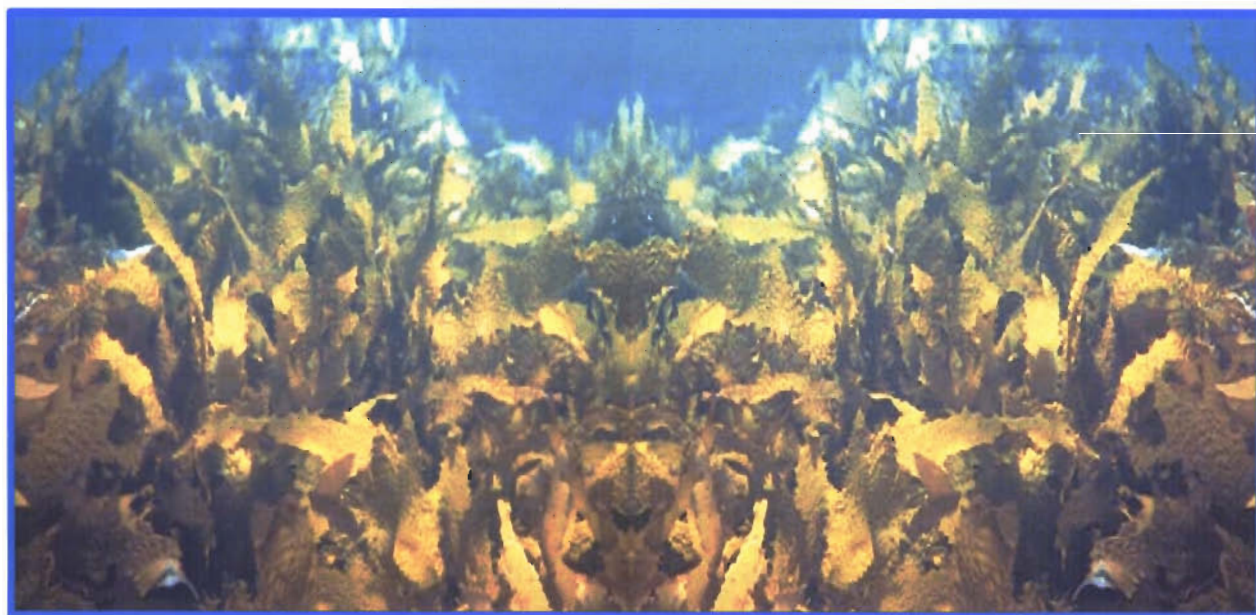




REGIONAL AND LOCAL PATTERNS IN KELP MORPHOLOGY AND BENTHIC ASSEMBLAGES



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Presented for the degree of Doctor of Philosophy

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July 2005



DECLARATION OF AUTHORSHIP

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Meegan Fowler-Walker

July 2005

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ABSTRACT

Most ecologists work at scales where complexity is greatest (i.e. local), and it is not surprising, therefore, that we tend to be captivated by the description and explanation of local variation whilst being pessimistic about the existence of broader patterns. Using a character (kelp morphology) known for its local and unaccounted variation, the morphology of the canopy-forming algae *Ecklonia radiata* (Phaeophyta) was quantified across > 5000 km of temperate Australian coastline, (i) between different configurations of algal stand (i.e. monospecific vs mixed-species stands) and (ii) across multiple spatial scales. A key result was that despite variation at local scales (km), differences between stands became increasingly clear at broad scales (1000's km), which supports the idea that large-scale patterns can emerge from apparent stochasticity at small scales.

Within each stand, regional scale differences in morphological characters were evident (i.e. Western Australia = South Australia ≠ Eastern Australia). These characters correlated with geographic and environmental variables to indicate that the majority of morphological variation across temperate Australia was accounted for by longitude, wave exposure, water temperature and plant density. Morphological differences associated with environmental factors may reflect a plastic response to the local environment, or alternatively may reflect genetically fixed traits (i.e. ecotypes). An independent test of morphological variation associated with wave exposure environments, using a reciprocal transplant experiment, revealed that morphological plasticity was the mechanism enabling *E. radiata* to adopt different morphologies between exposure environments.

The presence of kelp canopies has strong spatial relationships with organisms growing underneath them, and variation in the morphology of these canopies may facilitate distinct assemblages within the understory habitat. Variation in the morphology of *E. radiata* was found to be associated with the structure of understory assemblages, over broad spatial scales. This canopy-understorey association revealed two 'types' of kelp forest; one characteristic of Western and Southern Australia and the other of Eastern Australia. Patterns of canopy-benthos association have mostly been done on

horizontal surfaces and experimental tests showed that such patterns on horizontal surfaces were not representative of vertical surfaces, which enables us to recognize the conditions for which we can reliably anticipate the structure of benthic organisms, thereby improving the predictive power of models that account for widespread patterns in subtidal heterogeneity.

In conclusion, this thesis suggests that there are fundamental differences between the ecology of kelp forests at local scales (i.e. between types of stand) and at regional scales (i.e. between the south and east coast of temperate Australia), reflecting differences in kelp morphology that may be caused by environmental conditions (e.g. exposure) and may influence associated taxa (e.g. understory). Consideration of such local-scale variation (specificity) when testing for the existence of broad-scale phenomena (generality) not only strengthens our understanding of the ecology of subtidal forests, but will also improve the predictive power of further research in this system.

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Chapter 2

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Chapter 3

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This work could not have been completed without the support of T. Elsdon, P. Goodsell and E. Vytopil. This work was supported by an ARC Discovery grant to S.D.C and B.M.G and an ARC QEII Fellowship to B.M.G.

Chapter 6

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Appendix A

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Appendix B

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CHAPTER 1: General Introduction

CHAPTER 1

GENERAL INTRODUCTION

Canopy-forming vegetation (e.g. tropical and temperate rainforests, 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). Kelp forests (broadly defined as large brown algae: Steinberg and Kendrick 1999), define the character of temperate subtidal rocky reefs, by adding structure and complexity to create a three-dimensional environment, and can grow large enough to form floating canopies at the surface of the ocean (e.g. the Giant Kelp, *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. the Common Kelp, *Ecklonia radiata*, and various furoid algae in the genera *Cystophora* and *Sargassum*).

Kelp forests typically occupy broad geographic ranges and monopolise space on rocky coasts ranging from wave exposed coastlines to sheltered embayments (Steinberg and Kendrick 1999), and intertidal areas to depths of ~ 40 m. While contributing significantly to global primary production (Mann 1973), kelp forests also facilitate considerable quantities of secondary primary production by providing structurally complex habitat for phylogenetically diverse assemblages of flora and fauna (Duggins et al. 1989; Steneck et al. 2002; Graham 2004).

The wide distribution of kelp forests has stimulated a great deal of research regarding their morphology (e.g. Rice et al. 1985; Cheshire and Hallam 1989; Kalvas and Kautsky 1993; Blanchette et al. 2002), growth and productivity (e.g. Mann 1973; Gerard and Mann 1979; Fairhead and Cheshire 2004), and their influence on associated benthos (e.g. Duggins et al. 1990; Kennelly and Underwood 1993; Edwards 1998; Connell 2005). Yet much of our understanding of patterns and processes within kelp forests has

been largely 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 1984; Dayton 1985b; Schiel and Foster 1986; Kennelly and Underwood 1992; Foster and Van Blaricom 2001). These inconsistencies are often 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 (e.g. Wernberg et al. 2003). Where direct attempts have been made to quantify variability over regional scales (~ 1000 km), it has been concluded that as more sites are examined, fewer generalizations are possible (Choat and Schiel 1982; Schiel 1990). However, such conclusions may be premature due to the lack of replicated sites over appropriate spatial scales, which makes it difficult to distinguish true differences in hypothesised patterns from inherent spatial variability within, let alone among, broad sections of coastline.

The potential for large-scale patterns to emerge from stochasticity at small scales has been recognised (Chesson 1996). Indeed, individuals may respond to locally varied environments, while populations may be shaped over vast areas across which their ecology is regulated by powerful constraints (Chesson 2000). In this way, heterogeneity at small spatial scales may average out to produce patterns at large spatial scales. To properly address generality within and among biogeographic regions, both Foster (1990) and Underwood and Kennelly (1990) advocate using multiple sites that span the range of regions of interest, and importantly, to provide 'within-region' estimates of spatial variability (e.g. Fowler-Walker and Connell 2002; Edwards 2004; Irving et al. 2004). Noticeably, studies that have compared several locations (separated by 100s to 1000s of kilometres), using several local samples (separated by kilometres), and have not used replicate samples to estimate the within-region variation, have not surprisingly failed to detect patterns at regional scales (e.g. Wernberg et al. 2003). This latter situation can be avoided by hierarchical sampling (Green 1979; Underwood 1997) to provide an estimate of the contribution of each spatial scale to the total variation across regions. Studies that have adopted this approach have often detected considerable consistency (i.e. generality) of pattern among sites within defined regions (Choat and Schiel 1982; Kennelly and Underwood 1993; Estes and Duggins 1995; Fowler-Walker and Connell 2002; Irving et al. 2004). Indeed, by understanding the

proportion of total variation that is attributable to each scale, we are in a stronger position to identify the scales at which general patterns, rules and laws may emerge (Noda 2004). A major objective of this research was to implement a fully nested design, using multiple sites that span the range of regions of interest, to test whether regional patterns in kelp morphology existed, a hypothesis that was at odds with a previous study which emphasised high local variation and the lack of morphological pattern of the same kelp species (*Ecklonia radiata*) across similar regions (Wernberg et al. 2003).

There are costs involved in the search for generality (Wiens 1989). These costs often sacrifice specific information for breadth and ignore some special feature of the environment which, when taken into account, could improve predictive power. An emerging realisation is that large ecological differences may not just occur between the presence and absence of kelp canopies, but also among canopies of varying composition (Dayton et al. 1984; Goodsell et al. 2004; Irving et al. 2004). Whereas terrestrial ecologists recognise that stands of vegetation can occur in both monospecific and mixed species compositions (Cannell et al. 1992), subtidal ecologists have generally restricted their observations to monospecific stands (e.g. Santelices and Ojeda 1984; Kennelly 1987c; Underwood et al. 1991; Foster and Van Blaricom 2001). As a consequence, the extent to which patterns observed in monospecific stands relates to those of mixed-species stands of canopy-forming algae is poorly understood, despite evidence that mixed stands do exist (Chapman and Johnson 1990; Collings and Cheshire 1998). 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). In this way, if some local variable (e.g. kelp morphology) is strongly associated with an unrecognised feature of the environment (e.g. type of stand), then tests of broad scale patterns may be compromised.

The physical environment of the subtidal reef is dynamic. Kelp forests may experience changes in environmental parameters such as wave exposure, water temperature, and water nutrient concentration, and may inhabit areas of varying water depth and biogeography (i.e. latitude and longitude). The ability of macroalgae to change the shape of their thallus in response to the environment may be of functional and

ecological significance for the alga. Wave exposure is probably the most commonly identified cause of morphological variation in macroalgae (e.g. Gerard and Mann 1979; Cheshire and Hallam 1988; Ralph et al. 1998; Hurd 2000; Blanchette et al. 2002), and such variation is essential for macroalgae to persist over a range of environments without compromising their ability to efficiently photosynthesise and grow (Gerard 1982; Hurd et al. 1996), and to prevent breakage or dislodgement (e.g. Dudgeon and Johnson 1992; Blanchette 1997). While morphological differences associated with environmental factors have been used as evidence for a plastic response to the local environment (Norton et al. 1982), such associations may alternatively reflect genetically fixed traits (i.e. ecotypes) that are the result of speciation in the face of strong selection by environmental factors (e.g. Chapman 1974; Serisawa et al. 2003; Roberson and Coyer 2004). Transplantation experiments have commonly been used to differentiate between these two competing models, with the results of these experiments differing depending on the species involved and the environmental condition examined (e.g. De Paula and De Oliveira 1982; Blanchette et al. 2002; Serisawa et al. 2003; Roberson and Coyer 2004).

The subtidal rocky coasts of temperate Australia support widespread forests of canopy-forming algae, that primarily comprise species from the orders Laminariales and Fucales (Womersley 1987). Of these canopy-formers, the common kelp *Ecklonia radiata* (C.Ag.) J. Agardh comprises a large proportion of these forests (Goodsell et al. 2004) and exerts strong influences on the types of organisms that can exist underneath them (Kennelly 1987c; Melville and Connell 2001). The widespread and abundant nature of *E. radiata* has meant it has been the subject of numerous investigations in both Australia and New Zealand.

Consistent with globally-observed patterns, forests containing *E. radiata* are associated with assemblages of understory organisms that differ greatly from those organisms observed where canopies are absent (i.e. encrusting algae beneath canopies and erect algae where canopies are absent) (Kennelly 1987b; Melville and Connell 2001; Fowler-Walker and Connell 2002; Kendrick et al. 2004). Such canopy-understorey associations have been documented in monospecific forests of *E. radiata* over 1000's of km of temperate Australia (Fowler-Walker and Connell 2002) and can vary according to the composition of the canopy (i.e. between monospecific and mixed stands: Irving et al.

2004). Despite this observation, substantial variation in understory structure is often recognised within monospecific stands of *E. radiata* and the degree to which morphological variation of the canopy is correlated to such variation in the understory is unknown. Furthermore, much of our understanding of the relationship between canopy-forming species and benthic organisms is based on work done on horizontal surfaces, yet the orientation of substratum is known to have striking and widespread effects on benthos (e.g. horizontal vs vertical: Hurlbut 1991; Baynes 1999; Glasby 2000). An explicit quantitative understanding of the extent to which habitat related patterns on horizontal surfaces are representative of vertical surfaces is currently lacking and is needed before we can sensibly propose models that account for some of the major sources of subtidal heterogeneity.

This thesis follows a progression of ideas that test hypotheses about morphological variation of *Ecklonia radiata* across space, the potential factors that are related to this variation, and how the morphology of *E. radiata*, as well as other factors, are associated with and affect the structure of assemblages that live beneath the canopy.

Chapter 2

Kelp morphology is known for its local and unaccounted variation (e.g. Rice et al. 1985; Cheshire and Hallam 1989; Rice and Kenchington 1990a). This chapter deals with conceptual and methodological issues about the description of pattern over large spatial scales (generality), while incorporating knowledge of local variation (specificity). This chapter tested the hypothesis that the morphology of *E. radiata* differs between monospecific and mixed stands (specificity) across temperate Australia, and that regional patterns of variation exist (generality). In a broader context, this chapter provides the observational basis for understanding how heterogeneity at small scales relates to the existence of patterns at larger scales.

It was important to specifically test for the existence of regional patterns (Chapter 2), in isolation to potential causes of this pattern (Chapter 3). While Chapter 2 emphasises high local variation in morphology that is imbedded within regional patterns, this model is at odds with a previous study that emphasises high local variation and the lack of

morphological pattern of the same species across similar regions (Wernberg et al. 2003). Differences between these two studies are largely conceptual and methodological, and the reviewing process showed that this needed to be addressed as a separate issue before the biological work (Chapter 3) could be addressed (i.e. on why regional patterns may occur).

Chapter 3

Intra-specific variation in morphology is common among marine algae and may allow plants to occupy broad geographic ranges across a wide variety of environments (e.g. Rice et al. 1985; Kalvas and Kautsky 1993; Blanchette et al. 2002). The morphological variation described in Chapter 2 paved the way for Chapter 3 where I tested for relationships between the surrounding environment and the morphology of *E. radiata* across southern Australia. This chapter also assesses whether measures of morphological dissimilarity are greatest among locations that are separated by the largest geographic distances.

Chapter 4

A range of variables have been identified as influencing the morphology of marine macroalgae, for which wave exposure is probably the most common (e.g. Gerard and Mann 1979; Cheshire and Hallam 1988; Hurd 2000; Blanchette et al. 2002). In this chapter I tested the hypothesis that the morphology of *E. radiata* varies between exposed and sheltered sides of replicate islands. Reciprocal transplantation of juvenile sporophytes, between sheltered and exposed environments, was used to determine whether the morphology of transplanted *E. radiata* can change to match the morphology of individuals at the new environment, or whether they maintain the morphology of their native site (i.e. morphologically adaptive vs fixed traits).

Chapter 5

Associations between the presence of kelp canopies and the structure of understory assemblages have been documented in monospecific forests of *E. radiata* over 1000's of km of temperate Australia (Fowler-Walker and Connell 2002). Despite such documentation of canopy effects, substantial variation in understory structure is often recognised within monospecific stands of *E. radiata* (e.g. Fowler-Walker and Connell 2002; Irving et al. 2004). Given that canopies of *E. radiata* exert strong influences on

the types of organisms that can exist underneath them (via physical abrasion and provision of shade: Connell 2003a; Connell 2003b), and that the environment created by kelps can vary as a function of the canopies morphology (e.g. longer fronds create more abrasion and less light: Velimirov and Griffiths 1979; Kennelly 1989; Holbrook et al. 1991), I tested whether differences in the morphology of *E. radiata* (within monospecific stands) are associated with variation in the structure of understorey (benthic) assemblages over large spatial scales.

Chapter 6

Much of our understanding of the relationship between canopy-forming species and benthic organisms is based on work done on horizontal surfaces (e.g. Reed and Foster 1984; Edwards 1998; Jenkins et al. 1999a; Fowler-Walker and Connell 2002).

However, an explicit quantitative understanding of the extent to which well-described patterns of habitat association (i.e. canopy *vs* no canopy) on horizontal surfaces are representative of vertical surfaces is currently lacking. In this chapter I experimentally tested hypotheses about the interactive effect of habitat and orientation on benthic assemblages to provide a quantitative understanding of the nature and magnitude of such effects, and to identify the conditions for which we can reliably anticipate the structure of benthic organisms. Such a quantitative understanding of patterns is needed before we can sensibly propose models that account for some of the major sources of subtidal heterogeneity.

Notes on Chapter Style

Each chapter of this thesis that presents original data (Chapters 2 – 6) has been written in a style suitable for publication in a scientific journal and can be read as a separate study. 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, and describes the contributions of all co-authors to the research therein. Tables and figures appear within the text, and all references cited in this thesis are compiled at the end of the thesis (not at the end of each chapter).



Stand of monospecific *Ecklonia radiata*



Stand of mixed algae (*E. radiata* / fucal complex)

CHAPTER 2

CHAPTER 2 PREAMBLE

Chapter 2 tests for morphological differences in *E. radiata* between monospecific and mixed stands of canopy-forming algae across temperate Australia. Sampling was done at multiple spatial scales across > 5000 km of temperate Australia (Western, South and Eastern Australia) by all authors, and tests for the existence of patterns across multiple spatial scales and provides the necessary observations for broad-scale comparisons.

This chapter was published in the journal *Marine Biology* in 2005 (vol **147**: 823-831), with myself as senior author and Sean Connell and Bronwyn Gillanders (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).

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Short stipe, large thallus morphology of *Ecklonia radiata* growing in monospecific stands in South Australia



Long stipe, small thallus morphology of *E. radiata* growing in monospecific stands in Eastern Australia

CHAPTER 3

CHAPTER 3 PREAMBLE

Chapter 3 addresses biological questions on why regional patterns in the morphology of *E. radiata* may occur. This chapter attempts to couple the morphological variation of *E. radiata* across temperate Australia to geographic and environmental variables.

At the time this thesis was submitted (August 2005), this chapter was accepted for publication with the journal *Marine and Freshwater Research* in 2005 (in press), with myself as senior author and Sean Connell and Bronwyn Gillanders (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 C).

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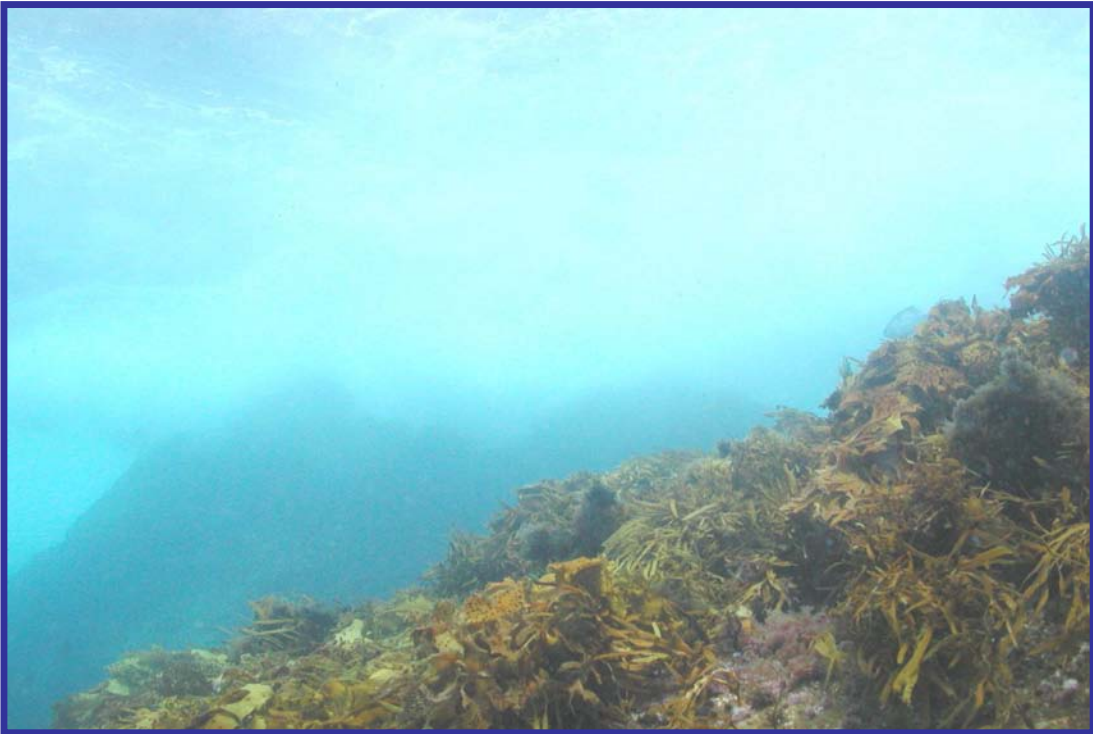
Date:.....

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Marine and Freshwater Research v.56 (6) pp 877-887

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Ecklonia radiata and other macroalgae inhabiting a
wave exposed environment.

CHAPTER 4

CHAPTER 4 PREAMBLE

Chapter 4 represents data from two experiments: one mensurative, testing for morphological differences of *E. radiata* between wave exposed and sheltered sites at two islands; and one manipulative, testing for morphological differences of juvenile *E. radiata* that have been reciprocally transplanted from the exposed to sheltered side of an island.

At the time the thesis was submitted (August 2005), this chapter was under peer-review with the journal *Marine Biology*, with myself as senior author, and Thomas Wernberg and Sean Connell (Adelaide University) as co-authors. It is therefore written in plural.

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Understorey organisms inhabiting the substratum beneath canopies of monospecific *Ecklonia radiata*, in Eastern Australia

CHAPTER 5

CHAPTER 5 PREAMBLE

Chapter 5 tests for patterns of association between kelp morphology and understory assemblages across temperate Australia.

This chapter was published in the journal *Estuarine, Coastal and Shelf Science* in 2005 (vol 63: 133-141), with myself as senior and corresponding author and Bronwyn Gillanders, Sean Connell and Andrew Irving (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 C).

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Estuarine, Coastal and Shelf Science v.63 (1/2) pp 133-141 April 2005

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Benthic organisms living on horizontal and vertical surfaces in stands of monospecific *Ecklonia radiata* and in habitats devoid of canopy-forming algae.

CHAPTER 6

CHAPTER 6 PREAMBLE

Chapter 6 presents the results of a manipulative experiment designed to test the extent to which patterns of habitat association on horizontal surfaces are representative of vertical surfaces, by experimentally testing for an interaction between the factors 'habitat' and 'orientation'.

At the time this thesis was submitted (August 2005), this chapter was under peer-review with the *Journal of Experimental Marine Biology and Ecology*, with myself as senior author and Sean Connell (University of Adelaide) as co-author. It is therefore written in plural.

Contributions and signatures of authors:

MEEGAN J. FOWLER-WALKER

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

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SEAN D. CONNELL

Constructed experiment, sampled data and supervised development of research, data interpretation, and manuscript evaluation.

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Chapter 6

Subtidal habitat heterogeneity: understanding unique combinations of canopy-cover and substratum-orientation on Benthos

Now cited as:

Fowler-Walker, M. J., and Connell, S. D. (2007)

Habitat heterogeneity as a consequence of substratum-orientation and kelp-canopy: relating interdependent responses to common patterns

Journal of Experimental Marine Biology and Ecology Article in press, corrected proof, available online 30 January 2007

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CHAPTER 7: General Discussion

CHAPTER 7

GENERAL DISCUSSION

This thesis provides quantitative evidence of changes in morphology across small to large spatial scales and the relationship between canopy-forming algae and understory assemblages (algae and sessile invertebrates) on subtidal rocky coasts of temperate Australia. In Chapter 2 I tested whether regional generalities were possible, even though previous studies appeared pessimistic. Specifically, I tested for and detected regional patterns in the morphology of *Ecklonia radiata*, results that were at odds with a previous study which emphasised high local variation and the lack of morphological pattern of the same species across similar regions (Wernberg et al. 2003). Differences between these two studies were largely conceptual and methodological, and the reviewing process showed that this needed to be addressed as a separate issue before the biology of such patterns could be addressed (i.e. Chapter 3). While testing for these general patterns in morphology emphasis was placed on detecting patterns from small through to large spatial scales, and partitioning observations into the type of stand in which canopy-forming algae grow (i.e. monospecific *vs* mixed stands). Results from chapter 2 showed that despite local variation large-scale patterns can emerge, which paved the way for Chapter 3 where I tested for, and detected, relationships between the surrounding environment and the morphology of *E. radiata* across southern Australia. Using transplantation experiments (Chapter 4), I demonstrated that at local scales the morphology of *E. radiata* can have a plastic response to wave exposure environments. The relationship between canopy-morphology and organisms living beneath canopies was tested at regional scales (Chapter 5), and these canopy-understorey associations were further tested in Chapter 6, where the effect of kelp forests was found to interact with the effect of surface orientation.

This chapter provides a summary of the key findings presented in this thesis. For expanded discussion of the points made here, and for the details that have been omitted, the reader can consult the relevant text in Chapters 2 through to 6.

7.1 DETECTION OF PATTERN ACROSS MULTIPLE SPATIAL SCALES

Much of our understanding of patterns and processes within kelp forests has been based on research done at relatively small spatial scales (i.e. km's) compared to the extensive distribution of kelp forests along the southern coastline of Australia. Understanding the extent to which complexity at local scales generates large-scale patterns is a continuing challenge to ecologists, and is fundamental to the search of ecological patterns across local to global scales (i.e. spatial generality). Knowledge of nested spatial patterns, spanning the range of regions of interest, is essential in testing for generalities of patterns within and among biogeographic regions (Foster 1990; Underwood and Kennelly 1990). By using a hierarchical sampling design an estimate of the contribution of each spatial scale to the total variation across regions can be provided (e.g. Edwards 2004; Irving et al. 2004), thereby identifying the scales at which general patterns, rules and laws may emerge (Noda 2004). Across > 5000 km of the coastline of temperate Australia I tested for differences in the morphology of *E. radiata* between monospecific and mixed stands, across multiple spatial scales using a hierarchical sampling design. Despite substantial local variation, differences between stands became increasingly clear at broader scales, such that the frequency of inconsistent differences between stands was greatest at local scales, intermediate at intermediate scales, and least at regional scales.

There are three key outcomes from this research. First, unaccountable variation at local scales (i.e. variation among sites) need not impede tests for similar patterns at broader scales (i.e. across regions), and that indeed large scale patterns can emerge from apparent stochasticity at small scales. Second, clear differences in the morphology of *E. radiata* between monospecific and mixed-species canopies indicate that failure to distinguish between these superficially similar types of habitat may present misleading conclusions about the ecology of Australia's algal forests. Third, the striking regional-scale differences within each type of stand (Western Australia = South Australia ≠ Eastern Australia) highlight the need to cautiously extrapolate results among regions, and warn that comparison of single, small-scale studies among regions can be mistakenly used to suggest overwhelming variation at all scales. We are becoming increasingly aware that ecologists are working at scales where complexity is often

greatest (i.e. local) and is likely to be explained by special and unique events (Underwood and Chapman 1996; Fowler-Walker and Connell 2002; Anderson et al. 2005). The results of Chapter 2 are encouraging in that they clearly demonstrate that patterns can emerge from complexity at local scales to provide new opportunities to answer some of the more interesting questions about how patterns and processes relate across vast parts of the world's coast.

7.2 RELATIONSHIP BETWEEN MORPHOLOGY AND ENVIRONMENT

There is a growing body of evidence suggesting the existence of very real differences in the ecology of algal forests among regions of temperate Australia (Goodsell et al. 2004; Irving et al. 2004), to which my results contribute, showing regional patterns of variation in the morphology of *E. radiata* (i.e. WA = SA \neq EA: Chapter 2). Results from Chapter 3 reveal that ~ 74 % of such morphological variation can be accounted for by a combination of geographic and environmental variables, in both monospecific and mixed stands. The majority of this variation is related to longitude, with wave exposure, water temperature and plant density contributing considerably. The possibility of morphological differences arising through restricted gene flow with increasing distances cannot be discounted, as large differences in morphology are consistently detected between locations separated by the greatest distances (> 2500 km). A promising area for further research involves the genetic differentiation of western and eastern populations of *E. radiata*, and the integration of historical and oceanographic evidence that pertains to the temperate Australian coastline.

Wave exposure is one of the most commonly identified causes of morphological variation in macroalgae (e.g. Molloy and Bolton 1996; Hurd 2000; Blanchette et al. 2002; Roberson and Coyer 2004), yet much of our understanding of patterns and processes between kelp morphology and wave exposure has been largely based on research done at local scales (i.e., km), often with little or no spatial replication. I firstly assessed whether the morphology of *E. radiata* differs between sheltered and exposed environments using replicated observations of exposure, and secondly whether such morphological differences were genetically fixed or were inducible responses to the local environment. A combination of observational and experimental analyses revealed that a large proportion of morphological characters responded consistently to

differences in exposure, and that morphological plasticity was the mechanism enabling this alga to display different patterns in morphology between exposure environments.

Variation in the morphology of *E. radiata* exists across southern Australia (Chapter 1), and this variation may be related to genetic differences or to a range of environmental and geographic factors (Chapter 2). However, at the scale of kilometres, the results of Chapter 3 confirm that environmentally specific forms of *E. radiata* in wave exposed and wave sheltered environments are the result of a plastic response to the local exposure environment and do not reflect genetically fixed traits (i.e. ecotypes). This is a useful distinction if we are to understand the population-biology of kelps (i.e. genetically isolated populations versus well mixed populations that respond to local conditions).

7.3 CONSISTENCY IN CANOPY-UNDERSTOREY ASSOCIATIONS

The presence and absence of canopy-forming algae forms predictable associations with the distribution and abundance of organisms living beneath the canopy (e.g. Reed and Foster 1984; Kennelly and Underwood 1993; Edwards 1998). Canopies of *E. radiata* exert strong influences on the types of organisms that can exist underneath them (Connell 2003a, b), and associations between the canopy and understorey have been documented in *E. radiata* forests over 1000's of km of temperate Australia (Fowler-Walker and Connell 2002). Despite such documentation of canopy effects, a substantial amount of variation in understorey structure is often recognised within monospecific stands of *E. radiata* (e.g. Fowler-Walker and Connell 2002; Irving et al. 2004). Results from Chapter 5 reveal that within monospecific stands, variation in morphology of *E. radiata* is associated with understorey structure across 1000s of kilometres of temperate Australia, and may therefore explain such variability.

Much of our understanding of the relationship between canopy-forming species and understorey organisms is based on work done on horizontal surfaces, and the extent to which such patterns are representative of vertical surfaces is unknown. By experimentally testing hypotheses about the interactive effect of habitat and orientation on benthic assemblages, Chapter 3 demonstrated that (1) that patterns of habitat association (kelp vs open) occurring on horizontal surfaces are not relevant for vertical surfaces, and (2) that the effects of orientation (horizontal vs vertical) are habitat

specific. Such interactive effects enables us to recognize the conditions for which we can reliably anticipate the structure of benthic organisms, thereby improving the predictive power of models that account for widespread patterns in subtidal heterogeneity. These results also provide a quantitative basis on which to propose models that integrate current understanding of processes that until now have been specific to habitat (i.e. presence *vs* absence of canopies) and orientation (i.e. vertical *vs* horizontal substratum).

7.4 FUTURE RESEARCH

- The striking regional pattern identified in Chapter 2 (WA = SA ≠ EA) begs explanation. Within this thesis, I have discussed the two main competing models that may contribute to the origin and maintenance of this pattern (i.e. genetic differences *vs* environmentally driven differences). Where possible, I have supplemented such arguments with supporting evidence pertaining to ocean boundary currents and ancient land bridges, and to environmental variables and ecological processes (Chapter 2 and 3). Importantly, such models are yet to be tested over the appropriate spatial scales and will require carefully designed hypotheses and experimental tests. Concerted effort in explaining the causes of observed regional-scale differences represents a promising area for future research (e.g. O'Hara and Poore 2000).
- Results of Chapter 2 also highlight that if some special feature of the environment (e.g. type of stand) is ignored in the search for generality, then tests of broad scale patterns may be compromised. Therefore, future research on the ecology of temperate kelp forests may well benefit from a renewed focus on which components of the system are usefully partitioned, as this may enhance the predictive power in a system where overwhelming spatial variation is often emphasised (e.g. Wernberg et al. 2003).
- In Chapter 2 and 3 I showed that variation in the morphology of *E. radiata* exists across southern Australia and that this variation may be related to a range of geographic and environmental variables, or to genetic differences occurring across

this regional scale. In Chapter 4 I showed that at local scales (i.e. 1 – 10 km's) morphologically distinct forms of *E. radiata* are the result of a plastic response to the local exposure environment. Examining the relative contributions of regional vs local-scale processes may provide useful insights into explaining the patterns observed across Southern Australia and contribute to this topical field of contemporary ecology (see Huston 1999 for further discussion). However, given the range of spatial scales involved, acquiring the evidence needed to distinguish between the role of processes operating at regional and local scales will require carefully designed hypotheses and experimental tests across these scales.

- In this thesis I have tested for the existence of an association between the morphology of *E. radiata* and the structure of understory assemblages across temperate Australia (Chapter 3). While clear associations were evident, future research on causal relationships between kelp morphology and understory would benefit from testing the potential importance that morphology may have on mechanisms such as light penetration and physical abrasion by fronds. In Chapter 6 I showed that the effects of kelp forests and surface orientation on benthic assemblages are interdependent, and suggest that the manipulation of these factors (habitat and orientation) under different regimes of light, sedimentation and physical abrasion by kelp will further our understanding of processes that drive such relationships. Importantly, future research would benefit from simultaneously testing multiple factors to identify potential synergies (e.g. Irving and Connell 2002) that would contribute to a better mechanistic understanding of the ecology of algal forests.
- Within this thesis, the use of morphological groups to quantify benthic organisms has been employed (Chapter 5 and 6). This approach can undoubtedly sacrifice information about fine-scale heterogeneity (i.e. species-specific responses) in favour of broad generalisations, and although may not be useful for all ecological tests (e.g. Phillips et al. 1997; Benedetti-Cecchi 2000), show considerable promise and receives increasing use in marine ecology (e.g. Warwick and Clarke 1996; Chapman 1998). Using such means of classification has been deliberate in my attempts to identify generality in the response of understory to canopies across vast distances,

and is often considered advantageous for achieving predicative outcomes (e.g. Steneck and Dethier 1994; Keddy 2001). 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.

7.5 CONCLUSIONS

The data presented in this thesis have demonstrated fundamental differences between the ecology of kelp forests at local scales (i.e. between types of stand) and at regional scales (i.e. between the south and east coast of temperate Australia). Importantly, differences between stands became increasingly clear at broad scales, despite unaccountable variation at local scales, which is encouraging for those inspired by similarities (repeatable patterns). Within each type of stand morphological differences were recognised among regions (WA = SA \neq EA), usefully identifying spatial limits for attempts to extrapolate results among regions. Variation in morphology across regional scales may be caused by a range of geographic and environmental conditions, and at smaller scales, reflects a plastic response to different wave exposure environments. The relationship between morphology and associated taxa (e.g. understorey) is recognised across regional scales, and interactions between the effect of kelp canopies and the orientation of benthic surfaces is evident.

The combination of sampling over broad-scales with small-scale experimentation, facilitated new insights into the generality and consistency of patterns and responses within some of the world's most widespread and abundant habitats (forests of *Ecklonia radiata*). There is considerable potential in using a combination of both broad-scale and local-scale studies to provide a general context for local studies, and for local studies to provide clues about which components of a system may be generally repeatable across broad scales. While few ecologists may be directly concerned with the morphology of kelp, the lessons learnt in this thesis have general implication, particularly that broad-scale patterns do exist and can be identified, despite large variation occurring at local scales. Consideration of local-scale variation (specificity) when testing for the existence of broad-scale phenomena (generality) not only strengthens our understanding of the ecology of subtidal forests, but will also improve the predictive power of further research in this system.

APPENDIX A

APPENDIX A PREAMBLE

Appendix A tests the hypothesis (1) that *Ecklonia radiata* does not primarily occur as monospecific stands, rather it occurs more often in stands of mixed algae, and (2) that different types of stands contain different assemblages of invertebrate species. This paper was written during my PhD, and is an integral part of this thesis as it provides the basis of testing for differences between monospecific and mixed stands of canopy-forming algae.

This chapter was published in the journal *Austral Ecology* in 2004 (Vol 29: 350-357), with Paris Goodsell as senior author and myself, Bronwyn Gillanders and Sean 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 C).

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Date:.....

MEEGAN J. FOWLER-WALKER

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

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BRONWYN M. GILLANDERS

Sampled, supervised development of research and assisted with manuscript evaluation.

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Date:.....

SEAN D. CONNELL

Sampled, supervised development of research and assisted with analysis and manuscript evaluation.

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Date:.....

Goodsell, P. J., Fowler-Walker, M. J., Gillanders, B. M., Connell, S. D. (2004)
Variations in the configuration of algae in subtidal forests: Implications for
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APPENDIX B

APPENDIX B PREAMBLE

Appendix B tests the hypothesis (1) that there are consistent broad-scale patterns in assemblages of algae between kelp forests and open habitats, and (2) that patterns are discernable within locations and across regions, which are not apparent at smaller spatial scales. This paper was written during my honour degree, and is an integral part of this thesis as it tests for broad-scale patterns across multiple spatial scales using a hierarchical sampling design (relevant to Chapter 2), and tests for canopy-understorey associations across southern Australia (relevant to Chapter 6).

This chapter was published in the journal *Marine Ecology Progress Series* in 2002 (Vol 240: 49-56), with myself as senior author and Sean Connell (University of Adelaide) as co-author. It is therefore written in plural. Permission from the publisher to reproduce this manuscript herein has been granted (see Appendix C).

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

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SEAN D. CONNELL

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

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Date:.....

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APPENDIX C

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CHAPTER 2

Chapter 2 was published online in the journal *Marine Biology* in 2005. The full citation is:

Fowler-Walker, M. J., Connell, S. D., Gillanders, B. M. (2005) Variation at local scales need not impede tests for broader scale patterns. *Marine Biology* **147**: 823-831

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APPENDIX B

Appendix B was published in the journal *Marine Ecology Progress Series* in 2002. The full citation is:

Fowler-Walker, M. J., Connell, S. D. (2002) Opposing states of subtidal habitat across temperate Australia: consistency and predictability in kelp canopy-benthic associations. *Marine Ecology Progress Series* **240**: 49-56.

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