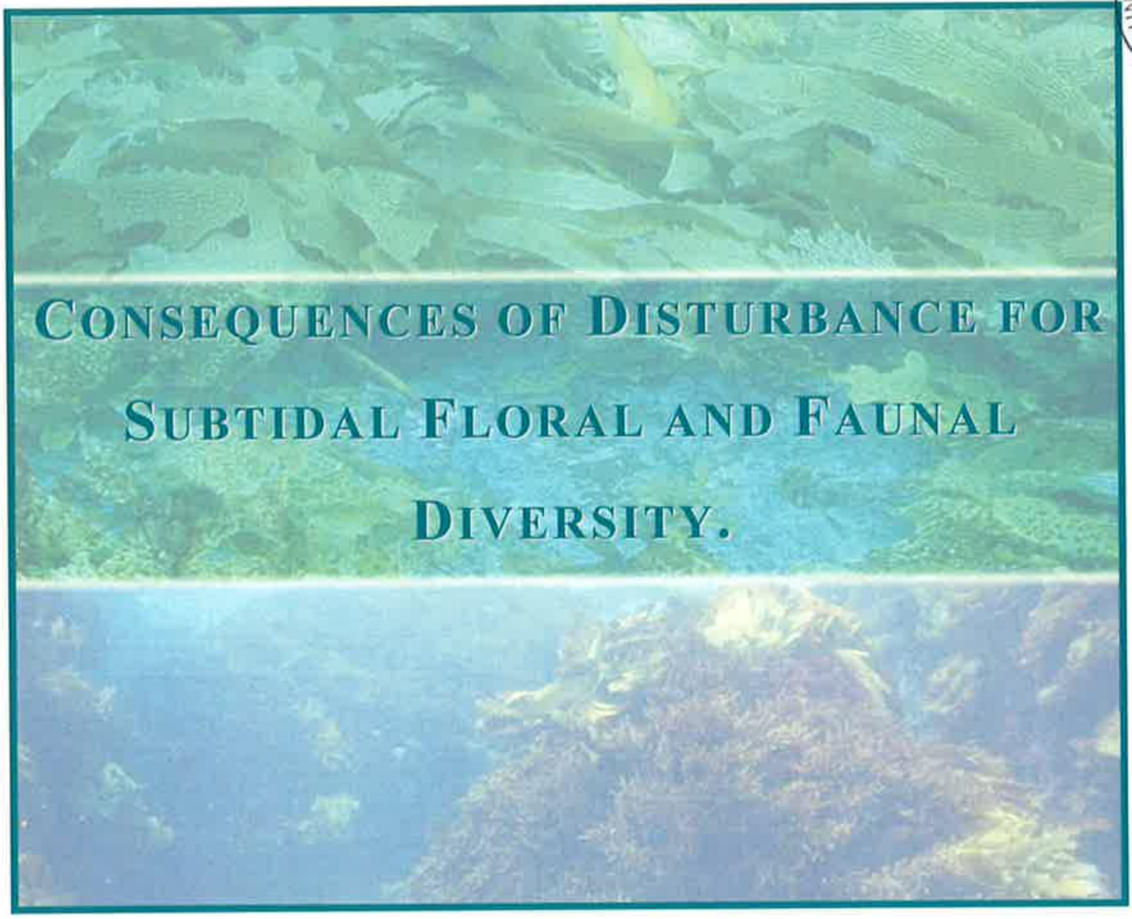

CONSEQUENCES OF DISTURBANCE FOR SUBTIDAL FLORAL AND FAUNAL DIVERSITY.

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AUSTRALIA

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ABSTRACT

Disturbance is a key determinant of the organisation of many natural systems, yet our ecological understanding of the response of mobile animals to disturbance in subtidal systems is limited. I assessed the impact of common disturbances (storms and herbivory) on subtidal forests of canopy-forming algae, *Ecklonia radiata* (Phaeophyta) and the consequences of disturbance and subsequent habitat modification on the diversity of associated invertebrates. This was done by testing hypotheses derived from a series of models that attempted to account for (i) the ways in which the composition of habitats of *E. radiata* are affected by disturbance, (ii) the effects of disturbance to habitat on the diversity of mobile invertebrates, (iii) the consequences of variation in composition of habitat for invertebrate diversity at local through to regional scales and (iv) whether the patterns of invertebrate diversity between habitats of different composition are a result of changes in local turnover.

Localised loss of monospecific canopies of *E. radiata* initiated a diverse recruitment of canopy-forming algae (taxa of fucalean algae) to potentially create mixed stands (i.e. species of fucalean algae interspersed with *E. radiata*). Such mixed-species stands were found to be equally as extensive as monospecific stands of *E. radiata* across temperate Australia (32% of reef covered by monospecific stands vs 31% stands of mixed algae). This thesis provides a unique assessment of whether such complexity in the composition of algae affects the diversity (composition and relative abundance) of invertebrates that rely on canopy-forming algae for habitat.

The next step was to determine the impact of disturbance events on the diversity of invertebrates associated with the holdfast of *E. radiata*. The initial loss of *E. radiata* habitat had important consequences for the diversity of mobile invertebrates, but their response was largely dependant on the configuration of habitat (density) prior to the disturbance. Considering that differences in the configuration and composition of habitat can be driven by disturbance and can influence the outcome of future disturbance events, ecological models that account for the dynamics of kelp systems will be stronger if we incorporate small-scale complexity in the structure of subtidal habitats.

Subsequently, I investigated the consequences of complexity in the structure of habitat (as driven by disturbance) on the diversity of mobile animals. Differences in invertebrate diversity between monospecific stands of *E. radiata* and stands of mixed algae were identified at a single location in South Australia. I therefore, tested the hypothesis that differences in invertebrate diversity between monospecific stands of *E. radiata* and stands of mixed algae are evident at local through regional scales across the temperate coastline of Australia. The composition and relative abundance of invertebrates differed between monospecific stands of *E. radiata* and stands of mixed algae, at most sites, most locations and all regions across Australia. There was a greater richness of taxa in monospecific stands than stands of mixed algae. This result highlights that complexity in the composition of subtidal habitats at small-scales, has important implications for patterns of animal diversity in ways predictable across broad scales. Finally, I investigated whether differences in mixed-species stands and monospecific stands of *E. radiata* were influenced by differences in local turnover of invertebrates among habitats of *E. radiata*. I tested the specific hypothesis that colonisation of distant habitats of *E. radiata* is affected by the nature of the intervening habitat (fucalean algae vs relatively bare space). The presence of fucalean algae between distant habitats of *E. radiata* (e.g. mixed stands) allowed for greater colonisation of *E. radiata* than a matrix of bare substratum.

I conclude that localised disturbance can generate considerable patchiness in the structure and composition of subtidal habitats which is a key determinant of differences in the diversity of associated assemblages of invertebrates. Consideration of such small-scale complexity within subtidal forests of algae and its affect on animal diversity not only strengthens our understanding of the ecology of subtidal forests, but will also increase the predictive capacity of further research in this system.

All in the golden afternoon
Full leisurely we glide;
For both our oars, with little skill,
By little arms are plied,
While little hands make vain pretence
Our wanderings to guide.

Ah, cruel Three! In such an hour,
Beneath such dreamy weather,
To beg a tale of breath too weak
To stir the tiniest feather!
Yet what can one poor voice avail
Against three tongues together?

Imperious Prima flashes forth
Her edict "to begin it"-
In gentler tone Secunda hopes
"There will be nonsense in it!"
While Tertia interrupts the tale
Not *more* than once a minute.

Anon, to sudden silence won,
In fancy they pursue
The dream-child moving through a land
Of wonders wild and new,
In friendly chat with bird or beast-
And half believe it true.

And ever, as the story drained
The wells of fancy dry.
And faintly strove that weary one
To put the subject by,
"The rest next time-" " It *is* next time!"
The happy voices cry.

Thus grew the tale of Wonderland:
Thus slowly, one by one,
Its quaint events were hammered out-
And now the tale is done
And home we steer, a merry crew,
Beneath the setting sun...

-Lewis Carroll 1907

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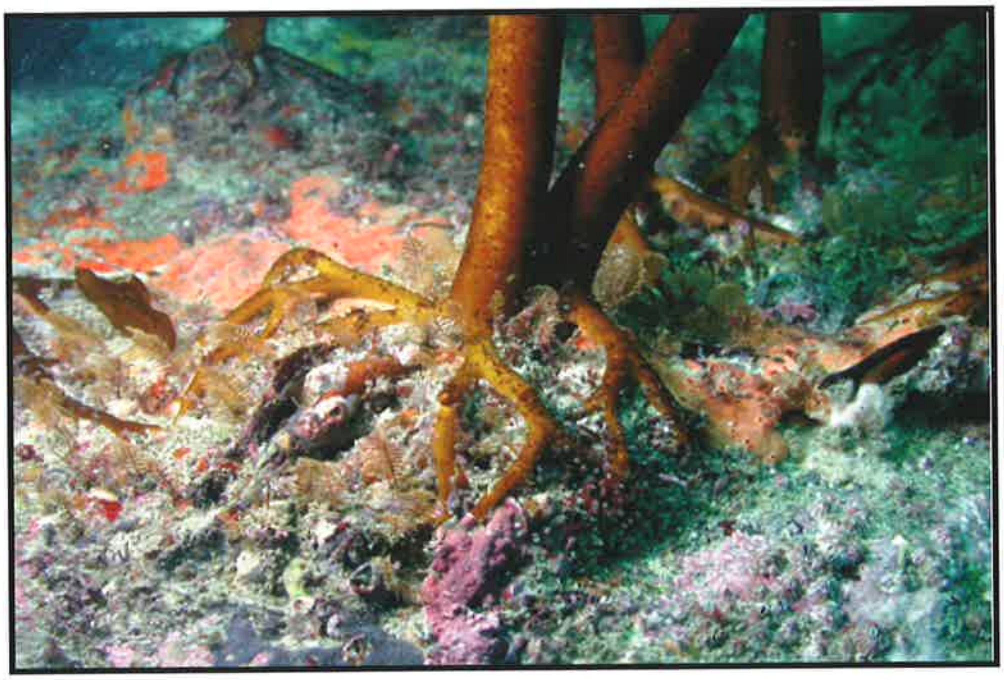


Holdfast of *Ecklonia radiata*,

New South Wales

CHAPTER ONE: INTRODUCTION

"The re-establishment of habitat complexity…and the associated recovery of populations of organisms that require it beg additional study."

-W. P. Sousa 2001

CHAPTER ONE

GENERAL INTRODUCTION

Questions about the processes that initiate and maintain diversity are of fundamental importance in ecological studies. Adequate conservation of biodiversity must initially involve the identification of patterns of diversity and then determination of the ecological processes by which they are structured (Hengeveld 1996). Whilst much attention of both the scientific and general public is focused on conserving biodiversity of terrestrial systems, marine environments contain a vast majority of the world's diversity of plants and animals (Norse 1995, Phillips 2001). Investigating the processes that initiate, maintain and modify patterns of diversity of marine systems is obviously critical.

Over thirty years ago Dayton (1971) pioneered the idea that disturbance plays an central role in the organisation and structure of assemblages in marine systems. Prior to this sovereign work, it was widely acknowledged that populations were maintained at or near equilibrium by a balance between biological interactions such as competition and predation (Weins 1977). Disturbances were viewed as rare events that only temporarily influenced the dynamics of populations (Odum 1969). It is currently understood, however, that disturbances can significantly alter biological interactions that shape assemblages and instigate long term changes in the composition and abundance of organisms (Pickett & White 1985b, Sousa 2001).

The use of the term disturbance is often ambiguous in ecological investigations and such a lack of definition impedes the progress of our understanding of the impacts of disturbance (McGuiness 1987). Disturbance can either refer to the force that causes physical damage to individuals or alternatively, describe the damage or mortality experienced per capita of population. One of the more tractable definitions of disturbance is a discrete event that kills or damages individuals thereby disrupting the dynamics of populations, assemblages or ecosystems (Pickett & White 1985a, Petraitis et al. 1989). Following Sousa (2001), I use the term disturbance to describe the effect of external agents i.e. the damage caused rather than the agent of damage.

Grime (1977) distinguishes between stress (impedance of growth) and disturbance (removal of biomass); here I use the latter definition. I am primarily concerned with natural physical and biological agents of disturbance that remove or damage local assemblages.

Disturbance is a key determinant of the initiation of the coexistence of species (Petraitis et al. 1989) via the creation of new space and liberation of resources (Connell 1972, Sousa 1984a). The intermediate disturbance hypothesis (Connell 1978) is one of the most widely cited hypotheses predicting the diversity of assemblages re-invading disturbed patches. It reasons that when disturbances are severe or frequent only a few resilient species can survive whilst in the absence of disturbance (or at very low levels) competitive species usually dominate. Diversity is initiated by moderate levels of disturbance because a balance is reached between competitive exclusion and opportunities for re-invasion (Connell 1978, Petraitis et al. 1989). This hypothesis, however, is not a universal reality (Mackey & Currie 2000, Dial & Roughgarden 1998) and further understanding, via experimental research, on the responses of animals and plants to disturbance is still necessary.

The dynamics of disturbance and subsequent recovery of disturbed areas are complex, hence predictions or models about the consequences of disturbance are difficult to apply to all kinds of habitats. The assemblage of species that re-invade disturbed areas depends on a number of factors all of which are variable; the frequency, severity, location and timing of the disturbance events, and the densities and reproductive abilities of species (Sousa 1984b, Pickett & White 1985b). The environmental characteristics of the disturbed patch (shape, heterogeneity, proximity to fertile stands) can also have strong influence on the diversity of assemblages of plants that re-invade disturbed areas (Whittaker & Levin 1977, Peterson & Pickett 2000). The relative and interactive effect of these variables creates tremendous complexity and research is well directed toward separating the consequences of the many components of disturbance on the diversity of natural systems.

Most conceptual models that attempt to explain the response of organisms to disturbance were developed from research done on intertidal, rocky coasts (e.g. Connell 1961, Paine & Levin 1981, Sousa 1985, Underwood 1998, 1999). Whilst these models can guide our understanding of disturbance in marine environments it is imperative to asses their reality in other marine environments. Subtidal systems contain some of the most productive and diverse assemblages of marine plants and animals (Suchanek 1994, Norse 1995, Gray 1997, Witman & Dayton 2001). Manipulative experiments which can identify the processes initiating and maintaining diversity are difficult in submerged habitats hence relatively little is known about processes that shape subtidal assemblages. Temperate coastal reefs of Australia are, however, increasingly threatened by human development (e.g. Gorgula & Connell in press) especially because temperate regions are highly populated (Sydney, Melbourne, Adelaide, Perth). Investigating the consequences of the loss and modification of subtidal habitat for animal diversity provides critically needed information to guide conservation and management practices.

Macroalgae of the orders Fucales and Laminariales (Phaeophyta) form the major structure for subtidal habitat of temperate rocky coastlines of the world (Shepherd & Womersley 1970, Choat & Schiel 1982, Santelices & Ojeda 1984, Underwood & Kennelly 1990, Jones & Andrew 1993). Whilst there is a large amount of ecological literature on the dynamics and biology of kelp communities in the northern hemisphere (e.g. North 1971, Chapman1984, Dayton et al. 1984, Dayton 1985), forests of canopy-forming large brown algae on the temperate coastline of Australia may not be comparable with their counterparts in the northern hemisphere. The common kelp, *Ecklonia radiata* (Laminariales) (C. Argardh) J. Argardh), is one of the most conspicuous and widespread subtidal alga across temperate Australia (Shepherd & Womersley 1970, Underwood et al. 1991) forming stipitate canopy at heights approximately 1-2 m. The understorey is composed of encrusting, filamentous and turfing forms of algae rather than understorey of other large brown algae (Shepherd & Womersley 1970, Underwood & Kennelly 1990, Connell 2003). Forests of *E. radiata* provide critical habitat for the majority of near shore assemblages of fish and invertebrates (Choat & Ayling 1987). Despite the increasing amount of experimental research done on macroalgae of Australian reefs (e. g. Kennelly 1983, 1987a, b, 1989, Andrew 1994, Kendrick et al. 1999, Wernberg-Møller 2002, Connell 2003) our understanding of the ecology of these forests remains poorly understood relative to temperate regions of the northern hemisphere (Underwood & Kennelly 1990).

Significant small-scale variability in the structure and composition of algae is evident in forests of canopy-forming algae of Australian (Shepherd &Womersley 1970, Kennelly 1983, Andrew & Jones 1990, Underwood et al. 1991, Andrew & O'Neill 2000). Whilst much research is done on monotypic arrays of *E. radiata*, in an attempt to reduce variation among replicates (Taylor 1998a, Underwood et al. 1991, Fowler-Walker & Connell 2002, Goodsell & Connell 2002), ecological predictions are made stronger by understanding the causes and consequences of variability in space and time (Kolasa & Pickett 1991, Palmer et al. 1997). Disturbance is a key process creating patchiness and increasing variability in the structure of marine habitats (Paine & Levin 1981, Jones & Andrew 1990, Syms & Jones 2000). Common agents of disturbance in forests of kelp include wave action and herbivory from urchins and fish, both of which can significantly alter the structure of kelp canopies (Dayton 1985, Andrew & Jones 1990, Jones & Andrew 1990). Disturbed patches in forests of kelp are often Type I (*sensu* Connell & Keough 1985, Sousa 1985); where removal or damage of individuals has occurred in areas bounded by survivors rather than catastrophic large scale damage (Kennelly 1987a, b, Andrew & Jones 1990).

Changes in the composition and abundance of organisms are common outcomes of disturbance yet much debate has arisen about the 'end point' or stability of alternate configurations following disturbance (Connell & Sousa 1983, Petraitis & Dudgeon 1999, Petraitis & Latham 1999). Determining whether assemblages have reached an alternate configuration is fraught with difficulty and in this thesis I am concerned with the initiation of diversity rather than its maintenance (*sensu* Petraitis & Latham 1999). Patterns of colonisation and diversity following disturbance have been studied for many years (Clements 1916) and the survival and persistence of species is primarily a function of interspecific interactions and competitive ability (Scheibling & Raymond 1990, Suding & Goldberg 2001); the investigation of such concepts requiring a different approach to the one in this thesis. Whilst local (within patch) diversity (alpha) can be initiated but not maintained, diversity at regional scales (beta) can persist (Pickett & White 1985a). Landscapes are often composed of a mosaic of patches in different successional stages because asynchronous disturbance events have altered the dynamics of assemblages in a number of patches within a landscape (Scheibling 1986, Turner 1987, Sousa 2001). A major objective of this research was to investigate the effects of disturbance in forests of canopy-forming algae in southern Australia and the consequences of heterogeneity in the structure and composition of forests for the diversity of associated fauna.

Many of the models developed to explain the response of organisms to disturbance are based on the response of sessile organisms such as plants. It is critical, however, that ecologists extend this understanding to mobile animals and assess their response to the loss or modification of their habitat as a result of disturbance. In 1984 (b) Sousa protested that knowledge of the response of mobile organisms to disturbance was lacking, due to the difficulty of observing and quantifying the response of mobile organisms. Almost twenty years later Sousa's plea remains (Sousa 2001). It is a concern that a whole suite of organisms (mobile) are under-represented in the ecological knowledge about the effects of disturbance.

Dramatic and long term changes to animal diversity are likely to stem from indirect effects of disturbance via the alteration of their habitat. Disturbance is a major regulator of the structure of habitat (Sousa 2001) hence processes that control populations of animals which are mediated by habitat (Southwood 1977) are likely to be modified by disturbance (Hanski 1991, Jones & Syms 1998). For example, animals that remain in disturbed habitats may suffer increased competition due to habitat loss and therefore migrate to find unoccupied or more suitable habitats (Smith 1982). Reductions in the quality of habitat following disturbance may also reduce populations of animals that remain in the disturbed area (Onuf & Quammen 1983). Alternatively, disturbances can promote faunal diversity by increasing the heterogeneity of the environment (Tilman 1982). Increased diversity and complexity in vegetative habitat increases the palatability and quantity of local food resources (Hansson 1979) and can positively influence the abundance and richness of animals (Bell et al. 1991). Variations in the composition, structure, and quality of habitat during succession can promote the diversity and abundance of animal populations (Southwood et al. 1979, Dean & Connell 1987a, b, c, Haddad et al. 2001).

Attempts to understand the consequences of disturbance on mobile animals are difficult but possible. The base of *E. radiata* is attached to the ground by a holdfast whose many haptera form a discrete habitat for a diverse group of invertebrates including crustaceans, polychaetes, molluscs and echinoderms (Smith et al. 1996). The fauna in holdfasts of *E. radiata* are highly mobile and exhibit rapid exchange of individuals (Gunnill 1982a, b, Howard 1985, Virnstein & Curran 1986, Jørgensen & Christie 2003). These habitats form effective patches (*sensu* Hanski 1991, Moore 1973a) which can be easily manipulated with replication. In addition, the response of the whole assemblage (diversity), as well as that of individual species, can be determined by sampling the complete habitat (individual holdfast). These factors render holdfasts valuable systems for investigations of the role of disturbance to habitat and on the diversity of animal assemblages. Furthermore, invertebrates make up a significant portion of the world's biodiversity but their conservation is often a case of 'out of sight out of mind' (New 1993) hence it is fundamentally important to understand the consequences of disturbance for invertebrate taxa.

The objective of my research was twofold. First, to determine the impact of common disturbance events on the diversity of subtidal assemblages of plants and animals. Second, to investigate associations between variation in the composition of habitat (generated by disturbance) and patterns of animal diversity. My research involved the following steps: (a) experimental determination of changes in the composition of macroalgae caused by disturbance (Chapter Two), (b) experimental investigation of the effects of disturbance to habitat (macroalgae) on the diversity of animal assemblages (Chapter Three), (c) identification of the extent of variation in composition of algae (from a) across Australia (Chapter Four), with assessment of the consequences of this variation for animal diversity at local (Chapter Four) and regional scales (Chapter Five) and (d) determination of whether patterns of animal diversity in relation to habitat complexity (observed in c) are a result of changes in local turnover (Chapter Six).

The experiments were designed to chiefly use analysis of variance to detect significant changes in assemblages in response to experimental conditions (e.g. Underwood 1997). Most experiments involve tests of hypotheses about the simultaneous response of assemblages, and relative abundance of individuals; NP-MANOVA (Anderson 2001) was used for these analyses. Non metric multi dimensional scaling plots (nMDS) or canonical discriminant ordinations were used to provide a visual estimation of the multivariate variability among and within samples (Legendre 1990, Clarke & Warwick 1994).

This thesis follows a logical flow of models that account for the ways in which the structure and composition of habitats are affected by disturbance and how this in turn affects the diversity of associated animals. The research for each chapter also involved testing hypotheses about novel ideas within each of the main objectives listed above and, as such, each chapter can be read as a separate piece of research. The additional objectives are as follows:

Chapter Two

Disturbances can vary in severity and can remove canopy but not liberate space on the substratum. Parts of plants remaining on the substratum increase the heterogeneity of the disturbed area and may promote diversity of recruit assemblages (e.g. Connell & Keough 1985, Bourget et al. 1994, Suding & Goldberg 2001). This chapter details research that assessed the effects of canopy versus substrate availability following disturbance on the recruitment of canopy-forming algae. In a broader context this chapter provides a basis for understanding how heterogeneity and patchiness at small-scales can be initiated within temperate subtidal reefs.

Chapter Three

Configuration of habitat (e.g. density) has strong influence on ecological processes that control populations of animals e.g. predation, recruitment (Bell & Hicks 1991, Anderson 1994, Levin & Hay 1996). Whilst the historical configuration of habitat i.e. that prior to disturbance, is often important in shaping the response of organisms to future events, history is often over-looked in ecological investigations of the effect of disturbance (Tanner et al. 1996). This chapter tested the hypothesis that the density of habitats of *E. radiata* before disturbance affects the initial response of mobile invertebrates to different severities of disturbance. More broadly, the research establishes information about the ways in which mobile organisms respond to initial disturbance to their habitat.

Chapter Four

This chapter quantifies small-scale variation in the composition and configuration of canopy-forming brown algae across southern Australia. The research involves a preliminary mensurative experiment to test the hypothesis that animal assemblages differ between different, but equally widespread configurations of brown algae; stands of monospecific *E. radiata* and stands of mixed alage (*E. radiata*/fucalean algae complex). This chapter forms the basis of the broad-scale study in Chapter Five.

Chapter Five

With aim to define the domain or extent to which a real pattern holds true i.e. the generality of patterns (Levin 1992), in this chapter I tested the hypothesis that differences in diversity of invertebrates between monospecific stands of *E. radiata* and stands of mixed algae observed at small spatial scales (Chapter Four) are evident at broader scales across the temperate coastline of Australia. Chapter Four and Five assessed whether patchiness at small-scales within temperate reefs, a common configuration of disturbed landscapes (Sousa 2001), is associated with differences in the diversity of animals.

Chapter Six

Reductions in the amount of habitat following disturbance leads to increased spatial isolation of remnant habitats threatening the ability for species to utilise resources (Andrén 1994). Connectivity of fragmented habitats can depend on the characteristics of the matrix (areas of non habitat surrounding habitats) (Fahrig & Merriam 1985, Ricketts 2001). In this chapter, I assessed whether colonisation of spatially isolated habitats of *E. radiata* was modified by the presence of alternate species of algae between primary habitats (*E. radiata*) i.e. stands of mixed algae relative to monospecific stands. This work fits into a broader context of the effects of habitat fragmentation on biodiversity and such field-based assessments are a rarity in this field of landscape ecology.

This chapter has outlined the necessary background (observations and review of literature) that lead to the generation of the hypotheses tested in the following chapters. The last chapter (Chapter Seven) provides a general discussion and synthesis of the data from Chapters Two - Six and concludes the major findings of this body of work. Note that each chapter is written in the style of a scientific paper and can be read as separate studies. Tables appear within the text and figures are presented at the end of each chapter. Appendices are numbered sequentially but included at the end of the relevant chapter. The references are compiled at the end of the thesis.

Juvenile *Ecklonia radiata* attached to adult holdfast of *E. radiata*, collected from Western Australia

***Sargassum fallax* attached to adult holdfast of *E. radiata*, collected from Western Australia**

CHAPTER TWO

DISTURBANCE INITIATES DIVERSITY IN RECRUITMENT OF CANOPY-FORMING ALGAE: INTERACTIVE EFFECTS OF CANOPY-THINNING AND SUBSTRATUM AVAILABILITY

2.1 INTRODUCTION

Disturbance is a key initiator of variability in the composition of taxa in many forest habitats (Pickett & White 1985b, Kolasa & Pickett 1991). Competition between neighbouring individuals often results in the dominance of a few or single species (Sousa 1979a, b, Paine & Levin 1981), which restricts the establishment of alternate species. Disturbance is hence a principal process that initiates, and often maintains, the diversity of habitats through the loss of all, or parts of established individuals (Sousa 1984b, Petraitis et al. 1989).

The severity of disturbance events and therefore the type of damage caused can be highly variable; not all disturbed patches are the same. Knowledge of the extent to which variation in the attributes of disturbed patches affect re-invasion is key to our understanding the consequences of disturbance (Whittaker & Levin 1977, Peterson & Pickett 2000). In marine systems tests of hypotheses about the effects of the characteristics of disturbed patches tend to focus on their size, shape or location (Connell & Keough 1985, Wernberg-Møller 2002, Airoldi 2003). Severe disturbances where all organisms are removed are rare in marine systems (Foster & Sousa 1985), yet there is little assessment of whether re-invasion is influenced by fragments of organisms remaining in disturbed patches.

Forests of brown algae are the major habitat for many marine animals of the temperate world (Witman & Dayton 2001). Three main types of assemblages of canopy-forming algae have been observed along rocky subtidal coastlines of Australia; monospecific *Ecklonia radiata* (C. Agardh) J. Agardh (Laminariales: Alariaceae) (Kendrick et al. 1999, Underwood et al. 1991), diverse assemblages of fucalean algae (Fucales) (Shepherd & Womersley 1970, Collings & Cheshire 1998), and complexes of fucalean species mixed with *E. radiata* (Chapter Four). Forests of *E. radiata* are commonly disturbed by storms and herbivory (Kennelly 1987b, Andrew & Jones 1990, Jones & Andrew 1990) and these agents of disturbance may drive the observed variation in the composition of forests of algae.

Depending on the particulars of the disturbance, removal of established canopy-forming algae often creates opportunities for the recruitment of alternate species, thereby increasing the diversity of the canopy (Kirkman 1981, Reed & Foster 1984, Scheibling 1986). Dense canopies can inhibit recruitment of canopy-forming algae by modifying the physical environment; such as light intensity (Reed &Foster 1984, Schiel 1985, Kennelly 1989), water motion (Eckman et al. 1989) and physical interference (Velimirov & Griffiths 1979, Connell 2003). The recruitment and establishment of canopy-forming algae, therefore, relies on the removal of all, or part of the surrounding adult plants. Algal settlement is, however, not only dependant on space liberated in the canopy but also on the availability and structure of the substratum (Dayton et al. 1984, Fletcher & Callow 1992). The two most extensive types of substrata available to recruits are holdfasts of canopy species or bare rock (Anderson et al. 1997).

Canopies of *E. radiata* are commonly thinned rather than completely removed (Kennelly 1987b). Moreover plants can be wholly dislodged or can be partially removed leaving parts of the plant (usually the holdfast and/or stipe) remaining on the substratum (Kennelly 1987b, Andrew & Jones 1990). This means that whilst space is liberated in the canopy, the substratum is still occupied by residual holdfasts. In this study, I tested the hypothesis that a greater diversity of canopy-forming algae recruits to areas where canopies of monospecific *E. radiata* have been thinned and the availability of substratum is increased (i.e. fewer holdfasts without thallus remain attached to the substratum).

2.2 METHODS

This study was done on a subtidal reef (Spit Reef) off West Island, South Australia (35° 37′ S, 138° 35′ E) (Fig. 2.1). The reef is granitic boulders 3-5 m deep and subject to primarily south-westerly swell. Stands of monospecific *E. radiata* were predominant, forming canopy ~ 600 mm high at the time of this study. Stands of mixed fucalean algae were observed interspersed with *E. radiata*. Detailed descriptions of the structure of assemblages of algae and environmental descriptions at West Island are given by Shepherd & Womersley (1970). The damage of *E. radiata* wrack ($n = 50$) was counted and assessed after a winter storm (Austral winter of 2002). A disproportionately large number of individuals did not have holdfasts intact ($n = 40$), providing a biological basis for manipulations of the interactive effects of canopy-thinning and availability of substratum.

In Australia, disturbed patches of *E. radiata* are seldom greater than a few square meters (Kennelly 1987b). I manipulated areas (1 m^2) within forests of monospecific *E. radiata* in very dense stands (14 - 15 individuals/m^2) to simulate common disturbance events (e.g. herbivory and storms). The cover of canopy was manipulated at two levels; moderately dense (7 individuals/m^2) and sparse (3 individuals/m^2) by removing whole plants (thallus and holdfast). Individuals with holdfasts of similar size were selected at random from each plot and removed by levering the holdfast and plant off the substratum with a dive knife. This was done so the amount of free substratum (e.g. high under sparse canopies vs low under moderately dense canopies) created by removing plants was similar among plots within the two categories of canopy cover. Orthogonal to levels of canopy cover, the availability of substratum was manipulated to create moderately dense (7 holdfasts/m^2) and sparse (3 holdfasts/m^2) covers of holdfasts on the substratum without thallus attached (thallus removed from the base of the stipe). Criteria for density were based on distinction between 'dense' and 'sparse' canopies of *E. radiata* that influence the growth of understorey algae at the above-mentioned levels (Melville & Connell 2001).

Juvenile macroalgae visible to the naked eye were infrequent but if present were removed during manipulations from all plots. Six replicates of each treatment were randomly allocated on the reef. A procedural control tested for artifacts associated with the cutting of stipes by comparing plots of naturally very dense forests (14-16 individuals/m^2) to plots in which cut stipes were attached to intact plants by cable ties ($n = 6$). This control tests for any chemicals that may be released by cutting stipes and may inhibit the recruitment of algae. No artifacts were detected in this comparison (ANOVA: $F_{1,10} = 0.572$, $P > 0.05$).

Manipulations were done in November (Austral spring) of 2002. The experiment was maintained over four months of the Austral spring and summer during which time the most abundant taxa of canopy-forming brown algae recruit at West Island (Alariaceae, Cystophoraceae and Sargassaceae) (Emmerson & Collings 1998, Hotchkiss 1999). Such a length of study is often used to determine factors important to the initiation of patterns of re-invasion (Kennelly 1983, Benedetti-Cecchi & Cinelli 1993, Melville & Connell 2001) and is sufficient for recruits to be identified as canopy-formers (~5-10 cm high) (Kennelly 1987b, Kendrick & Walker 1994, Emmerson & Collings 1998). I acknowledge that other factors such as density-dependant competition (Schiel 1985, Reed 1990) and grazing (Kennelly 1983, Scheibling & Raymond 1990) are more influential in structuring and maintaining the composition of assemblages over longer periods of time.

Sampling in each plot was done by counting the species (> 5 cm in height) that form canopy as adults (similar to Kennelly 1987b, Emmerson & Collings 1998, Hotchkiss 1999). This also ensured that recruits were well established and should persist through permanent attachment to the substratum underneath holdfasts (Fletcher & Callow 1992) as residual holdfasts decay (after > 6 months) (Anderson et al. 1997). No recruits were counted within 10 cm from the edge of the plot to avoid the effects of edges (Emmerson & Collings 1998). In each plot the amount of substrate free from holdfasts is inversely proportional to the total amount of residual and living holdfasts. For additional information counts were partitioned into two categories: recruits attached to the substratum and recruits attached to residual holdfasts (without stipes) (only two individuals were observed on holdfasts with thalli attached). Counts were initially pooled to assess total recruitment in response to the treatments (canopy cover vs substrate availability-the inverse of holdfast density) in analysis of variance. Type specimens were preserved and identified using keys from Womersley (1987).

2.3 RESULTS

Seven species of algae were identified as recruits; Cystoseiraceae: *Cystophora moniliformis* (Esper), *C. monilifera* (J. Agardh), *C. grevillei* (Agardh) J. Agardh) and

Acrocarpia paniculata (Turner), Sargassaceae: *Sargassum fallax* (Sonder), Seirococcaceae: *Syctothalia dorycarpa* (Turner) Greville), and Alariaceae: *Ecklonia radiata.*

Loss of canopy resulted in greater number of species (richness) (pooled rock and holdfast counts) when holdfasts were sparse but not when they were denser, i.e. when there was a greater availability of substratum (Table 2.1, Fig. 2.2). Analysis of variance (ANOVA) of species richness detected a significant interaction between the effects of canopy cover and the availability of substratum (Table 2.1). Reduction in the density of residual holdfasts also reduced the species richness of recruits when the cover of canopy was moderately dense but not sparse (Table 2.1, Fig. 2.2).

No difference in the abundance of individual species (pooled rock and holdfast counts) was detected among treatments, except *C. monilifera* (greater under sparse than moderately dense canopy ANOVA: $F_{1,20} = 10.29$, $P < 0.05$). Large variation between replicates (similar to Schiel 1985, Reed 1990, Santelices 1990) may have hampered the ability of ANOVA to detect statistically significant differences in patterns of recruit abundance between plots with different densities of canopy and substratum availability. Observation of the raw data indicates that rank abundance of *C. grevillei* and *E. radiata* under denser canopies was higher where residual holdfasts were denser than sparse (Fig. 2.3). Under sparser canopies this pattern was evident for *E. radiata*, but reversed for *C. grevillei* and not apparent for *S. fallax* (Fig. 2.3).

Table 2.1. (a) ANOVA of the species richness of recruits (mean number of species) between different covers of canopy (moderately dense vs sparse) and number of residual holdfasts (denser vs sparser) (substratum availability). Data were homogenous (Cochran's *C*-test: $P > 0.05$). 'Canopy Cover' and 'Substrate Availability' were treated as fixed and orthogonal. (b) SNK tests for the significant interaction between canopy cover and substratum availability. Not significant (ns): $P > 0.05$

(a) ANOVA

Source of variation	df	MS	F	*P*
Canopy cover	1	0.167	0.36	ns
Substratum availability	1	0.167	0.36	ns
Canopy cover × Substratum availability	1	4.167	8.93	0.007
Residual	20	0.467		

(b) SNK tests

Moderately dense canopy	Denser > Sparse holdfasts
Sparse canopy	Denser = Sparse holdfasts
Denser holdfasts	Moderately dense = Sparse canopy
Sparse holdfasts	Moderately dense < Sparse canopy

Three species were frequently observed on residual holdfasts; *C. grevillei*, *E. radiata*, and *S. fallax*. Again, due to large variation in the number of recruits among plots, statistically significant differences in the mean abundance of recruits between dense and sparse canopies were not detected by ANOVA: *C. grevillei* ($F_{1,20} = 2.82$, $P > 0.05$), *E. radiata* ($F_{1,20} = 0.01$, $P > 0.05$), and *S. fallax* ($F_{1,20} = 0.87$, $P > 0.05$). There does however appear to be a positive association between holdfast density and the rank abundance of recruits under denser but not sparse canopies (Fig. 2.4). It is noteworthy that more experimental plots had greater rank abundance (total number of recruits for all replicates) of recruits on residual holdfasts than on bare substratum under denser than sparse canopies for *C. grevillei* (Fisher's exact test: $P < 0.05$), *E. radiata* (Fisher's exact test: $P < 0.05$) and *S. fallax* (Fisher's exact test: $P < 0.01$) (Fig. 2.4).

2.4 DISCUSSION

Thinning canopies of monospecific *E. radiata* created a more diverse assemblage of canopy-forming recruits only where fewer holdfasts remained on the substratum. This experimental evidence supports the model that the loss of established algae within monospecific stands provides opportunities for the recruitment of alternate species of algae (Kirkman 1981, Reed & Foster 1984, Scheibling 1986, Emmerson & Collings 1998, Wernberg-Møller 2002), but is unique in establishing this model for species of algae that form canopies rather than understorey. Importantly, the greater species richness initiated in disturbed areas was neither a simple function of gaps created in the canopy nor free space on the substratum, but due to a combination of both factors.

Under moderately dense canopies, establishment of juveniles is often limited by the availability of light (Dayton et al. 1984, Reed & Foster 1984, Edwards 1998). In this study, however, thinning canopies lead to a greater richness of recruits only when greater amounts of space were available on the substratum (i.e. space free from holdfasts). I suggest that whilst residual holdfasts may not persist for more than a year (Anderson et al. 1997), canopy-forming algae are influenced by their presence in the early stages of recruitment and establishment. Permanent attachment of juveniles to the substratum underneath holdfasts is likely as the plants develop (Fletcher & Callow 1992) such that juveniles would persist as residual holdfasts decay. This study highlights the need for awareness of the nature of the substratum when assessing the effects of canopies on the re-invasion of disturbed patches (e.g. Scheibling & Raymond 1990, Minchinton 2001).

Juveniles of canopy-forming algae rarely establish under adult canopies (Rosenthal et al. 1974), but authors report significant numbers of recruits of *Cystophora* (Hotchkiss 1999) and *Sargassum* species established under canopies (Kendrick & Walker 1994). I suggest that it is difficult for juveniles to establish under canopies of

E. radiata in South Australia because the substratum is generally covered by topographically smooth encrusting coralline algae (Fowler-Walker & Connell 2002) and the substratum is continually abraded by the fronds of nearby adults (Connell 2003). I believe that the greater densities of recruits attached to residual holdfasts versus bare substrata under denser canopies is a consequence of the greater complexity provided by the holdfasts. Complexity of substratum is important for the recruitment and survival of plant propagules (Fletcher & Callow 1992, Anderson et al. 1997, Minchinton 2001) and their subsequent growth (Irving & Connell 2002). Holdfasts of *E. radiata* have numerous intertwined haptera which create crevices that may provide increased sites for attachment and protection from scour (Kennelly 1989, Connell 2003) or predation (Bodkin 1988, Anderson et al. 1997), which may be more intense under denser canopies.

Forests of algae can be maintained by the persistence of juvenile understorey plants or microscopic 'seedbanks' (North 1971, Edwards 2000). This has been noted for species of *Cystophora* (Hotchkiss 1999), *Sargassum* (Kendrick & Walker 1994) and *E. radiata* (Kirkman 1981, Andrew & Jones 1990). I acknowledge that the recruits in our study may not have arrived via dispersal but existed as a population of tiny understorey juveniles that were able to grow to form part of the canopy population following the manipulations. This possibility does not detract from the primary conclusion that thinning the canopy as well as increased space available on the substratum initiates greater diversity of recruits of canopy-forming algae. Further research will identify the stage(s) at which such recruitment is primarily affected by these types of disturbances.

Disturbance can modify the competitive interactions of species (Wilson & Keddy 1986) thereby influencing the composition of habitats. The expansive nature of the fronds and large holdfast of *E. radiata* allows the persistence of this species in monospecific arrays (Schiel 1988). It is clear, however, that this hierarchy (*E. radiata* vs fucalean algae) was not maintained for some months after disturbance. The conditions created by disturbance may allow a change (fucalean algae vs *E. radiata*) consistent with the competitive change hypothesis (Suding & Goldberg 2001). Fucalean algae may be able to procure resources (space and light) more rapidly than *E. radiata* after disturbance (Bolton & Anderson 1994, Hotchkiss 1999).

While I do not infer that the greater diversity of recruits translates to greater diversity of adult canopies, I do highlight the complex and interactive role that different attributes of disturbed patches have in initiating changes in the composition of forests of algae.

Whilst the initiation of local diversity (within patches) may not persist, regional diversity (among patches) can be maintained by asynchronous disturbance events in a number of patches such that the landscape is a mosaic of different successional stages; each patch varying in composition (Thrush 1991, Sousa 2001). Indeed, variability in the composition of taxa at small spatial scales is characteristic of forests of subtidal algae in Australia (Underwood et al. 1991, Kennelly & Underwood 1992, Andrew & O'Neill 2000). It is important to ascertain and separate processes that both initiate and maintain diversity (Petraitis & Latham 1999) and further research is needed to understand the mechanisms of succession and the interactions among adult species (e.g. Scheibling & Raymond 1990, Benedetti-Cecchi & Cinelli 1993, Minchinton et al. 1997).

In conclusion, high productivity and biomass of forests of canopy-forming algae make these habitats important components of coastal systems in temperate Australia (Walker & Kendrick 1998). Substantial small-scale variation in species composition of these forests has important consequences for understorey species of algae (Irving et al. 2004) and animals that rely on them as habitat (Chapter Four). Knowledge of the consequences of such variability provides the basis for understanding of the ecology of forests of algae that dominate so much space and have such a strong influence on subtidal assemblages of rocky coastlines in temperate Australia.

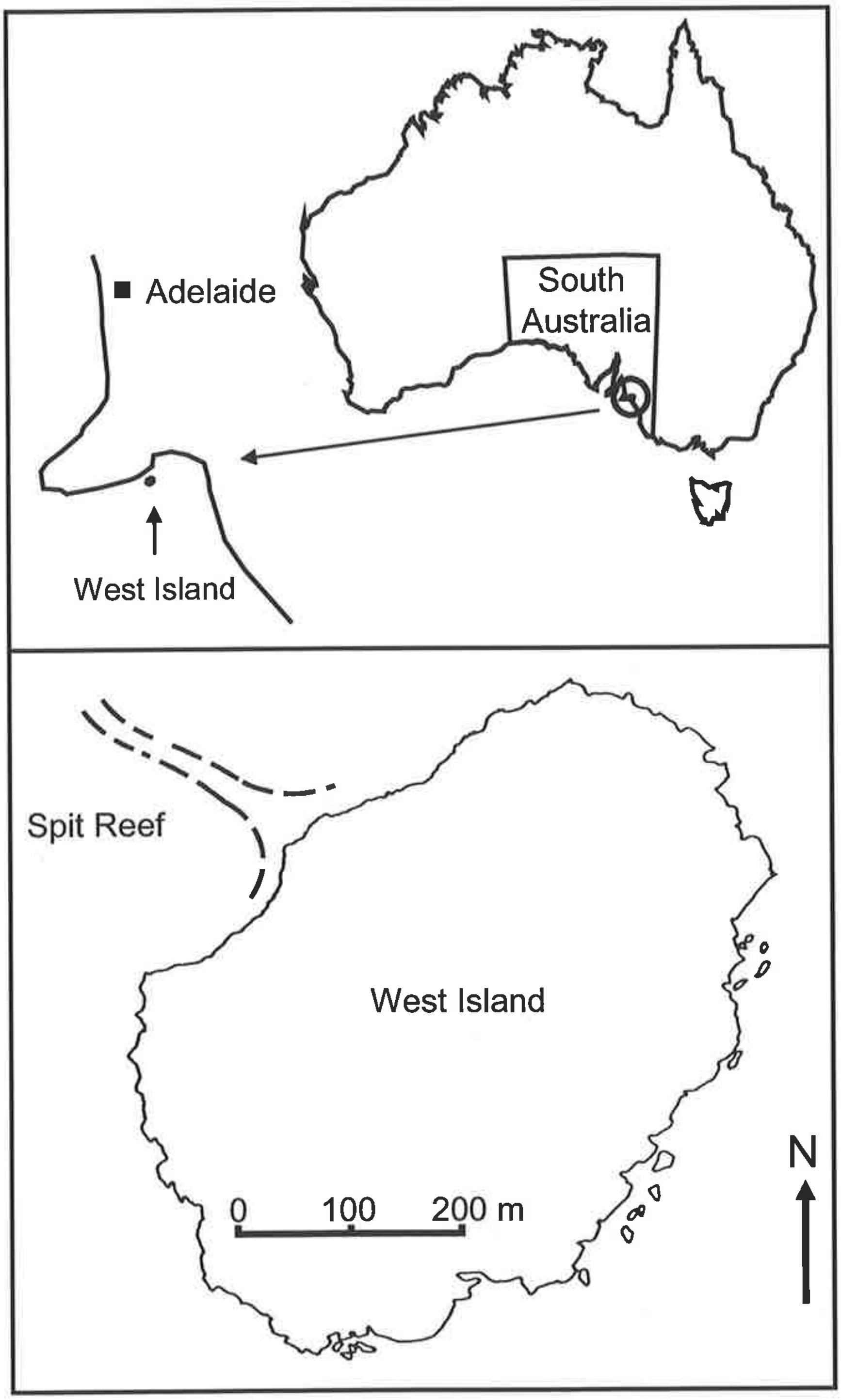


Figure 2.1 Location of study site; Spit Reef, West Island, South Australia.

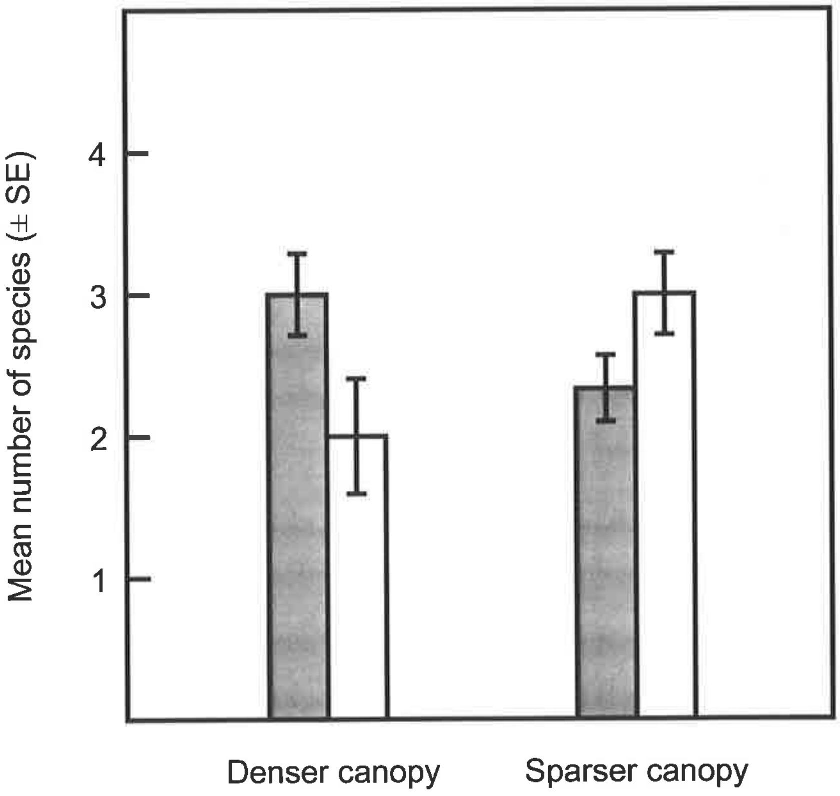


Figure 2.2 Mean number of species (± SE) of recruits of canopy-forming algae where residual holdfasts were denser (shaded bars) and sparse (open bars) under denser and sparse canopies ($n = 6$ replicates per treatment).

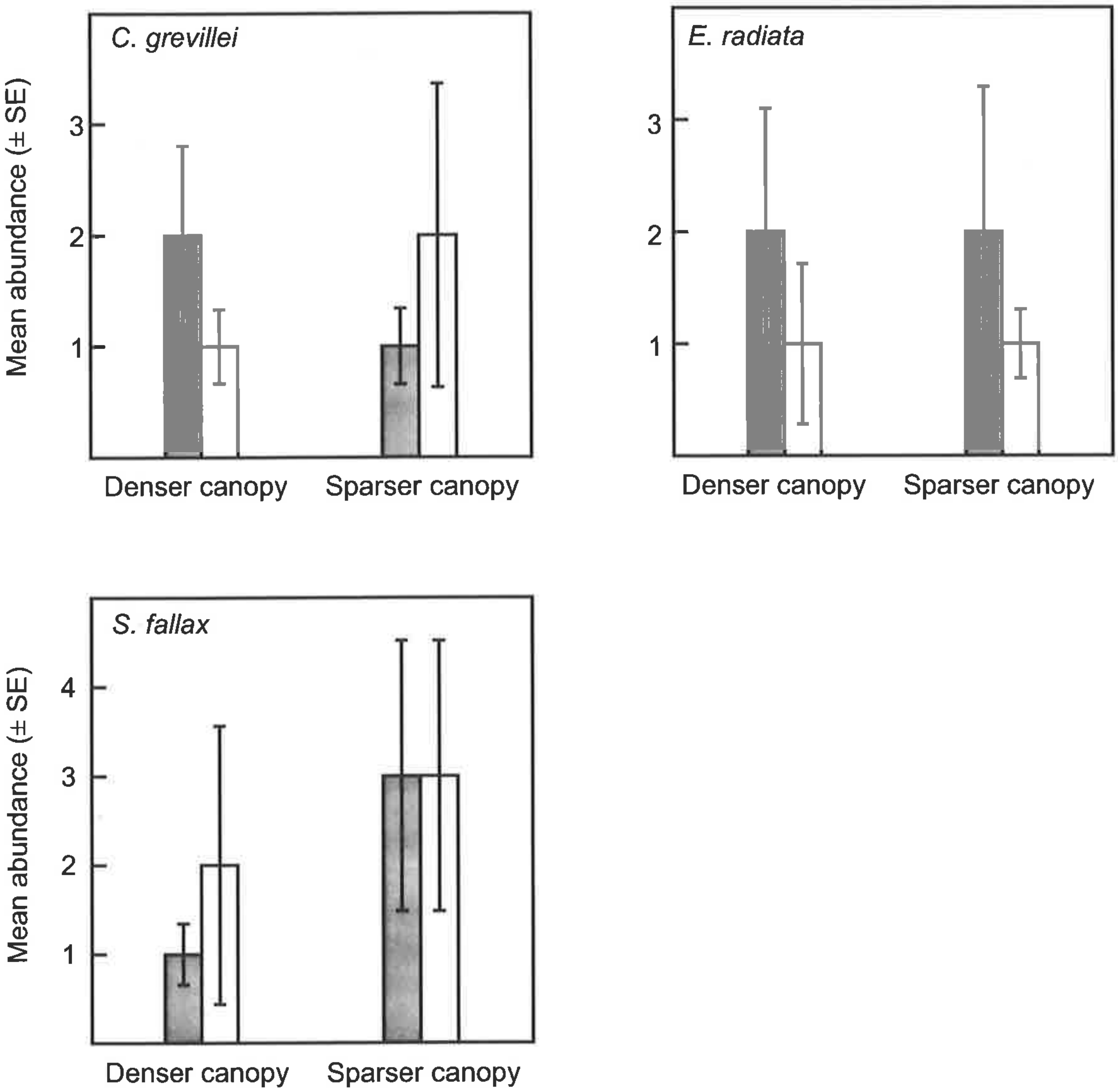


Figure 2.3 Mean abundance (± SE) of individual species that responded to different levels of availability of substratum; denser holdfasts (shaded bars) vs sparse holdfasts (open bars) under different covers of canopy (denser vs sparse) (*n* = 6 replicates per treatment).

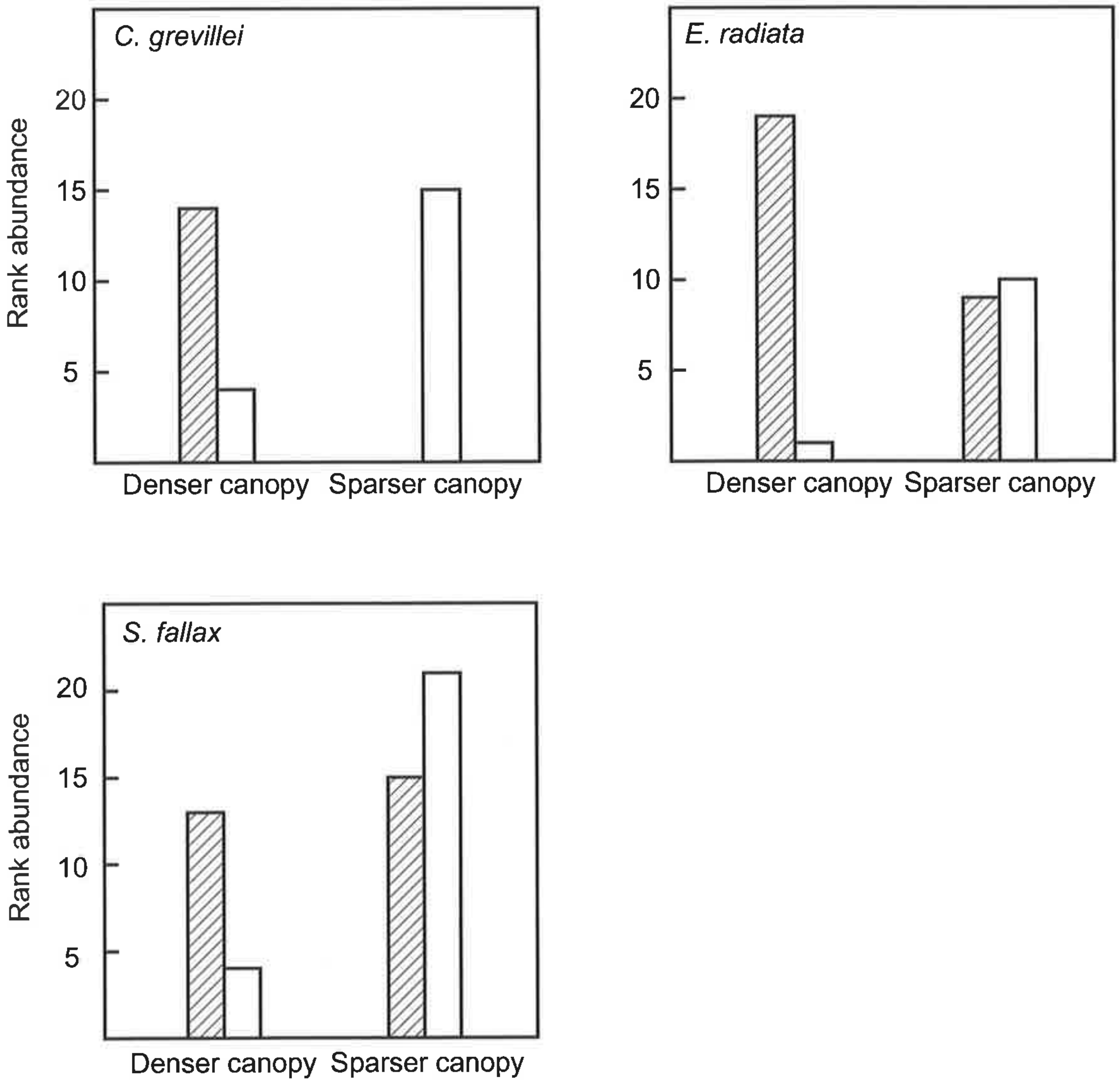


Figure 2.4 Rank abundance of particular recruits observed attached to holdfasts remaining on the substratum (striped bars) and relatively bare substrata (open bars) under denser and sparse canopies.

Holdfast of *Ecklonia radiata* without thallus attached; indicative of selective feeding on meristem by the fish *Odax cyanomeles*, New South Wales

CHAPTER THREE

CHAPTER THREE

HISTORICAL CONFIGURATION OF HABITAT INFLUENCES THE EFFECTS OF DISTURBANCE ON MOBILE INVERTEBRATES

3.1 INTRODUCTION

Disturbance events alter the dynamics of biological interactions that determine the likelihood of coexistence and the persistence of organisms (Dayton 1971, Wilson & Keddy 1986, Petraitis et al. 1989). Current understanding of these effects, however, is primarily derived from research done on organisms that are sessile as adults (e.g. Sousa 1979a, b, Paine & Levin 1981, Scheibling 1986, Kennelly 1987a, b). Unfortunately, we know relatively little about the ways in which disturbance affects the diversity of mobile animals that rely on sessile organisms for habitat.

The structure of habitat influences many of the processes that determine the diversity and abundance of mobile animals (McGuiness & Underwood 1986, Levin 1993). Hence disturbance, via alteration of habitat and availability of resources, can have significant, albeit indirect effects on mobile animals (Syms & Jones 2000, Sousa 2001). Most assessments of the effects of disturbance on animals involve comparisons of abundance in undisturbed to disturbed habitats, where habitats are similar to each other before the disturbance (Bodkin 1988, Christie et al. 1998, Hoffmann & Andersen 2003). While it is imperative that we understand the response of organisms to habitat change (Underwood 1993), it is also necessary to consider that the characteristics of the pre-disturbed habitat or system can influence the impact of any future event (Ricklefs & Schluter 1993, Hughes 1989, Briske & Anderson 1992).

Where attempts have been made to understand the effects of history, ecologists are concerned primarily with the regime of disturbance to which systems have been subject; how many and how often the system has experienced disturbance (Hughes & Connell 1999, Fukami 2001, Kwitt & Platt 2003). As many processes that structure populations of animals are mediated by their habitat (Southwood 1977, Rosenzweig 1995), the ways in which animals are affected by disturbance may depend on the historical characteristics of their habitat (Tanner et al. 1996, Farji-Brener et al. 2002). The current study is a rare experimental investigation of whether differences in the configuration of habitat, prior to disturbance, affect how animals respond to disturbance (but see mensurative experiments in Farji-Brener et al. 2002, Kiss et al. 2004).

Small-scale variation in the configuration of subtidal, vegetative habitats is considerable in temperate regions of the world (Dayton et al. 1984, Underwood et al. 1991, Andrew & O'Neill 2000). In Australia, forests of the common kelp, *Ecklonia radiata* provide the major habitat structure for many marine organisms. In particular, the holdfast of *E. radiata* support a large diversity of mobile invertebrates (Smith et al. 1996) and the diversity of these assemblages are strongly affected by the density of their *E. radiata* habitat (Goodsell & Connell 2002). It is likely, therefore, that the direction and extent of change in the diversity of invertebrates, when subject to the same disturbance (type and severity), will depend on the historical density of *E. radiata*.

Disturbance events that cause complete removal of habitat are relatively infrequent in subtidal forests compared to those which cause less severe or partial damage (Foster & Sousa 1985). In forests of *E. radiata* partial damage to habitat is a common event (Kennelly 1987b), but experimental tests that compare the response of mobile animals to different severities of disturbance are rare. A particularly conspicuous agent of disturbance in forests of *E. radiata* is herbivory by the odacid fish *Odax cyanomeles* (Andrew & Jones 1990, Jones & Andrew 1990), yet we know little of the consequences of this agent of disturbance on assemblages of animals that rely on *E. radiata* as habitat.

Selective herbivory by *O. cyanomeles* on the meristem and primary laminae of individuals of *E. radiata* creates a holdfast that remains on the substratum without thallus attached. Direct mortality from this kind of disturbance is not a likely consequence for invertebrates in holdfasts, but they may be indirectly affected by changes in the suitability of their habitat. Diversity of invertebrates may increase following disturbances, if resources were previously limited by dominant taxa (e.g. Connell 1978), alternatively diversity may decrease via reductions in the suitability of resources in the habitat caused by disturbance (Sousa 2001). In the current study, I tested the hypothesis that the historical density of *E. radiata*, influences the effects of differential severity of disturbance (herbivory) on invertebrate diversity.

3.2 METHODS

Manipulation of the severity of disturbance was done in monospecific stands of different densities of *E. radiata* at Edithburgh, South Australia (35° 5′ S: 137° 45′ E), at an average water depth of 3-5 m. A previous study at the same location has shown that the diversity of invertebrates in holdfasts of *E. radiata* is different between dense (> 5 individuals/ m^2) and sparse (4-5 individuals/ m^2) habitats of *E. radiata* (Goodsell & Connell 2002). In the afore-referenced study, reducing the density of *E. radiata* from dense to sparse caused significant changes in the diversity of invertebrates after 2 months (Goodsell & Connell 2002). In the current study, to ensure conditions were similar prior to experimental procedures, the effect of density was removed prior to experimental manipulations by thinning dense areas (1 m^2, n = 18) of *E. radiata* to be sparse. These plots were maintained for two months after which assemblages were assumed to be at similar levels to naturally occurring sparse plots.

The severity of disturbance was manipulated at three levels (0%, 50% and 100%) orthogonal to the two levels of forest density (dense vs sparse). To simulate the partial disturbance created by *O. cyanomeles*, 50% and 100% of the fronds of *E. radiata* were removed from the base of the stipe. A central plant was left intact and tagged for sampling at the end of the experiment. Different severities of disturbance were randomly allocated to the thinned plots and in areas of forest where *E. radiata* was dense. Holdfast samples were collected after 2 months; a sufficient time for significant changes in invertebrate assemblages to occur to due the effects of disturbance (Bell & Hicks 1991, Edgar 1992).

Holdfasts were removed by cutting the fronds away, enclosing the holdfast in a plastic bag sealed to the substratum and levering the holdfast into the bag. Samples were fixed in a 10% formalin and seawater solution. Holdfasts were dissected and their contents sieved through a 1 mm mesh to separate infauna. Identification was done to the finest possible taxonomic resolution.

3.3 RESULTS

An interaction between the historical density of habitat and the severity of disturbance was detected for the relative abundance and composition (diversity) of invertebrates (Table 3.1a). Post hoc comparisons reveal that assemblages from undisturbed habitats in sparse arrays were different to those from undisturbed habitats in dense arrays and this difference was consistent at 50% and 100% of disturbance (Fig. 3.1, Table 3.1b). Differences in diversity between historically dense and sparse habitats were smallest when 50% of the habitats were disturbed (Table 3.1b; t-values).

Intermediate (50%) and severe (100%) levels of disturbance caused differences in the diversity of mobile animals in habitats that were sparse before disturbance (Table 3.1b). Where habitats were historically dense, only the most severe (100%) disturbance caused assemblages to differ from those in habitats with no disturbance; assemblages differed between habitats with 50% and 100% disturbance (Table 3.1b).

Observation of the raw data shows that assemblages had the lowest number of taxa (richness) when plots were not disturbed, intermediate numbers with 50% disturbance and highest numbers with 100% disturbance in habitats that were historically both sparse and dense (Fig. 3.2, Table 3.2b, Appendix 1). The average number of taxa was greater in habitat that were dense than sparsely distributed for 0%, 50% and 100% disturbance (Fig. 3.2). Differences in the number of invertebrate taxa were significantly different between habitats that were historically sparse and dense for all levels of disturbance (Table 3.2a).

Table 3.1 (a) NP-MANOVA (Anderson 2001) testing the effects of the historical density of habitat (dense vs sparse) and different severities of disturbance (0% vs 50% vs 100%) on the relative composition and abundance of invertebrates. 'Density' and 'Disturbance Severity' were fixed and orthogonal (*n* = 6). Data were fourth root transformed to provide equal weighting of frequently occurring and numerous taxa, to those less frequent and less numerous. (b) Pair-wise comparisons for the significant interaction. Not significant (ns): *P* > 0.05, *: *P* < 0.05, **: *P* < 0.01, ***: *P* < 0.001.

(a) NP-MANOVA

Source of variation	df	MS	F	*P*
Density	1	501.253	3.115	***
Disturbance severity	2	384.205	2.388	***
Density × Disturbance severity	2	263.318	1.636	*
Residual	30	160.962		

(b) Pairwise comparisons		t	*P*
Dense	0% vs 50%	1.156	ns
	0% vs 100%	1.402	*
	50% vs 100%	1.342	*
Sparse	0% vs 50%	1.477	*
	0% vs 100%	1.980	**
	50% vs 100%	1.571	**
0%	Dense vs Sparse	1.540	**
50%	Dense vs Sparse	1.278	*
100%	Dense vs Sparse	1.571	**

An important result was that the magnitude of differences in the diversity of invertebrates, caused by increasing the severity of disturbance, was greater where habitats were historically sparse than where habitats were dense (Fig. 3.1, Table 3.1b; t-values). Variation in the number of invertebrate taxa among plots with 0%, 50% and 100% disturbance was similarly greater where habitats were sparse than dense before the disturbance (Fig. 3.2).

Table 3.2 (a) ANOVA testing for the effects of the historical density of habitat (dense vs sparse) and different severities of disturbance (0% vs 50% vs 100%) on the number of invertebrate taxa. 'Density' and 'Disturbance Severity' were fixed and orthogonal (*n* = 6). Data were homogenous (Cochran's *C*-test: $P < 0.05$) and not transformed. (b) SNK tests for levels within disturbance severity. Not significant (ns): $P > 0.05$.

(a) ANOVA

Source of variation	df	MS	F	*P*
Density	1	1201.778	36.04	0.000
Disturbance severity	2	415.028	12.45	0.000
Density × Disturbance severity	2	41.194	1.24	ns
Residual	30	33.344		

(b) SNK tests

0% < 50%

0% < 100%

50% < 100%

Table 3.3 (a) ANOVA testing for the effects of the historical density of habitat (dense vs sparse) and different severities of disturbance (0% vs 50% vs 100%) on the mean number of crustacean and polychaete taxa. 'Density' and 'Disturbance Severity' were fixed and orthogonal ($n = 6$). Data were homogenous (Cochran's *C*-test: $P < 0.05$) and not transformed. *: $P < 0.001$. (b) SNK tests for disturbance severity.

(a) ANOVA		Crustacean taxa	Polychaete taxa
Source of variation	df	F	F
Density	1	17.76*	34.46*
Disturbance severity	2	6.23*	12.12*
Density × Disturbance severity	2	1.84	1.74
Residual	30		
(b) SNK tests			
		0% < 50%	0% < 50%
		0% < 100%	0% < 100%
		50% = 100%	50% < 100%

The greater abundance and richness of invertebrate taxa in disturbed areas to non-disturbed areas was a consequence of increases in the abundance of most taxa and increases in the richness of particular groups. For example, the abundance of polychaete and crustacean taxa was greater in disturbed to undisturbed treatments but increasing severity (50 vs 100%) did not exacerbate this effect (Fig. 3.3, Table 3.3b). Polychaete richness was greater in treatments with both 50% and 100% disturbance than in undisturbed treatments (Fig. 3.3, Table 3.3b). The richness of crustacean taxa was greater in disturbed to undisturbed treatments, but an increase in severity of disturbance (50 vs 100%) did not lead to a greater number of crustacean taxa (Fig. 3.3, Table 3.3b). The abundance of crustacean and polychaete taxa were affected by the severity of disturbance (Table 3.3a), but this affect was not detected for the abundance of gastropods (ANOVA: $F_{2, 30} = 0.91$, $P > 0.05$) nor echinoderms (ANOVA: $F_{2, 30} = 0.72$, $P > 0.05$).).

3.4 DISCUSSION

Increasing the severity of disturbance caused changes in the diversity of mobile invertebrates, but this response was not independent of the historical configuration of habitat. There is a tendency for ecologists to study the most severe type of disturbances i.e. complete removal of habitat (Ebeling et al. 1985, Tegner & Dayton 1987, Minchinton et al. 1997, Christie et al. 1998, Underwood 1999). The few experiments that have manipulated severity of disturbance, however, report significant differences in patterns of re-colonisation with changes in the severity of disturbance (Kennelly 1987b, Airoldi 1998, Underwood 1998). Compared to the most severe level of disturbance (100%), I found that intermediate levels of disturbance (50%) caused smaller, but detectable changes in the diversity of invertebrates and are thus likely to play an important role in structuring assemblages of mobile invertebrates. Less severe disturbances, such as herbivory, that do not remove all habitats (e.g. 100%) are persistent and regular in forests of kelp (Kennelly 1987b, Jones & Andrew 1990) and maybe under-valued as a contributing process affecting the diversity of marine invertebrates. Indeed, herbivory is known to exert strong influence on the structure of biogenic habitat in many systems and has profound, albeit indirect effects, on associated animals (Scheibling & Raymond 1990, Huntly 1991).

In Australia, a large amount of subtidal research on rocky coasts focuses on the effects of the extensive and complete removal of kelp from urchin herbivory (*Centrostephanus rodgersii*) (Jones & Andrew 1990, Andrew 1994, Hill et al. 2003). Given that this type of herbivory may be most restricted to eastern coast of Australia (Fowler-Walker & Connell 2002), I highlight the need to recognise that variable and partial disturbance of *E. radiata* caused by selective feeding of *Odax cyanomeles* can have strong impact on the diversity of associated invertebrates. Indeed, *O. cyanomeles* is the most densely and widely distributed fish associated with *E. radiata* forests across Australia (Connell & Gillanders unpubl. data) and the thinned forests they create are a conspicuous aspect of *E. radiata* forests across Australia (Goodsell pers. obs.). *O. cyanomeles* herbivory can have strong affect on the structure of forest of *E. radiata* (Andrew & Jones 1990) and I show here that this agent of disturbance has important consequences for associated invertebrates.

It is often predicted that disturbance of habitat will indirectly reduce the abundance of associated mobile animals (Ebeling et al. 1985, Jones & Syms 1998). Interestingly, in the current study the number of invertebrate taxa was greater in disturbed to undisturbed habitats. This result appears to be primarily driven by increases in the abundance and diversity of polychaete and crustacean taxa in disturbed habitats. Taxa that were present following disturbance, but absent in undisturbed habitats, may represent poor competitors that are best able to exist through opportunistic colonisation associated with disturbance (Connell 1978, Petraitis et al. 1989, Farji-Brener et al. 2002). Determining the competitive hierarchies of holdfast assemblages would provide a better understanding of the observed increases in taxonomic richness and abundance of taxa following disturbance (e.g. Dean & Connell 1987a, b).

In conclusion, the effects of disturbance for the diversity of mobile animals can be modified by the historical structure of their habitat. Increasing the severity of disturbance had greater effects on diversity in habitats that were sparse prior to disturbance. Whilst many studies have shown that characteristics of the disturbance themselves, or the regime of disturbance, are key factors influencing the outcome of disturbance, I stress that the structure of the pre-disturbed habitat is an important factor to consider in assessments of the effects of disturbance (Farji-Brener et al. 2002). This is particularly the case for systems such as subtidal forests in which considerable small-scale complexity in structure exists (Underwood et al. 1991, Jones & Andrew 1990) and disturbance events are common. With an increasing recognition of the role of history in shaping biodiversity (Knick & Rotenberry 2000, Fukami 2001), there is great promise in future research that combines an understanding of historical events with contemporary processes.

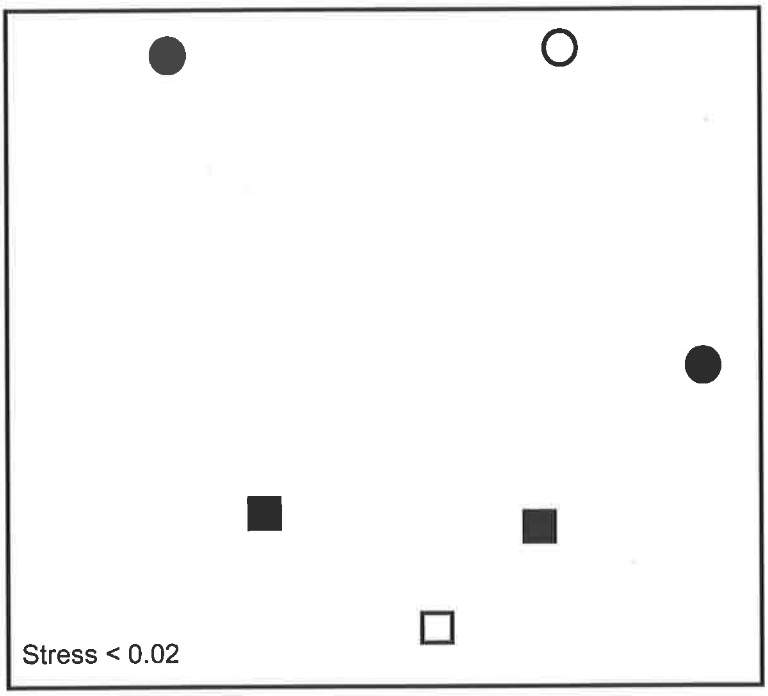


Figure 3.1 nMDS plot of the diversity of invertebrates from habitats of *E. radiata* that were historically dense (squares) and sparse (circles), in undisturbed plots (open symbols), plots with 50% of habitats disturbed (shaded symbols) and 100% of habitats disturbed (filled symbols).

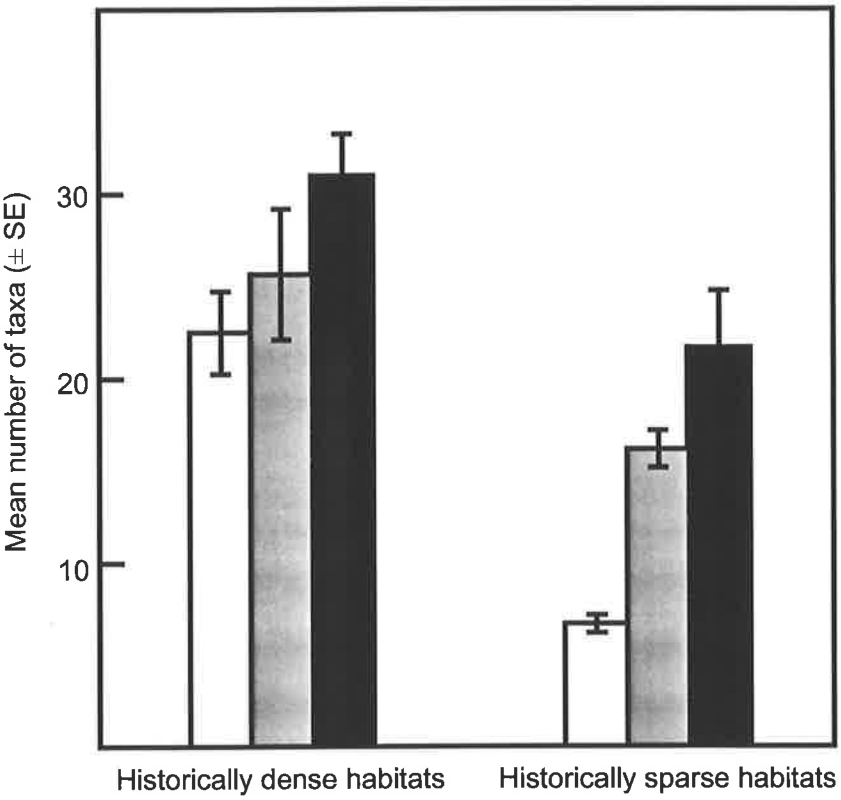


Figure 3.2 The mean number of mobile taxa (± SE) in habitats of *E. radiata* that were historically dense and sparse, in undisturbed plots (open bars), plots with 50% of habitats disturbed (shaded bars) and 100% of habitats disturbed (filled bars).

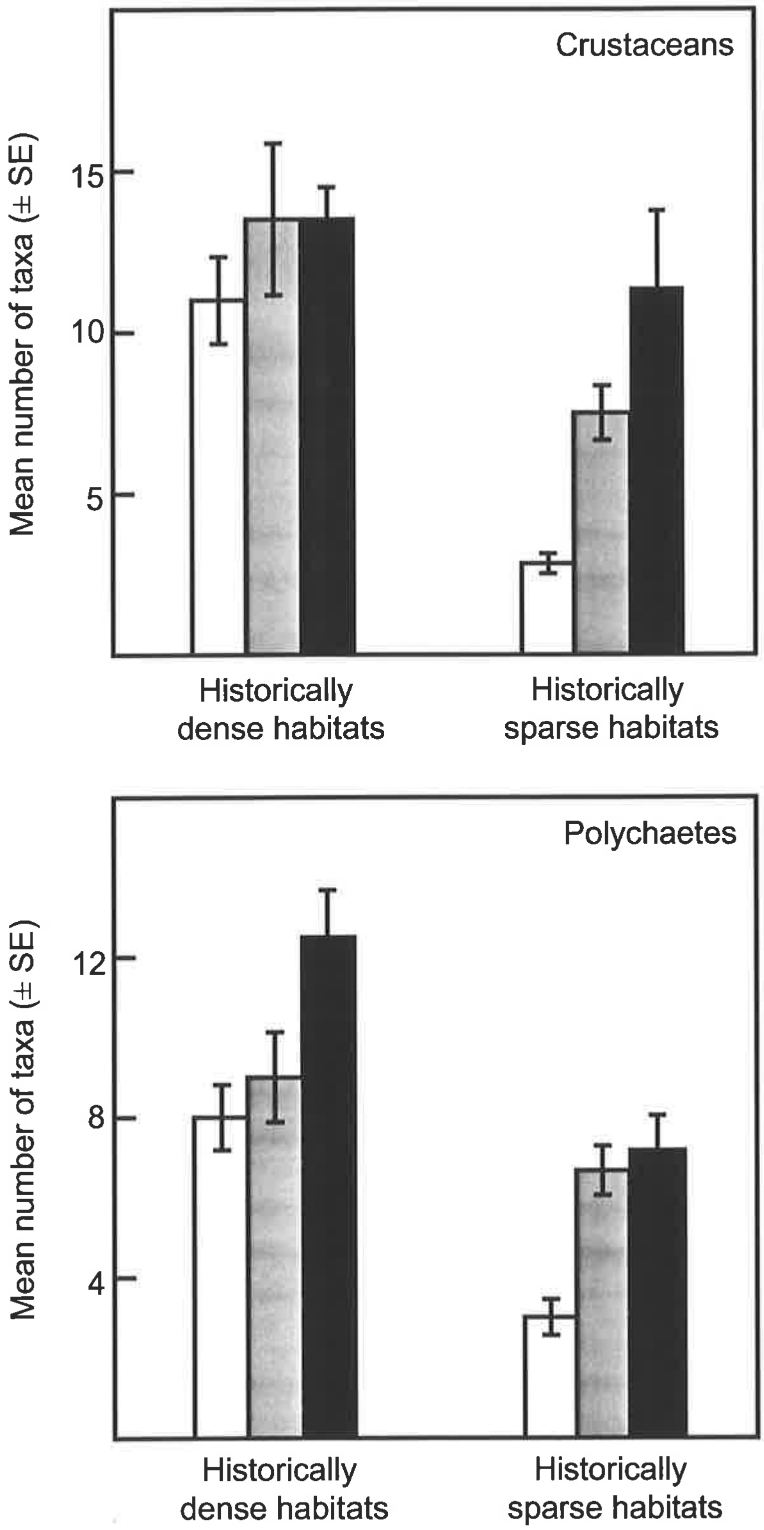


Figure 3.3 The mean number of crustacean and polychaete taxa (± SE) from habitats of *E. radiata* that were historically dense and sparse, in undisturbed plots (open bars) and plots with 50% of habitats disturbed (shaded bars) and 100% of habitats disturbed (filled bars).

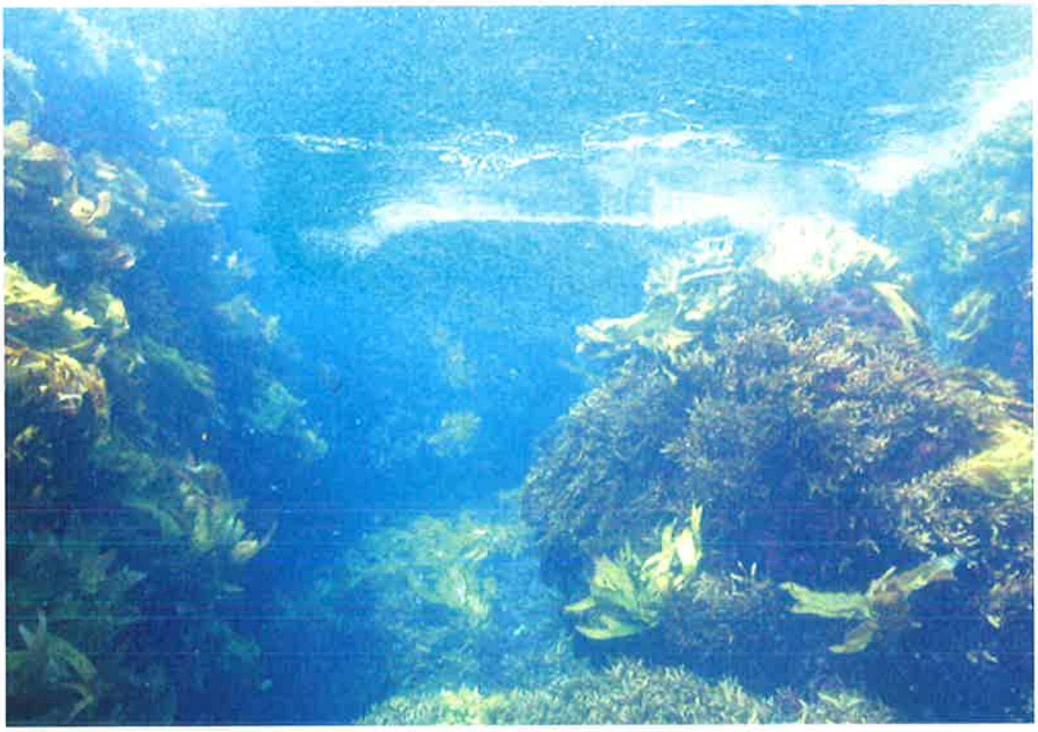
APPENDIX 1

List of the total number of invertebrate taxa associated with the holdfast of *E. radiata* from areas where habitats of *E. radiata* were historically dense and sparse, in undisturbed plots (0%) and plots with 50% of habitats disturbed and 100% of habitats disturbed ($n = 6$ for each treatment).

Historical density of habitat	**Dense**			**Sparse**		
Disturbance	**0%**	**50%**	**100%**	**0%**	**50%**	**100%**
ANNELIDA						
Polychaeta						
Armandia/Polyophthalmus spp.	1	2	0	0	1	0
Autolytinae sp. 1	8	11	13	2	13	7
Autolytinae sp. 2	0	0	1	0	0	0
Autolytinae sp. 3	1	1	0	0	0	0
Boccardia spp.	0	1	2	0	0	0
Capitellidae spp.	2	4	0	0	0	0
Cerethrium spp.	0	7	1	0	0	2
Chrysopetalum sp. 1	3	4	15	1	1	1
Cirratulidae spp.	1	1	0	0	0	0
Eunice spp.	5	16	6	5	0	16
Eurysyllis sp. 1	0	1	0	0	0	0
Exogone sp. 1	5	23	11	0	11	12
Lepidonotus sp. 1	2	1	2	0	2	0
Lysidice spp.	2	0	1	0	3	0
Maldanidae sp. 1	18	38	47	4	15	15
Microspio spp.	1	1	1	0	1	1
Nereididae sp. 1	12	26	21	4	10	15
Phyllodocidae sp. 3	2	0	0	0	0	0
Phyllodocidae sp. 4	0	1	0	0	0	0
Phyllodocidae sp. 5	0	5	1	0	0	1
Phyllodocidae sp. 7	0	0	1	0	0	0
Phyllodocidae sp. 8	0	2	0	0	0	0
Sphaerosyllis sp. 1	0	7	10	0	6	6
Syllinae sp. 1	21	28	34	14	13	12
Syllinae sp. 14	6	5	12	2	4	10
Syllinae sp. 3	5	12	13	1	11	6
Syllinae sp. 4	0	0	2	0	0	0
Trypanosyllis sp. 1	0	1	0	0	0	0
Trypanosyllis sp. 2	0	0	0	0	1	1
Trypanosyllis zebra	0	2	1	0	1	0
ARTHROPODA						
Crustacea						
Acidostoma spp.	4	2	2	0	2	0
Ampeliscidae spp.	1	8	1	0	1	0
Ampithoe sp. 1	6	2	17	0	4	1
Anthuridae spp.	1	2	2	1	2	2
Aora maculata	28	44	70	7	22	23
Apseudidae spp.	7	8	13	0	4	12
Bemlos spp.	19	36	35	8	47	15
Ceradocus spp.	0	12	13	0	0	4

Historical density of habitat		**Dense**			**Sparse**	
Disturbance	**0%**	**50%**	**100%**	**0%**	**50%**	**100%**
Crustacea						
Cirolanidae spp.	2	2	7	0	6	3
Corophidae sp. 1	3	2	26	0	7	0
Corophidae sp. 3	2	2	0	0	1	0
Gammaropsis sp. 3	3	4	5	0	8	2
Gammaropsis sp. 5	2	12	7	0	3	0
Gammaropsis sp. 6	0	6	27	0	9	3
Gitanopsis sp. 1	0	0	3	0	0	0
Gnathiidae spp.	1	3	2	0	1	3
Halicarinus spp.	1	0	0	0	0	0
Haswellia emarginata	0	0	1	0	1	0
Hyalidae spp.	2	0	1	0	0	0
Leucothoe gracilis	0	2	10	0	2	0
Leucothoe sp. 6	0	1	2	0	0	1
Limnoriidae spp.	5	3	9	1	4	0
Maera mastersi	17	27	51	4	10	21
Melitidae sp. 1	11	15	9	1	4	2
Ochlesis sp. 1	2	2	1	1	1	1
Paradexamine sp. 1	4	8	2	0	10	0
Pilumnus spp.	2	1	1	0	2	0
Plakarthrium spp.	0	0	0	0	0	1
Porcellana dispar	1	0	0	0	0	0
Quadimaera viridis	0	4	8	0	2	1
Shrimp spp.	3	1	1	0	0	1
Stenetriidae spp.	15	10	19	3	13	11
Syndexamine runde	0	1	1	0	0	0
Tanaidacea spp.	8	10	13	8	10	14
Tethygeneia spp.	2	0	8	0	3	2
Amphipoda sp. 1	5	3	12	0	1	1
Amphipoda sp. 2	13	14	19	5	5	6
Pycnogonida						
Pycnogonida spp.	1	0	0	0	0	0
ECHINODERMATA						
Dendrochirotida sp. 1	2	7	7	0	3	0
Ophiuroidea spp.	4	2	3	2	3	5
MOLLUSCA						
Chiton spp.	1	1	1	0	0	0
Nudibranchia spp.	1	3	0	0	0	0
NEMATODA						
Nematoda spp.	3	6	2	0	6	3
NEMERTEA						
Nemertea spp.	7	10	5	0	9	2
PLATYHELMINTHES						
Platyhelminthes spp.	0	0	0	0	1	0
SIPUNCULA						
Sipuncula spp.	0	1	0	0	0	0

Note: Taxa match other lists in this thesis and are based on a reference collection held within the Southern Seas Ecology Laboratories at the University of Adelaide.



Mosaic forest of canopy-forming brown algae with stands of mixed algae (right) and stands of monospecific *Ecklonia radiata* (left), Western Australia

CHAPTER FOUR

CHAPTER 4 PREAMBLE

Chapter 4 quantifies the small-scale variation in the composition and configuration of canopy-forming brown algae across southern Australia. A preliminary investigation of whether animal assemblages differ between different configurations of algae is included. This chapter is a precursor to the broader scale study in Chapter Five.

This chapter is collaboration with Meegan Fowler-Walker, Sean Connell and Bronwyn Gillanders and is published in Austral Ecology (2004) with me as senior and corresponding author. It is, therefore, written in plural. Bronwyn Gillanders instigated the mapping of habitat and I developed the idea to partition the observations between monospecific and mixed stands of canopy-forming algae. Sean Connell and Bronwyn Gillanders, with the assistance of Meegan Fowler-Walker, quantified the abundance of different types of algal stands at many spatial scales across South Australia and Western Australia. M. Fowler-Walker and S. Connell analysed this data and assisted with the evaluation of the manuscript. I sampled invertebrates from different stands of algae at a single location, analysed this data and wrote the manuscript.

Signatures of co-authors:

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Sean D. Connell

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Signed

Meegan J. Fowler-Walker

VARIATIONS IN THE CONFIGURATION OF ALGAE IN SUBTIDAL FORESTS: IMPLICATIONS FOR INVERTEBRATE ASSEMBLAGES

4.1 INTRODUCTION

Forests typically form a landscape made up of several different types of stands, where canopy-species vary in their relative abundance and arrangement in space (Safriel & Ben-Eliahu 1991, Lertzman et al. 1996). Terrestrial ecology has long recognised that plants form associations that can be identified and defined based on a repeated association of more than one species (Mueller-Dombois & Ellenberg 1974). This terminology has not yet entered the realm of marine ecology, although there are some descriptions of associations of algae in the Mediterranean (Haritonidis 1978, Ballesteros 1993, Panayotidis et al. 1999). In Australasia, canopy-forming forests of algae are usually labeled according only to the presence of the obvious taxa. However, it may be important to realise that heterogeneity can occur within marine forests (i.e. between stands) and that this may be accompanied by variation in assemblages of animals that rely on forests as habitat.

Many theories predict that a greater diversity of assemblages of plants will support a greater abundance and diversity of species of animals (Connell & Orias 1964, Lawton 1978, Rosenzweig 1995). Historically, correlations between heterogeneity in the habitat and the abundance of animals have been observed for many birds (MacArthur & MacArthur 1961), mammals (Simpson 1964) and marine invertebrates (Heck & Wetsone 1977). Given that patterns of species richness can often be explained by the arrangement of habitats in space (Bell et al. 1991), diversity of animals may respond to the arrangement of different species of plants in heterogenous habitats (e.g. Hiebeler 2000), rather than a measure of habitat diversity *per se*.

Subtidal ecology often focuses on the effects of the large-scale features of a habitat (presence or absence of macroalgae) in tests of habitat utilisation or association (Choat & Ayling 1987, Anderson 1994, Fowler-Walker & Connell 2002). However, animals may respond to the features of a habitat at smaller spatial scales (e.g. plant density), nested within the major type of habitat (Fisher et al. 1998, Crook et al. 2001). Such small-scale variation can generate large-scale patterns observed at regional scales (Wootton 2001). It is prudent therefore to assess the effect of finer scale variation within one of the most widespread and abundant habitats on subtidal coasts of temperate Australia.

Canopy-forming algae, particularly large brown algae of the order Laminariales and Fucales often dominate subtidal rock from 5 – 25 m depth and exert strong effects on the subtidal ecology of rocky coasts throughout the temperate world (Santelices & Ojeda 1984, Witman 1985, Johnson & Mann 1988, Underwood & Kennelly 1990). Along the rocky reefs of southern Australia and northern New Zealand, the common kelp *Ecklonia radiata* (Order Laminariales) makes up a large proportion of these forests (Shepherd & Womersley 1970, Choat & Schiel 1982, Underwood et al. 1991, Kendrick et al. 1999). This species has received considerable attention as a habitat that strongly influences the abundance of benthic algae, invertebrates and fish. We reviewed 45 studies published since 1970 on the ecology of forests of algae containing *E. radiata* (Appendix 2). Only four of those papers attempted to define whether *E. radiata* occurred as monospecific stands or were associated with other species of algae; the remainder described the habitat simply as '*E. radiata* forest'.

We were concerned with whether *E. radiata* primarily occurs as monospecific stands or in stands of mixed canopy-forming algae, and whether these different configurations affect the ecology of the associated biota. Strong canopy-benthic associations in stands of monospecific *E. radiata* have been documented across Australia (Fowler-Walker & Connell 2002), but we questioned whether monospecific stands represent the predominant form in which this species occurs across Australia. It is known that certain characteristics of stands of monospecific *E. radiata* (e.g. density) influence the species composition and relative abundance of understorey assemblages of animals (Goodsell & Connell 2002). Hence it is likely that variation in the configuration of algae may also influence these assemblages of animals.

We tested, within the extent of forests containing *E. radiata* on Western and South Australian coasts, the degree to which stands of monospecific *E. radiata* were the typical configuration and whether the assemblage of invertebrates in monospecific stands was representative of those in stands of mixed algae. We tested the hypotheses that *E. radiata* does not primarily occur in monospecific stands and that invertebrates associated with *E. radiata* holdfasts differ between stands of monospecific *E. radiata* and different configurations of algae within stands of mixed algae. At a 1 m^2 scale we recognised three main configurations within forests of algae (hereafter called stands): *E. radiata* that occur as; (i) monospecific stands; (ii) clumps (≥ 4 individuals together) surrounded by species of Fucales; or (iii) individual plants (or clusters of < 3 plants) interspersed among species of Fucales.

4.2 METHODS

Choice of size of sampling unit

A key sampling decision involved the choice of size of sampling unit (1 m2) (Andrew & Mapstone 1987); the larger the sampling unit the greater the probability of sampling stands of mixed algae rather than monospecific E. radiata. We chose the scale of 1 m^2 because preliminary sampling revealed stands of monospecific E. radiata (> 80 % of the canopy is E. radiata) rarely occurred at ≥ 1 m^2. This scale is appropriate to sample invertebrates in the holdfasts of E. radiata because of known experimental effects of the structure of E. radiata canopies measured at 1 m^2 on understorey algae (Melville & Connell 2001) and invertebrates within holdfasts (Goodsell & Connell 2002). Sampling a smaller area would have increased the probability of detecting monospecific E. radiata in places that they occur, but this configuration would contain very few plants. Likewise sampling of holdfasts was not replicated within stands as the target holdfast was categorised by the configuration of surrounding algae within 1 m^2 (see below).

Relative abundance of monospecific E. radiata vs mixed algae

The relative abundance of each stand within mosaic forests of algae was quantified in two regions, Western Australia (WA) and South Australia (SA), spanning 2100 km (linear distance) of the southern coastline of Australia (Fig. 4.1) in Austral summer (January-February 2002). Regions were separated by 1000s of kilometres but all locations were between latitudes 33° 37'S and 37° 06'S. Within each region, four locations were selected (separated by 100s of kilometres) and within each location, three sites were chosen (separated by kilometres). All sites were chosen so that they were of similar exposure and connected to the mainland.

At the 1 m^2 scale stands were identified as: 'monospecific' when $\geq$ 80% of the canopy was *E. radiata* and 'mixed' when canopies contained a ratio of 40-60% of both *E. radiata* and species of Fucales (e.g. *Cystophora* spp. and *Sargassum* spp.). In order to better understand heterogeneity we identified the two most likely arrangements of *E. radiata* in stands of mixed algae; 'clumped' where $\geq$ 4 individuals of *E. radiata* were clustered together and surrounded by species of Fucales (i.e. at least one *E. radiata* plant was completely surrounded by conspecifics), and 'interspersed' when individuals (or clusters of $<$ 3 plants) of *E. radiata* were scattered among species of Fucales.

At each site the relative abundance of different stands of algae and other subtidal habitats (e.g. turfing algae, stands of Fucales, mussel beds) were quantified along four 100 m × 1 m transects > 10 m apart. Tape measures were laid out perpendicular to the shoreline and started as close to mean or low water as the prevailing conditions would allow. Observers (S. D. Connell, M. J. Fowler-Walker, B. M. Gillanders) swam along each tape and recorded the distance at which the type of stand changed. Sampling stopped at 100 m irrespective of whether the reef extended further from the shore. Where the extent of the reef was shorter than 100 m, sampling ended at that distance.

Structure of holdfast assemblages in monospecific E. radiata vs mixed algae

Six replicate holdfasts from each type of stand (monospecific vs clumped vs interspersed) were sampled in an independent array in a mosaic forest of algae at Edithburgh, South Australia (35° 5′ S: 137° 45′ E) in Austral summer 2001. In 'monospecific' stands the target holdfast was surrounded by conspecific *E. radiata* plants, in 'clumped' stands target holdfasts were sampled on the edge of an *E. radiata* clump, such that the holdfast was surrounded by both *E. radiata* and species of Fucales, and in 'interspersed' stands the target holdfast was surrounded only by species of Fucales. Replicates were chosen at the 1 m^2 scale based on results from previous experimental work that showed these organisms respond to the structure of the canopy measured at this scale (Goodsell & Connell 2002). The canopy cover of all canopy-forming algae (per m^2) in each stand was constant (> 80 %). The density of *E. radiata* affects the diversity of invertebrate assemblages within holdfasts (Goodsell & Connell 2002), hence each stand from which samples were collected contained only sparse quantities of *E. radiata* (1-5 plants/m^2).

Holdfasts were removed by cutting the plant at the base of the stipe then sealing an open plastic bag to the substrate, enclosing the holdfast. The holdfast was levered off the substratum with a dive knife into the bag, which was quickly closed over the holdfast. The haptera (branches) of each holdfast were dissected and the contents sieved through a 1 mm mesh. The contained fauna were enumerated and where possible identified to species. As the volume of holdfasts increases the diversity of organisms increases (Smith et al. 1996), so care was taken to collect holdfasts of similar size for all replicates, and these did not differ among stands (ANOVA: $P > 0.05$).

NP-MANOVA (Anderson 2001) was used to detect differences in the composition and relative abundance (diversity) of invertebrate taxa in assemblages from the three stands. Bray-Curtis distances were calculated using fourth root-transformed data. Analysis used permutations of raw data for one-way analysis (Anderson 2001). Weather conditions caused a replicate to be lost from the factor 'monospecific' and this was replaced by averaging the other five collected.

4.3 RESULTS

Relative proportion and percentage covers of different stands of algae

No differences were detected in the relative proportion of the three types of stand at the scale of regions (1000s kilometres) or locations within regions (100s kilometres) (Fig. 4.2, Table 4.1). Across both Western and South Australia, stands of monospecific *E. radiata* occurred in similar proportion (32%) to interspersed (31%) and clumped (33%) stands (4% contained both interspersed and clumped that was not included in the analysis). Hence within forests containing *E. radiata*, stands of monospecific algae were half as abundant as stands of mixed algae, averaged across both regions.

Table 4.1. ANOVA testing the relative percentage cover of different stands of algae (monospecific vs clumped vs interspersed) among regions and locations. To ensure independence of the data, analysis used one type of stand per transect so that there were three replicates per location. Hence the term 'Residual' also incorporates the effect of Stand × Site interaction. The analysis treated 'Stand' and 'Region' as fixed and crossed factors, and 'Location' as a random factor nested within region. Data were not transformed. Cochran's *C*-test was used to test the homogeneity of the variance and data were non-significant ($P > 0.05$). Non-significant (ns): $P > 0.05$.

Source	df	MS	F	*P*
Stand	2	152.71	0.23	ns
Region	1	14.65	0.04	ns
Location (Region)	6	358.08	0.89	ns
Stand × Region	2	422.59	0.67	ns
Stand × Location (Region)	12	662.06	1.64	ns
Residual	48	403.76		

Table 4. 2. ANOVA testing differences in the percentage cover of individual stands of algae (monospecific, clumped, and interspersed) among regions, locations and sites. 'Region' was a fixed factor, 'Location' was random and nested within region and 'Site' was random and nested within region and location. Arc-sine transformation was used to meet assumptions of homogeneity of variance (Cochran's *C*-test: $P > 0.05$). Non-significant (ns): $P > 0.05$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

		(a) monospecific			(b) clumped			(c) interspersed		
Source	df	MS	F	*P*	MS	F	*P*	MS	F	*P*
Region	1	1193.13	0.44	ns	13.16	0.01	ns	3042.82	2.20	ns
Location (Region)	6	2691.55	3.13	*	1532.79	2.11	ns	1381.14	6.70	**
Site (Region(Loc))	16	861.51	12.09	ns	727.78	5.72	***	206.01	1.94	*
Residual	72	71.23			127.32			106.41		

Whilst the percentage cover of individual stands did not vary across regions, the cover of stands of (a) monospecific *E. radiata* was variable among locations (100's kilometres) but not sites (kilometres), (b) clumped algae was variable at sites but not locations, and (c) interspersed algae was variable at both sites and locations (Fig. 4.3, Table 4.2).

Structure of holdfast assemblages in monospecific E. radiata vs mixed algae

Assemblages of invertebrates in the holdfast of *E. radiata* differed among algal stands (NP-MANOVA: $F_{2, 15} = 1.690$, $P < 0.05$). Post hoc comparisons detected significant differences between monospecific and interspersed stands ($t = 1.303$, $P < 0.05$), interspersed and clumped stands ($t = 1.319$, $P < 0.05$), but not between monospecific and clumped stands ($t = 1.183$, $P > 0.05$) (Fig 4.4). Notably, assemblages of invertebrates in interspersed stands had the highest level of within group variance (Fig. 4.4). Univariate ANOVA failed to detect any differences between the number of species (species richness) in assemblages from the three different stands (ANOVA: $F_{2,\,15} = 0.53$, $P > 0.05$).

4.4 DISCUSSION

Forests containing *E. radiata* occupied most of the space (61 %) sampled on the rocky coast of Western and South Australia (Fig. 4.2), but did not primarily occur as monospecific stands (32 % of forests sampled). None of the stands we identified at the 1 m^2 scale were dominant at the scale of region or location within the forests of canopy-forming algae sampled across Western and South Australia. Interspersed stands of mixed algae are possibly very different habitats for understorey animals, to both stands of monospecific *E. radiata* and clumped stands. We acknowledge this effect was only tested at one locality, but suggest that the arrangement of *E. radiata* in stands of mixed algae, rather than the composition of canopy species *per se*, is an important consideration for future studies.

In subtidal marine systems where forests of *E. radiata* act as a primary form of habitat, only monospecific forests have been the focus of broad-scale research (Underwood et al. 1991, Fowler-Walker & Connell 2002), and smaller scale studies (Taylor 1998a, Goodsell & Connell 2002). We have shown that such spatial homogeneity is not the dominant form in forests of temperate waters, as is the case for many undisturbed terrestrial forests (Burrows 1990). Whilst the occurrence of monospecific stands will always be of interest to marine ecology, they only represent one configuration across Western and South Australia. It will be useful to recognise this pattern and include it in ecological tests of hypotheses about *E. radiata* as habitat for subtidal biota.

Much of the variation in relative proportion of stands is likely to be at the scale of sites, however it was not possible to test for this effect with the modified sampling design as sites were treated as samples to ensure independent replication. Despite the absence of a dominant type of stand at the regional scale, at smaller spatial scales most of the variation in percent cover occurs at a different spatial scale for each type of stand. This may reflect multiple forcing factors operating on different configurations of stands at different spatial scales, adding further cause for careful identification of stands within algal forests.

It is widely accepted that the presence of vegetation (algae, seagrass, understorey algae) is correlated with greater abundances and diversity of animals than similar areas without vegetation. Yet spatial heterogeneity is common within forests in many terrestrial, freshwater and marine systems (Menge et al. 1985, Freemark & Merriam 1986, Burrows 1990, Jones & Andrew 1993). Insightful research from riverine systems is beginning to uncover that small animals (e.g. fish and invertebrates) respond to smaller scale features of the habitat nested within larger scale features (Palmer et al. 2000, Crook et al. 2001). We have continued this vein and show that the presence of small-scale spatial heterogeneity (i.e. between stands) in mosaic forests of subtidal algae has the potential to influence the diversity of associated biota.

Differences in invertebrate composition and abundance rather than number of taxa accounts for most of the variation observed between different stands. This was suggested by the lack of variation in the number of invertebrate taxa among the three stands. Despite the frequent reports of positive correlations between plant diversity and animal diversity (MacArthur & MacArthur 1961, Murdoch et al. 1972, Southwood et al. 1979, Haddad et al. 2001), some evidence suggests that the particular type of plants in an assemblage influences animal assemblages more than the number of plants (Parker et al. 2001). The composition of forests by itself, however, may not be a precise enough variable on which to consider the ecology of forests of subtidal algae, because assemblages of invertebrates respond to the spatial arrangement of plants rather than the presence of particular algae.

We must emphasize that these observations were made at a fine spatial scale of 1 m^2. We acknowledge that the results from sampling of holdfasts are limited to interpretations at this scale only. Yet much of our understanding of the responses of understorey algae and invertebrates to variation in the configuration of *E. radiata* (e.g. density) occurs at this scale (Melville & Connell 2001, Fowler-Walker &

Connell 2002, Goodsell & Connell 2002). In this study as the size of sampling unit is increased (> 1 m^2) the probability would also increase that mixed stands (of both types) will contribute to the outcome of ecological hypotheses tested. Larger sampling units, however, tend to incorporate more than one type of algal stand in South Australia and 1 m^2 seems to be an appropriate scale for many future tests.

In conclusion, *E. radiata* form one of the most widespread and conspicuous subtidal habitats in temperate Australasia, but despite suggestions to the contrary (Jones & Andrew 1993), *E. radiata* did not predominate as monospecific stands in Western and South Australia. Most studies have either considered the ecology of these forests without clarification of the species composition and arrangement, or have focused on stands of monospecific *E. radiata*. This approach has not accounted for the potential small-scale heterogeneity within forests of kelp, nor the effect this may have on biota that rely on them as habitat. Consequently, our current understanding of forests containing *E. radiata* may be over simplified.

We suggest researchers should clearly define the configuration and composition of species within the forest they study. Biodiversity and heterogeneity can vary strongly at local scales (Tuomisto et al. 1995) and classification of heterogeneity in vegetative habitats can only promote more insightful and logical research. We are not advocating a reductionist approach, but better definitions of forests may provide opportunities to uncover patterns that are repeatable and may eliminate potential limits to generalisations. In the marine environment, this kind of rigour may help explain why differences occur among studies testing similar hypotheses. We suggest, therefore, that preliminary information on the spatial configuration of canopy-forming algae may assist in planning and interpretation of more insightful studies on the ecology of kelp forests.

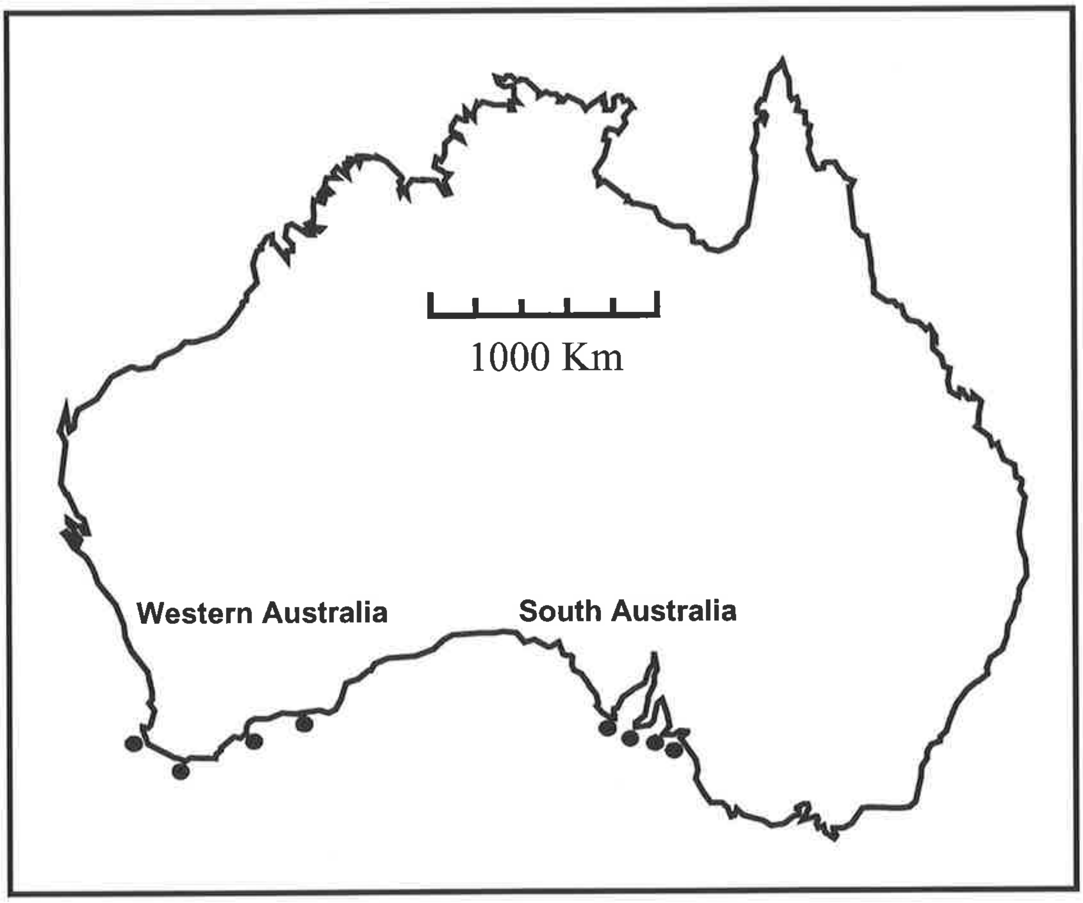


Figure 4.1. The regions and locations of sampling (33° 37' S and 37° 06' S). Locations from left to right: Cape Leeuwin, Albany, Bremer Bay and Esperance (Western Australia); and Eyre Peninsula, Yorke Peninsula, northern Fleurieu Peninsula, and southern Fleurieu Peninsula (South Australia).

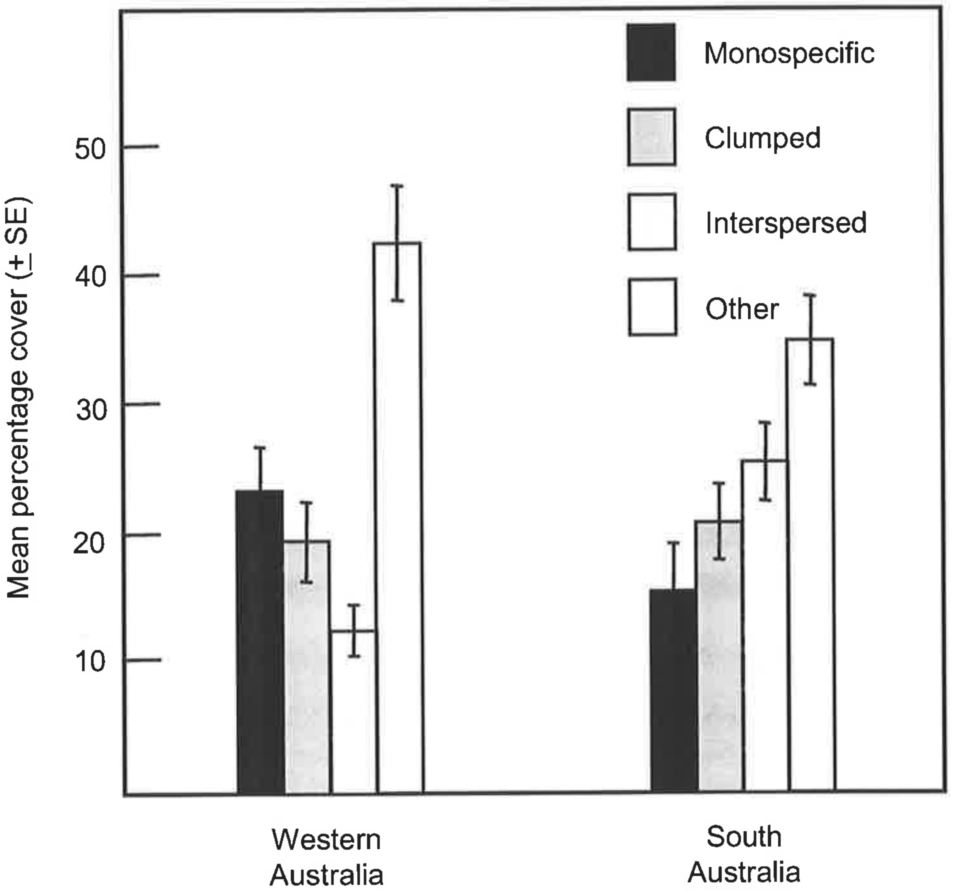


Figure 4.2. Mean percentage cover (± SE, $n = 48$) of three different stands of algae within canopy-forming forests containing *E. radiata* and other subtidal habitats in Western Australia and South Australia.

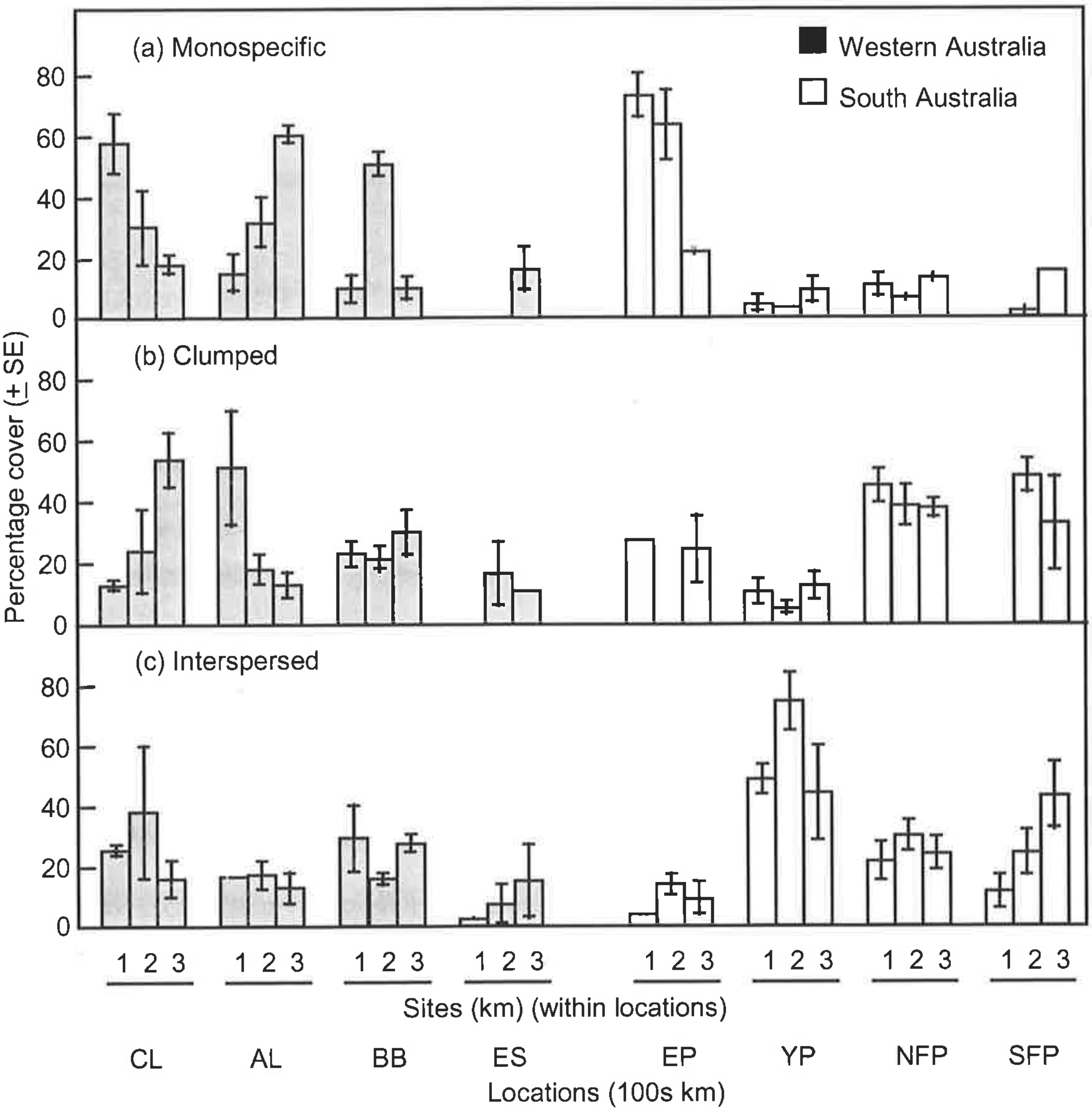


Figure 4. 3. Mean percentage cover (± SE) of each stand for three sites (*n* = 4), within each of 4 locations within Western Australia and South Australia. Locations: CL: Cape Leeuwin, AL: Albany, BB: Bremer Bay, ES: Esperance in Western Australia: and EP: Eyre Peninsula, YP: Yorke Peninsula, NFP: northern Fleurieu Peninsula, SFP: southern Fleurieu Peninsula in South Australia.

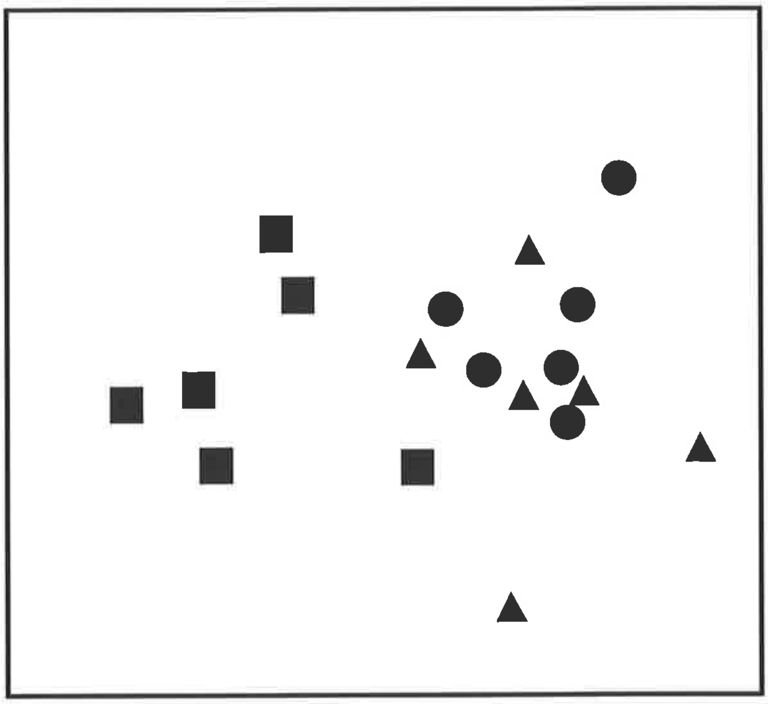


Figure 4. 4. Canonical ordination of the composition and abundance of invertebrates among three stands of algae in which holdfasts were surrounded by ▲ = conspecifics (monospecific), and ■ = species of Fucales (interspersed), ● = species of both taxa (clumped).

APPENDIX 2

Papers reviewed were sourced from 19 journals (Austral Ecology; Australian Journal of Ecology; Australian Journal of Marine and Freshwater Research; Aquatic Botany; Botanica Marina; British Phycological Journal; Diseases of Aquatic Organisms; Ecological Monographs; Hydrobiologia; Journal of Applied Phycology; Journal of Experimental Marine Biology and Ecology; Journal of the Royal Society of New Zealand; Marine and Freshwater Research; Marine Biology; Marine Ecology Progress Series; Marine Pollution Bulletin; New Zealand Journal of Marine and Freshwater Research; Oecologia; Phycologia) between 1970-2002 inclusive. The search used the keyword "*Ecklonia radiata*", and papers were selected if they tested ecological hypotheses.

Close up of canopy in a monospecific stand of *Ecklonia radiata,*
Western Australia

Close up of canopy in a stand of mixed algae (*E. radiata*/fucalean complex),
Western Australia

CHAPTER FIVE

CHAPTER 5 PREAMBLE

Chapter 5 investigates the repeatability of the associations between animal diversity and the composition of their macroalgal habitat, observed in Chapter 4 across the temperate coastline of Australia.

This chapter is submitted to Marine Ecology Progress Series as a multi-authored paper, with me as senior and corresponding author. The manuscript is authored by P. Goodsell, S. Connell and B. Gillanders. This chapter is, therefore, written in plural. The co-authors assisted in the collection of holdfasts and helped instigate the idea of making local through broad scale observations of diversity. Field work was funded by grants from the Australian Research Council of Australia to Sean Connell and Bronwyn Gillanders. I did the analyses and their interpretations are mine.

Signatures of co-authors:

Signed

Sean D. Connell

Signed

Bronwyn M. Gillanders

ASSOCIATIONS BETWEEN MACROALGAL AND INVERTEBRATE DIVERSITY AT LOCAL THROUGH REGIONAL SCALES

5.1 INTRODUCTION

Fundamental to understanding patterns of biodiversity is knowledge of the scales at which general patterns emerge and scales at which patterns are most variable. Describing patterns in nature without doing so over a broad range of spatial (and temporal) scales has been a criticism of the progress of ecological research (Keddy 1989, Peters 1991). Extreme variability in patterns of abundance and diversity at small scales (Underwood & Chapman 1998, Benedetti-Cecchi 2001) can restrict inferences to the site of study (Lawton 1999) and hence offer little insight into patterns that may be applicable at larger scales.

Detection of general phenomena in ecology often proceeds after the repeated documentation of patterns over large scales. Sampling a range of spatial scales, such that smaller scales are nested within progressively larger scales, allows detection of the scales at which variations in pattern exist and general patterns emerge (Andrew & Mapstone 1987, Underwood & Petraitis 1993, Gaston & McArdle 1994). This approach enables an understanding of the extent to which results from small scale controlled and replicated experiments may predict patterns at regional scales (Levin & Hay 2002).

In terrestrial systems, associations between the diversity of vegetative habitats and animal diversity have interested ecologists for decades (MacArthur & MacArthur 1961, Simpson 1964). Theory predicts that more diverse habitats support a greater diversity of animals via increased complexity of resources (Connell & Orias 1964, Lawton 1978, Rosenzwieg 1995). The model that complexity in the structure and composition of vegetative habitats affects the abundance and composition of animals, have been investigated in seagrass (Eggleston et al. 1999, Parker et al. 2001). Yet, little assessment of whether differences in the composition of macroalgae in subtidal habitats affects the diversity of associated animals has been undertaken (but see Levin & Hay 1996).

A widely observed pattern in marine systems is the strong influence of the structure of habitat (e.g. morphology, spatial configuration and composition) on the abundance and diversity of associated animals (Irlandi 1994, Levin & Hay 1996, Jones & Syms 1998). In subtidal habitats, ecological research has primarily focused on assessing the association of animals with large-scale features of habitat, such as the presence or absence of vegetative structure, e.g. macroalgae (Choat & Ayling 1987, Anderson 1994). Animals are often, however, also influenced by complexity in habitat structure (e.g. species composition) at smaller spatial scales, nested within the major type of habitat (Jenkins & Sutherland 1997, Fisher et al. 1998, Crook et al. 2001).

Forests of canopy-forming brown algae (Orders Laminariales and Fucales) provide the major habitat for many animals on rocky coasts across temperate regions of the world (Witman & Dayton 2001). Despite the predominance of work in Australasia within monospecific stands of the common kelp Ecklonia radiata (Laminariales) (Taylor 1998b, Underwood et al. 1991, Fowler-Walker & Connell 2002, Goodsell & Connell 2002), this monotypic configuration is not dominant in temperate waters. Instead a disproportionately large extent of forests within individual sites on Australia's coastline consist of stands of E. radiata/fucalean algae complex; hereafter referred to as mixed stands (Chapter 4). Such small-scale variation in composition of forests of algae is substantial (Kennelly & Underwood 1992, Kendrick et al. 1999) and has the potential to generate ecological patterns observed at regional scales (Wootton 2001, Irving et al. 2004).

E. radiata is habitat for an astonishingly diverse assemblage of invertebrates associated with the branched holdfast that provides networks of space and substrata (Smith et al. 1996). Diversity of holdfast assemblages differed between monospecific stands of E. radiata and stands of mixed algae at a single location (Chapter 4), but further information is needed to test whether this is a general pattern in temperate Australian waters. The current study was designed to test whether differences in invertebrate diversity between monospecific stands of *E. radiata* and stands of mixed algae observed at small spatial scales (kilometres apart) are consistent at larger (100s kilometres apart) and regional (western Australia, southern Australia and eastern Australia; 1000s kilometres apart) scales across the temperate coastline of Australia.

5.2 METHODS

Sampling methods

We sampled assemblages of invertebrates in holdfasts of *E. radiata* from stands of mixed algae and monospecific *E. radiata* across temperate Australia in the Austral summer of 2001/2002. We used a nested hierarchical design to sample over three spatial scales (Fig. 5.1). Four randomly chosen sites (separated by kilometres) were sampled within each of four locations (separated by 100s kilometres), randomly chosen within each of three regions; western, southern and eastern Australia (separated by 1000s kilometres). Sampling was done between the latitudes 33° 37′ S and 37° 06′ S to restrict latitudinal variation. All sites were chosen so they were highly exposed to oceanic swell and were connected to the mainland. The majority of samples were taken from a depth range of 3-10 m (average 7.9 ± 0.4 SE) and did not differ among regions (ANOVA: $F_{2,9} = 0.70$, $P > 0.05$), but extensive kelp beds at this range of depth were not present at Eden in eastern Australia where samples were taken from 8-12 m. Greater depths at this one location did not, however, have any effect on regional patterns observed (see Results, Fig 5.5).

Within each site, holdfasts were sampled from five replicate plants (separated by 1-10 m) within monospecific stands of *E. radiata* (> 80 % of the canopy was *E. radiata*) and stands of mixed algae (40-60% of the canopy was *E. radiata* and the remainder species of Fucales). These levels were based on results from Chapter 4 which show that monospecific stands of *E. radiata* and stands of mixed algae, defined at these levels, contain different assemblages of invertebrates. Cover was measured within $1m^2$ quadrats at each site prior to sampling the holdfasts. Flora of the canopy in stands of mixed algae was mostly of the families Cystoseiraceae (*Cystophora* spp., *Acrocarpia* spp.), Seirococcaceae (*Syctothalia* spp.) and

Sargassaceae (*Sargassum* spp.). Stands were generally no greater than 2 m^2 and interspersed among one another within the extent of the forest. The majority of samples (> 62%) were taken from stands with densities of *E. radiata* greater than 5 individuals/m^2 (> 5 plants/m^2) because at densities below this level different abundances and composition of invertebrates are associated with holdfasts of *E. radiata* (Goodsell & Connell 2002).

Holdfasts were sampled by cutting the stipe at its base and sealing a plastic bag to the substratum over the stipe and holdfast. The holdfast was levered off the substratum into the bag with a dive knife and the bag quickly closed over the holdfast. Holdfasts were fixed in 10 % formalin/seawater solution. The haptera of each holdfast were dissected and the contents sieved through a 1 mm mesh to separate the fauna. Mobile fauna were identified to the lowest possible taxonomic resolutions, identification to the species level was preferred but some animals could only be identified with certainty to family or class. Specimens were stored in 90 % alcohol and kept as a specimen library.

Analytical methods

Multivariate associations of the composition and relative abundance (diversity) of invertebrates between the two stands were tested by a 4-factor mixed model NP-MANOVA using Gower's distance measures. The factors were: stand (2 levels, fixed and orthogonal), region (3 levels, fixed and orthogonal), location (4 levels, random and nested within region) and site (4 levels, random and nested within each combination of region × location). Data were fourth root transformed to provide more equal weighting of taxa that occurred frequently and were numerous, to those less frequent and less numerous (Clarke 1993). Permutations (4999) of residuals were done. The same model was used on untransformed data in ANOVA to test for differences in the number of invertebrate taxa (richness) and of individual taxonomic groups between the two stands.

5.3 RESULTS

A total of 316 mobile taxa from > 100 families and 7 phyla (Annelida, Arthropoda, Echinodermata, Mollusca, Nemertea, Platyhelminthes, Sipuncula) were identified in holdfasts across temperate Australia (Appendix 3). Members of the phylum Arthropoda were the most numerically abundant and taxonomically diverse across Australia, particularly the amphipods and isopods. Polychaete worms were the most diverse and abundant taxa of the phylum Annelida.

A significant interaction between stand and site was detected by multivariate ANOVA (Table 5.1). Post hoc comparisons reveal that the composition and relative abundance of invertebrates (diversity) differed between stands of monospecific *E. radiata* and stands of mixed algae in 40 of the 48 sites across Australia. Similarities between stands occurred at a few sites only in a few locations within southern and western Australia, but not eastern Australia.

Variation in patterns of diversity between stands observed at small-scales did not, however, obscure the general pattern at regional scales (Table 5.1; significant effect of region). Assemblages of invertebrates within monospecific stands of *E. radiata* are distinct from those within stands of mixed algae in nMDS plots of average values at the scale of regions (Fig. 5.2) and locations (Fig. 5.3), despite the marginal non-significance of the effect of stand (Table 5.1). Among regions, differences in patterns of diversity (relative abundance and composition) were greatest between eastern Australia and both southern and western Australia, whilst southern and western Australia were the least different (Fig. 5.2, Table 5.1b). The relative abundance and composition of invertebrates was similar among locations (separated by 100s kilometres) within each region (Table 5.1).

Table 5.1 (a) Four-factor NP-MANOVA testing differences in the composition and relative abundance of invertebrates between monospecific stands of *E. radiata* and stands of mixed algae, among randomly chosen sites (separated by kilometres), nested within randomly chosen locations (separated by 100s kilometres) nested within three regions (western, southern and eastern) across temperate Australia ($n = 5$ for each site). (b) Post hoc comparisons among regions. Data were fourth root transformed to provide more equal weighting of taxa that occurred frequently and were numerous, to those less frequent and less numerous. Not significant (ns): $P > 0.05$, *: $P < 0.05$, **: $P < 0.001$.

(a) NP-MANOVA

Source	df	MS	F	*P*
Stand	1	4310.635	10.223	0.093
Region	2	6990.175	8.203	*
Location (Region)	9	852.145	2.572	ns
Site (Region × Location)	36	331.317	2.230	**
Stand × Region	2	1327.661	3.149	ns
Stand × Location (Region)	9	421.652	2.061	ns
Stand × Site (Location × Region)	36	204.555	1.377	**
Residual	384	410.559		

(b) Pairwise comparisons of regional effect	t	*P*
WA vs SA	3.341	**
WA vs EA	6.701	**
SA vs EA	6.754	**

The number of taxa (richness) between the two stands varied among sites (Table 5.2). Monospecific stands of *E. radiata* supported greater numbers of taxa than stands of mixed algae at most spatial scales (Fig. 5.4, 5.5, SNK tests). No sites, however showed significant differences occurring in the opposite direction to this general pattern. Whilst taxonomic richness was variable among locations in each region (Table 5.2), no interaction between stand and location was detected (Fig. 5.4, Table 5.2). Importantly, the magnitude of difference in richness between the two stands appears greater in eastern Australia than southern and western Australia (Fig. 5.4), notwithstanding the marginal non-significance of the stand by region interaction (ANOVA: $F_{2,9} = 3.72$, $P = 0.067$, Table 5.2).

Generally, monospecific stands of *E. radiata* contained greater richness and abundance of all phyla and most taxa than stands of mixed algae in all regions (Fig. 5.6, Table 5.3). Patterns of abundance and richness between the two stands at the scale of region differed for the most abundant taxa; polychaeta, isopoda and amphipoda (Table 5.4, Fig. 5.6). Differences in the abundance of isopods and polychaetes, and the richness of isopods between stands, were only significant in eastern Australia (Fig. 5.6, Table 5.4b,c; significant stand × region interaction). Polychaete richness differed among the two stands in each region (Fig. 5.6, Table 5.4c, SNK tests). The richness and abundance of crustacean taxa was greater in western Australia than in eastern or southern Australia, but the richness and abundance of polychaete taxa was greatest in eastern Australia than the other regions (Fig. 5.6, Table 5.4). Furthermore, southern Australia seems to be the most depauperate region for both abundance and richness of these three taxonomic groups (Fig. 5.6, Table 5.4).

Table 5.2 ANOVA of the number of species (species richness) of invertebrates from monospecific stands of *E. radiata* and stands of mixed algae among randomly chosen sites (separated by kilometres) nested within randomly chosen locations (separated by 100s kilometres) nested within three regions (western, southern and eastern) across temperate Australia ($n = 5$ for each site). Data were homogenous (Cochran's *C*-test: $P < 0.05$) and not transformed. Not significant (ns): $P > 0.05$.*: $P < 0.05$, **: $P < 0.001$.

Source	df	MS	F	*P*
Stand	1	4136.002	22.43	**
Region	2	4246.008	5.34	*
Location (Region)	9	795.657	5.13	**
Site (Region × Location)	36	155.155	2.68	**
Stand × Region	2	685.058	3.72	0.067
Stand × Location (Region)	9	184.401	1.66	ns
Stand × Site (Location × Region)	36	111.383	1.93	**
Residual	384	57.829		

Table 5.3 Total abundance of some frequent (occurred in >40% of all samples) and numerous taxa in holdfasts of *E. radiata* in monospecific stands (MO) and stands of mixed algae (MX) across temperate Australia. For each region, abundance is given in bold as total number of individuals/number of taxa (richness). Number of taxa in all samples is given in parentheses. Echinoderms and Molluscs were grouped at the level of class, and Nemerteans, Platyhelminthes and Sipunculans grouped at phyla.

	Eastern Australia		**Southern Australia**		**Western Australia**	
	MO	**MX**	**MO**	**MX**	**MO**	**MX**
ARTHROPODA (209)	3228/132	1466/108	2791/82	2583/85	1154/80	1301/69
Amphipoda (155)	**2239/96**	**1829/56**	**972/78**	**785/55**	**1817/61**	**879/44**
Aora maculata	376	366	176	120	74	96
Quadrimaera viridis	697	603	125	46	0	42
Tethygenia spp.	85	65	22	37	56	24
Isopoda (33)	**834/29**	**655/24**	**406/22**	**281/18**	**688/22**	**196/18**
Gnathidae spp.	43	28	57	10	148	17
Limnoridae spp.	119	77	52	52	70	8
ANNELIDA (92)	2594/57	1569/49	1810/65	1139/42	8358/40	3299/55
Polychaeta (90)	**2546/56**	**1563/41**	**1766/48**	**1126/39**	**8115/63**	**3266/53**
Nereididae sp. 2	102	50	63	57	410	319
Spionidae spp.	95	23	82	3	950	196
Syllinae sp. 2	1211	750	529	427	2831	1117
ECHINODERMATA(6)	137/3	113/6	924/4	105/4	132/5	347/4
MOLLUSCA (4)	38/3	36/4	210/4	19/2	28/2	109/3
NEMERTEA	26	32	169	178	60	263
PLATYHELMINTHES	3	6	57	2	1	1
SIPUNCULA	234	109	218	3	64	76

Table 5.4 ANOVA of the abundance and richness of the most frequently occurring and taxonomically diverse groups of invertebrates: (a) Amphipoda, (b) Isopoda and (c) Polychaetea, from monospecific stands of *E. radiata* and stands of mixed algae among three regions (western, southern and eastern) across temperate Australia ($n = 80$ for each region). Stand and region were treated as fixed and orthogonal factors. Data were transformed to ln (x + 1) such that variances were homogenous (Cochran's *C*-test: $P > 0.05$). Non significant (ns): $P > 0.05$.*: $P < 0.05$, ** $P < 0.001$.

		Abundance		Richness	
Source	df	F	*P*	F	*P*
(a) Amphipoda					
Stand	1	3.96	0.078	1.06	ns
Region	2	2.66	NS	1.82	ns
Stand × Region	2	2.48	NS	1.83	ns
Residual	384				
(b) Isopoda					
Stand	1	12.52	*	6.77	*
Region	2	17.46	**	17.92	**
Stand × Region	2	6.92	*	4.59	*
Residual	384				
(c) Polychaeta					
Stand	1	32.36	**	34.17	**
Region	2	9.16	*	8.97	*
Stand × Region	2	4.79	*	3.24	0.087
Residual	384				

5.4 DISCUSSION

The composition and relative abundance of invertebrates associated with the holdfast of *E. radiata* was consistently different between monospecific stands of *E. radiata* and mixed stands of algae at local through regional scales across temperate Australia. There was greater abundance and richness of invertebrates in monospecific stands of *E. radiata* than in stands of mixed algae. This relationship varied at scales of kilometres, but became progressively consistent at larger scales; 100s kilometres and 1000s kilometres.

Greater diversities of vegetative habitat have historically been associated with greater diversity of animals (e.g. MacArthur & MacArthur 1961, Murdoch et al. 1972, Southwood et al. 1979), but we show here that the reverse can be true for forests of algae; a greater number of holdfast invertebrates exist in monospecific than diverse (i.e. mixed stands) habitats. Interestingly, predictions that coexistence will be enhanced in diverse habitats were also not apparent for invertebrate fauna in seagrass habitats (Heck & Wetstone 1977, Eggleston et al. 1999). Models that greater diversity of vegetative habitat is synonymous with complexity of habitat (Dean & Connell 1987c, Orth 1992), which can positively influence the diversity of animals (Bell et al. 1991) may be oversimplified in light of weak relationships between habitat and faunal diversity detected in both marine (Parker et al. 2001) and terrestrial systems (Symstad et al. 2000).

Rather than responding to measures of diversity *per se* (number of plant taxa), invertebrates may be strongly influenced by the specific chemical, structural and morphological traits of plants, related to the identity of the plant species that make up their habitat (Parker et al. 2001). In the current study, the amount of resources available to invertebrates may not be increased by algal diversity. The presence of other species of canopy-forming algae may be detrimental to rates of local turnover for animals that are closely associated with the holdfasts of *E. radiata*. Fauna of holdfasts tend to move horizontally along the bottom between kelps rather than by swimming in the water column (Edgar 1992, Jørgensen & Christie 2003) and fucalean algae do not have branched holdfasts that are suitable as habitat for invertebrates, hence diversity may be reduced in stands of mixed algae.

Stands of mixed algae comprised a greater percentage of temperate reefs than stands of monospecific algae in western and southern Australia (Chapter 4). The natural or anthropogenic removal of monospecific canopies of *E. radiata* (Gorgula & Connell in press) promotes invasion of alternate species of algae (Kirkman 1981a, Emmerson & Collings 1998, Chapter 2) and has the potential to generate stands of mixed algae. If stands of mixed algae represent a disturbed, alternate state (but see discussion in Petraitis & Latham 1999), sparse densities and smaller richness of invertebrate taxa in holdfasts of *E. radiata* from mixed stands versus monospecific stands is a potential concern. Such concern may be particularly relevant to the eastern region of Australia, because the greatest differences in faunal diversity between stands was observed at this region and it is also the most human-dominated (i.e. New South Wales). Further investigation is needed into the key aspects of habitat structure that influence animal populations, combined with information on the life history of fauna, if we are to understand differences in the ecology of diverse (mixed) versus monospecific habitats (Cannell et al. 1992, Bartelink 2000).

Patterns of invertebrate diversity in eastern Australia were most different to that of western and southern Australia, despite the consistent differences in diversity between monospecific stands of *E. radiata* and stands of mixed algae across Australia. The greater magnitude of difference in abundance of polychaetes and isopods between monospecific and mixed stands in eastern Australia, as well as the greater overall richness of taxa, may account for the greater distinction in patterns of diversity between eastern Australia and both western and southern Australia. Why such exaggerated differences in the diversity of holdfast fauna between diverse and monospecific habitats occurs in eastern Australia relative to the rest of the southern coast, is an important biogeographic question requiring further investigation. Such studies must incorporate knowledge about the ecological requirements of holdfast fauna, as well as assessment of the many processes, both local and regional, which are key to the organisation of these assemblages (Poore 1994).

Disproportionately large differences in the ecological patterns of eastern Australia compared to the rest of the temperate coastline is emerging as a general pattern for many aspects of the ecology of forests of canopy-forming algae, including associations between canopy and understorey algae (Fowler-Walker & Connell 2002, Irving et al. 2004) and morphology of *E. radiata* (Fowler-Walker et al. in review). Considering that most of our knowledge of the ecology of these forests is derived from eastern Australia (Irving et al. 2004), greater awareness of the ecological differences of this well studied region with the rest of temperate Australia can only increase our understanding of the ecology of Australian subtidal habitats.

A key result of the current study was that local-scale associations between the diversity of subtidal habitats and the diversity of associated invertebrates in the holdfasts of *E. radiata* were consistent across Australia. Variability in the patterns of abundance and distribution of marine organisms at small spatial-scales has been well documented (Kennelly 1987a, b, Underwood & Chapman 1998, Benedetti-Cecchi 2001) and often such variability is reduced as the spatial scale of observation is increased (Underwood & Chapman 1996, Fowler-Walker & Connell 2002). In the current study, the strongest patterns of diversity between holdfast fauna and their habitat, occurred at scales of 100s kilometres, as there was little variation in patterns among locations. There is much debate about the relevance of variation or generality in ecological studies (Peters 1991, Keddy 1989, Lawton 1999), yet awareness of the scales at which general patterns become inconsistent remains a useful tool to assess general patterns in ecology (Levin 1992, Underwood 1996). Once the scale at which patterns of diversity vary or become consistent is identified, hypotheses about the relevant processes that determine patterns of diversity and the scale at which they operate can be developed (Gaston & Blackburn 1999, Huston 1999).

Site to site variation in patterns of diversity is most likely a function of variability in behavioural responses to the nature of their immediate habitat (scales of < ms) (Underwood & Chapman 1996, Eggleston et al. 1999). Such variability among small spatial scales did not, however, obscure the ability to detect general differences in patterns of invertebrate diversity in mixed and monospecific forests of algae. In the current study, regional differences in patterns of invertebrate diversity were a result of both differences in abundance and identity of taxa; each region contained a different compliment of taxa occurring in different relative abundance. This suggests that the influence of historical (e.g. divergence of land masses or speciation events) or regional processes (oceanographic) which control speciation and dispersal and hence the composition of taxa (Levin 1992, Ricklefs & Schluter 1993), interact with contemporary processes acting at smaller scales (environmental factors) to control the abundance of populations (Poore 1994).

In conclusion, variation at small spatial scales in the composition of forests of canopy-forming algae is widespread and has important implications for the ecology of these forests. Whilst patterns of diversity were variable at small scales, differences in the diversity of invertebrates within holdfasts of *E. radiata* between mixed and monospecific habitats were detected at broader spatial scales. Historical and regional phenomena must contribute to the biogeographic patterns we detected, but our results suggest that there is potential to infer predictions about associations between plant and animal diversity from manipulative experiments done at local-scales to broader scales. Such results encourage further manipulative tests of hypotheses about the nature of the relationship between subtidal habitat and animal diversity, considering that conclusions from such experiments have the potential to be broadly relevant across temperate Australia. Whilst the detection of repeatable patterns is a main goal of ecology, investigations need not be restricted to the detection of species-specific responses, rather associations between the structure of habitat and a broad suite of taxa (316 mobile taxa from > 100 families and 7 phyla) appear in this study, as a generality. This observation suggests that repeatable patterns in ecology may exist (Lawton 1999) and that the science of ecology can be much more than the description of idiosyncratic responses of certain taxa to particular conditions at particular locations.

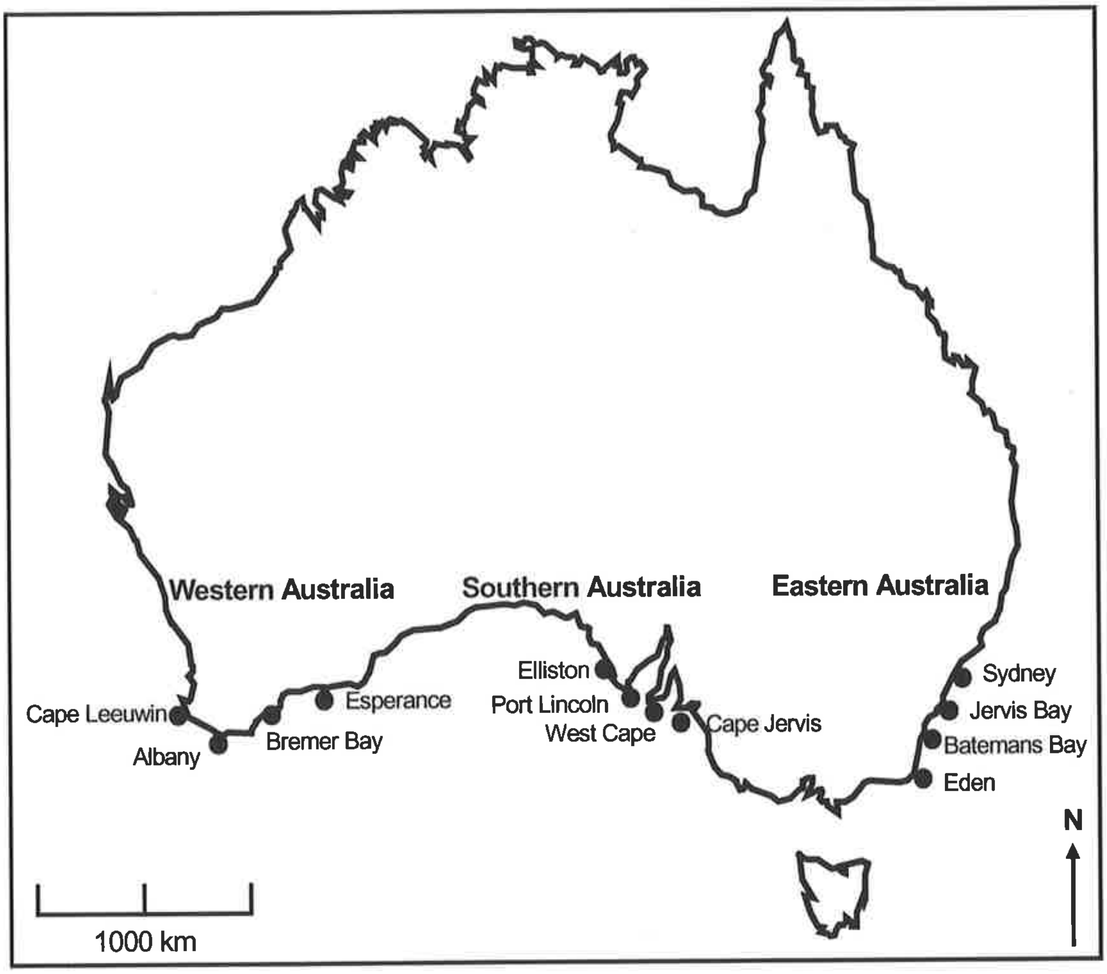


Figure 5.1 Position of locations (separated by 100s kilometres) within three regions; western, southern and eastern Australia (separated by 1000s kilometres) where sampling was done within the temperate region of Australia.

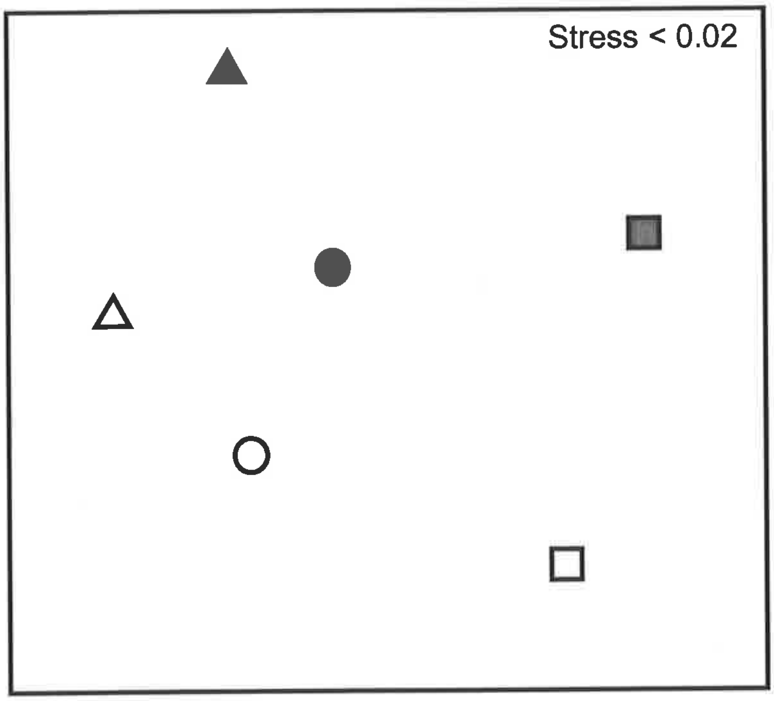


Figure 5.2 nMDS plot of the diversity of invertebrates between monospecific stands of *E. radiata* (open symbols) and stands of mixed algae (shaded symbols) in each of three regions; ▲ = western Australia, ● = southern Australia and ■ = eastern Australia (averaged over locations).

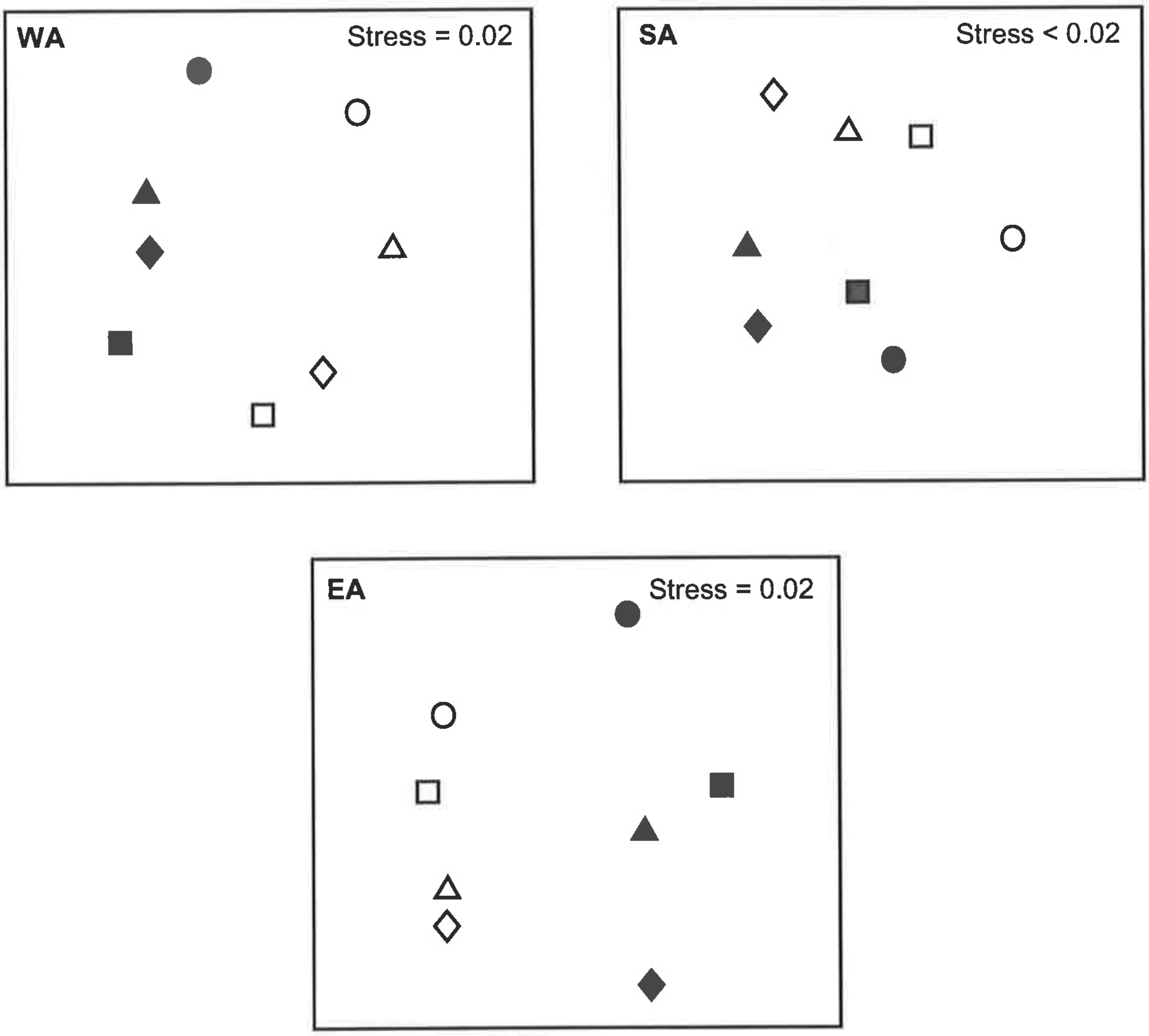


Figure 5. 3 nMDS plots of the diversity of invertebrates between monospecific stands of *E. radiata* (open symbols) and stands of mixed algae (shaded symbols) at the scale of location (averaged over four sites) within three regions; WA = western Australia, SA = southern Australia and EA = eastern Australia. Within each region, circles represent the eastern most location, and from west to east locations are represented by triangles, diamonds and squares (the western most location).

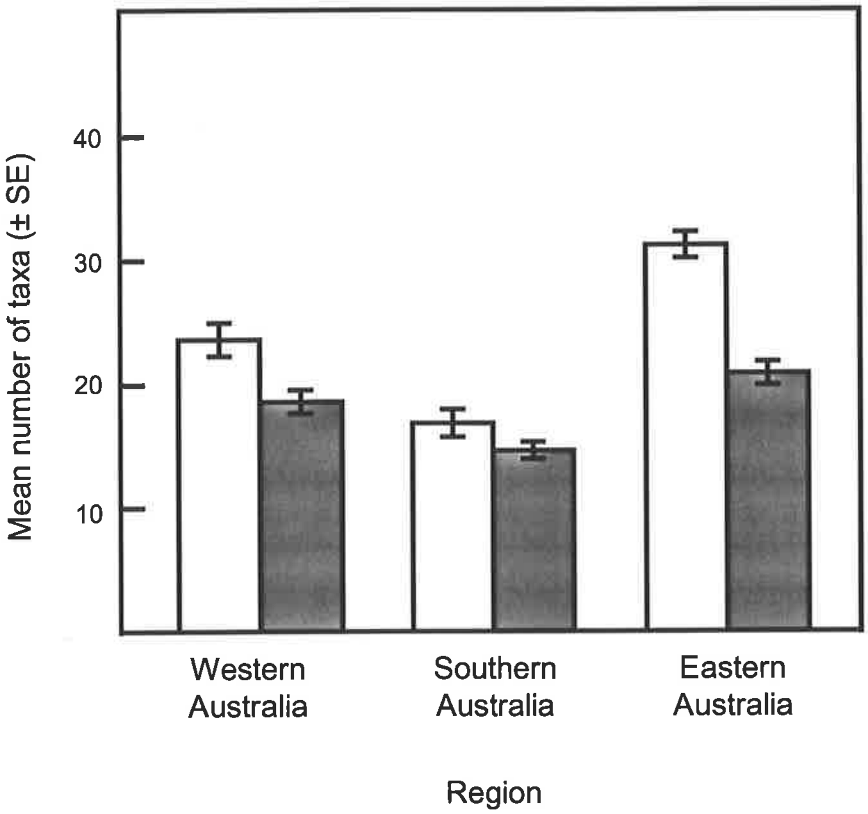


Figure 5.4 Mean number of taxa (± SE) between monospecific stands of *E. radiata* (open bars) and stands of mixed algae (shaded bars) among regions separated by 1000s kilometres across temperate Australia.

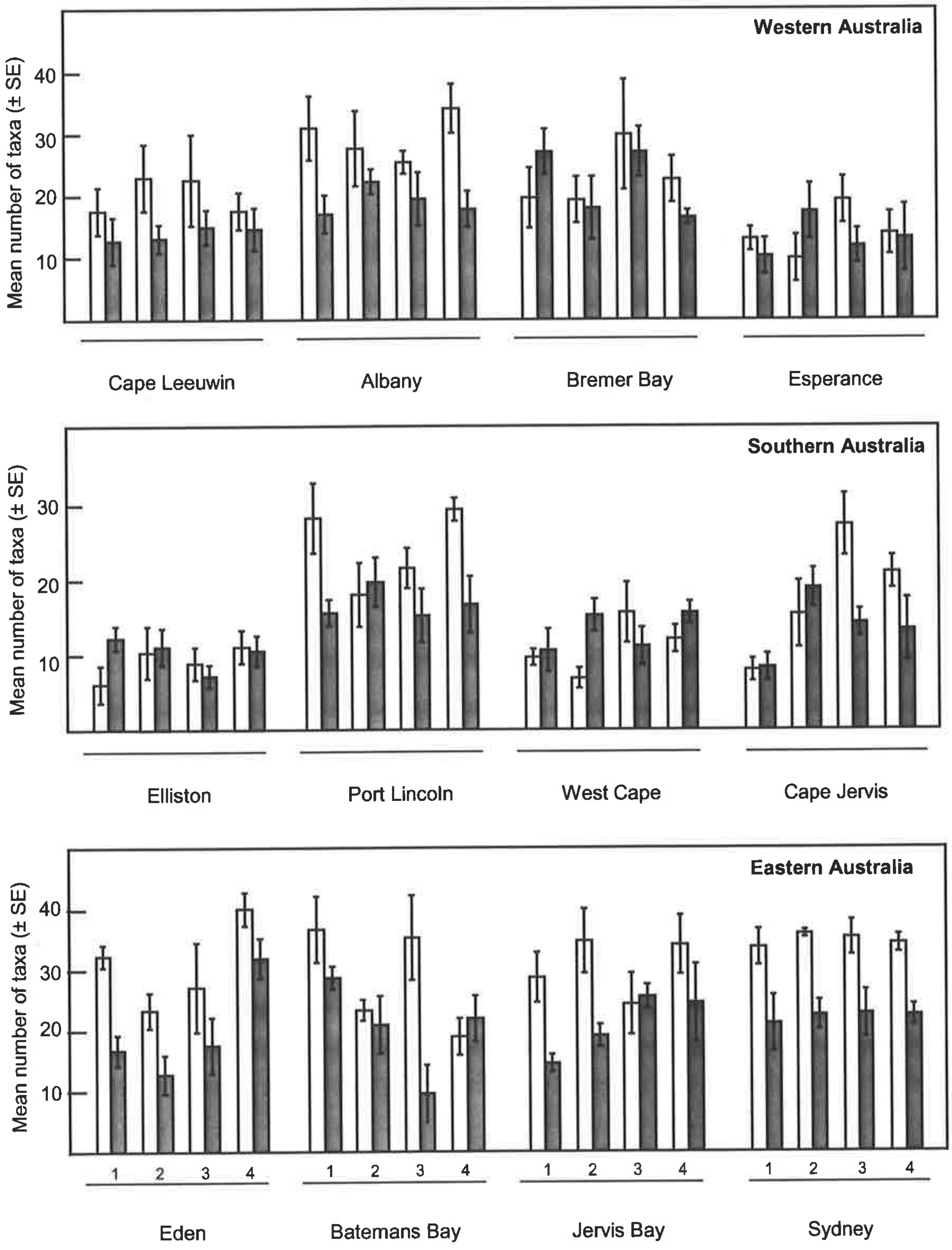
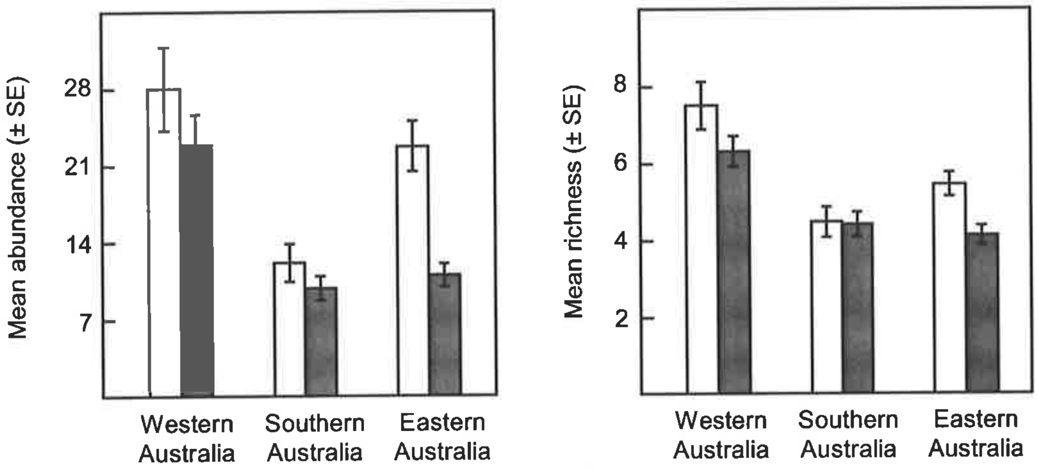
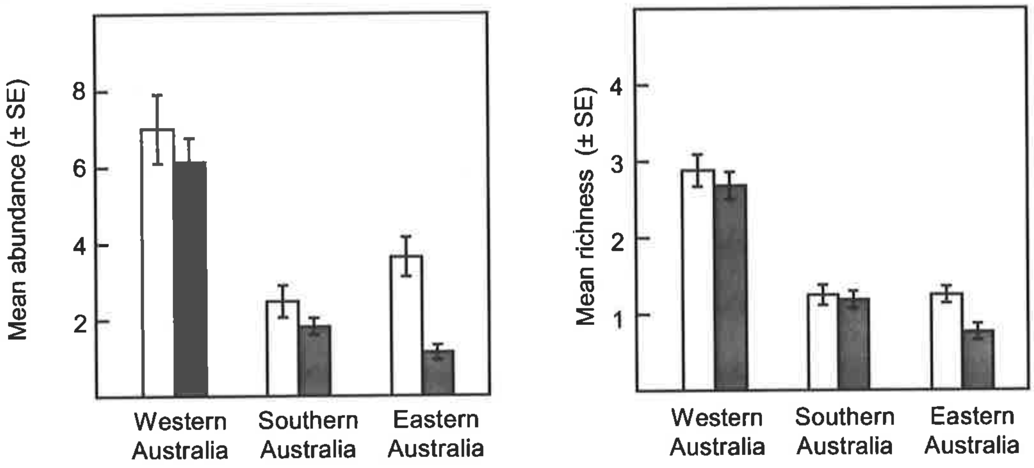


Figure 5.5 Mean number of taxa (± SE) between monospecific stands of *E. radiata* (open bars) and stands of mixed algae (shaded bars) among sites (kilometres apart) within locations (100s kilometres apart) for each region across temperate Australia.

(a) Amphipods



(b) Isopods



(c) Polychaetes

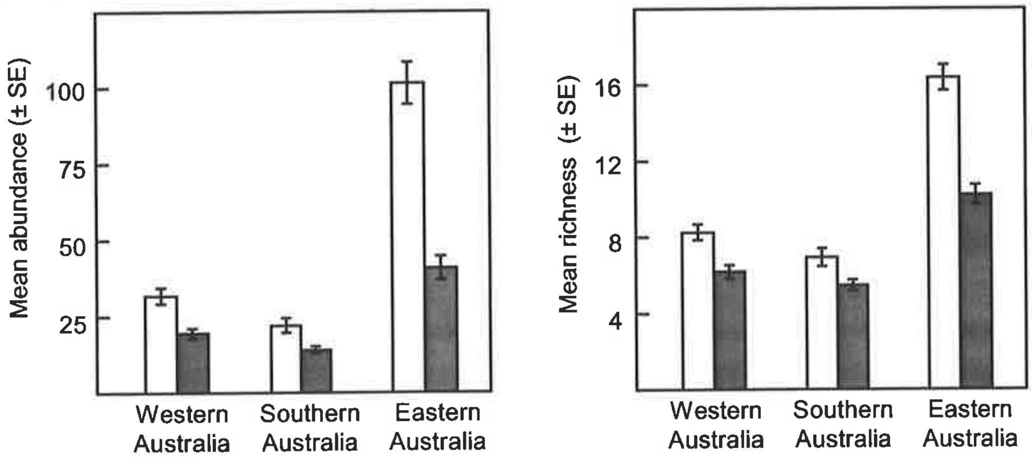


Figure 5.6 Mean number and richness (± SE) of the most frequently encountered and taxonomically diverse groups of invertebrates: (a) Amphipoda, (b) Isopoda and (c) Polychaeta between monospecific stands of *E. radiata* (open bars) and stands of mixed algae (shaded bars) among regions separated by 1000s kilometres across temperate Australia.

APPENDIX 3

List of taxa found across temperate Australia. Total abundance is given, for more detail see Table 5.3.

	ORDER	FAMILY	SPECIES	TOTAL
ANNELIDA				
Polychaeta	Eunicida	Dorvilleidae	Dorvilleidae sp. 1	7
			Dorvilleidae sp. 2	1
		Eunicidae	*Eunice* spp.	826
			Lysidice spp.	280
			Marphysa spp.	14
			Nematonereis spp.	44
		Euphrosinidae	Euphrosinidae sp. 1	4
		Lumbrineridae	*Lumbrineridae* spp.	307
		Oenonidae	*Arabella* sp. 1	19
			Notocirrus sp. 1	1
			Oenonidae sp. 2	1
		Onuphidae	*Rhamphobrachium* sp. 1	45
			Onuphidae sp. 1	3
			Onuphidae sp. 2	112
	Phyllodocida	Chrysopetalidae	*Chrysopetalum* sp. 1	85
		Glyceridae	*Glycera* sp. 1	12
		Hesionidae	Hesionidae sp. 1	2
			Hesionidae sp. 2	33
			Hesionidae sp. 4	1
		Lacydoniidae	*Lacydonia* sp. 1	1
		Nereididae	*Nereis spinigera*	4
			Nereididae sp. 1	252
			Nereididae sp. 2	1019
		Phyllodocidae	Phyllodocidae sp. 1	25
			Phyllodocidae sp. 2	28
			Phyllodocidae sp. 3	2
			Phyllodocidae sp. 4	14
			Phyllodocidae sp. 5	11
			Phyllodocidae sp. 6	18
			Phyllodocidae sp. 7	20
			Phyllodocidae sp. 8	2
			Phyllodocidae sp. 9	1
		Polynoidae	*Harmothoe phillipensis*	20
			Harmothoinae sp. 1	3
			Harmothoinae sp. 2	9
			Harmothoinae sp. 3	1
			Herdmanella sp. 1	1
			Lepidasthenia australiensis	2
			Lepidasthenia sp. 1	3
			Lepidonotus sp. 1	204
			Lepidonotus sp. 3	20
			Lepidonotus sp. 4	18
			Lepidonotus sp. 7	1
		Sigalionidae	*Eupholoe* sp. 1	1
			Sthenelanella sp. 1	2
		Sphaerodoridae	Sphaerodoridae sp. 1	4

	Order	Family	Species	Total
Polychaeta	Phyllodocida	Spionidae	Spionidae spp.	1349
		Syllidae	*Amblyosyllis* sp. 1	17
			Amblyosyllis sp. 2	1
			Autolytinae sp. 1	241
			Autolytinae sp. 2	164
			Brania sp. 4	71
			Eurysyllis sp. 1	22
			Eusyllinae spp.	89
			Exogone sp. 1	681
			Haplosyllis sp. 1	247
			Procerastea sp. 1	2
			Sphaerosyllis sp. 1	20
			Sphaerosyllis sp. 3	122
			Streptosyllis sp. 1	1
			Syllinae sp. 1	120
			Syllinae sp. 2	6865
			Syllinae sp. 3	1942
			Syllinae sp. 4	228
			Syllinae sp. 7	628
			Syllinae sp. 14	5
			Syllinae sp. 15	155
			Syllinae sp. 17	35
			Syllinae sp. 18	21
			Syllinae sp. 19	60
			Trypanosyllis sp. 1	18
			Trypanosyllis sp. 2	44
			Trypanosyllis zebra	408
	Scolecida	Arenicolidae	*Branchiomaldane* sp. 1	6
		Capitellidae	Capitellidae spp.	200
		Maldanidae	Maldanidae sp. 1	858
		Opheliidae	*Armandia* spp.	18
		Orbiniidae	*Naineris* sp. 1	10
			Proscoloplos bondi	126
			Scoloplos Scoloplos spp.	9
			Orbiniidae sp. 3	1
			Orbiniidae sp. 4	7
			Orbinidae sp. 5	1
		Questidae	*Questa* sp. 1	1
		Scalibregmatidae	Scalibregmatidae sp. 1	71
	Spionida	Chaetopteridae	Chaetopteridae sp. 1	4
		Spionidae	*Aquilaspio* sp. 1	23
			Minuspio cirrifera	1
	Terebellida	Cirratulidae	Cirratulidae spp.	386
Polychaeta			Polychaete sp. 1	2
			Polychaete sp. 2	5
			Polychaete sp. 3	1
ARTHROPODA				
Chelicerata				
Arachnida	Scorpiones		*Scorpiones* spp.	1
Pycnogonida			Pycnogonida spp.	80
Crustacea				
Malacostraca	Amphipoda	Ampeliscidae	*Ampelisca* sp. 1	13

	ORDER	FAMILY	SPECIES	TOTAL
Crustacea	Amphipoda	Ampeliscidae	Ampeliscidae sp. 2	2
		Amphilochidae	*Gitanopsis* sp. 1	16
			Gitanopsis sp. 2	3
			Stanthoe sp. 2	1
			Amphilochidae sp. 1	4
			Amphilochidae sp. 4	19
			Amphilochidae sp. 5	6
			Amphilochidae sp. 6	3
			Amphilochidae sp. 7	18
		Amphithoidae	*Ampithoe* sp. 1	271
			Ampithoe sp. 3	7
			Ampithoe sp. 5	29
			Ampithoe sp. 6	22
			Cymadusa sp. 1	72
			Cymadusa sp. 2	12
			Pleonexas sp. 2	4
			Pleonexes sp. 1	2
			Ampithoidae spp.	41
		Anamixidae	*Anamixis* sp. 1	2
		Aoridae	*Aora maculata*	1208
			Bemlos cf arkoolus	15
			Bemlos sp. 2	8
			Bemlos sp. 3	24
			Bemlos sp. 4	1
			Bemlos sp. 5	31
			Bemlos sp. 6	17
			Bemlos strigilis	52
			Bemlos trudis	88
			Aoridae sp. 1	1
			Aoridae sp. 2	1
			Aoridae sp. 3	2
			Aoridae sp. 4	1
			Aoridae sp. 5	1
			Aoridae sp. 6	9
			Aoridae sp. 7	1
			Aoridae sp. 8	4
			Aoridae spp.	35
		Colomastigidae	*Colomastix* sp. 1	5
			Colomastix sp. 2	12
			Colomastix sp. 3	5
			Yulumara wallanger	7
		Corophiidae	*Ampelisciphotis* sp. 1	35
			Chevalia sp. 1	35
			Corophiodea sp. *A*	6
			Corophiodea sp. *B*	9
			Corophiodea sp. *C*	3
			Corophium sp. 1	1
			Corophium sp. 2	5
			Corophium sp. 3	1
			Gammaropsis sp. 1	47
			Gammaropsis sp. 10	3
			Gammaropsis sp. 2	115

	ORDER	FAMILY	SPECIES	TOTAL
Crustacea	Amphipoda	Corophiidae	*Gammaropsis* sp. 3	157
			Gammaropsis sp. 4	2
			Gammaropsis sp. 5	204
			Gammaropsis sp. 6	10
			Gammaropsis sp. 7	12
			Gammaropsis spp.	5
			Gammoropsis sp. 11	14
			Grandidierella sp. 1	2
			Photis sp. *A*	466
			Corophiidae sp. 10	2
			Corophiidae sp. 11	1
			Corophiidae sp. 6	17
			Corophiidae sp. 7	1
			Corophiidae sp. 9	3
			Corophiidae spp.	8
		Cyproideidae	*Austropheonoides* sp. 1	10
			Austropheonoides sp. 2	2
			Cyproidea ornata	18
			Cyproidea sp. 2	1
			Cyproidea sp. 4	1
			Cyproidea sp. 5	1
		Dexaminidae	*Paradexamine frinsdorfi*	27
			Paradexamine goomai	18
			Paradexamine sp. 1	6
			Paradexamine sp. 3	5
			Polycheria sp. 1	50
			Syndexamine runde	18
			Syndexamine sp. 2	1
			Syndexamine sp. 4	2
			Syndexamine wane	10
			Syndexamine wunda	32
			Dexaminidae sp. 1	1
			Dexaminidae sp. 4	2
			Dexaminidae sp. 5	8
		Eusiridae	*Tethygeneia* spp.	289
			Eusiridae sp. 1	2
			Eusiridae sp. 3	26
			Eusiridae sp. 6	6
			Eusiridae sp. 7	9
			Eusiridae sp. 8	40
		Eusiridae	Eusiridae sp. 9	54
			Eusiridae spp.	4
		Hyalidae	Hyalidae sp. 1	78
			Hyalidae sp. 2	1
		Iciliidae	*Icilius* sp. 1	7
		Iphimediidae	*Iphemedia* sp. 1	3
			Ochlesis sp. 1	12
			Iphimediidae sp. 2	3
		Ischyroceridae	*Cerapus* sp. 1	5
			Ericthonius sp. 1	348
			Ericthonius sp. 2	3
			Jassa sp. 1	19

	ORDER	FAMILY	SPECIES	TOTAL
Crustacea	Amphipoda		*Ventojassa* sp. 1	260
		Leucothoidae	*Leucothoe gracilis*	182
			Leucothoe sp. 1	69
			Leucothoe sp. 10	32
			Leucothoe sp. 2	2
			Leucothoe sp. 3	5
			Leucothoe sp. 5	2
			Leucothoe sp. 6	8
			Leucothoe sp. 7	3
			Leucothoe sp. 8	1
			Leucothoe sp. 9	26
			Leucothoidae spp.	3
		Liljeborgiidae	*Liljeborgia* sp. 1	59
		Lysianassidae	*Amaryllis maerophthalma*	9
			Amaryllis spp.	28
			Tryphosella spp.	1
			Lysianassidae sp. 1	29
			Lysianassidae sp. 2	4
			Lysianassidae sp. 3	36
			Lysianassidae sp. 4	161
			Lysianassidae sp. 5	1
			Lysianassidae sp. 6	2
			Lysianassidae spp.	28
		Melitidae	*Ceradocus ramsayi*	21
			Ceradocus rubromaculatus	94
			Ceradocus sellickensis	163
			Ceradocus serratus	4
			Ceradocus spp.	10
			Dulichiella australis	35
			Elasmopus spp.	44
			Hoho marilla	119
			Maera mastersi	623
			Maera sp. 3	3
			Maera sp. *A*	79
			Maera sp. *B*	5
			Mallacoota subcarinata	194
			Melita sp. 1	3
		Melitidae	*Quadimaera viridis*	1543
			Melitidae sp. 1	88
			Melitidae sp. 2	1
			Melitidae spp.	21
		Philantidae	Philantidae sp. 1	1
		Phoxocephalidae	Phoxocephalidae sp. 2	1
			Phoxocephalidae spp.	15
		Plioplateidae	*Plioplateia* sp. 2	1
		Podoceridae	Podoceriidae spp.	43
		Stenothoidae	*Stenothoe* sp. 1	2
			Stenothoe sp. 2	18
	Amphipoda		Amphipoda spp.	77
	Caprellida	Caprellidae	Caprellidae spp.	141
	Cumacea		Cumacea sp. 1	2
	Decapoda	Diogenidae	Paguriidae spp.	34

	ORDER	FAMILY	SPECIES	TOTAL
Crustacea	Decapoda	Hymenosomatidae	*Halicarinus australis*	3
			Halicarinus ovatus	33
			Hymenosomatidae sp. 1	1
		Galatheidae	*Munida* spp.	1
		Pilumnidae	*Pilumnus* spp.	473
		Porcellanidae	*Porcellana dispar*	17
			Porcellana sp. 2	5
		Xanthidae	*Xanthidae* spp.	1
	Decapoda		Crab spp.	1
			Shrimp spp.	151
	Isopoda	Arcturidae	Arcturidae spp.	16
		Anthuridae	Anthuridae spp.	151
		Cirolanidae	Cirolanidae spp.	18
		Jaeropsidae	*Jaeropsis* spp.	95
		Idoteidae	Idoteidae sp. 1	1
		Gnathiidae	Gnathiidae spp.	303
		Limnoriidae	Limnoriidae spp.	378
		Munnidae	Munnidae sp. 1	1
		Paranthuridae	Paranthuridae spp.	4
		Plakarthriidae	*Plakarthrium* sp. 1	10
		Sphaeormatidae	*Amphoroidea* sp. 1	185
			Amphoroidea sp. 3	1
			Cerceis bidentata	2
			Cerceis tridentata	7
			Cymodocella sp. 1	68
			Dynamenella sp. 1	1
			Haswellia cilicioides	74
			Haswellia emarginata	22
			Haswellia tridentata	2
			Ischyromene sp. 1	181
			Oxinasphaera islaya	20
			Paracilicaea septendetata	4
			Sphaeromatidae sp. 1	1
			Sphaeromatidae sp. 3	1
			Sphaeromatidae sp. 4	3
			Sphaeromatidae sp. 5	2
			Sphaeromatidae sp. 6	4
			Sphaeromatidae sp. 7	3
			Sphaeromatidae sp. 8	2
			Sphaeromatidae sp. 9	1
			Sphaeromatidae sp. 10	5
			Sphaeromatidae spp.	4
	Tanaidacea	Stenetriidae	Stenetriidae spp.	209
		Apseudidae	Apseudidae spp.	262
		Kalliapseudidae	Kalliapseudidae sp. 1	38
			Kalliapseudidae sp. 2	2
		Leptocheliidae	Leptocheliidae sp. 1	321
		Paratanaidae	*Paratanais* spp.	614
		Pseudotaniadae	*Pseudotanais* sp. 1	2
		Tanaidae	*Tanais* sp. 1	40
	Tanaidacea		Tanaidacea spp.	2

	ORDER	FAMILY	SPECIES	TOTAL
ECHINODERMATA				
Asteroidea			Asteroidea spp.	31
Crinoidea			Crinoidea spp.	3
Echinoidea			Echinoidea spp.	16
Holothurioidea	Dendrochirotida		*Dendrochirotida* sp. 1	549
			Holothuroidea sp. 1	1
Ophiuroidea			Ophiuroidea spp.	1158
MOLLUSCA				
Gastropoda			Gastropoda spp.	264
Polyplacophora			Chiton spp.	149
	Nudibranchia		Nudibranchia spp.	21
NEMATODA			Nematoda spp.	647
NEMERTEA			Nemertea spp.	728
PLATYHELMINTHES	Turbellaria		Platyhelminthes spp.	70
SIPUNCULA			Sipuncula spp.	704

Note: Taxa match other lists in this thesis and are based on a reference collection held within the Southern Seas Ecology Laboratories at the University of Adelaide.

Holdfast of *Ecklonia radiata* surrounded by alternate species of algae,
South Australia

CHAPTER SIX

DETERMINATION OF CONNECTIVITY AMONG FRAGMENTED HABITATS REQUIRES MORE THAN MEASURES OF DISTANCE: INTERACTIVE EFFECTS OF MATRIX ON DISTANCE

6.2 INTRODUCTION

The fragmentation, or break up, of continuous habitat results in unsuitable or less suitable habitat separating resources by varying distances (Fahrig 2003). Remnant patches of habitat, however, can remain connected within fragmented landscapes because they are neither too distant nor the intervening environment impermeable. Our challenge, if we are to understand the consequences of habitat fragmentation, is to detect the components of landscape pattern that facilitate (or hinder) the persistence of populations via dispersal among & colonisation of remnant habitats (Fahrig & Merriam 1985, Hanksi 1994).

The persistence of populations requires that rates of immigration are sufficient to overcome local extinction in patches of habitat (Brown & Kodric Brown 1977). Biodiversity is threatened in fragmented landscapes because greater mortality is associated with travelling larger distances, through relatively inhospitable habitat, to utilise or supplement resources in remnant patches (Hanski & Gilpin 1997, Hanski et al. 2000). The extent to which remnant habitats are available to organisms and thereby structural connectivity of the landscape, is often assessed using a measure of distance between remnant habitats (Collinge & Forman 1998, Flather & Bevens 2002, Fahrig 2002). Recent research, however, suggests that the availability of habitats is also likely to be affected by the characteristics of the surrounding landscape; i.e. the matrix (Fahrig & Merriam 1985, Gascon et al. 1999, Jonsen et al. 2001, Ricketts 2001).

The type of vegetation, or lack thereof, in the matrix can determine the ease at which animals are able to move within the landscape. The matrix can be a barrier to colonisation because movement among fragmented habitats is physically impeded

(Johnson et al. 1992, Malcom 1997). Alternatively, colonisation of distant habitats may be facilitated because the matrix provides structure similar to the primary habitat (Gascon et al. 1999). It is likely, therefore, that connectivity of fragmented landscapes is not only a function of the distance among primary habitats but correlated with the nature of cover in the matrix through which animals disperse.

This experiment was done within one of the most productive habitats of temperate coastlines of the world; forests of kelp which support a majority of the diversity of marine fauna (Witman & Dayton 2001) and are increasingly threatened by human development in Australia (Gorgula & Connell in press). The focus species; the common kelp *Ecklonia radiata*, is particularly conspicuous and widespread across temperate Australia (Chapter Four). Each plant forms discrete habitat for a diverse assemblage of invertebrates (including crustaceans, polychaetes, molluscs and echinoderms) via the holdfast that attaches the plant to the substratum (Smith et al. 1996).

Many invertebrates are highly mobile exhibiting rapid exchange of individuals across small spatial scales (Gunnill 1982a, Howard 1985, Virnstein & Curran 1986) and most species of holdfast fauna move among kelps rather than remain associated with one individual plant (Edgar 1991, Norderhaug et al. 2002). Discrete patches of habitat like that provided by the holdfast of *E. radiata* can be thought of as a patch habitat (Gunnill 1982a, b, 1983, Thiel & Vásquez 2000) and the characteristics of the invertebrates render these excellent model systems for tests of hypotheses about colonisation of fragmented habitats (Goodsell & Connell 2002).

This study was designed to test the hypothesis that colonisation of fragmented patches (close vs far) is affected by the nature of the intervening matrix (alternate vegetation vs relatively bare space). I predicted that the presence of vegetation in the matrix between habitats would better facilitate colonisation compared to matrices of bare space. Hence, assemblages that colonise close habitats would be similar to those that colonise far habitats when alternate vegetation exists in the matrix, but not when the matrix is bare. I also assessed whether the structural or chemical nature of plants in the matrix had most influence on the colonisation of fragmented habitats. Whilst many authors realise that structural connectivity of fragmented landscapes depends on the distance between habitats as well as the presence of corridors or matrix (Taylor et al. 1993, Fahrig & Meriam 1994, Rosenburg et al. 1999, Ricketts 2001), to my knowledge this is the first experiment to separate the effects of the distance among remnant habitats and the nature of the intervening matrix in field conditions.

6.2 METHODS

Study system

Manipulations of the distance between fragmented habitats and matrix cover were done in forests of *E. radiata* on the rocky coastline of Edithburgh, South Australia (35° 5′ S, 137° 45′ E) at depths of 3-6 m. Two main types of matrix occur in fragmented forests of *E. radiata*; (i) canopy-forming species of fucalean algae (which have different physical and/or chemical characteristics to the primary habitat *E. radiata*), and (ii) relatively bare space that lack canopy-forming algae (algae > 20 cm in height). The structure of the holdfast of fucalean algae is unbroken and does not provide crevices as habitat for mobile invertebrates, whereas the holdfasts of *E. radiata* has a branched structure that provides space and refuge for mobile invertebrates (Smith et al. 1996). Direct tests of hypotheses about the effects of the structure of vegetation are difficult (Kelaher 2002) hence I tested the hypothesis that the chemical nature of algae within the matrix rather than its physical structure influences colonisation.

Manipulation of matrix cover and distance between habitats

Forests of monospecific *E. radiata* were fragmented by removing individuals to establish low densities (5 plants per m^2) of the primary habitat *E. radiata* in replicate plots (1 m^2, $n = 48$). A central plant (target sample) in each plot was separated from all neighbouring habitats of *E. radiata* by 'far' (20-25 cm), or 'close' (10 cm) distances via the removal of surrounding individuals. A previous experiment at the same location showed that the diversity of invertebrates from areas where holdfasts of *E. radiata* were separated by 10cm was different to areas where holdfasts where were separated by ~20 cm(Goodsell & Connell 2002).

Invertebrates present in the central plant (target sample) were removed by immersing the holdfast in 2% solution of formalin and freshwater above the sea-surface (Gunnill 1982a, Edgar 1992). Each central plant was removed by securing a plastic bag around the holdfast and then carefully levering it off the substratum. After the fauna was removed, the plant was rinsed in clean aerated seawater for 24 hours to remove any traces of formalin or freshwater. No tissue damage was obvious after this period and residual odour was negligible (see also Gunnill 1982a, Edgar 1992). The holdfast of each plant was then attached, using cable ties, to a plastic mesh grid (mesh size 25 mm) ready to be re-planted within the experimentally fragmented arrays.

Three different covers of matrix habitat were affixed to mesh grids; (i) intact individuals of fucalean algae, hereafter referred to as alternate algae; (ii) crushed fucalean algae such that the chemical but not structural nature was retained, hereafter referred to as alternate algae without structure; and (iii) bare where all canopy-forming individuals were removed. To construct matrices of crushed fucalean algae (ii) approximately 3 individuals (~ 10 cm in length) of fucalean algae (*Sargassum* spp.) were crushed and placed inside cloth mesh bags which were attached to grids. Empty mesh bags were a procedural control for the presence of mesh bags in this treatment which did not affect the colonisation of invertebrates to either close (NP-MANOVA: $t = 1.423$, $P > 0.05$) or far (NP-MANOVA: $t = 1.324$, $P > 0.05$) habitats. Bare matrices consisted of a bare plastic mesh grid.

Grids with the vacant holdfast and the matrix grids were 'planted' randomly within the previously fragmented plots so that one cover of matrix ($n = 6$ for each) surrounded the vacant holdfast. All existing individuals of *E. radiata* were either close to or far from the target holdfast (Fig. 6.1). Grids were anchored to the bottom by a metal stake driven into the substratum.

Fauna within the alternate algae (both crushed and intact) were removed by the above-mentioned method before planting/crushing so that reinvasion was not confounded by taxa more commonly associated with the matrix rather than primary habitat (see Malcolm 1997) and to un-confound differences in the treatment of habitat and matrix species in the study. The volume of holdfasts is known to have significant effects on diversity of assemblages (Smith et al. 1996) hence each target holdfast was chosen so that the volumetric measurements of holdfasts (done after the experiment) were not different among samples (ANOVA: $F_{3, 40} = 1.17$, $P > 0.05$).

The experiment was left for a period of three days; re-colonisation of invertebrates to vacant habitats is rapid (within days) and little changes occur in diversity thereafter. Similar experiments using natural and artificial habitats of kelp have reported colonisation and stability of assemblage structure of similar invertebrates within days (Howard 1985, Virnstein & Curran 1986, Edgar 1992, Taylor 1998b, Norderhaug et al. 2002). The target holdfast was sampled by sealing a plastic bag to the substratum around the holdfast, gently levering it off the substratum and quickly enclosing the plastic bag around the holdfast. Each sample was fixed in 10% formalin solution, dissected and the infauna separated through a 0.5 mm sieve. Identification of mobile animals was carried out to the level of family and diversity in each sample was used as a measure of colonisation.

6.3 RESULTS

NP-MANOVA (Anderson 2001) detected a significant interaction between the type of matrix and the distance between habitats on colonisation (the composition of taxa and their relative abundance in vacant holdfasts) (Table 6.1a, Fig 6.2). Post hoc comparisons revealed that the diversity of assemblages in close habitats was different to that in far habitats when the matrix was bare. The addition of alternate algae in the matrix, however, caused this difference between close and far habitats to disappear (Fig. 6.2, Table 6.1b).

Assemblages in habitats in close proximity were more affected by the nature of the matrix than those in habitats situated further apart. Furthermore, there was no difference in diversity of crushed versus intact matrix of fucalean algae (Table 6.1b). Hence the model that the structural characteristics of the plant-matrix are more influential than the chemical nature is rejected.

Table 6.1. (a) Two-way NP-MANOVA (Anderson 2001) testing the relative and interactive effects of the distance between habitats (close vs far) and the matrix separating habitats (bare vs alternate algae vs crushed alternate algae vs control) on the composition and relative abundance of invertebrates. Data were fourth root transformed to provide more a more equal weighting of numerically less dominant and more dominant species, than would be the case with untransformed data. (b) Post hoc comparisons relevant to the hypotheses for the significant interaction term. Not significant (ns): $P > 0.05$, *: $P < 0.05$, **: $P < 0.01$.

(a)NP-MANOVA

Source	df	MS	F	*P*
Proximity	1	128.013	5.219	**
Matrix	3	35.880	1.463	0.087 (ns)
Proximity × Matrix	3	40.560	1.654	*
Residual	40	24.526		

(b) Pairwise comparisons		t	*P*
Proximity			
Bare	Close vs Far	1.824	0.005
Alternate algae	Close vs Far	1.394	0.045
Matrix			
Far	Bare vs Alternate algae	1.056	ns
Close	Bare vs Alternate algae	1.660	0.031
Close	Alternate algae vs Crushed alternate algae	1.270	ns

I found 41 taxa with an average of 10 species and 80 individuals per holdfast. The most frequent and numerous fauna were amphipods and isopods. Surprisingly, ANOVA of the number of taxa (taxonomic richness) detected a greater number of taxa in habitats that were far apart than in those close together (Table 6.2, Fig. 6.3).

Table 6.2. Two way ANOVA testing for differences in the number of taxa in habitats separated by different distances (close vs far) and matrices of (i) alternate algae, (ii) crushed alternate algae, (iii) bare and (iv) control. 'Proximity' and 'Matrix' were treated as fixed factors and orthogonal. Variance values were homogenous at $P > 0.05$ (Cochran's *C*-test). Not significant (ns): $P > 0.05$.

Source of variation	df	MS	F	*P*
Proximity	1	111.021	7.86	0.008
Matrix	3	2.854	0.20	ns
Proximity × Matrix	3	13.243	0.94	ns
Residual	40	14.129		

6.4 DISCUSSION

Few habitats are truly isolated (Weins 1992) and the nature of the matrix between remnant patches of habitat plays an important role in the connectivity of fragmented landscapes (Fahrig & Merriam 1985, Weins et al. 1997, Ricketts 2001). The isolation of habitats-by-distance remains an influential determinant of dispersal among animal populations in fragmented habitats. Yet distance does not act independently of the nature of the matrix within fragmented landscapes. My results suggest that only when the matrix is very different to the primary habitat (e.g. no vegetation), does the distance between habitats exert strong effect on the colonisation of fragmented habitats.

The extent to which the matrix differs from the primary habitat affects the difficulty with which animals disperse across fragmented landscapes (Kotliar & Weins 1990, Weins et al. 1993, Taylor et al. 1993). The current study and other experimental work in marine systems show that decreases in colonisation of fragmented habitats occur when patches are separated by a matrix contrasting with the primary habitat (Holmquist 1998). These results warn that assessment of the connectivity of fragmented landscapes may not be adequate when based on predictions of distance alone; the nature of the matrix must be considered.

An important result was that the chemical nature of the matrix of alternate algae (fucoids) was more important than the structural characteristics. Many authors are aware that the morphology of plants is often correlated with variation in the diversity and abundance of fauna (Taylor & Cole 1994). My results support concerns that the qualitative aspects of plant identity may play a major role in the dynamics of animal populations (i.e. the idiosyncratic hypothesis; Lawton 1994, see Parker et al. 2001). I suggest that there is a need for knowledge of the characteristics of matrix environments (e.g. chemical composition of plant species) as they are likely to be key to understanding connectivity within fragmented landscapes.

Many species are capable of using the matrix as habitat (Laurence 1991, Gascon et al. 1999). In the current study the nature of the matrix was only important when habitats were close together supporting ideas that the matrix may be particularly important when sources of immigrants are close by (Gascon et al. 1999). The nature of the matrix may not be an important factor for invertebrates capable of dispersal over large distances. Surprisingly, assemblages that colonised close habitats separated by a matrix of fucalean algae resembled those that colonised habitats situated further apart (regardless of the type of matrix).

It seems plausible that particular assemblages of invertebrates are more strongly associated with landscapes that are heavily fragmented (primary habitats are far apart) or have alternate vegetation in matrices between habitats. Most of the fauna that colonised vacant holdfasts were crustacean taxa (brooders with adult dispersal) and those that appeared in most replicates of most treatments (common) were small-bodied and compact individuals with large shield like coxae (Lysianassidae, Colomastigidae and Ostracoda). This body shape is notable for its resistance to buffeting from wave action (Yassini et al. 1995) and capacity for dispersal (Franz & Mohammed 1989) which could explain their ability to colonise fragmented habitats regardless of the distance or the intervening matrix.

There is an increasing amount of evidence, at least for invertebrates, that diversity of faunal assemblages is not always suppressed by increasing distance between habitats. Both Gunnill (1982b) and Virnstein & Curran (1986) reported greater abundance of invertebrate taxa in habitats that were dispersed compared to aggregated habitats. Greater volumes of water surrounding dispersed habitats may facilitate colonisation because a greater diversity of invertebrates can resettle from suspension in the water column (Orth et al. 1984, Edgar 1992, Taylor 1998b). It is becoming apparent that the effects of fragmentation are as likely to be positive as they are negative (Lee et al. 2001, Fahrig 2002). The processes affecting dispersal, migration and survival of invertebrate taxa await further testing under field conditions (e.g. Hunt & Scheibling 1997).

Controlled and replicated experimental procedures are necessary to uncover the effects of fragmented landscapes on biodiversity to enabling future models to reflect the reality of natural systems (McGarigal & Cushman 2002). This is extremely difficult because of obvious ethical concerns associated with the manipulation of many components of landscape pattern, especially at scales appropriate to organisms with large ranges of dispersal. While the intention of models of colonisation among fragmented landscapes is to increase the efficiency of management strategies, tests of their predictions in the field are required to audit their outcomes. Given that small animals perceive their landscape at small scales (e.g. Goodsell & Connell 2002), experiments at small scales are often the most plausible. Furthermore they provide useful links between experimental ecology, modeling research and correlative work at larger scales (Weins et al. 1997, Lee et al. 2001).

In conclusion, the distance between remnant habitats on biodiversity was not independent of the nature of the matrix intervening in fragmented landscapes. The nature of the matrix is particularly important when animals disperse small distances between fragmented habitats. This finding suggests that adequate conservation of reserves or remnant areas of vegetation requires recognition of both the distance between primary habitats and the surrounding matrix. Sustainability of biodiversity in fragmented landscapes relies on connectivity among remnant patches and their relative isolation is a product of distance and the nature of the intervening matrix.

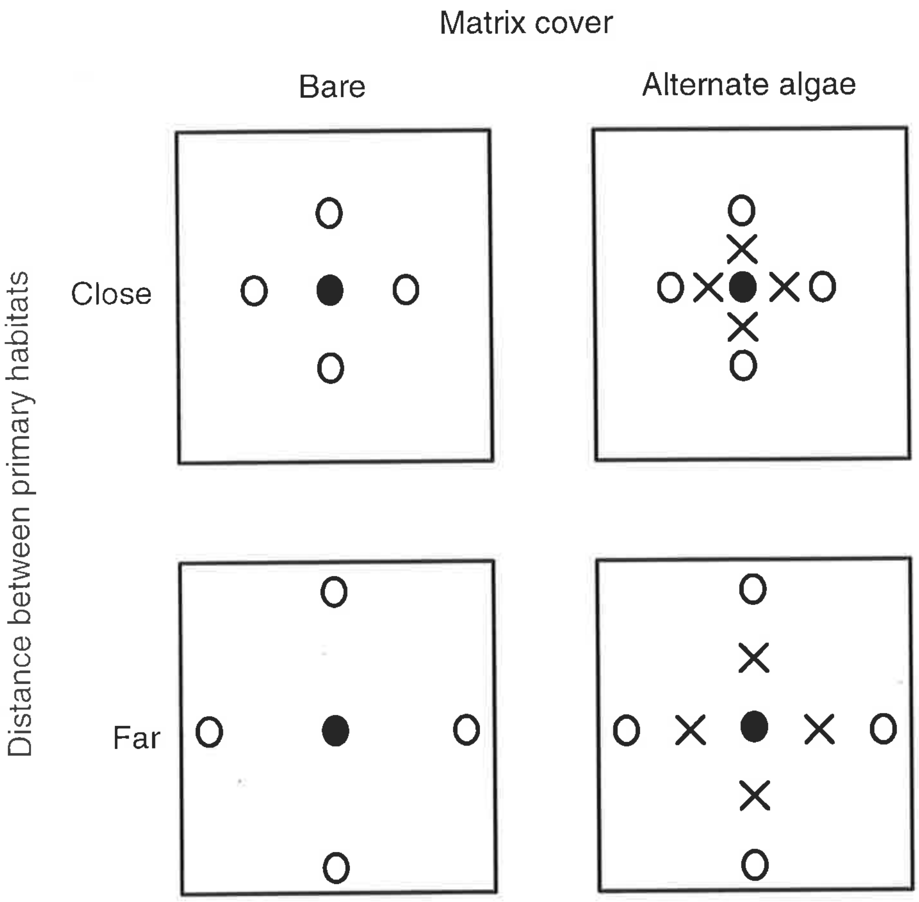


Figure 6.1. Diagram representing the experimental arrays of far and close distances between primary *E. radiata* habitats (○ = holdfasts) with the presence and absence of alternate species of algae (×) in the matrix. Filled circles represent the vacant holdfast that was sampled.

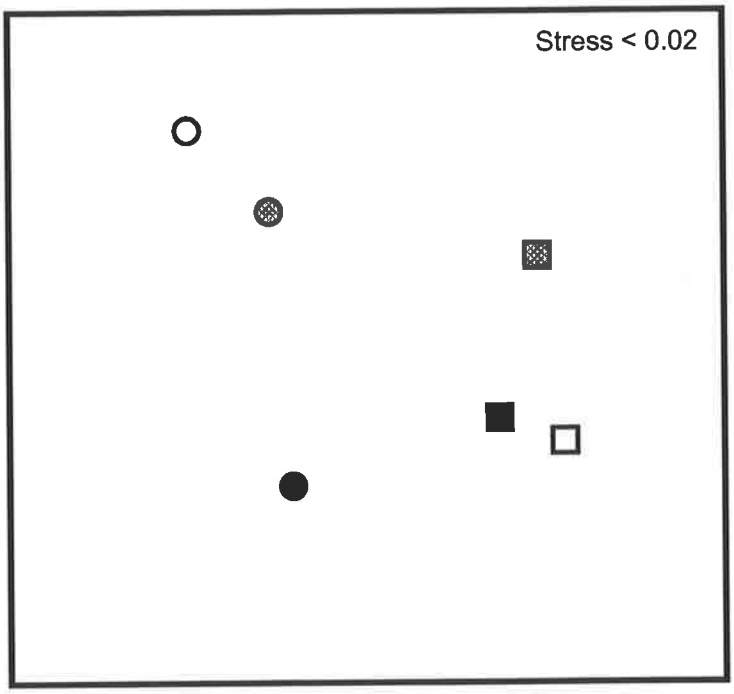


Figure 6.2. nMDS plot of the average composition and relative abundance of taxa from close (circles) and far (squares) habitats with different types of matrix. Open symbols represent samples with bare matrix between suitable habitats, filled symbols represent samples from habitats with a matrix of alternate species of algae, and shaded symbols represent samples with a matrix of crushed alternate algae. Data were fourth root transformed.

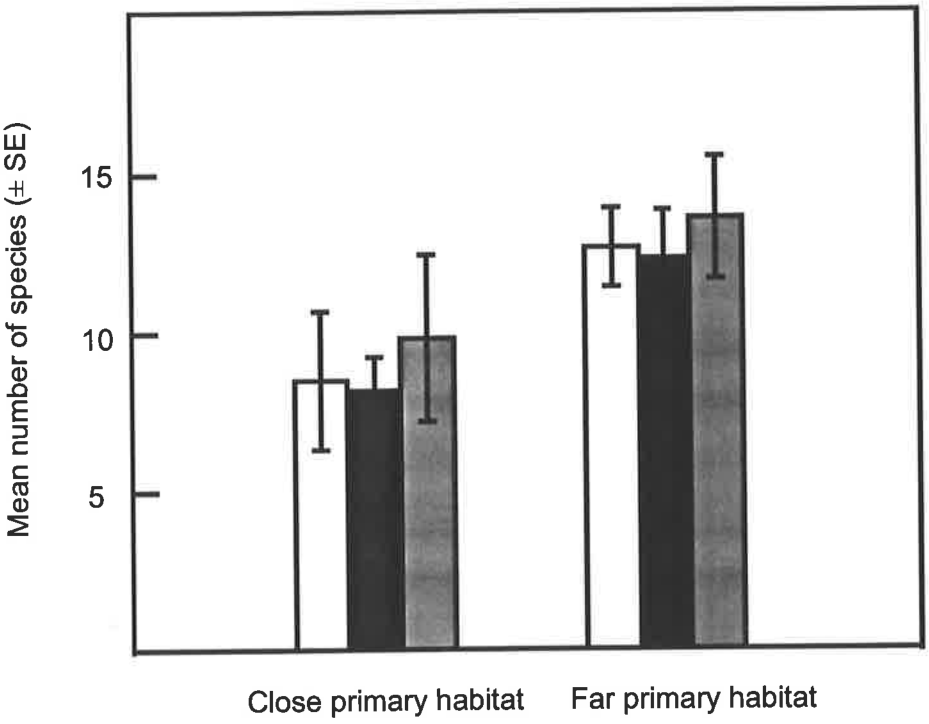


Figure 6.3. Graph showing the number of taxa (taxonomic richness ± SE) in close and far habitats separated by different types of matrix. Open bars represent samples with bare space in the matrix, filled bars represent samples from habitats with a matrix of alternate species of algae and shaded bars represent samples with a matrix of crushed alternate algae.

APPENDIX 4

Total number of taxa colonising holdfasts of *E. radiata* at far and close distances with matrices of fucalean algae or bare rock ($n = 6$).

Proximity of *E. radiata*	**Far**		**Close**	
Matrix	**Algae**	**Bare**	**Algae**	**Bare**
ANNELIDA				
Polychaeta				
Eunicidae spp.	0	0	0	0
Nereididae spp.	12	33	10	10
Maldanidae spp.	0	1	0	0
Phyllodocidae spp.	6	0	0	0
Polynoidae spp.	0	0	0	0
Spionidae spp.	0	0	0	0
Syllidae spp.	14	16	4	1
ARTHROPODA				
Crustacea				
Amphilochidae spp.	0	0	1	1
Amphipoda spp.	0	0	0	0
Ampithoidae spp.	1	0	0	0
Aoridae spp.	16	17	18	7
Anthuridae spp.	0	1	0	0
Apsuedidae spp.	3	4	0	0
Caprellidae spp.	0	0	1	0
Cirolanidae spp.	0	1	7	1
Colomastigidae spp.	35	62	50	13
Corophiidae spp.	3	2	0	0
Cyproididae spp.	0	2	0	0
Eusiridae spp.	4	9	1	3
Gnathiidae spp.	6	2	1	0
Hyalidae spp.	38	34	59	10
Jaeropsidae spp.	5	3	0	3
Liljeborgiidae spp.	0	0	0	0
Limnoridae spp.	11	15	4	9
Lysianassidae spp.	174	186	251	219
Melitidae spp.	2	7	0	4
Mysidae spp.	4	4	0	0
Nebaliidae spp.	0	0	0	0
Paratanaidacea spp.	1	3	2	0
Podoceridae spp.	1	0	0	0
Sphaeromatidae spp.	1	11	1	0
Stenetriidae spp.	1	0	0	0
Tanaidacae spp.	0	2	0	0
Ostracoda				
Ostracoda spp.	62	183	48	46
ECHINODERMATA				
Holothuroidea spp.	1	0	0	0
Ophiuroidea spp.	0	0	0	0

Proximity of *E. radiata*	**Far**		**Close**	
Matrix	**Algae**	**Bare**	**Algae**	**Bare**
MOLLUSCA				
Gastropoda				
Gastropoda spp.	0	2	0	0
Nudibranch spp.	1	0	0	0
Polyplacophora				
Chiton spp.	1	0	0	0
NEMATODA				
Nematoda spp.	10	11	4	0
SIPUNCULA				
Sipuncula spp.	0	0	0	0

Note: Taxa match other lists in this thesis and are based on a reference collection held within the Southern Seas Ecology Laboratories at the University of Adelaide.

CHAPTER SEVEN: GENERAL DISCUSSION

"A unifying goal [of seascape ecology] is an understanding of the processes that create and maintain patchiness at each scale, and the ways in which different organisms respond to this heterogeneity."

- G. P. Jones & N. L. Andrew 1993

GENERAL DISCUSSION

This thesis was designed to investigate the role of disturbance in shaping the composition of macroalgae and the diversity of associated invertebrates on subtidal rocky reefs in temperate Australia. This was done by testing hypotheses derived from a series of models that account for the effects of common disturbance events (i) on habitats of *Ecklonia radiata* (Chapter 2), (ii) on the diversity of associated invertebrates (Chapter 3) and (iii) the consequences of changes in the composition of macroalgae (generated by disturbance) for the diversity of invertebrates (Chapters 4-6). The research was motivated by dearth in our ecological understanding of the effects of disturbance in subtidal, relative to intertidal systems (Underwood & Kennelly1990, Witman & Dayton 2001) and the need for experimental tests of the consequences of disturbance for mobile animals (Sousa 1979b, Jones & Syms 1998, Sousa 2001).

7.1 Disturbance generates small-scale complexity in habitat composition

Subtidal forests of canopy-forming algae are frequently subject to disturbance, mainly from storms and herbivory by urchins and fish (Dayton 1984, Jones & Andrew 1990). The damage created by such disturbances is often localised and has the potential to induce small-scale complexity in the structure of forests of macroalgae (Kennelly 1987a, b, Andrew & Jones 1990). Indeed, research over the last couple of decades has emphasized small-scale variability in patterns of distribution and abundance in Australasian subtidal forests of algae (Kennelly 1987b, Underwood et al. 1991, Kennelly & Underwood 1992, Jones & Andrew 1993, Collings 1996). In this thesis, I determined that localised thinning of canopies of monospecific *E. radiata* can create opportunities for the recruitment of alternate species of algae, via the liberation of space available for establishment in both the canopy and substratum (Chapter 2). Whilst such patches of higher diversity may not persist (see arguments in Connell & Sousa 1983, Petraitis & Latham 1999), it is likely that many asynchronous disturbance events result in stands of mixed algae interspersed within monospecific stands of *E. radiata* (e.g. Turner 1987, Thrush

1991, Sousa 2001); a pattern observed at regional scales (Chapter 4). Our development of models about the ecology of forests of algae, will progress through further understanding of the role of disturbance in generating heterogeneity in the structure of habitat (Jones & Syms 1998, Scheibling 1986, Wernberg-Møller 2002), especially when this is combined with assessment of the consequences of such variability in habitat structure on animal diversity.

7.2 Invertebrate diversity is initially affected by disturbance

One of the main goals of this thesis was to improve our understanding of the consequences of disturbance and subsequent changes in the structure of subtidal habitat for mobile invertebrates. I first assessed whether similar kinds of disturbance, which induced changes in the composition of *E. radiata* habitats (Chapter 2), would also influence the diversity of invertebrates associated with *E. radiata* (Chapter 3). Importantly, small-scale differences in the density of *E. radiata*, prior to disturbance, habitat changed the severity of disturbance experienced by invertebrates. This result further highlights the importance of recognising and incorporating small-scale complexity in the structure of subtidal macroalgae. Not only are different assemblages of invertebrates associated with different configurations of kelp (Chapter 4, 5) but such differences in habitat structure can also alter the response of invertebrates to future disturbance events (Chapter 3, see also Tanner et al. 1996, Fukami 2001).

It is noteworthy that the changes in diversity of invertebrates in response to disturbance did not support the intermediate disturbance hypothesis. Whilst intermediate levels had significant effects on invertebrates, the diversity of assemblages was not highest at intermediate levels (Chapter 3). One of the criticisms of ecology as a science is an adherence to hypotheses without assessment of whether they can adequately predict the dynamics of populations in natural systems (Peters 1991, O'Neill 2001). The intermediate disturbance hypothesis seems to lack a body of experimental evidence demonstrating it as a widespread phenomenon (Mackey & Currie 2000) that justifies the current preoccupation ecologists have with it. It is, however, important to recognise the effect of different degrees of disturbance and variation in the extent of damage caused by disturbance can contribute to variability in the recovery of both sessile and mobile organisms (Airoldi 1998, Underwood 1998, Sousa 2001).

In both Chapter 2 and Chapter 3, I simulated less severe disturbance events that cause localised and partial damage in forests of canopy-forming. "Catastrophic" disturbances causing complete removal of all habitats are often the focus of ecological assessments of the effect of disturbance (Ebeling et al. 1985, Tegner & Dayton 1987, Minchinton et al. 1997, Christie et al. 1998). In Australian forests of *E. radiata*, however, the most regular and persistent agents of disturbance; odacid herbivory and storm action, do not remove whole plants, but rather the fronds or fronds and stipes (Kennelly 1987b, Andrew & Jones 1990). A major outcome of this thesis is an understanding that localised and less severe disturbances can generate significant variability in the structure of forests of *E. radiata* (Chapter 2) (Jones & Andrew 1990, Kennelly 1987b) and importantly, affect the diversity of associated assemblages of animals (Chapter 3).

7.3 Disturbance-driven changes in habitat affect invertebrate diversity

Explaining patterns of animal diversity with regard to the complexity in structure and composition of their habitat has been an area of ecological interest for many decades (Dean & Connell 1987a, b, c, Bell et al. 1991, Kolasa & Pickett 1991, Palmer & Poff 1997). In habitats of seagrass, experimental investigations of the effects of habitat architecture (Hacker & Steneck 1990), composition (Parker et al. 2001) and the spatial arrangements of different types of patches (Bell & Westoby 1986, Irlandi 1994, Bell et al. 2001) on the diversity of mobile invertebrates are substantial. The research in this thesis represents one of the few comprehensive investigations of the role of complexity in composition and configuration of forest of macroalgae (generated by disturbance) on the diversity of associated invertebrates in subtidal systems (but see Edgar 1992, Smith 1996, Taylor 1994, 1998b).

The diversity (composition and relative abundance) of mobile invertebrates was consistently different in stands of mixed algae to stands of monospecific *E. radiata* at local through regional scales across southern Australia (Chapter 4, 5). Small-scale complexity in patterns of composition and abundance of subtidal organisms has been argued to inhibit the progress of general models about the ecology of subtidal forests of algae (Schiel & Foster 1986, Choat & Schiel 1982). Results from Chapter 5, however, provide encouraging evidence that different assemblages of invertebrates are associated with small-scale differences in the composition of algae at broad scales across Australia. Such consistency provides an opportunity to establish whether particular local processes that exclude or facilitate taxa from local areas generate patterns that can be observed at regional scales (Thrush et al. 1997, Wootton 2001). At the very least, it rejects the notion that processes operating at regional scales are obscured by variability at small scales. While historical and regional phenomena may interact with local scale processes (Poore 1994), the results in this thesis suggest that there is potential to infer predictions about associations between the complexity of habitat and diversity of fauna from local-scale manipulative experiments to regions across Australia. Awareness that disturbance can generate small-scale complexity in habitat structure, which is associated with underlying differences in invertebrate assemblages, will improve conceptual models that account for ecological patterns in subtidal forests of algae at large scales (e.g. Chesson 1997, Syms & Jones 2000).

Interestingly predictions that coexistence is enhanced in diverse versus monospecific habitats (MacArthur & MacArthur 1961, Murdoch et al. 1972, Southwood et al. 1979) do not appear a reality for subtidal assemblages of invertebrates inhabiting both hard (Chapter 5) and soft bottom assemblages (Heck & Wetstone 1977, Eggleston et al. 1999). The richness of invertebrate taxa in holdfasts of *E. radiata* was consistently greater in monospecific stands of *E. radiata* than in stands of mixed algae across Australia (Chapter 5). The amount of resources required to sustain high levels of coexistence of invertebrate taxa may not be provided simply by a greater diversity in algae that make up their habitat. To better understand the consequences of variation in the composition of algae, I tested the model that differences in rates of local turnover among individual *E. radiata* account for the observed differences in diversity between mixed-species stands and monospecific stands of *E. radiata* (Chapter 4, 5). The presence of fucalean algae between distant habitats of *E. radiata* (e.g. mixed stands) allowed for greater colonisation of *E. radiata* than a matrix of bare substratum, although only when habitats of *E. radiata* were close to each other (Chapter 6). It seems holdfast fauna rely on refuge that is structurally complex (pebbles, rocks, remnant holdfasts, other species of algae) (Waage-Nieslon et al.

2003) rather than areas of non-complex substratum. Together with the results from Chapters 4 and 5, I suggest that whilst fucalean algae may provide some refuge for holdfast fauna, especially if primary habitats (*E. radiata*) are further apart, they are a less suitable habitat for the invertebrates studied in this research (see also Norderhaug et al. 2002). Hence, the use of measures of habitat diversity *per se* (i.e. number of plant taxa) to predict patterns of invertebrate diversity, may not be appropriate for marine invertebrates, at least those that inhabit holdfasts of *E. radiata*. Rather, aspects of the specific chemical, structural or morphological traits of plants; related to the identity of the plant species that make up their habitat, play a more influential role in structuring invertebrate assemblages (Parker et al. 2001). In the light of weak relationships between habitat and faunal diversity detected in both marine (Parker et al. 2001) and terrestrial systems (Symstad et al. 2000), it would be useful to continue research toward uncovering the processes that structure assemblages in mixed-species versus monospecific subtidal habitats.

The results of this thesis show that colonisation of habitat and local turnover of holdfast invertebrates is affected not only by disturbance (Chapter 3), but by the subsequent changes that can occur in habitat structure as a result of disturbance (Chapter 4, 5, 6). Investigations of the species specific responses of holdfast taxa to disturbance and their life-history characteristics are progressing for the northern hemisphere counterparts of *E. radiata* (e.g. *Laminaria* spp and *Macrocystis* spp) (Jones 1973, Moore 1981, 1985, Norderhaug et al. 2002, Jørgensen & Christie 2003, Waage-Nielsen et al. 2003), and this type of research is critically needed for the southern hemisphere (but see Ojeda & Santelices 1984). Many of the fauna I observed in holdfasts have not been previously described (Walker-Smith pers. comm.) and little is known of their biology or ecology. This thesis has preliminarily identified that disturbance to habitats of *E. radiata*, and subsequent changes in the composition of forests of algae, can significantly affect the diversity of invertebrates. A greater understanding of the effects of disturbance and the processes that shape subtidal hard-bottom assemblages (e.g. Hunt & Scheibling 1997) would benefit from research directed toward understanding the biology and life history of holdfast fauna (e.g. Moore 1981, Thiel & Vásquez 2000).

The maintenance of biodiversity is a fundamental scientific, political and social concern, and ecologists would do well to include assemblages of invertebrates in their investigations of patterns of diversity and the processes that drive them. Phyletic diversity, in contrast to species diversity, implies a greater variety of fundamentally different life history strategies and as most phyla occur in the coastal zone, subtidal systems can be considered the most phyletically diverse realm on earth (Ray 1991). As evident from the research in this thesis, holdfast fauna have great potential to be used as model systems for testing the reality of predictions about the consequences of habitat loss and its modification (disturbance) on animal diversity (Jones 1973, Moore 1973a, b, Sheppard et al. 1980). Such systems are particularly useful where logistics and ethics prevent experimental simulation of disturbance on large scales (e.g. Collinge & Forman 1985,Virnstein & Curran 1986, Weins & Milne 1989, Weins et al. 1997, Eggleston et al. 1999, McGarigal & Cushman 2002). That said, "most biodiversity is, and much of any such loss will be, invertebrates" (New 1993) and considering that invertebrates make up a large proportion of marine diversity (Norse 1995) assessing the impacts of disturbance on these assemblages is necessary in its own right.

7.4 CONCLUSION

The importance of disturbance-induced complexity in the structure of habitats for the ecology of natural systems is well recognised (Weins 1976, Pickett & White 1985a, Bell et al. 1991, Jones & Andrew 1993, Palmer et al. 1997). In southern Australia, significant variability exists in the configuration, density and composition of macroalgae (e.g. Underwood et al. 1991, Andrew & Jones 1990, Kennelly 1987a, b, Chapter 4). This thesis demonstrates that differences in the composition of algae can be generated by localised disturbance (Chapter 2), which can manifest as extensive small-scale complexity across Australia (Chapter 4). Such complexity has significant consequences for the diversity of invertebrates associated with holdfasts of *E. radiata* in ways predictable across broad scales (Chapter 5) that may be caused by changes in the availability of suitable refugia (Chapter 6), notwithstanding the mediating effect of differences in habitat configuration on the effect of disturbance for mobile animals (Chapter 3). Local or small-scale complexity in the composition of forests of algae increases the magnitude of variability inherent within marine systems (e.g. Syms & Jones 2000). This realisation is important because individual patches within a habitat may be the 'unit' within which key biotic interactions act to structure assemblages of animals (Southwood 1977) and in marine environments, interactions among patches of different types are likely (Syms & Jones 2000). Consequently, recognition that localised disturbances can generate variability in the structure of subtidal algae, which is associated with variation in animal diversity, combined with investigations of the dynamics among different patches, will enable ecologists to better understand the ecology and dynamics of subtidal forests.

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