PATTERNS AND RESPONSES OF BENTHOS TO HABITAT
HETEROGENEITY IN ALGAL FORESTS OF
AUSTRALASIA AND ANTARCTICA

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Cover photo: Thallus of the canopy-forming alga *Ecklonia radiata* (Laminariales) associated with an understorey assemblage monopolised by encrusting coralline algae (photo by the author).
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Habitat heterogeneity is a pervasive feature of natural systems that has profound consequences for the distribution and abundance of taxa across landscapes. Across >2000 km of temperate Australian coastline, the scales of patchiness within subtidal habitat created by canopy-forming algae (*Ecklonia radiata* and species of Fucales) were quantified. Three major habitats were identified: i) monospecific canopies formed by the laminarian alga *Ecklonia radiata*, (ii) mixed-species canopies containing *E. radiata* interspersed with canopy-forming species of Fucales (e.g. *Cystophora* spp., *Sargassum* spp.), and (iii) gaps among canopies of algae. The extent of individual patches of habitat generally varied over scales of metres (i.e. 1-10 m). The consequences of such heterogeneity for the structure of understorey assemblages (algae and sessile invertebrates) were tested across >5000 km of temperate Australasian coastline (Western Australia to New Zealand). Large and predictable differences in the structure of understorey assemblages were frequently observed among all three habitats, with the magnitude and direction of differences often consistent from local (km) to regional scales (1000's km). A key result was that patterns varied among regions sampled (i.e. western Australia = southern Australia ≠ eastern Australia ≠ New Zealand).

Models accounting for the observed differences in the structure of understorey assemblages among habitats were experimentally assessed. The experimental assembly of understorey algae and invertebrates to rocky substrata among all three habitats was consistent with patterns observed on natural coasts, highlighting how canopies of algae can act as a filter to limit which subsets of species from the locally available pool are able to assemble beneath them. Abrasion of the substratum by algal canopies had large negative effects on the abundance of articulated coralline algae and turfs of filamentous algae, which was consistent with natural patterns in their abundance (i.e. sparse beneath canopies and extensive within gaps). Moreover, monospecific canopies exerted a greater negative effect on articulated corallines than mixed-species canopies, which was also consistent with natural patterns.
The experimental removal of algal canopies caused understorey encrusting coralline algae to bleach from red/pink to white, which was associated with a decline in their photosynthetic activity. An independent test demonstrated that shade provided by the canopy appears key to preventing bleaching and concomitant declines in photosynthetic activity of encrusting corallines. Knowledge of such responses of encrusting coralline to canopy-loss was used to predict patterns and responses on a polar coast (Antarctica), where such knowledge did not exist. Remarkably similar results to those observed on tropical and temperate coasts were obtained from Antarctica, suggesting the response of encrusting corallines to canopy-loss may have predictive properties across large distances and environmental gradients (at least temperate-polar).

In sum, this thesis provides a broad-scale perspective of the role of habitat heterogeneity in shaping and maintaining the distribution and abundance of understorey taxa within subtidal forests of canopy-forming algae; vegetation that is widely considered as ‘key’ to shaping the ecology of much of the world’s rocky coastline. This thesis also provides a clear demonstration of how knowledge of nested spatial patterns, such as those quantified across temperate Australia, can increase confidence in predictions of the spatial extent of similarities, and the scales at which differences occur, as well as provide fresh insight when relating patterns and processes across space.
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- words of encouragement from Sean Connell (Ph. D. advisor)

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A forest of the perennial laminarian alga *Ecklonia radiata*, growing on subtidal rocky coast in South Australia (photo by the author).
CHAPTER 1

GENERAL INTRODUCTION

Variation in the configuration and composition of habitat (often termed ‘habitat heterogeneity’) is a pervasive feature of natural systems that was recognised by plant and animal biogeographers during the early 19th-century (McIntosh 1991; Wiens 2000). In recent times, knowledge of the causes of habitat heterogeneity and its consequences for biotic communities was sacrificed for many years (~1950’s – 1970’s) in favour of searching for unifying ecological theories through an understanding of population dynamics within spatially homogeneous and temporally stable habitats (Wiens 2000). As a consequence, the role of natural heterogeneity in community ecology remained largely unappreciated until the pioneering work of MacArthur and Levins (1964) and Levin and Paine (1974) laid much of the intellectual and theoretical foundation upon which our current ecological understanding of heterogeneity is based.

Over the past 35 years, considerable progress has been made in understanding the role of temporal and spatial heterogeneity of habitat for the origin and maintenance of patterns in the distribution and abundance organisms (e.g. Pickett and White 1985; Levin et al. 1993; Tilman and Kareiva 1997; Hutchings et al. 2000). Variation of the physical, chemical, and biological properties of habitats is frequently associated with variation in the distribution and abundance of organisms that depend on particular resources. Intrinsic to this observation is that the conditions imposed by a particular habitat are favourable for some taxa, but are unfavourable for others (e.g. Jones et al. 1997). Moreover, conditions that are favourable to an organism at a certain life-history stage may be unfavourable at another (e.g. larvae vs adult). Consequently, habitat heterogeneity often plays a critical role in ecological models of species interactions and community dynamics (Peterson and Pickett 2000; Syms and Jones 2000; Goodsell and Connell 2002). An emerging realisation is that patterns associated with heterogeneity may be observed across multiple spatial scales, such that patterns at local-scales (e.g. km) can be repeated with great fidelity over much larger distances (e.g. 1000’s km; Callaway et al. 2002). Even so, understanding the
scales at which habitat heterogeneity manifests (i.e. the ‘patchiness’ of a habitat) underpins decisions about ecologically meaningful scales for tests about natural heterogeneity.

Many of the world’s habitats exist because of the presence of particular organisms. Various terms such as ‘ecosystem engineers’ (Jones et al. 1994), ‘foundation species’ (Dayton 1975a; Dayton et al. 1984), and ‘keystone species’ (Paine 1969; Estes and Palmisano 1974; Wilson and Agnew 1992), familiar examples include trees and shrubs, salt marsh plants, reef-building corals, mangroves, seagrasses, and kelps. Habitat-formers can have large effects on the distribution and abundance of other organisms through direct (e.g. provision of food) and indirect pathways (e.g. amelioration of physically harsh conditions). While such effects can be positive, negative, or neutral (Callaway and Walker 1997; Jones et al. 1997; Bertness et al. 1999; Stachowicz 2001), they can also change direction under particular environmental conditions (e.g. negative interactions become positive in physically stressful environments; Bertness and Leonard 1997; Callaway and Walker 1997; Bertness and Ewanchuk 2002). In many environments, it is now clear that strong positive and negative associations among organisms often exist because habitat-formers facilitate the presence of specific sets of taxa, while excluding others (Jones et al. 1997; Bruno and Bertness 2001). As a result, heterogeneity in the distribution and abundance of habitat-formers has large effects on the distribution and abundance of associated species.

Canopy-forming vegetation (e.g. tropical and temperate rain forests, oak woodlands, alpine forests, mangroves, kelp forests) create widespread habitats in terrestrial and aquatic environments throughout much of the world. Accordingly, forests of algae constitute one of the most extensive, conspicuous, and highly productive of all marine habitats at temperate latitudes (Mann 1973; Dayton 1985a; Schiel and Foster 1986; Witman and Dayton 2001). Primarily comprising species belonging to the Phaeophyta (‘brown algae’), algal forests often monopolise space on rocky coasts, ranging from the intertidal to depths of ~40 m. Subtidally, algal forests can grow large enough to form floating canopies at the surface of the ocean (e.g. the largest marine alga, *Macrocystis pyrifera*, which grows up to 45 m long), but more typically form sub-surface canopies reaching ~0.5 – 3 m in height (e.g. *Ecklonia* spp.,
Laminaria spp., Pterygophora californica). While contributing significantly to global primary production (Mann 1973), algal forests also facilitate considerable quantities of secondary production by providing structurally complex habitat for phyletically diverse assemblages of flora and fauna (Duggins et al. 1989; Steneck et al. 2002; Graham 2004).

The persistence of algal forests is dependent on complex interactions among factors that influence the dispersal and recruitment of spores, growth and reproduction of adults, and ultimately, deforestation (Estes et al. 1978; Duggins 1983; Chapman 1984; Dayton et al. 1984; Santelices 1990; Vadas et al. 1992; Kendrick and Walker 1994; Johnson and Brawley 1998). Of key significance are factors that influence deforestation (e.g. storms, herbivores, harvesting), as well as spatial and temporal variation in the recruitment and survival of spores (Dayton 1985a; Schiel and Foster 1986; Steneck et al. 2002). As a consequence, forests of algae are widely thought of as heterogeneous systems typified by patchiness in the presence and composition of canopies (Duggins 1983; Dayton et al. 1984; Harrold and Reed 1985; Schiel and Foster 1986; Chapman and Johnson 1990; Dayton et al. 1992; Konar and Estes 2003; Goodsell et al. 2004). Despite widespread acceptance of this concept, the spatial scales over which such heterogeneity manifests have rarely been quantified (but see Underwood et al. 1991 and Dayton et al. 1992: Table 2).

Forests of algae form strong positive and negative associations with many species of flora and fauna (Steneck 1986; Witman and Dayton 2001; Graham 2004) that are largely predictable across space (Fowler-Walker and Connell 2002). Accordingly, heterogeneity in the structure of algal forests has large effects on the distribution and abundance of associated organisms (Dayton 1975b; Goodsell et al. 2004; Graham 2004). One of the most striking and frequently cited patterns from temperate rocky coasts around the world is that the type and abundance of benthic algae and sessile invertebrates occurring beneath canopies of algae (i.e. as ‘understorey’) differs greatly from that observed within gaps among canopies (e.g. north-west Atlantic: Chapman and Johnson 1990, Alaska: Dayton 1975b, Italy: Benedetti-Cecchi et al. 2001; Bulleri et al. 2002, United Kingdom: Hawkins and Harkin 1985, California: Reed and Foster 1984; Edwards 1998, Australia: Kennelly 1987a; Fowler-Walker and Connell 2002, Chile: Ojeda and Santelices 1984). While extensive covers of
algae with prostrate forms of growth (e.g. encrusting coralline algae) are frequently associated with canopies (Steneck 1986; Witman and Dayton 2001; Connell 2003a), such taxa may coexist with erect species of algae, such as articulated corallines (e.g. Dayton et al. 1984; Santelices and Ojeda 1984a; Kennelly 1987a; Schiel 1988; Clarke 2004). In other cases, erect algae that form ‘turfs’ (sensu Hay 1981) are sparse beneath canopies but are primarily associated with gaps (e.g. Hawkins and Harkin 1985; Figueiredo et al. 1996; Benedetti-Cecchi et al. 2001; Melville and Connell 2001; Bulleri et al. 2002). Irrespective of their nature, canopy-undersorey associations can be repeated with great consistency across scales of kilometres to 1000’s km (Fowler-Walker and Connell 2002).

An emerging realisation is that large ecological differences may not just occur between the presence-or-absence of canopies, but also among canopies of varying composition (Dayton et al. 1984; Goodsell et al. 2004). Broadly, canopies of algae may be described as ‘monospecific’ or ‘mixed-species’ (Shepherd and Womersley 1970; Dayton et al. 1984; Schiel 1988; Chapman and Johnson 1990; Dayton et al. 1992; Emmerson and Collings 1998; Goodsell et al. 2004; Valentine and Johnson 2004), yet surprisingly few studies have tested for ecological differences between these two types of habitat (in contrast to our understanding of terrestrial forests, e.g. Cannell et al. 1992). Qualitative (e.g. Shepherd and Womersley 1970), and some quantitative evidence points to ecological differences between monospecific and mixed-species canopies of algae (e.g. abundance of associated algae: Dayton et al. 1984, diversity of holdfast fauna: Goodsell et al. 2004), but such information is remarkably rare. Where differences do exist, partitioning observations between these two types of habitat may reduce seemingly ‘unexplained’ variation and therefore enhance predictive power in a system where enormous spatial variability is often emphasised (e.g. Wernberg et al. 2003).

Conspicuous positive and negative effects of algal canopies on understorey taxa have been observed through experimental manipulations of canopies (e.g. Dayton 1975b; Reed and Foster 1984; Benedetti-Cecchi and Cinelli 1992; Kennelly and Underwood 1993; Bertness et al. 1999). Where canopies are cleared, the structure of understorey assemblages typically becomes similar to that observed within gaps (Ojeda and Santelices 1984; Edwards 1998; Benedetti-Cecchi et al. 2001). Likewise, when
canopies are added to gaps, assemblages become similar to those observed beneath natural canopies (Melville and Connell 2001). Responses of understorey to the presence-or-absence of algal canopies can occur quickly (within weeks: Ojeda and Santelices 1984; Melville and Connell 2001) and may persist for years (Kennelly and Underwood 1993; Benedetti-Cecchi et al. 2001; Edwards 2004), potentially inhibiting a reversal to the former assemblage (i.e. ‘positive-feedback switches’ sensu Wilson and Agnew 1992, also see Kennelly 1987b). Experimental manipulations of the presence-or-absence of canopy-formers have clearly demonstrated that canopies of algae act to facilitate and exclude taxa from the understorey. While such outcomes are widely recognised, knowledge of the specific mechanisms driving such effects is limited.

Positive and negative effects of algal canopies on understorey taxa appear primarily caused by the modification of various physical properties of the local environment by canopy-formers (e.g. Bertness et al. 1999), which creates vastly different physical conditions to those experienced where canopies are absent (e.g. within gaps). Most notably, the intensity of light is greatly reduced by canopies, with intensities at the substratum typically only 1 – 10 % of that sampled within gaps (Reed and Foster 1984; Kennelly 1989; Connell 2003a; Clark et al. 2004). The effects of shade provided by canopies on understorey have been most widely tested, and appear to have strong effects on understorey (particularly organisms with photosynthetic obligations, i.e. algae) that are consistent with the experimental provision of shade (e.g. Kennelly 1989; Duggins et al. 1990; Connell 2003a). Algal forests can also reduce water flow (Jackson and Winant 1983; Duggins and Eckman 1994), and concomitantly increase rates of sediment deposition and possibly accumulation beneath canopies (Eckman et al. 1989; Connell 2003b). Reduced water flow may contribute towards differences in understorey composition by affecting the dispersal and delivery of spores to suitable understorey habitat (Santelices 1990). Additionally, enhanced sedimentation appears to favour taxa that tolerate burial (e.g. sediment-trapping algae that form ‘turfs’; Stewart 1989; Airoldi 1998, 2003), but excludes taxa susceptible to such disturbance (e.g. prostrate filter-feeding invertebrates: Irving and Connell 2002; Airoldi 2003). A direct effect of canopies on understorey is caused by the action of the laminae of canopy-formers ‘sweeping’ over the substratum (known as ‘abrasion’ or ‘sour’) (Velimirov and Griffiths 1979;
Morphological differences among species of canopy-formers mean that not all canopies abrade the substratum (e.g. erect algae with stipes that exceed the length of their lamian; Reed and Foster 1984). Where abrasion occurs, however, it can have strong negative effects on understorey algae (Cheroske et al. 2000), sessile invertebrates (Jenkins et al. 1999; Leonard 1999; Connell 2003b), and mobile herbivores (e.g. urchins; Konar and Estes 2003).

Recent studies have identified synergistic effects of factors modified by canopies of algae in the assembly and maintenance of benthic assemblages (e.g. Bertness et al. 1999; Irving and Connell 2002; Connell 2005). Where positive and negative forces interact, one factor can overwhelm the influence of the other to produce a net effect (e.g. positive effects of shade are offset by negative effects of abrasion to produce a net negative effect on the recruitment of invertebrates beneath canopies; Connell 2003b). Such knowledge provides a more comprehensive account of the specific mechanisms modified by canopies of algae that act to facilitate and exclude species as understorey.

It is important to observe that much of our understanding of patterns and processes within algal forests is based on research done at local scales (i.e. km), often with little or no spatial replication. Comparisons among these local-scale studies often reveal substantial variability in the magnitude, and sometimes direction, of observed patterns and effects (e.g. Dayton et al. 1984; Santelices and Ojeda 1984a; Dayton 1985b; Schiel and Foster 1986; Kennelly and Underwood 1992; Foster and Van Blaricom 2001). While comparing among studies can be useful for assessing generality (Underwood and Denley 1984; Gurevitch et al. 1992), differences among local-scale studies have been used to suggest that overwhelming variation occurs at local scales (i.e. from site to site), which reinforces the idea that few spatial generalisations are possible (Foster and Schiel 1988; Foster 1990; Kennelly and Underwood 1992). Such conclusions may be premature because a lack of replicated sites makes it difficult to distinguish true differences in hypothesised patterns and effects from inherent spatial variability within, let alone among, broad sections of coastline. Indeed, an alternate explanation is that inconsistencies among local-scale comparisons actually reflect patterns that emerge at broader scales, whereby the
current set of local-scale observations effectively represent a spatial sub-sample of these broad patterns. To properly assess generality within and among biogeographic regions, both Foster (1990) and Underwood and Kennelly (1990) advocated using multiple sites that span the range of regions of interest, providing ‘within-region’ estimates of spatial variability. Noticeably, studies that have adopted this approach have often detected considerable consistency (i.e. generality) of pattern among sites within defined regions (e.g. Choat and Schiel 1982; Kennelly and Underwood 1993; Estes and Duggins 1995; Fowler-Walker and Connell 2002).

The search for generality and predictability in nature is a perennially topical and unifying theme in contemporary ecology (Dayton 1984; Underwood and Denley 1984; Underwood and Petraitis 1993; Beck 1997; Lawton 1999; Tilman 1999), and is of increasing relevance given our expanding knowledge of large-scale impacts of human activities and global change (Vitousek et al. 1997; Walther et al. 2002). It is recognised, however, that research efforts in ecology often emphasise the search for new details in the description and explanation of local variation (Underwood and Petraitis 1993; Underwood et al. 2000), which may increase confidence in an understanding of local-scale complexity, but contribute little towards the development of ecological generality (Peters 1991; Keddy 2001). Spatial and temporal consistency of patterns and responses gives weight to arguments that it may be possible to scale up knowledge from small-scale ecological experiments to large-scale natural communities (Thrush et al. 1997), and underpins insightful discussion about the relative importance of local vs regional scale processes (e.g. Huston 1999). In a notoriously heterogeneous world, such outcomes provide encouragement for those searching for generality and predictability in nature; an endeavour that is often judged as one of the more progressive avenues of ecological inquiry (Peters 1991).

This thesis provides a quantitative understanding of canopy-understorey associations and interactions within forests of algae on subtidal rocky coasts. Using a combination of sampling (from local to broad scales) and manipulative experiments (local scales), I present research addressing four main objectives:
1) Identify the scales of habitat heterogeneity (monospecific canopies vs mixed-species canopies vs gaps) within subtidal forests of canopy-forming algae (Chapter 2)

2) Test for (i) consequences of such heterogeneity for associated understorey organisms (algae and sessile invertebrates), and (ii) the spatial consistency of these effects (Chapters 3 and 4)

3) Identify mechanisms driving positive and negative effects of canopies on understorey taxa (Chapters 5 and 6)

4) Assess the generality of positive effects of canopies on understorey taxa with an independent experimental test on a rarely-studied coastline (Antarctica) (Chapter 7)

The research presented herein was done subtidally in the productive waters of the vast Southern Ocean, comprising the temperate coastlines of Australia (primarily) and New Zealand, and the polar coastline of Antarctica.

Comparable to the majority of temperate coastlines around the world, the subtidal rocky coasts of temperate Australia support widespread forests of canopy-forming algae that provide habitat for diverse communities of flora and fauna. While forests of the giant kelp, *M. pyrifera*, occur in the southern-most locations (e.g. Tasmania), most canopy-forming algae in temperate Australia form shorter canopies (0.3 – 2 m in height) below the surface of the water. These canopies primarily comprise species from the orders Fucales (61 species, of which 51 are endemic) and Laminariales (4 species) (Womersley 1987). Of these canopy-formers, a laminarian alga, *Ecklonia radiata* (C. Agardh) J. Agardh, frequently occurs in such great abundance throughout temperate Australia (as well as New Zealand and South Africa) as to be the species by which researchers typically classify Australia’s algal forests (e.g. ‘*Ecklonia* forest’; Goodsell et al. 2004).

Despite the ubiquity of *E. radiata*, algal forests of temperate Australia exhibit considerable structural heterogeneity, typified by patchiness in the presence and composition of algal canopies (e.g. Underwood et al. 1991; Goodsell et al. 2004).
E. radiata can form dense monospecific stands, but also exists in mixed-species aggregations with many canopy-forming species of Fucales (e.g. Cystophora spp., Sargassum spp., Scytotalia dorycarpa, etc.) (Shepherd and Womersley 1970; May and Larkum 1981; Goodsell et al. 2004). Additionally, canopy-forming fucoids can form dense canopies that do not include E. radiata. Regardless of their composition, established canopies are frequently punctuated by gaps, where several canopy-forming individuals have been removed by disturbances such as storms (Kennelly 1987a) and herbivores (Andrew and Jones 1990). The sizes of such gaps are known to vary between 0.5 – 60 m², but are typically < 10 m² (Kennelly 1987a). Although the heterogeneous structure of Australian algal forests is widely recognised, few attempts have been made to formally quantify the spatial scales of such patchiness (but see Kennelly 1987a; Underwood et al. 1991).

Consistent with globally-observed patterns, Australian algal forests are associated with assemblages of understorey organisms that differ greatly from those observed within gaps among canopies (Kennelly 1987a; Melville and Connell 2001; Fowler-Walker and Connell 2002; Kendrick et al. 2004). On the eastern coastline (New South Wales), where much of our ecological understanding of Australian algal forests is based, encrusting coralline algae and several types of erect algae (e.g. articulated corallines) often occur beneath canopies of E. radiata (Kennelly 1987a; Kennelly and Underwood 1992). Where canopies are absent, intense grazing pressure by abundant herbivores (e.g. the urchin Centrostephanus rodgersii) maintains extensive covers of encrusting coralline algae and sparse covers of erect algae to create habitat known as ‘urchin barrens’ (Fletcher 1987; Andrew 1993). In other regions (e.g. western and southern Australia), these associations appear reversed to the eastern coast (i.e. erect algae in gaps and encrusting algae beneath E. radiata), which is associated with much lower densities of herbivores capable of maintaining sparse covers of erect algae (Fowler-Walker and Connell 2002; Vanderklift and Kendrick 2004). Qualitative observations also suggest that differences occur in the composition of understorey between monospecific canopies of E. radiata and mixed-species canopies (E. radiata with Fucales) (Shepherd and Womersley 1970), but there are almost no quantitative descriptions of pattern or tests of particular mechanisms.
Experimental manipulations of Australian canopies have demonstrated their strong positive and negative effects on understorey (Kennelly 1987a, c; Kennelly and Underwood 1993; Melville and Connell 2001; Valentine and Johnson 2003), but there remain few quantitative tests of specific mechanisms. As suggested above, grazing by urchins appears important in maintaining rocky surfaces free of erect algae in eastern Australia (Fletcher 1987; Andrew 1993), while shade provided by canopies of *E. radiata* maintains understorey assemblages within forests (Kennelly 1989). Interestingly, Kennelly (1989) did not detect strong effects of abrasion by *E. radiata* on understorey taxa, while Connell (2003b), working in South Australia, observed large negative effects of abrasion that offset the positive effects of shade on the recruitment of sessile invertebrates. Connell has also demonstrated strong effects of shade beneath canopies (explaining ~ 50% of the variation in understorey composition; Connell 2003a), which appears to form a synergy with sedimentation that causes an early divergence in the assembly and subsequent maintenance of understorey assemblages (Connell 2005). In Western Australia, Toohey et al. (2004) also observed strong effects of shade on understorey algae.

Inconsistent results among local-scale tests of patterns and the effects of specific mechanisms between eastern vs western and southern Australia could be used to promote the idea that enormous local-scale (site to site) variation exists and that few spatial generalisations are possible (Kennelly and Underwood 1992). Discordant with this model, however, are observed spatial consistencies of pattern within regions (Kennelly and Underwood 1993), as well as consistent differences among regions (Fowler-Walker and Connell 2002). Such observations are encouraging because they help to reconcile apparent conflicts among locally-observed patterns (e.g. Connell 2003b vs Kennelly 1989), while usefully identifying generalities contingent on recognised spatial limits. Most importantly, such knowledge points to very real differences in the ecology of algal forests among large regions of temperate Australia.
Notes on chapter style

Each chapter of this thesis that presents original data (Chapters 2 – 7) has been written in a style suitable for publication in a scientific journal. Consequently, each chapter can be read as both as an individual contribution to knowledge, and as part of a collective that makes a more substantial contribution. Wherever possible, I have tried to preserve a logical progression of ideas as one advances through the chapters.

Each chapter is preceded by a preamble that briefly describes the content of the chapter, presents information on the publication status of the chapter at the time of thesis submission (where applicable), and describes the contributions of all co-authors to the research therein (signed and dated by each co-author).

All literature cited in this thesis is displayed in a separate section at the end of the thesis (not at the end of each chapter).
Heterogeneity of habitat within subtidal forests of algae on Australia’s temperate coasts: monospecific canopies of *Ecklonia radiata* (A), mixed-species canopies comprising *Ecklonia radiata* and species of Fucales (*Sargassum* spp.) (B), and gaps among canopies of algae (C) (photos by the author).
“In a very real sense, ‘heterogeneity’ has become the ecologist’s mantra.”

J. A. Wiens, 2000

The Ecological Consequences of Environmental Heterogeneity, p.11
Chapter 2: Preamble

Chapter 2 presents a quantitative test of the spatial scale of habitat heterogeneity within subtidal forests of canopy-forming algae on Australia's temperate coasts. Sampling was done at multiple spatial scales across > 2000 km of coastline (western Australia to southern Australia) to understand the spatial generality of locally observed patterns, and to provide a broad-scale perspective on heterogeneity within these extensive habitats.

I was responsible for the analysis and interpretation of the data presented in this chapter. The majority of data were sampled by Sean D. Connell and Bronwyn M. Gillanders (University of Adelaide), who also provided advice on data interpretation and chapter content.
CHAPTER 2

SCALES OF PATCHINESS WITHIN FORESTS OF CANOPY-FORMING ALGAE IN TEMPERATE AUSTRALIA

2.1 ABSTRACT
Identifying scales of patchiness among habitats provides the logical starting position from which to propose tests about natural heterogeneity. Across > 2000 km of temperate Australian coastline, the frequency and size (linear extent) of patches of habitat were quantified within subtidal forests of canopy-forming algae. Three types of habitat were identified: (i) monospecific canopies of Ecklonia radiata, (ii) canopies comprising *E. radiata* mixed with canopy-forming species of Fucales, and (iii) gaps among canopies of algae. The heterogenous structure of algal forests was evident over distances of ≤ 100 m. Individual patches of habitat were frequently 10 m or less in size, indicating that habitat mosaics within forests of canopy-forming algae generally vary at the scale of metres. Of the three habitats identified, patches of *E. radiata* mixed with Fucales occurred more frequently and were more extensive than either monospecific patches of *E. radiata*, or gaps among canopies. This result occurred at all spatial scales at which sampling was done (sites 1-10 km apart, locations 100’s km apart, and regions 1000’s km apart). Additionally, the mean sizes of patches observed in Australia were remarkably similar to those sampled on neighbouring (New Zealand) and distant coasts (California and Antarctica), even though the algal forests among these regions vary in species composition. Most importantly, establishing the scales of spatial variability (patchiness) within forests of canopy-forming algae provides a quantitative basis of ecologically relevant scales for tests of the processes that maintain or disrupt these widespread habitats.

2.2 INTRODUCTION
Variation in the configuration and composition of habitat (often termed ‘habitat heterogeneity’) is an inherent feature of natural systems that has been recognized since early 19th-century studies of biogeography (McIntosh 1991). For several years (~1950’s – 1970’s), a stylised search for unifying theories in community ecology, often emphasising equilibrium dynamics and a ‘balance of nature’, made research of
spatially homogeneous and temporally stable habitats philosophically and practically appealing (Wiens 2000). As a consequence, the role of natural heterogeneity in community ecology was largely ignored until pioneering work of MacArthur and Levins (1964) and Levin and Paine (1974), and many authors since (e.g. Pickett and White 1985; Hutchings et al. 2000), demonstrated heterogeneity of habitat as key to maintaining patterns of diversity and abundance across multiple spatial and temporal scales.

There can be no doubt that heterogeneity of habitat, be it physical, chemical or biological, has large effects on the distribution and abundance of organisms associated with particular habitats or environmental conditions (e.g. Peterson and Pickett 2000; Syms and Jones 2000; Goodsell and Connell 2002). Moreover, associations observed at local scales (i.e. km) can be sufficiently strong and repeated with great fidelity as to be observable across larger distances (i.e. 1000’s km) (e.g. Callaway et al. 2002; Chapter 3). Even so, understanding the scales of spatial heterogeneity in habitat configuration (i.e. ‘patchiness’) is key to identifying the appropriate scales at which observations and experimental tests are ecologically relevant.

Extensive forests of canopy-forming algae (e.g. kelps) often dominate space on subtidal rocky coasts in temperate regions (Dayton 1985a). These productive and structurally complex habitats are widely recognised as comprising a mosaic of different types of patch (e.g. monospecific canopies, mixed-species canopies, gaps among canopies) (Duggins 1983; Dayton et al. 1984; Harrold and Reed 1985; Schiel and Foster 1986; Chapman and Johnson 1990; Konar and Estes 2003; Goodsell et al. 2004). An understanding of the origin and maintenance of such heterogeneity has come from studies testing hypotheses about the persistence and maintenance of algal canopies (e.g. Dayton 1975b; Dayton et al. 1984; Schiel 1988; Dayton et al. 1992; Konar and Estes 2003; Edwards 2004). Factors such as deforestation through natural (herbivores, storms) and anthropogenic sources (harvesting, eutrophication), as well as temporal and spatial vagaries in the recruitment and survival of spores, appear to be key determinants of heterogeneity within algal forests (Dayton 1985a; Schiel and Foster 1986; Steneck et al. 2002). While patchiness within forests of algae is often recognized as having a large influence on the structure and dynamics of associated
floral and faunal communities (Edwards 1998; Fowler-Walker and Connell 2002; Graham 2004), the spatial scale over which heterogeneity occurs (i.e. the frequency and extent of different patches) has rarely been quantified (but see Underwood et al. 1991 and Dayton et al. 1992: Table 2). Such information is pertinent for identifying ecologically relevant scales for observational and experimental tests associated with the patchiness of canopy-forming algae.

On subtidal rocky coasts of temperate Australia, extensive forests of canopy-forming algae are created by several species of fucalean algae (Phaeophyta) and the laminarian alga *Ecklonia radiata* (C. Agardh) J. Agardh. *E. radiata* can form dense monospecific stands or may persist in mixed-species aggregations with species of Fucales (e.g. *Cystophora* spp., *Sargassum* spp., *Scyathalia dorycarpa*) (Shepherd and Womersley 1970; May and Larkum 1981; Goodsell et al. 2004). Additionally, established stands of canopy-formers are often punctuated by gaps where several individuals have been removed by disturbances such as storms (Kennelly 1987a) or herbivores (Andrew and Jones 1990). This chapter presents data quantifying the spatial scale of habitat heterogeneity (monospecific *E. radiata* vs mixed *E. radiata*-Fucales vs gaps) within forests of canopy-forming algae across > 2000 km of temperate Australian coastline. This information is used to identify ecologically relevant scales for observational and experimental tests associated with the heterogeneity of Australian algal forests.

### 2.3 Materials and Methods

Variation in the frequency and size of three different habitats within forests of canopy-forming algae (algae > 50 mm in height) was quantified across > 2000 km of temperate Australian coastline during the austral summer of 2001/2002. Two regions separated by at least 1000 km were identified (western and southern Australia), within which three locations (each separated by > 100 km) were randomly chosen (Fig. 2.1). Within each location, three sites (each separated by 1-10 km) were also randomly chosen. All sites were exposed to the predominant swell conditions and were between latitudes 34° 22' S and 35° 36' S to minimise bias of any effect of latitude.
Figure 2.1. Map of Australia showing regions sampled (WA = western Australia, SA = southern Australia), and locations sampled within each region (each black dot represents a location: CL = Cape Leeuwin, A = Albany, BB = Bremer Bay, PL = Port Lincoln, WC = West Cape, CJ = Cape Jervis). Three sites (not shown) were sampled within each location.
At each site, the frequency and size (linear extent) of individual patches of habitat were quantified from replicate 1 × 100 m transects (n = 4), each separated by > 10 m. Three habitats, known to affect the abundance and distribution of benthic flora (Chapter 3) and fauna (Goodsell et al. 2004), were identified in each transect: (i) monospecific stands of *E. radiata*, (ii) stands of *E. radiata* mixed with species of Fucales (e.g. *Cystophora* spp., *Sargassum* spp., *Scytolithia dorycarpa*, etc.), and (iii) gaps among canopies of algae. At a scale of 1 m², monospecific stands of *E. radiata* were recognized when ≥ 80 % of the canopy cover comprised *E. radiata*, while stands of *E. radiata* mixed with species of Fucales were recognized when 40-60 % of the canopy cover comprised *E. radiata* and the remainder comprised fucoid species (Goodsell et al. 2004). Only stands containing *E. radiata* with 40-60 % cover of fucoid species were classified as ‘mixed’ because such stands represent a more even mixture of canopy-forming algae than stands containing 20-40 % or 60-80 % fucoid species. Gaps among canopies of algae were recognized as rocky substrata that did not support canopy-forming algae > 50 mm in height.

Transects were oriented perpendicular to the shoreline and started as close to mean low water as the prevailing conditions would allow. The distance along each transect at which the type of habitat changed was recorded, providing data (linear extent) for every individual patch sampled (see Underwood et al. 1991 and Dayton et al. 1992 for similar methodology). At sites where the seaward extent of rocky substrata was less than 100 m, sampling ended at that distance. Relative differences in the frequency and size of patches were tested among habitats, regions, locations, and sites using ANOVA. For these analyses, ‘Region’ was treated as fixed, ‘Location’ and ‘Site’ were treated as random and nested within ‘Region’ and ‘Location’, respectively, while ‘Habitat’ was treated as fixed and orthogonal. The number of patches within or among replicate transects, however, was not equal for each type of habitat. Hence, a balanced analysis (ANOVA) of the size of patches was only possible when the mean size of each type of habitat within each transect was used as a single replicate (giving n = 4 per site).

A fundamental sampling decision was the choice of scale at which habitats were identified (1 m²), because this size established the minimum scale at which variation
could be detected (one metre). We considered that sampling at 1 m$^2$ was appropriate because the average width of an adult *E. radiata* thallus (laminae plus blade) is ~0.5 m (Womersley 1987), and therefore sampling at scales of less than one metre would provide information about the spatial variability of individuals rather than patches of canopy-forming algae. Additionally, casual observation suggested that distinct patches of habitat often occurred at sizes of ~1 m$^2$ (verified by our sampling: see Results), and therefore sampling at scales larger than 1 m$^2$ would overlook the occurrence of these smaller patches.

It is also worth noting that sampling the linear extent of individual patches along transects provides an estimate of patch size in one dimension, whereas patch size can also be estimated by sampling the area (two dimensions) of individual patches. In this study, the use of transects to estimate patch size facilitated sampling across a much greater proportion of coastline than would be possible if sampling the area of individual patches, resulting in increased replication and power of statistical tests. More importantly, sampling along transects oriented perpendicular to the shore also encompassed any natural variation in patch size with depth or distance from the shore, ensuring the data obtained were representative of the natural variation in patch sizes across subtidal coasts.

2.4 Results

*Frequency of habitats*

The total number of patches sampled within transects (i.e. the sum of all gaps, mixed stands and monospecific stands sampled) varied from site to site but was generally even among locations within each region, and also between regions (Table 2.1, mean ± SE number of patches per transect = 6.67 ± 0.64 in western Australia, 7.94 ± 0.74 in southern Australia). Among habitat types, patches of *E. radiata* mixed with fucoids occurred with greater frequency than either monospecific stands of *E. radiata* or gaps in both regions (Fig. 2.2, Table 2.2: SNK tests: mixed > monospecific = gaps). In western Australia, monospecific stands appeared to occur more frequently than gaps (Fig. 2.2), but post hoc (SNK) tests failed to detect this difference. The pattern detected at the regional scale was observed within four of six locations. At the remaining two locations (Albany and Cape Leeuwin), the frequency of mixed and monospecific stands was even (i.e. mixed = monospecific >
Table 2.1. Result of ANOVA testing for differences in the total number of patches among sites, locations, and regions across temperate Australia.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Region</td>
<td>1</td>
<td>29.39</td>
<td>0.30\textsuperscript{ns}</td>
</tr>
<tr>
<td>Location(Region)</td>
<td>4</td>
<td>98.85</td>
<td>3.04\textsuperscript{ns}</td>
</tr>
<tr>
<td>Site (Location(Region))</td>
<td>12</td>
<td>32.50</td>
<td>4.34***</td>
</tr>
<tr>
<td>Residual</td>
<td>54</td>
<td>7.49</td>
<td>-</td>
</tr>
</tbody>
</table>

Cochran’s C-test of homogeneity of variances: \( P > 0.05 \). *** \( P < 0.001 \), \textsuperscript{ns} \( P > 0.05 \).

Table 2.2. Result of ANOVA testing for differences in the relative frequency of habitats (monospecific vs mixed-species vs gaps) among sites, locations and regions across temperate Australia.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>2</td>
<td>263.41</td>
<td>18.24**</td>
</tr>
<tr>
<td>Region</td>
<td>1</td>
<td>9.80</td>
<td>0.30\textsuperscript{ns}</td>
</tr>
<tr>
<td>Location(Region)</td>
<td>4</td>
<td>32.95</td>
<td>3.04\textsuperscript{ns}</td>
</tr>
<tr>
<td>Site(Location(Region))</td>
<td>12</td>
<td>10.83</td>
<td>5.94***</td>
</tr>
<tr>
<td>Habitat × Region</td>
<td>2</td>
<td>45.24</td>
<td>3.13\textsuperscript{ns}</td>
</tr>
<tr>
<td>Habitat × Location(Region)</td>
<td>8</td>
<td>14.44</td>
<td>3.18*</td>
</tr>
<tr>
<td>Habitat × Site(Location(Region))</td>
<td>24</td>
<td>4.55</td>
<td>2.49***</td>
</tr>
<tr>
<td>Residual</td>
<td>162</td>
<td>1.82</td>
<td>-</td>
</tr>
</tbody>
</table>

Cochran’s C-test of homogeneity of variances: \( P > 0.05 \). * \( P < 0.05 \), ** \( P < 0.01 \), *** \( P < 0.001 \), \textsuperscript{ns} \( P > 0.05 \).
Figure 2.2. Mean (± SE) frequency of patches per transect for each type of habitat in western Australia (WA) and southern Australia (SA).
gaps), although the frequency of mixed-species patches was still ranked as greater than monospecific patches at both locations. Some site to site variation in the relative frequency of habitats was observed in each region (Table 2.2: Habitat × Site(Location(Region)) interaction), but mixed-species stands still occurred with greatest frequency (either significantly or by rank) at 16 of the 18 sites sampled.

Size of habitats
Within each region, the distribution of patch sizes was positively skewed for each type of habitat (Fig. 2.3a-f), such that the majority of patches sampled were ≤ 10 m in size (Table 2.3). Conformity of data to a normal distribution is one of the three main assumptions for ANOVA. Although ANOVA is quite robust to departures from normality (Underwood 1997), a log-transformation was done to remove skewness prior to the analysis of mean patch size. This analysis revealed that patches of E. radiata mixed with fucoids were larger than either monospecific stands of E. radiata or gaps in both regions (Fig. 2.4, Table 2.4: SNK tests: mixed > monospecific = gaps). In western Australia, monospecific patches of E. radiata appeared larger than gaps (Fig. 2.4), but post hoc (SNK) tests failed to detect this difference. Patterns similar to those detected at the regional scale were observed among locations, while differences in patch size among habitats varied among sites (Table 2.4: Habitat × Site(Location(Region)) interaction). Even so, mixed-species stands were observed to be larger than either monospecific stands or gaps at 15 of 18 sites.
**Figure 2.3.** Frequency distributions of the size (linear extent) of each type of habitat (monospecific *E. radiata*, mixed *E. radiata*-Fucales, and gaps) within western and southern Australia. Broken lines indicate the 10m size class.
Table 2.3. Percentage of patches that were ≤ 10 m in size in western Australia and southern Australia.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Western Australia</th>
<th>South Australia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monospecific</td>
<td>85.9</td>
<td>97.8</td>
</tr>
<tr>
<td>Mixed-species</td>
<td>86.7</td>
<td>71.3</td>
</tr>
<tr>
<td>Gap</td>
<td>88.9</td>
<td>100.0</td>
</tr>
</tbody>
</table>

Table 2.4. Result of ANOVA testing for relative differences in the mean size of habitats (monospecific vs mixed-species vs gap) among sites, locations and regions across temperate Australia.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>2</td>
<td>40.27</td>
<td>16.66**</td>
</tr>
<tr>
<td>Region</td>
<td>1</td>
<td>1.85</td>
<td>5.68ns</td>
</tr>
<tr>
<td>Location(Region)</td>
<td>4</td>
<td>0.33</td>
<td>0.50ns</td>
</tr>
<tr>
<td>Site(Location(Region))</td>
<td>12</td>
<td>0.65</td>
<td>1.81ns</td>
</tr>
<tr>
<td>Habitat × Region</td>
<td>2</td>
<td>5.95</td>
<td>2.46ns</td>
</tr>
<tr>
<td>Habitat × Location(Region)</td>
<td>8</td>
<td>2.42</td>
<td>2.01ns</td>
</tr>
<tr>
<td>Habitat × Site(Location(Region))</td>
<td>24</td>
<td>1.20</td>
<td>3.35***</td>
</tr>
<tr>
<td>Residual</td>
<td>162</td>
<td>0.36</td>
<td></td>
</tr>
</tbody>
</table>

Data were ln(x + 1) transformed. Cochran’s C-test of homogeneity of variances: $P > 0.05$. ** $P < 0.01$, *** $P < 0.001$, ns $P > 0.05$. 
Figure 2.4. Mean (± SE) size of patch for each type of habitat in western Australia (WA) and southern Australia (SA).
2.5 DISCUSSION

Variation in the spatial extent of habitat (i.e. patchiness) is a notable characteristic of natural systems and has profound consequences for the distribution and abundance of taxa across landscapes (Hutchings et al. 2000). Forests of canopy-forming algae are often considered spatially heterogeneous; comprised of numerous types of habitat that form a mosaic-like pattern (Duggins 1983; Dayton et al. 1984; Schiel and Foster 1986; Konar and Estes 2003). Despite widespread acceptance of this concept, few attempts have been made to formally quantify scales of patchiness within forests of subtidal algae (but see Dayton et al. 1992). Although rare, such information can be useful for justifying the use of a particular scale (e.g. quadrat size) as ecologically relevant in future research, and may also be indicative of the scales at which particular processes manifest within algal forests (e.g. disturbance to canopies by storms: Kennelly 1987a).

Across > 2000 km of temperate Australian coastline, subtidal algal forests comprised a heterogenous mixture of habitats that existed as a mosaic of patches over distances of ≤ 100 m (i.e. the length of the transect). By recognising three different types of habitat (monospecific *E. radiata* vs mixed *E. radiata*-Fucales vs gaps) known to affect the distribution and abundance of benthic plants (Chapter 3) and animals (Goodsell et al. 2004), it was found that most patches of all three types of habitat were 10 m or less in size. A key result from this research was that patches of habitat comprising *E. radiata* mixed with species of Fucales were more frequently sampled and were more extensive than either monospecific stands of *E. radiata* or gaps among canopies of algae (also see Appendix A). This result appeared general at all spatial scales at which sampling was done (i.e. sites: 1-10 km, locations: 100’s km, regions: 1000’s km). Such knowledge has clear implications for predicting the distribution and abundance of benthic plants and animals associated with particular types of habitat. Moreover, this result adds weight to the argument that the common practice of describing algal forests according to the presence of the most obvious species (e.g. ‘*E. radiata* forest’) can provide a simplified, if not misleading representation of the structure of these widespread habitats (Goodsell et al. 2004).

Comparing patterns among studies done in other places and with other species can be useful for assessing generality and contributing towards a more useful body of
predictive understanding (Underwood and Denley 1984; Gurevitch et al. 1992). While the concept of subtidal algal forests being arranged as a heterogeneous mixture of habitats is widely accepted, the scale over which such heterogeneity occurs appears remarkably similar among regions and canopy-forming species. The mean (+ SE) size of patches of habitat across Australia ranged from 1.26 ± 0.27 m for gaps in southern Australia to 12.72 ± 2.31 m for mixed-species canopies, also in southern Australia. Similar patch sizes have been observed within forests comprising E. radiata and Fucales on neighbouring coasts (e.g. Leigh, New Zealand: mean ± SE: 9.36 ± 0.90 m), and also within forests of the phaeophycean canopy-former Himantothallus grandifolius on more distant coasts (Casey, Antarctica: mean ± SE: 4.67 ± 0.88 m) (S.D. Connell and A.D. Irving, unpubl. data). Moreover, Dayton et al. (1992) observed similar patch sizes among three canopy-forming species found at comparable depths off Pt Loma, California (mean ± SE patch size over 8-18 m depth: 5.27 ± 1.41 m for Macrocystis pyrifera, 3.93 ± 0.63 m for Laminaria farlowii, and 5.30 ± 1.65 m for Pterygophora californica). In a notoriously variable world, such consistency of pattern provides encouragement for those searching for generality and predictability in nature; an endeavour that is often judged as one of the more progressive avenues of ecological inquiry (Peters 1991).

In conclusion, the data presented in this chapter provides a quantitative basis for understanding habitat heterogeneity within algal forests of temperate Australia. The key result was that the majority of individual patches of habitat were 10 m or less in size (linear extent). Knowledge of the scales of patchiness provides a basis for identifying ecologically relevant scales for sampling and experimentation with these habitats. Therefore, studies done at the scale of metres (i.e. between 1 and 10 m) appear well matched to natural scales of patchiness within forests of canopy-forming algae across much of temperate Australia. While most studies in temperate Australia have, by design or by chance, worked at this scale (e.g. Kennelly 1987a, c; Kennelly and Underwood 1993; Kendrick 1994; Emmerson and Collings 1998; Melville and Connell 2001; Goodsell et al. 2004; Kendrick et al. 2004), it is prudent to base this choice of scale within a quantitative understanding of natural history. It is not suggested, however, that hypotheses tested at larger scales (e.g. clearances of canopy > 10 m) are irrelevant, as human activity on some coasts have created homogeneous habitat on much larger scales than metres (e.g. Gorgula and Connell 2004). In
reality, it would be valuable to understand how such differences in the scale of habitat heterogeneity affect patterns and processes within algal forests, which are widely thought of as 'key habitats' that shape the ecology of much of the world's coastlines.
The monopolisation of understorey habitat by encrusting coralline algae. This photograph was taken within a monospecific stand of *Ecklonia radiata*. The holdfasts of two *E. radiata* can be seen at the top of the photo (photo by the author).
“...lack of replicated sites often makes it impossible to know how generally the results of studies at one or a few sites apply to even a few kilometres of coastline.”

M. S. Foster, 1990
*Hydrobiologia*, 192: p.22

“For proper biogeographic comparisons to be made...it is necessary to know how much spatial variation exists from one place to another within a biogeographic region.”

*Hydrobiologia*, 192: p.16
Chapter 3: Preamble

Chapter 3 presents data quantifying variation in the distribution and abundance of benthic algae and invertebrates associated with (i) the presence and (ii) variation in the composition of habitat created by canopy-forming algae. Sampling was done at multiple spatial scales across > 5000 km of temperate Australasia (Western Australia to New Zealand) to understand the spatial generality of local-scale patterns and provide the necessary observations for broad-scale comparisons.

This chapter was published in the journal *Marine Biology* in 2004 (vol. 144: 361-368), with myself as senior and corresponding author, and Sean D. Connell and Bronwyn M. Gillanders (University of Adelaide) as co-authors. It is, therefore, written in plural. Permission from the publisher (Springer-Verlag) to reproduce this manuscript herein has been granted (see Appendix B).

*Contributions and signatures of authors*

**ANDREW D. IRVING**

*Sampled, analysed, and interpreted all data, wrote manuscript as senior and corresponding author.*

Signed:................................. Date:..............................

**SEAN D. CONNELL**

*Supervised development of research, data interpretation, and manuscript evaluation.*

Signed:................................. Date:..............................

**BRONWYN M. GILLANDERS**

*Advised on aspects of research and manuscript evaluation.*

Signed:................................. Date:..............................
CHAPTER 3

LOCAL COMPLEXITY IN PATTERNS OF CANOPY-BENTHOS ASSOCIATIONS PRODUCE REGIONAL PATTERNS ACROSS TEMPERATE AUSTRALASIA

3.1 ABSTRACT
Across subtidal coasts of temperate Australasia, canopy-benthos associations are mostly understood from broadly defined studies of algal forests within eastern Australia and north-eastern New Zealand. We tested the hypotheses that (i) benthic assemblages differ between habitats comprising monospecific canopies of *Ecklonia radiata* and canopies that comprise *E. radiata* mixed with other canopy-forming species, (ii) patterns observed locally (i.e. within sites 1-10 km apart) match those observed among regions (> 1000 km apart) for which (iii) eastern Australia and north-eastern New Zealand are representative of other regions of temperate Australasia. Benthic assemblages almost always differed among monospecific canopies, mixed-species canopies, and gaps among canopies, indicating that failure to distinguish between superficially similar habitats (monospecific vs mixed-species canopies) can lead to over-generalised conclusions about the ecology of algal forests. Patterns of differences among habitats did not change between western and southern Australia, but differed from eastern Australia, and patterns from all regions were distinct from New Zealand (WA = SA ≠ EA ≠ NZ). While local patterns were complex, the major morphological groups that often characterise benthos (i.e. encrusting coralline algae and filamentous turf-forming algae) revealed patterns that could be related across space from local to regional scales. These findings demonstrate that knowledge about the configuration of algal canopies will improve confidence about the representativeness of results, and that any local complexity need not impede searches for generality when the spatial limits of patterns are also understood.

3.2 INTRODUCTION
Understanding the extent to which complexity at local-scales generates large-scale patterns is a continuing challenge to ecologists. Central to this challenge is the
discovery of patterns at local scales that are repeated at larger scales (Wootton 2001) to identify situations in which studies at smaller, tractable scales may be scaled-up (Thrush et al. 1997). Knowledge of nested spatial patterns spanning the range of regions of interest is fundamental to this work (Underwood and Petraitis 1993; Gaston and Blackburn 1999) and any attempt to establish relationships between scale-dependent patterns and process (Hewitt et al. 1996). Establishing the spatial limitations of patterns and responses is clearly dependent on the spatial extent of a study (Legendre et al. 1997). However, simply extending observations to identify the generality of response is insufficient unless potential confounding factors can also be incorporated into the experimental design (Thrush et al. 1997).

Canopy-understorey associations provide one of the more promising systems showing that patterns can be related across space such that small-scale phenomena have the potential to be related to conclusions at larger-scales. Canopies act to facilitate and exclude particular taxa as understorey (Bertness et al. 1999) to produce the phenomena of plant associations (Gleason 1926) that are repeated across regional to global scales (Callaway et al. 2002). On subtidal coasts, canopies of algae place sufficiently strong constraints on the types of organisms able to colonise and persist as understorey (Kennelly 1987a; Schiel 1988; Eckman and Duggins 1991; Edwards 1998; Connell 2003b) such that local patterns generate the phenomena of canopy-benthos associations observed within (Kennelly and Underwood 1993; Connell 2003a) and among biogeographic regions spanning several thousand kilometres (Fowler-Walker and Connell 2002). The spatial extent of such studies has been critical to identifying limits to extrapolation from particular regions, but potential confounding factors are seldom incorporated into the experimental design. Of emerging concern is the potential confounding of canopy-benthos observations between monospecific stands and mixed-species stands of canopy-forming algae (Goodsell et al. 2004).

Whereas terrestrial ecologists recognise that canopy-forming vegetation can occur as both monospecific and mixed-species states (Cannell et al. 1992), with ecological differences between what appears to be outwardly similar types of habitat (Martijena and Bullock 1994; Hölscher et al. 1998; Torti et al. 2001), subtidal ecologists have generally restricted their observations to monospecific canopies (e.g. Santelices and
Ojeda 1984a; Kennelly 1987c; Foster and Van Blaricom 2001; Connell 2003a), possibly to increase certainty of conclusions (i.e. increase precision). However, a trade-off between confidence and generality of results is seldom appreciated, probably because a greater emphasis on certainty, rather than generality, is prevalent in many ecological studies. As a consequence, the extent to which patterns observed in monospecific stands relate to those of mixed-species stands of canopy-forming algae is poorly understood, despite evidence that mixed-species canopies do exist (Dayton et al. 1984; Chapman and Johnson 1990; Collings and Cheshire 1998; Appendix A) and may occupy more space relative to monospecific canopies (e.g. 32% monospecific vs 64% mixed-species on both Western Australian and South Australian coasts; Goodsell et al. 2004; Chapter 2). Depending on the spatial extent of different types of habitat, failure to identify differences in canopy-benthos associations between monospecific and mixed-species canopies may lead to over-generalised or even misleading conclusions about the ecology of algal forests.

The stipitate kelp *Ecklonia radiata* (Phaeophyta: Laminariales) is extensively distributed on subtidal shores of temperate Australasia (Womersley 1987). Our current understanding of Australasia’s *E. radiata* forests is predominantly based upon research done in eastern Australia (46.6% of papers; Table 3.1) and north-eastern New Zealand, particularly in and adjacent to the Leigh Marine Reserve (26.7% of papers; Table 3.1). Although this work has greatly advanced our understanding of subtidal canopy-benthos associations, an appreciation of how their results relate to other parts of Australasia over the same latitudes remains clouded. This is disturbing given the potential for large-scale biogeographic differences (Fowler-Walker and Connell 2002). In accordance with studies of algal forests in other regions of the world, recognition of *E. radiata* forests as monospecific or existing in a mixed assemblage with other canopy-formers is rarely made (Goodsell et al. 2004). Given the extensive distribution of *E. radiata* and that the proportional abundance of mixed-species canopies incorporating *E. radiata* can be large relative to monospecific canopies of *E. radiata* (Goodsell et al. 2004), there is the potential for ecological differences between monospecific and mixed-species canopies to be widespread and detectable over a range of spatial scales.
Table 3.1. Division of papers (1972-2002) testing ecological hypotheses about forests of *Ecklonia radiata* according to Australasian regions.

<table>
<thead>
<tr>
<th>Region</th>
<th>Number of papers</th>
<th>Percent of total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western Australia</td>
<td>7</td>
<td>11.7</td>
</tr>
<tr>
<td>Southern Australia</td>
<td>4</td>
<td>6.7</td>
</tr>
<tr>
<td>Eastern Australia (Sydney)</td>
<td>28 (19)</td>
<td>46.6 (31.7)</td>
</tr>
<tr>
<td>New Zealand (Leigh Marine Reserve)</td>
<td>21 (16)</td>
<td>35.0 (26.7)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>60</strong></td>
<td></td>
</tr>
</tbody>
</table>

The term ‘*Ecklonia radiata*’ was entered into three journal article search engines: Biological Abstracts, ISI Current Contents and Cambridge Scientific Abstracts. Publications between 1972 and 2002 were selected if they tested ecological hypotheses about *E. radiata*. Five papers that were not detected by search engines were supplemented from personal libraries. Of these five, three presented data from Sydney and two from north-eastern New Zealand. Note that one paper presented data from three regions and was counted three times (making total number of papers = 60).
In this study, we tested the hypotheses that (i) differences in the structure and composition of benthic assemblages occur between monospecific and mixed-species canopies of *E. radiata*, and that these assemblages differ from those occurring within gaps among canopies (i.e. substrata without canopy-forming algae), (ii) this local complexity of pattern (i.e. within sites 1-10 km apart) matches that observed among regions (>1000 km apart), and (iii) canopy-benthos associations in the most heavily studied localities of Australasia (eastern Australia and the Leigh Marine Reserve) are consistent with those in other regions of temperate Australasia (western Australia and southern Australia).

### 3.3 Materials and Methods

Sampling of benthic assemblages was done over the austral summer of 2001/2002 and spanned more than 5300 km (linear distance) across temperate Australasia within set latitudinal limits (33° 37' S to 37° 06' S) that enabled broad scale comparisons. Sampling in Australia followed a fully-nested hierarchical design of three spatial scales: regions (separated by 1000's km), locations within regions (separated by 100's km) and sites within locations (separated by 1-10 km). Benthic assemblages were quantified from three types of habitat (monospecific canopies of *E. radiata*, canopies of *E. radiata* mixed with Fucales, and gaps among canopies of algae: see definitions below) at every site and hence the type of habitat was orthogonal to all levels of spatial separation. Replicates (n = 8) within each site were separated by 1-10 metres. The three regions sampled in Australia were western Australia (WA), southern Australia (SA) and eastern Australia (EA) (Fig. 3.1). Four locations were randomly chosen within each region, and four sites exposed to predominant oceanic swell conditions were randomly selected within each of these locations. Sampling was done between 3-10 m depth at all locations except one (Eden, EA) where sampling was done between 8-14 m depth (canopies of *E. radiata* were not observed at shallower depths). During January of 2003, benthic assemblages were quantified at four sites within the Leigh Marine Reserve (LMR) on the north-eastern coast of New Zealand (Fig. 3.1). Sampling methodology was identical to that used in Australia to permit comparisons between Leigh and Australia.
Figure 3.1. Map of Australasia showing the positions of sampled locations within each region (each black dot represents a location). For each location, four sites were also sampled (not shown). WA = western Australia, SA = southern Australia, EA = eastern Australia, LMR = Leigh Marine Reserve. Locations sampled were: CL = Cape Leeuwin, A = Albany, BrB = Bremer Bay, Es = Esperance, El = Elliston, PL = Port Lincoln, WC = West Cape, CJ = Cape Jervis, Ed = Eden, BaB = Batemans Bay, JB = Jervis Bay, S = Sydney and LMR = Leigh Marine Reserve.
Stands of canopy-forming algae were identified at the 1 m² scale as: ‘monospecific E. radiata’ when ≥ 80% of the canopy cover comprised E. radiata, and ‘mixed-species’ when E. radiata comprised 40-60% of the canopy cover and the remainder of the canopy consisted of fucoid algae (e.g. Cystophora spp., Sargassum spp., Scytothalia dorycarpa, etc.) (Goodsell et al. 2004; Chapter 2). Gaps among canopies encompassed rocky surfaces without canopy-forming algae.

Quadrats (1 m², n = 8) were haphazardly placed within each type of habitat and were positioned > 1 m from the edge of a habitat. Percentage covers of benthos were estimated for several morphological groups using the point intercept method (25 regularly spaced points within an area of 0.2 x 0.2 m; Meese and Tomich 1992). Algae < 50 mm high were classified as benthos; above this they were classified as canopy. Benthic algae were identified as morphological groups (encrusting coralline algae, encrusting non-coraline algae, articulated coralline algae, filamentous turf-forming algae, foliose (fleshy, non-coraline) algae, juvenile stages of canopy-forming algae) according to Steneck and Dethier (1994), and invertebrates were identified as sponge, ascidian, bryozoan, barnacle, serpulid and spirorbid polychaetes and coral. We further define turf-forming algae as upright branches of filamentous algae ≤ 10 mm tall that are packed so that each is in contact with its neighbours. In addition, the density of E. radiata within each 1 m² quadrat was recorded because density has the potential to affect assemblages of benthos (e.g. Kendrick et al. 1999).

Tests for multivariate differences in the structure of benthic assemblages were done using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) and tests for differences in percentage covers of individual morphological groups were done with analysis of variance following the procedures of Underwood (1981). For all analyses, ‘Region’ was treated as fixed and orthogonal, ‘Location’ and ‘Site’ were treated as random and nested within ‘Region’ and ‘Location’ respectively, and ‘Habitat’ was treated as fixed and orthogonal.

3.4 RESULTS

Comparison among Australian regions

Assemblages of benthos differed among types of habitat in all regions of Australia (Fig. 3.2, Table 3.2: Habitat x Region interaction). Post-hoc analysis of the
Figure 3.2. Non-metric ordination of centroid values for benthic assemblages beneath monospecific canopies, mixed-species canopies, and within gaps among canopies in each region of Australia and in the Leigh Marine Reserve, New Zealand. Unfilled shapes = gaps, cross-hatched shapes = mixed-species, and filled shapes = monospecific. Note that the level of replication at Leigh (n = 32) is ¼ that of Australian regions (n = 128). A stress value of 0.03 indicates an interpretable ordination of the multivariate data in 2-dimensions (Clarke 1993).
Table 3.2. Result of a four-factor PERMANOVA testing for differences in the structure of understorey assemblages among habitats (monospecific vs mixed-species vs gaps), sites, locations and regions.

<table>
<thead>
<tr>
<th>Source</th>
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<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>2</td>
<td>9.25</td>
<td>33.35***</td>
</tr>
<tr>
<td>Region</td>
<td>2</td>
<td>5.01</td>
<td>3.01*</td>
</tr>
<tr>
<td>Location(Region)</td>
<td>9</td>
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<td>5.77***</td>
</tr>
<tr>
<td>Site(Location (Region))</td>
<td>36</td>
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<td>6.15***</td>
</tr>
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<td>Habitat x Region</td>
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<td>37.47***</td>
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<td>0.28</td>
<td>2.07***</td>
</tr>
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<td>Habitat x Site(Location(Region))</td>
<td>72</td>
<td>0.13</td>
<td>2.87***</td>
</tr>
<tr>
<td>Residual</td>
<td>1008</td>
<td>0.05</td>
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</tr>
</tbody>
</table>

* = P < 0.05, *** = P < 0.001.

Table 3.3. Pair-wise comparisons of understorey assemblages among Australian regions for each type of habitat. WA = western Australia, SA = southern Australia, EA = eastern Australia.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Regional comparison</th>
<th>t</th>
</tr>
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<tbody>
<tr>
<td>Monospecific</td>
<td>WA vs SA</td>
<td>3.34***</td>
</tr>
<tr>
<td></td>
<td>WA vs EA</td>
<td>11.66***</td>
</tr>
<tr>
<td></td>
<td>SA vs EA</td>
<td>8.73***</td>
</tr>
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<td>Mixed-species</td>
<td>WA vs SA</td>
<td>2.92***</td>
</tr>
<tr>
<td></td>
<td>WA vs EA</td>
<td>7.29***</td>
</tr>
<tr>
<td></td>
<td>SA vs EA</td>
<td>5.40***</td>
</tr>
<tr>
<td>Gaps</td>
<td>WA vs SA</td>
<td>4.11***</td>
</tr>
<tr>
<td></td>
<td>WA vs EA</td>
<td>20.42***</td>
</tr>
<tr>
<td></td>
<td>SA vs EA</td>
<td>16.19***</td>
</tr>
</tbody>
</table>

*** = P < 0.001.
Habitat × Site(Location(Region)) interaction within each region revealed distinct assemblages among all three types of habitat (i.e. gap ≠ mixed ≠ monospecific) at 13 of 16 sites in WA and 8 of 16 sites in SA, but only 3 of 16 sites in EA. At the remaining 13 sites in EA, but only 3 sites in WA and 5 sites in SA, assemblages beneath mixed-species and monospecific canopies were similar but differed to assemblages within gaps (i.e. gap ≠ mixed = monospecific). Comparison of assemblages within each type of habitat across Australia revealed differences among all regions (Table 3.3). However, these tests also revealed that assemblages in WA and SA were more similar to each other than they were to assemblages in EA for each type of habitat (Fig. 3.2, Table 3.3: consistently smaller $t$-values for WA vs SA comparisons in contrast to $t$-values for WA vs EA and SA vs EA comparisons). Hence, a notable regional difference both within and among habitats is that patterns detected in EA were generally inconsistent with those in WA and SA.

Analysis of variance detected differences among habitats (gap vs mixed vs monospecific) within each region for the most abundant benthic groups (i.e. algae and invertebrates that collectively contributed to > 96% of the percentage cover; Table 3.4). However, the magnitude and direction of differences were often inconsistent among regions, whereby patterns detected in WA were similar to those in SA, but were different (often reversed) to those in EA (Fig. 3.3, Table 3.4). In WA and SA, encrusting coralline algae monopolised space beneath monospecific canopies, while articulated coralline algae and juvenile canopy-forming algae occurred in greatest abundance within gaps (Fig. 3.3a-c, SNK tests). In EA, however, encrusting corallines monopolised space within gaps, where articulated corallines and juvenile canopy formers were in their lowest abundance (Fig. 3.3a-c, SNK tests). While the abundance of filamentous turfs and foliose algae did not differ among habitats in EA, filamentous turf occurred in greatest abundance within gaps, and foliose algae in least abundance in monospecific stands in WA and SA (Fig. 3.3d-e, SNK tests). In SA and EA, the abundance of sponge was greatest beneath canopies but did not differ between types of canopy (i.e. gap < mixed = monospecific, Fig. 3.3f, SNK tests). A similar pattern was observed for sponge in WA (Fig. 3.3f), although SNK tests failed to detect any differences among habitats in this region.
Table 3.4. Results of four-factor ANOVAs testing for differences in the percentage cover of benthic morphological groups among habitats (monospecific vs mixed-species vs gaps), sites, locations and regions across Australia.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>df</th>
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<tbody>
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<td>Habitat</td>
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<td>31520.73</td>
<td>31.23***</td>
<td>6</td>
<td>6850.13</td>
<td>6.63**</td>
<td>2</td>
<td>7853.51</td>
<td>20.66***</td>
</tr>
<tr>
<td>Region</td>
<td>2</td>
<td>3320.71</td>
<td>0.82ns</td>
<td>4</td>
<td>8830.74</td>
<td>1.22ns</td>
<td>2</td>
<td>7363.32</td>
<td>7.71ns</td>
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<td>Location (Region)</td>
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<td>4025.37</td>
<td>6.98***</td>
<td>5</td>
<td>7261.74</td>
<td>9.34***</td>
<td>2</td>
<td>954.76</td>
<td>2.90ns</td>
</tr>
<tr>
<td>Site (Location (Region))</td>
<td>36</td>
<td>576.35</td>
<td>5.38***</td>
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<td>777.18</td>
<td>6.02***</td>
<td>2</td>
<td>329.24</td>
<td>3.65***</td>
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<td>4</td>
<td>98579.69</td>
<td>97.68***</td>
<td>8</td>
<td>43051.44</td>
<td>41.64***</td>
<td>2</td>
<td>5594.60</td>
<td>14.72***</td>
</tr>
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<td>18</td>
<td>1009.23</td>
<td>1.66ns</td>
<td>10</td>
<td>1033.84</td>
<td>2.57**</td>
<td>2</td>
<td>380.05</td>
<td>2.49*</td>
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<td>Habitat x Site (Location (Region))</td>
<td>72</td>
<td>607.45</td>
<td>5.68***</td>
<td>12</td>
<td>401.76</td>
<td>3.11***</td>
<td>2</td>
<td>152.56</td>
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<td>Residual</td>
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<td>129.01</td>
<td></td>
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<td>41288.63</td>
<td>66.71***</td>
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<td>20.55***</td>
<td>2</td>
<td>11947.37</td>
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<td>10.76*</td>
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<td>5.75***</td>
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<td>Habitat x Region</td>
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<td>8819.06</td>
<td>14.25***</td>
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<td>1786.04</td>
<td>8.17**</td>
<td>2</td>
<td>2504.18</td>
<td>6.65*</td>
</tr>
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<td>Habitat x Location (Region)</td>
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<td>618.88</td>
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<td>1.85ns</td>
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<td>Habitat x Site (Location (Region))</td>
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<td>321.06</td>
<td>5.93***</td>
<td>12</td>
<td>147.31</td>
<td>1.77**</td>
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<td>83.18</td>
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<td>83.77</td>
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</tbody>
</table>

Data were arcsine(%) transformed. Cochran’s C-test of homogeneity of variances: $P > 0.05$ for (a) and (b). ** = $P < 0.01$, *** = $P < 0.001$, ns = $P > 0.05$. Transformation failed to reduce heterogeneous variances for (c), (d), (e), and (f) (Cochran’s C-test: $P < 0.05$) and significance was judged at the more conservative $\alpha = 0.01$ (Underwood 1997). In such cases, * = $P < 0.01$, ** = $P < 0.001$, *** = $P < 0.0001$, ns = $P > 0.01$.  

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Figure 3.3. Mean percent cover (± SE) of benthic morphological groups among habitats (gaps vs mixed-species vs monospecific) within each region of temperate Australasia. WA = western Australia, SA = southern Australia, EA = eastern Australia, LMR = Leigh Marine Reserve.
The extent to which patterns of abundance among habitats detected at the site and location level were consistent with that quantified at the regional scale was variable. Inconsistencies from location to location within a region were detected for all groups, although only 3 of 72 comparisons of rank abundance (12 locations × 6 morphological groups) contradicted the regional pattern (i.e. although the pattern of abundance at a particular location may have been inconsistent with the regional pattern, the magnitude and direction of differences among habitats were rarely opposite to the regional pattern). At the level of site, patterns of abundance of encrusting corallines and filamentous turfs were strongly consistent with regional patterns (Table 3.5), suggesting robust predictability of pattern across spatial scales of 1-10 km to 1000's km. For articulated corallines, juvenile canopy-forming algae, foliose algae and sponges, considerable site-to-site variability of pattern was detected (101 inconsistencies of 192 comparisons that involved 48 sites × 4 morphological groups), but only 11 of these inconsistencies showed patterns opposite to the regional pattern (Table 3.5).

**Leigh vs Australia**

Benthic assemblages within the Leigh Marine Reserve differed among all types of habitat (i.e. gap ≠ mixed ≠ monospecific, Table 3.6). Comparisons with Australian locations showed that differences within each habitat were frequently greatest between Leigh and Australian locations, rather than among locations within Australia (as indicated by *t*-values from pair-wise tests). A striking feature of the ordination of assemblages from Leigh and Australia was that benthic assemblages beneath mixed-species canopies at Leigh were more similar to those beneath monospecific canopies in WA and SA and within gaps in EA (monopolised by encrusting coralline algae), while assemblages beneath monospecific canopies at Leigh were more similar to those beneath mixed-species canopies in WA and SA (greater abundance of erect algae) (Fig. 3.2). The magnitude and direction of differences in abundance among habitats for several morphological groups of algae also differed between Leigh and Australian locations. At Leigh, encrusting coralline algae occurred in greatest abundance under mixed-species canopies, in least abundance within gaps and at intermediate levels of abundance beneath monospecific canopies (i.e. gap < monospecific < mixed) which follows that the direction of these differences was reversed for articulated coralline algae (i.e. gap > monospecific > mixed, Fig. 3.3a, b,
Table 3.5. Patterns of rank abundance among habitats, with the number of sites \(n = 16\) per Australian region) that revealed patterns inconsistent with that detected at the scale of region (number of contradictory sites is shown in parentheses). G = gap, MX = mixed-species, MO = monospecific.

<table>
<thead>
<tr>
<th>Morphological Group</th>
<th>WA</th>
<th>SA</th>
<th>EA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Encrusting coralline</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regional pattern</td>
<td>(G &lt; MX &lt; MO)</td>
<td>(G &lt; MX &lt; MO)</td>
<td>(G &gt; MX = MO)</td>
</tr>
<tr>
<td>Inconsistent sites</td>
<td>0 (0)</td>
<td>5 (0)</td>
<td>5 (3)</td>
</tr>
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<td>Articulated coralline</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regional pattern</td>
<td>(G = MX &gt; MO)</td>
<td>(G &gt; MX &gt; MO)</td>
<td>(G &lt; MX = MO)</td>
</tr>
<tr>
<td>Inconsistent sites</td>
<td>6 (1)</td>
<td>8 (0)</td>
<td>6 (1)</td>
</tr>
<tr>
<td>Filamentous turf</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regional pattern</td>
<td>(G &gt; MX = MO)</td>
<td>(G &gt; MX = MO)</td>
<td>(G = MX = MO)</td>
</tr>
<tr>
<td>Inconsistent sites</td>
<td>1 (0)</td>
<td>3 (0)</td>
<td>2 (2)</td>
</tr>
<tr>
<td>Foliose algae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regional pattern</td>
<td>(G = MX &gt; MO)</td>
<td>(G = MX &gt; MO)</td>
<td>(G = MX = MO)</td>
</tr>
<tr>
<td>Inconsistent sites</td>
<td>8 (1)</td>
<td>13 (0)</td>
<td>2 (2)</td>
</tr>
<tr>
<td>Juv. canopy-formers</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regional pattern</td>
<td>(G &gt; MX &gt; MO)</td>
<td>(G &gt; MX &gt; MO)</td>
<td>(G &lt; MX = MO)</td>
</tr>
<tr>
<td>Inconsistent sites</td>
<td>12 (0)</td>
<td>13 (1)</td>
<td>10 (0)</td>
</tr>
<tr>
<td>Sponge</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regional pattern</td>
<td>(G = MX = MO)</td>
<td>(G &lt; MX = MO)</td>
<td>(G &lt; MX = MO)</td>
</tr>
<tr>
<td>Inconsistent sites</td>
<td>4 (2)</td>
<td>11 (0)</td>
<td>8 (3)</td>
</tr>
<tr>
<td>Total (out of 96)</td>
<td>31 (4)</td>
<td>53 (1)</td>
<td>33 (11)</td>
</tr>
</tbody>
</table>
Table 3.6. Result of PERMANOVA testing for differences in the structure of understorey assemblages among types of habitat (monospecific vs mixed-species vs gaps) in the Leigh Marine Reserve.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>2</td>
<td>22327.44</td>
<td>36.15***</td>
</tr>
<tr>
<td>Residual</td>
<td>93</td>
<td>617.65</td>
<td></td>
</tr>
</tbody>
</table>

*** = P < 0.001.

Table 3.7. Results of ANOVAs testing for differences in the percentage cover of benthic morphological groups among types of habitat (monospecific vs mixed-species vs gaps) in the Leigh Marine Reserve.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Encrusting coralline</td>
<td>2</td>
<td>22332.96</td>
<td>246.71***</td>
<td>27322.40</td>
<td>161.21***</td>
</tr>
<tr>
<td>(b) Articulated coralline</td>
<td>93</td>
<td>90.52</td>
<td>169.48</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(c) Filamentous turf</td>
<td>2</td>
<td>565.63</td>
<td>6.46*</td>
<td>1179.83</td>
<td>24.16***</td>
</tr>
<tr>
<td>(d) Sessile invertebrates†</td>
<td>93</td>
<td>87.56</td>
<td>48.84</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Data were arcsine(%) transformed. Cochran’s C-test of homogeneity of variances: P > 0.05 for (a) and (d). *** = P < 0.001. Transformation failed to reduce heterogeneous variances for (b) and (c) (Cochran’s C-test: P < 0.05) and significance was judged at the more conservative α = 0.01 (Underwood 1997). In such cases, * = P < 0.01, *** = P < 0.0001.

†Only sessile invertebrates that extend appendages to feed and/or respire were included in this analysis.
Table 3.7). The abundance of filamentous turfs at Leigh was least under mixed-species canopies, but did not differ between gaps and monospecific canopies (i.e. gap = monospecific > mixed, Fig. 3.3d, Table 3.7). For these three morphological groups, such patterns of abundance among habitats were not detected at any location in Australia. Moreover, the abundance of encrusting coralline beneath mixed-species canopies, articulated coralline in gaps, and filamentous turf beneath monospecific canopies at Leigh was far greater than that sampled in the corresponding habitats at any location in Australia (SNK tests). Covers of invertebrates that extend appendages to feed and/or respire (e.g. serpulid and spirorbid polychaetes, barnacles and the sponge Cliona celata) differed among all three habitats at Leigh with greatest cover beneath monospecific canopies and least cover within gaps (i.e. gap < mixed < monospecific, Table 3.7). Furthermore, the abundance of these invertebrates was greater beneath mixed-species and monospecific canopies at Leigh than mixed-species and monospecific canopies at any Australian location (SNK tests).

Does density of Ecklonia radiata explain regional patterns?
Across Australia, monospecific canopies generally comprised twice as many E. radiata plants than mixed-species canopies (12-13 vs 6 plants m$^{-2}$) but no effect of region or consistent effect of location and site on E. radiata density was detected for both mixed-species and monospecific canopies (ANOVA: $F_{2,9} = 0.89, P = 0.44$ for mixed-species canopies, and $F_{2,9} = 0.19, P = 0.82$ for monospecific canopies), suggesting that the density of E. radiata in Australia, at least at the scale of 1 m$^2$, does not offer an alternate explanation for the regional patterns detected. Mixed-species canopies at Leigh comprised similar E. radiata densities to mixed-species canopies in Australia but monospecific canopies comprised greater densities than 9 of 12 Australian locations (SNK tests).

3.5 DISCUSSION
A key finding was that canopies of E. radiata mixed with fucoids supported different assemblages of understorey algae and sessile invertebrates compared to monospecific canopies of E. radiata, particularly in western and southern Australia. The abundances of some morphological groups (e.g. encrusting coralline algae and juvenile canopy-formers) beneath mixed-species canopies were often intermediate
between those sampled from gaps and under monospecific canopies. The striking lack of differences between mixed-species and monospecific canopies in eastern Australia indicates regional limits to this generality and suggests that we still have much to learn about the patterns that show eastern Australia to differ from much of temperate Australia. Nevertheless, differences in the ecology of mixed-species and monospecific stands of terrestrial vegetation have been recognised for many years (Cannell et al. 1992) and until now, even qualitative evidence of differences among mixed-species and monospecific stands of subtidal vegetation has been rare (Shepherd and Womersley 1970; Choat and Schiel 1982; Collings and Cheshire 1998; also see Appendix A).

The frequency with which patterns of complexity detected at local-scales (among sites) matched those at regional-scales depended on the morphological group examined. Importantly, the morphological groups that typically characterise benthic assemblages across the south coast of Australia (encrusting coralline algae beneath monospecific canopies: Connell 2003a, and turf-forming algae within gaps: Copertino et al. 2005) exhibited strong consistency between sites (local scale) and the region in which the sites were located (regional scale). For several more morphological groups (articulated coralline algae, juvenile canopy-forming algae, foliose algae and sponges), differences in abundance among types of habitat at the regional scale (1000’s km) were consistent at the scale of location (100’s km) within each region, suggesting consistency of pattern from 100’s to 1000’s of km. However, these groups exhibited inconsistent patterns among sites within a region (also see Kendrick et al. 1999). This finding reinforces the idea that although the abundances of some morphological groups vary inconsistently across local-scales (1-10 km), consistent patterns emerge at increasingly larger scales (100’s to 1000’s km) (Fowler-Walker and Connell 2002).

Knowledge of the ecology of E. radiata forests centres on eastern Australia and New Zealand (Leigh Marine Reserve), therefore, it is particularly useful to understand how these localities contrast to comparable localities (similar latitude) across temperate Australia. Critically, benthic patterns in western and southern Australia were most similar to each other, but were distinct from eastern Australia and New Zealand, which also differed from each other (WA = SA ≠ EA ≠ NZ). This result
usefully identifies limits to extrapolation from studies done within these regions and helps resolve apparent conflicts (e.g. reversed patterns in Connell 2003a in SA vs Kennelly 1989 in EA), as well as highlighting potential generalities in patterns and process (e.g. Connell 2003a in SA vs Wernberg-Moller 2002 in WA).

A critical factor accounting for differences among Australian regions appears to be greater grazing pressure in eastern Australia (Fowler-Walker and Connell 2002) that maintains extensive covers of encrusting coralline algae outside canopies (Andrew 1993), a benthic pattern that is reversed in western and southern Australia where grazers are relatively sparse. Similar patterns have been observed between kelp forests in northern (abundant grazers) and southern New Zealand (sparse grazers) (Choat and Schiel 1982; Schiel 1990) and in eastern North America (Chapman and Johnson 1990), which has encouraged models proposing grazing pressure as crucial to determining the structure and composition of kelp forests. Several factors that manifest over large spatial scales may also account for regional differences, including gradients of water temperature (Leliaert et al. 2000), ocean boundary currents and even geological history (e.g. land bridges between the Australian mainland and Tasmania). In the context of this study, such models remain speculative until tested over appropriate spatial scales.

Benthic patterns within the Leigh Marine Reserve did not match patterns detected anywhere in Australia and we hypothesize this to be a function of the striking difference in morphology of E. radiata between Australia and Leigh (Bolton and Anderson 1994) and its effect on the physical environment (e.g. shade and disturbance). For example, physical abrasion of the substratum by canopies of E. radiata is affected by canopy morphology (Kennelly 1989) and this disturbance excludes many sessile invertebrates from the understorey, particularly those taxa sensitive to physical contact (Connell 2003b). It would follow, therefore, that the greatest covers of invertebrates likely to be most susceptible to abrasion (i.e. those that extend appendages to feed and/or respire) were at Leigh, where the morphology of E. radiata (stipes were six times longer and fronds two times shorter than in Australia: M. Fowler-Walker, unpubl. data) is consistent with less physical disturbance of benthos; i.e. longer stipe to frond ratios (Kennelly 1989).
In conclusion, most of our understanding of *E. radiata* forests is derived from broadly defined stands within eastern Australia and Leigh (New Zealand) and this study indicates limits to inferences from monospecific to mixed-species stands, and from these well-studied regions to western and southern Australia. Importantly, while local patterns can be complex, the major morphological groups that often characterise benthos (i.e. encrusting coralline algae and turf-forming algae) show patterns of complexity that can be related across space from local to regional scales. It may be possible, therefore, to produce predictions from small-scale studies that are relevant to larger-scales. Our findings show that increased knowledge about the configuration of canopies will improve confidence about the representativeness of results, and if such local complexity is understood it need not impede searches for generality provided the spatial limits of patterns are also understood. The challenge now is to relate patterns and process across space (Bertness and Ewanchuk 2002) and integrate these contemporary effects with historical events and regional processes (Graham et al. 2003).
An experimental patch reef constructed as ‘monospecific *Ecklonia radiata*’ at West Island, South Australia (photo by the author).
“…what [do] we need to know in order to predict how communities are assembled from the total species pool?”

J. M. Diamond, 1975

Ecology and Evolution of Communities, p.385

“Whether ecological communities are patterned structures…or idiosyncratic collections of species has long been a central issue of ecology”

J. A. Drake, 1990

Trends in Ecology and Evolution, 5: p.159

“It would be good to be able to take a short list of abiotic conditions and predict assemblage composition.”

E. Weiher & P. A. Keddy, 1999

Ecological Assembly Rules: perspectives, advances, retreats, p.261
Chapter 4: Preamble

Chapter 4 presents data from a manipulative experiment testing the effects of the presence and composition of algal canopies on the assembly of understorey algae to rocky substrata. Several physical variables are also quantified among treatments to provide the basis for process-oriented models accounting for the observed patterns.

At the time this thesis was submitted (May 2005), this chapter was under peer-review with the journal Oecologia, with myself as senior and corresponding author, and Sean D. Connell (University of Adelaide) as co-author. It is, therefore, written in plural.

Contributions and signatures of authors

ANDREW D. IRRING

Designed and implemented the experiment, sampled, analysed, and interpreted all data, wrote manuscript as senior and corresponding author.

Signed:........................................ Date:..........................

SEAN D. CONNELL

Supervised development of research, data interpretation, and manuscript evaluation.

Signed:........................................ Date:..........................
CHAPTER 4

PREDICTING UNDERSTOREY STRUCTURE FROM THE PRESENCE AND COMPOSITION OF CANOPIES: AN ASSEMBLY RULE FOR MARINE ALGAE

4.1 ABSTRACT
Assembly rules provide a conceptual framework for predicting community structure under defined environmental conditions. Habitat created by canopy-forming algae (e.g. kelps) provides a promising system to identify assembly rules because canopies typically have a large and predictable influence on understorey communities. Across > 1000 km of subtidal South Australian coastline, we quantified natural associations between assemblages of understorey algae and (i) monospecific canopies of *Ecklonia radiata*, (ii) canopies comprised of *E. radiata* mixed with Fucales (*Cystophora* spp., *Sargassum* spp., etc.), and (iii) gaps among canopies of algae. We were able to recreate these associations by testing the assembly of understorey algae on unoccupied substrata within experimental reefs constructed as monospecific *E. radiata*, mixed *E. radiata*-Fucales, and gaps. We propose the assembly rule that understorey communities on subtidal rocky coast in South Australia can be expected to be (i) monopolised by encrusting coralline algae beneath monospecific canopies of *E. radiata*, (ii) comprised of encrusting corallines, encrusting non-corallines, and sparse covers of articulated corallines, beneath mixed *E. radiata*-Fucales canopies, and (iii) comprised of extensive covers of articulated corallines and filamentous turfs, as well as sparse covers of foliose algae and juvenile canopy-formers, within gaps. Consistencies between natural patterns and experimental effects demonstrate how algal canopies can act as a filter to limit which subsets of species from the locally available pool are able to assemble beneath them. Moreover, the subsets of species that assemble to subtidal rocky substrata in South Australia appear predictable given knowledge of the presence and composition of canopies incorporating *E. radiata*.

4.2 INTRODUCTION
A central goal of community ecology is to achieve a predictive understanding of how different communities are assembled from a common species pool. Development of
theory known as ‘assembly rules’ has provided a conceptual framework for realizing this objective (Weiher and Keddy 1999). Formally introduced by Diamond (1975), and subsequently debated, rationalized and refined by many (e.g. Connor and Simberloff 1979; Drake 1990; Weiher and Keddy 1999), assembly rules define the conditions that cause pattern in community structure. Predicated on knowledge that such patterns are non-random (i.e. ‘communities’ are not merely coincidental collections of species) (Connor and Simberloff 1979), assembly rules predict which subset of the available species pool will occur in a specified habitat. As such, they may invoke numerous physical and biological ‘filters’ (sensu Keddy 1992) that allow some species to contribute to the structure of the community, while preventing others.

For decades, ecologists have debated whether plant communities represent repeatable associations structured by interdependence among species, or merely coincidental collections of taxa with similar adaptations to the abiotic environment (Callaway 1997). A remarkable quantity of observational and experimental evidence demonstrates interdependence among plant species, manifest through numerous positive (e.g. facilitation: Callaway 1995) and negative interactions (e.g. competition: Grace and Tilman 1990). Where the presence of one species facilitates or suppresses the distribution and abundance of others, such interactions may effectively direct the structure of the community, and therefore represent an assembly rule for that particular community. Assembly rules are believed to occur in plant communities (Diaz et al. 1998; Cody 1999), but have been considered by some to be difficult to detect because of subtle effect sizes and large variation in natural systems (e.g. Wilson 1999).

Habitat created by canopy-forming vegetation provides a promising system to identify assembly rules because canopies typically have a large and predictable influence on the distribution and abundance of understorey flora (e.g. Callaway 1995; McPherson and Weltzin 1998). Subtidal canopies of algae (e.g. kelp forests) form one of the most extensive marine habitats in the temperate world, and frequently coexist with understorey algae (e.g. encrusting and articulated coralline algae) that differ greatly from those observed within gaps among canopies.
(e.g. filamentous and foliose algae) (Kennelly 1987a; Chapman and Johnson 1990; Chapter 3). Experimental removal of canopies typically results in changes to the structure of the understorey community such that they become more similar to those naturally observed within gaps (Kennelly 1987a; Edwards 1998; Melville and Connell 2001), with such observations highlighting a clear influence of canopies on the assembly of understorey. As such, rules for the assembly of understorey may be broadly based on the presence-or-absence of canopies.

Heterogeneity in the structure of understorey communities is not just associated with the presence-or-absence of canopies, but also with variation in the composition of canopies. Broadly, canopy-forming algae can exist in monospecific stands and also as mixed-species aggregations (Chapman and Johnson 1990; Goodsell et al. 2004; Chapter 2). Even at this coarse level of classification, large differences are often observed in the structure of understorey communities (Chapter 3). Therefore, it is possible that more sophisticated rules of assembly for understorey could be proposed when the composition of canopies is considered additional to their presence. Few studies have addressed this possibility because research efforts around the world have largely focussed on understanding the responses of understorey to the presence-or-absence of canopies per se, where variation in the composition of canopies is rarely described (Goodsell et al. 2004). Such knowledge is worth pursuing, however, given that both monospecific and mixed-species stands of canopy-forming algae are conspicuous subtidal habitats on temperate rocky coasts (Chapman and Johnson 1990; Goodsell et al. 2004; Chapter 2).

The specific processes driving rules for the assembly of understorey algae are likely to involve numerous physical factors modified by canopies (e.g. light intensity: Edwards 1998; Connell 2003a, water flow: Jackson and Winant 1983; Duggins and Eckman 1994). Close agreement has been observed between natural patterns of understorey structure (e.g. canopies vs gaps) and results of experimental tests of particular factors on understorey (e.g. shade vs no shade: Kennelly 1989; Connell 2003a). This knowledge has contributed greatly to a process-oriented understanding of how canopies of algae can act as filters to facilitate or suppress species from the understorey (Dayton 1975b; Bertness et al. 1999; Connell 2003a). Importantly, such information is likely to enhance the accuracy of assembly rules for understorey algae.
by helping us to better understand the causes of natural variability in the structure of understorey communities (e.g. Chapter 3).

The subtidal rocky coasts of temperate Australia support extensive covers of the canopy-forming Laminarian alga *Ecklonia radiata* (C. Agardh) J. Agardh, which can persist in dense monospecific stands or as mixed-species aggregations with canopy-forming species of Fucales (*Cystophora* spp., *Sargassum* spp. etc.) (Shepherd and Womersley 1970; Goodsell et al. 2004). Additionally, canopies are frequently punctuated by gaps created by wave energy during storms (Kennelly 1987a). We tested for differences in the structure of assemblages of understorey algae among monospecific stands of *E. radiata*, stands of *E. radiata* mixed with Fucales, and gaps, across >1000 km of continuous coastline in South Australia. We then experimentally tested for differences in the assembly of understorey algae to unoccupied substrata within these three habitats, evaluating the model that differences observed on natural reef occur because of the presence of habitat configured as monospecific *E. radiata*, mixed *E. radiata*-Fucales, or gaps. If supported, such knowledge would provide a foundation for proposing assembly rules for understorey algae in South Australia, based on the presence and composition of canopies incorporating *E. radiata*. Although a process-oriented understanding of such assembly rules was beyond the scope of this study, we provide a framework for such research by testing for differences in the intensity of four physical variables (light, sedimentation, water flow, and lamina abrasion) among all three habitats.

4.3 Materials and Methods

*Natural canopy-understorey associations*

Assemblages of understorey algae were quantified across >1000 km of continuous South Australian coastline during the austral summer of 2001/2002. Four locations, each separated by at least 100 km, were randomly chosen from areas of coast exposed to the predominant swell (Fig. 4.1). Within each location, four sites were randomly chosen (each separated by one to ten km). At each site, understorey algae (<50 mm in height) were quantified from monospecific stands of *E. radiata*, stands of *E. radiata* mixed with Fucales, and gaps among stands of canopy-forming algae
Figure 4.1. Map of South Australia showing locations sampled (shaded) and the position of West Island (site of experimental reefs). Inset: Map of Australia with South Australia shaded.
Experimental design: Habitat × Site(Location). Habitats were identified on a scale of 1 m² as (i) monospecific *E. radiata* where ≥ 80 % of the canopy cover was *E. radiata*, (ii) mixed *E. radiata*-Fucales where 40-60 % of the canopy cover was *E. radiata*, with the remaining cover consisting of canopy-forming species of Fucales (e.g. *Cystophora* spp., *Sargassum* spp.), and (iii) gaps among canopies of algae where rocky substrata did not support canopy-forming algae > 50 mm in height (Chapters 2 and 3). The abundance (percentage cover) of understorey algae within each type of habitat was quantified using the point intercept method (25 regularly spaced points in a 0.2 × 0.2 m quadrat, *n* = 8 per habitat). Replicates were separated by four to ten metres and sampling was done between three to ten metres depth at all sites.

Understorey algae were quantified as morphological groups: encrusting coralline algae, encrusting non-coralline algae, filamentous turf-forming algae, articulated coralline algae, foliose (fleshy, non-coralline) algae and juvenile stages of canopy-forming algae, after Steneck and Dethier (1994). A test for multivariate differences in the structure of understorey assemblages among habitats, sites and locations was done using a mixed-model three-way permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). Data were fourth-root transformed with permutation of residuals (reduced model) done using Bray-Curtis distance measures. Non-metric ordination plots were constructed to represent multivariate patterns, using similarity values calculated from Bray-Curtis distances. Similarity percentages (SIMPER) were used to identify the contribution of each group of understorey algae to the multivariate differences among habitats (Clarke and Warwick 1994). Tests for differences in the percentage cover of individual morphological groups were done using ANOVA. For all analyses, ‘Location’ was treated as random, ‘Site’ was treated as random and nested within ‘Location’, and ‘Habitat’ was treated as fixed and orthogonal.

**Experimental assembly of understorey**

Experimental reefs were constructed at West Island, South Australia (Fig. 4.1), in December 2002 to represent the three habitats sampled across South Australia (monospecific *E. radiata*, mixed *E. radiata*-Fucales, and gaps; *n* = 7 per habitat). Granitic boulders colonised by algae were sourced from a natural boulder reef.
(Spit Reef) and were translocated into plastic crates (0.57 m long × 0.65 m wide × 0.10 m high) located adjacent to Spit Reef at 5 m depth. Boulders supporting adult *E. radiata*, *Cystophora* spp. or *Sargassum* spp. were used to construct reefs designated as monospecific *E. radiata* or mixed *E. radiata*-Fucales, while boulders that did not support canopy-formers were used to construct reefs designated as gaps. All boulders used to construct gaps were sourced from beneath canopies of algae. When all experimental reefs were constructed, a granite boulder (0.2 – 0.25 m diameter) devoid of visible life was taken from above the intertidal region of West Island and placed at the centre of each reef. The algae recruiting to these boulders were sampled at least monthly over 357 days using the point intercept method (25 regularly spaced points in the central 0.1 × 0.1 m of each boulder) and according to the morphological groups described above. Experimental reefs were separated by 2-5 metres, with treatments maintained on a monthly basis by replacing lost or damaged canopy-forming algae with healthy individuals from Spit Reef, and by removing juvenile canopy-formers recruiting to reefs designated as gaps. Single-factor multivariate (PERMANOVA) and univariate analyses (ANOVA) were done for the final day of sampling (357th day).

There was potential for pre-existing conditions on each experimental reef (i.e. the type of algae growing on boulders used to construct the reefs) to bias the assembly of algae on the bare boulders and confound our interpretation of differences among habitats. All reefs were constructed from boulders sourced from beneath natural canopies, which ensured the pool of potential colonists on experimental reefs at the start of the experiment were locally (i.e. within each reef) consistent among treatments. Moreover, spores of marine algae generally disperse over distances of up to tens of metres (Santelices 1990), meaning that the pool of potential colonists likely extended far beyond that produced locally (i.e. by algae growing on neighbouring boulders within each experimental reef).

*Quantification of the physical environment*

Four environmental variables (light intensity, sedimentation regime, water flow and lamina abrasion) were quantified among all three habitats to provide observations for process-oriented models of proposed assembly rules. The intensity of light
(µE m⁻² s⁻¹ of photosynthetically active radiation: 400 – 700 nm) reaching the understorey was quantified in each habitat using an underwater quantum sensor (Li-Cor® LI-192SA) and surface meter (LI-250) on a cloudless day. Five experimental reefs were randomly selected from the seven available replicates of each habitat, and five measurements of light intensity (each averaged over 15 seconds) were taken on each reef. The mean and variance observed among replicate readings on each reef were analysed separately to test for differences in the average light intensity and variation in light intensity among habitats (Benedetti-Cecchi 2003). All measurements were taken within one hour (30 minutes each side of solar noon).

Differences in the rate of deposition of sediments (organic and inorganic particles < 1 mm²) among habitats were tested using cylindrical sediment traps secured to experimental reefs (n = 5 per habitat; trap dimensions = 170 mm high × 50 mm diameter; aspect ratio > 3:1 as recommended by Håkanson et al. 1989). Traps were deployed on two occasions (once for 15 days and once for 4 days). To relate the rate of sediment accumulation on boulders to the depositional environment, accumulated sediments were resuspended and cleared away from boulders before traps were deployed, by gently increasing water motion over the surfaces of boulders (via a waving motion with one hand). When traps were collected, the amount of sediment that had accumulated on the upward-facing surfaces of boulders was sampled by vacuuming an area of 50 × 50 mm using a syringe. Both deposited and accumulated sediments were oven dried at 70 °C for 48 hours before being weighed (mass (g) m⁻² d⁻¹). The amount of accumulated sediment was further analysed as a percentage of that deposited on each reef.

Quantifying water flow beneath canopies and abrasion of the substratum by canopies can be problematic because abrasion is not independent of flow (i.e. flow causes canopies to abrade). We estimated flow and abrasion in each habitat by measuring the amount of dissolution of plaster clods, followed by a series of analyses to tease apart the amount of plaster lost due to flow from that lost due to abrasion. Fifteen clods were placed within each habitat and were evenly partitioned among three treatments: (i) no cage (exposed to flow and abrasion), (ii) full cage (protected from abrasion but exposed to flow), and (iii) partial cage as a procedural control (exposed
to abrasion and flow). Cages were constructed from 50 × 50 mm galvanised steel mesh, with partial cages consisting of a base and all four sides but no roof, which exposed clods to abrasion in the presence of a cage structure (experimental design: 3 habitat × 3 cage = 9 treatment levels, n = 5). All clods were oven dried (70 °C for 48 hours) and weighed prior to placement among experimental treatments, and again after three days of submergence, with the amount of plaster lost from each clod calculated as a percentage of the original mass.

Analyses proceeded in four steps. First, we tested for artefacts of cages on flow by comparing among all three ‘cage’ treatments in gaps only (no artefacts were detected). It was not possible to test for this artefact beneath canopies since clods were exposed to both flow and abrasion. Assuming that cages also did not alter flow beneath canopies, we (second) tested for differences in flow among habitats by comparing the percentage loss of plaster from clods that were fully caged in each habitat (i.e. clods protected from abrasion but exposed to flow). Third, we tested for artefacts of cages on the loss of plaster beneath canopies (i.e. the percentage lost due to the combined effect of flow and abrasion beneath canopies) by comparing uncaged clods with those that were partially caged (no artefacts were detected). Fourth, differences in abrasion among habitats were tested by subtracting the percentage loss of plaster from fully caged treatments (absence of abrasion but presence of flow) from the percentage loss of plaster from uncaged treatments (presence of abrasion and flow). For this final analysis, replicate values were obtained by randomly pairing uncaged replicates with fully caged replicates for each habitat (n = 5).

4.4 Results

Multivariate differences among habitats

Assemblages of understorey algae differed among all three habitats on natural reef across South Australia (Table 4.1), with results from experimental reefs consistent with this widespread pattern (PERMANOVA: F2,18 = 116.95, P < 0.001, gap ≠ mixed ≠ monospecific; Fig. 4.2). On natural and experimental reefs, understorey assemblages beneath mixed-species and monospecific canopies were more similar to each other than to assemblages in gaps (smaller t-values for comparison of mixed vs monospecific than for either mixed vs gap or monospecific vs gap, Table 4.1).
Table 4.1. Result of PERMANOVA testing for differences in the structure of assemblages of understorey algae among habitats (monospecific *E. radiata*, mixed *E. radiata*-Fucales, and gaps), locations and sites on natural reef across South Australia.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>2</td>
<td>7.48</td>
<td>18.76*</td>
</tr>
<tr>
<td>Location</td>
<td>3</td>
<td>2.86</td>
<td>15.43ns</td>
</tr>
<tr>
<td>Site(Location)</td>
<td>12</td>
<td>0.19</td>
<td>3.64***</td>
</tr>
<tr>
<td>Habitat × Location</td>
<td>6</td>
<td>0.40</td>
<td>6.13ns</td>
</tr>
<tr>
<td>Habitat × Site(Location)</td>
<td>24</td>
<td>0.07</td>
<td>1.28ns</td>
</tr>
<tr>
<td>Residual</td>
<td>336</td>
<td>0.05</td>
<td></td>
</tr>
</tbody>
</table>

Pair-wise tests among habitats

<table>
<thead>
<tr>
<th>Test</th>
<th>$t$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gap vs Mixed</td>
<td>7.84***</td>
</tr>
<tr>
<td>Gap vs Monospecific</td>
<td>12.66***</td>
</tr>
<tr>
<td>Mixed vs Monospecific</td>
<td>5.99***</td>
</tr>
</tbody>
</table>

* $P < 0.05$, *** $P < 0.001$, ns $P > 0.05$
**Figure 4.2.** Non-metric ordination of understorey assemblages sampled within gaps (circles), beneath mixed-species canopies (triangles), and monospecific canopies (squares) of *E. radiata* (a) at four locations across South Australia and (b) on experimental reefs after 357 days. For ease of representation, only a single point for each location × habitat combination is shown for (a), whereas each point represents a single replicate for (b).
Moreover, multivariate differences among habitats across South Australia did not vary greatly among locations or sites (Table 4.1: non-significant Habitat × Location and Habitat × Site(Location) interactions), indicating that local-scale multivariate patterns (i.e. differences among habitats within a site) are repeated across a large extent of the coastline of South Australia.

SIMPER analyses revealed that extensive covers of articulated corallines and filamentous turfs, and sparse covers of encrusting corallines, largely distinguished assemblages within gaps from those beneath mixed-species and monospecific canopies on natural and experimental reefs (Table 4.2: gap vs mixed, and gap vs monospecific). Similarly, greater covers of articulated corallines and encrusting non-coralines primarily distinguished assemblages beneath mixed-species canopies from those beneath monospecific canopies (Table 4.2: mixed vs monospecific). Encrusting non-coralines also contributed to differences between mixed-species canopies and gaps (Table 4.2).

Univariate differences among habitats
We plot natural patterns and experimental effects together (Fig. 4.3) to assist interpretation of the extent to which experimental effects explain naturally occurring patterns, but analyses were necessarily kept separate due to the differences in sampling design (natural patterns: n = 128) and experimental design (experimental effects: n = 7). Encrusting coralline algae monopolised space beneath canopies relative to gaps, forming more extensive covers beneath monospecific than mixed-species canopies on natural (Fig. 4.3a, Table 4.3a) and experimental reefs (Fig. 4.3a, ANOVA: \( F_{2,18} = 279.88, P < 0.0001 \), SNK tests for experimental reefs: gap < mixed < monospecific; Table 4.4). At three of four locations, articulated coralline algae and turfs of filamentous algae on natural reef were more extensive within gaps than beneath canopies (Fig. 4.3b, c, Table 4.3b, c). Experimental effects were consistent with this pattern for both groups of algae (Fig. 4.3b, c, ANOVA for articulated coralline: \( F_{2,18} = 15.37, P < 0.001 \); for filamentous turf: \( F_{2,18} = 41.13, P < 0.0001 \), SNK tests: gap > mixed = monospecific for both groups; Table 4.4). Articulated corallines were also more extensive beneath mixed-species than monospecific canopies at two locations (Yorke and Fleurieu); a pattern that was not observed on experimental reefs (Fig. 4.3b, Table 4.4).
Table 4.2. Summary of SIMPER analyses: percentage contribution of each group of understorey algae to the overall dissimilarity between habitats on natural and experimental reefs (pairwise comparisons of gaps, mixed-species canopies, and monospecific canopies). Dissimilarities were calculated from Bray-Curtis distance measures.

<table>
<thead>
<tr>
<th>Natural Reef</th>
<th>Gap vs Mixed</th>
<th>Gap vs Monosp.</th>
<th>Mixed vs Monosp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Encrusting coralline</td>
<td>16.70</td>
<td>18.48</td>
<td>10.47</td>
</tr>
<tr>
<td>Articulated coralline</td>
<td>15.77</td>
<td>18.05</td>
<td>23.01</td>
</tr>
<tr>
<td>Filamentous turf</td>
<td>30.57</td>
<td>28.42</td>
<td>13.34</td>
</tr>
<tr>
<td>Foliose algae</td>
<td>10.71</td>
<td>10.09</td>
<td>18.51</td>
</tr>
<tr>
<td>Encrusting non-coraline</td>
<td>17.73</td>
<td>12.47</td>
<td>19.48</td>
</tr>
<tr>
<td>Juv. canopy-formers</td>
<td>8.52</td>
<td>12.50</td>
<td>15.19</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Experimental reefs</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Encrusting coralline</td>
<td>22.43</td>
<td>30.56</td>
<td>10.25</td>
</tr>
<tr>
<td>Articulated coralline</td>
<td>16.57</td>
<td>22.48</td>
<td>24.18</td>
</tr>
<tr>
<td>Filamentous turf</td>
<td>20.57</td>
<td>24.40</td>
<td>0.00</td>
</tr>
<tr>
<td>Foliose algae</td>
<td>14.83</td>
<td>17.49</td>
<td>0.00</td>
</tr>
<tr>
<td>Encrusting non-coraline</td>
<td>21.25</td>
<td>0.00</td>
<td>65.57</td>
</tr>
<tr>
<td>Juv. canopy-formers</td>
<td>4.36</td>
<td>5.06</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Figure 4.3. Mean percentage cover (± SE) of morphological groups of algae sampled within gaps, beneath mixed-species canopies and monospecific canopies of *E. radiata* at four locations across South Australia (Natural patterns) and on experimental reefs over 357 days (Experimental effects).
Table 4.3. Results of ANOVA testing for differences in the percentage cover of morphological groups of algae among habitats (monospecific *E. radiata* vs mixed *E. radiata*-Fucales vs gaps), locations and sites on natural reef across South Australia.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>df</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>2</td>
<td>104883.50</td>
<td>39.97***</td>
<td>6</td>
<td>2623.94</td>
<td>5.59**</td>
<td>6</td>
<td>469.33</td>
<td>2.03**</td>
</tr>
<tr>
<td>Location</td>
<td>3</td>
<td>18288.15</td>
<td>21.94***</td>
<td>12</td>
<td>833.71</td>
<td>3.61***</td>
<td>12</td>
<td>469.04</td>
<td>2.36**</td>
</tr>
<tr>
<td>Site(Location)</td>
<td>6</td>
<td>2623.94</td>
<td>5.59**</td>
<td>24</td>
<td>469.33</td>
<td>2.03**</td>
<td>24</td>
<td>124.00</td>
<td>0.62ns</td>
</tr>
<tr>
<td>Habitat × Location</td>
<td>6</td>
<td>2623.94</td>
<td>5.59**</td>
<td>24</td>
<td>469.33</td>
<td>2.03**</td>
<td>24</td>
<td>124.00</td>
<td>0.62ns</td>
</tr>
<tr>
<td>Habitat × Site(Location)</td>
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<td>336</td>
<td>199.15</td>
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<td>90.67</td>
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</tr>
<tr>
<td>Habitat</td>
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<td>5.87*</td>
<td>2</td>
<td>989.14</td>
<td>5.87*</td>
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<tr>
<td>Location</td>
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<td>8.86**</td>
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<td>Site(Location)</td>
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<td>2.41**</td>
<td>12</td>
<td>243.07</td>
<td>2.41**</td>
<td>12</td>
<td>243.07</td>
<td>2.41**</td>
</tr>
<tr>
<td>Habitat × Location</td>
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<td>168.43</td>
<td>1.29ns</td>
<td>6</td>
<td>168.43</td>
<td>1.29ns</td>
<td>6</td>
<td>168.43</td>
<td>1.29ns</td>
</tr>
<tr>
<td>Habitat × Site(Location)</td>
<td>24</td>
<td>131.07</td>
<td>1.30ns</td>
<td>24</td>
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<td>1.30ns</td>
<td>24</td>
<td>131.07</td>
<td>1.30ns</td>
</tr>
<tr>
<td>Residual</td>
<td>336</td>
<td>100.66</td>
<td></td>
<td>336</td>
<td>100.66</td>
<td></td>
<td>336</td>
<td>100.66</td>
<td></td>
</tr>
</tbody>
</table>

Data were arcsine(%) transformed. Cochran’s C-test of homogeneity of variances: *P > 0.05* for a, b, c, and f. *P < 0.05*, **P < 0.01, ***P < 0.001, ns *P > 0.05*. Transformation failed to remove heterogeneous variances for (d) and (e) (Cochran’s C-test: *P < 0.05*) and significance was judged at the more conservative *α = 0.01* (Underwood 1997). In such cases, *P < 0.01, **P < 0.001, ***P < 0.0001, ns *P > 0.01.*
Table 4.4. Natural patterns vs experimental effects among habitats for understorey algae. G = gap, MX = mixed-species canopies, MO = monospecific canopies.

<table>
<thead>
<tr>
<th>Morphological group</th>
<th>Location</th>
<th>Natural pattern</th>
<th>Experimental effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Encrusting coralline</td>
<td>Eyre West</td>
<td>G &lt; MX &lt; MO</td>
<td>G &lt; MX &lt; MO</td>
</tr>
<tr>
<td></td>
<td>Eyre East</td>
<td>G &lt; MX &lt; MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Yorke</td>
<td>G &lt; MX &lt; MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fleurieu</td>
<td>G &lt; MX &lt; MO</td>
<td></td>
</tr>
<tr>
<td>Articulated coralline</td>
<td>Eyre West</td>
<td>G = MX = MO</td>
<td>G &gt; MX = MO</td>
</tr>
<tr>
<td></td>
<td>Eyre East</td>
<td>G &gt; MX = MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Yorke</td>
<td>G &gt; MX &gt; MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fleurieu</td>
<td>G &gt; MX &gt; MO</td>
<td></td>
</tr>
<tr>
<td>Filamentous turfs</td>
<td>Eyre West</td>
<td>G &gt; MX = MO</td>
<td>G &gt; MX = MO</td>
</tr>
<tr>
<td></td>
<td>Eyre East</td>
<td>G &gt; MX = MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Yorke</td>
<td>G = MX = MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fleurieu</td>
<td>G &gt; MX = MO</td>
<td></td>
</tr>
<tr>
<td>Foliose algae</td>
<td>Eyre West</td>
<td>G = MX &gt; MO</td>
<td>G &gt; MX = MO</td>
</tr>
<tr>
<td></td>
<td>Eyre East</td>
<td>MX &gt; G = MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Yorke</td>
<td>G = MX &gt; MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fleurieu</td>
<td>G = MX = MO</td>
<td></td>
</tr>
<tr>
<td>Encrusting non-coralline</td>
<td>Eyre West</td>
<td>MX &gt; G = MO</td>
<td>MX &gt; G = MO</td>
</tr>
<tr>
<td></td>
<td>Eyre East</td>
<td>MX = MO &gt; G</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Yorke</td>
<td>G = MX = MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fleurieu</td>
<td>MX &gt; G = MO</td>
<td></td>
</tr>
<tr>
<td>Juv. canopy-formers</td>
<td>Eyre West</td>
<td>G = MX &gt; MO</td>
<td>G = MX = MO</td>
</tr>
<tr>
<td></td>
<td>Eyre East</td>
<td>G &gt; MX &gt; MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Yorke</td>
<td>G = MX &gt; MO</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fleurieu</td>
<td>G = MX &gt; MO</td>
<td></td>
</tr>
</tbody>
</table>
Differences in the covers of foliose algae and encrusting non-coraline algae among habitats were spatially variable on natural reef, yet some consistent patterns emerged. Foliose algae were generally more extensive within gaps and beneath mixed-species canopies than monospecific canopies (but see Eyre East: Fig. 4.3d, Table 4.3d), while encrusting non-coralines, although infrequently sampled, were often most abundant beneath mixed canopies (Fig. 4.3e, Table 4.3e). On experimental reefs, foliose algae were also abundant within gaps (although not beneath mixed-species canopies: Fig. 4.3d, ANOVA: $F_{2,18} = 27.50, P < 0.0001$, SNK tests: gap > mixed = monospecific; Table 4.4), while encrusting non-coralines were only sampled beneath mixed-species canopies (Fig. 4.3e, ANOVA: $F_{2,18} = 262.05, P < 0.0001$, SNK tests: mixed > gap = monospecific; Table 4.4). Juvenile canopy-formers were generally more extensive within gaps and beneath mixed-species canopies than monospecific canopies on natural reef (Fig. 4.3f, Table 4.3f), but were rarely sampled on experimental reefs (Fig. 4.3f, ANOVA: $F_{2,18} = 2.36, P > 0.12$, SNK tests: gap = mixed = monospecific; Table 4.4).

Spatial variation of differences among habitats on natural reef was evident for all groups of understorey algae. Of 16 sites in total (4 sites $\times$ 4 locations), the number of sites showing patterns inconsistent with that detected at the scale of location was five for encrusting coralline, three for articulated coralline and one for filamentous turf. A greater number of sites were inconsistent for foliose algae (11 sites), encrusting non-coralines (9 sites) and juvenile canopy-formers (13 sites). Among locations, some minor variation of pattern was observed for encrusting and articulated corallines, filamentous turfs, and juvenile canopy-formers (Fig. 4.3a, b, c, f, Table 4.4). Variability of pattern was most apparent for foliose algae and encrusting non-coralines (Fig. 4.3d, e, Table 4.4). Importantly, while we observed such natural variation in patterns among sites and locations, key patterns often emerged that were consistent with experimental effects (Table 4.4).

Environmental variables
The mean intensity of light reaching the substratum in gaps was greatly reduced by canopies of algae, especially beneath monospecific canopies of E. radiata (Fig. 4.4a, Table 4.5a). Greatest variability in the light environment occurred beneath mixed-species canopies and least variability beneath monospecific canopies.
Figure 4.4. Differences in environmental variables among gaps (G), mixed-species canopies (MX) and monospecific canopies (MO) of *E. radiata.*
Table 4.5. Results of ANOVAs ($F_{2,12}$ for all variables) testing for differences in the physical conditions among habitats, with associated SNK tests identifying the location of detected differences (G = gap, MX = mixed-species canopies, MO = monospecific canopies).

<table>
<thead>
<tr>
<th>Variable</th>
<th>$F$</th>
<th>SNK tests</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Mean light intensity</td>
<td>123.80***</td>
<td>G &gt; MX &gt; MO</td>
</tr>
<tr>
<td>(b) Variation in light intensity</td>
<td>25.57***</td>
<td>MX &gt; G &gt; MO</td>
</tr>
<tr>
<td>(c) Sediment deposition – time 1</td>
<td>0.76ns</td>
<td>G = MX = MO</td>
</tr>
<tr>
<td>(d) Sediment deposition – time 2</td>
<td>1.13ns</td>
<td>G = MX = MO</td>
</tr>
<tr>
<td>(e) Sediment accumulation - mass</td>
<td>58.07***</td>
<td>G &gt; MX &gt; MO</td>
</tr>
<tr>
<td>(f) Sediment accumulation – % of deposition</td>
<td>49.48***</td>
<td>G &gt; MX &gt; MO</td>
</tr>
<tr>
<td>(g) Flow</td>
<td>4.97*</td>
<td>G &gt; MX = MO</td>
</tr>
<tr>
<td>(h) Abrasion</td>
<td>18.10***</td>
<td>G &lt; MX &lt; MO</td>
</tr>
</tbody>
</table>

Data were arcsine(%) transformed for (f), (g) and (h). Ln(x + 1) transformation for (b) and (e) was needed to meet the assumption of homogeneity of variances (Cochran’s C-test: $P > 0.05$ for all variables). * $P < 0.05$, *** $P < 0.001$, ns $P > 0.05$
The rate of sediment deposition did not differ among habitats during each period of sampling (Fig. 4.4c, d, Table 4.5c, d), although greater rates of sediment deposition were observed at time 2 compared to time 1 (probably due to resuspension of sediments by large waves during time 2, Irving pers. obs.). The mass of sediment that accumulated on boulders, and the percentage of deposited sediments that accumulated, was an order of magnitude greater in gaps than beneath canopies, while mixed-species canopies also accumulated greater amounts than monospecific canopies (Fig. 4.4e, f, Table 4.5e, f).

No artefacts associated with the structure of cages were detected for water flow within gaps (ANOVA: $F_{2,12} = 1.16, P > 0.34$) or for the percentage loss of plaster beneath mixed-species and monospecific canopies (ANOVA: Habitat $\times$ Cage interaction: $F_{1,16} = 0.70, P > 0.41$). Hence, the presence of cages did not confound interpretation of the effects of habitat on flow and abrasion. Among clods that were fully caged, loss of plaster was greatest in gaps but did not differ between mixed-species and monospecific canopies (Fig. 4.4g, Table 4.5g). We interpret this as a reduction in water flow beneath canopies relative to gaps. The difference in the loss of plaster between fully caged and uncaged clods was greater beneath monospecific than mixed-species canopies (Fig. 4.4h, Table 4.5h), indicating that the intensity of lamina abrasion is greater within monospecific stands. Calculations of the loss of plaster due to abrasion indicated that some loss occurred in gaps (~3%), where abrasion by canopies can not occur. This loss can not be quantitatively explained in the present study, but may represent effects of drift algae or suspended sediments abrading clods within gaps.

4.5 DISCUSSION

One of the most striking and frequently cited patterns from subtidal rocky coasts of the temperate world is that the type and abundance of benthic algae growing beneath canopies of algae (e.g. kelps) differs greatly from that observed within gaps among canopies (e.g. north-west Atlantic: Chapman and Johnson 1990, Alaska: Dayton 1975b, California: Edwards 1998, Australia: Fowler-Walker and Connell 2002; Chapter 3). Our observations from South Australia are consistent with this widespread pattern, highlighting associations of understorey algae with canopies (e.g. encrusting corallines) or gaps (e.g. articulated corallines and filamentous turfs).
that are repeated with great fidelity across > 1000 km of coastline. Additionally, we observed variation in the structure of understorey communities between canopies of different composition (i.e. monospecific vs mixed-species). Although ecological differences between monospecific and mixed-species canopies of terrestrial vegetation are well known (e.g. Cannell et al. 1992), such information is remarkably rare among stands of canopy-forming algae in marine systems. Nevertheless, consistent differences between monospecific and mixed-species canopies of *E. radiata* suggest that partitioning observations between these two types of habitat could enhance predictive power in a system where enormous spatial variability is often emphasised (e.g. Wernberg et al. 2003).

Manipulating the presence and composition of canopies (monospecific *E. radiata* vs mixed *E. radiata*-Fucales vs gaps) demonstrated that we could recreate natural patterns of understorey structure using experimental protocols. Such consistencies illustrate how the presence and composition of canopies can act as a filter to limit which subsets of species from the locally available pool are able to coexist with canopies (monospecific or mixed-species). The presence of canopies enhanced the abundance of encrusting corallines, with greater covers observed beneath monospecific relative to mixed-species canopies. Additionally, mixed-species canopies typically supported greater covers of encrusting non-coralline algae than either monospecific canopies or gaps. Both articulated corallines and filamentous turfs were more extensive in gaps than beneath canopies, although mixed-species canopies often supported greater covers of articulated corallines relative to monospecific canopies on natural reef, but not on experimental reefs. Considerable spatial variability in the abundance of foliose algae among habitats may be attributable to the large number of species (mainly Rhodophytes and Chlorophytes) included in this group. Species of Rhodophyta and Chlorophyta can vary greatly in their resource requirements (e.g. differing demands for light: Gómez et al. 2004), and therefore it is perhaps not surprising that ‘foliose algae’ exhibited no clear association with one type of habitat over another. Juvenile canopy-formers were typically most abundant within gaps and beneath mixed-canopies on natural reef, but poor recruitment to all experimental reefs precluded a meaningful comparison between natural and experimental results. Such inconsistencies may be due to a probable difference in the ages of experimental (~1 year) and natural communities.
(> 1 year), whereby insufficient time was allowed for the recruitment and growth of some types of algae on experimental reefs. Importantly, while some inconsistencies were observed, key patterns frequently emerged that were consistent between natural and experimental reefs.

Consistencies between natural patterns and experimental effects provide a foundation for proposing assembly rules for understorey algae. The general pattern emerging from this research is that the subsets of species that assemble to subtidal rocky substrata in South Australia are predictable given knowledge of the presence and composition of canopies incorporating *E. radiata*. Specifically, we propose the following assembly rule: subtidal assemblages of understorey algae on exposed rocky coasts of mainland South Australia (i.e. Chapter 3) can be expected to be (i) monopolised by encrusting coralline algae where *E. radiata* forms monospecific canopies, (ii) comprised of encrusting corallines, encrusting non-corallines, and sparse covers of articulated corallines, where canopies of *E. radiata* are mixed with Fucales (i.e. *Cystophora* spp., *Sargassum* spp.), and (iii) comprised of extensive covers of articulated corallines and filamentous turfs, as well as sparse covers of foliose algae and juvenile canopy-formers, where canopies are absent (i.e. within gaps). It is necessary to test the utility of this rule as a general predictor of ecological pattern. In other words, does this rule apply to all subtidal coasts supporting *E. radiata*? Spatial variability in canopy-understorey associations among biogeographic regions (e.g. southern vs eastern Australia: Chapter 3), and even within regions (e.g. Fig. 4.3, Table 4.4) suggests limits to the generality of this rule. Even so, we wish to emphasize the worth of proposing such rules for providing a testable framework that may increase our predictive understanding of how understorey communities assemble on rocky coasts.

The predictive power of assembly rules is likely to be enhanced where they include knowledge of the specific processes affecting the assembly of communities. Modification of the physical environment by canopies of algae appears key to explaining observed differences in the assembly of understorey. Monospecific and mixed-species canopies of *E. radiata* greatly reduced the intensity of light reaching the understorey. Such conditions favour the growth of encrusting corallines (Figueiredo et al. 2000; Chapter 6), but appear to inhibit the growth of articulated
corallines and filamentous turfs (Kennelly 1989; Connell 2005). Greatest variability in the intensity of light was observed beneath mixed-species canopies, which may contribute towards enhanced growth and survival of articulated corallines and foliose algae beneath mixed-species canopies relative to monospecific canopies. The rate of sediment deposition was similar among the three habitats, although the amount of sediment that accumulated on understorey boulders was greatly reduced beneath canopies. The combination of enhanced light and sedimentation conditions (i.e. within gaps) is known to facilitate erect species of algae that incorporate sediments into their structure (i.e. turf-forming and articulated coralline algae), whereas reduced light and sediment accumulation (i.e. beneath canopies) facilitates encrusting coralline algae (Connell 2005).

Water flow was slightly greater in gaps than beneath canopies, which is consistent with observations from other forests of algae (Jackson and Winant 1983; Duggins and Eckman 1994). Little information is available on the effects of variable water flow on understorey algae, but reduced amounts of flow may contribute toward differences in understorey by affecting the dispersal and delivery of spores to suitable substrata (Santelices 1990). Abrasion of the understorey by the lamina of canopy-formers generally has negative effects on the abundance of articulated corallines and filamentous turfs (Cheroske et al. 2000; Chapter 5). We observed that the intensity of abrasion was greater beneath monospecific than mixed-species canopies, which may contribute toward an explanation of why greater covers of articulated corallines are often observed beneath mixed-species canopies. In sum, it appears that canopies of *E. radiata* can strongly modify physical conditions to create heterogeneous but largely predictable patterns in the assembly and maintenance of understorey (Connell 2005).

Spatial consistency of pattern gives weight to arguments that it may be possible to scale-up knowledge from smaller to larger scales (Thrush et al. 1997) and increase our predictive understanding of natural systems. Encrusting corallines, articulated corallines and filamentous turfs characterise much of the benthic habitat across temperate Australia (Underwood et al. 1991; Chapter 3), and differences in their covers among habitats were largely consistent from site to site in South Australia. As such, constraints imposed by canopies on the assembly of these understorey
species to rocky substrata appear predictable from local-scales (i.e. within a site) to larger scales (i.e. among sites and locations) on comparable coastlines. In contrast, differences in the covers of other groups (e.g. foliose algae) among habitats were variable among sites and locations, suggesting poor predictability in knowledge of their association with canopy-formers.

Generalities in ecology may present themselves as broadly repeatable patterns and responses in nature (Lawton 1999; Fowler-Walker and Connell 2002). Similar to stands of marine algae, understorey vegetation within stands of terrestrial canopy-formers often differs greatly to that which occupies gaps (Callaway 1995). Removal of terrestrial canopies often enhances the abundances of fast-growing opportunistic understorey species (e.g. grasses and herbs in beech-hemlock forest: Peterson and Pickett 1995, oak woodlands: McPherson and Weltzin 1998). Greater covers of opportunistic species following of canopy-loss are also observed among stands freshwater (e.g. reed marsh: Lenssen et al. 1999) and marine vegetation (e.g. kelp forests: Edwards 1998), suggesting general responses of understorey to canopy-loss across widely differing environments. It would be valuable to know whether the processes driving such responses are similar among systems. For example, canopies typically reduce the intensity of light and understorey taxa often respond predictably (positively, negatively, or neutrally) to such changes in the light environment (e.g. tropical forests: Watling and Press 2000, marine forests: Chapter 6).

We acknowledge that differences in the extent of a canopy, its composition, and so on will modify the influence of light, but we wish to emphasise that there is potential for tests of generalities in the effects of canopies on the assembly of understorey communities within relatively similar environments (e.g. tropical vs temperate rain forest) and between widely different environments (e.g. oak woodlands vs kelp forests).

In conclusion, contemporary ecology is shifting towards a sophisticated understanding of the environmental factors that cause pattern in nature (Keddy 1999). To this end, the concept of assembly rules allows us to propose testable predictions about the structure of communities based on defined environmental conditions. We propose that the structure of subtidal understorey communities of algae in South Australia may be predicted from knowledge of the presence and
composition of canopies incorporating *E. radiata*. Testing whether this prediction can be generalized to other coastlines supporting *E. radiata*, or even to canopies formed by species other than *E. radiata*, would provide an indication of its spatial and taxonomic limitations. Regardless of the results of such tests, we emphasise the potential of assembly rules as a useful tool for increasing our predictive understanding of the organisation of understorey communities beneath subtidal canopies of marine algae. Indeed, where knowledge of generality and predictability in ecology is embraced (Peters 1991), assembly rules show great promise for progressive outcomes.
Effects of abrasion by canopies of *Ecklonia radiata* on articulated coralline algae: sparse covers of articulated coralline exposed to abrasion (top) vs extensive covers of articulated coralline protected from abrasion via caging (bottom) (photos by the author).
"What does a tree do in a forest?"


Ecology, 78: p.1946

"...biologically generated habitats set the stage for a multitude of positive, neutral, and negative species interactions…"

J. F. Bruno & M. D. Bertness, 2001

Marine Community Ecology, p.201
Chapter 5: Preamble

Chapter 5 presents the results of an experimental test for negative effects of algal canopies on the abundance of articulated corallines and filamentous turfs, including a test of the contribution that abrasion by the canopy makes to the negative effects of canopies per se. Differences in the effects of canopies and abrasion between monospecific and mixed-species canopies are also tested.

At the time this thesis was submitted (May 2005), this chapter was being prepared for submission to the journal Marine Ecology Progress Series, with myself as senior and corresponding author, and Sean D. Connell (University of Adelaide) as co-author. It is, therefore, written in plural.

Contributions and signatures of authors

ANDREW D. IRVING

Designed and implemented the experiment, sampled, analysed, and interpreted all data, wrote manuscript as senior and corresponding author.

Signed:................................. Date:.............................

SEAN D. CONNELL

Supervised development of research, data interpretation, and manuscript evaluation.

Signed:................................. Date:.............................
CHAPTER 5

PHYSICAL DISTURBANCE BY KELP ABRADERS ERECT ALGAE FROM THE UNDERSTOREY

5.1 ABSTRACT
Positive and negative interactions among organisms are key determinants of pattern in the distribution and abundance of species. Beneath subtidal canopies of the stipitate kelp *Ecklonia radiata* (Laminariales), we observed sparse covers of erect algae (articulated coralline algae and filamentous turf-forming algae) that were extensive where canopies were absent. Moreover, articulated corallines occurred in greater abundance beneath canopies of *E. radiata* mixed with canopy-forming species of Fucales than beneath monospecific canopies of *E. radiata*. We experimentally tested the hypotheses that (i) canopies negatively affect the abundance of articulated corallines and filamentous turfs, whereby (ii) abrasion by canopies contributes to these negative effects, for which (iii) effects on articulated corallines would be greater beneath monospecific canopies than mixed-species canopies, but effects on filamentous turfs would not differ between types of canopy. Experiments revealed large negative effects of canopies on the abundance of articulated corallines and filamentous turfs, to which abrasion made a substantial contribution (~70 – 80% for articulated coralline and ~60% for filamentous turf). Moreover, the intensity of abrasion was greater beneath monospecific than mixed-species canopies, which was consistent with differences in the effect of canopies and abrasion on articulated corallines (monospecific > mixed-species), but not filamentous turfs (monospecific = mixed-species). Although abrasion is one of many influences of canopies, our results show that it can contribute substantially to the heterogeneity of understorey habitat on subtidal rocky coasts. Understanding the role of abrasion relative to other local-scale processes (e.g. shading by the canopy) will provide greater insight into the mechanisms that establish and maintain patterns of canopy-benthos associations in kelp forests.
5.2 **Introduction**

Strong positive and negative associations among organisms often exist because habitat-forming species facilitate the presence of specific sets of taxa (positive association), but exclude others (negative association) (Jones et al. 1997; Bruno and Bertness 2001). Patterns of association among organisms are often well understood, and can be sufficiently strong and repeated with great fidelity to be observable from local (km) to regional scales (1000's km) (Callaway et al. 2002; Chapter 3). Even so, there is often much to learn about the mechanisms that shape and maintain them. Intensive research of positive and negative associations often demonstrates causation through numerous mechanisms that can act in isolation or combination and whose effects may vary across time and space (Callaway 1992; Leonard 1999; Bertness and Ewanchuk 2002). An essential prerequisite to such knowledge is to identify relevant factors that contribute to the establishment and maintenance of associations of interest (Leonard 1999; Bruno 2000).

Subtidal rocky coasts at temperate latitudes are characterized by the presence of extensive forests of canopy-forming algae (e.g. kelps) that are widely thought of as heterogeneous systems typified by patchiness in the presence and composition of canopies (Duggins 1983; Dayton et al. 1984; Harrold and Reed 1985; Schiel and Foster 1986; Dayton et al. 1992; Konar and Estes 2003). Algal forests create habitat for a phyletically diverse complement of flora and fauna (Steneck et al. 2002), yet their heterogeneous structure appears to have large effects on associated organisms. A striking pattern observed around the world is that the type and abundance of understorey algae that occupy space beneath algal canopies often differs greatly from that observed within gaps among canopies (Kennelly 1987a; Edwards 1998; Chapter 3). While extensive covers of algae with prostrate forms of growth (e.g. encrusting coralline algae) are frequently associated with canopies of algae (Steneck 1986; Witman and Dayton 2001), such taxa may coexist with erect species of algae, such as articulated corallines (e.g. California: Dayton et al. 1984; Clark et al. 2004; eastern Australia: Kennelly 1987a; north-eastern New Zealand: Schiel 1988; Chile: Santelices and Ojeda 1984a). In other regions, however, erect algae that form “turfs” (*sensu* Hay 1981) are sparse beneath canopies but are primarily associated with gaps among canopies (e.g. western and southern Australia: Melville and Connell 2001; Chapter 3; United Kingdom: Hawkins and Harkin 1985; Figueiredo et al. 1996; Italy: 87
Benedetti-Cecchi et al. 2001; Bulleri et al. 2002). Irrespective of their nature (direction), canopy-understorey associations in algal forests can be repeated with great consistency across scales of kilometres to 1000’s km (Fowler-Walker and Connell 2002).

Conspicuous effects of algal canopies on understorey algae have been demonstrated in many locations around the world through experimental clearances and additions of canopies (e.g. Dayton 1975b; Reed and Foster 1984; Kennelly 1987a). Where canopies are cleared, assemblages of understorey algae typically become similar to those observed within gaps (Ojeda and Santelices 1984; Edwards 1998; Benedetti-Cecchi et al. 2001). Likewise, assemblages within natural gaps become similar to those observed beneath canopies when canopies are added (Melville and Connell 2001). Such responses by understorey algae can occur quickly (within weeks: Ojeda and Santelices 1984; Melville and Connell 2001) and may persist for years (Kennelly 1987a; Benedetti-Cecchi et al. 2001). Experimental manipulations of canopy presence-or-absence have clearly demonstrated that canopies of algae act to facilitate and exclude algae from the understorey (also see Chapter 4). However, knowledge of the mechanisms driving these effects is limited.

Canopies of algae can modify many biological and physical properties of the local environment, creating vastly different conditions to those experienced away from the canopy (Jackson and Winant 1983; Eckman et al. 1989; Clark et al. 2004). Accordingly, numerous factors are likely to contribute to the large effects of canopies on understorey. Shade provided by canopies is probably the most widely tested, and is known to have large effects on the abundance of understorey taxa that are often consistent with the experimental provision of shade (Kennelly 1989; Duggins et al. 1990; Connell 2003a). However, the ‘sweeping’ action of laminae across the substratum (abrasion) is also thought to contribute to the effects of canopies on understorey by excluding taxa susceptible to such physical disturbance (Velimirov and Griffiths 1979). Morphological differences among species of canopy-forming algae mean that not all canopies abrade the substratum (e.g. erect algae with stipes that exceed the length of their laminae; Reed and Foster 1984). Nevertheless, where abrasion by the canopy occurs, experiments have consistently revealed strong negative effects on the abundance of sessile invertebrates (Jenkins et al. 1999;
Leonard 1999; River and Edmunds 2001; Connell 2003b). In contrast, the consequences of abrasion to understorey algae are poorly understood. Strong negative effects of abrasion on turf-forming species of filamentous algae were detected by Cheroske et al. (2000), but Kennelly (1989) failed to detect any substantial effect of abrasion on several species of understorey algae. Such inconsistencies highlight the need for a better understanding of the role of abrasion by canopies of algae for shaping the distribution and abundance of understorey algae.

The rocky subtidal coasts of temperate Australia support extensive covers of the canopy-forming Laminarian alga *Ecklonia radiata* (C. Agardh) J. Agardh and numerous canopy-forming species of Fucales (Womersley 1987). *E. radiata* can form dense monospecific stands (typically 0.3 – 2 m in height; Womersley 1987) or can exist in mixed-species aggregations with species of Fucales (e.g. *Cystophora* spp., *Sargassum* spp., *Scytosiphon dorycarpa*. etc.; Shepherd and Womersley 1970; Goodsell et al. 2004). Additionally, established canopies are frequently punctuated by gaps where canopy-forming individuals have been removed by disturbance (e.g. storms: Kennelly 1987a). Across the western and southern regions of temperate Australia, erect algae such as articulated coralline algae and filamentous turf-forming algae (a complex of closely packed, erect filaments of numerous species of algae; *sensu* Hay 1981) monopolise space within gaps but are sparse beneath canopies (Shepherd and Womersley 1970; Fowler-Walker and Connell 2002; Chapter 3). Even so, articulated corallines typically form more extensive covers beneath mixed-species canopies (*E. radiata* with Fucales) than beneath monospecific canopies of *E. radiata*, although filamentous turfs are conspicuously absent beneath both types of canopy (Chapter 3). While shade provided by canopies of *E. radiata* can explain much of the variation in the abundance of understorey taxa (Kennelly 1989; Connell 2003a, b), tests of abrasion by canopies of *E. radiata* have yielded inconsistent results (e.g. negative effects in Connell 2003b vs negligible effects in Kennelly 1989). We propose abrasion by the canopy as a mechanism to account for the negative association of articulated coralline algae and filamentous turf-forming algae with canopies of *E. radiata*.

In this study, we quantified natural associations of articulated coralline algae and filamentous turf-forming algae with monospecific canopies of *E. radiata*, canopies of
E. radiata mixed with species of Fucales, and gaps among canopies at our experimental site (West Island, South Australia) and at four nearby sites. We then tested the hypotheses that (i) the percentage cover of articulated corallines and filamentous turfs would be negatively affected by canopies (monospecific and mixed-species) if translocated from gaps to beneath canopies, and (ii) such negative effects of canopies would be reduced if articulated corallines and filamentous turfs were protected from abrasion beneath the same canopies (i.e. abrasion contributes to the negative effect of canopies). We further tested that (iii) the magnitude of this negative effect of canopies, including that of abrasion, would be greater beneath monospecific canopies than mixed-species canopies for articulated corallines, but that the negative effects of canopies and abrasion on filamentous turfs would not differ between monospecific and mixed-species canopies.

5.3 Materials and Methods

Natural patterns

Natural differences in the abundance (percentage cover) of articulated corallines and filamentous turfs were quantified among three benthic habitats (monospecific canopies of E. radiata, canopies of E. radiata mixed with species of Fucales, and gaps among canopies; see definitions below) at five sites spanning > 50 km of the coastline of South Australia (including the experimental site at West Island, 35° 37' S, 138° 35' E). All sites supported extensive covers of canopy-forming algae and were of similar exposure to wave energy. Three habitats, known to influence the abundance of benthic plants (Chapter 3) and animals (Goodsell et al. 2004), were identified on a scale of 1 m² as: (i) 'monospecific E. radiata' when ≥ 80 % of the canopy cover was E. radiata, (ii) mixed E. radiata-Fucales when 40-60 % of the canopy cover was E. radiata and the remaining cover consisted of canopy-forming species of Fucales (e.g. Cystophora spp., Sargassum spp., Scytothalia dorycarpa), and (iii) gaps among canopies when rocky substrata did not support canopy-forming algae (Goodsell et al. 2004; Chapter 2). At each site, quadrats (0.2 × 0.2 m) were haphazardly placed within patches of each habitat and were positioned > 1 m from the edge of a patch. The percentage cover of articulated coralline and filamentous turf was quantified using the point intercept method (25 regularly spaced points within the 0.2 × 0.2 m quadrat). Replicates (n = 8) were separated by one to ten metres and sampling was done between depths of three to nine metres at all sites.
Differences in the abundance of articulated corallines and filamentous turfs among habitats and sites were tested with ANOVA, treating ‘Site’ as random and ‘Habitat’ as fixed and orthogonal.

Experimental effects of canopies and abrasion

Experimental tests of the effects of canopies and abrasion on articulated corallines and filamentous turfs were done at Abalone Cove, West Island, where extensive forests of canopy-forming algae occupy space on the natural boulder reef at 2 – 5 m depth (Shepherd and Womersley 1970; Connell 2003b). An orthogonal manipulation of the type of canopy (monospecific vs mixed-species) and abrasion (presence vs absence) was used to test (i) the effect of canopies per se, and (ii) the effect of abrasion by canopies on the abundance of articulated corallines and filamentous turfs beneath each type of canopy. Small boulders (0.2 – 0.3 m diameter) that naturally supported extensive covers of articulated coralline algae (*Halimeda roseum* (Lamarck) Garbary & Johansen) or filamentous turf-forming algae (primarily a complex of *Feldmannia* spp., *Ectocarpus* spp., *Sphacelaria* spp. and *Giffordia* spp.; Copertino et al. 2005) were translocated from natural gaps to beneath monospecific and mixed-species canopies (*n* = 15 boulders each for corallines and turfs). Beneath each type of canopy, five boulders supporting corallines and five supporting turfs were exposed to all effects of canopies (including abrasion), while another five boulders (corallines and turfs) were protected from abrasion but still exposed to all other effects of canopies (shade, etc). Abrasion was prevented by caging boulders within 50 × 50 mm galvanized mesh, thereby eliminating physical contact between the canopy and experimental boulders. Possible artifacts of the cages were tested by placing the remaining five boulders (both coralline and turf beneath each type of canopy) within a partial cage that had elements of the full cage structure but still allowed abrasion (procedural control: a base and four sides but no roof). Any differences between the partial cage treatment and that where abrasion was allowed (no cage) would suggest an artifact of the cage structure. Cages were designed to allow access to small (< 50 mm) benthic herbivores (e.g. gastropods) but probably excluded larger herbivores (e.g. adults of the urchin *Heliocidaris erythrogramma*). *H. erythrogramma*, however, are sparsely distributed on the coastline of southern Australia relative to comparable coasts in temperate Australia (e.g. eastern Australia: Fowler-Walker and Connell 2002) and primarily feed on drift algae.
Immediately prior to translocation, the percentage cover of articulated coralline or filamentous turf growing on each boulder was estimated using the point intercept method (25 regularly spaced points in the central $0.1 \times 0.1$ m of the boulder). Once translocated, we ensured that the upward facing surface of each boulder was positioned the same distance away from the canopy as surrounding boulders by replacing a boulder naturally present beneath the canopy with the experimental boulder (and cage). The percentage cover of algae on each boulder was sampled irregularly throughout the duration of experiment (55 days for articulated corallines, 36 days for filamentous turfs). Differences in the percentage cover among treatments of coralline and turf retained on boulders at the end of the experiment were tested using two-way ANOVA, treating ‘Canopy’ and ‘Abrasion’ as fixed and orthogonal. In addition, we tested for differences in key variables (depth, density of $E. radiata$, length of $E. radiata$ stipe and thallus) between our experimental patches of monospecific and mixed-species canopies, because such variables can affect understorey taxa (e.g. Kendrick et al. 1999; Fowler-Walker et al. 2005) and the intensity of abrasion (Kennelly 1989).

The magnitude of the effect of canopies per se on articulated corallines and filamentous turfs, and the contribution of abrasion alone to this effect, was compared between canopies (monospecific vs mixed-species). The effect of canopies was estimated by calculating the differences between the final and initial percentage covers in treatments exposed to the entire effect of canopies (i.e. no cage). The contribution of abrasion to this effect was estimated by (i) calculating the difference between the final and initial covers in treatments protected from abrasion (i.e. effects of canopies in the absence of abrasion) and (ii) subtracting this value from the effect of canopies calculated above. Differences attributable to abrasion were obtained by randomly pairing one ‘protected’ replicate with one ‘exposed’ replicate boulder for each type of canopy, and were analysed using ANOVA.

The process of translocating boulders from gaps to beneath canopies is a physical disturbance that has the potential to affect the abundance of articulated corallines and filamentous turfs, and potentially confuse our interpretation of the effects of canopies and abrasion. Hence, all boulders were translocated over similar distances (between
3 - 10 m) and care was taken to ensure the original and final positions of boulders were at similar depths (addition of canopies, of course, was likely to alter factors such as shade, water flow etc.). Nevertheless, we tested for effects of disturbance by (i) lifting five boulders supporting corallines and five supporting turfs within natural gaps and replacing them in their original positions (vertical disturbance), and (ii) translocating five boulders supporting corallines and five supporting turfs from natural gaps into other natural gaps located 3 - 10 m away (horizontal disturbance).

The percentage cover of corallines (55 days) and turfs (36 days) on these boulders was compared to that on unmoved boulders (controls) located within gaps. Any differences between moved (lifted or translocated) and unmoved boulders would indicate an effect of translocation.

Assessment of abrasion

Relative differences in the intensity of abrasion beneath monospecific and mixed-species canopies were tested using two methods. First, following the method of Kennelly (1989), 14 white ceramic tiles (0.14 x 0.14 m) were coated with a thin layer of red water-soluble paint and placed beneath monospecific and mixed-species canopies (n = 7 tiles per type of stand). Tiles were positioned the same distance away from the canopy as surrounding natural boulders and were exposed to lamina abrasion for three minutes, after which the percentage of white tile exposed was quantified using the point-intercept method (25 regularly spaced points within the central 0.1 x 0.1 m of each tile). Rather than representing the average intensity of abrasion through time, the amount of white tile exposed was used simply as an indicator of the relative intensity of abrasion between monospecific and mixed-species canopies. A further seven tiles were placed in natural gaps for three minutes to provide an estimate of the dissolution of paint in the absence of abrasion, which was presumably due to water motion (flow) over the surface of the tile.

Second, the loss of mass from plaster clods beneath monospecific and mixed-species canopies was tested using the same design as that which tested the effect of canopies and abrasion on corallines and turfs (2 canopy x 3 abrasion treatments, n = 5 per treatment). Beneath canopies, attributing the loss of plaster to abrasion can be problematic because both abrasion (mechanical removal) and water motion (dissolution) can cause loss of plaster from clods. Hence, we interpret the difference
between the amount of plaster lost from clods that were exposed to abrasion (i.e. no cage and partial cage: abrasion and water motion) and those that were protected from abrasion (i.e. full cage: water motion only) as being attributable to abrasion. Partial cages were again used to test for artifacts of cages on the loss of plaster from clods. All clods were made from the same mixture of plaster and were oven dried at 70°C for 48 hours before being weighed. Clods were then placed into appropriate treatments during moderate to strong swell conditions for Abalone Cove (2 m swells vs 0.5 – 1 m average summer swells, Irving pers. obs.) and were left for 3 days before being collected, oven dried (70 °C for 48 hours) and weighed. The amount of plaster removed was measured as the percentage loss of mass from each clod. Plaster clods were also placed within natural gaps to indicate the amount of dissolution of plaster in the absence of abrasion but presence of water motion. Here, full and partial cages were again used in conjunction with a ‘no cage’ treatment, with the prediction that the percentage of plaster lost would not differ among the three treatments.

5.4 Results

Natural patterns

At four of five sites, articulated coralline algae occurred in greater abundance within gaps than beneath canopies, but were also more extensive beneath mixed-species than monospecific canopies (Fig. 5.1a, Table 5.1a, SNK tests: gap > mixed > monospecific). At site 4, similar covers were observed within gaps and beneath mixed-species canopies (i.e. gap = mixed > monospecific). The cover of filamentous turfs was greater within gaps than beneath canopies (i.e. gap > mixed = monospecific) at all sites except site 2, where no differences among habitats were detected (Fig. 5.1b, Table 5.1b).

Experimental effects on articulated corallines

At the beginning of the experiment, all boulders supported similar covers of articulated coralline algae among treatments (ANOVA: $F_{3,36} = 0.61, P > 0.75$). After 55 days, boulders protected from abrasion (full cage) still supported extensive covers of articulated coralline, similar to the covers sampled on boulders that remained within gaps (Fig. 5.2a). In contrast, the covers of articulated coralline on boulders exposed to abrasion (no cage and partial cage) were reduced relative to boulders.
Figure 5.1. Natural differences in the mean (± SE) percentage cover of (a) articulated coralline algae and (b) filamentous turf-forming algae among habitats (monospecific vs mixed-species vs gaps) at five sites on the coastline of South Australia.
Table 5.1. Results of two-way ANOVAs testing for differences in the percentage cover of (a) articulated coralline algae and (b) filamentous turf-forming algae among habitats (monospecific vs mixed-species vs gap) and sites (n = 5).

<table>
<thead>
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<th>Source</th>
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<td>(a) Articulated coralline</td>
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<td>(b) Filamentous turf</td>
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<td>196.32***</td>
<td>4</td>
<td>218.52</td>
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<td>13.99*</td>
<td>3</td>
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</tr>
<tr>
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<td>8</td>
<td>16690.93</td>
<td>196.32***</td>
<td>4</td>
<td>331.87</td>
<td>4.14*</td>
</tr>
<tr>
<td>Site x Site</td>
<td>28</td>
<td>419.64</td>
<td>5.24***</td>
<td>4</td>
<td>80.11</td>
<td></td>
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</tbody>
</table>

Data were arcsine(%) transformed. Cochran’s C-test of homogeneity of variances: $P > 0.05$ for articulated coralline algae. *** $P < 0.001$, ns $P > 0.05$. Cochran’s C-test of homogeneity of variances: $P < 0.05$ for filamentous turfs. Hence, significance judged more conservatively ($\alpha = 0.01$) (Underwood 1997). * $P < 0.01$, *** $P < 0.0001$. 
Figure 5.2. Mean (± SE) percentage cover of (a) articulated coralline algae and (b) filamentous turf-forming algae within gaps and among experimental treatments of canopy (monospecific vs mixed-species) and abrasion (exposed = filled symbols vs protected = open symbols) through time. Note that procedural control treatments designed to detect artifacts in the experimental design (cages and translocating boulders) have been omitted because no artifacts were detected.
Table 5.2. Results of two-way ANOVAs testing for effects of abrasion (protected vs exposed vs procedural control) and type of canopy (monospecific vs mixed-species) on the percentage cover of (a) articulated coralline algae and (b) filamentous turf-forming algae.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
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<tbody>
<tr>
<td>Abrasion</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Abrasion × Canopy</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td></td>
<td></td>
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</tbody>
</table>

Date were arcsine(%) transformed. Cochran’s C-test of homogeneity of variances: $P > 0.05$ for filamentous turfs. *** $P < 0.001$, ns $P > 0.05$. Cochran’s C-test of homogeneity of variances: $P < 0.05$ for articulated coralline. Hence, significance judged more conservatively ($a = 0.01$) (Underwood 1997). * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$. 
protected from abrasion (Fig. 5.2a, Table 5.2a; SNK tests: protected > exposed = procedural control, for both monospecific and mixed-species canopies). However, the reduction in the cover of corallines on boulders exposed to abrasion was dependent on the type of canopy (Fig. 5.2a, Table 5.2a: Abrasion × Canopy interaction), being greater beneath monospecific than mixed-species canopies (SNK tests: monospecific > mixed for exposed and procedural control treatments). Importantly, no artifacts of the cages were detected (exposed = procedural control in all pair-wise comparisons).

The magnitude of the negative effect of canopies per se on articulated coralline was greater beneath monospecific than mixed-species canopies (Fig. 5.3a, ANOVA: \( F_{1,8} = 30.99, P < 0.001 \)), with ~55% loss of cover beneath monospecific canopies, and ~29% loss of cover beneath mixed-species canopies. The contribution of abrasion to the removal of corallines was also greater beneath monospecific than mixed-species canopies (Fig. 5.3a, ANOVA: \( F_{1,8} = 15.24, P < 0.005 \)). Abrasion accounted for 69.0 ± 5.7% of the observed effects of mixed-species canopies, and 79.92 ± 7.8% of the observed effects of monospecific canopies.

**Experimental effects on filamentous turfs**

All boulders supported similar covers of filamentous turf among treatments at the start of the experiment (ANOVA: \( F_{8,36} = 0.66, P > 0.70 \)). After 36 days, the cover of turfs on all boulders translocated beneath canopies was reduced, while boulders remaining within gaps (controls) still supported extensive covers of turf (Fig. 5.2b). Boulders exposed to abrasion (no cage and partial cage) lost greater amounts of turf than boulders protected from abrasion (full cage) (Table 5.2b: Abrasion main effect). Importantly, this effect was not dependent on the type of canopy (Fig. 5.2b, Table 5.2b: non-significant Canopy × Abrasion interaction; SNK tests: protected > exposed = procedural control, for both monospecific and mixed-species canopies). No differences between ‘exposed’ and ‘procedural control’ treatments indicate that no artifacts of the cage structures were detected.

The magnitude of the negative effect of canopies per se on filamentous turfs was similar between monospecific and mixed-species canopies (Fig. 5.3b, ANOVA:
Figure 5.3. Magnitude of the negative effects of canopies and abrasion (mean ± SE) on the percentage cover of (a) articulated corallines and (b) filamentous turfs between types of canopy (monospecific vs mixed-species).
\[ F_{1,8} = 0.75, P > 0.40 \), and was equivalent to the removal of \( \sim 99 \% \) of the original cover of turfs on translocated boulders. The contribution of abrasion to the loss of turf on boulders was also of similar magnitude between canopy-types (Fig. 5.3b, ANOVA: \( F_{1,8} = 0.02, P > 0.80 \), and accounted for 59.4 \( \pm \) 11.8 \% of the effect of monospecific canopies and 58.5 \( \pm \) 6.0 \% of the effect of mixed-species canopies observed in this study.

**Test of translocation artifacts**

No effect of moving boulders (vertical or horizontal disturbance) was detected for the percentage cover of articulated corallines and filamentous turfs \( (P > 0.30 \) in both cases). Hence, the process of translocating boulders from gaps to beneath canopies does not confound interpretation of the observed experimental effects.

**Abrasive environment**

The laminae of canopy-formers were observed to make repeated physical contact with the surfaces of painted tiles, resulting in instant removal of paint at the point of contact. The amount of white tile exposed (amount of paint removed) was greater beneath monospecific than mixed-species canopies of *E. radiata* (Fig. 5.4a, ANOVA: \( F_{1,8} = 26.34, P = 0.0009 \)). Only small amounts of tile were exposed in the absence of abrasion (Fig. 5.4a: Gap), presumably due to ambient water motion.

Given that water motion is typically reduced within stands of canopy-forming algae (Jackson and Winant 1983; Eckman et al. 1989), we consider that differences in the amount of tile exposed between monospecific and mixed-species canopies are likely to be primarily caused by abrasion by the canopy and not ambient water flow.

Plaster clods that were exposed to abrasion (no cage and partial cage) lost a greater percentage of their original mass than clods protected from abrasion (full cage) beneath monospecific and mixed-species canopies (Fig. 5.4b, Table 5.3: Abrasion main effect; SNK tests: protected < exposed = procedural control). Differences in the loss of plaster between monospecific and mixed-species canopies were subtle, but detectable by ANOVA (Table 5.3: Canopy main effect). Clods exposed to abrasion beneath monospecific canopies lost a greater percentage of plaster than those exposed to abrasion beneath mixed-species canopies (SNK tests:...
Figure 5.4. (a) Mean (± SE) percentage cover of tile exposed after three minutes beneath monospecific and mixed-species canopies, as well as in natural gaps.
(b) Mean (± SE) percentage loss of mass from plaster clods exposed to and protected from abrasion beneath monospecific and mixed-species canopies, as well as among caging treatments within natural gaps (absence of abrasion).
Table 5.3. Result of two-way ANOVA testing for effects of abrasion (protected vs exposed vs procedural control) and type of canopy (monospecific vs mixed-species) on the percentage loss of mass from plaster clods.

<table>
<thead>
<tr>
<th>Source</th>
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<th>MS</th>
<th>F</th>
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<tbody>
<tr>
<td>Abrasion</td>
<td>2</td>
<td>83.08</td>
<td>19.41***</td>
</tr>
<tr>
<td>Canopy</td>
<td>1</td>
<td>62.99</td>
<td>14.72***</td>
</tr>
<tr>
<td>Abrasion × Canopy</td>
<td>2</td>
<td>9.25</td>
<td>2.16ns</td>
</tr>
<tr>
<td>Residual</td>
<td>24</td>
<td>4.28</td>
<td></td>
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</tbody>
</table>

Data were arcsine(%) transformed. Cochran’s C-test of homogeneity of variances: $P > 0.05$. *** $P < 0.001$, ns $P > 0.05$. 
monospecific > mixed for ‘exposed’ and ‘procedural control’ treatments), while clods protected from abrasion lost similar amounts of plaster beneath both types of canopy (Fig. 5.4b). No artifacts of cages were detected (SNK tests). Hence, the difference in the loss of plaster between clods that were protected from vs exposed to abrasion (i.e. the intensity of abrasion) is greater beneath monospecific canopies relative to mixed-species canopies. No differences were observed among treatments within gaps (Fig. 5.4b: Gap, ANOVA: $F_{2,12} = 1.16, P > 0.34$; SNK tests: full cage = no cage = partial cage), where the amount of plaster lost was similar to clods exposed to abrasion beneath monospecific canopies (Fig. 5.4b). From this result, we predict that the amount of plaster lost due to water motion in gaps is equivalent to the amount lost due to the combined effect of water motion and abrasion beneath monospecific canopies.

**Key variables**

No differences between monospecific and mixed-species canopies were detected for the thallus and stipe length of *E. radiata*, as well as the depth of experimental patches of habitat (ANOVA: $F_{1,8} = 1.16, P > 0.05$ in all cases). However, the density of *E. radiata* comprising monospecific canopies was greater (~13 plants m$^{-2}$) than that sampled from mixed-species canopies (~7 plants m$^{-2}$) (ANOVA: $F_{1,8} = 18.99, P < 0.01$).

**5.5 DISCUSSION**

One of the most striking and frequently cited patterns from temperate rocky coasts around the world is that the type and abundance of understorey algae occupying space beneath canopies of algae differs greatly from that observed within gaps among canopies (e.g. north-west Atlantic: Chapman and Johnson 1990; California: Edwards 1998; Italy: Bulleri et al. 2002; Australia: Fowler-Walker and Connell 2002; Chapter 3). Consistent with this observation, we sampled sparse covers of articulated coralline algae and filamentous turf-forming algae beneath algal canopies, but extensive covers within gaps among canopies on subtidal coast in South Australia. This pattern is similar to observations from other coastlines around the world that also support low densities of benthic herbivores (e.g. urchins) (Hawkins and Harkin 1985; Bulleri et al. 2002; Chapter 3). The experimental presence of canopies had negative effects on the abundance of articulated corallines and
particularly filamentous turfs, which were almost completely removed (~99 %) from boulders exposed to all effects of canopies. However, such negative effects were reduced where abrasion by canopies was prevented. Although abrasion is one of many influences of canopies, it made a substantial contribution to our observed effects of canopies (~70 – 80 % for articulated coralline and ~60 % for filamentous turf). Hence, the negative effect of abrasion by laminae demonstrates that direct physical contact with the benthos can contribute to the heterogeneity of understorey habitat on subtidal rocky coasts.

The heterogeneous structure of algal forests is often recognized as patchiness associated with the presence and composition of canopies, yet surprisingly few studies have tested for ecological differences between canopies of varying composition. Differences in the composition of understorey assemblages between monospecific and mixed-species canopies have been qualitatively described (e.g. Shepherd and Womersley 1970) but rarely quantitatively tested. At multiple sites in South Australia, we observed greater covers of articulated coralline algae beneath mixed-species canopies relative to monospecific canopies, but sparse covers of filamentous turf beneath both types of canopy. Consistent with these patterns, monospecific canopies had a greater negative effect on the covers of articulated coralline than mixed-species canopies, while negative effects of similar magnitude were observed between both types of canopy for filamentous turfs. Additionally, the intensity of abrasion appears greater beneath monospecific than mixed-species canopies, which is consistent with between-canopy differences in the effects of abrasion on articulated corallines (monospecific > mixed-species). These results point to very real differences in the ecology (patterns and their causes) of monospecific vs mixed-species canopies of subtidal vegetation, and contribute to a growing body of knowledge describing such variation (Dayton et al. 1984; Goodsell et al. 2004; Chapter 3). Recognising such differences may help to reduce large and apparently ‘unexplained’ variance among replicates, and improve the power of predictions about the nature of heterogeneity.

Observation of experimental boulders through time revealed differences in the way abrasion affected the abundance of articulated corallines and filamentous turfs. Abrasion primarily appeared to affect the abundance of articulated corallines
(H. roseum) through the loss of adventitious branchlets along the lower two-thirds of
the thallus (Irving unpubl. data), giving the alga a more stipitate morphology. The
decline in cover occurred uniformly over the surface of boulders subjected to
abrasion, exposing either underlying encrusting coralline algae or bare rock. In
contrast, the decline in the cover of filamentous turfs involved the complete removal
of thalli (filaments) to expose the underlying bare rock. While such effects occurred
uniformly over the surface of boulders exposed to abrasion, any remaining turf
persisted only as a short (< 5 mm long) and sparsely distributed “tuft”. Relative to
articulated corallines, a greater magnitude of decline over a shorter period of time
was also observed for filamentous turfs.

Experimental tests of abrasion within stands of E. radiata have revealed
inconsistencies among results from different studies. In eastern Australia, Kennelly
(1989) found abrasion to have negligible effects on several species of understorey
algae and sessile invertebrate. Using a similar experimental design to Kennelly
(1989), both Connell (2003b) and the present study detected large negative effects on
sessile invertebrates (Connell 2003b) and erect algae (present study) in southern
Australia. Models to account for such regional inconsistencies are yet to be assessed.
A promising model, however, centres on the morphology of E. radiata, which is
related to the intensity of abrasion. The intensity of abrasion correlates negatively
with stipe length (Kennelly 1989), and E. radiata in eastern Australia generally have
longer stipes than plants in southern Australia (mean ± SE = 11.0 ± 0.7 cm for
eastern Australia, 6.7 ± 0.2 cm for southern Australia), in addition to shorter laminac
relative to the stipe length (mean ± SE lamina-to-stipe length ratio = 4.5 ± 0.3 for
eastern Australia, 6.8 ± 0.4 for southern Australia) (Fowler-Walker et al. in press).
The morphology of E. radiata in southern Australia appears suitable for causing
strong effects of abrasion (e.g. for this study, mean ± SE stipe length = 6.8 ± 0.9 cm,
lamina-to-stipe length ratio = 6.7 ± 0.5). Hence, the intensity of abrasion and its
effects on understorey taxa could be less in eastern Australia than that detected in
southern Australia because of regional variation in the morphology of E. radiata.
This could also contribute to an explanation of why the abundance of articulated
corallines beneath canopies of E. radiata in eastern Australia is ~ 7 times greater
than beneath corresponding canopies in southern Australia (Chapter 3). Although
untested, this model may provide a causative link between a local-scale process
Notwithstanding the effects of abrasion detected in this study, several other factors associated with canopies may also contribute to differences in understorey between canopy presence-or-absence. Canopy-mediated shade appears to have consistently strong effects on understorey (Kennelly 1989; Duggins et al. 1990; Connell 2003a) and can explain up to half the variation in understorey composition within forests of *E. radiata* (Connell 2003a). Canopies of algae can influence many other environmental variables, including water flow (Jackson and Winant 1983) and sedimentation regime (Eckman et al. 1989; Connell 2003b). Some of these factors have synergistic effects with light intensity and cause the early divergence in the assembly and subsequent maintenance of understorey associated with the presence and absence of canopies (Connell 2005). Hence, future models may benefit from the incorporation of light intensity as a potentially interactive factor to obtain a better understanding of the effects of particular factors relative to shade (e.g. Connell 2003a) and potential synergies.

Perhaps the world’s best studied subtidal kelp forests are those characterized by *Macrocystis pyrifera* along the coastline of California. It is useful, therefore, to understand how the ecology of Australian forests compares with these well understood and widely cited habitats. The surface canopy of *M. pyrifera* often occurs above a sub-surface canopy formed by species of Laminarian algae (mainly *Pterygophora californica* and several species of *Laminaria*). These sub-surface kelps are similar in size to *E. radiata* (0.5 – 2 m in length) and their canopies, either alone or in combination with canopies of *M. pyrifera*, reduce ambient light intensity at the substratum by similar amounts as *E. radiata* (e.g. 91 – 98 % reduction by *P. californica*: Reed and Foster 1984; Clark et al. 2004, vs 95 % reduction by *E. radiata*: Kennelly 1989). In comparison to *E. radiata*, however, these sub-surface kelps make less physical (abrasive) contact with the substratum (Connell *pers. obs.*) and it follows that the understorey within these forests often supports extensive covers of erect algae, especially articulated corallines (Reed and Foster 1984; Edwards 1998; Clark et al. 2004). Hence, understanding the limits of generality between Californian and Australian kelp forests may benefit from realizing this physical difference in the kelps themselves.
The challenge of understanding the relative influence of positive and negative interactions in ecology has been revived in recent times (Bruno et al. 2003). Canopies of algae modify local environmental conditions and facilitate biased subsets of species as understorey (Bertness et al. 1999; Connell 2005). However, positive effects of canopies can be offset by negative effects (e.g. abrasion) to produce a net negative effect (Connell 2003b). Although the abundance of articulated corallines and filamentous turfs can be negatively affected by lamina abrasion (Cheroske et al. 2000; this study), such effects may indirectly have positive consequences for the abundance of other taxa by excluding competitors for space and releasing additional resources (e.g. Kastendiek 1982). Furthermore, the effects of abrasion may augment those of shade provided by canopies, which appears primarily responsible for the maintenance of extensive covers of encrusting coralline algae beneath canopies (Kennelly 1989; Figueiredo et al. 2000; Connell 2003a). Experimental tests of these factors to identify variability in the strength of their positive and negative interactions across large sections of coastline and through seasonal changes remain key to improving our knowledge of the maintenance of heterogeneity within these subtidal habitats.
Comparison of bleached (left) and non-bleached (right) encrusting coralline algae. For this photo, the boulder on the right was sourced from beneath a monospecific canopy of *Ecklonia radiata*, while the boulder on the left was found within a gap among the same canopy of *E. radiata* (photo by the author).
"...do assemblages of organisms exhibit any interdependence, and if so, how interdependent are they?"

R. M. Callaway, 1997
*Oecologia* 112: p144

"It is time to bring ecological theory up to date by including facilitation."

J. F. Bruno, J. J. Stachowicz, & M. D. Bertness 2003
*Trends in Ecology and Evolution* 18: p119
Chapter 6: Preamble

Chapter 6 presents the results of a manipulative experiment designed to test for positive effects of canopies of algae on understorey encrusting coralline algae. First, the effects of experimental canopy removal on the photosynthetic activity of encrusting coralline algae are quantified. Second, the role of shade provided by canopies is tested as a mechanism accounting for such effects.

This chapter was published in the *Journal of Experimental Marine Biology and Ecology* in 2004 (vol. 310: 1-12), with myself as senior and corresponding author, and Sean D. Connell and Travis S. Elsdon (University of Adelaide) as co-authors. It is, therefore, written in plural. Permission from the publisher (ELSEVIER) to reproduce this manuscript herein has been granted (see Appendix B).

Contributions and signatures of authors

ANDREW D. IRVING

*Designed and implemented the experiments, sampled, analysed, and interpreted all data, wrote manuscript as senior and corresponding author.*

Signed:.............................................. Date:..............................

SEAN D. CONNELL

*Supervised development of the research, data interpretation, and manuscript evaluation.*

Signed:.............................................. Date:..............................

TRAVIS S. ELSDON

*Advised on aspects of the research and manuscript evaluation.*

Signed:.............................................. Date:..............................
CHAPTER 6

EFFECTS OF KELP CANOPIES ON BLEACHING AND PHOTOSYNTHETIC ACTIVITY OF ENCRUSTING CORALLINE ALGAE

6.1 ABSTRACT
Canopy-forming algae often co-exist with an understorey of encrusting coralline algae that bleach following the loss of canopies. We tested the hypothesis that canopy loss causes a reduction in photosynthetic activity of encrusting coralline algae concomitant with their bleaching. When canopies were experimentally removed, corallines bleached and their photosynthetic activity was rapidly reduced to half their activity observed under canopies. This result prompted us to test, and subsequently accept, the hypothesis that exposure of understorey corallines to enhanced light intensity per se (simulation of canopy loss) acts as a mechanism causing bleaching and reduced photosynthetic activity. Despite bleaching, encrusting corallines maintained reduced levels of photosynthetic activity and this may explain why, under certain conditions, bleached corallines can persist in the absence of canopy-forming algae. Nevertheless, our data provide evidence that the positive association between canopy-forming algae and encrusting coralline algae is maintained because of shade provided by the canopy.

6.2 INTRODUCTION
Debate over the relative influence of positive (facilitative) and negative (suppressive) interactions for the assembly and maintenance of biotic assemblages has been renewed by suggestions that positive interactions are more common and more widespread than usually considered (Callaway 1995; Bruno et al. 2003). Rigorous evidence of positive interactions among species is building (e.g. Bertness and Leonard 1997; Callaway and Walker 1997; Bruno and Bertness 2001), and a greater appreciation of the role of positive interactions has undoubtedly contributed to a more complex understanding of how particular taxa can modify the physical environment to enhance the distribution and abundance of associated species (Shouse 2003). Importantly, the objective of rigorously testing for and determining the
mechanisms driving positive interactions remains as pressing as ever (Jones et al. 1997; Bruno and Bertness 2001).

On temperate coasts, amelioration of physically harsh conditions by canopy-forming algae generates positive interactions between the canopy species and understorey taxa (Bertness et al. 1999). In the absence of algal canopies, substrata are typically colonised by taxa different from those persisting beneath a canopy (Reed and Foster 1984; Chapter 3) and experimental clearances of algal canopies have demonstrated a predictable switch in the composition of benthic assemblages from canopy-present to canopy-absent states (Hawkins and Harkin 1985; Kennelly 1987c; Edwards 1998; Melville and Connell 2001). Notably, these experiments emphasise that algal canopies can both facilitate and suppress particular taxa from the understorey (also see Chapters 4 and 5).

Canopy-forming algae form a strong positive association with understorey encrusting coralline algae (non-geniculate coralline algae: Rhodophyta) throughout much of the world (Witman and Dayton 2001). Following the loss of canopy, light intensity at the substratum increases (Connell 2003a) and encrusting corallines are observed to ‘bleach’ from red/pink to white (Littler 1973; Hawkins and Harkin 1985). Bleaching is thought to be a consequence of photoinhibition (Littler 1973) and is associated with reduced productivity (Figueiredo et al. 2000), and even suggested as an indicator of death (Littler 1973; Hawkins and Hartnoll 1985). However, colour restoration of formerly bleached coralline has been observed following the provision of shade (Figueiredo et al. 2000), suggesting some physiological recovery is possible.

Across temperate Australasia, encrusting coralline algae form an association with stands of the laminarian canopy-former *Ecklonia radiata* (C. Agardh) J. Agardh (Fowler-Walker and Connell 2002; Chapter 3). We tested the hypothesis that the photosynthetic activity of encrusting coralline algae (based on estimates of electron transport rate) would be reduced following canopy removal and that such a response would occur concomitantly with bleaching of coralline. An independent manipulation of light intensity allowed a test of the mechanistic hypothesis that
exposure to enhanced intensities of light causes reduced photosynthetic activity in corallines and causes corallines to bleach.

6.3 Materials and Methods

Experimental design

Experiments were done at West Island, South Australia (see Connell 2003a) using semi-spherical boulders (approximately 0.15 – 0.2 m radius) that supported extensive covers of encrusting coralline algae (Lithophyllum sp.) located beneath monospecific canopies of *E. radiata*. To test the effects of canopy removal on photosynthetic activity and bleaching of corallines, fifteen boulders were partitioned among three treatments (*n* = 5 boulders per treatment): canopy removed (clearance), canopy present (untouched control) and a procedural control. Canopies were removed over an area of ~1.5 × 1.5 m by cutting the stipe immediately above the holdfast. Severing an *E. radiata* canopy from its holdfast can enhance the exudation of phlorotannins produced within the alga (Jennings and Steinberg 1994) and this may affect encrusting corallines. Hence, a procedural control was established by attaching freshly-cut sections of stipe to the stipes of other *E. radiata* plants that were not removed. Any difference between procedural controls and untouched controls would therefore suggest an artefact of cutting the kelp.

Photosynthetic activity of corallines was estimated using a pulse amplitude modulated (PAM) fluorometer (see below) immediately prior to canopy removal and on ten of the following 35 days (between 1200 – 1400 hrs each day). Three replicate samples were taken per boulder on each day and each replicate area of algae (1.96 × 10⁻³ cm²) was only sampled once. The same boulders were sampled over time because too few boulders supported *Lithophyllum* sp. in each clearance. Bleaching of corallines was assessed by photographing each boulder before (day 0) and after canopy removal (days 3 and 35 only) and comparing the colour of *Lithophyllum* sp. on each boulder to a scale of ten colours (ranging from white to crimson) established using colour charts supplied by Wattyl™ paints. Each colour on this scale was assigned a value from one (white) to ten (crimson) and the colour of *Lithophyllum* sp. on each boulder was assigned the appropriate value.
To test the influence of shade on photosynthetic activity and bleaching of corallines, 18 boulders were collected from beneath monospecific canopies of *E. radiata* and were evenly divided among three circular fibreglass tanks (2 m diameter) initially under shaded conditions. Photosynthetic activity of corallines was sampled as above and each boulder was photographed before being randomly allocated to one of two levels of shading (*n* = 3 per tank): no shade (exposure to natural sunlight) and shade (provided by 0.3 × 0.3 m pieces of fibro-cement (Hardi-flex®) secured 0.1 m above boulders). Sampling of corallines over the following three days was restricted to 1200 – 1500 hrs each day, with all boulders photographed after sampling on the third day.

**Estimation of photosynthetic activity**

Photosynthetic activity of encrusting corallines was estimated using pulse amplitude modulated (PAM) fluorometry (Schreiber 1986; Beer et al. 1998). Using high-frequency modulations of light, a diving PAM (Walz, Germany) allowed *in situ* estimates of the quantum yield of photochemical conversion (*Y*) of corallines. Coupled with measurements of photosynthetically active radiation (PAR: 400 – 700 nm) available to the corallines at the time of sampling, photosynthetic rates of electron transport (ETR) through photosystem II were calculated using the equation:

\[
ETR = Y \times PAR \times AF \times 0.5
\]

where AF is a constant that represents the absorption factor of the thallus (0.84) and 0.5 is a constant that assumes both photosystems I and II absorb equal amounts of photon energy during sampling.

For both experiments, ETR was calculated using the equation described above. However, the resulting value of ETR is clearly dependent on the amount of PAR available at the time of sampling. The presence of canopies/shading structures reduces the intensity of light incident upon encrusting corallines (Figueiredo et al. 2000) and hence, apparent differences in ETR among treatments are potentially an artefact of the necessity for ETR calculation to be partially based on PAR. To correct for this, it was necessary to standardise ETR to PAR (i.e. ETR:PAR) to
provide an estimate of ETR per unit of available PAR. This ratio was the response variable analysed in both experiments.

Estimates of photosynthetic activity in marine plants traditionally involves measuring O₂ evolution and/or CO₂/HCO₃⁻ uptake across a range of irradiances (Beer 1996). ETR-irradiance curves appear to correlate well with O₂-irradiance curves for some species of encrusting coralline (e.g. Kühl et al. 2001). To indicate whether ETR is a useful estimate of photosynthetic activity in Lithophyllum sp., we generated an ETR-irradiance curve by exposing the alga to a range of light intensities (provided by a metal-halide lamp) and compared the shape of this curve to published O₂- and ETR-irradiance curves for other species of encrusting coralline.

6.4 Results
Effects of canopy removal
In control and procedural control groups respectively, the average (± SE) amount of PAR reaching the substratum across days 1-3 was 20.7 ± 0.3 % and 20.1 ± 0.4 % of that in areas where canopies had been removed (Fig. 6.1, ANOVA: F₂,₂₇ = 37.67, P < 0.0001). From day 16 onwards, the average (± SE) amount of PAR reaching the substratum in controls and procedural controls increased to 43.2 ± 0.2 % and 45.1 ± 0.3 % of that in clearances, respectively. Removal of canopy caused a decline in ETR:PAR of corallines relative to controls, but this difference between the presence and absence of canopies was dependent on time (Fig. 6.2; Table 6.1: ANOVA: Time × Treatment interaction). Prior to experimental clearances, ETR:PAR did not differ between designated cleared (canopy absent) and uncleared (canopy present) treatments (Fig. 6.2: day 0), but upon clearance, corallines showed reduced ETR:PAR relative to controls for the following three days (SNK tests: canopy removed < control = procedural control, Fig. 6.2). On the sixteenth day, and for all subsequent days, no differences were detected between clearances and controls (SNK tests). Rank ETR:PAR values, however, were consistently smaller within clearances than untouched controls on all seven of these days; an unlikely result by chance alone (binomial (sign) test: P < 0.02; Underwood 1997). The colour of corallines in clearances was lighter than that beneath canopies (Fig. 6.3, ANOVA
Figure 6.1. Mean amount (±SE) of PAR incident upon boulders in controls and clearances of canopy. Data have been pooled across days 1-3.
**Figure 6.2.** Response of ETR:PAR to canopy removal over time. *Post-hoc* (SNK) tests detected reduced ETR:PAR for corallines in clearances compared to controls on days marked with a star. Error bars are ±SE.

**Table 6.1.** Results of ANOVA testing for differences in ETR:PAR of corallines among boulders and treatments over time.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
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<tbody>
<tr>
<td>Time</td>
<td>10</td>
<td>0.0457</td>
<td>32.05***</td>
</tr>
<tr>
<td>Treatment</td>
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<td>0.0427</td>
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</tr>
<tr>
<td>Boulder (Treatment)</td>
<td>12</td>
<td>0.0036</td>
<td>2.53**</td>
</tr>
<tr>
<td>Time × Treatment</td>
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<td>3.53***</td>
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<tr>
<td>Time × Boulder(Treatment)</td>
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<td>0.0014</td>
<td>1.11ns</td>
</tr>
<tr>
<td>Residual</td>
<td>330</td>
<td>0.0013</td>
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</tr>
</tbody>
</table>

Cochran’s $C$-test of homogeneity of variances: $P > 0.05$. ** = $P < 0.01$, *** = $P < 0.001$, ns = $P > 0.05$. 

118
Figure 6.3. Mean (±SE) colour values assigned to corallines in clearances and controls.
on day 3 alone: $F_{2,12} = 17.60, P = 0.0003$), which is consistent with bleaching of corallines following canopy removal.

**Effects of shade**

Experimental shade provided a PAR intensity of $28.9 \pm 0.3$ SE % of that incident upon boulders in unshaded treatments (Fig. 6.4, ANOVA: $F_{1,4} = 13.25, P = 0.022$), which is slightly less than the difference between clearances of canopy and controls across days 1-3 (compare Figs 6.1 and 6.4). Following similar ETR:PAR readings prior to manipulation, ETR:PAR was reduced in unshaded corallines relative to shaded corallines (Fig. 6.5) by the end of the experiment (Table 6.2). Importantly, no effect of tank or interaction of tank and shading treatment was detected. Colour changes only occurred for corallines exposed to full sunlight (Fig. 6.6, ANOVA day 3: $F_{1,12} = 109.71, P = 0.009$) and were consistent with bleaching.

**ETR-irradiance curve**

The ETR-irradiance curve generated for *Lithophyllum* sp. (Fig. 6.7) is similar to $O_2$- and ETR-irradiance curves published for several species of encrusting coralline (e.g. Kühl et al. 2001; Roberts et al. 2002; Chisholm 2003), suggesting that ETR values can be used as estimates of photosynthetic activity for *Lithophyllum* sp.
Figure 6.4. Mean amount (±SE) of PAR incident upon boulders in the presence and absence of shade. Data have been pooled across days 1-3.
Figure 6.5. Response of ETR:PAR to the presence and absence of shade over time. Error bars are ±SE.

Table 6.2. Results of ANOVA testing for differences in ETR:PAR between shaded and unshaded corallines on day 3.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
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<td>0.0005</td>
<td>1.20&lt;sup&gt;ns&lt;/sup&gt;</td>
</tr>
<tr>
<td>Shade</td>
<td>1</td>
<td>0.0198</td>
<td>62.79*</td>
</tr>
<tr>
<td>Tank × Shade</td>
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<td>0.0003</td>
<td>0.80&lt;sup&gt;ns&lt;/sup&gt;</td>
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<tr>
<td>Residual</td>
<td>48</td>
<td>0.0004</td>
<td></td>
</tr>
</tbody>
</table>

Cochran’s C-test of homogeneity of variances: P > 0.05. * = P < 0.05, ns = P > 0.05
Figure 6.6. Mean (±SE) colour values assigned to corallines in the presence and absence of shade.

Figure 6.7. ETR-irradiance curve generated for *Lithophyllum* sp. at West Island, South Australia. Error bars are ±SE.
6.5 DISCUSSION

Loss of canopy-forming algae triggers predictable and often rapid changes to the composition of benthic assemblages (Reed and Foster 1984; Santelices and Ojeda 1984a; Kennelly and Underwood 1993; Melville and Connell 2001) suggesting that canopy-formers have both positive and negative effects on understorey taxa and that such effects can be species specific (Duggins et al. 1990; Connell 2003b). We detected rapid reductions in the photosynthetic activity of encrusting coralline algae following the loss of canopy, the timing of which correlated with bleaching of the alga. Loss of canopy is associated with an increase in light intensity reaching the substratum (Schiel and Foster 1986; Connell 2003a; this study) and our manipulation of shade demonstrates that light intensity has a strong influence on photosynthetic activity and concomitant bleaching of encrusting corallines.

Despite the reduction in photosynthetic activity in clearances throughout the experiment, differences in estimates of ETR:PAR between clearances and controls were not detected from day 16 onwards because the estimates from controls declined to become similar to those in clearances (Fig. 6.2). As corallines in controls did not bleach like those in clearances, the reason for this observation is unclear. We speculate that this was caused by the natural thinning of the canopy from 16 days (Irving pers. obs.) and an associated increase of PAR beneath canopies (days 1-3: mean ± SE μmol quanta m⁻² s⁻¹ = 59.3 ± 5.6, 57.8 ± 7.6; days 16-35: mean ± SE = 114.4 ± 5.3, 118.5 ± 8.3 for untouched canopies and procedural controls, respectively). This reduction in differences in light intensity among treatments may account for the reduced differences in ETR:PAR among treatments from day 16 onwards.

Coralline bleaching has been considered an indicator of injury or death (Littler 1973; Hawkins and Hartnoll 1985), but there is evidence that bleached corallines can restore their colour once shaded (Figueiredo et al. 2000). Death of corallines should result in ETR:PAR values measuring zero but we did not detected this in either experiment despite obvious bleaching. Instead, we observed that following a rapid reduction of ETR:PAR over the first three days after canopy removal, ETR:PAR appeared to stabilise for the remainder of the experiment. This result suggests that rather than die, corallines may acclimate and persist in conditions of greater light.
intensity, albeit at reduced levels of productivity. Many marine algae are capable of photosynthetically acclimating to varying light environments by altering their concentrations of light harvesting pigment (Ramus et al. 1976a, b; Lüder et al. 2002). Therefore, rather than signifying injury or death, bleaching of corallines could indicate changing pigment levels that facilitate photoacclimation to stronger intensities of light. In locations that are subjected to intense grazing pressure from mobile invertebrates (e.g. urchins), encrusting corallines often monopolise space across extensive tracts of coast devoid of canopy-forming algae (Chapman and Johnson 1990; Fowler-Walker and Connell 2002; Chapter 3). These corallines are frequently bleached (Irving pers. obs.) but acclimation to elevated intensities of light offers an explanation why they are able to persist in the absence of canopy-forming algae.

The experimental provision of shade prevented corallines from bleaching and maintained high ETR:PAR relative to corallines exposed to full sunlight. The relative difference in the PAR environments between shaded and unshaded boulders (tank experiment) was comparable to differences between canopy clearances and controls (field experiment) and this difference created similar amounts of bleaching and reduction in ETR:PAR between experiments. This similarity in response provides evidence that enhanced light intensity is a key mechanism that drives reductions in photosynthetic activity and advancement of bleaching events. Importantly, the effects of light detected in this study are consistent with previous work showing light intensity has strong effects on the distribution and abundance of many benthic taxa, including encrusting corallines (Reed and Foster 1984; Kennelly 1989; Connell 2003a).

In conclusion, the decline in photosynthetic activity of corallines following canopy removal suggests that E. radiata canopies create positive environmental conditions (i.e. shade) for encrusting coralline algae. Although exposure to full sunlight causes corallines to bleach, our data suggests that they do not die but instead sustain a reduced rate of productivity, possibly acclimating to the increased light intensity by altering amounts of their light harvesting pigments. These observations could explain why bleached encrusting corallines can, on some coasts, monopolise extensive areas of substratum in the absence of canopy-forming algae but presence of
strong grazing activity. Nevertheless, canopy-mediated shade appears a critical factor explaining the greater productivity and extensive covers of encrusting corallines under canopies of kelp.
A specimen of the large canopy-forming alga *Himantothallus grandifolius* (holdfast at top of photo) sampled from subtidal rocky coast at Casey, Antarctica, 2004 (photo by Sean Connell).
"...generalisations should be able to withstand rigorous testing in new, as yet untested situations (e.g. on different continents)."

A. J. Underwood & E. J. Denley, 1984
*Ecological Communities: conceptual issues and the evidence*, p.153

"...in the absence of general principles, ecology becomes natural history."

P. A. Keddy, 2001
*Competition*, p.317
Chapter 7: Preamble

Chapter 7 presents an assessment of whether knowledge of the ecology of encrusting coralline algae from tropical and temperate coasts can be used to predict patterns and responses on a polar coast where such knowledge does not exist. Positive associations between encrusting coralline algae and canopy-forming algae are quantified on a subtidal coast in Antarctica. Subsequently, the bleaching and photosynthetic responses of encrusting coralline algae following the experimental removal of overlying algal canopies are tested.

This chapter was accepted for publication in the journal Marine Biology on the 29th of March 2005, with myself as senior and corresponding author, and Sean D. Connell, (University of Adelaide), Emma L. Johnston (University of New South Wales), Adele J. Pile (University of Sydney), and Bronwyn M. Gillanders (University of Adelaide) as co-authors. It is, therefore, written in plural. Permission to reproduce this manuscript herein has been granted (see Appendix B).

Contributions and signatures of authors

ANDREW D. IRVING

Sampled, analysed, and interpreted data, wrote manuscript as senior and corresponding author.

Signed: Date:

SEAN D. CONNELL

Sampled data, supervised development of research, data interpretation, and manuscript evaluation.

Signed: Date:

EMMA L. JOHNSTON

Sampled data, advised on aspects of research and manuscript evaluation.

Signed: Date: 5/4/05
ADELE J. PILE
Advised on aspects of research and manuscript evaluation.

Signed:  
Date: (April 2005)

BRONWYN M. GILLANDERS
Advised on aspects of research and manuscript evaluation.

Signed:  
Date:
CHAPTER 7

THE RESPONSE OF ENCRUSTING CORALLINE ALGAE TO CANOPY LOSS: AN INDEPENDENT TEST OF PREDICTIONS ON AN ANTARCTIC COAST

7.1 ABSTRACT

We assessed whether published observations of the ecology of encrusted coralline algae (Rhodophyta) from tropical and temperate coasts could be used to predict patterns and responses on a polar coast where such knowledge does not exist. On subtidal rocky coasts near Casey, East Antarctica, we detected a strong positive association of understory encrusting coralline algae with canopies formed by the endemic alga *Himantothallus grandifolius*. The experimental removal of *H. grandifolius* caused corallines to bleach from red to pink/white concomitant with a decline in their photosynthetic activity. The magnitude of this decline (mean ± SE = 56.85 ± 8.43 %) was remarkably similar to that observed on temperate coasts (45.98 ± 5.91 %). Positive effects of nutrient enrichment of the surrounding water, hypothesized to alleviate the negative effects of canopy loss on encrusting corallines, were not detected. Removing *H. grandifolius* increased the intensity of photosynthetically active radiation (PAR) and ultra-violet radiation (UVR) reaching the substratum by three orders of magnitude, providing the basis for models invoking enhanced irradiance as the primary cause of the negative effects of canopy-loss. Striking similarities among our results and those from tropical and temperate coasts suggest that responses of encrusting corallines to loss of canopies may have predictive properties across large distances and environmental gradients (tropical-temperate-polar).

7.2 INTRODUCTION

A central purpose of ecology is the formal development and refinement of quantitative explanations for observed phenomena (Underwood 1997), with progressive avenues of inquiry often judged by their predictive ability (Peters 1991). Contemporary research efforts in ecology tend to emphasise the search for new details in the description and explanation of local variation (Underwood et al. 2000), which may increase confidence in our understanding of local phenomena, but
contribute little towards the development of ecological generality (Keddy 2001). There is a need, therefore, to consider independent and repeated tests of fundamental concepts that may contribute towards a more useful body of predictive understanding (Gurevitch et al. 1992; Keddy 2001).

A promising area of predictive research centres on prominent differences in the structure of understorey communities between the presence and absence of canopies of algae (e.g. kelps) on subtidal rocky coasts (Chapman and Johnson 1990; Chapter 3). Central to the origin and maintenance of this heterogeneity is natural disturbance (Sousa 2001), which creates open space (i.e. gaps) through fragmentation and loss of canopy-formers (Dayton and Tegner 1984; Kennelly 1987a). Subsequently, large changes to local environmental conditions (e.g. enhanced intensities of light: Reed and Foster 1984; Connell 2003a) and the composition of understorey communities are frequently observed (Dayton 1975b; Edwards 1998; Melville and Connell 2001). Human activities further alter environmental conditions, which can modify the outcome of natural processes (Vitousek et al. 1997; Lindberg et al. 1998). For example, the growth of benthic algae that form ‘turfs’ (sensu Hay 1981) may be facilitated by the creation of gaps among canopies of algae (Hawkins and Harkin 1985; Benedetti-Cecchi et al. 2001; Melville and Connell 2001), and this effect may be amplified in nutrient-rich waters on human-dominated coastlines (Worm et al. 1999; Gorgula and Connell 2004). As human populations expand and increase their impacts on coastal environments, it is critical that we understand potential interactions between anthropogenic inputs and natural ecological processes (Vitousek et al. 1997; Lindberg et al. 1998; Benedetti-Cecchi et al. 2001).

Encrusting coralline algae (Rhodophyta) often form a disproportionately large component of the understorey beneath stands of canopy-forming algae (Witman and Dayton 2001; Connell 2003a), but can be sparse within other habitats (e.g. gaps among canopies; Chapter 3). On tropical and temperate coasts, encrusting corallines are observed to ‘bleach’ from red/pink to white following the loss of canopies (Littler 1973; Hawkins and Harkin 1985; Valentine and Johnson 2004), with a concomitant decline in their productivity also observed on temperate coasts (Figueiredo et al. 2000; Chapter 6). Nutrient enrichment of the surrounding water can positively affect the productivity of encrusting corallines (Smith et al. 2001). Hence, the negative
effects of canopy-loss on encrusting corallines may be alleviated by positive effects of nutrient enrichment. Understanding the integrated roles of such physical processes can assist the development of predictive models about the assembly and maintenance of heterogeneity of benthic communities and their potential disruption by humans (Connell 2005).

Subtidal rocky coasts in the nutrient-rich waters of Antarctica often support extensive covers of macroalgae (Barnes 1995; Wiencke and Clayton 2002), including dense stands of the large canopy-forming alga, *Himantothallus grandifolius* (A & E Gepp) Zinova (Desmarestiales: Phaeophyta). *H. grandifolius* is reported to co-exist with encrusting coralline algae (Amsler et al. 1995), yet there is little knowledge of whether encrusting corallines persist in other habitats such as gaps among canopies of *H. grandifolius*, or in association with other types of algae (e.g. the widespread foliose rhodophyte *Palmaria decipiens* (Reinsch) Ricker). Nevertheless, agents of disturbance to benthic marine life in Antarctica, such as physical abrasion by grounded icebergs and sea ice (Barnes 1999), are likely to remove canopies of *H. grandifolius* and expose understorey encrusting corallines, which often tolerate intense physical and biological disturbances (Steneck and Dethier 1994). If the responses of encrusting corallines to the loss of canopies on tropical and temperate coasts (i.e. bleaching and reduced productivity) are general phenomena, we predict similar responses of polar corallines following the loss of polar canopies. In contrast, observed positive effects of nutrient enrichment on encrusting corallines (e.g. Smith et al. 2001) may not be as profound on Antarctic coasts because ambient nutrient concentrations are relatively high (Dayton et al. 1994). Experimental tests of the response of encrusting corallines to a combination of natural (canopy-loss) and anthropogenic disturbances (nutrient enrichment) in polar waters would improve our understanding of the predictability of canopy-understorey patterns and processes.

This study assessed whether observations from tropical and temperate coasts regarding positive associations between encrusting corallines and canopies of algae, as well as negative effects of canopy-loss on encrusting corallines, could be used to predict patterns and responses on a polar coast (Antarctica) where such knowledge does not exist. We tested the hypotheses that (i) encrusting corallines would be positively associated with stands of canopy-forming algae (*H. grandifolius*) but not
other habitats (e.g. gaps among canopies or stands of the foliose alga *P. decipiens*), and (ii) the loss of canopies of *H. grandifolius* would cause a reduction in the photosynthetic activity of corallines concomitant with their bleaching. We further tested whether (iii) such negative effects of canopy-loss on encrusting corallines would be reduced where nutrient concentrations were experimentally elevated.

### 7.3 Materials and Methods

**Relative abundance and associations among algae**

We tested for associations of encrusting coralline algae with three types of benthic habitat observed on subtidal rocky coasts near Casey, East Antarctica (66° 17' S, 110° 32' E): canopies of *H. grandifolius* (Phaeophyta), stands of the foliose red alga *P. decipiens* (Rhodophyta), and gaps among stands of algae (see definitions below). This research proceeded in two steps. First, we quantified the abundance (percentage cover) of each habitat and tested their relative contribution to the total percentage cover of benthos. Second, we quantified the abundance (percentage cover) of encrusting coralline algae within each habitat.

The abundance of each habitat was quantified at two sites (Shirley Island and McMullin Island; Fig. 7.1) during the austral summer of 2003/2004. Habitats were identified at a scale of 1 m² as: (i) stands of *H. grandifolius* when > 80% of the algal cover was *H. grandifolius*, (ii) stands of *P. decipiens* when > 80% of the algal cover was *P. decipiens*, and (iii) gaps among stands of algae when rocky substrata did not support algae > 50 mm in height. At both sites, four 30 x 1 m transects were oriented parallel to the shoreline at two depths (6 m and 12 m; n = 4 transects per depth per site), and observers recorded the distance along each transect that each type of habitat started and finished. Within any transect, estimates of the abundance of each habitat across the entire length of the transect are negatively correlated (i.e. where one habitat covers a large amount of space, the other two habitats can only cover small amounts). Hence, the following procedure was used to ensure independent estimates of the abundance of each habitat were obtained from each transect. All transects were partitioned into thirty 1 m² quadrats, from which ten quadrats were randomly chosen and the proportion supporting only one of the three
Figure 7.1. Map of the coastline near Casey showing the two sites (marked with a star: Shirley Island and McMullin Island) at which sampling and experimental tests were done. Inset: Map of Antarctica showing the position of Casey.
habitats was used as a replicate estimate of the percentage cover of that habitat (e.g. eight of the ten quadrats supported *H. grandifolius*, therefore the percentage cover of *H. grandifolius* was estimated as 80%). This process was repeated three times for each transect (once for each habitat). Three-way univariate analysis of variance (ANOVA) tested the relative contribution of each habitat to the total percentage cover of benthos across all depths and sites.

A fundamental sampling decision was the choice of size at which habitats were identified (1 m²). Although the size of *H. grandifolius* can be large (> 10 m long and up to 0.4 m wide; Wiencke and Clayton 2002), we considered that using 1 m² quadrats was appropriate because individual *H. grandifolius* at the study sites were consistently oriented with their long axis normal to the shoreline (i.e. across the shore), whereas our transects were oriented parallel to the shoreline (i.e. along the shore). As such, we sampled across the short axis of *H. grandifolius* (~ 0.4 m wide) and therefore had the potential to sample several individuals within each quadrat, rather than sampling along the long axis of *H. grandifolius*, which could bias results by repeatedly sampling the same individuals in numerous quadrats. The systematic orientation of *H. grandifolius* might be explained by the near absence of large waves and swell in near-shore regions (protection afforded by extensive sheets of sea ice that surround the continent), resulting in calm subtidal conditions that are likely to cause little disruption to the orientation of *H. grandifolius*.

The percentage cover of encrusting coralline algae growing on rocky substrata was sampled within each habitat at both sites. Sampling within stands of *H. grandifolius* and *P. decipiens* was done at 12 m depth. However, gaps were sparse at 12 m depth (see Results) and adequate replication of this habitat could only be achieved at 6 m depth (where canopies of *H. grandifolius* were sparse). Given this difference of depth among habitats, we cautiously interpret comparisons of the abundance of encrusting corallines between gaps and stands of *P. decipiens* or *H. grandifolius*. Quadrats (0.2 × 0.2 m, *n* = 8) were haphazardly placed within each habitat but were positioned > 1 m from the edge of a habitat. Percentage cover of encrusting corallines was estimated using the point intercept method (25 regularly spaced points within the 0.2 × 0.2 m quadrat). We did not identify the species of encrusting coralline we sampled because we hypothesized that the patterns and responses of this
group ought to transcend location (e.g. tropical vs temperate vs polar) and species identity.

**Response of corallines to canopy-loss and nutrients**

The bleaching and photosynthetic response of encrusting coralline algae to the loss of canopies of *H. grandifolius* was tested by comparing five experimental clearances of canopies to five controls (untouched canopy) at both sites. Clearances (~ 2 x 2 m in size) were made by separating the thallus of individual *H. grandifolius* from its holdfast with a knife (leaving the holdfast attached to the substratum) and swimming the thallus away from the clearance. A further five clearances were made at each site, within which ambient nutrient concentrations were experimentally elevated to test the hypothesis that negative effects of canopy removal on encrusting corallines would be less severe where nutrient concentrations were elevated. Coated fertilizer pellets (Osmocote® Plus slow-release) were used to elevate nutrient concentrations. Four porous bags (nylon mesh), each containing 6 g of Osmocote, were added to each clearance (total mass of Osmocote per clearance = 24 grams). Each bag was attached to a loop of galvanized wire that was threaded through holdfasts of *H. grandifolius* that remained attached to the substratum after canopies were removed. This method of attachment necessitated that all Osmocote bags were positioned ≤ 0.3 m from the substratum. This method is also considered the most appropriate way to enhance nutrient concentrations in subtidal experiments over periods of up to 6-8 weeks (Worm et al. 2000), with additions of 12 g of Osmocote (i.e. half of what was used at Casey) known to enrich temperate waters (Russell and Connell 2005). All clearances were made at depths of 10-13 m and were of similar size to large natural gaps observed at Casey (unpubl. data). Treatments were maintained by ensuring thalli of neighbouring plants were not present in clearances and bags of Osmocote were still attached to holdfasts in clearances. Water samples were taken from clearances (ambient and elevated nutrient treatments; *n* = 2) for analysis of ammonia, nitrate, nitrite and phosphorous concentrations. Samples were collected after 16 days using syringes, with the opening of each syringe positioned ~ 0.2 m from the Osmocote bags in elevated nutrient treatments. All samples were filtered immediately (0.45 μm filter) and frozen in liquid nitrogen prior to analysis by colorimetry (Skalar® segmented flow analyser; Australian Water Quality Centre).
Negative effects of canopy-loss on understorey encrusting corallines can occur over time periods as short as 1 – 4 days on tropical and temperate coasts (Littler 1973; Chapter 6). Based on this knowledge, we allowed 16 days to pass before we sampled the photosynthetic activity of corallines in all clearances (ambient and elevated nutrient concentrations) and beneath untouched canopies of *H. grandifolius* (controls). Photosynthetic activity was estimated in situ using a submersible pulse amplitude modulated (PAM) fluorometer (see below). Two samples were taken from each replicate, the mean of which was used as a single replicate for statistical analysis. Bleaching of encrusting corallines was identified across all treatments at the same time photosynthetic activity was estimated. The colour of corallines was used to quantify bleaching by comparison to a range of colours supplied by Wattyl® colour charts and assigning a value ranging from 1 (white) to 4 (crimson) to each replicate.

**Estimation of photosynthetic activity**

The photosynthetic activity of encrusting coralline algae was estimated using pulse amplitude modulated (PAM) fluorometry (Beer et al. 1998) because this technique is known to provide accurate estimates of the photosynthetic activity of encrusting coralline algae in polar waters (Kühl et al. 2001). Photosynthetic rates of electron transport (ETR) were calculated from estimates of the quantum yield of photochemical conversion of light energy (Y), using the equation:

\[
ETR = Y \times PAR \times AF \times 0.5
\]

where PAR is the amount of photosynthetically active radiation available to the corallines, AF represents the absorption factor of the thallus, and 0.5 is a constant that assumes both photosystems I and II absorb equal amounts of photon energy (Beer et al. 1998). Y was estimated using the saturating-light pulse method, while PAR was measured with the Diving-PAM’s quantum sensor whenever Y was sampled. The actual AF was not determined in this study, so a value of 1 was used for all calculations. Since this makes the assumption that the AF did not change among replicates, we present ETR as ‘relative ETR’ (rETR). Canopies of *H. grandifolius* reduced the intensity of PAR available to corallines (see Results). To compare among treatments, therefore, it was necessary to standardise estimates of
rETR to PAR (i.e. rETR:PAR) among all replicates to provide estimates of rETR per unit of available PAR. This ratio was the response variable analysed. Further details of this method are provided in Chapter 6.

Quantifying natural irradiance
Bleaching and concomitant declines in photosynthetic activity of encrusting corallines can be strongly related to enhanced intensities of light (Figueiredo et al. 2000; Chapter 6). We sampled the intensity of PAR (400 – 700 nm) and ultra-violet radiation (UV-A: 320 – 400 nm, and UV-B: 280 – 320 nm) within experimental clearances and beneath canopies of *H. grandifolius* (*n* = 6) to quantify the effect that canopies have on ambient irradiance. Sampling was done at one site (McMullin Island) over solar noon on an overcast day using a Li-Cor LI-192SA underwater quantum sensor (PAR) and a TriOS RAMSES-ACC hyperspectral irradiance sensor (UV-A and UV-B). Sampling during an overcast day was more representative than sampling on cloudless days because cloudy days occur more frequently at Casey than clear days during summer months (November - March) (62.8 % cloudy days vs 13.8 % clear days; Australian Bureau of Meteorology 2005). Differences in the intensity of PAR, UV-A and UV-B between treatments (clearances vs canopies) were tested with ANOVA.

7.4 Results
Relative abundance of habitats and encrusting coralline algae
The relative contribution of each habitat to the total percentage cover of benthos was dependent on depth (Table 7.1: Habitat × Depth interaction) and also varied between sites (Table 7.1: Habitat × Site interaction) (Fig. 7.2a). *Post-hoc* comparisons (SNK tests) revealed that *P. decipiens* formed more extensive covers than either *H. grandifolius* or gaps at 6 m (*P. decipiens > H. grandifolius = Gaps), while *H. grandifolius* was more abundant than either *P. decipiens* or gaps at 12 m (*H. grandifolius > P. decipiens = Gaps*). Between sites, *H. grandifolius* at Shirley Island formed more extensive covers than *P. decipiens*, which was more abundant than gaps (*H. grandifolius > P. decipiens > Gaps*), while *H. grandifolius* and *P. decipiens* at McMullin Island occurred in similar covers and were more extensive than gaps (*H. grandifolius = P. decipiens > Gaps*). A consistent pattern between
Table 7.1. Result of three-way ANOVA testing for differences in the percentage cover of habitats (*H. grandifolius* vs *P. decipiens* vs Gap) between depths (6 m vs 12 m) and sites (Shirley Island vs McMullin Island).

<table>
<thead>
<tr>
<th>Source</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>2</td>
<td>5525.99</td>
<td>8.98 ns</td>
</tr>
<tr>
<td>Depth</td>
<td>1</td>
<td>398.63</td>
<td>38.53 ns</td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>3.43</td>
<td>0.03 ns</td>
</tr>
<tr>
<td>Habitat × Depth</td>
<td>2</td>
<td>7044.37</td>
<td>37.98 *</td>
</tr>
<tr>
<td>Habitat × Site</td>
<td>2</td>
<td>615.40</td>
<td>5.26 **</td>
</tr>
<tr>
<td>Depth × Site</td>
<td>1</td>
<td>10.35</td>
<td>0.09 ns</td>
</tr>
<tr>
<td>Habitat × Depth × Site</td>
<td>2</td>
<td>185.47</td>
<td>1.58 ns</td>
</tr>
<tr>
<td>Residual</td>
<td>36</td>
<td>117.02</td>
<td></td>
</tr>
</tbody>
</table>

Data were arcsine(%) transformed. Cochran’s C-test of homogeneity of variances: $P > 0.05$. * $P < 0.05$, ** $P < 0.01$, ns $P > 0.05$. ‘Habitat’ and ‘Depth’ treated as fixed and orthogonal to ‘Site’ (treated as random).

Table 7.2. Result of two-way ANOVA testing for differences in the percentage cover of encrusting corallines among habitats (*H. grandifolius* vs *P. decipiens* vs Gap) and sites (Shirley Island vs McMullin Island).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>2</td>
<td>14464.15</td>
<td>197.38 **</td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>144.60</td>
<td>2.42 ns</td>
</tr>
<tr>
<td>Habitat × Site</td>
<td>2</td>
<td>73.28</td>
<td>1.23 ns</td>
</tr>
<tr>
<td>Residual</td>
<td>42</td>
<td>59.81</td>
<td></td>
</tr>
</tbody>
</table>

Data were arcsine(%) transformed. Cochran’s C-test of homogeneity: $P > 0.05$. ** $P < 0.01$, ns $P > 0.05$. ‘Habitat’ treated as fixed and ‘Site’ as random.
Figure 7.2. Mean % cover (± SE) of (a) *H. grandifolius*, *P. decipiens*, and gaps at 6 m and 12 m depth at Shirley Island and McMullin Island, and (b) encrusting coralline algae beneath canopies of *H. grandifolius*, within stands *P. decipiens*, and within gaps, at Shirley Island and McMullin Island.
sites was that *P. decipiens* was more abundant than *H. grandifolius* at 6 m, whereas *H. grandifolius* formed more extensive covers than *P. decipiens* at 12 m (Fig. 7.2a). Furthermore, gaps were relatively sparse at both sites and were only sampled at 6 m depth (some gaps were observed at 12 m depth but were not sampled in transects).

Encrusting coralline algae monopolized space beneath canopies of *H. grandifolius* (12 m depth) but were sparse within stands of *P. decipiens* (12 m depth) and within gaps (6 m depth) (Fig. 7.2b, Table 7.2: SNK tests: *H. grandifolius > P. decipiens > Gap*). This pattern was consistent between sites.

*Experimental manipulation of canopies and nutrients*

Removal of canopies of *H. grandifolius* had a negative effect on the photosynthetic activity of encrusting coralline algae at both sites (Fig. 7.3a). rETR:PAR of encrusting corallines beneath canopies was greater (at least double) than that recorded from encrusting corallines sampled in clearances (Fig. 7.3a, Table 7.3a). Among experimental clearances, ANOVA did not detect differences in rETR:PAR between treatments of ambient and elevated nutrient concentrations (Fig. 7.3a, Table 7.3a: SNK tests: Clearance-Ambient = Clearance-Elevated < Canopy for both sites). Comparison of the rank values of rETR:PAR between nutrient treatments, however, revealed that corallines exposed to ambient nutrient concentrations consistently had greater values relative to corallines exposed to elevated nutrient concentrations (17 of 20 comparisons; Binomial test: *P < 0.01*). Comparison of the rank values of nutrient concentrations in the water surrounding corallines revealed greater values in elevated vs ambient treatments at Shirley Island (e.g. ammonia (mean ± SE): 0.059 ± 0.035 vs 0.025 ± 0.000 mg L⁻¹), but no appreciable difference at McMullin Island (0.021 ± 0.002 vs 0.020 ± 0.002 mg L⁻¹). ANOVA failed to detect differences in the concentration of nutrients between ambient and elevated treatments at Shirley Island (e.g. ammonia: *F*₁,₄ = 0.88, *P > 0.40*). This outcome may be explained by inadequate replication (*n = 2*), rather than the low temperature (-1.8 °C) and run time (16 days: c.f. slow-release fertilizer pellets enhance nutrients for up to 6 – 8 weeks at comparable temperatures: Worm et al. 2000).
Figure 7.3. Results of experimental manipulations at Shirley Island and McMullin Island after 16 days: (a) mean (± SE) rETR:PAR and (b) mean (± SE) colour values of encrusting coralline algae among treatments (Clearance-Ambient vs Clearance-Elevated vs Canopy).
Table 7.3. Results of two-way ANOVAs testing for differences in (a) rETR:PAR and (b) colour of encrusting corallines among treatments (Clearance-Ambient vs Clearance-Elevated vs Canopy) and sites (Shirley Island vs McMullin Island).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(a) rETR:PAR</td>
<td></td>
<td>(b) Colour</td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>0.0080</td>
<td>38.75 *</td>
<td>977.11</td>
<td>24.73 *</td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>0.0011</td>
<td>3.76 ns</td>
<td>116.03</td>
<td>6.97 *</td>
</tr>
<tr>
<td>Treatment × Site</td>
<td>2</td>
<td>0.0002</td>
<td>0.73 ns</td>
<td>39.51</td>
<td>2.37 ns</td>
</tr>
<tr>
<td>Residual</td>
<td>24</td>
<td>0.0003</td>
<td>16.65</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(a) Cochran’s C-test of homogeneity of variances: $P > 0.05$. * $P < 0.05$, ns $P > 0.05$.
‘Treatment’ was treated as fixed and ‘Site’ as random.

(b) Data were $x^3$ transformed (required to remove heterogeneous variances).
Cochran’s C-test of homogeneity of variances: $P > 0.05$. * $P < 0.05$, ns $P > 0.05$.
‘Treatment’ was treated as fixed and ‘Site’ as random.
The colour of corallines within clearances was lighter (smaller colour values) than those beneath canopies at both sites (Fig. 7.3b), which is consistent with bleaching of corallines following the loss of canopies. No differences in the colour of corallines were observed between ambient and elevated nutrient treatments within clearances (Fig. 7.3b, Table 7.3b: SNK tests: Clearance-Ambient = Clearance-Elevated < Canopy). Within clearances with ambient concentrations of nutrients, corallines at Shirley Island were a lighter colour than those at McMullin Island (Table 7.3b: ‘Site’ main effect).

**PAR and UVR**

The intensities of PAR, UV-A, and UV-B were all greater in clearances than beneath canopies of *H. grandifolius* (Fig. 7.4, ANOVA: PAR: $F_{1,10} = 35.72, P < 0.001$; UV-A: $F_{1,10} = 20.97, P < 0.002$; UV-B: $F_{1,10} = 14.41, P < 0.004$). The intensity of both PAR and UV-A in clearances was three orders of magnitude greater than beneath canopies, while UV-B was two orders of magnitude greater in clearances.
Figure 7.4. Mean intensity ($\pm$ SE) of PAR (400 – 700 nm), UV-A (320 – 400 nm) and UV-B (280 – 320 nm) irradiance at the substratum in clearances and beneath canopies of *H. grandifolius*. Data plotted on a log₁₀ scale. Note that standard error of the mean is plotted for each bar but is often not observable due to small variances.
7.5 DISCUSSION

A century of widespread sampling of benthic organisms across the rocky coasts of Antarctica has revealed much about the diversity, abundance and geographical distribution of marine algae in this region (Wiencke and Clayton 2002). The subtidal rocky coasts near Casey are similar to many of the exposed rocky coasts of the world that support extensive stands of macroalgae that form a strong positive association with understorey encrusting coralline algae (Witman and Dayton 2001). Loss of canopies of algae on temperate coasts often triggers large and predictable changes to the assemblage of understorey taxa (e.g. Edwards 1998; Melville and Connell 2001). We observed large negative effects of removing canopies of *H. grandifolius* on encrusting corallines growing beneath, with such effects consistent with predictions of previous research on tropical and temperate coasts. However, elevating concentrations of nutrients did not greatly reduce the magnitude of the negative effects of canopy removal. Nevertheless, our results suggest that disturbance (removal) to canopies of *H. grandifolius* has large consequences for those organisms associated with this widely distributed (circumpolar) species of canopy-forming algae.

*H. grandifolius* occurred more extensively at 12 m depth than at 6 m, a pattern consistent with previous research of the distribution of macroalgae from more intensively studied regions of Antarctica (e.g. Antarctic Peninsula: Brouwer et al. 1995; Quartino et al. 2001). Beneath these canopies of *H. grandifolius*, encrusting coralline algae formed extensive covers (70 – 80 % of substratum space) and bleached from red to a pink/white colour following the removal of canopies. Bleaching of encrusting corallines following the loss of canopies of algae has also been observed on tropical (e.g. Littler 1973) and temperate coasts (e.g. Hawkins and Harkin 1985; Valentine and Johnson 2004), and appears to be a global phenomenon. Concomitant with bleaching, we observed a decline in the photosynthetic activity of corallines in clearances relative to corallines beneath intact canopies of *H. grandifolius*. The association between bleaching and reduced productivity of encrusting corallines has also been observed on temperate coasts (Figueiredo et al. 2000; Chapter 6) but is yet to be sampled in the tropics. Remarkably, the magnitude of the decline in photosynthetic activity following loss of canopies (relative to controls) is similar between temperate (mean ± SE = 45.98 ± 5.91% in southern
Australia: Chapter 6) and polar coasts (56.85 ± 8.43% at Casey: this study). Since the photosynthetic activity of bleached corallines at Casey did not decline to zero, bleaching may not always indicate death of encrusting corallines, as suggested in earlier literature (Littler 1973; Hawkins and Harkin 1985). Indeed, encrusting corallines are known to monopolise space in some habitats where most other types of algae are absent (e.g. urchin barrens) (Steneck and Dethier 1994). While these corallines are photosynthetically active (Chisholm 2003; Connell unpubl. data), they can also display obvious bleaching (Irving pers. obs.).

Models to account for bleaching and concomitant declines in the productivity of encrusting corallines commonly invoke negative effects of enhanced intensities of light following the loss of canopies of algae. Loss of canopies typically increases the intensity of light reaching the substratum by > 90% on temperate coasts (e.g. Connell 2003a; Clark et al. 2004) and we observed increases of similar magnitude for PAR, UV-A and UV-B at Casey. Moreover, Figueiredo et al. (2000) observed that formerly bleached corallines can restore their colour once shaded, while in Chapter 6, we observed similar responses between corallines provided natural shade (beneath canopies of algae) and those provided experimental shade designed to mimic shade afforded by canopies. Hence, there is evidence from temperate coasts that enhanced intensity of light is a key mechanism causing bleaching and declines in photosynthetic activity of encrusting corallines. While we did not experimentally assess this model at Casey, it is a plausible explanation for our observed effects given the similarities between our results and those obtained from temperate and tropical regions of the world. Previous research on encrusting corallines in the Arctic, however, has shown minor declines in photosynthetic activity at enhanced irradiances (Kühl et al. 2001; Roberts et al. 2002). It is difficult to compare our results to this observation because, unlike our system, the corallines sampled were not associated with canopies of algae nor were they bleached when photosynthetic activity was sampled. Nevertheless, experimentally assessing the model that enhanced irradiance causes bleaching and declines in photosynthetic activity of polar corallines may help reconcile these observations. This knowledge is worth pursuing because changes to the abundance of encrusting corallines are frequently associated with changes to the abundances of many understorey taxa.
Further research of this canopy-understorey interaction may benefit from focusing on the physiological mechanisms causing bleaching and reduced photosynthetic activity following the loss of canopies. Many marine algae photoacclimate to variable light environments by altering the concentrations of their light-harvesting pigments (often reducing them when light intensity is enhanced) so that photosynthetic rates are optimized (Ramus et al. 1976a). Marine algae in polar climates also exhibit this phenomenon in response to gradual (e.g. increasing/decreasing day length) and rapid changes in the irradiance environment (e.g. break up of winter ice sheets) (Lüder et al. 2001, 2002). Hence, bleaching of encrusting corallines may represent a reduction in pigment concentrations, which facilitates photoacclimation to the new irradiance environment experienced where canopies are removed. As we did not sample corallines through time, we are unable to assess whether they had fully acclimated to enhanced irradiances after 16 days, whether this process was ongoing, or if the observed decline in photosynthetic activity was transient or enduring. These questions, in addition to a more detailed physiological understanding of processes associated with photoacclimation (e.g. changes in the activity of carbon-fixing enzymes, damage to the reaction centres of photosystems I and II after prolonged exposure to enhanced irradiances, etc.), require further study for those interested in a mechanistic understanding.

Anthropogenic perturbations (e.g. nutrient enrichment) may interact with natural disturbances (e.g. canopy-loss) to produce exceptional responses from organisms (Vitousek et al. 1997; Benedetti-Cecchi et al. 2001). Elevating the concentration of nutrients in clearances, which was only achieved at one site (Shirley Island), slightly exacerbated the negative effects of removing canopies of *H. grandifolius* on rETR:PAR of corallines. Outwardly, the absence of a large effect of nutrient enrichment is not entirely surprising given that the polar waters of Antarctica are relatively nutrient-rich (Dayton et al. 1994) and therefore benthic algae are unlikely to be nutrient limited. Nevertheless, even a slight negative effect of nutrient enrichment is intriguing given that many algae, including encrusting corallines, often respond positively to such conditions (e.g. Smith et al. 2001; Gorgula and Connell 2004). Greater rETR:PAR in clearances with ambient nutrient concentrations could potentially be explained by an indirect effect of overgrowth of corallines by epiphytic algae (Hawkins and Harkin 1985), which causes colour restoration in
bleached corallines (Figueiredo et al. 2000) and suggests that photosynthetic activity may also recover. This model does not appear to explain our observation, however, because at both sites we observed greater covers of epiphytic algae (chain diatoms) on corallines in clearances where nutrients were added (unpubl. data).

Knowledge of the spatial and temporal generality of patterns and processes is critical for making inferences beyond the scales of ecological experiments (see Thrush et al. 1997 for further discussion) and developing our predictive understanding of certain phenomena (Keddy 2001). Testing predictions derived from the results of previous experiments at new places and times or with new habitats and species can be useful for assessing generality (Underwood and Denley 1984; Gurevitch et al. 1992). Our observations of patterns (encrusting coralline-canopy association) and responses (bleaching and photosynthetic activity of corallines) in Antarctica are consistent with predictions from tropical and temperate coasts. This coherence among numerous independent tests using different species at different times and places suggests that such patterns and responses may be predictable across large distances and environmental gradients (i.e. tropical-temperate-polar). If ecology seeks to predict the abundances, distributions and responses of organisms to particular events, then this subtidal system (canopy-understorey patterns and processes) offers consistency, testability, productivity and simplicity, critical elements of predictive power (Fagerström 1987).
Where desert meets ocean: the inspiring coastline of the Great Australian Bight (photo by Travis Elsdon).
CHAPTER 8
CHAPTER 8

GENERAL DISCUSSION

This thesis provides quantitative evidence of interactions between canopy-forming algae and understorey assemblages (algae and sessile invertebrates) on subtidal rocky coasts of temperate Australia and beyond (New Zealand and Antarctica). The consequences of habitat heterogeneity within forests of algae for the distribution and abundance of understorey taxa are quantified across > 5000 km of the coastline of temperate Australasia. Emphasis is placed on experimentally identifying positive and negative effects of canopy-forming algae (mainly *E. radiata* and species of Fucales) on understorey taxa that frequently characterise benthic habitat on subtidal rocky coasts around the world (encrusting coralline algae, articulated coralline algae, and filamentous turf-forming algae). A deliberately recurring theme throughout this thesis is the assessment of generality and predictability in canopy-understorey patterns and responses. This is primarily achieved using four methods: (i) sampling from local (km) to regional scales (1000’s km) to identify consistency of pattern across multiple spatial scales (Chapters 2, 3, and 4), (ii) quantifying patterns and testing responses at different places (separated by large distances) and using different species (Chapters 6 and 7), (iii) using broad morphological groupings to classify understorey taxa (Chapters 3, 4, 5, 6, and 7), and (iv) placing my results within the context of appropriate published knowledge (all chapters).

This chapter provides a summary of the key findings presented in this thesis. For expanded discussion of the points made here, and for further details that have been omitted, the reader should consult the relevant text in Chapters 2 through to 7.

8.1 PATTERNS AND CONSEQUENCES OF HABITAT HETEROGENEITY

Habitat heterogeneity is a pervasive feature of natural systems that has profound consequences for the distribution and abundance of flora and fauna from local to regional scales (Hutchings et al. 2000). It is, therefore, prudent to understand the scales over which heterogeneity manifests in natural systems to identify ecologically meaningful scales for sampling and experimentation within habitats. Extensive
forests of canopy-forming algae (e.g. kelps) characterise subtidal coasts in temperate regions of the world, and are often considered to exhibit a great deal of patchiness in the composition of canopies and configuration of habitat (Harrold and Reed 1985; Dayton et al. 1992; Konar and Estes 2003; Goodsell et al. 2004). Across > 2000 km of subtidal temperate Australian coastline, the heterogenous structure of algal forests comprising *E. radiata* and several species of Fucales was quantified (Chapter 2). Individual patches of habitat (monospecific canopies vs mixed-species canopies vs gaps) were frequently 10 m or less in size, indicating that habitat mosaics within these forests of canopy-forming algae generally vary at the scale of metres. Of the three habitats identified, patches of *E. radiata* mixed with Fucales typically occurred more frequently and were more extensive than either monospecific patches of *E. radiata*, or gaps among canopies. Importantly, the mean sizes of patches observed in Australia were remarkably similar to those sampled on neighbouring (New Zealand) and distant coasts (California and Antarctica). From these data, I propose that studies done at the scale of metres (i.e. 1-10 m) appear well-matched to natural scales of heterogeneity within forests of canopy-forming algae across much of temperate Australia.

Variation in the presence and composition of algal canopies appears to have large consequences for the distribution and abundance of associated flora and fauna (Kennelly 1987a; Edwards 1998; Goodsell et al. 2004). Using knowledge of the natural scales of habitat heterogeneity identified in Chapter 2, I tested for differences in the composition of understorey assemblages (algae and sessile invertebrates) among monospecific canopies, mixed-species canopies, and gaps among canopies across > 5000 km of the coastline of temperate Australasia (Western Australia to New Zealand). Benthic assemblages almost always differed among all three habitats. The magnitude and direction of differences among habitats were similar between western and southern Australia, but were often reversed to eastern Australia, while patterns from all regions were distinct from New Zealand (WA = SA ≠ EA ≠ NZ). While local patterns were complex, the major morphological groups that often characterise benthos (i.e. encrusting coralline algae, articulated coralline algae, and filamentous turf-forming algae) revealed patterns that could be related across space from local to regional scales.
There are three key outcomes from this research. First, clear differences in the structure of understorey assemblages between monospecific and mixed-species canopies of algae indicate that failure to distinguish between these superficially similar types of habitat may present misleading conclusions about the ecology of Australasia's algal forests. Second, any local complexity of pattern (e.g. variation among habitats and sites) need not impede searches for broad-scale generalisations when the spatial limits of patterns are also understood (i.e. variation among regions). Third, the striking regional-scale differences highlight the need to cautiously extrapolate results among regions. To date, most of our knowledge of the ecology of Australasia's forests of *E. radiata* is based on local scale research done in eastern Australia (particularly Sydney) and north-eastern New Zealand (particularly in the Leigh Marine Reserve). The results of Chapter 3 clearly demonstrate that the canopy-understorey associations in either of these regions are not representative of the remaining two-thirds of the coastline of temperate Australia. Accordingly, the insight gained from research in any one particular region may not always be directly applicable to other regions. These results add to a growing body of evidence suggesting the existence of very real differences in the ecology of algal forests among these regions of temperate Australasia (e.g. Fowler-Walker and Connell 2002; Goodsell et al. 2004).

**8.2 Consistency in Canopy-Understorey Associations**

The large and consistent differences in the composition of understorey assemblages among habitats and across large portions of coastline suggest determinism in the assembly of taxa to understorey substrata. Such knowledge can be of use in the formal construction of assembly rules that predict how different communities are assembled from a common species pool (Weiher and Keddy 1999). By testing the assembly of understorey algae to unoccupied substrata within experimental habitats constructed as monospecific *E. radiata*, mixed *E. radiata*-Fucales, and gaps, I was able to recreate natural canopy-understorey associations observed across > 1000 km of South Australian coastline (Chapter 4). Hence, the subsets of species that assemble to subtidal rocky substrata in South Australia appear predictable given knowledge of the presence and composition of canopies incorporating *E. radiata*. Specifically, I propose the assembly rule that understorey communities on subtidal rocky coast in South Australia can be expected to be (i) monopolised by encrusting
coralline algae beneath monospecific canopies of *E. radiata*, (ii) comprised of encrusting corallines, encrusting non-corallines, and sparse covers of articulated corallines, beneath mixed *E. radiata*-Fucales canopies, and (iii) comprised of extensive covers of articulated corallines and filamentous turfs, as well as sparse covers of foliose algae and juvenile canopy-formers, within gaps among canopies.

The observed consistencies between natural patterns and experimental effects (Chapter 4) demonstrate how canopies of algae can act as a filter to limit which subsets of species from the locally available pool are able to assemble beneath them. Knowledge of the effects of canopies *per se* is useful for a predictive understanding of the distribution and abundance of understory, as well as forecasting the likely changes to understory following the loss or addition of a canopy, or any change to its composition (e.g. mixed-species to monospecific). Even so, an understanding of the mechanisms that act to facilitate and exclude species as understory remains a critical component of our ecological understanding of algal forests.

### 8.3 Positive and Negative Effects of Canopies

Positive and negative effects of habitat-forming organisms (e.g. canopy-forming algae) are often key determinants of pattern in the distribution and abundance of associated species (Jones et al. 1997; Bruno and Bertness 2001). Forests of *E. radiata* can greatly modify local environmental conditions (e.g. light intensity, water motion, etc.), which influence the assembly and maintenance of understory through numerous positive and negative effects on individual taxa (Kennelly 1989; Connell 2003b, 2005). The experimental addition of monospecific and mixed-species canopies above articulated coralline algae and filamentous turf-forming algae (which are both naturally sparse beneath canopies but extensive within gaps on natural reef: Chapter 3) revealed strong negative effects of canopies on the abundance of both groups of understory algae. Experimentally isolating the process of abrasion of the substratum by the laminae of canopy-formers highlighted a substantial contribution of abrasion to the observed effects of canopies *per se* (~ 70 – 80 % for articulated coralline and ~ 60 % for filamentous turf). The negative effects of canopies and abrasion on articulated corallines were greater beneath monospecific canopies relative to mixed-species canopies (consistent with patterns of abundance on natural reef), but did not differ among types of canopy for filamentous
turfs (also consistent with natural patterns). Such knowledge contributes to our understanding of ecological differences and similarities between monospecific and mixed-species canopies of algae.

Abraison is one of many influences of canopies, but I have demonstrated that it is a process that can contribute substantially to the heterogeneity of understorey habitat within subtidal forests of E. radiata (Chapter 5). Other factors modified by E. radiata, but particularly shade afforded by the canopy, can have strong effects on understorey and explain up to half the variation in understorey composition (Connell 2003a). A promising area for further research involves testing the role of abrasion relative to other local-scale processes, such as shading by the canopy, to not only provide greater insight into the mechanisms that establish and maintain patterns of canopy-benthos associations in kelp forests, but to also identify potential synergies (e.g. Irving and Connell 2002; Connell 2003a).

While abrasion by canopies of E. radiata has negative effects on articulated corallines and filamentous turfs, shade afforded by canopies has positive effects on understorey encrusting coralline algae (Chapter 6). Around the world, encrusting coralline algae form a strong positive association with canopies of algae (Steneck 1986; Witman and Dayton 2001), and a frequent observation following the loss of canopies is that the understorey encrusting corallines bleach from red/pink to white (Figueiredo et al. 2000; Valentine and Johnson 2004), which has been suggested as an indicator of death (Littler 1973; Hawkins and Hartnoll 1985). Experimental removal of canopies of E. radiata caused understorey encrusting coralline algae to bleach, which was associated with a decline in photosynthetic activity (electron transport rate) relative to corallines beneath intact canopies. However, the photosynthetic activity of bleached corallines did not decline to zero, demonstrating that bleaching did not indicate the death of corallines. Instead, bleaching may represent changing pigment concentrations to facilitate photoacclimation to enhanced irradiances (e.g. Ramus et al. 1976a; Lüder et al. 2002), which may explain why encrusting corallines, although bleached, are sometimes able to persist in the absence of algal canopies (e.g. urchin barrens). Nevertheless, an independent experimental test demonstrated that shade afforded by canopies plays a large role in the prevention of bleaching of encrusting corallines and maintenance of their photosynthetic
activity, and hence contributes to the maintenance of the positive association between canopy-forming algae and encrusting coralline algae.

8.4 Assessing Generality of Responses
Testing predictions derived from the results of previous experiments at new places and times or with new habitats and species can be useful for assessing the generality of patterns and responses (Underwood and Denley 1984; Gurevitch et al. 1992). The responses of encrusting coralline algae to canopy-loss (i.e. bleaching and a decline in photosynthetic activity) have been observed on tropical and temperate coasts and appear to be general phenomena, but knowledge of such responses occurring on polar coasts does not exist. On subtidal coasts at Casey, East Antarctica, I detected a strong positive association of encrusting coralline algae with canopies formed by the endemic alga Himantothallus grandifolius (Chapter 7). After removal of H. grandifolius, corallines bleached from red to pink/white concomitant with a decline in their photosynthetic activity. The magnitude of this decline (mean ± SE = 56.85 ± 8.43%) was remarkably similar to that observed on temperate coasts (45.98 ± 5.91%; Chapter 6). Shade provided by canopies has been shown to be important in preventing bleaching of corallines and maintaining their photosynthetic activity (Figueiredo et al. 2000; Chapter 6). Although this model was not tested at Casey, removing H. grandifolius increased the intensity of photosynthetically active radiation (PAR) and ultra-violet radiation (UVR) reaching the substratum by three orders of magnitude, suggesting enhanced irradiance is a likely explanation for the observed responses of corallines. Striking similarities among results from Casey and those from tropical and temperate coasts suggest that responses of encrusting corallines to loss of canopies may have predictive properties across large distances and environmental gradients (tropical-temperate-polar).

8.5 Future Research
As with most ecological research, the deeper we dig the more questions we find. To quote A. J. Underwood (1997) (p. 481),

"Another feature of biological experimentation that needs greater appreciation is that virtually all our work is preliminary. The hallmark of progressive ideas is that they progress!"
With this mindset, I now provide a grossly inexhaustive list of areas for further research.

- The striking regional pattern identified in Chapter 3 (WA ≠ SA ≠ EA ≠ NZ) begs explanation. Within this thesis, I have provided numerous models that may contribute to the origin and maintenance of this pattern (e.g. grazing pressure, effects of canopy morphology on environmental conditions, ocean boundary currents, ancient land bridges, etc.), supplementing with supporting evidence where possible. Importantly, such models are yet to be assessed over the appropriate scales. Concerted effort in identifying the causes of observed regional-scale differences, and similarities, represents a promising area for further research.

- In a similar vein, examining the relative influence of regional vs local-scale processes in structuring the patterns observed across Australasia (Chapter 3) may prove a challenging, yet rewarding endeavour. Regional-scale patterns may be the result of processes operating at regional scales, processes operating at local-scales that repeat themselves over large distances, or an interaction between the two (e.g. in one region, the effects of some local-scale process are negated by the influence of some regional-scale process). Given the range of spatial scales involved, acquiring the evidence needed to distinguish among these models will require carefully designed hypotheses and experimental tests. Such knowledge, however, could provide great insight for explaining current patterns, in addition to advancing this topical field of contemporary ecology (see Huston 1999 for further discussion).

- Canopies of algae greatly modify local environmental conditions (e.g. shade, water flow, etc.) that contribute to observed positive and negative effects of canopies on understorey. In this thesis, I have tested the role of two factors (abrasion and shade) in maintaining widespread canopy-understorey associations. While clear effects were often observed, further research would benefit from simultaneously testing multiple factors to identifying potential synergies (e.g. Irving and Connell 2002; Connell 2003a) that would
contribute to a better mechanistic understanding of the ecology of algal forests.

- Across temperate Australasia, habitat created by canopy-forming algae was identified as existing in monospecific (*E. radiata*) and mixed-species configurations (*E. radiata* with Fucales). Large differences in the composition of understorey assemblages (Chapter 3) and the effects of particular processes (i.e. abrasion: Chapter 5) were frequently detected between these superficially similar types of habitat. Therefore, it may not be surprising to find that mixed-species stands of algae represent distinct habitats that deserve study in their own right (as is the case in terrestrial systems, e.g. Cannell et al. 1992). Furthermore, my results suggest that partitioning observations between these two types of habitat could enhance predictive power in a system where overwhelming spatial variability is often emphasised (e.g. Wernberg et al. 2003).

- On Australian and Antarctic coasts, the removal of algal canopies caused understorey encrusting coralline algae to bleach, which was associated with reduced photosynthetic activity. Further research of this interaction may benefit from focussing on the physiological mechanisms driving such responses in corallines. Bleaching may represent changing pigment concentrations, which facilitates photoacclimation of corallines to enhanced irradiances. Knowledge of sub-cellular responses associated with photoacclimation (e.g. changes in the activity of carbon-fixing enzymes, damage to the reaction centres of photosystems I and II, etc.), may also contribute to a physiological viewpoint of this predictable canopy-understorey interaction.

- Throughout this thesis, the use of morphological groups to quantify understorey has been used, with occasional regard for species identity. Using such means of classification has been deliberate in my attempts to identify generality in the responses of understorey to canopies across vast distances, and is often considered advantageous for achieving such predictive outcomes (e.g. Steneck and Dethier 1994; Keddy 2001). This approach can
undoubtedly sacrifice knowledge of species-specific responses of understorey
in favour of broad generalisations. To this end, testing the responses of
particular understorey species of concern would prove insightful for those
interested in a detailed understanding of species-specific responses of
understorey to canopies.

8.6 Conclusions
The data presented in this thesis have demonstrated widespread heterogeneity in the
structure of subtidal algal forests of temperate Australia, which has large effects on
the composition of associated understorey assemblages (algae and sessile
invertebrates) across > 5000 km of coastline (Western Australia to New Zealand).
Importantly, the magnitude and direction of differences among habitats varied among
regions sampled (WA = SA ≠ EA ≠ NZ), usefully identifying spatial limits for
attempts to extrapolate results among regions. The assembly of understorey algae to
experimental habitats was largely consistent with patterns observed on natural coasts,
indicating that the structure of understorey assemblages appears predictable given
knowledge of the presence and composition of algal canopies.

The influence of canopies of algae on local environmental conditions had positive
and negative effects on understorey. Consistent with patterns of abundance observed
on natural coasts, I detected strong negative effects of abrasion by canopies on the
abundance of articulated coralline algae and filamentous turf-forming algae. In
contrast, I observed clear positive effects of canopies on encrusting coralline algae,
which are frequently associated with algal canopies. A broad-scale approach to
sampling and experimentation within forests of canopy-forming algae facilitated an
enlightening and unique perspective on the generality and predictability of patterns
and responses within these widespread habitats. Indeed, algal canopy-understorey
interactions show great promise for progressive outcomes where knowledge of
generality is sought and predictability is embraced.
Charismatic mesofauna of South Australia's rocky coasts, the Leafy Seadragon *Phycodurus eques* (photo by the author).
“...I found the surface of the island, where it was sandy and produced small shrubs, to be full of [sooty petrel] burrows. Penguins...had their burrows nearer to the water-side. A small species of kangaroo was also found. A party was sent on shore at dusk to collect petrels, and in less than two hours returned with sufficient to give four birds to every man in the ship.”

Matthew Flinders
Captain of the British vessel Investigator
Comments on the Isle of St. Francis, February 1802

“From their appearance, their aridity, and everything else which makes them distasteful, I am not surprised that they have been named after the two saints who made vows of poverty, for they provide the most perfect example it is possible to give of it”

Nicholas Baudin
Captain of the French vessel Le Geographe
Comments on the Isles of St. Francis and St. Peter, May 1802
Unlike Flinders, Baudin did not land a shore party
Appendix A: Preamble

Appendix A presents data quantifying the heterogeneity of algal habitat on the subtidal rocky coasts of an offshore island (St Francis Island, Nuyts Archipelago) in South Australia. Differences in the morphology of *E. radiata* are quantified among habitats, while associations of benthic algae with each type of habitat are also tested. This research was part of a scientific voyage to the Nuyts Archipelago, funded by the Department of Environment and Heritage (State Government of South Australia), and the South Australian Research and Development Institute.

This chapter was published in the journal *Transactions of the Royal Society of South Australia* in 2003 (vol. 127: 167-175), with myself as senior author, and Meegan J. Fowler-Walker and Sean D. Connell (University of Adelaide) as co-authors. It is, therefore, written in plural. Permission from the publisher to reproduce this manuscript herein has been granted (see Appendix B).

Contributions and signatures of authors

ANDREW D. IRVING

*Sampled, analysed, and interpreted data, wrote manuscript as senior author.*

Signed:................................. Date:.............................

MEEGAN J. FOWLER-WALKER

*Sampled, analysed, and interpreted data, wrote portions of the Methods and Results.*

Signed:................................. Date:.............................

SEAN D. CONNELL

*Supervised development of research, data interpretation, and manuscript evaluation.*

Signed:................................. Date:.............................
ASSOCIATIONS OF FOREST-TYPE WITH MORPHOLOGY OF ECKLONIA RADIATA AND ABUNDANCE OF UNDERSTOREY ALGAE

A.1 ABSTRACT
This study tested for ecological differences between monospecific and mixed-species stands of subtidal canopy-forming algae. At three sites on the northern shore of St Francis Island, we determined the proportional cover of four configurations of canopy-forming algae: (i) monospecific stands of Ecklonia radiata, (ii) E. radiata clumps (≥ 4 individuals) surrounded by species of Fucales (e.g. Cystophora spp. and Sargassum spp.), (iii) individual E. radiata plants (or clumps of < 3 plants) interspersed among fucoid species and (iv) fucoid dominated stands. Mixed E. radiata-fucoid and fucoid-dominated stands formed the most extensive types of canopy, comprising > 94% of forests sampled at all three sites. Using this information, we then tested whether the morphology of E. radiata plants and structure of understorey floral assemblages differed between monospecific E. radiata canopies and canopies of individual E. radiata plants interspersed among fucoids. The morphology of E. radiata showed no substantial differences between monospecific and mixed-species canopies. The structure of understorey assemblages, however, differed substantially among monospecific canopies, mixed-species canopies, and gaps among canopies of algae (rocky substrata without canopy-forming algae). These results suggest that while the morphology of mature E. radiata is not strongly influenced by forest composition, it is likely that understorey algae are strongly affected by the composition and relative covers of species in the overlying canopy.

A.2 INTRODUCTION
Despite differences in the physical environment and ecology of monospecific and mixed-species stands of vegetation that compose terrestrial forests (Cannell et al. 1992; Hölscher et al. 1998), few studies have tested for differences between monospecific and mixed-species stands of subtidal vegetation. Marine algae form
conspicuous habitats on subtidal rocky coasts at temperate latitudes (Chapman and Johnson 1990; Underwood et al. 1991; Witman and Dayton 2001) and recent evidence demonstrates widespread heterogeneity in composition and spatial arrangement of canopy-forming algae on mainland coasts (Goodsell et al. 2004; Chapter 2). Such heterogeneity may have large implications for the distribution and abundance of plants and animals (Schiel and Foster 1986; Goodsell et al. 2004). The presence or absence of an algal canopy appears to influence the composition and abundance of understorey biota (Reed and Foster 1984; Schiel and Foster 1986; Kennelly 1987c; Kennelly and Underwood 1993; Edwards 1998; Melville and Connell 2001; Fowler-Walker and Connell 2002) but there remain few quantitative tests of differences in the structure of understorey assemblages between monospecific and mixed-species canopies (but see Shepherd and Womersley 1970; Chapter 3). Moreover, the morphology of canopy-forming algae can vary over regional (i.e. 1000's km) through local spatial scales (i.e. metres) (Rice et al. 1985; Schiel and Foster 1986). Such morphological differences are often explained in terms of hydrodynamic variation at scales of cm to several km (see review by Hurd 2000). It is possible that the composition of canopies (i.e. monospecific vs mixed-species) may influence the morphology of the component species as a direct or indirect consequence of differences in the type and abundance of neighbouring individuals within a stand (Dayton 1975b; Schiel and Foster 1986).

We tested for differences in the relative abundance of four types of habitat (monospecific, mixed-clumped, mixed-interspersed and fucoid; see definitions below) created by canopy-forming macroalgae at three sites on the northern shore of St Francis Island, Nuyts Archipelago, South Australia. We then tested the hypotheses that (i) the morphology of *E. radiata* and (ii) the structural composition of understorey assemblages differ between monospecific and mixed-species canopies of algae.

**A.3 MATERIALS AND METHODS**

Three sites separated from each other by at least 1 km were sampled along the northern coastline of St Francis Island (Fig. A.1), which is relatively protected from the large southerly swells that the island is subjected to throughout the year.
Figure A.1. Map of St Francis Island showing the locations of the study sites and the position of St Francis Island relative to mainland South Australia. Inset: Map of Australia with South Australia shaded.
Canopy-forming algae were defined as stipitate algae greater than 50 mm in height.

Relative abundance of algal habitats

Habitats created by canopy-forming algae were identified at the 1 m² scale as: ‘monospecific E. radiata’ when ≥ 80 % of the canopy cover comprised E. radiata, ‘mixed-species’ when 40-60 % of the canopy cover comprised fucoid species (e.g. Cystophora, Sargassum, Myriodesma spp., and Scytothalia dorycarpa; see Shepherd and Womersley 1976 for a more complete list) and the remaining cover comprised E. radiata, and ‘fucoid’ when > 80 % of the canopy cover comprised fucoid species. Only canopies containing E. radiata with 40-60 % cover of fucoid species were classified as ‘mixed-species’ because such habitats were believed to represent a more mixed configuration of canopy-forming algae than canopies containing 20-40 % or 60-80 % fucoid species. Mixed-species canopies were further categorised as ‘clumped’ when ≥ 4 individuals of E. radiata were nearest neighbours and were surrounded by fucoid species, and ‘interspersed’ when individual E. radiata were scattered among fucoids so that nearest neighbours were not other E. radiata individuals. At each site, the relative abundance of each of the four habitats was quantified along four 100 × 1 m transects separated by > 10 m. Transects followed tape measures laid out normal to the shoreline and began as close to mean low water as the prevailing conditions would allow. Observers swam along each transect and recorded the distance at which the type of habitat changed. Sampling stopped at 100 m or the sandline, whichever occurred first. Univariate analysis of variance (ANOVA) tested the relative contribution of the different types of habitat across the three sites, treating ‘Site’ as random and ‘Habitat’ as fixed and orthogonal. However, for any given transect, the abundance of a particular type of habitat was not independent of the abundances of the other three types of habitat in that transect. Hence, the data for one of each type of habitat were randomly selected from each of the four original transects (e.g. the abundance of monospecific canopies from transect 1, mixed-clumped canopies from transect 2, mixed-interspersed canopies from transect 3 and fucoid canopies from transect 4), and were combined to generate a ‘new’ transect where the abundance of any one type of habitat was independent of that for any other type of habitat. This process was repeated until four ‘new’ transects were generated per site.
**Morphological measures of Ecklonia radiata**

Eight morphological characteristics were quantified from individual *E. radiata* (Table A.1) sampled from monospecific canopies of *E. radiata* and mixed-interspersed canopies only, because *E. radiata* appeared to be more evenly mixed with fucoids in these canopies than in mixed-clumped canopies. At each of the three sites, five quadrats (1 m²) were haphazardly placed within each type of habitat at a depth of 3–8 m to minimise possible bias of depth on morphology. Quadrats were separated by metres, and positioned > 1 m from the edge of a patch of habitat. A single *E. radiata* plant within each quadrat was cut off at the base of the stipe and brought to the surface to measure. Only mature plants (stage 3, *sensu* Kirkman 1981) were used to reduce any bias of age on the morphological measures. Two-way permutational multivariate analysis of variance (PERMANOVA: Anderson 2001) tested the relative and interactive effects of habitat and site on the morphology of *E. radiata*.

**Structure of understorey assemblages**

Assemblages of understorey flora were quantified beneath monospecific and mixed-interspersed canopies of algae, and also on surfaces of reef without canopy-forming macroalgae (referred to as ‘gaps’ among canopies of algae). Quadrats (1 m², *n* = 6) were haphazardly placed within each type of habitat at a depth of 3-8 m and were positioned > 1 m from the edge of a patch of habitat. The percentage covers of understorey algae were then quantified from each quadrat using the point-intercept method (25 regularly spaced points within an area of 0.2 × 0.2 m; Meese and Tomich 1992). Taxa were recognised as a component of the understorey if their height was < 50 mm, and the functional groups identified were encrusting coralline algae, articulated coralline algae, filamentous turf-forming algae, foliose (fleshy, non-coralline) algae and juvenile canopy-forming algae (*sensu* Steneck and Dethier 1994).
Table A.1. Morphological variables of *Ecklonia radiata* quantified. The terminology of (Womersley 1987) has been adopted for describing particular parts of the plant.

<table>
<thead>
<tr>
<th>Morphological Variable</th>
<th>Procedure for measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet Weight (g)</td>
<td>Excess water shaken off and weight of whole plant (without holdfast) measured on a spring balance.</td>
</tr>
<tr>
<td>Plant Length (cm)</td>
<td>Length of plant from base of stipe to tip of blade.</td>
</tr>
<tr>
<td>Stipe Length (cm)</td>
<td>From immediately above the holdfast to where the stipe widens into the meristematic region.</td>
</tr>
<tr>
<td>Blade Length (cm)</td>
<td>From base of meristematic region to the tip of blade.</td>
</tr>
<tr>
<td>Stipe Width (cm)</td>
<td>Immediately above the holdfast. Widest diameter if oval shaped.</td>
</tr>
<tr>
<td>Blade Width (cm)</td>
<td>Width measured at 50% of blade length.</td>
</tr>
<tr>
<td>Number Mature Laterals</td>
<td>Count of laterals &gt; ~ 30 mm in length (not including eroded apical laterals).</td>
</tr>
<tr>
<td>Number Eroded Laterals</td>
<td>Count of laterals that have undergone heavy degradation (usually near apex of blade).</td>
</tr>
</tbody>
</table>
A.4 RESULTS

**Relative abundance of algal habitats**

Most stands of canopy-forming algae contained *E. radiata* in some configuration, and monospecific canopies of *E. radiata* generally occurred in the lowest proportion of all habitat types (Fig. A.2). The spatial arrangement of the different types of habitat exhibited considerable heterogeneity at all depths greater than 3 m and the relative abundance of the four types of habitat varied in an inconsistent manner among sites (ANOVA: Habitat × Site interaction: $F_{6,36} = 310.77$, $P = 0.0463$; SNK-tests; Fig. A.2). Previous studies of the subtidal distribution of canopy-forming algae have identified depth-related zones of particular types of habitat (e.g. Shepherd and Womersley 1970, 1976; Grace 1983). In this study, ANOVA on the depths at which each type of habitat occurred did not provide any evidence for a correlation of canopy type with depth ($P > 0.05$ for all sites). This is not surprising given that the depths that transects stopped at ranged between 10.8 m and 17.6 m, which is well within the extent of the mid-sublittoral algal zone identified by Shepherd and Womersley’s (1976) study of the algal flora of St Francis Island.

**Morphology of *E. radiata***

The morphology of *E. radiata* generally did not differ between monospecific and mixed-species canopies (PERMANOVA: Habitat: $F_{1,2} = 2.25$, $P = 0.1768$), but did differ among sites (PERMANOVA: Site: $F_{2,34} = 2.28$, $P = 0.0410$) although post-hoc tests failed to distinguish among sites and the nMDS plot did not provide an indication of obvious differences among sites (Fig. A.3). There was, however, a consistent trend for plants to be larger from monospecific than mixed-species canopies (Fig. A.4), such that 20 of 24 comparisons (8 variables × 3 sites) showed morphological variables to be larger (i.e. heavier, longer, wider). While ANOVA did not detect significant differences between mixed-species and monospecific canopies (Table A.2), this observation (20 of 24 comparisons) is not expected by chance alone (Binomial test: $P < 0.01$; Underwood 1997).

**Understorey assemblages**

The structure of the understorey assemblages differed according to the type of habitat at each site (PERMANOVA: $F_{2,45} = 25.01$, $P = 0.0006$; monospecific ≠ mixed ≠ gap; Fig. A.5). A weak effect of site was detected (PERMANOVA: $F_{2,45} = 2.45$, 172
Figure A.2. Percentage cover (± SE) of different types of algal habitats \((n = 4)\) for three sites at St Francis Island.
Figure A.3. nMDS plot of *Ecklonia radiata* morphology between monospecific canopies (filled symbols) and mixed-species canopies (unfilled symbols) within each site ( ■ Site 1, ● Site 2, ▲ Site3).
Figure A.4. Measures of morphological variables (± S.E., n = 5) of *Ecklonia radiata* for monospecific and mixed-species canopies at three sites.
Table A.2. Two-way ANOVAs testing for differences of morphological characteristics of *Ecklonia radiata* among habitats (monospecific vs mixed-species) and sites \((n = 3)\). * = \(P < 0.05\), ** = \(P < 0.01\), ns = \(P > 0.05\).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>(F)</th>
<th>MS</th>
<th>(F)</th>
<th>MS</th>
<th>(F)</th>
<th>MS</th>
<th>(F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>1</td>
<td>0.04</td>
<td>1.33*</td>
<td>0.12</td>
<td>4.74*</td>
<td>0.10</td>
<td>4.67*</td>
<td>0.13</td>
<td>4.71*</td>
</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>0.06</td>
<td>5.57*</td>
<td>0.04</td>
<td>1.09*</td>
<td>0.06</td>
<td>0.89*</td>
<td>0.05</td>
<td>1.00*</td>
</tr>
<tr>
<td>Habitat × Site</td>
<td>2</td>
<td>0.03</td>
<td>2.31*</td>
<td>0.03</td>
<td>0.66*</td>
<td>0.02</td>
<td>0.35*</td>
<td>0.03</td>
<td>0.58*</td>
</tr>
<tr>
<td>Residual</td>
<td>24</td>
<td>0.01</td>
<td></td>
<td>0.04</td>
<td></td>
<td>0.06</td>
<td></td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>1</td>
<td>0.14</td>
<td>4.52*</td>
<td>0.09</td>
<td>3.71*</td>
<td>1.58</td>
<td>1.14*</td>
<td>0.17</td>
<td>0.76*</td>
</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>0.02</td>
<td>1.08*</td>
<td>0.23</td>
<td>4.94*</td>
<td>1.55</td>
<td>5.61**</td>
<td>0.07</td>
<td>0.45*</td>
</tr>
<tr>
<td>Habitat × Site</td>
<td>2</td>
<td>0.03</td>
<td>1.97*</td>
<td>0.02</td>
<td>0.52*</td>
<td>1.38</td>
<td>5.00*</td>
<td>0.23</td>
<td>1.56*</td>
</tr>
<tr>
<td>Residual</td>
<td>24</td>
<td>0.02</td>
<td></td>
<td>0.05</td>
<td></td>
<td>0.28</td>
<td></td>
<td>0.15</td>
<td></td>
</tr>
</tbody>
</table>

All measured data \((a, b, c, d, e, f)\) were \(\ln(x)\) transformed to render multiplicative treatment effects and to normalise the positive skew of the characters, and all count data \((g, h)\) were \(\sqrt{x + 1}\) transformed to homogenise the variances (Underwood 1981). The assumption of homogeneity (Cochran’s \(C\)-test) was met for all characters except for \((e)\), hence a more conservative \(\alpha\)-value was used \((\alpha = 0.01)\) (Underwood 1997). In this case, ns = \(P > 0.01\).
Figure A.5. nMDS plot of the structure of the understorey assemblages quantified beneath monospecific canopies (MO), mixed-species canopies (MX), and within gaps among canopies (G). All replicates are shown and sites are not distinguished.
although post-hoc tests failed to distinguish among sites. Taxa that primarily contributed to multivariate differences were identified by successively omitting the most numerically abundant taxa and repeating the multivariate analysis until no significant differences were detected. No significant difference only resulted after encrusting coralline algae, foliose algae and turfs of filamentous algae were all omitted (PERMANOVA: $F_{2,45} = 1.98$, $P = 0.128$). Univariate analysis of these three functional groups of algae revealed that the cover of encrusting coralline algae was greatest beneath monospecific canopies (monospecific > mixed > gap; Fig. A.6a), whereas the covers of foliose algae (Fig. A.6b) and turfs of filamentous algae (Fig. A.6c) were generally greatest within gaps (Table A.3).
Figure A.6. Mean percent cover (± SE) of (a) encrusting coralline algae, (b) foliose algae and (c) filamentous turf-forming algae quantified from three types of habitat (monospecific canopies, mixed-species canopies, and gaps) for each site.
Table A.3. Two-way ANOVAs testing for differences in the abundance of
(a) encrusting coralline algae, (b) foliose algae and (c) filamentous turf-forming
algae among different types of habitat (monospecific vs mixed-species vs gap) at
three sites. * = $P < 0.05$, *** = $P < 0.001$, ns = $P > 0.05$.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Encrusting coralline algae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>14518.52</td>
<td>130.75***</td>
</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>99.84</td>
<td>0.74ns</td>
</tr>
<tr>
<td>Habitat × Site</td>
<td>4</td>
<td>111.04</td>
<td>0.82ns</td>
</tr>
<tr>
<td>Residual</td>
<td>45</td>
<td>135.34</td>
<td></td>
</tr>
<tr>
<td>(b) Foliose algae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>3450.99</td>
<td>14.28*</td>
</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>56.24</td>
<td>0.48ns</td>
</tr>
<tr>
<td>Habitat × Site</td>
<td>4</td>
<td>241.62</td>
<td>2.08ns</td>
</tr>
<tr>
<td>Residual</td>
<td>45</td>
<td>116.42</td>
<td></td>
</tr>
<tr>
<td>(c) Filamentous turf-forming algae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>9552.58</td>
<td>125.29***</td>
</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>121.72</td>
<td>1.29ns</td>
</tr>
<tr>
<td>Habitat × Site</td>
<td>4</td>
<td>76.24</td>
<td>0.81ns</td>
</tr>
<tr>
<td>Residual</td>
<td>45</td>
<td>94.03</td>
<td></td>
</tr>
</tbody>
</table>

Data represent percent cover and so were arcsine(%) transformed prior to analysis.
Cochran's C-test for homogeneity of variances: $P > 0.05$ for encrusting coralline
algae and foliose algae; $P < 0.01$ for filamentous turf-forming algae, so significance
judged more cautiously at $\alpha = 0.01$ (Underwood 1997). In this case, *** $P < 0.0001$,
ns $P > 0.01$. 

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A.5 Discussion

The forests of subtidal algae on the northern shore of St Francis Island were not only identified to have occurred in different configurations (monospecific, clumped and interspersed stands of *E. radiata* and fucoid dominated stands) but also occurred in different proportions (6%, 33%, 33%, 28% of forests sampled, respectively), suggesting that there are at least three extensive types of habitat created by canopy-forming algae (clumped, interspersed and fucoid) in which monospecific canopies of *E. radiata* are relatively sparse. This result differs from that found by Goodsell et al. (2004) where monospecific canopies of *E. radiata* were found to exist in equal proportion to that of mixed-species canopies (clumped *and* interspersed) across several locations on mainland Western Australia and South Australia. Although very preliminary, differences between this study and that of Goodsell et al. (2004) raise the possibility that the proportional abundances of the types of habitat recognised here differs between offshore islands and the shores of mainland Australia.

Although only subtle differences in the morphology of *E. radiata* plants were evident between monospecific and mixed-species canopies, the structure of the understorey assemblages of algae varied strongly across sites according to the type of overlying algal canopy. While previous studies demonstrate that the abundance and distribution of understorey organisms can vary predictably according to the presence or absence of an algal canopy (Kennelly 1987c; Edwards 1998; Melville and Connell 2001; Fowler-Walker and Connell 2002), it is apparent that the structural composition of the understorey biota is also associated with the composition of the canopy and not just its presence or absence (Shepherd and Womersley 1970; Foster and Van Blaricom 2001; Chapter 3). Observations showing that there are several different types of canopy distributed across a large proportion of subtidal Australian coasts (Goodsell et al. 2004; Chapter 2; this study) and that biota may be affected by these differences suggests that further research may benefit greatly from treating different types of canopy separately rather than lumping them as a single habitat type (i.e. ‘canopy-forming algae’ or ‘*E. radiata*’), which is likely to elevate uncertainty and confusion about the extent of pattern because of large and seemingly ‘unexplained’ variance among replicates. Greater abundances of foliose (erect) algae and reduced abundances of encrusting (prostrate) coralline algae in mixed-species vs monospecific habitats (Fig. A.6) may be partially explained by differences in the
physical environment between these two stands. Our unquantified observations suggest that light transmission is greater, and rates of frond scour reduced, beneath mixed-species canopies, which may favour the development of understorey algae sensitive to reduced light availability and/or strong scour conditions.

It is not understood what factors contribute to the origin of mixed-species rather than monospecific canopies of canopy-forming algae. When *E. radiata* is removed from the substratum, several species of fucoid have been observed to recruit to the newly created bare space (Kirkman 1981; Kennelly 1987a, c; Schiel 1988; Kennelly and Underwood 1993). We therefore speculate that mixed-species canopies are more common in localities of greater local disturbance that has removed *E. radiata* allowing colonization by one or more fucoid species. The timing of disturbances that can remove *E. radiata* from the substratum (e.g. storms: Kennelly 1987a) is often unpredictable but appears to be important for the subsequent establishment of fucoids or re-establishment of *E. radiata* (Kennelly 1987a; Schiel 1988). Unquantified observations indicate that *E. radiata* tends to be a stronger competitor for space than most fucoids, but fucoids tend to be presented with more opportunities to colonise new space because, collectively, their propagules are in great abundance (Umezaki 1984) and appear capable of recruitment over longer periods of time (e.g. Kendrick and Walker 1994). Hence, local disturbances that create new space when *E. radiata* do not recruit may explain the presence of mixed-species canopies. These mixed canopies are likely to be younger than canopies of monospecific *E. radiata*, which may explain why *E. radiata* within them tend to be smaller. Thus, the canopies we see today may not be so much the product of current interactions but rather the result of past events responsible for their origin.

In conclusion, it is apparent that forests of canopy-forming algae can be composed of different types of habitat (e.g. monospecific and mixed-species canopies) and that the relative abundance of different habitats can have very real consequences for the distribution of understorey algae. This study provides evidence that there is a need to understand the extent to which types of habitat affect ecological patterns and processes within marine forests. Large differences in the composition of algal canopies may obscure or confound patterns that we base on loose definitions of
E. radiata habitat (i.e. any 1 m² with E. radiata present). Terrestrial ecologists have found that mixed-species forests deserve separate study to the extent that entire books have been dedicated to the subject: e.g. ‘The ecology of mixed-species stands of trees’ (Cannell et al. 1992). It may not be surprising to also find that mixed-species canopies of algae represent distinct habitats that deserve study in their own right.
Home away from home: West Island, South Australia (photo by the author)
Summary

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Yours sincerely,

John Love
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Sunrise at West Island (photo by the author).
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