of some of the factors deemed important in structuring macroalgal communities. It is important to keep in mind that while good levels of correlation have been demonstrated between various factors and the 'resultant' biotic structure, few studies have actually demonstrated a causal mechanism.

1.5.1 Substrate and water quality

Macroalgae are generally confined to hard substrates. In some studies successful recruitment was found to be largely independent of aspect or texture (e.g. Collings and Cheshire 1998; Greig 2000; Renaud *et al.* 1996), while in others differential recruitment was observed (e.g. Fletcher and Callow 1992; Harlin and Lindburgh 1977; Vandermeulen and Dewreede 1982). Notwithstanding, recruitment is often moderated by the presence of other organisms, which act to modify the substrate or alternatively modify another factor (e.g. reduce herbivore activity, Farrell 1991). In contrast, the presence of unconsolidated sediment over the substrate generally has an inhibitory effect (Renaud *et al.* 1996).

Seawater generally has a salinity of around 35 ppt, but may be lower near river mouths or higher in places where evaporation exceeds freshwater input. Decreases in diversity have been reported under conditions where salinity is less than (Middelboe *et al.* 1998) or greater than (Kendrick *et al.* 1990) than the average.

Linked with fluctuations in salinity is the presence of fresh water or marine inflows that can also variously contribute nutrients, suspended matter and pollutants to the near shore environment. Additionally agents that have an effect on water quality may also be contributed from other anthropogenic sources. These issues are covered in detail in Chapter 2.

1.5.2 Depth and wave exposure

Previous work in southern Australia has demonstrated a pattern of zonation in terms of algal flora, across gradients of depth and wave exposure, both on exposed coasts (Shepherd and Womersley 1970, 1971, 1976, 1981; Cheshire and Hallam 1988b, 1989b) and in the more sheltered gulfs (Collings and Cheshire 1998).

Wave exposure can be seen to encompass a suite of factors that change along the wave force gradient (Cousens 1982), including mechanical forces, turbidity, and gas exchange (Cheshire and Hallam 1988b, 1989b). As such, wave exposure has been implicated as a major process structuring marine systems (e.g. Denny and Shibata 1989; Gaylord *et al.* 1994; Shepherd and Womersley 1970, 1971, 1976, 1981; Underwood *et al.* 1991).

Two significant effects of increasing depth are the reduction in wave energy along with a reduction in the quality and intensity of light available to photosynthetic organisms (Lobban and Harrison 1994). Of these Shepherd and Womersley (1970, 1971, 1976, 1981), argue that within much of the photic zone it is the degree of water movement, modified by depth, which is the most important factor in determining community composition.

In South Australia, the conspicuous kelp, *Ecklonia radiata* has been observed to dominate both extremes of the wave exposure gradient, but appears less prominent in moderate wave environments where fucoids are abundant (Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976). Further east, the massive taxa *Macrocystis angustifolia* Bory and *Durvillaea potatorum* also dominate more exposed locations (Womersley 1984; Cheshire and Hallam 1988a, b, 1989b, a).

In the east fucoids are known to dominate areas of reduced wave exposure (Womersley 1990), whereas in South Australia fucoids (*Cystophora* spp. and *Sargassum* spp.) inhabit a range of depth and wave exposure regimes (Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976; Collings and Cheshire 1998). Notwithstanding, individual species tend to inhabit a smaller range (Shepherd and Sprigg 1976; Hotchkiss 2000; Turner and Cheshire 2003). The western species *Scytothalia dorycarpa* often dominates high-energy environments (Shepherd and Womersley 1970, 1971, 1976, 1981), while further east (but overlapping) *Seirococcus axillaris* (Turner) Greville dominates a similar habitat (Womersley 1987).

1.5.3 The influence of light on productivity

Macroalgal communities have long been thought of as highly productive in terms of both carbon fixation and biomass turnover (Cheshire *et al.* 1996b). At the heart of this productivity is the ability of macroalgae to photosynthesise efficiently, over a range of light conditions.

Light reaching an individual can be quite variable and as such, many taxa are able to adjust their photosynthetic apparatus to make best use of that available (Fairhead 2001). The advantage of this is that individuals are able to maximise their photosynthetic rate within the prevailing light environment, although lower light conditions are generally associated with a concomitant drop in net 24-hour productivity (Cheshire *et al.* 1996b). As a result, there is a lower limit beyond which carbon fixation is not sufficient to cover the individual's physiological requirements. These lower limits have been predicted using models for a range of light environments and subsequently confirmed through field observation (Turner and Cheshire 2003).

Light quality and quantity are affected by a number of factors that tend to be variable and interactive. At a broad scale, temporal factors such as the time of day and season result in changes to the overall intensity of light as well as the angle at which sunlight strikes the water column. This, along with other factors, results in variation in productivity through time (Cheshire *et al.* 1996b; Fairhead 2001; Copertino 2002), with seasonal changes more pronounced at the higher latitudes (Jackson 1987; Davison *et al.* 1991).

In clear waters, light is filtered within the column at different rates depending on wavelength, such that longer wavelengths (red, violet, orange, yellow) are lost at a shallower depth (Dawson 1966). This means that only part of the light spectrum is available for use by photosynthetic organisms.

The amount of turbidity within the water column also changes the degree to which light is scattered by particulate matter, and hence the depth to which light can penetrate. As a result, macroalgal communities growing in clear oceanic water can extend their range deeper compared with a more turbid, low wave energy environment (Lüning 1981; Turner and Cheshire 2003).

Shading can also affect the amount of light reaching an individual, as a temporary (e.g., fluctuations in cloud cover) or more permanent phenomenon (e.g., position within the canopy). Algae growing beneath a canopy tend to have a highly efficient photosynthetic apparatus, so much so that the sudden loss of the canopy often results in the bleaching of pigments from encrusting red algae along with a corresponding reduction in photosynthetic rate (Irving *et al. in press*).

1.5.4 Biotic interactions

Many of the physical and chemical properties described above are important in defining broad habitat suitability. The presence of different organisms exploiting a given area inevitably leads to some degree of interaction, creating another level of structural complexity within the system. Interactions between living members of a system take on many forms. Even a brief inspection of the literature will reveal numerous papers describing concepts including competition between individuals, predator-prey relationships (including herbivory), a host of defensive strategies employed by various individuals, and even a few synergies.

Macroalgae often coexist in assemblages comprising multiple layers and different assemblages are frequently observed in areas that appear to have similar overall conditions (Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976). Patch diversity appears to be maximised under open canopy conditions, i.e. those with a sparse cover of larger individuals, although some closed fucoid canopies also include a range of understorey taxa (Turner and Cheshire 2003). In contrast, diversity is low under *Ecklonia* canopies and mainly limited to smaller encrusting forms and turfing algae (Kennelly 1987; Kennelly and Underwood 1992, 1993; Turner and Cheshire 2003). Systems dominated by *Durvillaea* tend to be almost monospecific with no foliaceous macroalgae existing beneath the canopy (Cheshire 1985), whereas the presence of *Ecklonia* and numerous Rhodophytes under the taller *Macrocystis* canopy is not uncommon (Sanderson and Thomas 1987).

Competition occurs in nature when a resource that is required by two different organisms is in short supply (Cale *et al.* 1989; Hutchinson 1959). Although in its simplest form the idea has a lot of intuitive appeal, historically it was the focus of much debate within the scientific community (see Lewin 1983).

Limiting factors are likely to have different levels of importance for different species. In the case of macroalgae, the availability of suitable substrate has been implicated as a major defining aspect of the system (Renaud *et al.* 1996) and it is generally accepted that competition in this regard is likely to be significant. Competition for light may also occur with successive canopies shading those below. Similarly, recruitment trials have demonstrated that the upper side of experimental plates are generally algal dominated while the light reduced lower sides favour sessile animals (Greig 2000).

In addition to resource competition, interference (e.g. Worm and Chapman 1996) or exclusion (e.g. Worm and Chapman 1998) competition may also influence community structure. In South Australia, successional processes often lead to the patches dominated by large brown macroalgae (Emmerson and Collings 1998; Turner and Cheshire 2003). But, if turf communities pre-empt the space, then they have the capacity to exclude the larger taxa and persist for several years (Airoldi *et al.* 1995; Kennelly 1987).

Community dynamics are often further complicated by the presence of herbivory. Fluctuating levels of herbivory may further influence the outcome of competitive interactions described above (Gacia *et al.* 1999). Furthermore, herbivory acts as a disturbance event, and may result in a total denudation of an area of substrate (Chapman 1981; Schiel 1990).

1.6 Macroalgal Life History Strategies

Most of the larger, more common brown macroalgae found in temperate regions exhibit a seasonal reproductive cycle, with sexual maturity occurring around winter and spring in South Australia. Notwithstanding, reproductive events in *Ecklonia* appear more erratic, variously occurring in spring (Andrew and Jones 1990), summer (Kennelly 1983), autumn (Novaczek 1984), or winter (Kennelly 1983; Kennelly and Underwood 1992). Additionally, there are some species including *Hormosira banksii* (Turner) Decaisne which are fertile throughout the year (Clayton 1990).

Rather than describe the myriad of different strategies used by various taxa, the following aims to highlight strategies used by the canopy forming taxa covered in this study.

1.6.1 Order Laminariales

The Laminariales are the true kelps, and although found in abundance throughout the colder regions of the northern hemisphere, are only represented by three native genera in Australia. The first two, *Macrocystis* and *Lessonia* are only present in eastern Australia and Tasmania respectively, while *Ecklonia* has a wider distribution (Womersley 1990). Recently, the exotic and highly invasive Laminarialean *Undaria pinnatifida* (Harvey) Suringar was introduced to Australasian waters and is currently present in New Zealand, Tasmania and Victoria (Hay and Luckens 1987; Campbell and Burridge 1998; Sanderson 1990).

E. radiata occurs on the coastlines of all temperate states of Australia, and extending into Queensland. The species is also found in New Zealand and South Africa (Womersley 1987). Across this distribution, *E. radiata* is recognised as a dominant, mainly in the mid sublittoral (Kirkman 1989, 1981; Kennelly 1983; Novaczek 1981; Choat and Schiel 1982; Sanderson and Thomas 1987; Shepherd and Womersley 1970, 1971, 1976, 1981), although it has been observed growing abundantly from just below the surface down to 44 metres (Womersley 1987).

Ecklonia has often been observed in monospecific stands (Kennelly 1983; Kirkman 1989; Hatcher 1989), although more realistically patches exist within a larger matrix that may variously contain fucoid or turf dominated communities (Kennelly 1987; Collings and Cheshire 1998; Turner and Cheshire 2003; Underwood *et al.* 1991). Indeed studies in

South Australia often identified shared dominance with *Scytothalia dorycarpa*, *Sargassum* spp., and *Cystophora* spp. (Shepherd and Womersley 1971, 1976, 1981).

Ecklonia exhibits an alternation of heteromorphic generations (Clayton 1990) comprising a familiar large sporophyte and a microscopic gametophyte stage (Womersley 1987). Gametophytes are dioecious and produce oogamous gametes. Reproduction in the sporophyte phase takes place via unilocular sporangia in external sori, which develop on the surface of the central axis as well as on the primary and secondary laterals (Womersley 1987).

The fact that reproductive sori develop on the surface of existing tissue represents a large energy saving for the sporophyte. This is especially true when compared to the seasonal reproductive effort of some fucoids, where up to 90% of total biomass may be reproductive tissue (Hotchkiss 2000). Indeed, it has been argued that Laminarialean algae instead store their reproductive potential as gametophytes (Cheshire and Hallam 1988a) or as partially dormant juveniles under the canopy (Kirkman 1981).

Until recently, studies of productivity in *Ecklonia* were limited to rates of biomass accumulation (e.g. Novaczek 1984; Novaczek 1980; Kirkman 1984, 1989; Hatcher *et al.* 1987), and demonstrated that the species was most productive over spring and summer when light levels were greatest. Notwithstanding, several authors demonstrated that the productivity peak was delayed with increasing depth often by several months (Fairhead 2001; Kirkman 1989; Novaczek 1984). It was, however, argued that measurements of biomass accumulation would underestimate total productivity because of their failure to take into account internal processes or exudates (Larkum 1986). Furthermore, a more recent study utilising *in-situ* photo-respirometry demonstrated that *Ecklonia* is able to adjust the sensitivity of its photosynthetic apparatus and thus maintain high productivity throughout the year (Fairhead 2001). Acknowledging that growth is seasonal (Kirkman 1989; Larkum 1986), excess assimilation during periods of little tissue production allows for carbon storage, which can then be better utilised when inorganic nutrient supply or demands for tissue production are high and exceed the rate of carbon assimilation (Fairhead 2001).

1.6.2 Order Fucales

Southern Australia has a rich collection of fucoid macroalgae, many of which are community dominants, especially in South Australia and Western Australia (Womersley 1990).

Pioneering work by Shepherd and Womersley identified that these taxa occur over a wide range of conditions in South Australia. Locally, a number of different fucoid genera have been observed to co-dominate rocky reef environments with *Ecklonia radiata*. Additionally, where conditions are less suitable for *Ecklonia*, mixed fucoid communities are common (Choat and Schiel 1982; Collings and Cheshire 1998; Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976). Along the Adelaide metropolitan coastline, only two genera (*Cystophora* and *Sargassum*) are present in sufficient numbers to dominate reef habitat. Although, *Seirococcus axillaris* and *Scaberia agardhii* Greville are often observed further south (Shepherd and Sprigg 1976).

Fucoids have an alternation of generations with only one free living phase (Clayton 1990), which is the diploid sporophyte. During the reproductive phase, conceptacles containing oogonia and antheridia are generally born on special reproductive tissue, with meiosis occurring at gametogenesis (Womersley 1987). Many species develop conceptacles seasonally, while in others they are developed as the individual matures. As such, this second group may become fertile at different times (Womersley 1964). Gamete production and release occurs throughout the fertile period (Klemm and Hallam 1987), with eggs being observed sticking to the parent during fertilisation (Nizamuddin 1964; Lobban *et al.* 1985). Additionally, some fucoid zygotes (notably *Sargassum*) are larger than their Laminarialean counterparts because they are retained on the adult for up to 48 hours after fertilisation, leading to a higher proportion of localised recruitment (Deysher and Norton 1981; Coon *et al.* 1972). Dispersal from the adult is often localised, as with *Sargassum* where 96% of propagules were found within 25cm of the parent (Kendrick and Walker 1991). Timing of spore release to periods of low water movement and high light (Pearson and Brawley 1996; Pearson *et al.* 1998) also helps to increase fertilisation success.

Locally, species of *Cystophora* have been shown to direct up to 90% of new biomass into reproductive tissues as part of seasonal reproductive effort (Hotchkiss 2000). Furthermore, many species of *Cystophora* (Hotchkiss 2000) and *Sargassum* (Kendrick and Walker 1994) produce reproductive tissues seasonally and these are later shed.

Many species of *Sargassum* also have the ability to regrow from remnant tissues left after the adult has been ripped from the substrate (Kendrick and Walker 1994). Kendrick and Walker (1994) concluded that both this regeneration and recruitment via propagules were important to the taxa's ability to persist in an area, given the high rates of mortality experienced among adult individuals.

1.7 Stability and the existence of alternate states

The shallow subtidal reef areas of southern Australian are dominated by macroalgae. While many have been seen to change in recent time primarily because of anthropogenic impacts, those in more remote areas appear to have remained largely the same (e.g. Shepherd and Womersley 1976; c.f. Turner and Cheshire 2003). This lack of change, along with a variety of life history traits that lead to such persistence, are central to the concept of ecological stability and have been discussed by many authors (e.g. Dayton *et al.* 1984). However, the number of different definitions of stability, including the factors and scales they cover has led to a high degree of imprecision in the term (Grimm 1996). In the context of this thesis, rather than specifically define stability, a number of stability properties are identified and defined (Table 1.5).

Table 1.5 Properties of stability (based on Grimm 1996).

Constancy	Staying essentially unchanged
Resistance	Staying essentially unchanged despite the presence of disturbances
Resilience	Returning to the reference state (or dynamic) after a temporary disturbance
Elasticity	Speed of resilience
Domain of attraction	The state space from which the reference state (or dynamic) can be reached again after a temporary disturbance
Persistence	An ecological system remaining in the same state through time

Together, these factors describe the ways in which a population may continue to exist and hence avoid local extinction. Embodied within the concepts is also the notion that there is underlying structure to the system.

Properties of stability may be manifested through the varied life history strategies of different taxa. Careful scrutiny will also reveal that there is a lot of overlap between the different concepts and hence they cannot really be viewed in isolation. As an example, most of the canopy forming taxa mentioned previously, use strategies that promote localised recruitment. The presence of large numbers of juveniles under the adult canopy means that the probability of at least some of them surviving is quite high; hence, individuals in the canopy will probably be replaced by those of the same taxa. This leads to persistence of the stand through time, but localised recruitment also provides resilience as individuals in the sub canopy can quickly replace adults lost through some form of disturbance.

At the heart of discussions of stability is the concept of disturbance, which can be defined as any event that has the potential to bring about a change to the state of the system. It is important to note that ecological systems are rarely, if ever, static and as such the state of the system should be viewed dynamically. In the case of macroalgal systems examples of disturbance include destructive events such as storms or herbivory, or alternatively may involve increased competition due to the introduction of other taxa (Dayton *et al.* 1992; Kennelly and Underwood 1993).

To add further complexity, changes to the variable of interest need to be linked to some form of reference state or dynamic (Grimm 1996). Locally, communities of macroalgae are dominated by a number of different large brown taxa or even turfing species (Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976; Cheshire *et al.* 1998a; Cheshire and Westphalen 2000; Turner and Cheshire 2003). Additionally, reefs expected to be dominated by macroalgal communities may instead consist largely of sessile animals (e.g. mussels, Smith 2000; Cheshire and Westphalen 2000), or be maintained in a denuded state (e.g. urchin barrens, Chapman 1981; Andrew 1993).

Detection of an appropriate reference state may also be hampered by successional processes (e.g. Dayton *et al.* 1984). Indeed following disturbances of sufficient magnitude to denude an area (e.g. herbivory, Foster and Sousa 1985), pioneering taxa are likely to be the first to recolonise, with longer-lived, late successional species gaining dominance only at a later stage (Littler and Littler 1980). The ability of late successional species to dominate an area is thus closely linked to the frequency and severity of disturbances, with these taxa tending to dominate in more constant environments (Littler and Littler 1980; Lobban and Harrison 1994).

The size, shape, and location of a disturbance can have implications on recruitment and successional processes (Sousa 1985), with smaller patches colonising faster (Foster and Sousa 1985; Connell and Keough 1985), however larger disturbed areas are more likely to support greater diversity (Sousa 1985). Within a disturbed patch, proximity to the edge also affects recruitment, due to the influence of the surrounding canopy (Emmerson and Collings 1998).

Physical factors such as depth and exposure are known to have a broad influence on species composition and hence overall community structure (Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976). Yet there is a large overlap in ranges meaning that at any particular place, a number of different taxa may potentially dominate (Shepherd and Womersley 1981; Turner and Cheshire 2003). This is generally manifested in terms of a patch mosaic where different patches are dominated by different taxa in close proximity (Collings 1996; Collings and Cheshire 1998; Turner and Cheshire 2003).

The presence of different environmental conditions and life history strategies means that over time, assemblages may form and progress through to a number of alternate climax states. Once established these patches may persist for quite some time (decades) as has been observed on West Island, Encounter Bay, South Australia (Shepherd pers. comm. *sensu* Shepherd & Womersley 1970).

1.8 Concluding remarks

Numerous studies have examined the important influence that physical conditions have on macroalgal community structure. Notwithstanding, there are a number of unique facets to the southern Australian marine environment including high levels of both diversity and endemism, and the preponderance for fucoids to act as a canopy dominant. As such, the broad scale application of findings from other regions may have limited applicability locally. Hence, an understanding of this system is only likely to come from local studies.

A combination of factors may be seen to influence macroalgal community composition in any location. Physical parameters are obviously important in defining the suitability of an area for colonisation. Furthermore, the interaction between factors such as depth, exposure, and water quality with the resulting community, allows some coarse level of predictability. However, this predictability is likely to lessen at finer scales due to micro variation in physical parameters (such as topography), because of significant biological interaction and the effects of stochasticity.

Community composition is unlikely to be driven solely by existing conditions, but represents a product of both current and historic events. Hence, community composition at any point may appear in one of a number of alternate states. As an example, it may be argued that strong competitors will topple the weak, yet if a weaker competitor is allowed to establish initially then it may be able to persist indefinitely. Furthermore, successional processes may eventually favour one taxon over another, yet the process may be upset through regular disturbance, allowing intermediate states to persist (Connell 1978).

The implied existence of stability through persistence of assemblages in a given state provides a useful approach to observing structure and dynamics within macroalgal systems.

Chapter 2

State of the Environment, Gulf of St Vincent, South Australia

Following a global trend towards more ecologically sustainable development, all Australian State Governments adopted a national strategy in 1992. Part of this framework included the introduction of regular reporting on the state of the environment (State of the Environment Advisory Council 1996). The work in this chapter aims to provide the reader with an insight into many of the environmental issues of specific relevance to the Gulf St Vincent Environment.

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2.1 Introduction

Gulf St Vincent was considered uncharted waters until separate expeditions by Flinders and Baudin in 1802 claimed the territory for England and France respectively. Subsequently, a number of settlements have been established in the area, the largest being the City of Adelaide, founded in 1836 (Harbison 2002) on the eastern shores and about half way up the Gulf (Figure 2.1).

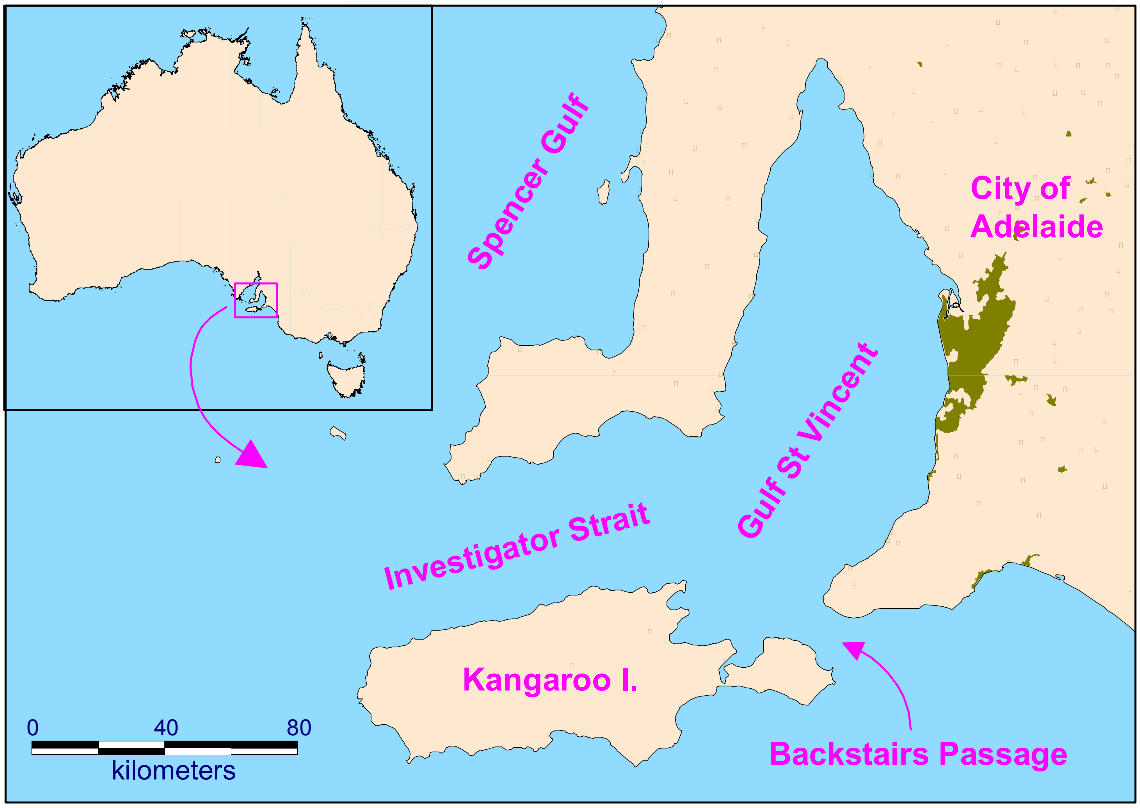

Figure 2.1 Map showing the location of Adelaide within Gulf St Vincent[5].

More recently, the Gulf has been recognised as a unique marine habitat and a number of initiatives are slowly being implemented in an attempt to curb further degradation. Notwithstanding, monitoring of coastal systems in close proximity to Adelaide has identified serious levels of degradation attributed to anthropogenic agents of stress including sewerage and contaminated stormwater (Nicolson *et al.* 2003).

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[5] This figure incorporates data that is © Commonwealth of Australia (Geoscience Australia 2003).

While coastal development continues largely unchecked (Nicolson *et al.* 2003), the potential for ecologically sustainable management is hindered by a fundamental lack of understanding of important processes. This emphasises the need for scientific programs with a sufficiently broad context to address system structure, and to be able to separate impacts of anthropogenic origin from natural environmental variation.

Due to the uniqueness of the Gulf St Vincent environment, an examination of local environmental conditions (both natural and anthropogenic), and how they interact, is necessary in order to understand macroalgal community structure.

The objective of this chapter is to describe the Gulf St Vincent environment in detail and to highlight important processes, including modifications resulting from anthropogenic activity over the past 170 years.

2.2 Natural history of Gulf St Vincent with special reference to the City of Adelaide

South Australia has a semi-arid environment with Mediterranean characteristics in the southern part. Summers are generally hot and dry, with most rain falling during the cooler winter months. Within the gulfs cool oceanic influences are combined with the semi-arid climate to produce a temperate region (Schwerdtfeger 1976). Rainfall is highest around the Mt Lofty ranges and associated systems where annual median values approach 1000mm in some areas, although typical values for the Adelaide Plains are less than 650mm (BOM 2002).

2.2.1 Oceanography

Depths within the gulf rarely exceed 40 metres and are substantially shallower towards the head (Grzechnik and Noye 1996). This shallow relatively calm water is subjected to large amounts of evaporation, leaving the top of the gulf in a hyper-saline state (Bye 1976). For this reason, Gulf St Vincent is defined as a reverse estuary.

The most important tidal influences on the gulf are astronomical in nature, being either solar or lunar driven, with each having a semidiurnal (travels west to east) and diurnal (travels east to west) component (Bye 1976). The two semidiurnal tides have periods of 12 hours and, 12 hours and 25 minutes for solar and lunar respectively (Grzechnik and Noye 1996).

The physical presence of Kangaroo Island means exchange of water with the open ocean is limited. Gulf St Vincent connects to the ocean via two water bodies, Investigator Strait and Backstairs passage. Tidally driven waves enter through these two openings such that high water is almost simultaneous at both entrances, which sets up a standing oscillation where the waves meet. As a result the tides make a rapid progression taking only twenty (Bye 1976) or thirty (Grzechnik and Noye 1996) minutes to travel from the western to eastern side of the gulf. In addition, tidal height increases in amplitude from the mouth of the gulf (Bye 1976; Grzechnik and Noye 1996).

Unusually, the two semidiurnal tidal components are of equal amplitude. Given their different periodicities (12 and 12 hours 25 minutes for solar and lunar respectively), every 14.77 days the two tides are in direct opposition and effectively cancel each other out leading to a couple of days per fortnight where the water is only moved by the weaker diurnal tides and is thus relatively still (neap tide). It was also noted by Matthew Flinders that the diurnal tidal component vanishes around the equinoxes and that this combined with a neap tide leads to several days of still water known as a dodge tide (Bye 1976; Grzechnik and Noye 1996).

Along much of the southern Australian coastline, tidal ranges average about one to 1.5 metres with some exceptions. Notably, ranges off Perth rarely exceed half a metre, while at Wilson’s Promontory and across northern Tasmania, ranges are in the order of 2.5 metres (Womersley 1984).

Within the two South Australian gulfs tidal ranges increase to three and four metres at the heads of Gulf St Vincent and Spencer Gulf respectively (Womersley 1984). Non-tidal water circulation within the gulfs also occurs and is caused by local wind, local thermal exchange at the water surface, and adjacent deep ocean circulation, with the first of these being most important (Bye 1976). Compared with the nearby coastline, wave energy within the gulfs is quite low, being moderate at the mouth and weakening towards the head.

2.2.2 Coastal erosion – shoreline recession and dune erosion

Adelaide's shoreline has been changing since sea levels stabilised 7000 years ago. Sand is being deposited on shore at an angle out of equilibrium with the existing (and recent) wave climate (Deans *in prep.*). Combinations of ocean swell and wind driven waves arriving at an angle to the coast cause beach sand deposits to be reworked and result in a net northward littoral drift. This drift, combined with the fact that Adelaide beaches receive very little natural sand supply (from rivers or eroding cliffs) means that sand is eventually lost from southern areas causing the shoreline recession (Deans *in prep.*).

Historically, the rate of northward drift (and hence recession) was lower than at present. The main reason for this is the loss of over 5000 ha of seagrass from the metropolitan coastline, that once acted to stabilise sediments and reduce near-shore wave energy (Deans *in prep.*).

As with all beach and dune systems, there are also cycles of dune erosion and rebuilding due to variations in wave sizes and water levels (e.g. storms and storm surges). The sand dunes dissipate wave energy during rough weather, eroding sand from the dunes onto the beach and offshore sand bar. The sand bars also help to break the larger waves and dissipate energy. When calmer periods return, sand is washed from the sand bars back onto the beach and is further blown up to reform dunes (Deans *in prep.*).

2.2.3 Biogeography

South Australia's two gulfs provide a sheltered habitat that supports vast seagrass ecosystems as well as coastal mangrove forests and highly productive macroalgal communities. Together these systems form the fundamental basis for much of the State's commercial and recreational fisheries as well as supporting a vast array of other marine life (Edyvane 1996).

Mangroves occur within the northern part of Gulf St Vincent, as far south as the Port River / Barker Inlet system. Further south, a few individuals have been planted along the banks of the Onkaparinga Estuary (Turner, *pers. obs.*). Stands within South Australia represent a monoculture of the grey mangrove *Avicennia marina* (Forsk.) Vierh (Fairhead 1995).

Occurring extensively throughout the gulf and occupying much of the sandy substrate are a number of seagrasses. In all, there are eight species represented, the most common being

Posidonia australis J.D.Hooker*,* *Amphibolis Antarctica* (Labillardière) Sonder & Ascherson *ex* Ascherson, *Heterozostera tasmanica*[6], and *Halophila australis* Doty & Stone (Shepherd and Sprigg 1976). *P. australis* has the most extensive distribution, often forming dense monospecific meadows. *A. antarctica* also has a wide distribution, but is better able to act as a primary coloniser than *P. australis* (Shepherd and Sprigg 1976).

In contrast to the seagrass occupation of soft sediments, hard surfaces are generally dominated by macroalgal communities (See Chapter 1).

Benthic animal communities within the gulf vary according to a number of physical parameters including water movement, light, depth, and substrate. Under conditions of gentle water movement and a muddy substrate, the most common animals are bivalves. Examples include the extensive razor fish communities at the top of the gulf as well as around Rapid Bay where oysters and scallops are also found (Shepherd and Sprigg 1976).

Bryozoans tend to be found in abundance in the deeper waters of the gulf as do sponges, while at intermediate depths ascidians, bivalves and seastars are prominent. Many of these organisms are also found in abundance on reefs, intermixed with macroalgae in shallower waters or as dominants beyond the limits of the photic zone. Additionally, a number of herbivorous taxa are found in areas that also contain macroalgal communities. Examples include sea urchins, and various gastropods (Shepherd and Sprigg 1976).

Two hundred and sixteen different species of fish have been collected from the waters of Gulf St Vincent with most being typical of the Flindersian biogeographical province. Of these, seven are believed to be endemic to the gulf, while another fourteen are of major commercial interest (Glover and Ling 1976).

2.3 Threats to Adelaide's coastal and marine environment

The following section includes a number of the factors that have affected the near shore marine environment. Included here are examples that are of particular relevance to this study. Knowledge of these factors is important, as they are likely to influence processes within the assemblages under study.

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[6] This species was recently renamed to *Zostera tasmanica* (Les *et al.* 2002).

2.3.1 Coastal Development

The majority of Australians live in relatively close proximity to the coastline and enjoy the lifestyle that it affords. In coastal cities such as Adelaide, seaside suburbs have been almost entirely developed meaning that very little of the natural coastal system remains. From an ecological point of view, coastal development has caused widespread vegetation clearance and habitat loss as well as a host other impacts related to human population expansion, most of which are covered in the sections below.

Although the problems associated with inappropriate coastal development are now recognised, development, in the form of housing, marinas and boat ramps, continues to proceed largely unchecked (Nicolson *et al.* 2003).

Historically, development of the Adelaide foreshore occurred with limited knowledge of either the ongoing shoreline recession or the dune erosion-rebuilding cycle (see previous section). As in many towns and cities worldwide, construction of roads and buildings occurred directly on the foreshore dunes. Soon after settlement, dunes eroded undermining the developments, and in response, occupants and governments built seawalls to protect their investment (Tucker 1985).

As is now well recognised, seawall construction, particularly vertical seawalls, disrupts the dune rebuilding part of the dune erosion-rebuilding cycle. The implications are twofold: back dunes are unavailable to be eroded as they have been built on and beach and fore-dunes do not reform as effectively following storms due to the high level of wave reflection off the seawalls (Deans *in prep.*).

While the dune erosion-rebuilding cycles were probably the main erosion process that brought on the early building of seawalls, this erosion process has since been understood to be of a secondary importance to that of ongoing shoreline recession (Deans *in prep.*).

As part of the development of Adelaide’s beaches, a number of groynes and breakwaters have also been built along the length of the coastline, further disrupting the natural progression of sand by causing a build up on the southern side and erosion from the northern side (Deans *in prep.*). This phenomenon can be clearly seen at the recently developed Holdfast Shores Complex (Figure 2.2) where moving sand around the structure costs 1.7 million dollars annually (Nicolson *et al.* 2003).

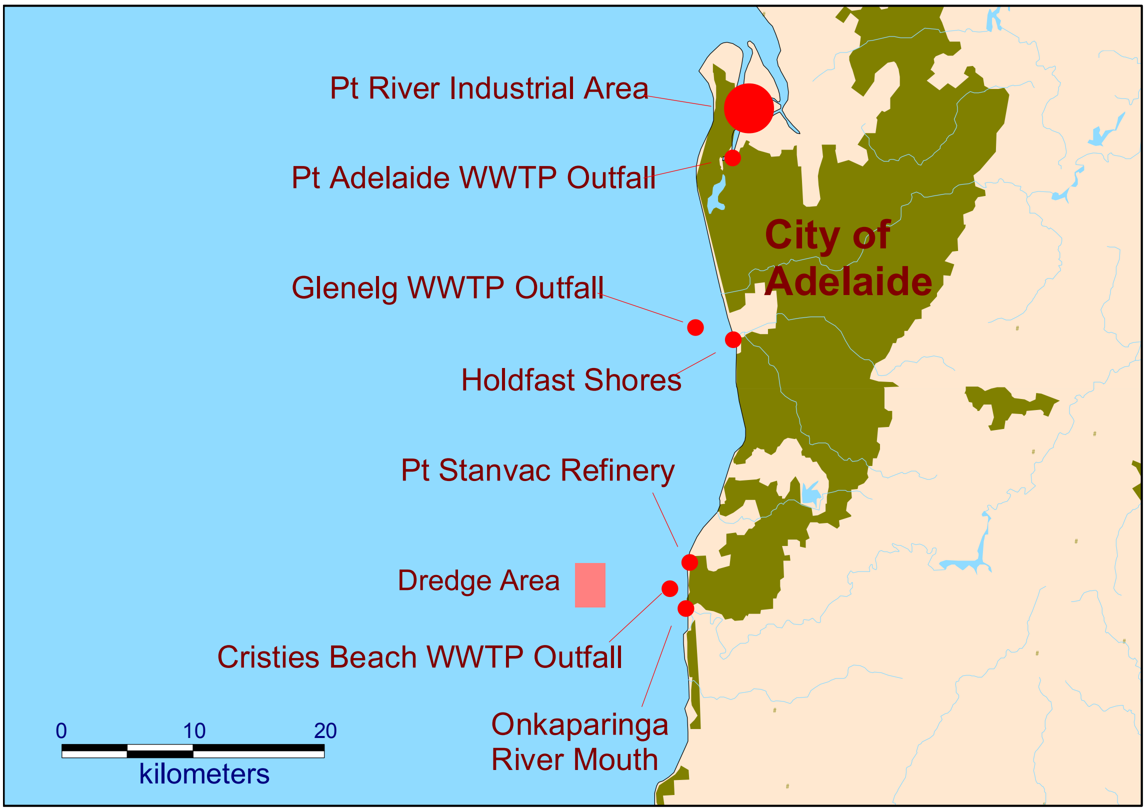

Figure 2.2 Problematic locations along Adelaide's metropolitan shoreline[7]. WWTP refers to waste water treatment plant. The largest plant at Bolivar is further north and not shown.

2.3.2 Sewage and industrial pollution

Sewage and industrial pollution are generally combined into a single waste system and referred to as 'wastewater'. The effluent produced by Adelaide's urban community is directed to one of four treatment plants (Figure 2.2) before being discharged into the sea (SA Water 2002). Local wastewater tends to contain high levels of organic material as well as a range of other contaminants including nutrients, biocides, heavy metals, micro-organisms, petrochemical products, and particulate matter (SA Water 2002).

Increased nutrient levels are considered to be a significant pollution issue within Gulf St Vincent (Steffensen *et al.* 1989b). Historically coastal waters were nutrient-poor due to the geological age of soils (Northcote 1976), limited nutrient runoff into the marine system (due to low rainfall), and the lack of an appreciable upwelling[8] (Jeffrey *et al.* 1990).

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[7] This figure incorporates data that is © Commonwealth of Australia (Geoscience Australia 2003).

[8] There is a small upwelling off the coast of Robe in the south east of South Australia (Northcote 1976).

Low nutrient concentrations are a major factor limiting plant (and algal) growth (Cosser 1997). Conversely, algal blooms and excessive epiphyte growth are often observed in eutrophic waters. Nutrient availability also stimulates phytoplankton growth that in turn promotes an increase in filter feeding organisms such as sponges, tubeworms and mussels (Brodie 1997).

Historically, wastewater discharge in South Australia involved minimal treatment, with everything (including sludge) being pumped into the ocean. There is strong evidence to suggest that this practice led to widespread seagrass loss (Cugley 2002). While sludge pumping has ceased and treatment continues to improve, the impacts of these outfalls are still recognisable (Fairhead 1995; Loo 2001).

More recently, a combination of public perception, water costs and technological advancements have led to improvements in both the level of treatment and the amount of water recycling (Nicolson *et al.* 2003).

Currently about 15% of Adelaide's wastewater is reused through a number of schemes, but the remainder (77 gigalitres) is still discharged to the gulf. Notwithstanding, a number of environment improvement programs are being undertaken (at a cost of A $240 million) to increase water reuse and reduce nitrogen levels in water discharged to the gulf (SA Water 2002). Indeed these programs aim to increase wastewater reuse to 30% by June 2005, and 50% in the long term.

Table 2.1 Christies Beach WWTP 2001-02 annual discharges (SA Water 2002).

Biochemical Oxygen Demand (BOD)	55 tonnes
Suspended solids (SS)	86 tonnes
Total Nitrogen (TN)	230 tonnes
Total Phosphorus (TP)	72 tonnes
Annual Effluent Discharged to GSV	8.75 gigalitres
Annual Effluent Reused	1.97 gigalitres (18%)

The Christies Beach wastewater treatment plant is of particular interest as the outfall is in close proximity to a number of reefs used in the current study. The plant is the newest in the metropolitan area and was upgraded in 2002 to reduce nutrient discharges into Gulf St Vincent. A summary of discharges to the marine environment is given in Table 2.1.

2.3.3 Catchment modification & stormwater channelling

Urban and nearby rural development has caused massive changes to the local catchments that feed into Gulf St Vincent. Land clearance has led to increased erosion (meaning increased sediment loads), while sealing of the ground with concrete and bitumen has increased runoff into the stormwater system.

Historically runoff from the Mt Lofty Ranges and Adelaide plains collected in the large flood plains and wetlands behind the coastal dune system. The routes of many natural waterways (e.g. Torrens River) have since been modified to bypass coastal wetlands and thereby facilitate further development (Deans *in prep.*).

In addition to particulate matter, catchment runoff carries with it a host of agricultural pesticides and fertilisers, while stormwater discharge in urban areas collects garbage and petrochemical by-products that are washed from the roads into the system. The result of all of this is large volumes of polluted, turbid, non-saline water entering the near shore marine environment (Steffensen *et al.* 1989a).

Annually about 110 gigalitres of stormwater is discharged directly into the sea. Unfortunately, this discharge is less regulated than effluent and the majority undergoes no treatment before reaching the coast. Notwithstanding, there have been a number of projects in recent years designed to address this issue, at least in metropolitan Adelaide. Around 20 gigalitres of stormwater is now recycled and used to irrigate parks and gardens (Nicolson *et al.* 2003), and several wetlands have been established throughout the metropolitan area.

Catchment Water Management Boards (CWMBs) have also been established with the aim of improving overall catchment health. A primary aim of these boards is to minimise the amount of pollution entering the stormwater system (South Australian Catchment Water Management Boards 2002). This is obviously important to the health of natural waterways, and has flow on benefits to the marine environment, as this is where most of the water finishes up.

Programs focus mainly around community education and include regional officers working with small and medium sized industry to encourage best management practices (South Australian Catchment Water Management Boards 2002).

The main locations where stormwater are discharged along Adelaide's metropolitan coast are through the Port River system, the Patawalonga Basin (now discharging via the Barcoo Drain), and the Onkaparinga Estuary (Figure 2.2). There are also numerous smaller drains scattered along the length of the coastline (Steffensen *et al.* 1989a).

In the north, the Port River system empties in close proximity to mangrove and seagrass communities, while the Barcoo drains into an area that was formerly occupied by seagrass. Further south, the Onkaparinga River empties amongst significant algal dominated reefs and nearby seagrass habitat.

The Onkaparinga River has undergone a number of major changes since the arrival of Europeans, including the construction of the Mt Bold reservoir and Clarendon weir, both of which have significantly altered the natural flow. In addition, the river also receives water from the Murray River via a pipeline. Other impacts have resulted from the urbanisation of parts of the river, especially around the estuary at the mouth. These include pollution, land clearance for agriculture and the dumping of rubbish (Onkaparinga Estuary Task Group 1990).

2.3.4 Resource exploitation

Currently most of South Australia's commercial fisheries are fully exploited (i.e. harvested at maximal sustainable levels, Nicolson *et al.* 2003). While commercial catch is regulated, activity in the recreational sector is more difficult to manage, with higher exploitation rates for several species including snapper and King George whiting (Nicolson *et al.* 2003).

Recreational fishing in particular is popular along the Adelaide metropolitan coastline and boats are often sighted around the reefs used in this study (Turner, *pers. obs.*). However fishing pressure is not uniform in the region due to the presence of aquatic reserves and other no take zones.

Of particular interest to this study is the Noarlunga aquatic reserve, which protects all marine life on the Noarlunga Reef. The reserve was declared in 1971 along with the adjoining Onkaparinga Estuary (Dalgetty and Edyvane 1996). The existence of the reserve is important because differences in fish abundance may influence grazing pressure as well as other community dynamics (e.g. McClanahan 1997).

The majority of dredging operations undertaken in South Australian waters are for the purpose of maintaining boating channels and harbours, and to facilitate the establishment of new coastal developments (Nicolson *et al.* 2003). However, sand mining has also been undertaken as part of beach replenishment programs in order to counter the ongoing shoreline recession (Deans *in prep.*) described in section 2.2.2 above. The majority of this dredging occurred during the 1990s at a site near Pt Stanvac (Figure 2.2). This program was responsible for the large sediment plume in 1997, described in section 2.5.2 below and thus is of particular relevance to the current study.

2.3.5 Introduction of feral species

A number of introduced taxa have already been confirmed within the waters of Gulf St Vincent (Cohen *et al.* 2002). These include the European sea squirt (*Ciona intestinalis* Linnaeus), Mediterranean fanworm (*Sabella spallanzanii* Gmelin), and the European shore crab (*Carcinus maenus* Linnaeus). More recently (2002) the highly invasive *Caulerpa taxifolia* (Vahl) C.Agardh was discovered in an artificial waterway that feeds into the Port River in the northwest of Adelaide and to date more than six million dollars has been spent in an attempt to eradicate it (Cheshire[9] *pers. comm.).* Following on from this, the other highly invasive *Caulerpa racemosa* (Forsskål) J.Agardh, was also found in the vicinity of the Port River (Cheshire *pers. comm.*).

Introduced species are not subject to the same sets of controls placed upon them within their natural habitat. In addition, many are opportunistic and are able to thrive in recently disturbed areas (Cohen *et al.* 2002). As such, the potential for them to spread is increased as local reef communities become degraded. Once they become established in a new area, they often have the potential to out compete and thereby further displace local taxa (Furlani 1996; Cohen *et al.* 2002).

A number of other invasive taxa are present in different parts of Australia but have not yet migrated into South Australia. Examples include Japanese kelp (*Undaria pinnatifida* (Harvey) Suringer) and the Northern Pacific sea star (*Asterias amurensis* Lutken), both of which are considered to pose a major threat to local marine ecosystems (Furlani 1996).

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[9] Chief Scientist of SARDI Aquatic Sciences.

Historically many of these taxa arrived by boat (as fouling communities or within ballast water), and this is still considered the most likely way in which future introductions will occur (Furlani 1996; Cohen *et al.* 2002). Ironically, while international guidelines have been in place for some time, similar guidelines do not cover interstate transport (Nicolson *et al.* 2003).

2.3.6 Sedimentation

Coastal works (2.3.1), effluent discharge (2.3.2), catchment modification (2.3.3), and seagrass loss (2.4.2) have all contributed to elevated levels of sediment within the near shore marine environment. Along with pollution, sedimentation is considered to pose a major threat to marine ecosystems in South Australia (Steffensen *et al.* 1989a; Cheshire *et al.* 1998a; Gorgula and Connell *in press*).

In a concurrent study, Greig (2000), measured rates of sedimentation on several reefs, also used as control sites in the current study (Hallett Cove, Southport, and Moana). The work was undertaken over the spring / summer period of 1999 / 2000 and measured considerably higher rates of sedimentation at Southport Reef (480 $g.m^{-2}.d^{-1}$) compared with the other two sites (Hallett Cove – 130 g, Moana – 90 g). It is plausible that the higher rates on Southport Reef are a consequence of its close proximity to the mouth of the Onkaparinga River.

While the above rates of sedimentation appear high, the majority of sediments were quickly dispersed, meaning that only a small volume was actually accumulated. According to Greig (2000), rates of sediment accumulation were high for both of the flat reefs (Hallett Cove – 3.5 $g.m^{-2}.d^{-1}$, Southport – 4.5 $g.m^{-2}.d^{-1}$) relative to Moana Reef (1.5 $g.m^{-2}.d^{-1}$). This implies that topographical aspect is likely to influence sediment accumulation. Interestingly, similar accumulation rates were observed on both flat reefs even though actual sedimentation was considerably higher at Southport. This is likely to be due to limits on the amount of sediment that can be ‘locked away’ (in cracks, crevices, and by the resident biota), as opposed to being re-suspended by water movement.

The impacts of sediments on macroalgal communities are central to this thesis and are covered in detail in Chapter 4.

2.4 Ecological consequences

2.4.1 Species decline and loss

Communities of primary producers that in turn provide food and habitat for numerous associated taxa, often dominate near-shore marine environments. Along the eastern shore of Gulf St Vincent, macroalgal communities are prominent on rocky reef environments while seagrasses cover huge areas of the sandy bottom. Further north mangroves are common in the intertidal mud, and samphires (salt marsh plants) populate the marsh.

Since the arrival of European colonists, huge areas of mangrove and samphire have been cleared, primarily to make way for industry (Edyvane 2000). The bi-products of this industry, along with that of residential households then polluted the waters causing the loss of thousands of hectares of seagrass (Cugley 2002). Pollution, along with elevated sediments resulting from seagrass loss and inappropriate developmental activities then affected the reefs, causing the resident macroalgal communities to degrade (Cheshire *et al.* 1998a; Cheshire and Westphalen 2000).

With the loss of these structural habitat components, there is likely to be a concomitant loss of numerous other species that have a reliance on them. Seafood species are further exploited by commercial and recreational fishing operations, placing additional stress on population numbers.

2.4.2 Seagrass dieback

Seagrass distribution around Australia is somewhat patchy with rich meadows scattered along the coastal fringe (State of the Environment Advisory Council 1996). In South Australia, a large proportion of the seagrass population resides within the two gulfs, and recently large amounts of dieback has been documented, attributed mainly to impacts associated with the larger urban centres (Edyvane 2000).

Over the last few decades, more than 5200 ha of seagrass have been lost from Adelaide's metropolitan coastline because of pollution and coastal development. Expanding blowouts are regularly observed, as is the increasing amount of bed fragmentation (Seddon 2002).

The general pattern consists of seagrass receding seaward along with increasing meadow fragmentation, a trend that appears to be extending southward (Fotheringham 2002).

Apart from the ecological value of seagrass meadows, they are also well-known sand stabilisers acting to both bind sediment and modify water flow. Furthermore the loss of seagrass along the Adelaide foreshore has led to increased rates of erosion and acceleration of northerly sediment movement, exacerbating the problem identified above (Department of Environment and Natural Resources 1997). In turn, this has led to further seagrass loss and a general worsening of the situation; hence cleaning up sources of pollution may no longer ameliorate the problem (Seddon 2002). Indeed recent observations indicate that the modified environment may no longer be able to support seagrasses meadows (Townsend 2002).

2.4.3 Degradation of macroalgal communities

Macroalgal communities have a number of separate strata and generally dominate subtidal reef systems particularly in shallow (<40 m) water. The upper canopy is usually made up of large phaeophycean species from Fucalean and Laminarialean orders (Womersley and King 1990).

Recent surveys designed to investigate the health of macroalgal communities found that the larger phaeophycean taxa were absent from Adelaide's northern metropolitan coastline (Cheshire *et al.* 1998a; Cheshire and Westphalen 2000). Although the reports did not cite historical evidence, these species were presumed to have been lost, probably because of declining water quality in the region (Cheshire *et al.* 1998a). This is a reasonable assumption given that similar areas on the other side of the gulf and in Spencer Gulf are known to support communities of large brown macroalgae (Turner, *pers. obs.*).

A benthic survey carried out in 1975 also reported the presence of Fucalean algae in deeper water (below ten metres) off the northern metropolitan coastline (R. K. Steedman & Associates 1976), adding further credence to the notion that absence of these taxa is due to recent losses.

In this northern area there is, however, a single artificial reef inhabited by dense *Ecklonia radiata* (Cannon 1987). Interestingly the *Ecklonia* population occupies only the vertical faces of the large concrete blocks (Turner, *pers. obs.*) and as such differs in aspect from the exclusively horizontal surfaces surveyed during the reef health program.

The presence of *E. radiata* on vertical but not horizontal surfaces led Cheshire *et al.* (1999) to hypothesise that elevated levels of sediment were primarily responsible for the loss of large phaeophycean taxa on the northern metropolitan coastline.

2.5 An opportunity to study impacts on reef environments

Good water quality is essential for a healthy aquatic environment and in recent years, significant progress has been made towards reducing the levels of pollutants entering the marine environment (Gaylard 2004). However, even without pollutants, water quality can be compromised by the presence of large volumes of suspended particles that increase turbidity and often smother sessile aquatic life.

Elevated levels of sediment in the water column arise from a number of sources including poorly managed coastal development, dredging, and increased sediment mobility following seagrass degradation (Nicolson *et al.* 2003). It is therefore important to understand the impact of increased sediments on marine environments so that this information may improve future management practices.

Reef systems provide an opportunity to study environmental perturbations within a discrete and easily identified environment.

2.5.1 Importance of southern Australian reef systems

There appears to be a number of fundamental differences between South Australian reefs and those elsewhere in Australia (e.g. Irving *et al.* 2004). One of these differences is the disproportionate high biodiversity and associated endemism relative to other comparable regions (Womersley 1990). Furthermore, in addition to *Ecklonia* dominated assemblages common across southern Australia, subtidal fucoid algae act as a canopy dominant, and are likely to have a large influence on overall community structure as well as underlying processes (Turner and Cheshire 2003).

Historically the value of natural environments has been largely viewed anthropocentrically and generally in terms of immediate returns (e.g. growing food). More recently, there have been attempts to place a monetary value on the complete range of ecosystem services provided by natural systems. In South Australia, this initiative identified aquatic systems as having the highest worth on an areal basis, with seagrass meadows topping the list

(Natural Resources Council of South Australia. Environmental Valuation Working Group 1999). Interestingly, reef environments were not assessed, possibly due to lack of available knowledge or their distance from the public eye. Notwithstanding this, local reef biota demonstrate higher productivity (Cheshire *et al.* 1996b; Westphalen and Cheshire 1997; Seddon 2000; Fairhead 2001; Turner and Cheshire 2003), greater diversity (Womersley 1990; Huisman *et al.* 1998), and more complexity of habitat (Shepherd and Sprigg 1976). As a result, reefs are likely to be at least as valuable, if not more so on a per hectare basis.

2.5.2 Creation of a sedimentation event

The eastern shore of Gulf St Vincent has undergone a number of detrimental changes since the arrival of Europeans less than two hundred years ago. While significant reductions in pollution entering the Gulf over the next few years are expected, management of sediments is less advanced (Nicolson *et al.* 2003).

Failure to foresee the impacts of a larger than average dredging operation led to the creation of a large sediment plume in November 1997 (see Chapter 4). The result of this was a large increase in the deposition of fine silts on two of Adelaide's metropolitan reefs, Noarlunga (Havenhand 1998) and Horseshoe (R Sandercock *pers. comm*).

Given the likely role of elevated sediments in reef degradation further north in the gulf (Cheshire *et al.* 1998a; Cheshire *et al.* 1999), this event (while regrettable) provided an opportunity to undertake an experiment into the impacts of sediments on a reef environment.

2.6 Rationale for the study

A large proportion of reef degradation that has been reported on Adelaide's northern metropolitan beaches has been attributed to declining water quality and in the case of macroalgal communities, increased sedimentation. This raises the issue of whether the sediment plume (associated with sand dredging in 1997) caused any impact on the resident macroalgal community.

The plume occurred towards the end of the recruitment period for the dominant canopy forming macroalgae (Cheshire *et al.* 1999). While Havenhand (1998) noted no initial impact, it was considered likely that the newly recruiting algae would be highly susceptible to the impacts of sediment deposition and furthermore, could easily have been overlooked due to their small size (Cheshire *et al.* 1999).

As a result, a study was commissioned into the impact of the plume on the reef's canopy forming macroalgal assemblages, which led to the production of a report for the relevant management agency (Cheshire *et al.* 1999). However, the initial analysis was not given sufficient scope to take into account temporal or spatial variation within the system, and was therefore unable to confidently delineate between the anthropogenic impact associated with the plume and other sources of perturbation or natural variation.

This thesis presents a substantial extension and expansion of the preliminary study (Cheshire *et al.* 1999). It incorporates a broad expansion of the temporal and spatial extent of both the field program and the analysis and interpretation of local environmental conditions as well as their likely influence on processes structuring the canopy forming macroalgal communities.

2.6.1 Specific aims of the study

- *To build an understanding of how local canopy dominated macroalgal systems are structured, and whether knowledge of the current state of a patch can be used to determine past or future states.*
- *To quantify the relationship between adult canopy structure and the underlying juvenile assemblage.*
- *To construct a model that effectively describes assemblage structure.*
- *To determine how the reefs in the study area change through time.*
- *To investigate the impact of elevated sediment levels as a pulse disturbance on the recruitment of canopy forming genera of macroalgae.*
- *To identify the longer-term effects of the sediment impact.*

Chapter 3

Population structure of canopy forming species in Gulf St Vincent

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The purpose of this chapter is to provide an understanding of the spatial structure displayed by canopy forming macroalgae within Gulf St Vincent. Many of the concepts developed here have been used to underpin the analysis and interpretation of a published account of macroalgal community structure from Nuyts Archipelago off the west coast of South Australia (Turner and Cheshire 2003). The usefulness of this approach both in the current context and in assessing the Nuyts communities indicates that these ideas have a broader applicability beyond the South Australian context.

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3.1 Introduction and rationale

The original examination of the impact of the dispersed sediment plume on macroalgal assemblages was undertaken by Cheshire *et al.* (1999), using the sampling program described in the methods section (3.2.1). The study concluded that local assemblages existed in one of four states, three of which were dominated by a singe genus, while the fourth comprised a lower density mixed assemblage. Furthermore, they confirmed a strong link between the structure of the adult canopy and that of the underlying juvenile assemblage.

Notwithstanding, there were a number of problems with the data analysis undertaken by Cheshire *et al.* (1999), which warrant a more thorough examination. In particular, the initial determination of community structure incorporated all locations; thus the effects of the sediment impact may have potentially confounded it. Secondly, the study did not deal with spatial non-independence and hence subsequent analyses were flawed.

As a result, this chapter aims to provide a more robust re-analysis of Cheshire *et al.* (1999), using a subset of sites that were not affected by the sediment plume, and taking into account the potential influence of spatial autocorrelation in the data.

While several South Australian studies have described macroalgal community structure under oceanic conditions (Shepherd and Womersley 1970, 1971, 1976, 1981; Turner and Cheshire 2003), few have surveyed within the gulf (but see Collings 1996; Collings and Cheshire 1998; Emmerson and Collings 1998). Furthermore, even these studies were undertaken near the mouth of the gulf; and as such, are not necessarily representative of the more northerly communities. There have only been a few studies of macroalgal communities off Adelaide's metropolitan coastline, the largest of which were a series of reports that assessed reef health in terms of both algal and animal communities (Cheshire *et al.* 1998a; Cheshire and Westphalen 2000; Cheshire *et al.* 1999). Additionally, several student theses have incorporated studies of macroalgal communities (e.g. Cannon 1987; Greig 2000; Smith 2000), while Shepherd & Sprigg (1976) also provided a general account of gulf communities.

Gulf St Vincent is a sheltered water body, deep at the mouth and shallow at the head. The presence of Kangaroo Island near the mouth acts to restrict water circulation (Grzechnik and Noye 1996). The Gulf's reverse estuarine nature means that salinity is also higher near the head, which further complicates the situation. Significant gradients also exist for wave energy, depth (also influencing temperature ranges) and water chemistry. The presence of the City of Adelaide on the eastern side of the gulf has also led to major changes in nutrient and freshwater influxes as well as considerable pollution (Nicolson *et al.* 2003).

Macroalgal community composition is known to change along the length of Adelaide's metropolitan coastline with southern reefs similar in composition to oceanic reefs elsewhere in the state, while those further north lack the large brown canopy forming species (Cheshire *et al.* 1998a; Cheshire and Westphalen 2000). This lack of canopy was interpreted as degradation due to declining water quality (Cheshire *et al.* 1998a; Cheshire and Westphalen 2000). The study also identified the central reefs (those used in this study) to be intermediate, with some showing signs of degradation.

Community structure is also likely to vary between the seaward and leeward sides of a reef due to differences in wave energy, and similarly across broad flat reefs. Additionally reef structure and proximity to point sources of perturbation (e.g. sewage outfalls, rivers etc.), will further influence composition. Notwithstanding, small-scale variability may result in patches on reefs with similar overall conditions to patches on other reefs, or at least the existence of assemblages in similar states.

Given the lack of a priori knowledge of assemblage structures off metropolitan Adelaide, and acknowledging the degree of patchiness in similar systems (Collings 1996; Collings and Cheshire 1998), an exploratory approach can be justified. Indeed a sampling protocol incorporating a number of spatial scales is not only pragmatic, but also provides the best opportunity to identify important patterns.

Processes underpinning community structure often act on different scales (Dayton and Tegner 1984; Palmer 1988) and sampling must match these scales if the complex nature of the system is to be adequately described. Indeed spatial scales relevant to the current study may include that of the patch, habitat, and reef (Collings 1996). By sampling at these scales, information about the nature of community structure may be used to further the explanation of scale-specific processes and help interpret hierarchical relationships (Allen and Starr 1982; Acker 1990).

In terms of the temporal aspect, attention should be given to annual variability in overall community structure, a topic that is addressed in Chapter 5.

It is also important to consider the age of individuals creating the overall population assemblage because recruits, juveniles, and healthy adults may respond differently to various environmental influences, including each other (e.g. Airoldi 2003). The overall structure of the stand may also be used to infer information on the stability of the population in the longer term (e.g. Johnson and Mann 1988; Dayton *et al.* 1984).

3.1.1 Objectives

Previous work has implicated sedimentation in the decline of canopy taxa from Adelaide's northern metropolitan reefs (Cheshire *et al.* 1998a; Cheshire and Westphalen 2000). Given the importance of canopy forming phaeophycean macroalgae in providing structure to the overall biotic assemblage of the reef, this study intends to focus on this group.

The objective of this chapter is to establish a level of understanding about the structure of macroalgal communities on a selection of Adelaide's metropolitan reefs. The chapter aims to address the nature of observed patterns and the degree to which assemblage structure differs across a number of scales.

A likely mechanism through which elevated sediment levels could cause the loss of canopy taxa would be as a result of reduced reproductive success caused by pre-emption of space and / or smothering (Airoldi 2003). As a result, special attention will be given to juvenile assemblages and their relationship to the adult canopy.

3.1.2 Layout of methods and results

This chapter contains a number of complex findings, many of which were identified using a relatively exploratory approach in which initial results led to the formulation of subsequent tests. In order to present a logical continuum (and thus aid readability), the method and results sections are divided into three parts. Part A describes the field methodologies and protocols used for classifying the different taxa and age cohorts. Following this, this issue of spatial independence is examined.

Part B is a re-examination of the work by Cheshire *et al.* (1999) using a more robust analysis protocol and taking into account developments identified in Part A. As such, this section provides detailed analysis of small-scale structure within canopy forming macroalgal assemblages and identifies the relationship between adults and juveniles.

Some of the findings from Part B are then modelled in Part C. The section then broadens the analysis in order to examine the emergent patterns over larger spatial scales.

3.2 Part A – Materials and methods

3.2.1 Field Program

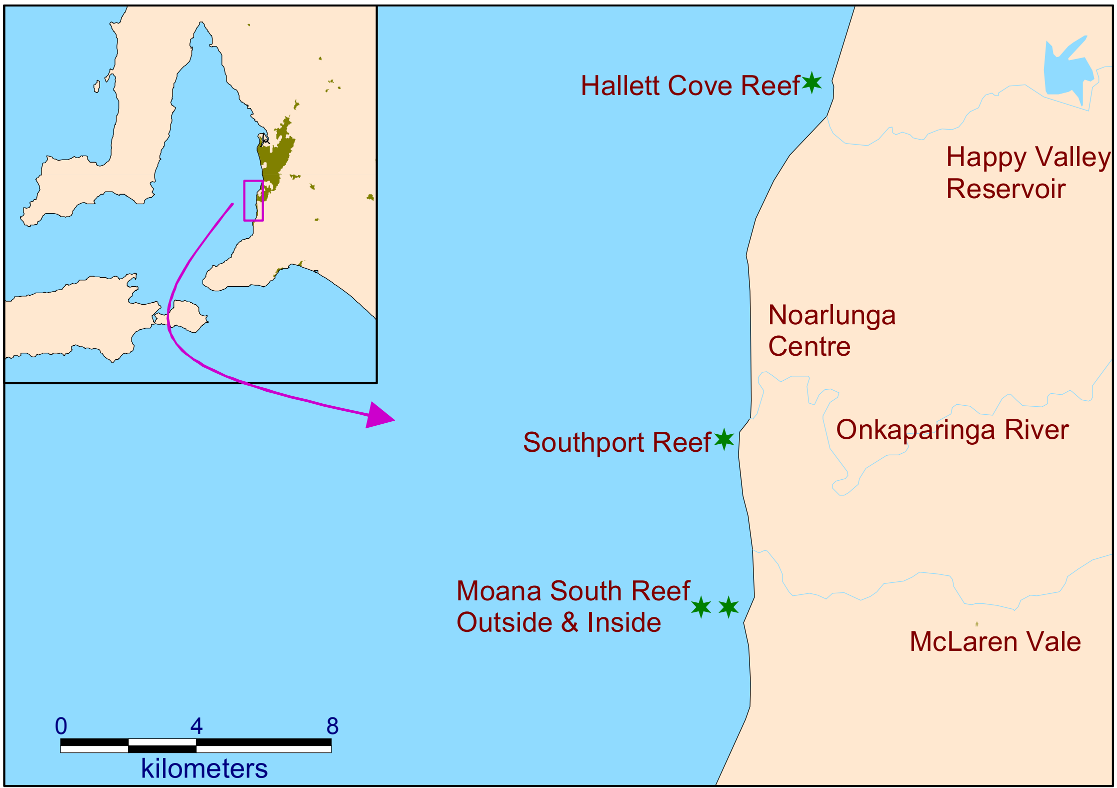

Figure 3.1 Map of the study area showing the location of reefs[10].

An assessment was made of canopy forming macroalgae on a number of Adelaide's central metropolitan reefs (Figure 3.1; Table 3.1) to obtain information on typical community assemblages. Reefs were chosen on the assumption that they were in relatively good health, based on Cheshire *et al.* (1998).

The survey collected spatially resolved information on the nature of both adult and juvenile community structure for the dominant species. Juveniles were distinguished based on approximate age as described in the following section (3.2.2). Field surveys coincided with the annual recruitment season (during August, 1998) and focused on shallow water communities (approximately five metres depth). All sampling was carried out using SCUBA.

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[10] This figure incorporates data that is © Commonwealth of Australia (Geoscience Australia 2003).

Table 3.1 Description of the reefs used in the first part of this study. Codes are those used to identify the sites in subsequent analysis. Locations describe the approximate midpoints of the reefs as latitudes and longitudes using the Geocentric Datum of Australia 1994 (GDA94).

Reef	Code	Location	Description
Hallett Cove	HAL	138.4878 -35.0768	Reef comprised of several long narrow rock strips running north/south, parallel to the shore. Algal cover was patchy, mostly *Sargassum* dominated, with some *Ecklonia* dominated patches.
Southport	SOU	138.4606 -35.1714	Flat top low profile platform elevated one to two metres from sea floor. Platform covered with large amounts of small rocks and pockets of sediment. *Sargassum* dominated with some mixed patches.
Moana South Inside	MSI	138.4617 -35.2155	Steep slope with many boulders and holes, high abundance patches of both fucoids and *Ecklonia*.
Moana South Outside	MSO	138.4521 -35.2155	Moderate slope with mixed fucoid and *Ecklonia* patches.

Each reef was characterised using three randomly placed transects that were comprised of a series of contiguous 0.6 m^2 quadrats (1m X 0.6m). In order to obtain sufficient replication for community analysis and interpretation, sampling along transect lines continued until twenty quadrats containing canopy forming macroalgae had been recorded.

For each quadrat, counts were made of all adult canopy forming macroalgae along with length measurements for all juveniles and recruits (<300mm; Table 3.2).

The choice of a generic level of classification of macroalgae was deemed suitable for this study, given that patch dominance tends to occur at this level (Turner and Cheshire 2003). Indeed, many of the larger taxa are locally restricted to only one species within the genus (e.g. *Ecklonia radiata*, *Scytothalia dorycarpa*), while Collings (1996) also found that smaller taxa within the gulf (e.g. *Cystophora* spp. and *Sargassum* spp.) often existed in mono generic stands comprising multiple species. Furthermore, such a choice also has pragmatic advantages given the difficulty in identifying some taxa when not sexually mature (especially species of *Sargassum*) *in situ*: this is especially true for juveniles, which lack the receptacles required for identification (Womersley 1987).

3.2.2 Age structure of juvenile canopy forming macroalgae

Information presented in Appendix I was used to determine the age / size classes described in Table 3.2 as a basis for categorising the macroalgal community. Additionally, many adult individuals from the genus *Sargassum* shed their laterals prior to the survey and thus existed only as a basal rosette. These individuals were differentiated from juveniles based on the 'woodiness' of their tissue.

This technique incorporated the available data on local juvenile growth rates, although it is acknowledged that there may be complications. Qualifications for this method of determining age classes are discussed in section 3.8.3.

Table 3.2 Juvenile macroalgae age / size class parameters.

Category	Size (mm)	Age of recruit
1	<15	New recruits
2	15-30	New recruits
3	31-50	One year old -
4	51-100	One year old
5	101-200	One year old +
6	201-300	Two year +

3.2.3 Testing for autocorrelation along a transect

Environmental gradients, biotic, and abiotic factors all influence community structure in both space and time. The resultant patchiness of the system means that variables used to describe community structure will take on different values according to their spatial location, and the time of the observation. As a result, values for these regionalised variables are likely to change along the length of a transect line. If, as in many cases, these changes happen in a predictable way then the variable is considered autocorrelated (Legendre *et al.* 2002).

Simply stated, if a variable is autocorrelated then neighbouring samples will be more or less similar to each other than to samples further away. Hence, the value of any particular sample will be partially dependent on the values of the surrounding samples (Liebhold and Gurevitch 2002).

This is important because most statistical tests assume that samples are independent of each other (i.e. no autocorrelation). Violation of this assumption reduces the overall degrees of freedom in an unpredictable way leading to an increased likelihood of false conclusions (Legendre *et al.* 2002; Liebhold and Gurevitch 2002). Furthermore, this lack of sampling independence cannot be circumvented easily with randomised sampling (Palmer 1988).

Violation of sampling independence can produce a number of unpredictable results hence the issue of autocorrelation needs to be embraced during any analysis and interpretation of spatial data.

Spatial autocorrelation along transect lines was explored using a Mantel correlogram in the following manner (Based on Legendre and Fortin 1989). All calculations were undertaken using a computer program written in PERL.

Bray-Curtis association

$$B = \frac{\sum_{i=1}^{n} \left| x_{ij} - x_{ik} \right|}{\sum_{i=1}^{n} (x_{ij} + x_{ik})}$$

Equation 3.1

Where x is the abundance of species i, and j and k are subscripts to the first and second quadrat respectively.

The Bray Curtis measure of association (B, Equation 3.1) was calculated for all pairs of quadrats using the abundance of adult individuals in each genus. The resulting values were subtracted from one and used to construct a true similarity matrix. A second matrix with the same overall layout was populated with values corresponding to the physical distance between quadrats pairs.

A normalised Mantel statistic (*r*, Equation 3.2) was then calculated between the dependent matrix (dissimilarity) and the predictor matrix (geographic distance). For each distance class, starting with one (for adjacent quadrats) and increasing with increasing distance, a separate distance matrix was produced. In this way, quadrat pairs separated by the required test distance were scored one while all other pairs received a zero.

Normalised Mantel statistic

$$r = \frac{1}{(n-1)} \sum_i \sum_j \left[\left(\frac{x_{ij} - \bar{x}}{s_x} \right) \left(\frac{y_{ij} - \bar{y}}{s_y} \right) \right] \quad \textbf{Equation 3.2}$$

Where x and y are the values from the dependent and predictor matrices at row i column j, and n is the number of distances in one of the matrices (excluding diagonals).

Test significance was evaluated via permutation procedures: rows and columns of the similarity matrix were randomly rearranged and Mantel's statistic recalculated 1000 times in order to produce a frequency distribution (Legendre and Fortin 1989). As a result, p values correspond to the proportion of runs where Mantel's statistic (based on real data) was larger than the value obtained during randomisation for positive and negative results respectively.

A correlogram was produced by plotting the resultant Mantel statistic on the y-axis against distance class on the x-axis. Given that the correlogram represented multiple tests, individual *P* values were Bonferroni adjusted and overall significance determined based on at least one *P* value being less than $\alpha=0.05$ (Legendre and Fortin 1989).

3.3 Part A - Results

3.3.1 Autocorrelation along transect lines

An examination of quadrat data obtained from reefs used in this chapter revealed the presence of canopy forming taxa in all cases. As a result, there was no need to account for gaps along transect lines.

A mantel correlogram using combined data from all sites revealed significant spatial autocorrelation. Along the length of the correlogram, there were a number of successive peaks and troughs, with the magnitude of Mantel's r generally decreasing with increasing distance (Figure 3.2).

On the figure, the horizontal axis indicates the distance class, and represents the number of quadrats that separate the assemblages being tested. As such, distance class one represents neighbouring quadrats, while distance class five represents quadrats with a gap of four quadrats (2.4 m) between the pairs.

The strongest correlation occurred at distance class one, indicating a high degree of similarity between neighbouring quadrats (in terms of community composition based on the Bray-Curtis measure) and implying that the samples were obtained from within the same clump. A peak at distance class three indicates the average distance between successive clump centres where the measure of similarity was maximised. The first trough at distance class two identifies the local minima in terms of similarity and hence defines the average edge of the clump. A second trough at distance class eight and peak at ten, points to repetition of this pattern.

A final peak at distance class eighteen points to a larger patch size at the transect scale (based on average transect length).

Given the effect of site differences in providing a coarse scale trend in the data, analyses were repeated on quadrat data for individual sites. Mantel correlograms identified a broadly similar pattern at each of the four sites (Figure 3.3). Although, the reduced number of replicates available led to more variability and meant that significant differences in the correlogram could only be defined as far as distance class ten. Notwithstanding the increased variability, troughs at distance classes of two and eight were identified at most sites.

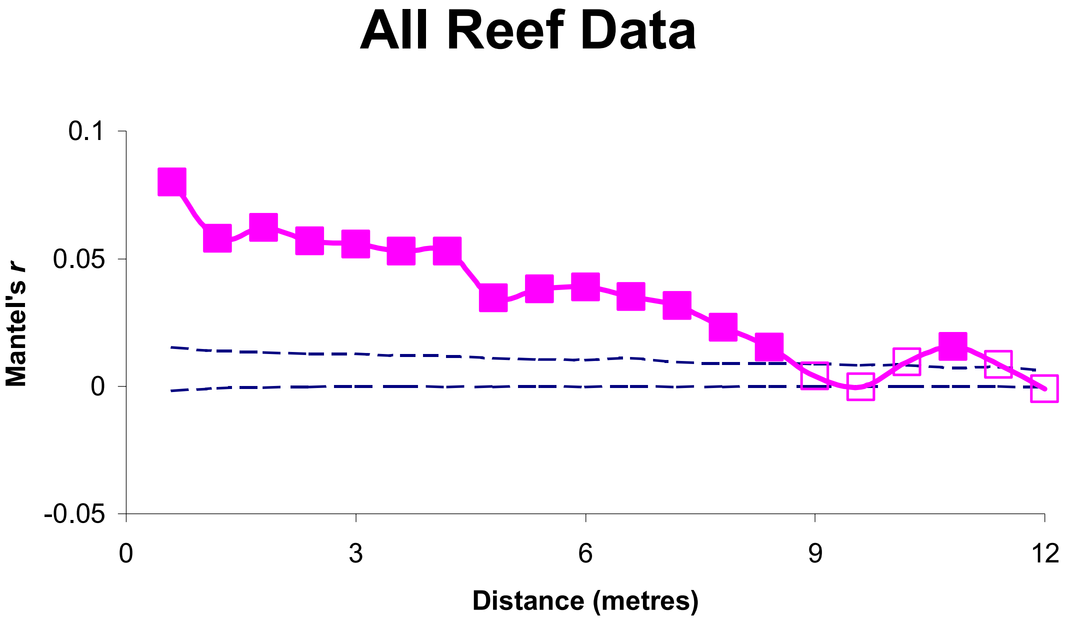


Figure 3.2 Mantel correlogram based on combined data from all sites. The dotted lines represent the upper and lower 95% confidence limits based on randomisation of data before multiple comparison adjustment. Solid squares indicate significance at a Bonferroni adjusted level of α=0.05 → *P*=0.0025.

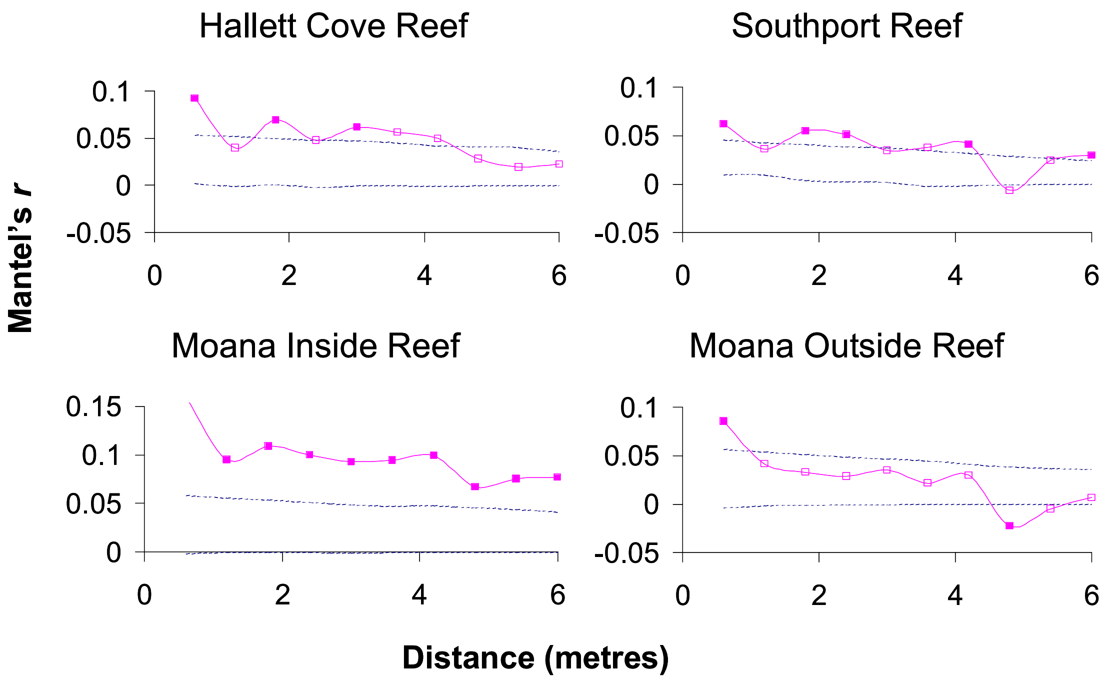


Figure 3.3 Mantel correlograms for each site. The dotted lines represent the upper and lower 95% confidence limits based on randomisation of data before multiple comparison adjustment. Solid squares indicate significance at a Bonferroni adjusted level of α=0.005.

3.4 Part B – Materials and Methods

3.4.1 Characterisation of adult community structure

Canopy composition on each transect at each site was described based on adult density information obtained during the field survey.

Differences in the canopy composition between sites was then tested using a non-parametric multivariate analysis of variance (NPMANOVA, Anderson 2000). To account for some of the variability within each site, transect data were nested within site. However, quadrat replicates on individual transects were spatially autocorrelated and thus non-independent (Part A, section 3.3.1). To compensate for this, new transects were produced by randomly selecting quadrats from across all transects within each site using the method of Manly (1997). Although this resulted in the loss of meaningful information about spatial patterns on individual transects, between sites comparisons (the focus of the current tests) were still valid.

Non-parametric measures of association (Spearman ρ and Kendall τ) were used to test for correlations between different genera at the scale of individual quadrats.

It is likely that the influence of the adult canopy on the underlying juvenile assemblage (see 3.4.2) would overshadow the affects of other environmental phenomena. As such, in order to maximise the chance of detecting an impact it was important for comparisons to be limited to similarly structured assemblages. Cluster analyses (Ward's method) were therefore used to identify assemblage types as the basis for subsequent comparison.

3.4.2 The relationship between adult and juvenile assemblages

Previous studies on South Australian coastal reefs (Turner 1995; Collings 1996; Collings and Cheshire 1998; Emmerson and Collings 1998; Cheshire *et al.* 1998a; Cheshire and Westphalen 2000; Turner and Cheshire 2003) have demonstrated that there is a high degree of variation in community structure even at relatively small spatial scales (within the length of a 20 m line transect). It has also been demonstrated that in many fucoid and *Ecklonia* dominated communities, the structure of the recruit/juvenile communities is strongly influenced by the nature of the adult canopy (Kennelly 1983; Velimirov 1983; Kennelly 1989; Kendrick and Walker 1994; Cheshire *et al.* 1999). In such situations, heterogeneity in the structure of the adult community is likely to result in heterogeneity in the structure of the recruit/juvenile communities.

The overall pattern of association between the adult and recruit communities was assessed to determine the extent to which the structure of the adult community was correlated with that of the juvenile community.

Correlation coefficients were used to identify the basic relationship between adult and juvenile members of each genus. Similarity matrices were then produced for all adult and juvenile data using the Bray Curtis measure of association (Bray and Curtis 1957). The resultant matrices were compared graphically using MDS ordination plots, and statistically using a mantel test (Douglas and Endler 1982). For the mantel test, probability levels were computed using 1,000 iterations of a Monte Carlo test similar to those described above.

Finally, the average numbers of juveniles for each taxon was calculated under each canopy type. Juveniles were grouped by age either as current season recruits, or as belonging to the one year or two year cohorts, based on size and using the age determination in Part A (Table 3.2).

3.5 Part B – Results

3.5.1 Adult Community Structure at the quadrat scale

Three canopy-forming genera of macroalgae (*Ecklonia*, *Cystophora* and *Sargassum*) were commonly found on transects and all were represented at each site to some degree (Figure 3.4). Another two fucoids (*Seirococcus axillaris* and *Scaberia agardhii*) were identified in the study area but were very rare, with only a few individuals observed on each reef. Hence they have been excluded from further analyses.

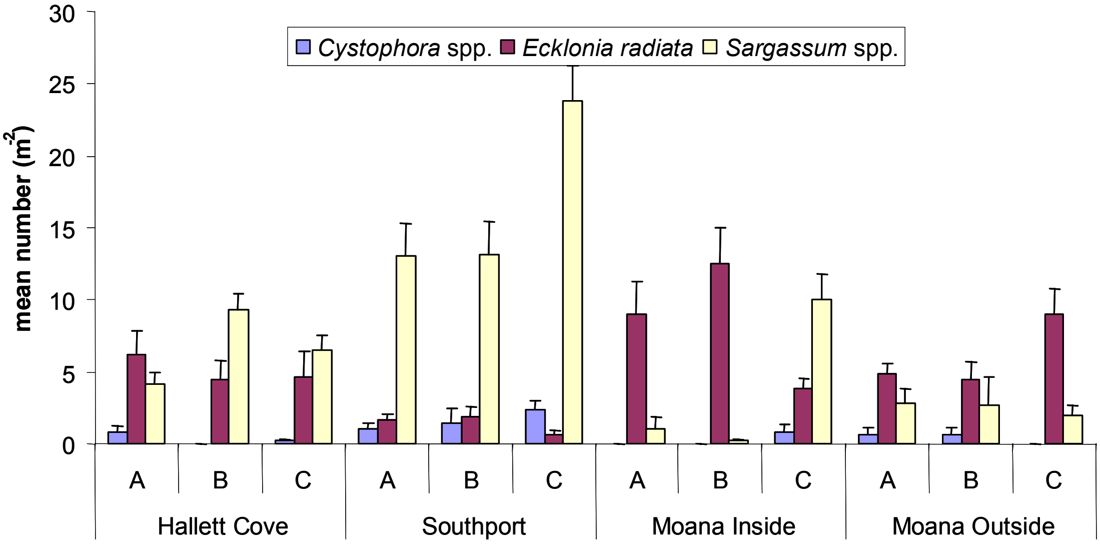


Figure 3.4 Number of adult canopy individuals (n m^{-2}) for each genus.
Shows that there was significant variation in community structure between sites. Densities also differed within sites although composition was more uniform. Error bars are standard error of the mean.

Average density of the common genera varied considerably between sites and between transects within the same site (Figure 3.4). Using randomised transects to correct for non-independence of quadrat replicates, assemblage composition was found to be significantly different between sites (NPMANOVA: Site $F_{3,8}$=90.8435, P=0.0001, Table 3.3).

Pair wise *a posteriori* comparisons showed that highly significant differences existed between all sites, with the two Moana sites showing the least difference (Table 3.4).

Acknowledging these differences, *Cystophora* was generally present at all sites in low density (<2-3 n m^{-2}), while *Sargassum* was more common on the two flat reefs; Hallett

Cove (>5 n m^{-2}) and Southport (>10 n m^{-2}). *Ecklonia* was also common on Hallett Cove Reef (~5 n m^{-2}) but found in greater density on both the seaward and leeward sides of Moana Reef (>5 n m^{-2}, Figure 3.4).

Table 3.3 NPMANOVA testing for site differences in macroalgal canopy composition.

Source	df	SS	MS	*F*	*P*
Site	3	164470.6	54823.52	90.8435	**0.0001**
Transect [Site]	8	4827.955	603.4944	0.3997	0.9952
Residual	216	326144	1509.926		
Total	227	495442.5			

Table 3.4 Pair wise *a posteriori* comparison between sites.

Pair wise comparison between		*t*	*P**
Hallett Cove	Moana South Inside	6.9745	**0.0006**
Hallett Cove	Moana South Outside	4.9199	**0.0012**
Hallett Cove	Southport	8.7701	**0.0006**
Moana South Inside	Moana South Outside	3.3368	**0.0150**
Moana South Inside	Southport	22.0661	**0.0006**
Moana South Outside	Southport	13.4544	**0.0006**

* *P* values Bonferroni adjusted for multiple comparisons

Within individual quadrats, a negative association existed between *Ecklonia radiata* and the other two genera indicating that it tends not to coexist with these taxa at this scale (Table 3.5). Tests of association between *Cystophora* and *Sargassum* were not significant.

In cases where numbers of individuals were sufficient to create a closed canopy, assemblages of canopy forming macroalgae (defined by the size of the quadrat) generally clustered according to a single dominant taxon. Under such conditions, groups were clearly dominated at the generic level by one or other of the common canopy forming taxa (*Sargassum* or *Ecklonia*). *Cystophora* was only found in sufficient density to dominate the patch in a few quadrats. However, when clustering was repeated using data from additional sites (see Chapter 4) *Cystophora* more frequently dominated assemblages (Figure 3.5).

Table 3.5 Tests of association between canopy forming genera.

Test of association		Spearman ρ	Kendal τ
Ecklonia radiata	*Cystophora* spp.	**-0.5234** **p=0.001**	**-0.4111** **p=0.001**
Ecklonia radiata	*Sargassum* spp.	**-0.1192** **p=0.001**	**-0.0902** **p=0.001**
Sargassum spp.	*Cystophora* spp.	0.0144 p=0.466	0.0125 p=0.421

Not all quadrats contained a dense adult canopy. In these instances, quadrats tended to be comprised of a mixture of two or more of the above genera in low abundance (<5 n m^{-2}, Figure 3.5).

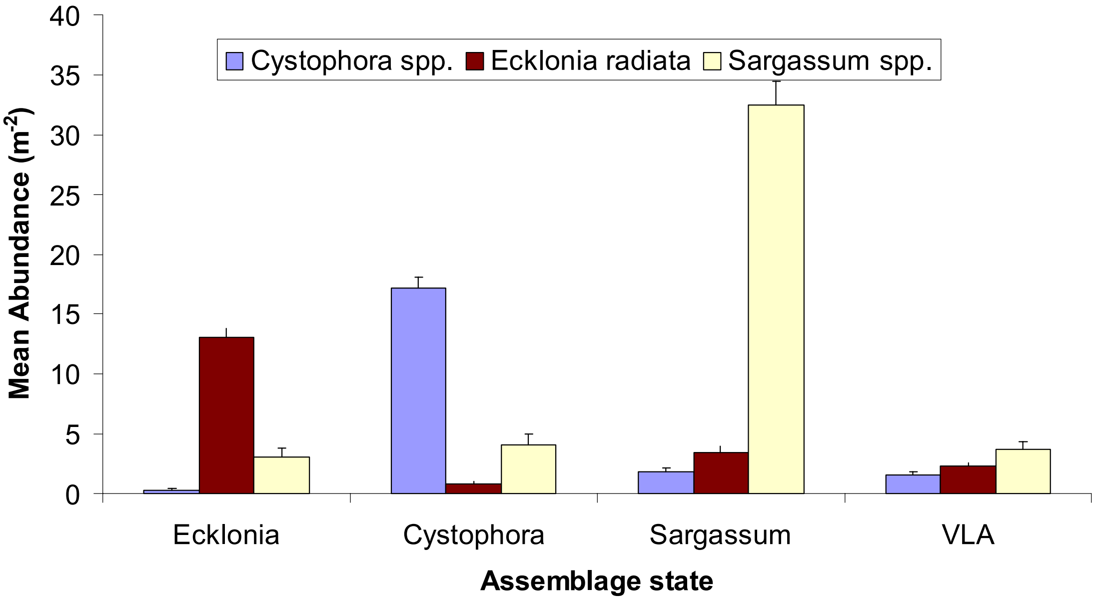


Figure 3.5 Composition of the identified assemblage states.
This indicates the presence of a low density mixed assemblage (VLA) as well as a number of higher density mono generic stands. Error bars are standard error.

Three of the four groups are hereafter referred to by their dominant genus while the fourth is termed VLA (Variable Low Abundance) due to its mixed canopy composition and low density. Plots of quadrat data in species space (Figure 3.6) show the VLA assemblages in the centre of the diagram where only a few individuals of each genus are present. As numbers increase, points are found further from the central region. Note that with increasing density, points tend to congregate around the axes confirming dominance by a single genus. Areas of the graph that would potentially represent greater numbers of individuals with shared dominance are virtually empty. The exception to this was in the area between *Sargassum* and *Ecklonia*.

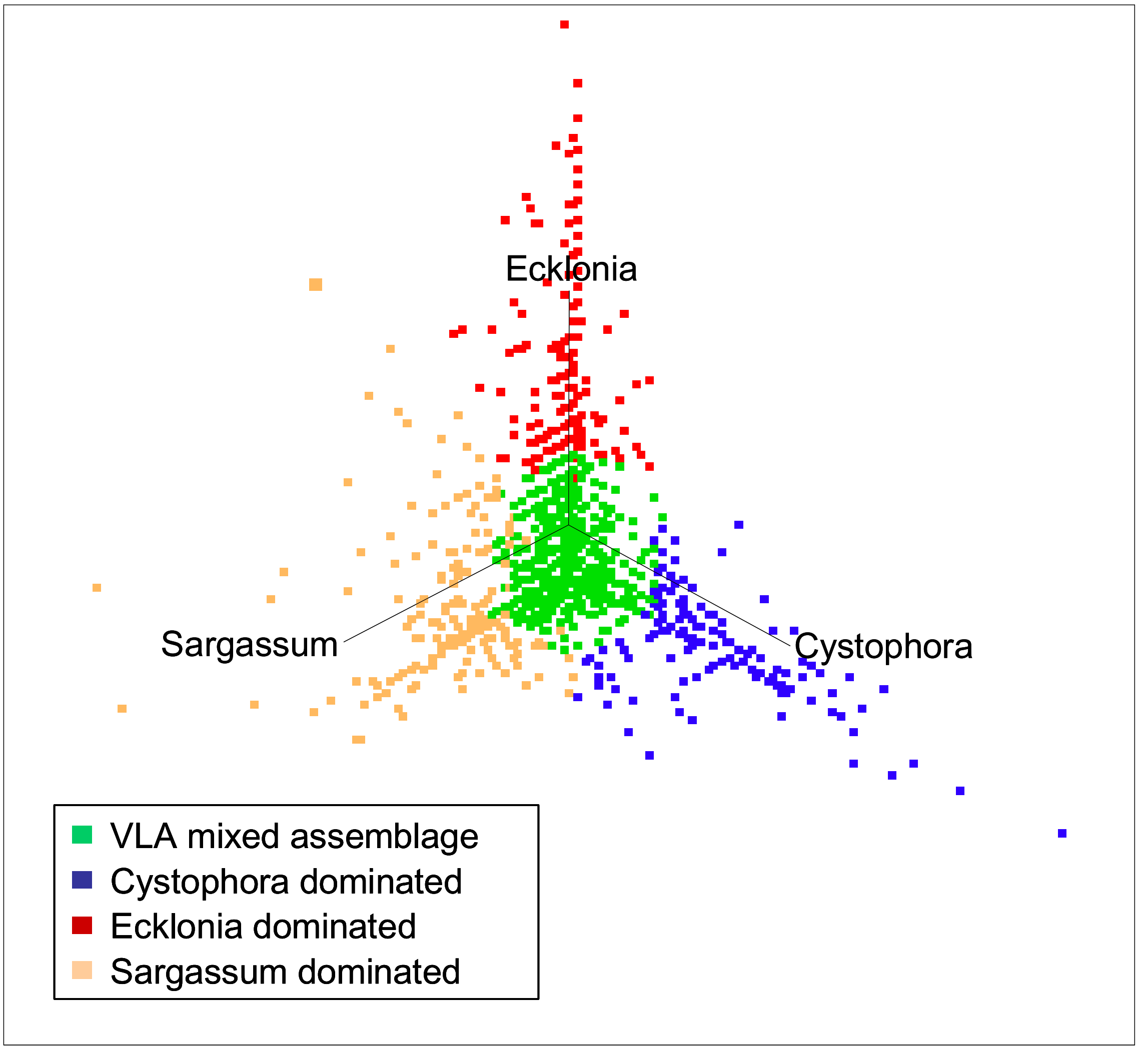


Figure 3.6 Graphical representation of quadrat data in genera space. Each point represents the abundance of the three dominant genera in 3D space for a given 0.6 m^2 quadrat.

3.5.2 The relationship between adult and juvenile assemblages

A high positive correlation was observed between the presence of adults of a given genus and juveniles of the same genus for all taxa (Table 3.6). In all cases, there was a strong negative association between the presence of adult *Cystophora* and juvenile *Ecklonia* and *vice versa* (Table 3.6).

Table 3.6 The relationship between the abundance of adult and juvenile plants. In all cases there is a significant (minimum p<0.0015) positive correlation between the presence of adults and juveniles of the same genera in a quadrat. There is also a strong negative correlation between adults and juveniles for *Ecklonia* and *Cystophora*.

	Juvenile		**Adult taxa**	
Juvenile taxa	**Size class**	***Cystophora***	***Ecklonia***	***Sargassum***
Cystophora	New	+	-	+
	One Year	+	-	+
	Two Year	+	-	+
Ecklonia	New	-	+	NS
	One Year	-	+	+
	Two Year	-	+	+
Sargassum	New	-	+	+
	One Year	-	NS	+
	Two Year	NS	NS	NS

+/- Indicates a significant (positive or negative) correlation for both the Spearman ρ and Kendall τ measures of association. NS = Non-significant correlation.

It needs to be recognised that age classes were assigned based on plant height. Given that *Sargassum* sheds its reproductive tissues following gamete release, very few juvenile individuals were distinguishable from the larger size categories. As a result, correlation analyses on larger individuals were found to be non-significant due to lack of replication. However, it was found in the smaller size classes that juvenile *Sargassum* were negatively associated with *Cystophora* and positively with *Ecklonia* and *Sargassum* adults. Adult *Sargassum* plants showed a positive association with juveniles of all taxa for most size classes (Table 3.6).

Ordination of one and two year old juveniles demonstrated a clear relationship between their structure and the overlaying canopy (Figure 3.7). This was however not the case for the current season's recruits.

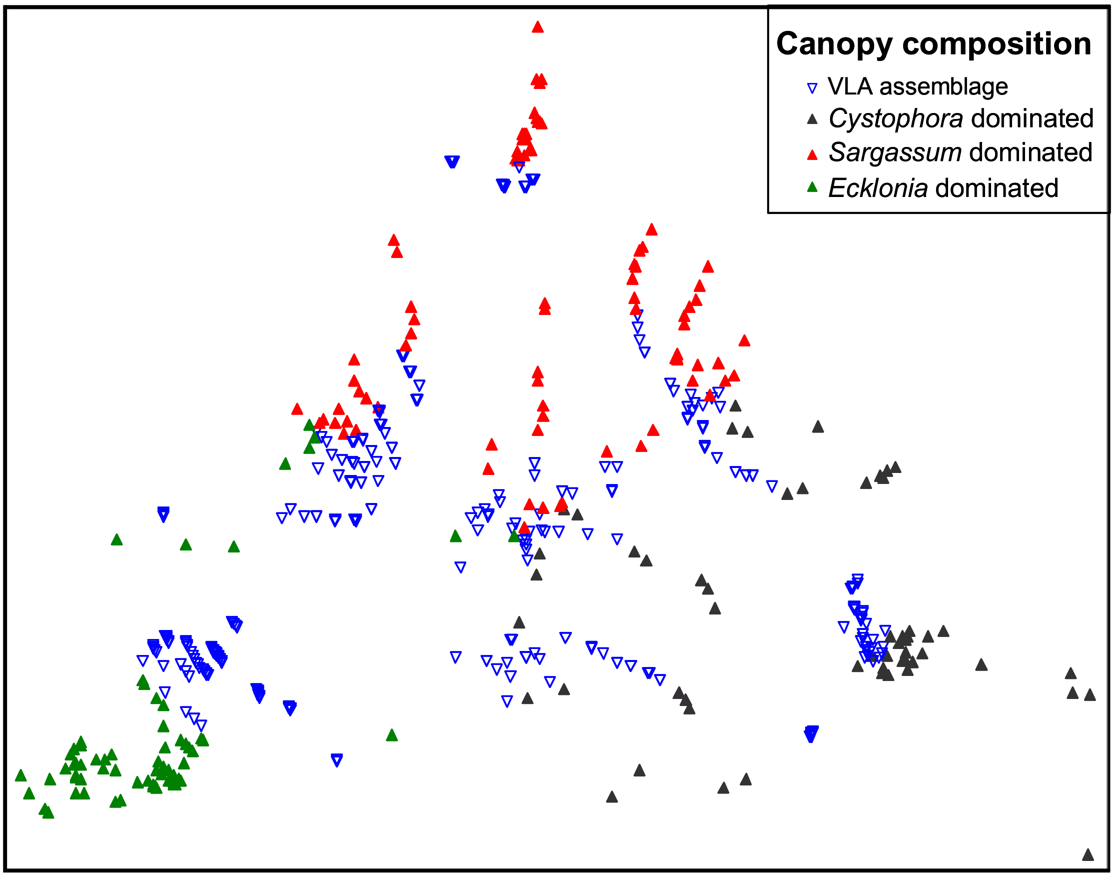
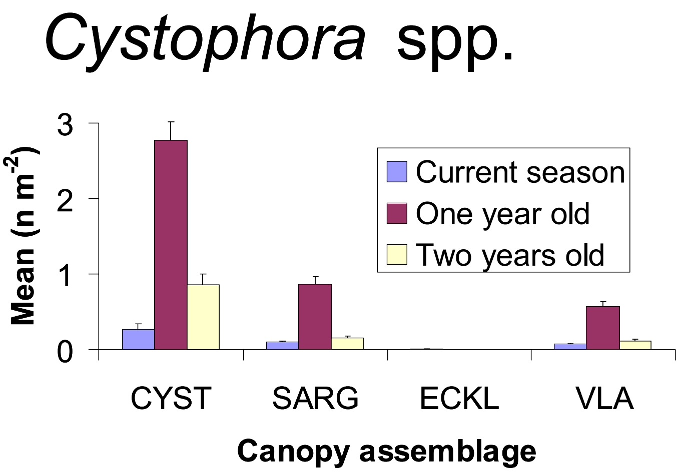
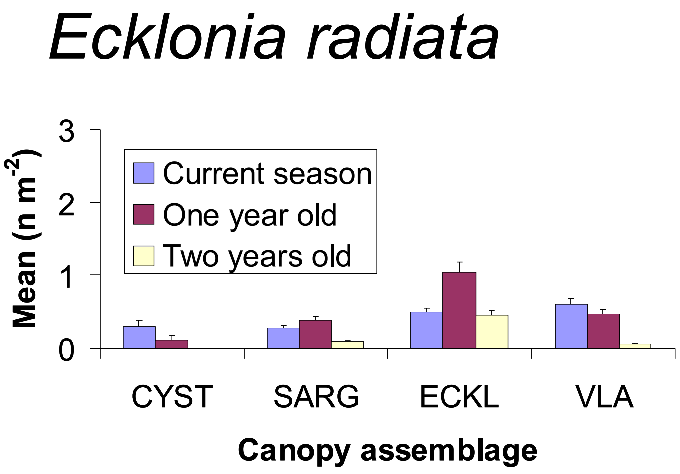


Figure 3.7 NMDS ordination of one-year-old canopy forming taxa. Different coloured symbols represent the type of overlying adult canopy, and demonstrate that the structure of the juvenile assemblage was clearly correlated with canopy composition. Two-year-old juveniles (not shown) demonstrated a similar trend.

Table 3.7 Mantel test of association between distance matrices. Comparisons were made between the adult matrix and juvenile matrices divided into age classes.

Age of juveniles	Standardised Mantel's r	*P* (type 1 error)
Current season recruits	-0.022964	0.021
One year old cohort	0.110387	0.001
Two year old cohort	0.073676	0.001





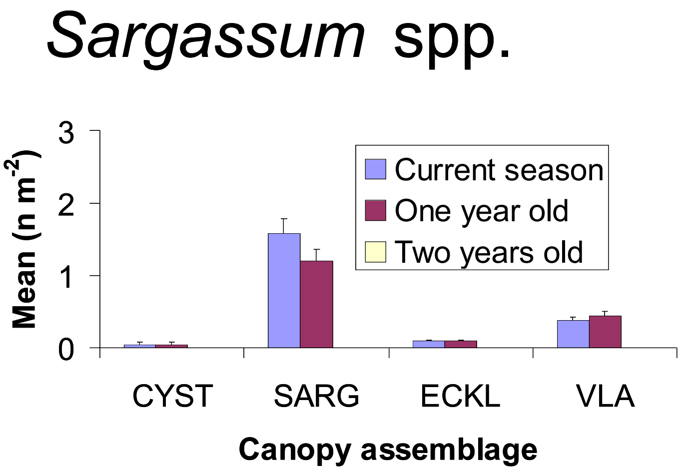


Figure 3.8 Average numbers of juvenile macroalgae under each canopy type. Juveniles of the genera *Cystophora*, *Sargassum* and *Ecklonia* are separated into age cohorts with average numbers per quadrat shown under each of the four canopy assemblages. Error bars indicate standard error of the mean.

Mantel tests were used to assess the level of association between similarity matrices derived from adult canopy individuals and those of juveniles in each age class. In all cases associations were found to be significant, however the type of association was not constant. As was expected the structure of the juvenile stand, based on the one and two year cohorts, was positively correlated with that of the adult stand. Interestingly, the opposite was observed for current season's recruits, which appeared to have a negative association with the adult stand (Table 3.7).

In all cases, recruitment of the three genera was greatest underneath a canopy of similar composition. Recruitment was next most successful under the open canopies of VLA assemblages (Figure 3.8). Lower average numbers of new recruits is most likely due to the timing of the survey, in that many individuals were too small to be noticed or alternatively had not yet recruited.

3.6 Part C – Materials and Methods

3.6.1 Modelling quadrats with co-dominant assemblages

In part B (section 3.5.1) it was determined that assemblages occurred as mono generic stands (*Ecklonia*, *Cystophora* or *Sargassum* dominated), wherever density was sufficient to create a closed canopy. Alternatively, at lower densities, assemblages existed in a state of variable low abundance (VLA). Few quadrats were found in which there was both a high density (>10 n m^{-2}) and a shared dominance of 2 or more taxa. In order to explore this feature of the system, data corresponding to co-dominant states were modelled and ordinated along with real data obtained during the field program. Modelled data were produced by applying a stochastic function to each genus in turn such that for any genus X:

Model values for genus X

$$X_i = \frac{\overline{X} + R}{C}$$ **Equation 3.3**

Where X_i is the abundance of genus X in the *ith* replicate, R is a random integer that lies within one standard deviation s ($-s \leq R \leq +s$). The mean was calculated from the mean of all mono generic quadrats divided by the number of co-dominant taxa C in the replicate in question.

Ordinations of modelled and real quadrat assemblages were computed using non-metric Multidimensional Scaling (nMDS) incorporating Bray-Curtis similarity.

3.6.2 Links between assemblages in space

The focus of previous analyses was to determine the nature and composition of macroalgal assemblages at relatively small scales. At these scales, assemblages appeared to exist as clumps (part A section 3.3.1) in one of a limited number of discrete states (part B 3.5.1).

As a logical continuation, an exploration was undertaken into how these clumps were spatially associated with one another. In the current context, transect data provided an opportunity to do this through an informal analysis of ecological grammars (e.g. Dale and Barson 1989).

The premise here was that if no structuring processes were acting to influence neighbouring clumps then distribution along the transect line at scales above that of the clump would appear to be random. As such, this formed a useful (but not perfect) null hypothesis[11].

It was likely, however, that the interaction of various structuring elements would change the probability of certain combinations occurring. Thus, certain combinations would occur either significantly more or less commonly than chance alone would suggest.

To test this hypothesis, each quadrat along a transect line was assigned an assemblage type (CYS, ECK, or SAR for *Cystophora*, *Ecklonia* or *Sargassum* dominated assemblages respectively, or VLA for assemblages existing in a state of variable low abundance; see results section 3.5.1 for more details). Relationships were first assessed at the clump (quadrat) level by scoring the frequency with which various combinations of neighbours occurred (e.g. VLA-VLA, CYS-ECK, SAR-VLA, etc.).

The significance of this distribution was tested with a randomisation procedure. The order of quadrats along the transect lines was randomly shuffled and cumulative frequencies recalculated one thousand times. *P* values for real observations less frequent than those randomly generated were determined by the number of times real values were larger that the permutated values. Conversely, where the observed frequency was higher than the randomly generated data, *P* values related to real values being smaller than permutated ones. In addition, sample mean and standard deviation were computed from the permutated data and used to standardise the real values.

Following this, multiple strings of the same state were reduced to single instances so as to assess structure at a ‘patch’ level (i.e. SSSVVVVVEEEEVVV became SVEV, where each letter represented an individual state abbreviation e.g. S=SAR, V=VLA). The above process was then repeated, acknowledging that the resulting frequency table would lack ‘like-like’ states (i.e. CYS-CYS or VLA-VLA).

Finally, the influence of VLA states on the system was discounted by assuming that they were simply representative of the boundary between states, and the process once again repeated (i.e. SVEVS became SES).

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[11] It is possible that the overall influence of several processes may yield a community structure which appears statistically random.

3.7 Part C - Results

3.7.1 Modelling assemblage states

The absence of shared dominance in the higher density states was confirmed in an nMDS ordination (Figure 3.9) combining real and modelled quadrat data. The three mono generic states were clearly separated with modelled co-dominant states appearing neatly between. There was very little overlap between the six states indicating that they are discrete in nature. However, *Sargassum* had a wide distribution and assemblages occasionally entering the neighbouring co-dominant states. VLA assemblages were scattered across the ordination and are not shown for purposes of clarity.

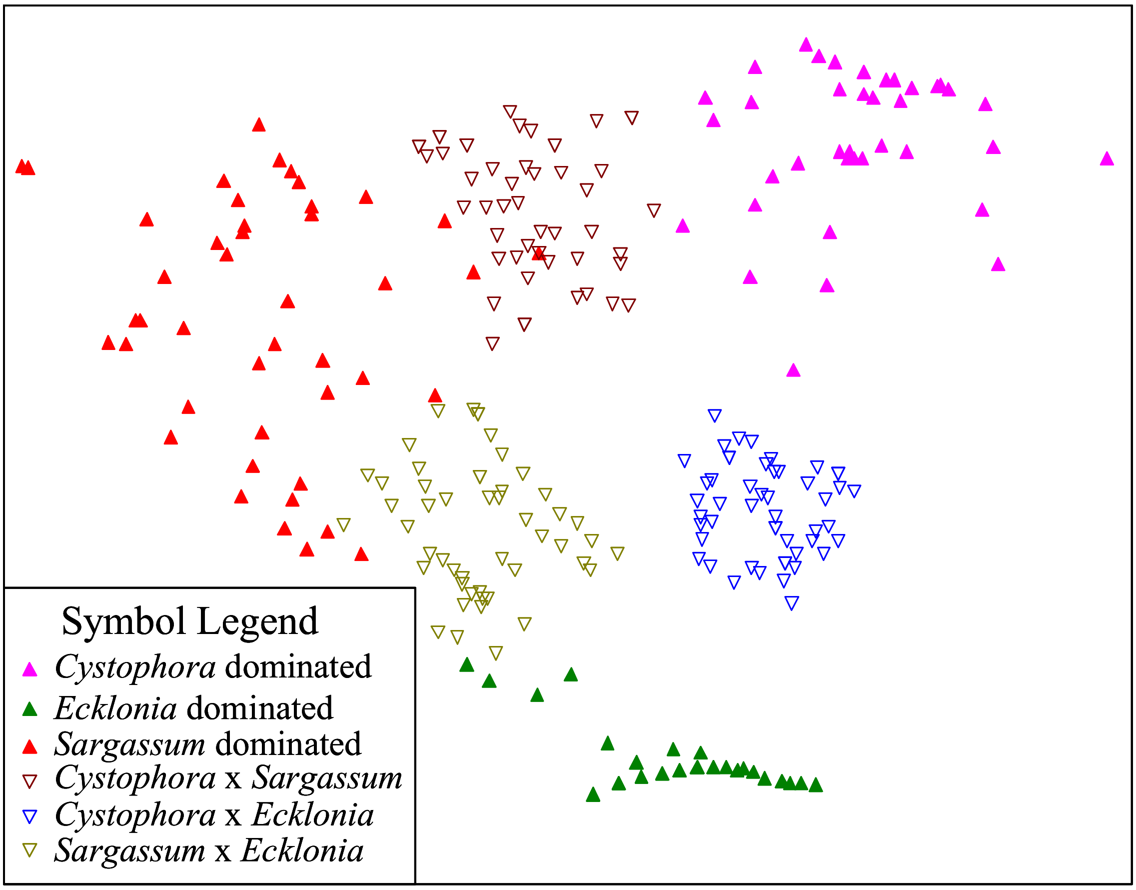

Figure 3.9 NMDS ordination of real and modelled quadrat data. Solid triangles represent the composition of real quadrats dominated by a mono generic assemblage. Open triangles represent modelled data such that assemblages were allowed to share dominance between two different genera. The figure demonstrates that the different groupings rarely overlapped.

3.7.2 Adult community structure at a larger scale – the relationship between neighbouring assemblages

If patch composition is limited to one of four assemblage types (VLA, CYS, SAR, ECK) then ten different permutations for neighbouring assemblages are possible (e.g. VLA – VLA, VLA – CYS, SAR – ECK etc.). The relative frequency with which these permutations will occur under random assignment will be linked to overall frequency of the different assemblage types.

For comparisons between neighbouring quadrats (clump level), the frequency of occurrence of the different neighbour combinations was found to be significantly different from a random arrangement in all cases except where two VLA assemblages acted as neighbours (VLA – VLA, Table 3.8).

Quadrats dominated by one of the three mono generic canopy-forming taxa tended to have neighbours with the same assemblage structure. This happened 3-4 times more often than random communities did (Table 3.8). Mono generic dominated assemblages neighboured VLA assemblages less than expected, while clumps with different mono generic states rarely acted as neighbours (Table 3.8).

Concatenating multiple strings in the same state allowed a 'patch' level view of the community. Mono generic states frequently neighboured VLA assemblages as above, however the observed frequency was only significantly greater than expected in the case of *Cystophora* dominated stands. Once again, different mono generic states rarely acted as neighbours (Table 3.8).

At the habitat level (discounting the existence of VLA states), the relationship between neighbouring assemblages was effectively the same as in the initial clump analysis (Table 3.8).

Table 3.8 Observed versus expected frequency for neighbouring patch configurations.

Neighbouring assemblages	Observed percentage	Expected^{+} proportion		Significance *P**	Outcome
		Mean	StDev		
Quadrat level observations (observations between neighbours)					
VLA-VLA	56.9	55.8	1.5	0.990	Not significant
CYS-CYS	5.0	1.2	0.5	**0.010**	Greater than expected
SAR-SAR	11.2	3.3	0.8	**0.010**	Greater than expected
ECK-ECK	8.3	1.9	0.6	**0.010**	Greater than expected
CYS-VLA	4.9	7.9	0.8	**0.010**	Less than expected
SAR-VLA	7.2	13.7	1.1	**0.010**	Less than expected
ECK-VLA	5.8	10.2	0.9	**0.010**	Less than expected
CYS-SAR	0.1	2.0	0.5	**0.010**	Less than expected
CYS-ECK	0.0	1.5	0.4	**0.010**	Less than expected
ECK-SAR	0.6	2.5	0.5	**0.010**	Less than expected
Patch level observations (concatenating quadrats in the same state)					
CYS-VLA	30.8	21.6	1.4	**0.006**	Greater than expected
SAR-VLA	35.7	35.8	1.6	0.990	Not significant
ECK-VLA	30.2	26.7	1.6	0.078	Not significant
CYS-SAR	0.5	5.3	1.1	**0.006**	Less than expected
CYS-ECK	0.0	3.9	1.0	**0.006**	Less than expected
ECK-SAR	2.7	6.7	1.3	**0.012**	Less than expected
Habitat level observations (same as above but excluding VLA)					
CYS-CYS	23.3	4.6	1.3	**0.006**	Greater than expected
SAR-SAR	27.4	12.7	1.9	**0.006**	Greater than expected
ECK-ECK	23.3	7.6	1.6	**0.006**	Greater than expected
CYS-SAR	9.6	24.6	2.6	**0.006**	Less than expected
CYS-ECK	2.7	19.2	2.3	**0.006**	Less than expected
ECK-SAR	13.7	31.3	2.7	**0.006**	Less than expected

$^{+}$ Values obtained from random permutation of transect data

* *P* values Bonferroni adjusted for multiple comparisons

3.8 Discussion

3.8.1 The presence of autocorrelation in the data

The Mantel correlograms (Figure 3.2; Figure 3.3) provide an opportunity to explore some of the underlying spatial patterning within the system. An understanding of autocorrelation is important from two standpoints. The first relates to the assumption of independence required by many statistical analyses while the second, more interestingly, allows for an investigation into community structure.

Assemblage composition at any particular location may be seen as a combination of three separate effects: the influence of local environmental factors (e.g. wave force, topography); biotic interactions (e.g. competition leading to a minimum inter-plant distance); and thirdly a spatially unstructured random error component (Legendre *et al.* 2002).

The four reefs surveyed are known to have different structure in terms of their physical composition, wave force, and topography. It is therefore highly likely that this broad environmental structure will have an influence on the structure and composition of the resulting biota. Notwithstanding this generality, correlograms from different reefs demonstrated a similar arrangement in terms of the spatial patchiness of canopy forming vegetation (Figure 3.3). As such, the autocorrelation identifiable in the data is likely to be primarily the result of the biological interactions along individual transects. In contrast, environmental conditions are likely to differ significantly between transects and sites and this will produce variation in both assemblage structure and overall species composition (Figure 3.4).

Data pertaining to canopy composition was not truly continuous along the length of the transect line, but rather it represented a series of contiguous quadrats. As such, the average patch size and distance to patch edge identified on the graph should be taken as approximate. Indeed if autocorrelation is assumed to be isotropic and clumps roughly circular in nature then a clump radius of two distance units (trough) would be inconsistent with the distance between clumps (peak) being three distance units.

Clumps as recorded along the constant depth contour (approx 5 m) appeared to encompass an area of about three quadrats (1.8 m). Importantly however, sampling was carried out in relatively shallow water. Hence, where sampling was undertaken on the sloped face of the reef, isotropy couldn't be assumed because of the likely influence of a depth gradient. This effect was not formally tested because all transect lines were carried out at the same depth.

3.8.2 The structure of a canopy covered macroalgal stand

Pioneering work by Shepherd and Womersley (1970, 1971, 1976, and 1981) demonstrated that reefs across South Australia tend to be dominated by large brown macroalgae in the sublittoral zone. The three genera abundant in the current study (*Cystophora*, *Sargassum*, and *Ecklonia*) are known to occur widely on Adelaide's rocky southern metropolitan coastline, along with a number of others present in lower numbers (Cheshire *et al.* 1998a; Cheshire and Westphalen 2000).

All three genera were represented at each study site although abundances were quite variable (Figure 3.4), with populations occurring in patches rather than as isolated individuals.

Ecklonia radiata had an average abundance of five plants (n m^{-2}), although this varied with the abundance of other taxa (Figure 3.4), indeed patches of around 20 n m^{-2} were common with density occasionally reaching more than 30 n m^{-2}. At these densities, *Ecklonia* formed a closed canopy monoculture. Similar densities were found in Western Australia commonly 15-25 n m^{-2} (Kirkman 1989) and up to 30 n m^{-2} (Kirkman 1984). Although Collings (1996) points out that average plant biomass within Gulf St Vincent was significantly lower (20-40g dwt $plant^{-1}$) than at oceanic sites (43-125g dwt $plant^{-1}$).

Sargassum abundance varied between five and ten plants (n m^{-2}) at most sites but averaged up to twenty at the Southport site (Figure 3.4). The genus was also observed as mono generic patches with densities of around 30 individuals (n m^{-2}). These figures are at the low end of those reported (32 – 58 n m^{-2}) for stands of *Sargassum* spp. growing at similar depths (6 m) on Rottnest Island, Western Australia (Kendrick and Walker 1994).

Finally, the genus *Cystophora* rarely occurred in sufficient abundance to dominate a patch (2-3 n m^{-2}, Figure 3.4) at the sites in this study. However, when analyses were extended to other sites (see Chapter 4) larger abundances were observed (average of 15 n m^{-2} at Horseshoe Outside – HSO and Noarlunga South Inside – NSI, Figure 4.3)

Rather than being uniform or even randomly distributed, it has been demonstrated that macroalgal assemblages are comprised of a mosaic of patches, (Collings and Cheshire

1998; Turner and Cheshire 2003; Underwood *et al.* 1991). This idea of a mosaic was also observed in the current study, with assemblages occurring in a number of discrete states (Figure 3.5).

The majority of these states were clearly dominated by a single genus of large brown macroalgae forming a closed canopy. An alternative state comprising an open canopy tended to contain a number of different taxa all in low abundance (VLA). States comprising closed mixed canopies were not found in this study.

Given that assemblage states were initially identified using a cluster analysis, boundaries between groups were by definition arbitrary (Canny 1981). If the different states simply represent a range of structures along a continuum, then it is possible that patches dominated by two or more different genera were simply divided between the more common mono generic or VLA states. However if this was the case, it should be visible on the ordination incorporating modelled mixed community states. Results showed little overlap between states, implying that states comprising mixed genera were not present at the time of the survey (Figure 3.9). The few points on the figure that showed a level of overlap may represent where quadrat sampling did occur across the boundary of two adjacent clumps in different states.

The existence of a finite number of states is important for any consideration of community pattern as well as postulating underlying processes (Cale *et al.* 1989). However, it must be acknowledged that this study was limited to areas containing canopy-forming macroalgae and hence does not represent the complete set of possible states[12].

The correlation between plant density and overall structure raises a number of important questions about the nature of processes driving canopy assemblages. It is postulated that the existence of high-density mono generic stands is a manifestation of properties of stability in these late successional taxa. Disturbances (although generally small scale) often result in the removal of adult biomass (Kim and Dewreede 1996) and may be used to explain the presence of patches of lower density (open canopy, VLA). Over a short time,

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[12] In the current context, transect lines at the four study sites were continuous across the substrate meaning that the four states identified do in fact represent the total number at the time of the survey. However, at other locations different patch configurations have been noted, including turf dominated patches and those dominated by mussels. This issue will be of greater importance in the following chapters.

and due to life history strategies creating resilience within the stand (Dayton *et al.* 1984), disturbed patches are likely to re-establish a closed canopy (e.g. Johnson and Mann 1993), thus returning to the mono generic state.

An examination of how neighbouring assemblages were associated in space demonstrated a strong degree of order, with different mono generic dominated patches rarely acting as neighbours (although *Sargassum* patches did occasionally act as neighbours to other assemblage types). Instead, there were generally one or more patches in the VLA state, separating different mono generic dominated patches (Table 3.8).

Comparisons between neighbouring assemblages showed that those in a mono generic state tend to form patches (often incorporating several quadrats), and that these patches are in turn bounded by areas in a VLA state (Table 3.8).

While at least some of these VLA areas are likely to represent a recent biomass loss through disturbance (such as when an area exists between two mono generic patches in the same state), they also appear to be acting as an interface between areas dominated by different mono generic stands. It is thus possible that these boundary areas are subject to a different set of dynamics, perhaps existing in a perpetual state of disturbance because of interference competition (Worm and Chapman 1996). Alternately, persistence (and possible expansion) of a patch may be juxtaposed against resistance from neighbouring patches to be overgrown (Worm and Chapman 1998), resulting in a dynamic equilibrium between the two opposing states. The outcome of these scenarios may lead to a stalemate in which the intermediate areas display characteristics of both stands, but neither is able to close the canopy and totally dominate.

This situation appears to be most evident between patches dominated by *Cystophora* and *Ecklonia*. While the clump level analysis (Table 3.8) showed that these two states never occurred as immediate neighbours in the current study, the habitat level analysis (Table 3.8) illustrated that they rarely occurred within close proximity. Thus, this observation may also relate to differential survivability in different habitats.

Sargassum on the other hand appeared to tolerate (or be tolerated by) the other two genera. A possible explanation for this lies in its seasonality of fronds, such that a large proportion of the plant's biomass is grown then shed annually (Kendrick and Walker 1994). The lack of this material at different times of the year would allow other canopy forming taxa to exploit the space. However, for this to be successful, *Sargassum* would need to possess the ability to re-establish itself leading up to the reproductive season.

3.8.3 Relationship between adults and juveniles

A comparison of adult canopy structure with underlying juvenile assemblages showed a remarkable degree of concordance for older individuals (> one year), but not so for the current season's recruits (Table 3.7). Indeed, there were a lot less new recruits counted than one-year-old individuals (Figure 3.8).

One likely explanation for this was that the survey was undertaken during the recruitment season and as such, many individuals would not have yet recruited or alternatively were too small to be noticed. A second explanation assumes that the results actually represent a substantial proportion of the year's recruitment and that survivorship of the new cohort had been incredibly poor. However given the number of one year old individuals recorded the following year (see Chapter 5), the first explanation is more likely to be correct.

It is also important to acknowledge that the age classes used in this study were determined from average growth rates based on available data (Appendix I). As a result, the classes are approximate and likely to be influenced by life history and local conditions. Thus different circumstances are likely to result in different growth rates and may potentially confound the classification. The obvious example being that growth rates tend to be faster amongst individuals in the open (Emmerson and Collings 1998) relative to those under a canopy where development may be retarded (Kirkman 1981). Notwithstanding, the juveniles used as a basis for comparison were those occurring under VLA stands. The open canopy nature of these assemblages would encourage relatively rapid growth of juveniles. As such, these rates of growth would be similar to those used in the studies that underpin the size classification.

Given the propensity for new recruits to establish within close proximity of the parent (Coon *et al.* 1972; Deysher and Norton 1981; Schiel and Foster 1986; Kendrick and Walker 1991), it is likely that a survey undertaken at the end of the recruitment season would identify a high level of association between recruit composition and canopy structure.

There are also a number of other strategies acting to inhibit the establishment of recruits from other taxa (creating resistance). In particular, the large fronds of *Ecklonia* act to reduce light levels by shading, and sweep the substrate, potentially dislodging smaller individuals. It is possible that *Ecklonia* recruits are less susceptible to these effects given that the species can increase photosynthetic efficiency to compensate for reduced light (Fairhead 2001), and propagules remain small in the presence of a canopy (Kirkman 1981). Other resistance strategies incorporate allelopathic interference, which has been identified in a number of taxa including *Sargassum* (Chen and Chou 1990).

Overall, these strategies may help explain the high degree of association between adults and juveniles of the older age classes (Table 3.7), and allow a number of inferences to be made. Firstly, it is likely that in recent history, canopy structures were similar (but see next section) and secondly because the majority of juveniles are of the same taxa as the canopy dominant, canopy structure is likely to remain similar at least in the near future. This feature demonstrates the ability of a patch to persist over a number of generations.

3.9 Summary and conclusions

The macroalgal communities of Southern Australia have already been shown to differ from their counterparts in other temperate regions due to the presence of a diverse array of subtidal canopy forming fucoids (Womersley 1990). Knowledge of the patterns and underlying processes within these systems remains fragmented, although a number of recent initiatives have begun to address this situation.

The macroalgal communities studied here are not assembled randomly but rather they appear to exist in patches that in turn are comprised of a number of discrete and finite states. Patches existed in high-density mono generic dominated states that were in turn bordered by lower density mixed assemblages (VLA). This structure appeared to be repeated in space with an average patch size of three quadrats (1.8 m). The regular repetition observed on these reefs highlights the importance of biological interactions in structuring these communities.

There was also a high degree of concordance between the adult canopy and underlying juvenile assemblage supporting the concept of stability in these systems. Indeed the majority of recruits under a closed canopy monoculture will be of the same type, giving a high probability that the patch will persist through time. Clumps were not observed in states representing a mixture of two or more genera at high density, implying that such states probably did not exist locally. As such, high-density mixed states are unlikely to provide a realistic mechanism for transition between different mono generic assemblages. It is more likely that state changes involve the clump passing through the VLA state. In terms of temporal dynamics, this concept will be explored further in later chapters.

In contrast to mono generic stands, low-density VLA assemblages comprise two or more different adult genera and similarly recruits. For this reason, future patch states become less certain. If held in check by the surrounding patches or subjected to frequent disturbance, they may remain in the VLA state. Alternatively, in the absence of these effects, VLA assemblages may tend towards one or other mono generic dominated state.

The observations made here have important implications on the way in which studies of macroalgal systems should be approached. Indeed, it could be argued from the above discussion that reef areas with similar measurable parameters could potentially support a number of different stable biotic configurations, and that each of these, in turn, may yield different outcomes following a disturbance event.

Knowledge of system states will be of fundamental importance in situations where an attempt is being made to compare two (or more) areas, for example in control – treatment style experiments. This understanding is relevant to the current study, underpinning the design of a program to assess the impact of sediments on a macroalgal community.

Chapter 4

Effect of elevated sediment deposition on algal recruitment

This chapter compares the structure of gulf algal assemblages from a series of control sites with those that were putatively impacted by a large sediment plume. The plume forms the basis of a natural experiment examining the impact of elevated sediments on reef health.

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4.1 Introduction and rationale

The process of sedimentation is important in the ecology of marine systems and is known to exert an influence on the composition, structure and dynamics of rocky coast assemblages (Airoldi 2003). While sedimentation is often a natural part of ecosystem functioning, anthropogenic activities have led to increasing rates variously through activities including catchment modification, coastal development and dredging. As such, increased sediment deposition poses a threat to marine ecosystem function (United Nations Environment Program 1995).

Sedimentation is simply the deposition of unconsolidated material (e.g. sand or silt) on the substrate. Rocky coastal habitats are very susceptible to the effects of increased sedimentation with numerous studies reporting dramatic changes in the nature of the benthos (Reviewed in Airoldi 2003).

In South Australia, coastal development and catchment modification have both led to increased levels of sedimentation. The situation has been exacerbated by sediment mobilisation following seagrass loss (Fotheringham 2002), primarily the result of pollution entering the gulf (Cugley 2002). The gulf is also subject to pulse sedimentation events due to dredging, both to maintain shipping channels and also from sand mining (Deans *in prep.*).

An understanding of the effects of elevated sediments and the ability to predict threshold levels in different environments is thus of fundamental importance to sustainable management (Airoldi 2003).

4.1.1 An opportunity to study the effects of sedimentation

A central goal of the current study was to determine and quantify the biological effects of a dispersed sediment plume resulting from offshore sand dredging for beach sand replenishment. More generally, the ability to detect ecological impacts of anthropogenic origin and discriminate between them and natural variability has become a central focus for ecologists working within the field of marine management (Osenberg and Schmitt 1996).

Unfortunately, such impacts rarely, if ever, occur in isolation, confounding the outcomes (Underwood 1994; Osenberg and Schmitt 1996; Thrush *et al.* 1996). Furthermore, timetables rarely incorporate sufficient lead times in order to establish suitable pre-impact monitoring, or alternatively the impact is not foreseen (Piltz 1996). Either way, impact assessments are often limited to post hoc comparisons between the affected site and one or more control sites.

Beach erosion on Adelaide's Metropolitan coastline

A combination of coastal development and seagrass loss has led to acceleration of the natural rate of erosion and substantial beach sand losses along the Adelaide metropolitan foreshore (Deans *in prep.*). Historically many beach protection strategies failed to take into account the complexity of coastal processes (Tucker 1985). This was exemplified in the words of the Coastal Management Branch…

> *"In the early years and persisting into this period, coastal engineering was coloured by the prevailing attitude in the western world that man should dominate and subdue the hostile environment to serve his purposes. In the case of coastal erosion, the perceived enemy was confronted head-on, mainly with concrete walls, some vertical and curved to better reflect the waves back to the sea. This was done with a confidence which managed to survive failure after failure."*
>
> (Coastal Management Branch 1984)

Offshore dredging for beach sand replenishment

The extent and significance of shoreline recession associated with littoral drift became apparent in the late 1960s, along with the realisation that engineering structures must be in sympathy with the environment. At this time focus shifted away from vertical seawalls and groynes in favour of softer dissipative solutions including beach sand replenishment (Coastal Management Branch 1984).

The newly formed Coast Protection Board instigated a beach sand replenishment program in the summer of 1973/74 "as the most harmless way" to neutralise wave energy and counter foreshore recession (Coastal Management Branch 1984). The program initially involved trucking of sand from depositional areas in the north back to areas of erosion in the south including Glenelg and Brighton.

A series of reports were commissioned during the 1980s that reviewed the effectiveness of the beach replenishment program and identified the need to locate other suitable sand sources in order to effectively maintain it (Tucker 1985; Department of Environment and Natural Resources 1997; Coastal Management Branch 1984). Initially sand was carted from sources including Torrens Island, and a dredge area south of the outer harbour breakwaters, leading to an increase in the total volume on Adelaide's beaches as well as increasing the beach buffer in the southern area.

Further demand for sand led to an investigation into offshore sand sources for exploitation through a dredging operation (Tucker 1985). As a result, biennial dredging off Pt Stanvac (Figure 2.2) was undertaken throughout the 1990s (Department of Environment and Natural Resources 1997; Deans *in prep.*) along with environmental monitoring carried out by the University of Adelaide (Cheshire and Kildea 1993, 1994; Cheshire *et al.* 1996a; Cheshire *et al.* 1999; March 1996; Miller 1996).

Typically, the biennial dredging operation removed approximately 150,000 cubic metres of sand over a ninety-day period, with timing dependent on the availability of dredge plants travelling through the area (Deans *in prep.*).

The assessment of the dredging operation found a significant short-term impact on local epibenthic communities, which appeared to recover within twelve months. However, a number of caveats were placed on these finding due to the large spatial variability noted in the area and because of the lack of information on the system prior to the first dredging in 1991 (Cheshire *et al.* 1996a).

Small areas of seagrass were also observed to have been destroyed during the first dredging (Cheshire and Kildea 1993), with later reports advising against any further activity in close proximity to other areas of seagrass habitat (Cheshire and Kildea 1994; Cheshire *et al.* 1996a).

Creation of a large sediment plume in 1997

In the period 1972 – 2003, the quantity of sand brought onto metropolitan beaches from external sources (including the Pt Stanvac dredging operation) was approximately 2.5 million cubic metres. Of this, about a quarter was collected during a single operation in 1997 (Deans *in prep.*).

Access to a larger dredging plant in November of 1997 presented the opportunity for a greater volume of sand to be collected during a campaign to provide a ‘sand reservoir’ for littoral drift. This led to the extraction of 600,000 cubic metres of sand over a thirty-day period and represented a tenfold increase in intensity (25,000 $m^3.day^{-1}$) over previous dredging in the area (2,500 $m^3.day^{-1}$; Cheshire *et al.* 1999). The event created a large sediment plume (Figure 4.1) covering a wide area including around Noarlunga and Horseshoe Reefs (R. Sandercock *pers. comm.*).

Figure 4.1 Aerial photo showing the large plume created by the dredge. Photo courtesy of R. Sandercock.

Public concern about the effect of the plume led to a follow up survey by Flinders University (Havenhand 1998), which confirmed increased levels of sediment on Noarlunga Reef (up to 10 mm) but noted no immediately visible impacts to the reef’s biota.

Although no initial impact was observed, a number of other studies (review in Airoldi 2003) have documented the impact of sediments on recruiting macroalgae. Given that the dominant canopy forming phaeophycean macroalgae were recruiting at this time, it was acknowledged that these assemblages may have been adversely affected (Cheshire *et al.* 1999).

4.1.2 Impacts of increased sediments

Deposition in rocky reef environments is not uniform but dependent on hydrodynamic conditions and the nature of the sediment. As an example, in high wave energy environments finer sediments are quickly resuspended and only persist where entrapment occurs (crevasses or through biotic accretion, Airoldi 2003).

Many marine organisms are known to bind sediment thereby stopping re-suspension. Within Gulf St Vincent seagrass, assemblages effectively bind unconsolidated sediment on soft bottoms, although recent degradation of these communities is allowing re-suspension, leading to further erosion (Fotheringham 2002). On reefs, turf algal assemblages are well known to accrete sediment (Airoldi and Virgilio 1998), while larger kelps act to displace it through a sweeping action (Kennelly 1989), but see Moore, (1972).

Sediment deposition affects reef biota through a combination of smothering, scour, and by changing the physical characteristics of the substrate (Airoldi 2003). Through these mechanisms, small scale fluctuations in sedimentation rates have been shown to influence macroalgal community structure (e.g. Airoldi and Cinelli 1997; Kennelly and Underwood 1993).

In a recent review of the effects of sediments on rocky reefs, Airoldi (2003) identified a number of common changes to community structure. Generally, organisms that rely upon sexual reproduction are more vulnerable than those using vegetative means, probably due to the lack of substrate stability and likelihood of smothering of new recruits. In contrast, organisms with sediment trapping morphologies, opportunistic species as well as those with physical adaptations to sediment tend to do well in sediment-affected environments (Airoldi 2003).

Areas impacted by elevated levels of sediment often lose the larger canopy forming taxa, and tend to have lower diversity, often dominated instead by turf and opportunistic foliose red algae or species with vegetative or migratory life histories (Airoldi 2003).

4.1.3 Objectives of this chapter – testing for an impact

Circumstances surrounding the 1997 dredging led to the formation of a sediment plume that extended across at least two of Adelaide's metropolitan reefs. This scenario although regrettable, provided an opportunity to study how a discrete disturbance can affect the biological community on these reefs.

Biological communities utilise a number of different techniques for maintaining viable populations over time and many of these were embodied into the properties of stability presented in Chapter 1. Central to these concepts was the notion that populations were able to prolong their dominance of a patch by minimising the impact of disturbance and at the same time colonise new areas through reproduction. Factors that influence recruitment success are thus likely to be important in defining the overall structure of a habitat.

Sampling to determine whether an event has influenced a given community is ideally undertaken using a 'Beyond BACI' style design (Underwood 1991; Underwood 1994). Such a scenario would involve multiple controls and multiple impact sampling sites to account for natural variation; with sampling repeated on a number of occasions both before and after the introduction of a treatment effect.

Given that the creation of the sediment plume that washed onto Noarlunga and Horseshoe Reefs was un-intentional (i.e. unplanned), it was not possible to undertake any pre-impact sampling of the reef communities. Acknowledging this limitation, an experimental design was constructed to evaluate whether or not the plume had affected the resident macroalgal community. The first part of this process (and the focus of this chapter) was to determine whether putatively impacted macroalgal communities differed from the surrounding ones.

The review of sediment impacts presented in the previous section identified newly recruiting individuals as highly susceptible to the effects of elevated sediment deposition. As such, differences in assemblage structure between the control and impact sites would likely be evident in the juvenile cohort.

The lack of available 'before impact' data forces an assumption to be made about the prior state of the sediment affected reefs. Indeed, if these reefs were already different, then testing for a difference and then concluding that the difference was due to sedimentation would obviously be erroneous. Notwithstanding, sampling at a number of sites unaffected by the plume would allow for an indication of biotic variation, and whether impacted reefs fell within 'natural' limits. Temporal comparisons (discussed in Chapter 5) should also help ascertain if the above assumption is valid.

4.2 Materials and methods

4.2.1 Experimental design

A multiple control, multiple impact (referred to as 'treatment' for purposes of analysis) survey design was implemented. Sampling was undertaken at ten sites (the four control sites identified in Chapter 2 and an additional six putatively impacted sites located on Noarlunga and Horseshoe reefs; Figure 4.2, Table 4.1). At each site, sampling of adult and juvenile canopy macroalgae utilised the same method as outlined in section 3.2 and summarised below.

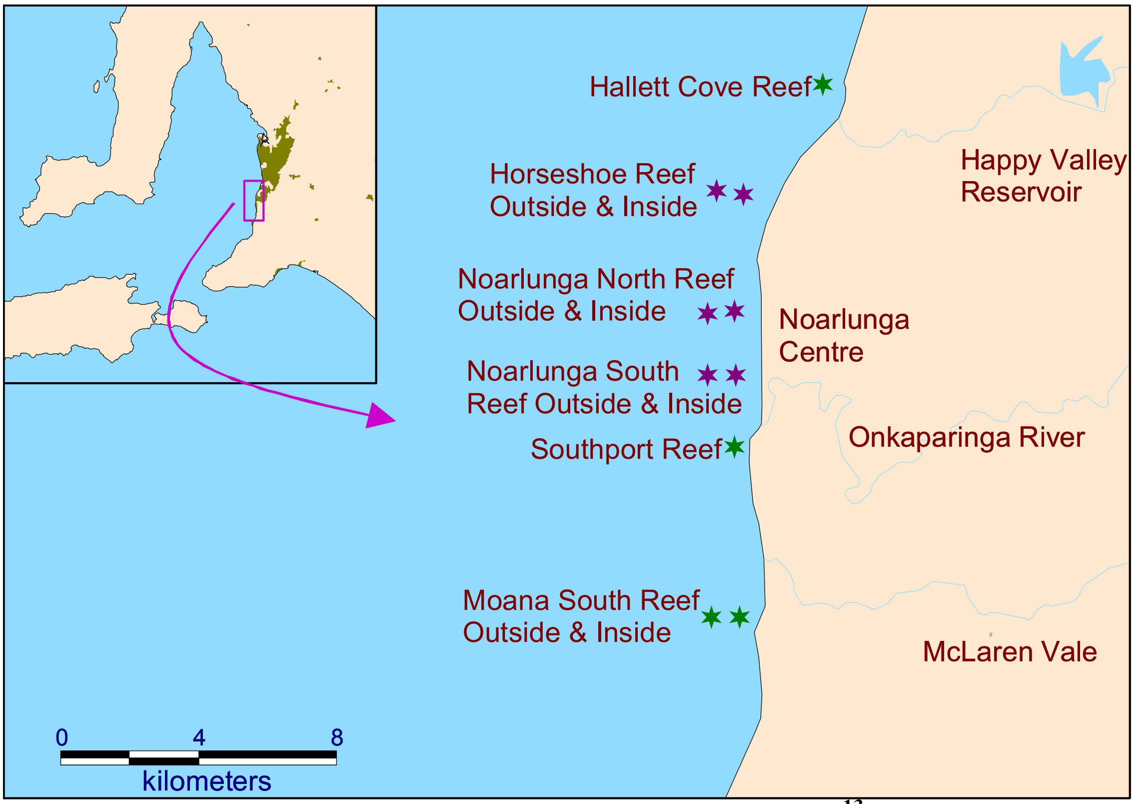

Figure 4.2 Map of the study area showing the location of reefs[13]. Control locations (from the previous chapter) are in green and putatively impacted locations purple.

Sampling of the additional reefs occurred at the same time as the control reefs described in the previous chapter (August 1998). At each site, contiguous quadrats were sampled along three transects. In each case, sampling continued until data had been obtained for twenty

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[13] This figure incorporates data that is © Commonwealth of Australia (Geoscience Australia 2003).

quadrats containing canopy macroalgae. For each quadrat (0.6 m^2), the number of adult canopy individuals was recorded for each genus along with length measurements for all juveniles (<30cm).

Table 4.1 Description of the treatment reefs used in the study.
Codes are those used to identify the sites in subsequent analysis. Locations describe the approximate midpoints of the reefs as latitudes and longitudes using the GDA94 datum.

Reef	Code	Location	Description
Horseshoe Inside	HSI	138.4538 -35.1042	Steep rocky slope with patchy mixed fucoid assemblages. Some areas have large amounts of coralline algae.
Horseshoe Outside	HSO	138.4629 -35.1051	Gentle rock slopes and platforms with patchy mixed fucoid communities.
Noarlunga North Inside	NNI	138.4600 -35.1357	Steep boulder slopes and platforms. Light and patchy algal cover. Generally, *Cystophora* dominated with some patches of *Sargassum* and *Ecklonia*. High cover of mussels.
Noarlunga North Outside	NNO	138.4510 -35.1366	Steep reef slope with many large boulders. High wave exposure. Heavily *Ecklonia* dominated, with dense tall canopy.
Noarlunga South Inside	NSI	138.4606 -35.1524	Near vertical slope with boulders at bottom. Slightly shallower than other sites. *Cystophora* dominated with some patches of *Sargassum* and *Ecklonia*. Patches dominated by mussels present.
Noarlunga South Outside	NSO	138.4510 -35.1524	Steep slope with large platforms. Mixed fucoid and Ecklonia patches. High wave exposure.

It is worth noting that the use of four control and six impact sites invariably leads to an unbalanced design. Obviously, site choice was constrained by the availability of reef habitat within suitable proximity to the site of the impact.

The initial intention was to pool data at the reef level (i.e. Noarlunga North, Noarlunga South, Horseshoe, Hallett Cove, Southport, and Moana South) to produce a balanced design with three control and three impacted locations. However, differences in reef topography and exposure increased the overall variability of the habitat. As such, a decision was made not to pool the data, as this would dampen many of the interesting emergent properties displayed by this environment.

Given that a pragmatic decision was made to record taxonomic information to the genus level, a follow up survey was undertaken in November 1998 to collect and identify canopy-forming taxa to the species level.

4.2.2 Comparison of adult structure

Community composition at each site was assessed in terms of overall adult numbers as well as the proportional representation of each of the four canopy assemblage types (as previously defined in section 3.4.1). Relationships between the various sites were then investigated with a canonical correlation analysis, undertaken using the JMP statistical package (SAS 1995).

Control versus treatment effects were then formally assessed using a non-parametric multivariate analysis of variance (NPMANOVA, Anderson 2000). Given the observed variability apparent between all sites, a nested design was opted for with sites nested within treatment. Unfortunately, the NPMANOVA analysis requires a balanced design with equal replication. Hence, it was necessary to omit two impact sites from the analysis. However, the analysis was then repeated with the omission of different sites to determine the overall robustness of the result, with Bonferroni adjustments made where necessary. Following the NPMANOVA, *a posteriori* analyses were conducted to quantify the differences between all pairs of sites.

4.2.3 Comparison of juvenile structure

Surveys were undertaken in August 1998, nine months after the initial sediment impact. Hence, by the time of the survey, the cohort most likely to have been affected by the plume would be approaching one year of age. Additionally, older juveniles provide a record of survivorship over two years, and may or may not have been directly impacted by the plume. Finally, increased sediment deposition was observed on several of the impacted reefs (during the 1998 survey), highlighting the possibility of continued interference with the current season's recruits. To aid investigation of these various phenomena, juveniles were separated into the three age cohorts (i.e. new recruits, one-year-old, and two-years-old), as described in section 3.2.2.

In Chapter 2, a clear relationship was established between the type of adult canopy and the underlying juvenile composition. Failure to account for this in analysis would likely confound any meaningful results. To address this, comparisons between juvenile assemblages were only undertaken using quadrats with similar adult canopy structure. Of the four assemblage types, only the VLA group was found sufficiently often to allow proper analysis (see 4.3.1).

Investigation of differences between control and impact sites was undertaken using canonical correlation, and was repeated for juveniles of each age cohort.

The subset of data used for juvenile comparisons involved uneven replication of quadrats within each site, due to the inclusion of only those assemblages under a VLA canopy. Furthermore, the unbalanced design meant that NPMANOVA was no longer a suitable analysis tool. As a result, differences between control and impacted sites were tested using a Multi Response Permutation Procedure (MRPP, Biondini *et al.* 1985). With a natural weighting n/sum(n) applied to groups to correct for uneven membership.

4.3 Results

4.3.1 Comparison of adults

The November 1998 survey identified five separate species each of *Cystophora* and *Sargassum* along with the kelp *Ecklonia radiata* (Table 4.2).

Table 4.2 Canopy forming taxa found commonly in the study area.

	Control sites				**Impact / treatment sites**					
Species	**HAL**	**SOU**	**MSI**	**MSO**	**HSI**	**HSO**	**NNI**	**NNO**	**NSI**	**NSO**
C. gracilis			+							
C. monilifera	+	+	+	+						
C. moniliformis	+	+	+				+		+	+
C. retorta	+		+	+	+	+	+		+	+
C. subfarcinata	+	+	+	+	+	+	+		+	+
E. radiata	+	+	+	+	+	+	+	+	+	+
S. decipiens		+		+						
S. fallax	+	+	+	+	+	+	+	+	+	+
S. linearifolium	+	+	+	+						+
S. paradoxum										+
S .tristichum	+									

On average, a density of twenty adult individuals m^{-2} were recorded during the study, although site averages ranged from fifteen (n m^{-2}, Hallett Cove – HAL, Moana South Outside – MSO) up to twenty-seven (n m^{-2}, Noarlunga North Outside – NNO, Figure 4.3). While assemblage compositions varied between sites, there were no differences between the control and putatively impacted sites. Notwithstanding, a number of the impact sites appeared to contain high numbers of *Cystophora* spp.

It was only at the impact sites that *Cystophora* existed in sufficient density to dominate patches of substrate, while *Sargassum* assemblages tended to be more common at control sites. With the exception of Southport (SOU) and NNO, sites were mainly comprised of the VLA assemblages (Figure 4.4).

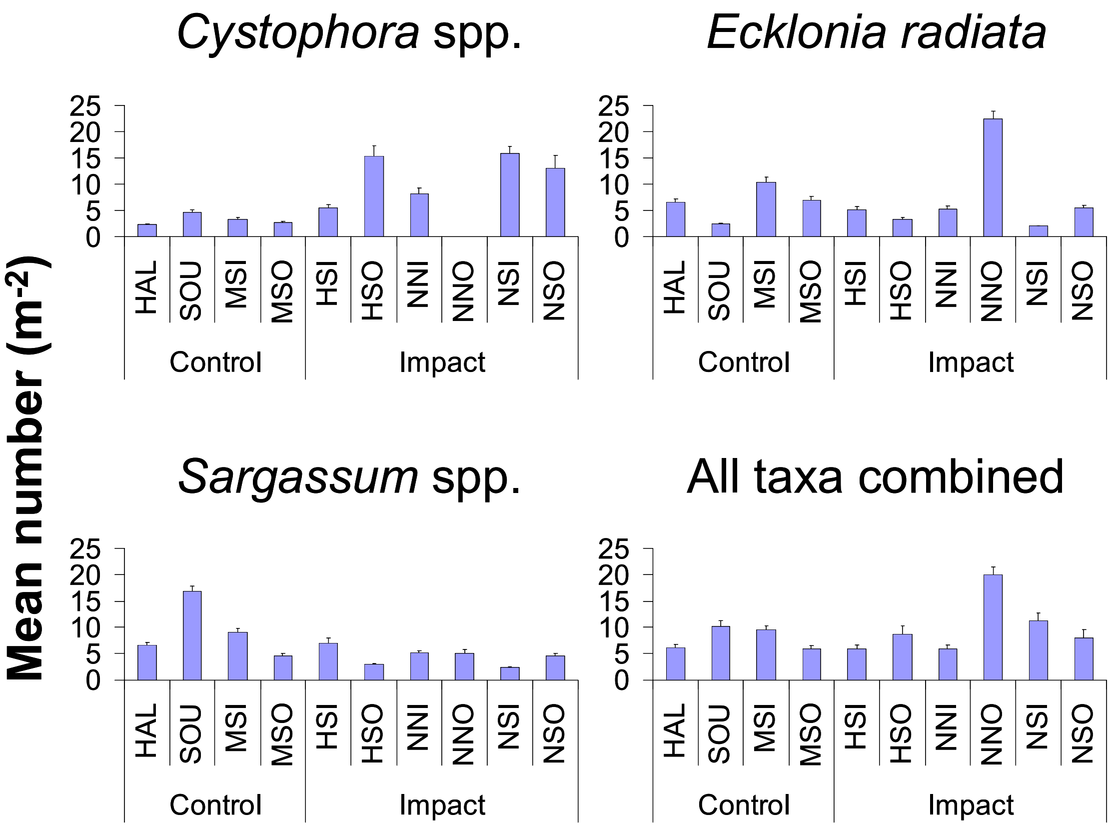

Figure 4.3 Average number of adult individuals (n m^{-2}) at each site. The four charts represent numbers for each genus and for all taxa combined. Error bars indicate standard error of the mean.

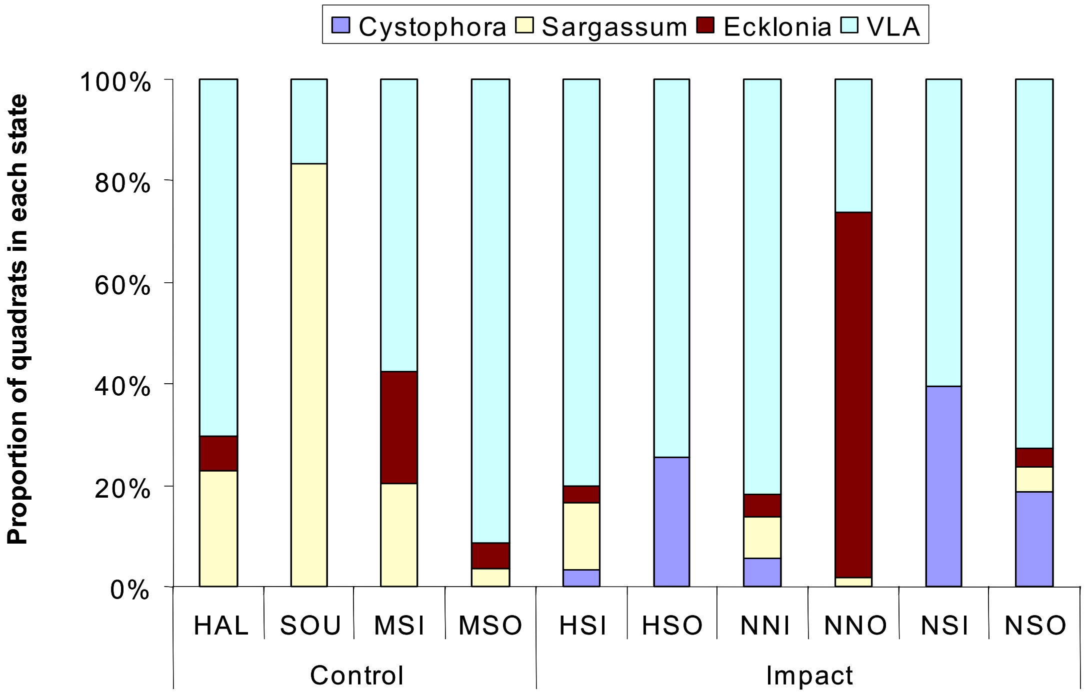

Figure 4.4 Composition of each site in terms of the four assemblage states. Based on the number of quadrats assigned to each state.

A difference in composition between sites was also observed in the canonical correlation analysis (Figure 4.5, Table 4.3). The analysis highlighted variability in structure between sites as well as a gradient from sites dominated by *Ecklonia* to those with high numbers of *Cystophora*. The two flat reefs (HAL, SOU) were also differentiated (Figure 4.5).

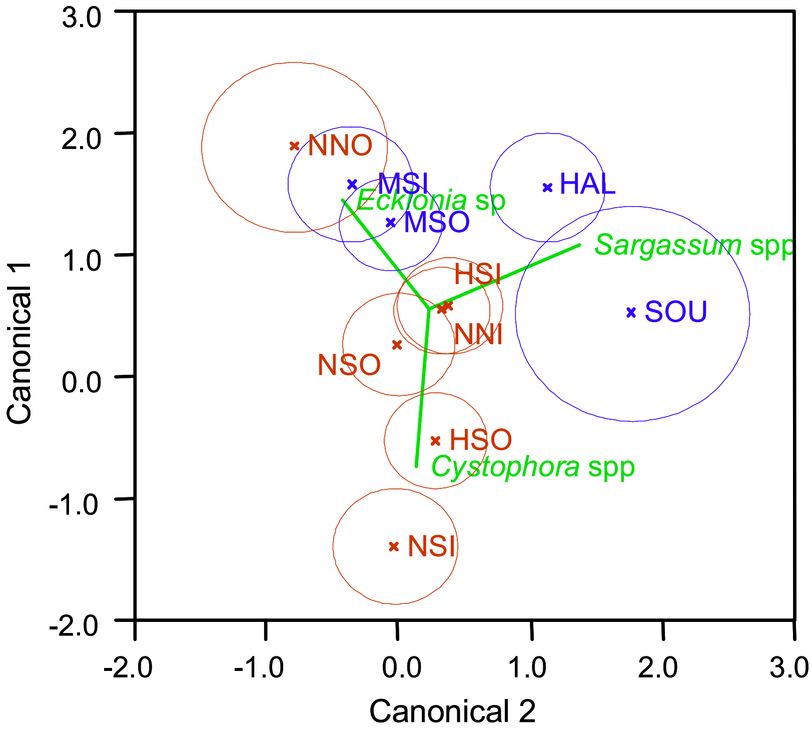

Figure 4.5 Canonical correlation based on adult canopy composition. Control sites are in blue and putatively impacted sites red. Ellipses represent the 95% confidence limits[14].

Table 4.3 Significance tests of canonical correlation in Figure 4.5

Test	**Value**	**Approx. *F***	**DF Num**	**DF Den**	**Prob>*F***
Wilks' Lambda	0.4059027	14.7189	27	1098.8	<.0001
Pillai's Trace	0.7197721	13.2576	27	1134	<.0001
Hotelling-Lawley	1.1671365	16.1958	27	1124	<.0001
Roy's Max Root	0.8528736	35.8207	9	378	<.0001

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[14] Both nMDS plots and canonical correlations were undertaken in these and subsequent analyses, with both methods yielding similar results.

Table 4.4 NPMANOVA testing for differences between sites.
(A) Table shows the results of a two-factor design with sites nested within treatment. In order to balance the design the two Horseshoe Reef sites were omitted, however different combination including these sites yielded similar results. (B) *A posteriori* tests undertaken between all sites.

Part A

Source	df	SS	MS	*F*	*P*	MS Denom
Control vs Impact	1	45503.48	45503.48	1.0355	0.4324	Site (C vs I)
Site (C vs I)	6	263655.1	43942.51	24.801	0.0002	Residual
Residual	312	552803.9	1771.807			
Total	319	861962.4				

Part B

Comparison		t	*P*	Comparison		t	*P*
HAL	SOU	5.3243	**0.0002**	MSI	NSO	3.4016	**0.0002**
HAL	MSI	3.4204	**0.0002**	MSO	HSI	2.799	**0.0006**
HAL	MSO	3.4639	**0.0002**	MSO	HSO	5.0756	**0.0002**
HAL	HSI	2.1728	**0.0012**	MSO	NNI	2.6608	**0.0004**
HAL	HSO	4.672	**0.0002**	MSO	NNO	4.9887	**0.0002**
HAL	NNI	1.7613	**0.0290**	MSO	NSI	6.8239	**0.0002**
HAL	NNO	7.2428	**0.0002**	MSO	NSO	3.391	**0.0002**
HAL	NSI	6.8078	**0.0002**	HSI	HSO	2.5254	**0.0002**
HAL	NSO	3.4767	**0.0002**	HSI	NNI	-0.3408	0.9990
SOU	MSI	7.301	**0.0002**	HSI	NNO	5.7942	**0.0002**
SOU	MSO	8.1863	**0.0002**	HSI	NSI	4.1765	**0.0002**
SOU	HSI	5.0264	**0.0002**	HSI	NSO	1.7535	**0.0172**
SOU	HSO	5.9228	**0.0002**	HSO	NNI	2.7747	**0.0004**
SOU	NNI	4.8891	**0.0002**	HSO	NNO	7.6564	**0.0002**
SOU	NNO	13.8634	**0.0002**	HSO	NSI	1.5752	0.0520
SOU	NSI	7.8065	**0.0002**	HSO	NSO	1.5104	0.0602
SOU	NSO	5.2379	**0.0002**	NNI	NNO	5.7752	**0.0002**
MSI	MSO	1.4729	0.1026	NNI	NSI	4.5031	**0.0002**
MSI	HSI	3.166	**0.0002**	NNI	NSO	1.9732	**0.0092**
MSI	HSO	5.1173	**0.0002**	NNO	NSI	9.5381	**0.0002**
MSI	NNI	3.063	**0.0002**	NNO	NSO	5.6851	**0.0002**
MSI	NNO	3.3453	**0.0002**	NSI	NSO	2.6939	**0.0004**
MSI	NSI	6.5945	**0.0002**				

While the difference in composition between control and treatment sites was notable, community structure at all sites was highly variable (Figure 4.5). Indeed differences between individual sites accounted for most of the observed variation (NPMANOVA $F_{6,312}$=24.801, P=0.0002). Considering the between sites variation using a nested design, insufficient additional variance was identified to reject the null model ($F_{1,6}$=1.0355, P=0.4324; Table 4.4), implying that no difference existed between the control and treatment sites. Nevertheless, pairwise comparisons undertaken between all sites were significant (P<0.05) for 41 out of 45 combinations (Table 4.4).

4.3.2 Juveniles

Two-year-old cohort

Analysis using the two-year-old cohort showed little distinction between control and treatment sites (Table 4.5; Figure 4.6). Overall less separation was observed between sites than for the adult assemblage, possibly due to the reduced numbers of individuals found in this cohort.

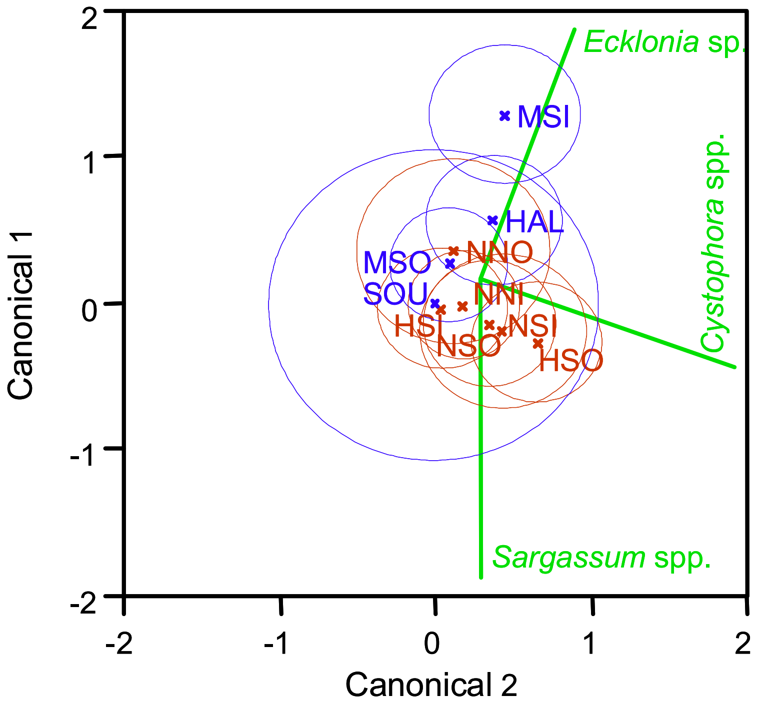

Figure 4.6 Canonical correlation using two-year cohort under a VLA canopy. Control sites are in blue and putatively impacted sites red. Ellipses represent the 95% confidence limits. NB: there were no two-year-old individuals identified from the Southport site.

Table 4.5 Significance tests of canonical correlation in Figure 4.6

Test	Value	Approx. F	DF Num	DF Den	Prob>F
Wilks' Lambda	0.7892983	3.2973	27	1054.9	<.0001
Pillai's Trace	0.2208893	3.2058	27	1089	<.0001
Hotelling-Lawley	0.2542012	3.3862	27	1079	<.0001
Roy's Max Root	0.1934019	7.8005	9	363	<.0001

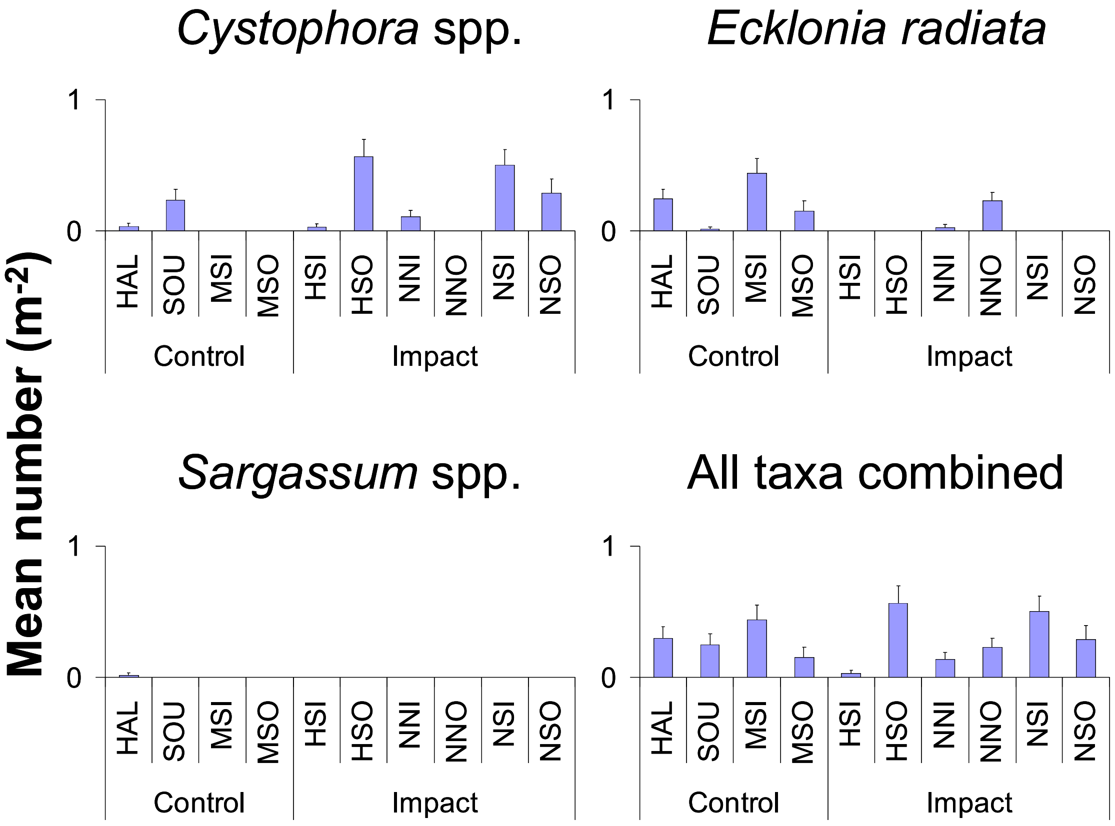

Figure 4.7 Average number of two-year-old individuals (n m^{-2}).
The four charts represent numbers for each genus observed under a VLA canopy, and for all taxa combined. Error bars indicate standard error of the mean.

Density of individuals in this cohort averaged less than one (n m^{-2}) indicating that individuals in this size class were comparatively rare. Nevertheless, the pattern formed was otherwise consistent with adult frequencies in terms of relative proportions by species (Figure 4.7 c.f. Figure 4.3).

Acknowledging the rarity of taxa in this size class, *Cystophora* juveniles appeared more common at certain treatment sites while *Ecklonia* favoured the control sites and NNO (Figure 4.7). *Sargassum* juveniles were rarely found in this age/size class due to seasonal shedding of laterals, with only a handful of individuals recorded at Hallett Cove and none elsewhere. When numbers of each taxon were combined, there was no significant difference or obvious trend between the control and treatment sites (Figure 4.7).

One-year-old cohort

Distinct separations were observed between control and treatment sites on the canonical plot (Figure 4.8; Table 4.6), and confirmed statistically (MRPP, *P*=0.0001). Significant variation was observed in terms of assemblage structure at the control sites and tended to mirror that of the adult assemblage. In contrast, treatment sites showed little variation in structure and clustered together.

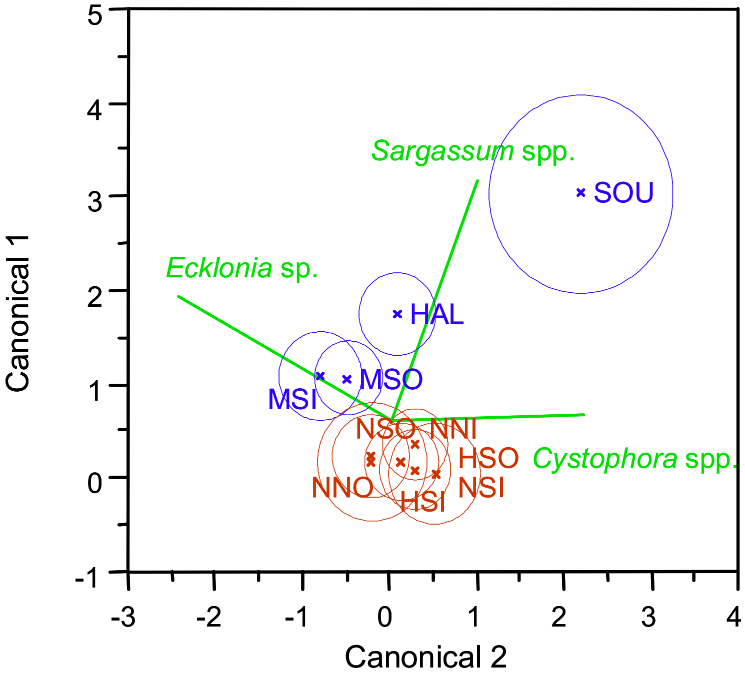

Figure 4.8 Canonical correlation using one-year cohort under a VLA canopy. Control sites are in blue and treatment sites red. Ellipses represent the 95% confidence limits.

Table 4.6 Significance tests of canonical correlation in Figure 4.8

Test	Value	Approx. F	DF Num	DF Den	Prob>F
Wilks' Lambda	0.5263921	9.6013	27	1054.9	<.0001
Pillai's Trace	0.5608664	9.2744	27	1089	<.0001
Hotelling-Lawley	0.7412837	9.8746	27	1079	<.0001
Roy's Max Root	0.4285721	17.2857	9	363	<.0001

Juvenile density of *Cystophora* fluctuated throughout the study area, although recruits were present at most sites. In contrast, *Ecklonia* and *Sargassum* recruits were more common at the control sites (Figure 4.9). Overall, recruitment was more successful at the control sites.

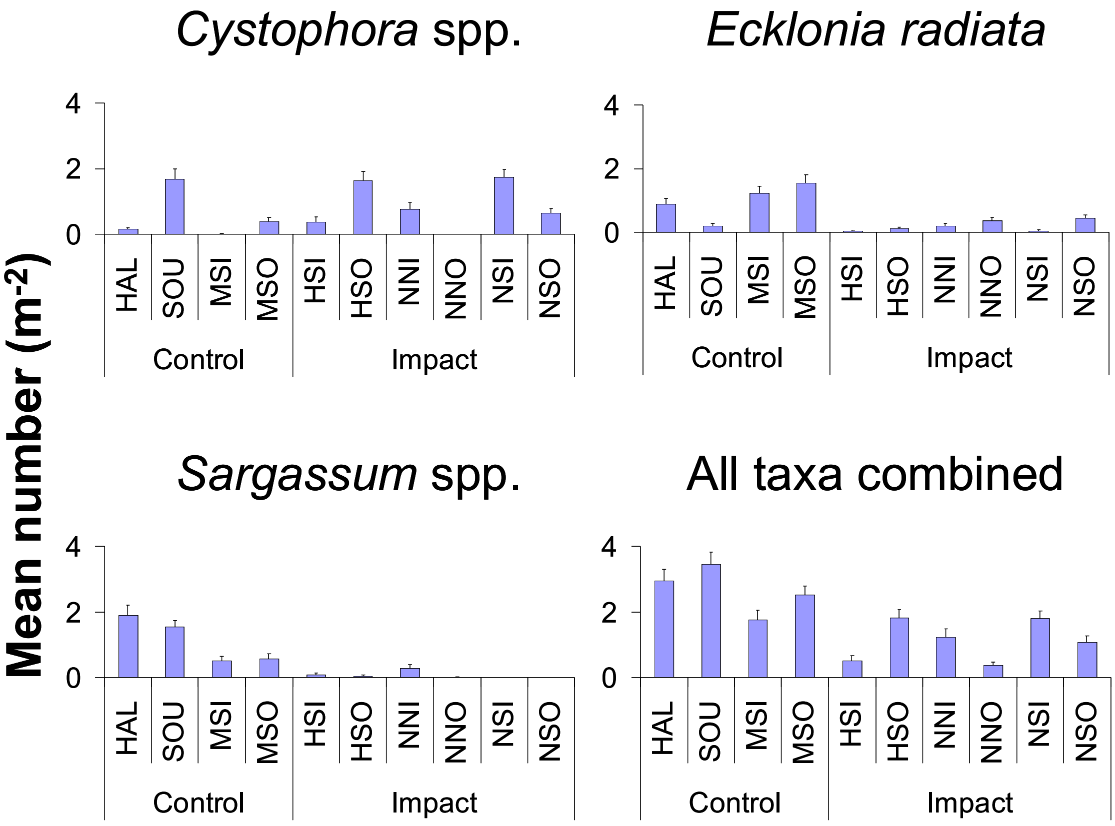

Figure 4.9 Average number of one-year-old individuals (n m^{-2}).
The four charts represent numbers for each genus observed under a VLA canopy and total numbers of recruits. Error bars indicate standard error of the mean.

Current season's recruits

The current season's recruits showed an obvious separation of the two flat control reefs (Hallett Cove – HAL and Southport – SOU) from the remainder (Figure 4.10; Table 4.7), leading to the significant MRPP result (*P*=0.0001) for control versus impact. However, the other two control sites (Moana South Inside and Outside, MSI and MSO) appeared more similar to many of the impact sites than to the flat reefs.

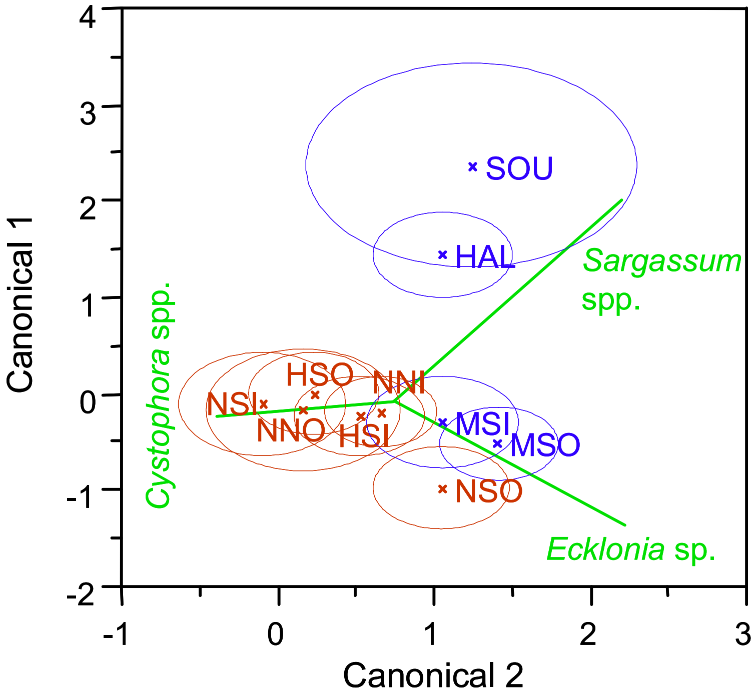

Figure 4.10 Canonical correlation using new recruits under a VLA canopy. Control sites are in blue and putatively impacted sites red. Ellipses represent the 95% confidence limits.

Table 4.7 Significance tests underpinning canonical correlation in Figure 4.10

Test	Value	Approx. F	DF Num	DF Den	Prob>F
Wilks' Lambda	0.5121529	10.0605	27	1054.9	<.0001
Pillai's Trace	0.5776758	9.6187	27	1089	<.0001
Hotelling-Lawley	0.7851354	10.4588	27	1079	<.0001
Roy's Max Root	0.4964059	20.0217	9	363	<.0001

Some *Cystophora* recruitment was recorded at most sites but at a lower density (approx 0.2 n m^{-2}) to that of the other two genera. Comparatively high levels of *Sargassum* (average of

2 n m^{-2}) were recorded on the two flat reefs while the other control sites had significant *Ecklonia* recruitment. Overall numbers of recruits were higher on the control reefs, with some treatment reefs (NNO and NSI) having virtually none (Figure 4.11). Total recruit density was less for this cohort than for the one-year group.

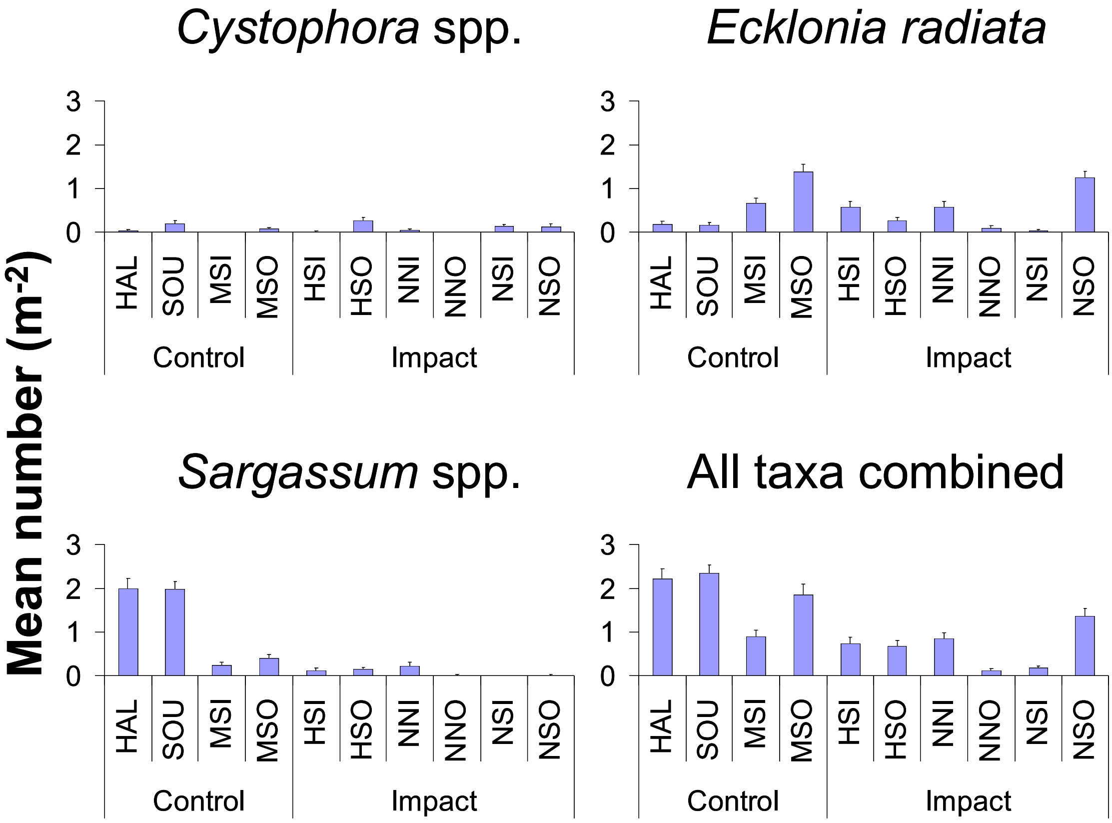

Figure 4.11 Average number of current season recruits (n m^{-2}).
The four charts represent numbers for each genus observed under a VLA canopy and for all taxa combined. Error bars indicate standard error of the mean.

4.4 Discussion

In order to undertake this natural experiment into the impact of the sediment plume, a number of pragmatic decisions had to be made and central to this was site choice. Reefs along Adelaide's metropolitan coastline had differing physical and biotic structure and were found to be in various conditions of health (Cheshire *et al.* 1998a; Cheshire and Westphalen 2000). Environmental heterogeneity limited the chance of replicate reefs being similar in nature (apart from the treatment affect), and thus must be considered in both the analysis and interpretation.

The unplanned nature of the impact meant that treatment sites were dictated by the location of the sediment plume and inevitably clustered together rather than being scattered across the study area. Such a design is far from perfect, and it is possible that community composition on these reefs may be different, due to localised environmental conditions unrelated to the sedimentation event. Furthermore, the pre-impact state of these reefs cannot be easily determined because of the lack of quantifiable data prior to the plume.

It is also important to consider the life history strategies of the dominant canopy forming taxa. Most large perennial taxa are generally considered to be late successional (Littler and Littler 1980), being iteroparous, having slow growth rates, and being generally characteristic of habitats with low levels of disturbance (Clayton 1990; Littler and Littler 1980).

During certain periods, excess carbon assimilation is stored by *Ecklonia radiata* and later used for rapid development during the winter growing season (Fairhead 2001). At this time, reproductive sori also develop on existing tissue resulting in minimal reproductive expenditure (Womersley 1987). The reproductive potential of the species is stored both as gametophytes (after Cheshire and Hallam 1989a; Clayton 1990) and as partially dormant juveniles under the canopy (Kirkman 1981).

While fucoids generally conform to the 'late successional' model (Littler and Littler 1980), local studies have shown that many species of *Cystophora* are pseudo-semelparous, shedding large amounts (up to ninety percent biomass) of spent reproductive material each season (Hotchkiss 2000). This phenomenon has also been reported for several species of subtidal *Sargassum* in Western Australia (Kendrick and Walker 1991, 1994) and *Cystoseira* in the United States (Schiel 1985). The allocation of such large amounts of biomass into reproductive structures is a strategy more commonly seen in opportunistic species (Littler and Littler 1980; Padilla and Allen 2000). The shedding of reproductive material following the production of large numbers of recruits results in a thinning of the canopy and thus provides sub canopy individuals with better opportunities for growth (Hotchkiss 2000).

4.4.1 Comparisons based on the adult stand

Biotic composition on reefs within the study area demonstrated large amounts of heterogeneity, consistent with work further south in the Gulf (see Collings 1996; Collings and Cheshire 1998). Reef topography appeared to be important, separating the two flat reefs (HAL, SOU) from the rest. This was, however, not simply an issue of wave exposure given sites with different energies often had similar compositions and *vice versa* (Figure 4.5). Any effect of a longshore gradient was also not readily apparent in the data summaries (Figure 4.5).

There did appear to be a degree of difference between the control and treatment sites, with most of the latter having patches dominated by *Cystophora* (Figure 4.4). However, given the amount of variability observed between all sites (Table 4.4), this may not be connected to the sediment plume. Furthermore, the site at NNO was largely dominated by *Ecklonia* and hence was more similar to the control sites (Figure 4.5).

Members of the genus *Cystophora* take about two years to reach adult size (see 3.2.2) and therefore the adult assemblage surveyed in 1998 was unlikely to have resulted from the plume. Furthermore, overall numbers of individuals on treatment reefs were not significantly different to those on control reefs (Figure 4.3). As such, it does not appear that the observable differences are attributable to the sediment plume, but more likely represent natural variability or possibly the presence of some other (possibly chronic) perturbation. The existence of such factors will be elaborated in Chapter 5.

Given the high degree of correlation between the community composition of the canopy and the underlying juvenile assemblage (3.8.3), it is important to consider the adult stand in recruitment studies. Heterogeneity in reef community composition means that subsequent analyses should only be undertaken on patches with similar canopy composition. In the current study, only VLA assemblages occurred in sufficient abundance to allow for suitably replicated inter-reef comparisons (Figure 4.4). These VLA assemblages were characterised as being made up of more than one canopy-forming genus, with a low overall density.

4.4.2 Comparisons based on juveniles assemblages

Recruitment must be sufficient to replace individuals that are lost in order for a macroalgal stand to persist through time. Numbers of juveniles in a patch represent a combination of the initial and post recruitment success of each taxon. This success is affected by many factors, including the availability of resources (e.g. light and suitable substrate, Cheshire *et al.* 1996b; Renaud *et al.* 1996), and a resilience to the physical environment (e.g. pollutants and physical disturbances, Bellgrove *et al.* 1997; Turner and Cheshire 2003). Furthermore, individuals need an ability to resist detrimental biotic interactions including herbivory and competition (Littler *et al.* 1983; Hackney *et al.* 1989; Chapman 1985). As an example, levels of recruitment will often be higher in open areas (following a discrete disturbance), than under an established canopy (Emmerson and Collings 1998). However if the disturbance is ongoing then the canopy may actually act as protection (Littler *et al.* 1983; Evans *et al.* 1993).

The type of canopy is also important in determining which species can successfully recruit under it. In similar communities to those of the current study, fucoids were shown to allow a greater diversity of taxa beneath their canopy than *Ecklonia* (Turner and Cheshire 2003). A similar phenomenon was observed at NNO where approximately 70% of the reef was dominated by *Ecklonia* (Figure 4.4), with the rest of the reef being VLA (mainly a mix of *Ecklonia* and *Sargassum* at lower density). The presence of the closed canopy over much of the reef resulted in small amounts of *Ecklonia* recruitment and little else. In contrast, approximately 80% of SOU comprised a *Sargassum* monoculture, but due to the seasonality of biomass, significant numbers of both *Sargassum* and *Cystophora* were able to recruit at the site.

In Chapter 3, it was postulated that VLA patches represented transitional states with mixed taxa in low abundance. The surrounding canopies will no doubt influence some of these, while many are likely to exist because of a recent disturbance (e.g. storm damage). In the latter case, recruitment may be encouraged because of the existence of free substrate and less competition with adult individuals (Emmerson and Collings 1998). The presence of several parent genera in the immediate vicinity will, however, increase the likelihood of recruitment by multiple different taxa.

The current study identified three cohorts of juveniles based on an age / size classification (see 3.2.2). By undertaking a survey near the start of the recruitment season, new recruits (<30mm) could be easily differentiated from the larger one year old individuals. Similarly, even larger specimens (>200mm) were estimated to be about two years of age.

At the time of the sediment plume (November 1997), the oldest of the three cohorts (two years of age at the time of sampling) would have been approximately one year old, with individuals probably ranging in size from 50-150mm. Inter-site comparisons showed that while reef specific differences existed (Figure 4.7), the resultant assemblage was similar to that expected, based on the composition of the canopy.

Elevated levels of sediment have been reported to affect macroalgal communities through actions such as smothering, scour and substrate modification, meaning that new recruits are especially vulnerable (Airoldi 2003). The lack of obvious difference between the control and treatment sites (Figure 4.6; Figure 4.7) is therefore not surprising as most of the individuals in the oldest juvenile cohort would have been large enough to resist many of the problems associated with sedimentation. It is important to note that this cohort recruited in the season prior to the sediment plume (1996). The lack of a significant difference in overall numbers means that similar levels of recruitment and subsequent survivorship occurred at control and treatment sites (Figure 4.7).

In contrast, there was a distinct difference between the control and treatment sites in terms of the middle cohort (which recruited around the time of the plume and was one year old at the time of the survey; Figure 4.8). Due to their small size, these juveniles would have easily been smothered, while many of those recruiting late in the season would have settled onto unconsolidated substrate and been dislodged easily. As a result, overall recruitment success appeared lower at the sites impacted by the plume (Figure 4.9).

At the control sites, the structure of the one-year-old juvenile stand mimicked that of the adult canopy (Figure 4.5; Figure 4.8) while the treatment sites lacked most of this definition. This result appears to be related to the continued survival of *Cystophora* recruits at some treatment sites while recruitment of *Ecklonia* and *Sargassum* largely failed (Figure 4.9).

The difference in overall success was also evident from analyses based on the newly recruited cohort (Figure 4.11). *Cystophora* numbers at each site were similar in proportion to that reported for the one-year cohort. At treatment sites, a higher level of recruit survivorship was noted for either *Ecklonia* or *Cystophora* but not both. Once again, *Sargassum* was common on the two flat reefs but not so elsewhere (Figure 4.11).

In terms of newly recruiting taxa, inter-site variation was most prominent at the control sites, and correlated well with that of the adult stand (Figure 4.10). At the treatment sites, more variation was observed in this cohort than in the one-year-olds. Nevertheless the dispersion was mainly along a gradient from low to high *Cystophora* abundance. The exception to this was NSO, which showed significant levels of *Ecklonia* recruitment.

The fact that numbers of new recruits were less than for the one-year cohort is most likely because the survey was undertaken during the reproductive season, hence many individuals either would not yet have recruited, or alternatively would be too small to be seen.

4.4.3 Impact of the dispersed sediment plume on canopy forming macroalgae

Dredging for beach sand replenishment created a plume that was observed to extend over Noarlunga and Horseshoe Reefs in November 1997. This event led to elevated levels of sediment on Noarlunga Reef shortly thereafter (Havenhand 1998); the condition of Horseshoe Reef at that time is unknown. At the time of this survey (August 1998), significant amounts of fine sediment were still visible on parts of the reefs, mainly on the inside of Noarlunga and over most of Horseshoe Reef.

All reefs in the study area were dominated by canopy forming macroalgae, although actual community composition was variable. As a result, there appeared to be a degree of difference between reefs acting as controls and those impacted by the sediment plume (Figure 4.5). Given the amount of heterogeneity both within and between sites (Table 4.4), these differences were not statistically significant but still need to be accounted for in any subsequent interpretation of an impact.

It is unlikely that differences in structure of the adult assemblages between the control and treatment sites resulted from the plume for the following reasons:

- No evidence of scour or tissue necrosis was observed in canopy taxa following the plume (Havenhand 1998).

- Smothering is unlikely as any material settling on the fronds of such large organisms would be quickly swept off by their constant movement in the water current (Kennelly 1989).

- Insufficient time had passed between the plume and this survey to allow smaller recruits (which were more likely to have been affected) to grow sufficiently large and thus to become part of the adult stand (see 3.2.2).

In contrast, juveniles of these species are quite susceptible to the impacts of sediment deposition (Airoldi 2003). However, because differences were observed in the adult stand unrelated to the sediment plume, and given the close link between canopy and the underlying juvenile assemblage (3.8.3), differences between control and treatment sites in the latter cannot simply be attributed to a specific event or impact. This is especially true due to the lack of quantitative information on the composition of the juvenile stand at these sites prior to the sediment plume.

Analyses using the older cohort of juveniles (representing the cohort that recruited in the year prior to the plume) demonstrated that the structure of the juvenile assemblage was closely related to the structure of the overlying canopy and that overall numbers of recruits were similar at control and treatment sites. This means that while differences did occur, these were predictable and indeed expected based on what was known about the processes operating in the stand (Chapter 2). More importantly, this shows that although differences in composition existed between sites, conditions at this time (1996) allowed for successful recruitment at both control and (pre) treatment localities. This observation helps to rule out the possibility of chronic impacts affecting treatment sites irrespective of the influence of the plume.

Considering the heterogeneity in the structure of canopy assemblages, control sites also demonstrated the expected pattern of recruitment for the one-year cohort (which recruited at the time of the plume). In contrast, treatment sites had reduced levels of recruitment, with almost total failure for the two genera *Ecklonia* and *Sargassum*. Given that no evidence of impact existed in the older cohort, recruitment failure in the one-year cohort is likely to represent a discrete disturbance linked directly to the sedimentation event rather than to a chronic legacy. Notwithstanding, recruitment failure was also apparent at treatment sites in the youngest (new recruits) juvenile cohort. Either implying that a chronic impact did exist or alternatively that elevated sediment levels were still having an affect on recruitment eight months after the dredging event.

Better correlation between adult and juvenile assemblages was observed at several treatment sites in terms of *Cystophora* recruit survivorship, with significant numbers of juvenile *Ecklonia* also being observed at NSO. The fact that the survey was conducted near the beginning of the season means, that this may represent a biased view of the 1998 cohort, as further recruitment would still be expected over the following months. The continued presence of elevated levels of sediment on certain reefs in 1998 would however help explain differences in recruitment success for that year's cohort.

4.5 Summary and conclusions

Recruitment failure was observed at treatment sites in the cohort that recruited at the time of the plume and the cohort in the following year. The fact that this was not the case in the season prior to the sediment plume (1996 cohort) implies that treatment reefs were not chronically impacted (at least in terms of recruitment). These findings are, however, tentative given the lack of *a priori* information on local reef structure, and because the treatment reefs were clustered together leading to a pseudo-replicated design (Hurlbert 1984).

Reduced levels of recruitment were most evident for *Ecklonia* and *Sargassum* while many treatment sites showed *Cystophora* had greater recruitment success. Unfortunately, taxa were not recorded to species, although a follow up survey in November revealed *C. subfarcinata*, *C. retorta*, and *C. moniliformis* to be common at treatment sites, while control sites were additionally populated by *C. monilifera* along with occasional sightings of *C. gracilis* at MSI (Table 4.2).

Interestingly, several local species of *Cystophora* display traits commonly found in more opportunistic species (Hotchkiss 2000). It is therefore possible that some of these species have a degree of tolerance to frequent disturbance and / or sedimentation. *C. subfarcinata*, in particular, produces large numbers of small eggs over a long duration (from late autumn, Hotchkiss 2000). As a result, early recruits would have been six months old at the time of the plume and may have been large enough to tolerate the sediment fallout.

The presence of opportunistic strategies in *Cystophora* may have aided the ability of members of the genus to recruit at the sediment-affected sites. However, these same strategies would also allow the taxon to persist normally under a more frequent disturbance regime. The presence of adults in mono generic stands may therefore indicate the existence of chronic effects at certain treatment sites. This is possible given the gradient from good to poor health of reefs along the metropolitan coastline (Cheshire *et al.* 1998a) and considering that, there are a number of sources of stress in the vicinity (see Chapter 5).

Confidence in the reported impact of the sediment plume could be significantly improved through a number of follow up surveys of the reefs. This would allow for an assessment of comparative recruitment success over a longer time scale and help differentiate between a one off problem (in the case of the plume) and a more general or chronic impact.

Chapter 5

Temporal change in adult and juvenile communities

The main purpose of this chapter is to broaden the analysis of assemblage structure to indicate parameters likely to give rise to spatial and temporal variability. By including several years of data, the likely influences of various parameters can be examined. This will allow the affect of the sediment plume to be better distinguished from other processes.

CHAPTER TABLE OF CONTENTS

5.1 Introduction

In Chapter 4, biotic structure at the putatively impacted sites was compared to that on a number of surrounding ‘control’ reefs. Subsequent analyses revealed differences in the structure of the juvenile population consistent with a sediment impact. However, a large amount of uncertainty surrounded this result, due to the lack of *a priori* knowledge about differences between the sites or the extent of other impacting processes. The need to account for other factors driving observed patterns was further highlighted through additional analyses, which revealed differences in the adult populations that could not be related to the sediment plume.

Two major problems need to be addressed in any experimental design concerned with detecting anthropogenic influences on biotic communities (Underwood 1994). The first of these relates to the large temporal variance exhibited in many populations creating large amounts of ‘noise’. This variation is likely to comprise both a structured component leading to somewhat coherent patterns (e.g. climatic fluctuations) and unstructured stochastic processes (Legendre *et al.* 2002).

The second of Underwood’s (1994) problems relates to the observation that populations in different locations often exhibit different temporal trajectories, leading to differences from place to place and a statistical interaction that may potentially confound analysis. These differences may be due to a variety of causes including the existence of different foundation events (e.g. Kim and Dewreede 1996; Anderson 1999; Camus 1994; Sousa 1984) or hysteresis within a population (e.g. Dayton *et al.* 1984; Farrell 1991; Thrush *et al.* 1996).

Generally, the framework for quantifying an environmental impact involves estimating the state of a system both in response to, and in the absence of a certain activity, then identifying the degree of uncertainty associated with the difference between these two estimates (Osenberg and Schmitt 1996). Quantifying this uncertainty involves an examination of the spatial and temporal variation relevant to the system under study.

In the current context, the signal of interest was the effect of the sediment plume on the local macroalgal flora. However, a number of other sources of variability have the potential to either mask or confound this signal. While it is not possible to specifically test for all sources of variability relevant to the study, closer examination of how these factors may influence assemblage structure will help place observed patterns in context (Thrush *et al.* 1996).

5.1.1 Likely affects of the sediment plume

Elevated levels of sediment, if prolonged, are likely to cause a loss of macroalgal diversity. In particular, slow growing taxa that rely on sexual reproduction are susceptible to smothering during the recruitment phase. This process has been implicated in the loss of larger canopy forming species in favour of more adventitious foliose and turfing forms (Airoldi 2003).

In the current context, the likely effect of the sediment plume would be to smother new recruits thereby causing a reduction in survivorship for the 1997 cohort. This would manifest during the 1998 survey, as a difference in numbers of one-year-old juveniles between control and treatment sites. Given that the plume was a pulse disturbance, excess sediments would eventually be washed free of the reef, and recruitment levels should become more similar between control and treatment sites over time.

By contrast, the constant sweeping action of larger individuals should leave the adult stand relatively unaffected (Kennelly 1989). Thus in the absence of other factors, there should initially be little observable difference between adult assemblages for either of the two treatments. Notwithstanding, the maturation of juveniles to replenish the adult stand means that the effects of the plume would eventually be propagated into the adult assemblages.

5.1.2 Temporal variability in environmental phenomena

Fluctuations in climatic and physical systems create variability in natural cycles and can influence biological communities over a broad area. The effects of these interactions are propagated through changes in biological processes, which ultimately manifest as an increase or decrease in recruitment, growth, or mortality.

At higher latitudes (such as in temperate regions), there are significant seasonal differences in a number of environmental parameters including water temperature, insolation, storm activity. These factors in turn influence a number of biological processes including photosynthesis, growth, mortality and the onset of reproduction (Gunnill 1980; Gomez and Wiencke 1997; Makarov *et al.* 1999; Hotchkiss 2000).

Inter-annual variability in climatic phenomena may also influence macroalgal communities (e.g. Dayton *et al.* 1999), and a knowledge of these is important for any interpretation of patterns in a temporal context.

More extreme fluctuations (such as those associated with El Niño events) often have large effects on biological systems (Dayton *et al.* 1999; Gunnill 1985). The existence of an El Niño event corresponds to a depression in the Southern Oscillation Index (SOI, Figure 5.1), which is the atmospheric pressure differential at sea level between the eastern and western sides of the Pacific Ocean. Due to the coupling of the two phenomena, they are often referred to as ENSO (Jaksic 1998).

A large depression in the SOI over the summer of 1997/98 was responsible for one of the most severe El Niño events of the twentieth century (Nicholls 1999). The event was of particular relevance to this study because it coincided with the dispersed sediment plume.

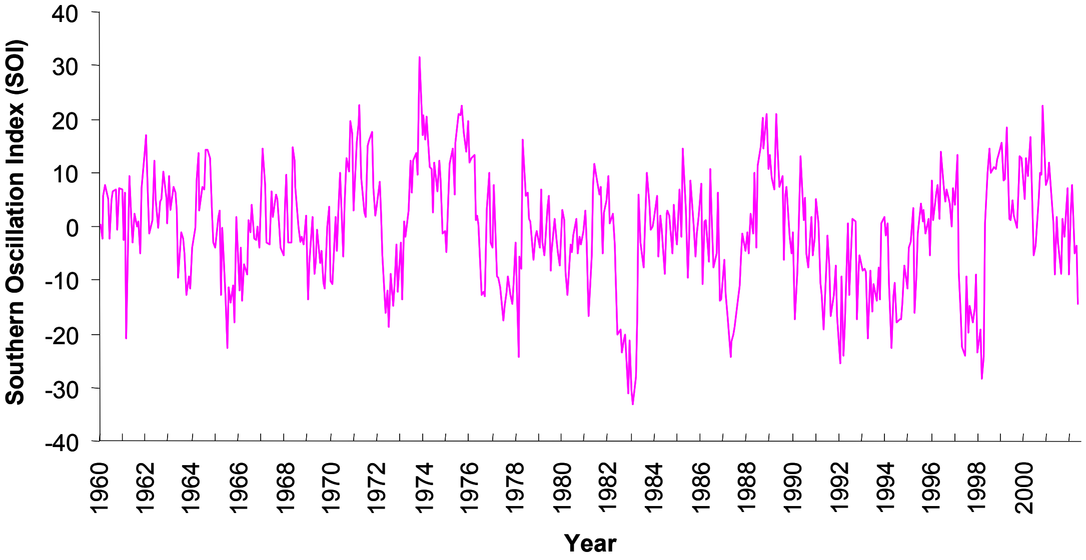

Figure 5.1 Southern Oscillation Index (SOI) data 1960 – 2002.
The chart shows a depression in the index during 1997/98 characteristic of an El Niño event. Data supplied by the Australian Bureau of Meteorology (BOM 2002).

The worldwide cost of the 1997/98 El Niño event was estimated to be $US 34 billion and affected 111 million people (NOAA-OGP 1999). Warmer than normal sea temperatures were recorded throughout much of the Pacific Ocean and were linked to coral bleaching in a number of areas. In Australia, above average sea temperatures have been documented during El Niño periods around Tasmania, and may extend westward into Western Australian waters (Jeffrey *et al.* 1990).

5.1.3 Differences between localities that may confound analysis

Reefs along Adelaide's metropolitan coastline represent different environments due to a host of natural influences including the north south gradient, differences in wave exposure, physical aspect (i.e. horizontal or vertical surfaces), and topography (Cheshire *et al.* 1998b). The development of Adelaide's coastal environment has also contributed a number of point sources of stress (Nicolson *et al.* 2003), the proximity to which is likely to further influence the structure of the reef community.

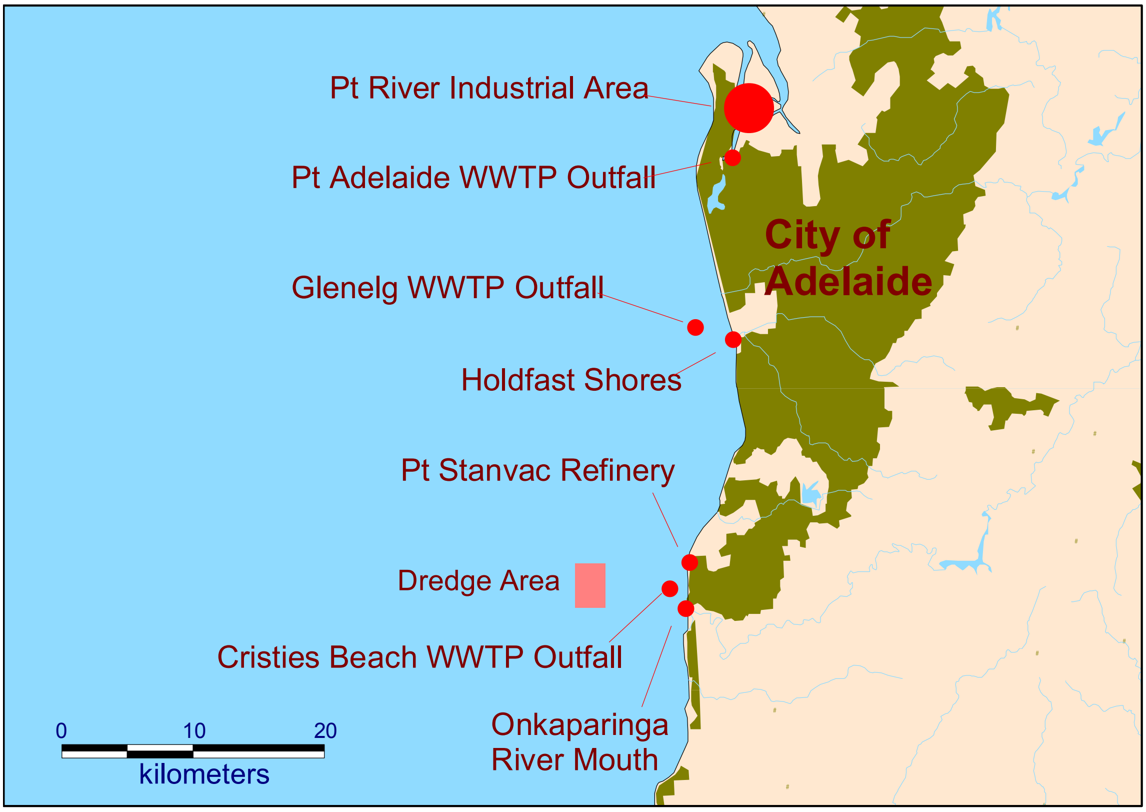

Figure 5.2 Problematic locations along Adelaide's metropolitan shoreline This figure is reprinted from Chapter 2[15].

In particular, the Christies Beach WWTP outfall is in close proximity to Horseshoe Reef, with Noarlunga Reef nearby. An examination of soft sediment fauna in the area has already demonstrated significant impacts of the outfall (Loo 2001) while studies elsewhere

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[15] This figure incorporates data that is © Commonwealth of Australia (Geoscience Australia 2003).

have identified effluent impacts on macroalgal communities (Burridge *et al.* 1996; Bellgrove *et al.* 1997).

Situated between the Noarlunga and Southport Reefs is the mouth of the Onkaparinga River. The poor water quality of this river continues to pose problems for the near shore marine environment (Edyvane 2000) although a number of suitable sites for wetlands have been identified to act as bio-filters (Onkaparinga Estuary Task Group 1990).

Noarlunga Reef is an aquatic reserve and thus is not subject to the same fishing pressures as other metropolitan reefs. Although not quantifiable, it is plausible that this may positively influence fish numbers, which in turn may have an effect on levels of herbivory.

At a smaller scale (e.g. on a single reef) factors such as proximity to a source of stress are likely to be more uniform, yet reef assemblages still exhibit a large amount of heterogeneity (Turner and Cheshire 2003). In Chapter 3 it was hypothesised that canopy forming assemblages occurred in a number of potentially stable states (dominated by a single genus), and one transitory state (a state of variable low abundance, VLA).

The presence of different states is likely to reflect past events altering the suitability of the environment to certain taxa. Events may include the timing of disturbance (especially in relation to recruitment and thus acting as a ‘foundation event’), the outcome of biotic interactions, and probably a stochastic (unquantifiable) element. The existence of different (and possibly stable) configurations highlights the importance of starting conditions in determining possible temporal trajectories. In terms of temporal studies or impact assessment, if not adequately understood, they may lead to confounding results.

Starting conditions may also affect the amount of hysteresis (i.e. time taken to undertake a given process). As an example, impacts on juvenile assemblages are likely to be propagated into the adult canopy. However, growth rates vary between species and under different environmental conditions, which may lead to different observations about the adult assemblage depending on the timing of a follow up survey.

5.1.4 Objectives of this chapter

A number of environmental factors operating over a range of scales influence the macroalgal communities used in this study. The net result of interactions between the elements of this system leads to large amounts of spatial and temporal heterogeneity.

Thus, in order to discern the longer-term effects of the dispersed sediment plume on the macroalgal communities, it will be necessary to account for a large proportion of this variability.

The aim of this chapter is to partition the variation in macroalgal community structure across relevant sources, in order to better assess the effects of the signal of interest (the dispersed sediment plume).

5.2 Materials and Methods

5.2.1 Summaries of climate data

Data for a number of environmental parameters relating to climate were obtained from third parties and summarised in order to determine the level of variability both prior to and over the duration of the study.

Water temperature data for the Pt Stanvac area and rainfall data for the Adelaide area was obtained from the National Tidal Facility and the Australian Bureau of Meteorology respectively. Data for the decade up to and including the study was summarised and reported as monthly means for relevant years. Additionally data from previous years were used to produce a composite mean value for each calendar month.

The Bureau of meteorology also supplied data on wind speed and direction that was used to produce a Relative Exposure Index (REI, Fonseca and Bell 1998).

Relative Exposure Index - REI

$$REI = \sum_{i=1}^{I} \left(F_i \times V_i \times P_i \right) \qquad \textbf{Equation 5.1}$$

Where I is the number of compass points (8), V_i is wind speed, P_i is wind duration, and F_i is the fetch length.

An average fetch length was used for each compass point (Figure 5.3) and the index calculated on a monthly basis. It was not considered necessary to use the more elaborate versions of this formula (which include bathymetry and tidal modifications) due to the regular bathymetry of Gulf St Vincent (Townsend 2002) and because the study was limited to subtidal populations (approx 5 m).

5.2.2 Temporal comparisons

Repeat surveys were undertaken annually in August 1999, 2000, and 2001 at the same ten locations identified in Chapter 4. The survey protocol also remained the same as outlined in Chapter 3, with two important exceptions: Firstly, where possible, members of the genus *Cystophora* were classified to species. This classification was not possible for *Sargassum* due to the lack of diagnostic features on the individuals at the time of the survey. Secondly, gap lengths were recorded in areas where the belt transects were discontinuous due to an absence of canopy forming algae. The importance of these measurements became apparent after the first survey due to the patchiness of the biota at certain sites.

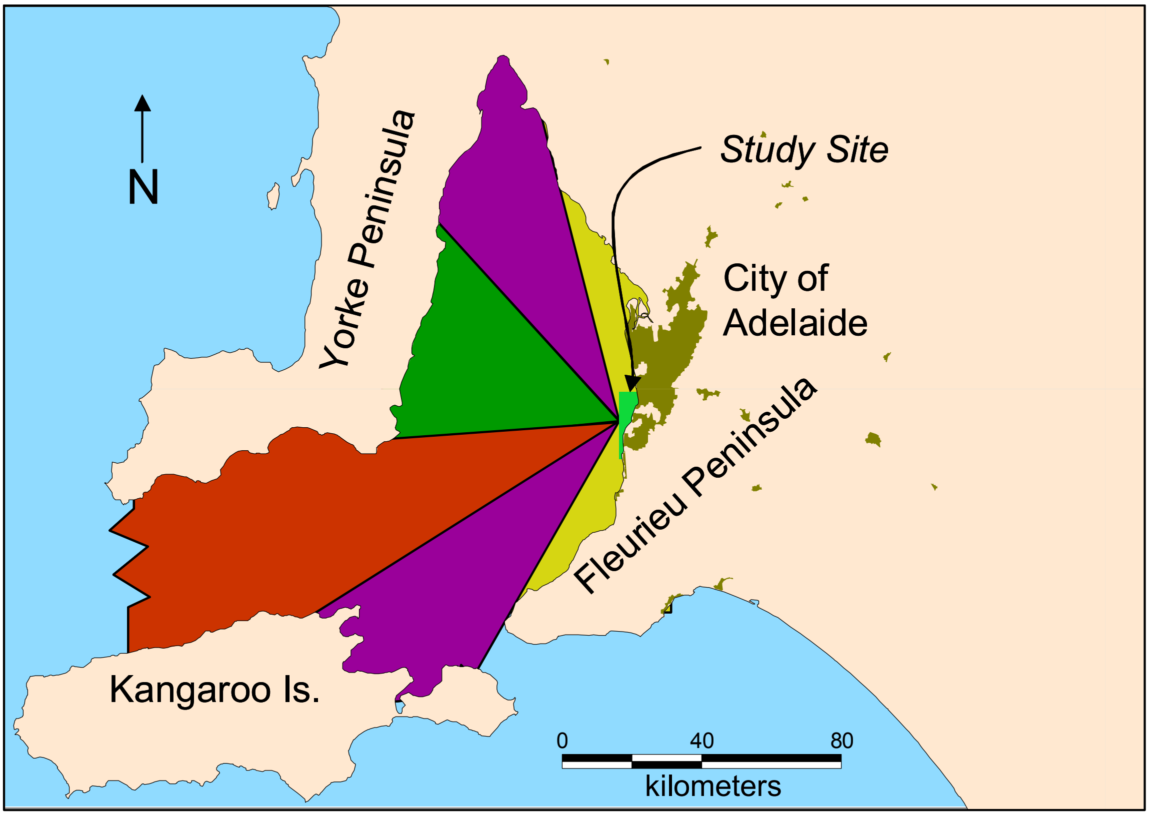

Figure 5.3 Map showing fetch lengths at the study site for different wind directions[16].

Analyses of the juvenile stand were limited to the one-year-old cohort for each survey to allow comparison with the individuals most likely affected by the sediment plume, as identified in previous chapters. Similar analyses to those in Chapter 4 were performed on the juvenile stand in order to compare control with treatment sites over the four years of the study.

Changes in the structure of the adult stand were compared in terms of population density and the relative proportion of community assemblages. Furthermore, it was identified in Chapter 4 that any differences between control and treatment sites in terms of the adult stand were unlikely to be the result of the sediment plume. Hence, for the purposes of analysis, the initial surveys of the adult stand may be viewed as representing the pre-

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impact state. While it is necessary to acknowledge this as an assumption of the following analysis, it allows for a far more robust assessment of the effect of the sediment plume.

Detection of the environmental perturbation was undertaken using a beyond BACI analysis incorporating the four surveys as described by Underwood (1992; 1994). Using this approach, sources of variation were partitioned and the impact tested using an asymmetrical Analysis of Variance (ANOVA). The method was upgraded to use a non-parametric multivariate version of the traditional ANOVA, and incorporate six (rather than one) treatment sites (Table 5.1).

Table 5.1 Asymmetrical ANOVA model for use with the Beyond BACI analysis. Sources of variation partitioned to identify the terms of interest (based on Underwood 1992, 1994).

Sources of variation	**df**	**Sources of variation (cont.)**	**df**
Before versus After (Q)	1	T(Q) × L	18
Among locations (L)	9	T(Before) × L	9
Impact versus Controls (Z)	1	T(Before) × Z	1
Among Impact sites (I)	5	T(Before) × I	5
Among Control sites (C)	3	T(Before) × C	3
Q × L	9	T(After) × L	9
Q × Z	1	T(After) × Z	1
Q × I	5	T(After) × I	5
Q × C	3	T(After) × C	3
Sampling times (Q) = T(Q)	2	Residual	421

Due to the complex and unbalanced design, each of the terms of interest needed to be calculated separately through multivariate multiple regression analysis (Anderson 2001; McArdle and Anderson 2001). The whole process was accomplished using DISTLM v.2 (Anderson 2003a) and XMATRIX (Anderson 2003b).

5.3 Results

5.3.1 Climatic variation

Variation in Sea Surface Temperature (SST)

Water temperatures were maximal in late summer and minimal in late winter, with values commonly a degree or more different in any particular month over consecutive years (Figure 5.4).

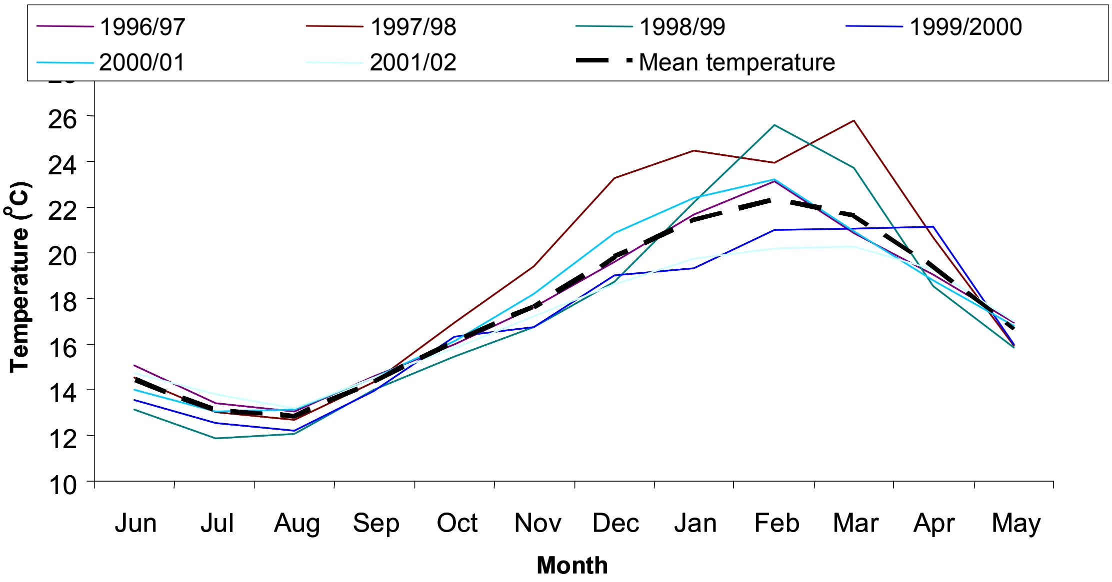

Figure 5.4 Average monthly sea temperatures at Pt Stanvac, South Australia. Mean temperature calculation is based on values over the decade 1993-2002.

Mean SST showed greater inter-annual variation over summer periods than in winter. In particular, a SST several degrees higher than average was recorded during the spring / summer period of 1997 / 98 and again during the following summer period (1998/99, Figure 5.4).

Monthly precipitation levels

Rainfall was highly variable both in terms of which months had the most rain and in terms of total annual precipitation (Figure 5.5). Monthly rainfall tended to oscillate between winter maximums and summer minimums.

Annual rainfall at Adelaide Airport in 1992 (730.8 mm), was considerably higher than the long-term 90th percentile (587 mm, BOM 2002). In contrast, the driest year of the decade was 1994, which had a total annual precipitation of 326 mm and corresponded to the long term 10th percentile (325.4 mm, BOM 2002).

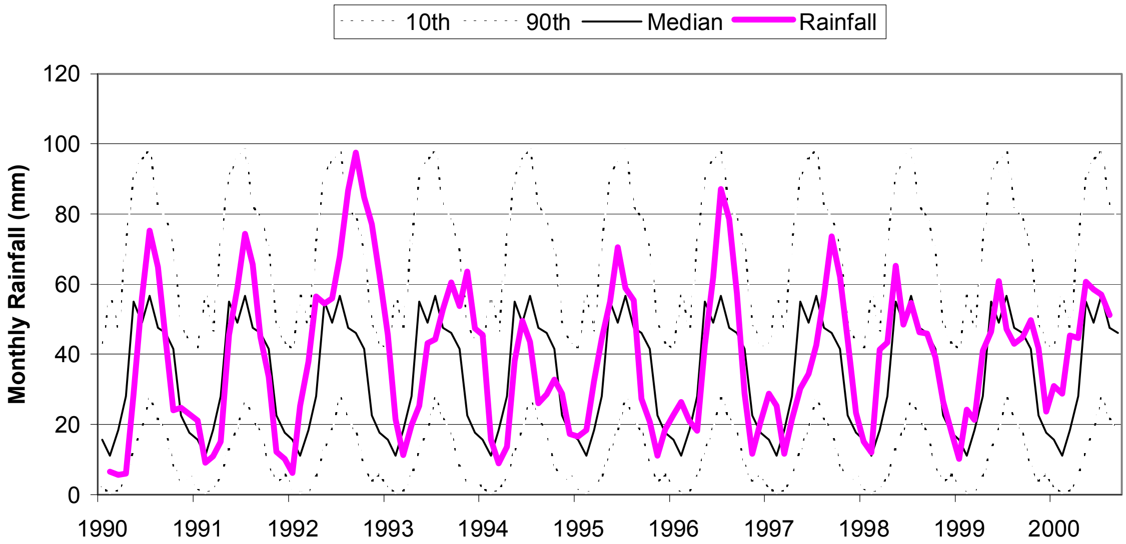

Figure 5.5 Total monthly precipitation for the Adelaide area (Adelaide Airport). Rainfall values are monthly totals smoothed with a 3 month running mean. Median and percentile data is based on long-term records from the Bureau of Meteorology.

Annual rainfall values for the rest of the decade were around or slightly lower than the long term median (466.2 mm, BOM 2002). However, differences were observed in monthly totals, with annual ranges tending to be smaller at the end of the decade (Figure 5.5).

Relative Exposure Index (REI)

A large amount of variability was observed in terms of both wind speed and direction over the course of the year. REI values generally oscillated between an autumn / winter low and spring / summer high indicating that the latter was characterised by a greater proportion of winds with a large fetch and / or higher speeds leading to greater wave energy at that time (Figure 5.6). Using this index, the calmest month was generally May (mean REI ≈ 14) with roughest weather peaking in November (mean REI ≈ 28).

Interestingly, wind data for the latter part of the 1990s (1996 on) produced lower index values implying that conditions moderated towards the end on the 1990s compared with the first part (Figure 5.6).

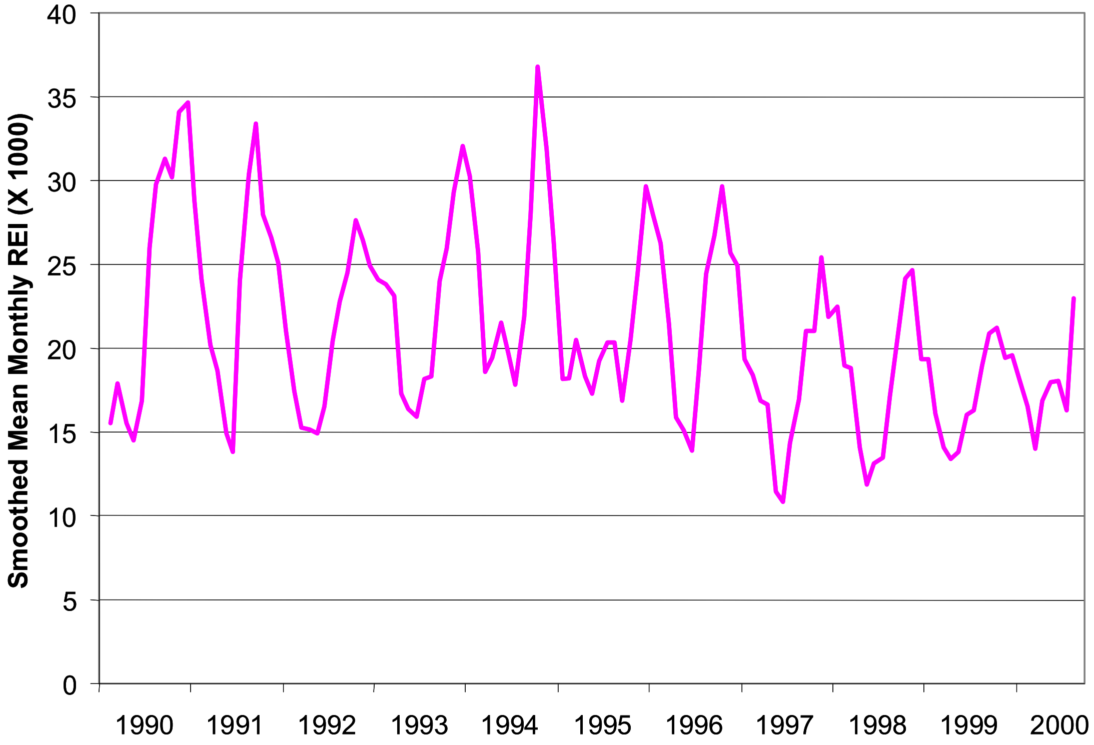

Figure 5.6 Relative Exposure Index (REI), 1990 – 2000 for the study area. Data points represent mean monthly values, calculated from daily REI values. All data have been smoothed by a three-month running mean.

5.3.2 Temporal comparisons based on the one year juvenile cohort

The 1998 survey recorded the lowest numbers of one-year-old *Cystophora* irrespective of site. Interestingly higher densities of this genus were recorded at impact sites than control sites in both 1998 and 1999. In 2000 / 2001, this trend was reversed due to both a considerable increase in numbers at control sites (mainly Hallett Cove and Southport) and a concomitant reduction at impact sites (Figure 5.7).

In all years, *Ecklonia* densities were greater at control sites than for the corresponding impact sites. Notwithstanding, numbers remained low during 1998 and 1999 before showing a similar increase to *Cystophora* in the following year (Figure 5.7).

Sargassum densities were also higher at control sites relative to the impact sites, but in contrast to the other genera, overall numbers were highest in 1998 and reduced in subsequent years (Figure 5.7).

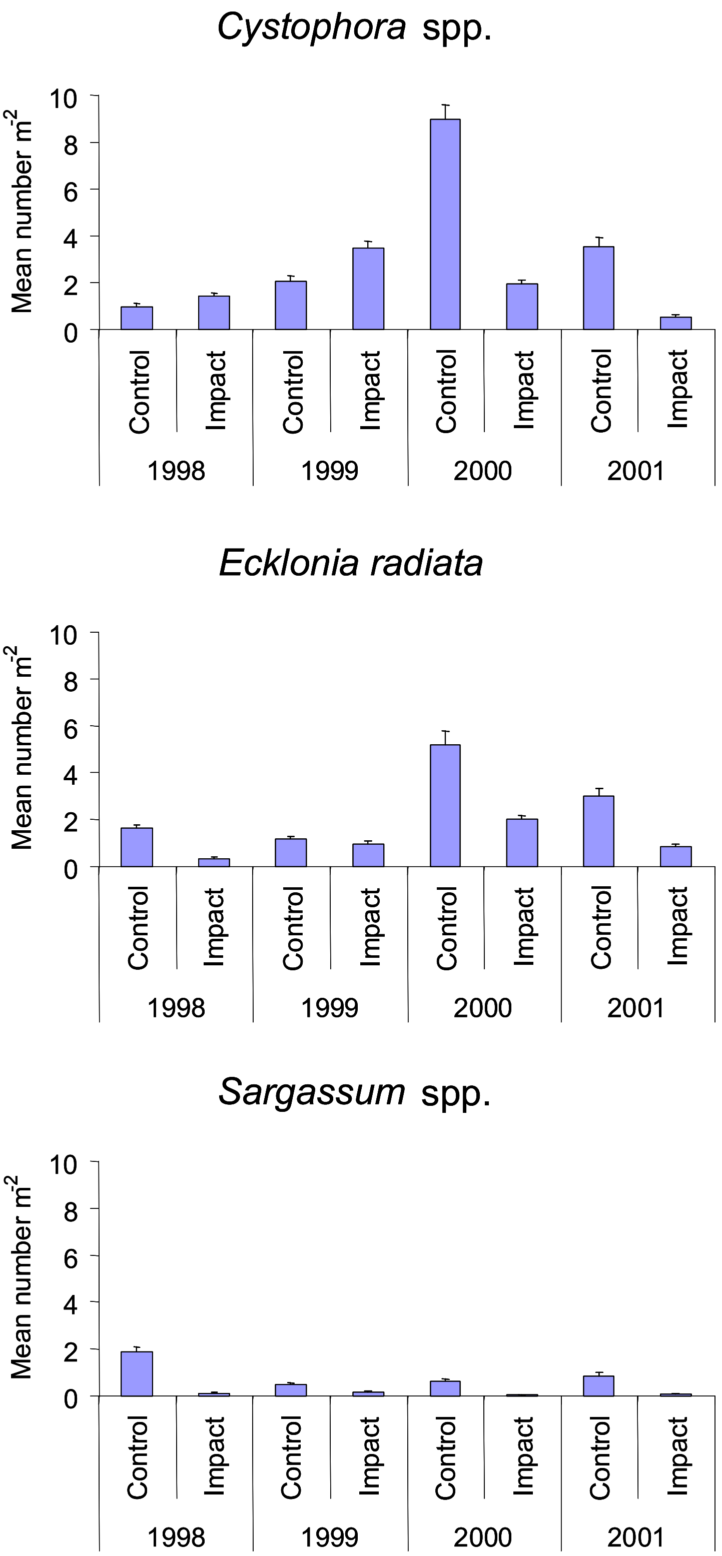

Figure 5.7 Density of one-year-old juveniles under VLA canopies. The three graphs indicate the mean density (n m^{-2}) at control and impact sites for each of the three common genera of canopy forming taxa. Error bars indicate standard error of the mean.

Canonical correlations using the one-year cohort provided an interesting summary of recruitment success over the duration of the study (Figure 5.8; Table 5.4). Comparisons were limited to assemblages occurring below a 'Variable Low Abundance' (VLA) type canopy.

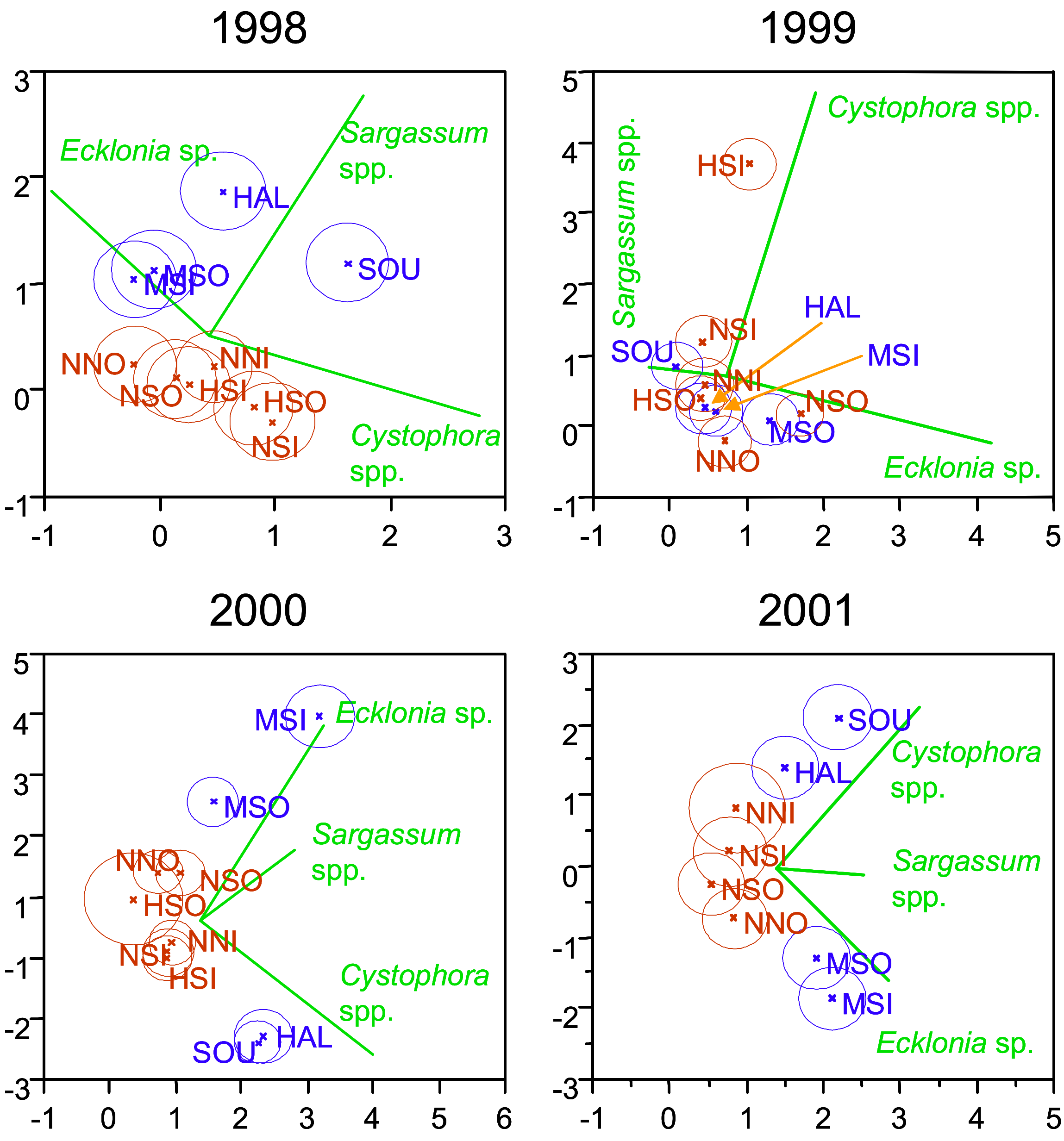

Figure 5.8 Canonical correlation of one-year-old juveniles under a VLA canopy. See Table 3.1 and Table 4.1 for site details.

In 1998, a clear separation was evident between the control and impact sites (Figure 5.8), as previously described in Chapter 4 (Section 4.4.2). In contrast, a division between control and impact sites was not evident from the 1999 survey, although there was some degree of separation between sites on the seaward side of the reefs and those on the leeward side (outside versus inside). The site at Horseshoe Reef Inside (HSI) was notably different from others due to the presence of large numbers of *Cystophora* recruits (Figure 5.8).

Table 5.2 Significance tests of canonical correlation in Figure 5.8

Test	Value	Approx. F	DF Num	DF Den	Prob>F
1998					
Wilks' Lambda	0.491975	17.8187	27	1750	<.0001
Pillai's Trace	0.611151	17.0841	27	1803	<.0001
Hotelling-Lawley	0.832115	18.4195	27	1793	<.0001
Roy's Max Root	0.456719	30.4986	9	601	<.0001
1999					
Wilks' Lambda	0.353552	29.3354	27	1852.2	<.0001
Pillai's Trace	0.794509	25.457	27	1908	<.0001
Hotelling-Lawley	1.430795	33.5265	27	1898	<.0001
Roy's Max Root	1.108284	78.3188	9	636	<.0001
2000					
Wilks' Lambda	0.188254	38.7377	27	1355.8	<.0001
Pillai's Trace	1.116	30.6709	27	1398	<.0001
Hotelling-Lawley	2.792861	47.8579	27	1388	<.0001
Roy's Max Root	2.153432	111.4999	9	466	<.0001
2001					
Wilks' Lambda	0.249576	23.9826	21	810.3	<.0001
Pillai's Trace	0.968734	19.349	21	852	<.0001
Hotelling-Lawley	2.167331	28.9666	21	842	<.0001
Roy's Max Root	1.708764	69.327	7	284	<.0001

The 2000 surveys once again identified a reasonable separation based on treatment (control versus impact), with recruit assemblages on the flat reefs (HAL, SOU) also differing from the sites at Moana South (MSI, MSO). A similar but less distinct separation was also observed the following year (2001) (Figure 5.8). Note: The two sites at Horseshoe Reef are not shown in 2001 due to lack of vegetation observed at the time of the survey.

5.3.3 Temporal comparisons based on adult assemblage

Density of adult canopy forming individuals in 1998 was similar between control and impact sites, averaging about 14 n m^{-2} (Figure 5.9). Significant increases were observed in 1999 with impact sites increasing to 20 n m^{-2} and control sites doubling to 30 n m^{-2}. Average density at control sites remained high in the following years while the number of adult individuals at impact sites declined to only 6 n m^{-2} by 2001, although losses were not uniform across all sites.

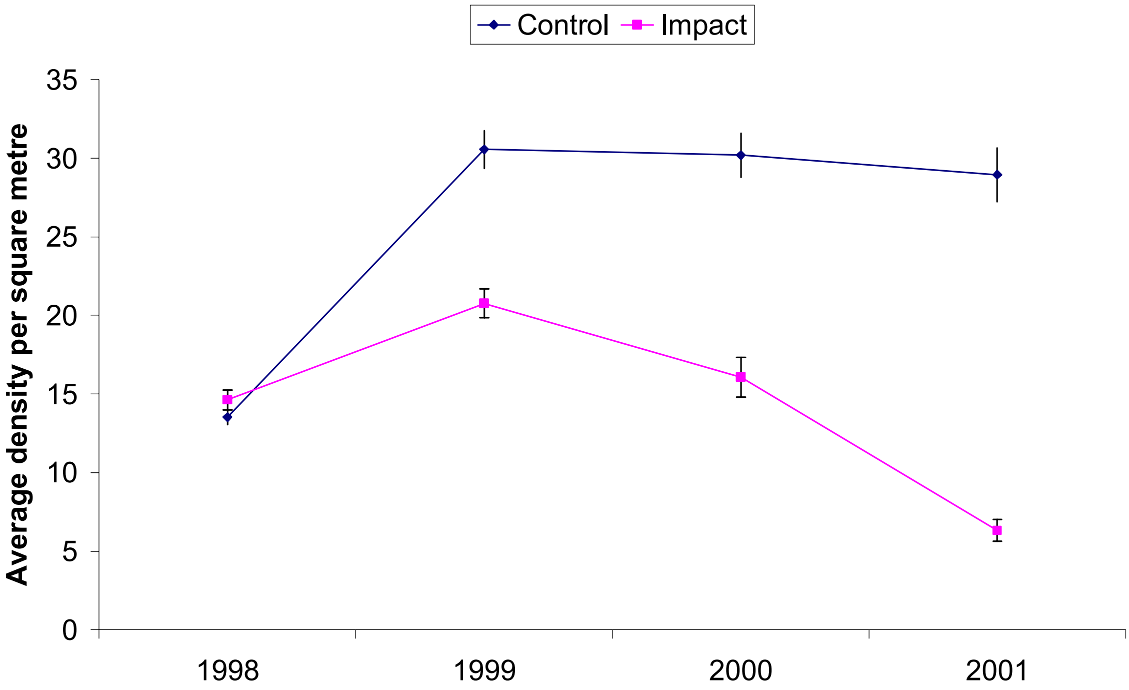

Figure 5.9 Average number of adult canopy individuals at each site. Repeated density measures take into account areas devoid of algae as encountered during the surveys (1999 – 2001 data only). Error bars indicate standard error.

Changes in abundance led to concomitant changes in the number of quadrats identified as VLA assemblages over the course of the study (Figure 5.10). In 1998 the number of VLA assemblages was high (>60%) at all sites except Noarlunga North outside (NNO). Over subsequent years of the study, the proportion of VLA state quadrats declined at control sites while reduced numbers of individuals (Figure 5.9) at impact sites elevated VLA frequency toward 100% (Figure 5.10).

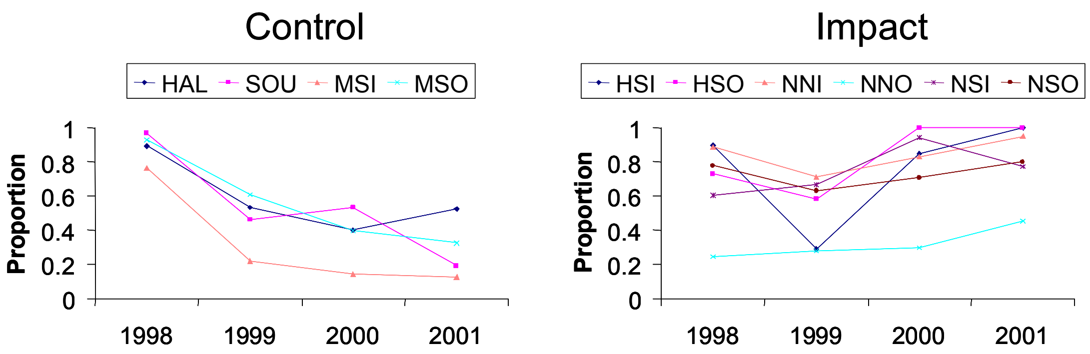

Figure 5.10 Total number of VLA type quadrats surveyed over the four years.

An examination of canopy structure in relation to the proportion of quadrats dominated by various assemblage states showed control sites transforming from mainly VLA dominated communities in 1998 (i.e. only about 10% mono generic dominated), towards about 70% of quadrats existing as mono generic dominated stands by 2001 (Figure 5.11). At impact sites, an initial elevation in the number of mono generic stands in 1999 (50%, over 1998 levels, 70%) was subsequently reduced to 30% by 2001. The majority of this 30% were *Ecklonia* dominated assemblages coming from one a single site (NNO; Figure 5.11).

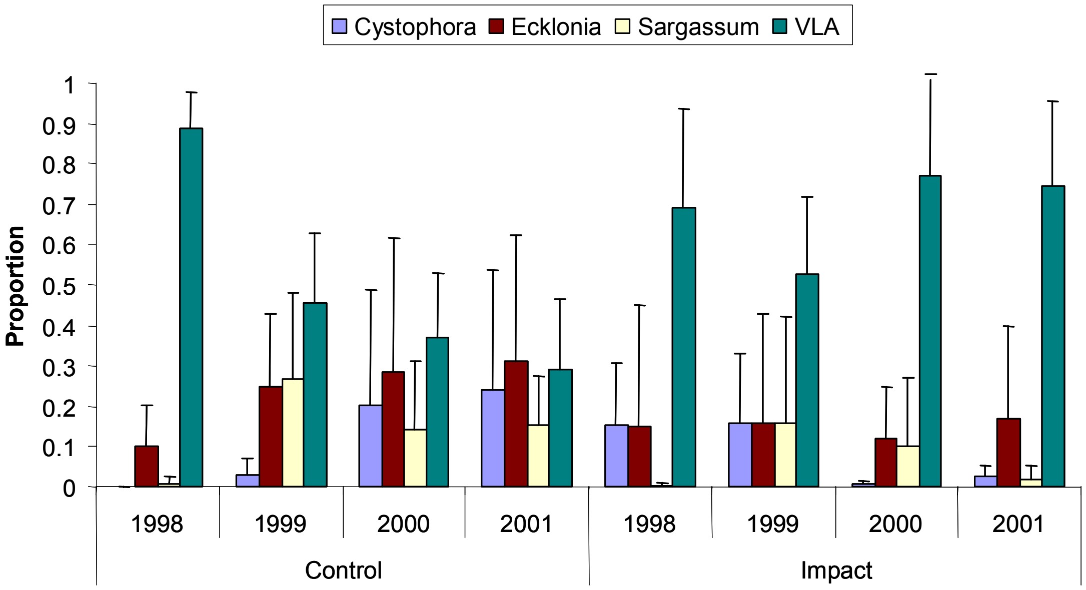

Figure 5.11 Average proportion of quadrats belonging to each community type. Data are grouped by treatment; error bars indicate standard error of the mean.

The Asymmetrical Non-Parametric Multivariate Analysis of Variance (ANPMANOVA) used as a basis for the beyond BACI assessment, identified a significant change in the structure of the impact sites following the putative start of the sediment plume. Interpretations follow those discussed in Underwood (1992; 1994) and are explained below (Table 5.3).

Table 5.3 Beyond BACI analysis, examining changes in adult assemblages. The table summarises the results of an asymmetrical non-parametric multivariate analysis of variance. Only relevant *F*-ratios are shown; * indicates *p*<0.05; **, *p*<0.01; ns, *p*>0.05. Some tests are two tailed because interactions may increase or decrease because of the impact.

Sources of variation	df	MS	*F*-ratio versus	*F*	Notes
Before versus After (Q)	1	1.92046			
Among locations (L)	9				
Impact versus Controls (Z)	1	9.90166			
Among Impact sites (I)	5	7.30900			
Among Control sites (C)	3	8.10794			
Q × L	9				
Q × Z	1	6.30708			
Q × I	5	2.16516			
Q × C	3	1.80611			
Sampling times (Q) = T(Q)	2	2.73830			
T(Q) × L	18				
T(Before) × L	9				
T(Before) × Z	1	0.27064	T(Before) × C	0.508^{ns}	
T(Before) × I	5	0.94181	Residual	5.789^{**}	
T(Before) × C	3	0.53314	Residual	3.277^{**}	
T(After) × L	9				
T(After) × Z	1	1.52892	T(After) × C	2.534^{*}	**A**
T(After) × I	5	2.13126	Residual	13.100^{**}	
T(After) × C	3	0.60348	Residual	3.710^{**}	**C**
Residual	760	0.16269			
Total	799				
2-tailed *F*-ratios					
T(After) × Z versus T(Before) × Z				5.650^{*}	**B**
T(After) × I versus T(Before) × I				2.263^{*}	
T(After) × C versus T(Before) × C				1.132^{ns}	**D**

There was a significant difference in the patterns of interaction between T(After) × Z and T(After) × C, and between T(After) × Z and T(Before) × Z (Table 5.3, Notes **A** and **B** respectively). The interpretation of this is that patterns at the impact sites changed relative to those at the control locations following the sediment event.

A short-term temporal interaction among control locations following the start of the disturbance was also detected (T(After) × C; Table 5.3, Note **C**). This implies that changes in assemblage structure were occurring out of phase in different places. Importantly though, interactions among control locations after the start of the impact (T(After) × C) did not change relative to those occurring before the impact (T(Before) × C; Table 5.3, Note **D**). As a result, it can be concluded that changes in assemblage structure at control locations were not related to a more general change at the time of the plume.

Although there were fluctuations in assemblage structure occurring throughout the study, the effect of the sediment plume led to an altered pattern of differences at impact sites relative to control sites following the start of the impact.

The temporal variability described in the ANPMANOVA can also be seen in the canonical correlations (Figure 5.12). Of the control sites, the two flat reefs (Hallett Cove and Southport) showed the greatest amount of variability, although this may be partially because of sampling differences due to patchiness of reef biota. While these reefs contained areas dominated by different genera, they were largely fucoid dominated. In contrast, the seaward and leeward sites at Moana South remained *Ecklonia* dominated during the course of the study.

In terms of the treatment sites, Noarlunga North Outside remained *Ecklonia* dominated throughout the study. The remainder of the sites initially showed no clear dominance (1998), but had a greater fucoid influence in 1999. By August 2000, *Cystophora* spp. was the most abundant taxa while in the following year (2001) dominance became more mixed (Figure 5.12; Table 5.4).

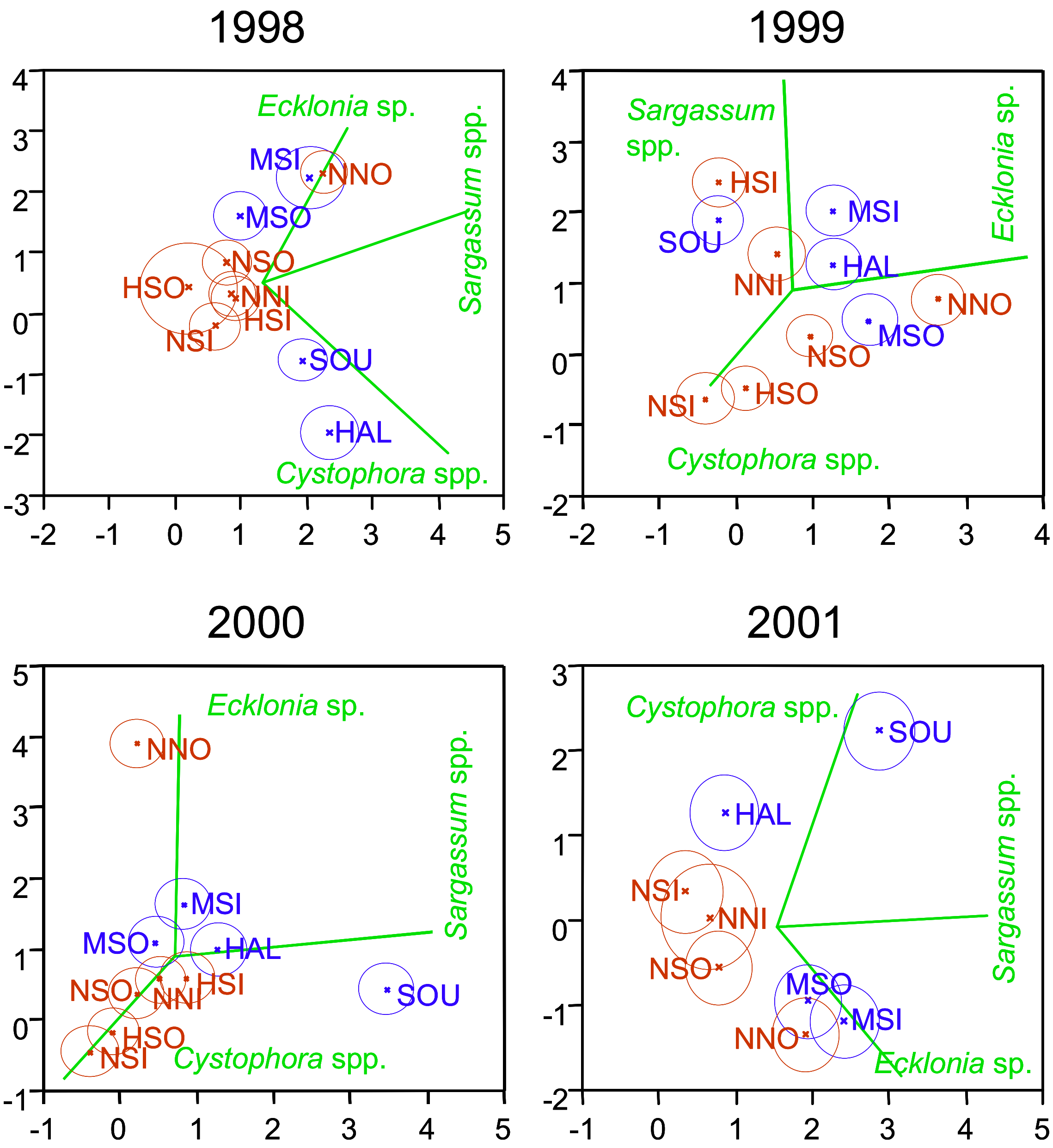

Figure 5.12 Canonical correlation of adult assemblages for each year of the study. See Table 3.1 and Table 4.1 for site details.

Table 5.4 Significance tests of canonical correlation in Figure 5.12

Test	Value	Approx. F	DF Num	DF Den	Prob>F
1998					
Wilks' Lambda	0.178633	52.084	27	1750	<.0001
Pillai's Trace	1.227972	46.2754	27	1803	<.0001
Hotelling-Lawley	2.557087	56.6032	27	1793	<.0001
Roy's Max Root	1.342523	89.6507	9	601	<.0001
1999					
Wilks' Lambda	0.263575	39.6964	27	1852.2	<.0001
Pillai's Trace	0.981587	34.3664	27	1908	<.0001
Hotelling-Lawley	1.880754	44.07	27	1898	<.0001
Roy's Max Root	1.009081	71.3084	9	636	<.0001
2000					
Wilks' Lambda	0.212931	35.0641	27	1355.8	<.0001
Pillai's Trace	1.130583	31.3141	27	1398	<.0001
Hotelling-Lawley	2.269345	38.887	27	1388	<.0001
Roy's Max Root	1.543754	79.9322	9	466	<.0001
2001					
Wilks' Lambda	0.20458	28.4679	21	810.3	<.0001
Pillai's Trace	1.127701	24.4365	21	852	<.0001
Hotelling-Lawley	2.382879	31.8474	21	842	<.0001
Roy's Max Root	1.525218	61.8803	7	284	<.0001

5.4 Discussion

Anthropogenic activities have a marked and often negative effect on natural ecosystems. However, given the inherent complexity and variability within these systems, it is often difficult to isolate the effect of interest from the background 'noise' (Osenberg *et al.* 1996). As a result, demonstrating a causal relationship between an observed effect and the putative anthropogenic cause is a challenge facing many scientists (Underwood 1994). Notwithstanding, knowledge of how individual impacts affect communities is important for planning and management of natural systems, in order to minimise future problems.

The spatial structure of the resident canopy forming, macroalgal assemblages was previously quantified (Chapter 3). Significant variation in the biotic composition was documented at spatial scales of metres, tens of metres, and hundreds of metres. At the smaller scales (metres) this variation was explained in terms of biological interactions driving recruitment processes (e.g. the influence of the species composition of the canopy on juvenile establishment and survivorship), whereas variation at larger scales was attributed to differences associated with wave exposure and aspect of sites.

Large-scale processes such as climatic conditions (particularly water temperature) may influence assemblage structure in a coherent way across all sites (e.g. through influencing algal reproductive ecology). Conversely, some climatic processes, such as inter-annual variation in rainfall, may act differentially across sites depending upon their proximity to river or stormwater inflows.

In the following discussion, the extent to which these factors may influence assemblage structure will be elaborated through an examination of the coherent temporal patterns of variability that appear to have influenced all sites similarly. In particular, inter-annual fluctuations in climatological phenomena and postulated causative links to the observed patterns are presented based on available literature. Following this, factors likely to have different effects throughout the study area are examined. Reference is made to starting conditions, physical aspect, and proximity to point sources of stress that are likely to influence biotic processes on certain reefs. In turn, these may result in different temporal trajectories (Underwood 1994) and thus potentially confound the signal of interest. Finally, the actual signal of interest (the impact of the dispersed sediment plume) is examined in light of the other sources of variability described above.

5.4.1 Coherent patterns of temporal variation in macroalgal structure

Temporal variation associated with large-scale climatic processes is identifiable and produces coherent patterns that may be extracted from the data. Inter-annual variability in water temperature may have significant consequences for many macroalgal species which are specifically adapted to certain temperature ranges (Bischoff and Wiencke 1993; Wiencke *et al.* 1994). Many larger taxa are especially sensitive to temperature increases and reductions in the abundance of phaeophycean taxa have been observed in response to changes in water temperature due, for example, to thermal pollution from power stations (Devinny 1980; Ravanko 1991; Gunnill 1985). Critical winter minimum temperatures have been implicated in controlling the production of fertile tissues (e.g. conceptacle development in fucoids, Lobban and Harrison 1994). More generally, increases in temperature appear to have an inhibitory effect on algal recruitment (Van Den Hoek 1982) and / or on the subsequent development of the sporophyte (Gunnill 1985; Gerard 1997).

Water temperatures around the time of the dispersed sediment plume were atypical and probably influenced by the strong El Niño event during the 1997/98 seasons. Over the period 1992-2002, water temperatures generally showed little deviation from seasonally adjusted means except between October 1997 and April 1998, and again the following summer when sea temperatures at Pt Stanvac (directly inshore from the dredge site) were several degrees above the long-term mean (Figure 5.4).

It is possible therefore, that the higher than normal water temperatures recorded during the 1997 recruitment period (August and December) and again over summertime the following year (Figure 5.4), would have affected juvenile populations by reducing abundances of recruits. It was notable that low numbers of both *Cystophora* and *Ecklonia* juveniles were observed during the 1998 and 1999 surveys (relative to the numbers observed in the subsequent two years; Figure 5.7). Given that this difference was observed across all sites it is likely that it was related to a broad influence across the study area (such as elevated sea temperatures) and not a point source of disturbance.

In contrast, *Sargassum* numbers appeared higher in 1998, a result that superficially contradicts the above explanation (Figure 5.7). However, unlike the other two genera, *Sargassum* is known to have a wide geographical distribution (from cold temperate through to tropical waters) and while individual species have a smaller range it is possible that the genus is less susceptible to the effects of warmer temperatures (Womersley 1987). In addition, *Sargassum* readily regenerates from basal fragments and it is likely that a significant proportion of the juvenile *Sargassum* observed, actually resulted from fragment regrowth rather than sexual reproduction[17].

Broad scale climatic processes also determine the amount and seasonality of rainfall, as well as the associated stormwater discharge. Unlike water temperature however, stormwater inputs may not have a uniform influence across the study area. Stormwater enters the marine environment through both creeks and rivers as well as through engineered drainage systems. Areas close to stormwater discharges are likely to experience periods of reduced salinity (e.g. Phillip and Lavery 1997; Recher *et al.* 1993) and exposure to an array of dissolved and suspended pollutants that may be problematic for marine life (March 1996).

Rainfall (precipitation) across this area of South Australia was generally higher in winter than summer but with substantial inter-annual fluctuations over the period 1992-2002 (Figure 5.5). Rainfall was higher during the winters of 1995-1997 than the median values although annual totals were generally consistent with long-term data. In contrast, seasonally adjusted rainfall patterns for the remainder of the decade were more consistent with monthly median values (Figure 5.5).

Higher than average wave energies associated with storm events have often been implicated in localised disturbances on rocky reef communities. Rough weather is most likely to affect larger individuals, which are subject to greater hydrodynamic forces and thus more likely to be damaged or torn free of the substrate (Lobban and Harrison 1994).

The use of a relative exposure index (REI) based on wind speed and fetch demonstrated that rough weather (south-westerly winds) mainly occurred during the second half of the year (August – December) and peaked in November (Figure 5.6). Furthermore, relative

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[17] Furthermore, if one accepts the hypothesis, that lower densities of adult plants in 1998 resulted from removal of plants during previous periods of rough weather, then this would likely result in many basal fragments being left on the reef. Regrowth of these fragments would then augment the subsequent re-establishment of the *Sargassum* population on these reefs.

exposure during the latter part of the 1990s (post 1996) was lower than in the previous years (Figure 5.6).

The greater frequency of rough weather prior to 1996 therefore provides a plausible explanation for the low densities of canopy forming algae observed in the first year of this study (1998), relative to later years (at control sites, Figure 5.9). A similar trend was also observed over a wider geographical area during the reef health surveys (Cheshire *et al.* 1998a; Cheshire and Westphalen 2000), with lower densities recorded in 1996 compared with 1999.

Table 5.5 Climatic conditions and their likely effects on macroalgal assemblages

Year	**Climatic conditions over the spring / summer period**	**Likely effect on the local canopy forming macroalgae**
Prior to 1996	Generally rougher conditions in the few years prior to 1996.	Greater damage to and loss of larger individuals.
1996 / 1997	Some rough weather and increased rainfall during winter and spring.	As above, increased rain may also bring with it, increased turbidity during the recruitment season (spring).
1997 / 1998	El Niño; Calmer and warmer than normal, with increased rainfall during winter and spring. Seas remained warm during summer, but with less than average rainfall.	Calm conditions would allow sediments to persist on the reefs for longer periods. Warmer conditions would have an inhibitory affect on recruitment.
1998 / 1999	Calm, average rainfall, warmer sea temperatures during summer	As above
1999 / 2000	Calm, average rainfall, sea temperatures less than average	Continued calm conditions would allow larger individuals to persist longer.

While the parameters reported here only represent a portion of those likely to influence macroalgal processes, they serve as a useful indicator to the types of events that may have led to temporally coherent patterns of change in the structure of these macroalgal assemblages. In broad terms, there was a consistent shift (at control sites) away from assemblages composed of a low density of adult individuals, with relatively open canopies (VLA type assemblages) towards assemblages largely dominated by a single genus.

This change in assemblage structure at control sites was largely consistent with the hypothesis presented in Chapter 3, where it was postulated that the VLA state was transitional. In the absence of continued disturbance, patches in this state would, over time, progress towards a closed canopy dominated by a single genus. The large number of VLA stands observed across reefs in the 1998 surveys would therefore be indicative of a broad scale disturbance of all assemblages for some period prior to the surveys.

The less favourable climatic conditions around this time, including above average wave exposure, may therefore provide a plausible mechanism for the low numbers of adult individuals reported in both the 1998 survey (this study) and the 1996 reef health surveys (Cheshire *et al.* 1998a).

Following the 1997 El Niño, climatic conditions became more typical (based on the long-term data: BOM 2002). Improved conditions correlate well with the increased densities of plants observed at control sites during subsequent surveys and similarly, reported by Cheshire & Westphalen (2000) over a broader geographical area. Indeed, assemblages at control sites became more similar in structure to those observed elsewhere in South Australia (Collings and Cheshire 1998; Turner and Cheshire 2003).

Overall, environmental conditions prior to and during the study were likely to have had a significant influence on macroalgal assemblages. There is evidence from the surveys that, at the time of the dispersed sediment plume, macroalgal assemblages across the study area, including those on impacted and control reefs, were in the process of recovering from an already degraded situation.

5.4.2 Different temporal trajectories

Phenomena that influence biological communities at more local scales may lead to differences between or within sites. This variability has the potential to confound the examination of the effect of interest and in many cases may manifest in terms of different temporal trajectories (Underwood 1994).

In some instances, it may be possible to minimise inter-site variability by using locations with similar environmental conditions (e.g. wave exposure and aspect) and overall assemblage structure. However, in the current study, the location of the impact sites was determined by the pattern of dispersal of the sediment plume (4.1.1), and control sites were subsequently chosen based on their proximity. As a result, several potentially confounding factors need to be addressed.

Environmental conditions between sites varied due to natural gradients in the system (e.g. longshore gradients relating to wave exposure) and proximity to point sources of stress (stormwater discharge and agricultural runoff through rivers and creeks or wastewater disposal). The presence of these different environmental conditions no doubt influenced the structure of macroalgal assemblages, with significant inter-site variation throughout the study (e.g. Figure 3.4; Table 3.4; Figure 4.5).

Another likely source of variation in algal assemblage structure is the physical aspect (flat or sloped) of a site or in its location on the reef (seaward or leeward) all of which are known to be important in influencing wave energy (Cheshire *et al.* 1998a; Turner and Cheshire 2003). In turn, differences in wave energy may influence both the biotic (e.g. growth morphology, Lobban and Harrison 1994) and abiotic conditions on the reef (e.g. settlement and re-suspension of particulate matter, Lewis 1968) and thereby strongly influence algal assemblage structure (Collings 1996; Collings and Cheshire 1998; Turner and Cheshire 2003).

The pattern of sediment removal appeared to be related to the level of wave exposure, with the more exposed seaward sides of the reefs clearing at a faster rate. Unquantified observations in 1999 identified similar levels on the seaward sides of Noarlunga and Horseshoe Reefs to that at Moana (an un-impacted site), whereas the more sheltered inner slopes still had elevated levels relative to Moana. Sediment levels on the insides of these reefs remained slightly higher over the following two years implying that conditions at these sites may naturally allow more sediment to persist.

The main point sources of stress present in the study area were concentrated in close proximity to the same sites that were affected by the sediment plume (treatment sites, Figure 5.2). It is possible therefore, that these sites experienced chronic impacts prior to the plume, and thus not surprising, that differences in adult assemblage structure (unrelated to the plume) were observed during the first survey (1998) when the impact sites were compared with the control sites (Table 4.4).

Biotic assemblages at individual sites responded differently to their localised environmental conditions, leading to temporal fluctuations in patterns from one place to another. For adult assemblages, these were revealed through the ANPMANOVA analysis (Table 5.3) as highly significant interactions ($p<0.01$) between survey year and treatment

(T(Before) and T(After) versus both Controls and Impact sites). This interaction can be illustrated by contrasting the changes in algal assemblage structure at different sites over the course of the study. The assemblages at the two flat reefs (Hallett Cove and Southport) were initially dominated by VLA assemblages and progressed towards a system largely dominated by the genus *Cystophora*. In contrast, the sites at Moana were essentially dominated by *Ecklonia radiata* (Figure 5.11, Figure 5.12) with density increasing throughout the period of the study. There is some indication from these findings that *Cystophora* is resilient to increased rates of sedimentation (which is naturally higher on flat versus sloping reef surfaces) and, as discussed below, the impact sites uniformly showed higher rates of recruitment of *Cystophora* relative to the other two genera.

Table 5.6 Environmental parameters that potentially influence inter-site variability.

Site	Exposure	Sedimentation†	Potential sources of stress
HAL	Flat	Moderate	None
HSO	Seaward	Decreased quickly	Christies Beach WWTP, Christies Creek
HSI	Leeward	Decreased slowly	
NNO	Seaward	Decreased quickly	Onkaparinga River, possibly Christies Beach WWTP. No fishing therefore possibly higher levels of herbivory than on the other reefs
NNI	Leeward	Decreased slowly	
NSO	Seaward	Decreased quickly	
NSI	Leeward	Decreased slowly	
SOU	Flat	Moderate	Onkaparinga River
MSO	Seaward	Constantly Low	None
MSI	Leeward	Constantly Low	

† Sediment observations are described in the text below.

5.4.3 The impact of the dispersed sediment plume

High levels of sediment were reported on Noarlunga Reef shortly after the occurrence of the dispersed sediment plume in 1997 (Havenhand 1998). Furthermore, although no observations were made at Horseshoe Reef, it has been assumed that it was also heavily impacted because the plume was observed to cover this area (R. Sandercock, *pers. comm. based on aerial observations*). In both cases, elevated levels of sediments (relative to levels at control sites) were still present at the time of the first survey (August 1998), and these declined over the following couple of years.

It was hypothesised that the most likely effect of the elevated sediment would be to increase mortality amongst newly recruiting individuals[18] and this was demonstrated to be the case (Chapter 4). Thus, the impact caused by the plume was evidenced in reduced numbers of juvenile algae surviving to one year of age at the impact sites relative to control locations (Chapter 4). Furthermore, these differences in the structure of the juvenile assemblage propagated through to the adult assemblage over subsequent years (Figure 5.11). Importantly it is likely that this chain of events led to further changes in the structure of juvenile assemblages, because of the known influences of adult canopy on recruitment, and it would be a number of years before the effects ceased being significant.

Notwithstanding the reduced numbers of juveniles at impact sites in 1998 it was expected that recruitment levels would recover in 1999 and beyond. This however did not happen and the number of juveniles[19] recruiting to VLA assemblages was substantially reduced in all years at the impact sites when compared to the control sites (Figure 5.7).

It is not clear, based on an analysis of the numbers of recruits under the adult canopy, why these differences persist into subsequent years. There were however, a number of confounding influences likely to have had a profound influence on the fate of these algal assemblages.

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[18] Defined as individuals that had recruited during the 1997 season and would have been 1 year old during the 1998 survey.

[19] This was not uniform across all species, with *Cystophora* showing higher levels of recruitment at impact sites during 1998 and 1999. This is discussed later.

Smith (2000) undertook an ecological study on interactions between the mussel *Xenostrobus pulex* and large canopy forming Fucalean algae at Horseshoe Reef. The study was motivated by observations that during the period 1996-1999 there had been a substantial change in macroalgal assemblage structure on both Horseshoe and Noarlunga reefs, with large areas being replaced by mussels (Cheshire and Westphalen 2000). The study concluded that reductions in density of the algal canopy had allowed mussels to become established. Once established, these mussel matrices inhibited subsequent algal recruitment and resulted in a persistent change in the structure of the assemblages.

This change in the assemblages was not anticipated at the time of the 1998 survey and therefore the survey design did not allow quantification of large areas of algal replacement. In fact this effect was so profound that the 2001 survey of Horseshoe Reef (this study) resulted in no algae being recorded on the Reef (and it has therefore been excluded from the analyses presented above; Figure 5.8, Figure 5.12).

Although survivorship amongst juveniles was low in 1998, *Cystophora* appeared to be less affected by the elevated sediments than the other two genera. Significant numbers of individuals were recorded at impacted sites during the first two surveys (1998, 1999; Figure 5.7). This possibly relates to the fact that members of this genus, although long lived and perennial, also display many traits of more adventitious taxa (Hotchkiss 2000).

Furthermore, even in the absence of more chronic impacts, differences are likely to persist for an extended period following the removal of excessive sediment. Arguably, assuming the average age of canopy plants is 5 years (inferred from Hotchkiss 2000) and that juvenile macroalgae take around 2-3 years to reach a size where they are classed as adults; it may be seven or more years before the effects of this disturbance are no longer observable.

5.5 Conclusions

Variability in the structure of canopy forming macroalgal assemblages at control sites appeared to be driven by two main processes. The first of these related to the adverse conditions prior to the plume, which resulted in a biomass loss evident on most metropolitan reefs (This study and Cheshire *et al.* 1998a). Following the establishment of more favourable climatic conditions, control reefs exhibited increasing population density and a transition towards mono generic-dominated stands as described in the previous section (5.4.1). This process was also evident initially (1998 → 1999) at the impacted sites, but was not sustained. Over the following two years (2000, 2001), there was a reversal of the above trend resulting in a significant reduction in adult numbers and a high proportion of VLA state assemblages.

The reasons for the decline in adult numbers at impact sites related to a recruitment failure, which appeared to be a direct result of elevated sediment levels from a dispersed sediment plume. Low levels of recruitment success were evident in both the 1997 and 1998 cohort. New recruits take between two and three years to reach adult size, depending on local conditions, meaning that these two cohorts would be expected to become adults between 1999 and 2001. The low numbers of recruits from these two cohorts were insufficient to replace adults lost through mortality, and thus led to the observed decline in adult numbers at impacted sites.

The second process leading to variability in the structure of the adult stand related to differences in local environmental conditions that led to a unique set of dynamics at individual sites. As a result, site conditions were variously suitable to each of the three dominant genera, leading to differences in the proportions of assemblages in each of the mono generic dominated states.

It is also worth noting that the impact sites used in this study were also subject to a number of other more chronic stresses including the Christies Beach WWTP and the Onkaparinga River. The fact that these perturbations are not new, but have been around for a few years may explain why the adult assemblages on Noarlunga and Horseshoe Reefs differed from those on the control reefs at the start of the study. In particular, higher levels of disturbance on these reefs may be linked to the higher proportion of *Cystophora* compared with control sites; given the genus has opportunistic life history traits.

Chapter 6

Summary and conclusions

This chapter provides a summary of the research undertaken in this thesis. It begins by briefly reiterating some of the important background information that led to the development of this study. This is followed by a summary of the major findings of the program, which are then placed in context by way of synthesis. An indication of future research directions is also presented.

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6.1 Background

Macroalgal communities dominate near shore reef systems across southern Australia and are an important structuring component of temperate marine environments (Shepherd and Sprigg 1976). However, a lack of systematic studies across relevant scales means that as a group they remain relatively poorly understood (Underwood and Kennelly 1990). This is especially true for South Australia because a significant proportion of taxa are unique to the area (Womersley 1990). As such, the ideas developed about macroalgal systems elsewhere may have limited relevance locally (Cheshire *et al.* 1998b).

Communities of macroalgae are often comprised of a number of separate strata, with large phaeophycean taxa tending to dominate assemblages in relatively shallow (< 15 m depth) environments in southern Australia (Shepherd and Sprigg 1976; Turner 1995; Turner and Cheshire 2003). The canopies formed by from these assemblages, exert a considerable influence on the remainder of the stand, and help create habitat complexity (Cheshire *et al.* 1998b).

Macroalgal assemblages tend to display large amounts of both spatial and temporal heterogeneity, much of which is likely to be driven by differences in environmental conditions on local as well as broader scales. Physical factors such as depth and wave exposure are known to have a strong influence on the composition of the stand (Shepherd and Womersley 1970, 1971, 1976, 1981), as are climatic conditions and biotic interactions. The interactions of these factors are likely to be multiplicative, and hence the combined effects on the system are likely to be complex, and not easily separated.

In addition to the influences that natural heterogeneity places upon macroalgal assemblages, Gulf St Vincent's eastern coastline has also changed over the last couple of hundred years as a result of the establishment of the City of Adelaide (Harbison 2002). Considerable urban development leading to increased nutrient and freshwater input along with pollutants and changes to natural regimes have all been implicated in the degradation of near shore marine communities (Cheshire *et al.* 1998b). The worst affected areas are those along Adelaide's northern coastline, where widespread loss of seagrass habitat and reef degradation is well documented (Cheshire *et al.* 1998a; Cheshire and Westphalen 2000; Seddon 2002; Cugley 2002).

In terms of macroalgal assemblages, anthropogenic impacts appear to have resulted in the loss of the large canopy forming taxa from reefs on Adelaide's northern metropolitan coastline (Cheshire *et al.* 1998a). There is also evidence to support a concomitant increase in systems that are structurally simpler, such as those dominated by turfing algae (Gorgula and Connell *in press*) or mussels (Smith 2000).

Elevated levels of sediment (review in Airoldi 2003), and pollution (Walker and Kendrick 1998; Gorostiaga and Diez 1996; Wu 1995; Hardy *et al.* 1993; Bellgrove *et al.* 1997; Soltan *et al.* 2001) are known to have a major impact on macroalgal communities, and are seen as the main anthropogenic sources of stress in South Australia (Steffensen *et al.* 1989a). Over the last few years, a considerable amount of effort has been put into reducing pollution loads entering Gulf St Vincent, largely due to improvements in wastewater management (Nicolson *et al.* 2003; Gaylard 2004). Unfortunately, issues of sedimentation have been less well addressed and are likely to remain a problem for a number of years (Nicolson *et al.* 2003).

Degradation of marine communities in areas south of Adelaide appears to be a more recent phenomenon and likely to be at least in part attributed to the increased amount of urban development in these southern suburbs over the last few decades. The reefs used in the present study were described as being in good to moderate health (Cheshire *et al.* 1998a) with some changes evident between 1996 and 1999 (Cheshire and Westphalen 2000).

There is therefore a need to build upon other local studies (Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976; Collings 1996; Collings and Cheshire 1998; Emmerson and Collings 1998; Cheshire *et al.* 1998a; Cheshire and Westphalen 2000) in order to develop an understanding of structure and dynamics within local macroalgal systems. In particular, knowledge needs to be compiled about patterns and processes under both natural and altered conditions in order to facilitate ecologically sustainable management of these ecosystems.

The aim of this thesis was to address some knowledge gaps relating to canopy forming macroalgal assemblages in South Australia. In particular, to look at the structure and stability of these systems under a range of conditions, as well as how they respond to / recover from anthropogenic impacts including elevated rates of sedimentation.

A large sediment plume, created during dredging in 1997 led to significantly elevated levels of sediment on two metropolitan reefs and provided a focal point for the research. Furthermore, the accidental creation of the plume enabled the impact to be experimentally examined at a scale that would not otherwise have been ethically possible.

6.2 Summary of key findings

Examination of canopy forming macroalgal assemblages on reefs within Gulf St Vincent revealed a structure that was largely comprised of a mosaic of patches. These canopy dominated patches appeared to exist in one of a finite number of states (Chapter 3). Most of the observed states tended to be dominated by a single genus, with individual plants present in sufficient density to produce a closed canopy. In the absence of disturbance, these assemblages appeared likely to persist through time due to emergent properties of stability linked to the life history strategies of the various taxa. In particular, a strong correlation was identified between the composition of the canopy and underlying juvenile assemblage (Chapter 3). As a result, it is proposed that members of the adult stand are highly likely to be replaced by juveniles of the same taxa, leading to a longer-term persistence of the state.

The alternative to the mono generic-dominated state described above, was a lower density state that was generally comprised of two or more different canopy forming genera. This alternative state was dubbed ‘Variable Low Abundance’ VLA. It is argued that this VLA state is transitory (Chapter 3) whereby processes of succession, operating on the stand through time, would favour the shift to one of the more stable mono generic dominated states. As such, the existence of patches in the VLA state indicated the presence of recent or ongoing disturbance at the scale of the patch.

Large numbers of VLA type assemblages were present at most sites surveyed in 1998 (Chapters 3 & 4), implying that algal communities on reefs across the study area were in a relatively degraded state. This degradation was attributed to unfavourable climatic conditions prior to the study (Chapter 5). In particular, it was argued that the area was subject to higher than average wave energies and extreme climatic conditions surrounding an El Niño event in 1997/98.

With the resumption of more typical climatic conditions, VLA assemblages were replaced by higher density mono generic stands, most notably at control sites. The reasons why this did not transpire at the sediment affected sites is addressed below.

In addition to the temporal changes observed during this study, a large amount of spatial heterogeneity was also documented. Broad scale variation in macroalgal community structure between sites, appeared to be consistent with the different environmental conditions exhibited at those sites. In particular, factors affecting wave energy as well as proximity to point sources of stress appeared to influence the overall structure of the stand. This had a confounding effect on the study because the sites impacted by the plume were also those most affected by other anthropogenic impacts. As a result, differences in the structure of adult stands were identified between the control and impact sites at the start of the study (Chapter 4), and it was argued that these were unrelated to the 1997 sediment plume. Notwithstanding, it is possible that these differences reflect a chronic effect of previous dredging.

At smaller scales, there may also be microhabitat effects, although the main driving forces involved biotic interactions such as competition and dispersal. Patches of canopy forming macroalgae were not randomly distributed across the substrate; instead, they displayed a level of structure. In particular, patches in alternate mono generic dominated states rarely abutted one another. Instead, an area of VLA generally acted as a buffer between the two. It was hypothesised in Chapter 3 that the presence of the VLA state under this particular circumstance might be indicative of strong biotic interactions between the two areas of closed canopy.

Having examined the key structural aspects of canopy forming macroalgal assemblages, their response to broad scale climatic influences, and changes associated with chronic disturbance, the impact of the dispersed sediment plume was addressed.

The initial impact of the plume appeared to be limited to elevated mortality amongst newly recruiting individuals. This led to widespread recruitment failure of the 1997 cohort, with diminished levels also apparent at impacted reefs in the following year. Over the following years of the study, low levels of recruitment success in 1997 and 1998 were propagated into the adult stand, resulting in lower densities of canopy forming taxa relative to that observed on the control reefs.

6.3 Stability and succession within macroalgal stands

Processes of succession have been documented in most ecosystems with the onset and duration of particular phases as well as the phases themselves being site specific (Kim and Dewreede 1996; Foster and Sousa 1985; Kennelly 1983). This study concentrated on large canopy forming macroalgae that are generally seen as being late successional species (Clayton 1990; Littler and Littler 1980), although some members of the genus *Cystophora* have been shown to possess a number of more adventitious characteristics[20] (Hotchkiss 2000). Furthermore, it appears that all the taxa examined are capable of forming persistent mono generic assemblages in environments with low disturbance regimes (Chapter 3, Turner and Cheshire 2003).

At the scale of the patch, mono generic stands appear to be resilient to small disturbances due to local recruitment and the ability of some offspring to survive below the canopy (Coon *et al.* 1972; Deysher and Norton 1981; Schiel and Foster 1986; Kendrick and Walker 1991). In an environment with higher levels of disturbance however, these mono generic patches may change to become a VLA assemblage (Chapter 5).

Under such circumstances the VLA state is essentially transitory and observations have shown that the composition of the underlying juvenile assemblage is more varied (Chapter 3, Turner and Cheshire 2003). As such, the composition of any future ‘climax’ state will be less certain and dependent on the surrounding environment, including both physical factors and the influence of other biological assemblages in close proximity (Kim and Dewreede 1996; Foster and Sousa 1985; Kennelly 1983). Hence, the patch may be seen as less stable over the longer term due to the increased uncertainty of future state, following disturbance (Horn 1974).

Within the reef environment, natural disturbances such as storm damage or herbivory tend to create point impacts, and it is unlikely that any particular event will completely denude a large area (Witman 1987; Sousa 1984). Thus at any time, only certain recently disturbed patches should exist in the VLA state, and it is expected that in the absence of further

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[20] As an example, *C. subfarcinata* is the most commonly found taxon across most of these reefs and has a number of adventitious traits (Kildea *unpublished data*; Hotchkiss 2000). In contrast, other taxa such as *C. monilifera* have a more late successional character (Hotchkiss 2000).

disturbance, secondary succession will occur (Kim and Dewreede 1996; Foster and Sousa 1985; Kennelly 1983; Horn 1974).

At any location, there will be a number of alternative stable states that the VLA patches may progress toward, and these will be influenced strongly by the suitability of different taxa to the local environment (Kim and Dewreede 1996; Foster and Sousa 1985; Kennelly 1983). In the event that a single genus has a clear advantage, this would be the likely outcome of the successional process. However, surrounding conditions may be confounding, and thus influence patch succession in two or more different but alternative directions (Kennelly and Underwood 1993; e.g. Santelices and Ojeda 1984; Worm and Chapman 1996). For example, if *Cystophora* bordered one side of a patch and *Ecklonia* the other, then the resultant biological interactions may disrupt successional process creating a state of perpetual imbalance. This would explain why patches in these two dominant states were never found to abut one another in this study (Figure 3.9).

Differences in the timing and extent of disturbances along with processes controlling the rate and direction of subsequent succession will (at broader scales, e.g. reef) lead to the appearance of a mosaic of patches (Sousa 1984; Turner and Cheshire 2003). It is likely that this mosaic will comprise of all locally suitable climax states, as well as transitional states (Horn 1974). Thus, uncertainty and state heterogeneity at small scales becomes an integral foundation for the emergence of complexity of structure over broader scales.

A simplified transition-state model representing this system is provided in Figure 6.1. In this model the VLA state is defined by the symbol V; Q is used to represent an assemblage in any of the alternative states with a mature closed canopy (*Ecklonia*, *Sargassum* or *Cystophora*). The model identifies a number of processes leading to persistence in any given state. In the case of the Q state successful recruitment leads to maintenance of a closed canopy. In the V state recruitment failure results in the community persisting in the VLA condition. Transitions between states include both recruitment driven processes (persistent failure leading to a shift from Q to V and recruitment success leading to a shift from V back to Q. Finally, the capacity for the system to quickly change from Q to V is driven by accelerated mortality (e.g. storm damage) leading to loss of many of the canopy individuals and degradation in the overall state of the community.

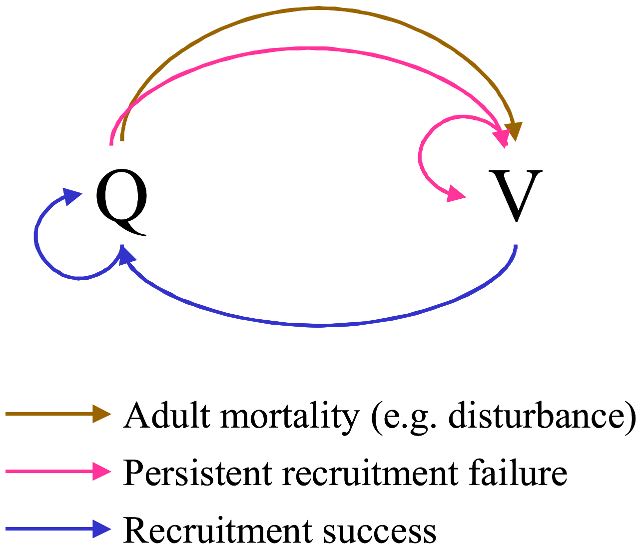

Figure 6.1 Basic transition state model.
The model shows the various pathways that would result in an assemblage persisting in a given state or transforming into the opposite state. V represents a low density mixed assemblage state (VLA) whereas Q may represent any mono generic dominated high-density state.

If the model is expanded to incorporate information about the spatial context of any individual patch (Figure 6.2) then the influence of heterogeneity in the system and the relative importance of transitions from a closed canopy state to a VLA state can be illustrated. In the examples shown, recruitment failure and/or the effects of physical damage can be used to illustrate the development of both transitory and persistent VLA states.

The model largely encapsulates the processes referred to in the preceding discussions and acknowledges the influence of disturbance processes on the survival of canopy plants, on recruitment processes and on spatial variability. Together these processes work to control (or influence) the structure of the resultant macroalgal communities.

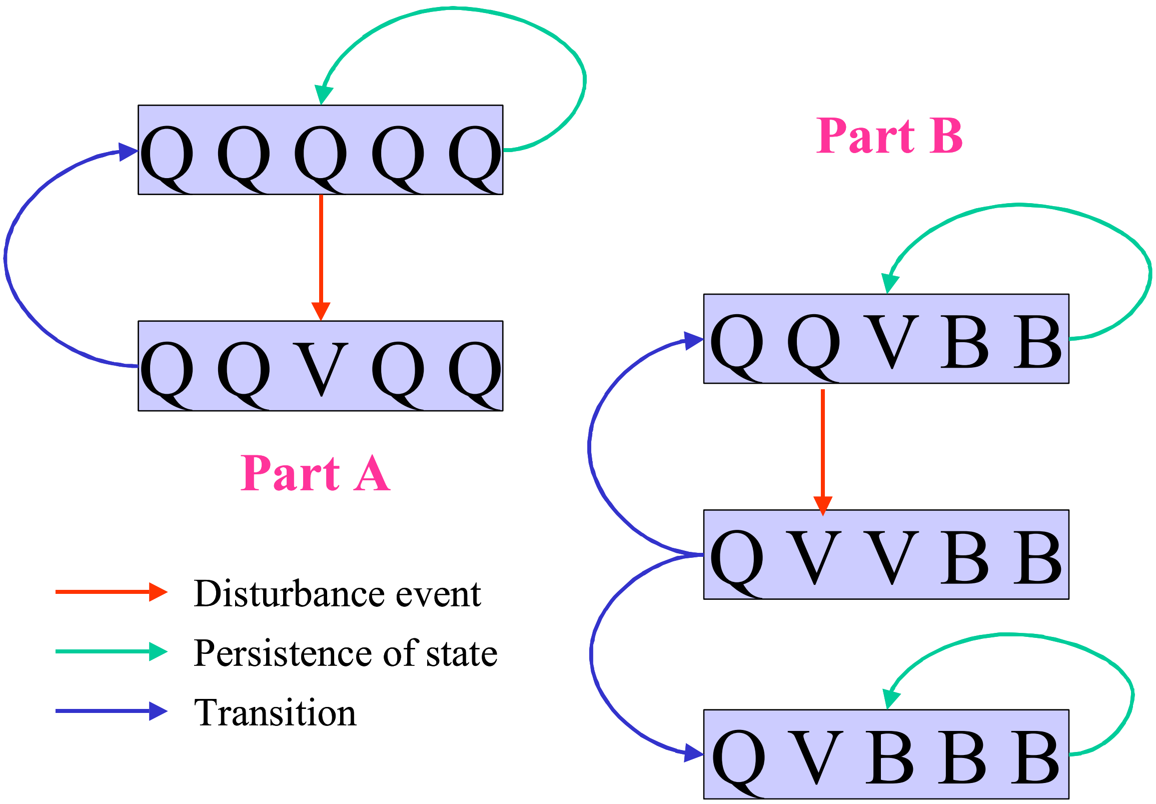

Figure 6.2 Transition state model using a spatial context.
V represents the VLA state while Q and B represent two alternative high-density mono generic dominated states. Part A: Illustrates the effect of a disturbance on a patch with neighbours in the same state. Part B: Shows that where the local environment comprised more than one state, persistent V states exist at the boundary, and following disturbance, succession may occur down more than one pathway.

In this model (Part A), the transitory VLA state (V) is taken to represent a patch that is changing through time in response to recovery from some form of disturbance. The model also hypothesises the existence of persistent VLA states. Although evidence for the existence of such systems is lacking, the model includes a speculative scenario in which high levels of inter-specific competition control recruitment in areas that sit between patches dominated by different species (e.g. a VLA patch sited between an *Ecklonia* and *Cystophora* dominated patch). Evidence for negative interactions and suppression of juvenile numbers of competing species has been widely reported including evidence for interference competition (Worm and Chapman 1996) or competitive exclusion (Worm and Chapman 1998). Similarly, Kennelly and Underwood (1992, 1993) report on the effect of an *Ecklonia* canopy in limiting sub-canopy diversity and Cheshire (1985) discussed similar processes operating to reduce sub-canopy diversity in *Durvillaea* dominated systems.

Formal testing for the existence of persistent VLA patches at the conjunction between mono generic patches of competitive species (e.g. *Ecklonia radiata* and *Cystophora* spp.*)* would need to be verified experimentally.

6.4 What remains to be done

There is a need for further research to follow macroalgal assemblages through time. In particular, it would be appropriate to formally test whether some VLA states are transitional (by examining whether they progress toward a mono generic state) and whether others are persistent (do not progress toward a mono generic dominated state).

In attempting to ascertain the existence of these two qualitatively different VLA states it would be useful to develop an experimental approach to examine the dynamic processes under different scenarios of neighbourhood conditions (i.e. sitting between patches of like vs. unlike species).

Other work that would support contentions developed within this thesis includes long term studies on recruitment success versus average water temperature conditions across the course of the reproductive season. This would evaluate the relative extent to which reproductive output of the 3 taxa (*Cystophora*, *Ecklonia* and *Sargassum*) changes over inter-annual time scales in response to temperature and explicitly whether inter-annual variability in recruitment of *Sargassum* (the pan-tropical genus) is less influenced by periods of elevated temperature than for the other two genera. Such studies would need to be undertaken at a species level to account for adapted taxa within each genus.

Collectively this will allow an analysis of the extent to which the putatively degraded state of the communities at the start of this study could be attributed to the unusual (El Niño and elevated storm frequency) climatic conditions over the 1996-1998 period.

It would be useful to also examine the influence of the spatial scale of impacts on the predictability of future states. Explicitly, whether areas formerly occupied by mono generic stands of one taxonomic group (e.g. *Ecklonia*) can change subsequent to a disturbance to dominance by another taxonomic group (e.g. *Cystophora*). Such a scenario was discussed by Collings (1996) who observed changes in the structure of macro-algal dominated communities from sites at Cape Jervis (further south in Gulf St Vincent).

This study demonstrated that macroalgal assemblages are equipped (under natural conditions) to handle ‘normal’ environmental fluctuations (such as inter-annual variability). However, the additional stress associated with certain anthropogenic impacts has the potential to push them over the limit, causing degradation. The loss of canopy macroalgae reduces the structural complexity of the system, leading to a concomitant reduction in their ability to recover. As such, these findings are of particular relevance to those charged with the responsibility for managing near-shore marine environments.

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Appendix I

Age determination in canopy forming macroalgae

In recent years, a number of studies have included information on growth rates in South Australian macroalgal stands (e.g. Emmerson and Collings 1998; Hotchkiss 2000; Fairhead 2001; Copertino 2002). Early growth of macroalgae tends to be a roughly exponential until factors such as self-shading and competition for space begin to limit this process (Emmerson and Collings 1998).

Juvenile *Cystophora spp.* reaches a length of 30 mm in an average time of 110 - 130 days. To reach 40 mm takes 130 - 160 days, and 50 mm, 150 - 200+ days, depending on local conditions. This rate is fastest where the plants recruit into open space (Emmerson and Collings 1998). Individual *Cystophora* plants recruiting onto settlement plates in the 1998/99 season achieved an average length of 106mm ±45mm by May 1999 (Copertino 2002).

Growth rates in *Sargassum* were slightly slower, taking 130 - 150 days to reach 30 mm in length and 160 - 200 days to reach 40 mm (Emmerson and Collings 1998).

Generally the recruitment period for macroalgae occurs between July and December each year (allowing for variation in local environmental conditions, Hotchkiss 2000).

These above studies indicate that individuals larger than 30 mm in length are likely to be at least 3 to 4 months old. Given surveys were carried out near the start of the recruitment season (August), individuals of this size or larger are highly unlikely to have recruited in the current season. Similarly the maximal lengths obtained in a twelve-month period are unlikely to be more than 200 mm; hence the majority of larger individuals (>200 mm) will be older than one year.

This information was used as the basis for the age / size classes described in Table 3.2 as a basis for categorising the macroalgal community.

Table I.1 Juvenile macroalgae age / size class parameters.

Category	Size (mm)	Age of recruit
1	<15	New recruits
2	15-30	New recruits
3	31-50	One year old -
4	51-100	One year old
5	101-200	One year old +
6	201-300	Two year +