

DISTURBANCES THAT INFLUENCE PATTERNS OF BENTHIC ASSEMBLAGES



One of my study sites, Coffin Bay National Park

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DECLARATION OF AUTHORSHIP

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ABSTRACT

Understanding the influence of disturbance, both natural and human-induced, is a persistent challenge in ecology. Recently, attempts to predict future environments have focused on the consequences of broad scale disturbances. In this thesis I focus on environmental and trophic disturbances as shapers of benthic assemblages. There is growing recognition of the need for greater scientific investment in understanding environmental disturbances to balance the continuing focus of research assessing trophic theories (e.g. herbivory). Historically, it is these theories that have provided a cornerstone to describe and manage subtidal rocky coasts worldwide. In this thesis, therefore, I first assess how our ecological perception of such disturbances (i.e. water pollution and harvesting grazers) may vary as a consequence of the choice of taxonomic classifications used to observe benthic patterns (Chapter 2). I then assess how mechanical disturbance (i.e. wave exposure) may affect the morphology of benthic habitat (Chapter 3) and how temperature disturbances (i.e. oceanographic, cold water pulsing) may affect the consumers of these habitats (Chapter 4).

The critical first finding centred on the effectiveness of alternate scales and metrics of taxonomic classification to detect the effects of water pollution (i.e. nutrient enhancement) as the largest disturbing agent on the benthos, and that this effect may be exacerbated by loss of grazers. While observations of the benthos as morphological groups detected the effects of enhanced nutrients, species diversity (as a measure of phylogenetic relatedness) was the only one of the chosen measures sensitive enough to detect the interaction of both top-down and

bottom-up stressors. This chapter highlights the importance of choice of classification (e.g. morphology *v.* species) and indices (e.g. Shannon index *v.* ABC curves and phylogenetic diversity) in their potential to predetermine our perception of ecological change and thereby predict future environments.

Mechanical disturbance (i.e. wave exposure) has been widely studied as a mechanism that creates new space for colonisation by alternate species, but is less well studied as a force that can change the shape of communities by mediating their morphology. Macroalgal morphology varies in response to wave exposure such that individuals at high exposures are often smaller than individuals in more sheltered environments. Observations not only confirmed these patterns for a general assemblage on a wave exposed southern coast, but reciprocal transplants of assemblages between exposures also revealed that morphological differences were likely to be a product of flexibility in morphological response of algae to local environments (Chapter 3). In contrast to the often multi-directional responses of a complex suite of morphological characters (e.g. smoothness, stipe length, frond width), overall size has the potential to be used as a broad and predictive tool to identify hydrodynamic stressors across an entire exposure gradient or geographic range.

Strong trophic interactions are often considered characteristic of aquatic systems and due to their perceived ubiquity on temperate rocky coasts, there has been an emphasis in the literature on the influence of herbivores in determining assemblages. Given the importance of the link between herbivores and assemblage structure, in my final chapter I investigated the potential for

disturbance to act indirectly on benthos by affecting the survivorship of an herbivorous urchin (Chapter 4). I used observations of variable temperature regimes in a region of upwelling to design an experiment that tested whether this temperature variation could negatively affect the survivorship of settling sea urchins (*Heliocidaris erythrogramma*). When exposed to cold water, mortality increased by up to 70 %, within 12 h of settlement, representing a massive loss of benthic consumers within a very short time scale. This result was used to assess the potential of temperature to indirectly influence benthic habitats across several spatial scales, a process that may have been profoundly underestimated.

In summary, this thesis provides insight into environmental and trophic disturbances as shapers of benthic assemblage patterns, both as natural and human-induced phenomena. I show that our perception of ecological response to the combination of such disturbances can be contingent on the organisational scales and metrics used. Subtle differences in initial choice of such observational units may not only have large effects on the kinds of benthic patterns and disturbances ecologists detect, but also those that they pursue. I recognise that while some physical disturbances can appear subtle (e.g. morphological variation) or strong (e.g. high mortality rate of herbivores), their relative impacts on the broader assemblage (e.g. understory flora and fauna) will often be dependent on biogeography. Integrating local-scale biological interactions with regional-scale physical processes, therefore, appears to be a potentially progressive line of future enquiry. Indeed, consideration of responses from the physiological through to physical and biogeographical scales will not only strengthen our understanding of

the effects of alternate disturbance regimes, but also our predictive power to anticipate future change.

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CHAPTER 2

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CHAPTER 3

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CHAPTER 4

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CHAPTER ONE: GENERAL INTRODUCTION



CHAPTER ONE

GENERAL INTRODUCTION

Ecologists have long sought to provide accurate assessments of environmental change as a product of both naturally and human derived events. Despite this effort, there remains considerable uncertainty about how to measure change, and the primary drivers of change. As the global population faces an ever increasing number of unprecedented changes (e.g. Scheffer et al. 2001), it is critical that we achieve a better understanding of the effectiveness of our tools of observation and the effects of natural and human drivers of change. The ability to discriminate among the effects of specific types of drivers of change may enable us to identify those drivers that are likely to create most change into the future. Indeed, recent reviews of ecological change convey a sense of urgency for greater investment in our understanding of change to our contemporary environments and predictive capacity to forecast future environments as a consequence of both natural and human phenomena (e.g. Vitousek et al. 1997, Jackson et al. 2001, Hughes et al. 2005).

Indisputably, disturbance is a key agent creating change that shapes the composition and relative abundances of organisms within communities. Here, it is defined as any discrete event in time that disrupts ecosystem, community or population structure and changes resources, habitat availability or the physical environment (White and Pickett 1985). Although this definition is broad, it incorporates both human and naturally derived events, enabling us to understand the environment as product of both natural and human phenomena.

Communities may respond to disturbance either by persisting in the same state (i.e. resistance), recovery to their natural state (i.e. resilience), or by shifting to a new, alternative state (i.e. regime-shifts). These different responses to disturbance provide a framework for understanding the influence of different kinds and intensities of disturbance and have been well studied (e.g. Sousa 1980, Connell and Sousa 1983, Sousa 1984, Dayton et al. 1984) and reviewed (Sousa 2001, Minchinton 2007). The activity of predicting the dynamics of change forms the core of disturbance ecology, the success of which depends on understanding how agents of disturbance affect community patterns and shape ecosystems.

Agents of disturbance may be physical (wind, waves, temperature change) or biological (predation, disruption of soft-bottom via foraging, creation of bare patches) (see Sousa 2001 and Minchinton 2007 for a comprehensive review of agents), each with a specific magnitude, measurable by its intensity and severity. The response of a community to disturbance, whether by resisting change, returning to a stable state post-disturbance or changing to a new alternative state will often depend both on the magnitude of disturbance and the biological interactions of the original assemblage. For example, the capacity for a community to regenerate will depend on the severity of disturbance and how this impacts processes such as recruitment and re-establishment (Connell et al. 1997; Dayton 1975; Menge and Sutherland 1987; Paine and Levin 1981; Sousa 1980). Further, recolonisation and stability of an assemblage may be dependent on species diversity (Steneck et al. 2002; Tilman 1999), consumer mobility (Breitburg 1996) and species competition (McCook et al. 2001).

Conflict in the way that ecological phenomena, such as disturbance, are viewed often centres on differences in the scale at which they are observed (Levin 1992). Fine scale observations can detect patterns and changes that may otherwise be missed with coarse scale observations (e.g. Phillips et al. 1997). Alternatively, coarse scale information can detect general patterns within and across systems, and can be used to develop theories on the processes mediating ecological change (e.g. Tilman 1999). It is perhaps not the choice of a single scale that is important as much as it is the choice of a range of scales within which to integrate the information across scales of interest (Keddy 1990). Understanding scale-dependency of patterns and processes may be one of the more challenging activities in the science of ecology (Thrush et al. 1997).

Perhaps the more heavily contested aspects of scale is that of species level observations versus higher organisational groups (such as species grouped by morphology), particularly in detecting changes in composition and abundance of sessile assemblages (see Padilla & Allen 2000 for review). Species-specific changes may have little over-riding influence on the whole assemblages (Littler and Littler 1980; Steneck and Dethier 1994), however, coarse scale groupings may lack the sensitivity to detect change, particularly in algal assemblages that may be relatively insensitive to environmental gradients compared with species-specific responses (e.g. Phillips et al. 1997). Coarse scales represent the sum of variation across finer scales to create simplistic observations. In this case, strong responses may reflect patterns of abundance of the most abundant species, and weak responses may simply be the sum of strong negative and positive responses

within assemblages. Understanding how the ecological patterns we observe maybe dependent on the way we classify organisms is a fundamental component of understanding ecological change *per se* (Chapter 2).

Ecosystem change also transcends several scales of both space and time.

Spatially, for example, loss of kelp forest habitat may occur at a local scale (i.e. localised intensive grazing and creation of barrens, e.g. Wright et al. 2005) or regionally (i.e. loss of kelps and replacement by turf-forming algae along entire coastlines; e.g. Benedetti-Checchi et al. 2001). Temporally, seasonal storms may result in higher loss of kelps during winter than summer (e.g. Kennelly 1987a, Paine & Levin 1981), and habitats may be exposed to mechanisms creating change on a daily (e.g. tidal cycles; Bellgrove et al. 2004) to decadal scale (e.g. El Nino Southern Oscillation; Stenseth et al. 2002).

Our perception or description of change in communities becomes dependent on the scale we use to make these observations (Levin 1992). The risk becomes two-fold; are we detecting a real change (i.e. not natural variability); and perhaps of greater concern, are we missing a change because of the scale we have adopted. The key to unraveling these complications is not to dwell on the benefits and costs of the use of different scales, but, armed with that knowledge, ascertain the most appropriate and effective scale to use specific to experimental design. Few studies consider the effectiveness of the most commonly used scales of change with the experimental practices on which we currently base our management decisions.

Not only is the issue of scale important in assessing ecological change, but also understanding the effect of the combined mechanisms (or ‘disturbances’) that drive change. As much as 30 years ago, there was a growing realization that natural physical disturbance may play as great a role in community dynamics as biological interactions such as predation and competition (Sousa 1984), that had previously dominated ecological research. It was suggested then, that the interplay between disturbance and biological processes could account for a major portion of the ecological patterns observed in natural communities (Sousa 1984). Despite this, the influence of disturbances acting in combination have only recently begun to be explored (Paine et al. 1998), where the multiplicative nature of disturbances may make ecosystems more vulnerable to change (Connell 2007b). With the increasing pressure of human-derived disturbances on coastal systems, understanding the influence of compounded disturbances will undoubtedly be key for contemporary management solutions (Paine et al. 1998).

This thesis follows a progression of ideas that tests the effectiveness of different scales and types of classification of organisms on our ability to detect real change, then progresses to assesses the influence of two common physical mechanisms of disturbance (temperature, exposure) on structuring patterns of benthic assemblages.

Chapter 2

Human activities alter the composition and abundance of benthic organisms by mediating both productivity (e.g. water pollution) and consumption (e.g. modification of herbivore numbers). The predominant habitats of rocky

temperate coasts (i.e. macroalgae) represent naturally disturbed systems (Witman and Dayton 2001) that are susceptible and sensitive to human-induced disturbances. Productivity can be altered by nutrient rich run-off in urbanized coastal areas, facilitating opportunistic, fast growing and resilient species of turf-forming algae at the expense of longer-lived kelp and other canopy-forming algae (Airoldi 2001; Connell 2007a; Worm et al. 2000b). In addition, consumption can be affected by harvesting and subsequent population declines in herbivores (Andrew et al. 2002), or fishing apex predators, triggering a population increase in herbivores (Estes et al. 1998). There is not only a growing need to understand and build on recent knowledge of how these disturbances act in synergy (Russell and Connell 2005), but to understand how choice of organizational (e.g. classification) and statistical scale (e.g. indices, abundances) may predetermine our perception of change, and ultimately, forecasts for future ecosystem change.

While a substantial portion of current literature is motivated by the complexity and interpretation of scale (see above), it was important to test the effectiveness of the most common methods currently adopted to assess ecosystem change.

Chapter 2 emphasises that the use of particular measures of change should not be based solely on perception, costs or benefits, rather the appropriateness of the measure in its capacity to reliably detect change under experimental constraints.

Chapter 3

Physical disturbance dominates the range of elements identified as contributing to change in marine macroalgal morphology (Gaylord et al. 1994; Hurd 2000;

Stewart and Carpenter 2003), although the majority of studies are limited to species specific responses, rarely testing the response of whole assemblages (Airoldi 2001). In this chapter, I tested the effect of exposure on the size of assemblages, firstly with the hypothesis that macroalgae were larger on sheltered than exposed coasts. Once validated, I tested the change in early-succession assemblages when reciprocally transplanted to a site of opposite exposure (i.e. adaptation or change to an alternative state). In this chapter, it was important to test whether a coarse classification of algal assemblages (i.e. overall size) could be applicable to detecting responses to physical disturbances. Intra-species variation in response to exposure (e.g. depending on site, latitude) can make the adoption of general theories challenging. Coarse scale changes may therefore increase the predictability of assemblage change in response to physical disturbance.

Chapter 4

Herbivores, particularly sea urchins, are important habitat determiners, contributing to creation of barrens habitats (Scheibling et al. 1999), patchiness, and decreased algal species diversity (Jones and Andrew 1990). While theories of herbivory are strong and quite general (e.g. Steneck et al. 2004), there is considerable uncertainty about the general application of this theory across the globe. For example, in Southern Australia alone, studies of disturbances that shape benthic patterns highlighted both the fundamental role of strong herbivory on the eastern coast, compared with the emphasis of physical processes on the south and western coast (Connell 2007a). As with any debated topic in experimental ecology, it is difficult to balance both views of the importance of the

primary processes shaping benthic communities. However, this chapter demonstrates the importance of understanding the interactive associations of physical disturbance on echinoid populations, and the potential shift in community dynamics resulting from subsequent changes to herbivory.

Despite comprehensive literature on the role of sea urchins in structuring benthic communities, the majority of research focuses on the direct decline of sea urchin populations following removal and exclusion (e.g. Hill et al. 2003) or disease (e.g. Scheibling et al. 1999). There exists a paucity of research on the influence of varying physical disturbances, such as temperature, and further, the consequential indirect influence of varying temperature on habitat structure. In this chapter, I tested the hypothesis that extreme shifts in temperature could reduce survivorship and recruitment of *Heliocidaris erythrogramma*. Further, I conducted some preliminary tests of the existence of cold water fluxes on local sites, and whether these may explain the persistent patterns observed in algal abundance. It was important in this chapter to begin to address the idea of indirect and direct influences of a single mechanism of change, perhaps of equal consideration as the compounded effect of multiple mechanisms.

Notes on chapter style

Each chapter in this thesis (Chapter 2 – 4) presents original data and can be read as a separate, discrete study. The chapters are written in a style suitable for publication in a scientific journal. Each chapter is preceded by a preamble that briefly described the content of the chapter, the publication status at the time of submission and the contributions of any co-authors. Tables and figures are

embedded within the text, and all references are compiled at the end of the thesis, rather than at the conclusion of each chapter.

NOTE: This figure is included on page 25 of the print copy of the thesis held in the University of Adelaide Library.

One of the experimental reefs used in this study to test the effects of compounded perturbations on early succession benthic algal communities (photo: SD Connell)

CHAPTER TWO



CHAPTER 2

PREAMBLE

Chapter 2 tests the effectiveness of several scales and units of observation commonly used to assess the response of algal composition, abundance and diversity to environmental impacts. I was responsible for initiating the idea to test for this ‘effectiveness’, analysis, and interpretation of data. My co-author was responsible for the idea of testing it on a combination of physical (nutrients) and biological (herbivory) impacts, designing and constructing the experimental units (experimental reefs) and assisting with broader ecological interpretations and submission. This chapter was accepted for publication in the journal Marine Ecology Progress Series in 2007 (in press), 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 (Appendix A).

Contributions and signatures of authors:

Bethany K. Roberts

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

Signed

Date.....

Sean D. Connell

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

Signed

Date.....

CHAPTER TWO

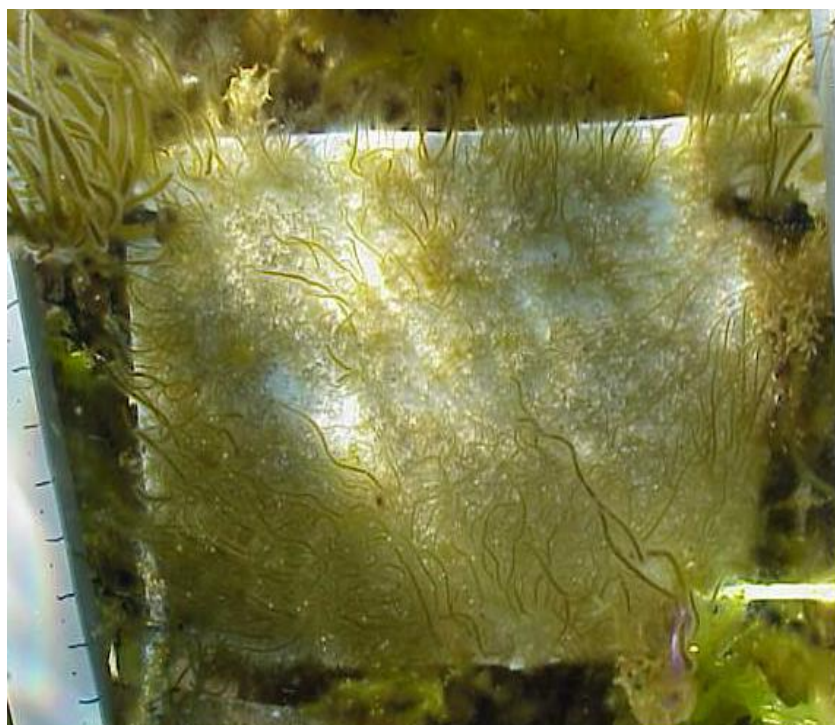
DETECTING BENTHIC RESPONSES TO HUMAN-INDUCED CHANGE: EFFECTIVENESS OF ALTERNATE TAXONOMIC CLASSIFICATION AND INDICES

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Settlement plates showing early succession algal assemblages (6 wk growth) typical of the high (above) and low (below) exposure sites studied.

CHAPTER THREE



CHAPTER 3

PREAMBLE

Chapter 3 represents data from two experiments: one mensurative, testing for morphological differences in benthic algal assemblages between wave exposed and sheltered sites; and one manipulative, testing for morphological differences between early succession assemblages that have been reciprocally transplanted from the exposed to sheltered and vice versa. This chapter tests the effectiveness of the morphological character of size of individuals within an assemblage as a broad scale predictive tool to assess the effects of exposure.

CHAPTER THREE

MORPHOLOGICAL PLASTICITY OF ALGAL ASSEMBLAGES BETWEEN EXPOSED AND SHELTERED WAVE EXPOSURES

ABSTRACT

Macroalgae have the ability to vary their form and shape in response to the physical forces of both exposed and sheltered environments. However, hydrodynamic challenges differ between species, and variation across all morphological characteristics, other than size, is neither consistent nor predictable. This study tested for differences in the size (i.e. large *v.* small morphology) of individuals within benthic algal assemblages in exposed and sheltered environments. Reciprocally transplanted early-succession assemblages (on settlement plates) between environments were used to determine if assemblage size was a fixed trait, or a response to the local environment. Differences between natural assemblages were consistent with the paradigm that size increases as exposure decreases. The reciprocal transplant confirmed that early succession assemblages responded to local environmental conditions, albeit with uneven rate of response between sheltered and exposed environments. Rapid changes in assemblages transplanted to an exposed site contrasted with the relatively slower change in assemblages transplanted to the sheltered environment. These results suggest that stressors in exposed environments may exert greater pressure on the size of macroalgal assemblages than those typical of sheltered environments. Second, the morphological characteristic of size alone

has the potential to be used as a broad-scale predictive tool to assess the effect of exposure.

INTRODUCTION

Shallow benthic communities of temperate coasts are characterised by macroalgae, which significantly contribute to biodiversity of temperate ecosystems (Mann 1973; Shiel and Foster 1986). Macroalgal communities not only play a key role as the dominant primary producers of near shore benthic ecosystems (e.g. Duggins et al. 1989), but are also important habitat formers for a suite of benthic fauna (*see* Steneck et al. 2002 *and references therein*).

Understanding the processes that influence macroalgae is an important aspect of the structure and function of temperate coasts.

Of the suite of environmental factors that exert pressure on patterns of macroalgal communities, hydrodynamics is perhaps one of the most ubiquitous mediating factors. Water motion can influence many factors that control macroalgal production; including rates of nutrient uptake (Hurd 2000), light levels (Wing et al. 1993) (where turbidity determines light refraction), photosynthesis (Stewart and Carpenter 2003) and propagule dispersal (Bobadilla and Santelices 2005). Extreme water motion can cause damage (through breakage) or dislodgement of individual thalli (Thomsen 2004), a stressor that can cause macroalgae to counteract via morphological variation (Gaylord et al. 1994). Morphological variation may confer selective advantages to species in certain environments (Blanchette et al. 2002) and ultimately extend their range and distribution (Denny

1988), by increasing survival and productivity across a broad range of hydrodynamic conditions.

Many species of macroalgae exhibit a range of morphologies across hydrodynamic gradients. For example, a larger boundary layer at a plants surface is typical of low flow environments (Stewart 2004), limiting nutrient uptake and ultimately productivity and growth (Hurd 2000). Typical characteristics of kelp species to combat limited productivity in low exposure environments include morphological adaptations such as larger (Fowler-Walker et al. 2006; Stewart and Carpenter 2003) , wider (Hurd 2000; Wernberg and Thomson 2005) and thinner (Blanchette et al. 2002; Duggins et al. 2003) fronds with ruffled or undulated margins (Roberson and Coyer 2004) and increased flexibility (increased drag and nutrient exchange) of thalli (Denny and Gaylord 2002; Stewart 2004). In contrast, strength increasing (e.g. thicker stipes and larger holdfasts) and drag decreasing (smaller, thicker fronds) morphologies characterise kelps in high exposure environments to minimise breakage and maximise productivity (see review by Hurd 2000).

Kelp canopies and understory assemblages interact in predictable patterns in time and space, where certain morphologies of understory may be either promoted or suppressed depending on the morphology of the canopy (Melville and Connell 2001). The common occurrence of loss of canopies due to wave action can therefore rapidly alter the ecological conditions and ultimately the understory assemblage (Kennelly 1987b; Wernberg and Thomson 2005). Given this inter-dependent relationship, it is therefore important to understand not only the

environmental conditions that influence morphological variation of kelp, but also that of understory assemblages. The influence of hydrodynamics on morphological plasticity of understory assemblages has received surprisingly little attention to date.

While several morphological characters vary with level of exposure, there remains an overriding viewpoint that hydrodynamic forces imposed by ocean waves primarily limit the size of nearshore organisms where the more exposed the shore, the smaller the individuals (Denny 1999; Gaylord et al. 1994). In a critical review of the literature, Thomsen and Wernberg (2005) found that thallus size alone could dictate the force required to break or dislodge many macroalgal species. This evidence supports the importance of size as a critical morphological character, albeit size alone is rarely considered as an *a-priori* hypothesis. I reviewed 40 studies published since 1980 investigating the morphology of macroalgae in wave-exposed compared to sheltered environments (Appendix B.2). Of these studies, 73 % concluded that morphological characters that contribute to an overall smaller thallus size typically dominated responses to increased wave action or water motion (i.e. high exposure), and consequently, characters contributing to larger thallus size dominated responses to low exposure regimes. This pattern transcended 3 divisions and 8 orders of benthic macroalgae, suggesting that this morphological association may affect the size of entire assemblages.

To investigate the effect of exposure on size of individuals (i.e. small v. large morphology) in assemblages, first I tested the prediction that macroalgae are

larger on sheltered than exposed coast. Once validated, I tested 1) that the morphology of transplanted assemblages would change to become more similar to the surrounding natural assemblages (i.e. transplanted site) and 2) be different from assemblages at the original site.

METHODS

Study Site & quantification of exposure

Morphology of subtidal macroalgal assemblages quantified during the Austral summer in 1999, and 2001-2003 at two adjacent sites at Coffin Bay, South Australia (35°61'S, 135°30'E). The northern (*hereafter* high exposure) site is separated from the southern (*hereafter* low exposure) site by a sub-tidal reef running perpendicular to the shore (Fig. 3.1). Water velocity (as a measure of exposure) was calculated by measuring the maximum drag force at each site using a maximum velocity recorder (Bell and Denny 1994). Five spring scales were deployed at each site at a depth of 1-2 m for two consecutive days. Drag measurements ($n = 5$ per site, two dates) were subsequently converted to water velocities using the calibration calculations from Bell & Denny (1994). A two-factor ANOVA tested for differences in water velocities between sites and days. Site was treated as fixed and orthogonal and date as random and orthogonal. Data conformed to homogeneity of variance. The analysis of water velocity showed significant differences between exposed (mean \pm SE; = $10.78 \pm 1.73 \text{ ms}^{-1}$) and sheltered ($6.16 \pm 0.75 \text{ ms}^{-1}$) sites ($F_{1,1} = 1191.87, p = 0.02$).

Natural patterns of algal abundance

Long term percentage cover of natural benthic macroalgae was sampled along three transects (50 m × 2 m), separated by at least 15 m, at each site (exposed and sheltered) during Austral summer of four years. Quadrats (1 m², $n = 8$, comprising 25 randomly placed points) were haphazardly placed along each transect, to a maximum depth of 2 m, and percentage cover of algae quantified using the point-intercept method (Meese and Tomich 1992). Algae were categorised into 4 morphological groups, modified from Steneck and Dethier (1994); 1) filamentous turf-forming algae and articulated coralline algae (classed as turfs 5 – 50 mm in height); 2) canopy-forming algae; 3) encrusting coralline algae (growing prostrate to the substratum) and 4) foliose algae (fleshy non-coralline) (e.g. Ulvales).

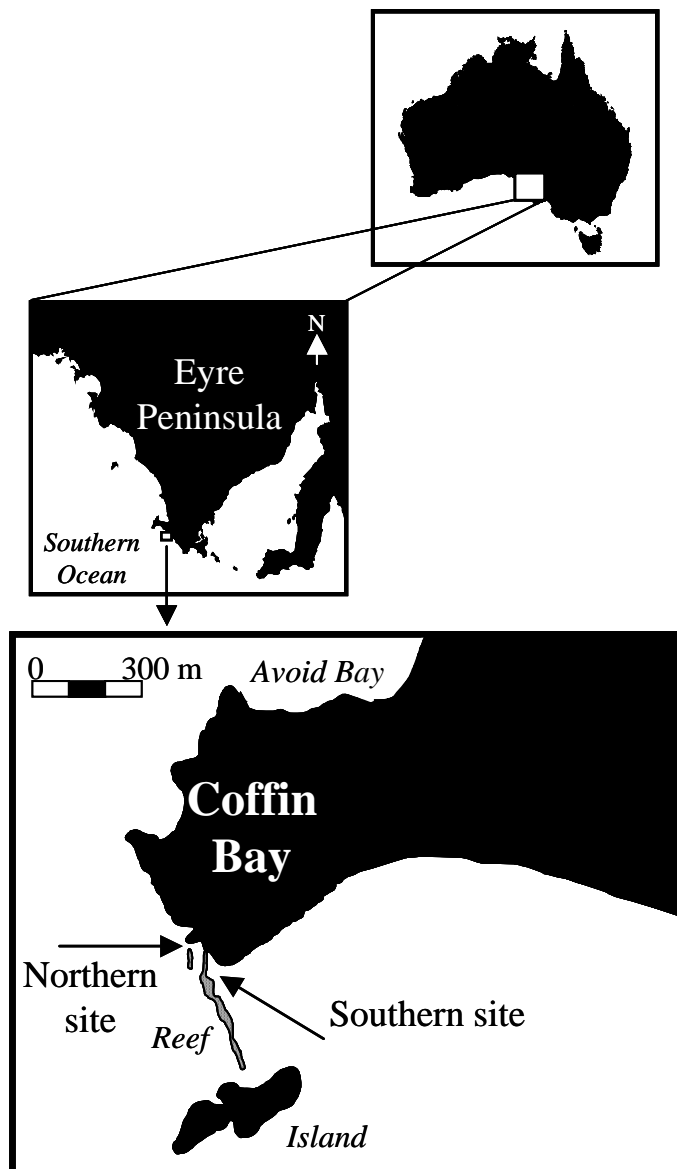


Figure 3.1 Schematic of field site; Northern site = high exposure, Southern site = low exposure

Statistical analysis of natural patterns

Multivariate analyses (PERMANOVA) tested for the effect of exposure (high v. low) and year ($n = 4$) on assemblage structure. Data were fourth-root transformed and a non parametric MDS plotted the centroid (average) of replicate quadrats ($n = 8$) for each transect in each of the four years sampled. Multiple pairwise comparisons were used to test for differences in assemblage structure between sites and among years. Percentage of similarity analysis (SIMPER) was used to determine the morphological groups that had the greatest contribution to dissimilarity in assemblage structure between treatments (Clarke 1993). Exposure was treated as fixed and orthogonal and year as random and orthogonal.

In order to test *a priori* hypotheses of differences in size of understorey algae between sites of differing exposure, understorey algae were grouped into small (encrusting and articulated coralline algae, filamentous algae and branched, terete algae 0 – 50 mm) and large (foliose, fleshy and terete algae > 50 mm) morphological groups and the difference in percentage cover between high and low exposure sites tested using a 2-factor ANOVA (Exposure \times Year). Data were tested for homogeneity of variance (Cochran's *C* test) and transformed accordingly.

Tests of morphological plasticity: reciprocal transplants of algal assemblages

To test the plasticity of algal morphology with differing levels of exposure, settlement plates were deployed at each site for 45 days before a reciprocal

transplantation between sheltered and exposed sites. Plates were constructed from 15 × 15 cm sheets of Flexi-board[®], and the outside surface sanded to create a topographically rough surface for successful recruitment (Irving and Connell 2002). In November 2003, 30 plates were attached at each site comprising three treatments, control, transplant procedural control and transplanted (*hereafter* experimental), $n = 10$ plates per treatment. Plates were attached to mesh secured on boulders, with horizontal orientation, at a depth of 1 - 2 m (below mean low water) at each site. Plates were deployed for a total of 90 days to coincide with the peak of the Austral summer (end February) to avoid the confounding effects of algal senescence with the onset of cooler water (Russell and Connell 2005).

Loss of settlement plates from the high exposure site during a storm event in the first 45 days forced the experimental design to be altered *in situ* (i.e. replication was reduced from 10 to 6 plates per treatment of procedural control and experimental). Experimental plates were removed, placed in a dive-bag, and re-attached at the reciprocal site, maintaining orientation and depth. Procedural control plates were removed in the same manner, and re-attached at the site of origin. Forty-five days post-transplantation (February 2004), plates were photographed (1 × optical zoom), placed in individual zip-loc bags and transported back to the laboratory for use as voucher specimens. Finally, I recognise the interpretational difficulties of observations and reciprocal transplants between two sites (one exposed and one sheltered) (Underwood 1997). The results of these observations and experiments, therefore, are interpreted with the note of caution that this study would need multiple and independent sheltered

and exposed sites for the inferences to be as strong as is often accepted in the discipline of marine ecology (Underwood et al. 2000).

Quantification of experimental algal assemblages

Percentage cover of algae was estimated by placing a grid of 100 evenly spaced points over projected photographs of each plate (Drummond and Connell 2005). In order to maintain a comparison with natural assemblages, each point was classified as either 1) bare space, 2) prostrate coralline algae 3) filamentous or branched turf-forming and articulated coralline algae (classed as turfs 0 – 10 mm in height) algae or 5) foliose or terete (fleshy, non coralline) algae (> 10 mm). Comparison with voucher specimens was used for confirmation of morphology from photographs where required. Only the inner 12 × 12 cm of assemblages was quantified to avoid possible edge effects.

Statistical analysis of experimental patterns

The design of the reciprocal transplantation experiment tested the plasticity of algal assemblages to exposure with two predictions, 1) assemblages transplanted between levels of exposure ('experimental') will differ to assemblages transplanted within exposure levels at the site of origin ('control') and 2) experimental assemblages will not differ from assemblages at the recipient site (i.e. Experimental sheltered = control exposed; and Experimental exposed = control sheltered). Multivariate analyses (PERMANOVA) of fourth-root transformed data tested for the effect of exposure (high v. low) and treatment

(natural v. experimental) on assemblage structure (using morphological groups). Multiple pairwise comparisons were used to test for difference in assemblage structure between exposure and treatment. Multivariate analysis of dispersion (PERMDISP), (based on untransformed Bray-Curtis dissimilarity), was used to test the effect of level of exposure and site of origin on dispersion of assemblages within the same site.

Finally, algae were grouped into coarse morphological groups of small (encrusting and articulated coralline and filamentous and branched turf-forming algae 0 – 10 mm) and large (Foliose, fleshy and terete algae > 10 mm). A two-factor ANOVA, with both origin (sheltered or exposed) and treatment (procedural control or transplanted) treated as fixed and orthogonal tested for differences in percentage cover of large and small morphologies between natural and experimental assemblages. Homogeneity of variances was tested using Cochran's *C* test, and heterogeneous data arc-sin transformed.

RESULTS

Natural patterns of algal abundance

Morphology of assemblages differed between the sheltered and exposed sites (Fig. 3.2, PERMANOVA, Table 3.1), but only significantly in two of the years (1999 and 2002). Assemblage structure was consistent within sites for all years, with the exception of 1999 and 2001 at the low exposure site (Table 3.1).

Analysis of dissimilarity revealed encrusting corallines contributed to 32 % of the difference between assemblages of understory algae at each site, followed by foliose (24 %) and articulated turf-forming (< 50mm) algae (12 %) (Table 3.2). In terms of understory algae, turf-forming morphologies (articulated corallines, filamentous and branched turfs) were in greater abundance at the high exposure than the low exposure site, but only in 2000 and 2001 (ANOVA: Exposure \times Year; $F_{3, 184} = 3.04$, $p = 0.03$; SNK: High exposure > Low exposure; Fig. 3.3a).

Greater cover of foliose algae at the low exposure site over time was marginally non significant (ANOVA: Exposure \times Year; $F_{3, 184} = 2.43$, $p = 0.067$), although there is a trend toward greater cover at the low exposure site over the first two years of sampling (Fig. 3.3b). Coralline algae were more abundant at the high exposure site in 2002 (ANOVA: Exposure \times Year; $F_{3, 184} = 3.34$, $p = 0.02$), more than twice that at the low exposure site (20 % cover *v.* 40 %, Fig. 3.3c).

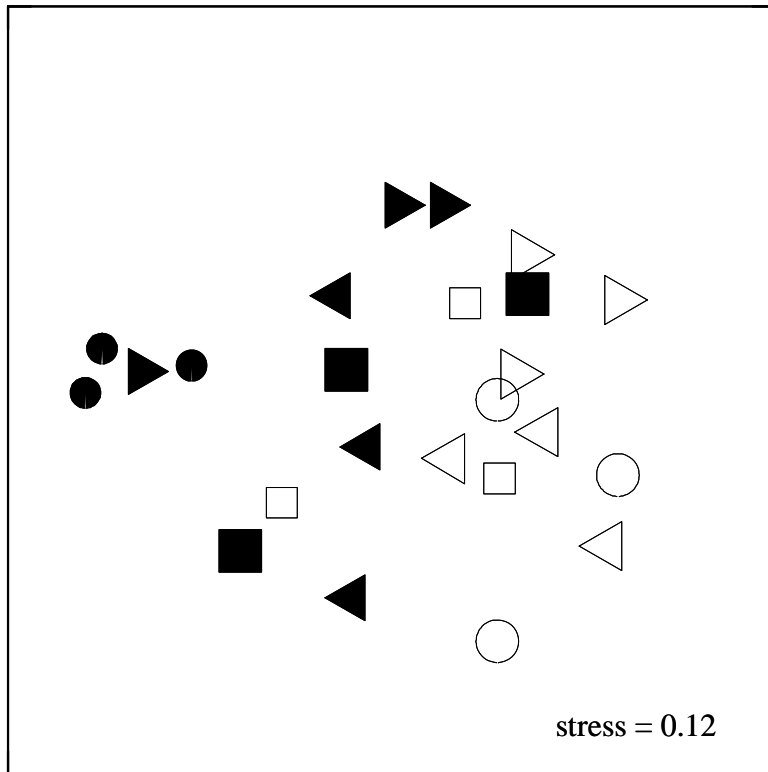


Figure 3.2 Non-parametric multi-dimensional scaling analyses showing associations of benthic algal assemblages between low exposure (filled symbols) and high exposure (open symbols) over 4 years, 1999, 2001, 2002 and 2003, ●, ◀, ◀, ▶, ■ respectively.

Table 3.1 Results of a) 2-factor PERMANOVA testing for differences in benthic algal assemblages between low and high exposure environments over a 4-year period and (b) pair wise comparisons of significant terms of exposure and year.

(a) Treatment	df	MS	<i>F</i>	<i>p</i>
Exposure	1	2042.54	6.53	*
(Exp)				
Year (Ye)	3	168.49	1.81	ns
Exp × Ye	3	311.97	3.36	*
Residual	16	92.86		
Total	23			

(b) Pair wise comparisons			<i>t</i>	<i>p</i>
Site	High vs low exposure		2.92	*
Year (exposure)	1999	Low vs High	4.34	*
	2001	Low vs High	1.48	ns
	2002	Low vs High	3.12	*
	2003	Low vs High	1.10	ns
	Low exp.	1999 vs 2001	3.34	*
		1999 vs 2002	2.08	ns
		1999 vs 2003	2.03	ns
		2001 vs 2002	1.91	ns
	2001 vs 2003	0.77	ns	
	2002 vs 2003	1.44	ns	

(Table 3.1 continued)

High exp.	1999 vs 2001	0.46	ns
	1999 vs 2002	1.90	ns
	1999 vs 2003	1.65	ns
	2001 vs 2002	1.37	ns
	2001 vs 2003	1.26	ns
	2002 vs 2003	1.48	ns

Not significant (ns): $p > 0.05$, $*p < 0.05$

Table 3.2 Average dissimilarity between algal assemblages from high and low exposure environments for percentage cover of morphological groups

Algae	Contribution %	Cumulative %
(a) Morphological group		
Encrusting coralline	32.49	32.49
Canopy forming	31.59	64.08
Foliose	24.39	88.47
Turf forming (< 50 mm)	11.53	100.00

Morphological groups are listed in order of decreasing contribution to the average dissimilarity (contrib. %) between high and low exposure sites. Average dissimilarity between sites was 56.87%.

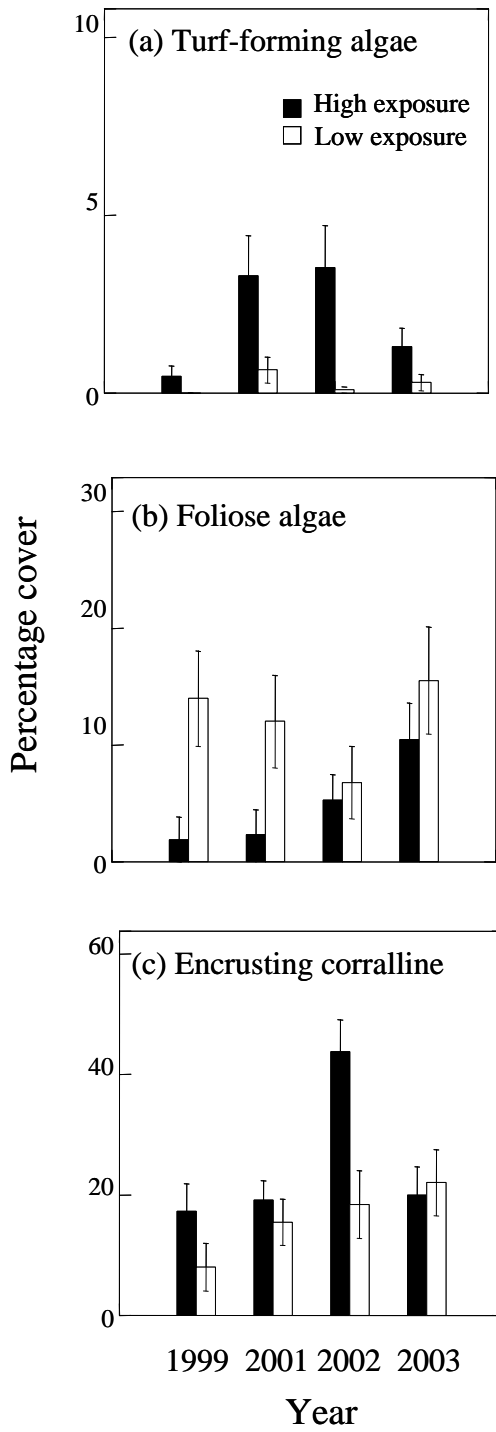


Figure 3.3 Percentage cover of morphological groups of understorey algae between high and low exposure sites over 4 years (\pm SE; n=24).

Small algae (prostrate, articulated and filamentous or branching turf-forms, < 50 mm) were more abundant at the high exposure site (Fig. 3.4, SNK: low exposure < high exposure). Conversely, large algae (delicate foliose forms, > 50 mm height) were more abundant at the sheltered site (SNK: low exposure > high exposure). This was detected as a significant interaction between exposure (low v. high) and morphology (small v. large) (Table 3.3).

Experimental algal abundance patterns

Differences between assemblages from each site were clearly visible where extensive cover of large algae, primarily composed of foliose morphologies (fleshy, delicate, non coralline), dominated at the low exposure site. In contrast, crustose and small turf-forming species (branched, filamentous, prostrate and articulated corallines < 10mm) were the only morphologies present at the high exposure site. This was detected as a significant interaction between exposure and treatment (multivariate: experimental v. control), where pair wise comparisons supported visible differences between control assemblages at each site (i.e. high exposure \neq low exposure) (Fig. 3.4, Table 3.4a).

No difference in morphological structure was detected between experimental assemblages from both sites (low transplant = high transplant). This asymmetrical response of transplanted assemblages will be discussed further below, however, can be partially explained by differences in morphology of control and experimental assemblages. This occurred only at the low exposure site (i.e. low exposure: control \neq experimental, high exposure: control = experimental) (Fig.

3.5). Multivariate analysis of dispersion (PERMDISP) showed no significant difference between assemblages for either of the two factors (exposure, treatment) (Table 3.4b) within each site.

Using the coarse classification scale of size, percentage cover of small and large algae transplanted to the high exposure site did not differ from the control assemblages naturally found there (i.e. low exposure transplanted to high exposure = high exposure control). Percentage cover of small and large algae in assemblages transplanted from the high exposure site did not differ from assemblages originating there (i.e. high exposure transplanted to low exposure \neq low exposure controls).

This is demonstrated by a significant univariate interaction between exposure and treatment at the coarse classification scale of size (Table 3.5). However, the *a priori* patterns of large *v.* small algae were more apparent for assemblages originating at the low exposure site. The dominance of large, foliose algae was replaced by small encrusting, articulated and turf-forms in experimental assemblages (Small: experimental > control; Large: experimental < control). The effect of transplanting from low to high exposure was large and more rapid (i.e. Large algae: control = 53 %, experimental = 3 %; Small algae: control = 32 %, experimental = 69 %) than transplanting from high to low exposure (i.e. Large algae: control = 0.8 %, experimental = 1.5 %; Small algae: control = 76 %, experimental = 85 %).

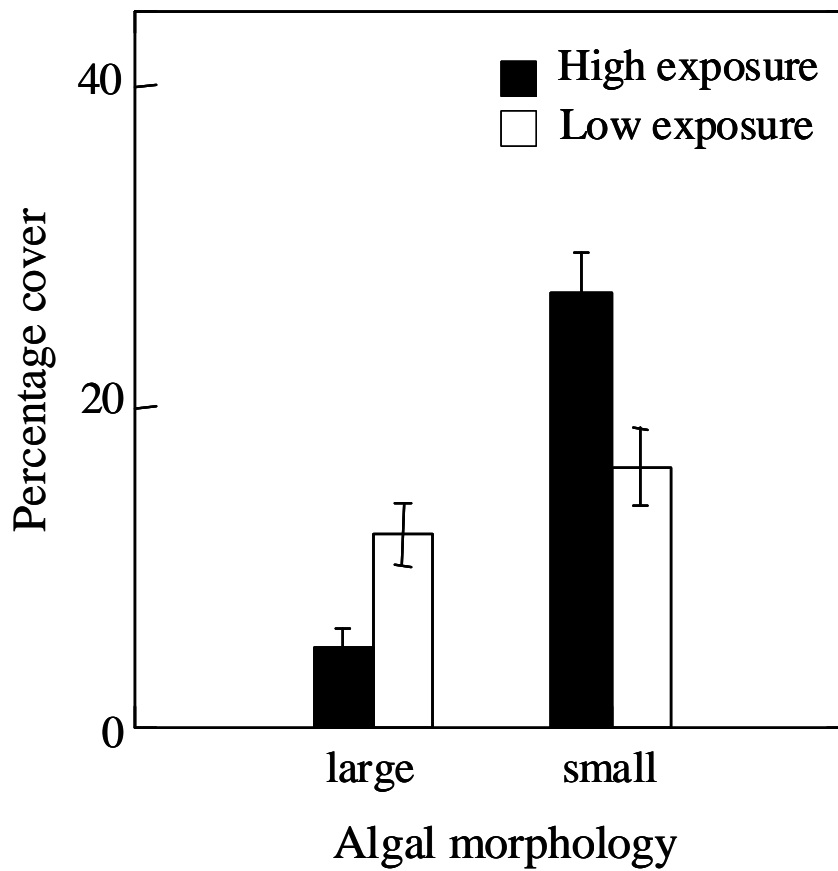


Figure 3.4 Percentage cover (\pm SE) of (a) large (delicate, >50mm) and (b) small (prostrate and articulated < 50mm) of natural understorey algal morphologies at high and low exposure sites (pooled years, $n = 96$).

Table 3.3 (a) Results of a two-factor ANOVA testing for the effect of Exposure (high v. low; pooled years) on the percentage cover of different morphology of understorey algae (small v. large) and (b) SNK-tests for the significant interaction of exposure and morphology.

(a) Treatment	df	MS	F	<i>p</i>
Exposure (Exp)	1	356.51	0.87	ns
Morphology (Mor)	1	16708.57	40.60	***
Exp × Mor	1	7794.01	18.94	***
Residual	380	411.50		

(b) SNK tests	
Small algae	Low exposure < High exposure
Large algae	Low exposure > High exposure
Low exposure	Large = small algae
High exposure	Large < small algae

Not significant (ns): *** $p < 0.001$

Data were $\ln(x + 1)$ transformed to conform to homogeneity of variance (Cochran's *C* test).

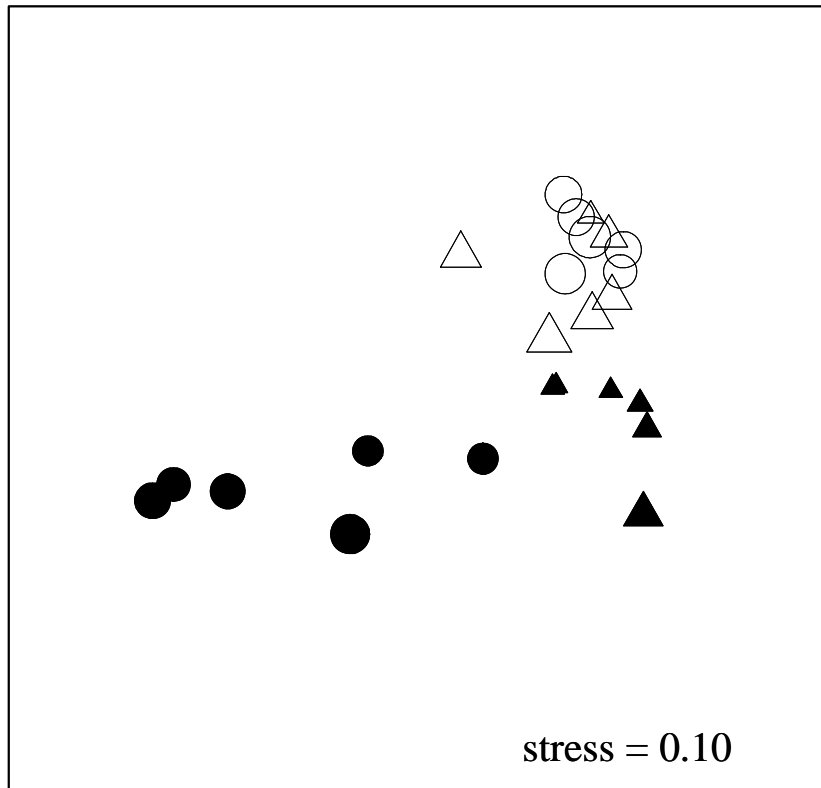


Figure 3.5 Non-parametric multi-dimensional scaling analyses showing associations of natural (filled symbols) and experimentally transplanted (open symbols) benthic algal assemblages from low and high exposure habitats (● and ▲ respectively).

Table 3.4 Results of a) two-factor PERMANOVA testing for difference in early-succession algal assemblages between low and high exposure environments, and pair wise comparisons of significant terms of exposure and treatment, and (b) PERMDISP testing for differences in multivariate dispersion of assemblages originating from high and low exposure sites and pair-wise comparisons.

(a) Treatment	df	MS	<i>F</i>	<i>p</i>
Exposure (Exp)	1	4615.70	6.26	**
Treatment (Tr)	1	5230.52	7.10	**
Exp × Tr	1	9278.52	12.59	***
Residual	20	737.16		

Pair wise comparisons		<i>t</i>	<i>p</i>
Low v. High exposure	Control assemblages	4.02	**
	Experimental assemblages	1.29	ns
Control v. experimental assemblages	Low exposure	4.67	**
	High exposure	1.29	ns

(b) Source	df	MS	F	<i>p</i>
Exposure (Exp)	1	263.86	2.99	0.11
Treatment	1	1.25	0.01	0.90
Exp x Tr	1	106.05	1.20	0.29
Residual	20	88.34		

Not significant (ns): ** $p < 0.01$, *** $p < 0.001$

Table 3.5 (a) Results of a two-factor ANOVA testing for the effect of Exposure (high *v.* low) on the percentage cover of different morphology of understorey algae (small *v.* large) and (b) SNK-tests for the significant Exposure \times treatment interaction. Control = assemblages representative of high and low exposure sites, Experimental = assemblages transplanted to a site with the opposite level of exposure (e.g. high to low, low to high).

(a) Treatment	df	MS	<i>F</i>	<i>p</i>	MS	<i>F</i>	<i>p</i>
		(i) small algae arc sin			(ii) large algae arc sin		
Exposure (Ex)	1	2169.18	24.22	**	3379.75	40.39	***
Treatment (Tr)	1	1295.49	14.46	*	2435.2	20.10	***
Ex \times Tr	1	437.01	4.88	*	2621.42	31.33	***
Residual	20	89.57			83.63		

(b) Morphological group	Low exposure	High Exposure
Small algae	Experimental > Control	Experimental = Control
Large algae	Experimental < Control	Experimental = Control

$p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$

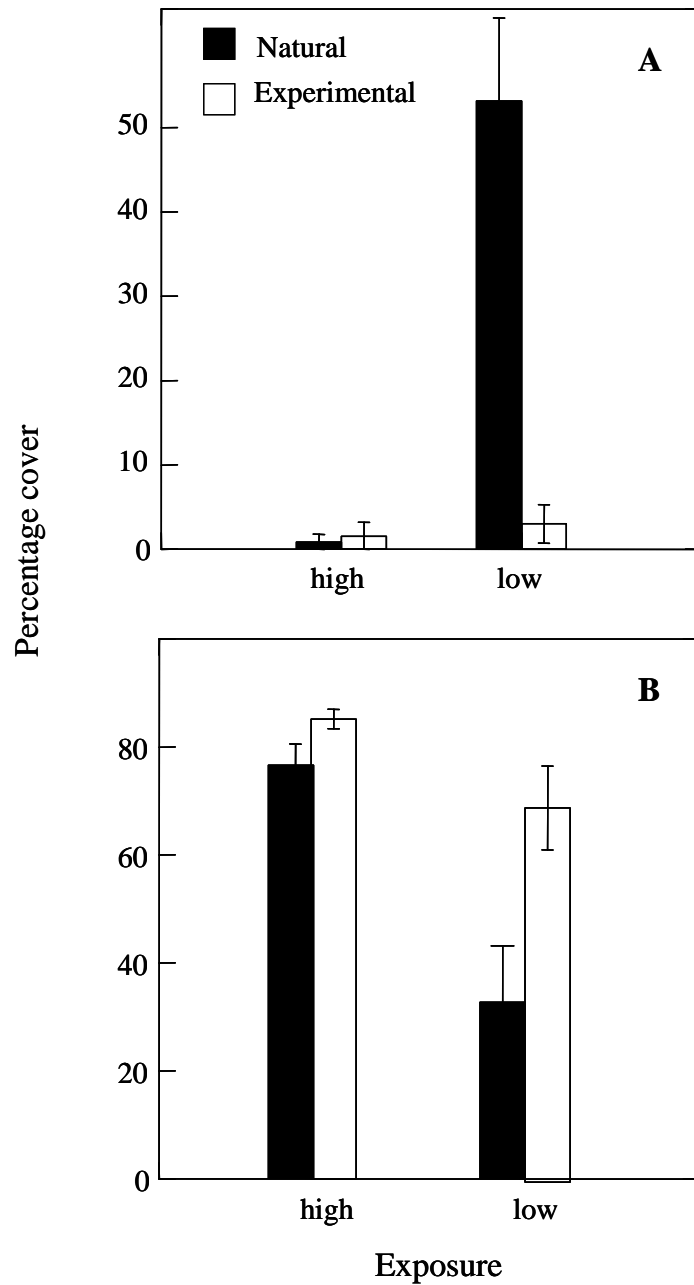


Figure 3.6 Percentage cover (\pm SE, $n = 6$) of (a) large (delicate, > 10mm) and (b) small (prostrate and articulated \leq 10mm) morphological groups of early succession algal communities on settlement plates representative of natural (control) and experimental (transplanted) assemblages.

DISCUSSION

The key finding was that size of macroalgal assemblages (in terms of the dominance of large and small morphologies) differed between the exposed and sheltered site, and that this was a plastic response to the environment. The greater proportion of small algal morphologies within established assemblages at the exposed site (dominated by prostrate corallines and complexes of turf-forming algae) and larger, foliose and more delicate morphologies at the sheltered site is consistent with this finding. These findings are not only consistent with documented biomechanical variations that counteract hydrodynamic stressors (Hurd 2000), but also support the paradigm that thallus size alone (rather than a complex array of different morphological characters c.f. Fowler-Walker et al. 2005) can account for the variation in morphology with exposure.

The response of morphological groups to variation in exposure within natural assemblages varied considerably over time. While there existed a trend toward differences in percentage cover of foliose, prostrate coralline and turf-forming algae, these differences were rarely significant. Incorporating a coarser scale of classification (i.e. size of understory) not only revealed significant responses of whole assemblages, but allowed generality of the pattern of assemblage response that may be useful on broader spatial scales. For example, there exists a controversy within the marine literature to the classification and use of the term “turf-forming algae”. Turfs may consist of a variety of combinations of filamentous, articulated corallines, terete and corticated foliose algae (Airoldi

2001; Benedetti-Cecchi et al. 1998; Coleman 2003; Connell 2003; Milazzo et al. 2004; Russell and Connell 2005; Worm and Chapman 1998). Although composed of several morphological groups, turfs are densely packed together and often grow to similar sizes (i.e. consistent height) (Airoldi 2001). Importantly, algae growing within turfs may therefore respond similarly to wave forces, independent of individual morphology, and perhaps assemblage size is the overriding important morphological feature (Airoldi 2001).

The dominance of large and small morphologies of early succession assemblages varied within sites. As expected, the abundance of small morphologies was three times that of larger morphologies (more susceptible to breakage) at the exposed site. However, the proportions of small and large morphologies at the sheltered site were not different. This may be because water flow at the sheltered site may not have been low enough to be limiting for productivity (via an increased boundary layer). Values of wave exposure are rarely reported within the literature, making comparison between categories of “exposed” and “sheltered” difficult. Although the sheltered site in this study experienced water velocities almost half that of the adjacent exposed site, this was still in the upper range of 1 – 5 ms⁻¹ reported for similarly classified sites worldwide (Bell and Denny 1994; Fowler-Walker et al. 2006; Kitzes and Denny 2005; Prathep et al. 2007; Roberson and Coyer 2004; Thomsen 2004). Even so, the analysis of dispersion (PERMDISP) between transplanted assemblages indicates that the assemblages responded by a shift in structure (i.e. abundance of large and small morphologies), rather than simply becoming either more or less variable within each site. The

differences in morphology of early-succession understorey assemblages were therefore plastic responses to the local environmental conditions.

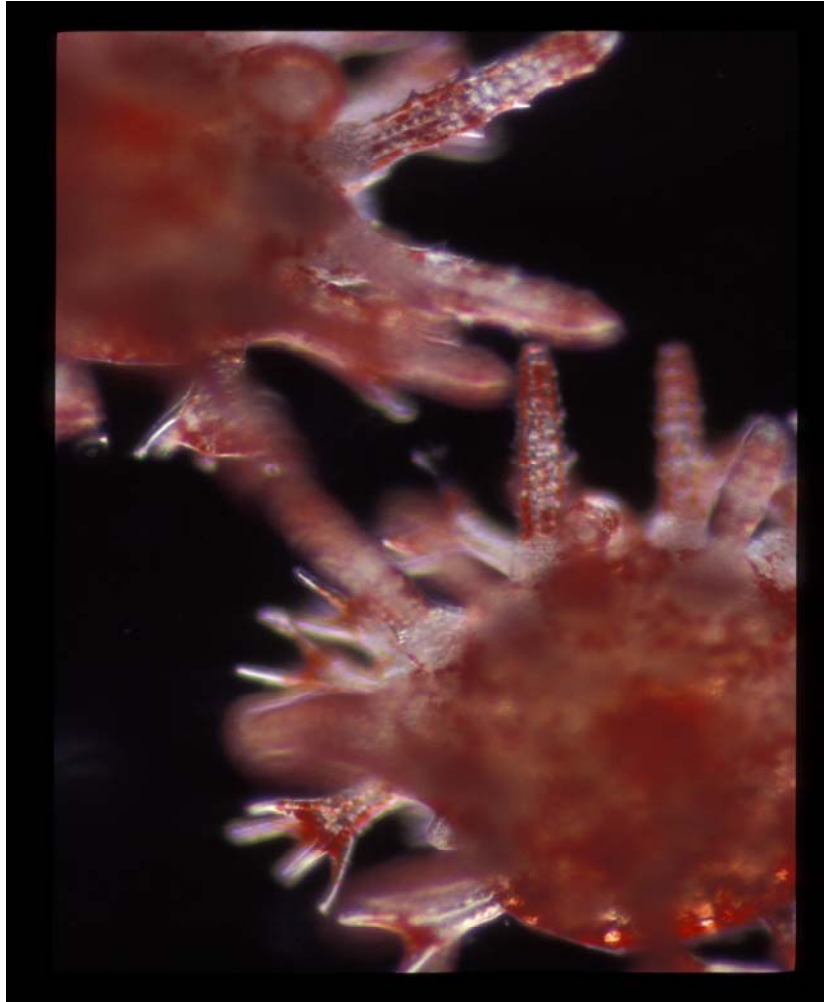
Transplanted assemblages from the sheltered site underwent large and rapid changes consistent with expectations of loss of large, foliose algae, being replaced with smaller, more robust morphologies resistant to drag and breakage in high water velocities (Thomsen and Wernberg 2005). Interestingly, these changes did not occur at the same rate for transplanted assemblages from the exposed site. While large, delicate morphologies were evident, experimental assemblages remained largely dominated by small morphologies, typical of their site of origin. There are a number of explanations for this disproportionate response between transplants. The lack of large forms colonising assemblages transplanted to the sheltered site may be a result of competition for space (e.g. Paine & Levin 1981). Assemblages transplanted to the exposed site rapidly lost large foliose morphologies quickly creating new space, which contrasts with those transplanted to the sheltered site, where dislodgement and breakage was minimal (*pers. obs*). Alternatively, the limiting thickness of the boundary layer (determined by the rate of flow; e.g. Carpenter and Williams 1993) that promotes fast growing more delicate forms in low flow environments may occur only in velocities much lower than tested here. Exposed sites may represent particular stressors (such as drag and breakage) that are either not represented, or relaxed at sheltered sites (Fowler-Walker et al. 2006), and that stressors such as nutrient limitation at sheltered sites may affect morphology only under extremely low flow conditions. Finally, given that larger morphologies recruited and grew simultaneously at the sheltered site,

the disproportionate response of assemblages at the exposed site is likely neither lack of recruitment or time for growth of larger morphologies.

The disproportionately longer response of transplanted assemblages from exposed to sheltered environments has also been demonstrated for a dominant kelp species, *Eklonia radiata* (Fowler-Walker et al. 2006). If we are to truly grasp the nature of the association between kelp canopies and understory assemblages (Fowler-Walker et al. 2005; Kendrick et al. 1999; Wernberg et al. 2003), understanding phenotypic plasticity of understory as a morphological group is important.

Although the need to validate these results with replication at other sites of varying exposure is necessary, this study suggests that variation in size of whole assemblages of macroalgae include plastic responses to the local physical environment.

Finally, while the use of coarse classifications such as size may result in a loss of information at the fine scale (i.e. species-specific responses), in contrast to the species dependent multi-directional response of a complex suite of morphological characters (e.g. length, width etc), overall size has the potential to be used as a broad and predictive tool to identify hydrodynamic stressors across an entire assemblage range and wide biogeographical areas, regardless of the species present.



Two three-day old juvenile *Heliocidaris erythrogramma* sea urchins 2 h post-settlement (10 x obj). Primary spines and tube-feet visible. Photo: B. Roberts

CHAPTER FOUR



CHAPTER 4

PREAMBLE

Chapter 4 tests the survivorship of the juvenile sea urchin, *Heliocidaris erythrogramma*, exposed to cold water pulses, and tests whether such variation in temperature may exist at a site within the Great Australian Bight, an area of well-documented summer upwelling. This chapter investigates the link between oceanographic phenomena and biological processes, such as herbivory, which are known to be pivotal agents structuring benthic assemblages.

CHAPTER FOUR

THE EFFECT OF VARIABLE TEMPERATURE ON SURVIVAL OF JUVENILE URCHINS: IMPLICATIONS FOR BENTHIC COMMUNITIES

ABSTRACT

Sea urchins can play a pivotal role in structuring benthic algal communities and understanding the factors that affect their abundance is therefore fundamental to understanding ecological processes. The influence of variation in temperature has been the focus of decades of benthic research, however, little attention has been focussed on the direct effect of lower sea surface temperatures on urchin mortality. I tested the effect of cold water pulses on post recruitment mortality of a common sea urchin (*Heliocidaris erythrogramma*). Laboratory studies revealed that exposure to these cold pulses reduced survivorship of newly recruited sea urchins by up to 70%. In addition I tested the theory that temperature variation (i.e. cold water pulses) may exist within the Great Australian Bight. Survivorship of newly settled urchins in the field was significantly lower at a site exposed to cold water pulses, when compared to a control site. My results show that variation in temperature can substantially reduce survivorship of a potentially important habitat determiner (i.e. grazers). This novel research may provide a more complete understanding of the link between oceanographic features that deliver cooler waters to coastal habitats and their influence on both a habitat determiner, and potentially the habitats themselves.

INTRODUCTION

Variations in cold water pulsing, associated with mechanisms such as high frequency upwelling, are globally extensive. Temperature can decrease from 2-10°C and period of change varies between 10 minutes and 14 days (Leichter and Miller 1999; Leichter et al. 2003; Menge et al. 2003). Such cold water intrusion on coastal benthic communities is known to affect near-shore communities in a variety of ways, among the most documented being a positive association with algal abundance (Diaz-Pulido and Garzon-Ferreira 2002; Leichter et al. 2003). However, in most studies, the increase in algal abundance is attributed to the pulsed increase of nutrients often associated with cold water intrusion. The effect of cold temperature on grazer mortality is rarely validated. Whilst the availability of nutrients can have important direct effects and consequences on primary productivity of an algal population, other biotic influences, such as herbivore pressure also play a key role in algal community dynamics. For example, variation in consumer pressure and activity has been shown to play a pivotal role in structuring marine benthic communities (e.g. Wright et al. 2005).

Herbivores, in particular sea urchins, are important grazers, exerting a significant influence on algal biomass in tropical (e.g. Levitan 1988), temperate (e.g. Wright and Steinberg, 2001) and sub-Antarctic (Konar 2001) marine systems.

Destructive grazing and creation of barrens habitats (Hill et al. 2003; Scheibling et al. 1999) and contributing to patchiness and decreased algal species composition (Jones and Andrew 1990) can ultimately lead to complete shifts in community dynamics. Understanding the factors influencing variation in echinoid

populations is therefore important in understanding the community dynamics of benthic systems.

Whilst the role of sea urchins in structuring benthic communities has been intensively studied by ecologists, the majority of this research has focussed on the effect of declining populations, either by experimental removal and exclusion (e.g. Hill et al. 2003; Sumi & Scheibling 2005; Shears & Babcock 2002) or disease (e.g. Liddell & Ohlhorst 1986; Scheibling et al. 1999). Echinoid mortality outside these direct effects has been little studied. Variation in physical and seasonal influences such as exposure (Verling et al. 2005) and sea surface temperature (Barnes et al. 2001) have only recently been considered as directly influencing decline in sea urchins. However, the indirect influence of these parameters on algal communities (through reduction in grazing pressure) has not been considered.

For more than a century, ecologists have recognised the influence of temperature on geographical distribution of marine species where temperature tolerance of adults, in combination with critical temperatures required for successful spawning, can determine the range and distribution of marine populations (*sensu* Sewell & Young 1999). Cold temperature exposure, in particular, exhibits a negative influence at a number of trophic levels within a community, such as increased physiological stress in sessile species (Hirche et al. 1997; Sanford 2002) and reduction in predation efficiency (Sanford 1999). Whilst reduced recruitment and the ultimate decline in echinoid populations has been linked to cold temperature through mortality of adults (Beddingfield and McClintock 1994),

limited fertilization success (Sewell and Yound 1999) and inhibition of spawning (Barnes et al. 2001; Verling et al. 2005), the direct influence of temperature on post-settlement success of this important grazer has not been tested, specifically in temperate regions. Massive direct effects of release from herbivore pressure on algal biomass is well documented, however, the notion that cold temperature indirectly influences algal biomass, through grazer mortality and not just nutrient supply, has not been quantified. Such profound but indirect effects are often poorly understood and represented in marine ecological literature (Fairweather 1990).

I tested the hypothesis that temperature (e.g. cold water pulses) could reduce the survivorship of the sea urchin *Heliocidaris erythrogramma*, a consumer known to exert intense grazing pressure in some parts of temperate Australia (Connell and Vanderklift 2007; Wright et al. 2005). In addition, I conducted some preliminary tests of the hypothesis that cold water pulses exist within the Great Australian Bight, at Point AVOID. This region is characterised by upwelling of colder water during the Austral summer (Ward et al. 2006), and provides an environment experiencing pulsed water events that may affect sea urchins.

METHODS

Can pulsed water events reduce sea urchin survivorship?

Laboratory trials tested the effect of temperature (i.e. cold water pulses) on survivorship of newly-settled juvenile sea urchins. In order to test the effect of specific temperatures and periods of immersion of cold water pulsing, I based my laboratory manipulations on the pattern of temperature variation observed at Point Avoid. This pulsed regime was simulated in the aquarium, using a gravity-fed cold water system. Stored drums of cold water (6°C) were placed above the aquarium system such that when valves were opened, ambient water flow was replaced with cold water flow, at the same rate. Valves for the cold water drum were opened every 12 h to mimic the 10min packets of cold pulses experienced in the field at low tide (see below for temperature recording). Cohorts ($n=5$) of newly settled juveniles ($n = 100$) were either a) kept at 18°C or b) pulsed with 6°C seawater every twelve hours (at 0700 and 1900 daily) to simulate the return of the ebbing tide. It is important to note that in areas of high frequency coastal upwelling, transport of sea urchin larvae, and settlement from the water column may occur either (1) by the mechanism driving shoreward cold water intrusion (in this case, at low tide) or (2) with the incoming high tide. For this reason, two separate treatments were employed in the laboratory, based on frequency of pulsed water events at Point Avoid, where the initial cold water pulse commenced (1) 12 h post-settlement and (2) 6 h post-settlement. Each pulse lasted 10 minutes, mimicking the pattern observed in the field.

Survivorship of newly settled sea urchins was determined for both control and pulsed cohorts, following each pulse. Surviving urchins were easily recognised as settled on the bottom of each dish (following metamorphosis to the juvenile form). Individuals with abnormal metamorphosis had not settled and were, in most cases, floating. Only normally metamorphosed (normal appearance, not globular) individuals were counted as surviving (*sensu* Emlet and Hoegh-Guldberg, 1997). Control (not pulsed) and pulsed cohorts were subjected to 5 tidal cycles (60 h) (determined by the time at which survivorship remained constant for three consecutive pulses as above). Ambient seawater (18°C) flowed between pulses, and survivorship was quantified in each dish after each pulse. Three trials were conducted for 12h post-settlement pulse, however, the lack of reproductively active individuals limited the 6h experiment to one trial.

Survivorship of juvenile sea urchins was analysed using a two-way repeated measures ANOVA (pulse \times time, pooled trials for 12h experiment, $n = 3$). Data conformed to normality and homogeneity of variance (Cochran's C test). Post-hoc comparisons (SNK tests) tested for differences between control and pulsed cohorts for both 12h and 6h pulsed experiments.

Rearing juvenile Heliocidaris erythrogramma in the laboratory

Adult sea urchins were collected from shallow reefs (~1m depth) and maintained in flow-through tanks at the Lincoln Marine Science Centre. Culture methods were modified from Strathmann (1987). Spawning was induced by injection of

10ml 0.5 mol l⁻¹ KCl through the perioral membrane into the coelom. 0.2 ml of eggs (thoroughly rinsed in 0.2µm filtered seawater) from each of three females was fertilized with sperm from each of three males to maintain genetic diversity. Cultures were maintained at constant temperature (20°C) in 0.2µm filtered seawater. Juvenile settlement was induced at 84hrs post-fertilization (3.5 days) by adding crushed coralline algae to cultures.

Preliminary tests of the existence of cold water pulses in Great Australian Bight

Point Avoid in Southern Australia (35°61'S, 135°30'E) is situated within a region known to experience upwelling during the Austral summer (Ward et al. 2006) and characterised by an off-shore reef that divides the point. Temperature loggers (Stow-Away TidbitTM) were deployed at both north and south sites (depth ~ 1m), and temperature recorded at intervals of 2 minutes during the Austral summer (Dec – Feb 2003). Loggers were replaced every 30 days, and data downloaded using Boxcar^R for Windows software (Onset Computer Corp. version 3.51).

Effects of temperature variation in field conditions

Field trials tested survival of newly settled juvenile sea urchins at the north (ambient) and south (cold) sites at Point Avoid. Settlement pipes (150 x 40 mm PVC piping) were lined with 100x100 mm artificial turf (Balch and Scheibling 2000). Turf (10 x 10cm) was adhered to PVC using SikaFlex®-291 Marine Adhesive Sealant, left to dry overnight, then placed in flow-through aquarium to allow growth of a biofilm.

Fifteen sampling units were constructed on each side of the point, each 40 m from the low-tide mark (depth 0.5 -1.5m at low tide). Sampling units consisted of gutter guard fixed to permanent rock structures with cable ties, and placed within visual range of each other (2-4m). Each sampling unit housed one settlement pipe. To eliminate the possibility that transportation has a significant affect of juvenile survival, two controls ('control' and 'procedural control') were used and both housed in the laboratory aquarium. Control pipes tested the affect of the field environment on juvenile survival, whereas procedural control pipes tested the affect of handling and transportation (these were treated in the same manner as deployed pipes e.g. driven on rough roads and transported by foot on beaches before and after deployment).

Juveniles were reared following the same protocols as for laboratory trials. Immediately preceding induction of settlement, 150 juveniles were pipetted into each tube and covered with 110 mg/L calcein seawater for non-lethal, non-invasive florescent marking during re-capture analysis (Kaehler and McQuaid 1999; Mohler 1997) and capped. Pipes were stored submerged for 6 h in seawater at 20^oC, then transported to Point Avoid, in iced coolers, and deployed at low tide to the cold ($n = 15$) and temperate ($n = 15$) sites. Each pipe was uncapped underwater and secured horizontally to the sampling units. Once deployed, 10 mm x 10 mm mesh was attached to each end of the pipe and secured with cable ties, to prevent macropredation. Procedural controls ($n = 15$) were subjected to similar handling on return from Point Avoid (i.e. driving on dirt roads), and then deployed with control pipes ($n = 15$) in the aquarium.

Pipes were collected from Point AVOID on 6th Feb 2003 proceeding 5 tidal cycles (60h). Retrieval involved placement of the macropredation mesh inside the pipe and the ends capped. Pipes were transported back to the laboratory and stored in the control temperature room until rinsed. Each pipe was filled with 8% MgCl and left for 20 minutes, then vigorously rinsed with 30 L (3 × 10L rinses) of high velocity seawater. Samples were then sieved through 250µm sieves and fixed in 4% buffered formalin. The lack of reproductively active individuals and the short spawning season for this urchin limited the field experiment to one trial. Due to un-avoidable loss of pipes during a storm event, analysis was done using an un-balanced experimental design.

Samples were sorted under a dissecting microscope (× 10 obj), and all juvenile sea urchins removed. Juveniles were examined under an epifluorescence microscope for the calcein marker (excitation filter 495nm, emission 535nm), and compared to non-marked auto-fluorescing individuals. Marked and newly-recruited urchins were separated and a one-way ANOVA (site) used to analyse (1) survivorship of marked juveniles and (2) recruitment of un-marked juveniles at the cold and temperate sites. Data was transformed accordingly to satisfy the assumption of homogeneity of variance. One way ANOVA's tested the difference in both survivorship and recruitment of newly settled sea urchins between sites. Binomial sign test was used to test whether the probability of survivorship at the north site being higher than the south was greater than that occurring by chance (Underwood 1997), by permutating random ranks of paired data (n = 10 times) between north and south.

Throughout laboratory manipulations of juvenile sea urchins, mortality resulted in individuals no longer being settled, and retained free-floating in petri dishes. For the purposes of the field experiment, it was assumed mortality would result in a similar fate, and individuals would be washed away from experimental pipes with the flow of current and wave action. All individuals remaining within experimental pipes were therefore deemed either as survivors or new recruits.

Density of sea urchins at the site of temperature variation

At each site (south and north), I sampled the natural density of the dominant herbivore *Heliocidaris erythrogramma* along three transects (50m × 2m), separated by at least 15 m, at each site. Quadrats (1m², n = 8) were haphazardly placed along each transect, to a maximum depth of 3m, and number of adult urchins m² quantified. A two-factor ANOVA treated site as fixed and orthogonal and transect as random and nested (site). Pair-wise comparisons (SNK tests) were used to test for differences in adult urchin density between sites. Data was transformed appropriately to meet the assumption of homogeneity of variance (Cochran's *C* test, $p > 0.05$).

RESULTS

Survivorship of sea urchins pulsed with cold water

Survivorship of juvenile sea urchins pulsed 12-hours post settlement (mimicking recruitment with a pulsed water event) was significantly reduced in the laboratory by 25%, compared to controls (Fig. 4.1a, Table 4.1).

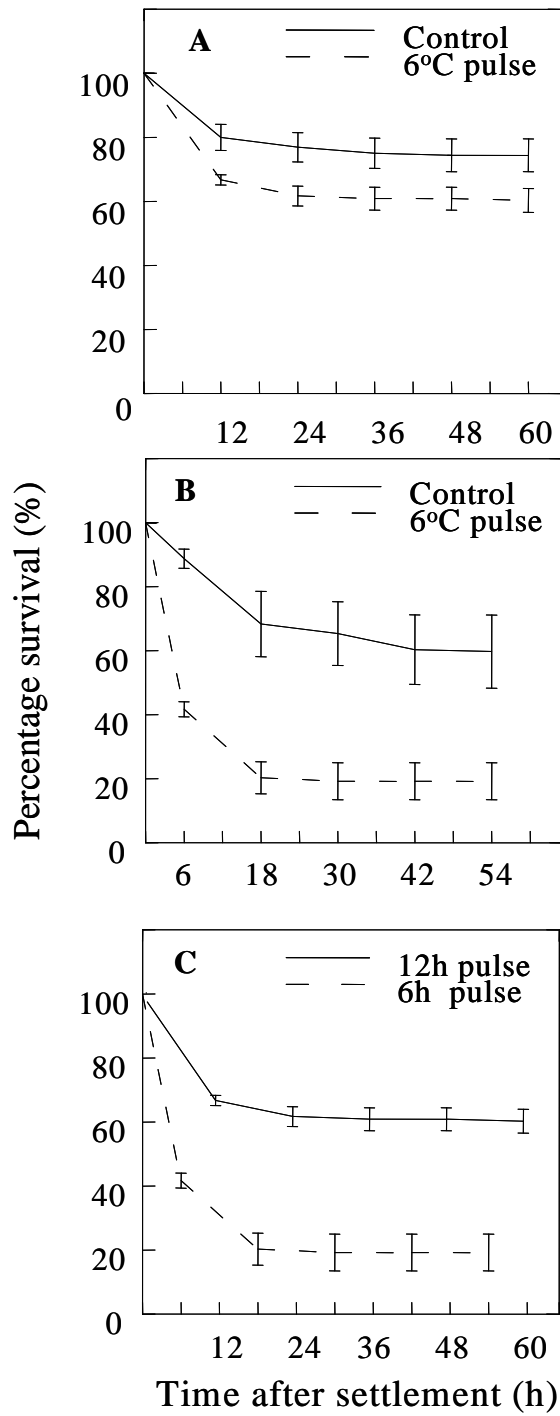


Figure 4.1 Mean survivorship ($n = 5$, \pm SE) of newly settled sea urchins, *Heliocidaris erythrogramma*, subjected to cold water pulses in aquarium conditions.

Table 4.1 (a) ANOVA testing for differences in mean survival of newly-settled sea urchins pulsed 12 h post-settlement in the laboratory and (b) post-hoc comparisons in terms of the main effect of pulse (pooled trials, $n = 3$). No pulse indicates ambient temperature (18°C) throughout the trial, pulse indicates cold water (6°C) pulse every 12h.

(a) Source	df	MS	F
Pulse (P)	1	7551.42	61.06**
Time (T)	4	181.21	1.47 ^{ns}
P x T	4	5.14	0.04 ^{ns}
Residual	140	123.67	

(b) Post-hoc comparisons	
Pulse	No pulse > pulse

Not significant (ns): ** $p < 0.01$

Table 4.2 (a) ANOVA testing for differences in mean survival of newly-settled sea urchins pulsed 6 h post-settlement in the laboratory and (b) post-hoc comparisons for the main effects of Pulse and Time (1 trial, $n = 5$ per time). No pulse indicates ambient temperature (18°C) throughout the trial, pulse indicates cold water (6°C) pulse every 12h.

(a) Source	df	MS	F
Pulse (P)	1	24822.59	109.43**
Time (T)	4	1166.85	5.14**
P x T	4	30.89	0.14 ^{ns}
Residual	40	226.84	

(b) Post-hoc comparisons	
Pulse	No pulse > Pulse
Time	6 > 18 > 30 = 42 = 54

Not significant (ns): ** $p < 0.01$

Pulses commenced (a) 12 h post-settlement (mean of three trials) and (b) 6 h post-settlement, and (c) comparison of sea urchins pulsed both 12h and 6h post-settlement. Sea urchins pulsed 6-hours post-settlement (mimicking recruitment at high tide) were also significantly effected by time and exposure to cold water pulses (Table 4.2), reducing survival by 70% when compared to non-pulsed juveniles (Fig. 4.1b). Post-hoc comparisons indicated that mean survivorship was significantly different between treatments, and decreased over the first 18h, after which remained constant within control and pulsed cohorts. Survivorship of newly settled sea urchins subjected to a 6°C pulse 6h post settlement is reduced up to 40% when compared to individuals pulsed 12h post settlement (Fig. 4.1c).

The existence of cold water pulses within the Great Australian Bight

Cold water pulses were observed in shallow subtidal waters at Point AVOID, where each site experiences differing temperature regimes. The south site experiences packets of short pulses of cold water on the ebbing tide, where temperature drops up to 10°C below ambient for a period of ten minutes. The north site has temperature profiles typical of temperate benthic communities, fluctuating between 14-19°C. Temperature anomalies occurred throughout the Austral summer (Dec-Feb 2003). The existence of these pulses, both in a region known to experience upwelling, and occurring at regular intervals (each tidal cycle) is a pattern of cold water intrusion typically associated with localised anomalies of upwelling (Leichter and Miller 1999). In order to enable visual differentiation of the temperature changes within hours, the first ten days of the summer profile have been graphically represented (Fig. 4.2)

Survivorship of sea urchins in field conditions

No differences were detected in recruitment or survivorship of sea urchins in the field between control and treatment controls. Similarly, recruitment of juvenile sea urchins was not significantly different between sites (Fig. 4.3a, Table 4.3a.). No difference in the survivorship of newly settled urchins was detected between sites. A second ANOVA testing survivorship between north and south Point Avoid only was conducted and indicated marginal non-significance (Table 4.3b, $p = 0.053$). Number of surviving urchins was ranked higher at the north site (mean = 7.2 indiv. \pm 1.4) than the south site (mean = 3.8 indiv. \pm 0.97) than expected by chance (Binomial sign test: $p = 0.02$) (Fig. 4.3b).

Density of sea urchins at the site of temperature variation

Density of *H. erythrogramma* was greater at the site of ambient temperature (north, Mean density = 0.875 ± 0.32 urchins m^{-2}) than the cold site (south, Mean density = 0 urchins m^{-2}) at Point Avoid (Table 4.4, Fig. 4.3a).

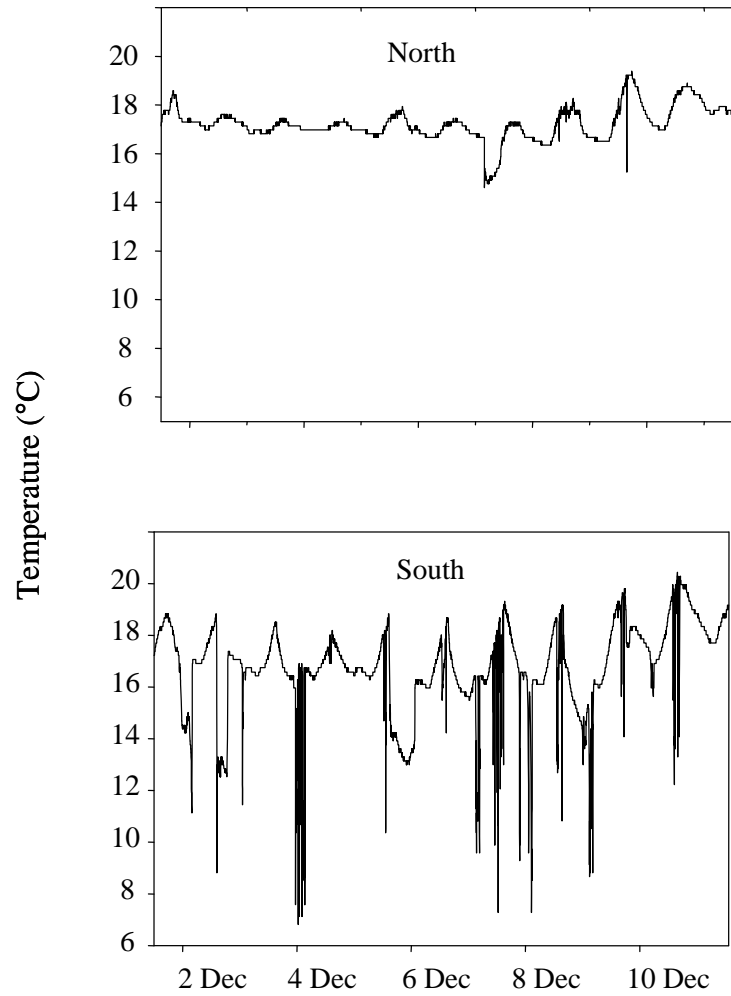


Figure 4.2 Field temperature regime at Point Avoid north (top) and south (bottom). Both sites have a baseline temperature of 15°C. Cold pulses occur at the South site every low tide, in packets of 2 or 3, lasting for 10 mins at a time, whereafter temperature returns to ambient.

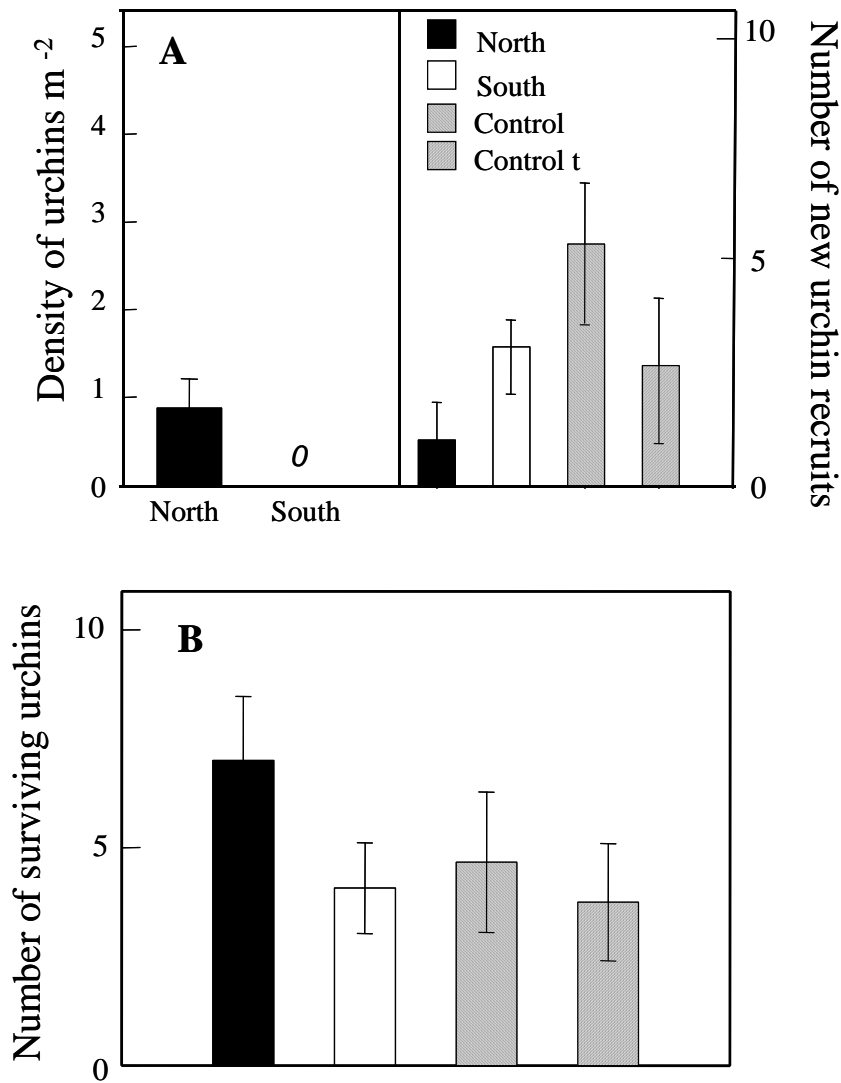


Figure 4.3 Mean number of *Heliocidaris erythrogramma* a) adults per m^2 and newly recruited individuals and b) surviving newly-settled individuals. New recruits and survivors were those in settlement pipes at Point AVOID ($n = 15 \pm SE$) ($10cm^2$ settlement substrate). Pipes were deployed for three days (exposed to 5 pulses). Control (t) indicates treatment control.

Table 4.3 ANOVA testing for differences in (a) mean recruitment (n=14) of newly-settled sea urchins at the north and south sites and (b) survival (n=14) of marked newly-settled sea urchins deployed at the north and south sites for 3.5 days (60h or five tidal cycles).

(a) Recruitment			
	df	MS	F
Site	1	4.321	0.262 ^{ns}
Residual	28	16.49	
(b) Survivorship			
Site	1	92.89	4.109*
Residual	28	22.61	
Sign test			
	Count	<i>P</i>	
North >South	11	0.02	
Not significant (ns): * $p = 0.053$			

Table 4.4 Analysis of variance (ANOVA) testing for differences in density of the dominant grazer, the sea urchin *Heliocidaris erythrogramma*, between north and south Point AVOID (per m⁻², $n = 24$) and (b) post-hoc comparison of the main effect of site.

(a) Source	df	MS	F
Site	1	2.0033	15.32*
Transect (site)	4	0.1307	0.69 ^{ns}
Residual	42	0.1907	

(b) Post-hoc comparison	
Site	South < North

Not significant (ns): * $p < 0.05$

DISCUSSION

I demonstrate that cold water pulses can have a direct negative effect on a habitat determiner (i.e. grazing urchins) by reducing survivorship of newly settled sea urchins by up to 70%. Understanding the effect of early post-settlement mortality of recruits is a fundamental aspect of ecological research as early life-history can influence spatial variation in benthic populations (e.g. Connell 1985, Gosselin & Qian 1997, Hunt & Scheibling 1997). These results show that the lack of adult sea urchins at the site of cold water pulsing may be the result of reduced recruitment of early post-settlement juveniles, due to high mortality.

Echinoid mortality outside that directly caused by mass-mortality (following disease outbreak, or uncommonly high temperature) has received minimal research (Verling et al. 2005). Evidence for the influence of regular, even predictable, physical disturbances has had little attention within the literature. Only two studies have examined the influence of prolonged lower sea surface temperatures on urchin mortality, where population decline is a result of recruitment failure linked to prolonged lower sea surface temperatures (Barnes et al. 2001; Verling et al. 2005). My study demonstrates that high frequency cold water pulsing can cause substantial mortality of a newly settled consumer. It therefore follows that sustained cold water intrusions could have a direct and continuing influence on populations densities of major algal consumers.

If factors affecting the juvenile abundance of herbivores (e.g. cold water) can alter the structure of echinoid populations (Barnes et al. 2001), they may indirectly

affect algal habitats. As sea urchins play a pivotal role in structuring benthic algal communities in many parts of the world, (e.g. Scheibling 1999, Jones & Andrew 1990, Guilliou et al. 2002), understanding sources and magnitude of such grazers have important implications for understanding variation in their influence on coastal ecosystems. Marine communities often exist in a mosaic of alternative states as a direct result of variation in grazing intensity (e.g. Konar & Estes 2003). For example, sea urchins often trigger a switch in temperate algal species, where foliose and canopy-forming algae is consumed and replaced by coralline algae or bare substrate (Hill et al. 2003; Wright et al. 2005).

The affect of cold water pulses on sea urchin mortality may have large-scale implications on ecosystems. Loss of kelp via destructive sea urchin grazing, and subsequent simplification of benthic habitats is associated with major changes in foraging activity of fishes (Jones and Andrew 1990) and associated coastal productivity (Scheibling et al. 1999). Understanding this interaction between macroalgae and the key herbivores of benthic systems is therefore important in the management of coastal areas and fisheries. Currently, disease is the only environmentally-induced mechanism documented for large scale transition from diverse algal assemblages to barrens via herbivore mortality (*sensu* Mumby et al. 2006).

While this study indicates that mortality of sea urchins as a consequence of exposure to cold water pulsing has the potential to impact at larger spatial and temporal scales, the field experiment is constrained by pseudoreplication (i.e. temperature treatments are not replicated). This brings some difficulty to the

interpretation of the results. Although survivorship differed between the two sites of variable temperature regimes, this difference cannot be conclusively separated from inherent site specific variation (e.g. Hurlbert 1984). This study would therefore benefit from replication at at least one other site impacted by frequent cool-water intrusion in order to differentiate between mortality as a consequence of cold water exposure, or simply the stochasticity of conditions experienced at a site (e.g. exposure, substrate, shelter) (Hurlbert 1984). Such replication, although necessary to substantiate interpretation of these results, would require substantial effort to locate a second site in which similar temperature regimes were a prominent physical feature. Nevertheless, it is recognised that this approach would complete an understanding of how the extent and magnitude of large temperature pulses is directly correlated with changes in benthic assemblages.

In conclusion, there is a relatively long history of study on the effects of urchin grazing in Australasia and throughout the world due to their key role in maintaining habitat heterogeneity. There has, therefore, been a substantial amount of research that assesses the factors that shape variation in the abundances of urchins, primarily their recruitment (Breitburg 1996; Scheibling et al. 1999; Wright and Steinberg 2001) and subsequent mortality (Ebert 1982; Gosselin and Chia 1995; Guillou et al. 2002). However, this study demonstrates the potential role of oceanographic processes (e.g. cold water pulses) to influence variation in population density of important grazers. If such oceanographic factors are strong and widespread, their potential to directly influence benthic habitats at local through to regional scales could have been underestimated. This chapter, therefore, is relatively pioneering, albeit preliminary, in that it provides

Australia's first link between oceanography and processes that can directly affect a habitat determiner, and potentially the habitats themselves.

CHAPTER FIVE: GENERAL DISCUSSION



CHAPTER FIVE

GENERAL DISCUSSION

A combination of both abiotic (i.e. climate, nutrient input, exposure) and biotic (e.g. predation, herbivory) disturbances shape the short-term and long-term dynamics of natural systems (Sousa 1980). Disturbance may be triggered by an obvious physical disturbance event (such as enhanced nutrients, exposure or temperature, Ch 2- 4), and counter-balanced by biotic feedbacks (e.g. competition and predation) that resist change (Scheffer et al. 2001). The aim of disturbance ecology is to predict the dynamics of disturbances and its impact on natural systems. Key to this aim is testing the independent and inter-dependent influences of biological and physical processes on the composition and structure of ecological patterns.

An ongoing challenge in disturbance ecology is matching patterns of disturbance to ecological patterns, simply understanding the combined effects of multiple processes may not lead to a predictive understanding of observed patterns (McArdle et al. 1997). Disturbance occurs across a range of scales in space and time, and, as such, it remains important to combine large and small-scale influences. For example, while large-scale physical processes can predict general patterns (e.g. Sanford 1999, Menge et al. 2003); localised biological processes such as herbivory and competition can emerge as important agents of heterogeneity in patterns that interact with large scale processes (Thrush et al. 1997). Hence, there is a need to understand the influence of disturbance across

several scales to improve the ability to generalise the impact of disturbance; a persistent challenge in ecology (Thrush et al. 2000).

This thesis provides quantitative evidence of the effects of varying agents of disturbance on changes and patterns of habitat structure and function (e.g. loss of key grazers, change in algal morphology; Chapters 2 - 4), the processes affected (e.g. recruitment, herbivory; Chapters 3 and 4) and interpretation of the ecological consequences of disturbance (i.e. resilience, recovery, stability; Chapters 2 - 4).

The effectiveness of measuring ecological impact with current methods: human-derived change

Detecting and forecasting ecological change not only requires research into understanding the agents of change (*hereafter* disturbances), but also the most effective methods to detect change. Understanding how pattern changes with scale of description is fundamental to the development of laws for simplification, aggregation and scaling (Levin 1992). A recurring issue concerns the choice of scale of variables used to describe ecological patterns and responses (e.g. molecules, species, functional groups, habitats) (Littler and Littler 1980; Padilla and Allen 2000; Steneck and Dethier 1994). In Chapter 2, I assessed how patterns caused by single and multiple disturbances change with scale and type of description using an experimental design common to experimental research. Previous work demonstrates that changes in the benthos already stressed by declining water quality (e.g. increased nutrients), may be exacerbated by the loss of grazers (e.g. Worm et al. 2000a, Russell and Connell 2005). While

observations of the benthos as morphological groups detected the effects of enhanced nutrients; species diversity (as a measure of phylogenetic relatedness) was the only measure sensitive enough to detect the interaction of top-down (i.e. loss of consumers) and bottom-up stressors (i.e. enhanced nutrients). Different types of costs and benefits are associated with different scales of observation (Connell, 2007b; Figure 14.1). Whilst recognising that smaller units provide greater resolution and detail, larger units of observation may provide the basis for which general patterns emerge. An unfortunate aspect of broader level taxonomic classifications is that they provide no species-specific information needed in some of the more successfully applied indices I used (Chapter 2). In this assessment, I recognise the costs of broader-level classifications, which is only being hastened by the downfall of the systematics marine algae in Australia (e.g. Entwisle and Huisman 1998).

Detecting patterns of community change with natural disturbance

The morphology of algae varies substantially and predictably across wave exposed gradients (Chapter 2). Indeed, wave exposure is commonly identified as the physical catalyst of natural morphological change (Blanchette et al. 2002; Hurd 2000). It is widely accepted that morphological adaptation translates to a competitive advantage in disturbed environments (e.g. Stewart 2004, Chapter 3), yet our understanding of the processes and patterns of morphology and wave exposure is based on species specific responses, particularly kelp (Fowler-Walker et al. 2006; Roberson and Coyer 2004; Wernberg and Thomson 2005). Rather than using an array of morphological descriptors (e.g. length, width, shape,

texture), few studies test the morphological response of an entire assemblage (Airoidi 2001) using coarse scale descriptive tools such as overall size. Substantial evidence demonstrates a size limitation for organisms inhabiting exposure shores (Denny 1999), and it stands to reason that this paradigm should transcend to algal assemblages. Results from Chapter 3 reveal that size of algal assemblages can describe the natural patterns of understory across gradients of exposure, where smaller algae inhabit high exposure, and large algae inhabit low exposure environments. Further, using manipulative transplant experiments, size of assemblages responded consistently to differences in exposure, potentially via morphological plasticity.

Species-specific responses to disturbance may be multi-directional and inherently “noisy” at a localised scale (e.g. Hay 1994; Chapter 2), where the use of coarser scale classifications may enable general patterns to emerge when using simple descriptive tools such as abundance (Chapter 2 & 3). Size has the potential to be used as a broad and predictive tool to identify generality in responses to hydrodynamic stressors, in contrast to the species dependent multi-directional response of a complex suite of morphological characters (Chapter 3). This is a useful tool if we are to better understand the fine through to large scale physical processes contributing to the establishment of ecological patterns.

While physical disturbance can result in a shift in assemblage structure via directly impacting bottom-up processes (Chapter 3), modification of top-down processes (e.g. herbivory) can also be pivotal in determining community structure and function (Wright et al. 2005). Substantial research has focused on the key

role of sea urchins (as a habitat determiner) in maintaining habitat heterogeneity (Guillou et al. 2002; Hill et al. 2003; Jones and Andrew 1990), however, the role of oceanographic disturbances (such as temperature) directly influencing this role remains little tested. Chapter 4 provides direct evidence of reduction in recruitment of the juvenile sea urchins, *Heliocidaris erythrogramma* by up to 70% when exposed to variable temperature regimes commonly found to occur in regions of upwelling. The majority of this mortality occurs within the first 12 hours of settlement, potentially eliminating recruitment of juveniles to sites that may experience continual pulses of variable temperature.

Physical features such as cold water upwelling are widespread (Leichter and Miller 1999; Pineda 1991; Roughgarden et al. 1991), and if recruitment can be directly removed from a system by such processes, their potential to influence benthic habitats across several spatial scales may have been dramatically underestimated. Top-down (herbivore removal) and bottom-up (nutrient flux) processes can interact to alter algal habitats (Chapter 2), therefore understanding the direct link between oceanography and herbivores is important in understanding the patterns of change in benthic habitats.

Very few natural mechanisms of change remain independent of human activity (Minchinton 2007), none more prevalent than the link between greenhouse warming and consequent slowing of ocean circulation and intensification of temperature contrasts (Bakun 1990). Given the potential influence of variable temperature regimes in structuring benthic communities (Chapter 4), the consequent shifts in communities may be compounded by human driven

disturbances. Unfortunately, as expressed by Paine et al. (1998), the possible synergistic interaction between human driven and natural disturbances remains merely an afterthought of modern ecological literature with little empirical testing.

Future directions

In Chapter 2, I assessed the effectiveness and validity of current methods for detecting ecosystem change to human-induced disturbances. A major step forward would be to understand how these methods and scales of description may be applied across different biogeographic provinces (e.g. Connell and Irving, in press) that exhibit ranges of nutrient concentrations (eg. comparison with eutrophic coastlines) and intensity of grazing (e.g. coasts with and without urchin barrens). If we can understand the result of increasing and decreasing the breadth of our taxonomic identities (i.e. where simplifications and complexities result) we may increase the integration of ecological observations and concepts across very different regions and ecologies of our planet.

These considerations have profound implications for management, particularly the need for information to understand the consequences of management action and inaction. For example, it is possible that different management strategies are required for different biological regions (i.e. biogeography) where the processes influencing change in communities may differ (Connell 2007b). Understanding the context dependency (i.e. biogeography) of ecological responses may assist local researchers understand the extent to which the phenomena they study are

representative of the broader biological region. Knowledge of regional patterns can reconcile a seemingly discordant series of local-observations because they can be related to a larger-scale pattern (e.g. Fowler-Walker et al. 2005). If most ecological research is set to continue to be done at local scales and favourite study places, integration of research across scales will be needed if we are to adequately inform management, a process itself which primarily operates at broad scales (Liu and Taylor 2002).

In Chapter 3 and 4, I demonstrated the change in benthic communities as a response to natural disturbances. My models involved the use of coarse scale classification of assemblages to predict responses to different levels of exposure would benefit from further investigation, again at a regional scale. It is at these scales that intra-species variation exists in morphological response to exposure, and it would be interesting to test the applicability of assemblage size, rather than specific morphological traits, as a morphological response across these environmental gradients.

In Chapter 4, I showed that oceanographic phenomena contributing to a stochastic physical environment may reduce recruitment to such a level as to decimate populations of herbivores. This represents a promising new avenue of research, as the link between physical oceanography and biological processes has only begun recently and has been little considered in the structuring of benthic communities (Witman et al. 2004). The interaction between regional scale oceanographic processes and habitat structure warrants further investigation at other sites experiencing documented influences such as upwelling, tidal bores and

temperature pulses. For example, in Eastern Australia, onshore upwelling during the warmer months is a well-known phenomenon among recreational and commercial SCUBA divers that is poorly recognised in benthic researchers of Australia. The potential for such a large scale phenomenon to combine with local processes (e.g. grazing) and shape extensive, but regionally constrained patterns is well recognised as a critical determinant of rates and patterns of ecological processes (Menge et al. 2003).

Conclusions

Linking the results of localised field experiments and observations to physical events that may shape entire communities at local and broader scales is a challenge that is likely to become addressed in greater vigour as global issues such as climate change gain traction with funding agencies. Spatial and temporal variation in the strength of disturbances is difficult to predict, particularly as they interact with local variation in physical and biological heterogeneity.

Nevertheless, embracing such variation will be critical before general conclusions regarding physical disturbances can be drawn (e.g. Helmuth et al. 2002).

Understanding the influence of disturbances with scale of organisation (e.g. molecules, physiology, species, populations, communities, ecosystems) seems a particularly important aspect of the multidisciplinary work that is required. I assessed how our perception of ecological response of disturbance may be contingent on the organisational scales and metrics used, however, it is apparent

that understanding the links between physiological responses of individuals and the ecological consequences (i.e. community patterns) is a promising direction. To anticipate the effects of disturbance, particularly climate on ecological phenomena, investment in responses from organism, to physiological (e.g. morphology, herbivory) and through to biogeographical (e.g. oceanographic phenomena) scales will be needed (Hughes 2000).

APPENDICES



APPENDIX A PERMISSION TO REPRODUCE PUBLISHED CHAPTER

Summary

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APPENDIX B CHAPTER APPENDICES

Appendix B documents the appendices referred to within Chapters 2 and 3.

APPENDIX B.1

Chapter 2

Papers reviewed were sourced from 14 journals between 1993 and 2006 inclusive. They included Marine Biology, Journal of Experimental Marine Biology and Ecology, Biological Bulletin, Aquatic Botany, Marine Ecology Progress Series, Journal of the Marine Biological Association of the United Kingdom, Journal of Phycology, Australian Journal of Marine and Freshwater Research, Estuarine Coast and Shelf Science, Aquaculture, Phycologia, Marine Pollution Bulletin, Journal of Planktonic Research and Journal of Sea Research. The search was limited to marine and freshwater research journals, using the keywords ‘field’ and ‘experiment’, and were selected if they used manipulative experiments to test assemblage responses.

APPENDIX B.2

Chapter 3

Papers reviewed were sourced from 18 journals (Annales Botanici Fennici, Aquatic Botany, Biological Bulletin, Botanica Marina, Ecological Monographs, Ecology, European Journal of Phycology, Journal of Experimental Biology, Journal of Experimental Marine Biology and Ecology, Journal of Marine Systems,

Journal of Phycology, Marine and Freshwater Research, Marine Biology, Marine Ecology Progress Series, New Zealand Journal of Marine and Freshwater Research, Phycologia, Sarsia, Transactions of the Royal Society of South Australia) between 1980 and 2006, inclusive. The search used the keywords alga, morphology and exposure. Ninety papers were found, 40 of which were relevant.

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