



**SPATIOTEMPORAL VARIATION OF MACROALGAL
COMMUNITIES OF SOUTHERN FLEURIEU PENINSULA,
SOUTH AUSTRALIA**

by

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For those who have inspired a love of learning

...and those who are equally inspirational in their quiet support.

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List of Abbreviations

AIPW	Average Individual Plant Weight
ANOVA	Analysis of Variance
B5	The Bluff (5 metres)
CJE5	Cape Jervis East (5 metres)
CJN5	Cape Jervis North (5 metres)
CJN9	Cape Jervis North (9 metres)
GI5	Granite Island (5 metres)
NMDS	Non Metric Multidimensional Scaling
PCC	Principal Canonical Correlation
SSH	Semi-Strong Hybrid Analysis
SV5	Second Valley (5 metres)
UPGMA	Unweighted Pair-Group Method using Arithmetic Averages
WI5	Wright Island (5 metres)
WI9	Wright Island (9 metres)

Standard International units are used throughout the thesis

Mass expressed as dry weight (either g dwt m⁻² or kg dwt m⁻²)

Summary

The temporal dynamics of eight subtidal mixed macroalgal communities were quantified. These were situated along a 100km region of coastline at the foot of Fleurieu Peninsula (South Australia) and encompassed a broad range of wave exposure regimes. Biomass, abundance and average plant weight were examined using 3-monthly sampling over 27 months in order to identify seasonal and annual variation. Composition and dynamics of these communities were related to the exposure of the sites using a combination of univariate (ANOVAs and regression) and multivariate (Bray-Curtis association measures, UPGMA classification and SSH ordination) statistical methods.

The nature of the spatial patterning at scales ranging from 10cm to 4km was examined at two sites of differing composition using a spatially structured sampling regime. The stretches of coast where this sampling was undertaken were physically uniform, in order to obtain an estimate of the variation attributable to biological interactions and processes. Mapping, univariate statistics, multivariate techniques and semivariates analyses were applied to these data in order to describe the spatial scales of the patterns observed.

A total of 84 species and species complexes were identified across the course of the study, with 15 of these being found in the canopy, and the remainder in the understorey. Of these fifteen, between 7 and 14 species were found at any one site, with the most exposed sites supporting the lowest number of canopy species, presumably because of the inability of some species to tolerate the extreme conditions.

Biomass, which ranged between 500g dwt m⁻² and 1700g dwt m⁻², was maximal at sites of medium to high water movement. It was significantly lower at the most exposed of the sites.

Species richness of the canopy was highest in samples of moderate biomass, the implication being that high biomass samples were generally dominated by a single species capable of producing high biomass stands, while low biomass stands may also have low species richness because of a disturbance event or unsuitability of the substrate.

Some, but not all, of the communities demonstrated relationships between density and average weight which were in concordance with the 3/2 thinning law. In those which did display such a relationship, the height of the boundary line varied considerably, demonstrating log K values of between 3.8 and 4.6.

The temporal changes demonstrated by these communities were quite considerable, with 2 to 6-fold variation in biomass levels of each of the species. In some species the fluctuations were seasonal and relatively predictable, while others varied significantly in an unpredictable, non-cyclic manner.

Multivariate assessment of the temporal fluctuations, using a novel method developed in this study, demonstrated a remarkable degree of similarity in seasonal change across the eight sites and two years. The exception to this was the spring change, which was highly variable between sites, probably the result of recruitment events. This was reflected in the ordination and classification of the community composition supported by the sites in each season. Typically, the summer composition was quite dissimilar to the other seasons, but the non-summer seasons were in two groups representing the two years. The composition of the non-summer seasons was most closely related to the summer preceding them, indicating that the

effects of the unpredictable spring change are felt throughout the following year, until the next spring.

These results were discussed in terms of the implications for sampling programs in the future and the reliability of previous work. The conclusion was that the high seasonal and annual variation necessitated sampling regimes which incorporated these changes if reliable estimates of community composition were to be obtained.

Spatial variation appeared to be greatest at the smallest scales (10 centimetres), which, it is proposed, was the result of microtopographical differences and highly localised dispersal. In general, progressively less variance was expressed as the scale increased, while the physical environment remained relatively uniform. However, for several species, significant differences were apparent between areas separated at different scales. In general, the temporal change was not as great as the spatial variation within the study sites (in terms of the variation between 1m² samples).

Species associations were remarkably similar between sites, and across scales, ranging from 10cm to 2km. In each case, there were four relatively clear associations. *Sargassum* species formed one group, with the *Cystophora* species constituting a related, but still distinct group. A third association consisted of the rarer species, and the fourth group was comprised of larger species which were not so much associated with each other, as disassociated from all other species. This, it was proposed, was a result of their size and ability to outcompete other nearby species. By contrast, *Cystophora* and *Sargassum* species, which were smaller, tended to coexist far more readily.

Importantly, this work provided a basis for the proposal of the important structuring processes which affect these communities. The magnitude of variation within an area of uniform physical environment is an indication that biological interactions are of enormous importance in the patterns and dynamics of these communities. Large scale patterns may in fact be due to the cumulative effect of biological interactions over extended periods of time. This view represents a deviation from previous studies of mixed macroalgal stands in these waters which have concentrated on physical factors such as light and water movement.

Declaration

This thesis contains no material which has been submitted or accepted for a degree or any other award in any university. To the best of my knowledge and belief, the thesis also contains no material previously published or written by another person, except where due reference is made in the text.

I consent to the thesis being made available for copying and loan, if accepted for the award of the degree.

Gregory Collings.

Acknowledgments

“So he took hold of Pooh’s front paws and Rabbit took hold of Christopher Robin and all
Rabbit’s friends and relations took hold of Rabbit, and they all pulled together....
And for a long time, Pooh only said “Ow!”...
And “Oh!”...

A.A. Milne
Winnie - the - Pooh

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Chapter 1 Overview and Aims

1.1 General Rationale

The most comprehensive review of macroalgal ecology in southern Australia (Underwood and Kennelly 1990a) described the paucity of temporal and spatial community descriptions as astonishing. They went on to say;

"A major challenge for future research by Australian algologists and marine ecologists is to design and complete a series of detailed quantitative studies to describe the patterns of distribution and abundance of inter- and subtidal algae at many more locations around the coast. To be of any value, these must include appropriate spatial and temporal replication to estimate variances among and within shores and among years and seasons. These would form the basis for geographic and regional comparisons that are currently impossible, and would also provide a firm base for comparing Australian assemblages with those in other parts of the world. The *next* stage (my italics) of investigation will then be more experimental analyses of the processes causing the observed patterns."

The present study aims to address this object with a detailed investigation of the temporal and spatial patterns demonstrated by the subtidal macroalgal communities of lower Fleurieu Peninsula (South Australia). Whilst it is restricted to a region of coastline of approximately 100km, the sites represent a wide range of habitats. This should provide the opportunity for wider comparison and the formulation of informed hypotheses concerning the processes which control the system.

1.2 Thesis Layout

This first section presents a rationale for the study and describes the layout and specific aims.

This is followed by Chapter 2 which is a summary of our knowledge of the ecology of macroalgal stands of southern Australia. Chapter 3 describes the geographic and physical setting of each of the study sites while Chapter 4 describes the macroalgal communities supported by these sites and makes cross site comparisons. In Chapter 5, a multivariate methodology for the comparison of temporal changes is developed and tested on simulated data sets. This technique was developed to provide a tool for the analysis of temporal changes in communities presented in Chapter 6. In this chapter the temporal changes which these communities demonstrated are detailed and their generality and likely causes discussed. Chapter 7 investigates the spatial patterns exhibited by two of the communities at scales ranging from centimetres to kilometres and discusses the processes which may be involved and the implications for future study of these systems. The eighth chapter acts as a synthesis which puts spatial and temporal variation into perspective. This allows a general picture to be assembled which describes the relative contribution of temporal and spatial variation (at each of the scales measured) to the overall community structure. The final chapter concludes the thesis by detailing the important findings of the study, their implications and the suggested directions of future research.

1.3 Specific Aims

In providing the first properly replicated description of the temporal fluctuations and spatial patterns in subtidal mixed macroalgal stands of southern Australia, there are several specific aims to be addressed:

- To identify the common canopy-forming species of the region and assess their relationship with wave exposure.
- To assess the relationship between density and average plant weight of these communities in

light of the 3/2 thinning law (Yoda *et al.* 1963).

- To determine if there is a relationship between biomass and species richness and attempt to propose likely explanations.
- To develop an effective methodology for the comparison of multivariate change across sites of differing composition. This was necessary after it became obvious that the traditional method was inadequate.
- To quantify the seasonal and annual changes of these communities in order to;
 - a) assess the need for incorporating temporal change in the estimation of community composition of communities in these waters.
 - b) compare fluctuations with those of communities at other locations.
 - c) provide an informed basis for the proposal of hypotheses to explain the dynamics of these communities.
- To investigate the spatial patterning of the biota apparent at two sites at a variety of scales in order to;
 - a) provide a properly replicated and described baseline for future comparison both within Australia and overseas.
 - b) quantify the amount of variation attributable to different spatial scales within uniform physical environments.
 - c) make informed proposals regarding the important structuring processes within these communities.
 - d) assess previous sampling regimes with a view to improving these in future studies.
- To quantify the partitioning of the biotic variance between temporal and spatial variation.

Chapter 2 Background

2.1 The importance of spatial and temporal scales and their description in ecology - a theoretical rationale

Community ecology is the study of the patterns of distribution and the processes and interactions which give rise to these (Diamond 1986; Wiegand 1989). It is an immensely complex subject which continually beggars attempts to provide universal answers (Foster 1990). These attempts have largely resulted in gross oversimplifications (Caffey 1985; Schiel 1990; Kennelly and Underwood 1993; Underwood and Petraitis 1993) which have often hindered the progress of our understanding (Kennelly and Underwood 1990).

Processes may be responses to the physical environment, or may involve biotic properties of the organisms (eg reproductive effort, dispersal mechanisms, longevity) or interactions between members of the community (eg mutualism, competition and predation) (Roughgarden and Diamond 1986). Clearly these categories are not exclusive. For example, competition, a biotic interaction, depends on limiting levels of one or more physical resources (Schoener 1983; Begon *et al.* 1986; Yodanis 1986). Stochasticity, ie the unpredictable effect of chance events, such as disturbance, can also play an important role in shaping the community (Connell 1978; Dayton and Tegner 1984; Sousa 1984a and b; Chesson 1986; Pickett *et al.* 1989; Chaneton and Facelli 1991; Haydon *et al.* 1993). Thus the community structure at any point in time is the result of an accumulated history of abiotic factors, biotic properties and stochastic events. With so many interacting variables, it is unsurprising that generality is such an elusive quality. In light of this, the most productive course for ecology, one supported by Underwood and Denley (1984), May (1985) and Schiel and Foster (1986), is investigating the generality of

phenomena in order to provide a series of rules which typically apply to given types of communities under specified situations.

One of the problems associated with recognizing community types and situations is the question of scale. There are two types of scale which must be considered - spatial and temporal (Butler 1991). Processes act on different scales to produce complex and often nested patterns (Dayton and Tegner 1984; Sousa 1984a and b; Palmer 1988; Acker 1990; Kotliar and Wiens 1990; Orians and Wittenberger 1991; Irlandi 1994). Spatial scales may range from the micrometres involved in questions of pheromones and microtopography (eg Maier *et al.* 1992) to the biogeographic scale involving thousands of kilometres (eg Womersley 1990). Temporal scales of importance vary widely, according to the individual in question and the feature under investigation (Dayton and Tegner 1984). This may be as short as the milliseconds involved in lightflecks and their impact on photosynthesis to the tens to millions of years involved in questions of evolutionary significance. While it is clear that different processes may act on different scales (eg competition and temperature tolerance), a single variable may act on widely disparate scales (see Deysher and Norton 1982; Collins and Glenn 1990). For example, wave force may be consistent along hundreds of kilometres of coastline, yet also vary considerably because of local features such as reefs (eg Shepherd and Womersley 1981; Hatcher 1989).

Dealing with the complexity of multiple scales

A useful way of viewing the problem of multiple scales is presented by hierarchy theory (eg Allen and Starr 1982; Urban *et al.* 1987; Kolasa 1989; Acker 1990; Kotliar and Wiens 1990; Lavorel *et al.* 1991; Fox 1992). This perspective involves portraying a system as a series of hierarchical relationships. A single level of the hierarchy may then be thought of as a component of the level above. Similarly, the level above operates to set constraints on the behaviour of lower levels (Acker 1990). This then acts as a framework which can be used to

demonstrate relationships of entities at different levels. It should be added that while this allows the dissection of a single level from a complex spatiotemporal context (Fox 1992), it is unusual that only one hierarchy is important. In general, principals derived at one level are not necessarily applicable at another (O'Neill *et al.* 1986 cited by Fox 1992; Farmer and Adams 1989). Constraints of an upper level may be clear at lower levels, but only rarely is it possible to predict higher level behaviour from lower level phenomena. Sometimes this is because not all the lower level properties are known. However, it is frequently due to the fact that the behaviour of the whole is not equal to the sum of the component parts. Higher order interactions (eg Worthen and Moore 1991; Wissinger and M^cGrady 1993) and synergisms (Underwood 1989), whereby factors have complex, often unpredictable interplay, are commonly the cause of this occurrence.

It is imperative that ecologists carefully choose the spatial and temporal scales of their study to match those of the phenomena that they are dealing with (Pickett *et al.* 1987; Underwood and Petraitis 1993). Too many ecologists either fail to do this (eg Padisak 1994 - see Wilson 1994a), or expect to see similar patterns at vastly different scales, where different processes could be expected to act (eg Gladfelter *et al.*'s (1980) comparison of their results with those of Sale and Dybdahl (1975)).

However, in selecting a scale, choices have already been made about the nature of the results and the conclusions which will be inferred (Canny 1981; Wiens *et al.* 1986; Wiegand 1989; Lavorel *et al.* 1991). While certain interactions may be discernable at the chosen level of scale, the researcher has become blinded to processes operating on different scales (Dayton and Tegner 1984). It is thus important to remain cognizant of the fact that the ecosystem is a multi-level hierarchy (Foster 1982; Acker 1990) and choose scales of observation carefully whilst remaining open to the possibility of interactions from other levels. This holds for any

level of study from the investigation of a single factor (eg Caffey 1985; Poiani and Johnson 1989), to theoretical concepts such as community stability and perturbation (Sutherland 1981; Dayton *et al.* 1984; Sousa 1984a).

Too often ecologists restrict the scale of their experiments in order to produce tractable, publishable results (Dayton and Tegner 1984). This practice, particularly in the case of experimental studies, leads to a proliferation of studies proclaiming the importance of certain processes. Over time, these hypotheses may reach the status of paradigms without any structured effort to determine their generality (Underwood and Denley 1984; Foster and Schiel 1988; Foster 1990). Foster (1990), for example, demonstrated that the widespread influence of urchins on kelp forests was far from the general effect which it was purported to be. Studies of this nature are vital in order to assess the generality of processes objectively.

The effects of scale on ecological systems

While it has been demonstrated that questions of scale are central to the intentions of the researcher, perhaps of greater importance is the way in which the biota interacts with its environment at different scales (see Kotliar and Wiens 1990). Scale is not only a question of human perception; its boundaries have an effect on processes themselves (Sousa 1984b; Gillanders and Brown 1994). Theories such as island biogeography (MacArthur and Wilson 1967; MacArthur 1972), metapopulation dynamics (Levins 1969; Kareiva 1986; Menges 1990; Collins and Glenn 1991; Hanski and Gilpin 1991) and even the intermediate disturbance hypothesis (Connell 1978; Wilson 1994a) depend intrinsically on the effects of spatial and temporal scale. Central to the concept of island biogeography and metapopulations are questions of the scale of separation of habitable areas and dispersal/migration distances of the biota (Day 1995). Perhaps the most obvious consequence of spatial boundaries is the effect on density. Effects arising from differing density are diverse, ranging from modification of animal

behaviour (eg Nagoshi 1967 cited by Gascon and Travis 1992) through effects on plant size (eg Cousens and Hutchings 1983; Cheshire and Hallam 1988a), survivorship (eg Begon *et al.* 1986) and fecundity (eg Watkinson and Davey 1985) to questions of gene flow and evolution (eg Lande 1988).

The roles of descriptive studies

Numerous authors have stated that experimental manipulation is required to prove and disprove hypotheses (eg Levins and Lewontin 1980; Underwood and Denley 1984; Diamond 1986; Shipley and Keddy 1987; Mentis 1988; Wiegleb 1989; Underwood and Kennelly 1990a). Ecology has become increasingly enamoured with the use of experiments to determine the actions of processes (Andrew and Mapstone 1987) to the detriment of quantitative descriptive work. While the requirement for hypothetico-deductive techniques is not denied, properly designed quantitative description still has a very real place in the advancement of ecological knowledge (Schiel 1988).

Descriptive studies, if properly designed, are an extremely important initial step in the understanding of an ecosystem (Andrew and Mapstone 1987). Popper (1959) espoused a view of scientific endeavour which has been adhered to by many ecologists for decades (Diamond 1986). This involves the rigorous testing of hypotheses which have been derived from inspiration (Mentis 1988). Apart from the obvious practical difficulties in keeping hypotheses from becoming influenced by knowledge, it is also counter-productive (Suppe 1977; Diamond 1986). However, while the utility of a pluralistic approach to ecology has been widely promoted (Allen and Starr 1982; Diamond 1986; Mentis 1988), any cursory examination of the marine ecological literature reveals that descriptive study "has become the poor cousin of experimental work" (Andrew and Mapstone 1987). In systems which are not well understood, descriptive study provides the basis on which to hypothesise as well as design

appropriate sampling strategies (Palmer 1988). It is the proper precursor to experimental work which allows minimisation of the time otherwise wasted in testing wild conjectures (Diamond 1986; Mentis 1988).

-the formulation of hypotheses

The most common role for descriptive studies is in the generation of hypotheses (eg ; Andrew and Mapstone 1987; Rice and Kenchington 1990a and b). The scales at which variation is demonstrated and the features which are associated with that variation give an important insight into the factors and processes which are *likely* to be important to the community under observation (Andrew and Mapstone 1987; Mentis 1988). From this, it is possible to objectively assess the generality of patterns and propose experimental design to investigate processes which are implicated.

-assisting experimental design

One of the shortfalls of many ecological studies is the problem of pseudoreplication, which involves drawing unjustifiable conclusions from experiments where treatments are not replicated (Hurlbert 1984). No amount of replication of samples within the treatment can remedy this. An example might be the comparison of two areas which differ in terms of a given environmental factor. Any conclusion that a difference between two populations is caused by a given environmental factor is confounded by the fact that different patches may have different biota, regardless of the environmental factor under consideration. Given the constraints of time and resources which typically dog ecological research (Green 1979; Dayton and Tegner 1984), it may not always be possible to sample the entire area or length of coastline. Sampling may in that case be assisted by a knowledge of the patch structure of the community in question. If large scale patches are evident in the vegetation across an area

representing a "treatment" (see the "natural experiments" of Diamond (1986) or "mensurative experiments" of Hurlbert (1984)), then it may be necessary to conduct experiments in each to interpret the effect in an unbiased manner (Hurlbert 1984; Andrew and Mapstone 1987; Morrissey *et al.* 1992).

A related problem which often occurs unnoticed in ecological studies is lack of independence (Underwood 1981a; Underwood and Denley 1984). This is technically a form of pseudoreplication (Hurlbert 1984). Independence of replicate measurements is essential for the application of inferential statistics such as ANOVA and regression techniques (Sokal and Rohlf 1981; Underwood 1981a; Zar 1984). Furthermore, no transformations can solve the problem and non-parametric equivalents are also invalidated (Palmer 1988). In a statistical sense, independence implies that there is no level of predictability associated with any underlying feature not considered in the model. The assumption of independence is violated when, for instance, samples are separated by less than the distance of a known patch size. In that case, two quadrats would fall in the same patch and therefore given a knowledge of one, it is possible to predict that the biota of the other is likely to be similar. If, however, the samples are spaced by more than the size of the patch, there is no level of predictability. It is a fallacy that random placement of samples overcomes this (Palmer 1988). The problem becomes recognizable only through pattern description, and even then it may demonstrate that there is no way to sample the system without violating the assumption of independence. This is, however, better than ignorance of the problem.

Power analysis acts as an important guide to sampling efficiency and to the level of certainty associated with a statistical conclusion (Underwood 1981a; Andrew and Mapstone 1987). As a post-hoc analysis, it is used to demonstrate the likelihood that statistical significance was not achieved because of the true lack of difference, as opposed to an insufficient level of sampling

(Sokal and Rohlf 1981; Zar 1984). Conversely, this form of analysis can be applied to pilot study data in order to design an efficient sampling program which is likely to detect significant differences if they truly exist (Underwood 1981; Zar 1984; Andrew and Mapstone 1987). These power analyses may address simple questions such as the required number of replicates a t-test requires for reasonable surety of obtaining a correct result, or they may be complex cost-benefit studies applied to nested ANOVAs (eg Irish and Clarke 1984; Kennelly and Underwood 1984). Whatever the level of sophistication, they are based on a knowledge of the levels of variance exhibited by the community under question.

Accurate description of the patterns in the biota is an important step which both prepares for a sound research program and allows a more thorough interpretation of the results obtained (Andrew and Mapstone 1987; Foster 1990; Underwood *et al.* 1991). Hypotheses can be generated in a far more informed manner, effective sampling programs can be designed, the possibility of pseudoreplication and lack of independence can be assessed, and the generality of conclusions can be appraised quantitatively. Descriptive studies, while not in favour amongst some ecologists because of their lack of controlled experimental manipulation (Diamond 1986), still have an extremely important role in our understanding of ecological systems (Andrew and Mapstone 1987; Mentis 1988; Underwood *et al.* 1991; Kennelly and Underwood 1992).

Rationale for this study

Underwood and Kennelly (1990a) reviewed the status of marine ecology in Australia and concluded that quantitative descriptive studies which assess spatial and temporal variation were extremely rare. Furthermore this was a problem which had to be addressed in order to facilitate our understanding of both the individual systems and the development of general ecological theories. To date, a lack of this knowledge has rendered comparison with overseas

studies an impossible task. Until accurate knowledge of the scales of spatial and temporal variation is obtained, we have no knowledge of the generality of our conclusions (Foster 1990; Schiel 1990; Underwood and Kennelly 1990a; Kennelly and Underwood 1992; Morissey *et al.* 1992).

This thesis aims to address the concerns of these authors through a study of the mixed macroalgal communities of southern Fleurieu Peninsula. It examines temporal variation on a seasonal basis across a period of more than two years and investigates the spatial patterning apparent on scales from 10cm to ≈ 100 km. This work should act as the basis for well designed studies investigating the processes which control these communities as well as assisting interpretation of both previous and future studies.

2.2 Introduction to Southern Australian Phaeophycean

Dominated Macroalgal Stands

Overview

Southern Australian macroalgal ecology remains poorly understood in comparison to the adjacent intertidal areas and subtidal macroalgal stands elsewhere in the world (Underwood and Kennelly 1990a). While there has been a significant amount of research in the field, it has not been done systematically, resulting in a fragmented view of the system (Underwood and Fairweather 1986; Underwood and Kennelly 1990a). Thus, much of our knowledge more closely represents the distributions of the biologists rather than the distributions of the biota (Womersley 1981a; Underwood and Fairweather 1986). The scale of ecological research is often reduced to ensure tractable results (Dayton and Tegner 1984) and because of the financial considerations of scientific research (Foster 1990). The result has been proliferations of different types of research in a few different areas. Subsequently, we have little idea of the generality of the findings across the distributions of the species (Underwood and Denley 1984) or the generality of processes in different community types. Thus, when we try to draw this knowledge together, we suffer from an "assumption of homogeneity and the illusion of generality" (Foster 1990).

The southern Australian coastline is vast and varied. It extends for 5,500 km and takes in both warm and cold temperate regions. Water temperatures are in the range 10⁰C to 19⁰C with an annual variation of around 5⁰C at any particular location (Womersley 1990). It should be added that sheltered bays and inlets will demonstrate a wider range as they are more influenced by air temperatures. This part of the Australian coastline expands over three biogeographic provinces, the Flindersian (including the Maugean subprovince), Peronian and the southern

portion of the Dampierian province (Fig. 2.1), and supports an extremely rich algal flora (Womersley 1984).

The Peronian province, which is classified as warm temperate, is represented by southern Queensland and New South Wales, while the Flindersian province is cooler and stretches across Victoria, Tasmania, South Australia and the southern part of Western Australia (thus encompassing all sites used in this study). The Maugean subprovince, which exists within the Flindersian province, includes Victoria, all of Tasmania and extends into South Australia as far west as Robe. It is here that a cool water upwelling ceases and with it the higher nutrient levels associated with this phenomena. It is significant that the two most massive genera of the Australian flora (*Durvillaea* Bory and *Macrocystis* C. Agardh) are found no further west than this. Womersley (1981a) asserts that the algal flora is consistent with the scheme of Tasmania and Victoria being classified as cold temperate (and hence a subprovince) while the rest of southern Australia, to the west of Robe (which is part of the Flindersian Province), is transitional cool to warm temperate.

Knowledge of southern Australian macroalgal stands is geographically fragmented, partly due to the distributions of the biota and partly to the interests and areas of Australia's phycologists. A broad brushstroke picture of Australian macroalgal ecological research reveals that most of the work in Western Australia has centred around *Ecklonia radiata* (C. Agardh) J. Agardh (eg Kirkman 1981, 1984, 1989; Hatcher *et al.* 1987; Wood 1987) and species of the genus *Sargassum* C. Agardh (Kendrick and Walker 1991, 1994; Kendrick 1994). South Australia is noted for the pioneering studies of Shepherd and Womersley (1970, 1971, 1976, 1981) which investigated the patterns in the biota as they related to depth and waveforce at various sites across the state. Tasmanian work is a mixture of ecological descriptions (eg Sanderson 1987a and b; Sanderson and Thomas 1987) and more recently, studies on the invasive Japanese alga,

Undaria pinnatifida (Harvey) Suringer (Sanderson and Barrett 1989; Sanderson 1990). New South Wales has produced a substantial quantity of work on the structure of *Ecklonia radiata* forests and the interactions within them, much of which addresses the question of large scale generality, at least within that state (eg Underwood *et al.* 1991; Kennelly and Underwood 1992, 1993). The bulk of the knowledge concerning the giant *Durvillaea potatorum* (Labillardiere) Areschoug emanates from Victoria, but covers the extent of the distribution (Cheshire and Hallam 1985, 1988a and b, 1989a and b).

The remainder of this introduction is a precis of our knowledge of these systems and the processes which operate within them. Where possible, an attempt will be made to gauge the generality of the findings through comparison between studies.

Macrocystis

Macrocystis is, along with *Durvillaea*, Australia's most massive genus. Belonging to the order Laminariales Kylin, it is one of the few true kelps that exist in southern Australia, where it is apparently represented by two species - *M. pyrifera* (Linnaeus) C. Agardh and *M. angustifolia* Bory. However, the distinction between these two species is dubious (H.B.S. Womersley pers. comm.). *Macrocystis* is restricted to the cooler, nutrient rich waters of the south and east, being found through Victoria, Tasmania and as far west as Robe (South Australia) (Womersley 1987).

Ecological work on *Macrocystis* in Australia is restricted to Tasmania, where it occurs extensively. However, in only one case (Sanderson 1987b) is *Macrocystis* the focus of the research. In other cases, the emphasis has been on the community composition and ecology of a whole area, certain parts of which were dominated by *Macrocystis* (eg Sanderson and Thomas 1987). Sanderson and Thomas (1987) concluded that *M. pyrifera* tends to form

patches of overstorey canopy when depth is greater than 9m, while Womersley (1987) places the upper limit at 6m. *M. angustifolia* however (assuming that it is a separate species), can dominate at depths of less than 1m (personal observations). According to Sanderson and Thomas (1987), the understorey typically consisted of species of Rhodophyta and occasional *Ecklonia radiata* plants.

It is not surprising, with the paucity of ecological work on this genus in Australia, that our understanding is based largely on the voluminous literature of the northern hemisphere (eg Dayton *et al.* 1984, 1992; Dean and Jacobsen 1984; Dayton 1985a; Ebeling *et al.* 1985; Gerard 1986; Reed 1987; Burgman and Gerard 1990) rather than knowledge of our own systems. However, from the work of Sanderson and Thomas (1987), it would appear that light is the principal factor involved in the distribution of communities. Water movement was also important, but played a secondary role. This is perhaps oversimplified and is better explained by Shepherd and Womersley (1970), who discriminated between vertical and horizontal distributions and concluded, for the systems that they were investigating, that while light was the principal influence on vertical (depth) distributions, water motion was the main influence on horizontal distribution. While these communities were not *Macrocystis* communities, this appears to represent a better way of expressing the findings of Sanderson and Thomas (1987).

Growth rates of *M. pyrifera* were maximal in terms of number of blades produced in spring, but achieved greatest extension in winter. It is proposed that this anomaly is the result of the plant trying to maximise light reception when the light levels are low by getting maximal photosynthetic area to the water surface (Sanderson 1987a). When light levels are high, in summer, the photosynthetic area is maximised, but the proximity to the surface appears not to be as important, perhaps because depth becomes less critical in a higher light environment.

Ecklonia radiata

Amongst Australia's most widespread macroalgal species, *Ecklonia radiata* (hereafter referred to as *E. radiata* or simply *Ecklonia*) is distributed around the mainland coast from Caloundra in Queensland, to Kalbarri in Western Australia and throughout Tasmania (Womersley 1987). The global distribution also includes New Zealand and South Africa. It grows at depths from 44m to almost the subtidal fringe; these extremes being dependent on the water movement at that site, with high water movement required for it to exist at great depth, but considerably less if it is to survive toward the upper limit of its depth distribution (Womersley 1987).

Ecklonia radiata's ubiquitous nature and its propensity to form dense forests with a monospecific canopy make this system a common target for research, a fact reflected in the large proportion of the literature which deals with the system (Underwood and Kennelly 1990a). While voluminous in nature, the work is fragmented by the fact that the studies are often constrained for logistic reasons to the general vicinity of the particular biologist. For this reason, research on a particular field is often restricted in its geographical extent and consequently the broad applicability of the findings is unknown. Despite this problem, *Ecklonia* forests remain the best understood of our macroalgal communities. Furthermore, the problem of large scale geographical consistency has recently been addressed in several studies on the coast of New South Wales (eg Underwood *et al.* 1991; Kennelly and Underwood 1992, 1993).

Structure of *Ecklonia radiata* stands

Ecklonia is generally recognized as a dominant of the mid sublittoral zone across its Australian distribution as demonstrated by Kirkman (1981, 1984) in Western Australia, Shepherd and Womersley (1970, 1971, 1976, 1981) in South Australia and Kennelly (1983, 1987a) in New South Wales. In New Zealand, it appears similarly important (Novaczek 1981; Choat and

Schiel 1982; Schiel 1988, 1990). While studies across the breadth of the continent have demonstrated that *Ecklonia* has the capacity to form monospecific closed canopy forests (Kirkman 1981, 1984, 1989; Kennelly, 1983, 1987a and b; Van der Velde and King 1984; Hatcher 1989), viewed on different scales, the forests consist of a mosaic of patches (Kennelly 1987b) as well as being a component patch of a larger vegetation pattern (Underwood *et al.* 1991).

Data on the biomass of *Ecklonia* in the forests of eastern Australia is not available, but density estimates of around 30 plants m⁻² (Kennelly 1987a, but note the high spatial and temporal variability demonstrated by Underwood *et al.* 1991) are similar to those found in Western Australia (eg 20 - 30 plants m⁻² (Kirkman 1984); 15-25 plants m⁻² (Kirkman 1989)). Shepherd and Womersley (1970, 1971, 1976, 1981) found *Ecklonia* demonstrated maximum biomass of between 1.5 kg wet weight m⁻² (Waterloo Bay) and 10 kg wet weight m⁻² (West Island) in their studies of the South Australian coastline. Hence biomass was generally lower than that found in the Western Australian *Ecklonia* forests where 6-18kg wet weight m⁻² were in evidence (Kirkman 1984). However it must be acknowledged that, with the exception of the West Island value, the South Australian communities usually demonstrated shared dominance, with *Scytothalia dorycarpa*, *Cystophora sp.* and/or *Sargassum sp.* being present in the canopy, unlike the almost monospecific stands described elsewhere (eg Kirkman 1984).

With the exception of the studies of Shepherd and Womersley (1970, 1971, 1976, 1981), the general picture gleaned from the above studies is that *Ecklonia* forms high biomass, largely monospecific forests with a low (<2m) canopy. However, the 'forest' is in fact a mosaic of patches which represent an alternation between dense kelp cover and turfing species of the order Dictyotales Kjellman without canopy, or "barren grounds" (Kennelly 1983, 1987c; Kennelly and Larkum 1983; Underwood *et al.* 1991; Kennelly and Underwood 1992).

Typically, the understory consists of crustose corallines in fairly large quantities (Underwood *et al.* 1991) and a highly variable assemblage of principally dictyotalean turfing algae (Kennelly and Larkum 1983; Kennelly 1987a, b and c; Kennelly and Underwood 1992, 1993).

The concern with most of the above studies is that study sites have generally been chosen *because* they are monospecific kelp forests and thus are unsuitable to gauge the generality of *Ecklonia* forest structure (see Underwood *et al.* 1991 for a contrast). In the parlance of Foster (1990), this tends to perpetuate the illusion of generality. Shepherd and Womersley (1970, 1971, 1976, 1981) demonstrate that *Ecklonia* is found coexisting with fucoid species (Order Fucales Kylin) in several habitats, but give no indication of whether this represents a homogeneous mix or a series of monospecific patches. Choat and Schiel (1982) and Schiel (1988) found that in New Zealand, the kelp canopy was generally fragmented in shallower (<8m) waters and more continuous below this depth.

Ecklonia has earned the sobriquet, "the dominant algal species (cover and biomass) in the subtidal reefs of most of southern Australia" (Kirkman 1981; Womersley 1981b cited by Kirkman 1984). However, Schiel (1990) speaks of the dominance of fucal algae at depths of less than 10m in New Zealand and claims the situation is similar in Australia, also quoting Womersley. (However, the reference is missing from Schiel's paper). Similarly, in areas which support both *Ecklonia* and fucoids within the same habitat (Shepherd and Womersley 1970, 1971, 1976, 1981), there is no indication of the patchiness or homogeneity of canopy composition. The need to assess the dominance of *Ecklonia* across a variety of scales in an unbiased, quantitative manner is clear.

Processes in *Ecklonia radiata* stands

Processes implicated in defining the structure of *Ecklonia* forests are affected by factors

intrinsic to the plant and those forced on it by its environment. Reproduction, growth and mortality are the broad categories of process which may be affected. The factors include the plant's genetic and biochemical composition (eg Cheshire and Hallam 1985 concerning *Durvillaea*; Steinberg 1989 for a more general example), competition from other algae (eg Kirkman 1981 for intraspecific; Kennelly 1987c for interspecific), herbivory (eg Choat and Schiel 1982; Andrew and Jones 1990; Jones and Andrew 1990; Jones 1992), wave force (eg Kirkman 1984; Hatcher 1989) and light (eg Shepherd and Womersley 1970, 1971, 1976, 1981 for implication in community composition; Wood 1987 for deleterious effect; Kirkman 1989 for beneficial effects). These effects are probably not additive - in many cases interaction of factors may result in effects which the action of the individual factors could not predict (eg the interaction of predation and herbivory demonstrated by Paine (1966), Connell (1975) and Menge and Sutherland (1976) amongst others). Despite the caveat concerning the questionable nature of broad scale generalizations, it would be remiss not to summarise the knowledge gleaned from the past 15 years of research on processes operating in kelp forests.

Ecklonia exhibits a life cycle referred to as an alternation of heteromorphic generations (Clayton 1990). The macroscopic sporophyte stage gives rise to microscopic male and female gametophytes. These produce gametes which fuse to form a zygote, which develops into a juvenile sporophyte.

Recruitment periods for *Ecklonia* are not well established. They appear to occur in pulses, but the timing of those pulses is somewhat unpredictable. Andrew and Jones (1990) stated that there was a recruitment period in spring. Kennelly (1983, 1987a), demonstrated that recruitment occurs in pulses in both summer and winter. Subsequently Kennelly and Underwood (1992) demonstrated a winter recruitment event which occurred in some forests, but was absent in others.

Schiel (1981, cited by Schiel 1988) found that like many marine algae (see Anderson and North 1966; Dayton 1973; Deysher and Norton 1982; Schiel 1985a and b; Kendrick and Walker 1991), recruitment of *Ecklonia* was distinctly localised, with 75% of recruitment occurring within 8m of the adult plant. However, this represents wider dispersal than that of similar sized fucoids (3-4m for *Sargassum sinclairii*, *Landsburgia quercifolia* and species of *Carpophyllum* - Schiel (1981) - *op cit*; 96% settlement within 25 cm (Kendrick and Walker 1991)). The wider dispersal area is probably due to the smaller propagules of laminarian algae taking longer to settle than those of fucalean algae (Schiel 1988).

Cheshire and Hallam (1989b) implied that laminarian algae, such as *Ecklonia*, store their reproductive potential as gametophytes. However, Kirkman (1981) demonstrated that juvenile sporophytes of *Ecklonia* act as a seed bank, their growth held in check while they are shaded by adult canopy. When storms dislodge adult plants, the juveniles grow rapidly into the canopy. In this way, the stand maintains its dominance. However, where large areas (rather than individual plants) are removed, this phenomenon is repressed (Kirkman 1981), probably through the agency of grazing. When odd plants are removed, the vulnerable juveniles are protected from herbivores by surrounding adults. This is not the case when large areas are denuded. A similar situation is described for *Laminaria pallida* by Velimirov and Griffiths (1979) and Velimirov (1983). There is an important temporal aspect involved in the recolonization of disturbed patches within a kelp forest. Kennelly (1987a) demonstrated that only when clearances were made in winter, did *Ecklonia* recolonize the patch. In other seasons, relatively persistent patches of dictyotalean algae established.

Growth and production in *Ecklonia* is affected primarily by light (eg Novaczek 1984), temperature (eg Hatcher *et al.* 1987), nutrients (eg Probyn and McQuaid 1985) and water movement (Kirkman 1989). Production appears to be similar on the east and west coasts of

Australia, being in the order of $3.5\text{kg dwt m}^{-2}\text{ yr}^{-1}$ (assuming 6:1 wet weight:dry weight ratio) (Kirkman 1984; Larkum 1986). These figures are comparable despite the studies being carried out at 1.5m in New South Wales (Larkum 1986) and from 2 to 7m in Western Australia (Kirkman 1984). However, beyond this depth, experiments utilizing artificial shading suggest that production is light limited during winter and autumn (Kirkman 1989).

Seasonal fluctuations in production are quite marked; Kirkman (1984) made biomass estimates of Whitford's reef across a two year period (1979-1980) and demonstrated that it varied between $7\text{kg wet weight m}^{-2}$ in winter and $42\text{kg wet weight m}^{-2}$ in late summer. In a subsequent study, Kirkman (1989) demonstrated similar levels in 1982/83 at the nearby Marmion reef. Exactly when production peaks is apparently dependent on depth, with the growth phase delayed with increasing depth (Kirkman 1989). At 1.5m in New South Wales, Larkum (1986) found that production peaked around September, while Kirkman (1989) found that the production peaked in October at 5m (in Western Australia). However, at the same location in Western Australia, at a depth of 10m, peak production occurred in December (Kirkman 1989). It was in this period that Sanderson (1987a) found maximal growth of *Ecklonia* on a reef off Tasmania (the depth was not reported).

Maximal biomass of individual plants lagged behind the period of maximal growth, occurring 4 months afterwards in the case of Kirkman's 5m site and 2 months afterwards at the deeper 10m site. At a 1.5m site (Fairlight Bay, N.S.W), Larkum (1986) found the lag was in the order of 3 months.

Water temperature has been implicated as a factor influencing the latitudinal limits of *Ecklonia* (Hatcher *et al.* 1987). Certainly, growth was negatively correlated with water temperatures above 20°C in the warm waters of the high latitudes of Western Australia. However, they concluded that other factors must also have an important influence. Kirkman (1984) found

that growth was negatively correlated with water temperatures above 18°C in the cooler waters off Perth (W.A). He acknowledged however, that the cooler waters of winter and autumn were associated with higher nitrate levels and greater water movement (which minimises "boundary layer" effects). Either or both of these factors may explain why production does not peak in summer when light levels are highest. In addition, while tissue production may not be maximal during this period, photosynthetic carbon fixation may in fact be high, storing photosynthates for use in growth at another point in time, perhaps when conditions are more appropriate.

Interactions with other species of algae also affect the distribution of *Ecklonia*. Shepherd and Womersley (1970) proposed that this explained the dominance at West Island of the fucoids in zones of intermediate wave energy, while *Ecklonia* dominated both the extremes. Like most canopy plant interactions, this observation has yet to be tested experimentally.

In contrast, interactions between canopy and understorey have been quite extensively researched. Besides Kirkman's (1981) assertion that the presence of the kelp canopy kept growth of juvenile *Ecklonia* in a suspended state, Kennelly (1987b, 1989) elucidated several aspects of the effects of the kelp canopy on its understorey. Amongst these was the assertion that it was principally shading by the canopy which affected the growth of the understorey. Scouring, another effect implicated in studies elsewhere in the world (eg. Velimirov and Griffiths 1979), was found to exert little influence on any of the common species.

Interactions between canopy and understorey are not one sided. It has also been shown that turfing algae such as *Zonaria* C Agardh, *Lobophora* J. Agardh and *Padina* Adanson form patches which resist colonization by kelps. This resistance continues even after the turfs have been removed, possibly through the agency of a lingering chemical effect (Kennelly 1987c).

Even in areas which were dominated by kelps, removal of these in any season except winter resulted in the establishment of persistent turfing communities (Kennelly 1987a).

Numerous authors have implicated herbivory as a factor affecting the patterns in kelp forests. Kirkman (1981) asserts that in the Western Australian stands which he studied, direct grazing was rarely seen in adult *Ecklonia* plants and that damage and/or loss was generally caused by storms. However, he did propose that herbivores can stop the establishment of juvenile *Ecklonia* if there was not a canopy above to protect them. Kennelly (1983) concurs with the influence of invertebrate grazers, but went further to suggest that, at least in the location he was dealing with, predation by fish kept this herbivory in check to some degree. This situation may parallel the sea otter - urchin - kelp relationship described by Dayton and Tegner (1984) and the effects of other predators on urchins (eg lobsters (Tegner and Levin 1983) and sheephead (Cowen 1983)).

In their 1990 review, Jones and Andrew assessed the impact of urchins and fish on the rocky shores of southern Australia. They concluded that there were different mechanisms behind the patches created by these types of herbivores. Urchins are *restricted* to certain patches, while fish *choose* to browse preferentially on patches of the rocky reef environment. These patches may be related to either topography or biotic elements. While urchins such as *Evechinus chloroticus* and *Centrostephanus rodgersii* can maintain large persistent barren areas through intense grazing, the effects of fish are more transitory or occur at smaller spatial scales (Jones and Andrew 1990).

The transitory nature of the barrens created by the kelp eating fish *Odax cyanomelas* is due to a behavioural trait linked to reproductive behaviour. The result is that patches, approximately 1 to 100m² in size, are heavily grazed in the same areas each year for a short period of time. Apparently the timing of the reproductive phase of the kelp sporophyte is such that the area is

immediately repopulated by kelps which then grow until the same time the following year (Andrew and Jones 1990). This is in contrast to the findings of Kirkman (1981) who found that areas of this size (36m^2) denuded of kelps were not repopulated by kelps for at least 9 months. However, Kirkman's (1981) clearance experiment was not temporally replicated - clearance was only effected once, in November 1979.

Having summarised our knowledge of *Ecklonia* forests, it is important to assess the generality of the situation (Schiel and Foster 1986; Foster 1990; Underwood and Kennelly 1990a).

Although no studies have examined aspects of structure and dynamics across the distribution of the species, two studies have examined generality across a range of habitats spanning large spatial scales. In the first of these, Kennelly and Underwood (1992) examined the fluctuations in abundance of species in several kelp forests along a stretch of coastline 140km long. This study concluded that "when kelp forests are described using quantitative data at several spatially replicated scales, few general conclusions can be made about these assemblages". The second study, Kennelly and Underwood (1993), examined the effects of artificial clearance at the same four locations used in the previous study. In this case, they concluded that despite significant small scale patchiness, effects were consistent within a single kelp forest, but differed between forests, which were separated by between 200m and 140km. The lack of consistency applied to the timing of changes in abundance and the actual species which constituted a successional phase. As with earlier studies (Kennelly 1987a, b and c) however, "guilds" of species could be identified. Opportunistic filamentous algae recruit soon after the disturbance, to be replaced subsequently by foliose species. *Ecklonia* recruited in some, but not all cases and generally only at the edge of the clearance.

In summary, while many aspects of the structure and processes within *Ecklonia* forests may be unpredictable (Kennelly and Underwood 1992), a broad pattern can be discerned (Kennelly

and Underwood 1993). *Ecklonia* stands are relatively resilient to most disturbances, with an understorey of juvenile plants ready to take their place in the canopy should an adult plant be removed. However, large scale disturbance, which removes a substantial quantity of the canopy, leaves the juveniles open to attack from grazers and may result in the occurrence of patches of turfing species (Kirkman 1981; Kennelly 1987a). Through encroachment from surrounding kelp plants on the edge of the patches, *Ecklonia* may dominate again, but this takes an extended period of time (Kennelly 1983; Kennelly and Underwood 1993). The exception to this rule appears to be the influence of herbivores which may have devastating effects on the kelp forest. They can reduce it to a barren which may be maintained for many years (in the case of urchins) or fluctuate between barrens and one year old age stands of kelp, as is the case with some herbivorous fish (Jones and Andrew 1990). Other fish may, in fact, be of benefit to the kelp through predation of potential grazers (Kennelly 1983).

Fucoids

While *Ecklonia* has dominated much of the Australian literature, it is often the order Fucales (members of which will hereafter be called fucoids) which dominate in terms of the number of species present in the canopy. The common canopy forming genera in South Australian waters are *Cystophora*, *Sargassum*, *Scytothalia*, *Seirococcus* and *Acrocarpia*. *Cystophora* and *Sargassum* alone have 38 species between them which are found in Australia, many of which are endemic (Womersley 1987). These are often the dominant genera of macroalgal stands, sometimes in pure fucoid stands, sometimes mixed with *Ecklonia* plants (see references below). *Scytothalia* and *Seirococcus* are common co-dominants with *Ecklonia* or, where wave force is more extreme, *Scytothalia* or *Acrocarpia* may dominate alone (Shepherd and Womersley 1970, 1971, 1976, 1981).

Despite the prevalence of fucoids in Australia, little ecological work on this group exists in the published literature. Exceptions to this are the community studies of Shepherd and Womersley cited above and the studies of Shepherd and Sprigg (1976), Edgar (1983a and b), Sanderson (1987a), Sanderson and Thomas (1987), and Hatcher (1989). The work on *Sargassum* by Kendrick and Walker (1991, 1994) and Kendrick (1994), and the studies of *Xiphophora gladiata* (Labillardiere) Montagne ex Kjellman presented in Rice and Kenchington (1990a and b) represent the best autecological studies of fucoid species in Australia.

Fucoids have a diplontic life history, with only the diploid phase prominent, the haploid phase being merely the gametangia (Womersley 1987). This is generally considered to be an alternation of generations with no free living phase (Clayton 1990). Growth occurs from an apical cell or cells which are sunken in a depression (Clayton 1990). Reproduction is oogamous, with the oogonia and antheridea being housed, along with hairs, in a cavity known as a conceptacle (Womersley 1987). These may be either monoecious or dioecious depending on the species (Womersley 1987).

Xiphophora

While *Xiphophora gladiata* does not occur in this study, it is a common fucoid of southern Australian waters and therefore deserves mention. Rice and Kenchington (1990a and b) investigated the morphological variation present in *Xiphophora gladiata* ssp *gladiata* (Labill.) Mont. ex Kjell. across its entire geographic range (the coast of Tasmania). Using the partitioning demonstrated by ANOVA results, they concluded that the bulk of the variation was at the 10cm scale and most of the remainder at geographic (hundreds of kilometres) scales. Variation at the 10cm scale resulted in quite distinct clumps of this size with abrupt boundaries. Intermediate scales did not add significantly to the variation (Rice and Kenchington 1990a). Discriminant analysis further revealed that the geographical variation

observed was irregular and not associated with along-shore distances of gene flow. Rather they were associated with physical properties of the water bodies and were relatively distinct, rather than representing a gradual cline (Rice and Kenchington 1990b).

Sargassum

Our knowledge of Australian *Sargassum* stands is restricted to Western Australia, where Kendrick and Walker (1991, 1994) and Kendrick (1994) have investigated the importance of recruitment dynamics to the persistence of the stand. Kendrick and Walker (1994) concluded that both recruitment from propagules and vegetative regeneration from crusts left by dislodged plants were important, particularly given the high mortality rates and seasonal variation exhibited by these stands. Dispersal was remarkably localized, with 96% of propagules being found within 25cm of the parent plant (Kendrick and Walker 1991). Survival of recruits was considerably decreased (three-fold reduction) by the presence of natural adult canopy (Kendrick 1994). Additionally, survival of recruits was partially dependent on the density of those recruits, but density independent mortality was considerable. Causes for this high level of density independent mortality were unknown, but warranted further study (Kendrick 1994).

Durvillaea potatorum

Durvillaea potatorum, while recently placed in the order Durvillaeales, was previously included in the Fucales owing to its similar diplontic life history and conceptacle structure (Womersley 1987). While the geographic distribution of *Durvillaea potatorum* has been covered, the work is largely autecological and community dynamics remain poorly understood. At up to 75 kg wet weight plant⁻¹, *D. potatorum* is one of the two largest macroalgal species in southern Australia (Cheshire and Hallam 1988a). It is principally a cold water species, being

distributed from southern New South Wales, throughout Tasmania and Victoria, and extending as far west as Cape Jaffa in South Australia (Womersley 1987). While it is primarily associated with the high surge and surf of the intertidal fringe, where it forms almost monospecific stands, it has also been found to depths of 15m (personal observation).

Existence in such a high energy environment requires a high level of morphological and biochemical adaptation. In the high energy intertidal, plants are typically longer, more braided and have shorter stipes. With increasing depth or decreasing wave energy, *D. potatorum* takes on a much less streamlined form which maximises photosynthetic ability (Cheshire and Hallam 1988b). Geographic location plays an important, but secondary, role in determining morphology (Cheshire and Hallam 1989a). In addition to a high degree of plasticity in its morphology, the level of alginates (cell wall constituents) is higher than in any other species - 50-65% of the dry weight of *D. potatorum* is composed of alginate (Cheshire and Hallam 1985), resulting in an extraordinarily tough plant, well adapted to the high stress environment in which it lives.

The lack of any similarly adapted species in this region often leads to almost monospecific high density stands of *Durvillaea* in the intertidal fringe. These stands have a large proportion of juveniles which act as the reproductive potential of the stand in the same way that gametophytes may in laminarian stands (Cheshire and Hallam 1989b). Kirkman (1981) would, however, argue that it is the juvenile sporophytes of the laminarian, *Ecklonia radiata* which act in the same way. This will be discussed in more detail subsequently. Cheshire and Hallam (1989b) concluded that the highest adult densities occurred in those stands which contained few very large individuals. The resultant populations, with a density of up to 23.5 plants m⁻² and biomasses in the range of 4 to 108kg wet weight m⁻², appear to demonstrate a carrying

capacity some five times higher than reported in any other plant population (Cheshire and Hallam 1988a).

Mixed Phaeophycean Stands

In their geographically dispersed studies, Shepherd and Womersley (1970, 1971, 1976, 1981) found that furoid species inhabited a wide range of wave force environments, which is unsurprising, given the number of species in the order. Distributions of individual species were circumscribed principally by light and the level of water movement. They stated that horizontal distribution was determined primarily by wave force, while vertical distribution was largely a product of available light (Shepherd and Womersley 1970).

Shepherd and Womersley's series of surveys of the rough coasts of South Australia allowed the development of a schema which saw the sublittoral divided into three main bands: the upper, mid and lower sublittoral. Defined by their biota, these zones were variable in extent, depending on the water movement at the location. Unfortunately, there has subsequently been a tendency to describe communities in terms of these three zones, even when the data does not support such a schema (eg Farrant and King 1982; Edgar 1983b, both cited by Underwood and Kennelly 1990a). While there are common species, the assemblages which defined these zones were fairly loose, with the presence of many species being variable. Add to this the fact that the zones may either be distinct or exhibit gradual intergrade, with several species common to adjacent zones, and the schema would appear to be a generalization that, while being inspirational to later studies, has outlived some of its usefulness (Underwood and Kennelly 1990a). For most species, there are just too many complicating factors controlling distribution.

From the studies of Shepherd and Womersley (1970, 1971, 1976, 1981) and Shepherd and Sprigg (1976), generalizations can be made concerning the distribution and abundance of fucoids. Canopy forming fucoids are typically associated with moderate water movement and depths from the subtidal fringing zone to the depth at which the Rhodophyta dominate. Depending on the wave energy of the location and water quality, this can begin at a depth of 50cm (8m in rough conditions) and descend to below 30m (10m in turbid waters) (Womersley 1981a). In general, the fucoids could be described as quite adaptable, with many able to cope in rough conditions from about 5m to well below 30m (Shepherd and Womersley 1970, 1976). There are exceptions, such as *Cystophora intermedia*, which is restricted to a narrow band at the subtidal fringe in high water movement conditions. It should be noted that *Ecklonia radiata* generally exists deeper than the fucoids (Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976).

It is not uncommon to find that fucoid species, particularly *Cystophora* and *Sargassum*, tend to form associations discrete from those areas dominated by *Ecklonia* (eg Shepherd and Womersley 1970; Collings 1989). Competition has been implicated in this feature (Shepherd and Womersley 1970), but the theory has not been put to experimental test. Schiel (1988) has detailed several important differences between laminarian algae (eg *Ecklonia*) and the fucoids. These included differences in morphology which greatly influence the number of individuals required to form a closed canopy (far more fucoids are required), space preemption by holdfasts (*Ecklonia* has much larger holdfasts) and life history differences which result in two distinct heteromorphic phases in *Ecklonia*. Fucoids, which utilize a direct reproductive cycle, release fewer spores, but they are better developed and therefore have higher survival rates (Schiel 1988).

The common furoid species which have distributions indicating a tolerance of rougher conditions are *Scytothalia dorycarpa* (Turner) Greville, *Acrocarpia paniculata* (Turner) Areschoug, *Sargassum fallax* Sonder, *Cystophora intermedia* J. Agardh and *C. moniliformis* (Esper) Womersley and Nizamuddin *ex* Womersley (Womersley 1981a). At the other end of the spectrum is *Scaberia agardhii* Greville, a furoid species commonly found subtidally in extremely low water movement conditions (Shepherd and Sprigg 1976); Womersley 1981a). In slightly less benign conditions, *Sargassum verruculosum* (Mertens) C. Agardh, *S. varians* Sonder, *Cystophora brownii* (Turner) J. Agardh and *C. monilifera* J. Agardh are often found (Shepherd and Womersley 1970, 1971, 1976, 1981). Having noted this, it is important to remember that these species do exist at higher energy environments, just as the high energy furoids can be found at great depth or in far calmer conditions (eg *Acrocarpia paniculata* at a depth of 35m (Shepherd and Womersley 1971)). With an ability to cope with such a wide range of conditions, it seems likely that biotic interactions have a major influence on the distributions observed within the wider constraints imposed by the physical environment.

2.3 Summary

The breadth of distribution of many Southern Australian macroalgal species has resulted in a diverse array of communities. While it has been possible to make some generalizations on the basis of previous work, too often generalizations have been drawn from inadequate or inappropriate data. Dynamics and processes within these systems may vary substantially, depending on the physical environment and the composition of the communities. The applicability of the small scale studies, typical of the literature, to the regional scale is often unknown. Descriptive studies which are appropriately replicated in time and space are an important key for identifying the scales over which generalizations are likely and designing experiments to test such hypotheses. Given that appropriate generalization is one of the most

important goals of community ecology (MacArthur 1972; Schoener 1986), the need for such descriptive studies is clear.

Chapter 3 Study Sites and Methods

This section details the sites and methods used for site comparisons (Chapter 4) and the investigation of temporal dynamics (Chapters 5 and 6).

Eight sites in six locations, representing both gulf and oceanically influenced sites, were sampled and described (Table 3.1). Four sites were located in Gulf St Vincent, South Australia and the remaining four in Encounter Bay, South Australia. These covered a range of about 90km (Fig. 3.1).

3.1 Study Sites

Gulf Sites

Cape Jervis North 5m and 9m (CJN5 and CJN9)

Geographic location: Plate 3.1, Fig. 3.1

Two adjacent sites, representing 5m and 9m depths are located at the southern tip of Fleurieu Peninsula (95 km southwest of Adelaide) 1km northwest of the boat ramp. This location has a westerly aspect and as such is partially open to the predominantly south-westerly swell, although Kangaroo Island offers a degree of protection. These two sites rank as the roughest of the gulf sites, with the 5m site being the roughest and the 9m site slightly less exposed because of the amelioration of wave energy with depth.

Both sites experience extreme tidal current to the extent that a diver often cannot hold on to a boat. The currents run parallel to the coast, generally in a north - south direction as the tide runs out of the gulf. While the northern extent of the current is unknown, the southern extent

is a spot about 700m south of the study sites, where churning water can be seen even on the calmest days.

Geologically, the sites consist of a series of ridges running parallel to the shore. The rock is a Kanmantoo group schist and is common to much of the lower Fleurieu Peninsula (SA Mines Department 1954).

Second Valley (5m) (SV5)

Geographic location: Plate 3.2, Fig. 3.1

Second Valley is situated 80 km southwest of Adelaide (15 km northeast of Cape Jervis). It is calmer than Cape Jervis North 5 and 9m, but rougher than Cape Jervis East. It is gulf influenced, rather than being subjected to oceanic swell and its west north-westerly aspect leaves it partially protected. Strong currents were never encountered during the period of the study. Rock type was the same as Cape Jervis - Kanmantoo schist, but rather than ridges, extensive, low horizontal platforms supported the biota.

Cape Jervis East (5m) (CJE5)

Geographic location: Plate 3.3, Fig. 3.1

Cape Jervis East is situated 1km south-southeast of the Cape Jervis boat ramp (2km from the Cape Jervis North sites). As Kangaroo Island protects it from the south, its southerly aspect leaves it less exposed than either Cape Jervis North or Second Valley. Thus, it was the calmest of the sites. Occasionally, moderate currents were experienced at this site. The rock type was Kanmantoo schist, but unlike the ridges of Cape Jervis North, rocky platforms were the dominant form.

Oceanic Sites

Granite Island (5m) (GI5)

Geographic location: Plate 3.4, Fig. 3.1

Granite Island is located in Encounter Bay, 75 km south of Adelaide. It is oceanically influenced and directly exposed to the swell. As the study site is on the seaward side of the island, there is no local protection at all. It is by far the roughest of the sites. The substratum is composed of large granite boulders. Currents were never noticeable at this site.

The Bluff (5m) (B5)

Geographic Location: Plates 3.4 and 3.5, Fig. 3.1

The Bluff, also known as Rosetta Head, is at the westernmost tip of Encounter Bay. The sample site was tucked into the lee of the head, affording it some local protection from the incoming southwesterly swell. Nevertheless, substantial swell is refracted around the head, so the site still experienced moderate to strong water movement (of slightly greater magnitude than Wright Island 5m). No current was ever observed and the substratum consisted of granite boulders.

Wright Island 5m and 9m (WI5 and WI9)

Geographic Location: Plates 3.4 and 3.5, Fig. 3.1

Like Cape Jervis North, this location provided two adjacent sites of 5 and 9m depth. Wright Island is 3 km southwest of Granite Island. The study sites were on the leeward side of the island and as such are offered a moderate degree of protection. For this reason, the 9m site is

rated as the calmest of the oceanic influenced sites, followed by Wright Island at the 5m depth. Despite being the calmest of the oceanic sites, Wright Island at 9m was rougher than the roughest of the gulf sites (Cape Jervis North 5m). Like Granite Island, there is no noticeable current and the substratum consists of granite boulders at both sites.

3.2 Field, Laboratory and Analytical Methods

The benthic flora of each of the eight sites described above was sampled. Sampling was done every 3 months in order to elucidate seasonal change over a period of 27 months (Table 3.2).

Collections in winter and spring 1993 were not possible at the oceanic sites because prolonged inclement weather at the times of sampling made diving too hazardous. Our up-side down boat was an adequate demonstration of this.

3.2.a Field Methods

Sampling was conducted mainly using SCUBA apparatus, although a hookah was utilized on a few occasions. Depending on the conditions, a dive of approximately 90 minutes was sufficient to sample each site.

Each site was represented by an area approximately 60m by 20m which was repeatedly sampled through the course of the study. Sampling was done by destructively harvesting eight replicate 1m by 1m quadrats which were arbitrarily dispersed across the area. After swimming ten finstrokes with eyes shut, the quadrat was dropped. Truly random placement was impracticable because of the water movement of the rougher sites. If the quadrat landed on an area of unconsolidated substratum (sand or rubble), it was moved to the nearest section of solid substratum, allowing a 50 cm margin to minimise boundary effects. A 50 cm buffer was

chosen, as this is approximately the size of the largest plants in those areas where the substratum was partially unconsolidated.

The destructive harvest involved collecting all individuals greater than 4cm high of species which were found in the canopy of the community. Presence-absence was scored for understory species in each quadrat. All quadrats were harvested into individual nylon mesh sacks with drawstrings. At the conclusion of the dive, all eight full sacks were brought to the surface and stored in large bins. These were returned to the laboratory and kept in a 4°C cold room until the samples had been analysed. The condition of the plants was similar to that when first removed from the water.

Choice of quadrat size and level of replication were made on the basis of a limited pilot study, detailed in Appendix A.

3.2.b Laboratory Methods

Each quadrat was sorted into its component taxa as classified by Womersley (1984, 1987) and by personal communication with Professor H. B. S. Womersley. In some cases, similarity in morphology made species level taxonomy too time consuming to be repeated for each individual and several species or genera were classified as a functional morphological group. There are several sound biological and pragmatic reasons for this (see Butler 1986; Warwick 1988; Hatcher 1989). Warwick (1993) points out that species level identification can be a major time and cost consideration and often a luxury that gains little information. Given the focus on canopy, species level identification was employed only for canopy species while understory individuals were assigned to higher order groups.

For each of the canopy species, the number of individuals was counted and the dry weight recorded for each quadrat. Drying was done in a glasshouse with heaters and fans. The

temperature was kept at 40° C. Plant weights were recorded when the mass of selected "test plants" did not decrease over a period of 24 hours. Those used as "test plants" were the largest, as they were the slowest to dry.

In later collections (Autumn 1993 onwards) the wet weight of each individual was recorded. This was done in order to obtain an estimate of population structure (eg DeWreede 1984; Cheshire and Hallam 1989b). When the dry weight was obtained for the sum of all individuals of that species for that particular quadrat, it was then apportioned according to the individual wet weights, allowing an estimate of the dry weight for each individual plant. It was not possible to count individuals or obtain individual weights for any species of *Sargassum* because they fragmented in the harvesting process.

Examples of each species were pressed and kept as herbarium sheets and are lodged at the Botany Dept., University of Adelaide.

3.2.c Data Storage

Data was stored initially on DBase IV databases (Ashton-Tate 1988), but was later transferred onto a Microsoft Access (Microsoft 1994) database. Four basic files were used and then the information conjugated and/or filtered when necessary. The files were;

- a) **Herbarium** database - which contained species codes, the species they represented and associated data on family, order and its status as an understorey or canopy plant.
- b) **Quadrat** database - which contained the quadrat number, the site it came from, and the date of harvest.
- c) **Quantities** database - which consisted of the quadrat number, species code,

biomass and number of individuals. Each record therefore represented the summed weight and abundance of a species for a given quadrat.

d) A **modified quantities** database for those collections where each individual was weighed. The same fields as above were used, with the exception that frequency was omitted. Thus, each record represented a single individual. This database was summed where necessary to provide data in the same format as the original "quantities database".

3.2.d General Methods of Analysis

Analysis was of two basic types - univariate and multivariate. Univariate analysis was used to test for differences in site and season in single measures such as biomass of a particular species, total biomass or diversity. Multivariate analyses are designed to detect patterns in overall community structure. That is, they take all species into consideration in the one analysis to detect and quantify differences in the community as a whole. Gauch (1983) provides a good overview of the objectives and methods of multivariate analysis.

Univariate analysis took the form of basic graphical methods such as column graphs with error bars, regression analyses and ANOVAs. The statistical package used was JMP (SAS Institute 1995). Multivariate analysis was done using PATN (Belbin 1992). Typically these analyses involved creating a Bray-Curtis association matrix followed by a UPGMA fusion to produce a dendrogram and then semistrong hybrid analysis (SSH) to create an ordination in two dimensions. Principal canonical correlation (PCC) analysis was sometimes applied to give species/genus vectors which show which direction on the ordination is associated with an increase in the abundance of those species.

In addition to the individual species, *total* biomass and *total* abundance are also analysed.

Total biomass in the case of this study refers to the dry weight per square metre of those species which generally exist in the canopy. This reflects the fact that the canopy is the focus of the study, as well as the pragmatic consideration that complete collection, identification and measurement of all understorey species was too time consuming. With the exception of *Ecklonia radiata*, all species belong to the order Fucales. The species which were included in this measurement were;

Acrocarpia paniculata (Turner) Areschoug

(referred to hereafter as *Acrocarpia*)

Ecklonia radiata (C. Agardh) J. Agardh

(referred to hereafter as *Ecklonia*)

Cystophora brownii (Turner) J. Agardh

C. expansa (Areschoug) Womersley

C. monilifera J. Agardh

C. moniliformis (Esper) Womersley & Nizamuddin *ex* Womersley

C. subfarcinata (Mertens) J. Agardh

Sargassum decipiens (R. Brown *ex* Turner) J. Agardh

S. fallax Sonder

S. lacerifolium (Turner) C. Agardh

S. linearifolium (Turner) C. Agardh

S. varians Sonder

S. verruculosum (Mertens) C. Agardh

Seirococcus axillaris (R. Brown *ex* Turner) Greville

(referred to hereafter as *Seirococcus*)

Scytothalia dorycarpa (Turner) Greville

(referred to hereafter as *Scytothalia*)

Thus the total biomass is the sum of the weights of these species in each square metre. It is also referred to as canopy biomass. Total abundance is the total number of individuals per

square metre of the same set of species, with the exception of *Sargassum* species which were not counted individually.

The general comparison of sites is made using the same data which were collected for the investigation of temporal change. Chapter 4 investigates the relationships between the sites without reference to seasonal change. Sites are described by all quadrats, regardless of collection. Conversely, Chapters 5 and 6, because they examine the temporal dynamics of the sites, take collection into account. The specific analyses used in each investigation will be detailed in the relevant chapter.

Chapter 4 Biotic Comparison of Sites and General Trends

4.1 Chapter Overview

This chapter acts as an introduction to the communities supported by each of the sites. It is based on an amalgamation of the temporal dataset without making distinction between different collections (which is the preserve of the following chapters). The chapter presents an overview which details the response of the species to the habitat represented by each site and compares those sites in terms of overall parameters such as total biomass and diversity. These responses are viewed in the light of the water movement gradient which they represented and compared with other studies of the region. Additionally, it provides the opportunity to examine the relationship between canopy biomass and species richness, and the application of self thinning principles to mixed macroalgal communities.

The chapter has four major topics;

- 1) A comparison of sites (in multivariate terms as well as in terms of diversity, total biomass and species composition).
- 2) An investigation of the response of each of the species to the habitat represented by the site.
- 3) An examination of the relationship between biomass and the species richness of the sample.
- 4) An application of the 3/2 thinning law to the mixed macroalgal stands supported by these sites.

These topics are addressed within separate sections, each of which is divided into methods, results and discussion. The chapter ends with a summary of the important conclusions.

4.2 Background

There are many physical factors which may influence the composition of subtidal macroalgal communities. Principal amongst these are temperature, nutrient levels of the waters, substratum type, light quality and quantity and water movement (see Dayton 1985a for a review). Within a limited area such as the one dealt with in this study, temperature and nutrient levels are unlikely to vary greatly. The fact that Shepherd and Womersley (1970) use data from a site similarly distant to my sites to describe nutrient levels at West Island supports this assumption, as do personal records of dive temperatures. Similarly, only solid substratum was sampled, so differences in this factor are likely to have little impact on the community composition. Thus, the two factors which are likely to differ most between sites are the level of water movement (also termed "exposure" in this study) and light. It is these two which have been most consistently implicated in the structuring of mixed macroalgal stands in the region (Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976; Sanderson and Thomas 1987; Collings 1989; Hatcher 1989). Total biomass, species biomass, community composition, and alpha and beta diversity were examined in light of these two factors, and compared with results obtained elsewhere.

The "3/2 thinning law", first proposed by Tadaki and Shidei (1959, cited by White 1981) describes the relationship between plant density and individual plant weight. Popularised by Yoda *et al.* (1963) and White and Harper (1970), the rule describes a boundary condition which cannot be exceeded and is defined by the equation

$$\log w = \log K - 3/2 \log p$$

where [w= average plant weight; K="thinning constant"; p= plant density]

Individuals in a population will grow, resulting in an increase in average plant weight until this boundary state is achieved. At this point, plants may continue to grow, but mortality will occur, thereby decreasing density. Figure 4.1 demonstrates this graphically. The relationship between these two variables follows the "3/2 thinning line" in an astounding variety of cases, from mosses to redwood forests (White 1981).

This law and its explanation have been sources of enormous debate amongst ecologists (eg White 1977 v Westoby 1977a and b; Schiel and Choat 1980 v Cousens and Hutchings 1983).

One of the causes of debate is the fact that K, which determines the height of the line, and hence the point at which thinning occurs, is somewhat variable. Log K is generally accepted to have a maximum of around 4.3 (White 1981; Cousens and Hutchings 1983). However, Cheshire and Hallam (1988a) claimed that, in the *Durvillaea potatorum* community which they studied, if the 3/2 thinning law did apply, then log K must have been at least 5.

Although originally applied to even-aged, monospecific stands which suffered from overcrowding, the rule has been applied to an increasingly wide range of community types (White 1985). However, to date, the only studies of the applicability of the law to macroalgal communities have centred on monospecific stands. This is the first to investigate the situation in mixed macroalgal stands.

4.3 Comparison of Sites

4.3.a Methods

Multivariate Measures

Classification and ordination were used to examine the biotic relationships between the sites.

The data set was simplified by working with the average composition of each collection at each site, rather than the individual quadrats. Thus each site was described by the points which represent the average community at each time of collection. Data was range standardized in order to even out the contribution of each species to the analysis (Belbin 1992; Clarke 1993).

A Bray Curtis association matrix (Bray and Curtis 1957) was created to define the relationships between the objects (collection averages of each site). This association measure is popular amongst ecologists for its invariance under transformation, its ability to standardize and the irrelevance of "joint absences" in its calculation (Field *et al.* 1982; Faith *et al.* 1987; Clarke 1993). Classification was performed, using a UPGMA dendrogram, which represents an intermediate between the weakly clustering algorithms such as the "furthest neighbour" and the intensely clustering Ward's (1963) method (see Belbin 1992). While ordination utilized Belbin's (1992) semi-strong hybrid (SSH) algorithm, histograms of association measures did not support the hybrid use of interval and ordinal measures. Ordinal measures were therefore utilized for all analyses, making them free of assumptions of distribution (Kenkel and Orloci 1986; Clarke 1993). Thus the analysis was in essence a non-metric multidimensional scaling (NMDS) procedure such as that developed by Shepard (1962a,1962b) and Kruskal (1964a,1964b) and advocated by Field *et al.* (1982), Clarke (1993) and Warwick (1993) amongst many others.

Two multivariate data sets were analysed in this section.

1. - An **average presence-absence** was calculated for each species by scoring the number of samples in which that species occurred. Given that each temporal collection at each-site consisted of 8 quadrats, this measure ranged between 0 and 8.
2. - the **average biomass** (g dwt m⁻²) of each species in each quadrat is used to analyse the system in a more intensive manner.

Using both of these levels of analysis not only depicts the relationships of the sites in terms of their biota, but also allows comparison of the results of the two methods. This is relevant because of the much greater effort required to obtain the biomass data.

Diversity

Diversity of the sites may be measured in different ways, each of which may reveal different features. Species richness has been described both at the scale of the whole site and at the scale of the 1 m² quadrat. The sites are compared in terms of total species richness, canopy species richness and understorey species richness at the scale of both site and quadrat.

Levinton (1982) argues that a description of diversity should not only reflect the number of species present, but also the homogeneity of the distribution. That is, it must also measure how evenly the biomass or abundance is apportioned to the species present. The simplest of these indices is the Shannon-Weaver Index (Shannon 1948 cited by Zar (1984));

$$H' = - \sum_{i=1}^K P_i \log P_i$$

where K = the number of categories (species), and P_i is the proportion of the total abundance or biomass contributed by category (species) i.

Communities with an even spread of biomass across all the species have high diversity indices. While the index is typically based on abundance (counts), because no counts were made of *Sargassum* species (which contributed considerably to the diversity of some sites), biomass data was used. Note also that, because biomass data was used, it was the canopy diversity which was described.

ANOVA's with post-hoc Tukey tests were used to determine the significance of differences in species richness per square metre between sites. Data was transformed using

$$X' = \sqrt{(x + 3 / 8)} \text{ (Freeman and Tukey 1950)}$$

as this appeared to best normalise the data. Where variances were significantly heteroscedastic (using Levene's test), Welch's ANOVA (Welch 1951 cited by SAS Institute 1995) was performed. Statistical comparison of the site level diversity was not possible as there was only a single measure for each site and thus no measure of variance.

Total Biomass

Total biomass (g dwt m⁻²) was calculated for each quadrat by summing the biomasses of the individual species, allowing the calculation of a mean and estimate of variance. Differences between the sites were assessed using ANOVA and localized with Tukey tests. Data was transformed using $X' = \sqrt{(x + 3 / 8)}$ to satisfy the assumption of normality.

Species Composition

The composition of each of the communities in terms of biomass is presented graphically, in order to provide an overview of the situation. Statistical analysis is left to the following section which investigates the response of each of the species to the different sites.

4.3.b Results

Multivariate Measures

Some sites supported a relatively distinct biota, while others were not clearly distinguished. Classification of the collection averages in terms of average presence-absence of the canopy species demonstrated that the major division was between the two low energy sites (CJE5 and SV5), and the remainder of the sites (Fig. 4.2a). Note that throughout this thesis, "collection average" and "site/collection average" both refer to the mean composition of one site at one collection date. Further subdivision resulted in the clear distinction of five sites. All four gulf sites were distinct, as was GI5. The remaining oceanic sites, B5, WI5 and WI9 were indistinguishable from each other. Ordination of the same data (Fig. 4.3a) also revealed that CJN5 and CJN9 supported biota which was intermediate in nature between the low energy sites which were dominated by *Cystophora* and *Sargassum* species and the oceanic sites which were dominated by *Ecklonia*, *Seirococcus* and/or *Scytothalia*.

Those sites which were situated in the gulf environment were clearly differentiated, in terms of their biota, from those which were oceanically exposed (Fig. 4.3a). The ordination also demonstrated that all gulf sites supported a distinct biota, as did GI5. Furthermore, the biota appeared to reflect the wave force experienced at the site - the roughest and calmest sites differed most in terms of their biota, with other sites intermediate, their biota generally defining a position on the ordination consistent with the water movement experienced by the site.

However, it should be noted that the assemblage supported at CJN9 was closer in composition to the oceanic sites than CJN5, which is not what would be expected if water movement were the only control.

In terms of biomass of the species (as opposed to presence-absence), the distinction between sites SV5 and CJE5 is not as clear. The classification (Fig. 4.2b) was unable to separate SV5 and CJE5, nor was it able to clearly separate GI5 and B5. Ordination of this data (Fig. 4.3b) showed a similar picture to that demonstrated by the coarser presence-absence analysis but was unable to separate SV5 and CJE5.

The calmest sites, SV5 and CJE5, supported communities rich in *Cystophora* and *Sargassum* species (refer to species vectors on Figs 4.3a and 4.3b). By contrast, the oceanic communities were dominated by *Ecklonia*, *Seirococcus* and *Scytothalia*. The higher energy gulf sites, CJN9 and CJN5, had a species composition which represented a mixture of these groups of species.

Diversity

Total species richness for the entire region (all sites together) was 84 species/species complexes. This consisted of 15 **canopy species** and 69 **understorey species**.

Total species richness for the whole site was highest at the gulf sites (Fig. 4.4). At CJE5, 59 species/species complexes were found, 47 at CJN5, 46 at SV5 and 42 at CJN9. By comparison, the oceanic sites supported 43, 38 and 35 species at WI9, WI5 and B5 respectively and GI5, with 34 species, demonstrated the lowest site diversity. It was not possible to measure variance at this level as there is only a single figure which describes this variable.

Canopy species richness for the whole site was highest at the 4 gulf sites, where CJE5, CJE5 and CJE9 supported 14 species, while SV5 supported 13 (Fig. 4.4). At the oceanic sites, 11 canopy species were in evidence at WI9, WI5 and B5. Only 7 canopy species occurred at GI5.

Understorey species richness for the whole site was again generally highest at the gulf sites (Fig. 4.4). With 45 understorey species, CJE5 was the most diverse in this respect. SV5, CJE5 and WI9 had considerably less, with 35, 33 and 32 understorey species respectively. Of the gulf sites, CJE9 demonstrated the lowest understorey richness, with 28 species. WI5 and GI5 both supported 27 species and B5 had the least rich understorey, with only 24 species.

In general the analysis of **total species richness per square metre** and **canopy species richness per square metre** (Figs 4.5a and 4.5b) revealed similar pictures to those portrayed by the overall site values described above. In terms of total and canopy species richness, CJE5 and CJE5 were significantly richer than all other sites ($\approx 16 \text{ sp. m}^{-2}$; $\approx 9 \text{ canopy sp. m}^{-2}$). In terms of total and canopy species richness, SV5 and CJE9 were less diverse ($\approx 10-11 \text{ sp. m}^{-2}$; $\approx 6.2-7.5 \text{ canopy sp. m}^{-2}$), but it was the oceanic sites which were least diverse ($7-9 \text{ sp. m}^{-2}$; $3-4 \text{ canopy sp. m}^{-2}$).

Understorey species richness per square metre was not consistently higher at the gulf sites (Fig. 4.5c). While CJE5 supported a significantly richer understorey than all sites except CJE5 ($\approx 6.5 \text{ understorey sp. m}^{-2}$), both SV5 and CJE9 had an understorey which was no richer (at significance level of .05) than any of the oceanic sites. These six sites supported, on average, 3-5 understorey species per square metre.

The **diversity of an average square metre, as described by the Shannon-Weaver Index**, was significantly higher at CJE5 than all other sites (Fig. 4.5d). SV5 and CJE5 supported a

less diverse biota than this, but more so than CJN9. All oceanic sites were of significantly lower diversity than the gulf sites. No significant differences were found between the diversity of the biota at any of the oceanic sites.

Partitioning the diversity between scales

Given that 93% of all canopy species were found at each of three of the gulf sites (Table 4.1a), it would appear that while differences in site cause a difference in composition, the diversity increase caused by different habitats contributes little to the overall species richness. Most of the species richness was attributable to alpha or within site diversity. Similarly, 65% of the understorey diversity of the entire study was demonstrated by a single site (Table 4.1b).

The gulf sites generally supported a greater proportion of their site level richness in any given square metre than did the oceanic sites (Table 4.1a). At two sites (CJE5 and CJN5), more than 2/3 of the canopy richness of the site was found in an average square metre. At SV5, 57% of the total canopy richness was found at the scale of the square metre. In fact, of the gulf sites, only CJN9 (44%) failed to support half of the site's canopy diversity in an average square metre. Despite lower site canopy richness, the oceanic sites still displayed an even lower proportion of this total in each square metre (36 - 44%). However, understorey species richness at the scale of the square metre was far lower than at the scale of the site (Table 4.1b). Diversity of the understorey in a square metre accounted for less than 20% of the site richness and less than 10% of the overall regional richness.

Total Biomass

The lowest total biomass was supported by the two low energy sites, CJE5 and SV5 ($\approx 500\text{g dwt m}^{-2}$), with maximal biomass being found at WI5 and B5 ($\approx 1700\text{g dwt m}^{-2}$) (Fig. 4.6). All

other sites were intermediate ($\approx 1100\text{g dwt m}^{-2}$) and did not differ significantly among themselves. The variance was higher at the oceanic sites than at the gulf sites.

Species Composition

The general trend was for the biomass to be dominated by two or three species, with the exception of the two lowest energy sites (CJE5 and SV5), which demonstrated a more even spread amongst several species (Fig. 4.7). *Ecklonia* and *Scytothalia* dominated the oceanic sites, with *Acrocarpia* and *Seirococcus* making sizeable contributions in some cases. *Ecklonia* dominated with *Seirococcus* at CJN5, and with *Seirococcus* and *Scytothalia* at CJN9.

Dominance was shared amongst more species at the two low energy sites (Fig. 4.7). Several *Cystophora* and *Sargassum* species made sizeable contributions to the biomass of **Cape Jervis East (5m)**, most notably *Cystophora expansa* (35%), *C. moniliformis* (17%), *C. subfarcinata* (9%) and *Sargassum linearifolium* (8%). A similar situation was evident at **Second Valley (5m)**, but here *Ecklonia* made a more sizeable contribution (19%). Other major contributors to the total biomass were *C. expansa* and *C. subfarcinata* (20% each), *Sargassum linearifolium* (12%), *C. moniliformis* and *S. varians* (8%).

At all other sites, *Ecklonia* made a greater contribution. At **Cape Jervis North (9m)** it was responsible for 60% of the biomass, with *Scytothalia* and *Seirococcus* contributing 16% and 18% respectively. Slightly shallower at **Cape Jervis North (5m)**, *Ecklonia* (34%) shared dominance with *Seirococcus* (37%). While many other species contributed, only *Sargassum fallax* (6%) was responsible for more than 5%. It is noteworthy that *Scytothalia* was responsible for only 3% at CJN5, in contrast to the 16% which it contributed at CJN9.

Wright Island (9m) was heavily *Ecklonia* dominated (73%), with *Scytothalia* (16%) and *Seirococcus* (10%) being the only other species to make sizeable contributions. At **Wright**

Island (5m), *Ecklonia* (76%) and *Scytothalia* (19%) were the principal canopy dominants.

The situation was similar at **the Bluff (5m)**, where *Ecklonia* and *Scytothalia* again dominated with contributions of 49% and 44% respectively. At **Granite Island (5m)**, these two species were again dominant (30% and 56% respectively), but here *Acrocarpia* contributed a sizeable 13% of the total biomass.

4.3.c Discussion

One of the problems of mensurative experiments (Hurlbert 1984) is that there is very little control over the "treatments" or regulation of the independent variables (Diamond 1986). In this study, a variety of sites were chosen principally to identify the level of consistency in the temporal changes of the communities. While some sites are more similar than others, each of the sites represents a "treatment" and as such can not be replicated. This is an example of what Hurlbert (1984) describes as "pseudoreplication" - essentially a difference ascribed to one factor (for example, wave force) is confounded by all the other factors that may differ with site. This concern is, however, partially offset by reference to results described by other studies of the algal communities in the region.

Associated with the above problem is the fact that we do not know how representative each of the sites is of their general environment. This issue is taken up in Chapter 7, where the concept of large scale spatial variability is addressed for two of these sites.

Nevertheless, the conclusions represent indications which merit experimental study, rather than direct answers. In this, they are consistent with the general aim of the study which is to provide an informed background for the formulation of hypotheses.

Multivariate Comparisons of Sites

The multivariate analysis revealed that wave force appeared to exert an influence on the structure of these communities. That the level of water movement should exert such an effect on the biotic composition of macroalgal communities was to be expected. Wave force has been found to be influential in several aspects of autecological work. In several species, it has been demonstrated that morphology is related to the level of water movement experienced by the individual (eg Norton 1969; Cousens 1982; Rice *et al.* 1985; Cheshire and Hallam 1988b, 1989a; Klinger and DeWreede 1988; Rice and Kenchington 1990a, 1990b). Growth and production are also affected by exposure to wave force (eg Gerard and Mann 1979), as is reproductive biology (Back *et al.* 1991). Furthermore, community composition of macroalgal stands has consistently been linked to the level of water movement experienced (eg Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976; Dayton *et al.* 1984; Dayton 1985a and b; Sanderson and Thomas 1987).

It is interesting that the biota of CJN9 was more similar to the oceanic sites than CJN5. This is contrary to what would be expected on the basis of the level of water movement. It would appear that the increased depth is associated with factors which are more typically associated with oceanic waters. One possibility is the light environment. Whilst not measured, it is likely that the rougher waters of the oceanic sites will keep more sediment suspended and subsequently reduce light to levels comparable with CJN9. Thus the lower light levels of CJN9 may override the effect of water movement. Such a hypothesis is not without precedent. Schiel (1990) found that *Ecklonia* was likely to dominate the biota in deeper waters (>5m depth) because of the far slower growth rates demonstrated by furoids at these depths, presumably a light related phenomenon. While growth rates of the furoid species of this study are unknown, it is possible that a similar situation exists in southern Australia.

It must be accepted that the other possibility is that the area chosen as CJN9 was not representative of the communities of lower wave force 9m sites. As there was only a single site representing this type of environment, the design was pseudoreplicated (Hurlbert 1984). This possibility is investigated further in Chapter 7. The interplay of light and water movement deserves further attention.

Ordination based on biomass data added information to the data set which was lacking in the average presence-absence analysis. This extra information content was not, however, reflected in the ability to differentiate sites. While the result was similar to that of the average presence-absence ordination, the analysis based on biomass failed to distinguish CJE5 and SV5. This is because the added variance contributed by the biomass estimates was large enough to overshadow the differences demonstrated in the coarser presence-absence analysis. It is important to remember that the aim of an ordination is simply to accurately represent the relationships between the samples (Field *et al.* 1982; Gauch *et al.* 1982; Begon *et al.* 1986), not necessarily to form distinguishable groups (Belbin 1991). Thus, the greater differentiation demonstrated by the presence-absence analysis does not necessarily make it a *better* analysis, it merely represents a *different* level of the system. However, it is clear that examination using coarser levels of data analysis can tell the investigator things which are obscured by greater detail. This is a point rarely addressed by surveys. For maximum benefit, future studies should not restrict analysis to a single level, just because that level is the most detailed possible.

Many managers and biologists have been concerned that the time and costs involved in field survey and subsequent laboratory analysis are prohibitive (Warwick 1993). For this reason, it is worth considering that an excellent picture has been achieved by using a coarse level of data definition, the collection of which requires far less time and resources than those required if biomass were measured. Several authors have demonstrated the utility of using higher

taxonomic levels in the analysis of biological communities (eg Hatcher 1989; Gray *et al.* 1990; Cheshire and Kildea 1993; Warwick 1993; Warwick and Clarke 1993). This has resulted in significant time savings, while losing little definition. While the effect of using coarser data types (eg presence-absence rather than biomass or abundance) has received little attention in the marine literature, more general texts have concluded that presence-absence data is inferior (Greig-Smith 1964; Clifford and Stevenson 1975). However, this study has demonstrated that it has utility and, that depending upon the question being addressed, this may be important in designing pragmatic survey techniques.

Comparisons of Sites in Terms of Diversity

Species richness was comparable to other studies in the region (Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd and Sprigg 1976). While the understorey richness was approximately half that found by these other authors, this was probably because of the use of species complexes in the present study. Canopy species richness was generally higher than reported at a single depth in previous work on sites of this region. West Island (Shepherd and Womersley 1970) supported between 4 and 7 species which would have been classified as canopy in the present study. A range is detailed here rather than an absolute figure because each of the previous studies sampled more than one site at each location in order to assess differences in wave force. Pearson Island (Shepherd and Womersley 1971) supported between 2 and 8 species, while St. Francis Island demonstrated between 4 and 10 canopy species. Waterloo Bay (Shepherd and Womersley 1981) supported between 3 and 10 canopy species. The sites sampled in this study supported between 7 and 14 canopy species. It is worth noting that Shepherd and Womersley (1970, 1971, 1976) did not employ a sampling regime as intensive as that of the present study and generally claimed that further sampling would have revealed more species.

In all the studies detailed above and that of Shepherd and Sprigg (1976), canopy species richness was minimal under conditions of extreme water movement. It was intermediate levels of exposure which resulted in the highest canopy richness. This study revealed a similar pattern over the more extensive inter-location scale.

It is worth noting that my judgement of exposure is not independent of the studies which have been described. Womersley and Thomas (1976) published a photograph of the precise location of my Granite Island site, with the caption "high energy coastline". However, my low energy sites were probably subject to more water movement than the low energy sites reported in the studies of Shepherd and Womersley (1970, 1971, 1976, 1981) as the latter are distinctly locally protected.

It is not a simple matter to put the scales at which diversity was measured into context with the concepts of alpha, beta and gamma diversity (Whittaker 1972; Cody 1993). Gamma diversity is typically evident at the largest scale. It is determined by factors such as barriers to dispersal and is often associated with speciation (Cody 1993). Within any geographic province there are, of course, many different habitat types. It is the differences between these habitats which give rise to beta diversity (Knoll 1986), while alpha diversity represents the species richness *within* a habitat type (Whittaker 1972; Knoll 1986; Cody 1993; Haydon *et al.* 1993; Schluter and Ricklefs 1993). However, defining "habitat" is problematic - there are many features of the environment to which species may respond and they do not vary concurrently.

The biogeographic provinces defined by Womersley (1981a, 1990) and Poore (1995) are determined by large scale factors such as oceanic currents and sea temperatures. Thus, they probably could be considered to encompass the gamma diversity. Within each of these provinces, several habitats can be distinguished. One could consider each of the study sites as a different habitat, or the gulf as one habitat and the ocean as another, with the sites representing

within-habitat diversity. For the sake of this exercise, each of the sites was considered to represent a different habitat. Hence beta diversity was defined as the species richness of the entire study and alpha diversity was considered to be represented by the number of species within a site. Species richness at the scale of the square metre therefore represents a component of alpha diversity (hereafter "sub-alpha diversity"), which Schluter and Ricklefs (1993) would ascribe to "niche space components within the local sample".

On the basis of this terminology, sub-alpha diversity of the canopy represented a remarkably high proportion of the alpha diversity of the canopy of each of the gulf sites (Table 4.1a). At the oceanic sites, sub-alpha diversity represented a lower proportion of the alpha diversity of each site. This difference was magnified when the average sub-alpha diversity of each site was expressed as a function of the beta (all sites) diversity. At three of the gulf sites, considerably more than half of all canopy species found across all sites were found in an average square metre. However, at the oceanic sites, no more than 30% was accounted for by sub-alpha diversity. CJN9 represented an intermediate between the diversity partitioning of the gulf and oceanic sites. It is noteworthy that this site supported significantly more *Ecklonia* than the other gulf sites.

There are clearly factors which operate at the scale of the site to partially determine diversity. Given the associations demonstrated between water movement and community composition (eg Shepherd and Womersley 1970,1971,1976,1981; Shepherd and Sprigg 1976; Schiel and Foster 1986; Sanderson and Thomas 1987; Collings 1989; Santelices 1990a) and the clear differences in exposure evident at the sites of this study, it is not unreasonable to suggest that the level of water movement may be an important determinant of diversity at the scale of the site.

While this may be a direct effect, removing those plants which are structurally or morphologically unsuitable, it may also be indirect. Numerous examples exist in the literature of distributions which, while associated with water movement, were in fact controlled by interactions with other species, themselves restricted by water movement (eg Menge 1978; Choat and Schiel 1982; Santelices 1990a). Studies such as Paine (1966), Menge and Sutherland (1976) and Menge (1978) have demonstrated that disturbance events can act to remove an important predator (or as in this case, a herbivore). While it is possible that the higher water movement of the oceanic sites dislodged potential herbivores and allowed competitive exclusion (Gause 1934) to occur, it is unlikely for two reasons. Firstly, no visible difference was apparent in the numbers of herbivores present across sites (although it must be admitted that no quantitative measurement was made), and secondly, if herbivory was occurring, we might expect to see a decrease in biomass. Rather, the low diversity sites tended to support high biomass.

One possibility worthy of consideration is that certain species are better able to exploit a given environment than others and tend to produce higher biomass stands. In doing so, they competitively exclude other species. *Ecklonia*, with its ability to easily form closed canopies (Schiel 1988), is a very good candidate for this type of species.

At the smaller scale, which determines sub-alpha diversity, species interactions are likely to be of great importance (Pacala and Silander 1990; Watkins and Wilson 1992; Schluter and Ricklefs 1993). By examining the proportion of site diversity demonstrated by an average quadrat, we eliminate site scale effects. Those sites which demonstrate high proportions of *Ecklonia* generally do not demonstrate a high proportion of the site diversity at the scale of the square metre. It is proposed that *Ecklonia* is a particularly good competitor which severely restricted the presence of other canopy species in its immediate vicinity. While other species

may exist, they do so in patches largely separate from *Ecklonia*. This is consistent with the mosaic nature of the "*Ecklonia* forests" described both in Australia (eg Kennelly 1987c; Kennelly and Underwood 1992) and in New Zealand (Choat and Schiel 1982; Schiel 1988). This hypothesis is addressed more directly by the relationship at the quadrat level of *Ecklonia* biomass and canopy species richness (Sections 4.3c and 4.4c) and in Chapter 7, where species associations are investigated.

While the total number of understorey species supported at a site was generally higher at the gulf sites, the same cannot be said at the scale of the square metre. Although the understorey richness per square metre is higher at CJE5 than any oceanic site, there was very little to separate the other sites. Thus, while the environment of the more exposed sites precludes a number of species, approximately the same number coexist within a square metre as in the more benign environments. There are several possible explanations; one possibility might involve the "core-satellite hypothesis" (see Gotelli and Simberloff 1987; Glenn and Collins 1990). According to this view, there are a few "core species", which are relatively ubiquitous, and many "satellite species" which are much rarer. It may be that many of the satellite species are unable to survive the oceanic sites at all and at the gulf sites occur only very rarely, thereby elevating site richness, but having little effect on the species richness of an average quadrat. However, while there are 6 species which occur at all sites, they are far from common, with many of them found in only one or two quadrats (of a total of 56 or 72). The only species complex to occur consistently in a high proportion of quadrats at all sites was the *Zonaria* complex, which comprised species of the genera *Zonaria*, *Padina* and *Lobophora*. Thus, this explanation is not sufficient to explain the observed pattern.

Another possibility is that diversity may be determined by the competitive interactions of understorey species. While some sites supported a greater number of understorey species

across the entire site, only a few generally coexisted in any small area. This would correspond with the competitive exclusion principle of Gause (1934). Furthermore, the greater exposure of the oceanic sites may have resulted in more consistent levels of disturbance, retarding the mechanism of competitive exclusion (eg Connell 1975; Paine and Levin 1981; Sousa 1984a and b; McGowan and Walker 1993), thereby helping to maximise diversity within the constraints applied by the environment. At the gulf sites, disturbance through wave action may be more infrequent, resulting in greater opportunity for competitive dominants to exclude others. The result is that at the level of the square metre diversity of the oceanic sites is maintained by disturbance levels, while at the gulf sites, it is the higher alpha diversity of the site which buoys diversity (ie a greater range of species are available to colonise when a rare disturbance occurs).

Comparisons of Sites in Terms of Total Biomass

The levels of biomass reported in this study were consistent with levels found in other studies of southern Australian macroalgal communities. The aforementioned studies of Shepherd and Womersley (1970, 1971, 1976, 1981) demonstrated that biomass varied between locations, between sites of different exposure within the location, and with depth within that exposure regime. Most sites supported a canopy biomass of less than 1000g dwt m^{-2} . However, West Island, which neighbours my "oceanic sites", supported 1730g dwt m^{-2} (Shepherd and Womersley 1970), which is very similar to the levels demonstrated by the present study. Similarly, *Ecklonia* forests of Marmion Reef (Western Australia) fluctuated seasonally between approximately 1000g dwt m^{-2} and 3000g dwt m^{-2} (Kirkman 1984; converted using a 6:1 wet:dry ratio).

The present study demonstrated highest canopy biomass at sites representing intermediate exposure conditions. This is not surprising as the optimal level of exposure represents a

compromise whereby water movement must be high enough to efficiently transfer waste from, and nutrients to, the plant (Lobban and Harrison 1994) without causing detachment. However, studies of macroalgal communities in the region reveal no consistent trend to relate exposure and biomass. Kirkman's (1984) study demonstrated no difference between exposed and protected reefs, and while Shepherd and Womersley (1981) demonstrated a minimal biomass at extreme levels of water movement, this is not mirrored by their 1970, 1971 and 1976 studies.

4.4 Species Response to Site

4.4.a Methods

The biomass of each canopy species was investigated as it differed across the sites. Statistical comparison between sites was made using ANOVA and subsequent Tukey tests. Data was transformed $\left(\sqrt{x + 3/8}\right)$ to comply with the assumption of normality, and Welch's ANOVA was applied where variance was heteroscedastic.

Average individual plant weight was calculated for each species by dividing its biomass in a sample by its abundance;

$$AIPW = \frac{biomass}{abundance}$$

Each quadrat then acts as a replicate, rather than each plant. This concern is addressed by Hairston (1989), who concluded that this generally led to conservative results because the decreased variance was more than compensated for by the decreased degrees of freedom involved in the analysis. ANOVA and Tukey tests were used to detect significant differences. Data had to be normalized using fourth root transformation. Again, Welch's ANOVA was used when variance was heteroscedastic.

4.4.b Results

This section describes, for each species, the differences in biomass, abundance and average individual plant weight between the sites. Each canopy species is presented, generally in descending order of biomass, with a brief description. All descriptions and distributions are from Womersley (1987). All species are distributed to the south of the eastern and western limits which are stated.

Ecklonia radiata

Ecklonia radiata is a true kelp (Order Laminariales) and belongs to the family Alariaceae Setchell and Gardiner. While the order is distributed across the world and contains such ecologically and commercially important species as *Macrocystis pyrifera*, *Ecklonia radiata* is restricted to Australia, New Zealand and South Africa. Within Australia it is found along the southern Australian coast from Kalbarri (Western Australia) to Caloundra (Queensland). It demonstrates intercalary growth and a heteromorphic alternation of generations between the microscopic gametophyte and the large (50cm - 2m long) sporophyte. It is distinguished by a hapterous holdfast, cylindrical stipe and broad laminae with one central blade and secondary laterals (Womersley 1987).

Biomass

By far the dominant species in the region at this depth in terms of biomass, *E. radiata* was most prevalent at the oceanic sites (Fig. 4.8a). Generally, the oceanic sites supported a greater biomass than the gulf sites, although appreciable levels of the species were found at the Cape Jervis North sites. WI5 supported significantly higher *Ecklonia* biomass than any other species, with 1438g dwt m⁻², which represented 76% of the total canopy weight.

Approximately 750g dwt m⁻² of *Ecklonia* was found at WI9, B5 and CJN9, which represented respectively 73%, 49% and 60% of the total canopy biomass. Significantly less *Ecklonia*

was present at GI5 and CJN5, which supported approximately 400g dwt m⁻² (34% and 29% of canopy biomass respectively) and less still at SV5 (88g dwt m⁻² but note that this still represents 20% of the total biomass). CJE5 supported significantly less *Ecklonia* than any other site, with only 12g dwt m⁻², which represented only 2% of the total biomass.

Average Individual Plant Weight

Ecklonia plants were the most massive of any species found in this study. The highest average weight per plant (Fig. 4.9a) was found at the oceanic sites. Within this group of sites, average plant weight decreased as wave force increased, a trend not evident in the gulf sites. WI9 clearly supported the largest individuals ($\approx 125\text{g dwt plant}^{-1}$). *Ecklonia* plants were smaller at WI5 and B5 ($\approx 80\text{g dwt plant}^{-1}$) and smaller still at GI5 ($43\text{g dwt plant}^{-1}$). Of the gulf sites, CJN9 and CJN5, had on average, the largest plants ($\approx 40\text{g dwt plant}^{-1}$). CJE5 and SV5 supported *Ecklonia* plants of the lowest individual plant weight ($20\text{g dwt plant}^{-1}$). Note that WI5 supported higher *Ecklonia* biomass than WI9. This implies that at WI5 there are more plants, each weighing less than their counterparts at WI9. At the Cape Jervis North sites, the difference between the 5m site and the 9m site was not significant.

Scytothalia dorycarpa

Scytothalia dorycarpa is a member of the order Fucales, family Seirococcaceae Nizamuddin. It is endemic to southern Australia, being restricted to an area from Point Lonsdale in Victoria to Geraldton, Western Australia. It consists of a terete, slightly flexuous axis with similar primary branches. The laterals are flat and linear to curved. The plant grows to 2m in length, but is typically about 60cm long. It grows from an apical meristem and has leaf shaped receptacles in the axils of the laterals. These receptacles contain the conceptacles which release gametes (Womersley 1987).

Biomass

Oceanic sites generally supported more *Scytothalia* biomass than gulf sites. In general, there was a trend for increased *Scytothalia* biomass with increasing water movement (Fig. 4.8b). The two sites of lowest exposure to water movement (CJE5 and SV5) supported no *Scytothalia* and the two roughest sites (GI5 and B5) supported most (approx. 680g dwt m⁻²). WI5, with 365g dwt m⁻² had significantly less than these, and WI9 and CJN9 (≈165g dwt m⁻²), significantly less again. Of those sites which supported *Scytothalia*, CJN5 demonstrated the lowest levels (41g dwt m⁻²). Thus, *Scytothalia* appeared to be a plant which is highly tolerant of high water movement and as this increased, it demonstrated an increasing level of dominance, presumably through an ability to cope with the physical conditions.

Average Individual Plant Weight

The average weight per plant of *Scytothalia* followed almost the same trend as the biomass. B5 and GI5 supported plants of significantly higher weight (≈ 27g dwt plant⁻¹) than all other sites, which did not differ significantly amongst themselves (≈ 15g dwt plant⁻¹) (Fig. 4.9b).

Seirococcus axillaris

Seirococcus axillaris is almost identical in morphology to *Scytothalia dorycarpa*. The major difference lies in the receptacles. Like *Scytothalia*, they are located in the axils of the laterals. However, the shape differs in that the leaf-like structures of *Scytothalia* are replaced by short (2mm), terete, hairlike structures in *Seirococcus*. It has a similar eastern distribution limit to *Scytothalia* (Point Lonsdale), but is found no further west than Port Lincoln (South Australia) (Womersley 1987).

Biomass

Biomass of *Seirococcus axillaris* was maximal at the highest energy gulf sites and low at both extremes of the exposure gradient (Fig. 4.8c). CJN5 supported the highest biomass, having $\approx 480 \text{ g dwt m}^{-2}$. CJN9 had significantly less, with about 200 g dwt m^{-2} , but this was still significantly greater than that of WI9 which supported $\approx 110 \text{ g dwt m}^{-2}$. All other sites supported significantly less again ($< 40 \text{ g dwt m}^{-2}$). *Seirococcus* was not found at SV5.

Average Individual Plant Weight

Average individual plant weight of *Seirococcus* did not appear to demonstrate any relationship with exposure (Fig. 4.9c). Similarly, there was no consistent difference between those sites representing the gulf habitat and those representing the oceanic. Highest average plant weight was found at CJE5, CJN5 and B5 ($\approx 35 \text{ g dwt plant}^{-1}$). The lowest average plant weight was found at WI5 ($\approx 15 \text{ g dwt plant}^{-1}$). All other sites were intermediate.

Acrocarpia paniculata

Acrocarpia paniculata is a member of the order Fucales, family Cystoseiraceae Kuetzing. It is restricted to southern Australia, in particular from Pt. Stevens in New South Wales to the Great Australian Bight. It consists of a very short stipe with several long (20-100cm) rough surfaced primary branches and irregular secondary branches. Laterals and ramuli are slender to moderately robust. Reproduction is achieved via the release of gametes from bisexual conceptacles within receptacles developed on the ends of the ramuli. Like all members of the Cystoseiraceae, they demonstrate apical growth (Womersley 1987).

Biomass

Biomass of *A. paniculata* was significantly higher at GI5 ($\approx 145 \text{ g dwt m}^{-2}$) than at any other site (Fig. 4.8d). CJE5, B5 and WI5, with approximately 50 g dwt m^{-2} , were the only other sites to support appreciable amounts of *Ecklonia*. Whilst found elsewhere, it contributed less than 8 g dwt m^{-2} at these sites (CJE5, SV5, CJE9 and WI9). It should be added that the high variance associated with the means made it impossible to statistically separate WI5 from these low biomass sites.

Average Individual Plant Weight

Acrocarpia plants were generally smaller than *Seirococcus*, *Scytothalia* and particularly *Ecklonia*. Maximum average plant weight was found at GI5, where individuals weighed only 17 g dwt on average (Fig. 4.9d). However, this was statistically inseparable from all other sites except for CJE5, where plants averaged only 5 g dwt .

Cystophora brownii

Cystophora brownii belongs to the order Fucales, family Cystoseiraceae. It grows to about 60 cm long, and consists of multiple coarse, broad, highly flexuous axes with retroflex residues of old laterals or secondary axes. It has receptacles developed from the ends of the ramuli and is distributed across NE Tasmania and on the mainland from Victor Harbor (South Australia) to Port Denison (Western Australia) (Womersley 1987).

Biomass

Cystophora brownii was only a minor component of the canopy, with the highest biomass being supported at SV5 and CJE5 where approximately 16 g dwt m^{-2} was found (Fig. 4.8e).

The other two gulf sites (CJN5 and CJN9) had significantly lower biomass ($<2.4\text{g dwt m}^{-2}$).

None of the oceanic sites supported any *C. brownii*.

Average Individual Plant Weight

There was no significant difference ($p>.05$; ANOVA) in average weight per plant of *C. brownii* between the three sites which supported it (Fig. 4.9e). The plants weighed, on average, $4\text{--}11\text{g dwt plant}^{-1}$.

Cystophora expansa

Cystophora expansa is widely distributed, ranging from Long Bay (New South Wales) to Yallingup (Western Australia). It is endemic to Southern Australia. In terms of morphology, it is rather similar to *C. brownii*, although not as robust. In addition, the lower portion of the primary axes is often denuded and small ovoid vesicles are scattered on the laterals.

Receptacles are usually simple, being developed from the ends of the ultimate branches (Womersley 1987).

Biomass

C. expansa made its greatest contribution to the total biomass at CJE5, where 198g dwt m^{-2} were supported (Fig. 4.8f). SV5 supported significantly less (92g dwt m^{-2}), but this is still significantly more than that found at CJN5 (35g dwt m^{-2}). At CJN9 and WI9, only trace amounts ($<1\text{g dwt m}^{-2}$) were found and none was found at any of the other oceanic sites.

Average Individual Plant Weight

The highest average weight of plant was found at CJE5, SV5 and CJN5, at around $9\text{--}11\text{g dwt plant}^{-1}$ (Fig. 4.9f). At CJN9 and WI9, AIPW was around 2g dwt plant^{-1} , but *C. expansa* was

found in only a single quadrat at WI9 and was therefore not considered to be reliably estimated.

Cystophora monilifera

Cystophora monilifera is morphologically very similar to *C. expansa*, the most obvious differentiation being that where *C. expansa* has ovoid vesicles, they are spherical in *C. monilifera*. It has a distribution stretching from Long Bay (New South Wales) to Nickol Bay (Western Australia) (Womersley 1987).

Biomass

Cystophora monilifera was found at more sites than *C. expansa*, but not in particularly large quantities, the greatest being 40g dwt m⁻² at CJE5 (Fig. 4.8g). About 11g dwt m⁻² was found at CJN9 and CJN5, while SV5 supported significantly less (1g dwt m⁻²). WI9, SV5, WI5 and B5 supported less than 5g dwt m⁻² and GI5 supported none.

Average Individual Plant Weight

There was no significant difference in average plant weight of *C. monilifera* across the seven sites at which it occurred (Fig. 4.9g). Average plant weight ranged between 3 and 15g dwt, but the lowest estimates (WI5 and B5) are unreliable as there were too few replicates.

Cystophora moniliformis

This species of *Cystophora* has an extremely flattened primary axis which shows nothing of the flexuous nature of most *Cystophora* species. The laterals, however, are more similar, having a complanate nature, growing from the edges of the main axis. It generally grows to a maximum of 2m long, although more extreme examples have been reported (Womersley 1987).

Biomass

Like most of the species of *Cystophora* found in the area, *C. moniliformis* demonstrated its maximum biomass at CJE5 (Fig. 4.8h). Here, 94g dwt m⁻² was supported, significantly more than SV5 (38g dwt m⁻²). The next tier was represented by CJN5, WI5 and B5 (6-23g dwt m⁻²). *C. moniliformis* was found at CJN9, WI9 and GI5, but only in trace (<2.5g dwt m⁻²) amounts.

Average Individual Plant Weight

Average individual plant weight ranged from 30g dwt at CJN5 to 7g dwt at WI5 (Fig. 4.9h). However, the high level of variance associated with these averages meant that while WI9 supported significantly smaller plants than all other sites on average, none of the other sites could be differentiated.

Cystophora subfarcinata

C. subfarcinata is distributed from Wilson's Promontory (Victoria) to Nickol Bay (Western Australia). It has a slightly flexuous primary axis growing to 80cm long, which tapers to the edges. From the faces of the primary axes grow the flexuous, non-complanate laterals. Receptacles are quite large (generally 1 - 3 cm long, 1-2mm thick) and develop from the ramuli (Womersley 1987).

Biomass

Although *Cystophora subfarcinata* was found at all sites, only the gulf sites supported appreciable quantities (Fig. 4.8i). Biomass was maximal at SV5 (93g dwt m⁻²), but this was not significantly different to CJE5 which supported ≈50g dwt m⁻². These two sites supported significantly more *C. subfarcinata* than CJN5, where 33g dwt m⁻² was apparent. All other sites supported less than 7g dwt m⁻² and were statistically inseparable.

Average Individual Plant Weight

While the highest average plant weight was found at WI9 (25g dwt plant⁻¹), this was not significantly different from the average plant weight of any of the gulf sites (10-14g dwt plant⁻¹) (Fig. 4.9i). The other oceanic sites supported significantly smaller plants (1-5g dwt plant⁻¹).

Sargassum decipiens

While *Sargassum* C. Agardh is a highly cosmopolitan genus, found throughout temperate regions across the globe, *S. decipiens* is endemic to southern Australia, with a distribution from Westernport Bay (Victoria) to Cape Naturaliste (Western Australia). It has stipes of 2-15cm length, with large laterals which occur seasonally and are shed as part of the reproductive period. Like most *Sargassum* species, it has basal laterals which are different in morphology to the upper laterals. However, the difference is not as marked as in many other *Sargassum* species. The primary branches, which carry the fertile material, grow to 40cm in length. The laterals are 1-4cm long on the basal portion of the branch and 1-3 cm long in the upper (fertile) region of the branch. The difference lies in the form. In the lower laterals, the form is generally sub-terete and simple, or once or twice divided, while the upper laterals are filiform, terete and much divided. The branches are shed at the end of the fertile period, leaving only a short stipe behind (Womersley 1987).

Biomass

Sargassum decipiens was not a dominant feature of the canopy at any of the sites, but occurred at all except GI5 and WI9 (Fig. 4.8j). It was best represented at SV5 and CJN5, where biomasses of 20.6 and 18.3g dwt m⁻² were present. CJE5 and CJN9 supported

approximately 5g dwt m⁻², while the oceanic sites supported either no *S. decipiens* or trace (<0.5g dwt m⁻²) amounts.

Sargassum fallax

Sargassum fallax shows much greater differentiation between upper and lower laterals than *S. decipiens*, with broad (4-10cm long, 0.5-1.5cm wide) leaf-like lower laterals and much smaller, branched filiform upper laterals. It possesses large subterete vesicles in the upper ramuli and grows to about 50cm in length. *S. fallax* is distributed from Ballina (New South Wales) to Houtman Albrohos (Western Australia). Like the other *Sargassum* species, it undergoes marked changes in seasonal morphology with the loss of the primary branches (Womersley 1987).

Biomass

S. fallax was found at all sites, but CJN5 (70g dwt m⁻²) supported significantly more than any other site (Fig. 4.8k). CJN9, with 34g dwt m⁻² was the site with the next highest *S. fallax* biomass, and CJE5 followed with 18g dwt m⁻². The lowest biomass of *S. fallax* was found at SV5 (9g dwt m⁻²), which makes it comparable with the oceanic sites. The oceanic sites did not differ significantly among themselves and demonstrated *S. fallax* biomasses ranging from less than 1g dwt m⁻² to 12g dwt m⁻².

Sargassum lacerifolium

This species was recorded at only two sites, CJE5 and SV5 and even then, in small amounts (0.1 and 3.4g dwt m⁻² respectively) (Fig. 4.8l). It is reported only because it fits my definition of a canopy species. It is not a species of any real importance to these communities.

Sargassum linearifolium

Sargassum linearifolium is a member of the subgenus *Sargassum*. It is characterised by a short (1-3cm) stipe with long (10-45cm) primary branches which are shed after the fertile period. The upper laterals are flat, 1.5-8cm long and 1-3mm broad. Lower laterals are 3-8cm long and 3-5mm broad. The species is found from New South Wales to Port Dennison (Western Australia) (Womersley 1987).

Biomass

The greatest quantities of *Sargassum linearifolium* were found at the gulf sites (Fig. 4.8m). It made its maximal contribution at SV5, where 56g dwt m⁻² are supported. Similar, but significantly lower amounts were supported at CJN5 and CJE5 (41-47g dwt m⁻²). All other sites supported less than 3g dwt m⁻².

Sargassum varians

Sargassum varians shows the most marked differentiation between laterals of all *Sargassum* species found throughout the study. The lower laterals are flat, large (3-8cm long), pinnate and retroflex. In contrast, the upper laterals are filiform, terete and much smaller (0.5 - 2cm long). Vesicles are petiolate and subspherical, 3-6mm in diameter. Receptacles are found bunched in the axils of the ramuli (Womersley 1987).

Biomass

Like *Sargassum linearifolium*, *S. varians* was found principally at the gulf sites (Fig. 4.8n). CJE5 and SV5 supported the highest biomass (≈ 40 g dwt m⁻²), while at CJN5, *S. varians* contributed ≈ 25 g dwt m⁻². All other sites supported little (< 0.5 g dwt m⁻²) or no *Sargassum varians*.

Sargassum verruculosum

S. verruculosum is distributed from Maroubra (New South Wales) to south west Western Australia. Like *S. varians* it is in the subgenus *Phyllotrichia* and shows marked difference between its broad pinnate lower laterals and the shorter filiform upper laterals. In common with all of the *Sargassum* species involved in this study, it drops the large primary branches after the fertile period, leaving just a stipe (Womersley 1987).

Biomass

The biomass of *S. verruculosum* was maximised at CJE5, where it was responsible for 28g dwt m⁻² (Fig. 4.8o). With 10g dwt m⁻², CJN5 was the only other site to support a significant amount of *Sargassum verruculosum*. All other sites had less than 2g dwt m⁻² and GI5 had none at all.

A Note on Size Structure of the Populations

Average individual plant weight gives a useful indication of the size of the plants supported, but a more comprehensive description of population structure must include a size-frequency histogram (or weight-frequency in this case). On the basis of the final 4 collections, size-frequency histograms were drawn for each species at each site where more than 25 individuals were measured. In all cases except one, the community demonstrated an abundance of smaller individuals in the 0-4g dwt size-class, with larger plants becoming progressively rarer as the size increased. An example of a typical size frequency histogram is shown in Figure 4.10a. The only exception to this was *Ecklonia* at GI5, which demonstrated a more uniform distribution of plant sizes (Fig. 4.10b).

Summary of species response to site

An overview of the relationship between species distribution and the water movement of the

site indicates that *Acrocarpia paniculata* and *Scytothalia dorycarpa* are the species which preferred the most extreme levels of water movement (Fig. 4.11). While *Ecklonia* can tolerate these conditions, it has an extremely broad range of tolerance and is better adapted to moderate to strong levels of water movement. *Seirococcus* was also best represented in the intermediate environments, but clearly occupied a position lower on the exposure gradient than *Ecklonia*. While some species of *Cystophora* were represented at all or most sites (*C. monilifera*, *C. moniliformis* and *C. subfarcinata*), they clearly preferred the gulf habitat and were generally best represented at CJE5 and SV5, the sites of lowest water movement. The only thing that can be said about the response of *Sargassum* species to the level of water movement exhibited by the sites is that they were best represented in the gulf habitat. Within this group of sites, there was no apparent relationship to water movement.

4.4.c Discussion

It is worthwhile to compare the species response to the hypothesised exposure gradient with other studies involving the same species. In general, there was consistency between the findings of this study and other studies of community composition in the region. The sites examined in this study span a wide range of habitats and sampling was considerably more intense than has previously been the case, so it is not surprising that several of the species of this study have not been described in ecological papers elsewhere.

The biomass of *Ecklonia* was similar to that reported by Shepherd and Womersley (1970, 1971, 1976, 1981) and Kirkman (1984). The fact that it was the sites of high (but not extreme) water movement which supported the greatest biomass of *Ecklonia* is consistent with the studies of Shepherd and Womersley and Shepherd and Sprigg (1976). In contrast, Kirkman's (1984) study of *Ecklonia* forests on the coast of Western Australia demonstrated no difference in biomass between exposed and protected reefs. However, communities at 10m demonstrated

lower biomass than those at 5m. This was calculated using average individual plant weight data of Kirkman (1989) and abundance data of Kirkman (1984 and 1989). Given that in his 1989 study, he uses his abundance estimates from his 1984 paper to estimate production, it was assumed that the studies were comparable. While this is consistent with the fact that WI5 has higher biomass than WI9, the situation is reversed at CJN9 and CJN5. It appears that the relative biomass supported by different depths is dependent upon location.

Average individual plant weight of *Ecklonia* plants was significantly higher at WI9 than all other sites. This could be interpreted as a requirement for moderate to high levels of water movement, juxtaposed against the increased plant damage caused by higher water movement. Shepherd and Womersley (1970) made note of a similar phenomenon at West Island, where individuals were smaller under conditions of extreme exposure. However, Kirkman (1989) demonstrated that at Marmion reef, average plant weight did not change with depth between 5 and 10m. Kirkman (1984) compared standing stock and production between reefs of similar depth but different exposure, but unfortunately used pooled estimates of average plant weight, so comparison was not possible. Average individual plant weight ranged from 16g dwt plant⁻¹ to 130g dwt plant⁻¹ in the studies quoted above, which is comparable with what has been demonstrated in this work.

Scytothalia biomass increased with increasing wave force. This is consistent with the assertion of Womersley (1987) that it is a species generally found on rough water coasts. Similarly, Shepherd and Sprigg (1976), in their study of the Gulf St. Vincent, found that *Scytothalia* was one of the few species suited to the roughest conditions and furthermore was found in stronger water movement than *Ecklonia*. This is supported by the findings of Shepherd and Womersley (1970, 1976, 1981) at West Island, St Francis Island and Waterloo Bay. While Shepherd and Womersley (1971) found *Scytothalia* on the highly exposed seaward shore of Pearson Island, it

existed at between 34 and 50m depth. It is clearly a plant well suited to extreme exposure, but able to tolerate low water movement in combination with the low light levels found at great depth. Where light levels are high, such as in the present study, it appeared to be outcompeted at sites where water movement was low. The fact that this species is well suited to the extreme environment is confirmed by the fact that average plant weight was maximal at the two sites of highest water movement.

Given the morphological similarity of *Seirococcus* to *Scytothalia*, it is puzzling that the former is clearly not suited to conditions of high to extreme water movement. Maximal biomass was found at CJN5, indicating a preference for a more moderate environment. This is consistent with Shepherd and Sprigg (1976), who described its preferred gulf habitat as strong to moderate. Of all the sites studied by Shepherd and Womersley, only West Island fell within the geographic distribution of *Seirococcus*. At this site *Seirococcus* was found under calmer conditions than *Ecklonia* and *Scytothalia*. While significant differences in average plant weight were detected, there was no apparent relationship with wave force. It is quite possible that the AIPW (average individual plant weight) reflects the extent of recruitment events which act to decrease AIPW through the addition of a flush of juvenile plants.

Of all the species examined, *Acrocarpia* is the one which appears to benefit most from extreme water movement. This is not to say it "is best suited to extreme water movement", because there is only $\approx 150\text{g dwt m}^{-2}$ at the roughest site, while the same site supports $\approx 380\text{g dwt m}^{-2}$ of *Ecklonia* and 650g dwt m^{-2} of *Scytothalia*. However, the amount of *Acrocarpia* at GI5 is more than twice that found anywhere else, while in the case of *Scytothalia*, just as much is supported by B5, and in the case of *Ecklonia*, more than four times the biomass of GI5 is supported at sites of lower exposure. This conclusion on its own would be tentative because of the pseudoreplicated nature of the design (Hurlbert 1984) - the higher biomass at GI5 could

be due to factors unrelated to water movement. However, qualitative comparison with other studies strengthens this inference. *Acrocarpia* biomass was maximised in areas of extreme exposure at West Island (Shepherd and Womersley 1970). Similarly, it occurred in the highest water movement of any of the canopy plants at Pearson Island and Waterloo Bay (Shepherd and Womersley 1971, 1981).

All *Cystophora* species reported in this study demonstrated their highest biomass at the calmest site, and lowest biomass at the roughest site. SV5, the next calmest site, generally supported relatively high levels of all *Cystophora* species. Of these, only *C. moniliformis*, *C. monilifera* and *C. subfarcinata* were found at the oceanic sites, with *C. brownii* and *C. expansa* being restricted to gulf sites. This is consistent with the biota of West Island (Shepherd and Womersley 1970), where the first three species were indeed present in small amounts and the latter two were not supported. A similar situation was reported at Pearson Island and St Francis Island (Shepherd and Womersley 1971, 1976), with the exception of the fact that *C. brownii* also existed in small amounts under sheltered conditions. Waterloo Bay supported a wide variety of *Cystophora*, with ten species present between 5 and 10m (Shepherd and Womersley 1981). These included all of the species identified in the present study. As was the case in the present study, *C. brownii* and *C. expansa* were restricted to areas of low water movement.

Sargassum species were typically most prevalent at the gulf sites. In a listing of some of the common canopy species of Gulf St Vincent, Shepherd and Sprigg (1976) identified all species found in the present study with the exception of *S. verruculosum*. The major consistency between their study and the present one was that *Sargassum fallax* is described as a rough water gulf plant, which is what is indicated by the biomass levels described in this study. In contrast, *S. lacerifolium* is a common species at this depth according to Shepherd and Sprigg

(1976), whereas it appears only in trace quantities at two of the sites of this study and not at all at any of the others. This is an indication that the sites sampled in the present study do not encompass the range of habitats exhibited by the gulf. It is unfortunate that Shepherd and Sprigg's study, which was quite extensive, failed to present any quantitative data to allow comparison. While Shepherd and Womersley (1970, 1971, 1976, 1981) found all *Sargassum* species with the exception of *S. lacerifolium* at at least two of their sites, only the fact that they are generally inhabitants of calmer waters is consistent. This is principally because within the gulf habitat, only *S. fallax* appeared to demonstrate a relationship with the exposure of the site. This could be an instance of an apparent relationship which is in truth due to chance alone, but the fact that Shepherd and Womersley (1970) report it as existing in the "rough" zone of West Island is consistent with the original interpretation.

4.5 Relationship Between Biomass and Species Richness

4.5.a Methods

The relationship between the measures of biomass (total biomass, *Ecklonia* biomass and fucoid biomass) and species richness (both canopy richness and understorey richness) was examined graphically. Statistical analysis was not attempted as there was no real central tendency evident in the data. Rather, an upper boundary appeared to exist which defined what level of species richness was possible, given a certain biomass. It is worth noting that no *a priori* assumption is made about causation in this relationship - diversity levels may be influenced by canopy biomass, or it may be the case that both variables are driven simultaneously by another.

4.5.b Results

When relationships between biomass and species richness are investigated, it is clear that there was no central tendency (Figs 4.12a-4.12f). Rather, upper boundaries were apparent which

defined "allowable states". For a given biomass, species richness could be anything up to a certain limit imposed by the boundary. While the boundary which was drawn (as is the case in some of the relationships) dictated that low biomass quadrats may have high species richness, many such samples will have low species richness. Thus what is defined by the boundary for any given biomass is the *maximum* species richness which is likely to occur, rather than giving any indication of the *average*.

Total Biomass v Canopy Species Richness

Canopy species richness is maximal at intermediate levels of biomass (Fig. 4.12a). While richness is clearly depressed in quadrats with less than 1000g dwt m⁻² of canopy biomass, it is above 1700g dwt m⁻² that the greatest decrease in species richness occurs. With the exception of a single outlier, no quadrat with biomass greater than 2000g dwt supports more than seven canopy species (c.f. up to 13 species in quadrats of intermediate biomass).

***Ecklonia* Biomass v Canopy Species Richness**

The relationship between *Ecklonia* biomass and canopy species richness demonstrated no intermediate maximum (Fig. 4.12b). Rather, species richness demonstrated a uniformly high boundary at all *Ecklonia* biomasses less than 700g dwt m⁻². Between this and 2000g dwt m⁻², there is an inverse relationship between canopy species richness and *Ecklonia* biomass.

Beyond this point, the boundary evident in canopy species richness is uniformly low.

Furoid Biomass v Canopy Species Richness

The relationship between furoid biomass and canopy species richness demonstrates a clear intermediate maximum (Fig. 4.12c). Canopy species richness peaked when furoid biomass was

approximately 700g dwt m⁻². Within the range of biomasses observed, there was no upper threshold beyond which species richness ceased to decline.

Total Biomass v Understorey Species Richness

Understorey species richness decreased as total biomass increased (Fig. 4.12d). Beyond 2500g dwt m⁻² understorey species richness demonstrated a uniformly low upper limit. Similarly, the boundary appeared unaffected by any changes in biomass at levels below 800g dwt m⁻².

***Ecklonia* Biomass v Understorey Species Richness**

Unlike the above instance, there is no lower limit of biomass below which species richness is unaffected when *Ecklonia* biomass is considered (Fig. 4.12e). Even low levels of *Ecklonia* were associated with a dramatic decrease in the species richness of the understorey. However, the decline in species richness with increasing biomass became more gradual with increases beyond 500g dwt m⁻².

Furoid Biomass v Understorey Species Richness

Understorey species richness was dictated by a boundary condition which was uniform across the range of furoid biomasses up to 1000g dwt m⁻² (Figure 4.12f). Beyond this, understorey species richness declined. While an intermediate maximum may appear at first glance to exist at ≈700g dwt m⁻², this is based on only three rich samples and is therefore not reliable.

4.5.c Discussion

The relationships between biomass and canopy richness are not simple cases of cause and effect. In considering the relationship between canopy richness and total biomass, it is evident that species richness is restricted in both very high and very low biomass samples. At the high biomass extreme, it was hypothesised (section 4.3c) that a single species, with the ability to

form high biomass stands, is able to outcompete and exclude many of the other canopy species.

The fact that the almost monospecific stands of *Ecklonia* reported throughout Australia have such high biomass (eg Kirkman 1981, 1984, 1989; Kennelly 1983, 1987a, 1987b; Larkum 1986) adds support to this theory, as do the monospecific, high biomass *Durvillaea* stands investigated by Cheshire and Hallam (1988a and b, 1989a and b). At the other extreme, it is likely that low biomass and low diversity are not linked in a causal relationship, but rather are *both* caused by something detrimental to the macroalgae. This might involve a permanent factor like poor substrate (although this was guarded against in the sampling), or some form of local disturbance, which has rendered the patch temporarily devoid of much of the macroalgal cover (see Sousa 1984a and b, 1985 for a discussion of disturbance). The latter would result in low biomass and low diversity, but would be a transitory phenomena.

When compared to the level of *Ecklonia* biomass, canopy species richness did not demonstrate a restriction at low levels of biomass. This is because those samples low in *Ecklonia* were typically dominated by fucoids, many of which commonly coexist. Conversely, at high *Ecklonia* biomass, species richness of the canopy was low because high levels of *Ecklonia* restrict the recruitment of other canopy species, a phenomenon demonstrated by Schiel (1990) and evident in the studies of *Ecklonia* mentioned in the previous paragraph. The ability of *Ecklonia* to form closed canopies much more easily (i.e. with fewer individuals) than the fucoid species may play an important role in this (Schiel 1988).

By contrast, when compared to fucoid biomass, canopy species richness was low at both high *and* low fucoid biomass. Some of the larger fucoids (*Scytothalia* and *Seirococcus*) also have the ability to form high biomass patches which tend to be reasonably monospecific in canopy composition. Thus the low canopy richness at high fucoid biomasses is unsurprising. In samples with low fucoid biomass, there are two possibilities - either the area supports little

biota as outlined previously, or *Ecklonia* is dominant. Both possibilities do occur and both result in low canopy richness.

Understorey species richness was restricted considerably by any increase in the biomass of *Ecklonia* up to 2000g dwt m⁻². Beyond this there was no additional detrimental effect on understorey richness - it was uniformly low. The taxa present under these conditions represent a cadre of species adapted to very low light levels and/or to a high degree of mechanical sweeping from the canopy. In contrast, furoid biomass had little effect on understorey species richness until it exceeded 1000g dwt m⁻². This indicates that, gram for gram, *Ecklonia* has a greater effect on the understorey richness than a furoid canopy. Schiel (1988) demonstrated that lower numbers of *Ecklonia* were required to form a complete canopy than was the case for furoid species, but this was presumably because of the greater size of the *Ecklonia* plants.

In the light of this study, it is clear that factors other than the amount of biomass contribute to the effect of the canopy on the understorey. Three non-exclusive explanations are proposed here; Firstly, differences in morphology could result in *Ecklonia* cutting out more light than a furoid species for a given amount of biomass. Secondly, the ability of kelps to maintain space around them through mechanical abrasion and sweeping has been demonstrated in the related species *Laminaria pallida* by Velimirov and Griffiths (1979) and Velimirov (1983). While it is not suggested that this does not occur in furoid plants, it may not be as efficient. However, Kennelly (1989) demonstrated that sweeping effects were negligible in an *Ecklonia* forest for most understorey species. The third possibility is that the *Ecklonia* plants have large holdfasts, which commonly cover more than 200cm². Thus in a kelp forest with more than 20 plants per square metre (Kirkman 1984; Kennelly 1987a), up to half of the area may be covered by *Ecklonia* holdfast, thereby denying much settlement space to many understorey species.

4.6 Relationship Between Density and Average Plant Weight

- "the 3/2 thinning law"

4.6.a Methods

Like the previous section, investigation of this relationship is restricted to graphical analysis. All samples are plotted simultaneously on a graph of log average plant weight (g dwt plant⁻¹) against log density (individuals m⁻²). Also plotted are a line representing the commonly accepted "3/2 thinning line", as defined in the chapter background, with a log K value of 4.3 (Cousens and Hutchings 1983), and a line, chosen on a subjective basis, which best describes the boundary for the population in question. Graphs were also constructed for each site separately to see if the situation differed between habitats and/or community types.

Self thinning is represented by a linear upper boundary, above which combinations of plant weight and density do not occur. The law applies only to self thinning populations. In cases where self thinning has not occurred, this should not be accepted as evidence of the falsification of the rule (eg Hickman 1979 cited by White 1981). It is necessary that the trajectory be followed *under conditions of self thinning*. Having said this, the present study does not follow a single aging population. Rather, in the manner of Cheshire and Hallam (1988a), it examines many samples at the same point in time, the majority of which may not have reached a thinning line. However, plotting all samples on the log w against log p graph may reveal some samples which are undergoing self thinning. The presence of several of these samples may provide an indication of a clear linear boundary. The lack of such a linear boundary would prove nothing either way, indicating either that self thinning was not occurring or that the thinning relationship was not a log linear one. A linear boundary with a slope

clearly different to $-3/2$ would, however, be strong evidence that the thinning rule in its standard form was not applicable to the stand under examination.

As *Sargassum* species were included in the biomass estimate, but not that of abundance, it was necessary to approximate their abundance. On the basis of field observations, it was assumed that *Sargassum* plants are similar in size to *Cystophora* plants. Having calculated the average weight for a *Cystophora* plant, the *Sargassum* biomass was divided by this figure to give an approximation of the number of individuals present. Average plant weight for a quadrat was calculated by dividing the biomass of a sample by the abundance within that sample. This technique has been justified by Petraitis (1995).

4.6.b Results

If all samples are taken into consideration concurrently (Fig. 4.13a), it appears that some samples breach the $3/2$ thinning boundary defined when $\log K = 4.3$, which is a commonly accepted maximum (Cousens and Hutching 1983). These samples were all from either B5 or WI5. If these samples were disregarded, a linear boundary would be apparent with a considerably lower slope (≈ -1). However, when each of the sites are analysed individually (Figs 4.13b - 4.13i), it is apparent that this is an artefact caused by the overlay of different sites, with different habitats.

Examination of the situation at each of the individual sites shows that not all sites displayed evidence of self thinning. SV5, B5 and WI9 (Figs 4.13c, 4.13g and 4.13h) demonstrated no linear slope, indicating that few, if any, samples at these sites were undergoing self-thinning.

The remainder of the sites appeared to demonstrate self thinning at a line with slope of $-3/2$. However, the $\log K$ value differed between each of these sites, indicating differences in carrying capacity. CJE5, CJN9, CJN5 and GI5 demonstrated thinning lines with $\log K$ values

of 3.8, 4.2, 4.2 and 4.2 respectively (Figs 4.13e, 4.13d, and 4.13f). The highest log K value, 4.6, was demonstrated at WI5 (Fig. 4.13i).

4.6.c Discussion

None of the communities studied constituted evidence contradicting the $3/2$ thinning law of Yoda *et al.* (1963) and White and Harper (1970). However, there were distinct differences in the relationship of average plant weight to density between the different sites. Some sites (B5, WI9, SV5) displayed no clear evidence of thinning, while others did appear to demonstrate a linear upper boundary. Where present, this upper boundary had a slope of approximately $-3/2$.

While the log K value differed between those sites which demonstrated self thinning, most are below the commonly accepted maximum of 4.3 - 4.4 (White 1981; Cousens and Hutchings 1983). However, WI5 apparently demonstrates a far higher log K value of approximately 4.6. While this value is high, it is still below White's (1985) revision of the upper limit to $\log K = 5.0$

Cheshire and Hallam (1988a) claimed that *Durvillaea potatorum* stands were exceptional in that they appeared to demonstrate a log K value of 5. This was clearly above the limit of 4.3 which Cousens and Hutchings (1983) had demonstrated in several monospecific stands of macroalgae. However, their work is flawed by the fact that they worked with fresh weight which is approximately five times greater than dry weight. After cross referencing the replotting in Cousens and Hutchings (1983) paper of Schiel and Choat's (1980) data, it can only be assumed that Cousens and Hutchings were dealing with dry weight. Furthermore, White (1985) states that weight should be expressed as dry weight. When Cheshire and Hallam's values are converted to dry weight, log K becomes precisely 4.3 and therefore no longer exceeds Cousens and Hutchings (1983) estimate of the maximum for seaweed stands.

The confusion is indicative of our lack of understanding of the mechanics behind the $3/2$ thinning law. Allometric explanations (Yoda *et al.* 1963) and interpretations involving leaf area indices (Westoby 1977a and b) have both met with criticism (White 1977, 1981), leaving us with an empirical rule and little understanding of the reasons behind it. The question has to be asked - "is fresh weight or dry weight more appropriate in applications of this rule?" To date there is no simple answer. However, for the sake of comparison and generalization the measures should be consistent, or at least stated in papers dealing with the issue. This becomes very important when generalizations are made not only between species of macroalgae, but also between terrestrial and marine habitats (eg Cousens and Hutchings 1983; Cheshire and Hallam 1988a) where wet:dry ratios are likely to vary considerably.

In light of the fact that the exceptionally high value of log K reported by Cheshire and Hallam (1988a) is scaled down to 4.3 when converted to dry weight, the community supported by WI5 demonstrates a thinning line (and therefore optimal carrying capacity) higher than this. However, Cheshire and Hallam's study gave no evidence to suggest that self thinning had occurred. Rather, they stated that log K must be *at least* 5 (re-estimated to be 4.3 by the present study) based on the maximum biomass found in their study. It is quite possible that the highest value they found was not on the thinning line. However, the fact remains that the present study has, in the case of WI5, demonstrated a thinning line higher than any described in a macroalgal stand before. Whether this is the result of the physical environment or the particular mixture of species supported by the site deserves further investigation.

The fact that CJE5 demonstrated the lowest boundary condition and WI5 the highest is not consistent with Cousens and Hutchings' (1983) assertion that light is the principal determinant of the level of this line. On the basis of this principle alone, it would be expected that the biota of CJE5 would conform to a higher log K value than that demonstrated by communities of the

more turbulent waters of GI5, or those of the deeper waters of CJN9. This may be the result of other physical factors such as water movement or an effect of the specific composition.

It must be accepted that there are two weaknesses in the study performed here. The first of these was the subjective nature of the estimation of thinning lines. The second was that the heterogeneous nature of the community means that some samples may breach the thinning line because the quadrat was bordered by areas of sparse biota. This would lead to an overestimate of interplant interaction and allow an artificially elevated biomass for the plant density observed. Of course the reverse situation could occur, but that would have little effect on the definition of the thinning line, so long as some unbiased samples remained.

To confirm the interesting findings of the present study, we should now look to the use of permanent quadrats. Through repeated nondestructive temporal sampling, these could be used to definitively demonstrate self thinning in these stands, removing the subjectivity necessary in this instance

Note on the relationship of Log (K) and carrying capacity

Previous authors (eg Cheshire and Hallam 1988a) have attempted to back-calculate the carrying capacity^a of some populations from estimate of log (K). This appears to be based on an extension of the thinning line to the point where log (plant density) is zero (ie the y axis).

There are two flaws which invalidate such back-calculation.

Firstly, when $\log(\text{plant density}) = 0$, this implies one plant per square metre, and there is nothing to stop further thinning beyond this density (with a corresponding increase in biomass).

To the contrary, the density of stands of large trees may be orders of magnitude less than this

(White 1981). To choose one plant per square metre as the point where stand biomass is maximised is arbitrary and inappropriate for many species.

The converse problem also exists. Carrying capacity is a function of features of the environment and of the species in question. Both of these may prevent an individual from growing to the point where it can monopolise an entire square metre (imagine a giant carrot!).

Clearly then, to extrapolate the density - plant weight relationship to this point is inappropriate, and to claim that this represents the carrying capacity disregards the very features which determine this variable.

Finally, the units of K demonstrate that the parameter is not a measure of biomass (Cheshire pers. comm.), as the following calculations prove;

If w is measured in g plant^{-1} and p is measured in plants m^{-2}

then assuming that $\log(w) = \log(K) - 3/2 \times \log(p)$

then $\log(\text{g plant}^{-1}) = \log(K) - 3/2 \times \log(\text{plant m}^{-2})$

therefore $\log(\text{g plant}^{-1}) + 3/2 \times \log(\text{plant m}^{-2}) = \log(K)$

$$\rightarrow (\text{g plant}^{-1}) \times (\text{plant m}^{-2})^{3/2} = K$$

$$\rightarrow \text{g plant}^{-1} \times \text{plant}^{3/2} \text{m}^{-6/2} = K$$

$$\rightarrow K = \text{g plant}^{1/2} \text{m}^{-3}$$

(See White (1981) for the general rule where units of w and p vary)

If K were an indication of carrying capacity, the units should be those of biomass, ie g m^{-2} , which they are clearly not. Rather, the units indicate that K is a complex measure involving weight, density and volume. This may relate to the manner in which the plants utilise the volume around them, which is a function of morphology.

4.7 Conclusions

This chapter made a comparison of sites in terms of the biota which they support. The data has been drawn from a sampling regime which deliberately incorporated temporal variability without bias, a rarity in macroalgal studies of southern Australian waters. While each of the sites in a mensurative experiment such as this represents a "treatment", the problem of pseudoreplication is countered to some degree by comparison with other studies of the region.

Apart from providing an overview of the biota of the sites as background for the subsequent investigation of temporal change, this chapter has made several important points:

1) Total biomass was maximised at sites of moderate to high wave energy. This was consistent with some studies, while other studies found biomass equally high under conditions of extreme exposure.

2) A replacement sequence can be postulated along the exposure gradient which is consistent with findings elsewhere in the region for communities at this depth. From high to low energy; *Acrocarpia* → *Scytothalia* → *Ecklonia* → *Cystophora* species → *Sargassum* species.

The latter two categories are very generalised. They in fact contain several species which overlap.

3) Despite the fact that site CJN9 was less similar to the oceanic sites than CJN5 in terms of the level of water movement, it supported a more similar biota. This may be due to the greater similarity in light environment, but requires further attention.

4) The gulf sites supported the highest species richness, with three of these sites each supporting 14 of the 15 canopy species found across the entire study. Furthermore, at these sites more than half of the canopy richness of the entire study could be found in the average

1m² sample. Oceanic sites supported lower species richness, probably because the more extreme environment excluded some species, and of those species which could tolerate the environment, many may have been suppressed by the high levels of *Ecklonia*.

5) Species richness of the canopy was highest in samples of intermediate biomass. Some large species (*Ecklonia*, *Scytothalia* and *Seirococcus*) produce high biomass stands and in doing so, appear to competitively exclude many of the other species. While few studies have examined multispecific canopies, the prevalence of monospecific *Ecklonia* canopy apparent in the published literature, if representative, would indicate that this mechanism is not uncommon. Low canopy richness at low biomass probably represents an early stage after disturbance.

6) Understorey species richness was lowest at both high *Ecklonia* and high fucoid biomass. However, it was diminished by even the smallest amounts of *Ecklonia*. Conversely, more than 1000g dwt m⁻² of fucoid biomass was required before understorey richness was affected. This may be due to morphological differences, differential sweeping potential, or the ability of *Ecklonia* to preempt space with its large holdfast. The relationship is unsurprising given the important interactions of *Ecklonia* canopy and understorey demonstrated by Kennelly (1989).

7) Analysis in light of the 3/2 thinning law revealed that some, but not all, sites appeared to demonstrate thinning. However, the height of the thinning line differed between sites. While the highest thinning line was within the range quoted for terrestrial systems, it was beyond any reported in monospecific seaweed stands.

8) The fact that CJN9 demonstrated a higher intercept of thinning line than CJE5 casts doubt on the assertion of some authors that the height of the thinning line is determined by light levels. In this case, another factor appears more important.

Chapter 5 Temporal Change - Development of a

Multivariate Methodology

“O investigator,
do not flatter yourself that you know
the things that nature performs for herself,
but rejoice in knowing the purpose
of those things designed by your own mind”

Leonardo da Vinci

5.1 Introduction

Before investigating the temporal change demonstrated by the communities described in the previous chapter, it is necessary to develop an effective methodology. While description of the fluctuations in the individual species is straightforward, the analysis of multivariate trajectories is not. This chapter describes the evolution of a strategy to address this problem.

Ordination is an excellent tool for investigating the relationships of multivariate entities such as biotic communities (Everitt 1978; Field *et al.* 1992; Clarke 1993). Multivariate ordination has become widely used in the assessment of the effects of disturbance (eg Warwick and Clarke 1991; Cheshire and Kildea 1993; Clarke 1993). In some cases, single communities have been repetitively sampled and represented on an ordination (eg Warwick 1993; Warwick and Clarke 1993; Griffin and Conran 1994). In this case, the temporal change is inferred from the trajectory between points representing the community at consecutive points in time. However this approach is ineffective when it becomes necessary to compare the trajectories demonstrated by different sites.

Using a modelling approach, artificial communities were created and underwent simulated seasonal changes. These were then analysed using NMDS ordination. The problems associated with the old method of comparison of trajectories (eg Griffin and Conran 1994; Williams *et al* 1994) are clearly detailed and a superior approach is outlined and demonstrated. Finally, the new method was assessed for its ability to detect consistent seasonal change when differing degrees of stochastic variation were introduced.

5.2 Demonstration of the Problem

Two major problems are inherent in the comparison of trajectories on an ordination. The first is that it is not known whether identical changes will be represented by identical trajectories on the ordination if the starting composition differs. The second is that trajectory lines differ in both direction and length, and there is no quantitative method of comparison. These problems will be demonstrated using the NMDS analysis of a set of simulated communities undergoing seasonal change.

5.2a Methods

A series of 8 "initial communities" was created, each representing one of the study sites. These were described by the biomass of each of the 15 major canopy species. The biomass allocated to each of these species was calculated from the field data described in the previous chapter. Biomass of each species at each site actually represented the average at that site across all temporal collections. Table 5.1 details the composition of these original communities.

While it may appear that averaging across all collections is not as appropriate as using the actual community composition of collection 1, the changes which were applied to the data do not correspond to any particular season, so an average is just as appropriate as choosing one of

the collections. Furthermore, this exercise is intended as an exploration of the behaviour of the analysis under known manipulations rather than a true representation of reality.

These "average communities" were set up in an Excel 5 (Microsoft 1993) spreadsheet as a matrix of species by sites with a biomass value for each. This block was then arithmetically manipulated to produce a second block which represented the species biomasses in the next season. The second block was then further manipulated to represent the next change of season, thereby producing a third block. This was repeated to simulate 8 seasons across two years.

The mathematical manipulations representing seasonal change

The basic set of manipulations involved a 75% loss of biomass in one season, followed by a linear increase over the course of the year until all biomass had regrown 12 months after the original loss. The biomass fluctuations can be represented as follows;

100% → 25% → 50% → 75% → 100% → 25% → 50% → 75%

However, the timing of these fluctuations was staggered to represent the fact that different species have biological cycles which are not synchronous. *Acrocarpia*, *Scytothalia* and *Seirococcus* follow the cycle detailed above, with a maximum biomass in the first and fifth seasons. The fluctuations of the *Cystophora* species lagged by a season, but otherwise followed the same pattern (ie 75% → 100% → 25% → 50% → 75% etc) and *Ecklonia* lagged by a further season (hence 50% → 75% → 100% → 25% → 50% → 75% etc). *Sargassum* species lagged by another season to demonstrate fluctuations described by the sequence 25% → 50% → 75% → 100% → 25% etc. Fig. 5.1 demonstrates this graphically.

The simulated communities were then analysed with NMDS ordination based on a Bray-Curtis association measure using the PATN (Belbin 1992) analysis package. Data were range standardised prior to analysis.

It is important to remember that the fluctuations which have been simulated are identical across all sites and the only difference is the starting composition of each of the communities. While the absolute magnitude of the change differs between sites, the relative magnitude is the same. This is considered appropriate because changes in biomass are usually proportional to the level which is present (see section 5.3a). If ordination trajectories can be legitimately compared, we should expect to see identical trajectories demonstrated by each of the sites.

5.2b Result and Discussion

While there are some similarities between trajectories demonstrated by different sites, it should be obvious that they are not identical (Fig. 5.2). Those sites which are similar in composition demonstrate roughly similar trajectories, but when there are differences in composition, the trajectories can be very different. For instance, the trajectory from season 4 to 5 at B5 runs at an angle of 90° to that of WI5 across the same seasonal change. The trajectories from season 2 to 3 at SV5 and CJN5 are similar in direction, but that at SV5 is three times longer.

Comparison of the trajectory between seasons 1 and 2 at CJE5 and GI5 shows that they differ by 90° in direction and approximately an order of magnitude in length.

The important point to note is that these discrepancies have occurred despite the same mathematical/biological changes occurring at the sites. Thus the conclusion drawn from the ordination, that sites underwent different changes, would be erroneous, the truth being that the species are fluctuating in an identical manner across all sites.

The inconsistency demonstrated by the trajectories of the different sites is a product of their different composition. A site which is dominated by a particular species is going to demonstrate its longest trajectory when that species undergoes its 75% biomass loss. Another site, dominated by a different species, will have its longest trajectory at a different time. Additionally, the fact that several species are being considered simultaneously means that the direction of trajectory will be a composite which is determined by the relative levels of those different species within that site.

Even when trajectories amongst sites of roughly similar composition are compared, a problem arises. It could be said that C³JN9 and W⁷I9 demonstrate similar trajectories from season 1 to 2 (Fig. 5.2). However, they differ slightly in angle. Is this discrepancy enough to say they are different or not? This demonstrates the lack of an objective quantitative method for comparison of the trajectories. Any conclusions which are drawn must be made on the basis of a subjective assessment of both length and direction simultaneously and consequently can not be made with confidence.

Thus, the problems which have been demonstrated by this section are two-fold. Firstly, there is no adequate objective method for the comparison of trajectories on an ordination plot. Secondly, trajectory length and direction are not consistent between sites of different composition despite undergoing identical fluctuations. In light of this, comparison of temporal paths using trajectories between points on the ordination is unsatisfactory and a new method is required.

5.3 The solution

The solution to this problem is based on the documented strengths of ordination. While no-one has demonstrated adequate comparison of trajectories (and the previous section

demonstrated that it is inappropriate), ordination excels in the ability to demonstrate the relationships between objects. The answer is thus not to plot points representing composition of community and infer change, but to actually plot the changes themselves.

5.3a Methods

Generally, the most biologically relevant method of representing change is as a proportion of the initial amount (ie before the change). This is because changes are in most cases related to the amount of the species which is present. For example, if a group of plants weighing 100g dwt undergoes reproductive shedding and subsequently weighs only 50g dwt, then each plant is losing half of its biomass. Hence we could assume that twice as many plants, which weighed 200g dwt, would also halve in biomass, resulting in 100g dwt. Similarly, if a storm affects a population of plants, it removes a certain *proportion* of those plants present, rather than an absolute quantity. Thus it appears most biologically reasonable to describe the changes in terms of proportional change.

To calculate these changes, the biomass of one season is divided by the biomass of the previous. As an example of the calculation, the following biomass readings:

$100\text{g dwt m}^{-2} \rightarrow 75\text{g dwt m}^{-2} \rightarrow 150\text{g dwt m}^{-2} \rightarrow 200\text{g dwt m}^{-2} \rightarrow 100\text{g dwt m}^{-2}$,

would result in the following description of changes:

0.75, 2.0, 1.33, 0.5.

Although it did not occur in these synthesised communities, it is possible that in a natural system a species may apparently become locally extinct or invade a site previously uninhabited by that species. However, given that all of the canopy species dealt with in this study were perennial and that it was generally only rarer species which appeared to demonstrate this

phenomenon, it was assumed that this was due to the sampling regime not being geared toward rare species. This would result in observing the species on some occasions, but not on others. Thus, wherever the absence of a species was reported at either of the two times required to calculate a change, that change was coded as missing data. However, this applied only to that change (or changes) where the species was absent; a species at a site may be coded with "missing data" across some seasons, but also show measured change between other seasons.

The imprecision (high variance : mean ratio; Andrew and Mapstone 1987) involved in estimation of the biomass of rarer species could result in extraordinarily large ratios. For instance, a species which had apparent biomass of 0.2 g dwt m^{-2} in one season and 4 g dwt m^{-2} in the next would apparently have put on a twenty-fold increase in biomass, when in fact the difference is due to the inadequacy of the sampling regime to adequately estimate such low means. This type of influence would swamp the more realistic (less dramatic) changes and remove their influence from the analysis. To overcome this, the magnitude of the change is categorized on a six point scale:

1	change < .25	(representing loss of more than 75% of the biomass)
2	change .25 to .5	(representing loss of between 50% and 75%)
3	change .5 to 1	(representing loss of less than half of biomass)
4	change 1 to 2	(representing increase of less than double)
5	change 2 to 4	(representing increase between double and fourfold)
6	change >4	(representing increase greater than fourfold)

The same dataset used to show the problem of comparing trajectories (section 5.2) is used to calculate change and demonstrate that this method represents a solution. Again, data were

range standardised and associations were calculated using a Bray-Curtis association measure before NMDS ordination was performed using the SSH algorithm of Belbin (1992).

5.3b Result and Discussion

The ordination of the changes revealed four quite distinct groups representing each of the four seasonal changes (Fig. 5.3). All groups sites were contained within each seasonal cluster, clearly indicating that there is great similarity in the seasonal change across all sites. Given that this is just how the communities were "programmed" to behave, this method of ordinating the changes can be considered a success.

It was also clear that despite the obvious distinction between the different seasonal changes and similarity between the behaviour of the sites, there was still a degree of variability displayed by the ordination (Fig. 5.3). This is represented by the spread of points within the seasonal grouping. If the changes were identical, then all points within the groupings should overlay each other, reducing the ordination to four points. The reason for the spread is that not all sites have exactly the same species. Where species were not present, they were coded as missing data, and this has caused the variation of the sites within the seasonal envelope.

Finally, the question of objective quantitative assessment of similarity appears to be solved. Similarity is now based simply on the distance between points rather than an ill-defined composite of direction and distance. If groups are well defined, as in this case, no further analysis is necessary. However, if they are poorly defined, a procedure such as ANOSIM (Warwick and Clarke 1991; Clarke 1993) may be employed to make a statistical distinction.

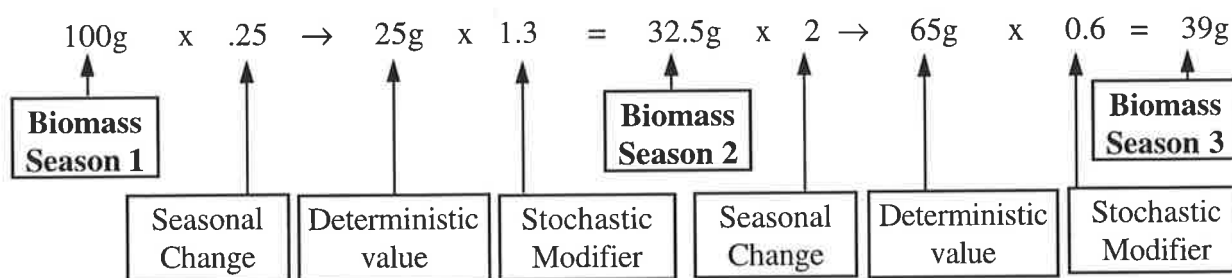
5.4 Proofing the Solution

Having proposed and demonstrated a useful method for making comparison of multivariate temporal change, it remains to see how robust to natural variation this technique is. It would be of little practical use if a low level of natural variation obscured the seasonal change. In order to test this, the same dataset was subjected to differing degrees of stochastic variation over and above the existing seasonal change.

Methods

The same seasonal fluctuations were applied to the dataset, with the exception that stochasm was built into the output of each change. After each seasonal change, the output was varied randomly (using the random function of Excel 5 (Microsoft 1993)) within certain bounds around the deterministic value. Three different levels of stochasm were applied; $\pm 20\%$, $\pm 50\%$ and $\pm 100\%$. Thus the possible ranges were 40% of the mean, 100% of the mean and 200% of the mean, in each case centred on the mean. Note that there is no central tendency to this stochastic range. All values within the specified range are equally probable. Furthermore, the next seasonal change is applied to the stochastically modified previous value.

The following example demonstrates the steps in the calculation of a few seasons and the resultant measurement of change (using $\pm 50\%$ stochasm, which corresponds to multiplication by a random number between 0.5 and 1.5):



The changes which would be calculated from this short sequence are .325 (season 1 to 2) and 1.2 (season 2 to 3) .

Results and Discussion

The ordinations (Figs 5.4a - 5.4c) indicate that the method is extremely robust with respect to stochastic variation. Although the envelopes representing the different seasonal changes grow wider with increasing stochasm, even at a level of $\pm 100\%$ variation about each of the means, the similarity of seasonal change across sites is quite evident. This result is an excellent demonstration of the robust nature of this sort of analysis.

The fact that such high levels of stochasm did not cloud the underlying mechanism (ie seasonal change) is one of the inherent benefits of multivariate analysis. While the fluctuations of a single species may be highly variable, a multivariate analysis incorporates all species simultaneously, thereby "averaging out" these individual stochastic fluctuations. In effect, simultaneous use of many species increases the accuracy of the estimation of community state, in much the same way that many samples are a better estimator of a univariate mean than a single one.

5.5 Conclusions

The methodology developed here is an accurate and robust technique for the comparison of temporal change amongst different communities. It is more accurate than comparison of inferred trajectories, and also allows a quantitative assessment of the similarity of changes. Both its robust nature and efficiency in allowing comparison of temporal change are derived from the inherent qualities of multivariate ordination. This technique took the step of ordinating change itself rather than inferring it from ordinated community states, and in doing

so has provided a very useful tool. Its utility will be demonstrated in the following chapter where it is applied to real community data.

Chapter 6 Temporal Variation

6.1 Introduction

The object of incorporating seasonal and annual change in this study was two-fold. Firstly, it ensured that the between site comparisons of Chapter 4 were made on the basis of a complete picture, rather than a single point in time, unrepresentative of the typical community state. Secondly, it made it possible to detail the seasonal changes and quantify their consistency across two years and eight sites.

Underwood and Kennelly's (1990a) review on the status of Australian macroalgal research highlighted the need to be cognizant of the temporal variation present in macroalgal stands. Dayton and Tegner (1984) are even more adamant - "Developing a proper temporal perspective may be one of the most important unresolved problems in ecology...". To date, few community studies have been designed to incorporate or detail seasonal changes, and fewer still have extended this to include interannual variation. Rather, the much maligned "snapshot view" (Schiel 1988) has dominated our research. While often necessary for pragmatic reasons, this approach has the potential to render a biased or misleading description of the system (West and Reese 1991).

The objectives of this chapter are to quantify the seasonal and annual changes demonstrated by the eight communities already described. As Andrew and Mapstone (1987) point out, studies of this nature act as "the building blocks of the models from which we generate hypotheses". Thus the nature of the patterns demonstrated across time, and their consistency across different sites, provide a basis for the proposal of the important structuring processes. Additionally, this work will allow an assessment of the legitimacy of previous studies which relied on the "snapshot" method, as well as appraising the need to include temporal variability in future

surveys of similar communities. Finally, this dataset also provides the opportunity to test the method of comparison of multivariate change described in Chapter 5 on a real set of communities and seasonal changes, rather than a set illustrating arbitrary levels of deterministic fluctuation and stochasm.

Changes in community composition of sites, separated by up to 100 km and differing considerably in physical environment and biotic composition, were followed across a 27 month period with sampling on a three monthly basis. Presented first are the trends evident in the univariate data. These include the fluctuations in biomass, abundance and average individual plant weight ("AIPW") of each species in addition to total biomass and total abundance. This is followed by a multivariate investigation which examines the changing compositions of the communities and compares the changes across time and site. A discussion of the results provides possible explanations and assesses previous studies in light of these findings.

6.2 Background

Autumn is almost universally recognised by the reds and yellows of falling leaves while mention of spring inevitably brings to mind pictures of wildflowers blooming (& itchy eyes, running noses and sneezing!). Such is the familiarity that even the most uninterested layman has with the changes in our terrestrial vegetation. By contrast, the seasonal cycles which our underwater communities demonstrate remain poorly understood, even amongst keen divers. Those few attempts to summarise these (eg Kain 1989) have concluded that there is little consistency between either the species or the environmental factors driving the changes.

Cognizance of temporal variation is important, not only to obtain an unbiased estimate of community structure and composition, but also because temporal dynamics themselves are important. Concepts central to our understanding of ecology such as succession (eg Connell

and Slatyer 1977; Harris *et al.* 1984), mechanisms of persistence (eg Cheshire and Hallam 1989b; Chapman and Johnson 1990), disturbance recovery dynamics (eg Sousa 1985; Kennelly 1987a,b and c; Kennelly and Underwood 1993) and the existence of alternative stable states (eg Ebeling *et al.* 1985; Johnson and Mann 1988) all rely upon effective description of temporal variation.

The temporal scale of observation, in terms of boundaries and grain, depends upon the process being investigated. Scales range from the seconds involved in the effect of fluctuating light regimes on photosynthesis and production (eg Chazdon and Pearcy 1986; Dromgoole 1987) to evolutionary timescales involving tens to thousands of years (eg Cohen *et al.* 1993). In the study of community dynamics, 1 to 10 year projects are the norm (Dayton and Tegner 1984), although foresight has seen the creation of some important long term vegetation records in terrestrial systems (eg Koonamore Vegetation Reserve since 1925 (Sinclair 1986)). Dayton and Tegner (1984) argue that based on mean generation times, between one and 15 years is required to study the dynamics of many of the large kelp forests. However, the grain of these studies should be such that important fluctuations occurring on a smaller scale can be detected. This necessitates sampling at least on a seasonal basis in order to accommodate the life history processes of the species involved (Schiel 1985b).

Macroalgal research in the northern hemisphere has for some time recognised the need to address issues at different temporal scales (eg Dayton and Tegner 1984, Wheeler and Druehl 1986). The work of Schiel and co-workers (eg Schiel and Foster 1986; Schiel 1990) in New Zealand also demonstrates the importance of these concerns. However, in Australia few authors have recognized this requirement. Much of the description of macroalgal communities is unreplicated at any temporal scale, and that which is may be spatially unreplicated.

Published Australian studies which are adequately spatially replicated and structured to elucidate both seasonal and interannual variation are rare (Underwood and Kennelly 1990a); often as a result of pragmatic considerations. To address accuracy and generality in space and time is often beyond the resources available. This brings with it the need to make compromises, and sacrifice one aspect in order to concentrate on another. For example, Kendrick and Walker's (1994) investigation of the role of recruitment in the structure of *Sargassum* beds uses monthly sampling across a period of two years to provide an excellent insight into the importance of this process. This allows both fine grain, and the assessment of generality between years, but the conclusions are restricted to a single cove on Rottnest Island, Western Australia, as it has not been possible to repeat the experiment across a broad geographical range.

Similarly, Kirkman (1984, 1989) provides excellent descriptions of the fluctuations in productivity, standing stock, density and individual plant weight of *Ecklonia radiata* across an extended period. However, while the study sites were separated along a 6km distance, they often represented different depths. Comparison between depths was the purpose of the latter study, but restriction of each depth to a single geographic location is the hallmark of "pseudoreplication" (Hurlbert 1984). This essentially means that the comparison of depth is confounded by unreplicated change in location. This does not invalidate the work, but it does mean that the conclusions must be tempered with a degree of caution.

May and Larkum (1981) produced an early study which detailed changes in species composition over a 5 year period. However, it suffered from a lack of spatial replication, as it consisted of a single transect. While this does not constitute pseudoreplication, as no comparisons are made other than through time, it does mean that the conclusions remain restricted to a single 60m line off Jervis Bay, New South Wales.

The works of Shepherd and Womersley (1971,1976) give good accounts of the changes in composition associated with depth and exposure within a localised area, but fail to address temporal variability. At West Island (Shepherd and Womersley 1970), data collection was carried out over a period of some years, but the design was not orthogonal (ie each depth and exposure level sampled at each time period) and as such comparisons of exposure levels or depths may be confounded by temporal change. Temporal changes were not addressed quantitatively, and appeared to be based on personal observations rather than by design. Similarly, Waterloo Bay (Shepherd and Womersley 1981) was sampled over five years, thereby incorporating long term change. However, the design was, again, not orthogonal, and different areas of the bay, representing different habitats, were sampled on different dates, once again confounding the observations. In this instance, sampling was largely restricted to October, in order to reduce any confounding effect of seasonal change, but a lack of annual change had to be assumed on the basis of qualitative observations.

Even Kennelly and Underwood, the foremost proponents of the recognition of temporal and spatial scale in Australian phycology, are forced to make compromises. Despite the elaborate and often extensive experimental design and sampling protocol (eg Kennelly 1983, 1987a,b and c and 1989; Kennelly and Underwood 1990b, 1992 and 1993), the studies rarely cover long enough time periods to draw conclusions of similarity between years. Even when the period of observation is extended, any experimental manipulation is carried out in only a single year.

My intention has not been to criticize the above authors and their work. On the contrary, they have been presented because their work has represented some of the finest insights we have into the structure and function of Australian macroalgal stands. This highlights the difficulty of simultaneously addressing questions requiring both fine grain (accuracy) and wide breadth

(generality). It also provides a framework with which to understand where the present study fits with respect to previous work. This current study is also a compromise, which allows a moderate degree of accuracy and generality, over an intermediate geographical distance, although it does encompass a wide range of physical conditions.

6.3 Methods

6.3a Field and Laboratory Methods

Site locations and characteristics were described in section 3.1 and field and laboratory methods were described in section 3.2. The dataset used in this chapter is the same as that of Chapter 4, although in this case distinction was made between the seasonal collections.

6.3b Methods of Analysis

Univariate

The features which were examined on a temporal basis at each site were:

- 1) Total biomass and abundance
- 2) Biomass of each species
- 3) Abundance of each species
- 4) Average individual plant weight (AIPW) of each species

The first category represents the major univariate parameters without respect to species. Total biomass and abundance represent the total biomass of, and total number of, canopy plants of all species combined (15 canopy species for biomass and 9 canopy species for abundance - see Chapter 3).

AIPW for each **individual species** was calculated by summing that species' biomass for the entire collection and dividing it by the abundance summed similarly across the entire collection. While this prohibited any measure of variance (because neither individual quadrats nor individual plants were recognized), it more accurately reflected the real average because individual quadrats often did not have enough plants to accurately estimate average plant weight.

Trends are represented and analysed by way of graphs, and ANOVAs. Where Levene's test (Levene 1960 cited by SAS Institute 1995) found significant heteroscedasticity, Welch's ANOVA (Welch 1951 cited by SAS Institute 1995) was used in place of the standard procedure.

The general procedure used to test for differences between means of collections was either standard ANOVA or Welch's ANOVA. Normally if hypotheses were being tested, it would be standard practice to follow this with a post-hoc procedure such as those devised by Tukey (1953). However, they were not deemed appropriate in this case as they are overly conservative for the comparisons which were required. The Tukey test is applicable when comparison is to be made between all means. In this case, not all means are to be compared, only those which are relevant. For instance, it may be useful to assess whether a parameter increased or decreased across consecutive seasons, or to compare the same season in different years. However, there is no logical planned reason to compare different seasons in different years (eg winter 1992 with summer 1994). Thus the number of comparisons to be made is lower than that assumed by the Tukey analysis. On the other hand, the dangerous practice of unprotected multiple t-tests also cannot be endorsed. Bonferoni adjustment of t-tests for the number of comparisons was avoided because it is also extremely conservative when many comparisons are involved (Wilkinson 1990), probably even more so than the Tukey test.

As a result of the inability of post-hoc multiple comparison tests to deal with the situation which is being analysed, and the fact that this study is designed to provoke hypotheses rather than test them, statistical post-hoc comparison was avoided. Rather, declaration of "seasonality" is based on a significant ANOVA result (at $\alpha=.05$ in all cases) and predictable trend, irrespective of the results of the Tukey test.

When non-significant ANOVA results are returned, a power analysis has been performed in order to demonstrate the probability of achieving a significant result if there really is a difference between the populations (collections). This is dependent on three factors - the magnitude of the difference between means, the variance exhibited by the samples, and the number of samples obtained. Power values range from 0 to 1, where 1 indicates that the ANOVA will definitely declare a significant difference if a difference exists, and 0 indicates a complete lack of ability to detect a significant difference. While significance, or the lack of it, is cited in the text, its level, and, where necessary, its power are to be found in Appendix B.

Analysis of the fluctuations in individual components of the biota was performed at the level of genus. Only *Cystophora* and *Sargassum* species were affected by this as these were the only canopy genera to contain more than one species. Analysis was performed at the level of genus because individual species in many cases could not be adequately estimated. Given the typical similarity of species within a genus in terms of morphology and life history, this was not an unreasonable pooling. Furthermore, the increased precision outweighed the inability to distinguish individual species.

Relationships of Abundance and AIPW to Biomass

As biomass is defined in an explicit relationship as the product of the average individual plant weight (AIPW) and the abundance of those individuals, fluctuations in biomass *must* be caused

by changes in one or both of these factors. This section investigates the relationship between AIPW and biomass as well as between abundance and biomass in order to determine whether one or the other are primarily responsible for the fluctuations in biomass which we observed.

The relationships were investigated by applying multiple linear regression analysis, using biomass as the dependent variable and AIPW and abundance as the independent variables.

This procedure allowed us to partition the variance in the biomass fluctuations and quantify the proportion of the fluctuations attributable to each of the independent variables. As there is a strict deterministic relationship between these variables ($\text{Biomass} = \text{abundance} \times \text{AIPW}$), there was no error term, so the proportions were based on the relative magnitude of the sums of squares of each of the independent variables.

Multivariate

Multivariate analysis was used to investigate three questions. The first of these examined the similarity of the changes across sites, which was assessed using the method developed in the previous chapter. Secondly, the relationships between the communities of the different sites at different times was considered, and finally variation within each of the temporal collections was incorporated.

The multivariate analysis involved the calculation of Bray-Curtis association measures on the basis of range standardised species biomass levels. Dendrograms were constructed using UPGMA classification which is a moderately intensive clustering algorithm. The dataset was also subjected to SSH ordination, which, with a cutpoint in the association values of zero, is analogous to non-metric multidimensional scaling (NMDS), a technique widely used in the ecological literature (Austin 1985; Clarke 1993).

Comparison of the seasonal changes demonstrated by the sites is made using the method described in Chapter 5. Once changes were calculated, they were ordinated in the same fashion as described above. A seasonal change describes the difference between the beginning of that season (when the collections were typically made) and the beginning of the next. Thus the winter 1993 change describes the difference between the community state in winter 1993 and that of spring 1993. Similarly, the spring 1992 change describes the change over the three months subsequent to the spring 1992 harvest.

6.4 Results

While significant fluctuations occurred in all genera at some sites, it was only *Ecklonia*, *Cystophora* and *Sargassum* which demonstrated consistent fluctuations which appeared cyclic. The other species (*Acrocarpia*, *Seirococcus* and *Scytothalia*) demonstrated considerable fluctuation at many sites, but these changes were neither consistent, nor cyclic in nature. Neither did they correlate with any known environmental events such as major storms. The cyclic fluctuations of *Sargassum* and *Cystophora* appeared in phase and correlated with known cycles in fertility of the species. *Ecklonia*, while demonstrating cyclic fluctuations was not in phase with the other two genera.

In sampling multispecies communities such as these, the rarer species are typically poorly estimated, as the sampling regime is not sufficient to adequately estimate all species. Thus in many instances, the fluctuations of the rarer species are not commented upon, as they are artefactual. Far more intensive or focussed sampling would have been required to adequately estimate all species.

6.4a Total Biomass and Abundance

Total biomass generally fluctuated in a manner which suggested biological seasonality (Fig. 6.1a). However, that seasonality differed between sites in amplitude and timing of fluctuations. At the oceanic sites, a cyclic trend is apparent, generally with a maximum in autumn of each year, and minimum in spring. The exception to this is B5 which peaks in winter and displays minimal biomass in both spring and summer. Of the gulf sites, CJE5 and SV5 show clear seasonality, with minimal biomass being supported in summer (although this had not occurred by summer 1994 at SV5). CJN5 shows seasonality, but the minimum appears to lag by a season compared with SV5 and CJE5, displaying minimal biomass in autumn. CJN9 shows no seasonality (ANOVA $p = .06$, power = .77). This power value indicates that there is a 23% chance of declaring no significant difference when there really was one. All other sites demonstrated fluctuations which were significant at $\alpha = .05$ as determined by ANOVA.

In general, seasonality was not as evident or consistent in total abundance as it was in total biomass. Total abundance differed significantly between seasons at all sites except WI5 and CJN9 (Fig. 6.1b). However, only CJN9, CJN5 and WI9 demonstrated fluctuations which could be interpreted as seasonal cycles. CJN9 and CJN5 demonstrated almost identical cycles, with minima in summer, and maxima in winter/spring. WI9 appeared to demonstrate a cycle out of phase with CJN5 and CJN9 by a season. At WI9, the maximum occurred in autumn and minimum in spring. None of the fluctuations displayed by other sites resembled a seasonal cycle.

6.4a Ecklonia

Biomass

A relatively consistent trend existed for *Ecklonia* biomass to be minimal in spring. *Ecklonia*

biomass tended to peak in winter 1992 followed by an almost universal drop to a minimum in spring before increasing again in summer 1993 (Fig. 6.2a). In 1993, it was again the spring collection which demonstrated the lowest biomass at CJN9, but it was delayed until summer 1994 at CJN5. The oceanic sites all displayed spring minima, but there were no winter or spring readings in 1993, so the generality of the pattern remains unknown. B5 ($p=.20$) and WI9 ($p=.05$) were the only sites not to demonstrate significant fluctuations, but the low power values (.52 and .72 respectively) indicate that the non-significant result is quite possibly due to undersampling, rather than a true lack of any fluctuations. However, the proposal of spring minima is supported by the fact that the trend, while statistically unsupported at B5 and WI9, occurs universally at all sites which supported a substantial *Ecklonia* biomass. However, CJE5 and SV5, which were the sites least dominated by *Ecklonia*, did not display any evidence of seasonality. Further support for the concept of a consistent spring minimum comes from the pilot study in spring 1991, where WI5 supported 662g dwt m⁻² of *Ecklonia*, representing another clear minimum.

Abundance

Of the sites which supported a considerable amount of *Ecklonia* and did demonstrate significant ($p<.05$) fluctuations in abundance, SV5, CJN5 and CJN9 were aseasonal and GI5, WI5 and WI9 demonstrated low abundance in spring/summer (Fig. 6.2b). The abundance of *Ecklonia* did not fluctuate significantly at B5 or CJE5. While GI5, WI5 and WI9 appeared to demonstrate minima in spring or summer, the gulf sites were neither similar, nor seasonal. At WI5 the pilot study of spring 1991 demonstrated a low abundance of 9.75 plants m⁻². While the fluctuations at B5 were not significant ($p=.21$), this may have been due in large part to the lack of power (.58) of the analysis. This interpretation is supported by the fact that the other oceanic sites demonstrate the same trend with statistical significance.

Average Individual Plant Weight

There is a striking similarity in the pattern of AIPW of *Ecklonia* at each of the sites. It is a loosely seasonal pattern, with maxima in summer and autumn and minima in winter and spring (Fig. 6.2c). SV5 and CJE5 support insufficient *Ecklonia* upon which to base estimates of AIPW for each season. Therefore, any apparent fluctuations at these sites are discounted. Despite the similarity of this trend across all sites (except CJE5 and SV5) in the first year, there is no evidence to suggest that the same trend is repeated in 1993. The two gulf sites, CJN5 and CJN9 demonstrate remarkably similar fluctuations, but the pattern is not seasonal. Nothing can be concluded about the pattern at the oceanic sites because of the failure to sample in winter and spring 1993.

6.4b Cystophora

Only at 3 sites, CJN5, CJE5 and SV5, was the sampling regime sufficient to accurately assess the biomass of *Cystophora*. It was too rare at other sites. The power of ANOVAs applied to these other sites was generally less than 0.6. Reporting of results is therefore restricted to CJE5, SV5 and CJN5.

Biomass

At those sites supporting substantial quantities of *Cystophora*, the dynamics appear strongly seasonal (Fig. 6.3a). In 1992, CJE5, SV5 and CJN5 all demonstrated a symmetrical annual cycle with maxima in winter and minima in summer. However, the differences at CJN5 were not significant, and stand only as support for the statistically significant patterns of the other two sites. In 1993, the same pattern was repeated at CJE5, but at SV5, the decrease toward summer was masked by an extraordinary increase in one species, *Cystophora subfarcinata* (Fig. 6.4a). The other *Cystophora* species demonstrated the expected minima (Fig. 6.4b

demonstrates one example). CJN5 did not support sufficient *Cystophora* biomass in 1993 to comment on the fluctuations.

Abundance

Abundance of *Cystophora* did fluctuate significantly at CJE5 ($p=.002$) and SV5 ($p=.018$), but not in a seasonal manner (Fig. 6.3b). CJE5 showed a long term increase to autumn 1993 and then a decrease, while SV5 increased significantly across the study period. All other sites showed no significant change in abundance of *Cystophora* across the timecourse of the project ($p>.05$). For reasons outlined above, the sampling was insufficient for any claims to be made concerning the fluctuations of *Cystophora* at the oceanic sites.

Average Individual Plant Weight

Average weight of individual *Cystophora* plants (Fig. 6.3c) generally appeared seasonal at the three gulf sites, where substantial levels of *Cystophora* were recorded. The fluctuations at these sites were similar to those displayed in terms of biomass. An annual cycle was apparent in both years at CJE5, as was the case at CJN5, although the latter was less well defined. At SV5, *Cystophora* AIPW followed a roughly annual pattern, but failed to decrease in summer 1994. This was again the result of *C. subfarcinata* growth. Figs 6.4a and 6.4b demonstrated the phenomenon as it occurred in the biomass data. The same was seen in AIPW data, but a separate set of graphs was not produced.

6.4c Sargassum

Biomass

The biomass of *Sargassum* (Fig. 6.5) displayed striking similarity in behaviour across all sites. This pattern was clearly seasonal at the gulf sites (except CJN9 which did not differ

significantly; $p > .05$, power = .56) with biomass reaching a minimum in summer each year. *Sargassum* undergoes a 5 to 6-fold change between its periods of maximum and minimum biomass. Similar fluctuations are evident at the oceanic sites. However, while there was a minor decrease at CJN5 and SV5 in winter of each year, this was exaggerated at the oceanic sites, to the extent that winter 1992 represented as much of a minimum as summer. All oceanic sites displayed the same pattern, but only WI9 and WI5 demonstrated statistically significant differences. Power of the tests for GI5 and B5 were only .43 and .57 respectively.

6.4d *Acrocarpia*, *Seirococcus* and *Scytothalia*

These species, while fluctuating significantly at several sites, did not do so in a consistent or cyclic manner in terms of biomass, abundance or AIPW. As a result, the fluctuations are presented in Figs 6.6a to 6.8c, in order to quantify and demonstrate the magnitude of the fluctuations, without discussion in the text. The only exception to this is the biomass of *Scytothalia*, which displayed some apparently seasonal cycles, but they were not consistent between sites.

6.4e Relationships of Abundance and AIPW to Biomass

While there was no consistent pattern either within a single site or across sites within one species, there was a tendency for the oceanic sites to be more influenced by abundance changes than the gulf sites (Table 6.1). Not all species can be investigated at all sites because of absence or rarity in many instances. However, of the 16 cases where it was possible to reasonably quantify the relationship between AIPW, abundance and biomass at the oceanic sites, the biomass fluctuations of 13 were primarily (>50%) influenced by changes in abundance. At the gulf sites, abundance was predominantly responsible for biomass

fluctuations in only 7 of 16 instances. In the remainder, it was changes in AIPW which were the major cause of biomass fluctuations.

6.4f Multivariate Comparison

Overview

This section compares both the *compositions* of the communities in different seasons, and the *changes* which occurred between each of the seasonal collections. These *changes* were calculated from the compositions in successive collections. The *composition* describes the community state at the beginning of the season in question, while the seasonal *change* refers to the change from the beginning of the season to the beginning of the next. For example, the "winter 1993 change" describes the change across winter 1993 (ie from the beginning of winter 1993 to the beginning of spring 1993) and was determined by calculating the difference between the *compositions* of winter and spring 1993.

In general, the composition of the communities fluctuated in a manner which indicated that any given seasonal change was consistent across all sites and both years, but differed between seasons. The only exceptions to this pattern were the spring changes, which were unpredictable and highly variable across sites and years. Because of the variability of the spring changes, the community *composition* in the subsequent summers was often dissimilar to that of all the other seasons. Sometimes, but not always, summer compositions were similar to each other. Inter-annual differences were demonstrated in the composition of the communities in non-summer seasons, indicated by the fact that these seasons often tended to group together in loose "year groups" on the ordinations. The non-summer community compositions were often more closely related to the preceeding summer, than the one following.

Comparison of Temporal Changes

As stated above, with the exception of spring, each of the seasons was associated with a distinct change in composition which was consistent across the eight sites and two years encompassed by the study (Fig. 6.9).

While the communities are the essential focus of this thesis, it is also necessary to comment on the actual ordination used to demonstrate the above finding, as it represents a field test of the multivariate technique developed in the previous chapter. Four groups of seasonal changes were depicted, each one representing a different season. The "summer group" contained every summer change except two (CJN9 and GI5 in 1993 were aberrant). All autumn changes, from all sites in both years, were found in the appropriate seasonal group. Winter changes were a little more variable, but still only two were found outside the envelope encompassing the bulk of the seasonal changes. The two exceptions were SV5 and WI9 in 1992. Spring changes could not be said to be similar across sites. Dissimilar to the other seasonal changes, they were also scattered widely on the ordination, indicating considerable variation across sites and years.

To summarise the tendency of the changes to fall into discrete seasonal envelopes:

- only two out of the sixteen summer changes fell outside the "summer envelope"
- two of the twelve winter changes fell outside the "winter envelope"
- only one of the twelve spring changes fell in the wrong envelope
- none of the twelve autumn changes fell outside the correct seasonal envelope

This represents an extraordinary similarity of change across sites of extremely varied composition and physical habitat and over two separate years.

Comparison of Composition

CJN5

In terms of the analysis of the averages, both the ordination (Fig. 6.10a) and dendrogram (6.10b) of the seasonal collections at CJN5 appeared to display two groups of non-summer samples, each representing one of the two years. Distinct from these are the summer 1993 sample and a group consisting of the other two (1992 and 1994) summer collections. The non-summer groups are more similar to the preceding summer than to the one subsequent.

Incorporation of the spatial variation at CJN5, as evidenced by the samples of each collection, supported the notion of a broad distinction between years, but none of the summers was particularly distinct (Fig. 6.10c).

SV5

The ordination and dendrogram of the average collections of SV5 (Figs 6.11a and 6.11b) demonstrated the same general phenomenon as CJN5. There was a tendency for summer collections to be distinct from non-summer collections. It differed from CJN5 in that the summers of each year are distinct both from the non-summer seasons, and each other. Again, the non-summer months cluster within year groups which are more closely related to the preceding summer than the one following.

Examination of the within-collection variation at SV5 (ie plotting all samples from all collections - Fig. 6.11c), revealed a similar picture to that demonstrated by the analysis of the averages. There appears to be justification for accepting two groups representing the summers of 1992 and 1993, and two groups representing the non-summer collections of 1992 and 1993. Furthermore, there appeared to be a tendency for the non-summer collections of 1992 to be

more similar to summer 1992 than summer 1993, while the non-summer 1993 collections tended to be more similar to summer 1993.

CJE5

A similar situation existed at CJE5, where the ordination (Fig. 6.12a) could be interpreted as distinguishing the summer collections (1992 and 1993) and two groups of non-summer collections clustered into year-groups, with the final summer collection being similar to the non-summer collections immediately prior to it. However, while the dendrogram (Fig. 6.12b) supported the notion of two distinct summer collections in 1992 and 1993, it is unable to distinguish two groups representing the two years of non-summer collections.

Ordination of the samples which comprise the temporal collections of CJE5 demonstrate a reasonably clear distinction of the summer samples, the 1992 non-summer samples and the 1993 non-summer samples (Fig. 6.12c). This interpretation is similar to that derived from the analysis of the averages, although the dissimilarity of summer 1994 to the preceding non-summer seasons is clearer here. There is no real evidence to indicate whether non-summer samples were more similar to the preceding rather than succeeding summer, because the first two summer collections did not differ substantially.

B5

Ordination and classification of the seasonal composition of B5 (Figs 6.13a and 6.13b) again distinguished summer 1992 and 1993 as distinct from all other collections. Summer 1994 was not grouped with any other collections. It was not possible to assess the presence of year classes, as no sampling was done at this site in winter and spring 1993.

The ordination of all samples taken from B5 (Fig. 6.13c) indicates that the interpretation of the averages analysis was only partially correct. While there is a tendency for summers 1992 and 1993 to group together, relatively distinct from samples of the other seasons, the remainder of the collections, including summer 1994 are not distinguishable from each other. Furthermore, it is clear that there is substantial variation within the summer collections which results in three of the summer 1992 samples being more similar to the group of "non-summer" collections.

WI9

The ordination and classification of the average collections of WI9 (Fig. 6.14a and 6.14b) appear to indicate a similarity between the summers of 1992 and 1994, with these two being distinct from the other collections. Summer 1993 is not distinct from non-summer collections, and two other non-summer sites stand distinct. With so few points, however, the ordination is difficult to interpret, as "grouping" become rather arbitrary.

Within - collection variation is considerable at WI9 and it was only possible to clearly distinguish two seasons - autumn 1992 and 1993 (Fig. 6.14c). This casts some uncertainty on the results of the ordination and dendrogram of the "average" communities.

WI5

A similar situation exists at WI5, where the ordination could be interpreted as demonstrating a distinction between summer collections and non-summer collections (Fig. 6.15a). However, as with WI9, the interpretation is tenuous because of the paucity of community states being plotted. The dendrogram (Fig. 6.15b) highlights this difficulty. If summer 1992 and 1994 were to be considered as a separate group, 5 groups would have to be accepted, which is not

particularly useful when only collections are being analysed. Thus, it appears that the most useful interpretation of the situation is that there are three main groups:

- 1) summer 1992 and 1994 with spring 1992
- 2) autumn 1992 and 1993 with winter 1992
- 3) summer 1993

Examination of the ordination of all samples from WI5 (Fig. 6.15c) demonstrates a high degree of within-collection variation. This variation makes it possible to distinguish only the autumn collections, with the samples from autumn 1992 and 1993 being relatively distinct from all others.

CJN9 and GI5

The ordinations of the collections of CJN9 and GI5 displayed no discernable pattern (Figs 6.16a and 6.17a). Similarly, the dendrograms demonstrated "chaining", with no distinct clusters (Figs 6.16b and 6.17b). The use of the more intensely clustering Ward's method failed to change this situation. It should be added that the final collection (summer 1994) at GI5 was very different in composition from any of the other collections.

Ordinations of all samples at each of these sites failed to detect any particularly distinct groups of samples (Figs 6.16c and 6.17c), with the exception of the summer 1994 collection at GI5 (Fig. 6.17c), which was distinct from all other samples.

6.5 Discussion

Total abundance and biomass

Most sites demonstrated fluctuations in total biomass which could be interpreted as being indicative of a seasonal cycle. However, the fact that the timing of these fluctuations differed between sites suggests that the processes underlying these cycles may differ between sites. There are several possibilities which might account for this. Firstly, the fluctuations could be linked to the annual reproductive cycles which typically involve biomass increase until the period of reproduction, and then a loss of biomass as reproductive material is shed. Given that different sites were dominated by different species, this may help explain the inconsistency between sites if the different species had cycles which were out of phase with each other. A second possibility is that the cycles were the result of the balance of synthetic and degradative processes in each of the species. Productivity varies across the course of a year, as does biomass loss through sloughing, reproductive shedding and storm damage. Again, these factors may differ between species. The third possibility is that biomass loss was due to the damaging effect of storms and regrowth alone, and that the effect of the storms is moderated by the location of the site.

A combination of the moderated effects of storms and changes associated with the reproductive cycle may be the best explanation for the situation. The minima demonstrated by most oceanic sites in spring is consistent with the damage caused across winter, when storm activity was highest (see Fig. 6.18). CJE5 and SV5 are far less exposed and unlikely to have been affected by storms to the same degree. The minimum in summer demonstrated at these sites is likely to correspond to the seasonal shedding of biomass associated with reproduction of the *Cystophora* and *Sargassum* species which dominate these sites and reach their fertility peak in spring (Womersley pers. comm.). It is possible that the spring minima demonstrated by

most oceanic sites are due to the reproductive cycle of the dominant species, *Ecklonia*, rather than winter storms. While this hypothesis is not supported by Kennelly and Larkum's (1983) observation that the major settlement event for *Ecklonia* occurred in autumn (at least for the kelp forest that they studied), Kennelly (1987a) states that the major recruitment event of *Ecklonia* along the New South Wales coast occurs in winter, which indicates that the spring minima may be attributable to life history-related fluctuations alone. Ultimately, it must be admitted that the possible causes are confounded, and either or both may explain the situation at the oceanic sites. However, at the gulf sites, life history-related biomass fluctuations are the best explanation.

The fact that total abundance did not demonstrate consistent seasonality at many sites where total biomass appeared seasonal is unsurprising given the complexity of the processes acting on abundance fluctuations (see Kennelly 1983; Reed 1990). Recruitment, which causes an influx of many juveniles, is known to be patchy (Sousa 1984b; Kendrick 1994), and determined to a large degree by the shading and scouring effects of adult plants (Kirkman 1981; Santalices and Ojeda 1984a and b; Kennelly 1987a and b; Cheshire and Hallam 1989b). Sousa (1985) suggests that, at least in the intertidal, disturbance is highly seasonal. On this basis, it might be predicted that winter/spring storms would result in an influx of many small plants which are taking the place of those adults which are removed (thereby freeing space and reducing shading and scouring). The data however does not support this hypothesis. Those fluctuations which we do see are not consistently related to the seasonal patterns we would expect to see in adult mortality. The conclusion is therefore that the lags and feedbacks involved in the system make the temporal dynamics of overall abundance largely uninterpretable without very controlled conditions. This finding is not restricted to mixed stands where the variety of species is likely to complicate the interactions, but also applies to the *Ecklonia* forests described by Kirkman (1984) which are practically monospecific. He

demonstrated that while significant changes in the abundance of stage III (mature large adult) plants occurred, they did not correspond to any seasonal cycle.

Quantifying the fluctuations within and between years has allowed the assessment of previous studies which used snapshot pictures, gleaned from sampling at a single point in time. It has also provided guidelines for future studies. Total biomass typically varied by between 100% and 200% across the course of the year, but there was little evidence to suggest great difference between the two years of this exercise. While a comparison of only two consecutive years is not definitive, it is clear that seasonal changes are extensive. Previous descriptive accounts based on a single sampling period are likely to be based on inadequate data, and the "snapshot view" should be avoided in future studies of these communities. It should be noted that other authors such as Bouxin and Gautier (1982) have specifically defended snapshot sampling in some terrestrial ecosystems as being legitimate and accurate. The macroalgal communities of southern Fleurieu Peninsula can not be treated similarly, and given the similarity in composition to other sites around the state (see Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd 1976; Collings 1989), this conclusion could be confidently extended to a far wider area.

Ecklonia

The fluctuations in biomass of *Ecklonia* are relatively consistent across the sites of this study, but they lag behind the cycle demonstrated by Kirkman (1984) in *Ecklonia* forests off the coast of Western Australia. While the minimum biomass is achieved in spring at the sites of this study, those of Kirkman (1984) reached a minimum in winter. It is proposed that the difference is the result of the severe storms which occurred after the winter collection in the present study (see Fig. 6.18). It should also be noted that replication across two years by Kirkman allows us to gauge the consistency across years and that this revealed up to two

months difference in the timing of minimum biomass between years. If this is the result of variation in the timing of these disturbance events (and Underwood 1981b would suggest that such variation is common, at least in NSW), then the minimum displayed in spring at most of my sites could be the result of the late winter storms. Given the close proximity of the oceanic sites, such variation cannot explain why there is such a decrease to winter 1992 at WI5. This remains an unexplained site-specific effect (eg episode of severe herbivory). Note, however, that there was no recovery in the following season - biomass remained low at the time when the other sites reached their minima.

The rapid regrowth demonstrated after the minimum is not surprising in light of Larkum's (1986) finding that production was maximised at this time for *Ecklonia* plants at a site in New South Wales. Kirkman (1984) also found production maximal in late spring in *Ecklonia* stands in Western Australia.

The importance of storm events is apparent again in the abundance fluctuations of *Ecklonia*. Of the sites which supported a considerable amount of *Ecklonia* and which did demonstrate significant ($p < .05$) fluctuations in abundance, the most sheltered sites showed no seasonality, while the exposed sites, GI5, WI5 and WI9, demonstrated low abundance in spring, which is indicative of storms removing entire *Ecklonia* plants. The fact that the abundance remained low in the following summer despite increased biomass can be explained by a combination of vegetative growth and recruitment. It would appear that initial biomass increases were the result of the regrowth of damaged plants and previously suppressed juveniles after the storm. However, there was no input of new juveniles until autumn.

Resilience of *Ecklonia* stands via a "store" of suppressed juveniles is in contrast to the hypothesis of Cheshire and Hallam (1989b). They proposed the lack of juveniles found in the *Pterygophora californica* communities of DeWreede (1984) was due to the fact that

laminarians such as *Pterygophora* have an alternation of heteromorphic generations and may store their reproductive potential in the form of the microscopic gametophyte stage. This was contrasted with *Durvillaea potatorum*, which undergoes direct reproduction like the fucoids and maintains large numbers of suppressed juveniles beneath the canopy. This study appears to demonstrate that even if *Pterygophora* does rely on gametophytes for storage of reproductive potential, it is not necessarily so for other laminarians such as *Ecklonia*. Fig.

4.10a demonstrates that most *Ecklonia radiata* communities in this study generally did have a preponderance of juveniles and they appeared to be utilized in much the same way as proposed for *Durvillaea*, growing to fill canopy gaps as adults are removed. Kirkman (1981) also found that *Ecklonia* used suppressed juveniles as a store of reproductive potential and a mechanism of persistence. This study would indicate that both mechanisms of persistence are utilised - sexual reproduction through gametophytes and suppression of juveniles beneath the canopy.

The dynamics of *Ecklonia* in this study are reasonably consistent with the findings of other studies dealing with the species. Kennelly (1983) detailed settlement of *Ecklonia radiata* in summer. Prior to this there was very little settlement of the species. If the "very high" growth rates of Kirkman (1981) are applicable in the communities under study here, then the autumn flush in abundance may be the result of juveniles which settled in summer growing to the "collectable" size of 4cm.

While Kennelly (1983) proposed reproductive periods in both winter and summer, in a subsequent paper (Kennelly 1987a), he demonstrated that when *Ecklonia radiata* is removed from large areas (2m x 2m), it will only recolonize if the clearance occurs in winter. Otherwise turfing species dominate. Similarly, Kirkman (1981) showed that clearance in late spring resulted in extremely limited recruitment by *Ecklonia*. These results may appear puzzling in light of the fact that this study has demonstrated that recruitment can proceed when

disturbance occurs in spring (if one equates major storm events and abundance and biomass loss with disturbance).

This apparent contradiction is interpretable in light of the experimental procedure. Both Kennelly (1987a) and Kirkman (1981) effected a complete clearance of kelp plants across areas of four and 36 square metres, which is unusually large for natural stands. A kelp canopy modifies the environment of its juveniles to such an extent that monospecific forests are common. With the canopy removed, settling juveniles are subject to a different hydrodynamic environment (Dayton and Tegner 1984), less protection from herbivores (Velimirov and Griffith 1979, Velimirov 1983), greater interspecific competition and importantly, particularly in shallow waters, increased exposure to harmful ultraviolet radiation (Wood 1987). All of these may act to decrease the growth and survival of *Ecklonia* recruits. Indeed, when kelp finally began to recolonize the clearances, it began on the edges. This indicates a preference for living under at least a partial kelp canopy. Thus, the survival of some adults and repressed juveniles and subsequent rapid growth is vital for the protection of the new cohort of juveniles, and ultimately the persistence of the stand.

Kirkman (1984) demonstrated fluctuations in average plant weight of mature *Ecklonia* plants which were very similar to the findings of this study. He also found minima in winter and spring and maxima in summer and autumn. His explanation for the fluctuations involved winter storms both damaging and removing plants, and regrowth of the adult plant over summer and autumn. However, in the case of the present study, it was early spring storms which damaged plants, thereby removing biomass. This was followed by rapid growth across *Ecklonia*'s period of highest productivity (spring/summer) (Kirkman 1984, 1989; Larkum 1986). The reason for the AIPW decreasing in winter in this study was probably not winter storms, but rather an artefact of the method of calculation. While this period may not entail

storm damage of the adults, it appeared to be the time when juveniles, which recruited during the storms of the previous spring, grow into the canopy. This influx of smaller plants causes the average weight to decrease.

The presence of other species appeared to have an effect on the fluctuations of *Ecklonia* biomass, abundance and AIPW. A good example of this is the failure of *Ecklonia* biomass to increase significantly at the summer 1994 collection at CJN5 and CJN9, the only two gulf sites to support significant quantities of that species. At CJN9, the failure to increase may be due in part to a substantial increase in *Scytothalia*. At CJN5 this normally high growth period may be being masked by an increase in *Sargassum* biomass, inconsistent with the general pattern. A similar argument could be made for the failure of *Ecklonia* AIPW to increase in the final summer. The *Ecklonia* stands of Kirkman (1984) represent the extreme monospecific case, and these demonstrated almost clinical annual cycles in biomass and AIPW. Abundance fluctuations also appeared to be affected by the presence of other species. The oceanic sites, where *Ecklonia* dominated, demonstrated far more predictable seasonality than the more species rich gulf sites. Thus it appears that the larger number of species in these mixed communities makes prediction of the dynamics of *Ecklonia* more difficult because of the interactions involved. It must be admitted that the converse situation may be applicable. *Sargassum* and *Scytothalia* may increase because of the lack of the normally dominant *Ecklonia*. Only manipulative studies can resolve this dilemma.

Cystophora

The fluctuations in biomass of *Cystophora* appear to be driven by the reproductive life history of most species of this genus. Fluctuations in biomass were associated with changes in AIPW rather than abundance. While the death of adult plants and recruitment of juveniles into the canopy do occur, they were not seasonal, and were thus not reflected in the trends we see in

biomass. As it is only at the gulf sites where *Cystophora* is found in quantities sufficient for analysis, it is not surprising that at these protected sites communities show little evidence of wave shear disturbance.

Most species of *Cystophora* undergo changes in morphology associated with reproduction. They put on substantial quantities of weight prior to the reproductive period in the form of fertile laterals and/or ramuli. These are often lost after reproduction, leaving the plant with reduced weight (Womersley pers. comm.; Hotchkiss unpubl. data). Given that the fertile period of many of these *Cystophora* species is spring, it is not surprising to find that summer is the period of both minimum biomass and AIPW. It would appear, however, that the adults generally regrow, leaving the juveniles to wait until canopy space is cleared through disturbance. In environments as physically benign as these, this is apparently common. This is supported by the fact that most adult *Cystophora* plants carry remnant scars of fertile laterals of previous years.

The only major deviation from the cyclic trend was caused by a single species, *Cystophora subfarcinata*, and this too can be interpreted in the light of cycles of fertility. Of the *Cystophora* species found at these sites, only *C. subfarcinata* does not reproduce solely in late spring. Rather, it is able to reproduce year round (Womersley pers. comm.; Hotchkiss unpubl. data), providing an explanation for the difference between its dynamics and those of the other species of the genus. It is possible that this species is opportunistic and is able, on occasion, to take advantage of the increased light levels caused by a thinning canopy.

Alternatively, it may have been that the sampling date was fractionally early to catch the major loss of biomass associated with reproduction. It is known that other species of fucoids have annual periods of reproduction cued by the full moon (Norton 1981; Kendrick and Walker 1991; May and Clayton 1991). It may be that for *C. subfarcinata*, the time to reproduce and

shed the majority of laterals was a single lunar cycle after the other species. This may have been just subsequent to the final sampling.

These results represent the first account of the biomass fluctuations of subtidal species of *Cystophora*, and as such there is little opportunity to make comparisons. However, if these communities are to be compared to others in the future, it is clear that different sampling designs and methods are needed where *Cystophora* shares dominance, or is sub-dominant. Poor power levels at the oceanic sites are clear evidence of this requirement. Permanent quadrats may be a more effective method of monitoring fluctuations under these circumstances.

Sargassum

The fluctuations described in this study are consistent with the major changes in morphology associated with reproduction of *Sargassum*, and the timing of such reproductive events.

Deysher and Norton (1982) described the propensity of *Sargassum* species to shed their large laterals at the end of the reproductive period. While their work concentrated on the ubiquitous invasive weed, *Sargassum muticum*, Womersley (1954) also demonstrated seasonal shedding of laterals associated with annual reproduction in the subgenus *Phyllotrichia*, and later (Womersley 1987) extended the generalization to species of the other 2 subgenera of *Sargassum*. These laterals make up the bulk of plant biomass, and typically all that is left is a stub which can subsequently regrow (Tsukidate 1984; Paula and Eston 1987; Kendrick 1994). Furthermore, Kendrick and Walker (1991) demonstrated that this reproductive event was at its height in late spring/early summer (November - December). Thus the fluctuations of *Sargassum* look to be clearly controlled by the changes in morphology associated with the life history of the genus.

Acrocarpia, Seirococcus and Scytothalia

These genera did not furnish any real evidence for seasonality of fluctuations. In many cases, the sampling was insufficient to detect significant differences, but even in those cases where significant differences were found, the patterns were rarely seasonal. However, while the fluctuations were not seasonal, they were, nonetheless, statistically significant and substantial in magnitude. Four-fold changes in biomass and abundance were not uncommon. Hence, future studies must be cognizant of this variation and incorporate it in their sampling regimes.

While the dynamics of *Scytothalia*, in terms of abundance and biomass, may appear seasonal at a number of sites, the fact that some sites are out of phase by up to 180° (6 months) is an indication that the fluctuations are not related to innate cycles of the species. Rather, they would appear to be related to site specific features (such as herbivory or the fluctuations of the remainder of the community, which varies in composition between sites). Dieckmann (1980), Kornfeldt (1984), Novaczek (1984b), and Kirkman (1989) have described lags in growth phase between different populations. However, these studies attributed the lag to differences in depth, with deeper sites lagging behind shallower by up to three months. In the present study, there were rarely differences in depth, and at Wright Island, where such a comparison was possible, it was the shallower site which lagged. For these reasons, it cannot be assumed that a similar explanation can be applied to the fluctuations of the sites of this study.

Relationship of AIPW and abundance to biomass

Biomass fluctuations were typically related to fluctuations in abundance at the oceanic sites, but far less so at the gulf sites. At the gulf sites, AIPW was more closely related to the biomass fluctuations than it was at the oceanic sites. This may represent the results of the balance between the effects of water movement and innate reproductive cycles. At the oceanic sites, wave shear is an important agent of disturbance (Sousa 1985), and acts through the

removal of plants. In contrast, the more protected environment of the gulf sites ameliorates the effects of water movement, and disturbance via this agency becomes far less common. Under these circumstances, loss of adult plants may be much rarer, and the fluctuations in AIPW associated with reproductive cycles become more prominent. Another possibility is that the lower level of water movement at the gulf sites dictated that plants were merely damaged, rather than removed totally. These two alternatives are not mutually exclusive.

There are few studies with which to compare these results. Kirkman (1984) presented data which describe the fluctuations in biomass at two adjacent sites in Western Australia which represented exposed and more protected environments. However, the abundance and AIPW fluctuations published in that study were based on pooled data, so comparison between protected and exposed could not be made. Nevertheless, on the basis of Kirkman's pooled data, the fluctuations in AIPW mirrored those of biomass while abundance fluctuations were dissimilar to both.

Multivariate Comparisons

The multivariate analyses have provided evidence not only for the distinction of summer community states, but also for differentiation between years. The distinction between years of the non-summer collection tends often to be related to the state of the community in the preceding summer.

It was apparent from the multivariate analyses that spring is a very important time for the structure of these macroalgal communities. The ordination of changes (Fig. 6.9) has demonstrated that this period of change, while dissimilar to all other seasonal changes, varied considerably between sites and years. The community compositions in summer (which are shaped by these spring changes) were generally quite dissimilar to the non-summer

compositions (Figs 6.10a - 6.17a). Furthermore, it is not uncommon for the non-summer collections to be more closely related to the preceding summer than to other summers. The inference is that the community changes across spring were large and varied, and have an important role in shaping the composition of the community for the remainder of the year.

Spring is an important time for the recruitment of many of the component species of the communities. Many of the furoid species found in this study are fertile or recruiting across spring and early summer (Womersley pers. comm. and Hotchkiss unpubl. data for *Cystophora* spp.; Kendrick and Walker 1991 and Kendrick 1994 for *Sargassum* spp). Similarly, it is in this period when, in the storm damaged oceanic communities, recruitment might occur on recently cleared substratum. Given the importance of these periods for the introduction of new individuals into the community, it is unsurprising that subsequent seasons are affected by the highly variable summer community state.

It must be admitted that the within-collection variation at WI5 and WI9 was substantial. Thus the trends in the analysis of the average community states, which tended to be similar to those demonstrated in the gulf sites, were obscured. Interestingly, in those cases where this was evident, it was the autumn collections in both years which appeared to be distinct at both sites. This is probably explained by the dominance of *Ecklonia* at these two sites (76% by weight), and the fact that this species reaches its maximum biomass in this period, resulting in a community which was relatively uniformly dominated by *Ecklonia*. High biomass of *Ecklonia*, and simultaneously little input from other species which are outcompeted results in a series of autumn samples which are relatively uniform, yet distinct from others.

Application of the multivariate method for comparison of changes allowed the opportunity to field test the method developed in the previous chapter. Despite the proofing done with simulated datasets, testing with a real dataset is necessary because the simulated seasonal

changes and associated levels of stochasm were chosen arbitrarily. If real ecosystems undergo much smaller levels of seasonal variation and are subject to a far higher degree of stochasm, the technique would be of little use for the analysis of actual communities.

Ordination of the real fluctuations of the communities has made it clear that the method is applicable to these types of communities. To have demonstrated so clearly the similarity in seasonal change across eight sites and 2 years is proof of the usefulness of the technique. It should be added, however, that other systems may not be so easily examined using this method. Systems with even greater stochasm, relative to the magnitude of the seasonal change, may be problematic, as would systems where annual plants dominate the community. The latter is a concern, because annual plants disappear each year, and the calculation of change used in this technique was not designed to deal with appearance and disappearance.

6.6 Conclusions

This study represents the first quantitative replicated study of the seasonal fluctuations in South Australian subtidal macroalgal communities. It has allowed hypotheses to be formulated to explain the fluctuations that the communities underwent. Additionally, it has demonstrated the need for incorporating seasonal and annual variation in future studies and has acted as a field test of the multivariate technique for comparison of change, formulated in Chapter 5.

Most changes in community state were similar across sites and years for any given season. However, the change from spring to summer is highly variable, resulting in summer community states which were often different to the community states at other times of the year and are highly unpredictable. Furthermore, in those sites where it was possible to assess this, it appeared that the community state in summer influenced the state of the community in the following seasons. It was proposed that the change from spring to summer is an important

time for the recruitment of many species, either because of storm damage to the community or because of the reproductive period of the dominant species.

The magnitude of the fluctuations casts doubt upon previous studies which have relied on sampling at a single point in time. Seasonal and interannual variation is such, that to adequately sample any of these communities, seasonal sampling across at least two years is necessary. Four-fold changes across the course of the year in many of the species make this clear.

As a field test of the technique for comparison of change developed previously, this study has demonstrated that the technique can be applied very successfully to natural communities. It has demonstrated a remarkable similarity of change within season across eight communities of widely varied composition and physical environment.

Fluctuations in the biomass of some of the individual genera were consistent with the changes in plant weight associated with the annual reproductive cycles and the seasonal effects of storms. *Ecklonia*, which dominated the more exposed oceanic sites, appears to demonstrate fluctuations related to disturbance through storm damage. In conjunction with the fluctuations in abundance, it appears that suppressed juvenile sporophytes play an important role in the maintenance of the community. *Sargassum* undergoes clear seasonal fluctuations which are dictated by well documented reproductive cycles. These cycles involve an increase in biomass to the reproductive period in spring and then loss of the large laterals before regrowing. *Cystophora* fluctuations also appear to be related to the annual reproductive cycle, which, like *Sargassum*, dictate a minimum in biomass in early summer. *Cystophora subfarcinata* is the only species to defy the general trend, but this is explained by its unusual ability to be reproductive year round, rather than having a narrow reproductive period like the other *Cystophora* species. In all cases, where the biomass was dominated by a variety of other

species, the fluctuations were confused, either through ineffective sampling or because of the interactive effects of the other taxa.

The fluctuations of *Acrocarpia* and *Seirococcus* provided no evidence of consistent seasonality. This could be related to their inability to dominate communities and consequently having fluctuations driven by the more dominant species. *Scytothalia* fluctuations could have been interpreted as seasonal, but the lack of consistency across sites made this possibility unlikely.

Chapter 7 Spatial Variation

7.1 Introduction and Rationale

The investigation of temporal change presented in the previous chapter represents one aspect of the total variation demonstrated by biological communities. Spatial variation is the other facet, and it is at least as important. There have been many mensurative (descriptive) experiments performed where the "treatment" involved comparisons between communities differing in environmental factors such as exposure (eg Cheshire and Hallam 1989a; Hatcher 1989), depth (eg Shepherd and Womersley 1970,1971,1976,1981; May and Larkum 1981) or geographic separation (eg Collings 1989; Rice and Kenchington 1990a, 1990b). Biotic factors such as plant-plant interactions usually operate on smaller scales (Pascala and Silander 1990; Watkins and Wilson 1992). The results of these processes and influences are represented by changes in the assemblages in space (ie spatial pattern) and will also be evident at different scales.

A knowledge of the manner in which macroalgal communities vary in space is indispensable as an aid to research direction, hypothesis generation, design of experimental studies and interpretation of results (Andrew and Mapstone 1987). With that point in mind, this chapter presents an investigation of the spatial pattern apparent in two macroalgal communities at a variety of scales from ten centimetres to four kilometres.

Specifically, the aim of this chapter is to investigate the spatial patterning of the biota at two sites at a variety of scales in order to;

- a) provide a properly replicated and described baseline for future comparison both within Australia and overseas.

- b) quantify the amount of variation attributable to different spatial scales within uniform physical environments.
- c) make informed proposals regarding the important structuring processes within these communities.
- d) assess previous sampling regimes with a view to improving these in future studies.

For the purposes of structure, a "small scale" section, with methods and results is presented separately to the "large scale" section. This is because they represented separate field exercises. However, they are linked by a single general discussion.

7.2 Background

An accurate description of the spatial patterning of an ecosystem is a vital prerequisite for developing an understanding of the mechanisms which control it (Townsend 1989; Underwood *et al.* 1991). It serves not only as the basis for proposing informed hypotheses, but also as an indicator of the sampling regime which should be implemented in order to test these hypotheses. Andrew and Mapstone (1987) decry the circumstances which have seen the accurate description of spatial pattern as "the poor cousin of experimental work". While no-one doubts the need for well designed manipulative experimentation, to proceed with this step with little prior knowledge of the patterns exhibited by the system is folly (Mentis, 1988). It is akin to being blindfolded and told to find the correct haystack before even starting to look for needles. Understanding the ecology of natural systems is difficult enough without ignoring the direction which patterns can give us in the search for relevant processes.

An excellent example of the failure to acknowledge the importance of descriptive work is the period in the 1960s and early 1970s where competition was seen as the universal structuring agent. Experimentation and subsequent theory was based almost solely on competition

(Townsend 1989). The blind acceptance of current generalizations such as this has been strongly criticised by Underwood and Denley (1984) and Foster (1990) amongst others. Properly designed descriptive studies would often have revealed patterns that did not implicate competition as a likely process of importance (eg Foster 1982). However, experimentation which reveals the *lack* of a process is not news and generally remains unpublished. The result is a view which artificially inflates the importance of studied structuring agents. Foster (1990) addressed this concern and concluded that many of the supposedly important processes in the marine communities of Nova Scotia were, in fact, rarely important. He points out that a few isolated experimental studies have been generalised to a geographic range that the studies do not truly represent. Much of this area does not appear to demonstrate the patterns which would be expected of systems dominated by these processes. Descriptive analysis can assist in assessing the likely generality of such processes.

The normal role for descriptive studies is in the construction of hypotheses (Andrew and Mapstone 1987). The patterns demonstrated by a community often provide clues as to the likely structuring agents. Thus accurate description of patterns will act as an important indicator of the processes which are most likely to be worth investigating with subsequent manipulative experimentation.

While several authors have warned of the inability of pattern description to clearly distinguish the action of a process (eg Levins and Lewontin 1980, Underwood and Denley 1984, Diamond 1986, Shipley and Keddy 1987), it is foolish to adopt an either/or approach to the investigation of ecosystems (Mentis 1988). Pattern description and manipulative experimentation should not represent alternatives. Rather, they should be complementary, pattern description acting as an important guide to the subsequent experimental work.

Aside from assisting in the proposal of hypotheses, knowledge of the spatial structure exhibited by a community can be used to shape sampling regimes (Andrew and Mapstone 1987, Underwood *et al.* 1991, 1993). Power analysis can be applied, given quantitative description of the communities, which predicts the sample size required to find significant differences where they exist (Sokal and Rohlf 1981, Zar 1984). This is possible only with prior knowledge of the variance structure of the communities to be studied. Of even more basic importance than this is the ability to plan the *structure* of the sampling regime. The need for stratification to incorporate known levels of variation in the community in order to create nested designs requires knowledge of the spatial structure of the system to be studied. One of the prime requirements of most statistical tests is independence of samples (Underwood 1981, Palmer, 1988). In order to ensure that the samples are independent, prior quantitative analysis of the spatial structure of the community is necessary.

Description of the spatial variation of individuals at a variety of scales in published accounts is surprisingly rare given its benefits. Andrew and Mapstone (1987) concluded that this probably represents a sad indictment of the attitude of many ecologists to the concept of variability.

Too many view natural variation as an inconvenience which must be avoided if significant results are to be achieved. For example, Gauch (1983) wrote of noise as the deviation from an interesting data structure. Wiegand (1983 as cited by Wiegand 1989) partitions variance into an "interesting" and "non-interesting" part, the latter being termed noise. This view may result in significance to the statistician, but fails to allow the community to "tell its own story" (and demonstrate what is truly biologically significant). Noise too has causative agents, and they may in fact contribute far more to the variation of the biota. Thus while it may not be of "interest" to the researcher, it may be of great importance to the community. It is thus important to realise that there is no such thing as "noise" to a community, it is a term which reflects the interests and prejudices of the researcher. Multiscale descriptive studies such

as this put the variation at different scales into perspective and truly allow the community to give an unbiased account of itself.

The most basic measurement of spatial pattern is that of the "clumpedness" of individuals (Andrew and Mapstone 1987). Assortment of individuals grades from clumped at one extreme, where there is a tendency for isolated patches of high density to form, to uniform at the other which results in a regular spacing of individuals. These represent the two ends of a continuum, with assortment between these extremes being known as random (Johnson and Zimmer 1985). These patterns are multi-scalar and may involve different patterns of organisation at different levels (Palmer 1988, Acker 1990). For example, small scale uniform pattern may be superimposed on large scale patchiness. Such a pattern might result from strong competitive effects within patches which are caused by the presence or absence of suitable substratum.

Knowledge of the spatial arrangement of individuals is extremely useful for developing proposals of structuring processes. Clumped assortments imply the presence of processes which make some patches more likely to be inhabited than others. This may be positive effect such as the presence of an adult plant dropping reproductive material close by, creating a patch around itself (eg Deysher and Norton 1982; Kendrick and Walker 1991) or it may be the result of a negative process such as grazing (eg Andrew and Jones 1990). Uniform assortment however, is likely to be the result of factors such as competition which tend to define strict density limits at appropriate scales.

Patches not only represent the effects of processes, they also influence the processes themselves. The community often substantially alters its own environment. Conditions internal, external and on the boundary of a patch are likely to differ significantly (Dayton and Tegner, 1984). These differences may include physical factors such as water movement

(Jackson and Winant 1983) and nutrients (Dayton and Tegner, 1984) or biological considerations such as sweeping effects (Velimirov and Griffiths 1979) and local spore dispersal concentrations (Deysher and Norton 1982; Santelices 1990b; Kendrick and Walker 1991). Indeed the whole field of metapopulation dynamics (Levins 1969) is based on patch properties and the dispersal/migration properties of the constituent individuals. To investigate the nature of these effects is beyond the scope of this study. Rather, it is restricted to identifying and quantifying the scale of the spatial variation of these macroalgal communities.

For the purposes of this study, a "patch" is an area, of any size, which supports a biota considerably different to the area which surrounds it. That difference may be defined in terms of any variable of interest, either individual species, total biomass/abundance or the "community types" defined by multivariate analyses. It should be pointed out that large patches may in fact be agglomerations of small patches which have merged and lost definition. Without temporal replication, this "snapshot" view can do little to elucidate this possibility other than to demonstrate that the same patch type occurs at smaller scales.

7.3 Small Scale Spatial Variation

This section identifies the smaller (10cm - 300cm) scales at which patchiness is exhibited and the microscale relationships demonstrated by the different species.

7.3a Field Methods

A destructive harvest of an area 1m x 3.5m was carried out at a depth of 5metres, 40metres south-southeast of the CJE5 sampling site. The physical environment was the same as described previously for CJE5. This area was subdivided into 10cm x 10cm squares, each of which was harvested individually and put into a separate numbered bag. Subsequently, the contents of the bags were divided into species and every canopy individual (defined in the

same manner as in the previous sections) was measured, dried and weighed. In this way, it was possible to map all individuals with a spatial resolution of 10cm. The collection was made on the 8th of January 1994.

This same census method was carried out at Cape Jervis North, but rather than a single 1 x 3.5m area, it was necessary to census two smaller areas of 1m x 1m and 1m x 2m.

Unfortunately it was not possible to relocate the first area and make it contiguous with the second. These areas were both approximately 40 metres south-southwest of CJN5 and shared the same physical characteristics. In all cases, the area to be harvested was chosen haphazardly by simply swimming down the anchor line and then 5m further in the same direction. The community composition was similar at each of the sites to those used in the study of temporal variation. The harvests were made a week after the CJE harvest, on the 15th and 16th of January 1994. There was no significant storm activity in the interim.

Data was stored in MS Access (Microsoft 1994) as a linear data matrix with a row for each individual which described the coordinates of the subquadrat in which it was found, the species, length and dry weight.

7.3b Methods of analysis

No single analysis can identify all spatial features of vegetation pattern. For this reason, a number of analyses were applied to the data in order to illuminate different facets of the pattern.

The pattern of distribution was statistically tested using Pielou's α (Pielou 1959) which differentiates between uniform, random and aggregated (clumped) pattern. This measure is

based on the distance from a series of random points to the nearest individual and is calculated by use of the equation $\alpha = \pi \cdot d \cdot \omega$,

where α = the index of aggregation, d = the density of organisms and ω = the mean squared distance between the random points and the nearest individual. If the distribution is random, then α will be 1, with regular distributions resulting in values significantly lower than this, and clumped pattern resulting in values significantly higher. The statistical significance of this result is tested against a chi squared distribution which required the calculation of the test statistic $\chi^2_{2n} = 2 \cdot n \cdot \alpha$ (Andrew and Mapstone, 1987), where n represents the number of random points used, which in this case was 50, after Underwood (1976). A value greater than the critical χ^2 for $p = .05$ was accepted as evidence of a clumped (aggregated) distribution, while a value less than the critical χ^2 for $p = .95$ indicated a uniform distribution. Between these two values, the distribution was considered random.

Only those species which were counted individually were analysed in this manner. Individuals were given the coordinates of the centre of the subquadrat from which they came. Thus coordinates were subject to ± 5 cm error in both dimensions. Dale and Powell (1994) made a similar approximation in their study of the spatial variation of *Solidago canadensis* L.

As this analysis had to be applied to many different data sets (different species at different sites), an algorithm was programmed in QuickBASIC (Microsoft 1988) to speed the process. This program was tested with simulated data sets and performed correctly.

While Pielou's α allows detection of aggregated and regular patterns, it gives no indication of the scale at which patches of aggregation might occur. For this purpose, a different approach was used, namely the calculation of the variance to mean ratio of the quadrat (the "coefficient of dispersion" of Blackman (1942)). As equality of mean and variance is a fact which

defines a Poisson distribution, a significant lack of equality is evidence for non-random distribution (Pielou 1969). This was then converted to the "index of dispersion" (Clapham 1936) in order to compare with a chi squared distribution. The statistic was calculated as follows:

$$I = (s^2/\bar{x}) \cdot (n-1),$$

where s^2 is the variance, $\bar{x}$ is the mean and n is the number of replicates. This was then compared with a χ^2 distribution with $(n-1)$ degrees of freedom (see Fisher 1970 cited by Andrew and Mapstone 1987). This is probably the most commonly used index of spatial pattern in marine ecology (Andrew and Mapstone 1987).

If the statistic I was higher than the critical χ^2 at $p=.05$, the individuals were considered clumped; if it was lower than the critical value for $p=.95$, then the individuals were considered to be arranged regularly. By aggregating contiguous quadrats to form larger quadrats, it was possible to repeat the analysis at different scales, to find the scales at which patches existed. Aggregation allowed the creation of three levels of quadrats - 10cm x 10cm, 20cm x 20cm and 50cm x 50cm. It was not possible to increase the size of the quadrats beyond this as there would be insufficient replicates (5 is the minimum according to Bateman (1950)). For the same reason, the 50cm x 50cm analysis was not possible at the small (1m x 1m) harvest at Cape Jervis North.

The above analysis was extended in the manner of Jumars (1975a and b) so that it was possible not only to detect patchiness at different scales, but also to determine if the species were evenly assorted amongst patches or whether they tended to form patches to the partial exclusion of other species. This was achieved through calculation of the index of dispersion (I) of the summed data (ie total biomass or total abundance) and the sum of the indices of dispersion for

each of the individual species. The difference between the two values is indicative of the degree of segregation of species and is termed "heterogeneity chi". Again, these were tested against a chi squared distribution.

Semivariates analysis was used in order to determine the scales at which quadrats remained independent. This is a relatively new type of analysis to ecology, based on fractal geometry developed by geostatisticians and soil scientists (see Burrough 1983 and Culling 1986). A series of quadrats, separated by known distances are all compared with each other to produce a list of differences in the parameter of interest and the associated distance between these samples. Semivariance can then be calculated for all possible distances of separation by use of the following formula;

$$\gamma(h) = \frac{1}{2N(h)} \cdot \sum_{i=1}^{N(h)} (z(i) - z(i+h))^2$$

where $\gamma(h)$ = the semivariance at distance of separation h

$N(h)$ = the number of pairs of points separated by distance h

$(z(i) - z(i+h))$ is the difference in parameter value of two points separated by h

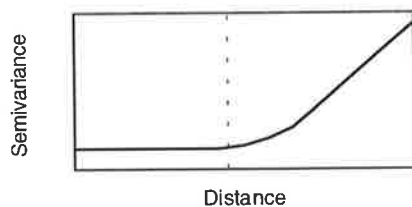
By plotting, on a log-log plot, semivariance against the distance of separation, a "semivariogram" is produced. Interpretation of the semivariogram is dependent on the slope of the line. The fractal dimension (D) can be calculated using the formula

$$D = (4-m)/2 \quad [\text{where } m = \text{slope of line on semivariogram (Burrough 1983).}]$$

D may range between 1 and 2, where 1 indicates complete spatial dependence (a slope of 2 on the semivariogram) and 2 indicates complete spatial independence (a flat line). Dependence is defined by an ability to predict the value of a sample based on those samples around it.

Conversely, independence denotes an inability to make predictions from knowledge of other

samples. This is indicated by a semivariogram where the slope is negligible. As the slope increases towards two, the fractal dimension decreases toward one, which indicates spatial dependence or "patchiness". The slope of a semivariogram need not be constant; the point at which the slope varies is indicative of the size of patches. For instance, the following semivariogram would indicate large scale dependence with independence at smaller scales (less than that indicated by the dotted line).



Another way of looking at this is that there are patches at the size of the dotted line which are homogenous (or at least non-patchy) within. A thorough discussion of this form of analysis is to be found in Palmer (1988).

Semivariates analysis in this instance was employed in an unusual manner. To date, most published accounts of the use of this method have been restricted to univariate measures (eg Palmer 1988), but in this case a multivariate form of semivariate analysis was used (although Turner (1995) demonstrated a similar technique based on squared Euclidean distance in an unpublished study). The difference between quadrats was calculated, not as the difference in a single parameter, but as the difference in terms of all species simultaneously. In this instance, the multivariate difference was described in terms of the Bray-Curtis distance measure. This value was then treated in the same manner as the difference in any univariate measure and was used in the standard formulation of semivariance. As this produced a series of 61,075 comparisons in the largest data set, a computer program was written to enable the calculation of semivariance.

In order to provide a more complete description of the community, the sweep areas of the canopy individuals are also considered. This is because macroalgae, unlike terrestrial vegetation, are not static, as water movement causes individuals to move. Thus the interactions of individuals are likely to be related to the overlap of the areas which each of the algae utilize. Individuals prescribe a rough circle as water motion sweeps them around. While the waves typically move them backwards and forwards, it is not uncommon for them to move in a circle rather than "whip" backwards and forwards. Thus a circle can be drawn around each plant which describes its "sweep area" or area of physical influence. This is calculated using $\pi.r^2$ where r represents the radius of the sweep circle which is actually the length of the plant. Calculation of the combined sweep area for the whole harvest is made under the assumption that the non-inclusion of the sweep areas of plants adjacent to the harvest (which therefore impinge in terms of sweeping) is balanced by the inclusion of the entire sweep areas of individuals whose sweep circles do not fall entirely within the area of harvest.

Comparison is made of samples under differing intensity of sweeping. However, while the assumption outlined above was useful in the calculation of total sweep area, it is inappropriate in the calculation of sweep intensity for any given 10cm x 10cm subquadrat. The level of sweeping on subquadrats close to the edge of the area cannot be calculated as we have no knowledge of the impinging effect of plants just outside the harvest area. Therefore a large boundary had to be drawn to exclude those subquadrats which were likely to have sweeping effects from outside the harvest area. As the maximum length of plants was about 40cm, a 40cm boundary was used which excluded all but the two central 10 cm strips in this comparison.

The relationships of the species at the 10cm x 10cm scale were analysed using multivariate ordination based on Bray-Curtis association measures. This was achieved by plotting species

in sample space rather than vice versa. In this manner, the species were described by the quadrats in which they were found. The result is that those species which occur close together in the ordination are generally associated with each other. The decision to analyse the relationships between these species by way of multivariate ordination was made on the premise that the biomass of any species in a multispecies community will be dependent on the presence of all other species rather than any single species in isolation (Epp and Aarsen 1989).

7.3c Results

Composition

The area sampled at Cape Jervis East was similar in composition to that described for the temporal survey (Table 7.1a). It was dominated by *Cystophora expansa* (31% by biomass), *C. subfarcinata* (22%), *C. monilifera* and *C. moniliformis* (14% each), with *Sargassum fallax*, *S. linearifolium*, *S. varians* and *S. verruculosum* present in less substantial quantities. *Acrocarpia paniculata*, *Caulocystis cephalornithos*, *Cystophora brownii*, *Sargassum decipiens* and *Ecklonia radiata* all occurred in trace quantities. Total biomass for the 3.5m² area was 1042g dwt which translates to 298g dwt m⁻². SSH ordination analysis confirmed that the community composition for this area is consistent with that of the summer collections of the temporal study (Fig. 7.1a).

The two areas involved in the study at Cape Jervis North were in a similar area, but were somewhat dissimilar in composition (Tables 7.1b and 7.1c). The smaller (1m x 1m) area was dominated by *Seirococcus axillaris* (82% of the biomass), while the larger (2m x 1m) area was dominated by both *Scytothalia* (51%) and *Ecklonia* (28%). A complete species list for each area, including understorey species, is presented in Appendix C. The difference in canopy between the two harvested areas is indicative of the variation present at a scale larger than 1m.

Despite the difference, the harvests were consistent, in terms of the multivariate community description, with the samples taken from this general area in the study of temporal variation (Fig. 7.1b).

Sweep Areas

Cape Jervis East

The summation of the sweep areas of the counted canopy individuals of Cape Jervis East resulted in an area approximately 17.5 times larger than the 3.5 m² from which they were harvested. The combined sweep area was 61.45 m², with the percentage of the area swept by each species (Table 7.2a) similar to the breakdown of species biomass. The only exception is *C. moniliformis*, which swept a disproportionately large area (comprises 27% of area and only 14% of biomass). This indicates a high length to biomass ratio in this species.

The fact that *Sargassum* species were not counted individually makes the estimate of total sweep area an underestimate. If one assumes that *Sargassum* species are of a similar morphology to that of *Cystophora*, biomass estimates would indicate that the increase in sweep area would be in the order of 22.5%. However, while this census was taken in summer, when both genera are typically at their lowest weight per individual plant, *Cystophora* and *Sargassum* lose the weight in a different manner. *Cystophora* loses weight through shedding of ramuli and secondary laterals, maintaining its length despite much loss in biomass. In contrast, *Sargassum* species lose their long fertile branches when shedding weight, maintaining wide basal "leaves" (Womersley 1987). Thus, in summer, the morphology in terms of length to weight ratio is likely to differ between the genera, with *Sargassum* having far less length per unit weight. Therefore the increase in sweep area when *Sargassum* is taken into account is

more likely to be in the order of only 5-10% which resulted in a total sweep area of approximately 65m².

The relationship between understorey species and the intensity of sweeping was investigated by plotting the sweep zone of each individual and scoring each 10cm x 10cm subquadrat for the number of plants which swept over it and the number of understorey species within it. There was no clear relationship between the presence of any of the understorey species and the sweep intensity. Understorey species richness appeared maximal in those quadrats with an intermediate level of sweeping (Fig. 7.2a), but this conclusion is based on only three subquadrats of higher species richness and is therefore unreliable.

Cape Jervis North

At Cape Jervis North, when the sweep zones of each individual were calculated and summed for the entire harvest, they covered 9.6 times the actual area in which they were constrained. This was remarkably consistent between the large and small areas (Tables 7.2b and 7.2c), but only half that of the sweep area of the community of Cape Jervis East (Table 7.2a). Generally, the percentage of the total area covered by each canopy species was similar to the proportions demonstrated by the biomass of the species. The notable exception to this was *Cystophora expansa* which constituted approximately 5 times more of the total area than it did biomass. This species clearly devoted a greater proportion of its resources to extension of length than do the other species at this site.

Like CJE, the understorey species richness at Cape Jervis North appeared to be maximised at the intermediate sweep intensities (Fig. 7.2b). However, this was again based on very few (four) richer subquadrats and clearly needs more intense investigation before trends can be declared with confidence.

Patchiness of Distribution

Even without quantitative analysis, it is clear that abundance and biomass appeared to demonstrate patchiness at both Cape Jervis East and North. While total biomass appeared to be highly variable between the 10cm subquadrats, there were larger patches which were more likely to contain a high biomass quadrat than other areas (Figs 7.3a, b and c). Similarly the abundance of each individual species appeared to be highly variable between the 10cm subquadrats, but for most species, there are areas where high abundance quadrats were more likely. *Cystophora expansa* at CJE provides an excellent example of this pattern (Fig. 7.4). Of note is the fact that when there were multiple individuals in a subquadrat, they were commonly of the same size.

Sargassum decipiens, *S. fallax* and *Cystophora brownii* were not present at high enough levels to allow interpretation. With these exceptions, all canopy species appeared to demonstrate a similar trend to that illustrated by *Cystophora expansa* as described above. Although subsequent analyses are capable of demonstrating aggregation at smaller scales, there appears to be a natural patch size of 1-2m which could not be demonstrated statistically in this study as the total area is not large enough for replication of patches of this size.

The microscale patterning of the biota at Cape Jervis East appeared to be extremely patchy at all scales between 10 and 50cm. Vegetation as a whole was clumped, ie some patches were of high abundance (of any species) while others were bereft of canopy plants (Pielou's α , $p < .001$). Additionally, each individual *Cystophora* species was significantly clumped according to Pielou's α ($p < .001$, χ^2 test ; Table 7.3a) with the exception of *Cystophora brownii* which was not present in large enough quantities to cast judgement. These results are summarised in Table 7.3a. Examination of the variance to mean ratio demonstrates that that there was heterogeneity or patchiness present in the biota, not only at the 10cm x 10cm scale at which

these samples were collected, but also at scales of 20cm x 20cm and 50cm x 50cm (these being created by aggregating the 10cm subquadrats) ($p < .001$, χ^2 test for all scales). This, allied with the clumped nature of individuals as a whole, demonstrated by Pielou's α , indicated that some areas were better than others for the growth and survival of the canopy species. Furthermore, these quadrats did not contain similar relative contributions from the different canopy species (χ^2 , $p < .001$). The species were segregated such that different species dominated different areas (mean:variance ratio, heterogeneity chi $< .001$; Table 7.4a). This occurred at all scales from 10 to 50 cm, the generalization holding for the analysis of both biomass and abundance.

A similar pattern occurred at Cape Jervis North with both areas demonstrating patchiness at all scales investigated. Like Cape Jervis East, both Cape Jervis North areas demonstrated aggregation (Pielou's α , $p < .05$) of the biota as a whole as well as in each of the species individually (Tables 7.3b and 7.3c). Furthermore, the mean to variance ratio showed that there was significant clumping at the 10cm, 20cm and in the case of the larger area, the 50cm scale ($p < .05$ using variance to mean ratio; Tables 7.4b and 7.4c). Analysis was not performed at the 50cm scale at the 1m x 1m site as there would have been only 4 replicates, too few for reasonable interpretation (Bateman 1950). In all cases, the species were segregated rather than occurring in similar proportions in each subquadrat ($p < .05$, "heterogeneity chi", after Jumars 1975a). This result was consistent for both biomass and abundance.

Semivariates analysis applied to the multivariate description of the differences between quadrats revealed that there was independence at all scales at both Cape Jervis East and North (Figs 7.5a, 7.5b and 7.5c). This essentially indicates that in a multivariate sense, a quadrat is just as likely to be similar to a neighbouring quadrat as it is to a quadrat at any distance (up to 3m) away. This result appears contrary to the patchiness exhibited by the community according to other analyses.

The contrast was actually the result of the high level of variance at the scale of the sample unit. A single species community was simulated with a densely populated circular patch of diameter 1m in the centre of the 3.5m x 1m area. Biomass in each of the 10cm subquadrats within the patch was 100g dwt m⁻² whilst each quadrat outside the patch supported only 10g dwt m⁻². The semivariogram which described this community (Fig. 7.6a) clearly demonstrated dependence up to the size of the patch. However, when stochasm was added to the system, such that the quadrats in the patch could range up to 100g dwt m⁻², while quadrats outside the patch ranged up to only 10g dwt m⁻², the slope of the semivariogram was far slighter and less defined (Fig. 7.6b). By applying a rule (on top of the previous 1m patch community) which dictated that randomly 1 in 3 quadrats would support no biomass, the community more closely approximated the highly variable, yet apparently patchy, real community. Under these conditions the semivariogram failed to demonstrate any clear evidence of the underlying 1m patch (Fig. 7.6c). Thus, the failure of the semivariogram to detect dependence at any scale was probably a reflection of the inability of semivariates analysis to deal with a community which displayed much of its variation at the scale of the sample unit, which in this case was 10cm x 10cm.

Small Scale Species Associations

Species associations, as demonstrated by a multivariate ordination of species in sample space, showed consistencies between Cape Jervis East and North (Figs 7.7a and 7.7b). In both cases, the *Sargassum* species tended to form a distinct group, although *S. fallax* was only loosely associated in both cases. At CJE, this entailed a separation between the *Cystophora* and *Sargassum* species. This indicates that the *Cystophora* species were positively associated and tended to be found together at the 10cm scale, as did the *Sargassum* species. The fact that *Ecklonia* and *Seirococcus* were not closely associated was probably due to the fact that it was

rare for them to share a quadrat with another species because of their large size. The other species are smaller and were therefore found co-occurring in the same subquadrat more often.

7.4 Large Scale Spatial Variation

The aim of this study was to investigate the levels of variation present at large scales.

Specifically, the scales were in the order of two metres, twenty metres, two hundred metres and two thousand metres. Both univariate and multivariate variation were examined.

7.4a Field Methods

Two linear transects, several kilometres in length, were run at a constant depth of 5m in the Cape Jarvis region. The first of these was 4.444 kilometres long and stretched northeast along the coast from Cape Jarvis North. The second was 2.444 kilometres long and stretched eastward from a point 50m south-southeast of Cape Jarvis East (Fig. 7.8). These transects were sampled by means of destructive harvest using a 1m x 1m quadrat positioned at specific intervals.

The distances between quadrats were designed to elucidate the major scales at which variation occurred (diagrammatically represented by Fig. 7.9). At Cape Jarvis North, three quadrats were separated by 2m (ie at the 0m, 2m and 4m points). This was repeated at the 20m mark (ie at the 20m, 22m and 24m points) and at 40m (at 40, 42 and 44m). This whole sequence of nine quadrats was repeated from the 200m mark (ie at 200, 202, 204, 220, 222, 224, 240, 242 and 244m). and similarly from the 400m mark. Finally this sequence of 27 quadrats was repeated 2km northeast and 4km northeast to give a total of 81 quadrats spaced to give an indication of the variance at scales of a few metres, tens of metres ("groups"), hundreds of metres ("sections") and thousands of metres ("sites"). The same exercise was carried out at Cape Jarvis East, but it was not possible to repeat the sequence beyond the second 2km

site as the rocky substratum was replaced by sand. Thus only 54 quadrats were harvested there.

Canopy plants (as defined in the previous chapter) were sorted into species, and the number of individuals of each species counted and weighed. Weights were converted from wet weight by drying ten individuals of each species and calculating an average wet/dry ratio. Understorey species were scored for presence in each quadrat.

The harvests were made consecutively across the period 13-20 December 1993.

7.4b Methods of Analysis

Analysis involved both univariate and multivariate methods. SSH analysis after the calculation of Bray Curtis association measures provided a multivariate view of the variability at different scales. These analyses were based on the biomass of the canopy species after range standardisation (division of biomass by maximum biomass of that species). A nested ANOVA was also applied to the canopy biomass data in the manner of Morissey *et. al.* (1992). The "factors" in this analysis were the levels of spatial nesting used in the survey, these levels being;

- a) the sites separated by 2km - "sites"
- b) the three sections within each of these sites separated by 200m - "sections"
- c) the three groups separated by 20m within each of these sections - "groups"
- d) the variance between the replicate samples in the groups

Significant differences found in any of the "factors" (spatial scales) represent patchiness at that scale in terms of the parameter under investigation.

F ratios were calculated as

$$F_{\text{sites}} = MS_{\text{sites}} / MS_{\text{sections}}$$

$$F_{\text{sections}} = MS_{\text{sections}} / MS_{\text{groups}}$$

$$F_{\text{groups}} = MS_{\text{groups}} / MS_{\text{error}}$$

This is in accord with the nested ANOVA design of Sokal and Rohlf (1981), Underwood (1981a) and Zar (1984). No attempt was made to apply post-hoc tests as the interest lay in demonstrating patchiness at certain scales. Their geographical location was irrelevant.

Welden and Slauson (1986) point out that significance in a statistical sense gives no indication of the relative importance of a factor as it is dependent on things such as the number of degrees of freedom. Their proposal is that the relative importance of a factor can be gauged by its contribution to the total sum of squares (see Morin *et al.* 1988 for an example). In the case of geographical nesting, such as used in this study, the related method of calculation of the variance components from the ANOVA is appropriate (Sokal and Rohlf 1981; Underwood 1981a; Morissey *et al.* 1992; Underwood and Petraitis 1993). The variance is calculated for each level using $(MS_a - MS_b)/n$, where b is a factor nested within factor a. The denominator n represents the total number of samples which are associated with the factor a. This equation can be applied at each level of nesting with the MS_{error} being subtracted from the MS of the lowest level. The proportion associated with the residual (MS_{error}) is indicative of the quadrat to quadrat variation on the smallest (2 metre) scale. Where the variance calculation associated with any level was negative, it was assumed to be zero (after Underwood 1981). These variances were then converted to percentages associated with each level.

The relationship between species was investigated at the different scales studied (scale of the quadrat, within the 20m area and within the 200m area). This was done by ordinating the species in sample space, as opposed to the normal method which involves ordinating the

sample in species space. In this way, the species are described by each of the samples rather than *vice versa*. Averaging species biomass for each group or section allowed the relationships to be examined at each of these scales.

7.4c Results

Multivariate Assessment of Large Scale Patchiness

The relationship of the sites used for the temporal studies to those of the larger scale spatial variation study is important in order to place the former in a proper perspective. By averaging the species composition for each of the 200m sections and averaging the temporal collections of CJE5 and also those of CJN5, it was possible to ordinate the points and determine whether the restricted area ($\approx 40\text{m}$) used for the temporal studies was representative of the whole area. The ordination (Fig. 7.10) revealed that in terms of canopy composition, the sites used for the temporal analysis were atypical of the general habitat. The site used at CJN5 for the temporal analysis had similar composition to the collection made in the same area in the investigation of spatial variation. However, this was quite dissimilar to any of the collections made at any distance (greater than 200m) away. The situation is similar at CJE5, where the average of the temporal collections was very different even to the nearest of the collections of the spatial exercise which was only 50m away.

Ordination of all samples in each of the transects (Figs 7.11a and 7.11b) indicates that there was a high degree of variation between those sites separated by 2km. This is indicated by the lack of any overlap between the envelopes representing the two sites of CJE and the fact that these sites occupy largely distinct regions of the ordination of the CJN samples, although in a strict sense, the envelopes do overlap slightly.

Within the envelopes representing each of these sites on the above ordinations, it is possible to distinguish the 200m sections in some, but not all, cases (Figs 7.12a and 7.12b). At CJE (Fig. 7.12a), the first 200m section was distinct, but there was no distinction between the second and third 200m sections of the first site. Within the site 2km east, none of the 200m sections were distinct. Within the first site of the CJN transect (Fig. 7.12b), all three 200m sections were largely distinct. Within the next site at CJN, one 200m section stood largely distinct, as was the case within the third site.

It is possible to focus on smaller scales by examining the distinction between the 20m groups within the 200m section. However, caution must be exercised in interpretation at this scale as there are only three replicates representing each of these groups. Notwithstanding this problem, it appeared that like the other scales, distinction occurred in some, but not all cases. There was no distinction between any of the 20m groups in the first 200m at CJE, but a number of these groups appeared distinct within the second and third 200m sections (Fig. 7.12a). The second site at CJE, which did not demonstrate any distinction between 200m sections, had two 20m groups which appeared to differ from the other groups within their 200m section (Fig. 7.12a). Similarly at CJN, some, but not all, 20m groups were distinct from the others in their 200m section (Fig. 7.12b).

In summary, there were few consistencies in the multivariate variation exhibited by the community in either transect at any scale. However, the important fact is that it has been demonstrated that patchiness can, and often does, exist at all scales studied.

Species Associations

Examination of the associations between species was done through inversion of the data matrices to ordinate species in sample space. Those species which were found close together

on the ordination typically occurred together. This analysis was carried out on the scale of the individual quadrat and repeated at the scale of the 20m group and the 200m section.

The species associations were not only consistent across scales, but also demonstrated real similarities across sites (Fig. 7.13). In each case, there was a core group of *Sargassum* and *Cystophora* species, a group of less common fucoid species and a group of species which are typically larger plants (*Ecklonia*, *Seirococcus*, *Acrocarpia* and *Scytothalia*). Furthermore, in both cases the core group of *Sargassum* and *Cystophora* species could be broken down into two distinct sections, one of which contained the *Sargassum* species and the other the *Cystophora* species. This was an indication that the *Cystophora* species tend to occur in the same place and that *Sargassum* species associate in a similar manner.

Membership of these three main groups and the *Cystophora* and *Sargassum* subgroups was almost identical. There were two exceptions to the pattern. Firstly *Cystophora expansa* appeared to be part of the *Cystophora* subgroup at CJE (albeit toward the periphery), but it was part of the group of large dominating plants at CJN. Secondly, *Cystophora brownii* tended to be associated with the other uncommon species at CJN, while it was more closely associated with the *Sargassum* subgroup at CJE.

Univariate Assessment of Large Scale Patchiness

The individual parameters examined (total abundance and biomass as well as the abundance and biomass of each species) varied across scales of 2m, 20m, 200m and 2000m. In many cases the areas sampled at these distances apart were significantly different, which demonstrated patchiness at that scale. Calculation of the proportion of the total sum of squares contributed by each level indicated that the magnitude of variation attributable to each scale differed between the parameters being measured. A graphical depiction of the relative

importance of the scales of spatial variation is presented in Fig 7.14 and the actual ANOVA tables are to be found in Appendix B.

Cape Jervis East

A nested ANOVA (ANOVA tables found in Appendix B) revealed considerable patchiness in the biomass of species at Cape Jervis East. Of the 14 species which were collected and weighed, ten differed significantly on at least one scale, and two (*Cystophora expansa* and *Seirococcus*) differed significantly at two of the three spatial scales measured (Fig. 7.14). Four species differed significantly at each of the three scales ($p < .05$). Only *C. brownii*, *Scytothalia*, *Sargassum varians* and *Sargassum fallax* did not display significant differences at any spatial scale. Total biomass varied significantly at the 20m scale.

The patchiness at Cape Jervis East was even more pronounced when the abundance of species was considered. All nine counted species differed significantly on at least one scale, and four (*Acrocarpia*, *Cystophora expansa*, *Ecklonia* and *Seirococcus*) showed significant ($p < .05$) differences at two of the three scales. Most species (all except *Cystophora monilifera*) displayed significant differences at the 20m scale, four did so at the 2km scale, while only *C. monilifera* differed significantly at the 200m scale. Total abundance varied significantly at the 20m scale ($p < .05$).

Cape Jervis North

Biomass patterns were patchy at Cape Jervis North. Twelve of 14 species differed significantly on at least one scale, and *Ecklonia radiata* did so on two of the three scales (Fig 7.14). Only *C. monilifera* differed significantly on the 2km "site" level, while seven species differed significantly between the 200m sections within the sites and five differed significantly between the 20m "groups". Total biomass demonstrated significant ($p < .05$) differences at this latter

scale. Figure 7.14 depicts the case for each species and the ANOVA tables may be found in Appendix B.

Abundance was also highly patchy at Cape Jervis North, where 8 of 9 species differed on at least one scale (Fig. 7.14). Only *Cystophora moniliformis* failed to demonstrate any significant difference at any scale. None, however, demonstrated significant variation on more than one scale. As with biomass, only *Cystophora monilifera* differed significantly at the site scale. Four species demonstrated significant differences between the 200m "sections" and three varied significantly at the 20m "group" scale. Total abundance differed significantly at the 200m scale.

Partitioning of Variance Components

Investigation of the partitioning of the variance components indicated considerable variation in the scales at which species displayed levels of variation (Fig. 7.14). Similarly, there was little consistency for any single species across sites. There are, however, some general points to be made. Firstly, the pattern of partitioning for a given species at any site was generally similar for the biomass and abundance analyses (*Acrocarpia* and *Cystophora brownii* at CJE were exceptions). Secondly, in the majority of cases, the largest proportion of variation was attributable to the smaller scales (Fig. 7.14, summarised in Table 7.5). In terms of biomass, in 18 cases (of 30 total), the greatest variation was seen at the 2m (quadrat to quadrat) scale. In six, the greatest variation was seen at the 20m "group" scale, while only four species demonstrated greatest variation at the 200m scale. Only two species displayed greatest variation at the 2km "site" scale - *Cystophora expansa* and the ubiquitous *Ecklonia radiata*. An analysis of abundance revealed a similar situation (Table 7.5).

7.5 General Discussion

With the exception of the associations of the species, the overall picture obtained from these exercises was not one of consistency. Rather, the vegetation appeared to represent a mosaic of patches of different sizes. However, this lack of consistency does not imply a lack of causative forces. The fact that there was patchiness is clear evidence of the processes at work. The reason for the lack of consistency may involve a long term temporal aspect.

Species associations

In contrast to the lack of consistency in patch sizes, the similarity in species associations across all scales and both sites was striking. The species coexisted with other members of their genus, although *Sargassum* and *Cystophora* species did have some degree of association. The other species fall into two groups - those which occurred relatively infrequently (*Caulocystis*, *Scaberia*, *Cystophora brownii*, *Cystophora retorta*) and a group of physically large species which can dominate communities, as evidenced by this exercise and the temporal studies. This latter group of species consisted of *Ecklonia*, *Seirococcus*, *Scytothalia* and to a lesser extent, *Acrocarpia*. *Cystophora expansa* could be included in this group at CJN, but appeared to be included in the *Cystophora* group at CJE.

The arrangement of these groups of species appears related to morphological and taxonomic traits. At CJN, the species within the group of "large" or "dominating" taxa were, at all scales, not so much associated with each other as disassociated with all others. That is, they tended to either dominate an area or be rare. They did not share co-dominance. At the small scale, it is indicative of the properties of individual plants to maintain space in their immediate area, while at larger scales it demonstrated the ability of a species, through time, to extend its localised distribution and dominate a growing patch. While the *Sargassum* and *Cystophora*

species can do this, their dominance is at the level of the genus rather than species. Several species of the genera may co-occur and, as a group, dominate the area. To a lesser (but still considerable) degree, there is an association between most *Cystophora* and *Sargassum* species. This is likely to be a reflection of the morphology of these plants. These species are not as massive as those belonging to the "large" group, and as a consequence tended to coexist with other species of their morphological type. The temporal CJE5 site is a good example of *Cystophora* - *Sargassum* coexistence and dominance. The presence of a member of one of the more massive species may represent the seed for an eventual turnover of species.

At CJE, the trends in species association were similar to those demonstrated at CJN. The composition of the groups is similar, although *Cystophora expansa* is more closely allied to the *Cystophora* group than the "large" group. It does, however, exist at the periphery of the group, indicating a tendency to not co-occur quite as readily as the other members of the group. The fact that the "large" group is, with the exception of *Scytothalia*, more tightly clustered than at CJN indicates that co-occurrence of these dominating species is more likely. Thus there is some flexibility in the outcome of species-species interactions within a reasonably consistent overall framework.

Explanations for the patchiness found at different scales

At the smallest scale measured (10cm), there was high variability in overall cover as well as the individual species. Analysis using Pielou's α demonstrated a high degree of clumping in all species and the mean to variance ratio indicated that this occurred at very small (10cm) scales. Some small areas were devoid of canopy while immediately adjacent areas supported several large plants. There are numerous possible causes for the variation seen at this scale. Processes which may be implicated here are the patchy nature of the settlement event, effects of microtopography and the allelopathic effects of understorey species. It is clear that several

plants can coexist in one small area while an adjacent area supports no canopy. This is an indication that at this scale competition between canopy plants is not the primary influence.

Microtopography is known to affect the settlement and subsequent recruitment of macroalgae (eg Foster (1975), but see Kennelly (1983) for opposing situation). This may be due to indirect effects such as the modification of water movement or refuge from herbivores as is granted by fissures (Kirkman 1981; Dayton 1985a; Keats 1991), or direct effects such as the inability of spores to adhere to certain substrates (Dayton *et al.* 1984).

Herbivory may be implicated, although whether this would occur in such a small scale patchy manner is unknown. There is little evidence from the literature to suggest that herbivory is quite so localised and intense. Rather, numerous accounts describe the destruction of larger areas (eg Estes *et al.* 1978; Vance 1979; Chapman 1981; Ebeling *et al.* 1985; Jones and Andrew 1990) or a more homogenous effect is inflicted (eg Dayton and Tegner 1984; Lawrence 1975). Fish are known to render areas devoid of macroalgae (eg Andrew and Jones 1990) in a territorial manner, but no evidence of this sort of behaviour was seen. It is accepted that lack of published accounts of microscale subtidal herbivory is more likely to be due to lack of study rather than absence of the effect.

While the term "spore rain" (Santelices 1990b) engenders images of homogeneity, the concept actually embodies several processes which give rise to patchy settlement. Not only is there often a far greater chance of spores falling close to the adult plant (Anderson and North 1966; Deysher and Norton 1982; Schiel 1988; Kendrick and Walker 1991), but on a smaller scale, macroalgae are also known to wipe "packets" of spores onto the substrate as the adult sweeps across it. This has been proposed by Cheshire (1985), but its applicability to the species of this study is unknown. A packet of spores may be wiped onto an area, leaving the adjacent area

free. If "wiping" is a common method of spore dispersal, then effects of microtopography may be magnified as small depressions are likely to be free of any sweeping effect.

The fact that in this study the "clumps" of algae consist of individuals of similar size may indicate that a single cohort is present. Either this patch is functionally annual and dies to be replaced by patches in different positions in the following year, or it is perennial and will persist for some years, denying the area immediately adjacent to any settling spores in the manner of Velimirov and Griffiths (1979). However these authors demonstrated this phenomenon with single plants maintaining an area clear of grazers around them. In this case, several individuals of similar size are clustered tightly. This would imply that they do not compete with each other to the point where plant removal occurs, but that they do alter their immediate environment to make it unsuitable for the subsequent microscopic juvenile stages. This sort of effect has been demonstrated in dense jungles where thick canopy inhibits recruitment of juveniles (eg Connell and Lowman 1989; Hart 1990; Hart *et al.* 1990).

The understorey may also exert an effect on the settlement of canopy species. While it is unlikely that understorey will outcompete an adult canopy individual, if a disturbance occurs it is possible that understorey species may preempt space (competition for space (Yodzis 1986)), denying the settling individuals any substrate on which to attach. This has been observed by Kennelly (1987c) in a study of the kelp *Ecklonia radiata*, where turfing algae maintained long term patches. Furthermore, even removal of this turfing algae did not result in kelp recruitment into these areas, suggesting a lingering allelopathic effect. If effects of the understorey are implicated, then such lingering effects must be assumed in subquadrats where neither canopy nor understorey exist.

Alternatively, the fact that this is a "snapshot" view of the spatial variation may hide the fact that the bare area was recently covered by a large alga which died or was torn out, ie the bare

patches may be shifting transitory phenomenon (Kennelly 1983). This effect may be exaggerated by the dislodged plant tangling with those nearby and causing their removal (Dayton and Tegner 1984).

At a slightly larger scale, both the small scale and large scale studies appeared to demonstrate patches which were around 1-2m in size. The problem with the small scale studies was that the total area surveyed was not large enough to demonstrate more than a single patch. However, the nested ANOVAs of the large scale section also demonstrated that this was an important scale of variation to most species. While topography may play a role at this scale, the strongest possibility is that these patches were caused by the dispersal patterns of the adult plants. Kendrick and Walker (1991) demonstrated that 98% of the spores of *Sargassum spinuligerum* fall within a circle with a radius of one metre around the adult plant. This would give a patch size of between one and two metres, which was often observed in this study. Anderson and North (1966), Deysher and Norton (1982) and Schiel (1988) have also demonstrated highly localised dispersal in various macroalgae. Urchins and other herbivores could also be implicated as they are known to create patches of approximately this size around home refugia (Vance 1979).

While the larger scales of 20m, 200m and 2000m did not contribute as much to the total variation in the biota, there was still a considerable amount of variation at these scales. Indeed, the individual species often displayed significant differences between patches at these scales. While the patchiness at scales of up to a few metres is explicable in the light of the processes which have been detailed, patchiness at the larger (20m+) scale does not immediately suggest any single factor. It is possible that the processes implicated at smaller scales are scaled up to operate at larger scales. However, topography was similar across all the sites within CJE and CJN, making this unlikely as a cause of the variation seen. Herbivory could cause the mosaic

which is seen, but there were no observable differences in the levels or types of herbivore present. It should be added that no attempt was made to quantify this observation. While not denying their importance in other systems and at other scales, it seems that another explanation is required to explain the mosaic.

Physical factors are most commonly reported as the cause of large scale variation, but the patches demonstrated in this study are unlikely to be the result of such abiotic influences.

While large scale factors such as temperature and nutrient levels will act to determine the suite of species available to the area under study (Acker 1990), it is substratum type, light and water movement which are most commonly associated with variation at the medium spatial scale from tens of metres to kilometres (eg Shepherd and Womersley 1970, 1971, 1976, 1981; Schiel and Foster, 1986; Underwood and Kennelly 1990a). However, in this study the location of the transects was deliberately chosen to maintain similar levels of water movement and constant depth (and therefore light levels). No major freshwater point discharges occurred along the length of the transect, which might have otherwise affected salinity (Norton and South 1969) and levels of suspended solids (and hence light levels) (eg Dayton 1985). This also eliminated siltation as a cause of variation. In summary, physical factors are unlikely to be responsible for the marked variation displayed at the larger scales in this study.

Having demonstrated that it is unlikely that the patterns observed are due to physical influences, as they were factored out of the study, it remains to propose an alternative. My proposal is that the larger scale patches are in fact extensions of the smaller (1-2m) scale patches caused by localised dispersal of propagules. This extension occurs through time, as the new generation of individuals will produce spores which are cast a further metre or more (eg Schiel 1988; Kendrick and Walker 1991). As time progresses, the patch grows (Velimirov and Griffiths 1979) until patches interact. If the patches represent a similar biota then they will

appear to merge and become a single larger patch. If, however, the two patches support different species, then competition will occur, resulting in the continuing expansion of the competitively superior patch and contraction of the other. This need not be an immediate phenomenon. The overlap of the patches may actually persist for some period of time, supporting members of both patch types.

Disturbance events on different scales interrupt this progression which would otherwise result in a single dominant species (Dayton *et al.* 1984; Sousa 1984a, 1985; Chaneton and Facelli 1991). These disturbance events give rise to bare space which may be resettled by either the dominant alga of the patch or another alga. Small scale disturbance usually results in recolonization by the species of the existing patch while large scale disturbance may see the colonization of new species (eg Kirkman 1981; Schiel and Foster 1986). Only those species which are fertile at this time are eligible to colonise the available area. The new species may take hold and, through competitive superiority, dominate the patch in which it has appeared. Alternatively, while an invader may itself succeed, the surrounding plants may outcompete any juveniles produced by this individual. Onto this mosaic of patches is superimposed the blanket of spores of different species which are suited to long range dispersal. These too may utilise bare space onto which they settle (Reed *et al.* 1988; Santelices 1990b).

The hypothesis above may explain the patterns observed in the biota, but it will remain untested speculation without further work. This will need to be of a more reductionist nature, involving the manipulation and observation of the species interactions between the more common species demonstrated here. However, without this preliminary work, the hypotheses on which to base these experiments would be undirected. While this would appeal to Popper's (1959) view of the progress of scientific endeavour, most agree that this is likely to result in much wasted effort (eg Diamond 1986, Andrew and Mapstone 1987; Mentis 1988) and would

prefer to see hypotheses based on well researched prior knowledge of pattern. Until now, without properly spatially replicated work, much of our prior knowledge of multispecies systems has been restricted to correlations with physical variables (eg Shepherd and Womersley 1970, 1971, 1976, 1981; May and Larkum 1981). While other factors such as dispersal and competition are acknowledged, their scales of operation and influence have remained unknown. This work provides a basis for the thorough investigation of these factors.

Previous investigations of spatial structure

Whilst rare in marine systems (Underwood and Kennelly 1990a) pattern analysis of this sort has previously been applied to terrestrial systems, particularly grasslands. Like this study, most concluded that there was a rich mosaic of patches on different scales which overlapped and were often nested within others. For example, Ver Hoef *et al.* (1989) found patchiness at scales of 30cm, 2m, 3m and 10m in a chalk grassland and concluded that "homogeneity in the usual phytosociological sense is illusory". They made no attempt to propose any cause. Davis *et al.* (1989) described patchiness at the 1-2m scale in post burn chaparral vegetation and related it to possible pre-burn characters. Watkins and Wilson (1992) used fine grain pattern analysis to support the concept of niche limitation at a scale of 2cm x 2cm in lawns of Fiji and New Zealand. Sousa's (1984) review of disturbance makes it clear that patches are observable in all biological systems at all scales.

Two examples of particular relevance to the present work are the studies of Hatcher (1989) and Morissey *et al.* (1992). Hatcher examined the spatial variation exhibited by the higher order taxonomic/functional classes of a Western Australian coastal lagoon and Morissey *et al.* examined the partitioning of variance into spatial scales of the soft-bottom benthos of Botany Bay (New South Wales). While these two were similar to this study in that they are marine and covered similar spatial scales, the present work is unique in addressing hard-bottom

macroalgal communities, an environment of great value both intrinsically and for the important fisheries which they support (Underwood *et al.* 1991).

Like this study, Hatcher (1989) found significant differences at some scale in the cover of most taxa, and significant differences at more than one scale (patches within patches) were reported. These scales ranged from kilometres, which represented offshore and nearshore reefs, through the hundreds of metres between sites within reef lines, to the tens of metres between community types. Whilst deliberately choosing to sample different community types appears a somewhat circular argument, there were clear differences attributed to the different reef lines and sites within these. The potential controls identified were exposure to swell, which operated at the largest scale, availability of food at the medium scale and biological interactions, microtopography and light at the smallest scale.

Morissey *et al.* (1992), using a nested hierarchical sampling design, demonstrated significant patchiness at scales from 10m to 3.5km in soft-sediment benthos. They made no attempt to propose any hypothesis to explain this. Rather they used the result to sound a warning for those designing procedures for environmental sampling and monitoring.

The present study is similar to that of Morissey *et al.* (1992) in that it did not set out to test spatial scales associated with known environmental gradients/disjoints (eg Wilkinson and Cheshire 1989; Wilson 1994b). To the contrary, it deliberately avoided these. The idea that such patchiness could be attributed to biological processes alone is not new (see Elton 1949), but it is one which is often ignored in the structure of surveys and experiments (Underwood and Kennelly 1990a). While Weir and Wilson (1987) point out that species - environment associations occur at scales of less than 1cm, there is no reason to suppose that this variation operated consistently at larger scales and caused the observed patches. Thus, this study also stands as a caution to future studies that there can exist significant variation within a stretch of

environmentally homogenous coastline. Homogenous physical environment should not be accepted as evidence for homogeneous biotic composition, even at larger scales. It should be admitted that this criticism could be reversed and applied to the present study - while a functionally homogeneous physical environment has been assumed on a qualitative basis, it has not been subjected to quantitative assessment.

Concerns raised by the findings

The findings of this exercise present serious problems for experimental and correlative studies in the area. At both a multivariate and single species level, they demonstrate that there are important distinctions to be made in the biota regardless of any proposed physical forcing or disturbance. The assessment of a single impact is made impossible without quantitative description of both the impact area and appropriate "controls" prior to the impact event. This is because the supposedly impacted area may naturally represent one of the many distinct patches in the biota. Furthermore, studies examining the effect of larger scale variables such as water movement must be extensive in spatial scale, because to sample too small an area may result in describing only one patch. This is a clear example of natural "pseudoreplication" (Hurlbert 1984). Although only demonstrated at two sites, the study provides a warning that this patchiness and its associated problems may be present in any area of study. In hindsight, this represents a caution for the site comparisons presented in Chapter 4 of this study.

Of particular concern to any quantitative ecologist is the fact that patchiness at these different scales may invalidate the use of any classical inferential statistics. This is because of the assumption of independence involved in these tests (Andrew and Mapstone 1987). Unlike many of the assumptions of parametric statistics, no amount of transformation helps this problem. Furthermore, while deviations from many of the assumptions are tolerated in tests such as the ANOVA because of its "robust" nature, the same cannot be said for the assumption

of independence (Sokal and Rohlf 1981; Underwood 1981a; Zar 1984). Patches represent a degree of predictability between quadrats which is the quality that defines non-independence (Underwood 1981a). Under these circumstances both non-parametric and parametric statistical tests are suspect. Random placement of samples does not solve this problem (Palmer 1988). The only cure is separation of the quadrats by a distance at least that of the size of the patch. In the case of the two areas under consideration in this study, depending on the species, independence is achieved only at a distance of at least 20 (and possibly greater than 2000) metres.

7.6 Conclusions

This chapter began by outlining four important consequences of a knowledge of spatial pattern; a refined direction of research, an informed ability to generate hypotheses, better experimental design and a framework within which to interpret results and allow quantitative comparison. The findings of this study have made contributions to each of these areas.

It is now clear that many of the most important variations in community structure occur within a single habitat type, where physical factors vary little. To date, studies have concentrated on larger scale physical phenomena (eg Shepherd and Womersley 1970, 1971, 1976, 1981; Shepherd 1976; May and Larkum 1981; Sanderson and Thomas 1987). While the importance of these factors is acknowledged, there now exists a demonstrable need to investigate smaller scale questions, where the physical environment is relatively uniform. The scales of this research range from the centimetres involved in patterns of recruitment through the interplant scale where competition appears important, to the scale of kilometres.

The patterns observed at the different scales have also provided a basis for the construction of hypotheses. For instance, the patchy nature of plants at the small scale and the general

consistency in size within these patches suggests that these patches may represent "packets" of zygotes wiped on to the substratum, as proposed by Cheshire (1985). Perhaps the most interesting suggestion from the findings of this study was that large patches of hundreds or thousands of metres may represent the scaled up effects of competitive interactions and disturbance across an extended timescale. Repetitive, non-destructive sampling of a series of adjacent patches, with particular attention to the boundary area may add significantly to our knowledge of the dynamics of these stands in addition to suggesting possibilities for other systems.

Sampling regimes for future studies now have a basis for more accurate assessment. Variance levels demonstrated by different aspects of the community have been detailed and may assist in ensuring adequate replication. However, non-independence of replicates appears to be a problem which must be addressed, or at least acknowledged in these communities, as it has been demonstrated that in many cases there is no distance of sample separation which allows independence. The conclusions drawn from inferential statistics are adversely affected by this problem. However, it is better to acknowledge the concern rather than work in ignorance of it.

Without properly replicated sampling design over a variety of scales, it is impossible to make meaningful comparison with macroalgal systems elsewhere in Australia and the world. This study has demonstrated that comparisons made on the basis of limited areas may be seriously flawed, as there is significant variation between areas within a region of relatively homogeneous habitat. Interpretations based on studies of this type are suspect, as the area sampled may not be representative of the habitat in question. Investigations where several sites are involved are less susceptible to this problem, but not immune. Proper quantitative analysis demonstrating the different scales of variation has enabled useful comparison with other systems.

Chapter 8 A Synthesis of Spatial and Temporal Variation

To this point, spatial and temporal variation have been viewed in isolation. This section endeavours to place in perspective the spatial and temporal variation demonstrated by these communities. That is, to determine the relative magnitude of spatial and temporal change in the community. In saying this, I examine only the spatial variation at the scale of the $\approx 40\text{m}$ area which described each temporally replicated site. Only at Cape Jervis North and Cape Jervis East can this be viewed with a knowledge of the spatial variation demonstrated at larger scales.

8.1 Methods

Two methods were used to examine the relative effects of spatial and temporal variation. Examination of the ANOVA tables of the temporal section allowed a univariate measure for each of the species. Additionally, multivariate comparison was made of the temporal change and spatial variation of each site.

Using the ANOVA tables of the temporal section, it was possible to partition the total sum of squares between the treatment effect, which was temporal change, and the residual which represents the spatial variation of the site. The proportion contributed by each to the total sum of squares is indicative of the magnitude of the variation attributable to them. This technique has been demonstrated and used previously by Sokal and Rohlf (1981), Caffey (1985), Welden and Slauson (1986), and Morin *et al.* (1988). Partitioning of the components of the variance was done on untransformed data (after Morissey *et al.* 1992).

Underwood (1981) and Underwood and Petraitis (1993) point out two important difficulties with the technique. Firstly, any interaction effect severely compromises the interpretation of

the variance components. A two way orthogonal ANOVA with site and collection as factors demonstrated such a significant interaction term, making it necessary to use a separate ANOVA for each site and restrict conclusions to a site by site basis. Additionally, if experiments such as this are used to compare effects between sites, it is important that they have the same design (Underwood and Petraitis 1993). As the oceanic sites were not sampled on two of the nine occasions, this invalidates comparison of oceanic and gulf sites. To circumvent this problem, analysis was restricted to the first year, when all sites were sampled during each season. Thus the comparison of temporal to spatial variation is really a comparison of seasonal variation across the first year to within site spatial variation.

The second technique involved plotting a series of points representing the average biotic composition of each of the seasonal collections and the points representing each quadrat in each collection simultaneously, using SSH ordination. This was done separately for each site and allowed a multivariate view which directly compared the amount of variation attributable to temporal change with the spatial variation of the site.

SSH ordination was also used to simultaneously plot the points representing the average biotic state of each site at every collection and the averages of each of the 200m sections of the large scale surveys. This was done in order to make comparison of the variation across sites representing different physical environments and the variation on a large scale within such an area. The analysis procedure was as outlined above.

8.2 Results

In general the ANOVAs used to analyse temporal change at each site revealed that the seasonal temporal variation was not as great as within site spatial variation (Table 8.1). In half of the cases seasonal variation contributed less than 20% of the total (seasonal + spatial)

variation observed, and in only about 10% of cases was seasonal variation responsible for half of the total variation. Of all the parameters measured, total biomass was most consistently affected by seasonal variation. Cape Jervis East had the greatest number of species showing a considerable effect of seasonal variation. At that site, 9 species (and total biomass) demonstrated a temporal variance component >20% of the total variation. The ANOVA tables themselves can be found in Appendix B.

By ordinating points which represented the average biotic composition at each temporal collection, and the points representing each of the individual samples, it was possible to gauge the relative magnitude of temporal change compared with the local (between quadrat) spatial variation. In most cases, the temporal variation across 1992 and 1993 was not as great as the spatial variation between quadrats. This was particularly the case at the oceanic sites (Fig. 8.1a), but less so at the gulf sites (Fig. 8.1b).

A multivariate analysis which placed the temporal averages for each collection at each site and the averages of the 200m "sections" of the large scale survey made several points clear (Fig. 8.2). Firstly, the temporal variation exhibited across 1992 and 1993 at CJN5 and CJE5 was not as great as the variation contributed by the 200m sections of these spatially surveyed sites. Secondly, the variation demonstrated along the coasts of CJN and CJE was quite considerable compared with the variation between the sites of the gulf. In fact, the spatial variation displayed by each of the sites was comparable to the between-site variation. Furthermore, when this variation was taken into account, it was not possible to distinguish Cape Jervis North from Second Valley (5m), despite the fact that the sites represented different physical environments. Cape Jervis East (5m), however, remained relatively distinct.

8.3 Discussion

The conclusion from these analyses appears to be that seasonal variation was typically responsible for about 30% or less of the total variation demonstrated within site. Exceptions to this generalization were the variation displayed by total biomass at most sites, and most species which were examined at CJE5. There were no consistent trends which could be related to site characteristics (eg wave force), nor any taxonomic consistency (eg consistency within genera).

The lack of consistency is not without precedent. Caffey (1985) found little consistency in temporal variation of the recruitment of barnacles between several sites separated by 11 - 555 kilometres. Similarly, Kennelly and Underwood (1992), after following fluctuations of *Ecklonia* forest species across a series of nested spatial scales, found complex patchiness at all scales examined and concluded that "few general conclusions can be made about the structure of these assemblages". In a later study, (Kennelly and Underwood 1993), they demonstrated a similar level of complexity and unpredictability in the response of kelp forests to disturbance. The conclusion to be drawn from the present study is that, like Kennelly and Underwood's kelp forests, the mixed communities of southern Fleurieu Peninsula also represent a complex mosaic of patches demonstrating few consistent qualities. Foster's (1990) assertion that generality of process and homogeneity of structure were illusory has now been demonstrated in mixed stands.

On the basis of Cape Jervis East and North, where both temporal and large scale spatial studies were conducted, it would appear that the greatest variation was typically (i.e. for most species) at the scale of a few metres (demonstrated by the temporal ANOVA partitioning). Taking this into account, and putting it into perspective with the partitioning demonstrated by the large scale spatial exercise, temporal variation and variation on the 20m scale contributed similar

amounts, but markedly less than the metre to metre scale. Variation at the 200m scale contributed still less, and the smallest contribution to the overall variation was demonstrated by differences between areas separated by kilometres.

Kennelly and Underwood (1993), in a study of the geographic consistency of the effects of disturbance in kelp forests, noted that the responses were not consistent between locations separated by tens to hundreds of kilometres (quite possibly representing different physical environments), but within kelp forests, the results were reasonably consistent. At smaller scales still (3 - 5m), the variation was maximised. This is consistent with the findings of the present study involving mixed communities. While this is only circumstantial evidence, it is interesting to note that in an earlier study, Kennelly (1987a) found that the majority of disturbed areas were smaller than 5m². The correlation of patch size and typical spatial extent of disturbance is worthy of further study.

It is also not possible to directly compare the variation on the 10 cm scale to the variation at larger scales. This is because the size of the sampling unit differed between the large scale and small scale studies (Andrew and Mapstone 1987). Effectively, this means that variance is being measured at a finer grain. While not quantitatively comparable, it has been demonstrated that there was a very high degree of variation at the 10cm scale. Although smaller scales were not investigated, it seems quite likely that these, down to the scale of the individual plant, would contribute significantly to the variability in the biota (eg Watkins and Wilson 1992).

The ordination of temporal change and spatial variation on a single plot was not directly comparable to the ANOVA results, as the latter are based on only the first four collections. However, the interpretation was similar. Generally temporal variation represented only a minor fraction of the overall variation demonstrated by the site, although CJE5 and SV5 demonstrated temporal variation of almost the same magnitude as the spatial variation

exhibited at each collection. A similar case could be made for GI5, a view which is inconsistent with the ANOVA result. This can be explained by the fact that much of the envelope of temporal change in the ordination is created by collection 9, which was not included in the ANOVA. It is, however, a demonstration of the important effect of catastrophic storms and a warning that relatively rare events such as this may not be apparent in a study limited to a single year. Similar quantum shifts in community structure as a result of catastrophe are not unusual in the marine ecological literature (eg Dayton and Tegner 1984; Harris *et al.* 1984; Ebeling *et al.* 1985; Chapman and Johnson 1990; see Sousa 1984a for a review). Kennelly (1987) demonstrated in an *Ecklonia radiata* forest of New South Wales that while disturbance is a natural and common feature, the spatial extent of disturbance was generally limited to $<5\text{m}^2$. Disturbances more extensive than this may have quite different effects (Sousa 1984a).

Simultaneous plots of collection averages and the 200m sections of the large scale survey demonstrated considerable overlap of sites representing different physical environments. This is clearly of great concern to those designing surveys and experiments investigating these physical factors. Furthermore, it demonstrates that differences in the physical environment must be quite considerable before they overshadow the biotic processes which create the mosaic of patches observed in these assemblages. Having said this, clear differences existed between communities representing the oceanic sites and those of the gulf sites. On this scale physical differences appear to have a clear overriding effect. This is consistent with the lack of generality over large (up to 100km) scales which Underwood and Kennelly (1993) found in the fluctuations of kelp forest species. The caveat to this statement is that it assumes that the oceanic sites did not display a degree of spatial variation (untested in this study) which would see them support patches of community like those of the gulf sites.

As a consequence of this study, it is possible to make decisions regarding sampling protocol. Knowledge of the scales of variation can be used as a guide to the levels and scales of replication required to answer specific questions (Andrew and Mapstone 1987). Similarly, depending on the question being examined, a decision can be made as to whether temporal variation should be addressed or whether, given limited resources, it would be more productive to concentrate on accurate assessment at fewer points in time, and accept temporal uncertainty. It should be added that this is not recommended, given the magnitude of temporal variation demonstrated in Chapter 6. Furthermore, patches at larger scales have made it abundantly clear that the problem of pseudoreplication (Hurlbert 1984) is likely to impact on studies of the macroalgal communities of these coasts. Future studies should structure sampling regimes to incorporate this variability rather than allow it to misguide interpretation.

The conclusions of this exercise could be strengthened considerably by the repeated measurement of permanent quadrats (eg Sokal and Rohlf 1981; Green 1993). Estimation of temporal change in the present study was made from independent sampling, and therefore the estimates of temporal change are subject to the inherent error due to spatial variation.

However, while permanent quadrats may make estimations of change more accurate, non-independence of readings (they belong to the same quadrat!) would have invalidated inferential statistics (Underwood 1981a). Given that it was not feasible to use both permanent and random quadrats, the decision was made to use random quadrats and accept the uncertainty arising from sampling error.

Additionally, a more complete picture could have been obtained by an orthogonal design which incorporated temporal change across nested spatial scales. For example, all eight sites would have been represented by samples within areas within larger sections within the "site" which encompassed an area of some kilometres (eg Caffey 1985; Kennelly and Underwood 1992,

1993). This would have allowed investigation of interaction effects and also given an indication of the generality of the spatial patterns which were observed. It should be remembered that both large scale sampling studies were conducted in the relatively calm gulf waters. Examination of the spatial variation of the oceanic communities may have seen a different result. Indeed the more extreme physical environment may have overridden the biotic processes to produce a more homogenous biota. Pacala and Silander (1990) and Watkins and Wilson (1992) suggest that at larger scales the biotic processes tend to have less impact while physical factors assume overriding importance.

The experimental structure chosen in this study was a compromise between the desirable and the practicable. Subtidal habitats are far from ideal in terms of efficient sampling because of the limits on submerged time and the practical difficulties presented by working in an environment resembling a manic washing machine. Thus time and resources precluded the sort of orthogonal design and repeated measurements described above. The exercises of this study were designed to provide as much information as possible on spatial and temporal variation in different subtidal habitats. They have demonstrated clear and significant effects of temporal variation and assessed its contribution relative to that of the local spatial variation.

Additionally, this local variation has been put in the perspective of larger scale variation both within one physical environment, and across differing physical environments. It has also indicated that the variability at a 10cm scale within the 1m x 1m sample is likely to be considerable.

Chapter 9 Conclusions and Future Directions

This study represents the first account of Southern Australian multispecies macroalgal systems to incorporate seasonal and annual fluctuations and investigate their spatial organization. The work was done in order to address a well founded criticism that Australian phycology was sadly lacking in properly replicated description of subtidal macroalgal communities at a variety of scales. The paucity of studies incorporating spatial and temporal variation prevented meaningful comparison between stands, both within Australia and internationally. In addition to providing a baseline for broader comparison, this study has, through description of pattern, allowed the formulation of informed hypotheses to explain the processes which drive these systems. Furthermore, it has provided data with which to examine the communities in light of current ecological theories. Finally, it is useful for its insights into sampling practice for future studies and for the development of an effective method for the comparison of change in multi-species communities.

The principal canopy species were distributed in a manner consistent with a wave force gradient. *Acrocarpia paniculata* and *Scytothalia dorycarpa* were typically associated with the most extreme environments, while *Ecklonia radiata*, which was the commonest species and the one which dominated most sites, was best represented in medium to high energy environments. *Seirococcus axillaris* never dominated any site alone, but was well represented at sites of moderate water movement. Some species of *Sargassum* and *Cystophora* were found in small quantities at exposed sites, but generally these genera were restricted to lower energy waters. These findings were largely consistent with previous research.

It appeared that the "3/2 thinning law" applied to some, but not all, of these populations.

While some sites demonstrated an apparent boundary in the density : average weight

relationship, communities at other sites never reached this thinning line. At those sites where a boundary was apparent, the gradient was approximately $-3/2$, but the log K value varied between 3.8 and 4.6. While some authors have suggested that variation in this figure could be attributed to light availability, the results of this study do not support this supposition.

Species richness was maximal at low to moderate levels of water movement, presumably because many species were unable to survive in high energy environments. Canopy species richness was highest in samples of intermediate biomass. This may be because the low biomass samples may be depauperate of both biomass and species richness as a result of a small scale disturbance event, or unsuitability of substrate in a certain patch. Conversely, high biomass samples often represent domination by a single large species such as *Ecklonia radiata* or *Scytothalia dorycarpa*, which have the capacity to form high biomass patches to the exclusion of other species.

Comparison of temporal change in these multispecies communities required the development of an effective quantitative method for multivariate comparison of changes. A technique was developed which classified the magnitude of the changes of each species and uses semi-strong hybrid analysis to ordinate the changes themselves. This allowed unambiguous assessment of the similarity of changes across sites of differing composition and, where necessary, statistical analysis. The technique was used to demonstrate a remarkable similarity in seasonal change across sites differing considerably in composition and physical environment, and consistency across years. Only the spring change was unpredictably variable, possibly as the result of recruitment of juveniles to the size necessary for collection.

Annual cycles were apparent in the biomass fluctuations of *Ecklonia*, *Cystophora* and *Sargassum* which involved two to six-fold changes across the course of the year. *Acrocarpia*, *Scytothalia* and *Seirococcus* also demonstrated significant changes across the course of the

study, but the fluctuations were unpredictable and not cyclic in nature. Annual variation was also apparent. This provides a clear warning for future studies that mixed macroalgal communities cannot be assessed adequately at a single point in time. The two year time-course of this study is the very least which should be considered acceptable for future work. This finding also casts some doubt on previous work which has not had the benefit of such an extended time frame.

It was on the smallest spatial scales studied (10cm x 10cm) that most of the variation occurred, a phenomenon which could be explained by the highly localised nature of the dispersal of the species which comprised the canopy of these communities, and the variable nature of the microtopography. While for most species it was clear that larger scales generally demonstrated a progressively lower proportion of the overall variation, there were some species which were at odds with this generalization. Variation at scales of metres to kilometres, along coasts which were relatively uniform in their physical characteristics, is evidence of the important influence of the biotic properties of the species on the patterning observed in the system and provides an indication of the need to incorporate this large scale variation in comparisons with other studies. Studies which investigate physical factors, and are not distributed on a broad enough scale, run the risk of a biased assessment because they may sample only one patch type of the many which are possible (and do exist) under the same environmental conditions.

The variability between square metre samples within a site was generally far greater than the temporal variation which occurred across the course of the study. Partitioning of the variation using ANOVA indicated that typically less than 30% of the overall variation was attributable to temporal change. The effects of severe storms increased this proportion, as did the dominance of genera with highly seasonal cycles, such as *Cystophora* and *Sargassum*.

This description of the temporal and spatial patterns demonstrated by these subtidal macroalgal communities has acted as a basis from which to propose the important structuring mechanisms which control the dynamics of these systems.

Probably the most important conclusion of this study was the fact that biotic properties of the species appeared to be of great importance in structuring communities. It appeared that within an area of uniform physical environment, the community consisted of a series of dynamic patches which grew and interacted, with the results dependent upon the biological properties (dispersal distance, competitive abilities etc.) of the different species. Disturbance events of differing magnitude had a modifying effect on this process, preventing competitive exclusion.

The above hypothesis could be verified by the mapping of patches, with particular attention to the borders between these. With repeated non-destructive sampling of these, it would be possible to document the changes and track the possible invasion of patches into others. Such adjoining patches could also be created artificially and monitored. Disturbances could be simulated on different scales to determine the effect on the progression of such an invasion. Supplemented with studies of the dispersal characteristics (timing, localization) of the common canopy-forming species and a series of competition experiments, a detailed model could be assembled which incorporated the biological properties of the species and a characterization of the disturbance regime (frequency and magnitude). Eventually, this could then be overlaid on our knowledge of the effects of the physical environment (light, wave energy etc.) to produce a probabilistic model which describes the likely communities under different conditions and times. With time, it should be a goal to recognize the generalizations which can be made in these dynamics, such that we are able to make the kind of legitimate generalizations that MacArthur (1972), Schoener (1986) and others would seek.

The above proposal for future research is a large undertaking, and not the work of a single

researcher over any short period of time. Nonetheless, this would appear to be a productive direction if we are to explain and predict the dynamics of the subtidal macroalgal communities of southern Australia.

This study has provided an important descriptive framework with which to begin such a research effort. It has indicated some of the mechanisms which are likely to be important in controlling the composition and dynamics of shallow mixed macroalgal stands. However, it is only the first step. It is imperative that the ideas gleaned from this study now be tested experimentally in order to understand and quantify the processes which structure these stands. By providing a basis for *informed* hypotheses, this study will better direct future research, thereby hastening our understanding of these hitherto poorly understood communities.

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**SPATIOTEMPORAL VARIATION OF MACROALGAL
COMMUNITIES OF SOUTHERN FLEURIEU PENINSULA,
SOUTH AUSTRALIA**

by

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Volume 2 - Plates, Tables, Figures and Appendices

Layout of Volume 2

This volume is divided into the same chapters as Volume 1. Plates, tables and figures referred to in Volume 1 can be found in the same chapter in Volume 2. Within each chapter, all plates are presented first, then tables and finally figures. The three appendices are found at the end of the volume.

Chapter 2



Fig. 2.1 The biogeographic provinces of Australia according to Womersley (1990). Southern Australia is encompassed by the Peronian, Flindersian and Dampieran (where it overlaps the Flindersian) provinces. The Maugean subprovince is a part of the Flindersian province which stretches through Victoria, Tasmania and as far west as Robe (S.A.). All sites in the current study fall within the Flindersian province.



Chapter 3



Plate 3.1 The Cape Jervis North study sites (CJN5 & CJN9) looking west. Both CJN9 and CJN5 were situated at this location. It was the roughest of the gulf sites, but not as rough as any of the oceanically influenced sites.



Plate 3.2 The Second Valley study site (SV5), looking north. Local protection made this one of the calmest sites.



Plate 3.3 The Cape Jervis East study site (CJE5). The calmest of all sites, CJE5 was protected by Kangaroo Island which can be seen in the background.



Plate 3.4 View of the “oceanic sites” looking west across Encounter Bay from Granite Island. The rough environment of the Granite Island (GI5) site is clearly evident in the foreground. On the horizon, the highest point is The Bluff (B5) with Wright Island (WI5 and WI9) visible in the bay to the right. To the left is West Island, well out of the bay, which was not included in this study.



Plate 3.5 Wright Island and The Bluff looking south into Encounter Bay. The two Wright Island sites (WI15 and WI19) were located slightly in the lee (just to the left) of Wright Island. The Bluff (B5) can be seen to the right of the picture.

Table 3.1 Physical environment of the sites. Each of the sites is described in terms of its ranked water movement, influence from oceanic swell, current strength and substratum type.

Table 3.2 Dates of each of the temporal collections. Collections were made in every season for 27 months, with the exception of collections 7 and 8 at the oceanic sites.

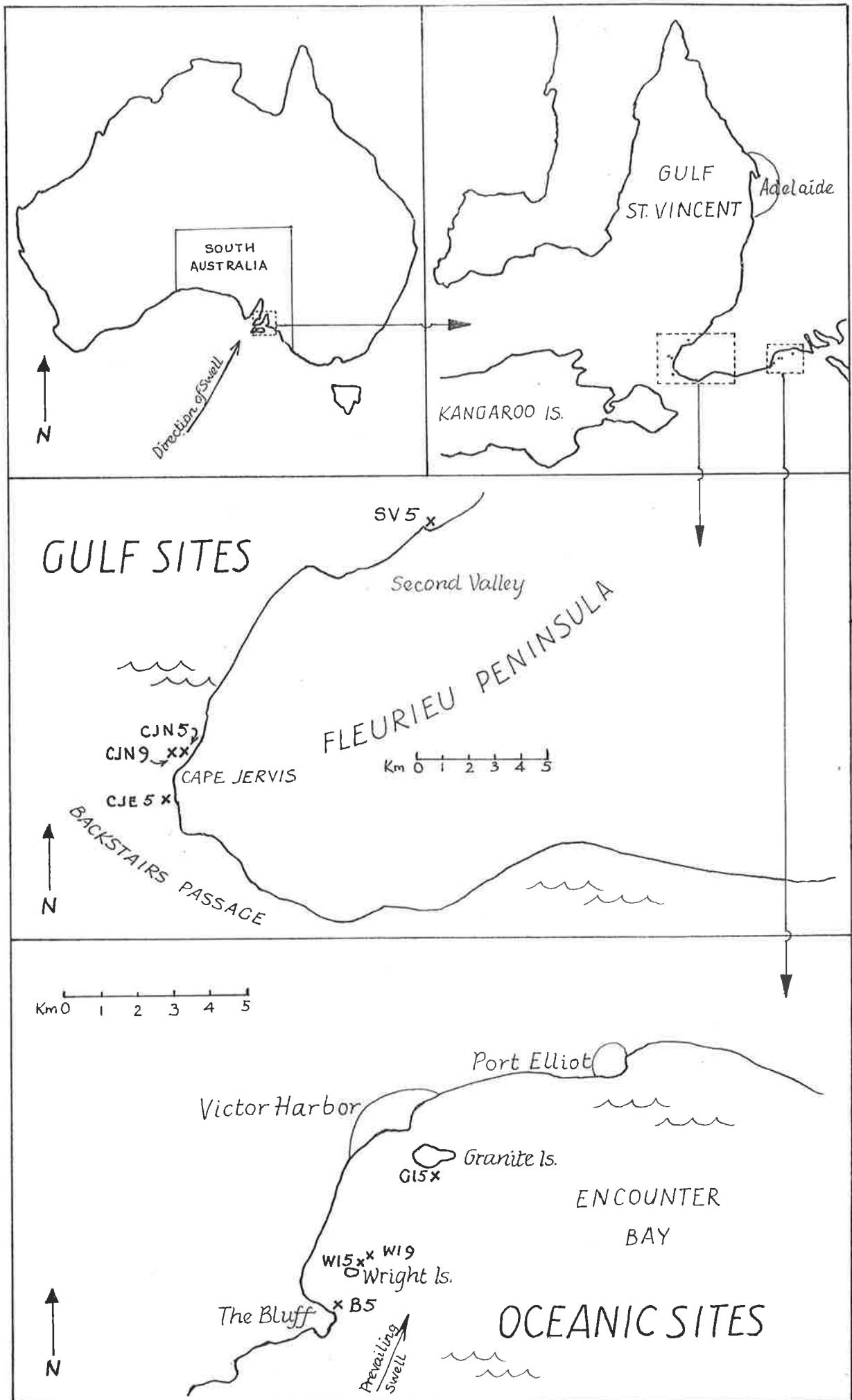
SITE	Water Mov^t (1=calm, 8=rough)	Gulf / Oceanic	Current	Substratum
Cape Jarvis East (5m)	1	Gulf	Moderate	Schist Platforms
Second Valley (5m)	2	Gulf	Slight	Schist Platforms
Cape Jarvis North (9m)	3	Gulf	Strong	Schist Ridges
Cape Jarvis North (5m)	4	Gulf	V. Strong	Schist Ridges
Wright Island (9m)	5	Oceanic	None	Granite Boulders
Wright Island (5m)	6	Oceanic	None	Granite Boulders
The Bluff (5m)	7	Oceanic	None	Granite Boulders
Granite Island (5m)	8	Oceanic	None	Granite Boulders

Collection number	Collection	Date
1	Summer 1992	December 1991 (6/12 - 16/12)
2	Autumn 1992	March 1992 (5/3 - 12/3)
3	Winter 1992	June 1992 (7/6 - 15/6)
4	Spring 1992	September 1992 (8/9 - 16/9)
5	Summer 1993	December 1992 (27/12 - 2/1)
6	Autumn 1993	March 1993 (24/3 - 28/12)
7	Winter 1993	June 1993 (25/6 - 30/6)
8	Spring 1993	October 1993 (7/10 - 9/10)
9	Summer 1993	December 1993 (20/12 - 23/12)

Fig. 3.1 Location of study sites. All sites were situated at the southern tip of Fleurieu Peninsula (S.A.). The four gulf sites were located at the southeastern end of Gulf St Vincent, while the four oceanic sites were situated off the coast of Victor Harbor in Encounter Bay. Other than Cape Jervis North (9m) and Wright Island (9m), all sites were situated at a depth of 5m below the mean low water mark.

Most northerly of the gulf sites was Second Valley (SV5) which was partially protected from wave movement by local features. Cape Jervis North (5m) (annotated CJN5) and Cape Jervis North (9m) (annotated CJN9) represented the roughest gulf sites, although the depth of CJN9 ameliorated the effects of wave force somewhat. Calmest of all sites was Cape Jervis East (CJE5). All of these sites were protected from direct oceanic swell by Kangaroo Island.

Of the oceanic sites, Granite Island (GI5) was the roughest, being afforded no protection from the oceanic swell. The Bluff (B5) was afforded slight local protection from the swell by "the Bluff", but being close to the seaward tip, refraction does not reduce the wave energy much. Wright Island (5 and 9m) (WI5 and WI9) were located toward the leeward side of the Wright Island. While this island was small, it reduced the wave action somewhat, making these sites the most protected within the oceanic environment. They were still far rougher than any of the gulf sites.



Chapter 4

Table 4.1a Partitioning canopy richness between regional, site and sample scales.

Columns represent;

- a) the number of canopy species found at each site as a proportion of the total found across all sites;
- b) the average number of canopy species found in a square metre at each site as a proportion of the canopy richness of that entire site;
- c) the average number of canopy species found in a square metre at each site as a proportion of the canopy richness of the entire study.

With the exception of CJN9, the gulf sites supported a greater proportion of the species richness displayed across all sites. Furthermore, a greater proportion of the site richness was found in any given square metre. The result was that considerably more than half of the total number of canopy species found across the entire study can be found in any given square metre at the gulf sites.

Table 4.1b Partitioning understorey richness between regional, site and sample scales.

Columns are as above, but describe understorey species richness rather than canopy.

While gulf sites supported a greater number of species at the site level, the proportion of these found in any square metre was at least as high at the oceanic sites. A far lower proportion of total study understorey richness was demonstrated at the level of the square metre than was the case with canopy species. There was no consistent difference between oceanic sites and gulf sites.

Note for tables 4.1a and 4.1b The relativity between sites for column A is of course equivalent to that demonstrated in Figure 4.4. Similarly, the relativity between sites in column C is demonstrated (and statistically analysed) in Figures 4.5b and 4.5c. This is because these columns divide all sites by the same denominator (entire study richness). The point of these tables was to demonstrate the extraordinary proportion of the large scale species richness found within only a square metre.

CANOPY

Site	Site Richness as % of Regional Richness	Average Richness of 1m ² as % of Site Richness	Average Richness of 1m ² as % of Regional Richness
CJE5	93	68	63
SV5	87	67	58
CJN9	93	44	41
CJN5	93	68	63
WI9	73	36	26
WI5	73	40	29
B5	73	40	29
GI5	47	44	21

UNDERSTOREY

Site	Site Richness as % of Regional Richness	Average Richness of 1m ² as % of Site Richness	Average Richness of 1m ² as % of Regional Richness
CJE5	65	15	10
SV5	51	11	6
CJN9	41	14	6
CJN5	48	19	9
WI9	46	16	7
WI5	39	17	7
B5	35	13	5
GI5	39	19	7

Fig. 4.1 Graphical depiction of self thinning line. Each of the points represents an aging population, at successive points in time, described by the log density (plants m^{-2}) (note that this is "abundance" in the parlance of this thesis) and log average plant weight (g dwt plant $^{-1}$) of the sample. T_1 represents the population at time 1, T_2 represents the same population at time 2 and so on. Note that the plants grow in weight until the point where they encounter the thinning line. Thereafter, increases in plant weight are offset by decreases in density such that the population moves from right to left along the thinning line. While the slope is almost universally accepted to be $-3/2$, the intercept ($\log K$) may vary depending on the population. The generally accepted limits for this are 3.5 to 5 (White 1985).

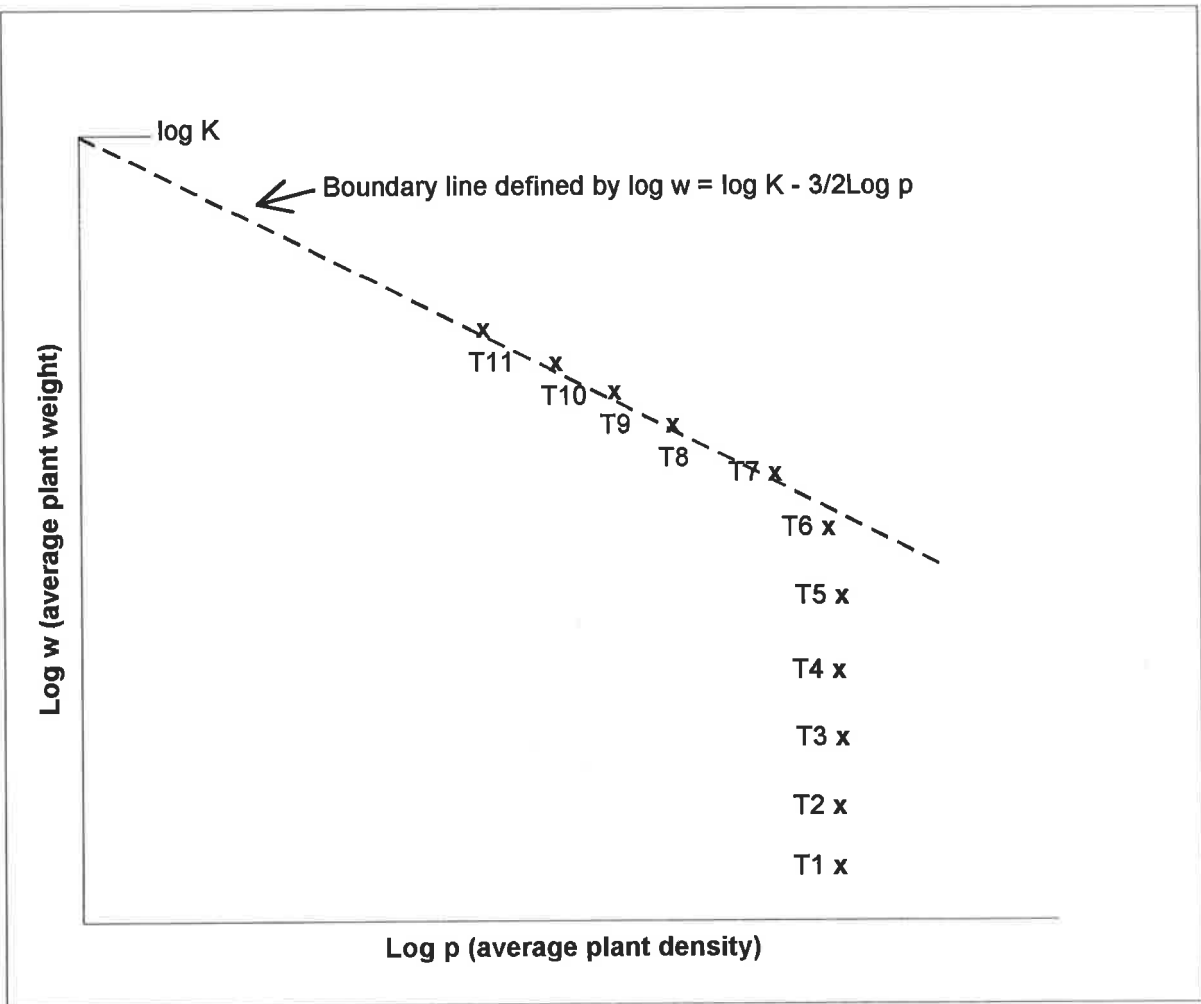


Fig. 4.2a Dendrogram of site / collection averages based on presence-absence. Because of the hierarchical nature of this UPGMA analysis, it is possible to make distinctions at different levels. The user defined (red and green) vertical lines intercept the horizontal grouping lines of the dendrogram. Where it does so, the boundary of a group is defined.

The labels used are a double digit number, where the first digit represents the site, and the second the collection date.

Site (first digit)	Collection (second digit)
1 CJS	1 Summer '92
2 SV5	2 Autumn '92
3 CJS	3 Winter '92
4 CJS	4 Spring '92
5 GS	5 Summer '93
6 B5	6 Autumn '93
7 WIS	7 Winter '93
8 WIS	8 Spring '93
	9 Summer '94

Thus the label 25 represents SV5 in Summer 1993.

The most basic distinction (red line) defines CJS and SV5 as separate from the remainder of the sites. However, finer resolution (the green line) distinguishes 7 groups which largely correspond to the different sites. The groups defined were [CJS], [CJS], [GS], [SV5], [CJS] and 2 groups which were a mixture of collections from oceanic sites.

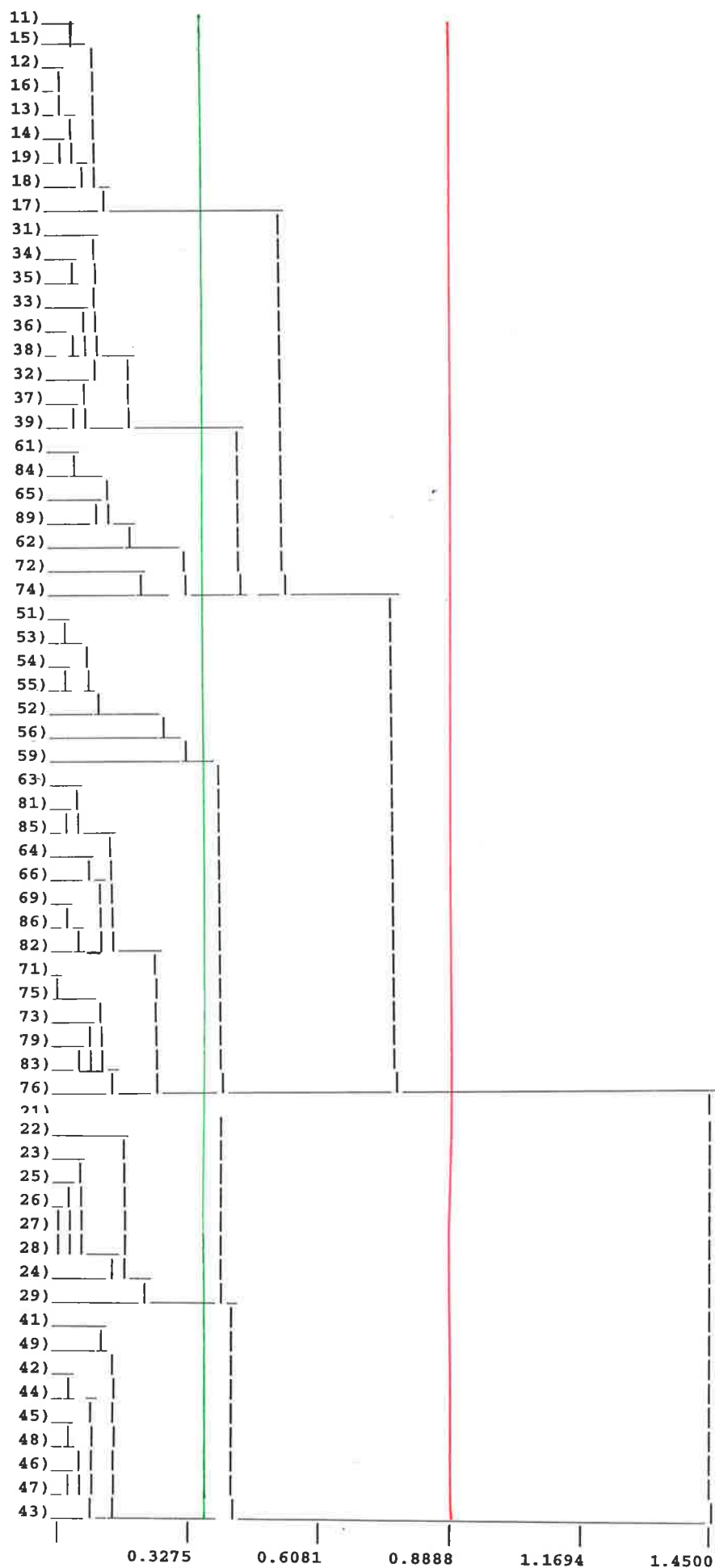


Fig. 4.2b Dendrogram of site / collection averages based on biomass data. This UPGMA analysis, using biomass data revealed three major distinctions (green line). The three relatively separate groupings were;

- a) the two calmest sites (CJE5 and SV5)
- b) CJN9 and the oceanic sites
- c) CJN5

There was very slight overlap with groups b and c.

Labels used were the same as Fig 4.2a; a double digit number representing site and date

Site (first digit)	Collection (second digit)
1 CJN5	1 Summer '92
2 SV5	2 Autumn '92
3 CJN9	3 Winter '92
4 CJE5	4 Spring '92
5 GI5	5 Summer '93
6 B5	6 Autumn '93
7 WI9	7 Winter '93
8 WI5	8 Spring '93
	9 Summer '94

Thus the label 21 represents SV5 in Summer 1992

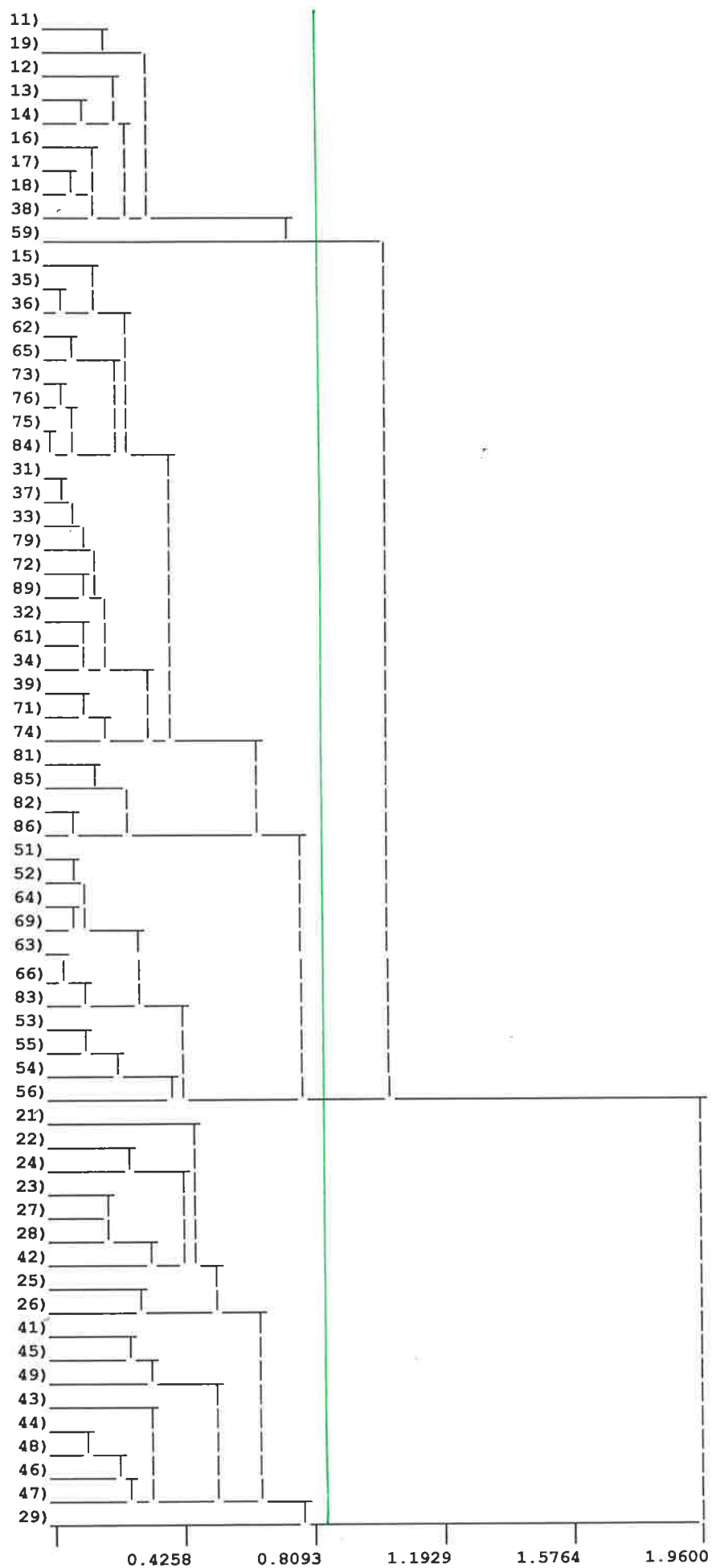


Fig. 4.3a Ordination of site / collection averages based on presence-absence. This ordination (non-metric multidimensional scaling) represents the relationships between the biota of the sites in two dimensions. Each point represents a site / collection average (average biota of a site on one collection date). Labelling system is explained in the caption of Figure 4.2a. Green envelopes represent a distinct group consisting of collections of a single site. Red envelopes contain points from more than one site. Stress = .09

The overlay of the species vectors is made using principal canonical correlation. Each letter represents a different species and all vectors originate from the same point and pass through the letter which labels them. Only 3 vectors (blue lines) are shown, in order to keep the figure as uncluttered as possible. These vectors represent an axis along which samples tend to contain increasing levels of the relevant species toward the head of the arrow. All species vectors were significant ($p < .05$; multiple regression).

Species Labelling:	A	<i>Acrocarpia paniculata</i>
	B	<i>Cystophora brownii</i>
	C	<i>C. expansa</i>
	D	<i>C. monilifera</i>
	E	<i>C. moniliformis</i>
	F	<i>C. subfarcinata</i>
	G	<i>Ecklonia radiata</i>
	H	<i>Sargassum decipiens</i>
	I	<i>S. fallax</i>
	J	<i>S. lacerifolium</i>
	K	<i>S. linearifolium</i>
	L	<i>S. varians</i>
	M	<i>S. verruculosum</i>
	N	<i>Scytothalia dorycarpa</i>
	O	<i>Seirococcus axillaris</i>

Most sites appeared distinct from each other with the exception of B5 and W19. CJE5 and SV5, the calmest sites, were associated with high levels of *Cystophora* and *Sargassum* species, while the oceanic sites were associated with high levels of *Ecklonia*, *Scytothalia* and *Seirococcus*. The two higher energy gulf sites, CJN5 and CJN9, were of intermediate composition and were particularly associated with *Seirococcus*.

Fig. 4.3b Ordination of site / collection averages based on biomass data. Species labelling system is described above, and site / collection labelling system is described in Figure 4.2a. Stress = .13 This NMDS analysis, using biomass data, revealed almost the same patterns as found in the average presence-absence data displayed above. The major exception is the inability to distinguish SV5 and CJE5. Species vectors demonstrated the same associations as above.

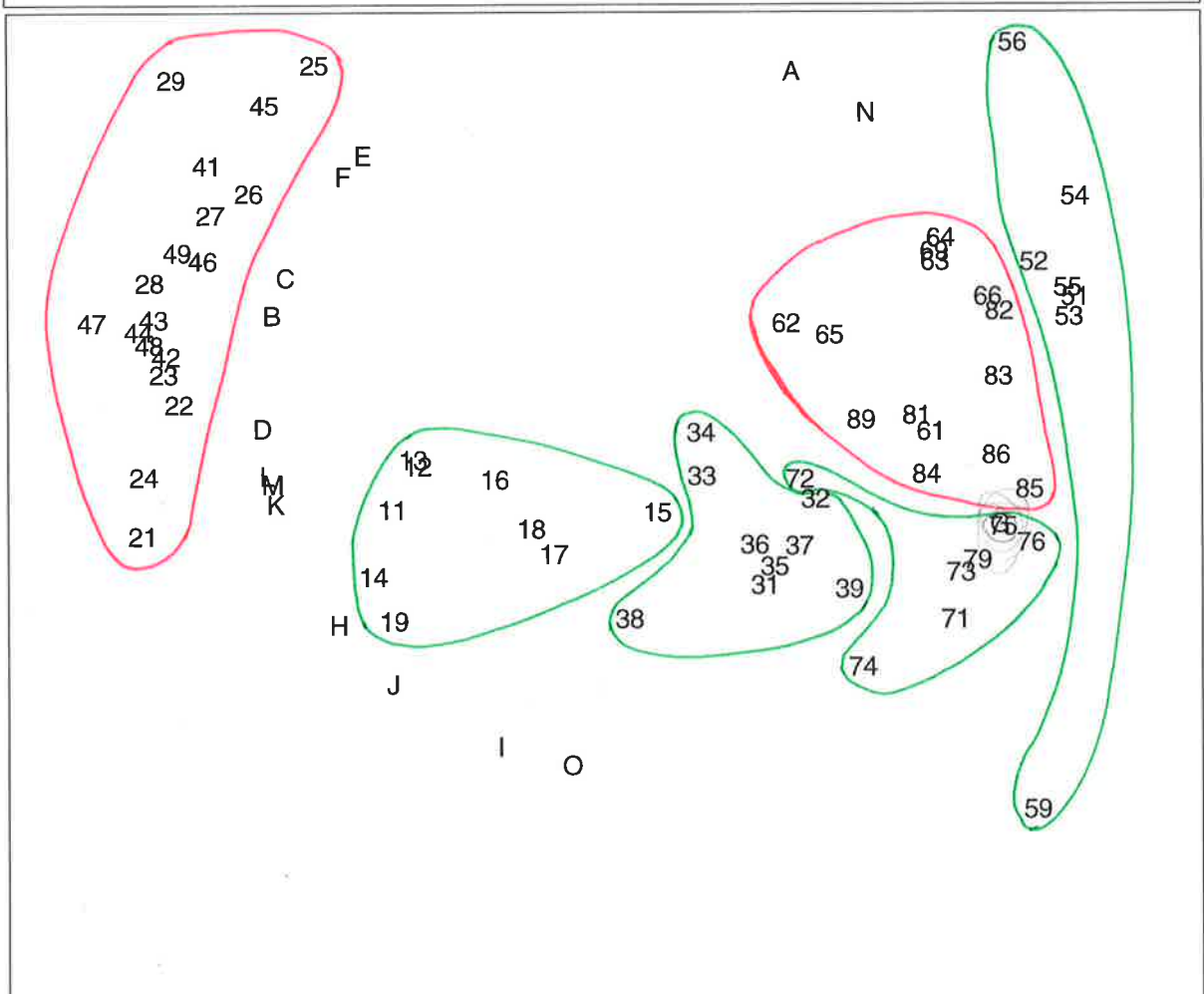
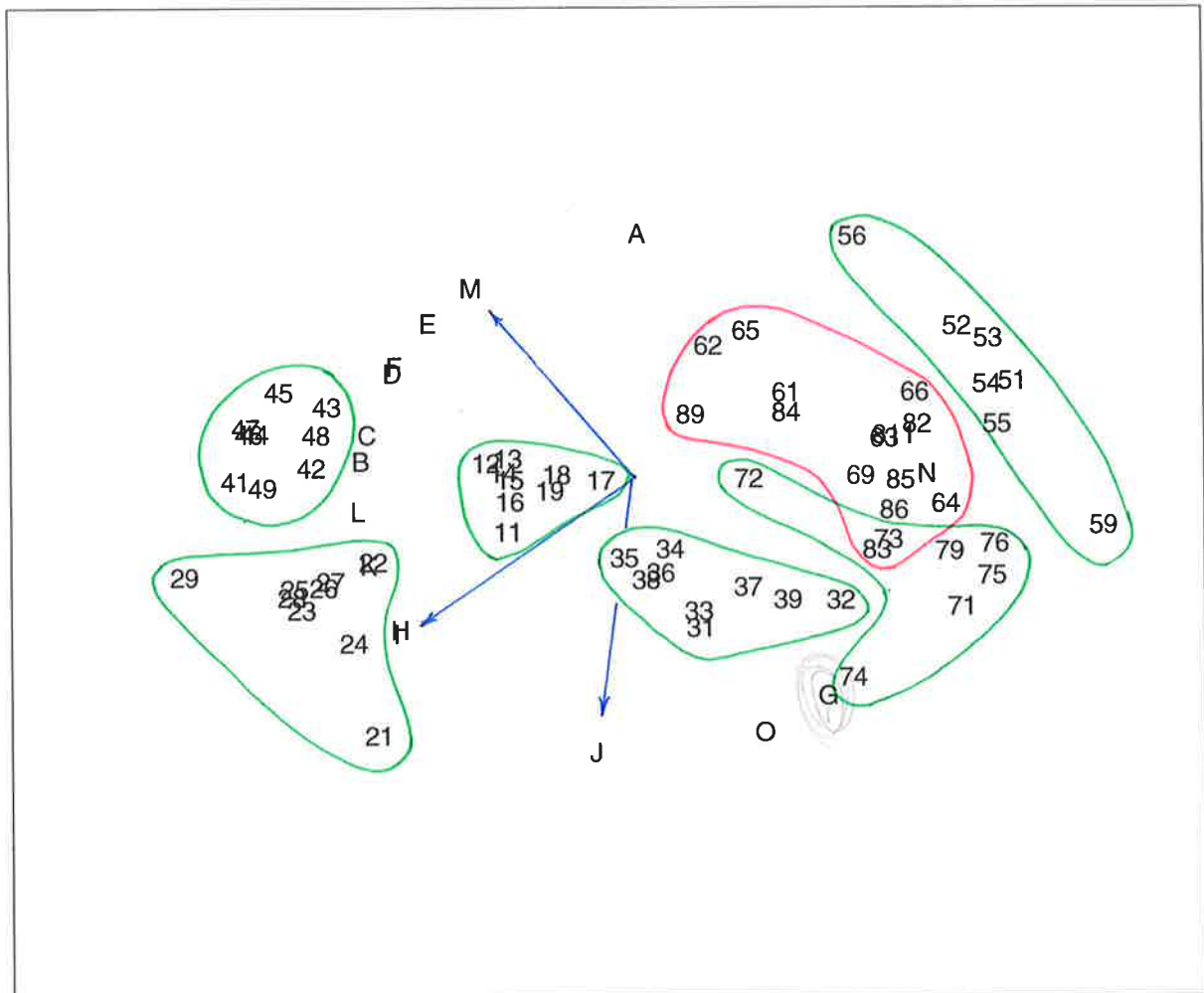


Fig. 4.4 Site level species richness (total, canopy and understorey). Site level species richness is a description of the number of species found at each site across the course of the entire study. Total species richness is represented by the height of the column, which is partitioned into canopy and understorey richness. The numbers within the columns indicate the number of species present. No measure of variation is possible since there is no replication. Sites are arranged in order of increasing water movement

CJE5 supported the highest understorey and canopy richness, and GI5 the lowest. Generally the gulf sites supported higher canopy and total richness. Understorey richness was not consistently higher in either oceanic or gulf habitats.

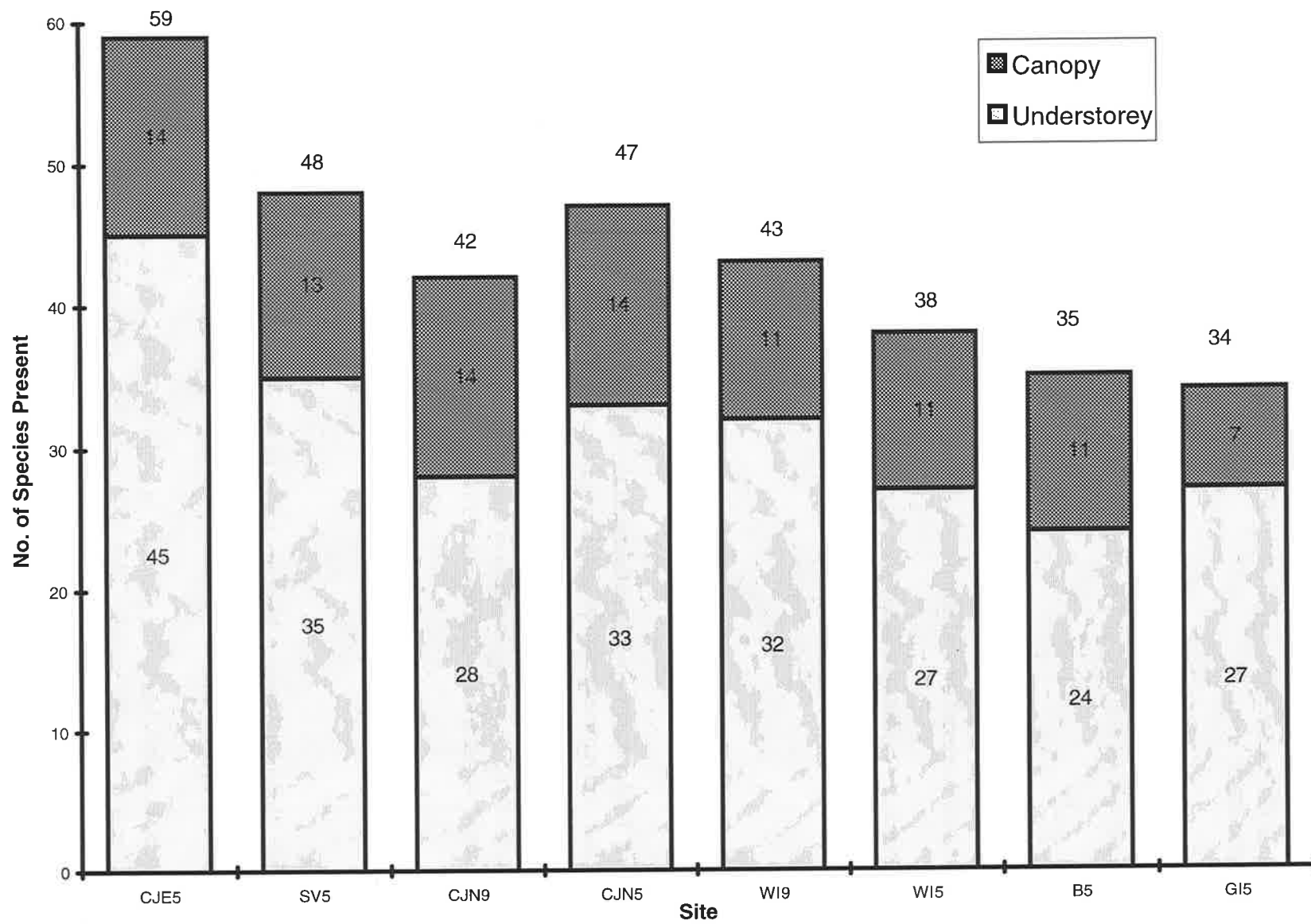


Fig. 4.5a Total species richness at the scale of the sample (1m²). Error bars represent $\pm$ 1 standard error. (n=72 for CJE5, SV5, CJN9 and CJN5; n=56 for WI9, WI5, B5 and GI5). The letters above the column demonstrate which sites are significantly different - those sites which share a letter are NOT significantly different (Tukey tests after ANOVA on $\sqrt{x + 3/8}$ transformed data)

Gulf sites demonstrated lower species richness at the scale of the square metre, although CJN9 was not significantly different to the Wright Island sites. CJE5 and CJN5 supported the highest total species richness, and B5 the lowest.

Fig. 4.5b Canopy species richness at the scale of the sample (1m²). Error bars, level of replication and representation of significant difference as above.

Similar trends are evident in canopy species richness as those described above. Highest canopy richness was found at the gulf sites, particularly CJE5 and CJN5. Lowest canopy richness was evident at GI5 and WI9.

Fig. 4.5c Understorey species richness at the scale of the sample (1m²). Error bars, level of replication and representation of significant difference as above.

Neither the gulf nor oceanic environment consistently supported greater understorey species richness. While CJE5 was again the most species rich, high variance levels meant that no other gulf site could be statistically differentiated from all oceanic sites.

Fig. 4.5d Shannon-Weaver diversity index at the scale of the sample (1m²). Based on biomass of the canopy species, this represents the diversity of the canopy. Error bars, level of replication and representation of significant difference as above.

This analysis revealed clearly that diversity, in terms of species richness and evenness, was higher at the gulf sites, particularly CJE5, SV5 and CJN5. All oceanic sites demonstrated statistically uniform low diversity indices.

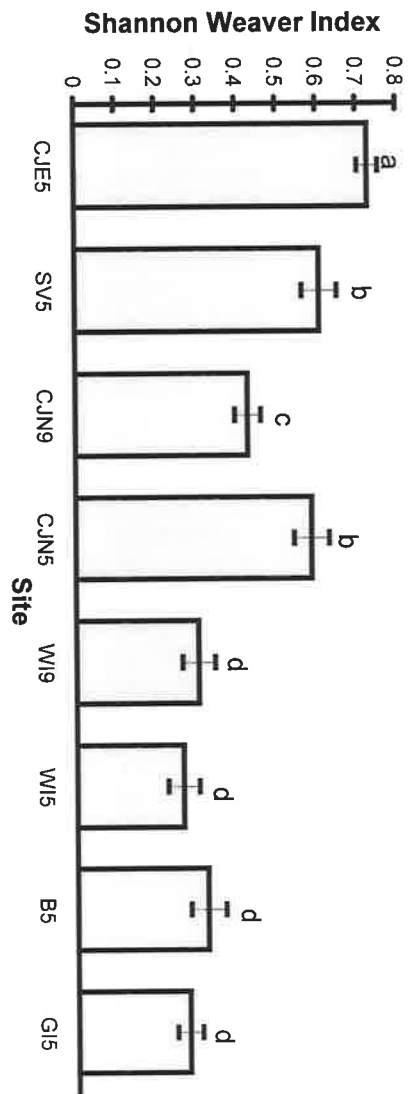
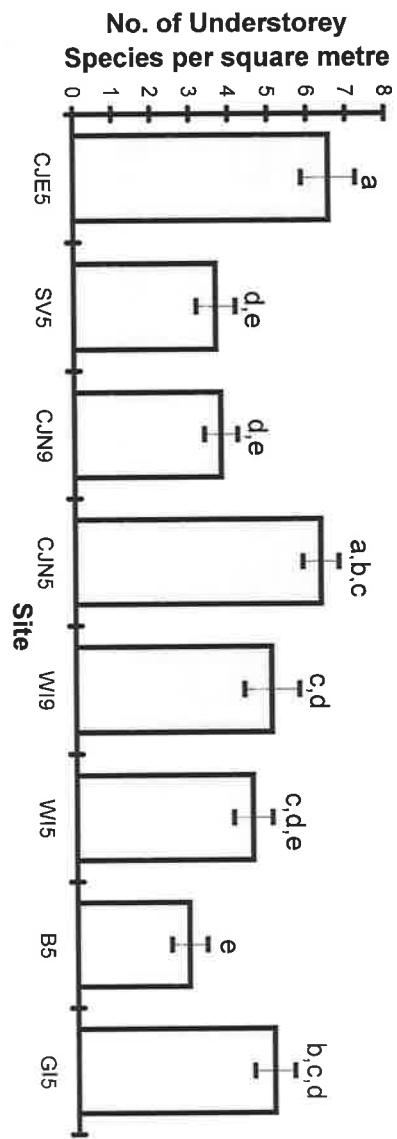
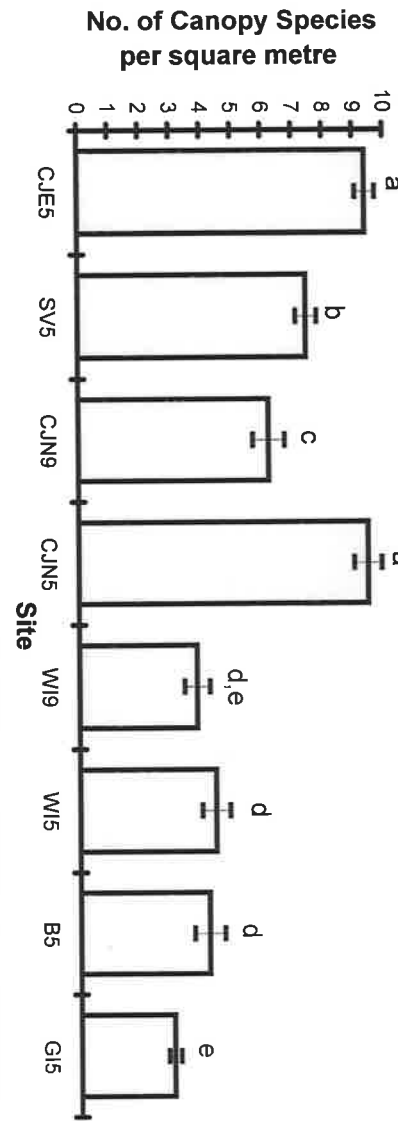
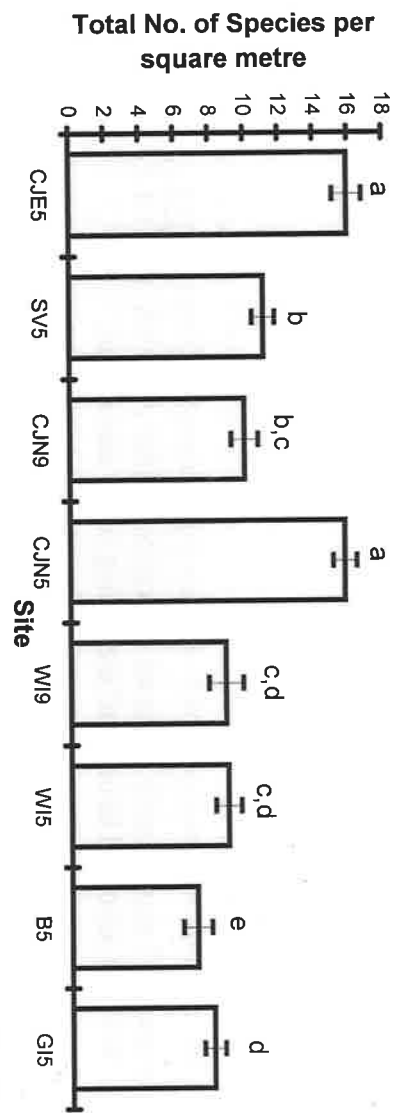


Fig. 4.6 Total biomass supported by each of the sites. Error bars represent ± 1 standard error. (n=72 for CJE5, SV5, CJE9 and CJE5; n=56 for WI9, WI5, B5 and GI5). The letters above the column demonstrate which sites are significantly different - those sites which share a letter are NOT significantly different (Tukey tests after ANOVA on $\sqrt{x + 3/8}$ transformed data). Sites are arranged in order of increasing water movement.

Biomass was maximal at sites of moderate to high (but not extreme) water movement. It was the calmest sites which supported the lowest total biomass.

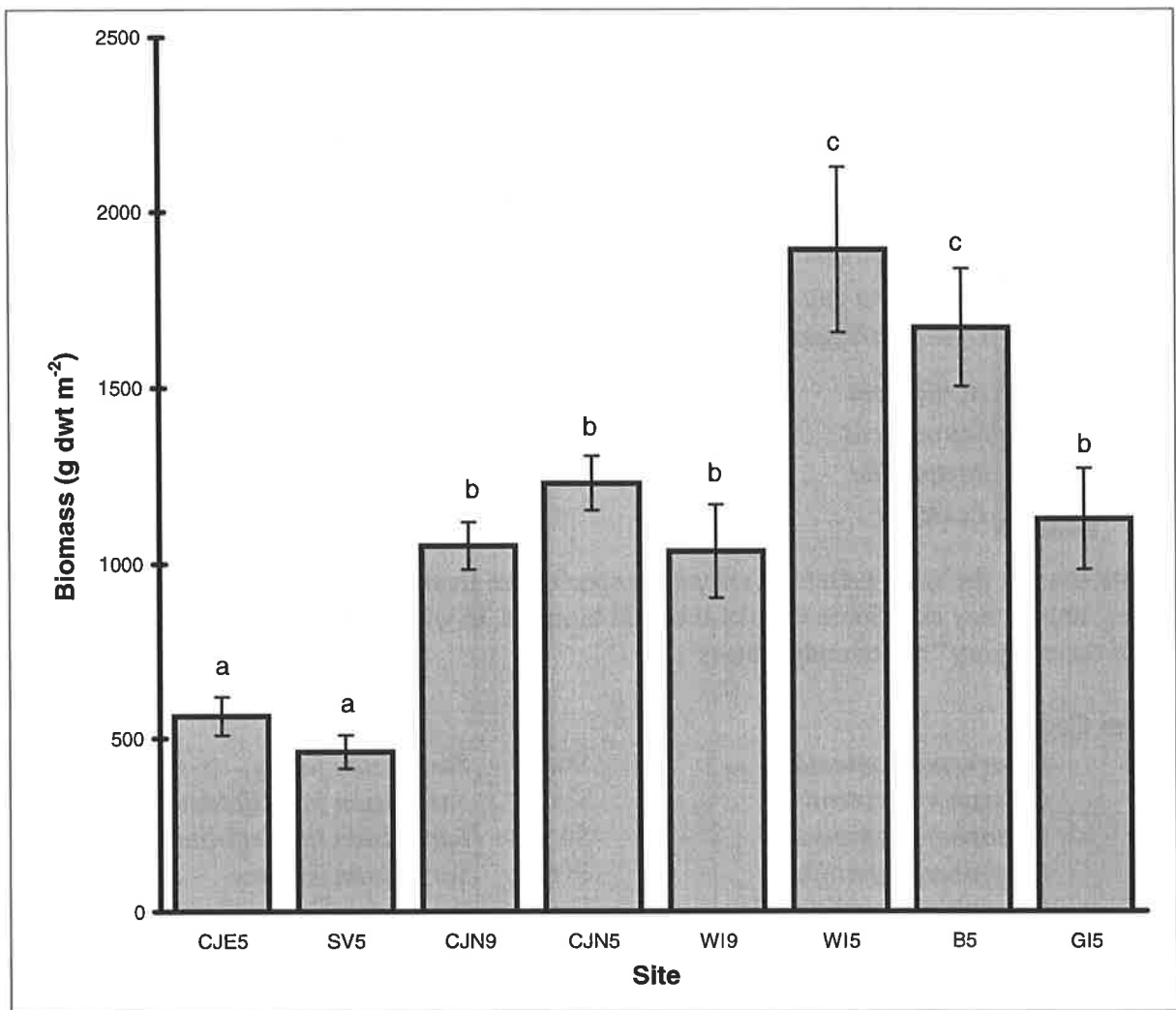
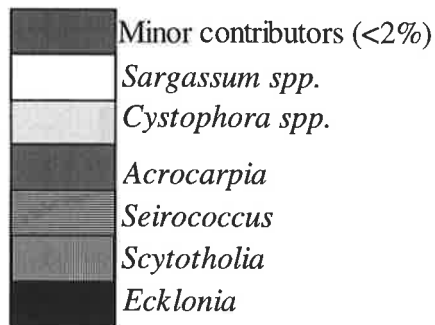


Fig. 4.7 Proportional contribution of each species to total biomass at each site. Total biomass of each site is represented by a pie chart partitioned according to the contributions by each species. Patterns used for each category are as follows;



Despite sharing the same pattern, *Cystophora* species are treated separately, as are *Sargassum* species, unless they contribute <2% of the total biomass, in which case they are aggregated as part of the category "minor contributors".

Species Codes

Apa	<i>Acrocarpia paniculata</i>	Sfa	<i>Sargassum fallax</i>
Cbr	<i>Cystophora brownii</i>	Sla	<i>Sargassum lacerifolium</i>
Cex	<i>Cystophora expansa</i>	Sli	<i>Sargassum linearifolium</i>
Cma	<i>Cystophora monilifera</i>	Sva	<i>Sargassum varians</i>
Cms	<i>Cystophora moniliformis</i>	Sve	<i>Sargassum verruculosum</i>
Csu	<i>Cystophora subfarcinata</i>	Sdo	<i>Scytothalia dorycarpa</i>
Era	<i>Ecklonia radiata</i>	Sax	<i>Seirococcus axillaris</i>
Sde	<i>Sargassum decipiens</i>		

In general, more species made significant contributions to the total biomass at the gulf sites, particularly at CJE5 and SV5 where many *Cystophora* and *Sargassum* species contribute. In contrast, the oceanic sites were dominated by only two or three species. Overall, *Ecklonia* is the species which most consistently made significant contributions to the biomass.

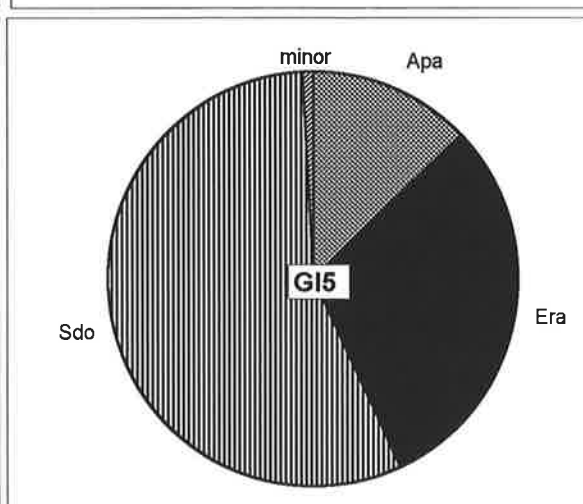
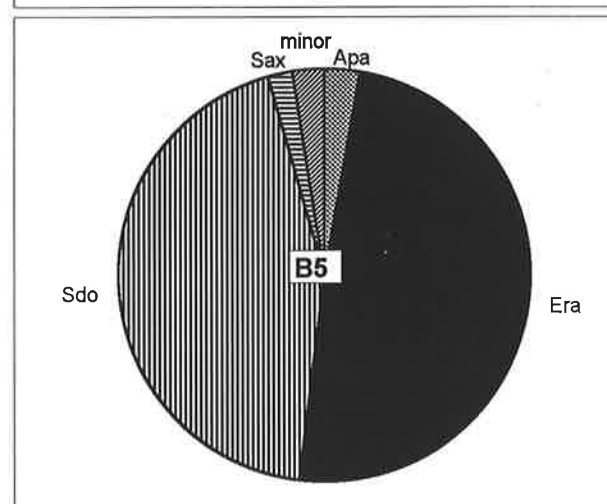
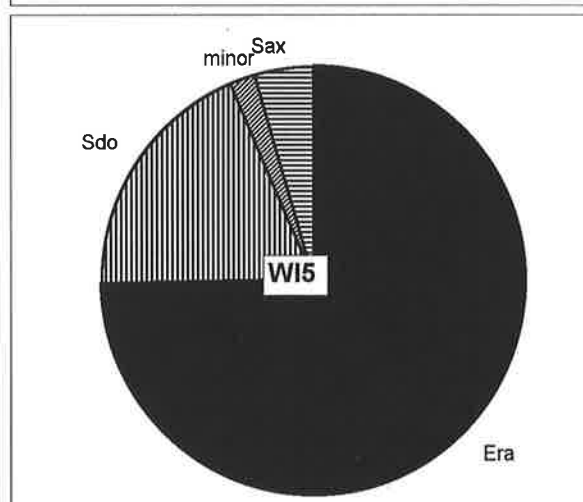
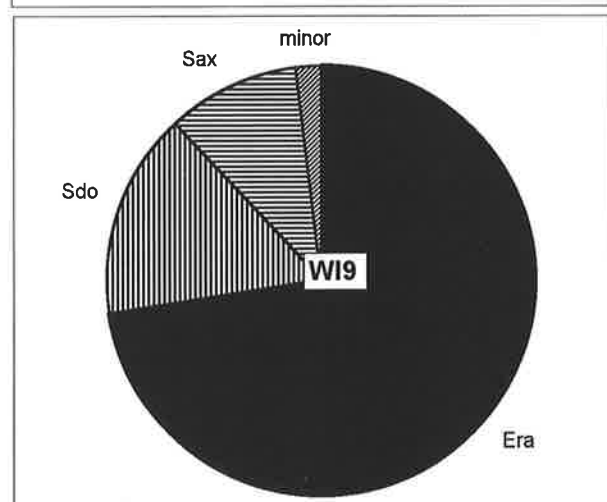
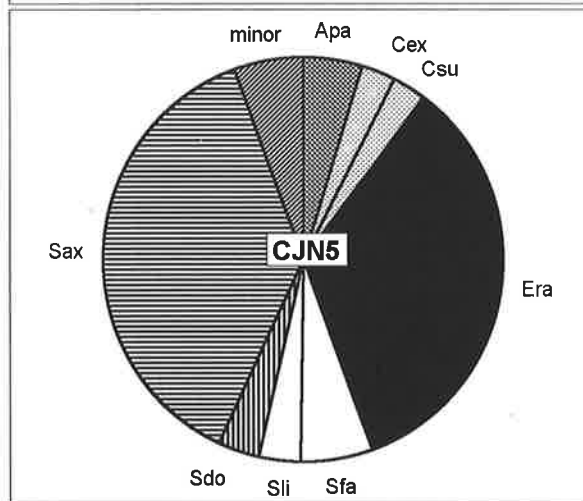
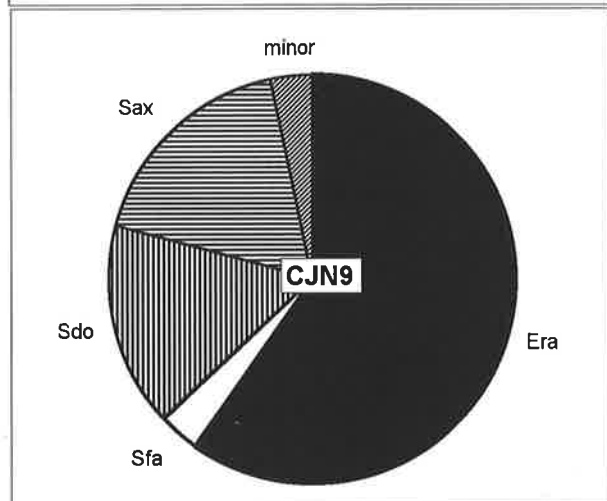
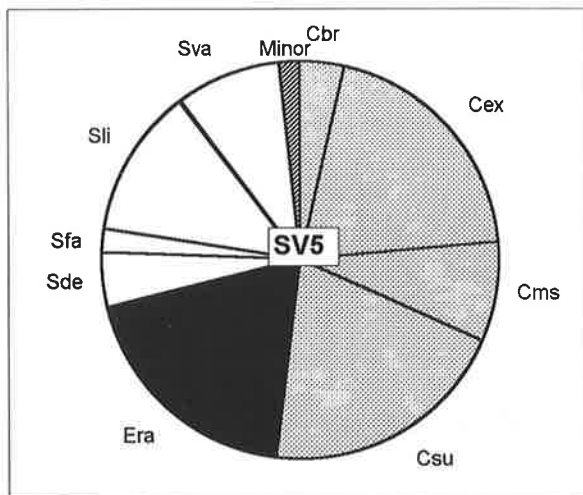
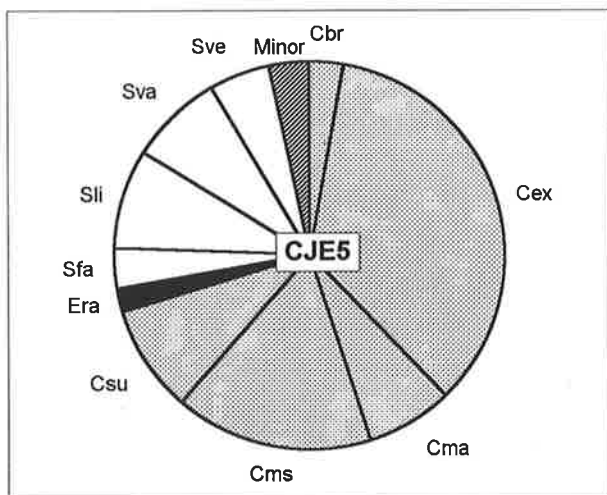


Fig 4.8a Biomass of *Ecklonia radiata* supported by each site. Error bars represent $\pm$ 1 standard error. (n=72 for CJE5, SV5, CJN9 and CJN5; n=56 for WI9, WI5, B5 and GI5). The letters above the column demonstrate which sites are significantly different - those sites which share a letter are NOT significantly different (Tukey tests after ANOVA on $\sqrt{x = 3/8}$ transformed data). Sites are arranged in order of increasing water movement. The numbers in brackets represent the proportion of the total biomass that this species represents at each site. Proportions are displayed only for *Ecklonia* because of its impact on the biomass of all sites.

Ecklonia biomass was maximised at the oceanic sites, particularly those with moderate to strong biomass. Of the gulf sites, it was CJN9 which demonstrated the highest biomass of *Ecklonia*. While significantly more biomass was supported by WI5 than WI9 this still represented approximately the same proportion of the total biomass.

Fig. 4.8b Biomass of *Scytothalia dorycarpa* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

This is clearly a plant which thrived in high energy conditions, being maximised at the two sites of highest exposure and completely absent at the two sites of lowest exposure.

Fig. 4.8c Biomass of *Seirococcus axillaris* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

Seirococcus biomass was maximised at moderate levels of water movement, supporting $\approx 450\text{g dwt m}^{-2}$ at CJN5. It was found at oceanic sites, but not in large quantities, as was the case for the sites of lowest exposure.

Fig. 4.8d Biomass of *Acrocarpia paniculata* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

Acrocarpia probably represented the species which prefers the most extreme water movement. Only at GI5, where $\approx 150\text{g dwt m}^{-2}$ was supported, was more than 70g dwt m^{-2} found. However, it was found at all sites in small quantities.

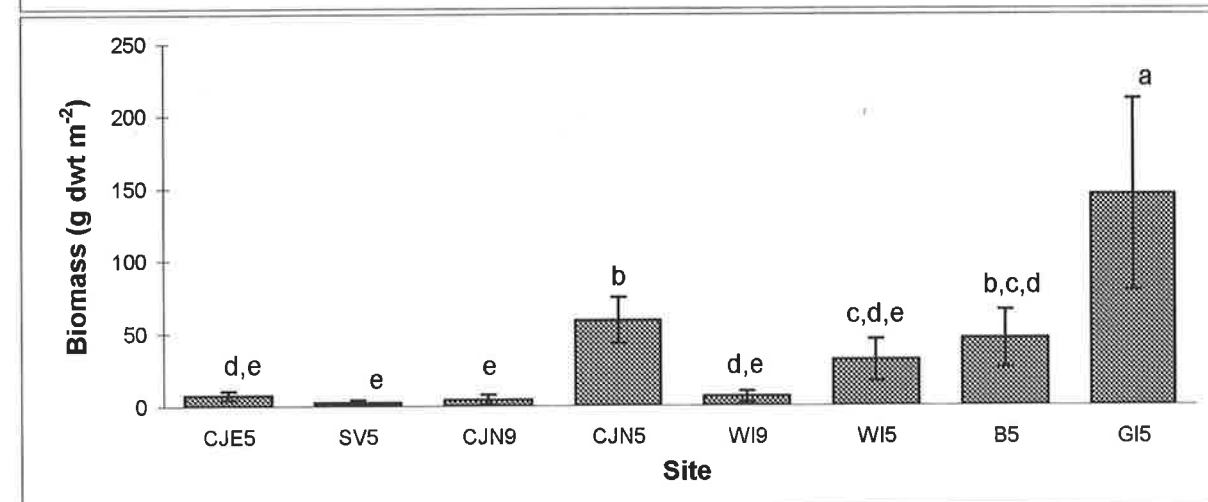
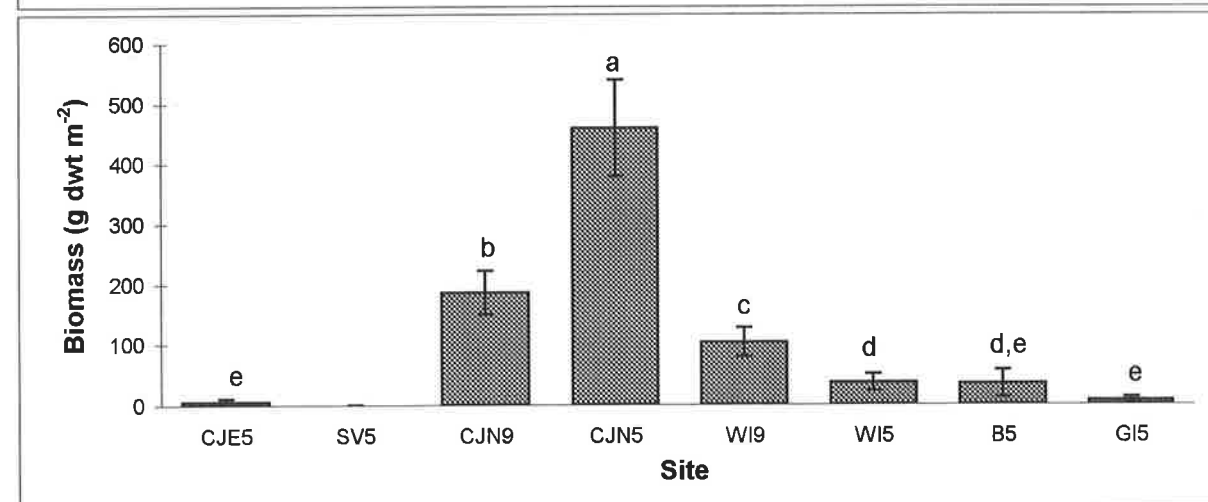
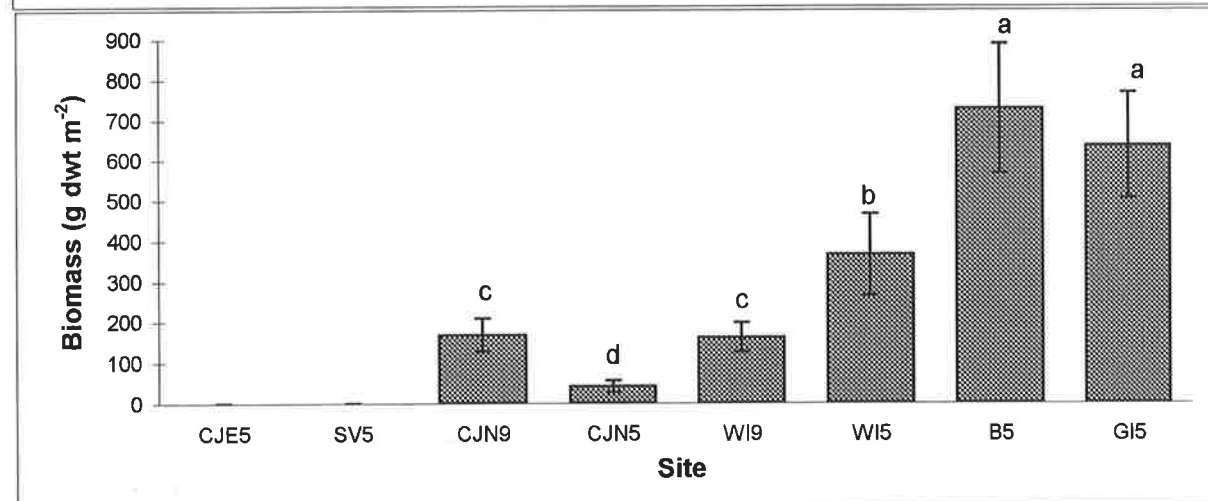
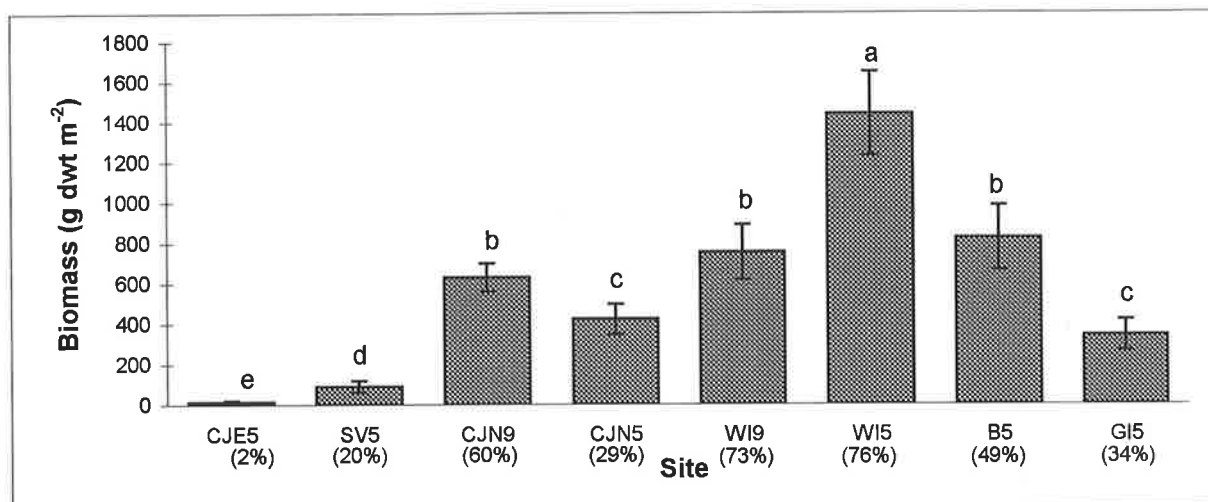


Fig. 4.8e Biomass of *Cystophora brownii* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

Cystophora brownii appeared to be a calm water species, being represented only at the gulf sites, and of those, CJE5 and SV5 supported the greatest biomass.

Fig. 4.8f Biomass of *Cystophora expansa* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

This species of *Cystophora* was supported in large quantities at CJE5, and occurred only at the gulf sites.

Fig. 4.8g Biomass of *Cystophora monilifera* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

While found at all sites except GI5, this species demonstrated maximal biomass at CJE5.

Fig. 4.8h Biomass of *Cystophora moniliformis* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

Cystophora moniliformis was found at all sites, but was maximal at CJE5.

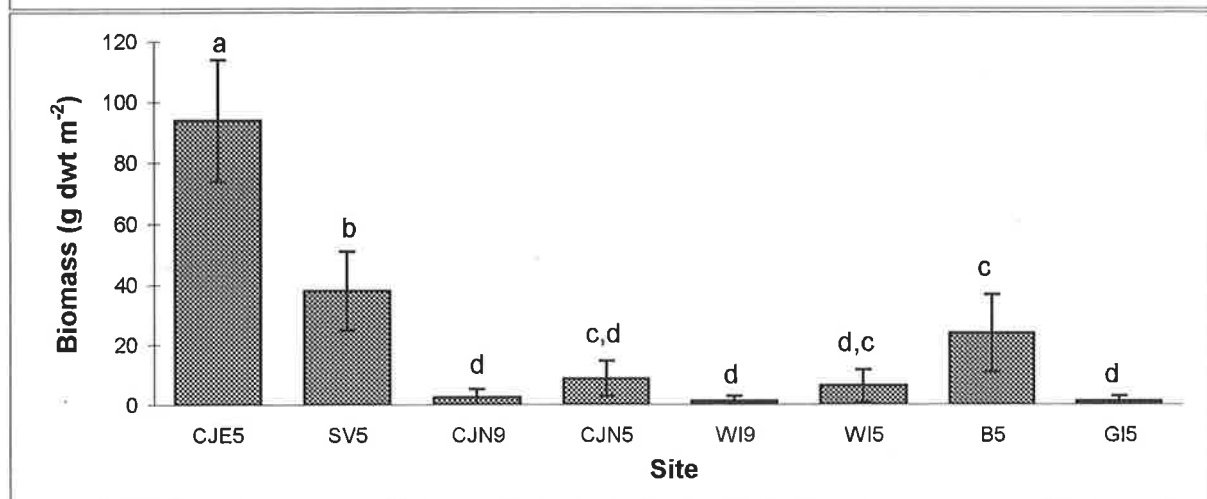
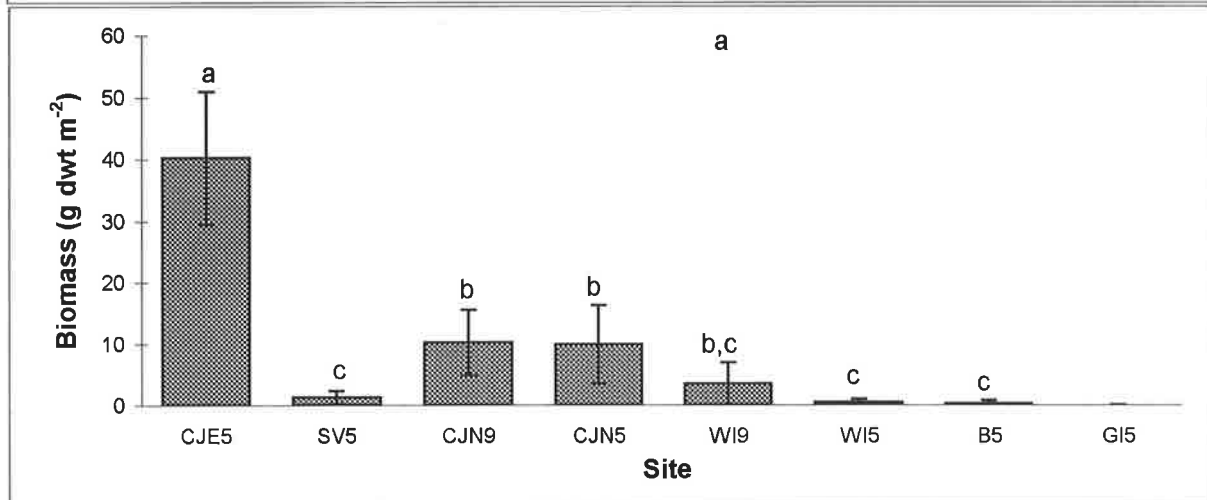
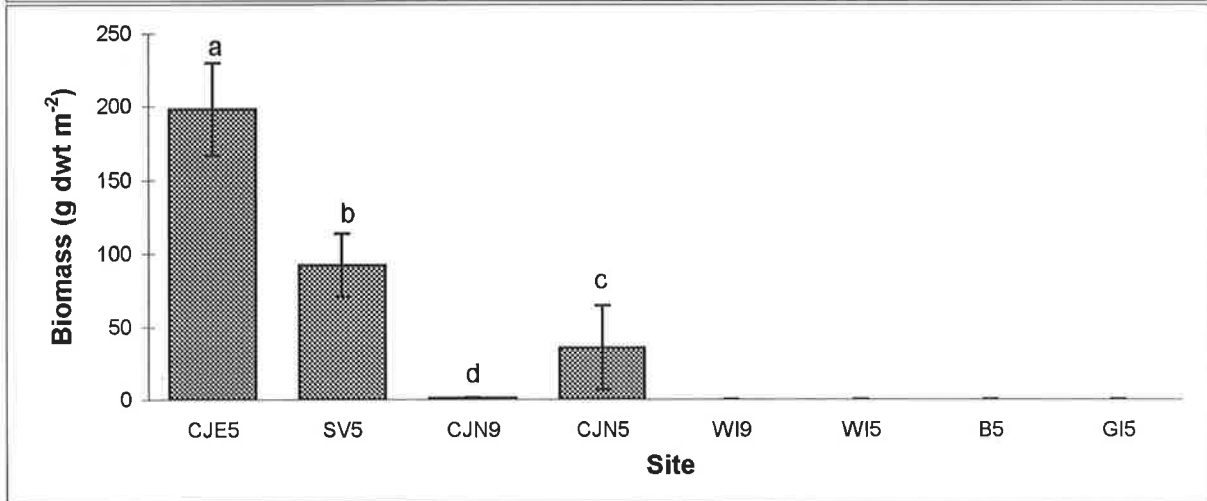
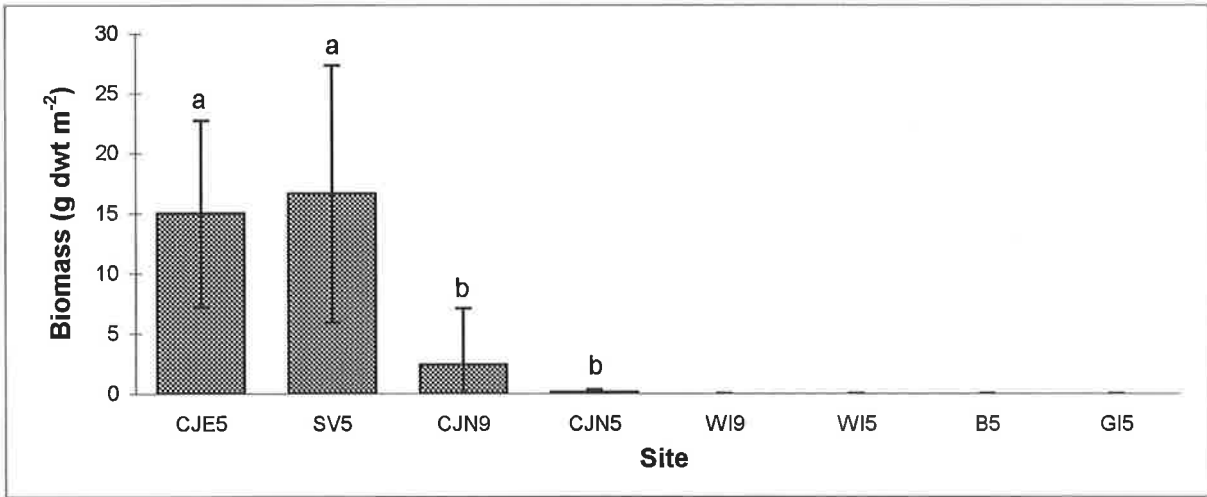


Fig. 4.8i Biomass of *Cystophora subfarcinata* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

Cystophora subfarcinata was found at all sites except GI5. However, it occurred only in trace quantities at sites other than CJE5, SV5 and CJN5. It appeared best suited to the gulf sites, with the exception of CJN9.

Fig. 4.8j Biomass of *Sargassum decipiens* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

Not represented well at any sites, this species displayed more than 10g dwt m⁻² only at SV5 and CJN5.

Fig. 4.8k Biomass of *Sargassum fallax* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

Sargassum fallax was supported by all sites, but it was at CJN5, and to a lesser extent CJN9, that biomass was maximal.

Fig. 4.8l Biomass of *Sargassum lacerifolium* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

Despite being reported by Shepherd and Sprigg (1976) as a common species of the gulf waters, it was extremely rare in this study.

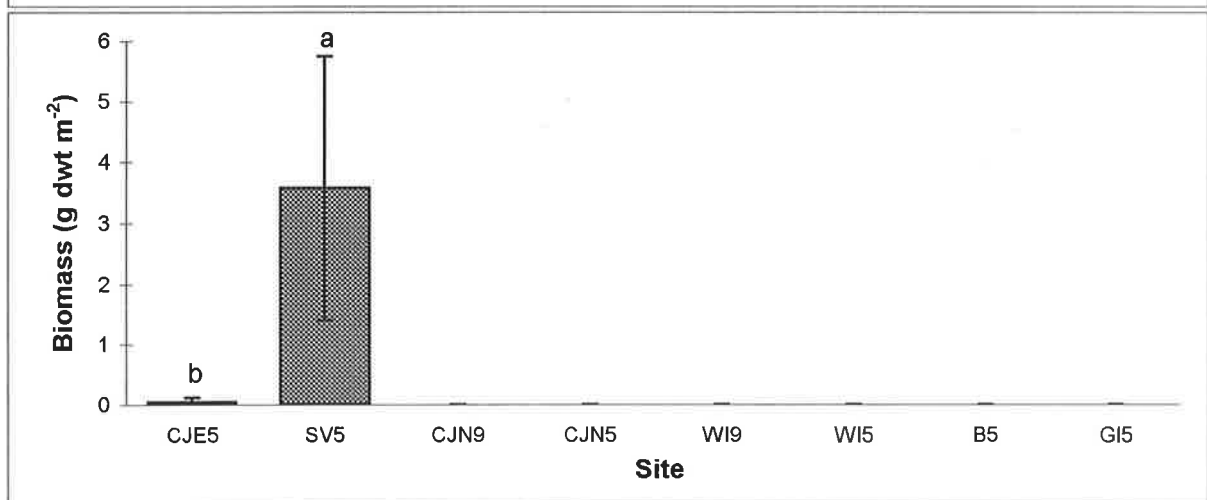
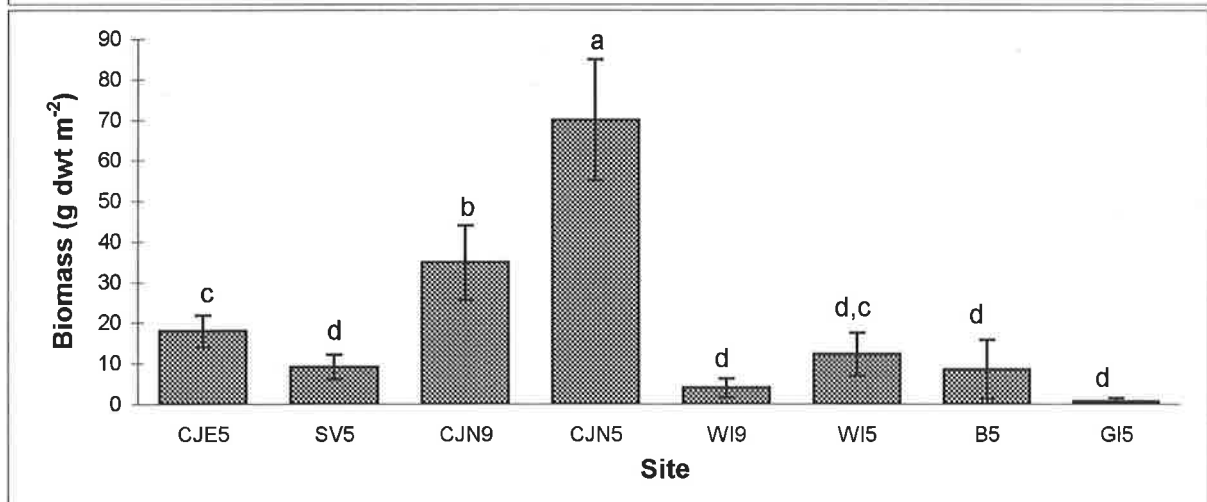
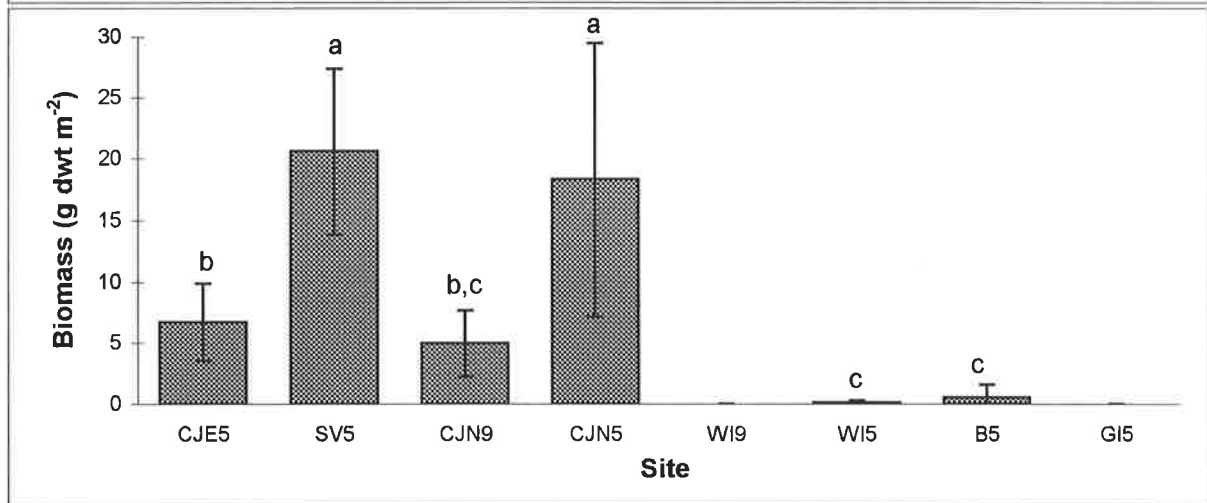
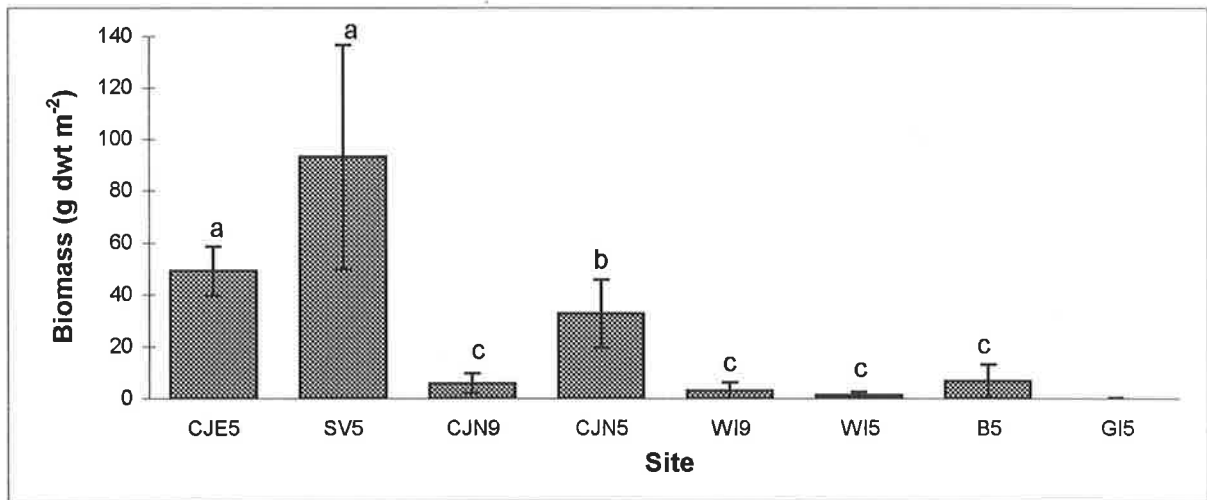


Fig. 4.8m Biomass of *Sargassum linearifolium* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

This species was principally found at the three 5 metre gulf sites. Other sites supported little or no *Sargassum linearifolium*.

Fig. 4.8n Biomass of *Sargassum varians* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

Like *S. linearifolium*, *Sargassum varians* was found in greatest quantity at the three 5 metre gulf sites. It was generally absent from the oceanic sites.

Fig. 4.8o Biomass of *Sargassum verruculosum* supported by each site. Error bars and the method of analysing and representing significant differences is the same as Fig. 4.8a.

Found only in small amounts, only CJE5 and CJN5 supported more than 10g dwt m⁻² of *Sargassum verruculosum*.

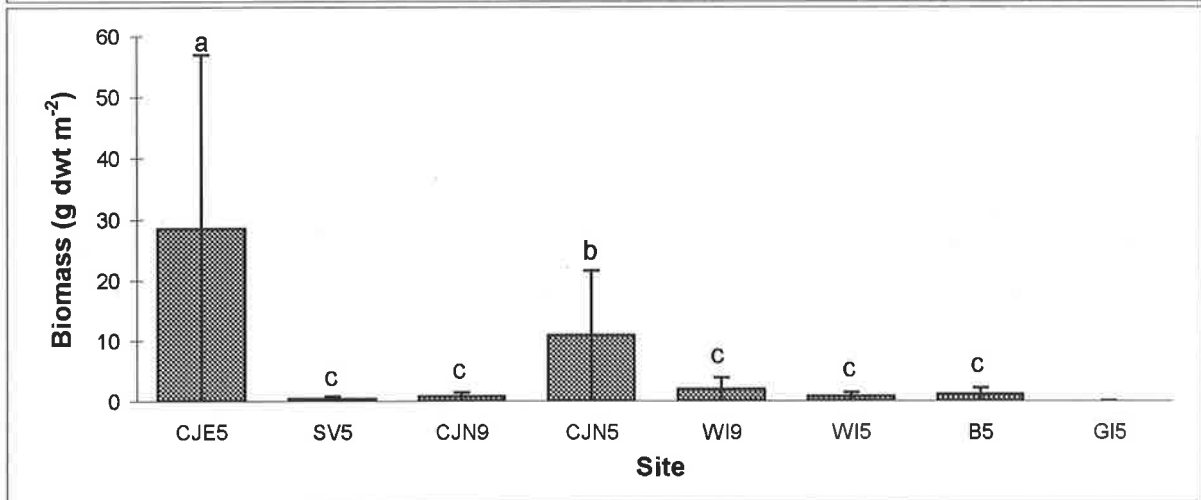
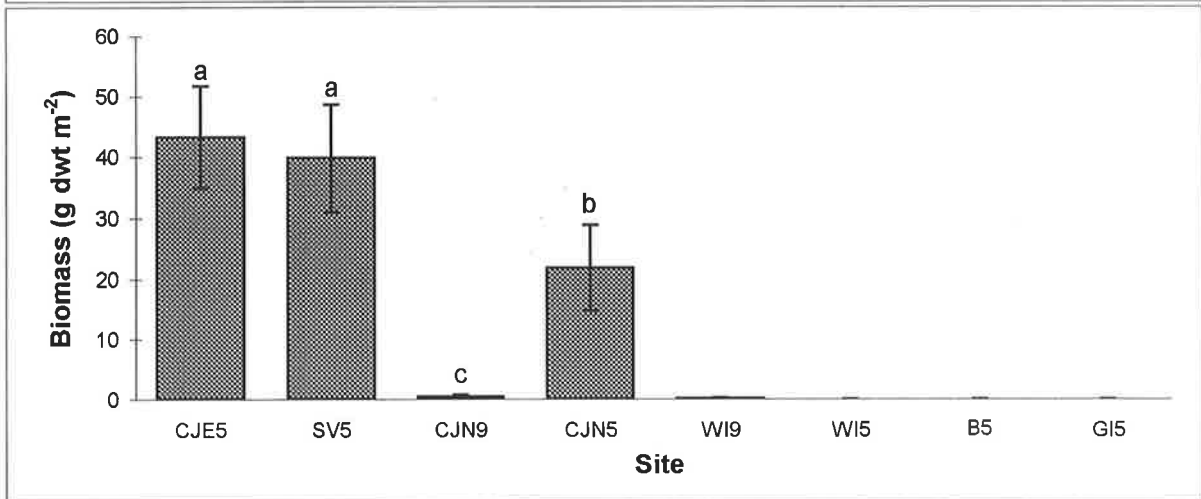
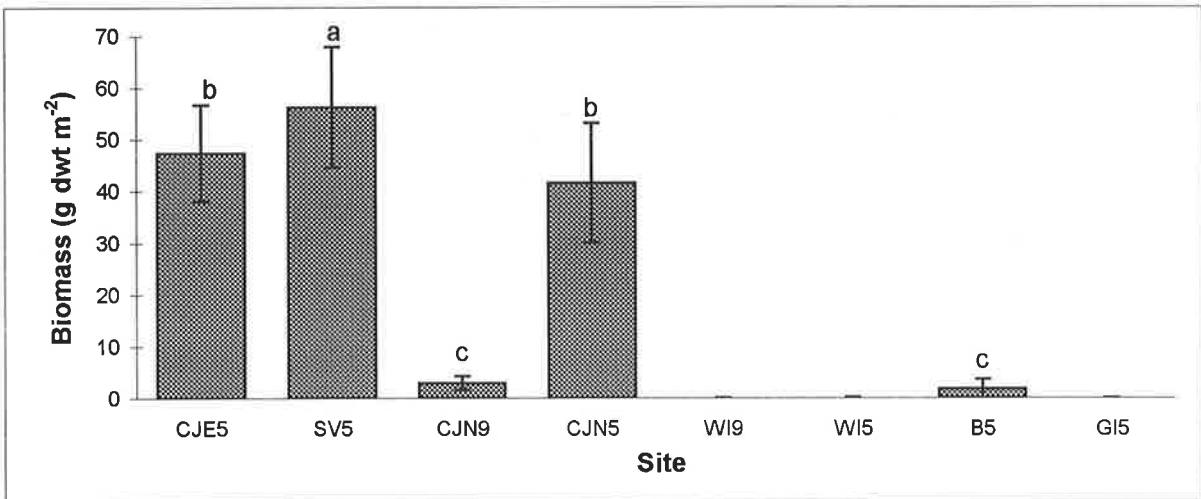


Fig. 4.9a Average Individual Plant Weight of *Ecklonia radiata* at each site. Error bars represent ± 1 standard error. Sites sharing a letter are not significantly different ($p < .05$; Tukey test after ANOVA on fourth root transformed data). Average individual plant weight was calculated by dividing biomass by the abundance for each quadrat and treating this as a replicate. Replicate number is printed in the relevant column in brackets.

The largest (by weight) *Ecklonia* plants were found at the oceanic sites, particularly WI9. *Ecklonia* plants were clearly larger than all other species, with an average plant weight of $\approx 130 \text{ g dwt m}^{-2}$ at WI9.

Fig. 4.9b Average Individual Plant Weight of *Scytothalia dorycarpa* at each site. Presentation and analysis are the same as described for Fig 4.9a.

Individual plant weight of *Scytothalia* increased with increasing wave force to be maximal at GI5.

Fig. 4.9c Average Individual Plant Weight of *Seirococcus axillaris* at each site. Presentation and analysis are the same as described for Fig 4.9a.

Maximum plant size occurred at CJE5, CJN5 and B5. There was no apparent relationship to wave force of the site.

Fig. 4.9d Average Individual Plant Weight of *Acrocarpia paniculata* at each site. Presentation and analysis are the same as described for Fig 4.9a.

Individuals of this species differed little between sites in terms of average weight.

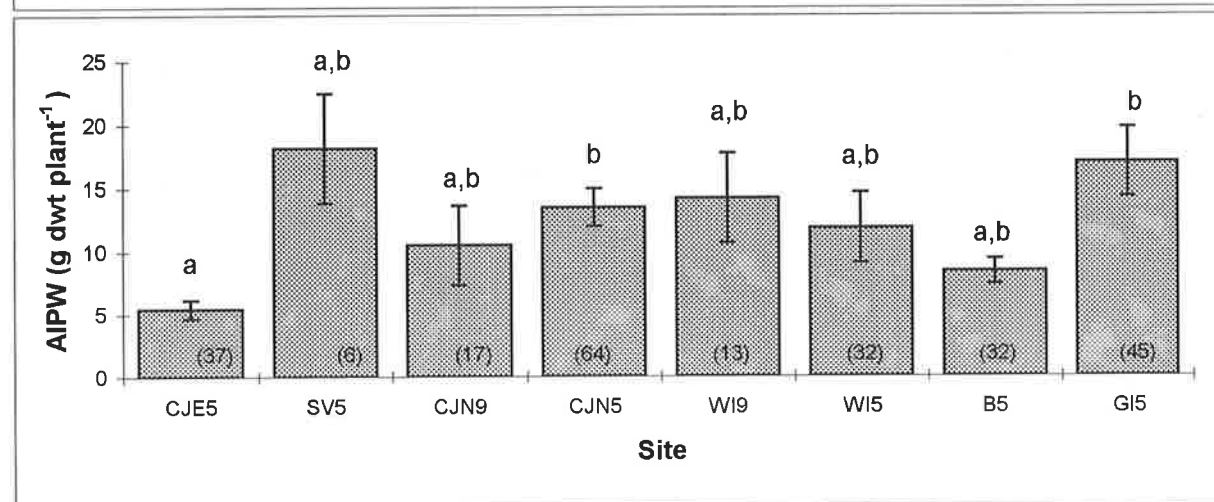
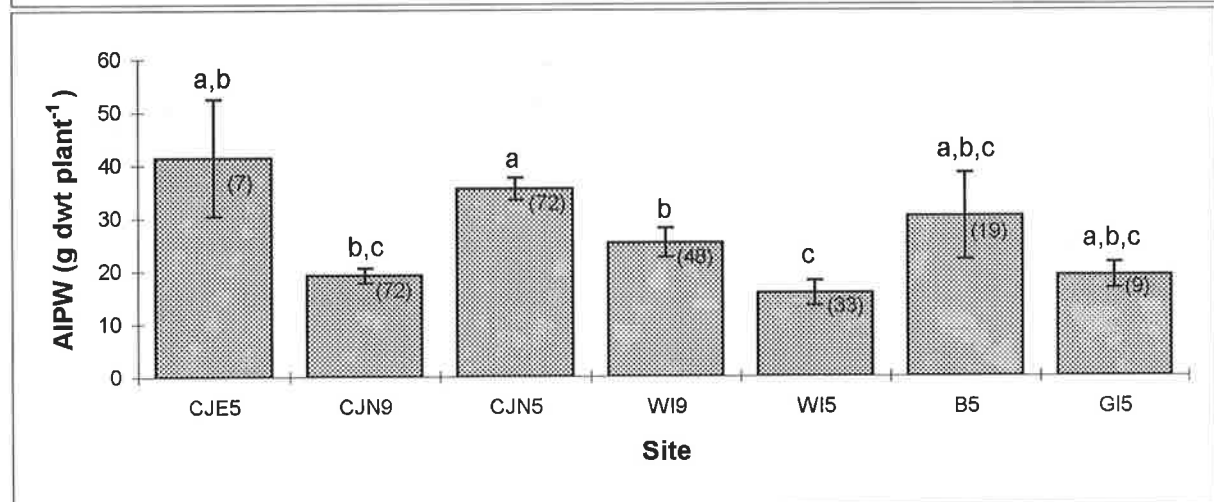
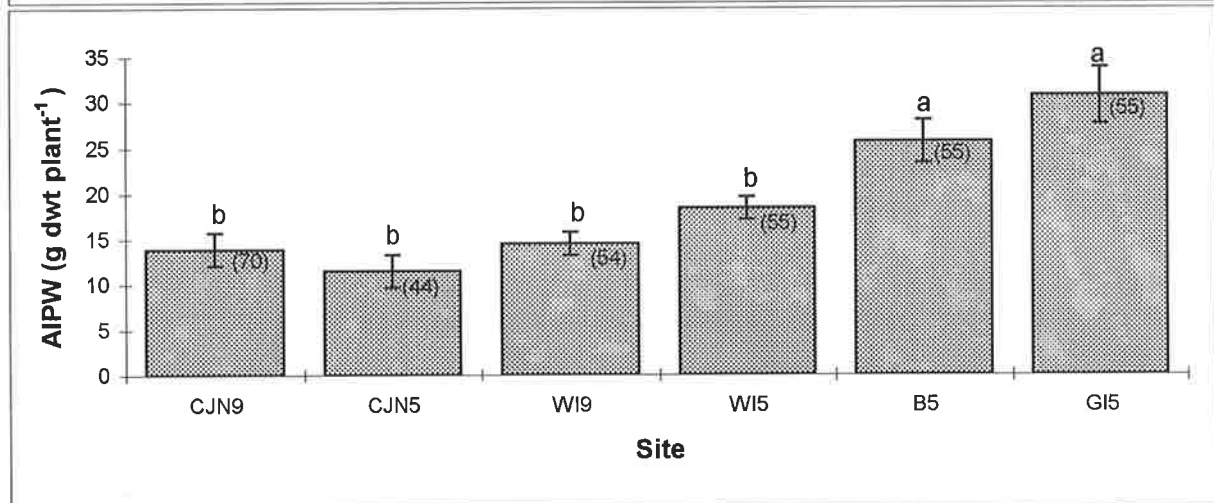
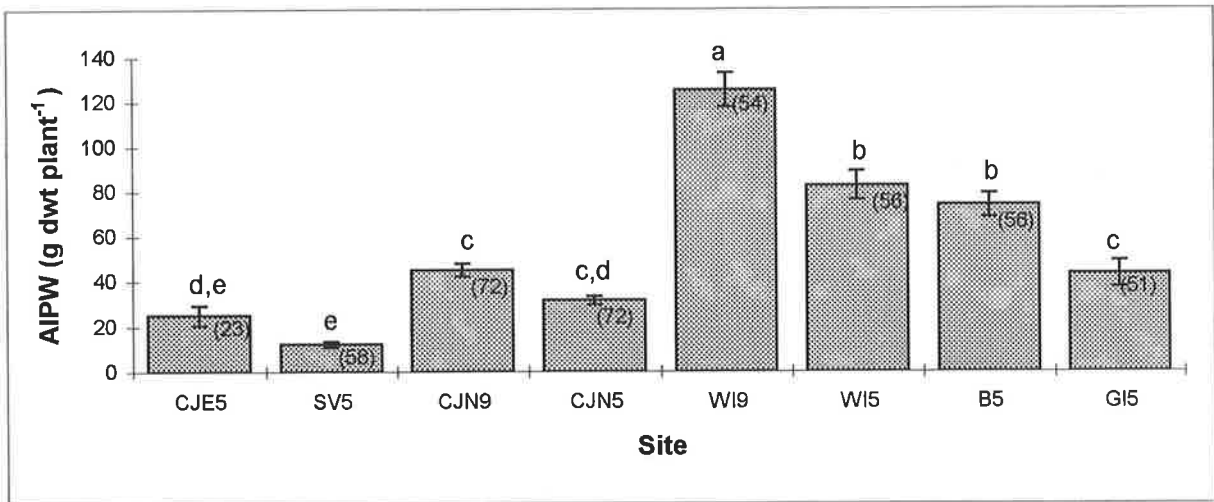


Fig. 4.9e Average Individual Plant Weight of *Cystophora brownii* at each site.

Presentation and analysis are the same as described for Fig 4.9a.

Cystophora brownii did not differ significantly among sites in terms of average individual plant weight ($p > .05$, ANOVA).

Fig. 4.9f Average Individual Plant Weight of *Cystophora expansa* at each site.

Presentation and analysis are the same as described for Fig 4.9a.

While CJN9 appeared to support smaller plants, this was based on only ten replicates. The other gulf sites supported plants of approximately the same size.

Fig. 4.9g Average Individual Plant Weight of *Cystophora monilifera* at each site.

Presentation and analysis are the same as described for Fig 4.9a.

Cystophora monilifera did not differ significantly among sites in terms of average individual plant weight ($p > .05$, ANOVA).

Fig. 4.9h Average Individual Plant Weight of *Cystophora moniliformis* at each site.

Presentation and analysis are the same as described for Fig 4.9a.

AIPW of this species did not vary in a manner consistent with the level of water movement. Few significant differences existed because of the high variance associated with this measure.

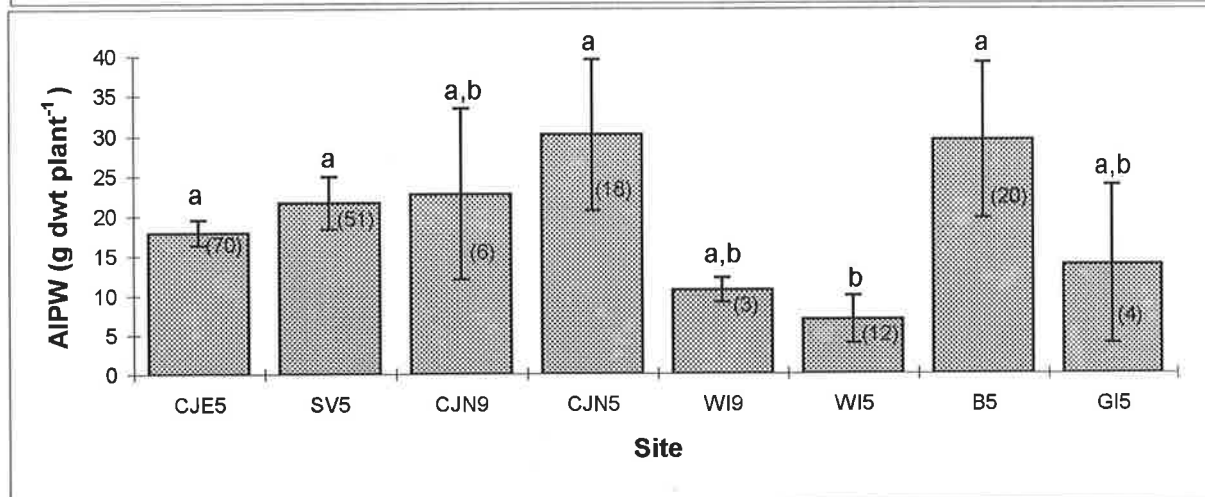
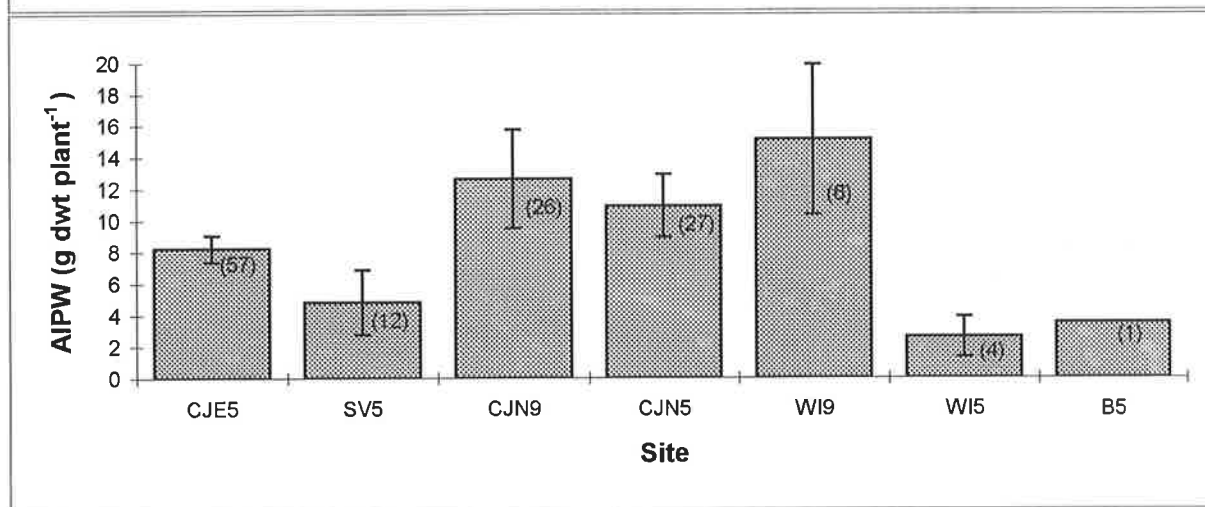
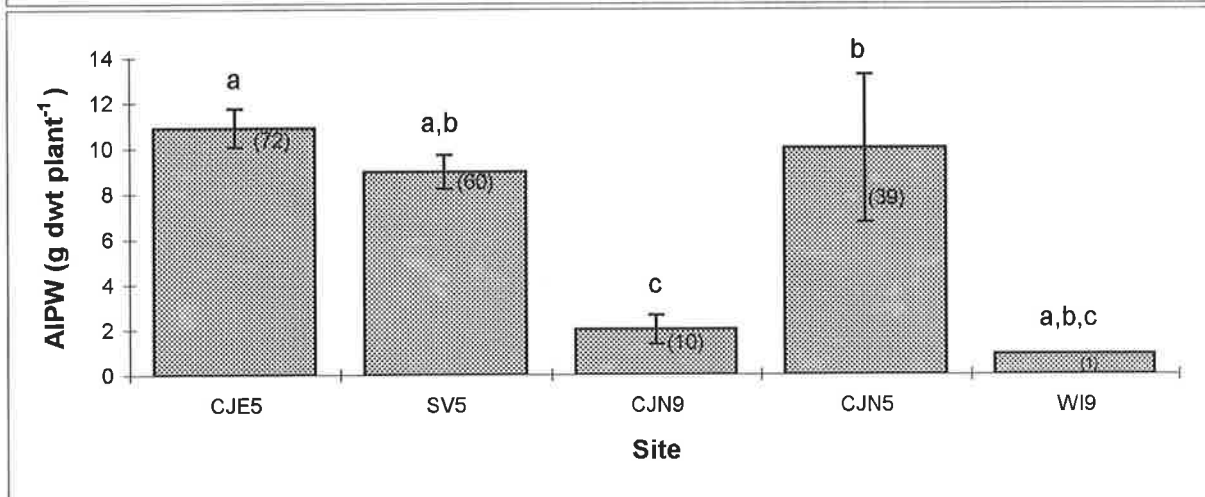
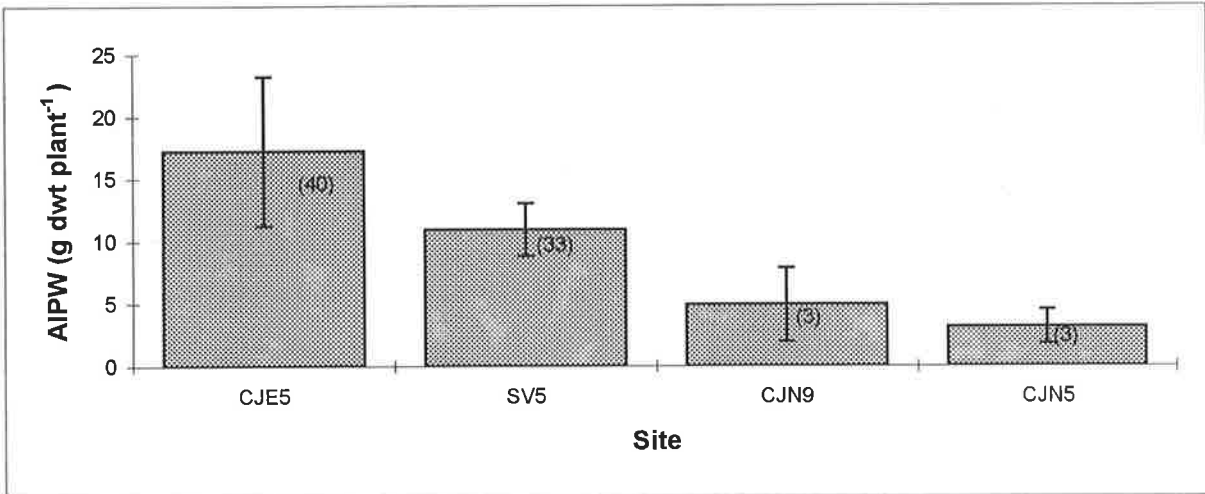


Fig. 4.9i Average Individual Plant Weight of *Cystophora subfarcinata* at each site.
Presentation and analysis are the same as described for Fig 4.9a.

High variance and low replicate numbers at some sites made significant differences rare. While W15, B5 and G15 appeared to support smaller plants, there really are too few replicates to make this conclusion.

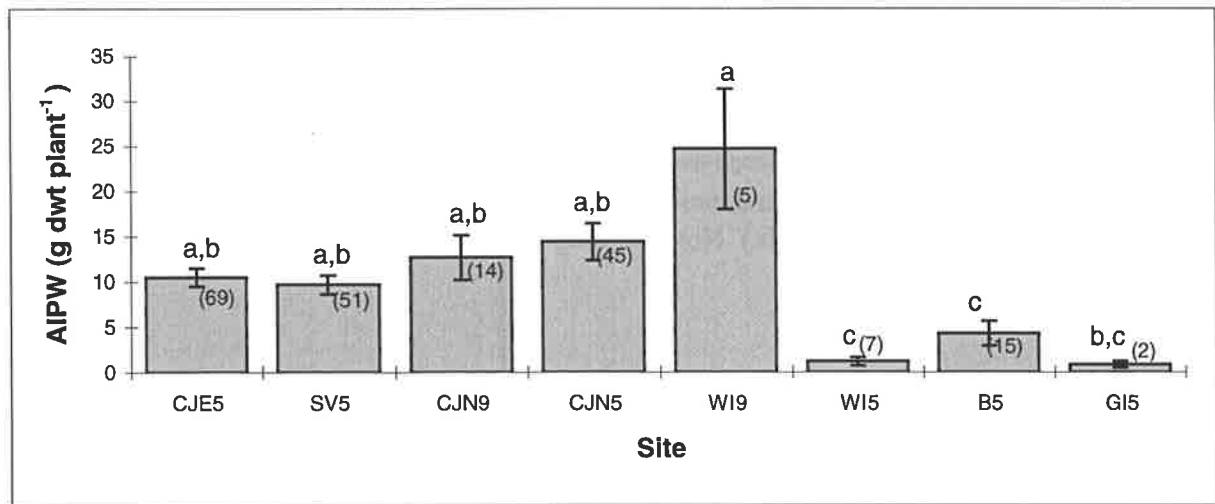


Fig. 4.10a Example of a typical size (weight) - frequency histogram.

This example represents the situation demonstrated for most species at most sites. (This example is actually *Ecklonia* at CJN5.) Note the preponderance of individuals in the smaller weight classes.

Fig. 4.10b Size (weight) - frequency histogram for *Ecklonia radiata* at GI5.

The size - frequency histogram for *Ecklonia* at GI5 was the only one not to demonstrate a preponderance of juveniles (<5g dwt). Rather, there was a more even spread across the weight classes.

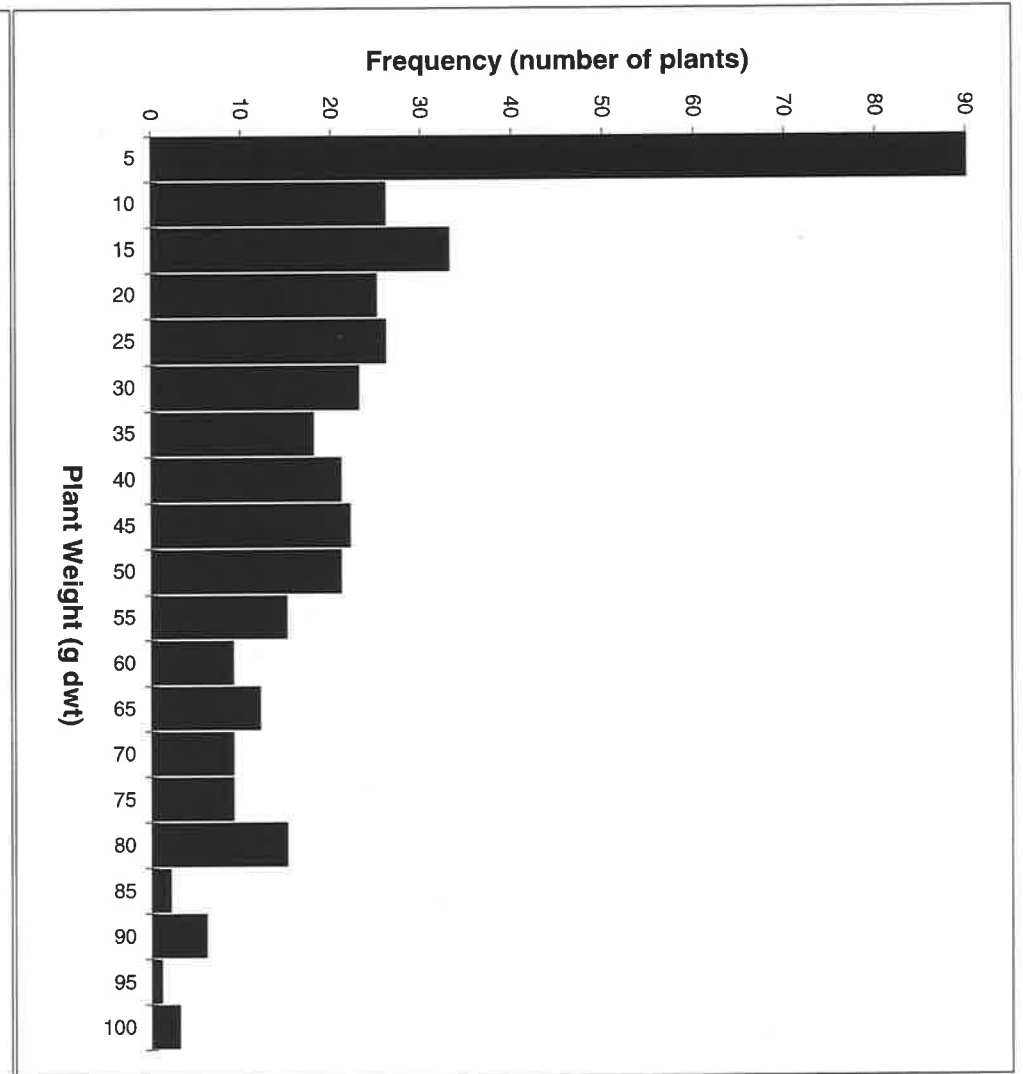
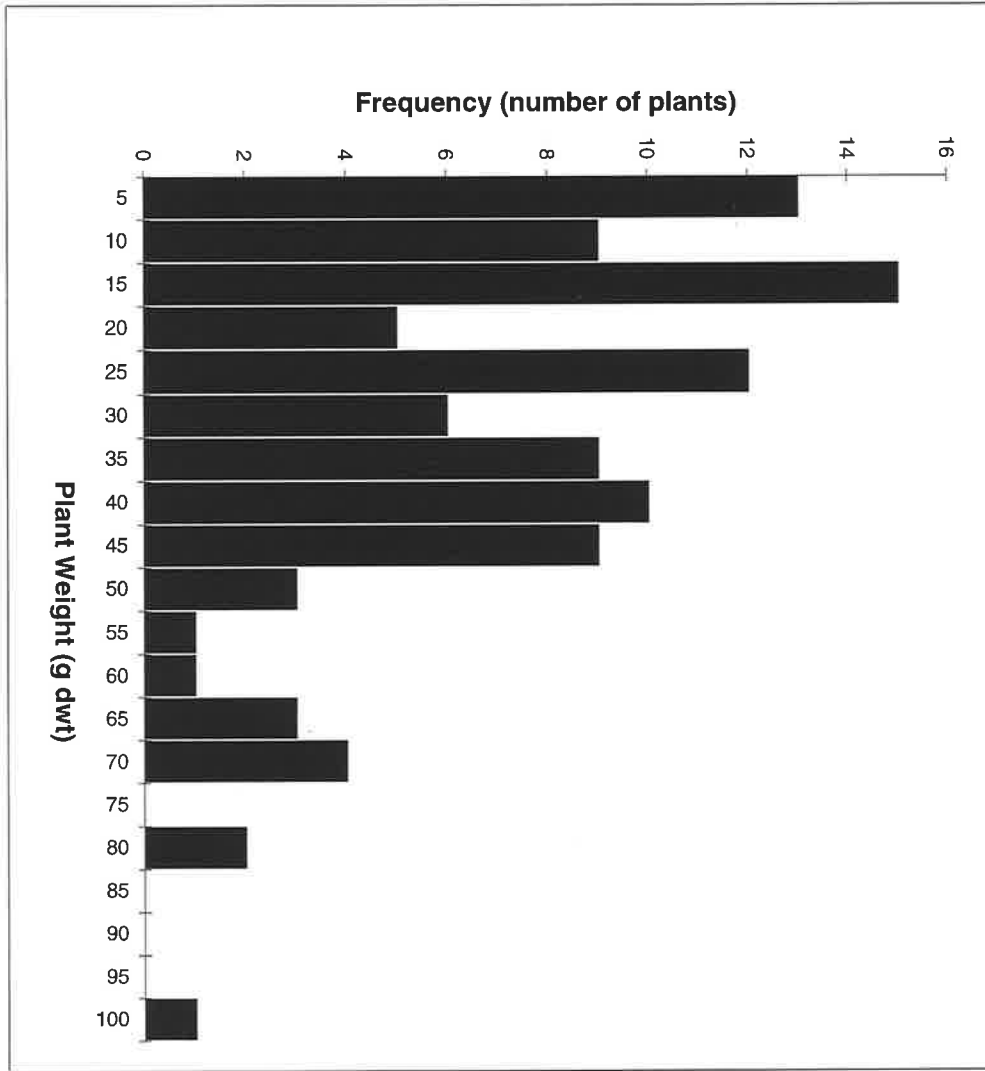


Fig 4.11 Summary of species response to site. The biomass of each species is represented by the level of the line. The lack of a line indicates that that particular species does not occur at the site; a dashed line indicates biomass of between .1 and 10g dwt m⁻²; a solid line represents biomass between 10g dwt m⁻² and 100g dwt m⁻²; a thick line indicates biomass above 100g dwt m⁻².

A replacement sequence can be proposed along the wave force gradient with *Acrocarpia* at the high energy extreme, along with *Scytothalia* and to a lesser extent *Ecklonia*. *Seirococcus* preferred intermediate habitats, and *Sargassum* and *Cystophora* species were best represented at the lower wave force end of spectrum.

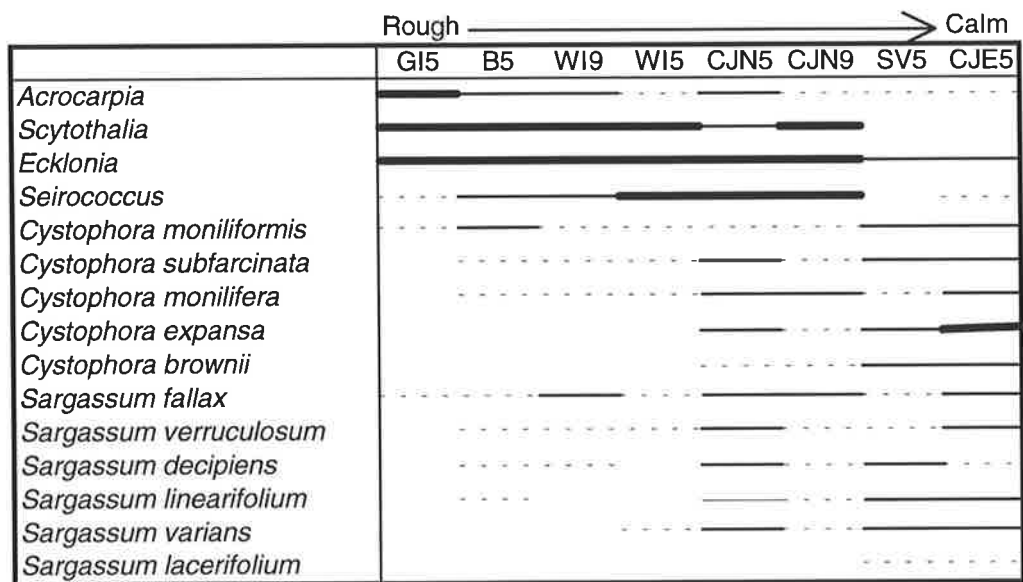


Fig. 4.12a Relationship between total biomass of samples and canopy richness. Each point represents a single sample (solid circle represents a sample with *Ecklonia* contributing >66% of biomass; a grey circle represents *Ecklonia* contribution between 33% and 66%; hollow circles represent samples with <33% contributed by *Ecklonia*). A boundary condition is evident (represented by the red line) below which any combination of biomass and richness can occur. There are very few outliers beyond this boundary.

Canopy richness was restricted in both high and low total biomass samples. Note the rarity of *Ecklonia* dominated quadrats (black circles) at high levels of species richness.

Fig. 4.12b Relationship between *Ecklonia* biomass and canopy richness. Layout as for above figure.

Low levels of *Ecklonia* did not seem to be associated with a restriction of canopy richness, but as biomass increases beyond $\approx 750 \text{ g dwt m}^{-2}$ species richness declined until approximately $2000 \text{ g dwt m}^{-2}$. Beyond this level, species richness was maintained below a uniformly low boundary.

Fig. 4.12c Relationship between furoid biomass and canopy richness. Layout as for above figure.

Both high and low levels of furoid biomass were associated with a restriction in canopy richness.

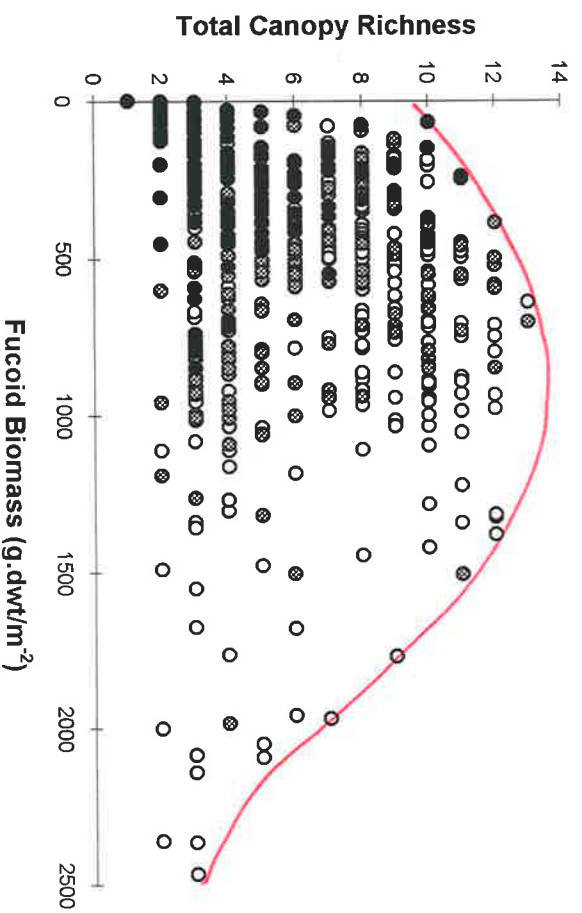
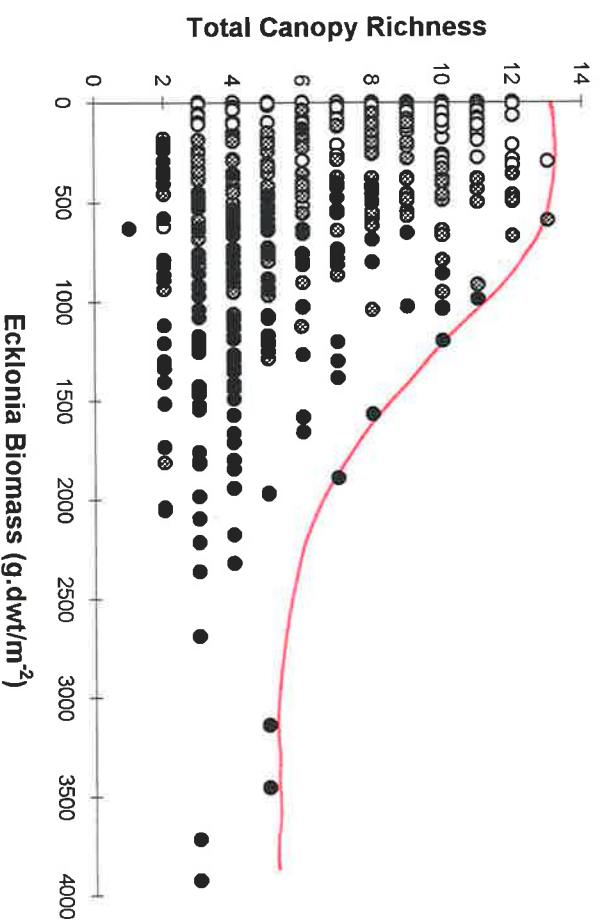
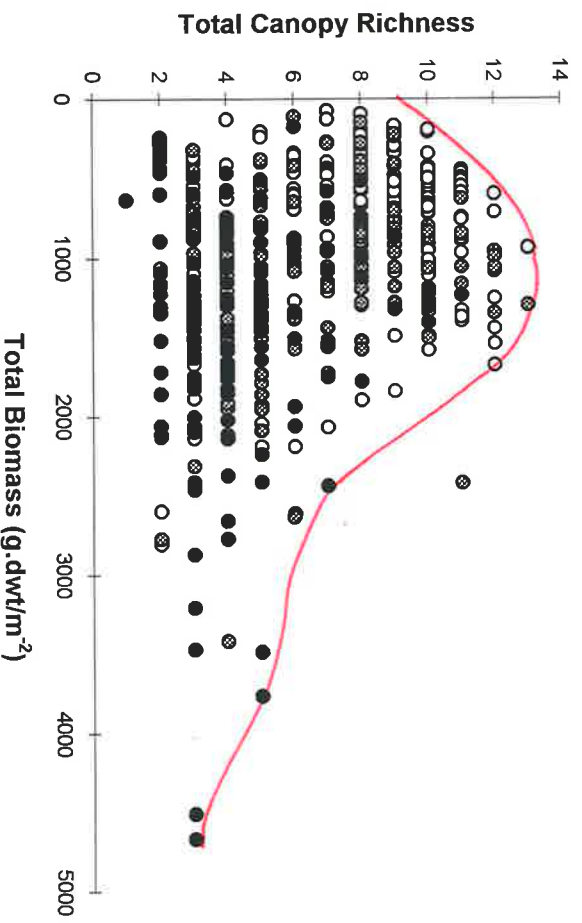


Fig. 4.12d Relationship between total biomass of samples and understorey richness.

Layout as for Figure 4.12a. Two outliers exist beyond the boundary, but generally, increasing biomass of samples appears to be associated with a decrease in understorey richness. Like canopy richness, understorey richness is maximal in those samples not dominated by *Ecklonia* (ie the hollow and grey circles).

Fig. 4.12e Relationship between *Ecklonia* biomass of samples and understorey richness.

Layout as for Figure 4.12a. A decrease in potential understorey richness is evident even at very low levels of *Ecklonia*.

Fig. 4.12f Relationship between furoid biomass of samples and understorey richness.

Layout as for Figure 4.12a. Unlike the relationship with *Ecklonia* biomass, furoid biomass must exceed $\approx 1000\text{g dwt m}^{-2}$ before increases are associated with a decrease in understorey richness. However, there were insufficient samples of high species richness to support the concept of an intermediate maximum.

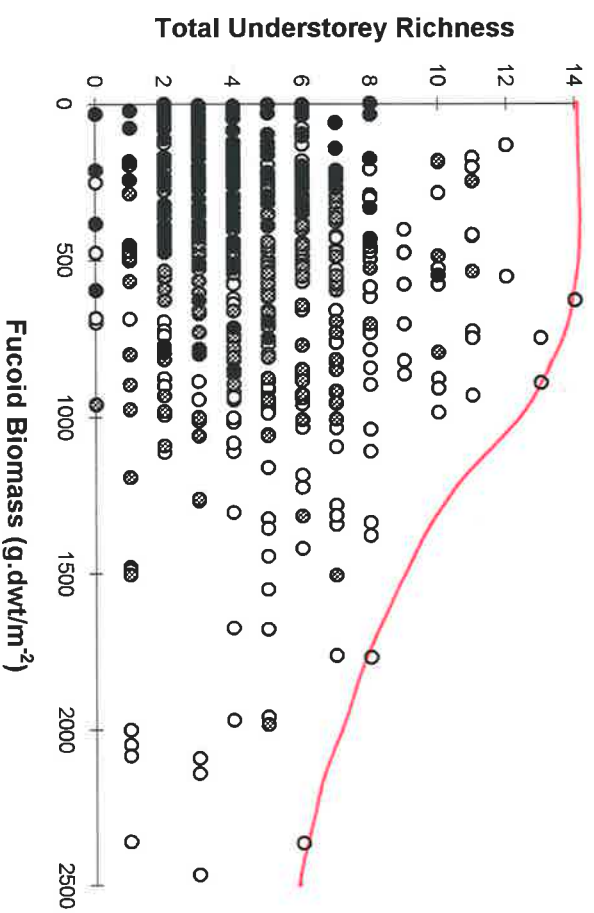
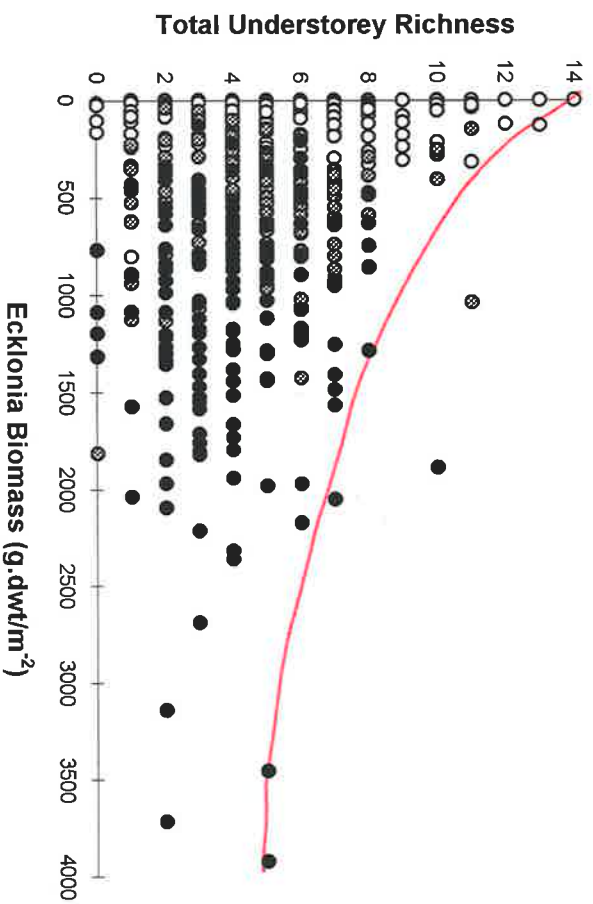
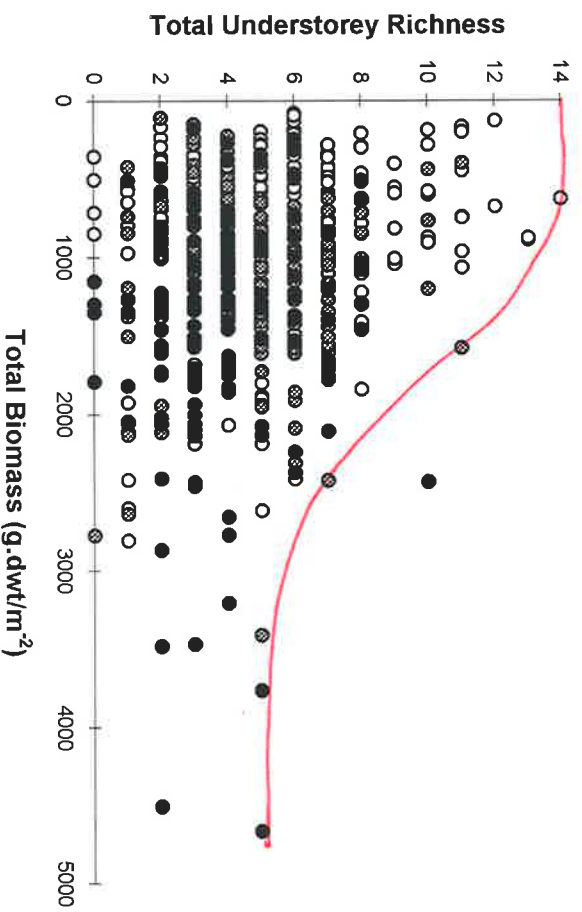


Fig. 4.13a Relationship between average plant weight and density (all sites). Plotting the average plant weight and abundance of each sample on a log- log graph allows assessment of the relationship in light of the 3/2 thinning law. Shading of circles represents the proportion of *Ecklonia* and is the same as in Figure 4.12a. The black line represents the -3/2 thinning line when $\log K = 4.3$ and is therefore described by the equation;

$$\log \text{average plant weight} = 4.3 - 1.5 \log \text{abundance}$$

Some points (mainly those dominated by *Ecklonia*) clearly breach this condition.

Fig. 4.13b Relationship between average plant weight and density (CJN5 only). Layout is as described in Figure 4.13a. Additionally, a line is plotted showing the hypothesised thinning boundary (in green).

While one sample exceeded this hypothesised boundary, this is thought to be due to the patchy nature of the community resulting in odd samples being edge affected and therefore not quite complying with the boundary. The hypothesised line, based on the bulk of the samples, demonstrated a slope of $\approx -3/2$ and $\log K$ value of ≈ 4.2 .

Fig. 4.13c Relationship between average plant weight and density (SV5 only). Layout is as described in Figure 4.13b.

Self thinning was not detectable at this site.

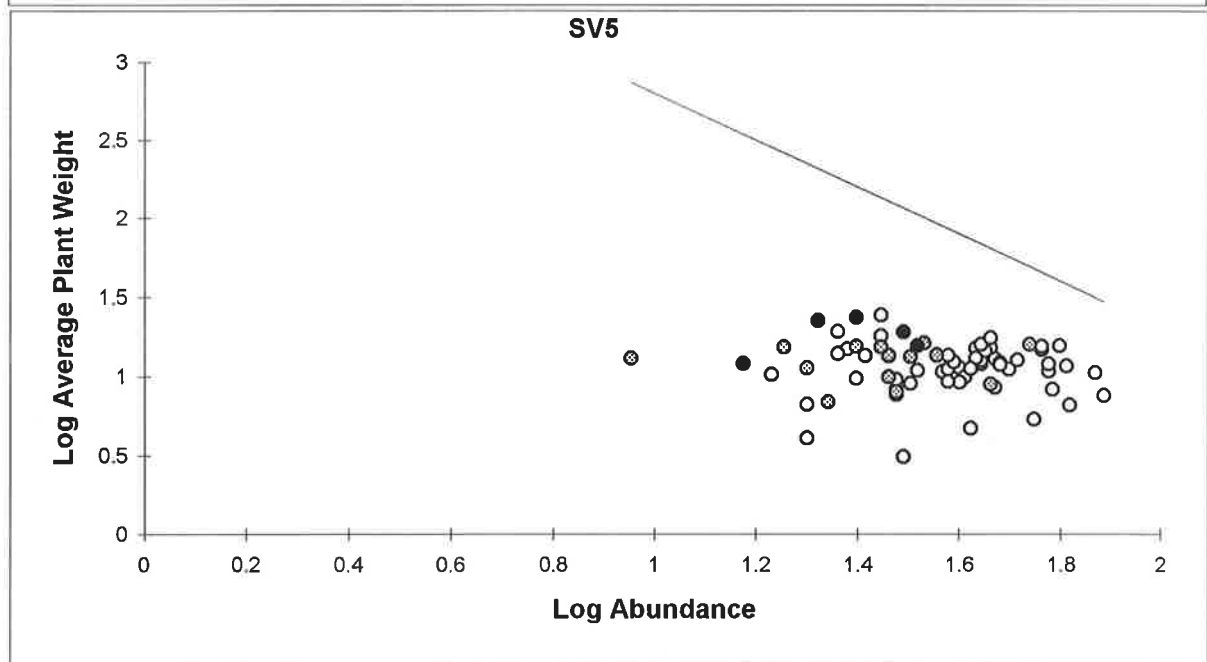
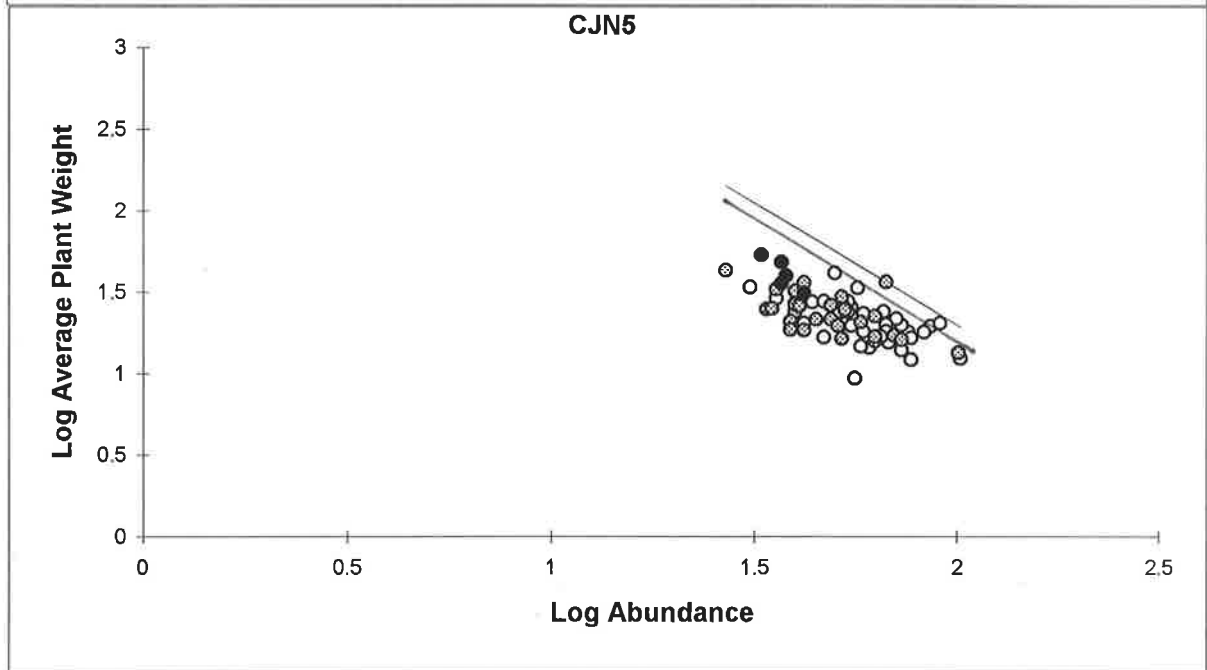
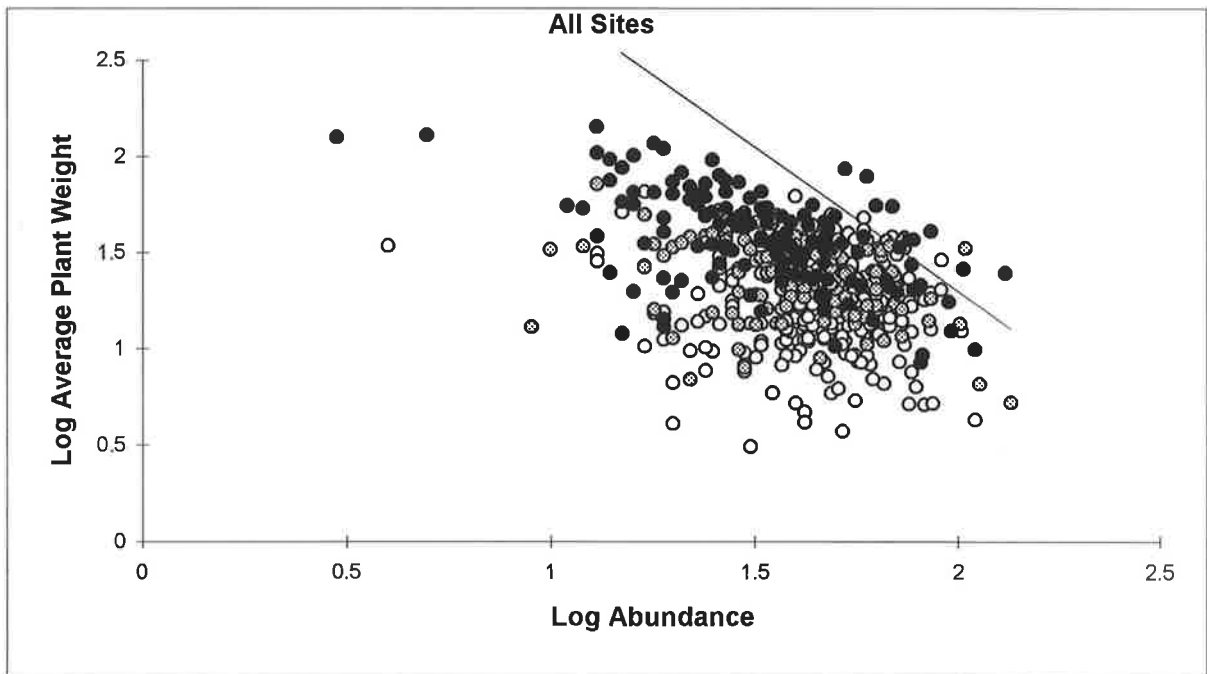


Fig. 4.13d Relationship between average plant weight and density (CJN9 only). Layout is as described in Figure 4.13b.

A thinning line was apparent (green line) which was parallel to, but lower than the boundary condition described when $\log K = 4.3$ (black line). This line appeared to have an intercept ($\log K$ value) of ≈ 4.2 .

Fig. 4.13e Relationship between average plant weight and density (CJE5 only). Layout is as described in Figure 4.13b.

A thinning line was apparent with $-3/2$ slope, but appeared to demonstrate thinning at quite low levels (green line). A $\log K$ value of approximately 3.8 appeared to be indicated.

Fig. 4.13f Relationship between average plant weight and density (GI5 only). Layout is as described in Figure 4.13b.

A thinning line with $\log K$ of approximately 4.2 was apparent (green line). The slope was approximately $-3/2$.

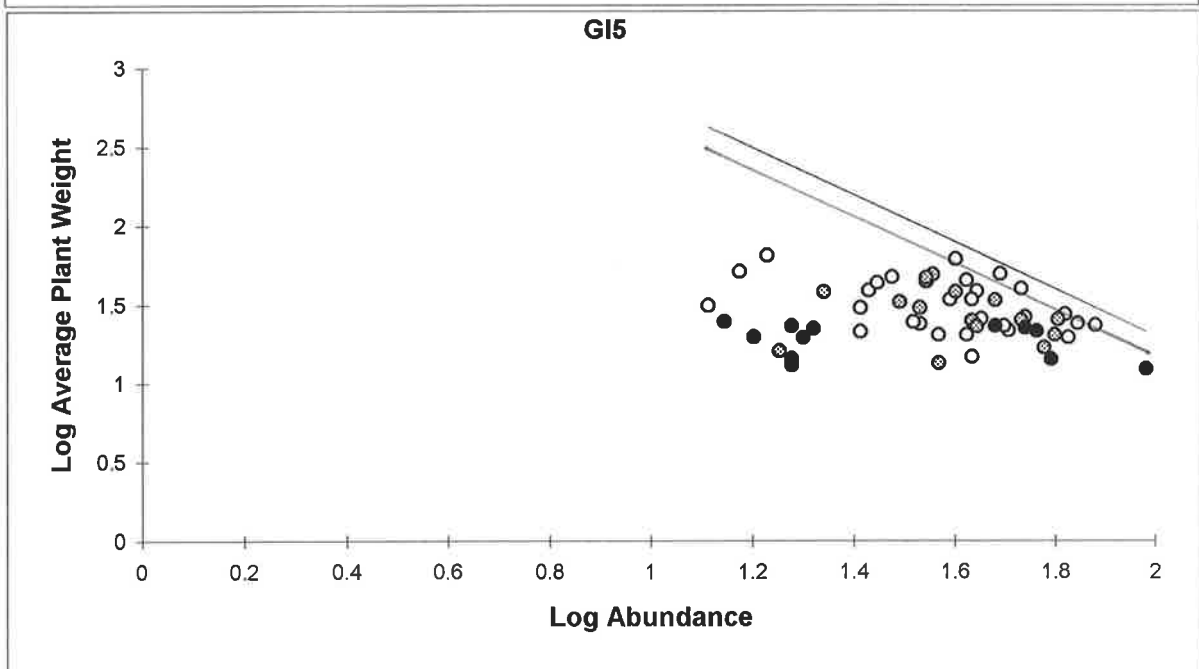
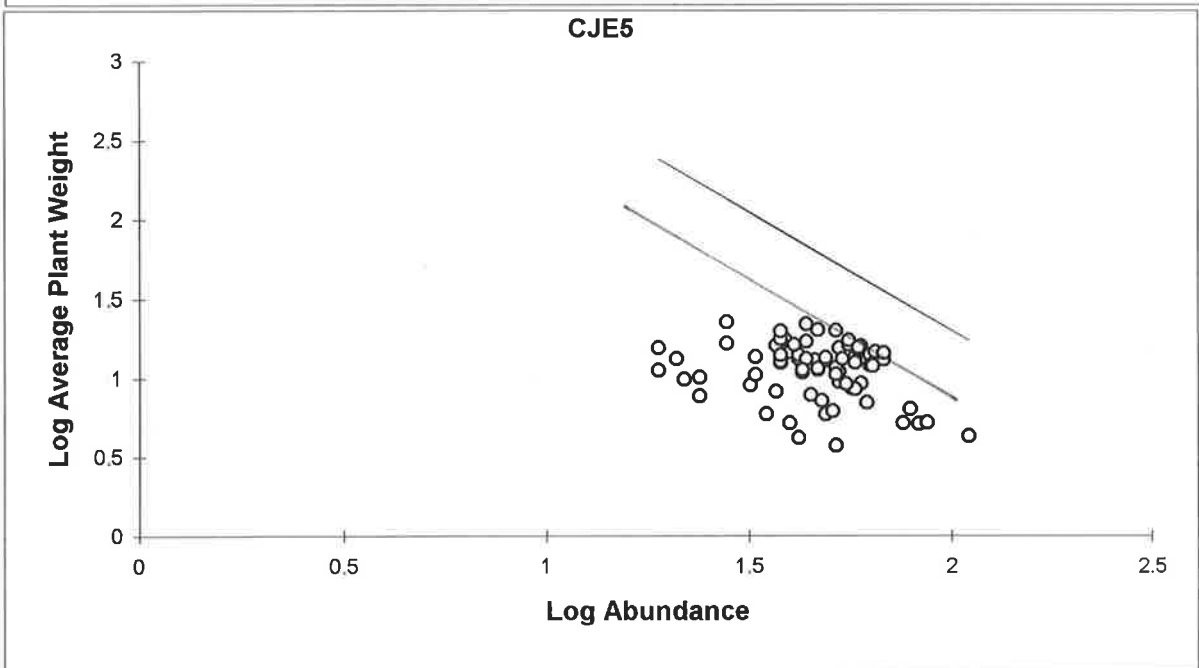
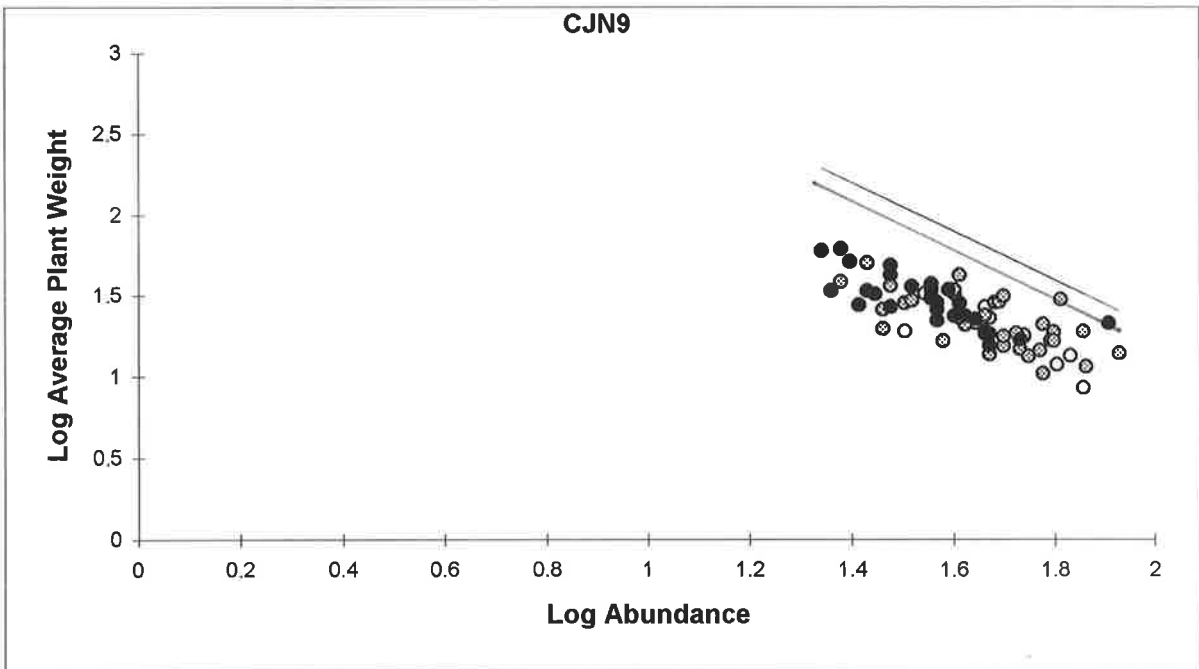


Fig. 4.13g Relationship between average plant weight and density (B5 only). Layout is as described in Figure 4.13b.

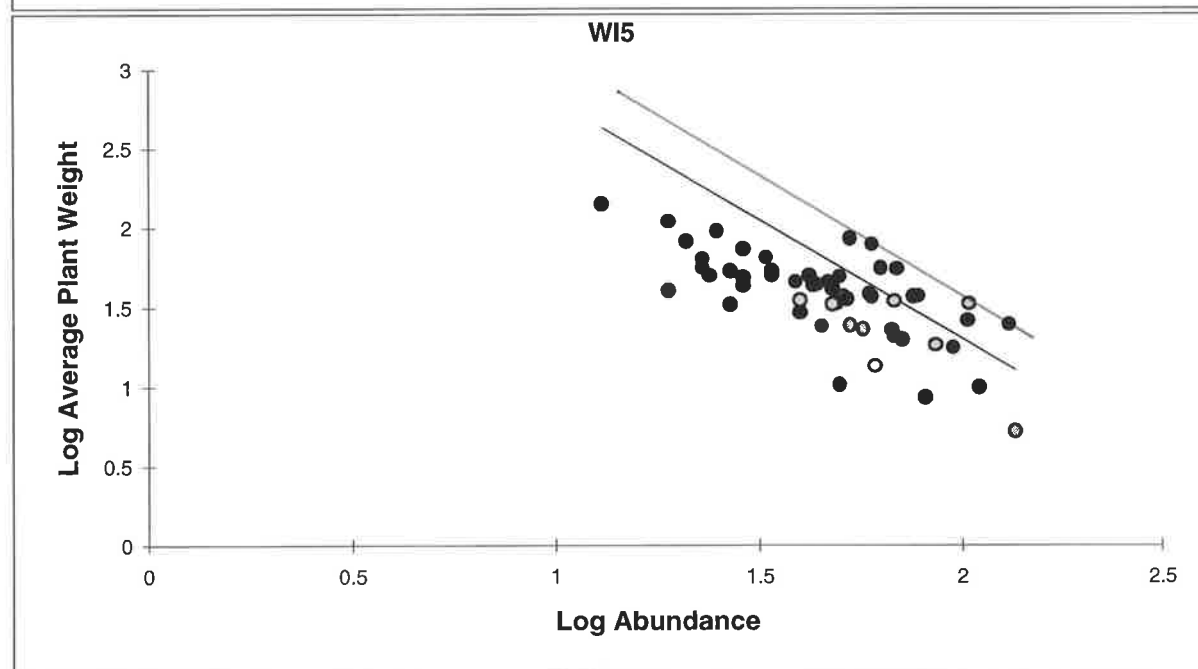
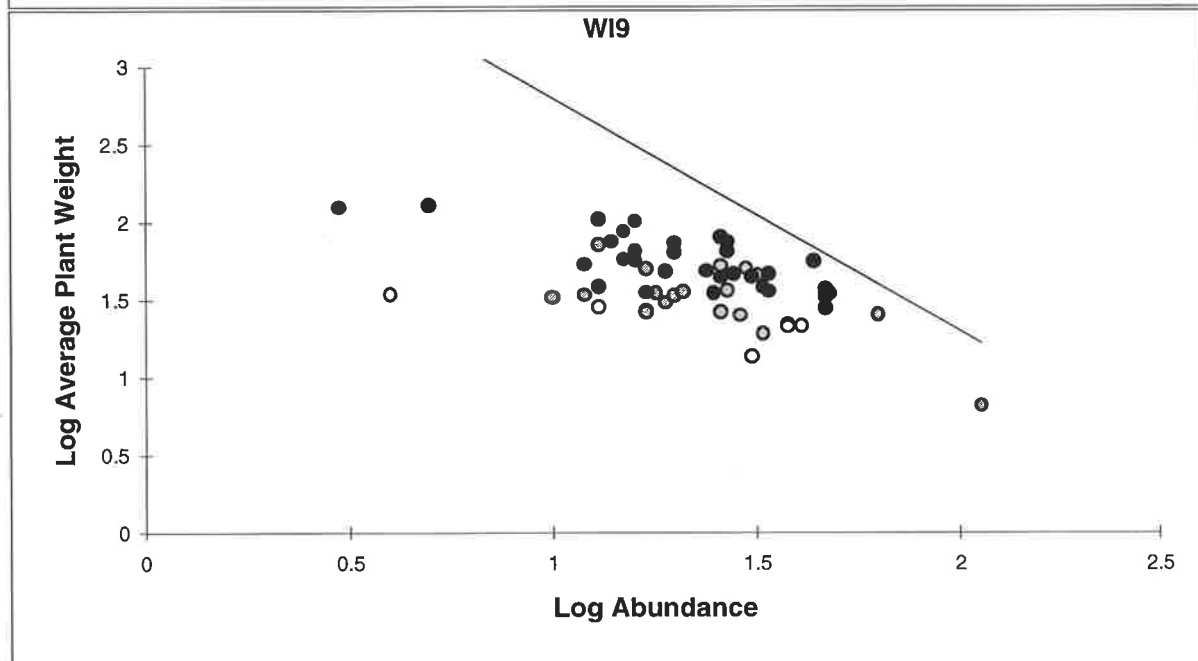
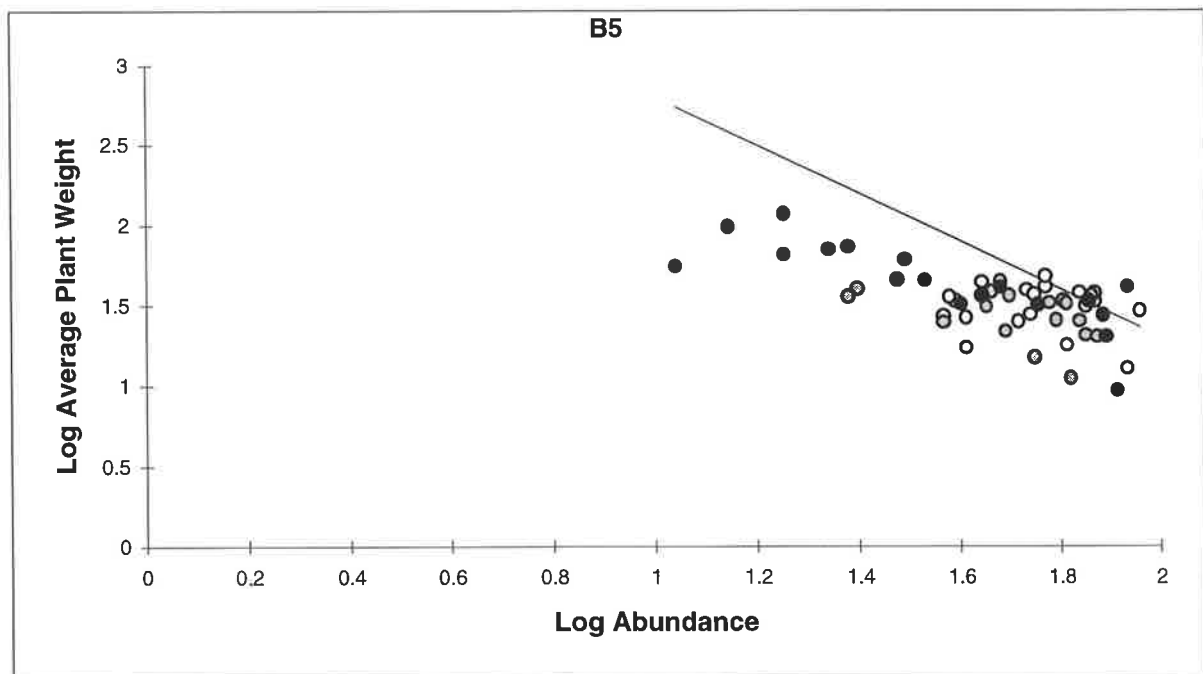
Despite the fact that samples of B5 breached the $-3/2$ thinning law defined when $\log K$ is 4.3, samples at this site displayed no evidence of self thinning.

Fig. 4.13h Relationship between average plant weight and density (WI9 only). Layout is as described in Figure 4.13b.

No samples breached the $-3/2$ thinning line defined when $\log K$ is 4.3, and self thinning was not evident.

Fig. 4.13i Relationship between average plant weight and density (WI5 only). Layout is as described for Figure 4.13b.

WI5 supported several samples which breach the $-3/2$ thinning line defined when $\log K = 4.3$. A thinning line was evident with a slope of $-3/2$, but a considerably higher carrying capacity was indicated than the other sites, with a $\log K$ value of ≈ 4.6 (green line).



Chapter 5

Table 5.1 Composition of initial communities used in simulation model. This table displays the composition of each of the communities used in the simulation model. The values represent the average biomass (g dwt m⁻²) for each site across all temporal collections. These compositions were then manipulated to represent seasonal change.

	CJN5	SV5	CJN9	CJE5	GI5	B5	WI9	WI5
<i>Acrocarpia paniculata</i>	58.4	2.0	4.1	7.1	144.9	45.8	6.1	31.0
<i>Cystophora brownii</i>	0.1	16.6	2.4	15.0	0.0	0.0	0.0	0.0
<i>C. expansa</i>	35.4	92.1	0.8	198.0	0.0	0.0	0.0	0.0
<i>C. monilifera</i>	9.9	1.2	10.2	40.2	0.0	0.3	3.5	0.4
<i>C. moniliformis</i>	8.6	37.8	2.4	93.8	1.1	23.7	1.1	6.2
<i>C. subfarcinata</i>	32.6	93.1	5.8	49.0	0.1	6.7	3.0	1.1
<i>Ecklonia radiata</i>	420.6	88.3	628.2	11.8	338.9	822.3	751.2	1438.2
<i>Sargassum decipiens</i>	18.3	20.6	4.9	6.7	0.0	0.5	0.0	0.1
<i>S. fallax</i>	70.0	9.0	34.8	18.0	0.6	8.5	3.9	12.2
<i>S. linearifolium</i>	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0
<i>S. lacerifolium</i>	41.5	56.2	2.9	47.4	0.0	1.7	0.0	0.1
<i>S. varians</i>	21.8	39.8	0.4	43.3	0.0	0.0	0.1	0.0
<i>S. verruculosum</i>	10.8	0.3	0.7	28.4	0.0	1.1	1.9	0.7
<i>Scytothalia dorycarpa</i>	41.8	0.0	167.6	0.0	634.7	726.7	161.6	365.4
<i>Seirococcus axillaris</i>	459.5	0.0	185.8	5.4	6.7	34.2	102.8	36.2

Fig. 5.1 The fluctuations simulated for each species. Each of the initial communities detailed in table 5.1 was manipulated in an identical manner to represent seasonal change. This change involved a loss of 75% biomass in one season and then a linear increase to build up the same amount of biomass on a 12 month cycle. However, the seasonal cycles for each species were not synchronous. *Acrocarpia*, *Scytothalia* and *Seirococcus* lost their biomass in the first season, the *Cystophora* species in the second and *Ecklonia* lost biomass in the third season. *Sargassum* species all lost their biomass in the final season.

(Note: This is not intended to represent the actual seasonal cycles of these taxa; it is simply for the purposes of a modelling exercise.)

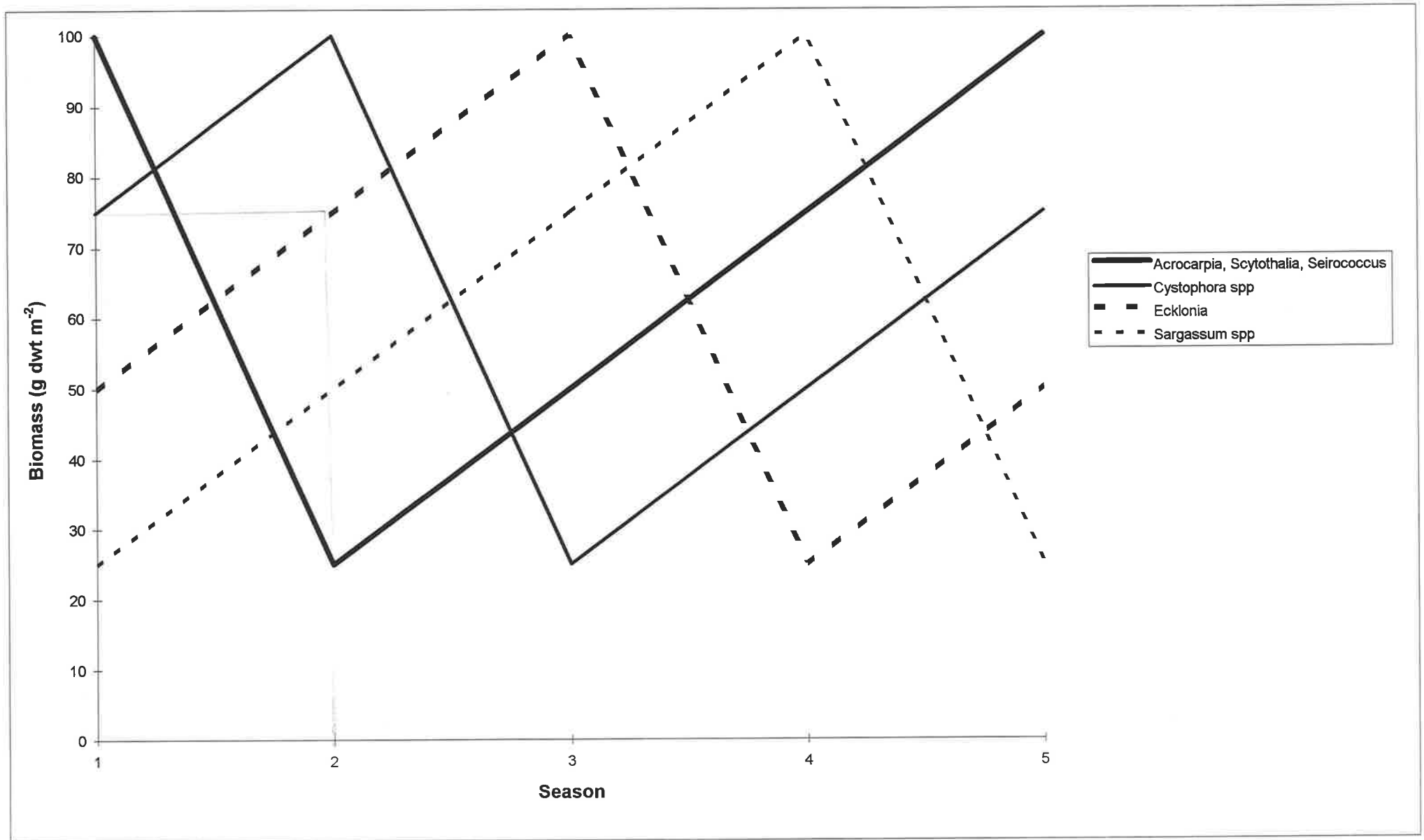


Fig. 5.2 Trajectories representing simulated seasonal change in simulated community. Ordination of the simulated communities across the course of a year. The first digit represents the site, and the second the season;

Site (first digit)

- 1 CJN5
- 2 SV5
- 3 CJN9
- 4 CJE5
- 5 GI5
- 6 B5
- 7 WI9
- 8 WI5

Some trajectories representing temporal change are illustrated using coloured arrows. Note that the simulation was carried on for two years, although it appears that only 4 seasons are plotted; in each case, the same season in different years overlies each other. For instance, the point marked "41" also represents "45" - they are identical. Stress = 0.18

The trajectories, although representing the same changes at each site, do not necessarily appear consistent on the ordination. For example, the green arrows represent the same change at SV5 and CJN5. They differ in length, but not direction. The blue arrows represent the changes from seasons 4 to 5 at B5 and WI5. Here, the length is similar, but the direction very different. The red arrows denote the changes from season 1 to 2 at CJE5 and GI5. They differ in both direction and length. Many such inconsistencies are to be found amongst the trajectories. The change from season 1 to 2 at CJN9 and WI9 is indicated by a black arrow. These are quite similar, but are they similar enough to be considered the same? This highlights the lack of any objective method of comparison - are these trajectories similar or not?

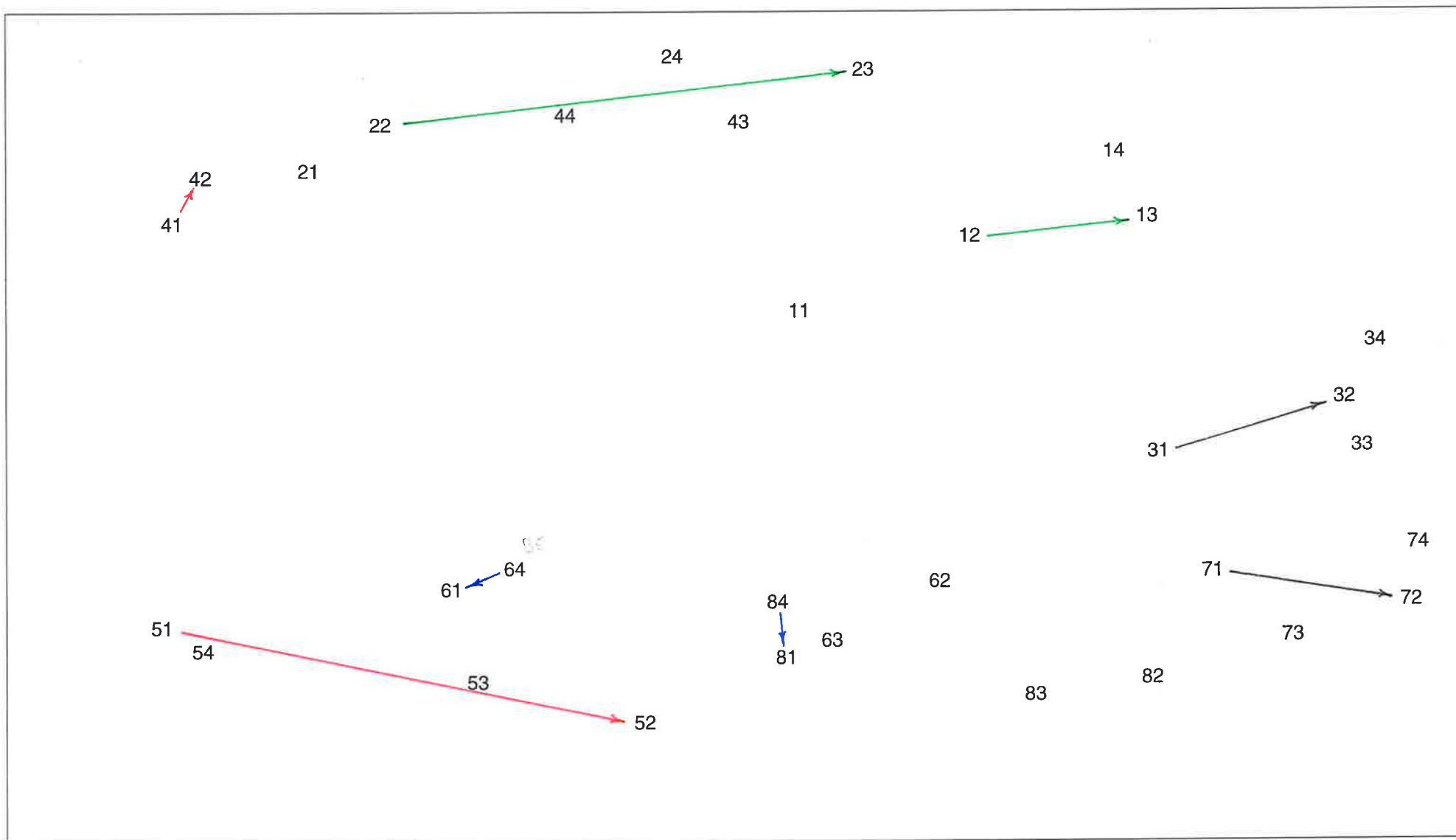


Fig 5.3 Ordination of the changes demonstrated by the sites. This NMDS ordination demonstrates the relationships of the changes directly, rather than inferring them from the trajectories between points. Labelling system is as used in Fig 4.2b - the first digit represents the site code, the second represents the change involved (eg "61" represents the change from season 1 to 2 at B5). As this represents a deterministic model, the second year is identical to the first. As a consequence, points representing the second year exactly overlie the same seasonal change of the previous year (eg 37 overlies 33; 66 overlies 62). Only the points representing the first year are shown, the corresponding point in the second year can be assumed to be at the same position. Envelopes represent the spread of the sites within each seasonal change. Stress = 0.15

It is obvious that each seasonal change is different, but any single change is similar across all sites. Points representing a single season do display some variability, but the similarity is clear. The slight spread of these points is due to some species not being present at some sites and therefore being coded as missing data.

51
71 81
31 41
21

22
42
82 32 72
52

23
43
33 63
73
53

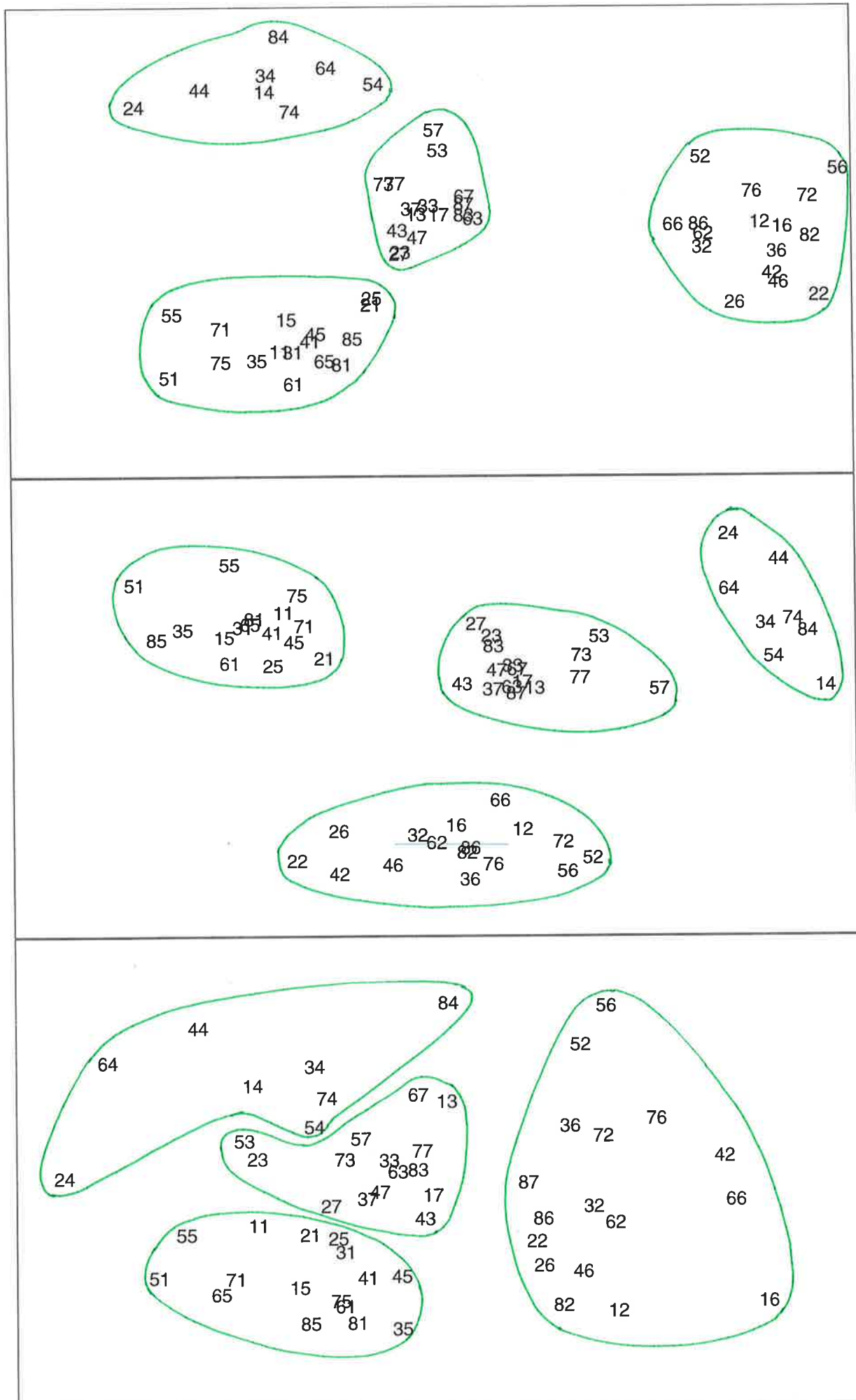
24 74 54
44 34
64

Fig 5.4a Ordination of change in community modelled with $\pm 20\%$ stochasm. This NMDS ordination of the changes, demonstrated by the same simulated community as Fig 5.3, differs only in that there was $\pm 20\%$ stochasm introduced to each species at each change. Note though, that the points representing changes in the second year no longer overlie the first year due to the drift in community structure resulting from the stochasm. Labels as for Fig 5.3. Stress = 0.14

Fig 5.4b Ordination of change in community modelled with $\pm 50\%$ stochasm. Stress = 0.15

Fig 5.4c Ordination of change in community modelled with $\pm 100\%$ stochasm. Stress = 0.24

In all cases it is clear that corresponding seasonal changes are similar across all sites, but there is a distinction between the different seasonal changes. As the level of stochasm is increased the ratio of within seasonal group variation to between seasonal group variation increases. However, the distinction between seasons and the similarity between sites is clear even when $\pm 100\%$ stochasm is introduced.



Chapter 6

Table 6.1 Summary of the relationship between biomass fluctuations and those of abundance and AIPW for each species at each site. The figure in each cell represents the percentage of the variance in biomass fluctuations which was attributable to the fluctuations in abundance. The remainder of the variation is attributable to variation in the average weight of the individual plants. The variance was calculated and partitioned according to multiple linear regression. Shading of the cell highlights the fact that abundance is responsible for less than half of the variation in biomass. Non shaded cells represent cases where abundance is responsible for more than half of the variation in biomass. A cell without a number indicates that there was not enough data to make a reasonable assessment.

Abundance was generally responsible for a greater proportion of the fluctuations in biomass at the oceanic sites than it was at the gulf sites. At the oceanic sites in 13 instances (of the 16 possible) abundance changes were responsible for more than half of the variation in the biomass data. In contrast, the gulf sites showed the importance of changes in AIPW. There, changes in abundance were responsible for more than half of the variation in biomass in only 7 (of 16) cases.

	<i>Ecklonia</i>	<i>Scytothalia</i>	<i>Seirococcus</i>	<i>Acrocarpia</i>	<i>Cystophora</i>	Overall
CJE5					6	7
SV5	100				88	61
CJN9	35	57	81		71	37
CJN5	0	55	43	1	7	31
WI9	94	93	92			90
WI5	23	51	84			35
B5	76	94		100		80
GI5	75	21		100		61

Fig. 6.1a Temporal fluctuations in total biomass. Upper graph displays gulf sites, lower displays oceanic sites. Error bars represent standard error (n=8). The red point represents the total biomass of the pilot study in spring 1991 at WI5. Replication was identical. Statistical analysis, however, did not include data from the pilot study.

With the exception of CJN9 ($p=.06$), all sites exhibit significant fluctuations. While the fluctuations appear seasonal, the sites are not all in phase.

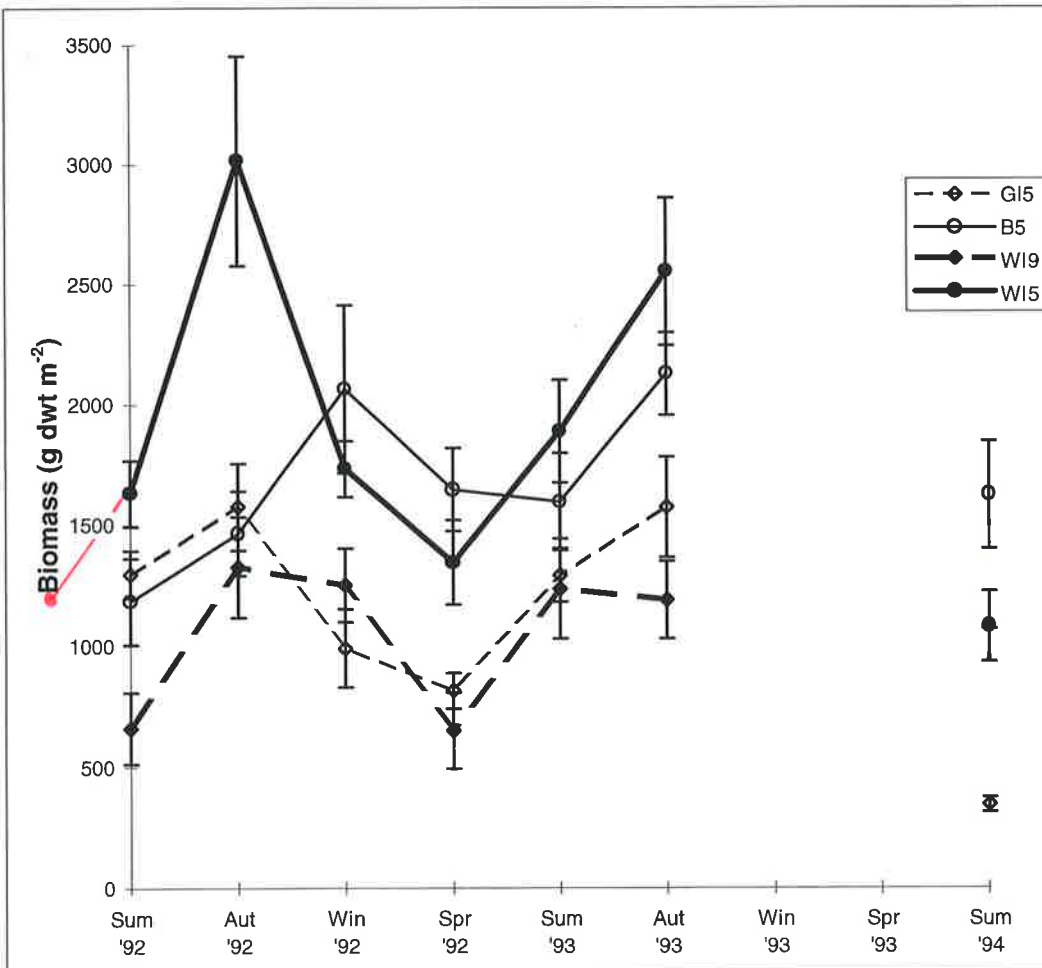
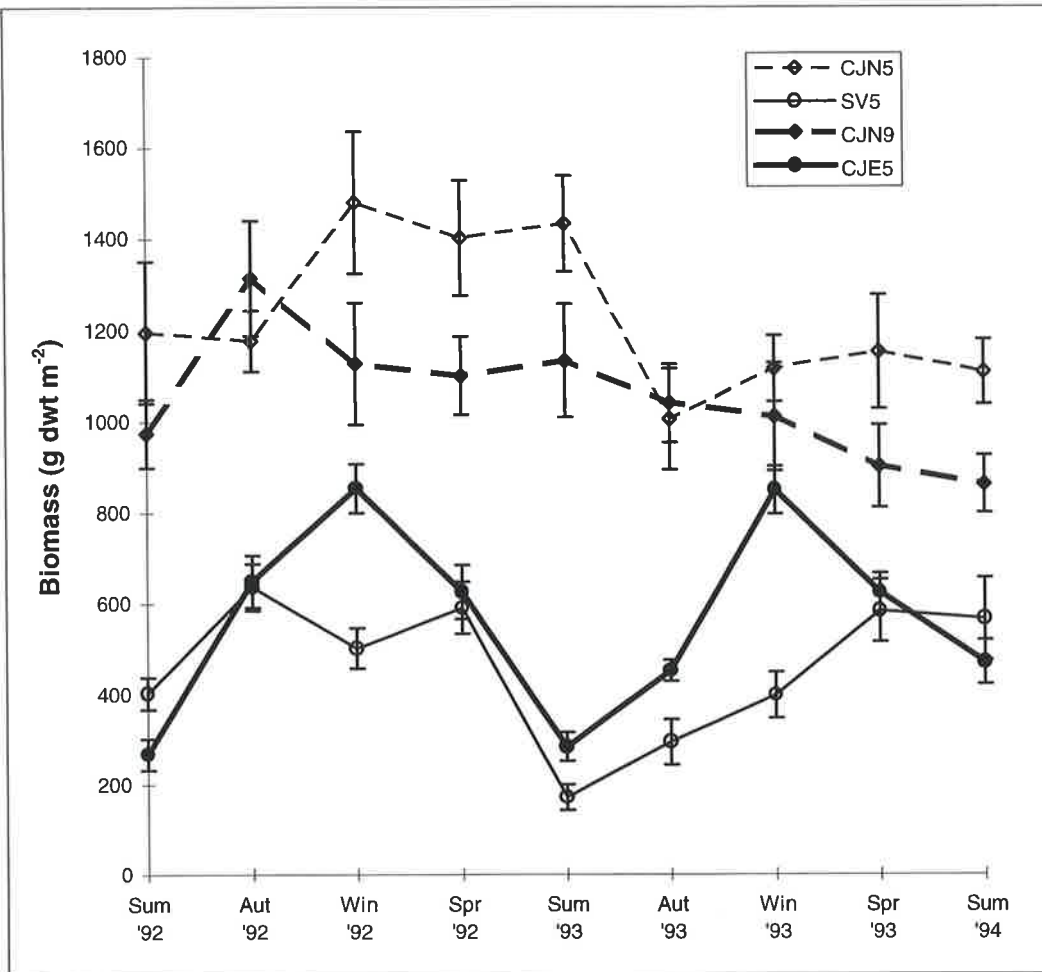


Fig. 6.1b Temporal fluctuations in total abundance. Layout and level of replication as for Fig. 6.1a. Red point represents the total abundance of pilot study in spring 1991 at WI5.

Total abundance fluctuated significantly at all sites except CYN9 and WI5 ($p=.08$ and $.07$ respectively). However, only CYN9, CYN5 and WI9 have fluctuations which could be interpreted as an annual cycle. CYN5 and CYN9 lagged behind WI9 by a season.

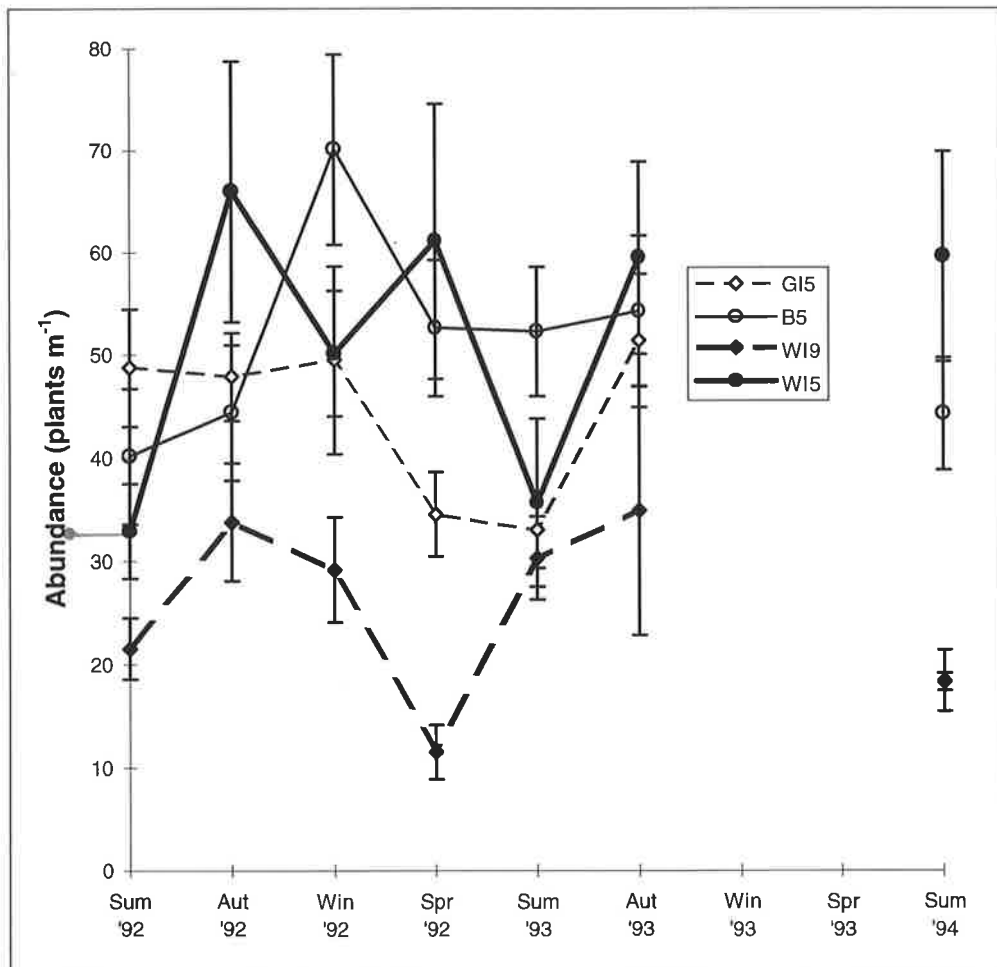
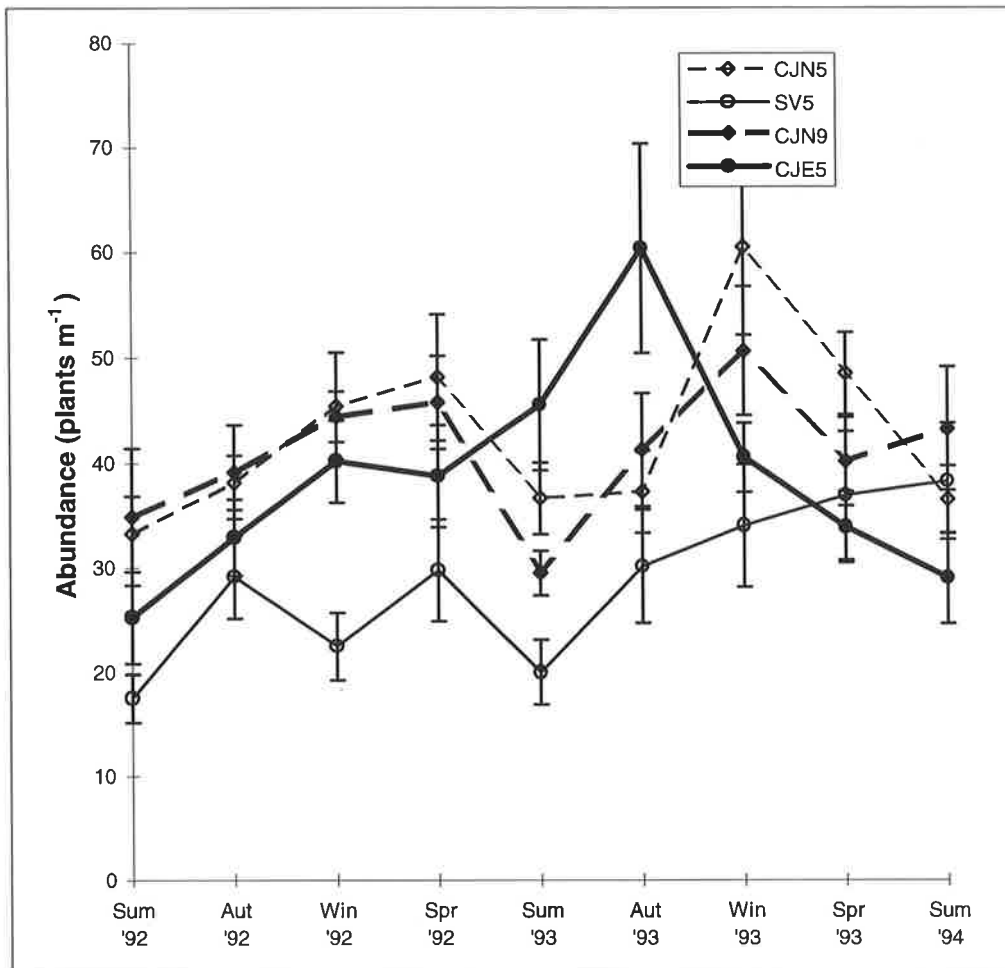


Fig. 6.2a Temporal fluctuations in *Ecklonia* biomass. Layout and level of replication as for Fig. 6.1a. Red point represents *Ecklonia* biomass of the pilot study in spring 1991 at WI5 (n=8).

A fairly consistent trend toward seasonal cycles with spring minima is evident. The fluctuations at all sites were statistically significant except B5 and WI9 ($p=.20$ and $p=.056$, respectively).

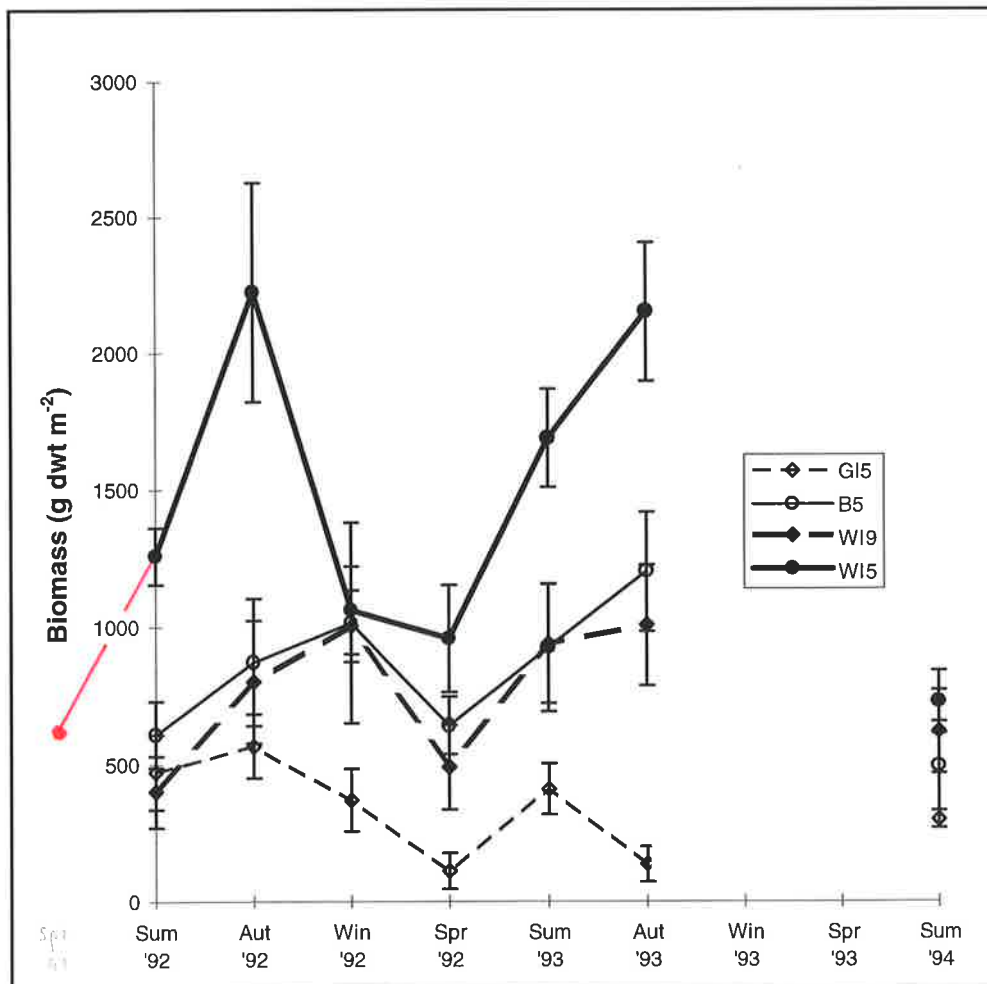
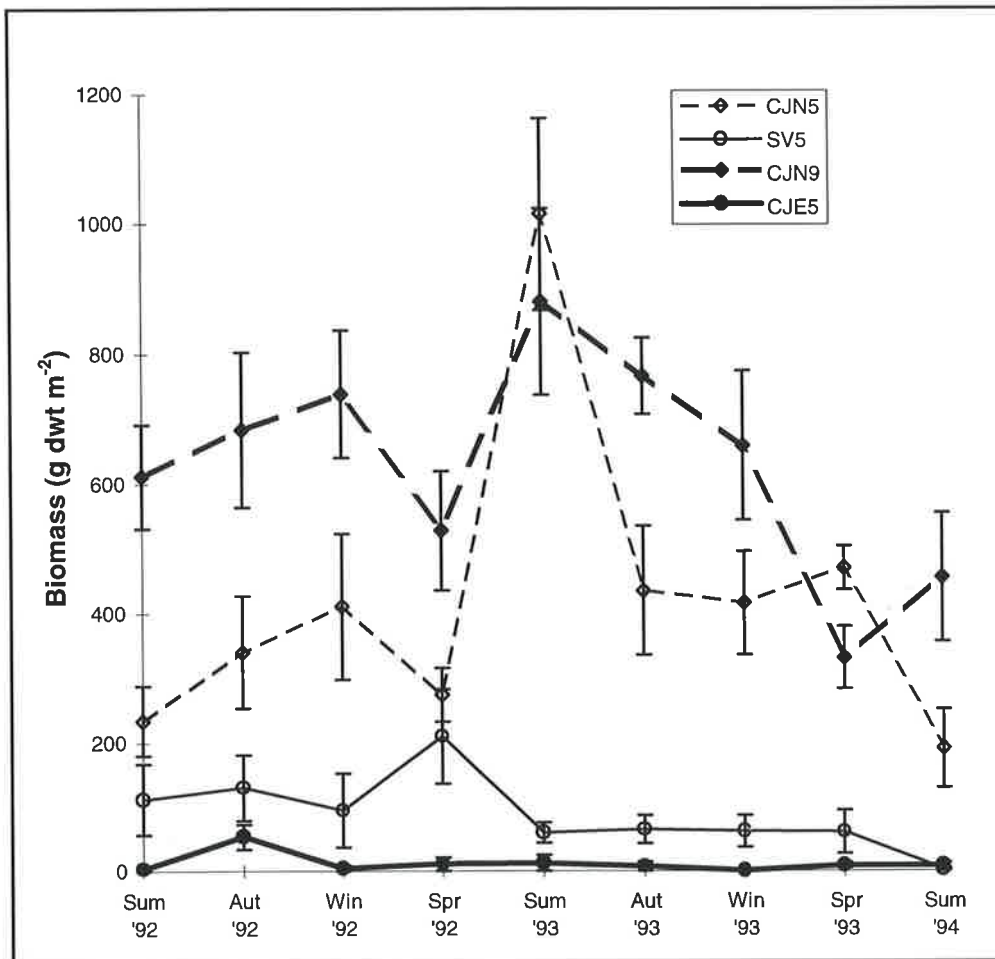


Fig 6.2b Temporal fluctuations in *Ecklonia* abundance. Layout and level of replication as for Fig. 6.1a. Red point represents *Ecklonia* abundance of the pilot study in spring 1991 at WI5 (n=8).

Fluctuations were significant at all sites except B5 ($p=.21$). SV5, CYN5 and CYN9 demonstrated aseasonal trends but the fluctuations of GI5, WI5 and WI9 appeared to demonstrate an annual cycle, with a minimum in spring or summer. CJE5 did not support levels of *Ecklonia* sufficient for judgement.

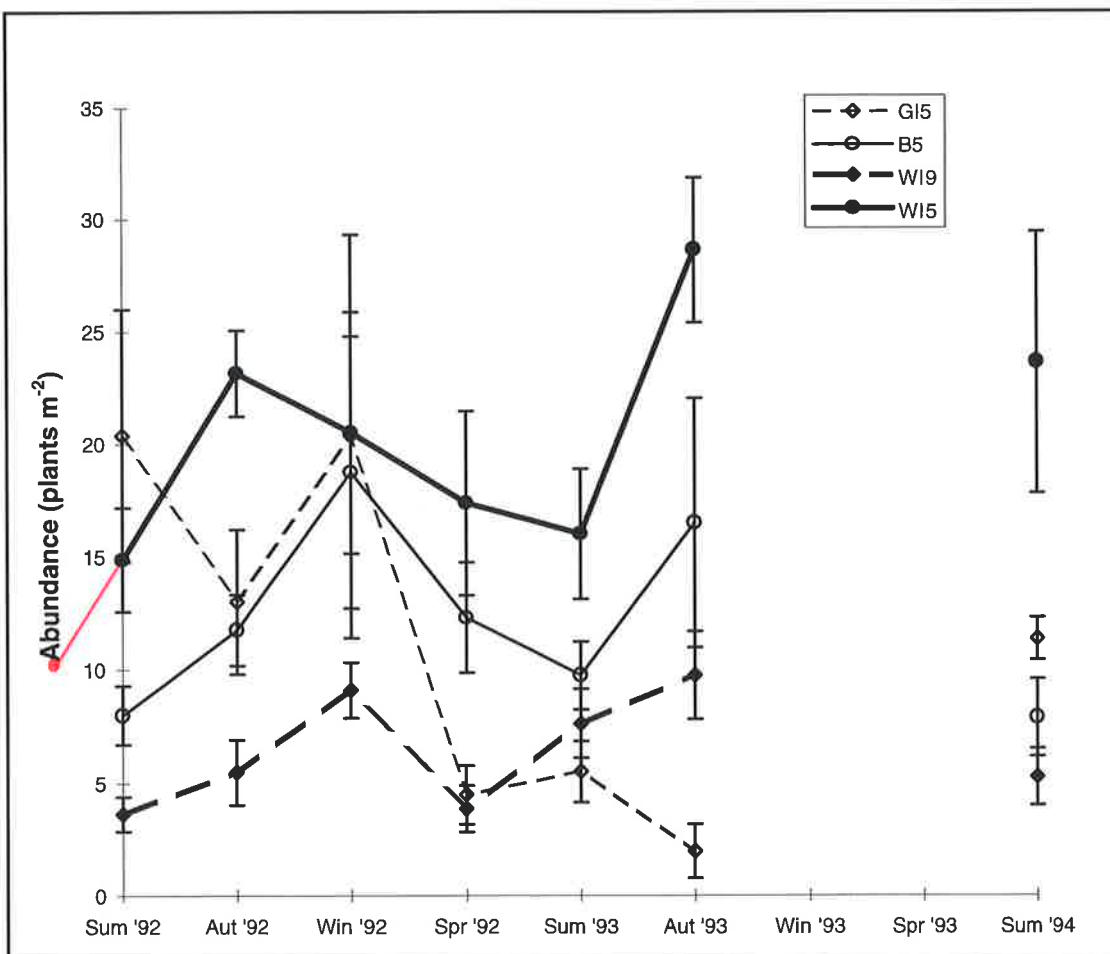
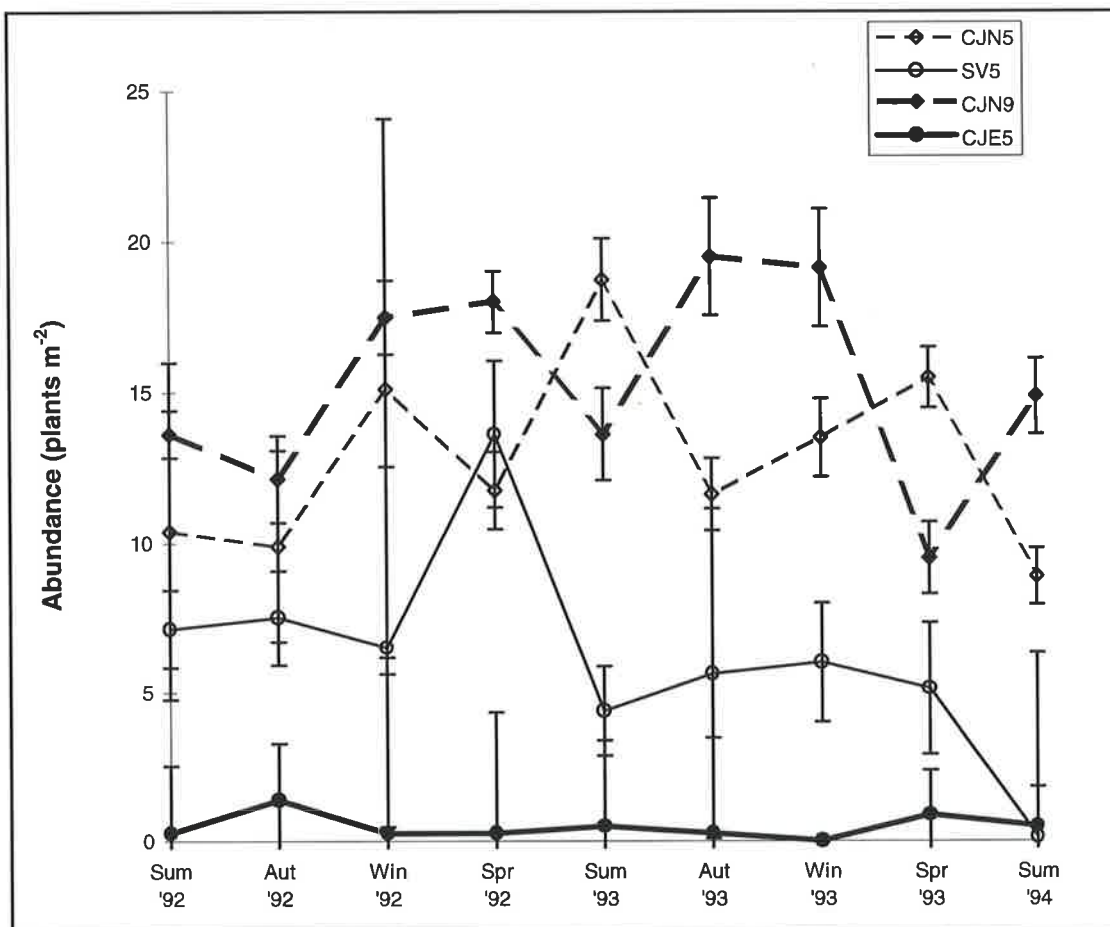


Fig 6.2c Temporal fluctuations in *Ecklonia* AIPW. Layout and level of replication as for Fig. 6.1a. Statistical tests were not possible as there is no measure of variance. Red point indicates *Ecklonia* AIPW for the pilot study in spring 1991 at WI5.

Fluctuations in AIPW appeared seasonal at most sites, with minima in winter and spring and maxima in summer/autumn. The exceptions to this are SV5 and CJE5 which did not support enough *Ecklonia* to make an accurate estimation of AIPW, and thus should be discounted.

Fig 6.3a Temporal fluctuations in *Cystophora* biomass. Layout and level of replication as for Fig. 6.1a.

Only at CJN5, CJE5 and SV5 was sufficient *Cystophora* supported to enable an accurate estimate of fluctuations. At these sites, there appeared to be a consistent annual cycle with maximum biomass in winter and minimum in summer. In the second year, only CJE5, the site supporting the greatest amount of *Cystophora*, displayed the same clear trend. CJN5 had only low levels and was thus poorly estimated. SV5 failed to demonstrate any loss of biomass. This was caused by only a single species -*Cystophora subfarcinata* - see text for details

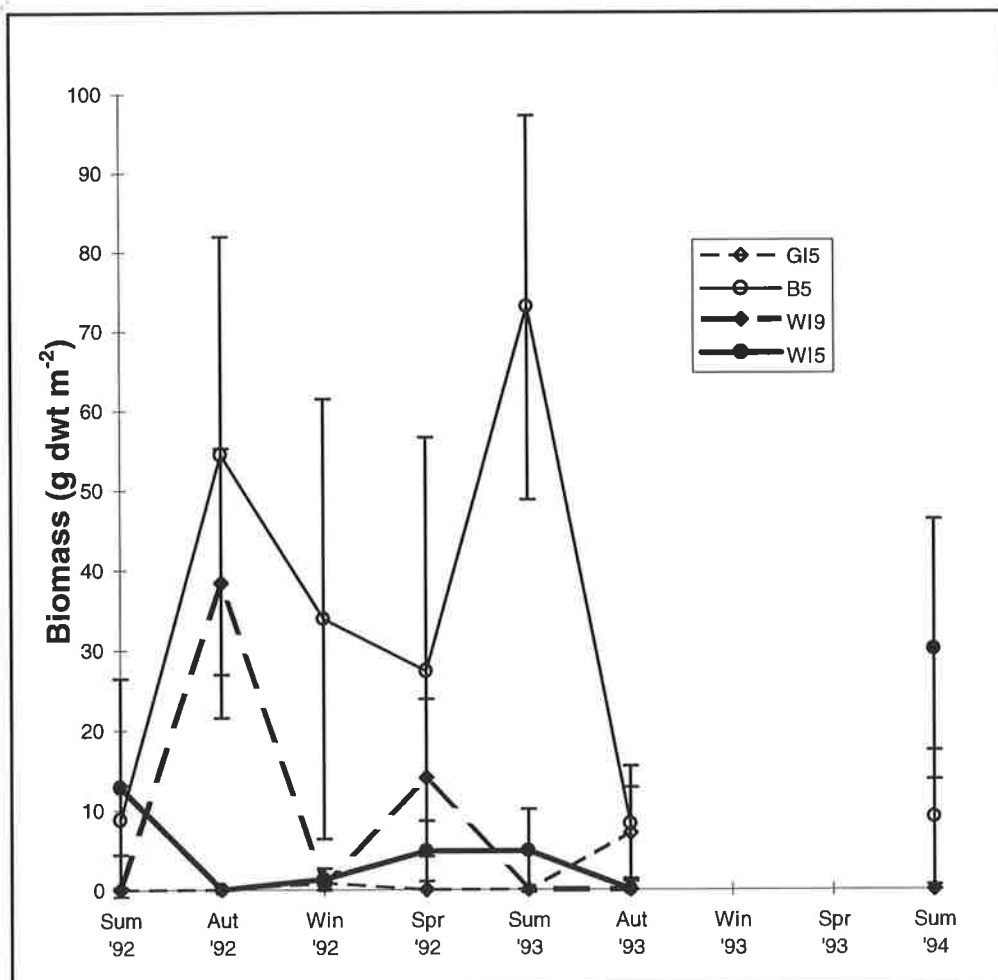
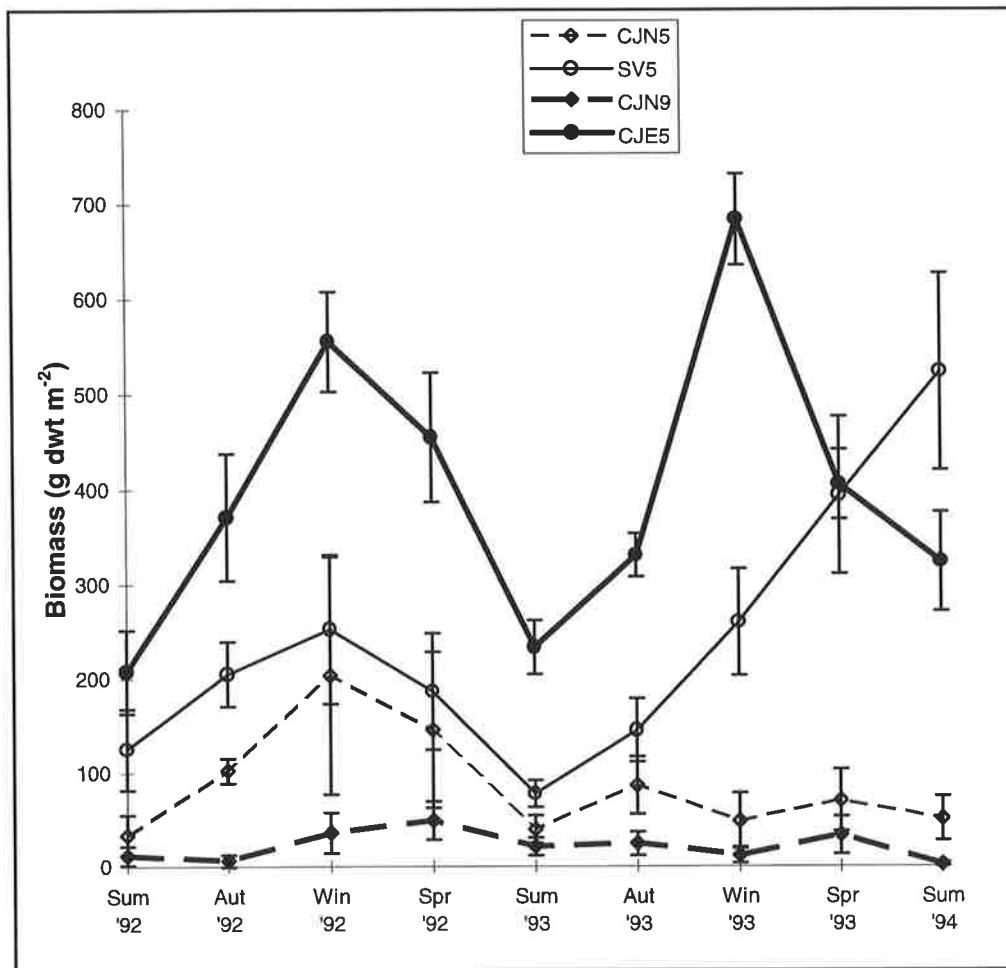


Fig 6.3b Temporal fluctuations in *Cystophora* abundance. Layout and level of replication as for Fig. 6.1a.

Significant fluctuations were recorded only at CJE5 and SV5 ($p=.002$ and $.018$), but these fluctuations did not appear seasonal. Biomass at SV5 increased across the course of the study period, while CJE5 increased to autumn 1993 and then decreased.

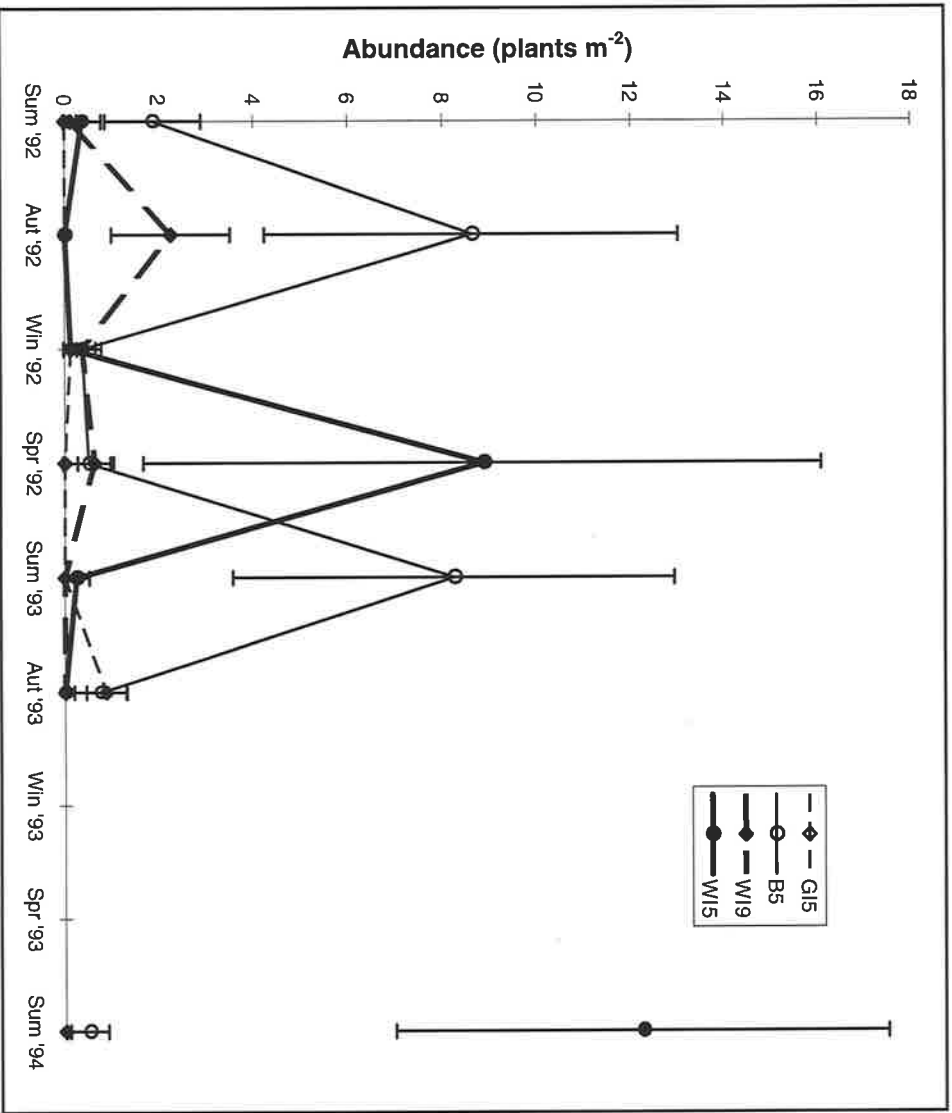
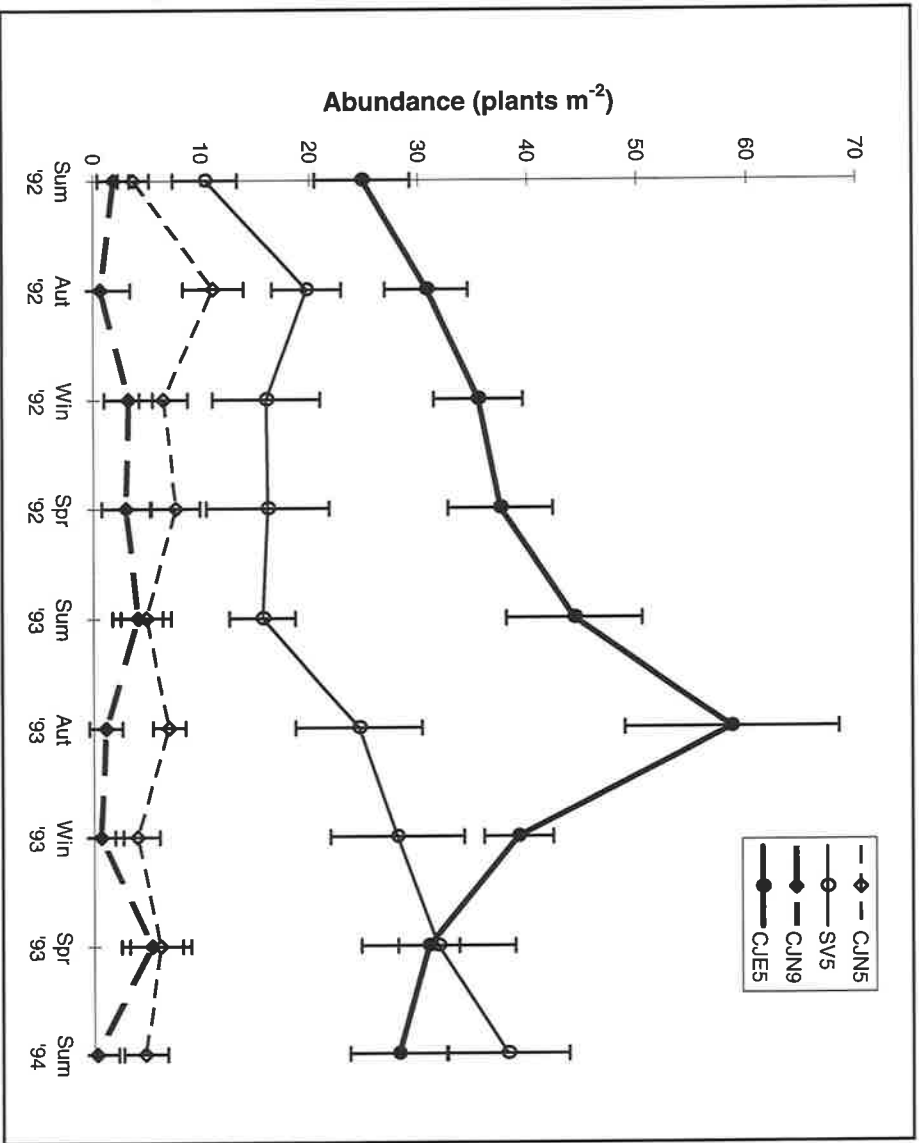


Fig 6.3c Temporal fluctuations in *Cystophora* AIPW. Layout and level of replication as for Fig. 6.1a.

AIPW fluctuations appeared roughly seasonal at the three sites where high enough levels of *Cystophora* were recorded (CJE5, SV5 and CJN5). While the tendency was for a late spring / early summer minimum, this did not occur in 1993 at SV5, again because of the effect of *Cystophora subfarcinata*.

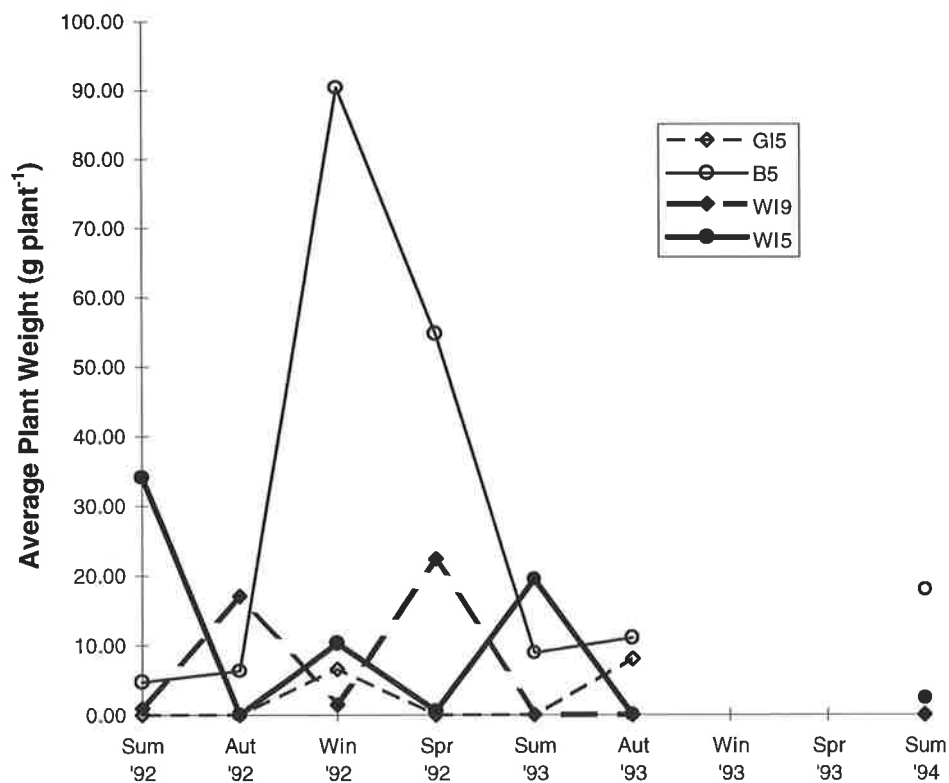
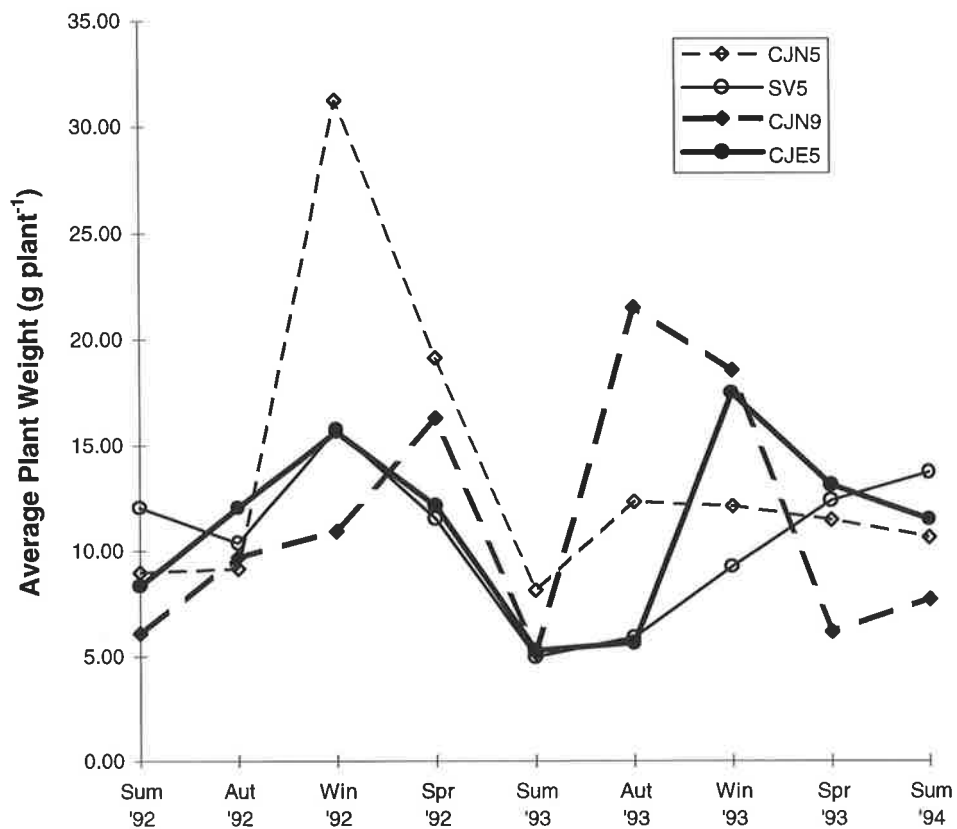


Fig 6.4a Temporal fluctuations of *Cystophora subfarcinata* biomass at SV5. Layout and level of replication as for Fig. 6.1a.

This species of *Cystophora* did not demonstrate the seasonal cycles typical of the genus. Rather, it maintained low levels until autumn 1993, when it increased rapidly to summer 1994, without the decrease found in the other species of *Cystophora*.

Fig 6.4b Temporal fluctuations of *Cystophora moniliformis* biomass at SV5. Layout and level of replication as for Fig. 6.1a.

Cystophora moniliformis demonstrated the type of biomass cycle typical of most species of *Cystophora* at SV5. A cycle with a minimum in summer each year is apparent.

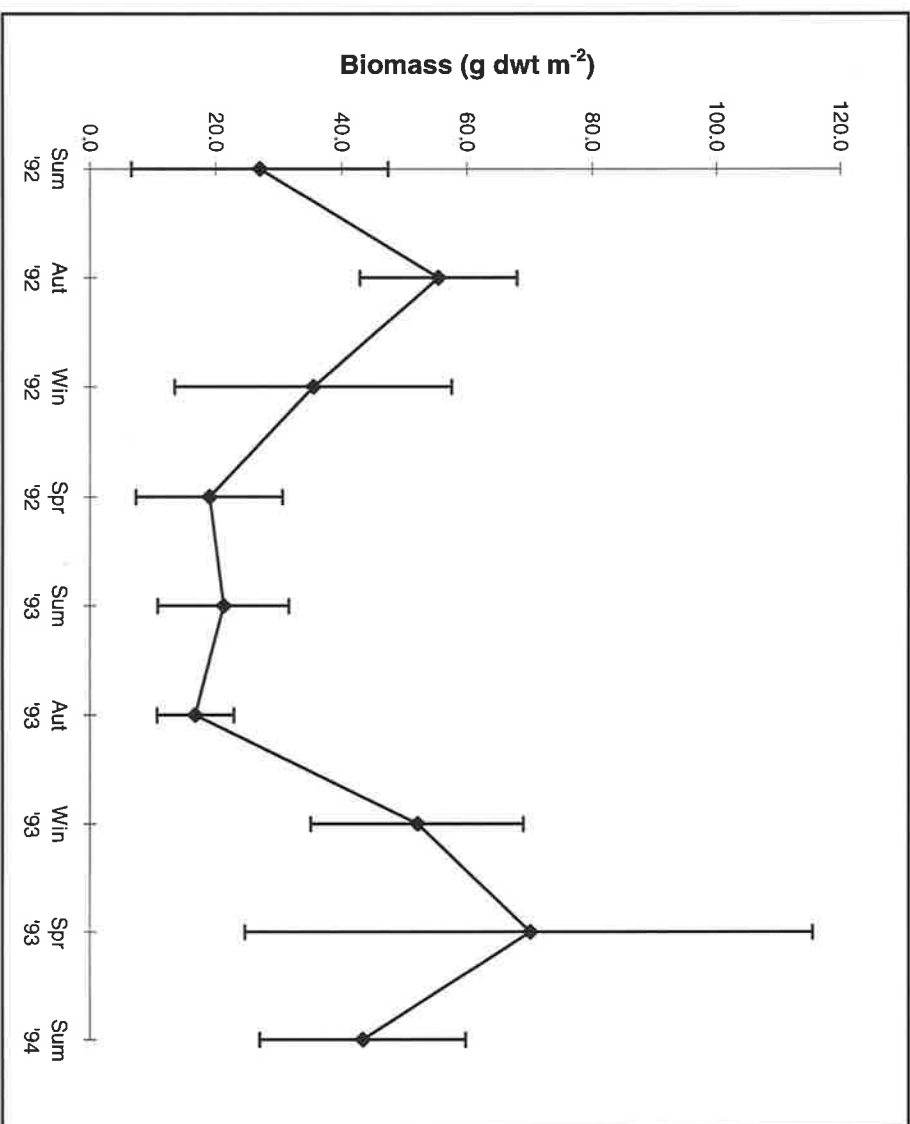
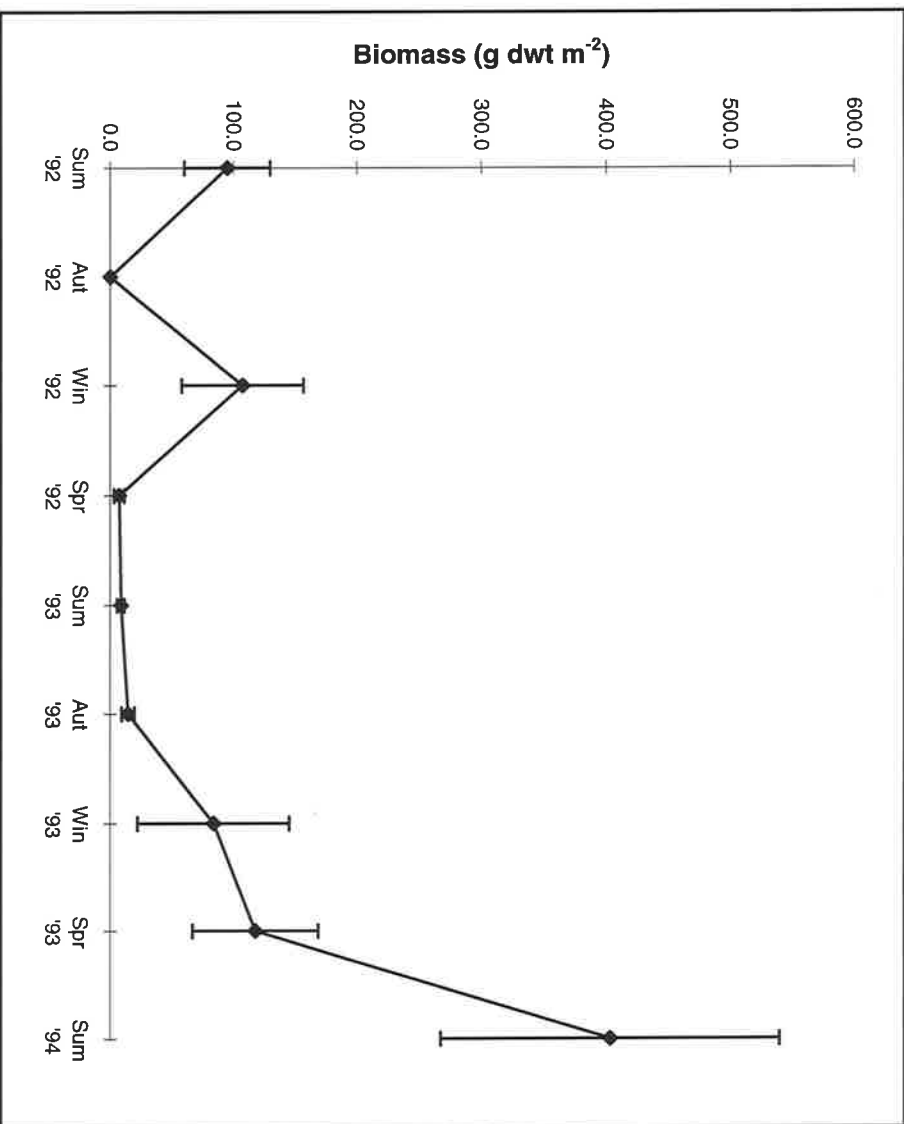


Fig 6.5 Temporal fluctuations in *Sargassum* biomass. Layout and level of replication as for Fig. 6.1a.

Fluctuations in *Sargassum* biomass were remarkably similar across sites. Seasonal cycles were apparent with a minimum in summer of each year. However, there was also a depression of *Sargassum* biomass in winter at most sites which was slight in the gulf sites, but great at the oceanic sites. All sites except CYN9, G15 and B5 demonstrated statistically significant differences between seasons.

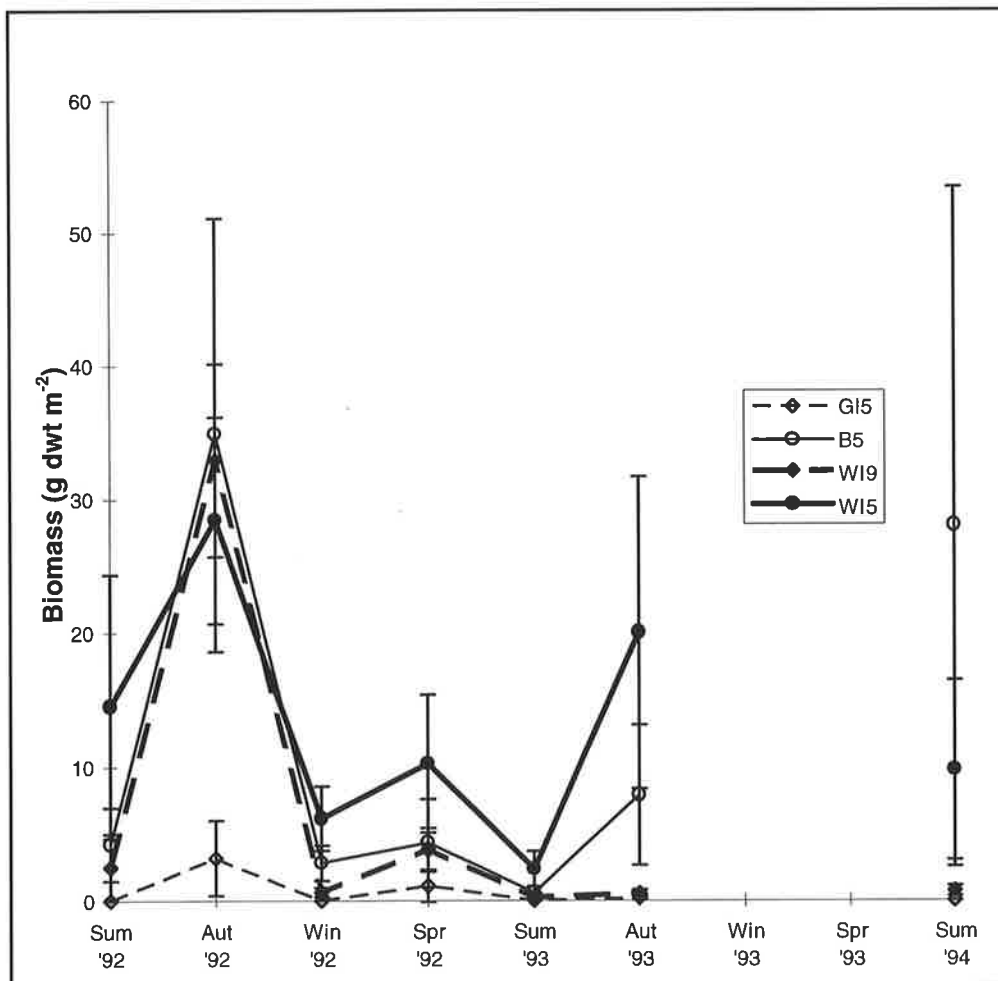
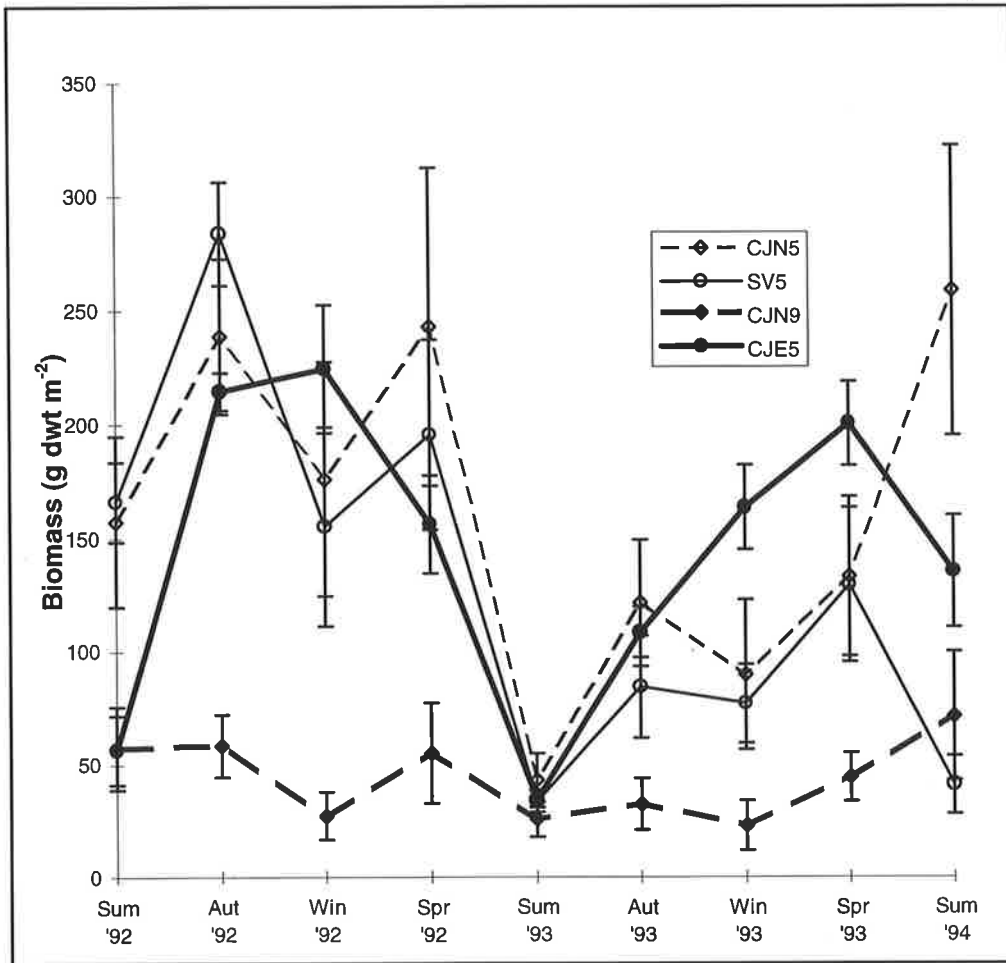


Fig. 6.6a Temporal fluctuations in *Acrocarpia* biomass. Layout and level of replication as for Fig. 6.1a

Only CYN5, W15, B5 and G15 supported sufficiently high levels of *Acrocarpia* for adequate estimation of fluctuations. At all of these sites, there were statistically significant fluctuations, but no annual cycle was apparent.

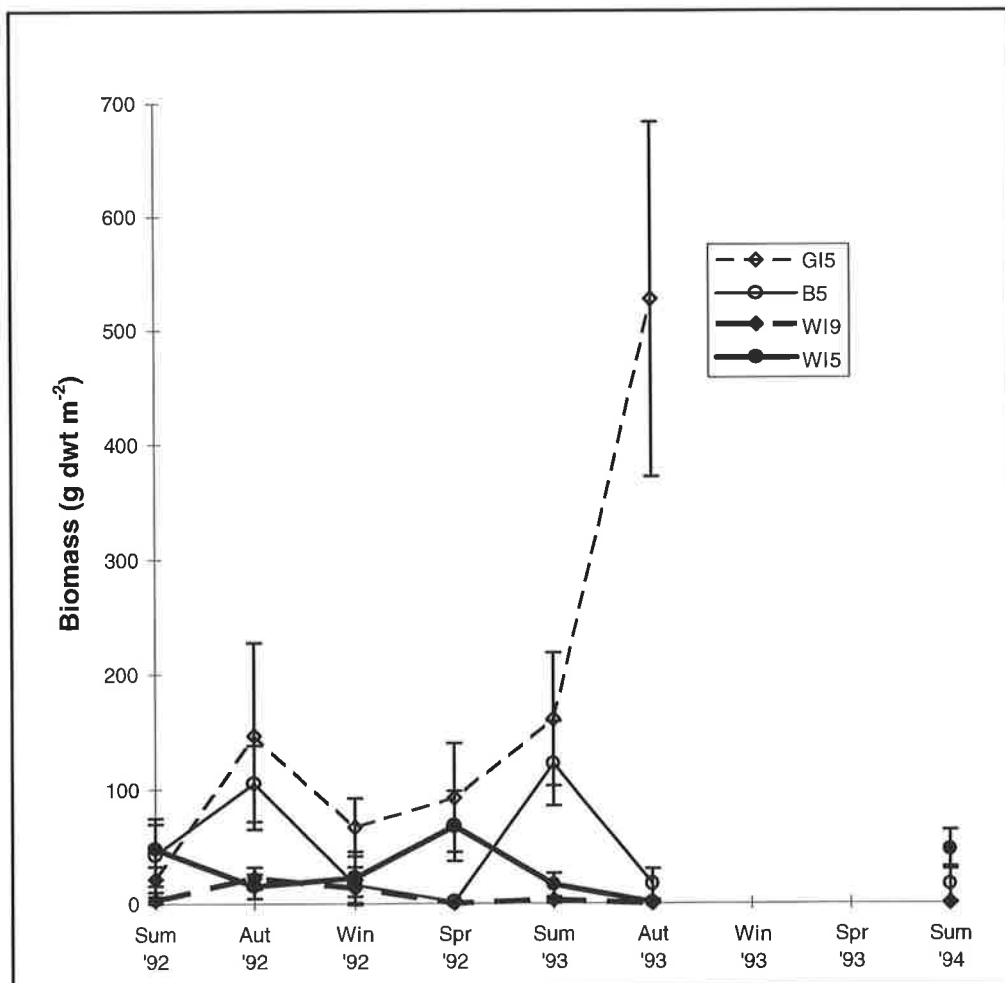
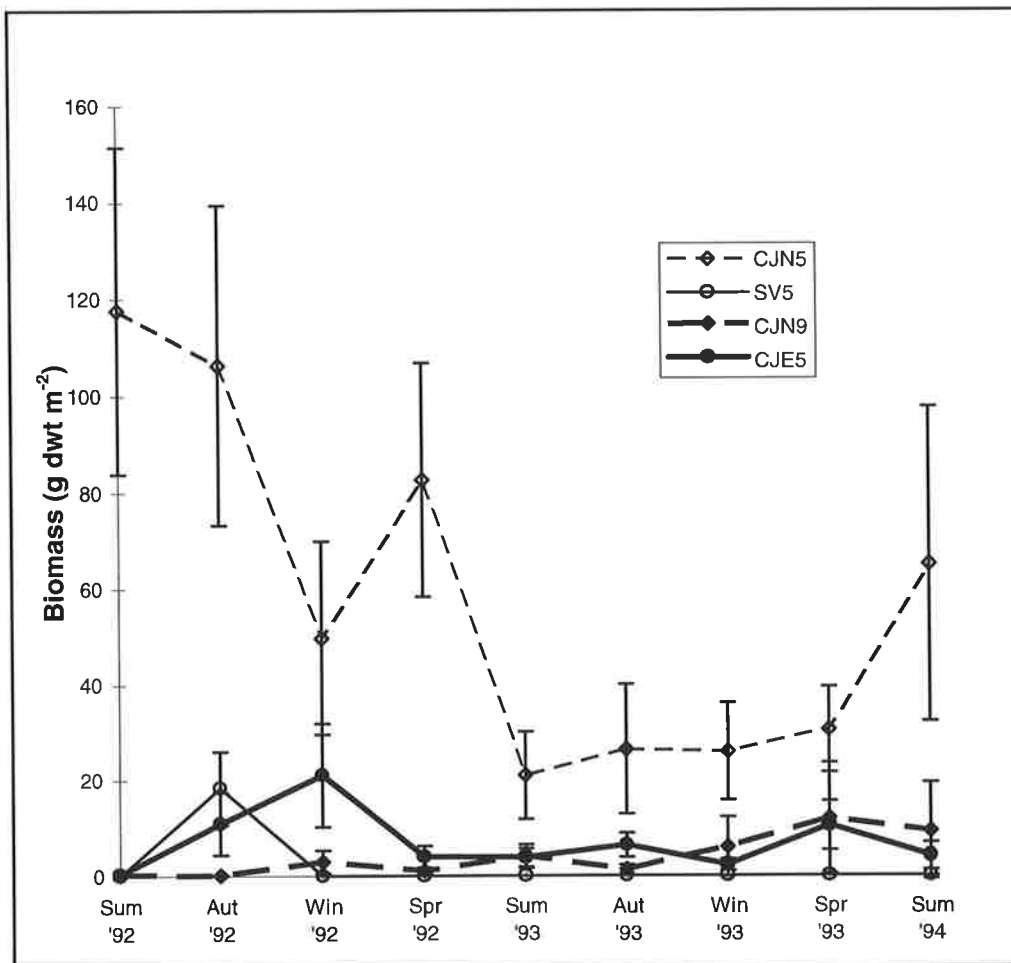


Fig. 6.6b Temporal fluctuations in *Acrocarpia* abundance. Layout and level of replication as for Fig. 6.1a

Of the sites with sufficiently high levels of *Acrocarpia* biomass (see Fig. 6.6a), only CJS5 failed to demonstrate significant fluctuations. There was no evidence of consistency between sites, nor any annual cycle.

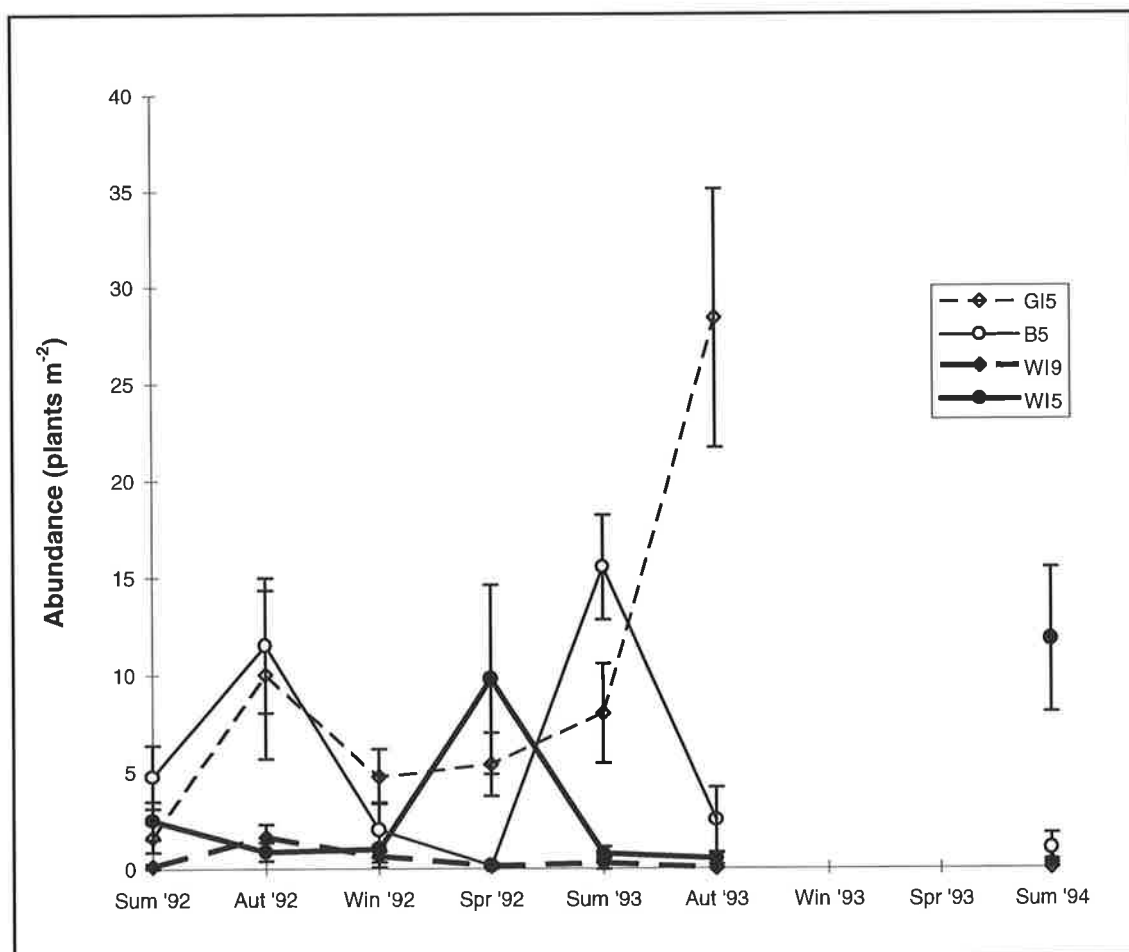
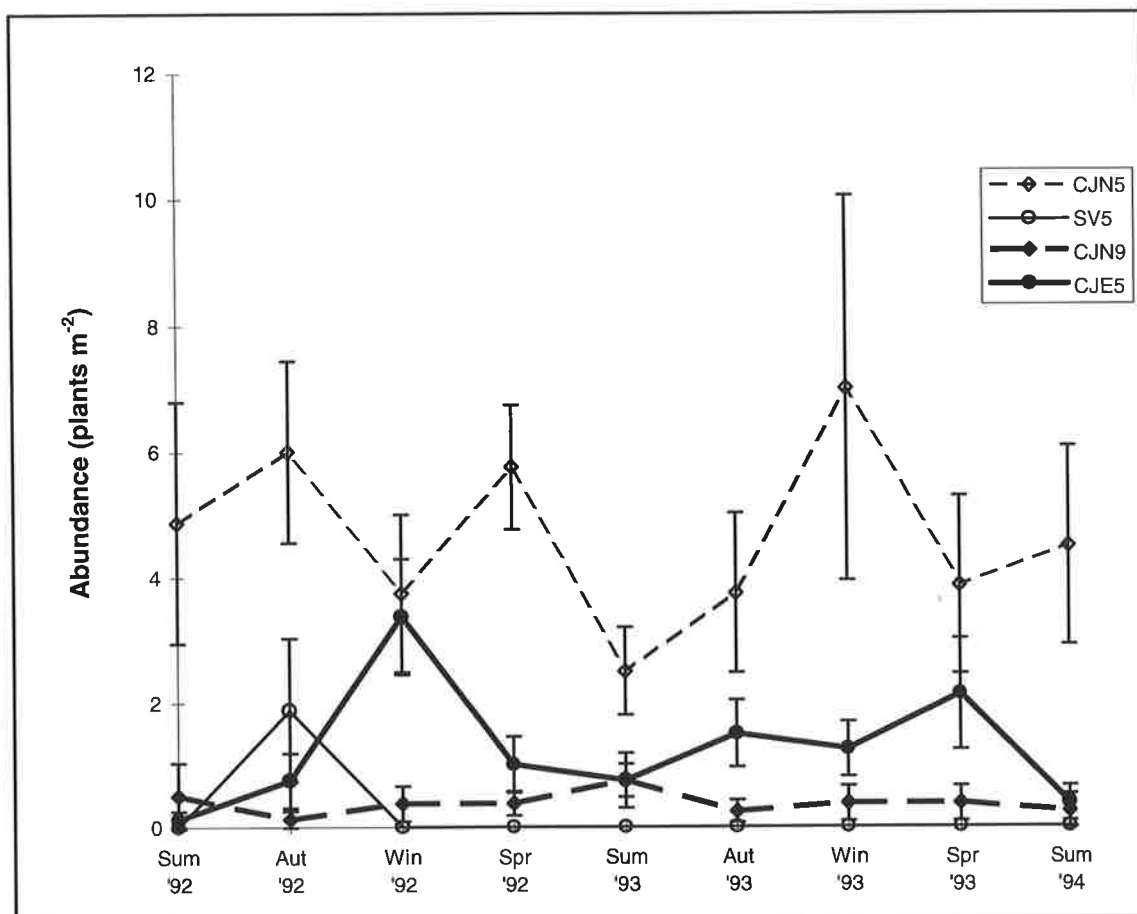


Fig. 6.6c Temporal fluctuations in *Acrocarpia* AIPW. Layout and level of replication as for Fig. 6.1a

Fluctuations did not appear to follow any annual cycle, and were not consistent across sites. WI9 and WI5, while appearing similar were not reliable, because of the low number of plants used to estimate AIPW.

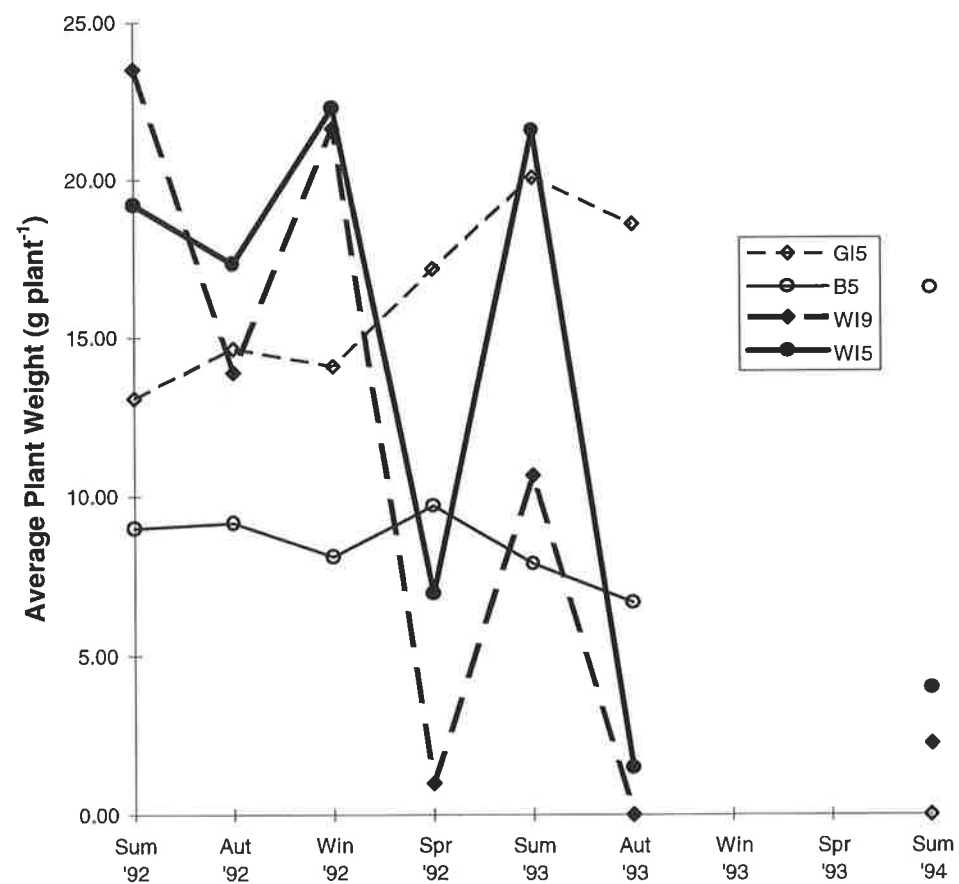
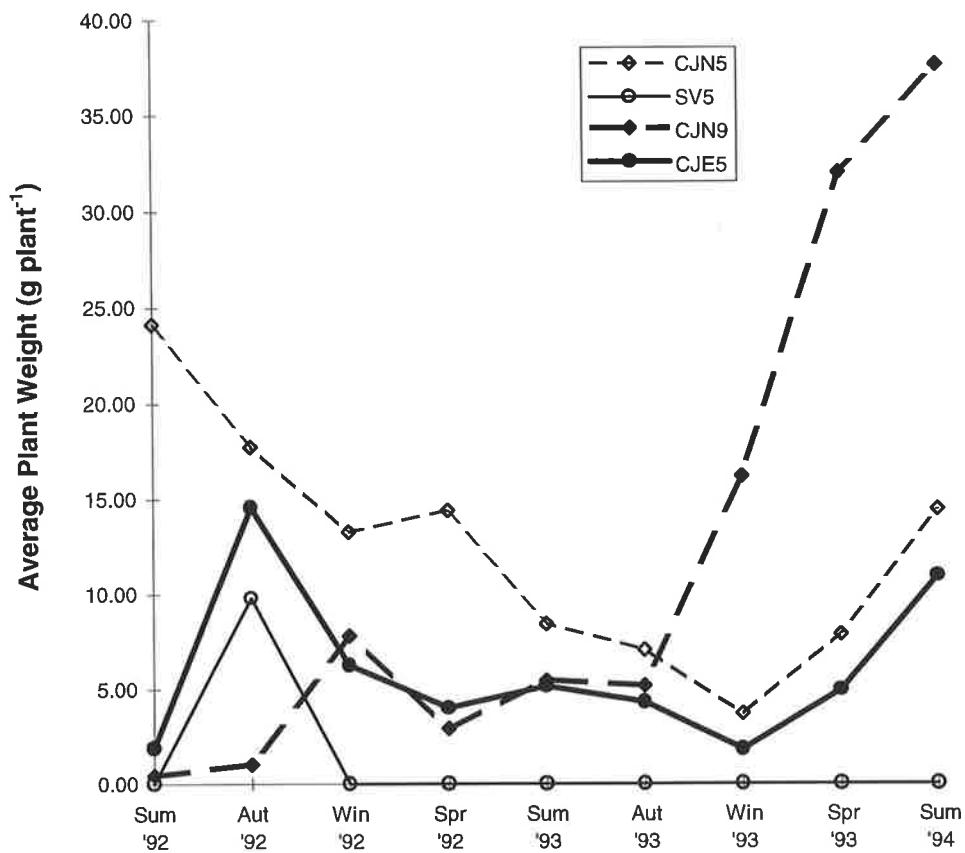


Fig. 6.7a Temporal fluctuations in *Seirococcus* biomass. Layout and level of replication as for Fig. 6.1a

Only CYN5, CYN9 and W19 supported enough *Seirococcus* for this sampling regime to be effective. Of these, only CYN9 demonstrated significant fluctuations, and this was restricted to a single short lived increase in spring 1993.

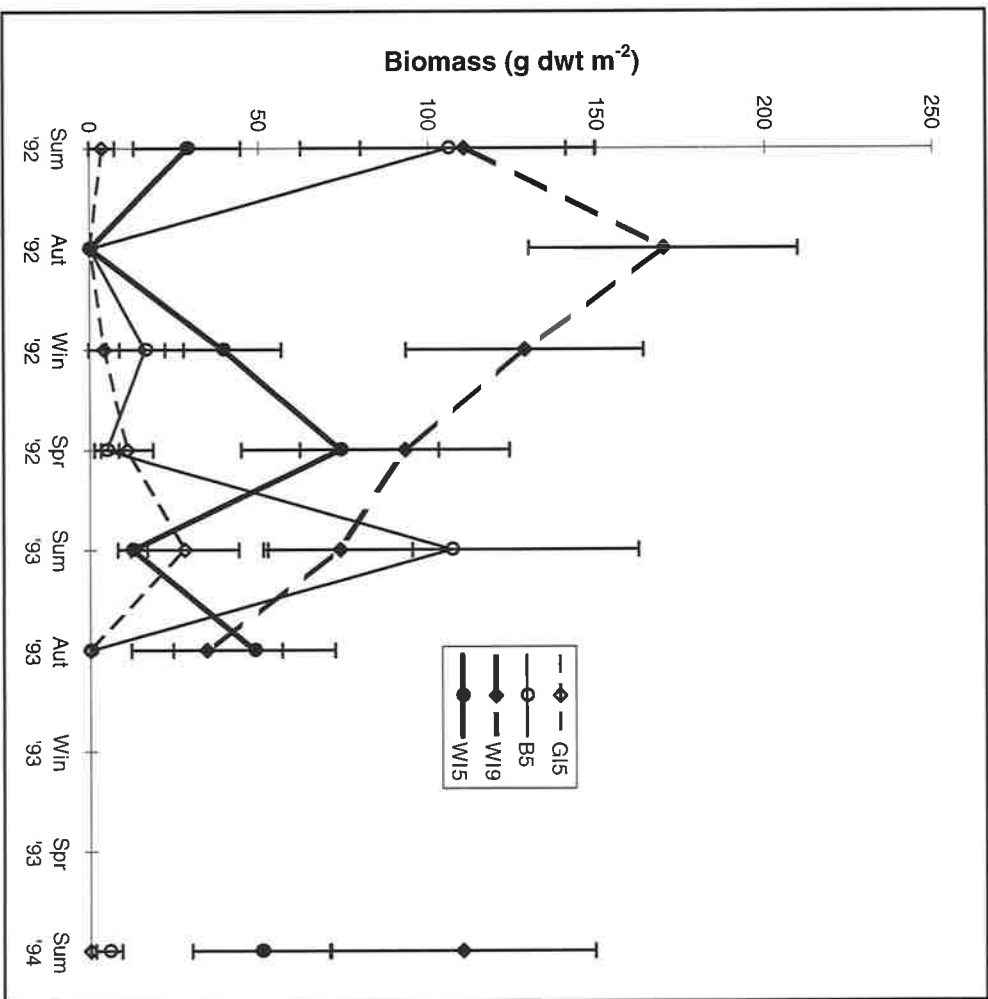
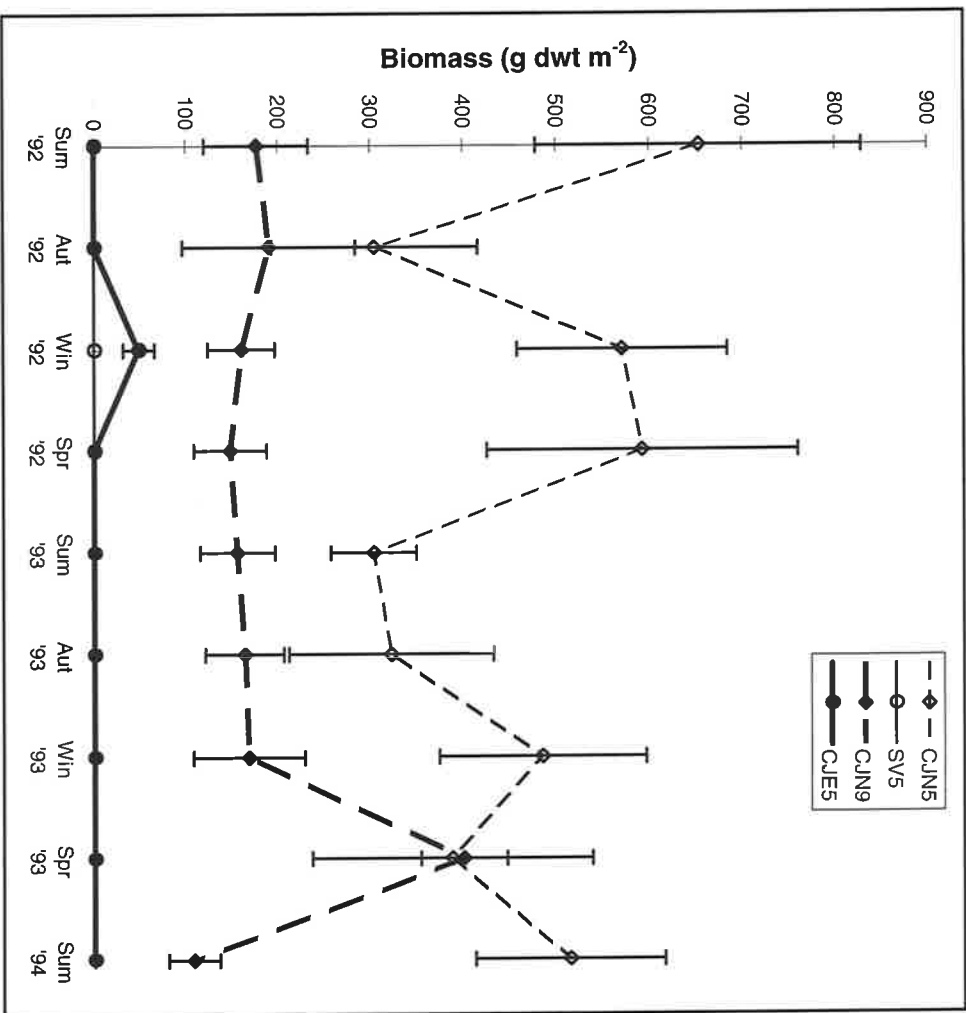


Fig. 6.7b Temporal fluctuations in *Seirococcus* abundance. Layout and level of replication as for Fig. 6.1a

Only CJN5, CJN9 and WI9 supported enough *Seirococcus* for this sampling regime to be effective. Only CJN9 demonstrated significant fluctuations, but this did not appear seasonal.

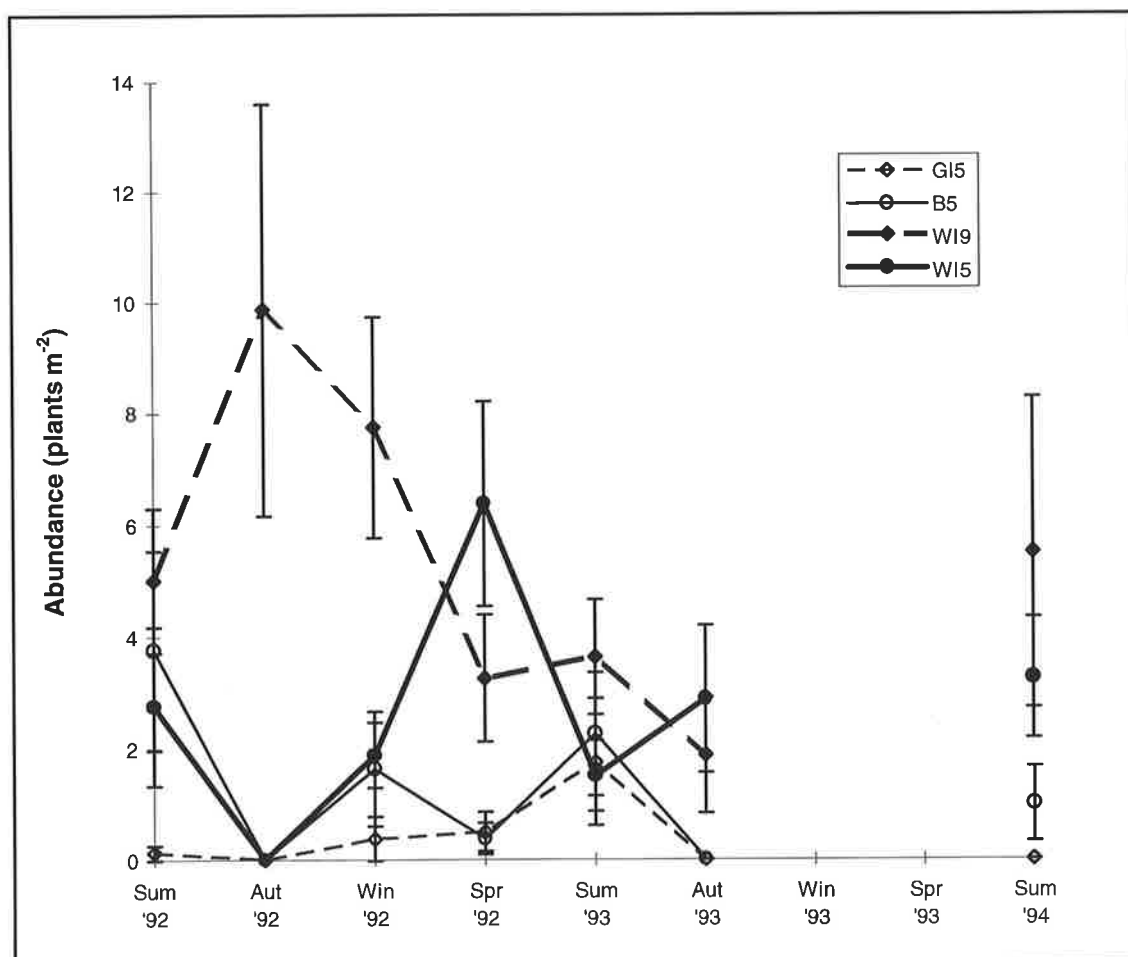
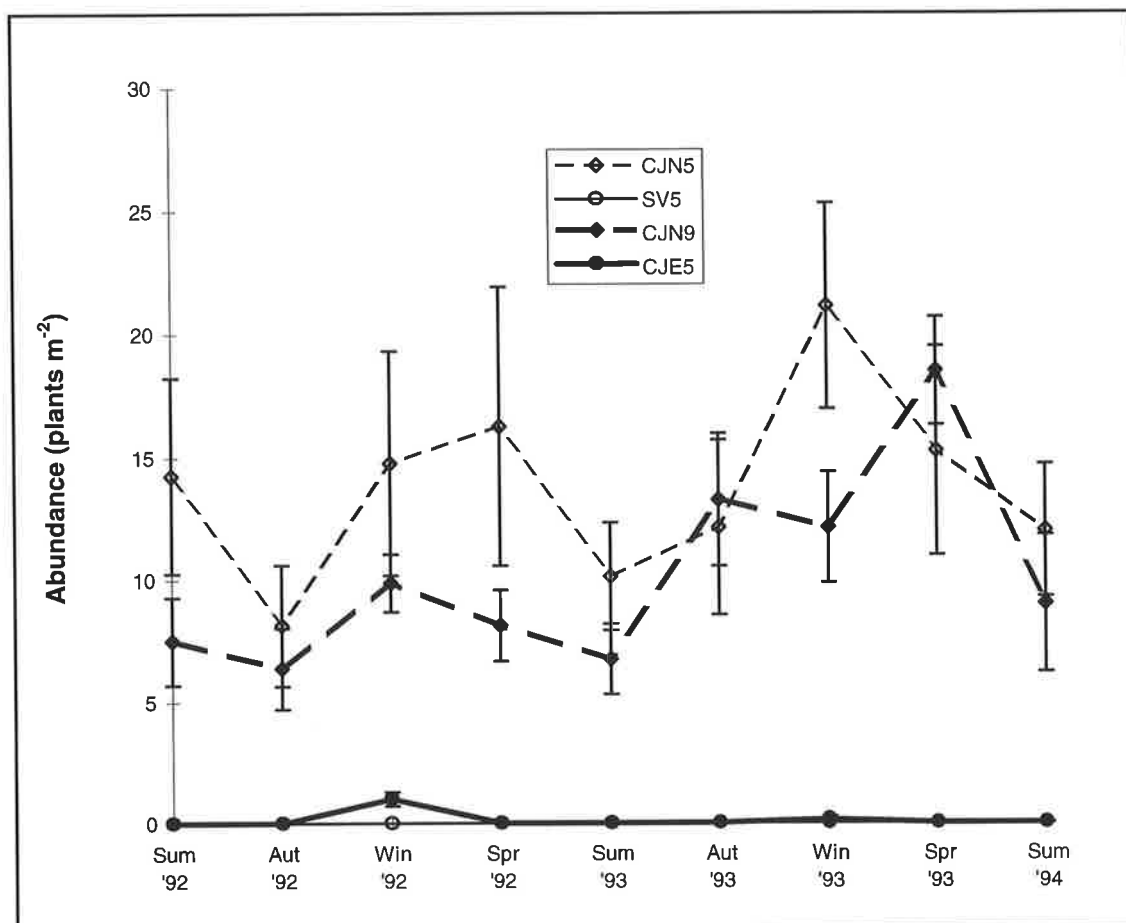


Fig. 6.7c Temporal fluctuations in *Seirococcus* AIPW. Layout and level of replication as for Fig. 6.1a

Only CJN5, CJN9 and WI9 supported enough *Seirococcus* for this sampling regime to be effective. None of these sites displayed any annual cycle, although CJN9 displayed an apparent 3 season (9 month) cycle, which is assumed to be coincidental.

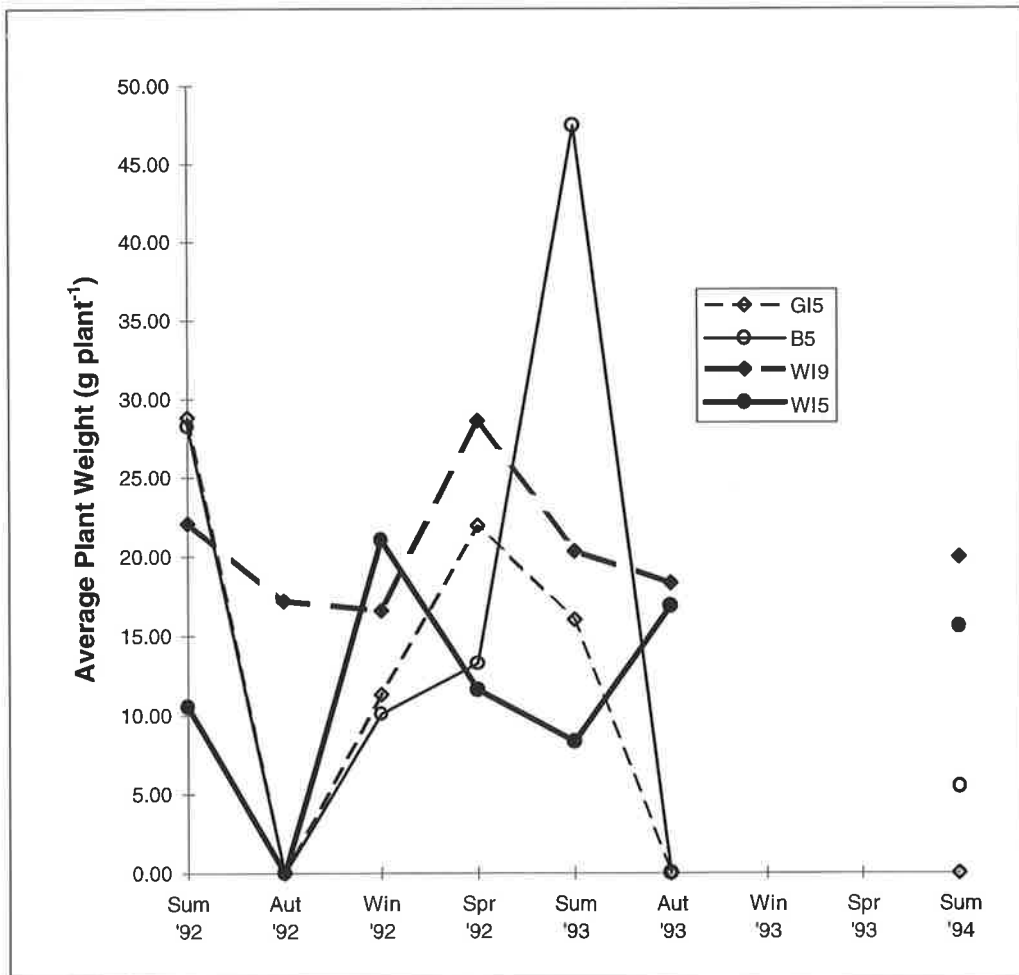
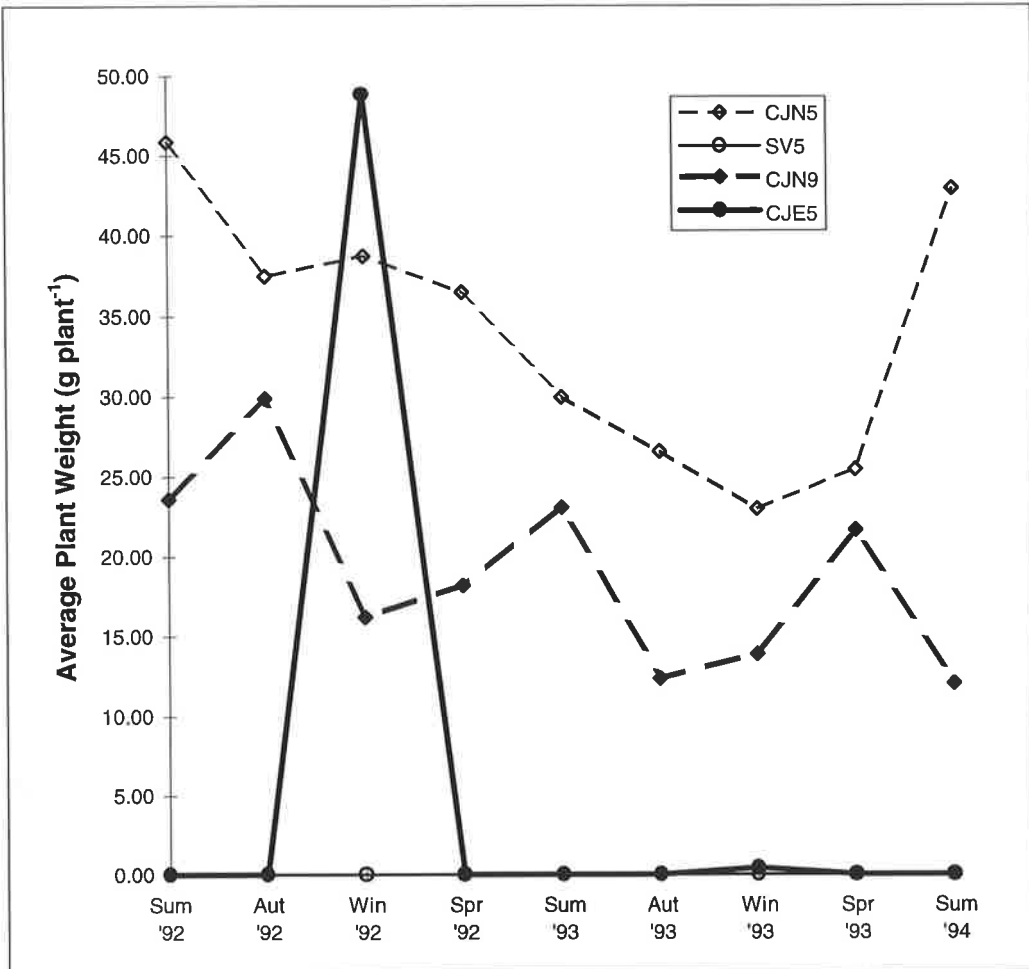


Fig. 6.8a Temporal fluctuations in *Scytothalia* biomass. Layout and level of replication as for Fig. 6.1a

All sites except CJE5 and SV5 displayed significant fluctuations, and seasonal cycles appeared possible at CJN5 and all oceanic sites. However, the lack of sampling in winter and spring 1993 makes this suggestion tenuous. If these do represent seasonal cycles, then the timing was inconsistent between sites.

Fig. 6.8b Temporal fluctuations in *Scytothalia* abundance. Layout and level of replication as for Fig. 6.1a

All sites except CJE5 and SV5 exhibited significant differences between seasons. Fluctuations were generally similar to those exhibited in *Scytothalia* biomass. Note that all sites demonstrated a minimum in summer 1993.

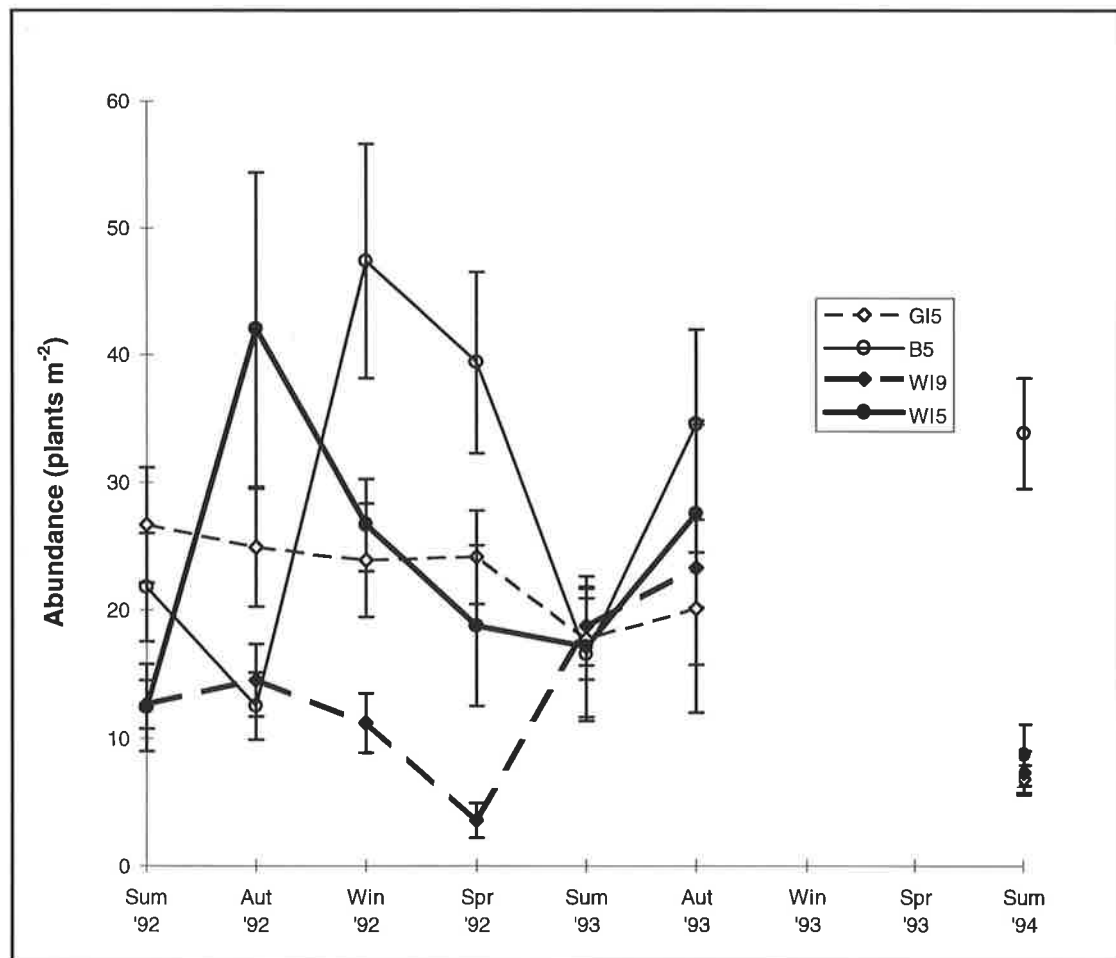
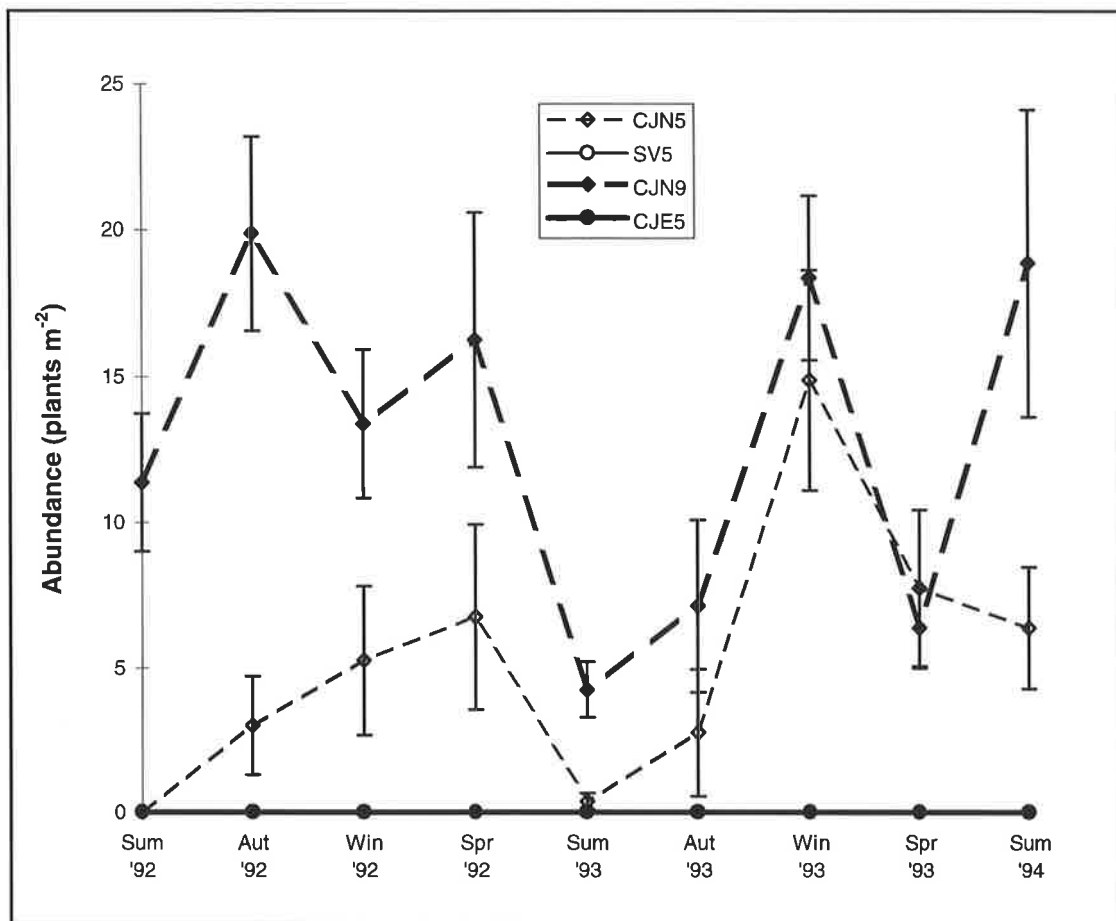


Fig. 6.8c Temporal fluctuations in *Scytothalia* AIPW. Layout and level of replication as for Fig. 6.1a

There was no evidence of seasonality or consistency between sites.

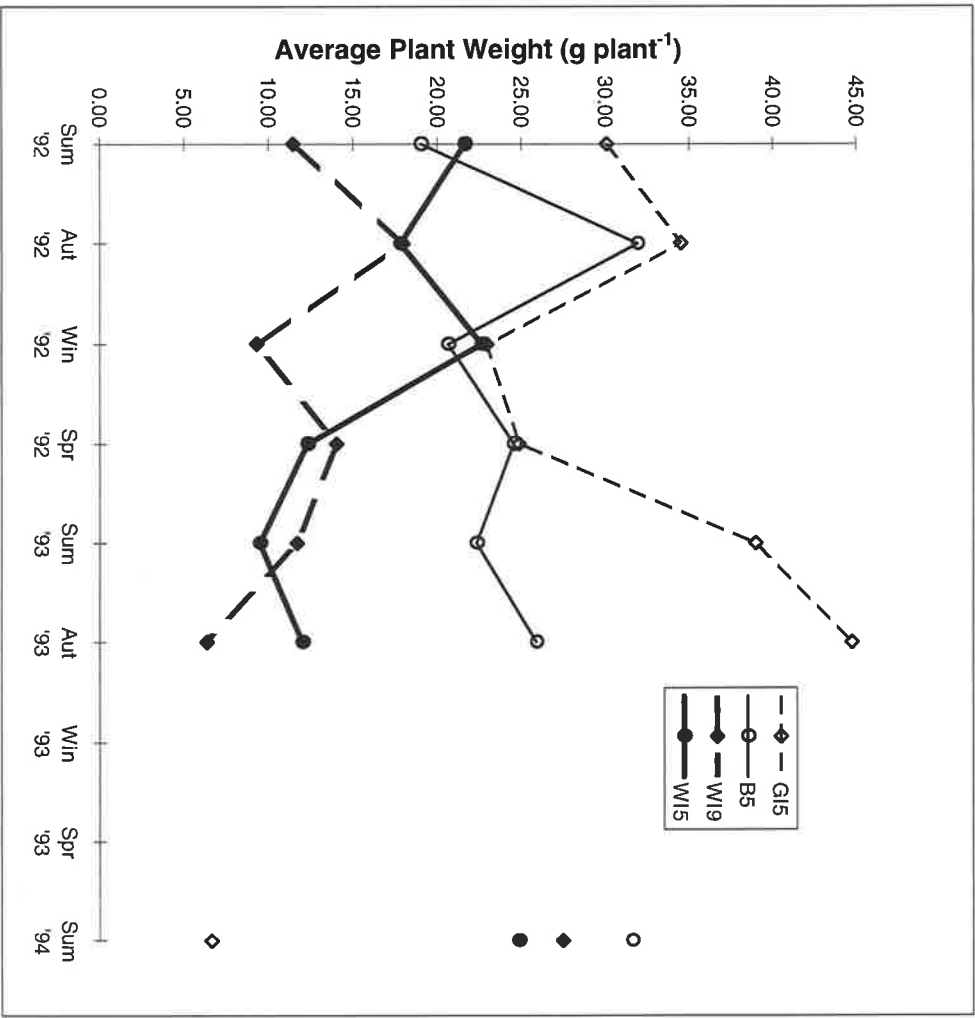
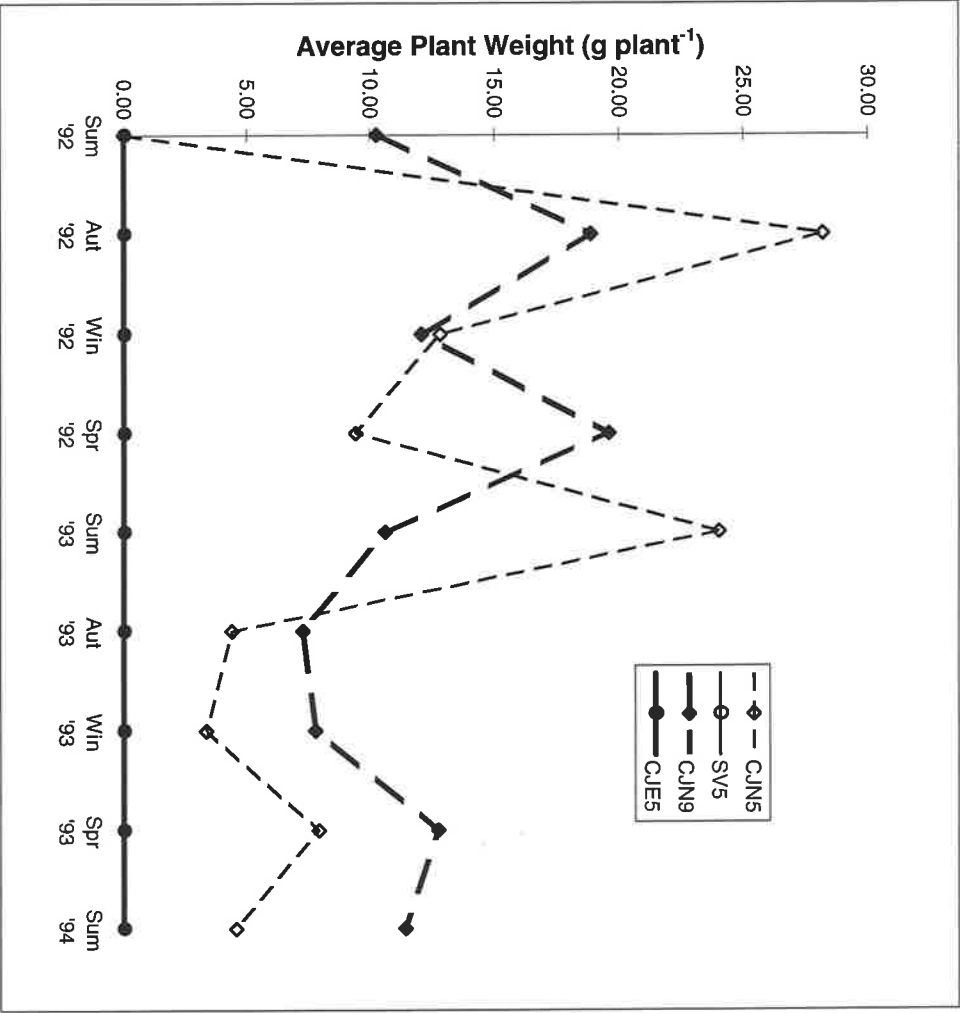


Fig. 6.9 SSH ordination of the temporal changes demonstrated by all sites. The points on this ordination represent the changes in composition which each of the communities underwent. The method of calculation of change was presented in Chapter 5. Proximity of points represents similarity of change. Alphanumeric label denotes the site and temporal change in question;

A	CJN5	1	Summer 1992
B	SV5	2	Autumn 1992
C	CJN9	3	Winter 1992
D	CJE5	4	Spring 1992
E	GI5	5	Summer 1992
F	B5	6	Autumn 1993
G	WI9	7	Winter 1993
H	WI5	8	Spring 1993

The major envelopes indicate the bulk of the samples for a particular season and include all sites and both years. Outliers are ringed separately.

Stress = .28 Note that this ordination was repeated in three dimensions, which reduced the stress value to .21, but rendered a similar picture. The two dimensional plot was presented as it is simpler than plotting and comprehending 3 sets of graphs representing all pairings of axes.

There appeared to be a remarkable consistency in seasonal change (indicated by the groupings). There were only five outliers in a total of 56 seasonal changes. Furthermore, this consistency existed across 8 sites and two years. The spring changes, while generally not found in any of the other seasonal envelopes were spread across the plot, indicating a great variety in change.

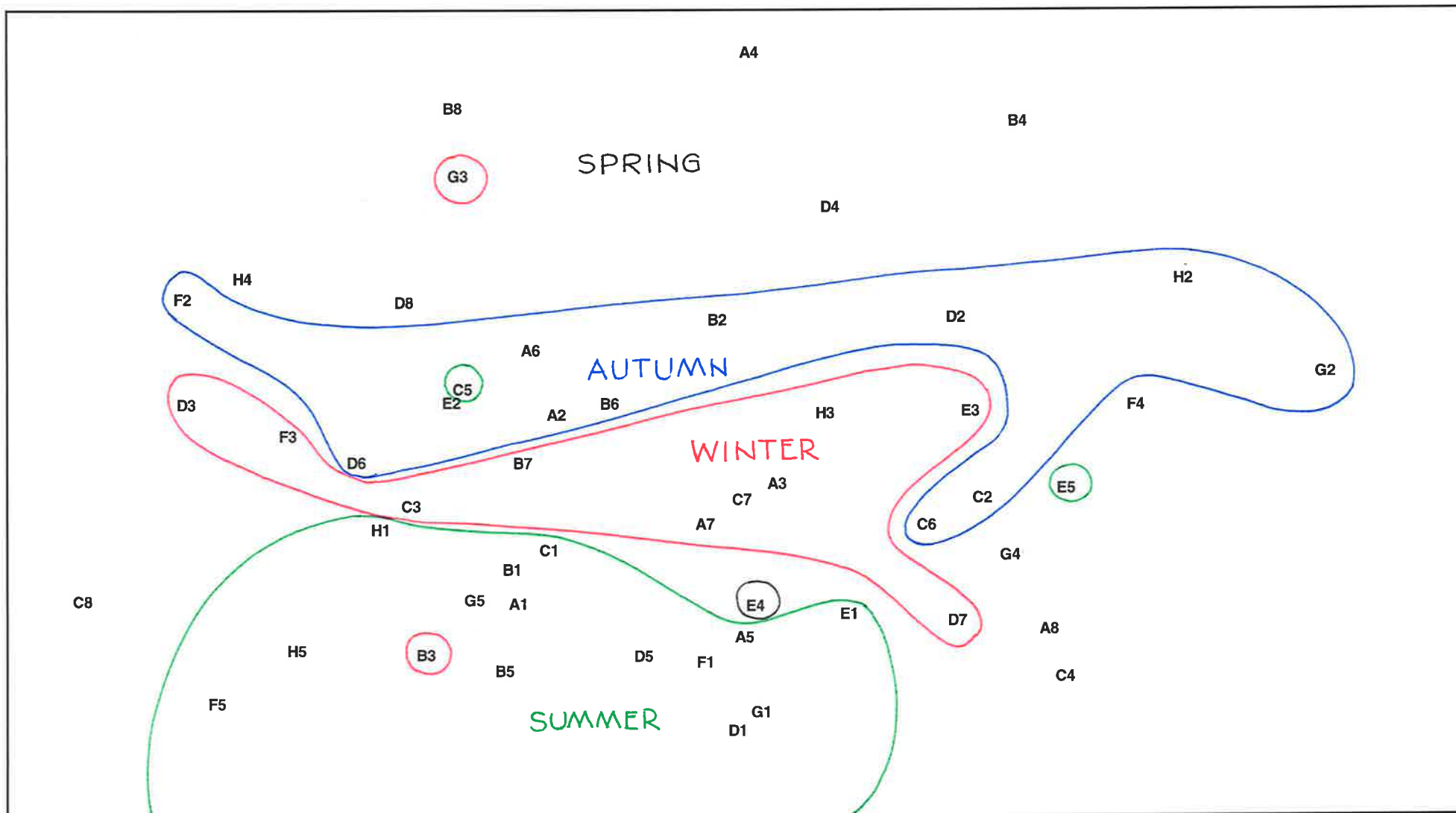


Fig. 6.10a SSH ordination of the average community compositions in each season at CJN5. The numeric labels denote the collection;

- 1 Summer 1992
- 2 Autumn 1992
- 3 Winter 1992
- 4 Spring 1992
- 5 Summer 1993
- 6 Autumn 1993
- 7 Winter 1993
- 8 Spring 1993
- 9 Summer 1994

Stress = .10

Note that the summer collections were distinct from the non-summer collections but that the non-summer collections were more similar to the summer immediately preceding than the one which succeeded them.

Fig. 6.10b UPGMA dendrogram of average community compositions in each season at CJN5. Labelling as above. Dashed vertical line denotes chosen cut point.

Dendrogram supports the above interpretation of ordination. Summer collections stand distinct with non-summer collections grouping within year. Non-summer seasons were more closely related to the preceding summer than the one which followed.

Fig. 6.10c SSH ordination of all samples taken from CJN5. Each sample (1m² quadrat) is represented by a point on the graph, with the label corresponding to the seasonal collection in which the sample was taken. Labelling as for Fig 6.9a.

Stress = .25

While no distinct collection groupings occurred, the bulk of the 1992 samples (collections 1,2,3 & 4) are found toward the upper left of the plot, while the 1993 samples (collections 5,6,7 & 8) are found toward the bottom right.

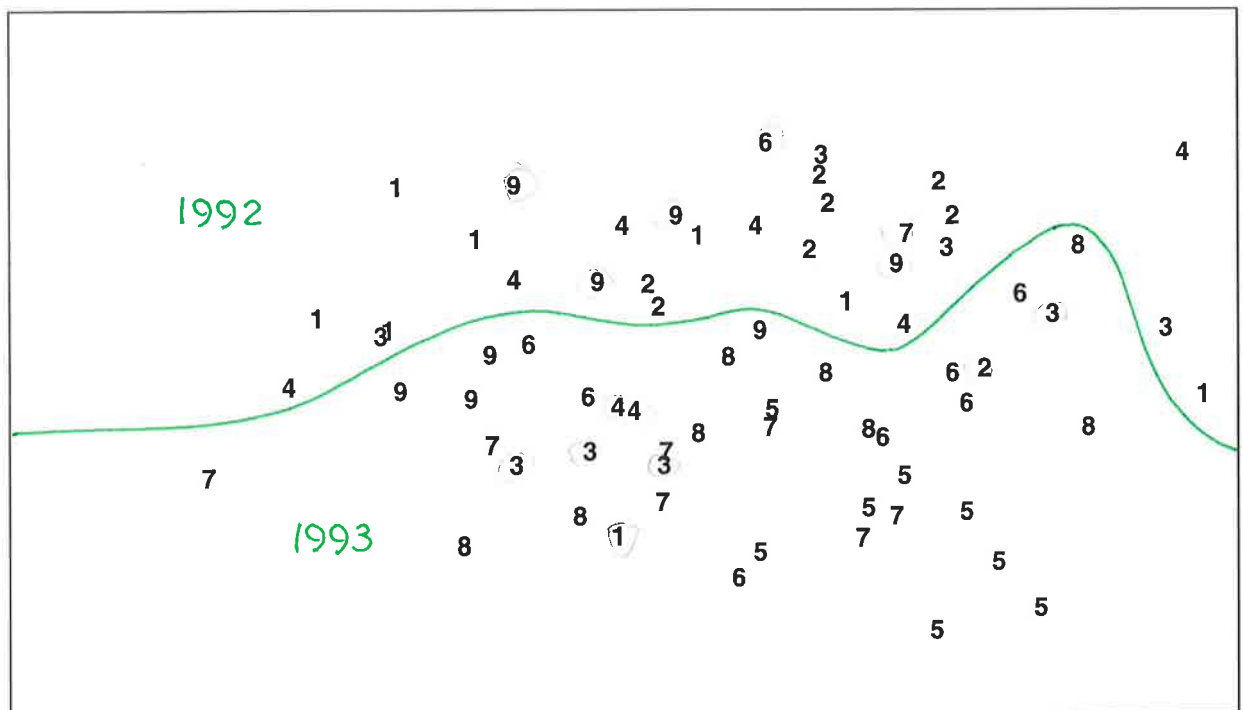
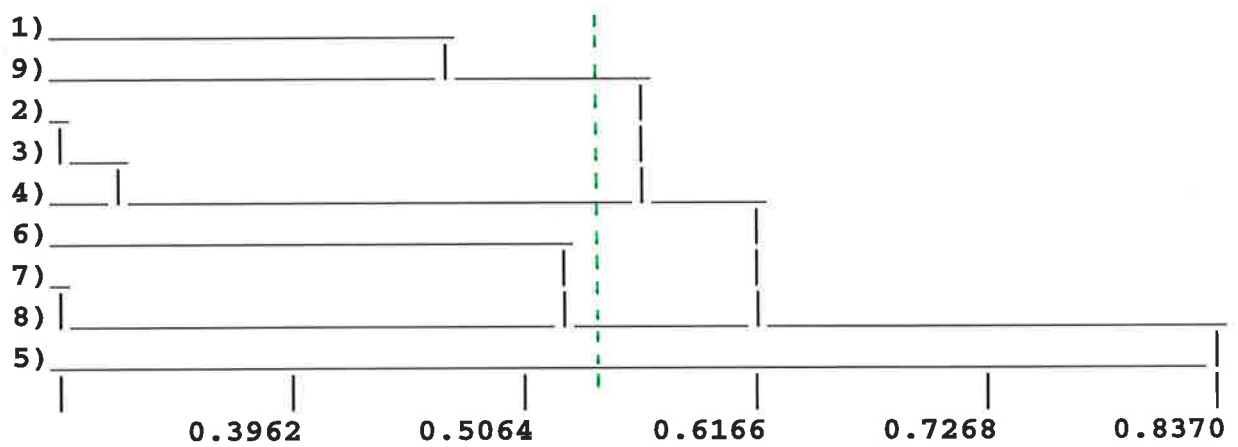
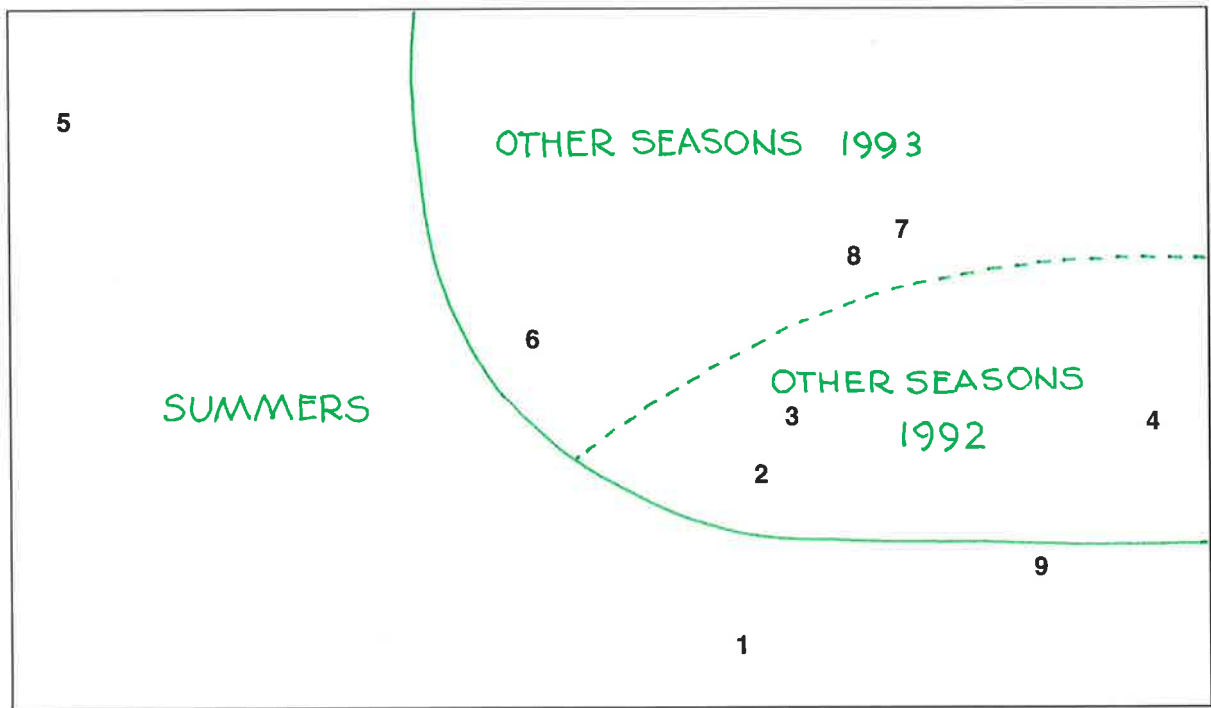


Fig. 6.11a SSH ordination of the average community compositions in each season at SV5. The numeric labels denote the collection;

- 1 Summer 1992
- 2 Autumn 1992
- 3 Winter 1992
- 4 Spring 1992
- 5 Summer 1993
- 6 Autumn 1993
- 7 Winter 1993
- 8 Spring 1993
- 9 Summer 1994

Stress = .08

Note that the summer collections were dissimilar to non-summer collections but there was no similarity between the summer collections. Also, the non-summer collections were more similar to the summer immediately preceding than the one which succeeds them.

Fig. 6.11b UPGMA dendrogram of average community compositions in each season at SV5. Labelling as above. Dashed vertical line denotes chosen cut point.

Dendrogram supports the above interpretation of ordination. Summer collections were distinct from each other as well as from the non-summer collections which group together in groups representing the two years. Non-summer seasons were more closely related to the preceding summer than the one which followed.

Fig. 6.11c SSH ordination of all samples taken from SV5. Each sample (1m² quadrat) is represented by a point on the graph, with the label corresponding to the seasonal collection in which the sample was taken. Labelling as for Fig 6.9a

Stress = .23

While few distinct collection groupings occurred, the bulk of the 1992 samples (collections 1,2,3 & 4) are found toward the bottom right of the plot, and the 1993 samples (collections 5,6,7 & 8) are found toward the top and left hand side. Within these broad groups it is possible to distinguish only the summer collection in each case.

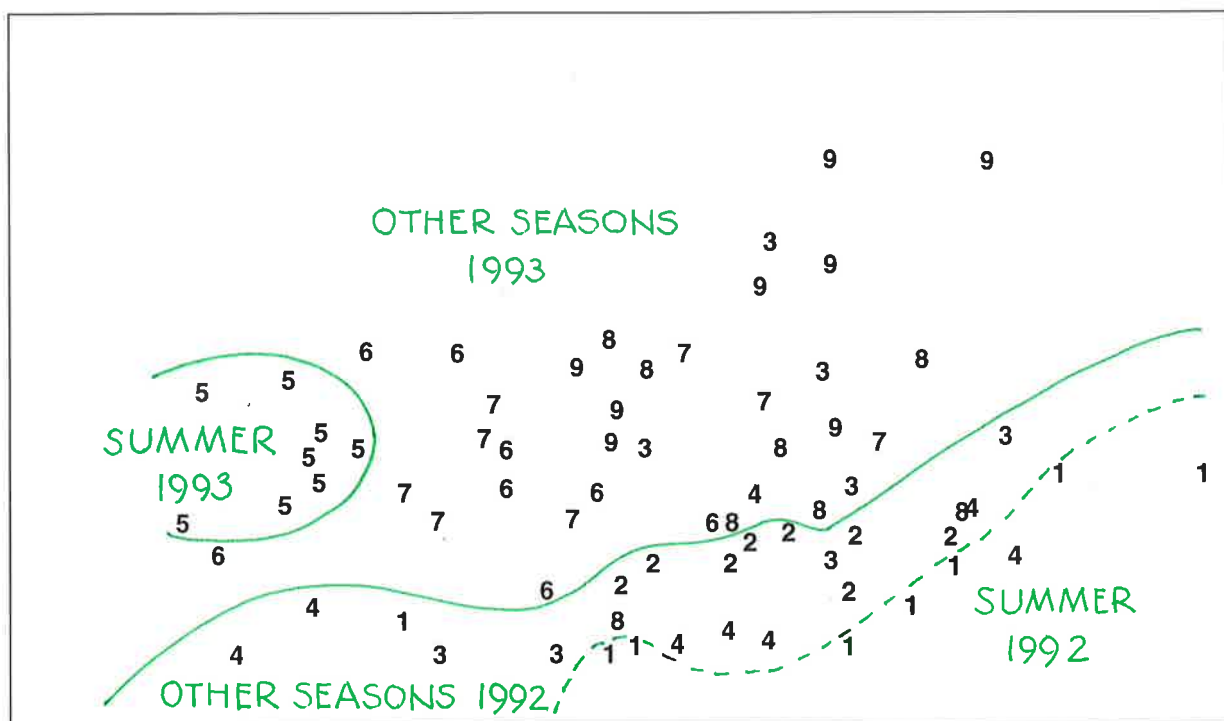
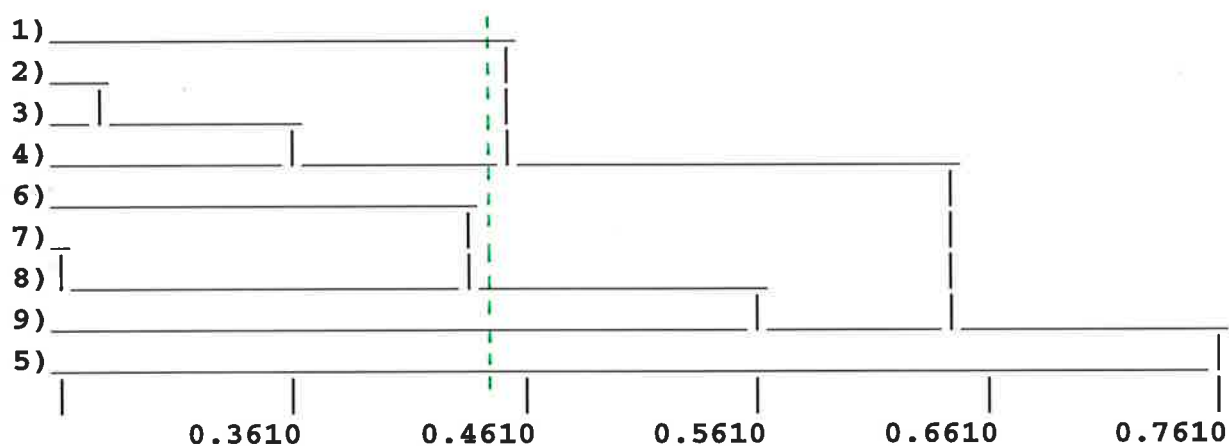
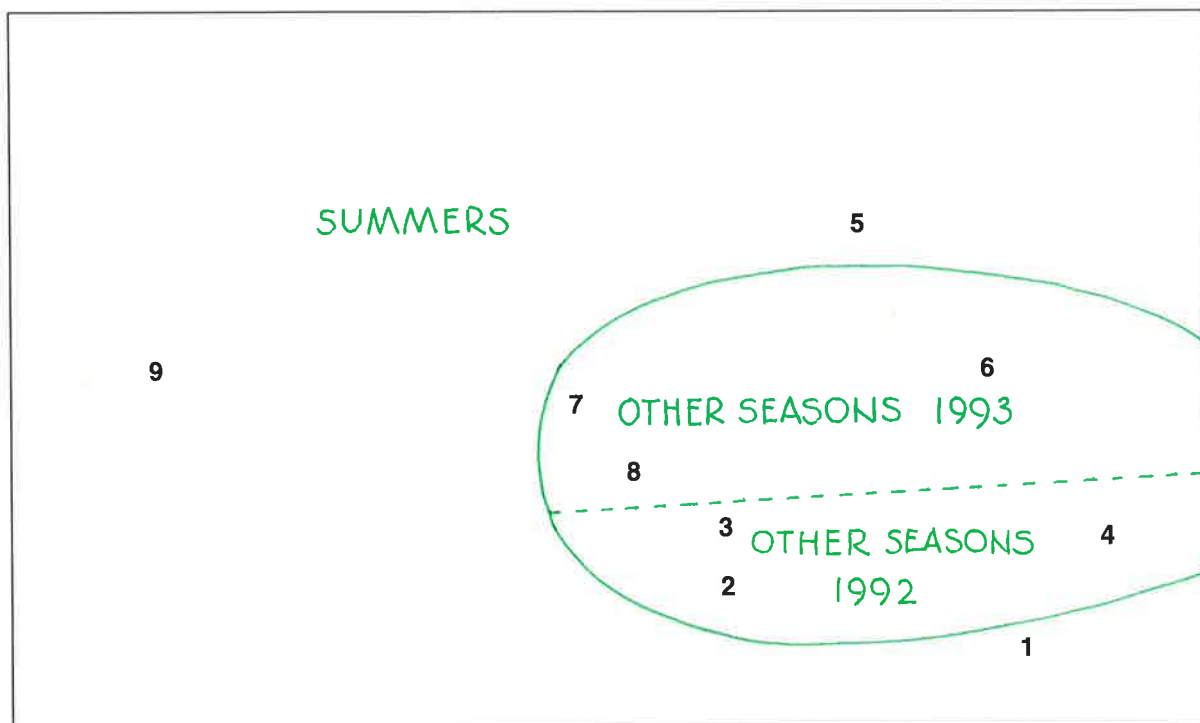


Fig. 6.12a SSH ordination of the average community compositions in each season at CJE5. The numeric labels denote the collection;

- 1 Summer 1992
- 2 Autumn 1992
- 3 Winter 1992
- 4 Spring 1992
- 5 Summer 1993
- 6 Autumn 1993
- 7 Winter 1993
- 8 Spring 1993
- 9 Summer 1994

Stress = .06

The summer collections were dissimilar to non-summer collections (less so in the case of summer 1994) and it appeared that the non-summer collections separate into the two year groups.

Fig. 6.12b UPGMA dendrogram of average community compositions in each season at CJE5. Labelling as above. Dashed vertical line denotes chosen cut point.

Dendrogram does not support the above interpretation of ordination. While it distinguishes the first two summers, the dendrogram is unable to separate the non-summer collections into year groups.

Fig. 6.12c SSH ordination of all samples taken from CJE5. Each sample (1m² quadrat) is represented by a point on the graph, with the label corresponding to the seasonal collection in which the sample was taken. Groupings roughly delineate

- a) summer 1992
- b) summer 1993
- c) summer 1994
- d) non-summer collections of 1992
- e) non-summer collections of 1993

Labelling as for Fig 6.9a

Stress = .26

This ordination supports the distinction of summers from other seasons and the distinction between years of the non summer seasons. However, little can be concluded regarding the similarity of non-summer seasons to the preceding summer because of the similarity of summer 1992 and 1993.

Fig. 6.13a SSH ordination of the average community compositions in each season at B5. The numeric labels denote the collection;

- 1 Summer 1992
- 2 Autumn 1992
- 3 Winter 1992
- 4 Spring 1992
- 5 Summer 1993
- 6 Autumn 1993
- 9 Summer 1994

Stress = .12

The summer collections of were dissimilar to non-summer collections. However, the summer compositions were also quite different to each other.

Fig. 6.13b UPGMA dendrogram of average community compositions in each season at B5. Labelling as above. Dashed vertical line denotes chosen cut point.

Dendrogram supports the above interpretation of ordination. Summers were distinct from all non-summer collections, as was spring 1992.

Fig. 6.13c SSH ordination of all samples taken from B5. Each sample (1m² quadrat) is represented by a point on the graph, with the label corresponding to the seasonal collection in which the sample was taken. Groupings roughly delineate

- a) Most of the samples from the first two summers
- b) The remainder of the samples

Labelling as for Fig 6.9a

Stress = .20

This ordination indicates that while the community composition in summer was generally distinct from the non-summer collections, there was a large degree of spatial variation involved. This resulted in 3 of the summer 1992 samples being more similar to the "non-summer" samples.

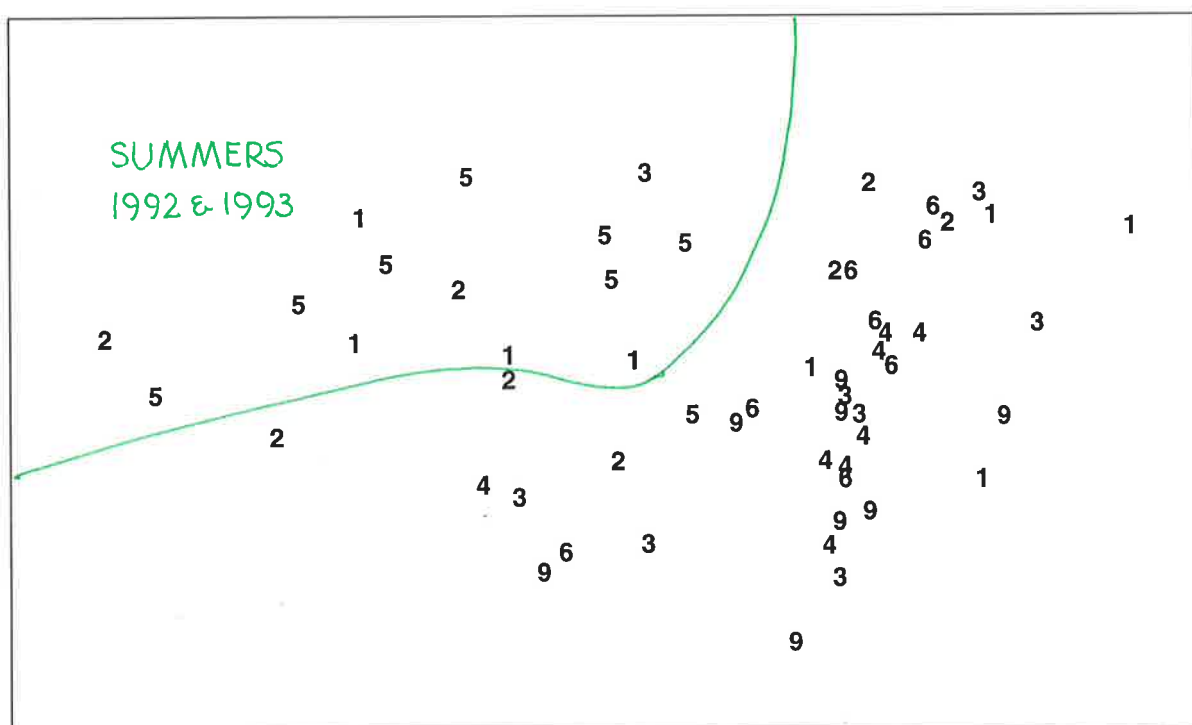
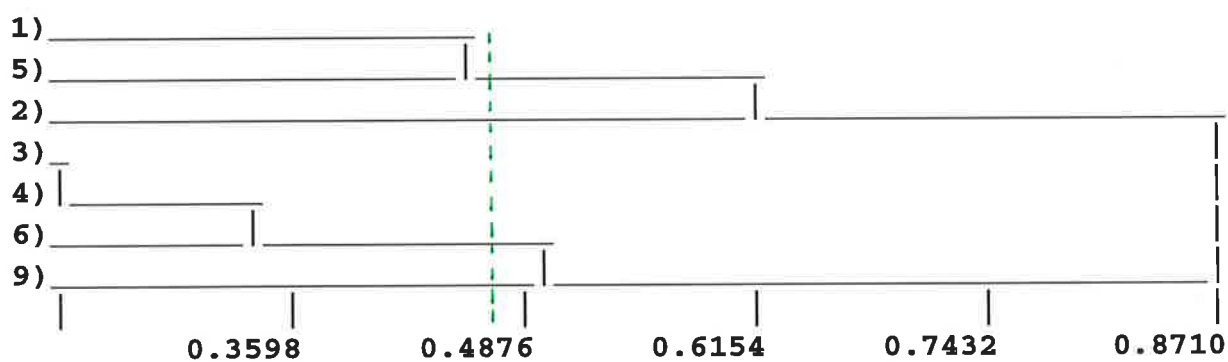
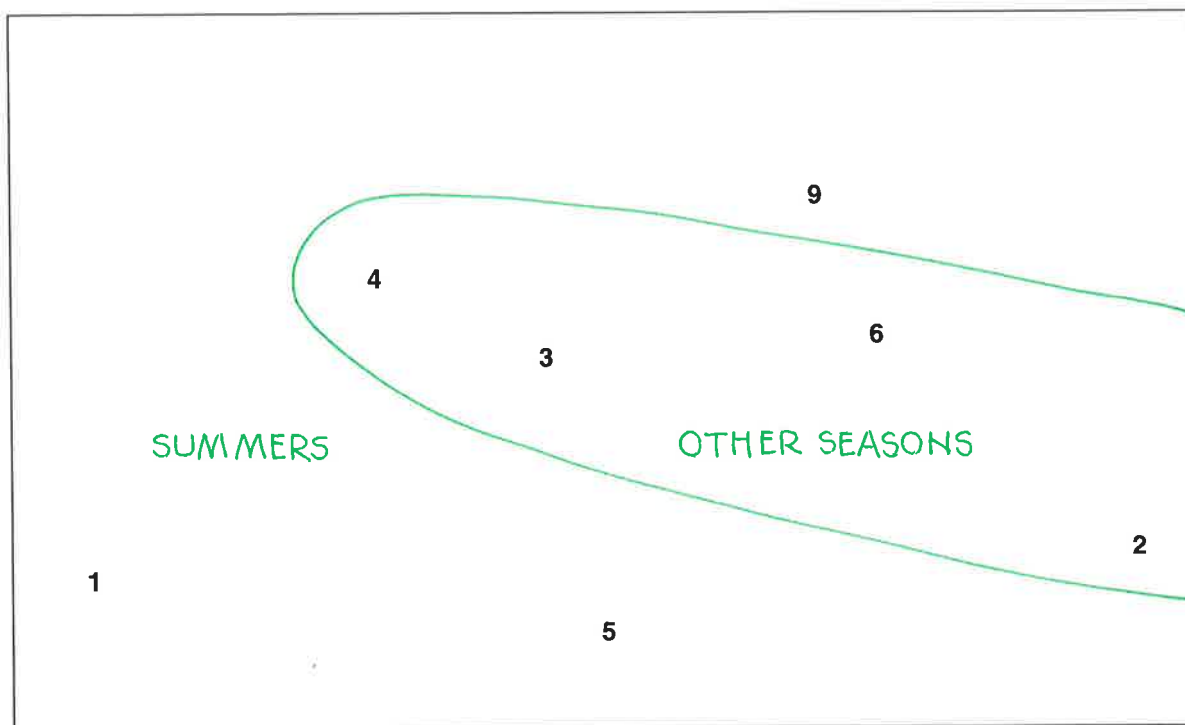


Fig. 6.14a SSH ordination of the average community compositions in each season at WI9. The numeric labels denote the collection;

- 1 Summer 1992
- 2 Autumn 1992
- 3 Winter 1992
- 4 Spring 1992
- 5 Summer 1993
- 6 Autumn 1993
- 9 Summer 1994

Stress = .12

With so few points on the plot, and no real outliers, it is difficult to interpret this ordination, other than to say that the summer 1992 and 1994 collections appear similar and could be considered distinct from the other collections. However, this means accepting that collections 2, 4 and 6 are distinct, which makes the interpretation pointless. Thus, no solid conclusion can be drawn from this ordination.

Fig. 6.14b UPGMA dendrogram of average community compositions in each season at WI9. Labelling as above. Dashed vertical line denotes chosen cut point.

Dendrogram indicates that summer 1992 and 1994 were similar and distinct from the other sites, but autumn and spring 1992 are also separate. For the reasons outlined above, again no solid conclusion could be drawn.

Fig. 6.14c SSH ordination of all samples taken from WI9. Each sample (1m² quadrat) is represented by a point on the graph, with the label corresponding to the seasonal collection in which the sample was taken. Envelopes represents the bulk of the autumn 1993 samples and the bulk of the autumn 1992 samples.

Labelling as for Fig 6.9a

Stress = .18

Only autumn 1992 and to a lesser extent autumn 1993 appeared distinguishable when within collection variation was taken into account

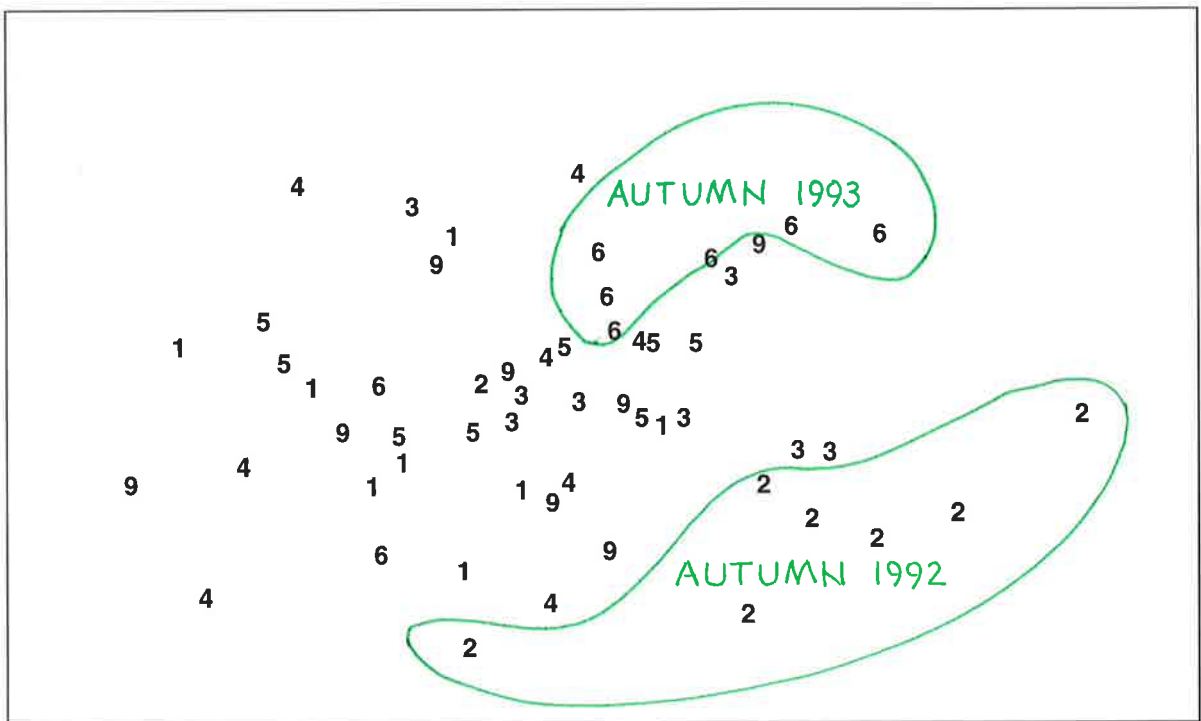
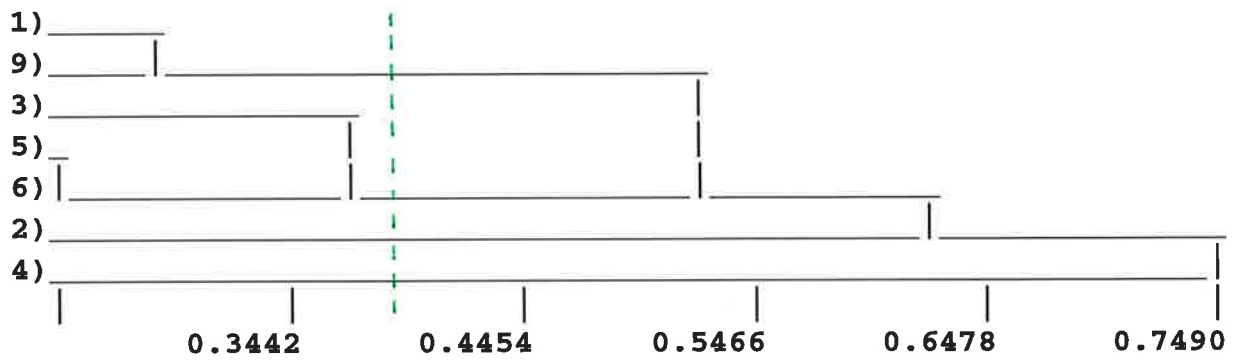
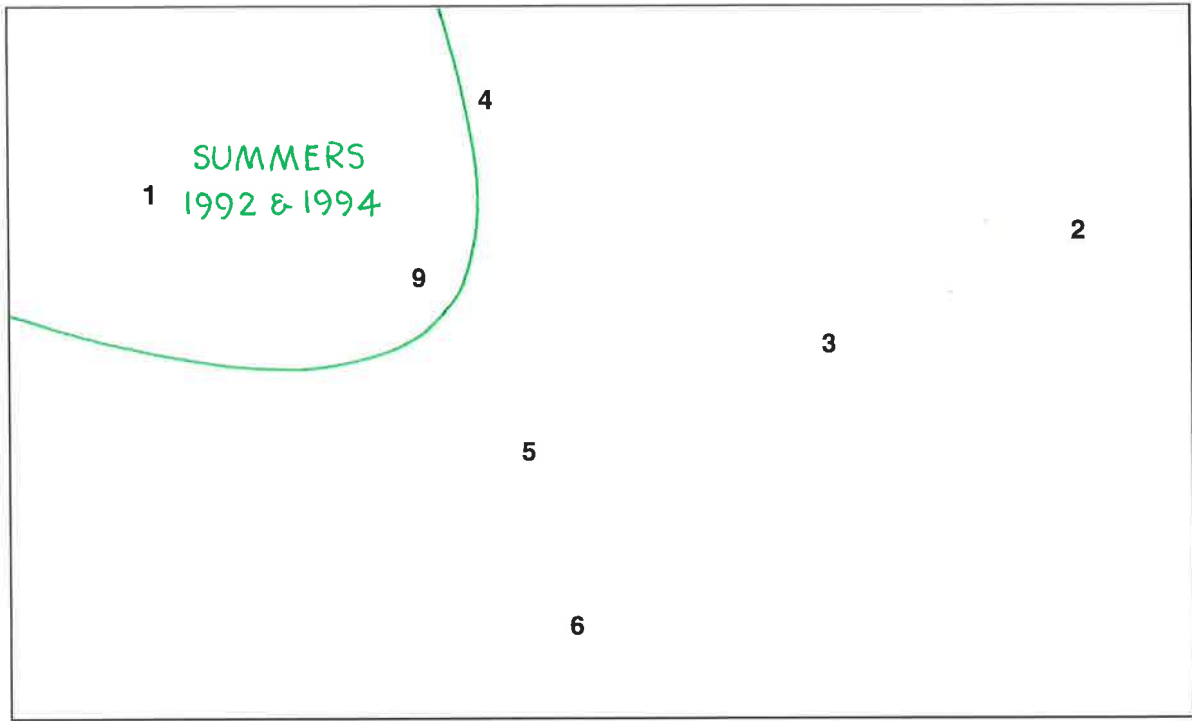


Fig. 6.15a SSH ordination of the average community compositions in each season at WI5. The numeric labels denote the collection;

- 1 Summer 1992
- 2 Autumn 1992
- 3 Winter 1992
- 4 Spring 1992
- 5 Summer 1993
- 6 Autumn 1993
- 9 Summer 1994

Stress = .04

While the summers appeared distinct from non-summer collections, it is difficult to interpret this ordination because of the lack of any clear groups.

Fig. 6.15b UPGMA dendrogram of average community compositions in each season at WI5. Labelling as above. Dashed vertical line denotes chosen cut point.

Dendrogram indicates that summer and spring 1992 and summer 1994 formed a group which is different from the composition at other times. Summer 1993 also appeared quite different from the bulk of the collections.

Fig. 6.15c SSH ordination of all samples taken from WI5. Each sample (1m² quadrat) is represented by a point on the graph, with the label corresponding to the seasonal collection in which the sample was taken. Envelope represents the bulk of the autumn 1992 and 1993 samples.

Labelling as for Fig 6.9a.

Stress = .23

Within collection variation was quite considerable for most seasonal collections. The only reasonably distinct group was one which comprised autumn 1992 and 1993.

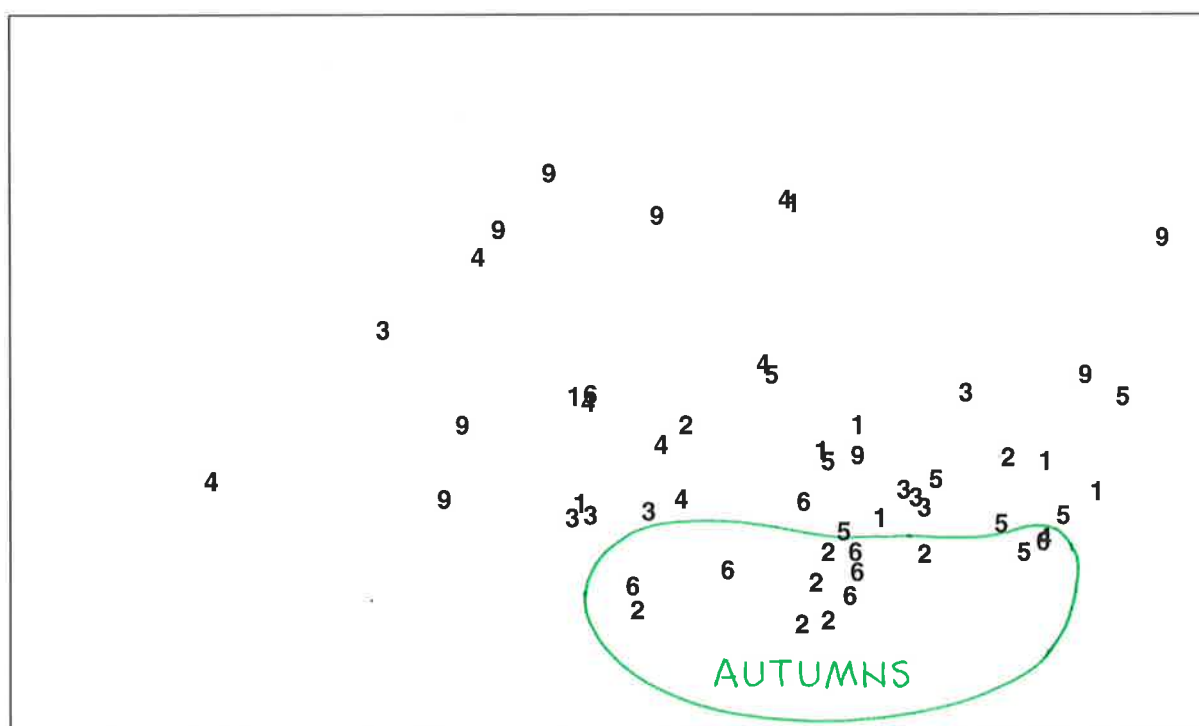
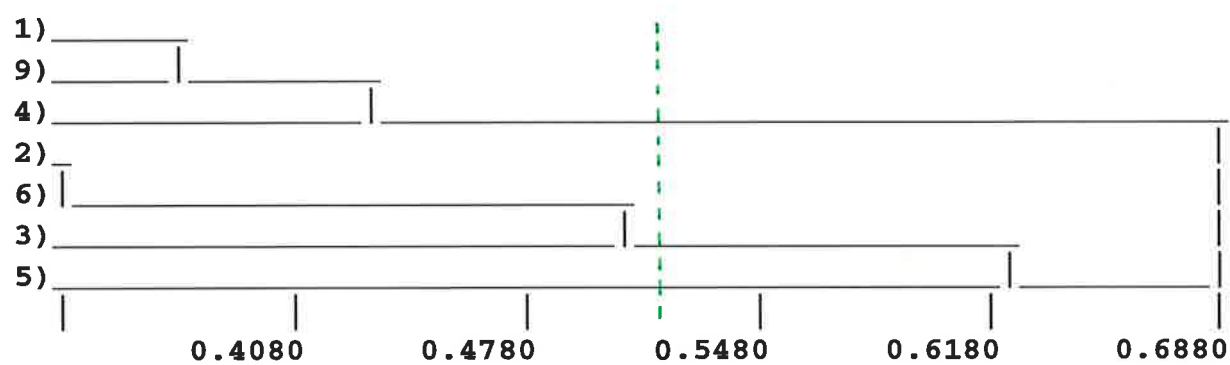
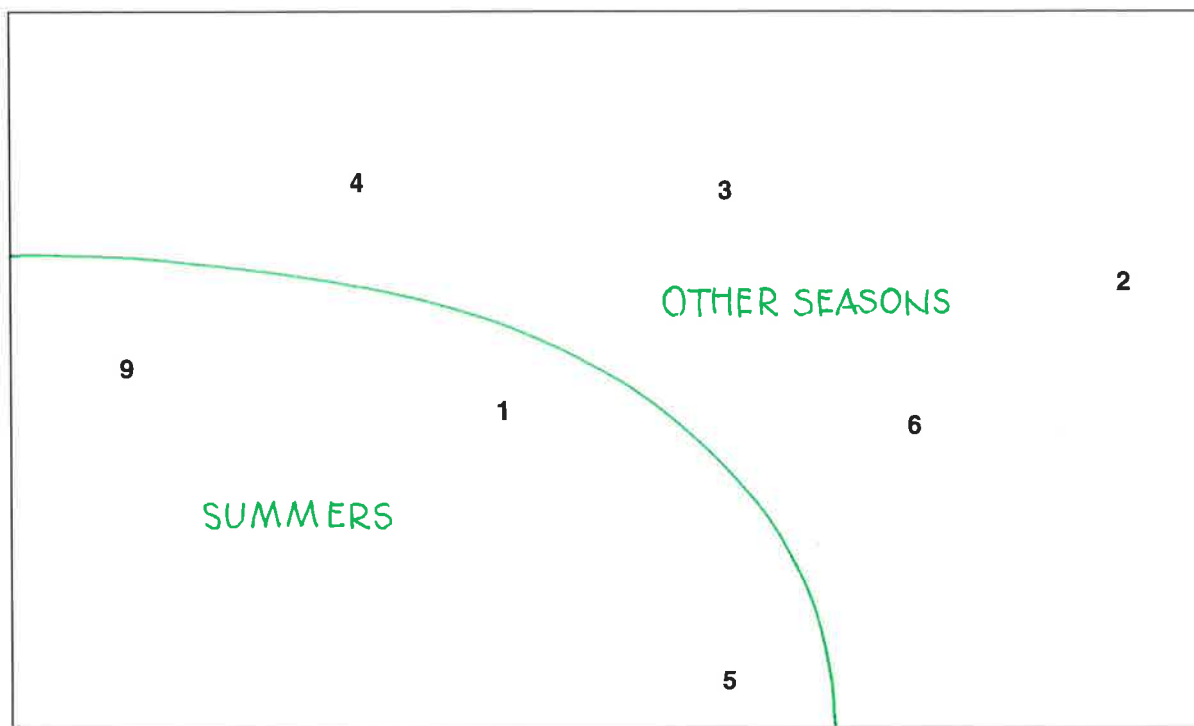


Fig. 6.16a SSH ordination of the average community compositions in each season at CJN9. The numeric labels denote the collection;

- 1 Summer 1992
- 2 Autumn 1992
- 3 Winter 1992
- 4 Spring 1992
- 5 Summer 1993
- 6 Autumn 1993
- 9 Summer 1994

Stress = .12

There appears to be no particular pattern to the temporal fluctuations of the community at CJN9. The final two collections appeared quite dissimilar to the bulk of the points representing the community composition at other times.

Fig. 6.16b UPGMA dendrogram of average community compositions in each season at CJN9. Labelling as above.

The "chaining" effect in the dendrogram indicates that there were no strong groupings.

Fig. 6.16c SSH ordination of all samples taken from CJN9. Each sample (1m² quadrat) is represented by a point on the graph, with the label corresponding to the seasonal collection in which the sample was taken.

Labelling as for Fig 6.9a

Stress = .23

None of the seasonal collections nor groups of these were particularly distinct.

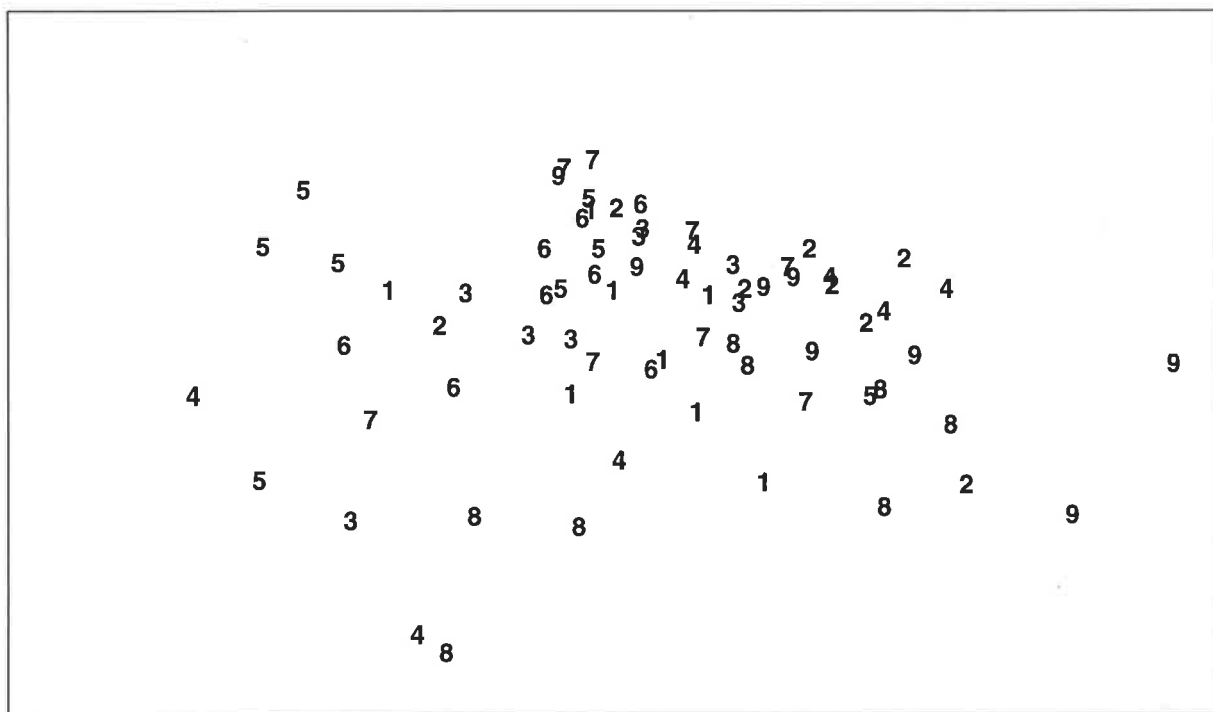
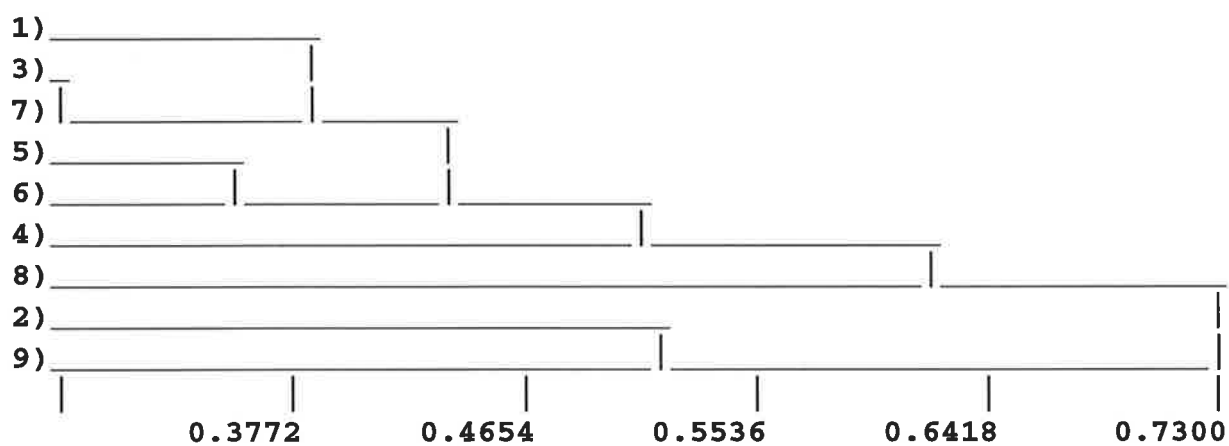
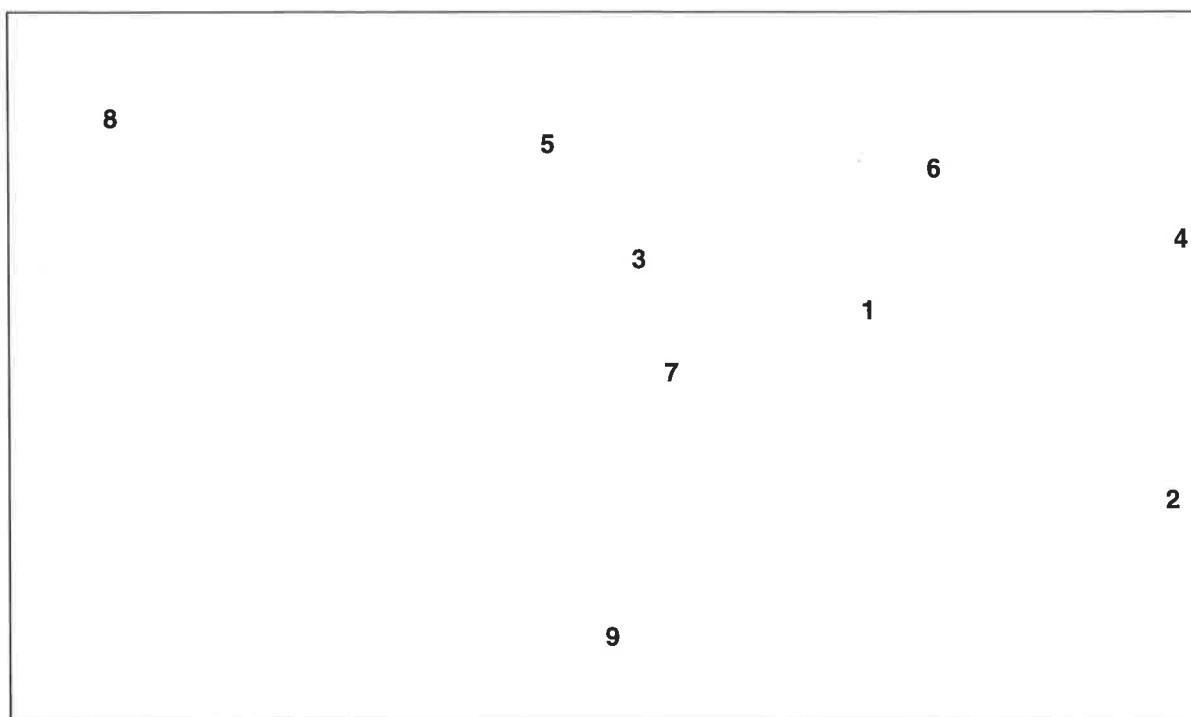


Fig. 6.17a SSH ordination of the average community compositions in each season at GI5. The numeric labels denote the collection;

1	Summer 1992
2	Autumn 1992
3	Winter 1992
4	Spring 1992
5	Summer 1993
6	Autumn 1993
9	Summer 1994

Stress = .09

There appeared to be no particular pattern to the temporal fluctuations of the community at GI5. The final collection appeared quite dissimilar to the bulk of the points representing the community composition at other times.

Fig. 6.17b UPGMA dendrogram of average community compositions in each season at GI5. Labelling as above.

The "chaining" effect in the dendrogram indicates that there are no strong groupings with the exception of summer 1994 which was, quite different to the remainder of the collections.

Fig. 6.17c SSH ordination of all samples taken from GI5. Each sample (1m² quadrat) is represented by a point on the graph, with the label corresponding to the seasonal collection in which the sample was taken. Envelope demonstrates the distinct composition of the community in summer 1994.

Labelling as for Fig 6.9a

Stress = .17

None of the seasonal collections nor groups of these were particularly distinct with the exception of summer 1994.

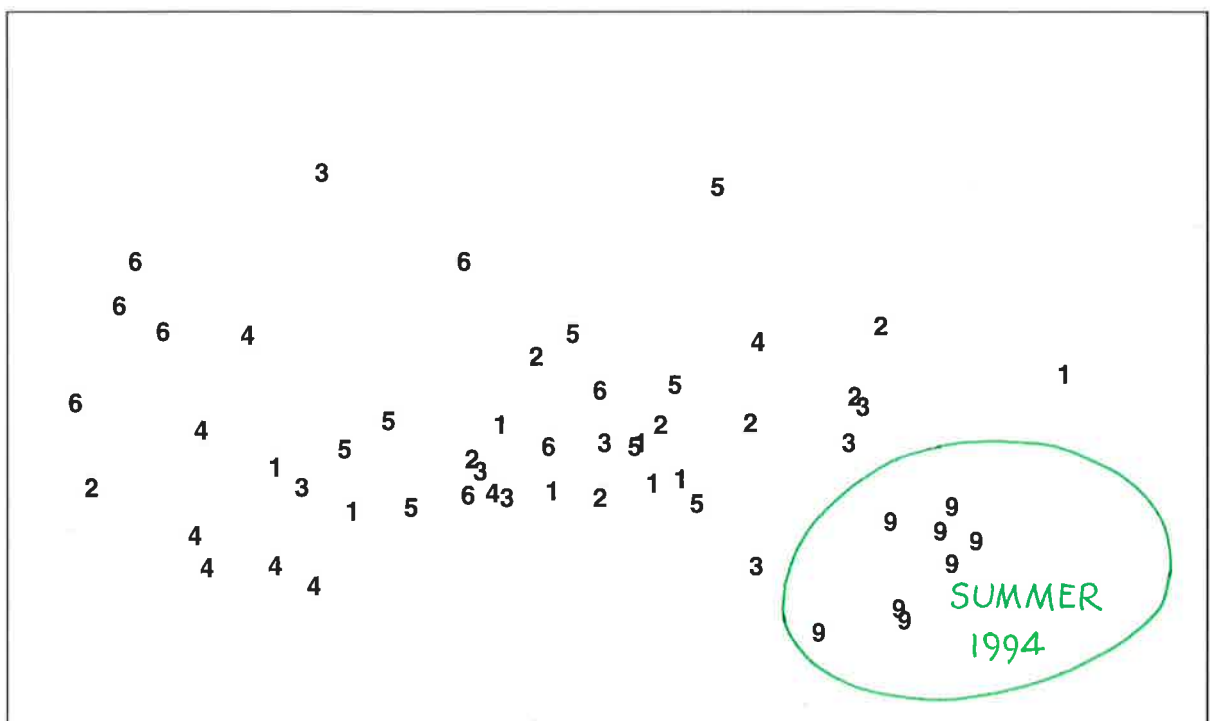
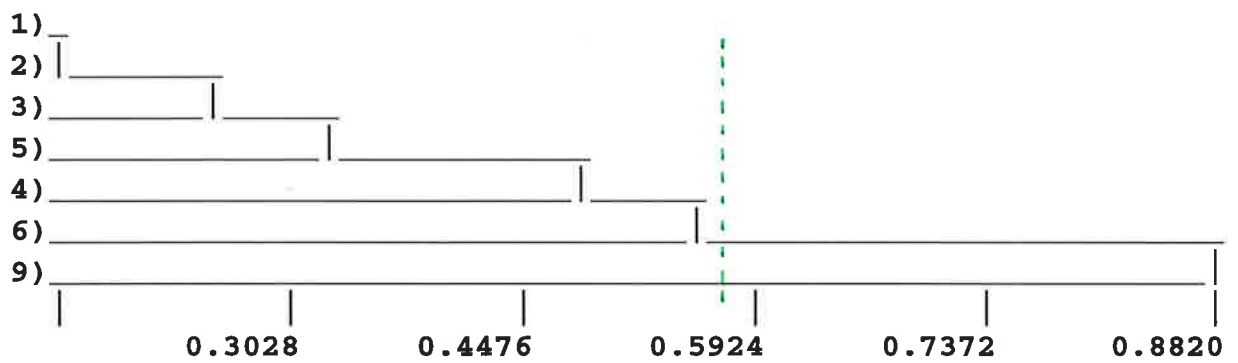
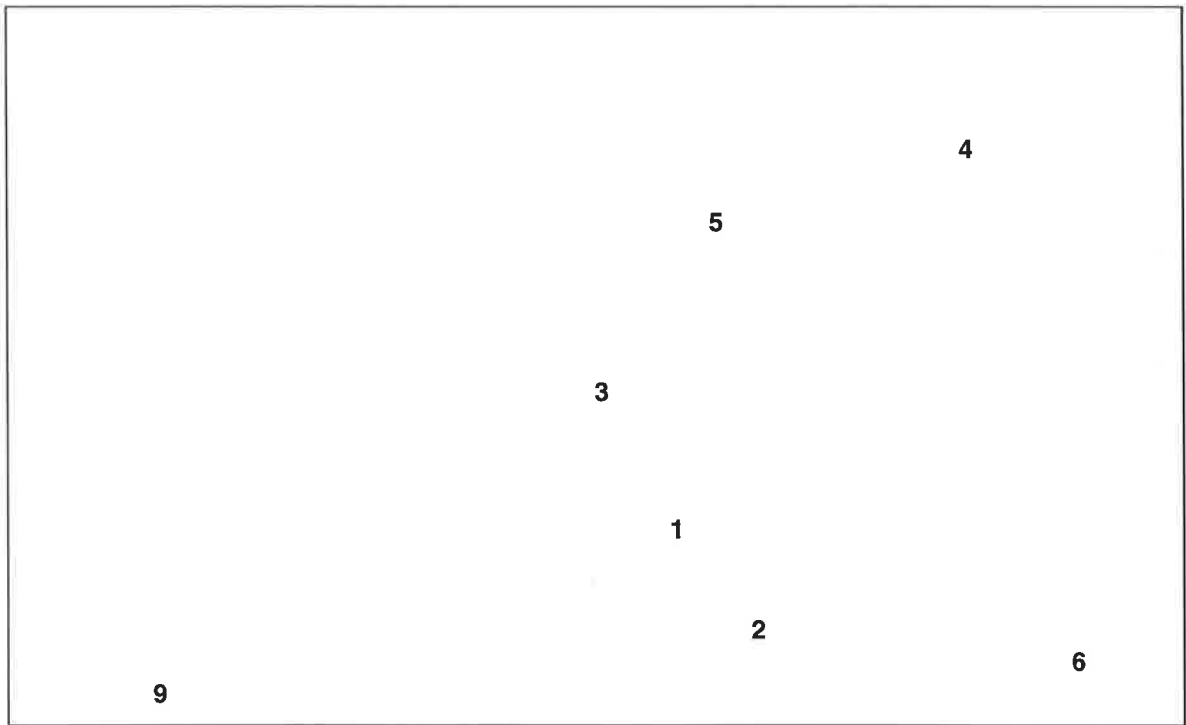
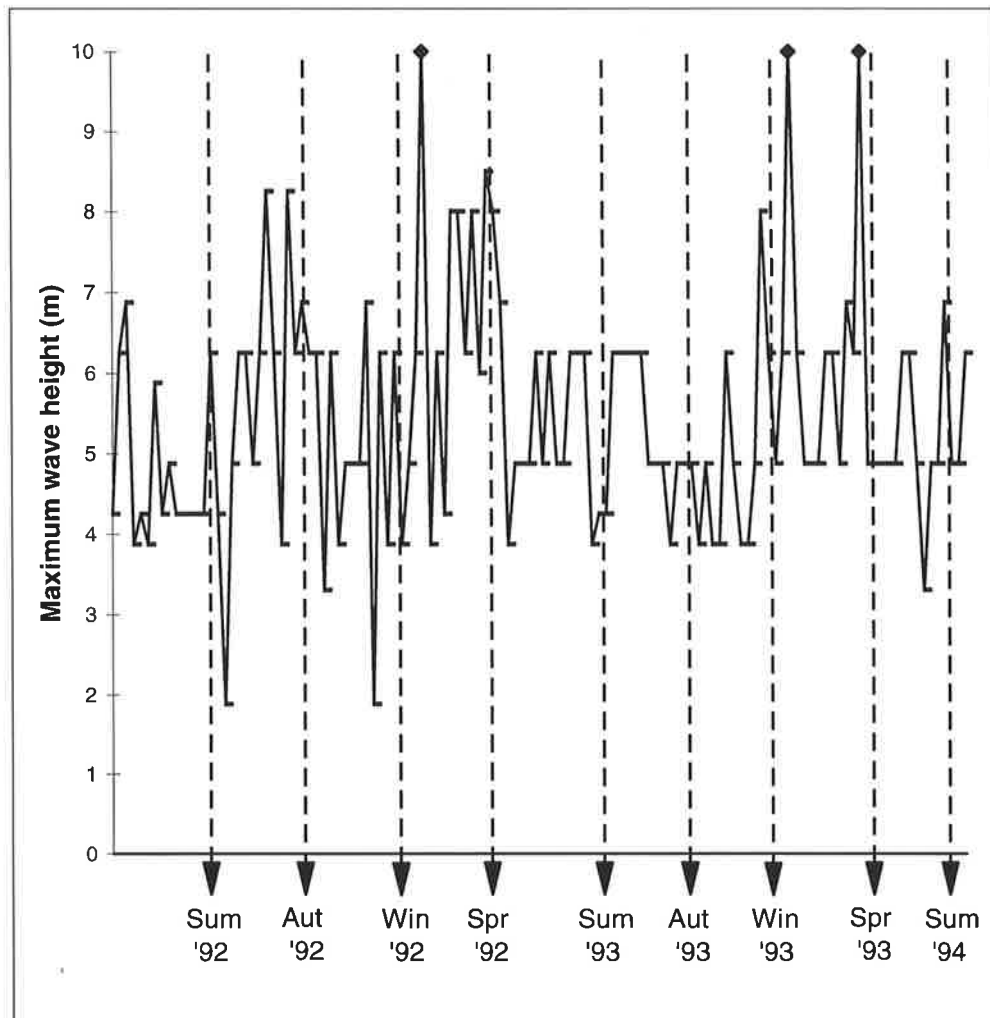


Fig. 6.18 Storm events across the timecourse of the study. This plot was created from the sea state records recorded at Cape Willoughby on Kangaroo Island and maintained by the Bureau of Meteorology. The points represent the maximum possible wave height for each week. They are calculated by the addition of the estimated swell height and the estimated sea height. Having made this calculation for each day, the maximum for the week was recorded and plotted. While it is unlikely that any wave actually achieved this height, it allows an estimate of the relative state of the sea at different times of the year. The dashed vertical lines represent the times when sampling occurred.

The principal period of extreme storm activity was prior to the spring collection in each year.



Chapter 7

Table 7.1a Composition of the Cape Jervis East canopy (small scale survey) by weight. Biomass (g dwt m⁻²) of each species and the percentage of the total biomass which each species comprised are presented.

The bulk of the biomass was contributed by fucoid species, particularly *Cystophora* spp.

Table 7.1b Composition of the canopy of the small Cape Jervis North harvest by weight. Biomass (g dwt m⁻²) and the percentage of total biomass which each species comprised are presented.

Seirococcus dominated this harvest.

Table 7.1c Composition of the canopy of the larger Cape Jervis North harvest by weight. Biomass (g dwt m⁻²) and the percentage of total biomass which each species comprised are presented.

Seirococcus and *Ecklonia* dominated this harvest.

Species	Biomass	Percentage
<i>Cystophora expansa</i>	91.4	31
<i>Cystophora subfarcinata</i>	64.9	22
<i>Cystophora moniliformis</i>	41.5	14
<i>Cystophora monilifera</i>	40.4	14
<i>Sargassum varians</i>	21.6	7
<i>Sargassum linearifolium</i>	14.1	5
<i>Sargassum verruculosum</i>	13.9	5
<i>Sargassum fallax</i>	5.5	2
<i>Acrocarpia paniculata</i>	3.5	1
<i>Sargassum decipiens</i>	0.6	<.5
<i>Cystophora brownii</i>	0.3	<.5
<i>Ecklonia radiata</i>	<.1	<.5
Total	297.6	

Species	Biomass	Percentage
<i>Seirococcus axillaris</i>	647.9	82
<i>Sargassum fallax</i>	43.3	5
<i>Ecklonia radiata</i>	39.6	5
<i>Acrocarpia paniculata</i>	23.3	3
<i>Sargassum linearifolium</i>	19.2	2
<i>Scytothalia dorycarpa</i>	4.2	1
<i>Cystophora expansa</i>	5.5	1
<i>Cystophora subfarcinata</i>	0.2	<.5
<i>Sargassum varians</i>	3.6	<.5
<i>Sargassum decipiens</i>	3.1	<.5
Total	791.7	

Species	Biomass	Percentage
<i>Seirococcus axillaris</i>	351.6	51
<i>Ecklonia radiata</i>	189.7	28
<i>Sargassum linearifolium</i>	34.5	5
<i>Cystophora expansa</i>	33.9	5
<i>Sargassum varians</i>	21.7	3
<i>Acrocarpia paniculata</i>	18.9	3
<i>Sargassum fallax</i>	15.5	2
<i>Sargassum verruculosum</i>	13.5	2
<i>Sargassum decipiens</i>	2.8	<.5
<i>Cystophora subfarcinata</i>	2	<.5
Total	684.1	

Table 7.2a Total sweep area of each species of the CJE small scale exercise. The combined sweep area of all individuals of a species calculated as the sum of the areas swept by each individual. By dividing by the area from which the plants came, the measure is standardised. Units are therefore m² sweep per m² substratum.

Cystophora species dominated, particularly *C. expansa* and *C. moniliformis*. The total sweep area demonstrated that, on average, any point was swept by more than 17 individuals.

Table 7.2b Total sweep area of each species of the CJN (1m x 1m) small scale harvest. Calculation and layout as described above.

Seirococcus dominated in terms of sweep area, contributing 86% of the sweeping. Total sweep area indicated that any point is swept by more than 9 individuals on average.

Table 7.2c Total sweep area of each species of the CJN (2m x 2m) small scale harvest. Calculation and layout as described above.

This harvest was co-dominated by three species; *Seirococcus*, *Ecklonia* and *Cystophora expansa*. Despite the difference in composition, the total sweep area was nearly identical to the smaller CJN harvest. It was however, only half that of the *Cystophora* dominated CJE harvest.

Species	Sweep area per m ²	Percentage
<i>Cystophora expansa</i>	6.34	36
<i>Cystophora moniliformis</i>	4.71	27
<i>Cystophora subfarcinata</i>	3.29	19
<i>Cystophora monilifera</i>	3.14	18
<i>Cystophora brownii</i>	0.03	<.5
<i>Ecklonia radiata</i>	<.01	<.5
Total	17.52	

Species	Sweep area per m ²	Percentage
<i>Seirococcus axillaris</i>	8.25	86
<i>Ecklonia radiata</i>	0.54	6
<i>Cystophora expansa</i>	0.47	5
<i>Acrocarpia paniculata</i>	0.34	4
Total	9.60	

Species	Sweep area per m ²	Percentage
<i>Seirococcus axillaris</i>	3.86	40
<i>Cystophora expansa</i>	2.55	27
<i>Ecklonia radiata</i>	2.39	25
<i>Acrocarpia paniculata</i>	0.76	8
<i>Cystophora subfarcinata</i>	0.02	<.5
Total	9.57	

Table 7.3a Pielou's aggregation analysis at CJE. The significance of Pielou's α as tested against a chi square distribution for each species, and *Cystophora* as a genus (which essentially represented the entire canopy).

Both the canopy as a whole and each of the individual species were aggregated.

Table 7.3b Pielou's aggregation analysis at CJNI (1m x 1m). The significance of Pielou's α as tested against a chi square distribution for *Seirococcus* and the canopy as a whole. Only *Seirococcus* occurred in great enough abundance to make it worth analysing.

Seirococcus and the canopy as a whole were aggregated.

Table 7.3c Pielou's aggregation analysis at CJNI (2m x 2m). The significance of Pielou's α as tested against a chi square distribution for each species, and the canopy as a whole

Canopy as a whole was aggregated, as were each of the canopy species.

Species	Alpha	Chi sq	p
All <i>Cystophora</i> sp	3.27	326	<.001
<i>C.expansa</i>	3.14	314	<.001
<i>C. monilifera</i>	2.12	212	<.001
<i>C. moniliformis</i>	4.34	434	<.001
<i>C.subfarcinata</i>	2.51	251	<.001

Species	Alpha	Chi sq	p
All Species	1.92	192	<.001
<i>Seirococcus axillaris</i>	1.88	188	<.001

Species	Alpha	Chi sq	p
All Species	1.87	187	<.001
<i>Seirococcus axillaris</i>	1.5	150	<.001
<i>Ecklonia radiata</i>	2.98	298	<.001
<i>Cystophora expansa</i>	2.94	294	<.001

Table 7.4a Mean / variance ratio at CJE at 10cm, 20cm and 50cm scales. The mean to variance ratio was calculated for both abundance and biomass at a scale of 10cm x 10cm, and then by aggregating subquadrats, at scales of 20cm x 20cm and 50cm x 50cm. Pooled chi represents the aggregation of the canopy as a whole, and "heterogeneity chi" is a demonstration of the level of segregation of the species. Statistic is tested against chi squared distribution (after Jumars 1975a; see text for details).

Significant aggregation of the canopy occurred at all scales in terms of both biomass and abundance. Additionally, in all cases, there was significant segregation of the species - ie the relative contribution of the species to the total varied across subquadrats.

Table 7.4b Mean / variance ratio at CJN (1m x 1m) at 10cm, 20cm and 50cm scales. Details as above.

Again, aggregation occurred at all scales in terms of abundance and biomass, and again, the species were segregated at all scales.

Table 7.4c Mean / variance ratio at CJN (2m x 2m) at 10cm, 20cm and 50cm scales. Details as above.

Aggregation occurred at all scales in terms of abundance and biomass, and again, the species were segregated at all scales.

Measure & Scale	Pooled Chi	Pooled p	Heterogeneity Chi	Heterogeneity p
Biomass 10 x 10	3437	<.001	11323	<.001
Abundance 10 x 10	1222	<.001	1638	<.001
Biomass 20 x 20	786	<.001	3209	<.001
Abundance 20 x 20	386	<.001	467	<.001
Biomass 50 x 50	302	<.001	691	<.001
Abundance 50 x 50	229	<.001	151	<.001

Measure & Scale	Pooled Chi	Pooled p	Heterogeneity Chi	Heterogeneity p
Biomass 10 x 10	9171	<.001	7338	<.001
Abundance 10 x 10	143.9	<.005	762	<.001
Biomass 20 x 20	2279	<.001	1804	<.001
Abundance 20 x 20	137.8	<.001	704.6	<.001

Measure & Scale	Pooled Chi	Pooled p	Heterogeneity Chi	Heterogeneity p
Biomass 10 x 10	17744.9	<.001	33164.2	<.001
Abundance 10 x 10	237.5	<.05	1070.2	<.001
Biomass 20 x 20	15314.5	<.001	34535.9	<.001
Abundance 20 x 20	294.1	<.001	1188.4	<.001
Biomass 50 x 50	609.2	<.001	1280.1	<.001
Abundance 50 x 50	15.1	<.05	60.4	<.001

Table 7.5 Number of species which demonstrated maximum variance at each scale.

This table summarises, for each scale, how many species (including the total) demonstrated maximum variance in biomass and abundance.

It was the smallest (2m) scale at which most species demonstrated maximum variance, and the largest (2km) scale where fewest species display maximum variance.

Scale	Biomass	Abundance
2000	2	1
200	4	4
20	6	5
2	18	10
Total	30	20

Fig. 7.1a Relationship of CJE small scale harvest to samples of temporal study. NMDS ordination of all samples from CJE5 in the temporal study and the CJE small scale spatial study. The point "X" represents the small scale harvest, with each of the other points representing samples from temporal collections. The number used to label the points indicate the collection from which the samples originate. Labelling system is as described in Fig 4.2a. Collection numbers 1, 5 and 9 represent the 1992, 1993 and 1994 summer collections. Stress = 0.24, which is high by the standard of Kruskal (1964b), but Clarke and Warwick (1994) contend that this does not invalidate the analysis.

The small scale collection was typical of a summer collection at this site.

Fig. 7.1b Relationship of CJN small scale harvests to samples of temporal study. NMDS ordination of all samples from CJN5 in the temporal study and the CJN small scale spatial studies. The points "Y" and "Z" represent the 1m x 1m and 1m x 2m small scale harvests respectively, with the numbered points representing samples from temporal collections. The numbers used to label the points indicate the collection from which the samples originated. Labelling system is as described in Fig 4.2a. Collection numbers 1, 5 and 9 represent the 1992, 1993 and 1994 summer collections. Stress = 0.25

The small scale collections were typical of this site.

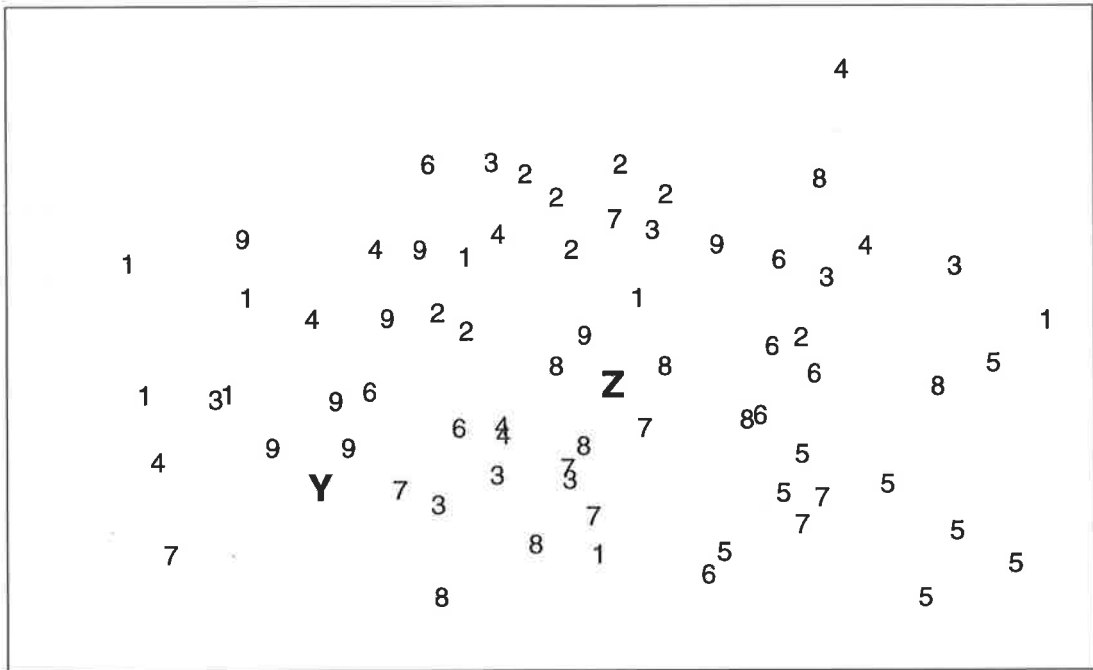
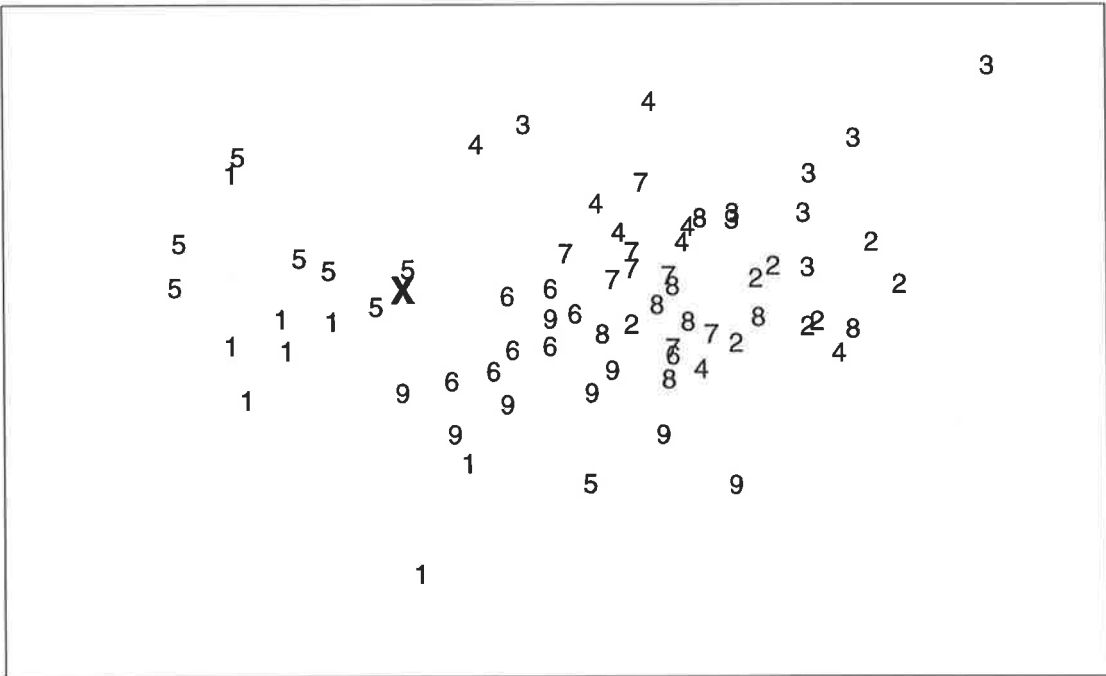


Fig 7.2a Relationship between understorey richness and sweep intensity at CJE. Each subquadrat was scored for the number of individuals which swept over it and the species richness of its understorey. Subquadrats within 40cm of the edge were not considered as sweeping from plants outside the sample could not be assessed. Each point on the plot represents a subquadrat.

There did not appear to be any clear relationship. An apparent intermediate maximum could not be supported because there were only three particularly rich quadrats.

Fig 7.2b Relationship between understorey richness and sweep intensity at CJN.

Layout as described above. In this instance, subquadrats from both CJN harvests were scored for the number of individuals which swept over it and the species richness of its understorey. Each point on the plot represents a subquadrat.

There did not appear to be any clear relationship. An intermediate maximum may have existed, but with only four species rich quadrats, the conclusion would be extremely tenuous.

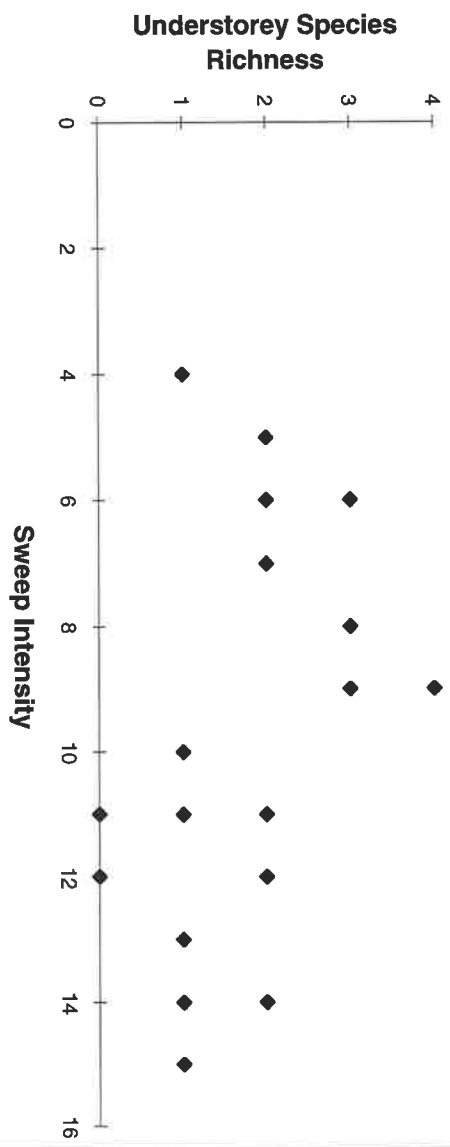
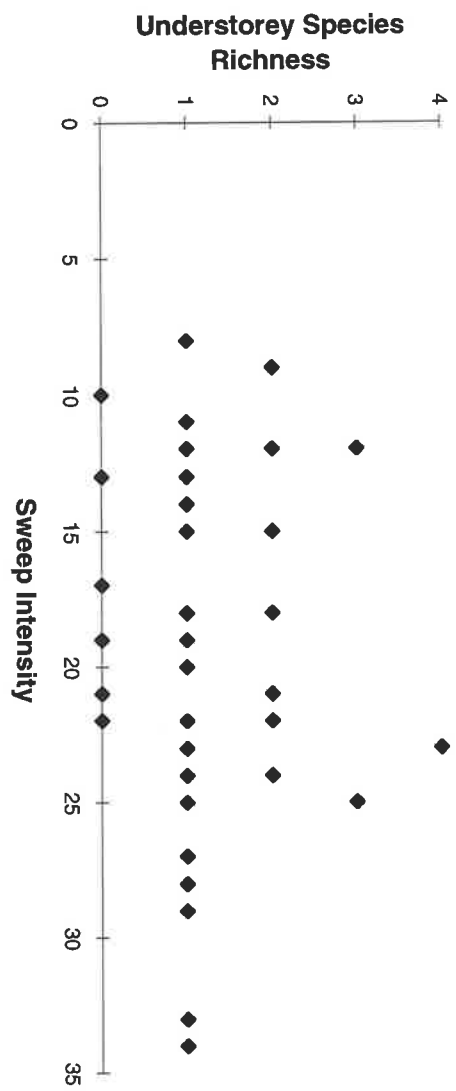


Fig. 7.3a Graphical representation of the variation of total biomass across CJE harvest. This representation demonstrates the relative total biomass of each of the subquadrats. The highest biomass for any subquadrat was 35.2 g dwt.

Total biomass was highly variable, with the highest biomass subquadrats often having neighbouring subquadrats which supported no canopy. There appeared to be a patch of about 1m to 2m in length, toward the centre which was more likely to contain high biomass subquadrats than the remainder of the harvest area.

Fig. 7.3b Variation of total biomass across the CJN (1m x 1m) harvest. Layout as above, with the highest subquadrat supporting a total biomass of 172g dwt.

Again, total biomass was highly variable at the scale of the subquadrat. It was common for high biomass subquadrats to be neighboured by subquadrats supporting no canopy plants. However, the area was too small to draw conclusions about patch size.

Fig. 7.3c Variation of total biomass across the CJN (2m x 2m) harvest. Layout as above, with the highest subquadrat supporting a total biomass of 196g dwt.

Total biomass was highly variable at the scale of the subquadrat. There appeared to be a patch, approximately 1m in length, which was more likely to contain high biomass subquadrats than the remainder of the harvest area. This may, however, have been one end of a larger patch which extended outside the harvested area.

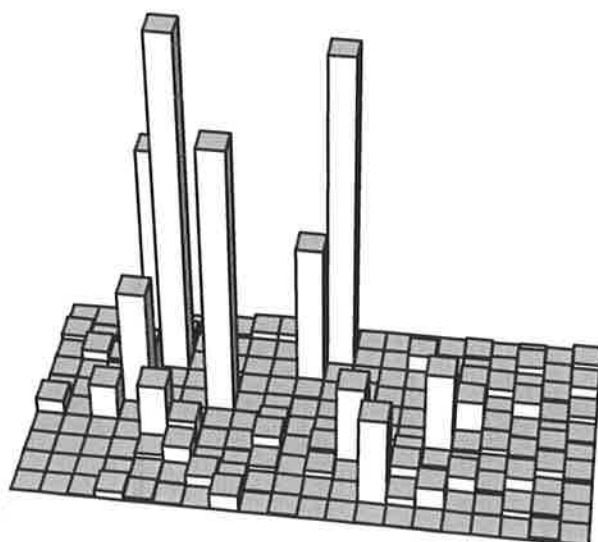
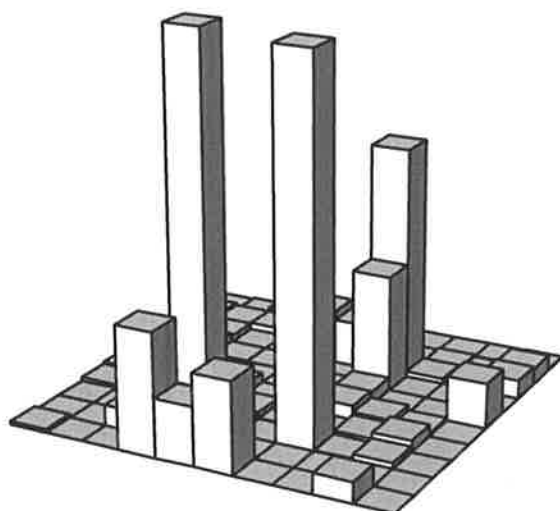
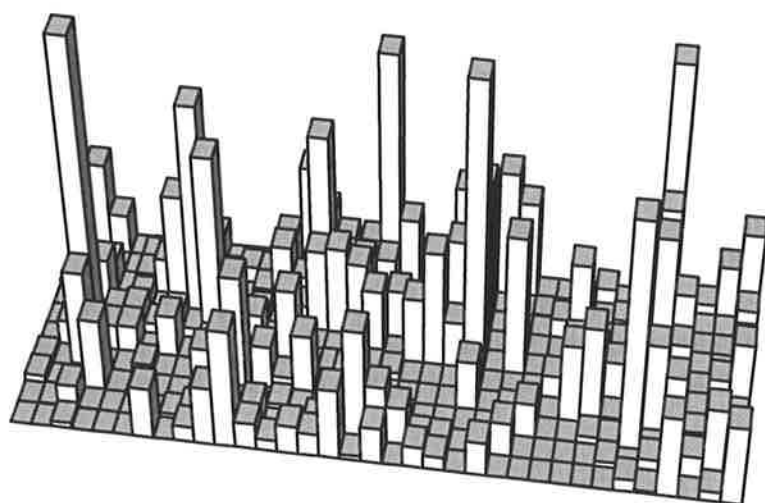


Fig. 7.4 Example of the patchiness of a single species. The abundance of *Cystophora expansa* at CJE is presented as an example to demonstrate how patchy the distribution of these plants was. Each dot represents a single *C. expansa* plant. Light grey patches indicate quadrats that support only understorey, and dark grey patches are devoid of both canopy and understorey.

This aggregation was typical of all common species. While there was clearly an area in which high abundance quadrats were more likely, there was enormous variance within this patch; it was quite common for a high abundance subquadrat to neighbour a quadrat with no canopy at all. Although it was not possible to portray it on the figure, plants in high density quadrats were generally of similar length, indicating that they probably belonged to a single cohort.

	0	1	2	3	4	5	6	7	8	9
0	•	•			•••	■	■	■	•	•
1				■		■				
2			■	■	■			•		
3			■	•	•		•		•	
4		•			•			■		
5					•		•	■		
6							•		■	■
7			■	•				■	■	
8					•	•			■	■
9	■				■			■	■	
10	■		■		■			•		
11	•	■	■	■			••	••		■
12	•••	■	■	■	■	■	■	■	•	
13	•••				•••	••		•	■	■
14	•••	•••			••	•	■		•	
15		•	■	•			■	■		
16	■			••	•	■			•	■
17	••	•	■				■		•	•
18	•••	•	■	•	•		■		•	
19		•	•	•	••				•	
20	••	••		•		•	■	■		
21	■		••	•			■	■		
22	•		••	•••						
23		•••	•	•	■					
24	■			•	•	■	■	•••	•	
25						■			•	
26			•		••		■	■		
27			•••		■	■	■	■		
28			■		•	■	■	■	••	
29			•			■	■	■	■	■
30				•		■	■	■	■	
31		■		■		■			■	■
32	•		••	•						
33	•		•				■			■
34				■		•				

Fig. 7.5a Semivariates analysis of community at CJE. The semivariates analysis is based on the multivariate difference between quadrats calculated from Bray Curtis association values. Samples are considered independent across scales (x axis) where the line is horizontal. The "squiggle" at the end of the line is mathematical artefact (Palmer 1988)

This analysis suggests that in a multivariate sense, the samples were independent at all scales measured (ie a neighbour was just as likely to be similar as a subquadrat at greater distance away).

Fig. 7.5b Semivariates analysis of community at CJN (1m x 1m). Calculation and layout as above.

Again, the subquadrats appeared to be independent at all spatial scales measured

Fig. 7.5c Semivariates analysis of community at CJN (2m x 1m). Calculation and layout as above.

The horizontal line across all scales indicates apparent independence of samples across all scales measured.

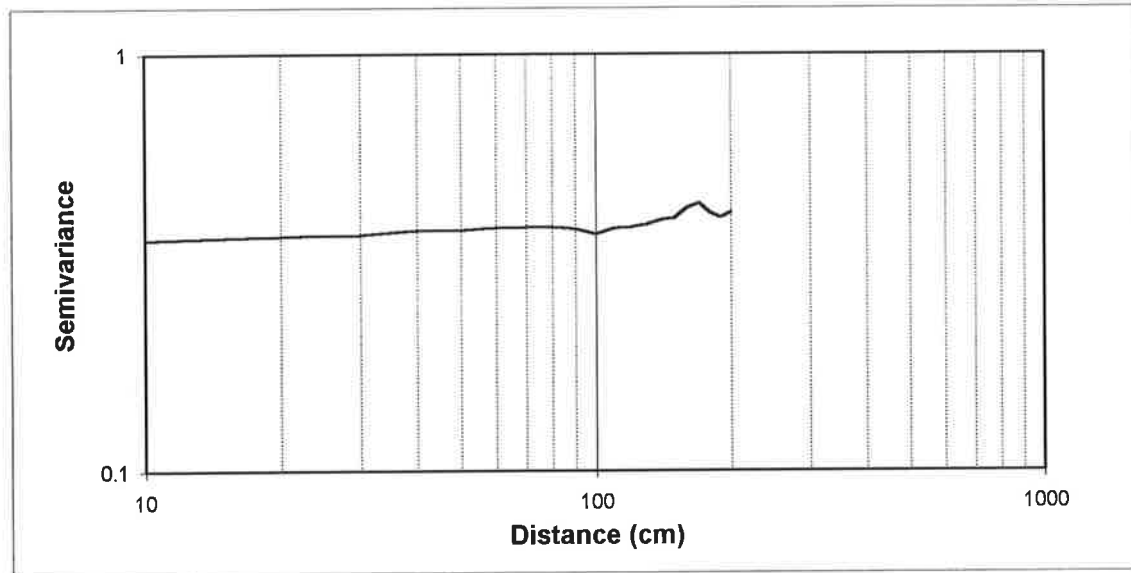
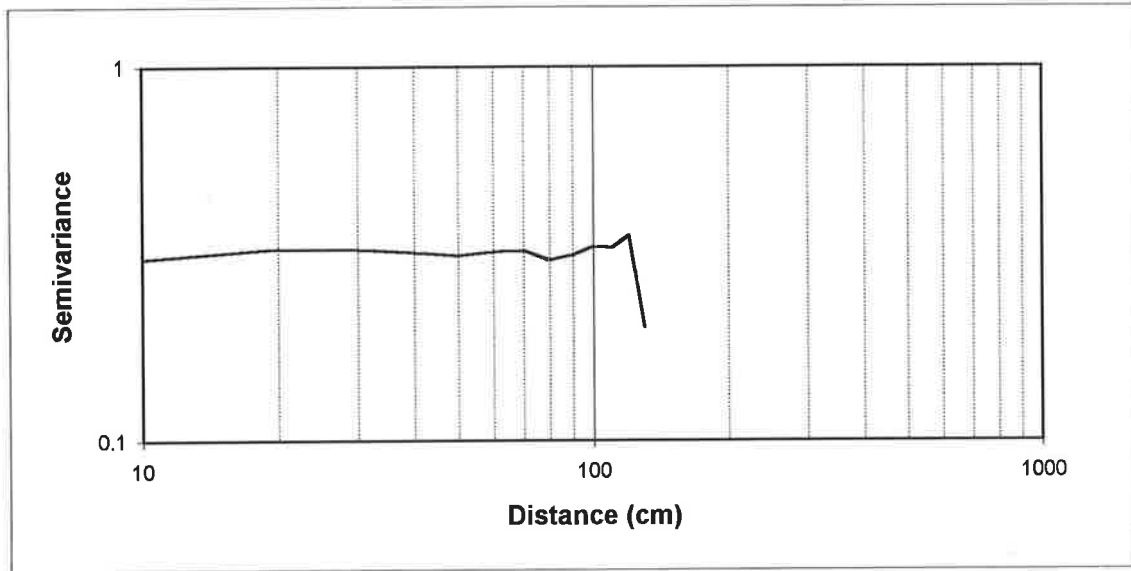
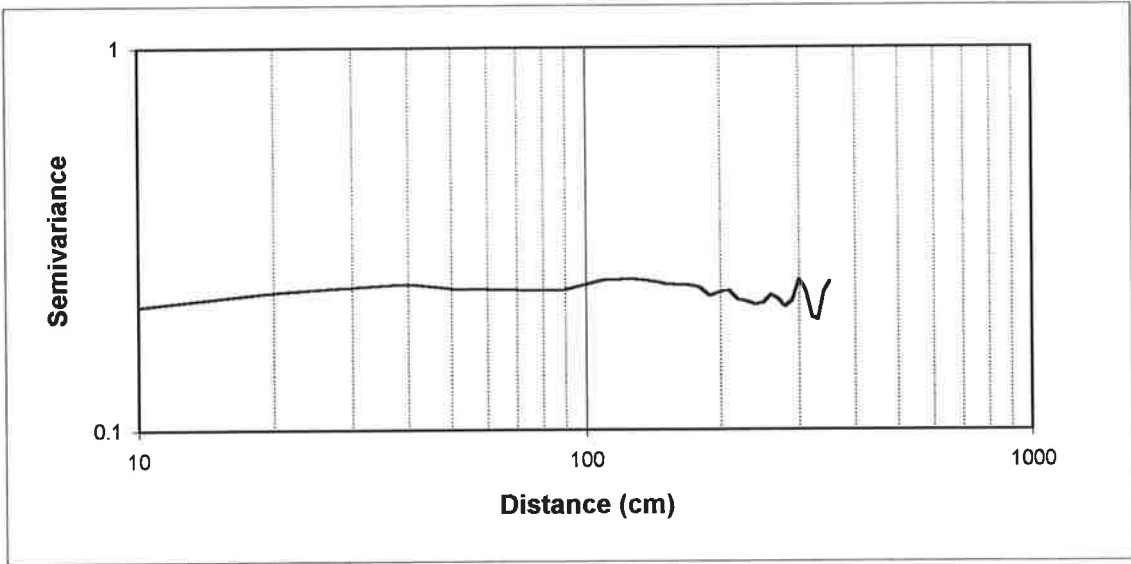


Fig 7.6a Semivariogram of a simulated community with 1m circular patch. The community analysed was simulated with high biomass in all subquadrats in a 1m circle, surrounded by low biomass subquadrats (see text for details). Dependence is indicated at all scales up to 1m by the sloping line which flattens at the 1m scale. This is the behaviour expected of a semivariogram under these conditions.

Fig 7.6b Semivariogram of the above with stochasm added. This community was the same as the above, except subquadrats were randomly allocated between 0 and 100g in the 1m patch but only 0 to 10g in the remainder of the "community". Dependence is still noticeable, but less so than in the deterministic model above. The line does not slope a great deal (the degree of dependence is indicated by the slope) and is variable.

Fig 7.6c Semivariogram of the above with stochasm added and random bare areas. This community, based on that of Fig. 7.6b, also incorporated the fact that randomly 1 in 3 subquadrats was devoid of algae. In this manner, it more closely mirrored the real, highly variable system.

It is clear that evidence of dependence (which is actually still present) is almost impossible to detect when this level of stochasm is incorporated. This is an indication that the results obtained for the real community may reflect the inability of the semivariogram to deal with high variance at the level of the sampling unit (in this case a 10cm x 10cm subquadrat).

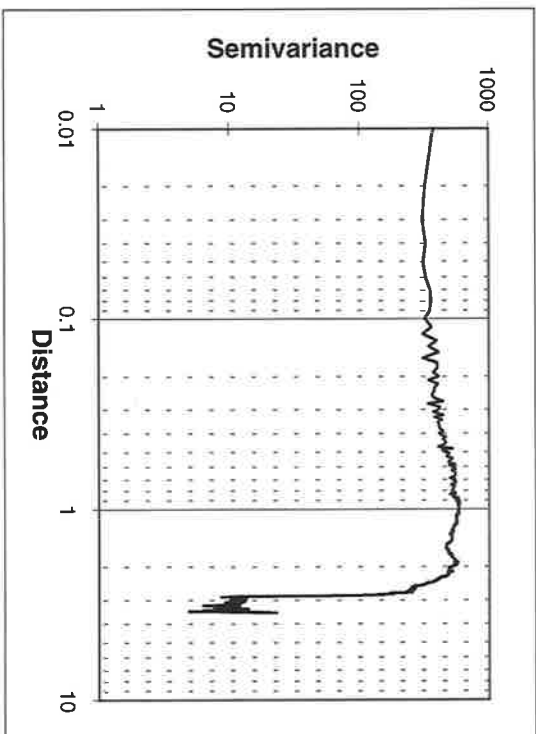
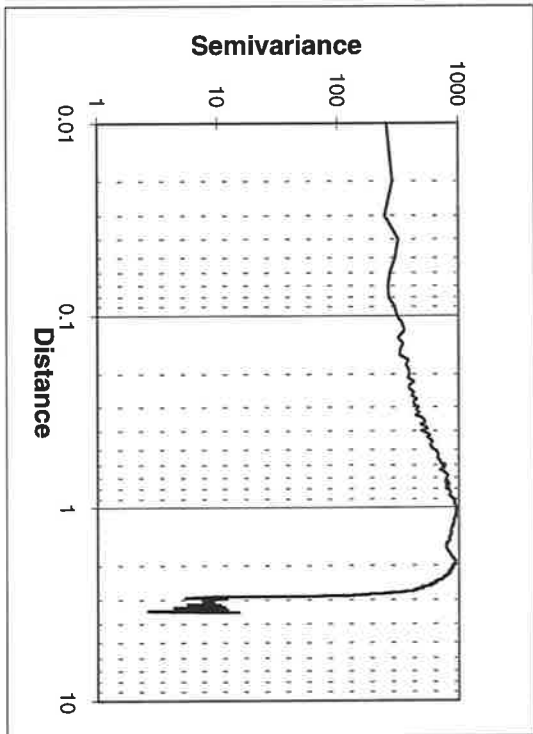
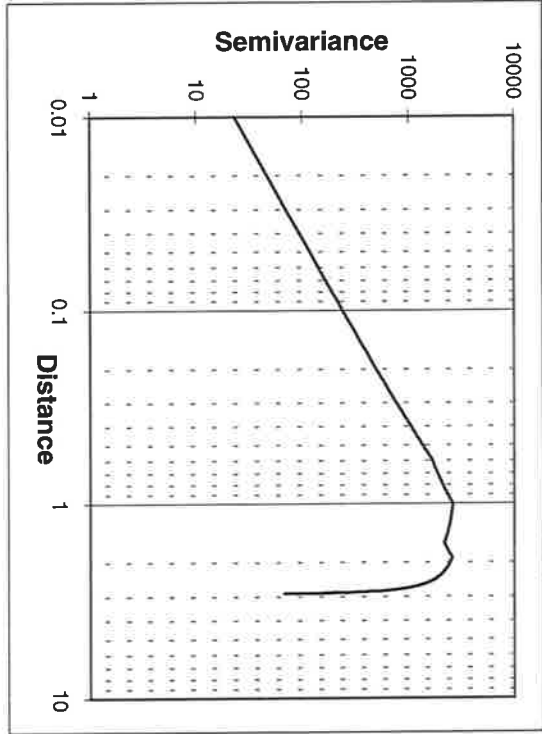


Fig 7.7a Species associations at the 10cm x 10cm scale at CJE. NMDS ordination of the relationships of the species as described in sample space. Species which are closer together are more highly associated (ie more commonly found together). Abbreviations are;

Apa: *Acrocarpia paniculata*

Cbr: *Cystophora brownii*

Cex: *C. expansa*

Cma: *C. monilifera*

Cms: *C. moniliformis*

Csu: *C. subfarcinata*

Era: *Ecklonia radiata*

Sfa: *Sargassum fallax*

Sli: *S. linearifolium*

Sva: *S. varians*

Sve: *S. verruculosum*

Sax: *Seirococcus axillaris*

The *Cystophora* species tended to associate, distinct from the *Sargassum* species.

Fig 7.7b Species associations at the 10cm x 10cm scale at CJNI (both harvests). Layout and labelling as above.

The *Sargassum* species had a tendency to associate, although *S. fallax* did so only loosely (as was the case with CJE above). The other species were not really associated with any others, a phenomenon probably indicative of their large size which precluded other species from sharing the subquadrat.

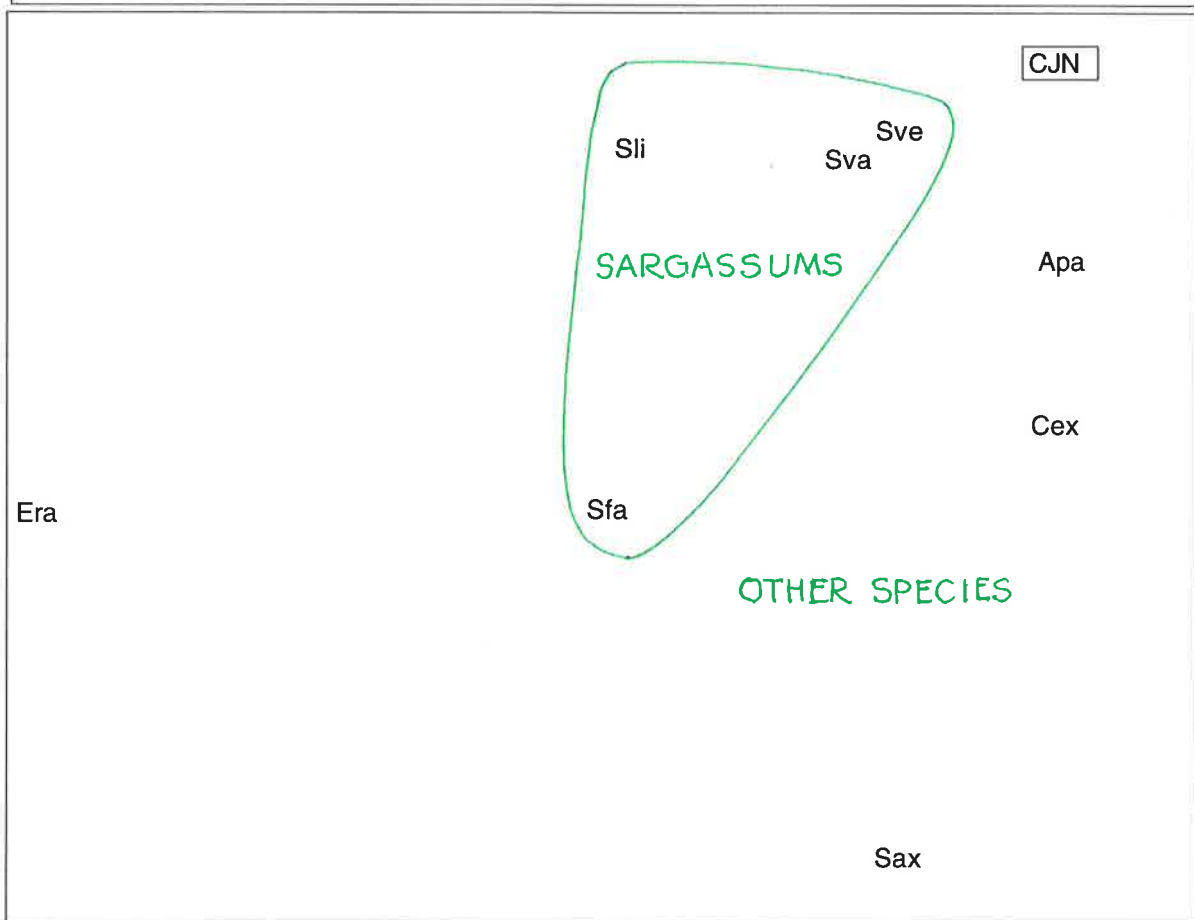
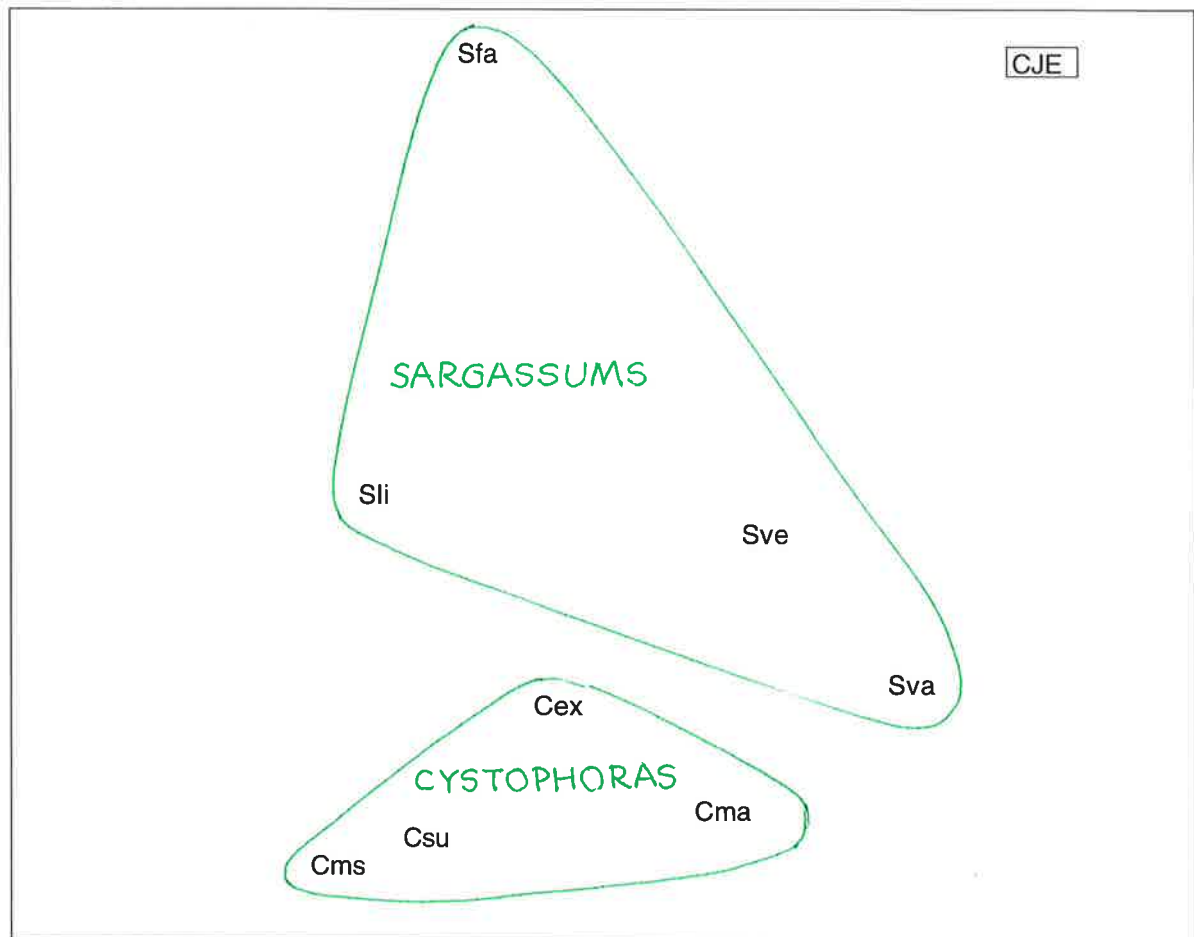


Fig 7.8 Map showing large scale transects. Two transects were surveyed at Cape Jervis. One, 4.5km long, known as Cape Jervis North. The other, 2.5km long, was known as Cape Jervis East.

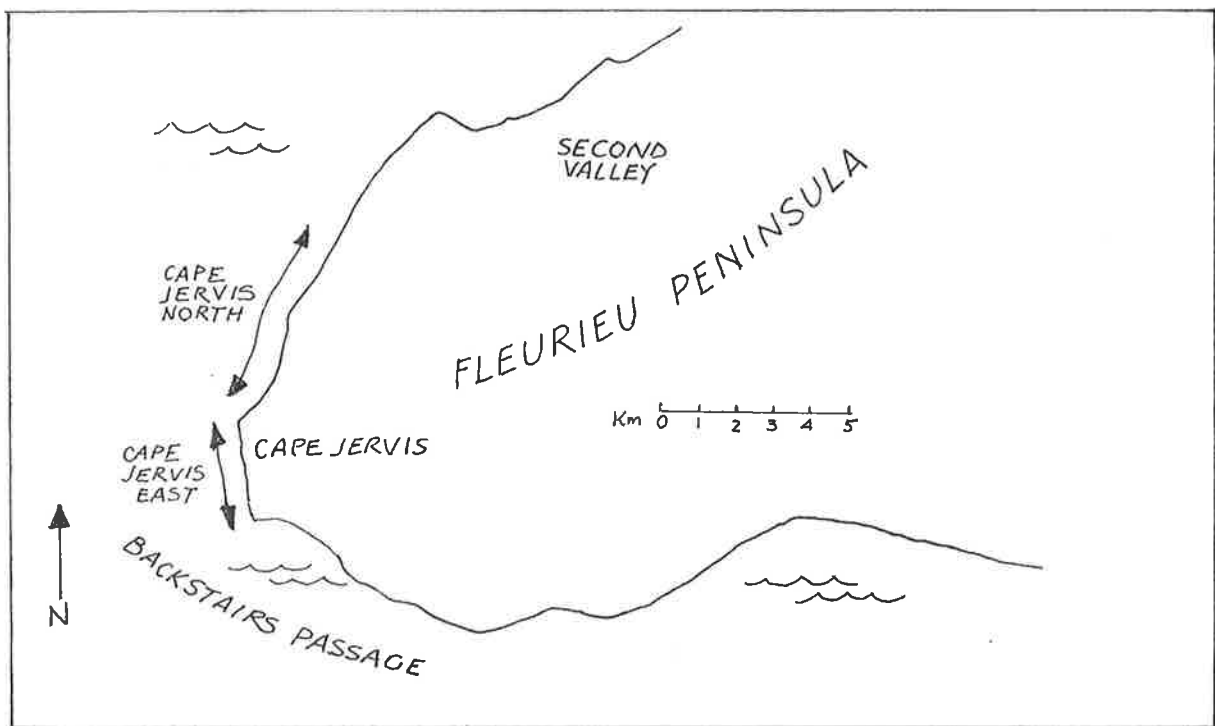
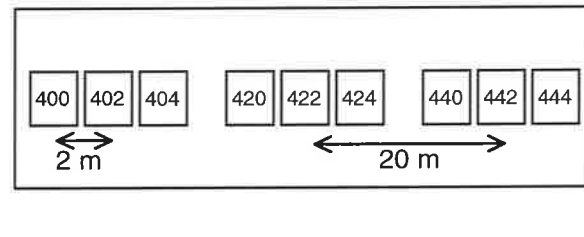
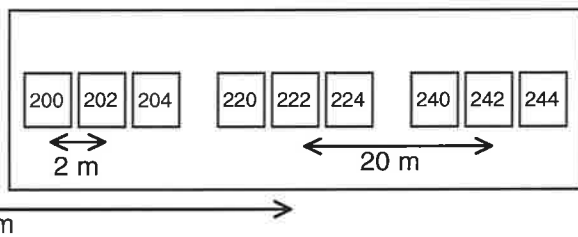
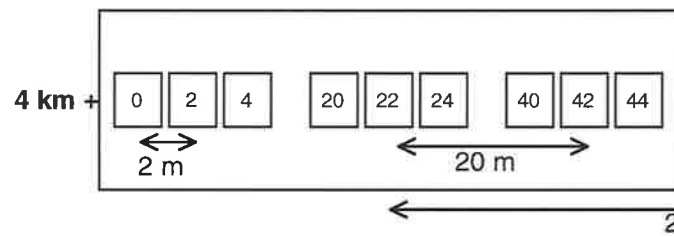
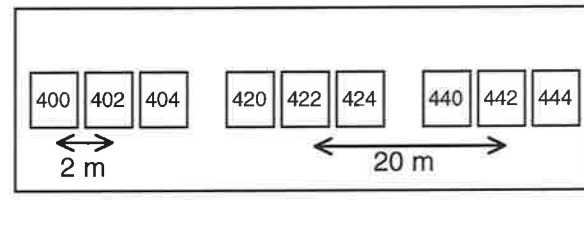
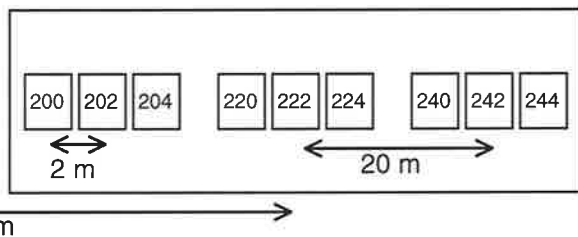
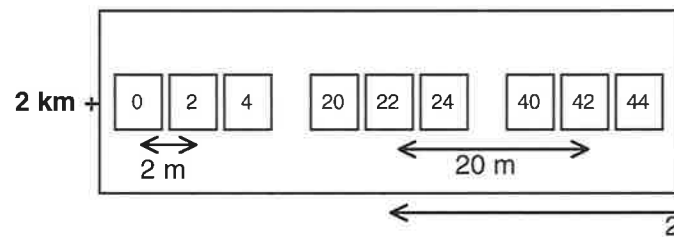
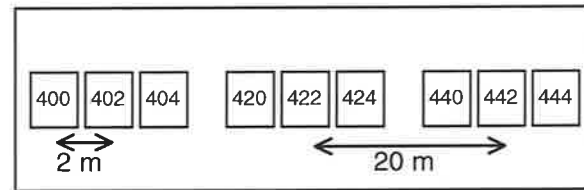
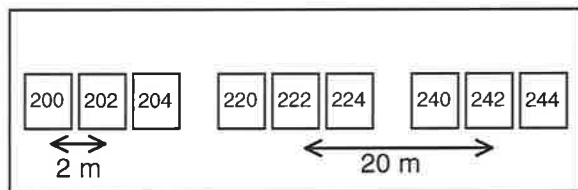
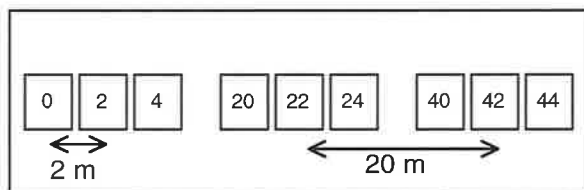


Fig 7.9 Layout of the 1m x 1m sample quadrats for large scale surveys. The numbers within the quadrats represent the distance along the transect at which these quadrats were harvested (gap distances not to scale). This allowed comparison to be made between samples separated by 2m, "groups" separated by 20m, "sections" separated by 200m and "sites" separated by 2000m. At CJN, three sites were sampled as indicated by the diagram, but at CJE only two sites could be sampled, so the bottom row is absent.



2 km

2 km

Fig 7.10 Relationship between temporally sampled sites and the 200m sections. This NMDS ordination examines the relationships between the average compositions of each of the 200m sections of the large scale surveys and the average of the two (CJE5 and CJN5) temporally sampled sites. The labels CJN5 and CJE5 represent the averages of the seasonally sampled sites. The double digit labels represent each of the 200m sections; the letter "N" signifying a CJN section, and the letter "E" signifying a CJE section. The number following indicates the section (increasing further away from the temporally replicated site in both cases). Stress = 0.12

They indicate that while CJN5 was typical of its immediate (200m) area, it was not typical of the rest of the section of coastline. The other temporally replicated site, CJE5 was quite dissimilar from the 200m section which began only 40m away (E1).

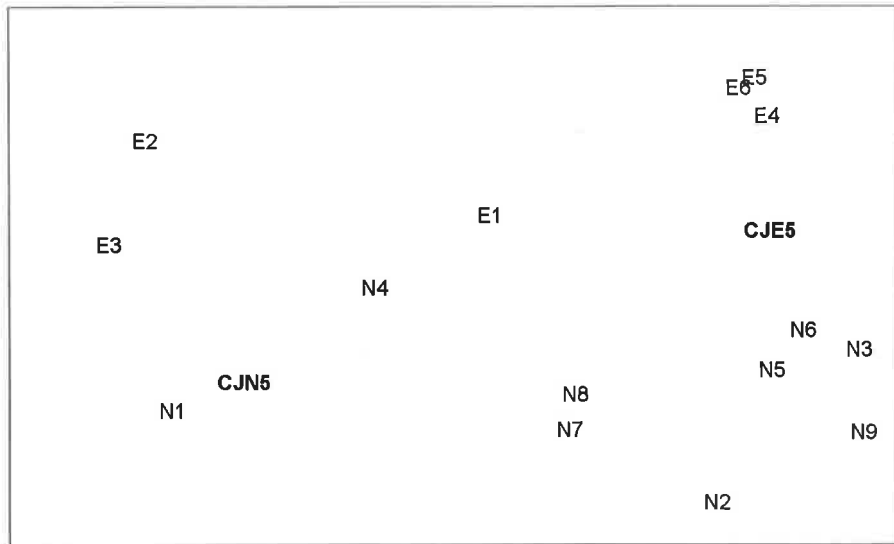


Fig. 7.11a Relationships between the "sites" of the CJN large scale survey. This NMDS ordination, based on Bray Curtis association values demonstrates the relationships between samples of the CJN large scale surveys. In particular, it is designed to demonstrate the relationships of the "sites" which the collection of samples represent. These sites are indicated by the overlaid "envelopes". The letters represent the 20m group from which the sample came (eg all "a" samples come from the first group). The number "1" denotes the 27th group because the alphabet wasn't designed with this project in mind and is too short. Stress = 0.20

Membership of sites and sections in terms of Groups

Site	Section	Groups
1	1	a,b,c
1	2	d,e,f
1	3	g,h,i
2	1	j,k,l
2	2	m,n,o
2	3	p,q,r
3	1	s,t,u
3	2	v,w,x
3	3	y,z,1

The sites were largely distinct, although there was a small area of overlap.

Fig. 7.11b Relationships between the "sites" of the CJE large scale survey. Description and layout as above with the exception that only two sites were sampled, rather than three. Stress = 0.17

In this case, the two sites of CJE were quite distinct, demonstrating no overlap.

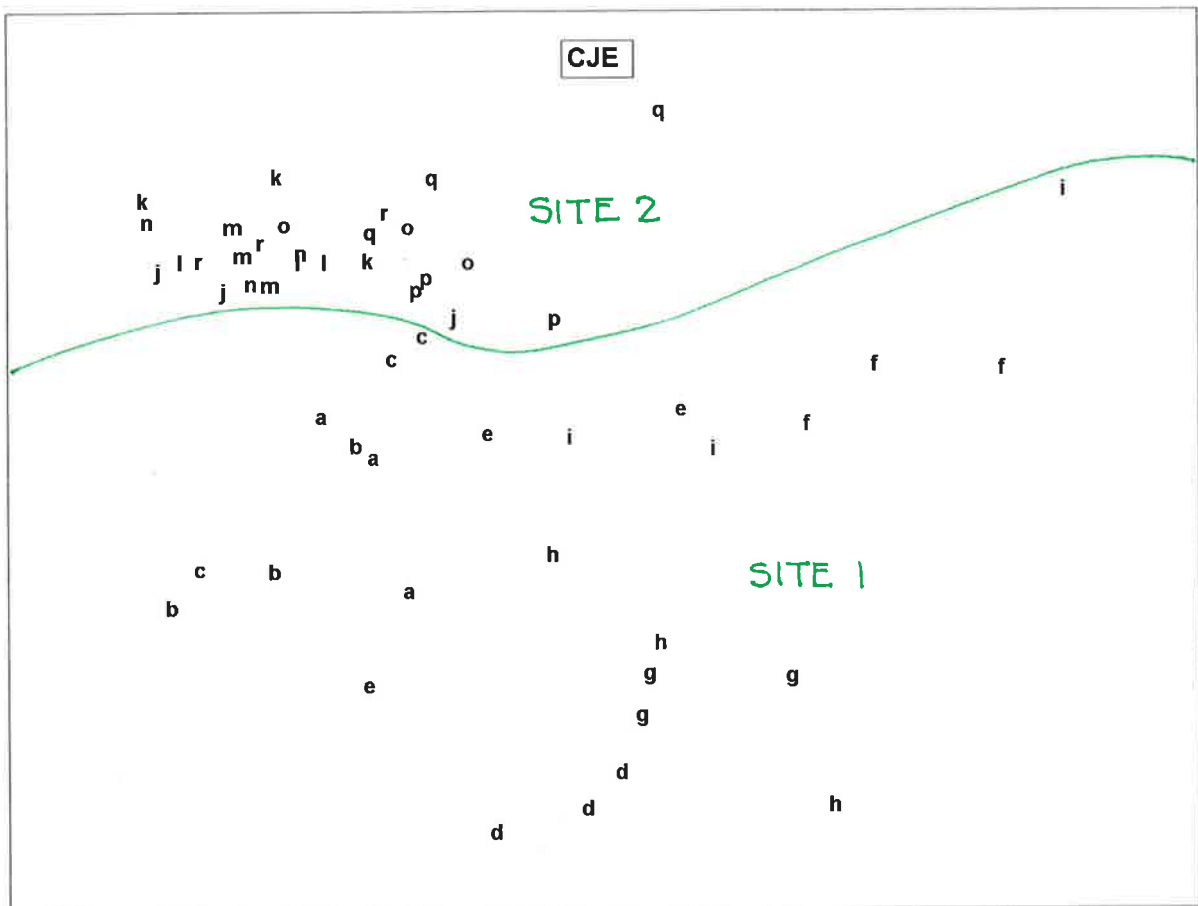
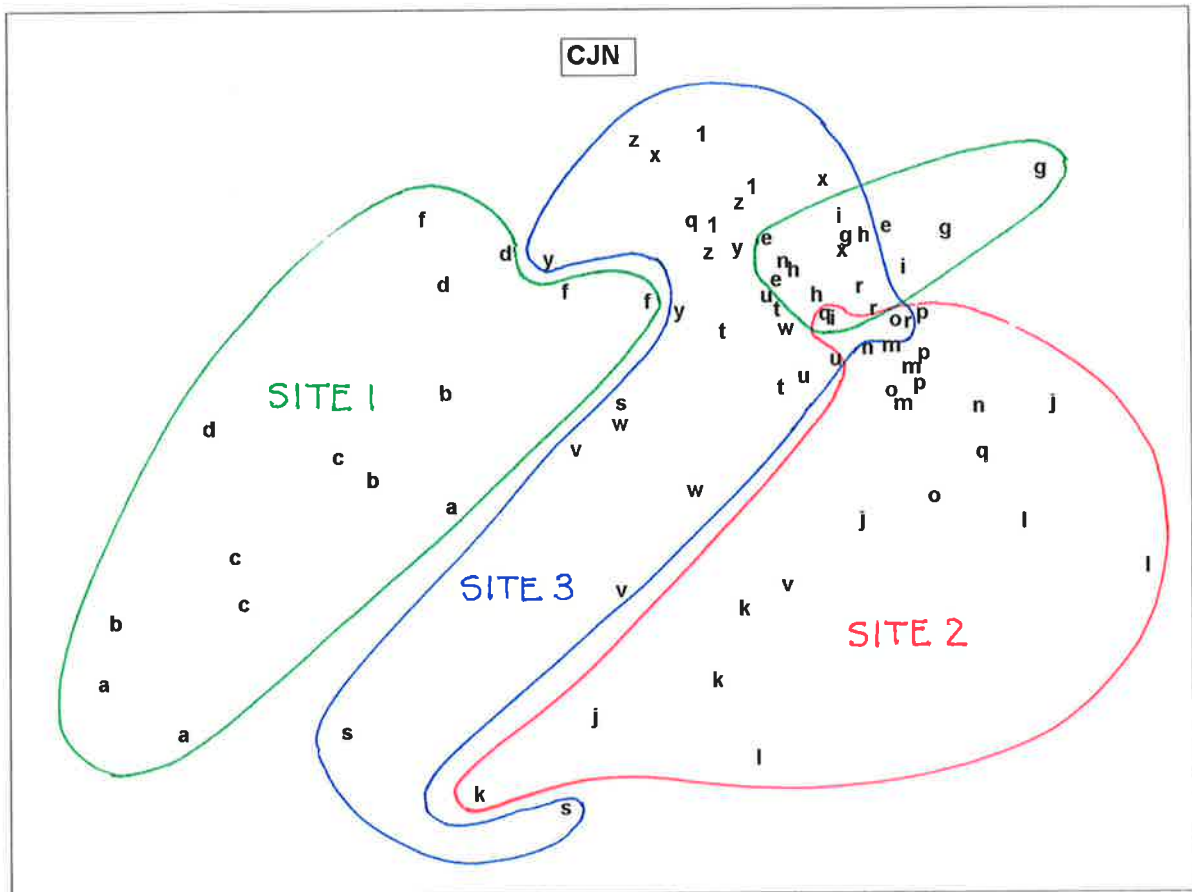
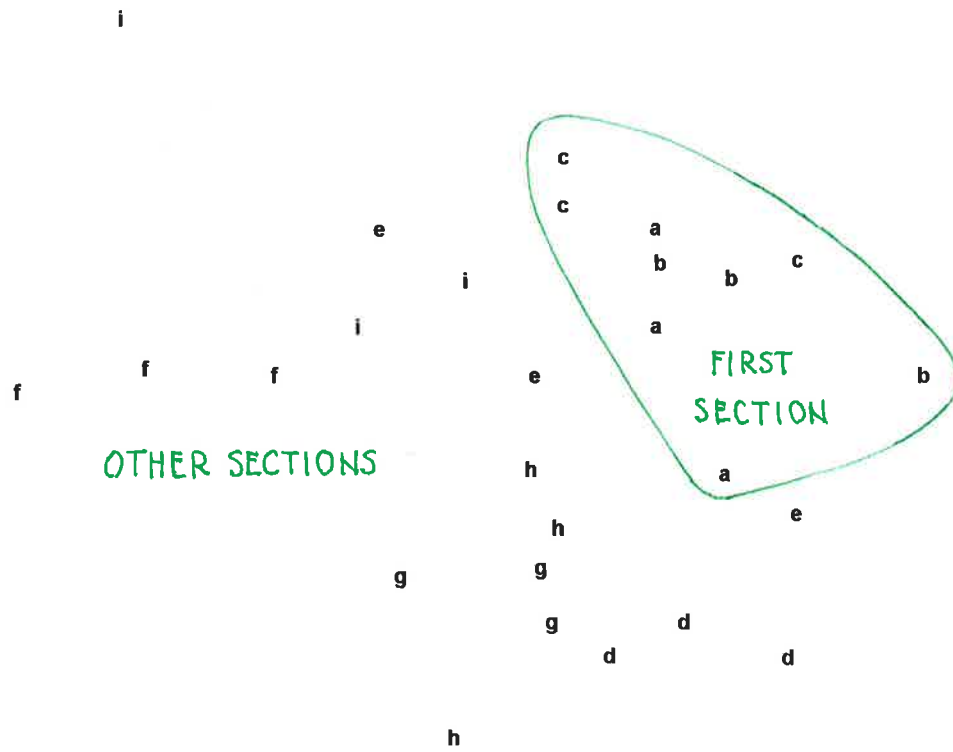


Fig 7.12 a Relationships of groups and sections within sites (CJE). The two NMDS ordinations demonstrate the relationships between samples within each of the two distinct sites of CJE. Note that the two ordinations represent separate analyses. Envelopes, where present, indicate a clustering of samples representing an entire 200m "section". Letter labels are as described for Fig 7.10a. Stress = 0.20 and 0.22 respectively.

The first 200m section was distinct from the others within the same site. However, the other two could not be reliably distinguished, and at the other site of CJE, no distinction could be made between any sections. Groups (represented by the same letter) sometimes appeared distinct, but there was no consistency to the pattern.

First Site



Second Site

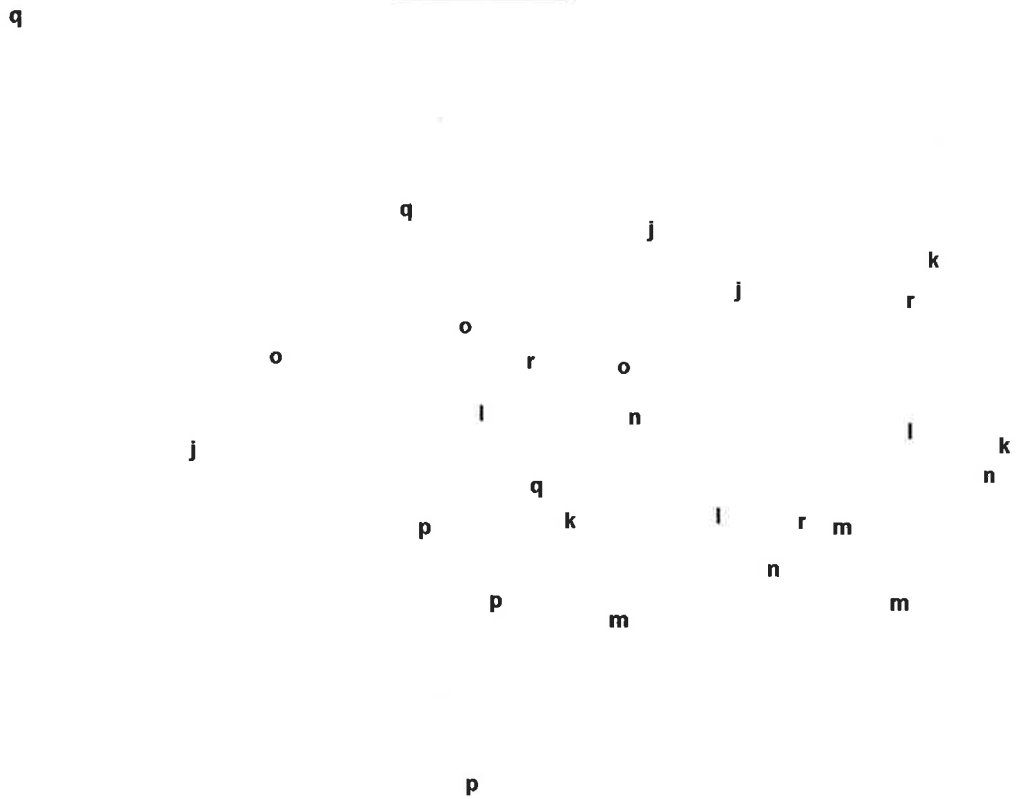


Fig 7.12b Relationships of groups and sections within sites (CJN). Analysis and layout as described in Fig. 7.12a. Stress = 0.13, 0.18 and 0.19 respectively.

Each site demonstrated a different degree of distinction of its 200m sections. At the first site, all three sections were distinct. At the second site, only one section was distinct, and even this involved some overlap. The third site had one distinct section. Within the section some, but not all, groups (denoted by the same letter) appeared distinct.

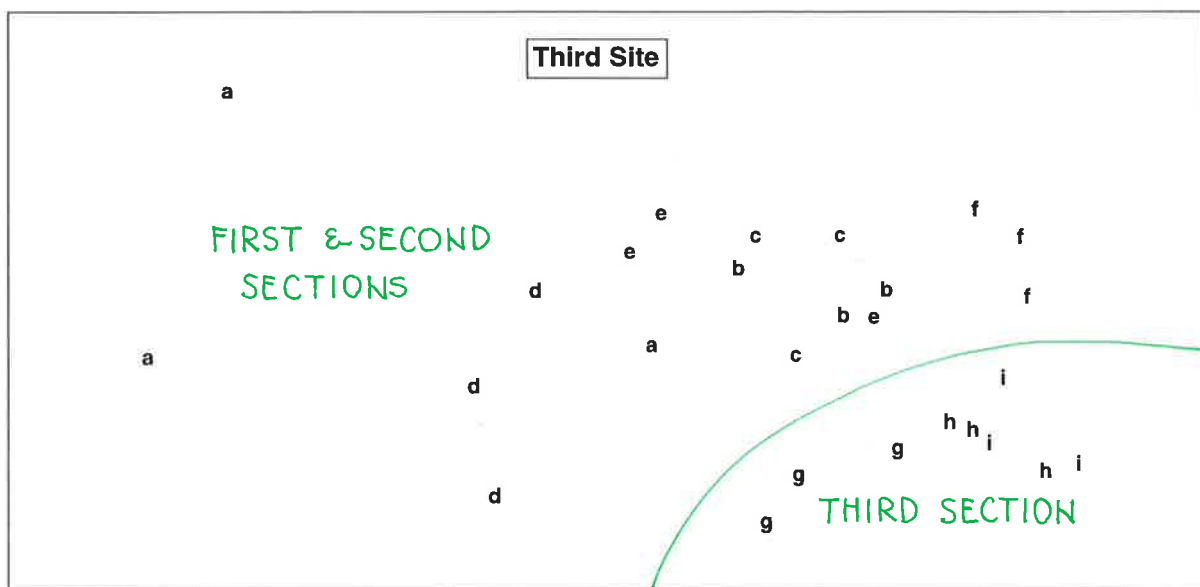
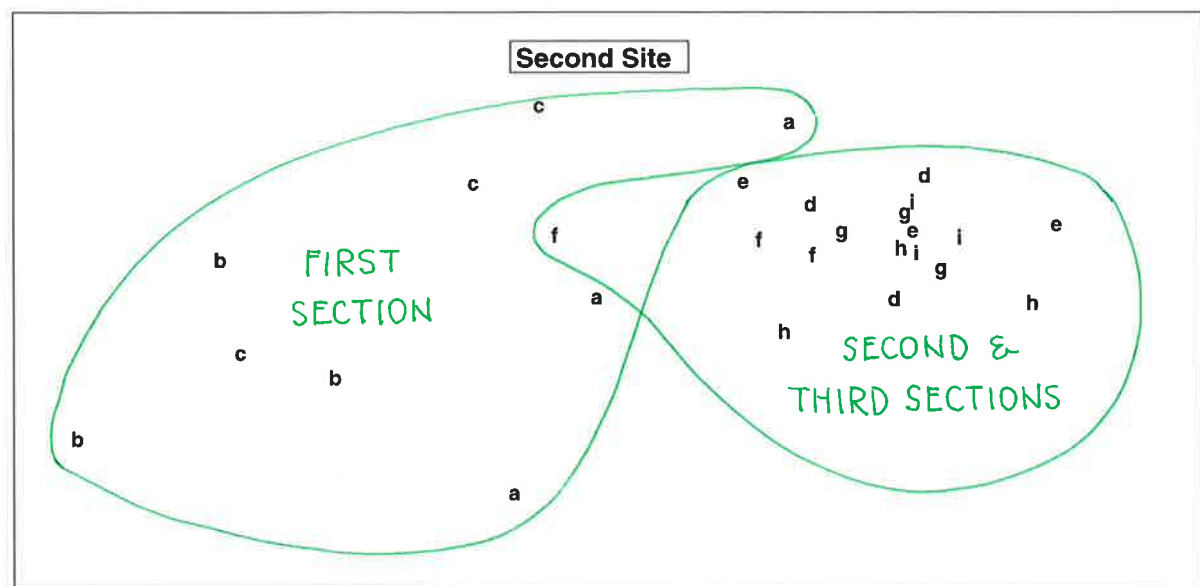
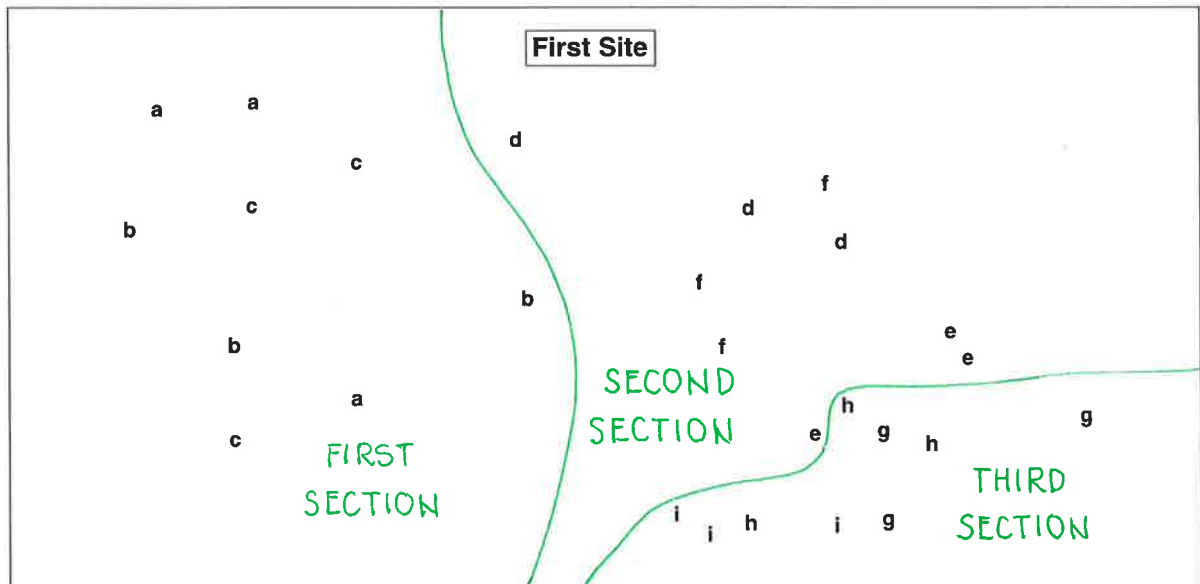


Fig 7.13 Species associations at the scales of quadrat, group and section (both sites).

These NMDS ordinations represent the associations between the species at the scale of the quadrat as well as the larger scales of 20m groups and 200m section. The dataset involved ordination of species in sample space, where "sample" represented each of the quadrats or each of the groups, or, at the largest scale, each of the sections. The ordination is based on Bray Curtis association measures, calculated from range standardised data. Labelling as follows:

Apa: *Acrocarpia paniculata*

Cbr: *Cystophora brownii*

Cex: *C. expansa*

Cma: *C. monilifera*

Cms: *C. moniliformis*

Csu: *C. subfarcinata*

Cce: *Caulocystis cephalornithos*

Era: *Ecklonia radiata*

Sfa: *Sargassum fallax*

Sli: *S. linearifolium*

Sva: *S. varians*

Sve: *S. verruculosum*

Sag: *Scaberia agardhii*

Sax: *Seirococcus axillaris*

Sdo: *Scytothalia dorycarpa*

Sde: *Sargassum deiripiens* ?

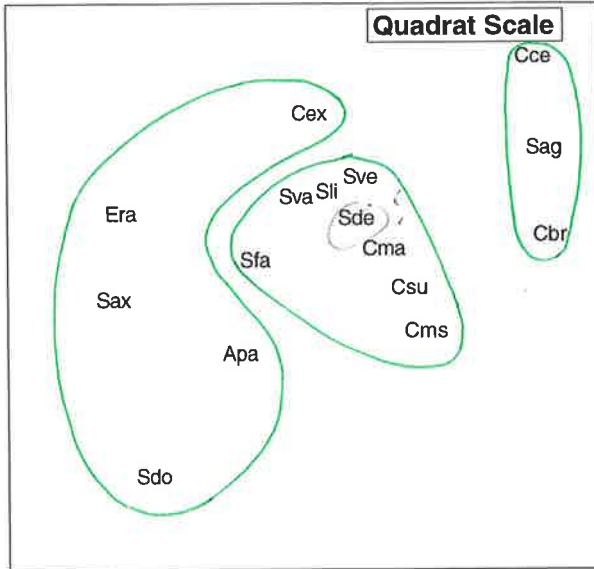
Stress levels are;

CJN	CJE
0.15	0.12
0.14	0.14
0.17	0.10

The point to notice from these ordinations was the similarity in associations both across scales and sites. In both cases, there was a tendency for four categories to form; a group of *Cystophora* species, a closely related, but still distinct *Sargassum* group, a group of rarer species, and a fourth group of physically large species, which were not so much associated with each other, as disassociated with all other species. Envelopes are drawn around these groups. There were only two exceptions to this pattern; *Cystophora brownii* was associated with the group of rarer species at CJN, but tended toward the other *Cystophora* species at CJE. Also, *Cystophora expansa* was associated with *Cystophora* species at CJE, but with the group of physically large species at CJN.

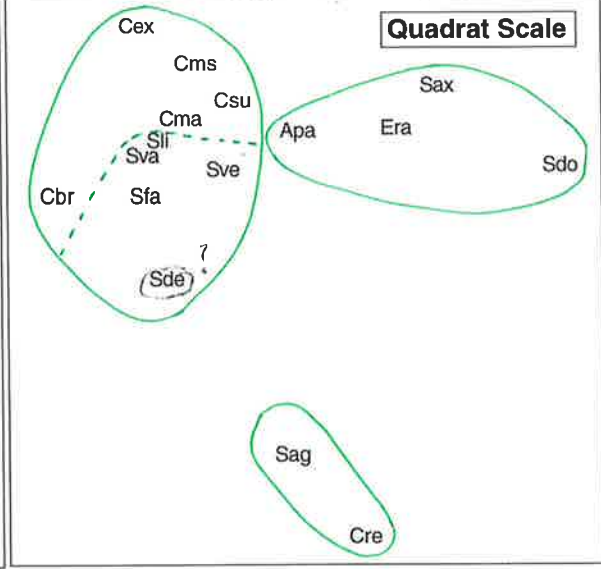
CJN

Quadrat Scale

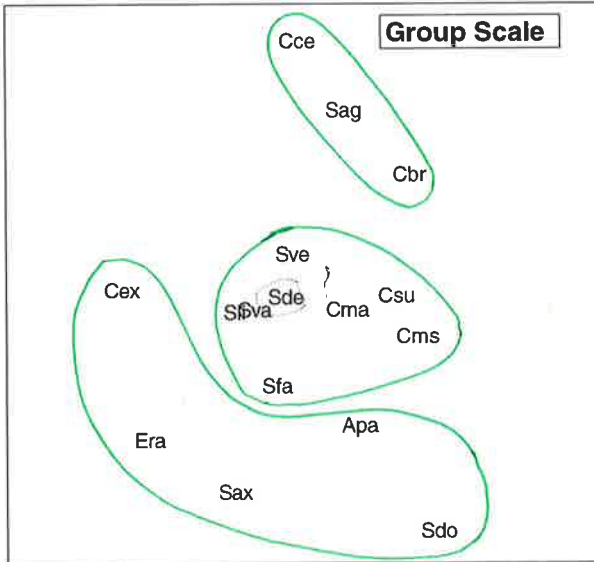


CJE

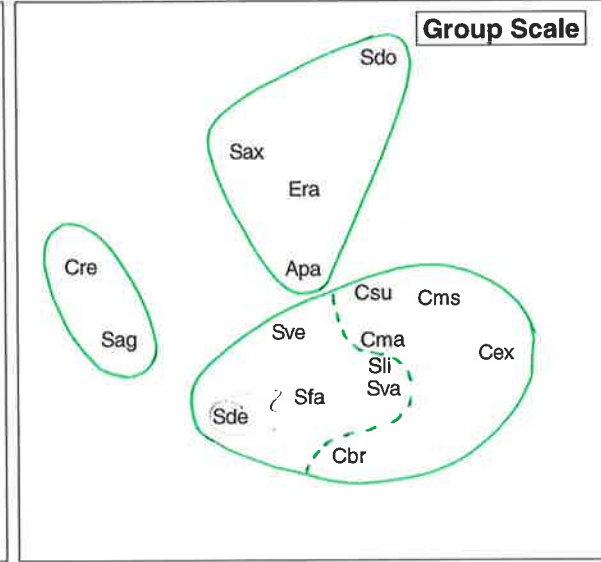
Quadrat Scale



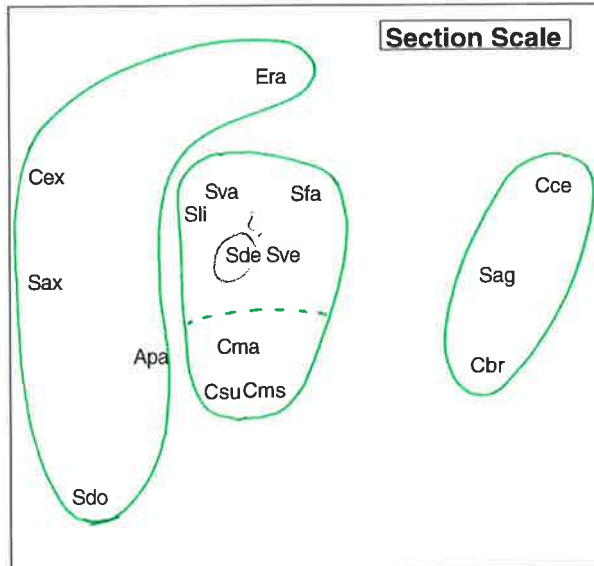
Group Scale



Group Scale



Section Scale



Section Scale

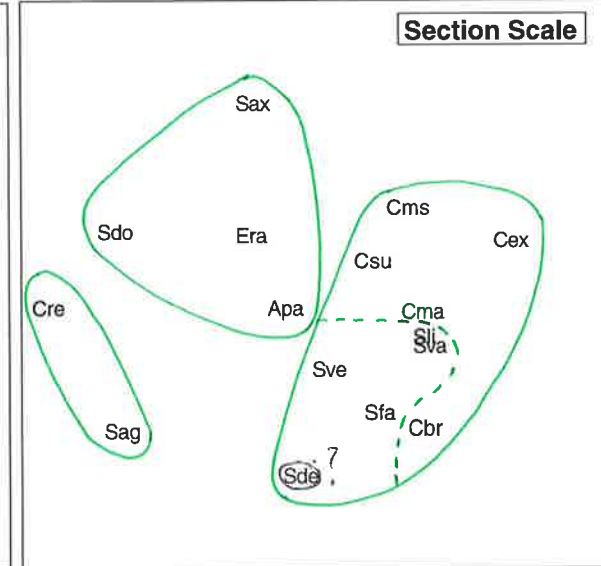
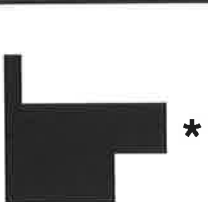
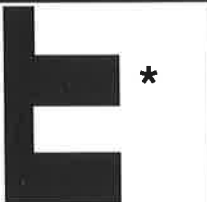
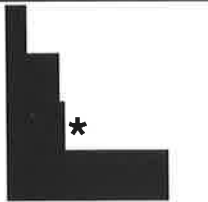
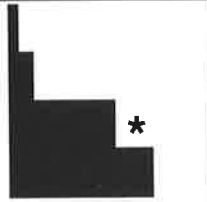
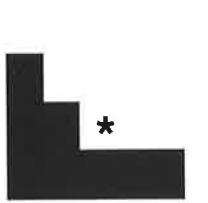
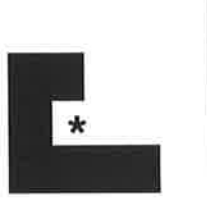
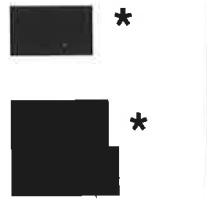
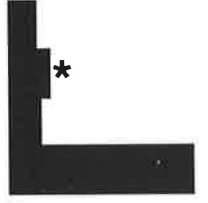
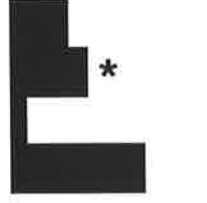
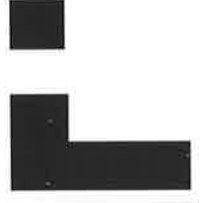
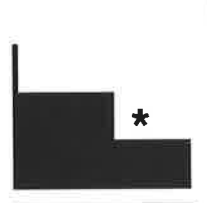
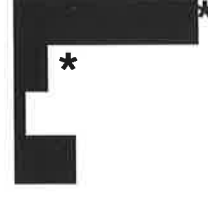
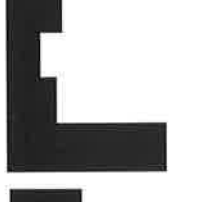
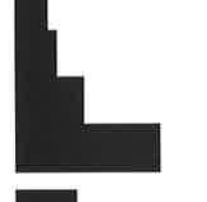
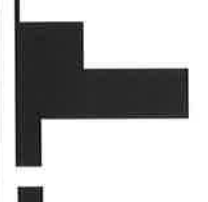
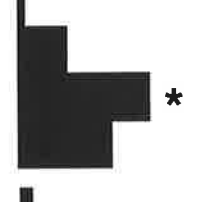
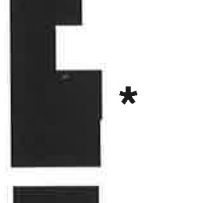
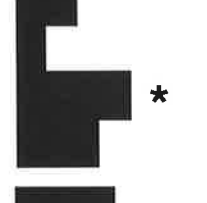
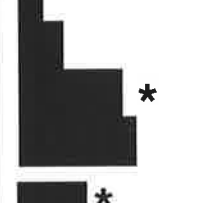
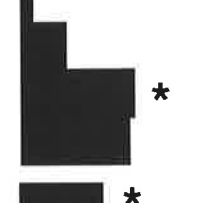
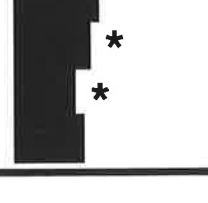


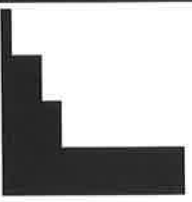
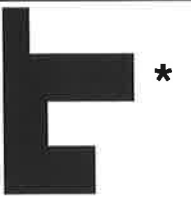
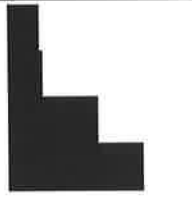
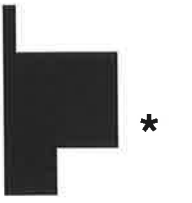
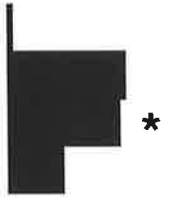
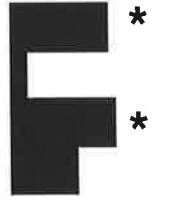
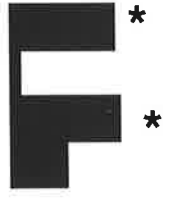
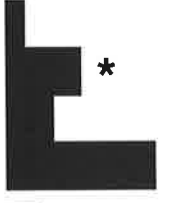
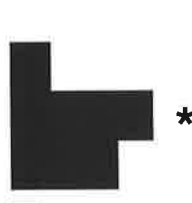
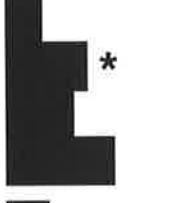
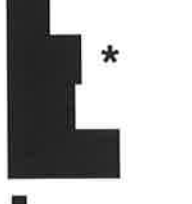
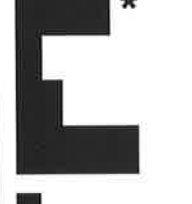
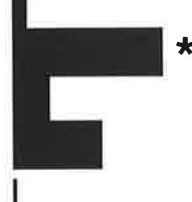
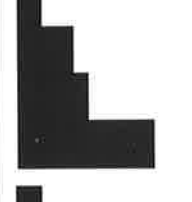
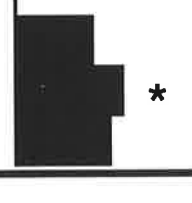
Fig 7.14 Variance partitioning of biomass and abundance across the spatial scales.

The length of each of the bars represents the proportion of the variance attributable to each level of scale (after Underwood 1981a). An asterisk indicates significance ($p < .05$) of that level in a nested ANOVA. Full ANOVA tables are presented in Appendix B. The four columns represent the results of biomass and abundance at each of the two sites.

The most important point to emerge from this figure is that most of the variation was usually (but certainly not always) displayed at the smallest scale, with the largest scale very rarely contributing a great deal of variance. Also, in most cases, statistically significant differences occurred on at least one scale.

Species	Scale	Cape Jervis North		Cape Jervis East	
		Biomass	Abundance	Biomass	Abundance
Total	2000 200 20 2				
<i>Acrocarpia paniculata</i>	2000 200 20 2				
<i>Cystophora brownii</i>	2000 200 20 2				
<i>Cystophora expansa</i>	2000 200 20 2				
<i>Cystophora monilifera</i>	2000 200 20 2				
<i>Cystophora moniliformis</i>	2000 200 20 2				
<i>Cystophora subfarcinata</i>	2000 200 20 2				
<i>Ecklonia radiata</i>	2000 200 20 2				

Continued on next page

Species	Scale	Cape Jervis North		Cape Jervis East	
		Biomass	Abundance	Biomass	Abundance
<i>Scytothalia dorycarpa</i>	2000				
	200				
	20				
	2				
<i>Seirococcus axillaris</i>	2000				
	200				
	20				
	2				
<i>Sargassum decipiens</i>	2000				
	200				
	20				
	2				
<i>Sargassum fallax</i>	2000				
	200				
	20				
	2				
<i>Sargassum linearifolium</i>	2000				
	200				
	20				
	2				
<i>Sargassum varians</i>	2000				
	200				
	20				
	2				
<i>Sargassum verruculosum</i>	2000				
	200				
	20				
	2				

Chapter 8

Table 8.1 Relative contribution of temporal variation to the total variation. The contribution of temporal variation to total (temporal + spatial) variation. This was calculated by expressing the sum of squares due to temporal change as a percentage of the total sum of squares. Analysis was a one way ANOVA with collection as the factor under consideration. The residual is considered to be variation due to within site spatial variation. Shading is to aid interpretation. Where contribution is < 20%, the cell is not shaded. A cell is shaded light grey where contribution is between 20 and 40%, and dark grey if contribution is >40%.

CJE5 seemed to be the site where most species demonstrated temporal variation which was responsible for a considerable proportion of the total. Total biomass was the variable for which temporal variation was most consistently a major contributor to overall variation.

	CJN5	SV5	CJN9	CJE5	GI5	B5	WI9	WI5
<i>Acrocarpia paniculata</i>	12			20	12	33	24	11
<i>Cystophora brownii</i>		10		11				
<i>Cystophora expansa</i>	7	30		57				
<i>Cystophora monilifera</i>	13		6	45				
<i>Cystophora moniliformis</i>	6	9		9		4		
<i>Cystophora subfarcinata</i>	12	30		4				
<i>Ecklonia radiata</i>	11	8	13	35	27	8	26	41
<i>Sargassum decipiens</i>	8	16	14	23				
<i>Sargassum fallax</i>	22	18	18	29				24
<i>Sargassum lacerifolium</i>								
<i>Sargassum linearifolium</i>	22	44		10				
<i>Sargassum varians</i>	5	9		42				
<i>Sargassum verruculosum</i>	12			65				
<i>Scytothalia dorycarpa</i>	18		26		8	22	39	29
<i>Seirococcus axillaris</i>	12		1	50	10	37	10	25
Total Biomass	14	36	17	73	43	76	37	51

Fig 8.1a Ordination of temporal and within site-spatial variation at oceanic sites.

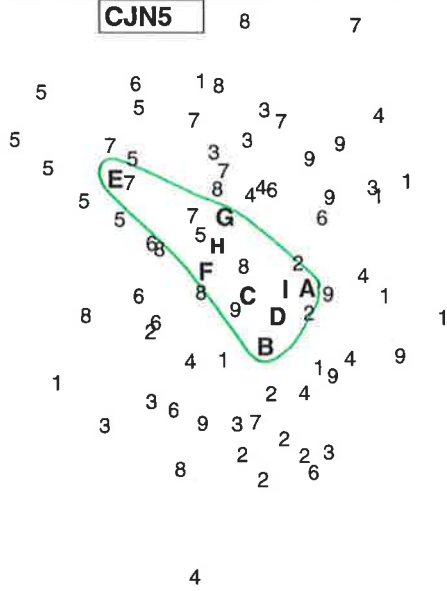
NMDS ordination plot of all samples in addition to superimposing the temporal averages. Samples are described by their collection number, and temporal averages by consecutive letters. The area described by the plotting of the averages is indicative of temporal variation (green envelope), while the area which encloses all the points of a single collection is indicative of the spatial variation at that time of collection. Stress levels: GI5 = 0.17; B5 = 0.20; WI9 = 0.18; WI5 = 0.21

Generally temporal variation was not as great as the spatial variation.

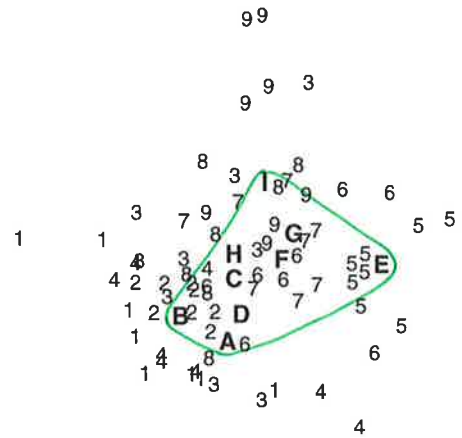
Fig 8.1b Ordination of temporal and within-site spatial variation at gulf sites. NMDS ordination plot of all samples in addition to superimposing the temporal averages. Samples are described by their collection number, and temporal averages by consecutive letters. The area described by the plotting of the averages is indicative of temporal variation, while the area which encloses all the points of a single collection is indicative of the spatial variation at that time of collection. Stress levels: CJN5 = 0.24; SV5 = 0.20; CJN9 = 0.23; CJE5 = 0.25

While temporal variation was not generally as great as the spatial variation, this was not as pronounced as it was at the oceanic sites

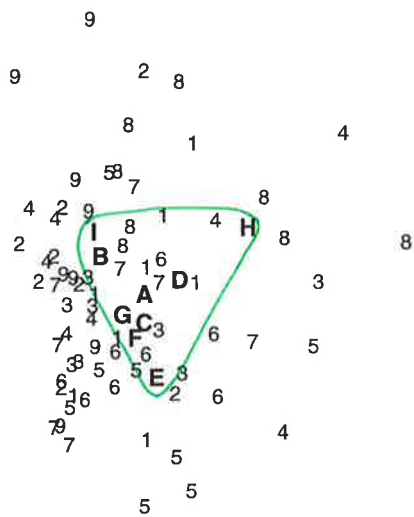
CJN5



SV5



CJN9



CJE5

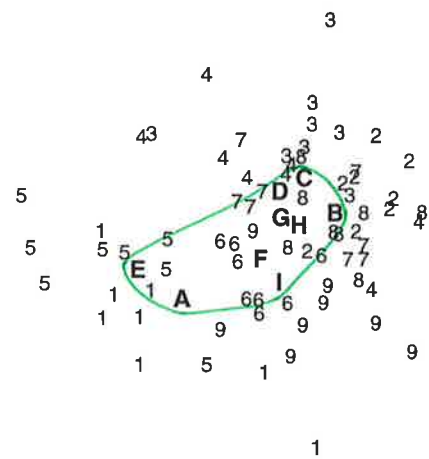


Fig 8.2 Ordination of temporal averages and large scale spatial variation. NMDS ordination demonstrating the relationships between the averages of the 200m sections of the large scale survey, and the site / collection averages from the temporal study. The bold letter-number combinations represent the average composition of a 200m section from the large scale survey, while the non bold two digit numbers represent the temporal collections from all sites. The same code is used for the two digit numbers as previously :

First digit = site; second = collection

1 C**J**N5

2 S**V**5

3 C**J**N9

4 C**J**E5

5 G**I**5

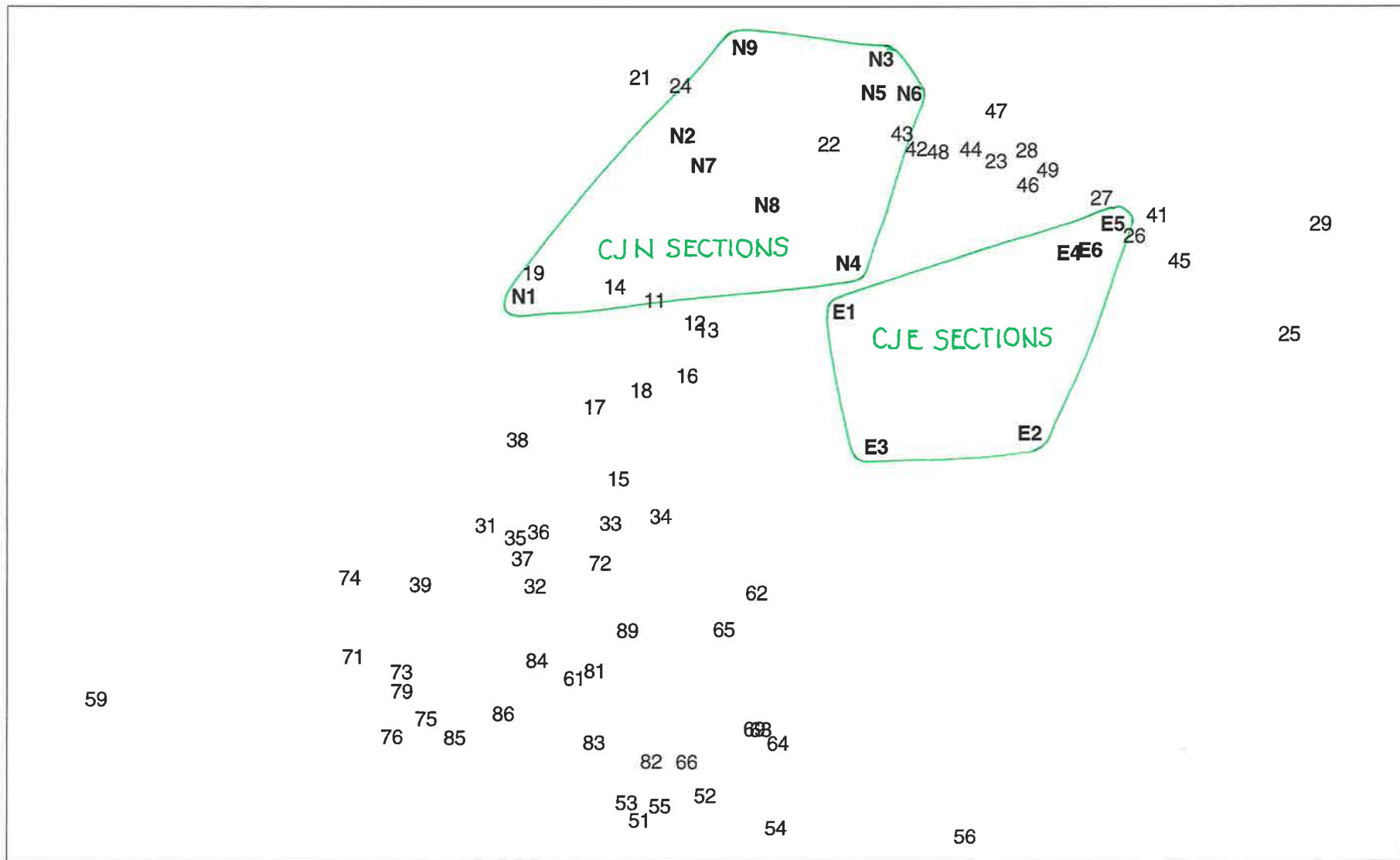
6 B**5**

7 W**I**9

8 W**I**5

In the case of the bold letter number labels, N refers to Cape Jervis North, while E refers to Cape Jervis East. The number following the letter signifies which 200m section it was, with 1 being geographically closest to the site used in the study of temporal variation (see Fig 3.1) and the largest number, the farthest away. Stress = 0.13

The spread of the 200m averages was quite considerable relative to the temporal variation demonstrated. Furthermore, it was of the same magnitude as the difference between sites of the temporal study, which represented different physical habitats.



Appendix A

Pilot Study

Details of a pilot study carried out at WI5 to assess quadrat size and replication for the main study of temporal variation.

Pilot Study

Before the study of temporal variation was undertaken, a brief pilot study was performed in order to determine the best size of quadrat. A single site (Wright Island (5m)) was chosen for this assessment. The object was to select the quadrat size which gave the best precision, which is defined as the ratio of standard error to mean, or;

$$\text{Precision} = \frac{\left(\frac{\text{Standard.Deviation}}{\sqrt{n}} \right)}{\text{Mean}} \quad (\text{Andrew and Mapstone 1987})$$

Low precision values imply better precision.

A series of four destructive harvests was made, each one using a different quadrat size (10cm x 10cm, 30cm x 30cm, 60cm x 60cm and 100cm x 100cm). All canopy species (as defined in Chapter 3) were harvested, identified and dried.

As pragmatic considerations required that sampling of a single site should be completed in a single dive (90-120 mins), as many quadrats were collected as possible on each dive. The object was to demonstrate which quadrat size had the best precision value given the number of quadrats which could be collected during a single dive.

Twenty random 10cm x 10cm quadrats were collected. Similarly twenty 20cm x 20cm quadrats were harvested. However, it was possible to harvest only ten 60cm x 60cm quadrats and eight 100cm x 100cm quadrats.

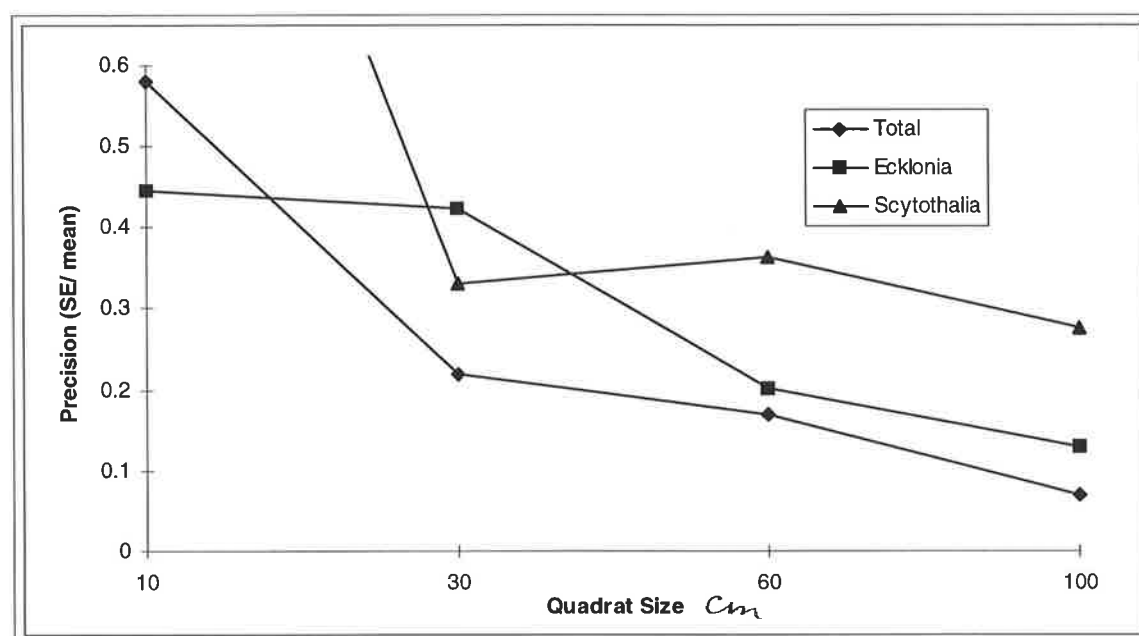
In order to scale the estimates up to the level of the square metre, the calculated means had to be multiplied by a modifier. (eg as the 10cm x 10cm quadrat represents only .01 of a square metre, the mean had to be multiplied by 100). The standard deviation must also be modified using the same multiplier (Sokal and Rohlf 1981; Zar 1984).

The standard errors were then calculated and divided by the mean to obtain an estimate for precision. Note that as the same population was being sampled with each of the different quadrat sizes, a single estimate of the mean was used in each case. This essentially meant that the best size quadrat was the one which displayed the lowest standard error.

The composition of the canopy was clearly dominated by *Ecklonia radiata* and *Scytothalia dorycarpa* ($\approx 90\%$ between them). Thus estimates of precision were made for *Ecklonia*, *Scytothalia* and total biomass.

Results

The graph below demonstrated that the precision value was lowest (ie best) for the 100cm x 100cm quadrats for all three variables measured.



The y axis is truncated to suppress a value of 1.3 for *Scytothalia* with 10cm x 10cm quadrats

Canopy composition was also calculated on the basis of the 100cm x 100cm quadrats for use in the temporal study;

Species	Biomass	Abundance
<i>Acrocarpia paniculata</i>	42.2	4.0
<i>Cystophora monilifera</i>	34.6	1.3
<i>Cystophora moniliformis</i>	12.6	0.8
<i>Cystophora subfarcinata</i>	13.4	1.9
<i>Ecklonia radiata</i>	661.7	9.8
<i>Sargassum spp</i>	30.0	?
<i>Scytothalia dorycarpa</i>	340.0	13.9
<i>Seirococcus axillaris</i>	101.3	4.0

Biomass is measured in g dwt m⁻² and abundance in individuals m⁻². Inexperience with the flora meant that *Sargassum* species could often not be differentiated at the species level. As with the main study, it was not possible to count individual *Sargassum* plants.

Conclusion

Given the restriction on the level of replication imposed by the length of the dive, the best quadrat size to use (of those tested) was 100cm x 100cm.

Appendix B

Details of Statistical Analysis of Data

Tables detailing results of statistical analyses used in this thesis. This appendix is divided into the chapters, and the type of analysis and variables are specified along with the relevant statistical results.

Chapter 6

Significance of BIOMASS fluctuations

Analysis: 1 way ANOVA
Treatment: Collection
Dependent Variable: Biomass

CJN5

Total Biomass				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	1761444.9	220181	2.4011
Error	63	5777041.6	91699	Prob>F
C Total	71	7538486.6		0.0250

Ecklonia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	3777235.8	472154	8.9198
Error	63	3334781.7	52933	Prob>F
C Total	71	7112017.5		0.0000

Seirococcus				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	1151466.8	143933	1.2903
Error	63	7027527.3	111548	Prob>F
C Total	71	8178994.1		0.2648

Cystophora				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	202294.6	25286.8	1.2015
Error	63	1325857.7	21045.4	Prob>F
C Total	71	1528152.3		0.3127
Power				

Scytothalia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	58081.96	7260.25	2.3986
Error	63	190693.82	3026.89	Prob>F
C Total	71	248775.78		0.0251

Acrocarpia

Levene p=0.0000

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
2.3618	8	25.923	0.0467

Sargassum

Levene p=0.0437

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
6.6986	8	25.384	0.0001

SV5

Acrocarpia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	2404.2678	300.533	6.5315
Error	63	2898.8287	46.013	Prob>F
C Total	71	5303.0965		0.0000

Cystophora

Levene p=0.0018

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
6.2223	8	25.234	0.0002

Ecklonia

Levene p=.0009

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
5.8862	8	23.545	0.0003

Sargassum

Levene 3.8086 8 63 0.0011

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
22.1880	8	24.923	0.0000

Scytothalia and Seirococcus

None supported at this site

Total Biomass

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	1558231.3	194779	8.9824
Error	63	1366125.5	21685	Prob>F
C Total	71	2924356.8		0.0000

CJN9

Acrocarpia

Levene 3.1898 8 63 0.0042

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
1.1849	8	24.679	0.3473

Power = .27

Cystophora

Levene 4.3417 8 63 0.0003

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
2.0350	8	24.556	0.0843

Power = 0.58

Ecklonia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	1816992.7	227124	3.3130
Error	63	4318931.3	68554	Prob>F
C Total	71	6135924.0		0.0032

Sargassum

Levene p=0.0303

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
1.2878	8	26.083	0.2924

Power=0.55

Scytothalia

Levene p=0.0000

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
4.5666	8	25.945	0.0015

Seirococcus

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	448644.5	56080.6	2.8813
Error	63	1226190.1	19463.3	Prob>F
C Total	71	1674834.6		0.0085

Total

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	1188378.8	148547	1.9995
Error	63	4680480.3	74293	Prob>F
C Total	71	5868859.2		0.0609

CJE5

Acrocarpia

Levene p=0.0001

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
3.1030	8	23.851	0.0151

Cystophora

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	1471696.3	183962	10.9743
Error	63	1056070.7	16763	Prob>F
C Total	71	2527767.0		0.0000

Ecklonia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	16354.137	2044.27	3.4724
Error	63	37089.756	588.73	Prob>F
C Total	71	53443.893		0.0022

Sargassum

Levene p=0.0085

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
65.0126	8	25.033	0.0000

Scytothalia did not occur and
Seirococcus occurred only in trace quantities

Total

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	2947519.0	368440	24.4599
Error	63	948971.4	15063	Prob>F
C Total	71	3896490.4		0.0000

GI5

Acrocarpia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	1532204.5	255367	6.8564
Error	49	1825009.1	37245	Prob>F
C Total	55	3357213.6		0.0000

Cystophora occurred only in trace quantities
as did Sargassum

Ecklonia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	1350342.7	225057	3.5606
Error	49	3097176.3	63208	Prob>F
C Total	55	4447519.0		0.0053

Scytothalia

Levene p=0.0151				
Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
21.1170	6	19.05	0.0000	

Seirococcus

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	4992.122	832.020	2.3798
Error	49	17131.046	349.613	Prob>F
C Total	55	22123.168		0.0426

Total

Levene				
	4.6521	6	49	0.0008
Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
36.7816	6	20.294	0.0000	

B5

Acrocarpia

Levene p=0.0378				
Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
4.1875	6	18.836	0.0077	

Cystophora

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	30637.17	5106.19	1.6469
Error	49	151924.12	3100.49	Prob>F
C Total	55	182561.29		0.1544
Power = 0.38				

Ecklonia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	3042177	507030	1.4949
Error	49	16619445	339172	Prob>F
C Total	55	19661622		0.1996
Power = .52				

Sargassum

Levene	4.3252	6	49	0.0014
Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
1.9849	6	19.692	0.1167	
Power=.57				

Scytothalia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	4796806	799468	2.5932
Error	49	15106614	308298	Prob>F
C Total	55	19903419		0.0292

Seirococcus

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	117862.09	19643.7	3.8372
Error	49	250842.50	5119.2	Prob>F
C Total	55	368704.59		0.0032

Total

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	5183726	863954	2.6004
Error	49	16279748	332240	Prob>F
C Total	55	21463474		0.0288

WI9

Acrocarpia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	3610.681	601.780	3.5736
Error	49	8251.519	168.398	Prob>F
C Total	55	11862.200		0.0051

Cystophora

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	10149.019	1691.50	4.4455
Error	49	18644.376	380.50	Prob>F
C Total	55	28793.396		0.0012

Ecklonia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	2999087	499848	2.2224
Error	49	11020795	224914	Prob>F
C Total	55	14019882		0.0564

Power=.72

Sargassum was only present in trace quantities

Scytothalia

Levene p=0.0031				
Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
8.2069	6	21.333	0.0001	

Seirococcus

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	86874.71	14479.1	2.0108
Error	49	352839.44	7200.8	Prob>F
C Total	55	439714.16		0.0820

Power=.67

Total Biomass

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	3932998	655500	3.3015
Error	49	9728767	198546	Prob>F
C Total	55	13661766		0.0083

WI5

Acrocarpia

Levene p=0.0096

Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
3.2433	6	18.691	0.0233	

Cystophora

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	5607.472	934.579	1.8879
Error	49	24257.004	495.041	Prob>F
C Total	55	29864.476		0.1018

Power=.64

Ecklonia

Levene p=0.0124

Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
7.7835	6	21.466	0.0002	

Sargassum

Levene p=0.0351

Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
2.8113	6	20.383	0.0371	

Scytothalia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	2354370.4	392395	3.5733
Error	49	5380838.3	109813	Prob>F
C Total	55	7735208.8		0.0051

Seirococcus

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	29658.06	4943.01	2.0600
Error	49	117578.94	2399.57	Prob>F
C Total	55	147237.00		0.0752

Power=.69

Total Biomass

Levene p=0.0010

Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
6.3257	6	21.519	0.0006	

Significance of ABUNDANCE fluctuations

Treatment: Collection; Dependent Variable: Abundance

CJN5

Acrocarpia

Levene p=0.0272

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio 1.3363 DF Num 8 DF Den 25.99 Prob>F 0.2701
Power=.35

Cystophora

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	333.7778	41.7222	1.2082
Error	63	2175.5000	34.5317	Prob>F
C Total	71	2509.2778		0.3089

Power=0.50

Ecklonia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	647.2778	80.9097	2.1623
Error	63	2357.3750	37.4187	Prob>F
C Total	71	3004.6528		0.0425

Scytothalia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	1320.3611	165.045	4.2018
Error	63	2474.6250	39.280	Prob>F
C Total	71	3794.9861		0.0004

Seirococcus

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	916.9444	114.618	1.0866
Error	63	6645.5000	105.484	Prob>F
C Total	71	7562.4444		0.3842

Power=.43

Total abundance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	4818.778	602.347	3.7931
Error	63	10004.500	158.802	Prob>F
C Total	71	14823.278		0.0011

SV5

Acrocarpia, Seirococcus and Scytothalia either didn't occur or did so in trace amounts

Cystophora

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	5185.000	648.125	3.4886
Error	63	11704.500	185.786	Prob>F
C Total	71	16889.500		0.0022

Ecklonia

Levene p=0.0027
Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
13.4123	8	23.641	0.0000

Total Frequency

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	3432.028	429.003	2.8061
Error	63	9631.625	152.883	Prob>F
C Total	71	13063.653		0.0100

CJN9

Acrocarpia occurred only in trace amounts

Cystophora

Levene p=0.0004
Welch Anova testing Means Equal, allowing Std's Not Equal
F Ratio DF Num DF Den Prob>F
1.8280 8 25.609 0.1177
Power=.058

Ecklonia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	751.2778	93.9097	3.1034
Error	63	1906.3750	30.2599	Prob>F
C Total	71	2657.6528		0.0051

Scytothalia

Levene 3.3337 8 63 0.0031
Welch Anova testing Means Equal, allowing Std's Not Equal
F Ratio DF Num DF Den Prob>F
6.9472 8 25.654 0.0001

Seirococcus

Levene 2.0937 8 63 0.0495
Welch Anova testing Means Equal, allowing Std's Not Equal
F Ratio DF Num DF Den Prob>F
3.5625 8 26.127 0.0064

Total Frequency

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	2446.111	305.764	1.8628
Error	63	10340.875	164.141	Prob>F
C Total	71	12786.986		0.0819

Power=.73

CJE5

Acrocarpia

Levene p=0.0000
Welch Anova testing Means Equal, allowing Std's Not Equal
F Ratio DF Num DF Den Prob>F
3.6017 8 25.457 0.0063

Cystophora

Levene p=0.0079
Welch Anova testing Means Equal, allowing Std's Not Equal
F Ratio DF Num DF Den Prob>F
2.4633 8 26.119 0.0390

Ecklonia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	8	11.194444	1.39931	2.5369
Error	63	34.750000	0.55159	Prob>F
C Total	71	45.944444		0.0184

Scytothalia and Seirococcus occurred in nil or trace amounts

Total abundance

Levene p=0.0110
Welch Anova testing Means Equal, allowing Std's Not Equal
F Ratio DF Num DF Den Prob>F
2.5963 8 26.162 0.0311

G15

Acrocarpia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	4324.7143	720.786	9.5633
Error	49	3693.1250	75.370	Prob>F
C Total	55	8017.8393		0.0000

Cystophora occurred only in trace amounts

Ecklonia

Levene p=0.0001				
Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
9.1018	6	21.334	0.0001	

Scytothalia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	2195.6071	365.935	3.4873
Error	49	5141.7500	104.934	Prob>F
C Total	55	7337.3571		0.0060

Seirococcus

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	19.107143	3.18452	1.9941
Error	49	78.250000	1.59694	Prob>F
C Total	55	97.357143		0.0845
Power= .68				

Total Frequency

Levene				
	2.7639	6	49	0.0215
Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
20.3932	6	19.581	0.0000	

B5

Acrocarpia

Levene p=0.0004				
Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
8.9698	6	18.985	0.0001	

Cystophora

Levene	5.3492	6	49	0.0003
Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
1.3683	6	21.075	0.2726	
Power=.8				

Ecklonia

Levene p=0.0037			
Welch Anova testing Means Equal, allowing Std's Not Equal			
F Ratio	DF Num	DF Den	Prob>F
1.5521	6	21.486	0.2093
Power=.58			

Scytothalia

Levene p=0.0032				
Welch Anova testing Means Equal, allowing Std's Not Equal				
F Ratio	DF Num	DF Den	Prob>F	
6.2867	6	21.322	0.0006	

Seirococcus

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	90.67857	15.1131	2.5296
Error	49	292.75000	5.9745	Prob>F
C Total	55	383.42857		0.0327

Total abundance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	4704.857	784.143	2.2906
Error	49	16774.000	342.327	Prob>F
C Total	55	21478.857		0.0500

WI9

Acrocarpia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	15.214286	2.53571	3.8231
Error	49	32.500000	0.66327	Prob>F
C Total	55	47.714286		0.0033

Cystophora

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	31.85714	5.30952	2.8241
Error	49	92.12500	1.88010	Prob>F
C Total	55	123.98214		0.0193

Ecklonia

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	290.85714	48.4762	3.7555
Error	49	632.50000	12.9082	Prob>F
C Total	55	923.35714		0.0037

Scytothalia

Levene p=0.0080

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
6.0583	6	21.462	0.0008

Total abundance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	3634.500	605.750	2.4672
Error	49	12030.625	245.523	Prob>F
C Total	55	15665.125		0.0365

WI5

Acrocarpia

Levene p=0.0003

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
2.6745	6	21.021	0.0435

Cystophora

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	1285.5000	214.250	2.6832
Error	49	3912.6250	79.849	Prob>F
C Total	55	5198.1250		0.0248

Ecklonia

Levene p=0.0077

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
2.8827	6	21.467	0.0322

Scytothalia

Levene p=0.0086

Welch Anova testing Means Equal, allowing Std's Not Equal

F Ratio	DF Num	DF Den	Prob>F
4.3119	6	21.293	0.0054

Seirococcus

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	185.92857	30.9881	3.4151
Error	49	444.62500	9.0740	Prob>F
C Total	55	630.55357		0.0068

Total Frequency

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	6	8247.750	1374.63	2.0758
Error	49	32448.375	662.21	Prob>F
C Total	55	40696.125		0.0732

Power = .68

Relationship of Abundance and AIPW to Biomass

Analysis: Multiple Regression

Treatments: Abundance, AIPW

Dependent Variable: Biomass

Acrocarpia

CJN5

Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
AcroW	1	1	7677.9999	40.4257	0.0004
AcroF	1	1	67.3069	0.3544	0.5704

GI5

Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
AcroW	1	1	305.10	0.6834	0.4549
AcroF	1	1	138362.65	309.9384	0.0001

B5

Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
AcroW	1	1	54.253	1.5212	0.2723
AcroF	1	1	16993.730	476.4832	0.0000

Cystophora

CJN5

Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Cystf	1	1	965.315	1.9948	0.2007
CystW	1	1	15424.787	31.8757	0.0008

SV5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Cystf	1	1	64102.730	12.1377	0.0102
CystW	1	1	8683.224	1.6441	0.2406

CJN9					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Cystf	1	1	1601.6779	19.3657	0.0032
CystW	1	1	653.0119	7.8955	0.0261

CJE5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Cystf	1	1	17314.04	4.3498	0.0755
CystW	1	1	229671.78	57.7009	0.0001

Ecklonia

CJN5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Ecklf	1	1	182.400	0.0108	0.9202
EckW	1	1	83556.395	4.9409	0.0616

SV5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Ecklf	1	1	20918.187	83.4506	0.0000
EckW	1	1	13.103	0.0523	0.8257

CJN9					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Ecklf	1	1	98688.05	15.5172	0.0056
EckW	1	1	183212.33	28.8075	0.0010

GI5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Ecklf	1	1	309238.05	26.1371	0.0037
EckW	1	1	100959.54	8.5332	0.0330

B5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Ecklf	1	1	366084.19	25.3627	0.0040
EckW	1	1	113672.62	7.8754	0.0377

WI9					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Ecklf	1	1	434433.97	89.9629	0.0002
EckW	1	1	25998.11	5.3837	0.0680

WI5

Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Ecklf	1	1	378775.3	3.5671	0.1176
EckW	1	1	1290083.8	12.1494	0.0176

Scytothalia

CJN5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Scytf	1	1	6036.8359	11.3984	0.0149
ScytW	1	1	4983.1607	9.4089	0.0220

CJN9					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Scytf	1	1	14878.424	3.9147	0.0884
ScytW	1	1	11112.507	2.9238	0.1310

GI5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Scytf	1	1	41617.47	5.6817	0.0629
ScytW	1	1	155653.09	21.2500	0.0058

B5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Scytf	1	1	541965.89	32.8689	0.0023
ScytW	1	1	34891.21	2.1161	0.2055

WI9					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Scytf	1	1	28587.390	14.6552	0.0123
ScytW	1	1	27384.648	14.0386	0.0133

WI5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Scytf	1	1	233358.61	20.6323	0.0062
ScytW	1	1	17852.12	1.5784	0.2645

Seirococcus

CJN5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
SeirF	1	1	64404.757	11.9467	0.0106
SeirW	1	1	86255.806	15.9999	0.0052

CJN9					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
SeirF	1	1	42293.880	20.0365	0.0029
SeirW	1	1	9737.202	4.6130	0.0688

WI9					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
SeirF	1	1	15110.860	145.3479	0.0001
SeirW	1	1	1382.920	13.3020	0.0148

WI5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
SeirF	1	1	2051.4614	51.3533	0.0008
SeirW	1	1	395.3434	9.8965	0.0255

Total Biomass

CJN5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
TotF	1	1	233805.70	30.5591	0.0009
TotAIPW	1	1	512087.96	66.9315	0.0001

SV5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
TotF	1	1	36584.713	8.7652	0.0211
TotAIPW	1	1	23257.214	5.5721	0.0503

CJN9					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
TotF	1	1	206603.85	42.2055	0.0003
TotAIPW	1	1	358518.02	73.2389	0.0001

CJE5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
TotF	1	1	17579.51	3.9318	0.0878
TotAIPW	1	1	236954.16	52.9968	0.0002

GI5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
TotF	1	1	306361.40	6.8753	0.0470
TotAIPW	1	1	194740.93	4.3703	0.0908

B5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
TotF	1	1	416908.13	16.6030	0.0096
TotAIPW	1	1	103714.98	4.1304	0.0978

WI9					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
TotF	1	1	904931.42	73.6944	0.0004
TotAIPW	1	1	103198.46	8.4041	0.0338

WI5					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
TotF	1	1	1107606.4	6.1039	0.0565
TotAIPW	1	1	2054736.6	11.3234	0.0200

Chapter 7

Partitioning of variance between spatial scales

Analysis: 3 level Nested ANOVA

Levels: 2km, 200m, 20m

Dependent Variables: biomass and abundance

Cape Jervis East

Biomass

Total Biomass

Scale	DF	SS	Propn	F	p
2000	1	311092	7	1.642	NS
200	4	757835	18	2.403	NS
20	12	946053	20	2.057	0.05
Residual	36	1379467	56		

Abundance

Total Abundance

Scale	DF	SS	Propn	F	p
2000	1	9022	3	1.34	NS
200	4	27032	8	1.45	NS
20	12	55753	38	3.20	<.005
Residual	36	52281	51		

Acrocarpia paniculata

Scale	DF	SS	Propn	F	p
2000	1	26613	33	5.375	NS
200	4	19805	19	5.816	<.005
20	12	10216	0	0.741	NS
Residual	36	41384	48		

Acrocarpia paniculata

Scale	DF	SS	Propn	F	p
2000	1	1076	28	10.87	0.05
200	4	396	0	0.56	NS
20	12	2127	34	3.72	<.005
Residual	36	1716	38		

Cystophora brownii

Scale	DF	SS	Propn	F	p
2000	1	993	18	6.226	NS
200	4	638	0	0.784	NS
20	12	2441	19	1.936	NS
Residual	36	3782	62		

Cystophora brownii

Scale	DF	SS	Propn	F	p
2000	1	0.9	0	0.06	NS
200	4	60.7	1	1.06	NS
20	12	172	36	2.70	0.05
Residual	36	191	63		

Cystophora expansa

Scale	DF	SS	Propn	F	p
2000	1	139415	65	14.29	0.05
200	4	39017	11	4.345	0.05
20	12	26937	3	1.446	NS
Residual	36	55893	21		

Cystophora expansa

Scale	DF	SS	Propn	F	p
2000	1	3700	75	37.56	<.005
200	4	394	2	1.44	NS
20	12	819	8	2.56	0.01
Residual	36	958	15		

Cystophora monilifera

Scale	DF	SS	Propn	F	p
2000	1	9	0	0.002	NS
200	4	14940	42	5.456	0.01
20	12	8215	13	1.896	NS
Residual	36	12995	45		

Cystophora monilifera

Scale	DF	SS	Propn	F	p
2000	1	66	0	0.66	NS
200	4	400	35	5.04	0.01
20	12	238	7	1.37	NS
Residual	36	521	58		

Cystophora moniliformis

Scale	DF	SS	Propn	F	p
2000	1	9491	0	0.174	NS
200	4	218712	1	1.024	NS
20	12	640686	88	24.62	<.005
Residual	36	78067	11		

Cystophora moniliformis

Scale	DF	SS	Propn	F	p
2000	1	641	0	0.47	NS
200	4	5474	2	1.10	NS
20	12	14889	51	4.22	<.005
Residual	36	10576	47		

Cystophora subfarcinata

Scale	DF	SS	Propn	F	p
2000	1	16907	8	2.108	NS
200	4	32089	4	1.267	NS
20	12	75968	31	2.649	0.01
Residual	36	86044	57		

Cystophora subfarcinata

Scale	DF	SS	Propn	F	p
2000	1	809	0	0.97	NS
200	4	3339	4	1.19	NS
20	12	8453	40	3.15	<.005
Residual	36	8049	56		

Ecklonia radiata

Scale	DF	SS	Propn	F	p
2000	1	112003	35	22.27	<.005
200	4	20118	0	0.493	NS
20	12	122469	12	1.664	NS
Residual	36	220764	54		

Ecklonia radiata

Scale	DF	SS	Propn	F	p
2000	1	134	42	11.40	0.05
200	4	47	2	1.18	NS
20	12	119	17	2.33	0.05
Residual	36	153	39		

Scytothalia dorycarpa

Scale	DF	SS	Propn	F	p
2000	1	21309	14	3.566	NS
200	4	23901	2	1.133	NS
20	12	63269	21	1.979	NS
Residual	36	95906	64		

Scytothalia dorycarpa

Scale	DF	SS	Propn	F	p
2000	1	93	22	4.71	NS
200	4	79	0	0.93	NS
20	12	254	47	5.64	<.005
Residual	36	135	31		

Seirococcus axillaris

Scale	DF	SS	Propn	F	p
2000	1	1658408	46	24.96	<.005
200	4	265797	0	0.448	NS
20	12	1779551	30	4.692	<.005
Residual	36	1137715	24		

Seirococcus axillaris

Scale	DF	SS	Propn	F	p
2000	1	2660	48	43.43	<.005
200	4	245	0	0.26	NS
20	12	2779	32	5.77	<.005
Residual	36	1445	20		

Sargassum decipiens

Scale	DF	SS	Propn	F	p
2000	1	0.07	0	0.002	NS
200	4	134	0	0.824	NS
20	12	488	50	4.011	<.005
Residual	36	365	50		

Sargassum fallax

Scale	DF	SS	Propn	F	p
2000	1	280	11	3.544	NS
200	4	316	3	1.295	NS
20	12	732	0	1.017	NS
Residual	36	2160	86		

Sargassum linearifolium

Scale	DF	SS	Propn	F	p
2000	1	3068	46	15.19	0.01
200	4	808	4	1.635	NS
20	12	1483	2	1.107	NS
Residual	36	4020	48		

Sargassum varians

Scale	DF	SS	Propn	F	p
2000	1	1347	6	1.665	NS
200	4	3237	15	2.351	NS
20	12	4131	12	1.539	NS
Residual	36	8053	67		

Sargassum verruculosum

Scale	DF	SS	Propn	F	p
2000	1	2096	0	0.786	NS
200	4	10673	51	9.959	<.005
20	12	3215	1	1.093	NS
Residual	36	8824	47		

Cape Jervis North**Biomass**

Total Biomass

Scale	DF	SS	Propn	F	p
2000	2	118595	0	0.21	NS
200	6	1511417	5		NS
20	18	3685678	57		<.005
Residual	54	2027249	38		

Abundance

Total Abundance

Scale	DF	SS	Propn	F	p
2000	2	3004	10		NS
200	6	5477	40		<.005
20	18	2648	10	0.89	NS
Residual	54	4623	40		

Acrocarpia paniculata

Scale	DF	SS	Propn	F	p
2000	2	12516	0	0.21	NS
200	6	151120	12		NS
20	18	250128	25		0.05
Residual	54	340244	62		

Acrocarpia paniculata

Scale	DF	SS	Propn	F	p
2000	2	11.6	0	0.15	NS
200	6	355	28		0.05
20	18	312	16		NS
Residual	54	507	56		

Cystophora brownii

Scale	DF	SS	Propn	F	p
2000	2	17309	6		NS
200	6	26345	13	0.67	0.05
20	18	20221	0	0.30	NS
Residual	54	119963	81		

Cystophora brownii

Scale	DF	SS	Propn	F	p
2000	2	53.4	13		NS
200	6	71.5	30		<.005
20	18	14.22	0	0.20	NS
Residual	54	124.7	56		

Cystophora expansa

Scale	DF	SS	Propn	F	p
2000	2	158733	0		NS
200	6	2327942	58		<.005
20	18	714432	9	0.89	NS
Residual	54	1216082	34		

Cystophora expansa

Scale	DF	SS	Propn	F	p
2000	2	266	0	0.45	NS
200	6	5883	59		<.005
20	18	1590	6	0.84	NS
Residual	54	3105	34		

Cystophora monilifera

Scale	DF	SS	Propn	F	p
2000	2	91129	35		0.05
200	6	22535	0	0.57	NS
20	18	69830	12	0.87	NS
Residual	54	125733	53		

Cystophora monilifera

Scale	DF	SS	Propn	F	p
2000	2	408	33		0.05
200	6	161	5		NS
20	18	310	12	0.89	NS
Residual	54	530	49		

Cystophora moniliformis

Scale	DF	SS	Propn	F	p
2000	2	70667	20		NS
200	6	41907	7	0.63	NS
20	18	62689	0	0.55	NS
Residual	54	205805	73		

Cystophora moniliformis

Scale	DF	SS	Propn	F	p
2000	2	31.6	9		NS
200	6	41.3	9		NS
20	18	68.7	10	0.79	NS
Residual	54	147.3	73		

Cystophora subfarcinata

Scale	DF	SS	Propn	F	p
2000	2	139309	25		NS
200	6	87548	6		NS
20	18	179300	28		<.005
Residual	54	174571	40		

Cystophora subfarcinata

Scale	DF	SS	Propn	F	p
2000	2	474	23		NS
200	6	220	0		NS
20	18	898	40		<.005
Residual	54	644	37		

Ecklonia radiata

Scale	DF	SS	Propn	F	p
2000	2	116937	27		NS
200	6	104534	25		0.05
20	18	84230	17		0.01
Residual	54	95891	31		

Ecklonia radiata

Scale	DF	SS	Propn	F	p
2000	2	740	29		NS
200	6	746	41		<.005
20	18	166	0	0.62	NS
Residual	54	486	29		

Scytothalia dorycarpa

Scale	DF	SS	Propn	F	p
2000	2	19332	0	0.26	NS
200	6	90489	9	0.65	NS
20	18	137145	0	0.58	NS
Residual	54	427359	91		

Scytothalia dorycarpa

Scale	DF	SS	Propn	F	p
2000	2	160	0		NS
200	6	841	53		<.005
20	18	277	6	0.80	NS
Residual	54	586	41		

Seirococcus axillaris

Scale	DF	SS	Propn	F	p
2000	2	292331	0		NS
200	6	3071626	34		NS
20	18	3067102	43		<.005
Residual	54	1383064	23		

Seirococcus axillaris

Scale	DF	SS	Propn	F	p
2000	2	122	0	0.37	NS
200	6	3896	35		NS
20	18	3700	41		<.005
Residual	54	1809	24		

Sargassum decipiens

Scale	DF	SS	Propn	F	p
2000	2	7939	0		NS
200	6	32971	28		0.01
20	18	20723	0	0.57	NS
Residual	54	66394	72		

Sargassum fallax

Scale	DF	SS	Propn	F	p
2000	2	20395	4		NS
200	6	46345	28		0.05
20	18	38245	15		NS
Residual	54	62081	53		

Sargassum linearifolium

Scale	DF	SS	Propn	F	p
2000	2	38547	8		NS
200	6	68019	24		0.05
20	18	61933	14	0.90	NS
Residual	54	104922	54		

Sargassum varians

Scale	DF	SS	Propn	F	p
2000	2	10012	0		NS
200	6	121450	59		<.005
20	18	28703	3	0.71	NS
Residual	54	71397	38		

Sargassum verruculosum

Scale	DF	SS	Propn	F	p
2000	2	818	0	0.09	NS
200	6	58976	19		NS
20	18	82299	36		<.005
Residual	54	72087	45		

Species Richness

Scale	DF	SS	Propn	F	p
2000	2	58.17	15		NS
200	6	53.63	8		NS
20	18	96	13	0.86	NS
Residual	54	179.3	65		

Chapter 8

Partitioning biotic variance between temporal change and within site spatial variation

Analysis: 1 way ANOVA on collections 1 to 5

Treatment: Collection

Dependent Variable: Biomass

CJN5

Acrocarpia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	21607.63	7202.54	1.2748
Error	28	158195.63	5649.84	Prob>F
C Total	31	179803.26		0.3022

Cystophora brownii				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0.6337500	0.211250	1.0000
Error	28	5.9150000	0.211250	Prob>F
C Total	31	6.5487500		0.4074

Cystophora expansa				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	65802.42	21934.1	0.6744
Error	28	910717.96	32525.6	Prob>F
C Total	31	976520.38		0.5750

C. monilifera				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	1464.817	488.272	1.3596
Error	28	10055.982	359.142	Prob>F
C Total	31	11520.800		0.2754

C. moniliformis				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2107.311	702.44	0.6167
Error	28	31894.446	1139.09	Prob>F
C Total	31	34001.757		0.6100

C. subfarcinata				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	15795.03	5265.01	1.3266
Error	28	111127.05	3968.82	Prob>F
C Total	31	126922.08		0.2855

Ecklonia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	145299.1	48433.0	1.1046
Error	28	1227744.7	43848.0	Prob>F
C Total	31	1373043.8		0.3638

Sargassum decipiens				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	11149.08	3716.36	0.8129
Error	28	128008.27	4571.72	Prob>F
C Total	31	139157.35		0.4975

S. fallax				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	21513.676	7171.23	2.6797
Error	28	74932.271	2676.15	Prob>F
C Total	31	96445.947		0.0661

S. lacerifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

S. linearifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	17674.721	5891.57	2.5835
Error	28	63853.924	2280.50	Prob>F
C Total	31	81528.645		0.0732

S. varians				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2114.826	704.94	0.4613
Error	28	42792.943	1528.32	Prob>F
C Total	31	44907.769		0.7116

S. verruculosum				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	3164.103	1054.70	1.2902
Error	28	22888.484	817.45	Prob>F
C Total	31	26052.587		0.2971

Scytothalia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	32929.96	10976.7	2.0315
Error	28	151289.51	5403.2	Prob>F
C Total	31	184219.47		0.1322

Seirococcus				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	573764.1	191255	1.3076
Error	28	4095455.6	146266	Prob>F
C Total	31	4669219.6		0.2915

Total Biomass				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	540661.4	180220	1.4980
Error	28	3368559.6	120306	Prob>F
C Total	31	3909221.0		0.2367

SV5

Acrocarpia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2028.6009	676.200	6.5315
Error	28	2898.8287	103.530	Prob>F
C Total	31	4927.4297		0.0017

C. brownii				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	13620.68	4540.23	1.0630
Error	28	119595.13	4271.25	Prob>F
C Total	31	133215.81		0.3806
Cystophora expansa				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	76997.15	25665.7	4.0899
Error	28	175712.46	6275.4	Prob>F
C Total	31	252709.62		0.0158
C. monilifera				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	33.6459	11.2153	0.2201
Error	28	1426.9813	50.9636	Prob>F
C Total	31	1460.6272		0.8816
C. moniliformis				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	5879.194	1959.73	0.9362
Error	28	58609.495	2093.20	Prob>F
C Total	31	64488.689		0.4363
C. subfarcinata				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	77015.40	25671.8	3.9888
Error	28	180205.56	6435.9	Prob>F
C Total	31	257220.96		0.0175
Ecklonia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	62203.34	20734.4	0.8273
Error	28	701793.00	25064.0	Prob>F
C Total	31	763996.34		0.4900
Sargassum decipiens				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	6373.691	2124.56	1.7556
Error	28	33885.268	1210.19	Prob>F
C Total	31	40258.959		0.1785
S. fallax				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	1469.0034	489.668	1.9922
Error	28	6882.1963	245.793	Prob>F
C Total	31	8351.1997		0.1380
S. lacerifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2028.8850	676.295	6.5620
Error	28	2885.7500	103.062	Prob>F
C Total	31	4914.6350		0.0017
S. linearifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	37075.148	12358.4	7.4393
Error	28	46514.176	1661.2	Prob>F
C Total	31	83589.325		0.0008

S. varians				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	4585.422	1528.47	0.9578
Error	28	44681.852	1595.78	Prob>F
C Total	31	49267.275		0.4263

S. verruculosum				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	58.12594	19.3753	1.4717
Error	28	368.62875	13.1653	Prob>F
C Total	31	426.75469		0.2436

Scytothalia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

Seirococcus				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

Total Biomass				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	256563.29	85521.1	5.3428
Error	28	448192.12	16006.9	Prob>F
C Total	31	704755.40		0.0049

CJN9

Acrocarpia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	40.91625	13.6387	1.2292
Error	28	310.68250	11.0958	Prob>F
C Total	31	351.59875		0.3176

C. brownii				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2750.971	916.990	1.0522
Error	28	24402.729	871.526	Prob>F
C Total	31	27153.700		0.3850

Cystophora expansa				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0.4534375	0.151146	1.9881
Error	28	2.1287500	0.076027	Prob>F
C Total	31	2.5821875		0.1386

C. monilifera				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	1644.071	548.024	0.6045
Error	28	25383.299	906.546	Prob>F
C Total	31	27027.370		0.6176

C. moniliformis				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	709.5938	236.531	1.5609

Error	28	4242.8750	151.531	Prob>F
C Total	31	4952.4688		0.2209

C. subfarcinata				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	822.4709	274.157	1.0056
Error	28	7633.8188	272.636	Prob>F
C Total	31	8456.2897		0.4049

Ecklonia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	319351.5	106451	1.3883
Error	28	2146923.2	76676	Prob>F
C Total	31	2466274.7		0.2669

Sargassum decipiens				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	884.1234	294.708	1.5205
Error	28	5427.1337	193.826	Prob>F
C Total	31	6311.2572		0.2309

S. fallax				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	7115.861	2371.95	2.0435
Error	28	32501.217	1160.76	Prob>F
C Total	31	39617.079		0.1305

S. lacerifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

S. linearifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	133.1513	44.3838	1.1562
Error	28	1074.8275	38.3867	Prob>F
C Total	31	1207.9787		0.3439

S. varians				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	4.986250	1.66208	0.9447
Error	28	49.262500	1.75938	Prob>F
C Total	31	54.248750		0.4323

S. verruculosum				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	1.503750	0.501250	0.8278
Error	28	16.955000	0.605536	Prob>F
C Total	31	18.458750		0.4898

Scytothalia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	366308.9	122103	3.3639
Error	28	1016358.3	36299	Prob>F
C Total	31	1382667.3		0.0326

Seirococcus				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	8386.12	2795.4	0.1070

Error	28	731290.16	26117.5	Prob>F
C Total	31	739676.29		0.9553

Total Biomass				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	470829.4	156943	1.9212
Error	28	2287357.6	81691	Prob>F
C Total	31	2758187.0		0.1491

CJE5

Acrocarpia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2013.738	671.246	2.3107
Error	28	8133.934	290.498	Prob>F
C Total	31	10147.671		0.0979

C. brownii				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	6937.798	2312.60	1.2124
Error	28	53409.163	1907.47	Prob>F
C Total	31	60346.960		0.3235

Cystophora expansa				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	247323.39	82441.1	12.3039
Error	28	187611.71	6700.4	Prob>F
C Total	31	434935.10		0.0000

C. monilifera				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	44355.484	14785.2	7.7186
Error	28	53634.355	1915.5	Prob>F
C Total	31	97989.839		0.0007

C. moniliformis				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	18409.48	6136.49	0.9459
Error	28	181641.83	6487.21	Prob>F
C Total	31	200051.32		0.4318

C. subfarcinata				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	3110.281	1036.76	0.3792
Error	28	76557.119	2734.18	Prob>F
C Total	31	79667.400		0.7687

Ecklonia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	13580.946	4526.98	5.0834
Error	28	24935.219	890.54	Prob>F
C Total	31	38516.165		0.0062

Sargassum decipiens				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	1991.6759	663.892	2.7176
Error	28	6840.2088	244.293	Prob>F
C Total	31	8831.8847		0.0635

S. fallax

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	3003.858	1001.29	3.8918
Error	28	7203.931	257.28	Prob>F
C Total	31	10207.790		0.0192

S. lacerifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0.7350000	0.245000	1.0000
Error	28	6.8600000	0.245000	Prob>F
C Total	31	7.5950000		0.4074

S. linearifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	3174.066	1058.02	1.0808
Error	28	27410.803	978.96	Prob>F
C Total	31	30584.869		0.3733

S. varians				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	17061.344	5687.11	6.6372
Error	28	23992.095	856.86	Prob>F
C Total	31	41053.439		0.0016

S. verruculosum				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	67978.25	22659.4	17.3549
Error	28	36558.13	1305.6	Prob>F
C Total	31	104536.38		0.0000

Scytothalia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

Seirococcus				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	14303.284	4767.76	9.3800
Error	28	14232.055	508.29	Prob>F
C Total	31	28535.339		0.0002

Total Biomass				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	1427402.4	475801	25.0592
Error	28	531638.8	18987	Prob>F
C Total	31	1959041.2		0.0000

GI5

Acrocarpia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	65219.75	21739.9	1.2916
Error	28	471294.13	16831.9	Prob>F
C Total	31	536513.88		0.2967

C. brownii				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

Cystophora expansa				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?
C. monilifera				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?
C. moniliformis				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	4.083750	1.36125	1.0000
Error	28	38.115000	1.36125	Prob>F
C Total	31	42.198750		0.4074
C. subfarcinata				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?
Ecklonia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	915442.5	305148	3.5266
Error	28	2422746.3	86527	Prob>F
C Total	31	3338188.8		0.0276
Sargassum decipiens				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?
S. fallax				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	54.21094	18.0703	1.1059
Error	28	457.52375	16.3401	Prob>F
C Total	31	511.73469		0.3632
S. lacerifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?
S. linearifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?
S. varians				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?
S. verruculosum				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

Scytothalia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	550310.6	183437	0.8426
Error	28	6095846.4	217709	Prob>F
C Total	31	6646157.0		0.4821

Seirococcus				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	504.3713	168.124	1.0152
Error	28	4637.1275	165.612	Prob>F
C Total	31	5141.4988		0.4007

Total Biomass				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2694748.2	898249	6.9387
Error	28	3624757.1	129456	Prob>F
C Total	31	6319505.3		0.0012

B5

Acrocarpia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	31679.9	10560.0	2.1084
Error	252	1262164.7	5008.6	Prob>F
C Total	255	1293844.6		0.0997

C. brownii				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2247.54	749.180	0.7922
Error	252	238316.78	945.702	Prob>F
C Total	255	240564.32		0.4992

Cystophora expansa				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	106522.8	35507.6	3.5063
Error	252	2551930.6	10126.7	Prob>F
C Total	255	2658453.4		0.0160

C. monilifera				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	5880.02	1960.01	2.3612
Error	252	209181.05	830.08	Prob>F
C Total	255	215061.07		0.0719

C. moniliformis				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	1335.78	445.26	0.1879
Error	252	597195.52	2369.82	Prob>F
C Total	255	598531.30		0.9046

C. subfarcinata				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	4561.32	1520.44	0.6010
Error	252	637568.69	2530.03	Prob>F
C Total	255	642130.01		0.6149

Ecklonia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	3672146	1224049	3.6853

Error	252	83700282	332144	Prob>F
C Total	255	87372427		0.0126
Sargassum decipiens				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	7007.81	2335.94	2.6089
Error	252	225637.78	895.39	Prob>F
C Total	255	232645.58		0.0521
S. fallax				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	11660.35	3886.78	3.7142
Error	252	263712.26	1046.48	Prob>F
C Total	255	275372.61		0.0121
S. lacerifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	261.0612	87.0204	3.4690
Error	252	6321.4988	25.0853	Prob>F
C Total	255	6582.5600		0.0168
S. linearifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	17587.72	5862.57	3.5951
Error	252	410943.90	1630.73	Prob>F
C Total	255	428531.62		0.0142
S. varians				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	5776.75	1925.58	1.6882
Error	252	287431.21	1140.60	Prob>F
C Total	255	293207.96		0.1700
S. verruculosum				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	9508.93	3169.64	4.0308
Error	252	198159.24	786.35	Prob>F
C Total	255	207668.17		0.0080
Scytothalia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	520817	173606	0.9847
Error	252	44427156	176298	Prob>F
C Total	255	44947973		0.4005
Seirococcus				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	92438	30812.5	0.5951
Error	252	13048577	51780.1	Prob>F
C Total	255	13141014		0.6188
Total Biomass				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	8015532	2671844	6.4064
Error	252	105098434	417057	Prob>F
C Total	255	113113966		0.0003

WI9

Acrocarpia

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	50488.38	16829.5	4.6798
Error	28	100692.49	3596.2	Prob>F
C Total	31	151180.87		0.0090

C. brownii CYSTBROW

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

Cystophora expansa

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

C. monilifera

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	18.37500	6.12500	1.0000
Error	28	171.50000	6.12500	Prob>F
C Total	31	189.87500		0.4074

C. moniliformis

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	3454.951	1151.65	0.3817
Error	28	84489.227	3017.47	Prob>F
C Total	31	87944.179		0.7670

C. subfarcinata

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	8085.516	2695.17	4.0156
Error	28	18792.894	671.17	Prob>F
C Total	31	26878.410		0.0170

Ecklonia

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	895021	298340	0.8054
Error	28	10371987	370428	Prob>F
C Total	31	11267008		0.5015

Sargassum decipiens

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	78.84375	26.2813	1.0000
Error	28	735.87500	26.2813	Prob>F
C Total	31	814.71875		0.4074

S. fallax

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	662.8425	220.948	2.9657
Error	28	2086.0325	74.501	Prob>F
C Total	31	2748.8750		0.0490

S. lacerifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

S. linearifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	633.6309	211.210	3.3750
Error	28	1752.2787	62.581	Prob>F
C Total	31	2385.9097		0.0322

S. varians				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

S. verruculosum				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	280.5159	93.5053	2.1850
Error	28	1198.2187	42.7935	Prob>F
C Total	31	1478.7347		0.1120

Scytothalia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2557240	852413	2.6731
Error	28	8928927	318890	Prob>F
C Total	31	11486166		0.0666

Seirococcus				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	59670.12	19890.0	5.5979
Error	28	99487.89	3553.1	Prob>F
C Total	31	159158.01		0.0039

Total Analysis of Variance				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	3245860	1081953	2.8980
Error	28	10453651	373345	Prob>F
C Total	31	13699512		0.0526

WI5

Acrocarpia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	13955.10	4651.70	1.1475
Error	28	113503.94	4053.71	Prob>F
C Total	31	127459.04		0.3472

C. brownii				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

Cystophora expansa				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

C. monilifera				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	26.14594	8.71531	1.7133
Error	28	142.42875	5.08674	Prob>F
C Total	31	168.57469		0.1870

C. moniliformis				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	845.061	281.687	0.8451
Error	28	9332.738	333.312	Prob>F
C Total	31	10177.799		0.4808

C. subfarcinata				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	5.703750	1.90125	1.4651
Error	28	36.335000	1.29768	Prob>F
C Total	31	42.038750		0.2453

Ecklonia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	8054290	2684763	6.4952
Error	28	11573596	413343	Prob>F
C Total	31	19627886		0.0018

Sargassum decipiens				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2.343750	0.781250	1.0000
Error	28	21.875000	0.781250	Prob>F
C Total	31	24.218750		0.4074

S. fallax				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	2798.707	932.902	2.9088
Error	28	8980.172	320.720	Prob>F
C Total	31	11778.880		0.0520

S. lacerifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

S. linearifolium				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

S. varians				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	0	0	?
Error	28	0	0	Prob>F
C Total	31	0		?

S. verruculosum				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	128.34375	42.7813	2.3289
Error	28	514.35500	18.3698	Prob>F
C Total	31	642.69875		0.0960

Scytothalia				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	1540370.4	513457	3.7640
Error	28	3819527.4	136412	Prob>F
C Total	31	5359897.9		0.0218

Seirococcus				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	22298.295	7432.76	3.0529
Error	28	68169.591	2434.63	Prob>F
C Total	31	90467.886		0.0448

Total Biomass				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	13189155	4396385	9.8957
Error	28	12439574	444270	Prob>F
C Total	31	25628729		0.0001

Appendix C

Species Lists

Species lists for the sites of Chapter 6 (temporal fluctuations) and Chapter 7 (spatial variation).

Species List for the Temporal Variation Study

This part of the appendix provides a species list for each site, separated into canopy and understorey. The number following the species represents the percentage of quadrats in which the species was found at that site.

Cape Jervis East (5m)	
Canopy	
<i>Acrocarpia paniculata</i>	51
<i>Cystophora brownii</i>	56
<i>Cystophora expansa</i>	100
<i>Cystophora monilifera</i>	79
<i>Cystophora moniliformis</i>	97
<i>Cystophora subfarcinata</i>	96
<i>Ecklonia radiata</i>	32
<i>Seirococcus axillaris</i>	10
<i>Sargassum decipiens</i>	46
<i>Sargassum fallax</i>	93
<i>Sargassum lacerifolium</i>	1
<i>Sargassum linearifolium</i>	97
<i>Sargassum varians</i>	97
<i>Sargassum verruculosum</i>	85
Understorey	
<i>Amphibolis antarctica</i> (Labillardiere) Sonder and Ascherson ex Ascherson	1
<i>Amphiroa anceps</i> (Lamarck) Decaisne	19
<i>Areschougia congesta</i> (Turner) J. Agardh	18
<i>Asparagopsis Montagne complex</i>	3
<i>Bellotia eriophorum</i> Harvey	3
<i>Botryocladia obovata</i> (Sonder) Kylin	3
<i>Caulerpa brownii</i> (C. Agardh) Endlicher	33
<i>Caulerpa cactoides</i> (Turner) C. Agardh	13
<i>Caulerpa flexilis</i> Lamaroux	6
<i>Caulerpa geminata</i> Harvey	1
<i>Caulerpa scalpelliformis</i> (R. Brown ex Turner) C. Agardh	3
<i>Caulerpa simpliciuscula</i> (Turner) C. Agardh	13
<i>Caulocystis cephalornithos</i> (Labillardiere) Areschoug	19
<i>Chlanidophora microphylla</i> (Harvey) J. Agardh	25
<i>Cirrulicarpus nanus</i> Womersley & Norris	10
<i>Cladosiphon filum</i> (Harvey) Kylin	3
<i>Codium pomoides</i> J. Agardh	15
<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbes & Sollier	11
<i>Corallina Linnaeus complex</i>	58
<i>Cutleria multifida</i> (Smith) Greville	1
<i>Dictyosphaeria sericea</i> Harvey	11
<i>Dilophus fastigiatus</i> (Sonder) J. Agardh	13
<i>Dilophus gunnianus</i> J. Agardh	19
<i>Erythroclonium muellerii</i> Sonder	29
<i>Gelidium Lamaroux / Pterocladia</i> J. Agardh complex	6
<i>Gloiosachion brownii</i> Harvey	14
<i>Haloplegma preissii</i> Sonder	1
<i>Halopteris Kuetzing complex</i>	7
<i>Laurencia Lamouroux complex</i>	3
<i>Liagora Lamaroux complex</i>	78
<i>Lobophora variegata</i> (Lamouroux) Womersley	42
<i>Lobospira bicuspidata</i> Areschoug	11
<i>Myriodesma integrifolium</i> Harvey	4
<i>Myriodesma tuberosum</i> J. Agardh	1
<i>Osmundaria prolifera</i> Lamaroux	1
<i>Perithalia caudata</i> (Labillardiere) Womersley	4
<i>Phloiocaulon spectabile</i> Reinke	8
<i>Plocamium Lamaroux complex</i>	1
<i>Rhabdonia verticillata</i> Harvey	18
<i>Rhodymenia Greville complex</i>	3
<i>Scaberia agardhii</i> Greville	21
<i>Sonderopelta coriacea</i> Womersley and Sinkora	1
<i>Thamnoclonium dicotolon</i> (J. Agardh) J. Agardh	14
<i>Zonaria complex</i>	86

Canopy

<i>Acrocarpia paniculata</i>	7
<i>Cystophora brownii</i>	46
<i>Cystophora expansa</i>	83
<i>Cystophora monilifera</i>	17
<i>Cystophora moniliformis</i>	71
<i>Cystophora subfarcinata</i>	71
<i>Ecklonia radiata</i>	81
<i>Sargassum decipiens</i>	82
<i>Sargassum fallax</i>	72
<i>Sargassum lacerifolium</i>	19
<i>Sargassum linearifolium</i>	96
<i>Sargassum varians</i>	97
<i>Sargassum verruculosum</i>	4

Understorey

<i>Amphibolis antarctica</i>	11
<i>Amphiroa anceps</i>	1
<i>Apjohnia laetevirens</i> Harvey	1
<i>Areschougia congesta</i>	8
<i>Bellotia eriophorum</i>	6
<i>Botryocladia obovata</i>	1
<i>Caulerpa brownii</i>	4
<i>Caulerpa cactoides</i>	1
<i>Caulocystis cephalornithos</i>	17
<i>Chlanidophora microphylla</i>	14
<i>Cirrulicarpus nanus</i>	1
<i>Cladostephus spongiosus</i> (Hudson) C. Agardh	10
<i>Colpomenia sinuosa</i>	10
<i>Corallina complex</i>	43
<i>Dictyosphaeria sericea</i>	17
<i>Dilophus crinitus</i> J. Agardh	3
<i>Dilophus fastigiatus</i>	3
<i>Dilophus gunnianus</i>	22
<i>Distromium multifidum</i> Womersley	1
<i>Erythroclonium muellerii</i>	3
<i>Gloiosachion brownii</i>	19
<i>Halopteris complex</i>	6
<i>Hydroclathrus clathratus</i> (C. Agardh) Howe	1
<i>Laurencia complex</i>	3
<i>Liagora complex</i>	10
<i>Lobophora variegata</i>	32
<i>Lobospira bicuspidata</i>	15
<i>Myriodesma integrifolium</i>	3
<i>Phloiocaulon spectabile</i>	8
<i>Polyopes</i> J. Agardh complex	3
<i>Rhabdonia verticillata</i>	6
<i>Scaberia agardhii</i>	4
<i>Sonderopelta coriacea</i>	3
<i>Zonaria complex</i>	76

Cape Jerisa North (9m)

Canopy

<i>Acrocarpia paniculata</i>	24
<i>Cystophora brownii</i>	4
<i>Cystophora expansa</i>	14
<i>Cystophora monilifera</i>	35
<i>Cystophora moniliformis</i>	8
<i>Cystophora subfarcinata</i>	19
<i>Ecklonia radiata</i>	100
<i>Scytothalia dorycarpa</i>	97
<i>Seirococcus axillaris</i>	100
<i>Sargassum decipiens</i>	38
<i>Sargassum fallax</i>	99
<i>Sargassum linearifolium</i>	56
<i>Sargassum varians</i>	15
<i>Sargassum verruculosum</i>	14

Understorey

<i>Amphiroa anceps</i>	46
<i>Areschougia congesta</i>	3
<i>Asparagopsis complex</i>	1
<i>Botryocladia obovata</i>	1
<i>Caulerpa brownii</i>	6
<i>Caulerpa flexilis</i>	1
<i>Caulerpa obscura</i> Sonder	1
<i>Caulerpa trifaria</i> Harvey	1
<i>Chlanidophora microphylla</i>	1
<i>Cirrulicarpus nanus</i>	26
<i>Corallina complex</i>	85
<i>Dictyopteris Lamaroux spp.</i>	1
<i>Distromium multifidum</i>	1
<i>Erythroclonium muellerii</i>	6
<i>Halopteris complex</i>	1
<i>Laurencia complex</i>	4
<i>Liagora complex</i>	15
<i>Lobophora variegata</i>	19
<i>Lobospira bicuspidata</i>	24
<i>Nizymenia Sonder complex</i>	1
<i>Plocamium complex</i>	28
<i>Polyopes complex</i>	4
<i>Rhabdonia verticillata</i>	4
<i>Rhodomenia complex</i>	15
<i>Scaberia agardhii</i>	1
<i>Sonderopelta corriacea</i>	18
<i>Zonaria complex</i>	60

Cape Jervis North (5m)

Canopy

<i>Acrocarpia paniculata</i>	89
<i>Cystophora brownii</i>	4
<i>Cystophora expansa</i>	54
<i>Cystophora monilifera</i>	38
<i>Cystophora moniliformis</i>	25
<i>Cystophora subfarcinata</i>	63
<i>Ecklonia radiata</i>	100
<i>Scytothalia dorycarpa</i>	61
<i>Seirococcus axillaris</i>	100
<i>Sargassum decipiens</i>	64
<i>Sargassum fallax</i>	100
<i>Sargassum linearifolium</i>	92
<i>Sargassum varians</i>	83
<i>Sargassum verruculosum</i>	74

Understorey

<i>Amphiroa anceps</i>	61
<i>Asparagopsis complex</i>	11
<i>Botryocladia obovata</i>	1
<i>Caulerpa brownii</i>	33
<i>Caulerpa cactoides</i>	3
<i>Caulerpa flexilis</i>	11
<i>Caulerpa geminata</i>	1
<i>Caulerpa scalpelliformis</i>	1
<i>Chlanidophora microphylla</i>	3
<i>Cirrularia nanus</i>	29
<i>Codium pomoides</i>	6
<i>Colpomenia sinuosa</i>	1
<i>Corallina complex</i>	99
<i>Dictyosphaeria sericea</i>	11
<i>Gelidium / Pterocladia complex</i>	7
<i>Gloiosachion brownii</i>	7
<i>Haloplegma preissii</i>	1
<i>Halopteris complex</i>	3
<i>Hydroclathrus clathratus</i>	3
<i>Laurencia complex</i>	3
<i>Liagora complex</i>	86
<i>Lobophora variegata</i>	31
<i>Lobospora bicuspidata</i>	40
<i>Myriodesma integrifolium</i>	3
<i>Nizymenia complex</i>	4
<i>Plocamium complex</i>	31
<i>Polyopes complex</i>	8
<i>Rhodomenia complex</i>	29
<i>Scaberia agardhii</i>	1
<i>Sonderopelta corriacea</i>	13
<i>Zonaria complex</i>	89

Wright Island (9m)

Canopy

<i>Acrocarpia paniculata</i>	23
<i>Cystophora expansa</i>	2
<i>Cystophora monilifera</i>	11
<i>Cystophora moniliformis</i>	5
<i>Cystophora subfarcinata</i>	9
<i>Ecklonia radiata</i>	96
<i>Scytothalia dorycarpa</i>	96
<i>Seirococcus axillaris</i>	86
<i>Sargassum fallax</i>	38
<i>Sargassum varians</i>	2
<i>Sargassum verruculosum</i>	16

Understorey

<i>Apjohnia laetevirens</i>	4
<i>Areschougia congesta</i>	71
<i>Asparagopsis complex</i>	11
<i>Botryocladia obovata</i>	4
<i>Caulerpa trifaria</i>	2
<i>Cirrularia nanus</i>	7
<i>Codium pomoides</i>	2
<i>Corallina complex</i>	7
<i>Dilophus fastigiatus</i>	4
<i>Erythroclonium muellerii</i>	11
<i>Gelidium / Pterocladia</i>	14
<i>Haloplegma preissii</i>	2
<i>Halopteris complex</i>	4
<i>Homostrichus sinclairii</i>	2
<i>Laurencia complex</i>	13
<i>Lenormandia marginata</i> Hooker and Harvey	2
<i>Lobophora variegata</i>	4
<i>Lobospora bicuspidata</i>	9
<i>Melanthalia concinna</i> J. Agardh	4
<i>Melanthalia obtusata</i> (Labillardiere) J. Agardh	14
<i>Nizyenia complex</i>	61
<i>Osmundaria prolifera</i>	36
<i>Phacelocarpus</i> Endlicher & Diesing complex	41
<i>Plocamium complex</i>	41
<i>Polyopes complex</i>	7
<i>Rhodopeltis australis</i> Harvey	2
<i>Rhodymenia complex</i>	88
<i>Sonderopelta coriacea</i>	16
<i>Thamnoclonium dicotolon</i>	5
<i>Ulva lactuca</i>	2
<i>Zonaria complex</i>	18

Wright Island (5m)

Canopy

<i>Acrocarpia paniculata</i>	57
<i>Cystophora monilifera</i>	7
<i>Cystophora moniliformis</i>	21
<i>Cystophora subfarcinata</i>	13
<i>Ecklonia radiata</i>	100
<i>Scytothalia dorycarpa</i>	98
<i>Seirococcus axillaris</i>	59
<i>Sargassum decipiens</i>	4
<i>Sargassum fallax</i>	75
<i>Sargassum linearifolium</i>	4
<i>Sargassum verruculosum</i>	7

Understorey

<i>Apjohnia laetevirens</i>	2
<i>Areschougia congesta</i>	14
<i>Asparagopsis complex</i>	7
<i>Caulerpa flexilis</i>	4
<i>Caulerpa obscura</i>	2
<i>Chaetomorpha coliformis</i> (Montagne) Kuetzing	2
<i>Corallina complex</i>	23
<i>Gelidium / Pterocladia complex</i>	61
<i>Halopteris complex</i>	29
<i>Homoestrichus sinclairii</i>	2
<i>Laurencia complex</i>	14
<i>Liagora complex</i>	2
<i>Lobospira bicuspidata</i>	5
<i>Melanthalia concinna</i>	14
<i>Melanthalia obtusata</i>	29
<i>Nizyenia complex</i>	21
<i>Osmundaria prolifera</i>	4
<i>Phacelocarpus complex</i>	57
<i>Plocamium complex</i>	27
<i>Polyopes complex</i>	18
<i>Rhodopeltis australis</i>	2
<i>Rhodymenia complex</i>	86
<i>Sonderopelta coriacea</i>	4
<i>Ulva lactuca</i> Linnaeus	4
<i>Zonaria complex</i>	23

Granite Island (5m)

Canopy

<i>Acrocarpia paniculata</i>	80
<i>Cystophora moniliformis</i>	7
<i>Cystophora subfarcinata</i>	4
<i>Ecklonia radiata</i>	91
<i>Scytothalia dorycarpa</i>	98
<i>Seirococcus axillaris</i>	16
<i>Sargassum fallax</i>	9

Understorey

<i>Areschougia congesta</i>	2
<i>Asparagopsis complex</i>	9
<i>Caulerpa brownii</i>	2
<i>Caulerpa geminata</i>	2
<i>Chaetomorpha coliformis</i>	2
<i>Corallina complex</i>	34
<i>Erythroclonium muellerii</i>	7
<i>Gelidium / Pterocladia complex</i>	27
<i>Halopteris complex</i>	11
<i>Laurencia complex</i>	16
<i>Liagora complex</i>	13
<i>Lobospira bicuspidata</i>	2
<i>Melanthalia concinna</i>	5
<i>Melanthalia obtusata</i>	9
<i>Nizymenia complex</i>	34
<i>Perithalia caudata</i>	2
<i>Phacelocarpus complex</i>	91
<i>Plocamium complex</i>	61
<i>Polyopes complex</i>	21
<i>Rhabdonia verticillata</i>	2
<i>Rhodopeltis australis</i>	7
<i>Rhodymenia complex</i>	48
<i>Sonderopelta corriacea</i>	61
<i>Thamnoclonium dicotolon</i>	9
<i>Zonaria complex</i>	30

The Bluff (5m)

Canopy

<i>Acrocarpia paniculata</i>	57
<i>Cystophora monilifera</i>	2
<i>Cystophora moniliformis</i>	36
<i>Cystophora subfarcinata</i>	25
<i>Ecklonia radiata</i>	100
<i>Scytothalia dorycarpa</i>	98
<i>Seirococcus axillaris</i>	34
<i>Sargassum decipiens</i>	4
<i>Sargassum fallax</i>	55
<i>Sargassum linearifolium</i>	9
<i>Sargassum verruculosum</i>	7

Understorey

<i>Areschougia congesta</i>	14
<i>Asparagopsis complex</i>	2
<i>Caulerpa cactoides</i>	4
<i>Cirrulicarpus nanus</i>	4
<i>Corallina complex</i>	5
<i>Dilophus fastigiatus</i>	7
<i>Gelidoptero complex</i>	27
<i>Griffithsia teges</i> Harvey	2
<i>Haloplegma preissii</i>	4
<i>Halopteris complex</i>	25
<i>Homoeostrichus sinclairii</i>	4
<i>Laurencia complex</i>	9
<i>Lobospira bicuspidata</i>	11
<i>Melanthalia obtusata</i>	7
<i>Nizymenia complex</i>	14
<i>Osmundaria prolifera</i>	9
<i>Phacelocarpus complex</i>	13
<i>Plocamium complex</i>	5
<i>Polyopes complex</i>	18
<i>Rhodymenia complex</i>	63
<i>Sonderopeltaaustralis</i>	2
<i>Zonaria complex</i>	43

Species List For the Small Scale Spatial Variation Surveys

Cape Jervis East	Cape Jervis North 1m	Cape Jervis North 2m
Acrocarpia paniculata	Acrocarpia paniculata	Acrocarpia paniculata
Cystophora brownii	Cystophora expansa	Cystophora expansa
Cystophora expansa	Cystophora subfarcin	Cystophora subfarcinata
Cystophora monilifera	Ecklonia radiata	Ecklonia radiata
Cystophora moniliformi	Sargassum decipiens	Sargassum decipiens
Cystophora subfarcinat	Sargassum fallax	Sargassum fallax
Ecklonia radiata	Sargassum linearifoliu	Sargassum linearifolium
Sargassum decipiens	Sargassum varians	Sargassum varians
Sargassum fallax	Scytothalia dorycarpa	Sargassum verruculosum
Sargassum fallax	Seirococcus axillaris	Seirococcus axillaris
Sargassum linearifolium	Areschougia congesta	Caulerpa brownii
Sargassum varians	Caulerpa brownii	Caulerpa geminata
Sargassum verruculosu	Caulocystis cephalornith	Cirrulicarpus complex
Areschougia congesta	Codium pomoides	Codium pomoides
Asparagopsis armata	Colpomenia sinuosa	Colpomenia sinuosa
Bellotia complex	Corallina complex	Corallina complex
Botryocladia obovata	Dictyosphaeria sericea	Coralline complex
Caulerpa brownii	Liagora complex	Gloiosachion complex
Caulocystis cephalornitho	Lobospira bicuspidata	Lobospira bicuspidata
Codium pomoides	Rhodymenia complex	Myriodesma tuberosum
Colpomenia sinuosa	Sonderopelta australis	Rhodymenia complex
Corallina complex	Zonaria complex	Sonderopelta australis
Dictyosphaeria sericea		Zonaria complex
Erythroclonium complex		
Gloiosachion complex		
Laurencia complex		
Liagora complex		
Lobospira bicuspidata		
Sonderopelta australis		
Thamnoclonium dicotolon		
Zonaria complex		

Bold type indicates canopy species

Species Lists for Large Scale Spatial Exercises

Acrocarpia paniculata
Cystophora brownii
Cystophora expansa
Cystophora monilifera
Cystophora moniliformis
Cystophora retorta
Cystophora subfarcinata
Ecklonia radiata
Sargassum decipiens
Sargassum fallax
Sargassum linearifolium
Sargassum varians
Sargassum verruculosum
Scaberia agardhii
Scytothalia dorycarpa
Seirococcus axillaris
Perithalia caudata
Apjohnia complex
Areschougia complex
Asparagopsis armata
Averainvillea complex
Bellotia complex
Botryocladia obovata
Caulerpa brownii
Caulerpa cactoides
Caulerpa flexilis
Caulerpa scalepaliformis
Caulerpa simpliciuscula
Caulocystis cephalornithos
Cirrulicarpus complex
Cladosiphon complex
Cladostephus complex
Colpomenia sinuosa
Corallina complex
Dictyosphaeria sericea
Erythroclonium complex
Glischercarrion complex
Gloiosachion complex
Halopteris complex
Liagora complex
Lobospira bicuspidata
Melanthalia complex
Osmundaria prolifera
Plocamium complex
Rhodomenia complex
Scytosiphon lomentaria
Sonderopelta australis
Sporochnus complex
Zonaria complex

Bold type indicates a canopy species