

THE ECOLOGY OF SUBTIDAL TURFS IN SOUTHERN AUSTRALIA



BAYDEN D. RUSSELL

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Dedication

I'd like to dedicate my thesis to Jarrod Stehbens, a great mate and all round great bloke. Much of the fieldwork in my Ph.D. was only possible because of Jarrod's willingness to help out, no matter what the conditions. I have never met anyone as capable in the field as Jarrod, and over our many months together he taught me more about the moods of the ocean and boating than I had learnt over years of fieldwork. Jarrod was tragically taken by a Great White Shark (*Carcharodon carcharias*) offshore from Adelaide at 3:57 pm on the 24th of August, 2005. Everyone who knew Jarrod misses him immensely.

The work contained within this thesis is my own, except where otherwise acknowledged. It contains no material previously published or written by another person, except where due reference is made.

There is no material within this thesis that has been accepted for the award of any other degree or diploma in any university.

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Bayden D. Russell
June 2005

Cover image: A gap that has formed in *Ecklonia radiata* canopy through natural removal. Turf-forming algae has already colonised much of the free space in the middle of the gap.
Photo in cover image: Andrew Irving.

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ABSTRACT

Assemblages of algae are altered by both bottom-up (e.g. nutrient availability) and top-down (e.g. herbivory) processes. As a result of the increasing human population in coastal areas, massive changes are forecast to benthic habitats in response to increasing coastal nutrient concentrations and a reduction in consumers. To identify the scales over which nutrients may have an effect, abundance of turf-forming algae growing as epiphytes on kelp (*Ecklonia radiata*) were related to water nutrient concentration across temperate Australia. In general, the percentage cover of epiphytes was greatest at sites with the greatest nutrient concentrations. By experimentally elevating mean nitrate concentration from the low $0.064 \pm 0.01 \mu\text{mol L}^{-1}$ to $0.121 \pm 0.04 \mu\text{mol L}^{-1}$, which was still only $\sim 5\%$ of that measured on a more eutrophic coast, I was able to increase the percentage cover of epiphytes to match those seen on nutrient rich coasts, despite not matching the nutrient concentrations on those coasts. Hence, it appears that the effects of elevated nutrients will be disproportionately large on relatively oligotrophic coasts.

Nutrient concentrations were also experimentally elevated to test whether the presence of an algal canopy or molluscan grazers were able to counter the effects of nutrient enrichment on algal assemblages. The loss of canopy-forming algae is likely to be a key precursor to nutrient driven changes of benthic habitats, because nutrients had no direct effect on algal assemblages in the presence of canopy-forming algae. In the absence of canopy-forming algae, space was quickly monopolised by turf-forming algae, but in the presence of elevated nutrients grazers were able to reduce the monopoly of turf-forming algae in favour of foliose algae. This switch in relative abundance of habitat may reflect greater consumption of nutrient rich turf-forming algae by grazers, possibly creating more space for other algae to colonise. Importantly, greater consumption of turf-forming algae in the presence of elevated nutrients may act as a mechanism to absorb the disproportionate effect of nutrients on oligotrophic coasts.

In southern Australia, canopy-forming algae have a negative impact on the abundance of turf-forming algae. To assess the mechanisms by which an algal

canopy may suppress turf-forming algae, abrasion by the canopy and water flow were experimentally reduced. Abrasion by the canopy reduced the percentage cover and biomass of turf-forming algae. In contrast to predictions, biomass and percentage cover of turf-forming algae were also reduced when water flow was reduced. Light intensity was substantially reduced when there was less water flow (because of reduced movement in algal canopy). However, the reduction in available light (shading) did not account for all of the observed reduction in biomass and percentage cover of turf-forming algae, suggesting that other factors are modified by water flow and may contribute to the loss of turf-forming algae.

Habitat loss and fragmentation are well known to affect the diversity and abundance of fauna in habitat patches. I used experimental habitats to assess how fragmentation of turf habitats affects the diversity and abundance of two taxa of macroinvertebrates with different dispersal abilities. I established that increased isolation of habitats reduced the species richness and abundance of invertebrates with slow rates of dispersal, while the species richness and abundance of invertebrates with fast rates of dispersal were greatest in habitats that were far apart.

In summary, this thesis provides an insight into some of the impacts associated with human populations in coastal areas, namely increased nutrient inputs, loss of grazers (e.g. harvesting), and loss of canopy algae and fragmentation of habitats. I show that increased nutrient concentrations in coastal waters can alter the relative abundance of algal species, and that some effects of elevated nutrients can be absorbed by the presence of grazers. I also show that elevated nutrients have no effect on algal assemblage in the presence of canopy-forming algae, and that canopies can suppress the colonisation of turf-forming algae. Finally, I show that the fragmentation of turf habitats affects taxa of invertebrates with different dispersal abilities in different ways. Whilst the contemporary ecology of much of the temperate Australian subtidal coast is considered to be relatively unaffected by human activity, this thesis shows that changes to top-down and bottom-up processes could have large consequences for habitats and their inhabitants.

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CHAPTER TWO

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CHAPTER ONE



GENERAL INTRODUCTION

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GENERAL INTRODUCTION

Disturbance has long been recognised as an integral part of ecosystems (Watt 1947; Pickett & White 1985). The frequency and magnitude of disturbances is thought to play a central role in determining community structure and the organisms that dominate particular ecosystems (Connell 1978; Petraitis et al. 1989). The ability of organisms to recover from different disturbances is also thought to determine, in part, the diversity and functioning of different systems (Gunderson & Pritchard 2002). Many natural disturbances are irregular and short in duration, and organisms are able to either resist or take advantage of disturbances, allowing communities to recover to their original state. As the world's population increases, however, there is an increasing trend for broad-scale, severe anthropogenic disturbances from which systems may not easily recover (Hughes et al. 2005).

As with disturbances, bottom-up (e.g. nutrient inputs) and top-down (e.g. predation and herbivory) processes were thought to structure communities. In the 1960's, top-down processes were proposed as the main processes that determine terrestrial communities (Hariston et al. 1960). It was later recognised, that the strength of top-down processes is possibly in response to the productivity of a system, which is controlled by bottom-up processes (Fretwell 1977, 1987). For many years, marine systems were thought to be structured by top-down processes, and that bottom-up processes had less effect (Menge 1992). More recent work has found that systems are often controlled by both processes, and that top-down processes tend to alter the effects of bottom-up processes (see review by Menge 2000). Recently, however, it has also been realised that both top-down and bottom-up processes are likely to be altered by human impacts, and the effects of altering these processes on marine systems needs to be better understood (Vitousek et al. 1997a; Vitousek et al. 1997b; Dayton et al. 1998; Tegner & Dayton 2000).

Anthropogenic disturbances are likely to alter bottom-up and top-down processes, and include the input of nutrients into coastal waters, harvesting of marine resources, and loss of habitat forming algae. Nutrient inputs can be point-source (e.g. sewage outfall: Littler & Murray 1975) or non point-source (see review by Carpenter et al. 1998). Point-source inputs are often short in duration and localised in their effect (e.g. storm runoff), whereas non point-source inputs tend to modify habitat in aquatic systems over broad scales (i.e. 100s to 1000s kms) (Vitousek et al. 1997a, b; Carpenter et al. 1998; Eriksson et al. 2002). Nutrient inputs across broad scales can adversely affect entire ecosystems (Duarte 1995; Eriksson et al. 2002), hence, understanding the relationship between nutrient concentrations and particular effects from local through regional scales may not only identify locations most likely to be affected by nutrients, but also allow us to forecast their effects across coasts where human populations are to expand and become more dense.

Harvesting of animals can have large effects on marine ecosystems and can cause large changes to benthic habitats (Tegner & Dayton 2000). In systems that have strong top-down control, for example, harvesting large predators can release predation pressure on herbivores, causing increased herbivory and a subsequent reduction in the abundance of the major habitat forming plants and algae (Estes & Duggins 1995; Silliman & Bertness 2002; Lafferty 2004). Such trophic cascades can cause a switch from habitats dominated by canopy algae to barrens (see reviews by Tegner & Dayton 2000 and Hughes et al. 2005). When harvesting is stopped, often through the use of protected areas, systems can revert to their original state (e.g. Shears & Babcock 2002). Direct harvesting of herbivores is also of concern, because herbivores may counter the effects of increasing coastal nutrients (Lotze et al. 2001; Hillebrand 2003), and loss of herbivores may reduce their ability to absorb the negative effects of increasing nutrient concentrations in coastal waters (Scheffer & Carpenter 2003). It is currently unclear, however, if consumption by herbivores in bottom-up controlled systems (i.e. systems with weak consumer pressure) is sufficient to absorb the effects of elevated nutrients.

Harvesting of marine animals may also affect non-target species and the habitat itself. For example, trawl harvesting can reduce the abundance and diversity of non-

target species (Kaiser 1998), such as a reduction in mollusc diversity within a scallop fishery (Edgar & Samson 2004). Trawl fisheries may also have direct impacts on the habitat structure, by removing the major algal habitat (Dayton et al. 1998). Loss of habitat often causes changes to assemblages of algae and fauna (e.g. Duggins et al. 1990; Benedetti-Cecchi et al. 2001; Vanderklift & Jacoby 2003; Edgar et al. 2004; Jenkins et al. 2004), and recovery of the disturbed area can take several years (Christie et al. 1998). The time that it takes for fauna to recolonise areas where canopies have been removed can depend on the dispersal rate of the fauna and the distance from the nearest undamaged habitat (Waage-Nielsen et al. 2003).

Large, canopy-forming algae, such as kelp, are often the major habitat forming algae on temperate coasts (Reed & Foster 1984; Christie et al. 1998), particularly in Australia (Goodsell et al. 2004; Irving et al. 2004b). Predictable associations exist between canopies of algae and the benthic understory (Kennelly & Underwood 1993; Bertness & Leonard 1997; Bertness et al. 1999; Bruno 2000; Bulleri et al. 2002; Irving et al. 2004b). These associations are maintained by the canopy-forming algae, and can be both positive (Bertness et al. 1999; Irving et al. 2004a) and negative (Kennelly 1989; Connell 2003b). When the algal canopy is lost, such as through storm damage, a new set of taxa often colonises and alters the covers of algae (Reed & Foster 1984; Kennelly 1987b, c). In Australia, fast growing, opportunistic species, such as filamentous turf-forming algae, are often suppressed by the presence of canopies (Kennelly 1987b; Kennelly & Underwood 1993), but dominate newly created space (Kennelly 1987b; Melville & Connell 2001). There is, however, an increasing trend for long-term intergenerational and perhaps permanent loss of canopy forming algae to occur along human-impacted coasts (Jackson 2001; Eriksson et al. 2002) as a consequence of nutrient enrichment (Worm et al. 1999). The trend towards long-term loss of canopies of algae is worrisome, because intergenerational loss of diversity may change perception of what is the “natural” state of communities, making detection of future human impacts difficult (Dayton et al. 1998).

On temperate coasts, increasing nutrient loading often favours small, fast-growing and opportunistic algae at the expense of slower growing and longer-lived algae that

form canopies (Worm et al. 1999). Filamentous algae have a physiology that is suited to rapid uptake of nutrients and rapid growth (Hein et al. 1995) and have total biomass turnover in 4 – 12 days (Carpenter 1985). These algae are often ephemeral, occupying all available space during the warmer seasons but losing biomass and cover with a decrease in productivity associated with reduced day length (i.e. reduced time for photosynthesis) (Copertino et al. 2005). In contrast, canopy-forming algae tend to be perennial, store nutrients in their tissue and have much slower growth rates (Jackson 1977; Bolton & Anderson 1994; Lobban & Harrison 1994). This difference in physiology often means that filamentous algae are able to rapidly respond to any source of elevated nutrients and occupy available space before canopy-forming algae. Furthermore, turf-forming algae tend to accumulate sediment between the filaments (Airoldi & Cinelli 1997) which can inhibit the recruitment of canopy algae (Kennelly 1987a), leading to long-term habitat switches.

Disturbances, such as nutrient inputs, can be short (pulse) or long (press) in duration. The effects that these two different durations of disturbance will have, or the response of organisms to the disturbance, can differ, and are often harder to distinguish (Glasby & Underwood 1996). For example, nutrient input may be quite short in duration, but cause a “press”, or long-term response. A single pulse of nutrients can increase the abundance of filamentous epiphytes, but not enhance the growth of the host (Worm & Sommer 2000). As events such as storm water runoff are often pulse events, but can be relatively frequent, such disturbances may increase the abundance of opportunistic algae without increasing the growth rate of canopy algae. On many temperate coasts of the world, there seems to be a loss of canopy-forming algae, in favour of turf-forming algae that has been attributed to increasing nutrient concentrations in coastal waters (Worm et al. 1999). Such switches in habitats are becoming more common globally (Scheffer & Carpenter 2003; Hughes et al. 2005) and can be considered a “press” response. Globally, these “habitat switches” from the dominant habitat to turf habitats seem to be long-term (e.g. Hughes 1994; Eriksson et al. 2002; Nilsson et al. 2004). If habitats are to revert to more desirable states, such as the re-establishment of canopies, a mechanism that removes algal turfs may be required, such as grazing by herbivores.

Choice of food by herbivores is complex, and can be based on food morphology, digestibility, or nutrient content (Nicotri 1980; Jensen 1983; Watanabe 1984; Norton et al. 1990; Kennish & Williams 1997). However, grazers often consume greater biomass of plants and algae that are higher in nitrogen content (Neckles et al. 1993; Williams & Ruckelshaus 1993; Karez et al. 2000; Silliman & Zieman 2001).

Furthermore, many herbivores preferentially consume filamentous algae (Jensen 1983; Williams & Ruckelshaus 1993; Hillebrand et al. 2000; Hillebrand & Kahlert 2001; Karez et al. 2004; but see Karez et al. 2000), the algae most likely to respond quickly to elevated nutrients. By consuming algae that is most likely to respond to elevated nutrients, herbivores can counter the effects of nutrient enrichment on algal habitats (Neckles et al. 1993; Hillebrand et al. 2000; Roll et al. 2005). Furthermore, as fast growing, opportunistic algae often have physiologies that allow the rapid uptake of available nutrients (Hein et al. 1995), grazers are likely to preferentially consume these algae soon after eutrophication events, possibly constraining outbreaks of fast growing algae (Roll et al. 2005) and reducing the possibility of long-term habitat switches being caused by short-term nutrient enrichment.

Most of the best-studied coasts of the world exist under strong consumer (grazer) control and their benthic habitats are probably able to moderate nutrient enrichment on macroalgal habitats. Over harvesting of large predators on these coasts is probably the primary concern, because of loss of algae through increasing urchin abundance (Estes & Duggins 1995; Steneck et al. 2002). However, there are large expanses of coastline, such as South Australia and Western Australia, which appear to be largely unaffected by grazing (Fowler-Walker & Connell 2002). Sparse densities of herbivores that “scrape” algae off the rock (i.e. completely remove algae) in southern Australia (Fowler-Walker & Connell 2002; Vanderklift & Kendrick 2004) compared to eastern Australia (Fletcher 1987; Andrew & Underwood 1993) and other parts of the world (Norton et al. 1990; Scheibling et al. 1999; Villouta et al. 2001) may, in part, explain this weaker grazing pressure. The interactive effects of nutrients and grazers on coasts with few grazers are not well understood, and these coasts would seem to be most vulnerable to increases in nutrient concentration because of a lack of functional groups able to remove opportunistic algae. Currently, however, there is little information to challenge or support this model.

With the increase in human populations in coastal areas, there is concern that human impacts will increase the frequency at which benthic habitats switch from more to less desirable habitats, such as the switch from canopy-forming to turf-forming algae. In this thesis, I present research that investigates factors that may contribute to, or counter these switches. My research focused on four main areas:

1. The scale over which coastal nutrient concentrations vary in southern Australia, and how the concentration of nutrients in the water affects the abundance of epiphytic algae (Chapter 2);
2. How nutrients and algal canopy, and nutrients and grazing, interact to determine the relative abundance of benthic algae (Chapters 3 & 4);
3. The effects of abrasion by algal canopies and water flow on the colonisation of turf-forming algae (Chapter 5); and
4. The effect of fragmentation of turf habitats on macroinvertebrate assemblage, species richness and abundance (Chapter 6).

Throughout this thesis, I attempt to maintain a logical progression of ideas, but each chapter is written as a separate paper and, as such, can be read independently. The objectives of individual chapters are as follows:

Chapter 2

Algal assemblages can vary over the same scale as the physical processes that form them, a pattern which seems to be true for epiphytic algae (Vanderklift & Lavery 2000; Lavery & Vanderklift 2002; Rindi & Guiry 2004). In Chapter 2, I compare the abundance of turf-forming algae growing as epiphytes on kelp (*Ecklonia radiata*) to the concentration of nutrients over multiple nested spatial scales, to identify whether there is a relationship between epiphyte abundance and nutrient concentration. The results conformed to my general model (i.e. positive correlation between nutrients and epiphytes), hence, I then assessed this relationship experimentally, by testing whether elevated nutrient concentrations increased epiphyte cover on an oligotrophic coast to match covers of epiphytes on nutrient rich coasts.

Chapter 3

In southern Australia, turf-forming algae and foliose algae dominate space (95% cover) in the absence of canopy-forming algae (Fowler-Walker & Connell 2002; Irving et al. 2004b), and turf-forming algae are the first to colonise space that is created with the loss of canopies of kelp (Melville & Connell 2001). Switches from canopy to turf dominated habitats on human dominated coasts are considered to be, in part, a response to increasing nutrient concentrations (Worm et al. 1999). In Chapter 3, I test whether (i) the presence of an algal canopy can counter the effects of nutrient enrichment on algal assemblages and (ii) molluscan grazers can counter the effects of elevated nutrients in the absence of canopies.

Chapter 4

Grazing by herbivores can counter the effects of elevated nutrients through consumption of greater biomass of nutrient rich plants and algae (Neckles et al. 1993; Williams & Ruckelshaus 1993; Karez et al. 2000; Silliman & Zieman 2001). Increased consumption of algae in the presence of elevated nutrients may be able to counter blooms of turf-forming algae (Roll et al. 2005), and be an important mechanism in absorbing the effects of nutrients on human-dominated coasts. In Chapter 4, I assess whether herbivorous molluscs will consume more turf-forming algae in the presence of elevated nutrients, and if this increased consumption creates more space, possibly leading to changes in relative algal abundance (as observed in Chapter 3).

Chapter 5

On human dominated coasts, there is an increase in habitat switches from those dominated by canopy-forming algae to turf-forming algae (Jackson 2001; Eriksson et al. 2002; Copertino et al. 2005). In South Australia, turf-forming algae dominates space in the absence of canopies (Fowler-Walker & Connell 2002; Irving et al. 2004b), but canopies seem able to suppress the colonisation of turf-forming algae, and remove turf-forming algae that has colonised. In Chapter 5, I identify the mechanisms that suppress the colonisation of turf-forming algae.

Chapter 6

Loss of habitat and habitat fragmentation have negative impacts on faunal assemblages, species richness and population size (see review by Fahrig 2003). The degree to which populations in neighbouring habitats interact depends on many factors, including individual habitat size (Anderson 1998; Fleishman et al. 2002), amount of habitat in a landscape (Delin & Andr n 1999; Lee et al. 2002; Fahrig 2003) and distance to other habitats (Golden & Crist 1999; Lomolino & Perault 2001; Fleishman et al. 2002). The degree to which these factors affect populations may also depend on the mobility of taxa, and the mode of adult dispersal. In Chapter 6, I used experimental turfs to investigate the effects of size of neighbouring habitat, and distance to it, on species richness and abundance of macroinvertebrates with contrasting dispersal abilities.

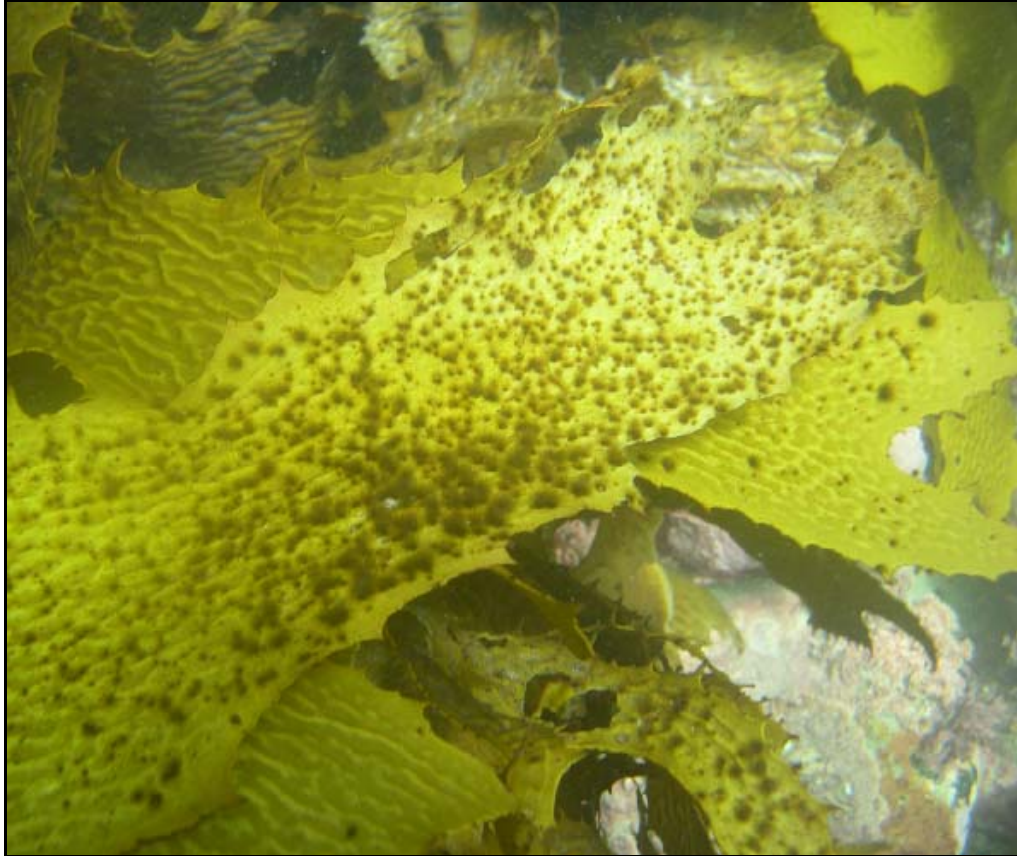
Chapter 7

In Chapter 7, I provide brief discussion of the preceding chapters, how they are linked and discuss directions for future research.

Notes on chapter style

Each chapter in this thesis (chapters 2 – 6) presents original data, and has been written in a style suitable for publication in scientific journals. As such, they can be read as individual papers, but as a collective, they form a thesis. Where possible I have attempted to maintain the logical progression of ideas. All tables and figures are embedded within the text of the relevant chapter, but literature cited in chapters is provided in a separate section at the end of the thesis, not at the end of each chapter.

Each chapter is preceded by a preamble that describes the content of the chapter and how this relates to other chapters, information on the publication status at the time of thesis submission (where applicable), and the contributions of the co-authors (where relevant).



Turf-forming algae growing as epiphytes on the laterals of *Ecklonia radiata*.
Photo: Andrew Irving.

CHAPTER TWO



NUTRIENTS INCREASE EPIPHYTE LOADS: BROAD SCALE OBSERVATIONS AND AN EXPERIMENTAL ASSESSMENT

CHAPTER TWO PREAMBLE

Chapter two investigates the relationship between water nutrient concentrations and the cover of epiphytes on kelp over broad scales (the temperate coast of Australia). Patterns that were observed were then experimentally assessed at a field site in South Australia by elevating nutrient concentrations.

This chapter is a co-authored paper in press in *Marine Biology*, and as such is written in plural throughout. It is included with permission of Springer Science and Business Media (see Appendix A). The paper can be cited as:

Russell B.D., Elsdon T.S., Gillanders B.M. and Connell S.D. 2005. Nutrients increase epiphyte loads: broad scale patterns and an experimental assessment. *Marine Biology* **147**: 551-558.

In this paper Bronwyn Gillanders and Sean Connell supplied funding and had input into the development of ideas relating to broad-scale sampling. Travis Elsdon assisted with the broad scale sampling and helped with acquisition of the chlorophyll images. I set up and ran the nutrient experiment, acquired and analysed chlorophyll images, did the data analysis and wrote the paper.

Signatures of co-authors:

Signed:

Travis S. Elsdon

Signed:

Bronwyn M. Gillanders

Signed:

Sean D. Connell

NUTRIENTS INCREASE EPIPHYTE LOADS: BROAD SCALE OBSERVATIONS AND AN EXPERIMENTAL ASSESSMENT

2.1 ABSTRACT

There is a global trend towards elevated nutrients in coastal waters, especially on human-dominated coasts. We assessed local to regional scale relationships between the abundance of epiphytic algae on kelp (*Ecklonia radiata*) and nutrient concentrations across much of the temperate coast of Australia, thus, assessing the spatial scales over which nutrients may affect benthic assemblages. We tested the hypotheses that (1) percentage cover of epiphytic algae would be greater in areas with higher water nutrient concentrations, and (2) that an experimental enhancement of nutrient concentrations on an oligotrophic coast, to match more eutrophic coasts, would cause an increase in percentage cover of epiphytic algae to match those in more nutrient rich waters. Percentage cover of epiphytes was most extensive around the coast of Sydney, the study location with the greatest concentration of coastal chlorophyll *a* (a proxy for water nutrient concentration). Elevation of nitrate concentrations at a South Australian location caused an increase in percentage cover of epiphytes that was comparable to percentage covers observed around Sydney's coastline. This result was achieved despite our inability to match nutrient concentrations observed around Sydney (< 5 % of Sydney concentrations), suggesting that increases to nutrient concentrations may have disproportionately larger effects in oligotrophic waters.

2.2 INTRODUCTION

Enhancement of nutrients in coastal waters is likely to cause large changes to benthic assemblages, such as a shift from slow growing macroalgae to fast growing turf-forming algae (Pedersen & Borum 1996; Worm et al. 1999; Gorgula & Connell 2004). Nutrient inputs can be point-source (e.g. sewage outfall: Littler and Murray 1975) and non-point source (see review by Carpenter et al. 1998), modifying habitat in aquatic systems over large scales (i.e. 100s to 1000s kms) (Vitousek et al. 1997a;

Carpenter et al. 1998; Eriksson et al. 2002). Nutrient inputs across large scales can adversely affect entire ecosystems (Duarte 1995; Eriksson et al. 2002), hence, understanding the relationship between nutrient concentrations and ecosystem effects from local through regional scales may not only identify areas of interest, but also place these patterns within their regional context.

Enhanced nutrient concentrations have strong positive effects on assemblages of fine filamentous algae that comprise ‘turfs’ (Gorgula & Connell 2004), which appear to be favoured on human-dominated coasts because their life-history and physiology are better suited to nutrient overloading (Hein et al. 1995; Pedersen & Borum 1996). Assemblages of turf-forming algae can respond to seemingly minor physical differences in substratum (Irving & Connell 2002). We chose to compare percentage cover of turf-forming algae on the most comparable substratum we could find, the laminae of *Ecklonia radiata* sourced from stands of similar age and density. The canopy-forming alga *Ecklonia radiata* is common and extensively distributed across temperate Australia (Fowler-Walker & Connell 2002; Goodsell et al. 2004). These stands form predictable associations with the benthos (Connell 2003a; Irving et al. 2004b) and represent a common habitat on which to base regional comparisons of benthic algae.

Perennial epiphytes on seagrass and macroalgae are often more abundant on the older portions of the host (Whittick 1983; Borowitzka & Lethbridge 1989). Kelp grows upwards from the meristem (located near the bottom of the stipe); thus, laterals at the top of each individual are the oldest (Kain 1963; Bolton & Anderson 1994). From this algal growth pattern, the upper part of individual kelp would be most likely to have greatest cover of epiphytes. Vertical gradients of perennial epiphyte abundance on kelp stipes exist (Whittick 1983), but it is not known whether such a gradient exists on the laterals of kelp. In contrast, a gradient may not exist with ephemeral epiphytes, such as turf-forming algae, because these epiphytes will not accumulate across years, as occurs with perennial epiphytes (Whittick 1983). Furthermore, it is unknown whether gradients of epiphyte abundance are altered by the concentration of nutrients in the water.

We assessed local to regional scale relationships between the abundance of epiphytic algae on kelp (*Ecklonia radiata*) and chlorophyll *a* (proxy for nutrient concentrations) across much of the temperate coast of Australia, to assess the locations and spatial scales over which nutrients may affect benthic assemblages. While *E. radiata* and their epiphytic turfs appear ideally suited for detecting spatial scales and localities likely to be affected by elevated nutrients, we acknowledge that any perceived relationship constitutes a correlation and may be explained by a host of alternate models. Hence, we took the additional step and directly tested the hypothesis that if we elevated nutrient concentrations in an oligotrophic system to match the most eutrophic system, the percentage cover of turfs in the nutrient poor system would increase to match those observed in the nutrient rich system.

2.3 MATERIALS AND METHODS

Regional epiphyte data

Percentage cover of turf-forming algae growing as epiphytes on *Ecklonia radiata* was quantified across temperate Australia in the Austral summer of 2001/2002. Sampling was constrained to the latitudinal limits of 33°37'S – 37°06'S so as not to be strongly influenced by latitudinal gradients. Sampling was done at hierarchical nested spatial scales of regions, locations, and sites; regions were separated by 1000s of kilometres, locations (within regions) separated by 100s of kms, and sites (within locations) separated by 1 – 10 km (Figure 2.1). Within each site, replicate *E. radiata* separated by 1 – 10 m ($n = 5$) were collected from approximately 3 – 10 m depth. Percentage cover of epiphytic turf-forming algae was quantified on the laterals of *E. radiata* at three heights from the holdfast (bottom, middle and top). Laterals on the lower half of the algae represent the “bottom”. The remainder of the algae was then divided in half again and defined as “middle” and “top” relative to the algal holdfast. Percentage cover of epiphytic turf-forming algae was estimated for the point of attachment to *E. radiata* within a 10 mm × 10 mm quadrat haphazardly placed within each lateral height ($n = 5$).

Coastal chlorophyll concentrations

A positive correlation can exist between water nutrient concentration and chlorophyll *a* concentrations in the water column (Evgenidou & Valiela 2002; Nedwell et al.

2002; Nielsen et al. 2002; Muslim & Jones 2003). We obtained a remotely sensed SeaWiFS satellite chlorophyll *a* image, spanning temperate Australia, from the Australian CSIRO Remote Sensing Facility. All satellite passes over the region during January 2002 were formed into a single monthly composite image. The month of January was selected, because it represented conditions half way through the regional sampling. The image spanned all regions and was analysed at a resolution of 1 km pixels. Study sites could not be accurately plotted on the image, thus, chlorophyll *a* concentrations were quantified for 10 pixels spanning across all sample sites at each location, and taken as a mean chlorophyll *a* concentration ($\mu\text{g L}^{-1}$) for each location.

Experimental manipulation of nutrients

The effect of elevated nutrients on turf-forming algae growing on *E. radiata* was experimentally tested at West Island, South Australia (35°36'S, 138°35'E), by comparing *E. radiata* from experimental reefs with different nutrient treatments (ambient *v.* elevated; $n = 5$ / treatment). Nutrient concentrations were manipulated on experimental reefs from December 2002 to March 2003 (Austral summer). Percentage cover of turf-forming algae on *E. radiata* was quantified at the peak of summer (beginning of March 2003), to avoid confounding effects of algal senescence with the onset of cooler water temperatures and shorter days (Worm et al. 2002). *E. radiata* was collected and percentage cover of turf-forming algae quantified using the same method as for the regional scale study.

Experimental reefs were made from metal frames on a concrete base (60 × 60 cm) set on sand and separated from the natural reef. Boulders were collected from the natural reef and placed on each experimental reef in November 2002, before the experiment commenced. Boulders were selected so that *E. radiata* were on experimental reefs in natural densities (9 – 11 m^{-2}).

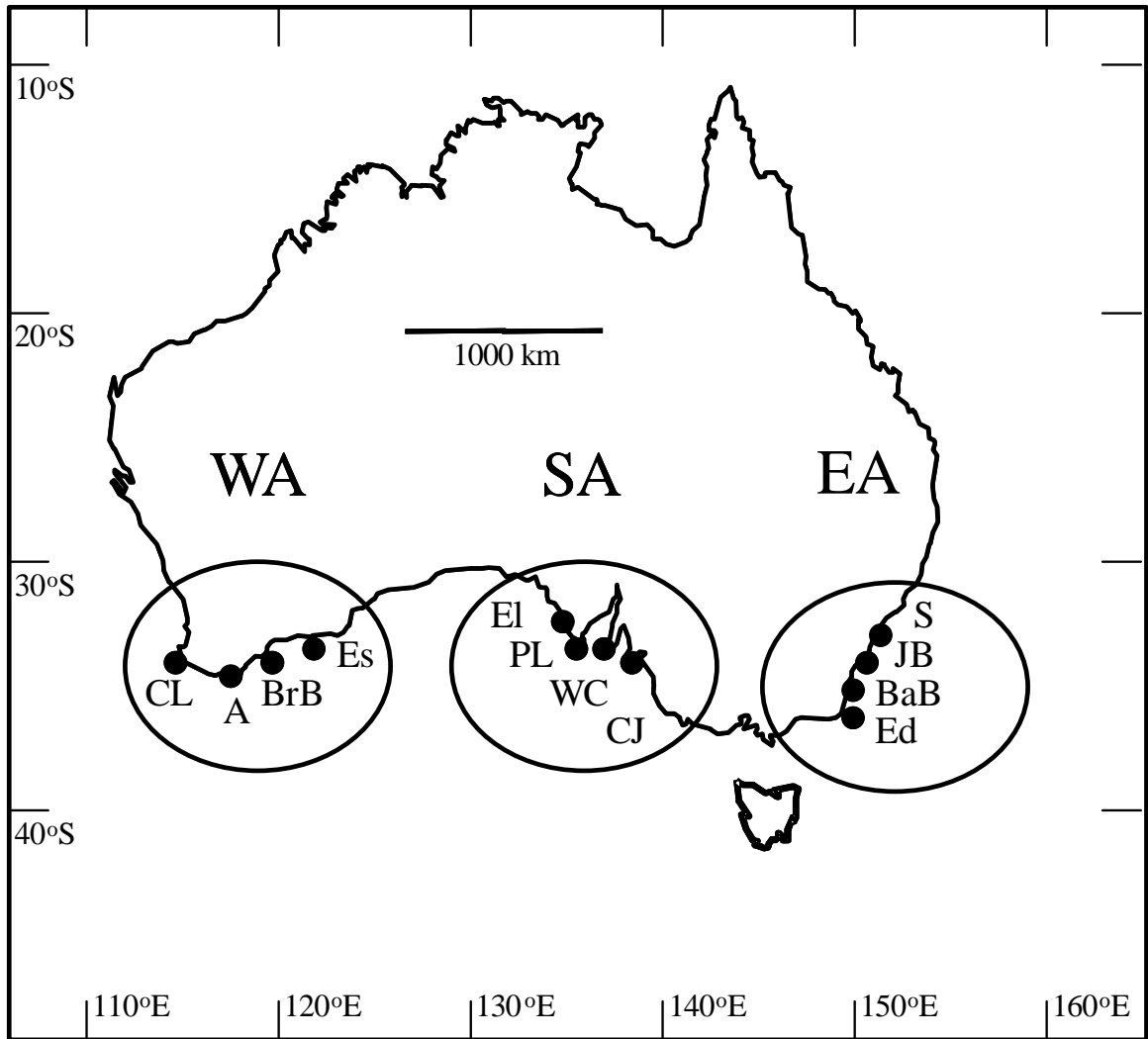


Figure 2.1 Map showing the locations sampled within regions across southern Australia. Regions: WA = western Australia, SA = southern Australia, EA = eastern Australia. Locations: CL = Cape Leeuwin, A = Albany, BrB = Bremer Bay, Es = Esperance, El = Elliston, PL = Port Lincoln, WC = West Cape, CJ = Cape Jervis, Ed = Eden, BaB = Batemans Bay, JB = Jervis Bay, and S = Sydney.

Treatments of elevated nutrients were manipulated by the addition of 12 g of Osmocote Plus[®] slow release fertilizer per nutrient reef (6 month release: 15,5,10 N-P-K). Nutrients were supplied in four nylon mesh bags (1 mm mesh size) filled with Osmocote[®] pellets and attached to stakes on the reef corners at the beginning of the experiment. Bags containing nutrient pellets were replaced every two months to ensure a continuous supply of nutrients; this approach has been tested and suggested to be the most appropriate method of elevating nutrients in subtidal experiments (Worm et al. 2000b) and has been successfully used in a previous experiment at the study site (Chapter 3). Control reefs were identical, without the addition of nutrients. Experimental reefs were separated by at least 5 m to ensure treatments were independent.

Water samples were collected at the end of February 2003 to ascertain whether nutrients were supplied at elevated concentrations on the experimental reefs. To test whether the nutrient treatments on neighbouring reefs were independent, water samples were taken from nutrient elevated reefs, their closest ambient (control) reef, as well as distant to all reefs (ambient water column nutrients) ($n = 4$). Samples were collected in 120 ml vials 10 cm above the experimental boulders. Ambient water column samples were taken at the same height above the natural substratum. On returning to the surface, all samples were filtered through 0.45 μm filters and frozen. Samples were sent to the Australian Water Quality Centre (South Australia) for analysis. It was assumed that if nutrient concentrations on control reefs did not differ from ambient water column concentrations, then nutrients were not flowing from elevated reefs to control reefs.

Analyses

The mensurative hypothesis was tested using a four-factor ANOVA; factors: region, location (nested within region), site (nested within region and location), and height on *E. radiata* (orthogonal). Region and height were treated as fixed factors, and site and location as random. Arc-sine transformation was used to reduce heterogeneity in the data, but variance remained heterogeneous, so significance was judged at the more conservative $\alpha = 0.01$ (Underwood 1997).

The experimental hypothesis was tested in two steps. First, a two-factor ANOVA tested for differences in percentage cover of epiphytes between nutrient concentrations (ambient *v.* elevated) among the three heights on the algae (bottom *v.* middle *v.* top). Both factors were fixed and orthogonal. Again, arc-sine transformation was used to reduce heterogeneity in the data, but variance remained heterogeneous, so significance was judged at $\alpha = 0.01$. Second, a two-factor ANOVA tested the extent to which percentage cover of epiphytes in treatments of elevated nutrients matched the covers observed around Sydney. Because replication differed between the mensurative and manipulative experimental designs, we compared the mean percentage cover of epiphytes at each of the four Sydney sites (i.e. sites were used as replicate samples) with the experimental responses (replicate samples were randomly reduced from 5 to 4 by deleting one replicate). Arc-sine transformation was successfully used to reduce heterogeneity in the data, and significance judged at $\alpha = 0.05$.

2.4 RESULTS

The turf-forming algae quantified had similar morphology, as identification to species requires examination of specimens under microscopes (which was impossible in field conditions). All turf-forming algae quantified were filamentous brown algae that grew in mats, generally to a vertical height of ≤ 20 mm. In South Australia, these algae were primarily composed of *Feldmannia lebelli* and *F. globifera*, which were morphologically similar to the turf-forming algae in WA and EA.

In southern Australia (SA) and western Australia (WA) the percentage cover of epiphytic turf-forming algae did not differ with lateral height on *E. radiata*, but turf-forming algae in eastern Australia (EA) showed different patterns, according to proximity to Sydney (Figure 2.2, Table 2.1; significant height \times location interaction; SNK tests). In EA, there were no differences among heights at the most distant location from Sydney (Eden), whereas at the two closer locations (Batemans Bay and Jervis Bay) the percentage cover was greater at the top and middle than bottom. At the Sydney location, the percentage cover of epiphytic algae was greatest on the top laterals and showed a clear gradient to the bottom laterals (top > middle > bottom). Percentage cover of epiphytic algae was more extensive in Sydney than all other

locations in EA, SA, and WA (Figure 2.2, Table 2.1) and no differences were observed among locations in SA and WA. In locations with higher water nutrient concentrations (see next paragraph) there was greater percentage cover of turf-forming algae on the top laterals of *E. radiata*. There was also higher variability in cover of epiphytes at locations with increasing water nutrient concentrations, causing significant site and location terms (Table 2.1).

There was a positive correlation between chlorophyll *a* concentration in the water column and mean percentage cover of epiphytic algae at locations ($r = 0.96$, $P < 0.001$; Figure 2.3). This correlation was partly driven by the Sydney location, and even though the relationship was non significant ($r = 0.58$, $P = 0.06$) when Sydney was removed from the analysis, there was still a positive trend. When SA was removed from the analysis, there was a strong correlation between chlorophyll *a* concentration and percentage cover of epiphytic algae ($r = 0.89$, $P = 0.007$). In EA, there was a north to south decrease in chlorophyll concentration. Chlorophyll *a* concentration was higher at Sydney than Jervis Bay, Batemans Bay, and Eden, and was > 3 times higher than all locations in SA and WA.

Table 2.1 Results of four-factor ANOVA testing differences in percentage cover of turf-forming algae growing as epiphytes at different heights on *Ecklonia radiata* laterals among regions, locations and sites within Australia. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability.

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Region	2	6064.98	3.79	NS
Location (Region)	9	1600.56	7.32	***
Site (Region × Location)	36	218.72	5.08	***
Height	2	718.73	5.41	NS
Region × Height	4	325.02	2.44	NS
Height × Location (Region)	18	132.94	2.64	**
Height × Site (Region × Location)	72	50.35	1.17	NS
Residual	576	43.03		

NS not significant ($P > 0.01$), ** $P < 0.005$, *** $P < 0.0001$. Arc-sine transformation was used to reduce heterogeneity in the data, but variance remained heterogeneous, so significance was judged at $\alpha = 0.01$ (Underwood 1997).

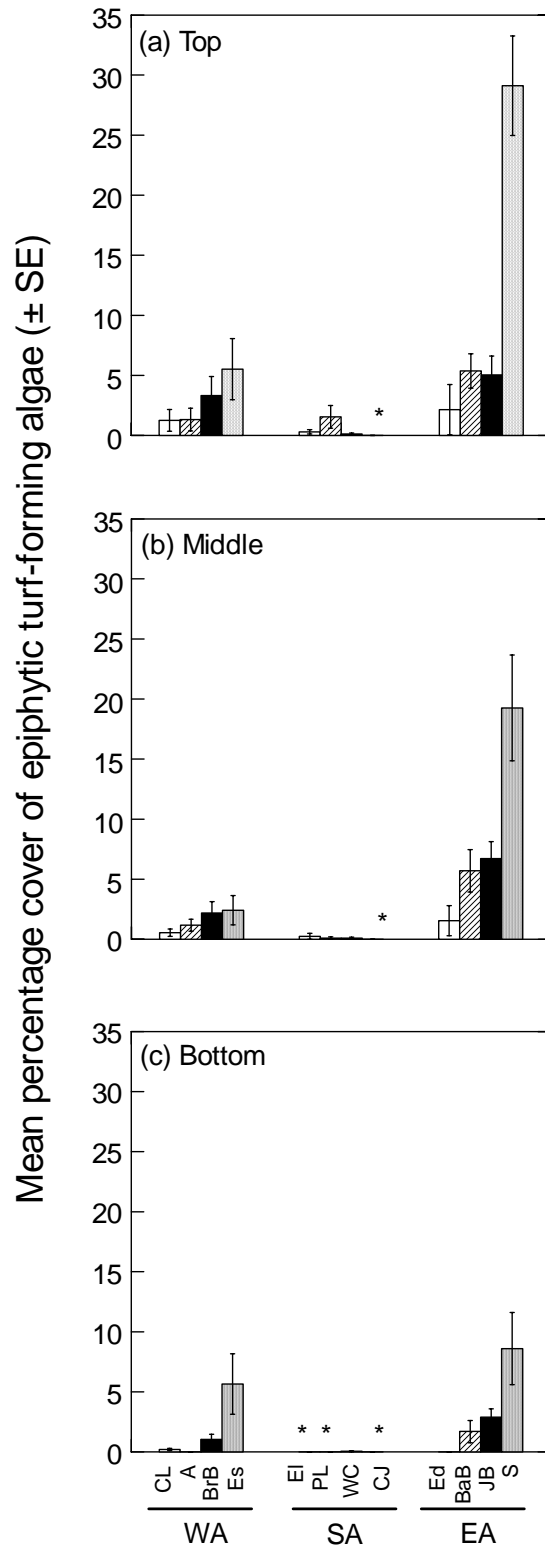


Figure 2.2 The percentage cover of turf-forming algae growing as epiphytes on (a) top, (b) middle and (c) bottom laterals of *E. radiata* across regions and locations (mean \pm SE). For region and location abbreviations see Figure 2.1. * = 0 % cover.

Experimental conditions created nitrate concentrations that were approximately 89 % higher on nutrient elevated (mean $0.121 \pm 0.04 \mu\text{mol L}^{-1}$) than ambient (mean $0.064 \pm 0.01 \mu\text{mol L}^{-1}$; ANOVA: $F_{2,5} = 16.78$, $P < 0.03$) reefs. Student Newman Keuls (SNK) comparison of means demonstrated that nitrate levels differed between elevated and ambient water samples, but did not differ between ambient nutrient reefs and water column samples, indicating that nutrients from elevated reefs were not detectable on control reefs, so the distance between experimental reefs was great enough that elevated and control reefs were independent of each other. Phosphate levels did not differ between ambient ($0.19 \pm 0.005 \mu\text{mol L}^{-1}$) and nutrient elevated reefs ($0.19 \pm 0.01 \mu\text{mol L}^{-1}$; ANOVA: $F_{2,5} = 3.1$, $P > 0.15$). The failure to detect enriched phosphorus is likely due to filtering of water samples, which removes most of the ionic phosphorus. The failure to detect elevated phosphate concentrations is not considered a problem because nitrogen, not phosphorus, is generally considered the nutrient limiting algal growth in marine waters (Hecky & Kilham 1988; Carpenter et al. 1998; Hodgkiss & Lu 2004).

Percentage cover of epiphytic algae was greater on *E. radiata* exposed to elevated nutrient concentrations than on those exposed to ambient concentrations of water nutrients (Figure 2.4, Table 2.2a). SNK comparison of means showed that percentage covers of epiphytic algae on *E. radiata* exposed to elevated nutrients did not differ from those observed on *E. radiata* around Sydney (Figure 2.4; Table 2.2b). Height on *E. radiata* also had a significant effect on the percentage cover of epiphytic algae, but there was no significant interaction with nutrient treatment (Figure 2.4; Table 2.2b).

Table 2.2 Results of a two-way ANOVAs testing the effects of experimental elevation of nutrients on the percentage cover of turf-forming algae growing as epiphytes at different heights on *Ecklonia radiata* laterals, (a) all experimental reefs compared (ambient *v.* elevated; $n = 5$ / treatment) and, (b) comparison of experimental reefs with Sydney (ambient *v.* elevated *v.* Sydney; $n = 4$ / treatment). Differences in replication ((a) *v.* (b)) reflect differences in mensurative and manipulative experimental designs (see Methods).

(a) Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Nutrient	1	6087.69	28.75	***
Height	2	196.59	0.93	NS
N × H	2	74.45	0.35	NS
Residual	24	211.76		

NS not significant ($P > 0.01$), *** $P < 0.0001$. Arc-sine transformation was used to reduce heterogeneity in the data, but variance remained heterogeneous, so significance was judged at $\alpha = 0.01$ (Underwood 1997).

(b) Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Nutrient	2	1671.98	11.16	**
Height	2	542.02	3.62	*
N × H	4	76.10	0.51	NS
Residual	27	149.76		

NS not significant ($P > 0.05$), * $P < 0.05$, ** $P < 0.001$. Arc-sine transformation was used to reduce heterogeneity in the data (Underwood 1997).

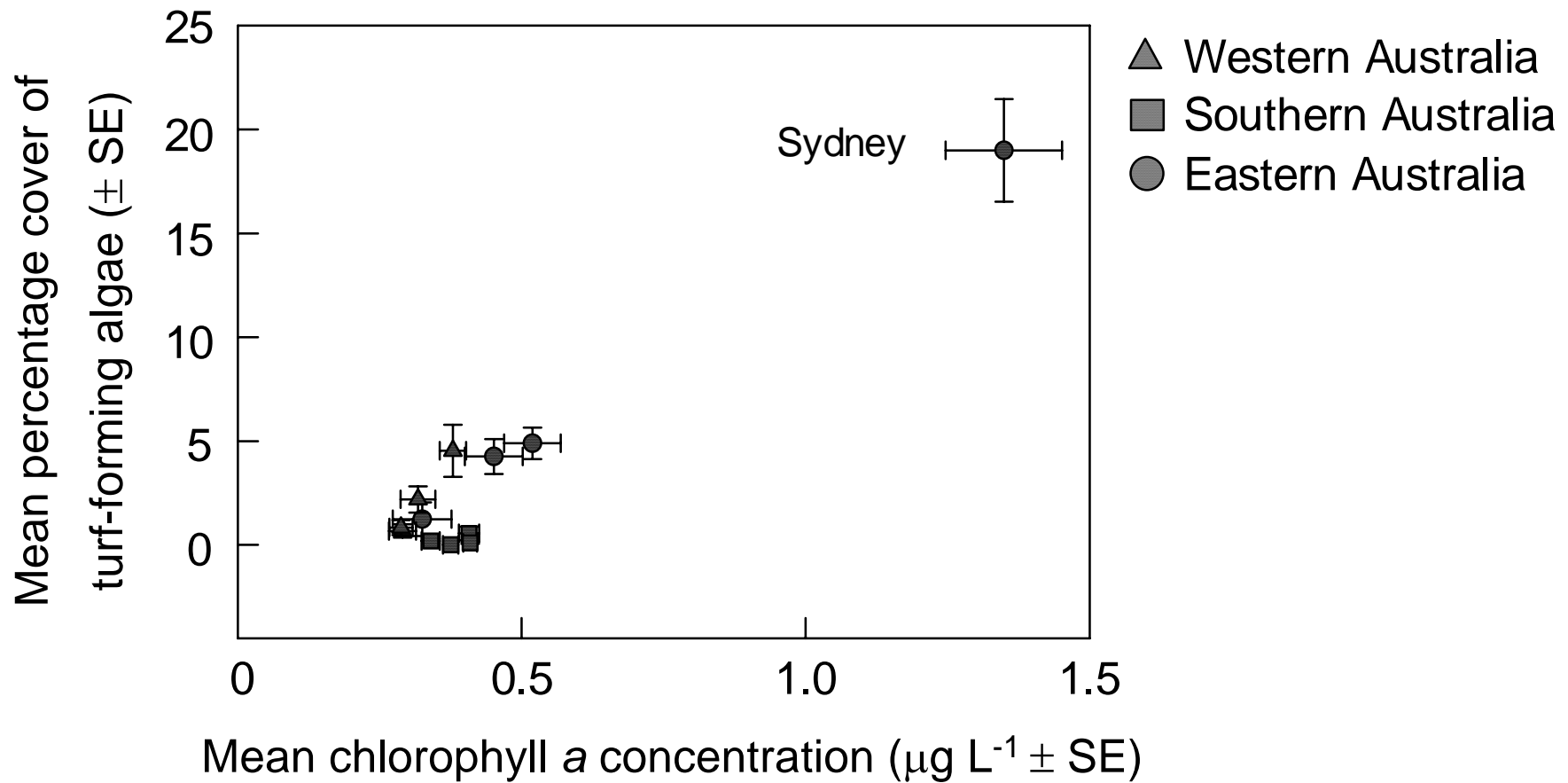


Figure 2.3 The relationship between concentration of chlorophyll *a* (mean \pm SE) and percentage cover of turf-forming algae (mean \pm SE) growing as epiphytes on *E. radiata* at all sampling locations across temperate Australia.

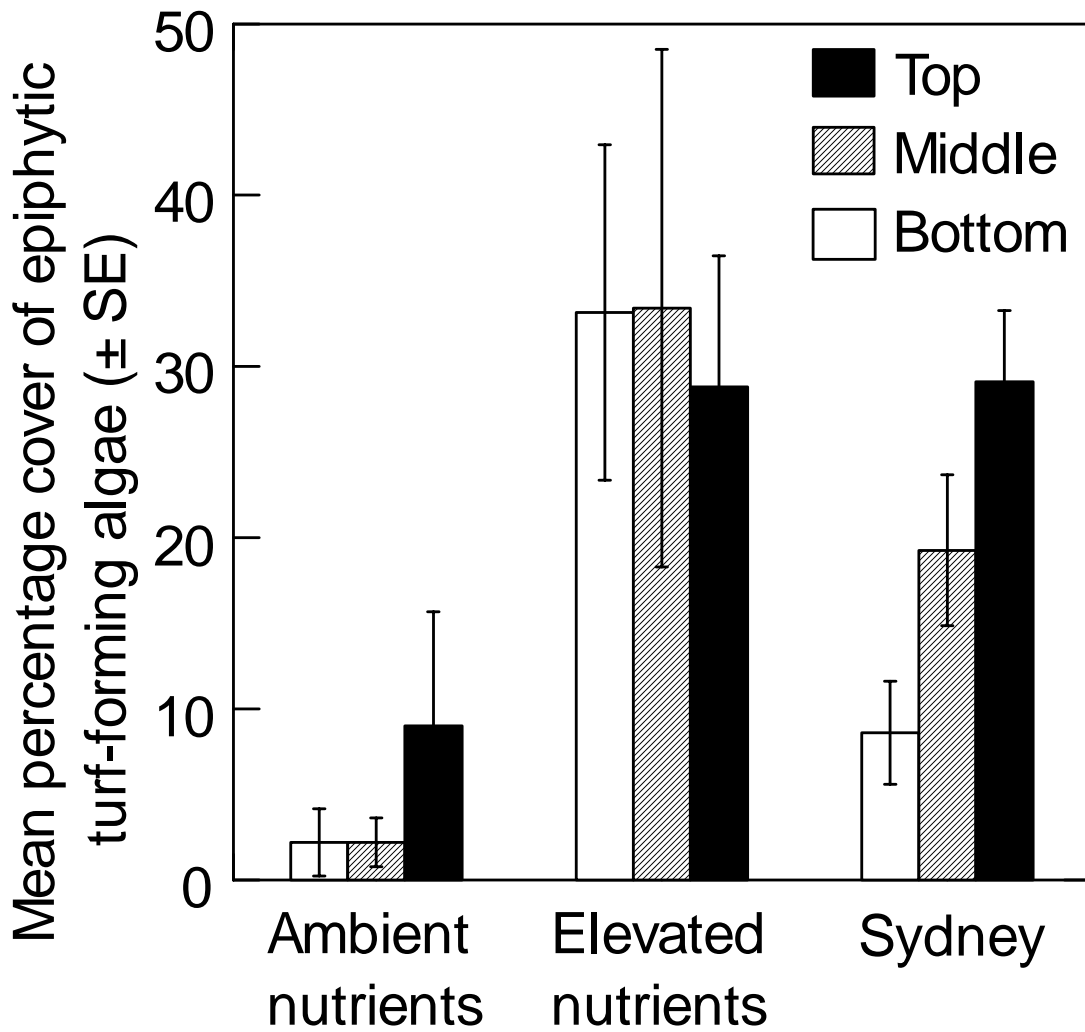


Figure 2.4 The effect of nutrients (ambient v. elevated) on the percentage cover of turf-forming algae growing as epiphytes on the top, middle, and bottom laterals of *E. radiata*, compared to natural percentage cover at Sydney.

2.5 DISCUSSION

Local through broad scale observations are fundamental to identifying localities and scales of patterns and the processes underlying them. Little information is currently available on the scales at which abundance of epiphytes vary. A key finding of this study was that the cover of epiphytic algae on *E. radiata* did not differ between southern Australia and western Australia. Importantly, the percentage cover of epiphytic algae in eastern Australia tended to increase from south to north, with covers at the Sydney location being greater than all other locations across temperate Australia, indicating that epiphyte covers can vary over scales of 100s kms.

Abundance of epiphytes on seagrass and some macroalgae has been shown to vary on the scale of kms, which is the scale of variation of physical environmental gradients (Lavery & Vanderklift 2002; Rindi & Guiry 2004). In this study, there was variation in cover among sites (kms) but the greatest differences were seen among locations (100s kms). Importantly, it is over this larger scale that we detected large differences in the concentration of ambient chlorophyll *a*.

The pattern of chlorophyll concentrations showed a positive relationship with the percentage cover of epiphytic algae. Chlorophyll concentrations were greatest at the Sydney location, which also showed the highest cover of epiphytic algae. Although chlorophyll *a* concentrations may not directly relate to the concentration of nutrients available to turf-forming algae (because of nutrient use by phytoplankton), a separate broad-scale study in 2004 showed ambient water nutrient concentrations above the substrate were higher in Sydney than in locations of comparable latitude in South Australia and Western Australia (mean \pm SE; Sydney 3.8 ± 0.89 ; SA 0.26 ± 0.036 ; WA $0.59 \pm 0.091 \mu\text{mol L}^{-1}$; Connell, S.D. unpubl. data). As turf-forming algae can benefit from increased nutrient levels (Rönnerberg et al. 1992; Hein et al. 1995; Worm et al. 2000a), we suggest that the greater nutrient concentrations observed around Sydney cause the greater covers of epiphytic algae observed in that location.

At most locations in this study there was no pattern in the vertical distribution of turf-forming algae on *E. radiata* laterals. However, in EA locations with the highest chlorophyll *a* concentrations, an increase in cover of turf-forming algae with increasing height on *E. radiata* was found. It is unknown why higher nutrient levels

should cause this vertical pattern. It is unlikely that there is an increase in the cover of epiphytes with age of the host, because the turf-forming algae are ephemeral and not likely to increase biomass across years. Epiphytes have been shown to preferentially settle at specific sites on the host, such as wounded parts (Pearson & Evans 1990) and the apices of seagrass, possibly because the apices receive the most sunlight (Borowitzka & Lethbridge 1989). It is possible that with increased nutrients epiphytes show an increase in photosynthetic productivity and either settle or survive in greater abundance on the upper laterals of *E. radiata*, causing a change in the vertical distribution. The pattern in vertical distribution of epiphytes also seems to vary, depending on the host. Perennial epiphytes can show greater abundances on the older parts of kelp stipes (Whittick 1983) and seagrasses (Borowitzka & Lethbridge 1989). However, no pattern of zonation was observed in a study of the epiphytes of fucoid algae (*Cystoseira* spp.: Belegreatis et al. 1990).

Our experimental enhancement of nutrient concentrations under field conditions resulted in an increase in the percentage cover of epiphytic algae, which was comparable to the covers observed at Sydney. Elevated water nitrate concentrations in this experiment were approximately 80 % greater than ambient water concentrations. Ambient nitrate concentrations were higher in Sydney than locations of comparable latitude in South Australia and Western Australia (Connell, S.D. unpubl. data, see previous paragraph). Mean nitrate concentration at a Sydney site in January 2000 (records were unavailable for 2002) was $3.36 \pm 1.6 \mu\text{mol L}^{-1}$ (CSIRO Port Hacking record station), indicating that the elevated concentrations used in this experiment were < 4 % of the ambient concentrations recorded at Sydney in January 2000 and 2004. Even with this relatively low concentration of nutrients, we were able to achieve covers of epiphytic algae similar to those recorded at the Sydney location. This disproportionate response to increased nutrients may be a function of nutrient limitation (Neckles et al. 1993; Hein et al. 1995; Karez et al. 2004) and level of response may be greater when in nutrient limited waters. As the growth response of epiphytes is not proportional to the increase in nutrients (Duarte 1995), response of epiphytes in oligotrophic waters (such as South Australia: Gorgula and Connell 2004; Chapter 3) is likely to be greater than in waters with higher nutrient concentrations (such as Sydney and other human dominated coasts). Therefore,

nutrient inputs on oligotrophic coasts may have larger effects than on coasts with high ambient nutrient concentrations (such as regions of seasonal nutrient upwelling), or coasts already impacted by human nutrient inputs (e.g. Western Baltic: Worm et al. 2000a).

Although anthropogenic nutrient inputs surrounding Sydney are large (e.g. 9.2×10^8 L d⁻¹ of sewage discharged at Port Hacking; Dela-Cruz et al. 2003), there is some seasonal upwelling in summer that cannot be dismissed as a source of nutrients (Gibbs 2000; Oke & Middleton 2001; Roughan & Middleton 2002). This wind driven upwelling is localised in extent (Pritchard et al. 2003), and is not associated with major upwelling caused by the East Australia Current, which splits off from the coast at about 32° S (compared to Sydney at ~ 34° S; Gibbs 2000). During upwelling events, sewage and estuarine nutrients make up only ~ 10 % of the total water nutrients (Pritchard et al. 2003). However, sources of nutrients are difficult to separate, possibly because of variability in hydrological conditions and difficulty in determining chemical signatures (e.g. Dela-Cruz et al. 2003). Thus, phytoplankton blooms and chlorophyll *a* concentrations in the Sydney region can be caused by anthropogenic (i.e. sewage outfall, Dela-Cruz et al. 2003), estuarine (Dela-Cruz et al. 2003), and upwelling nutrients (Dela-Cruz et al. 2002). It seems likely that because upwelling events can be short lived (McClellan-Padman & Padman 1991), anthropogenic and estuarine sources of nutrients are important, especially during the non-upwelling season (Pritchard et al. 2003), but more study is needed.

Eutrophication has been proposed as a cause of greater epiphyte abundance and biomass on developed coasts (Philippart 1995; Wear et al. 1999) and near point-source nutrient enriched areas, such as fish farms (Rönnerberg et al. 1992). Increased epiphytic cover may adversely affect health of host algae and seagrasses through reduced photosynthesis (e.g. Sand-Jensen 1977) and incidental consumption of host tissue by increased grazing on epiphytes (Williams & Ruckelshaus 1993; Karez et al. 2000). This reduction in the health of the host algae and plant has been shown for kelp (Scheibling et al. 1999), furoid macroalgae (D'Antonio 1985; Karez et al. 2000; Worm & Sommer 2000), and seagrass (Sand-Jensen 1977; Sand-Jensen et al. 1985).

Much of our knowledge about the ecology of *E. radiata* is from eastern Australia (see Irving et al. 2004b for a review of published studies), especially from sites close to and around Sydney. However, there is increasing evidence that generalisations based on information from this area may not be directly applicable to other regions of Australia (e.g. Fowler-Walker & Connell 2002; Irving et al. 2004b). We have shown that generalisations based on the percentage cover of turf-forming algae from Sydney are not indicative of patterns across temperate Australia. Furthermore, experiments on the effects of elevated nutrients, were they to be done in Sydney, may lead to different results than we found in the oligotrophic waters of South Australia, because nutrient concentrations are already elevated around Sydney. A limited response of epiphytic algae may be seen if ambient levels of nutrients are high relative to experimental increases (Karez et al. 2004). Indeed, predictions based on the effects of experimentally elevated nutrients may be limited to areas with similar nutrient regimes. Thus, generalisations about nutrient effects in oligotrophic waters can not be obtained from studies in already nutrient rich areas (natural or human impacted).

In summary, the cover of turf-forming algae growing on *E. radiata* was greater in Sydney than the rest of temperate Australia. Epiphytic algal abundance was correlated to chlorophyll *a* concentration, and thus, higher water nutrient concentration. We were able to show that elevated nutrients positively affect the abundance of turf-forming algae by experimentally elevating nitrate concentrations. These experimental results also suggest that increased nutrient concentrations have large effects on oligotrophic coasts, which requires further investigation. Understanding the different effects of elevated nutrients is important when considering management of coasts close to large sources of nutrients, such as agricultural and urbanised areas.



The artificial patch reefs used in many of the experiments. The top photo shows a reef with *Ecklonia radiata* and the bottom photo an open reef devoid of algal canopy.
Photos: Andrew Irving.



Turf-forming algae growing on a boulder at West Island (top) and a mixture of Turf-forming and Foliose algae (bottom).
Photos: Andrew Irving.

CHAPTER THREE



A NOVEL INTERACTION BETWEEN NUTRIENTS AND GRAZERS ALTERS RELATIVE DOMINANCE OF MARINE HABITATS

CHAPTER THREE PREAMBLE

Chapter three investigates the interactive effects of kelp canopy and nutrients, and nutrients and grazing, on the relative dominance of habitats by algae. This chapter follows on from Chapter 2 by further exploring the effects of elevated nutrients in subtidal habitats. Furthermore, the main experimental response was detected for turf-forming algae, the same algae that were growing as epiphytes on kelp in Chapter 2.

This chapter is a co-authored paper in press in Marine Ecology Progress Series, and as such is written in plural throughout. The paper can be cited as:

Russell B.D. and Connell S.D. 2005. A novel interaction between nutrients and grazers alters relative dominance of marine habitats. *Marine Ecology Progress Series* **289**: 5-11.

Sean Connell supplied funding and had input into the development of ideas behind nutrient dynamics and the experimental design. He also helped with data analysis and constructed a large number of experimental reefs. I helped in development of the ideas, constructed experimental reefs, ran the experiment and collected the data, did the data analysis and wrote the paper.

Signature of co-author:

Signed:

Sean D. Connell

CHAPTER THREE

This publication is included on pp. 45-59 in the print copy of the thesis in the University of Adelaide Library.

Russell, Bayden D., Connell, Sean D.

A novel interaction between nutrients and graziers alters relative dominance of marine habitats.


Marine ecology progress series 289:5-11 (2005)

<http://www.int-res.com/abstracts/meps/v289/p5-11/>



The northern (sheltered) side of West Island, the site used for experimental work (top) and a close up photo of my “home away from home”; the two huts on West Island (bottom).
Photos: Author.

CHAPTER FOUR



HISTORICAL AND CONTEMPORARY EFFECTS OF NUTRIENT
ELEVATION ON HERBIVORY: SUDDEN INCREASES IN
NUTRIENTS CHANGE RATES AND EFFECTS OF FORAGING

CHAPTER FOUR PREAMBLE

In Chapter 3, an observation was made that herbivorous molluscs seem to consume more turf-forming algae that has been exposed to elevated nutrients than to ambient nutrients. In Chapter 4, I experimentally test this observation. I also extended the experiments to test for differences in the effects of historical and contemporary nutrient concentrations to assess if grazers that historically have access to algae poor in nutrients will consume greater amounts when presented with algae rich in nutrients.

HISTORICAL AND CONTEMPORARY EFFECTS OF NUTRIENT ELEVATION ON HERBIVORY: SUDDEN INCREASES IN NUTRIENTS CHANGE RATES AND EFFECTS OF FORAGING

4.1 ABSTRACT

Herbivores can consume greater amounts of algae containing greater nutrient content and, therefore, may counter the negative effects of elevated nutrients. Understanding this observation may be useful for managing systems susceptible to monopolisation by opportunistic algae (e.g. turf-forming algae) as a consequence of sudden increases in nutrient loads (e.g. run-off from storm events). I used three successive field experiments to test the hypotheses that under intense regimes of herbivory: (1) molluscs would consume a greater percentage cover of turf-forming algae exposed to elevated nutrients, and consequently these turf-forming algae would have lower biomass than those exposed to ambient nutrients; (2) a greater number of herbivores would graze algae exposed to elevated nutrients; and (3) grazers exposed to sudden increases in nutrient rich algae would respond more strongly when historical nutrient loads were low. I was unable to reject these hypotheses and suggest that the apparent preference of grazers for nutrient rich algae may explain observations of intense herbivory that absorbs sudden eutrophication events which otherwise create algal blooms. Critically, these effects were greater when historical nutrient loads were low, suggesting that the response of grazers to sudden nutrient events would be greater on oligotrophic coasts where small increases in nutrient concentrations have disproportionately large effects.

4.2 INTRODUCTION

Opportunistic algae can form competitive dominants in the presence of elevated nutrients (Lotze et al. 2000), but grazers may counter this effect (Neckles et al. 1993; Hillebrand et al. 2000; Hillebrand 2003; Roll et al. 2005) by consuming greater biomass of plants and algae that are higher in nitrogen content (Neckles et al. 1993; Williams & Ruckelshaus 1993; Karez et al. 2000; Silliman & Zieman 2001). Greater

consumption of algae may occur as a function of densities of grazers (e.g. Karez et al. 2004; Roll et al. 2005), or through the greater consumption of biomass of nutrient enriched algae per individual (e.g. Nicotri 1980; Arrontes 1990). As opportunistic algae are often fast growing and have physiologies enabling the rapid uptake of available nutrients (Hein et al. 1995), grazers are likely to preferentially consume such algae soon after eutrophication events (e.g. runoff from storm events), possibly constraining outbreaks of fast growing algae (Roll et al. 2005).

The way in which the historical nutrient status of algae affects the food preference of herbivores is not well understood (Watson & Norton 1985). However, studies of food preference demonstrate that the feeding history and nutritional status of herbivores can determine feeding behaviour and food preference (Watson & Norton 1985; Norton et al. 1990; Bamstedt et al. 1999). If only low preference food is historically available, feeding rates of grazers often increase when a more preferred food is offered (Watson & Norton 1985; Norton et al. 1990). When given a choice between food with different nutritional values, herbivores are more likely to consume food with higher nutritional value (Nicotri 1980; Watson & Norton 1985; Arrontes 1990; Bamstedt et al. 1999). Further, it could be expected that herbivores with historical access to low nutrient food will consume greater amounts of nutrient rich food than herbivores that historically have access to food with high nutrient value. It is possible, therefore, that whilst nutrients may have disproportionately greater effects on oligotrophic coasts (Chapter 2), grazers on these coasts may have a greater compensatory response and reduce the effects of nutrients.

In South Australia, turf-forming algae appear to be competitive dominants on subtidal rock adjacent to heavily urbanised coast (Gorgula & Connell 2004) and constitute a large part of the diet of many of the herbivorous molluscs (Clarkson & Shepherd 1985), which are the most abundant benthic grazers of this region (Gorman & Connell, unpublished data). Under naturally intense regimes of herbivory, I tested the hypotheses that: (1) molluscs would consume a greater percentage cover of turf-forming algae exposed to elevated nutrients, and consequently these turf-forming algae would have lower biomass than those exposed to ambient nutrients; (2) a greater number of herbivorous molluscs would graze turf-forming algae on boulders

exposed to elevated nutrients than on boulders exposed to ambient nutrients; and (3) grazers exposed to sudden increases in nutrient rich algae would respond more strongly when historical nutrient loads were low.

4.3 MATERIALS AND METHODS

Natural patterns and experimental reefs

Experiments were done on experimental reefs in Abalone Cove, West Island, South Australia (35°36'S, 138°35'E). The study site consists of a sloping boulder reef that terminates in sand at ~ 5 m depth and supports diverse assemblages of algae (Shepherd & Womersley 1970) and dense populations of molluscan grazers (Clarkson & Shepherd 1985) which were 2 – 100 times greater than those observed at 6 sites on the adjacent coast (Fleurieu Peninsula; Table 4.1; Gorman & Connell, unpublished data). Experiments focused on *Clanculus* spp., *Turbo* spp., and *Astrarium aureum*. Alternate benthic grazers (e.g. echinoids, *Heliocidaris erythrogramma*) are rarely observed on adjacent coast of the mainland (Fleurieu Peninsula) and westward through to the Great Australian Bight (Gorman & Connell, unpublished data). The turf-forming algae quantified in this study comprised annual, fine filamentous algae that formed close-knit “turfs” < 2 cm in vertical height, primarily *Feldmannia lebelli* and *F. globifera*.

The experimental reefs used for all three experiments were constructed of 60 × 60 cm metal frames on a double concrete base (60 × 60 cm) set on sand (~ 5 m depth) at least 10 m from the natural reef. The upper concrete base was 20 cm above the lower base (set on sand) and created a platform for experimental boulders. Boulders were taken from natural reef and placed on the experimental reefs, leaving a gap in the middle of each reef for the “experimental” boulder. This design has been successfully used to exclude and test the effects of molluscan grazers (see Shepherd & Turner 1985 for a photograph of the experimental reefs), and made it possible to control the number of molluscan grazers on each experimental reef (see Chapter 3). At the beginning of each of the three successive experiments, boulders similar to those on experimental reefs, but devoid of marine life, were placed at the centre of each reef.

Effects of nutrients on grazing

In February 2003, 10 experimental reefs with high densities of grazing molluscs ($111 \pm 9.6 \text{ m}^{-2}$) were used to test whether the percentage cover of grazing marks of molluscs was greater on reefs exposed to elevated concentrations of nutrients ($n = 5$ reefs) than reefs with ambient concentrations of nutrients ($n = 5$ reefs). Percentage covers were quantified by placing a $100 \text{ mm} \times 100 \text{ mm}$ grid containing 25 points over the boulder and recording the presence of either turf-forming algae or grazing scars directly beneath each point (Drummond & Connell 2005). Molluscs consumed small filamentous algae down to the substrate (Clarkson & Shepherd 1985), leaving defined grazing scars, which were easily quantified. The effects of grazing were striking in their support for the hypothesis (see Results), but I was less secure about this effect at sparser densities of grazers (i.e. $< 50\%$ of initial densities). To increase our confidence, therefore, I retested this hypothesis at sparser densities of grazers ($46.7 \pm 5.4 \text{ m}^{-2}$; 0.8 – 43 times greater than 6 sites on the adjacent peninsula) using an extra replicate to detect a potentially smaller effect-size ($n = 6$ reefs per treatment) whilst also quantifying the biomass of turf-forming algae in addition to percentage cover. This second experiment was run for four weeks over December 2003 and algal biomass was sampled by placing the opening of a plastic jar (surface area of 14.52 cm^2) over the experimental boulder and removing all algae off the rock and into the jar. Algae were oven dried (70°C) for 48 hours, to constant weight, before being weighed. These experiments focus on the early and rapid phase of growth by turfs, the phase most likely to be affected by sudden increases in nutrient concentrations, and to either overwhelm the effects of grazers or be subjected to their control. Single-factor Analysis of Variance (ANOVA) was used to test for the effects of treatments on percentage cover and biomass of turf-forming algae (two levels of nutrient: ambient v. elevated).

Effects of historical v. contemporary nutrient status

The effects of historical (low v. high) and contemporary (ambient v. elevated) nutrient concentrations on grazing were tested together in a crossed design ($n = 6$ per treatment) (Figure 4.1). In January 2004, grazers were isolated to reefs with either high or low concentrations of nutrients (i.e. historical conditions), before being presented with algae from high and low concentrations of nutrients (i.e.

contemporary conditions). The translocated algae were cultured on boulders devoid of marine life, and had been placed on experimental reefs without herbivorous molluscs. After four weeks, these boulders were moved to experimental reefs that contained molluscs ($46.7 \pm 5.4 \text{ m}^{-2}$) that were associated with either historically low (natural) or high (experimentally enhanced) nutrient levels for three months. Two boulders were placed at the centre of each experimental reef, one that had been exposed to ambient nutrients and one that had been exposed to elevated nutrients (contemporary nutrient). Four weeks after boulders had been moved onto the experimental reefs, biomass of algae was sampled as above (previous subsection).

To test the hypothesis that greater densities of molluscs graze on turf-forming algae exposed to elevated nutrients compared to ambient nutrients, I counted the number of molluscs observed grazing each experimental boulder on two occasions; two weeks after commencement and the night before biomass samples were collected. Counts were done an hour after sunset because the molluscs at the field site were more active at night. As all boulders on experimental reefs were selected to be of similar size, the number of molluscs is expressed as per boulder (i.e. $\sim 300 \text{ cm}^2$). A two-factor ANOVA was used to detect differences in algal biomass, with two fixed, orthogonal factors, contemporary nutrient status (two levels: ambient *v.* elevated) and historic nutrient status (two levels: low *v.* high) ($n = 6$). The number of molluscs grazing on each boulder was analysed using the same two-factor ANOVA design.

Nutrient content of algae

To test the explicit assumption that nutrient content of algae exposed to elevated nutrients was greater than in algae exposed to ambient nutrients, samples of turf-forming algae were collected from boulders in January 2004 (ambient *v.* elevated; $n = 6$). Samples were dried using the same method as biomass samples from previous experiments (see above). Samples were ground using a porcelain mortar and pestle, weighed to the nearest 0.1 mg, and analysed for percentage of nitrogen using a GV Isoprime mass spectrometer. Data on the nitrogen content of algae were log transformed and a single-factor ANOVA used to test for differences in the nitrogen content of algal tissue.

Table 4.1 Comparison of natural nutrient concentrations (DIN: dissolved inorganic nitrogen = ammonia + nitrate + nitrite; $\mu\text{mol L}^{-1}$) and mollusc abundances (m^{-2}) at different sites within South Australia.

	Nutrient Concentration DIN ($\mu\text{mol L}^{-1}$)	Mollusc Abundance (individuals m^{-2})
West Island	0.29 ^a	113 ^b
Experimental reefs (high density)	0.15 ^c	111 ^c
Experimental reefs (low density)	No data	46 ^d
Adjacent coast	No data	1 - 25 ^e

^a Gorgula & Connell 2004; ^b Clarkson & Shepherd 1985; ^c Chapter 3; ^d This study;

^e Gorman & Connell, unpublished data

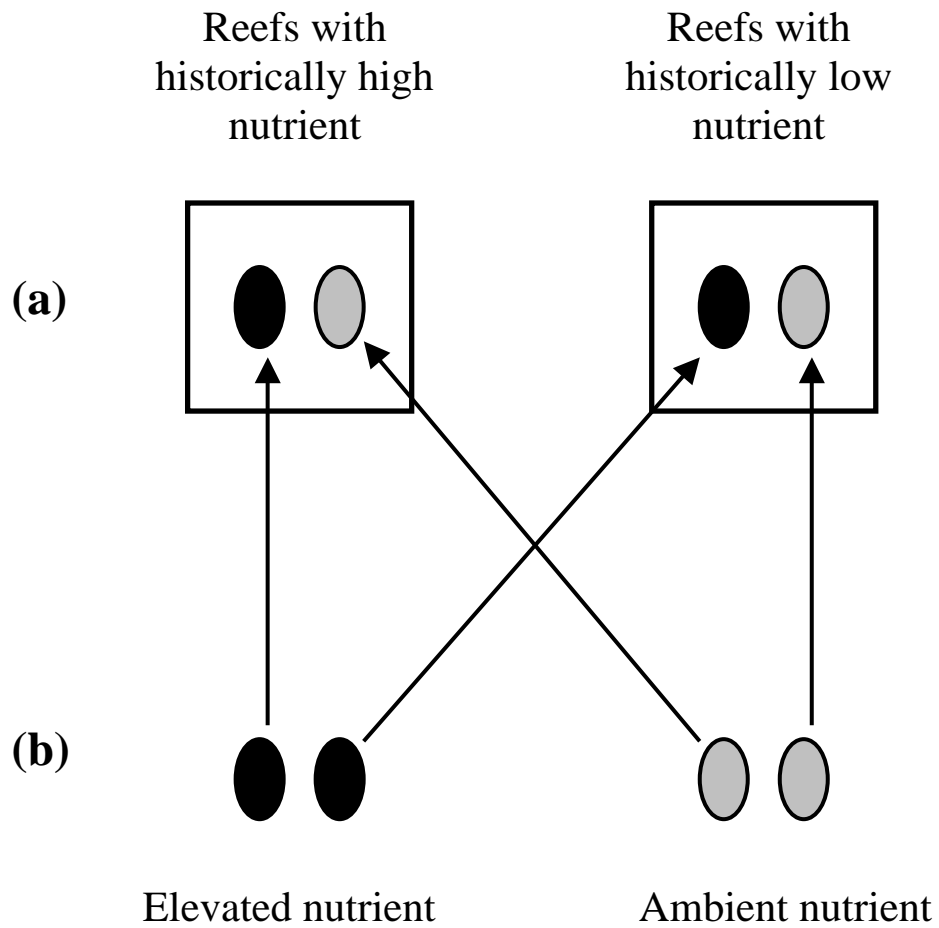


Figure 4.1 Schematic diagram showing how I created the conditions needed to test the effects of historical and contemporary nutrient loads on grazing. Initially, grazers were isolated to algae associated with (a) reefs of either high or low concentrations of nutrients (i.e. historical conditions) before (b) being presented with algae associated with both high and low concentrations of nutrients (i.e. contemporary conditions).

Nutrient addition

Nutrients were supplied as 12 g of Osmocote Plus[®] slow release fertilizer per nutrient reef (6 month release: 15, 5, 10 N-P-K). Four nylon mesh bags (1mm mesh size) were each filled with 3 g Osmocote[®] pellets and attached to the reefs at four sides of the central boulder using cable ties at the beginning of experiments (3 g × 4 bags = 12 g per boulder). Each bag was ~ 2 cm in diameter and was slightly below the top surface of the central boulder. This configuration of deployment does not modify water flow, or increase habitable surface on the boulder, and explicit tests for artefacts associated with this experimental protocol have shown that treatments do not confound the interpretation of experiments by artefacts (Gorgula & Connell 2004). Moreover, this approach has been tested against other experimental protocols and suggested to be the most appropriate method of elevating nutrients in subtidal experiments (Worm et al. 2000b). In this study, water samples were not collected for nutrient analysis because the same weight of fertilizer (12 g per boulder) has been used to successfully increase water nutrient concentrations at the same study site at the same time of year; nitrate concentrations were elevated by approximately 87 % above ambient concentrations (Chapter 3) and nitrate and phosphorus by approximately 90 % and 38 %, respectively (Gorgula & Connell 2004).

4.4 RESULTS

Effects of nutrients on grazing

Molluscs consumed more algae in the presence of elevated nutrients. The percentage cover of grazing scars of molluscs was greater on boulders that were exposed to elevated nutrients than ambient nutrients in February 2003 (mean ± SE; 44 ± 6.1 %; 20 ± 4.8 %, respectively; ANOVA: $F_{1,9} = 9.46$, $P = 0.015$). I retested this hypothesis using lower densities of grazers and more replicates, and detected a greater proportion of grazing marks on boulders exposed to elevated nutrients in January 2004 (Figure 4.2a, ANOVA: $F_{1,10} = 31.62$, $P < 0.001$). Moreover, this pattern translated into lower biomass of turf-forming algae on boulders exposed to elevated nutrients (Figure 4.2b, ANOVA: $F_{1,10} = 12.17$, $P < 0.01$). These biomass samples were Ln (X) transformed to meet assumptions of heterogeneity (Cochran's C-test) (Underwood 1997).

Effects of historical v. contemporary nutrient status

Both contemporary nutrient concentration (elevated) and historical nutrient status (low) had a negative effect on the biomass of turf-forming algae in the presence of grazers (Figure 4.3, Table 4.2). Biomass of turf-forming algae was less on boulders that had elevated contemporary nutrients than ambient nutrients (Figure 4.3, Table 4.2). On reefs with low historical levels of nutrients, mean biomass of turf-forming algae was an order of magnitude less on boulders exposed to elevated nutrients (mean \pm SE; 4.5 ± 0.9 mg, Figure 4.3) than boulders exposed to ambient nutrients (38.9 ± 13.4 mg, Figure 4.3). On reefs with historically high nutrient loads, contemporary differences in nutrients (ambient v. elevated) had no detectable effect on biomass of algae (Figure 4.3). A greater number of molluscs were present on boulders exposed to elevated rather than ambient nutrients after two weeks (Figure 4.4a, Table 4.3a), but this was marginally non-significant after four weeks (Figure 4.4b, Table 4.3b).

Nutrient content of algae

The mean nitrogen content of turf-forming algae was greater in treatments of elevated nutrients (mean \pm SE; 0.479 ± 0.047 %) than ambient nutrients (0.377 ± 0.016 %), but the test for the difference between these means was marginally non-significant (ANOVA: $F_{1,10} = 4.32$, $P = 0.06$). I retested for differences after removing an outlying sample (i.e. a low concentration from the treatment of elevated nutrients) and differences between the means were detected (elevated 0.504 ± 0.049 %, ambient 0.377 ± 0.016 %; ANOVA: $F_{1,9} = 7.892$, $P = 0.02$). I report both analyses so that the reader can assess whether the two reported means are likely to represent real differences (using $\alpha = 0.05$).

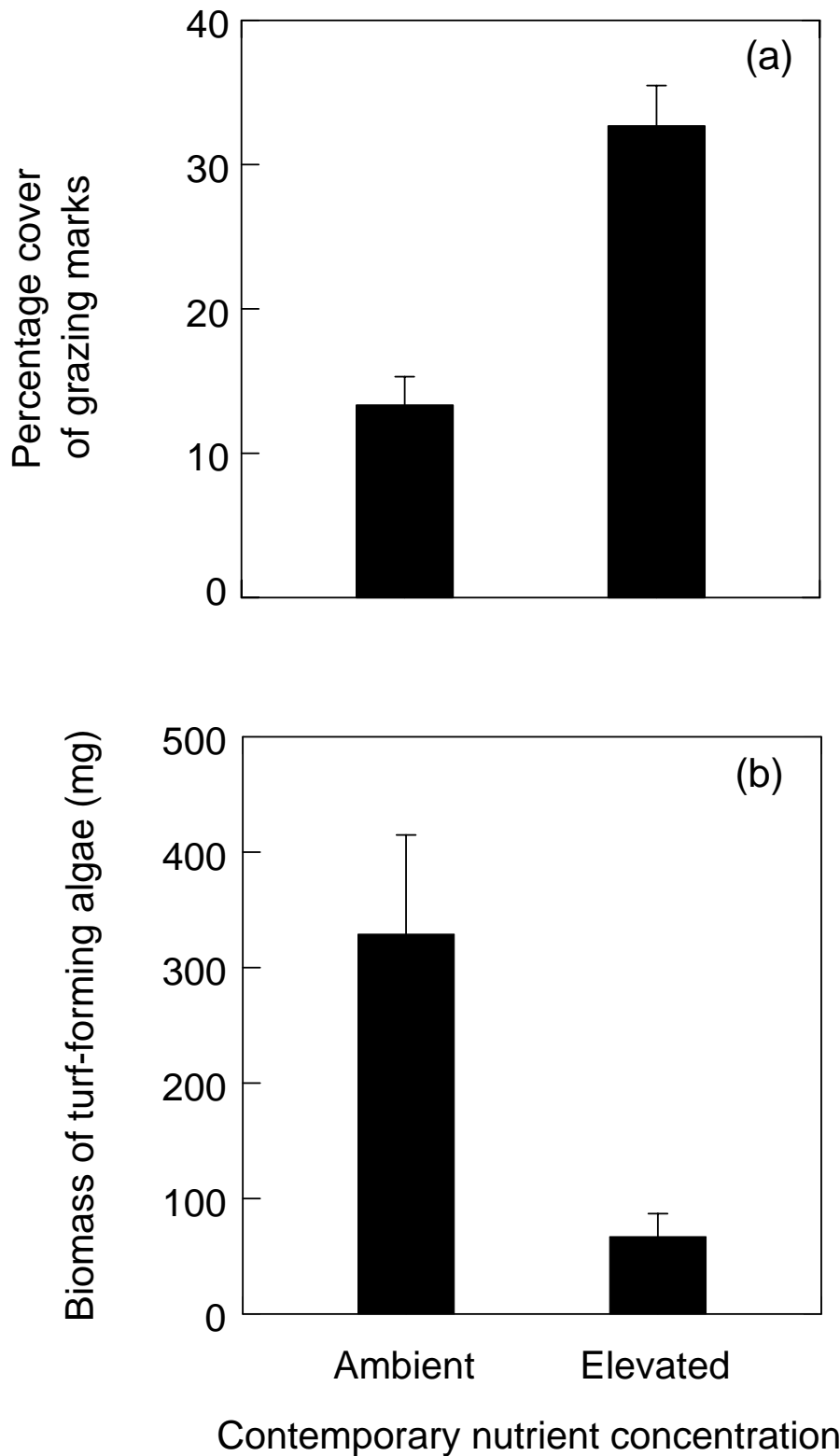


Figure 4.2 (a) The percentage cover (mean \pm SE) of grazing marks of molluscs and (b) biomass (mg; mean \pm SE) of turf-forming algae exposed to different nutrient concentrations (ambient *v.* elevated).

Table 4.2 Results of a two-factor ANOVA testing for the interactive effects of contemporary (ambient *v.* elevated) and historical (low *v.* high) nutrient concentration on the biomass of turf-forming algae on boulders after grazing by molluscs. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. Probability values in bold are significant. Ln (*X*) transformation was used to meet assumptions of homogeneity of data (Cochran's *C*-test) (Underwood 1997).

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Contemporary nutrient	1	13.12	4.65	0.040
Historical nutrient	1	16.62	5.89	0.025
C × H	1	0.59	0.21	0.650
Residual	20	2.82		

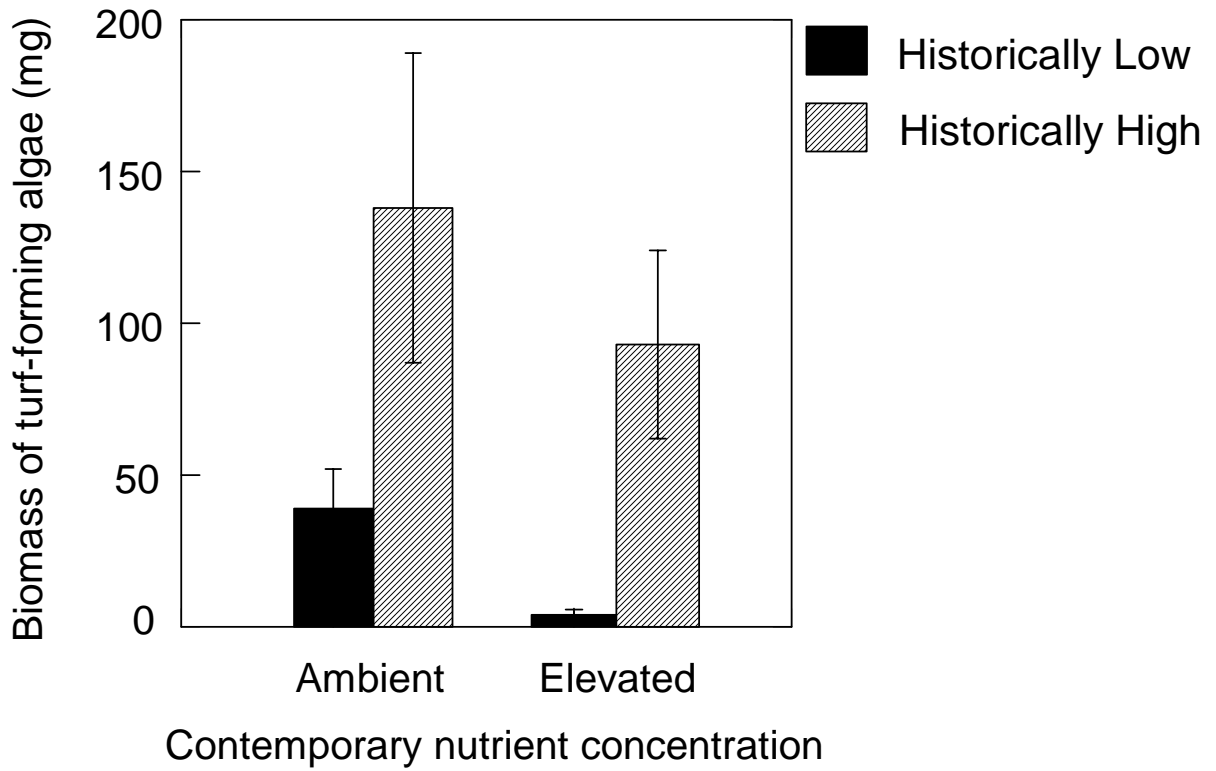


Figure 4.3 The biomass (mg; mean \pm SE) of turf-forming algae exposed to contemporary (ambient *v.* elevated) and historical nutrient concentrations (low *v.* high) after grazing by molluscs.

Table 4.3 Results of two-factor ANOVAs testing for differences in the number of molluscs grazing on boulders exposed to different contemporary nutrient concentrations (ambient *v.* elevated) and with different historical nutrient state (low *v.* high) after (a) two weeks and (b) four weeks. Probability values in bold are significant. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability.

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
(a) Two weeks				
Contemporary nutrient	1	35.04	11.98	0.002
Historical nutrient	1	2.04	0.70	0.413
C × H	1	1.04	0.35	0.557
Residual	20	2.93		
(b) Four weeks				
Contemporary nutrient	1	121.50	3.99	0.059
Historical nutrient	1	10.67	0.35	0.560
C × H	1	6.00	0.19	0.662
Residual	20	30.38		

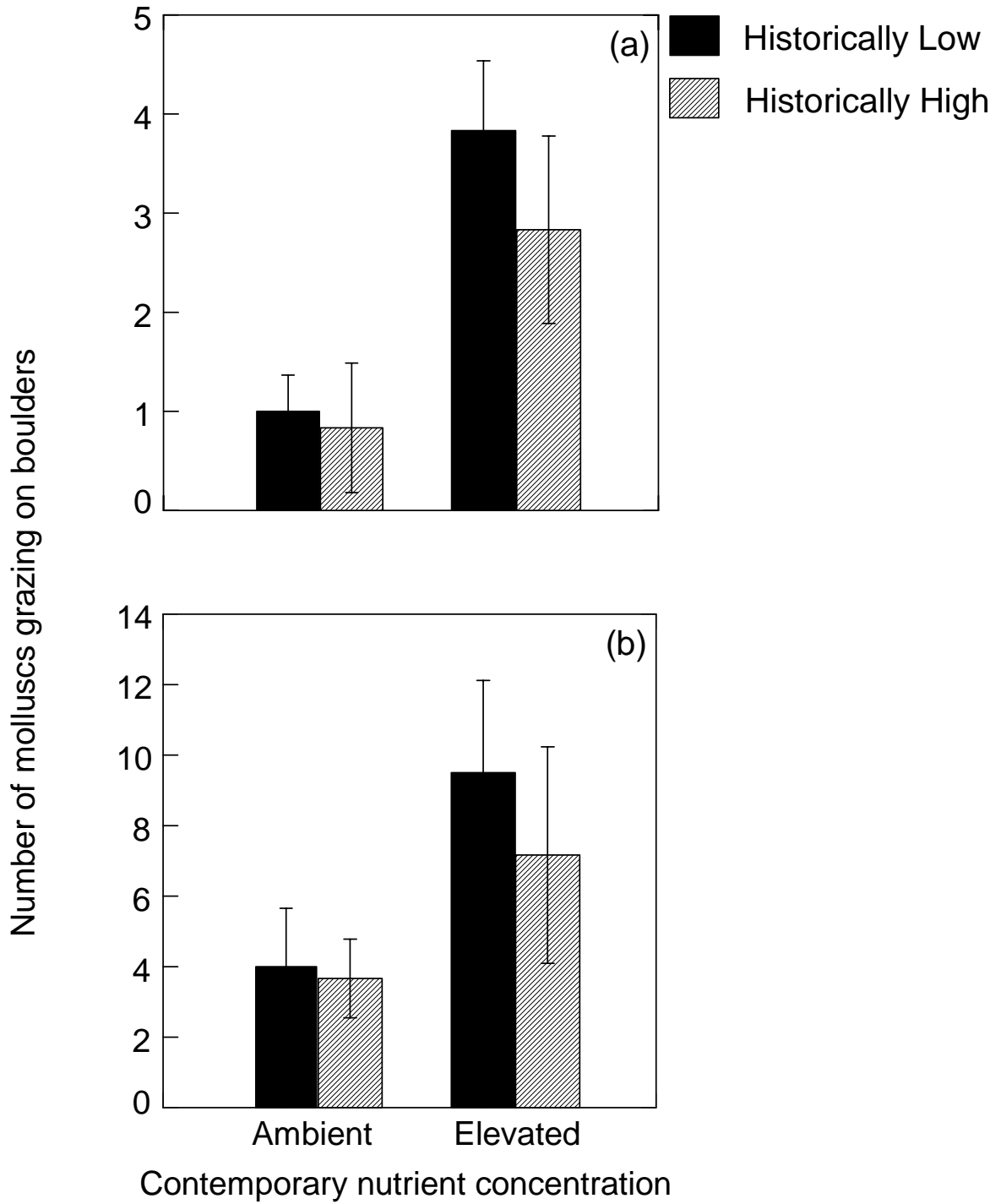


Figure 4.4 The number of molluscs (mean \pm SE) grazing on algae exposed to different contemporary nutrient concentrations (ambient *v.* elevated) and with different historical nutrient state (low *v.* high) (a) after two weeks and (b) after four weeks.

4.5 DISCUSSION

The key finding of this study was that under elevated nutrients, herbivorous molluscs reduced algal biomass at a greater rate than under ambient nutrient concentrations. Hillebrand et al. (2000) found similar effects, where the species of algae most positively affected by nutrient enrichment were also most negatively affected by grazing pressure. I show that grazers can remove nutrient rich algae at a rate that causes their biomass to be less than algae exposed to ambient concentrations of nutrients. Although grazing in the presence of elevated nutrients can cause a switch in the relative dominance of algae (e.g. Chapter 3), it still remains to be tested whether this observation can hold at broad-scales. It would be useful to understand whether the relative abundance of algae on entire reefs subjected to elevated nutrients can be held in check by grazers, and whether the lack of grazers on some reefs can explain shifts from perennial to opportunistic algae (e.g. Gorgula & Connell 2004).

Grazers exposed to sudden increases in nutrient rich algae responded more strongly when historical levels of nutrients were low. It appears that molluscs preferentially consumed more algae when they had historically low nutrients and were then exposed to elevated nutrients. Feeding history of herbivores is known to affect food choice (Watson & Norton 1985), hence, food with greater nutrient content is likely to be consumed preferentially by herbivores with historical access to low nutrient food. Grazers have been shown to consume more biomass of algae of greater nitrogen content (Neckles et al. 1993; Williams & Ruckelshaus 1993; Karez et al. 2000). Greater consumption of fast growing, opportunistic algae on coasts with historically low nutrient concentrations could be an important check on the effects of sudden elevation of nutrients (e.g. storm runoff), as it is possible that grazers in these areas are likely to consume the nutrient rich opportunistic algae at greater rates.

An increase in consumption of algae may occur as a consequence of either an increase in the number of grazers or by individual grazers increasing consumption. It is possible for consumers to increase in number through immigration to a location. However, the experimental reefs used in this study successfully limit the immigration of molluscs (Chapter 3), so grazing pressure on reefs appears to have increased through either an increase in consumption by each individual mollusc or by an

increase in the proportion of grazers from each reef grazing on the experimental boulder. In salt marsh, molluscs consume greater biomass of plant matter that has been exposed to elevated nutrients (Silliman & Zieman 2001). Further work is required in my system to distinguish between redistribution of foraging activity from increased per capita consumption. Nevertheless, our results suggest that changes in foraging effort are likely to be an important component of nutrient driven changes to foraging activity and its consequences.

I found that reefs exposed to elevated nutrients had lower biomass of turf-forming algae than on reefs exposed to ambient nutrients, as a consequence of greater grazing by molluscs. Despite this result, it is possible that grazers did not consume all of the algal biomass that was lost. Silliman and Zieman (2001) observed that although mollusc consumption of salt marsh plants increased with the addition of nutrients, not all plant matter was consumed, and a large proportion of plant biomass loss was because of plant mortality associated with damage by grazing. The proportion of damaged or dislodged algae not consumed by grazers is of concern to similar studies. I am cautious, therefore, in interpreting the difference in algal biomass between nutrient treatments as an overestimate of the consumption by molluscs. Nevertheless, such overestimates of consumption do not affect the outcome of tests of the effects of elevated nutrients, because the primary space created when algae is dislodged by grazing can be used by other species of algae (e.g. Chapter 3).

I emphasise two issues that challenged this study and may require care in future work and interpretations about the ability of grazers to absorb the effects of enhanced nutrient loads. First, tissue analysis and interpretation of nutrient status of turf-forming algae is challenging. In general, small filamentous algae with simple cellular structure (such as the turf-forming algae in this study) have high biomass turnover, high growth rates, and are likely to store less nutrients in their tissues (Hein et al. 1995; Pedersen & Borum 1996; Copertino et al. 2005), often making differences in tissue nutrient concentrations small and difficult to detect. Second, understanding the locations and spatial extent to which herbivores confer resilience to change of coastal habitat will vary as a consequence of the types and densities of grazers present in the immediate area of study and within the region the study is

imbedded (Fowler-Walker & Connell 2002). Grazers have spectacular effects in many parts of the world which are intensely studied (e.g. New Zealand, Shears and Babcock 2002; eastern Australia, Andrew 1993; Alaska, Estes and Duggins 1995; Nova Scotia, Scheibling et al. 1999), but models about the central role of grazing may not apply to large areas of the world's coast (western and southern Australia, Fowler-Walker & Connell 2002), which appear to be under the influence of alternate processes (e.g. Connell 2005). We may need to recognise biogeographic differences so that the importance of grazing is recognised, but not overstated.

The concomitant world wide increase in nutrient loading in coastal waters (Vitousek et al. 1997a), and loss of herbivores, is associated with an increase in rate at which systems switch from those dominated by canopy-forming algae to less desirable states dominated by smaller turf-forming algae (Worm et al. 1999). It is important, therefore, to understand mechanisms that may counter these effects. Increased grazing in the presence of elevated nutrients may inhibit blooms of fast growing macroalgae, reducing (Roll et al. 2005), if not countering, their effects. In this study I have shown that molluscs can respond to elevated nutrient concentrations by removing turf-forming algae at a greater rate. Although I was not able to determine if this represents increased per capita consumption, I did observe a redistribution of foraging effort at the small spatial scale of experimental reefs ($< 1 \text{ m}^2$). Importantly, molluscs responded positively to sudden increases in nutrient rich algae, and this response was greater on reefs with historically low nutrients. This observation suggests that grazers may have a greater response to increased nutrient concentrations on oligotrophic coasts where small increases in nutrient loads can have disproportionately large effects on opportunistic algae (Chapter 2). By preferentially consuming the more opportunistic, fast growing algae, molluscs may reduce the effects of elevated coastal nutrients by creating space for other, longer lived algae to colonise (e.g. Chapter 3). This compensatory response of herbivores to the effects of nutrients deserves tests over broader scales to understand its potential importance to coastal management, particularly because human harvesting of herbivores tends to be greater in locations of greater nutrient runoff (i.e. human-dominated coasts).



The artificial “kelp” used to test for the interactive effects of abrasion and water flow on turf-forming algae. Artificial “kelp” were used because it was not logistically possible to effectively reduce water flow on whole patch reefs. This photo shows a flow procedural control (partial cage).
Photo: Author.

CHAPTER FIVE



EFFECTS OF CANOPY-MEDIATED ABRASION AND WATER FLOW ON THE EARLY COLONISATION OF TURF-FORMING ALGAE

CHAPTER FIVE PREAMBLE

In Chapter 3, I showed that in the absence of kelp, turf-forming algae dominate available space. It is also known that algal canopies modify water flow and light conditions for the algal understorey. To understand how kelp suppress turf-forming algae, it would be useful to understand the interaction of these factors. In Chapter 5, I investigate the interactive effects of water flow and abrasion by algal canopy on turf-forming algae.

EFFECTS OF CANOPY-MEDIATED ABRASION AND WATER FLOW ON THE
EARLY COLONISATION OF TURF-FORMING ALGAE**5.1 ABSTRACT**

Algal canopies form predictable associations with the benthic understorey across thousands of kilometres of coast, and these associations may be maintained by canopy-mediated processes. With the increase in switches from habitats dominated by canopy-forming algae to turf-forming algae, it is useful to understand how algal canopies suppress the short term colonisation of turf-forming algae. Two canopy-mediated processes that are inherently linked are the amount of water flow through a canopy, and the amount of abrasion of the substrate by the canopy; there is an increase in abrasion by canopies with increasing water flow. I experimentally reduced both water flow through canopies and abrasion by canopies to test the hypotheses that (1) reduced abrasion by kelp canopies would allow greater percentage cover and biomass of turf-forming algae to colonise and (2) reduced water flow would allow greater percentage cover and biomass of turf-forming algae to colonise. When abrasion was reduced, the biomass of turf-forming algae was reduced, supporting the hypothesis. However, abrasion had a greater effect on the biomass of turf-forming algae than the percentage cover, suggesting that below a certain vertical height, filaments of turf-forming algae are less affected by the physical abrasion of canopies. In contrast to predictions, reducing water flow had a negative effect on the percentage cover and biomass of turf-forming algae, rejecting the hypothesis. It seems, however, that the negative effect was caused by a reduction in light intensity because of reduced canopy movement and not a reduction of water flow *per se*. None of the factors accounted for all of the change seen in algal percentage cover or biomass, indicating that it is important to study the interactive effects of physical processes to understand how algal canopies suppress or exclude other benthic organisms.

5.2 INTRODUCTION

Predictable associations exist between canopies of algae and the benthic understorey (Kennelly & Underwood 1993; Bertness & Leonard 1997; Bertness et al. 1999; Bruno 2000; Bulleri et al. 2002; Connell 2003a; Irving et al. 2004b). These associations are maintained by the canopy-forming algae, and can be both positive (Bertness et al. 1999; Irving et al. 2004a) and negative (Kennelly 1989; Connell 2003b). When the algal canopy is removed, such as through storm damage, a new set of taxa often assembles, altering the algal dominance (Reed & Foster 1984; Kennelly 1987b, c). Fast growing, opportunistic species, such as filamentous turf-forming algae, often dominate this open space (Kennelly 1987b; Melville & Connell 2001; Bulleri et al. 2002), and can inhibit the recruitment of canopy forming algae (Kennelly 1987a). To understand how canopy algae re-establish, it is useful to understand the mechanisms by which canopies of algae can suppress turf-forming algae.

Algal canopies alter water flow across the benthos by creating a physical barrier to the water (Eckman et al. 1989). In doing so, the canopy itself is moved by the water flowing through it. As the canopy is moved by the water, it sweeps across the substrate, causing surface abrasion. In areas of greater water movement, such as exposed coastlines, the canopy moves more, and subsequently causes more abrasion of the substrate (Kennelly 1989; Toohey et al. 2004). Therefore, it could be expected that in areas of less water movement, the effect of canopy abrasion may be less than in areas of greater water movement.

Physical abrasion of the substrate can alter the species composition of the understorey by directly excluding invertebrates (Connell 2003b) and algae (Velimirov & Griffiths 1979; Kennelly 1989) through physical removal. Abrasion by canopies may also have indirect effects on some species of algae. For example, the sediment enhances the growth of some species of algae, such as turf-forming algae (Airoldi & Cinelli 1997; Irving & Connell 2002), and removal of sediment from the substrate may limit the growth of these algae. When canopy abrasion is removed, a

different set of taxa tend to dominate space than when the canopy is present (Kennelly 1989; Bulleri et al. 2002).

In southern Australia, turf-forming algae dominate open space in the absence of an algal canopy (Fowler-Walker & Connell 2002), but are quickly lost from the benthos with the addition of a canopy (Melville & Connell 2001). On human dominated coasts, it is becoming increasingly common to see switches from habitats dominated by canopy-forming algae, to habitats dominated by turf-forming algae (Jackson 2001; Eriksson et al. 2002; Copertino et al. 2005). To understand how algal canopies are able to suppress the short term colonisation of turf-forming algae, and remove turf-forming algae that has colonised, it is useful to understand the effects of canopy-mediated processes. I experimentally altered the amount of water flow through canopies, and the amount of abrasion by canopies, to test the hypotheses that (1) reduced abrasion by kelp canopies would allow greater percentage cover and biomass of turf-forming algae to colonise and (2) reduced water flow would allow greater percentage cover and biomass of turf-forming algae to colonise.

5.3 MATERIALS AND METHODS

Study site

Experiments testing for the effects of canopy abrasion, water flow and shade on filamentous turf-forming algae were done on experimental reefs at West Island, South Australia (35°36'S, 138°35'E). The study site consists of a sloping boulder reef that terminates in sand at ~ 5 m depth and supports diverse assemblages of algae (Shepherd & Womersley 1970), including the canopy alga *Ecklonia radiata* and the filamentous turf-forming algae *Feldmannia lebelli* and *F. globifera*.

Natural v. artificial abrasion

It was not possible to limit water flow around experimental reefs containing *E. radiata*, so artificial “kelp” was used to assess the effects of water flow and abrasion on turf-forming algae. To assess the extent to which artificial kelp mimicked natural abrasion by *E. radiata* canopy, I compared experimental abrasion (present v. absent v. procedural control) to abrasion by *E. radiata* (present v. absent v. procedural control) in a crossed design ($n = 4$ per treatment). A two-factor ANOVA was used to

test for differences between natural and artificial abrasion, with the fixed, orthogonal factors of natural and artificial abrasion.

Effect of water flow and abrasion

The effects of canopy abrasion (present *v.* absent *v.* procedural control) and water flow (present *v.* reduced *v.* procedural control) on percentage cover and biomass of turf-forming algae were tested in a crossed design ($n = 4$ per treatment). Artificial “kelp” was used to simulate abrasion, as it was not logistically possible to limit water flow around experimental reefs with natural kelp. Data were analysed using a two-factor Analysis of Variance (ANOVA), with factors of flow and abrasion. Both factors were considered to be fixed and orthogonal.

Effect of shade

The intensity of light that reaches the substrate is also altered by canopies, and reduced light is thought to contribute to the effects of canopies on understory assemblages (e.g. Connell 2003a). To estimate the effect of reduced light intensity on turf-forming algae, I also experimentally reduced light in a concurrent experiment (full sunlight *v.* shade *v.* procedural control; $n = 6$ per treatment). The effect of shading on percentage cover and biomass of turf-forming algae was tested using a single-factor ANOVA. In all ANOVAs, Cochran’s *C*-test was used to test for heterogeneity in the data, and $\text{Ln}(X+1)$ transformation used to remove heterogeneity when necessary. Significance was judged at $\alpha = 0.05$ and SNK pairwise comparisons used when significant interaction terms were detected.

Colonisation and removal of turf-forming algae by canopies

Canopies formed by kelp suppress the colonisation of turf-forming algae, but can also remove turf-forming algae that has already colonised (e.g. encroaching from surrounding gaps in the canopy). To test the effects of kelp canopy on colonisation and removal of turf-forming algae, all experiments were done twice, once for the colonisation of turf-forming algae on bare settlement plates and once for the removal of turf-forming algae that had already established on settlement plates. To test for the effect of canopies on the colonisation of turf-forming algae, bare settlement plates were placed under experimental treatments and turf-forming algae allowed to grow.

Bare settlement plates were attached to experimental reefs, under the appropriate treatment, where they were left for 60 days before sampling. In all experiments assessing the effect of canopies on the colonisation of turf-forming algae, the final percentage cover and biomass of algae were compared among treatments, because no algae were present on plates at commencement of the experiments.

To test for the effect of canopies in removing turf-forming algae, settlement plates were attached to boulders on the natural reef to allow turf-forming algae to establish prior to being placed under experimental conditions. After 45 days, settlement plates were randomly re-assigned to an experimental treatment. Settlement plates were sampled 15 days after being placed under experimental conditions. For experiments assessing the removal of turf-forming algae, the change in percentage cover was calculated for each individual plate, and compared among treatments. Change in biomass was calculated by subtracting the mean initial biomass (see next subsection) from the final biomass of algae on each plate.

These experiments were designed to test for the effects of kelp canopies on the early colonisation of turf-forming algae, and how canopies can remove turf-forming algae over short periods. Turf-forming algae at the field site colonise to cover bare substratum outside canopies within 2 weeks (Chapter 3), but have very low abundance under canopies (< 5 % cover, Irving 2005). Although longer periods are required to test hypotheses about the longer-term maintenance of assemblages beneath canopies (e.g. 300 days: Connell 2003a), 60 days is sufficient time to observe the effect of canopies on the colonisation of turf-forming algae.

Sampling

Initial percentage cover of turf-forming algae was recorded for all settlement plates (see method next paragraph), but initial biomass could not be sampled because biomass sampling is destructive. To allow an estimate of the amount of biomass turf-forming algae removed by canopies, an estimate of mean initial biomass was calculated by destructively sampling four plates, which were not assigned to experimental treatments, at the start of the experiment.

At the completion of each experiment, the percentage cover of turf-forming algae on each settlement plate was quantified by placing a 10 cm × 10 cm grid containing 25 regularly spaced points over the plate and recording the number of points that had algae directly beneath them (Drummond & Connell 2005). Each plate was placed in an individual bag and returned to the laboratory. All algae in the central 10 cm × 10 cm area of each plate was scraped off and dried in an oven at 70°C for 48 hours, to constant weight, before being weighed to the nearest 0.1 gram.

Tests for differences in light and flow conditions

To test for differences in light conditions among experimental treatments, light intensities were recorded for all experiments ($n = 3$ measurements per treatment). Light measurements were taken using a Li-Cor meter, with the sensor placed slightly above the upper surface of settlement plates. Measurements were taken at midday on a day when no cloud was present, so that light conditions were as constant as possible. Data are presented as $\mu\text{moles m}^{-2} \text{ s}^{-1}$. Differences in light intensities in the flow *v.* abrasion experiment were analysed using a two-factor ANOVA, with the orthogonal factors of flow (three levels: present, reduced, procedural control) and abrasion (three levels: present, absent and procedural control). Single-factor ANOVAs were used to compare light levels between artificial and natural kelp (three levels: artificial kelp flow absent, artificial kelp flow present and natural kelp) and for the shading experiment (three levels: shade, open and procedural control).

To test for relative differences in flow among treatments, and to enable a relative comparison of water flow under artificial and natural kelp, plaster clods were attached to plates for the full experimental design. Clods were cylinders of casting plaster 4.5 cm diameter × 5 cm high. Before being deployed in the water, all clods were dried at 70°C for two days and weighed to the nearest 0.1 g. Clods were collected 7 days after being placed under experimental conditions and dried at 70°C for 2 days before being weighed to the nearest 0.1g. Percentage loss of clods was compared among treatments. All clods were made from a single batch of plaster, so dissolution rate should be constant for all clods. To test for differences in flow among treatments, a two-factor ANOVA was used for the full flow *v.* abrasion experimental design. A single-factor ANOVA was also used to test for differences

among artificial kelp, natural kelp and clods from open reef (four levels: artificial kelp reduced flow, flow present, natural kelp, open reef).

Experimental units

Settlement plates (11 cm × 11 cm) were made from Hardiflex fibreboard, which has a smooth and rough side to the board that is created in the manufacturing process. In this study, plates were attached with the rough surface facing upwards, as filamentous turf-forming algae readily colonise this surface (Irving & Connell 2002). Plates were slightly larger than the sampled area (10 cm × 10 cm) to avoid the possibility of edge effects altering experimental effects.

Each experimental plate was surrounded by 12 artificial “kelp”, each of which was a strip of shade cloth 10 cm wide and 50 cm long. Because shade cloth is slightly buoyant, each “kelp” blade was weighed down at the tip by a small lead weight (0.3 cm diameter), allowing the blade to scrape across the substrate in a similar manner to natural kelp. Frames to limit water flow were cubic wire frames (each side 30 cm long) surrounded by clear plastic on four sides, but open at the top and bottom. Frames that were only enclosed with plastic on two sides were used to test for artefacts of the frame. Cages to limit abrasion by artificial and natural kelp were made from wire mesh (5 cm square mesh) that totally enclosed settlement plates. Procedural control cages were incomplete cages that allowed kelp to abrade the surface of settlement plates.

Frames for the “shade” experiment were cubes (20 cm sides). Black Mylor[®] plastic roofs (20 cm × 20 cm) were attached to frames for the “shade” treatment, while clear Mylor[®] roofs were used to test for artefacts of the presence of frames and roofs. Unshaded plates were attached to boulders without frames or roofs.

5.4 RESULTS

Natural v. artificial abrasion

No difference was detected between natural and artificial abrasion on the colonisation of percentage cover or biomass of turf-forming algae (Figure 5.1a & b, Table 5.1). Abrasion had a significant negative effect on the colonisation of turf-forming algae, so that percentage cover was less when abrasion was present. However, Student Newman Keuls (SNK) comparison of means showed that percentage covers were the same when abrasion was present or absent, and that cover was greater when abrasion was absent (Figure 5.1a, Table 5.1). Abrasion had a significant negative effect on the colonisation of turf-forming algae, so that biomass was less when abrasion was present (Figure 5.1b, Table 5.1).

For the removal of percentage cover and biomass of turf-forming algae, there were no differences between natural and artificial abrasion (Figure 5.2a, Table 5.2). Biomass of turf-forming algae increased when abrasion was absent, but decreased when abrasion was present and for the procedural control (Figure 5.2b, Table 5.2).

Table 5.1 Results of two-factor ANOVAs testing for the effects of type of canopy (natural *v.* artificial) and abrasion (present *v.* absent *v.* procedural control) on the colonisation of (i) percentage cover and (ii) biomass of turf-forming algae. Ln (X) transformation was used on (ii) to remove heterogeneity from the data. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
		(i) Percentage cover			(ii) Biomass		
Canopy	1	486.00	0.47	0.500	0.723	1.17	0.294
Abrasion	2	4420.67	4.31	0.029	3.938	6.36	0.008
C × A	2	234.00	0.23	0.798	0.647	1.04	0.372
Residual	18	1025.56			0.647		

Table 5.2 Results of two-factor ANOVAs testing for the effects of type of canopy (natural *v.* artificial) and abrasion (present *v.* absent *v.* procedural control) on the removal of turf-forming algae, (i) change in percentage cover and (ii) biomass. Ln (X+1) transformation was used on (ii) to remove heterogeneity, but the data remained heterogeneous, so significance was judged at the more conservative $\alpha = 0.01$ (Underwood 1997). *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
		(i) Percentage cover			(ii) Biomass		
Canopy	1	640.67	0.98	0.336	0.006	0.11	0.741
Abrasion	2	1608.67	2.46	0.114	0.404	7.49	0.004
C × A	2	964.67	1.47	0.255	0.011	0.21	0.815
Residual	18	654.44			0.054		

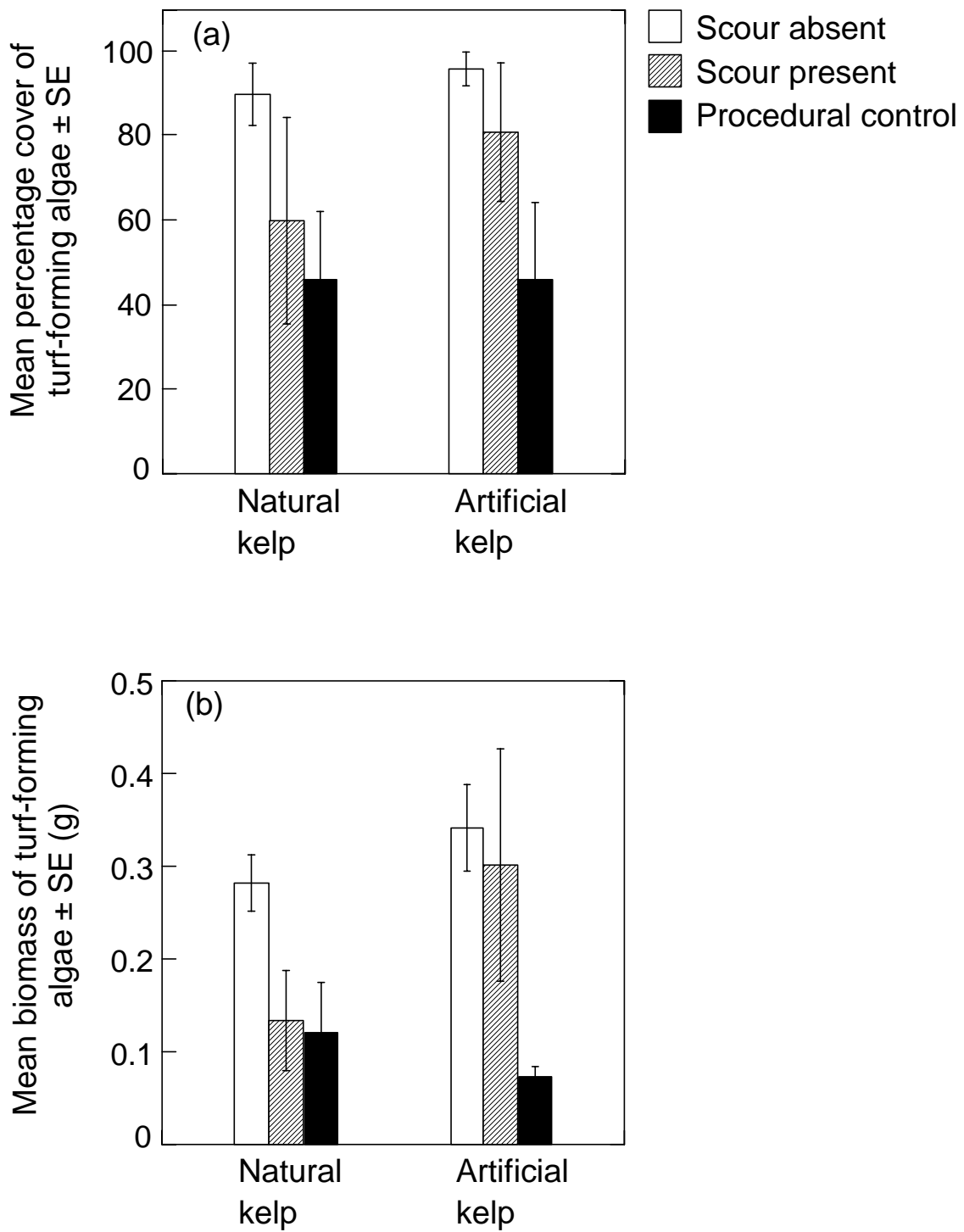


Figure 5.1 The effect of natural abrasion (absent *v.* present *v.* procedural control) and artificial abrasion (absent *v.* present *v.* procedural control) on the colonisation of turf-forming algae on bare settlement plates for (a) percentage cover and (b) biomass of turf-forming algae.

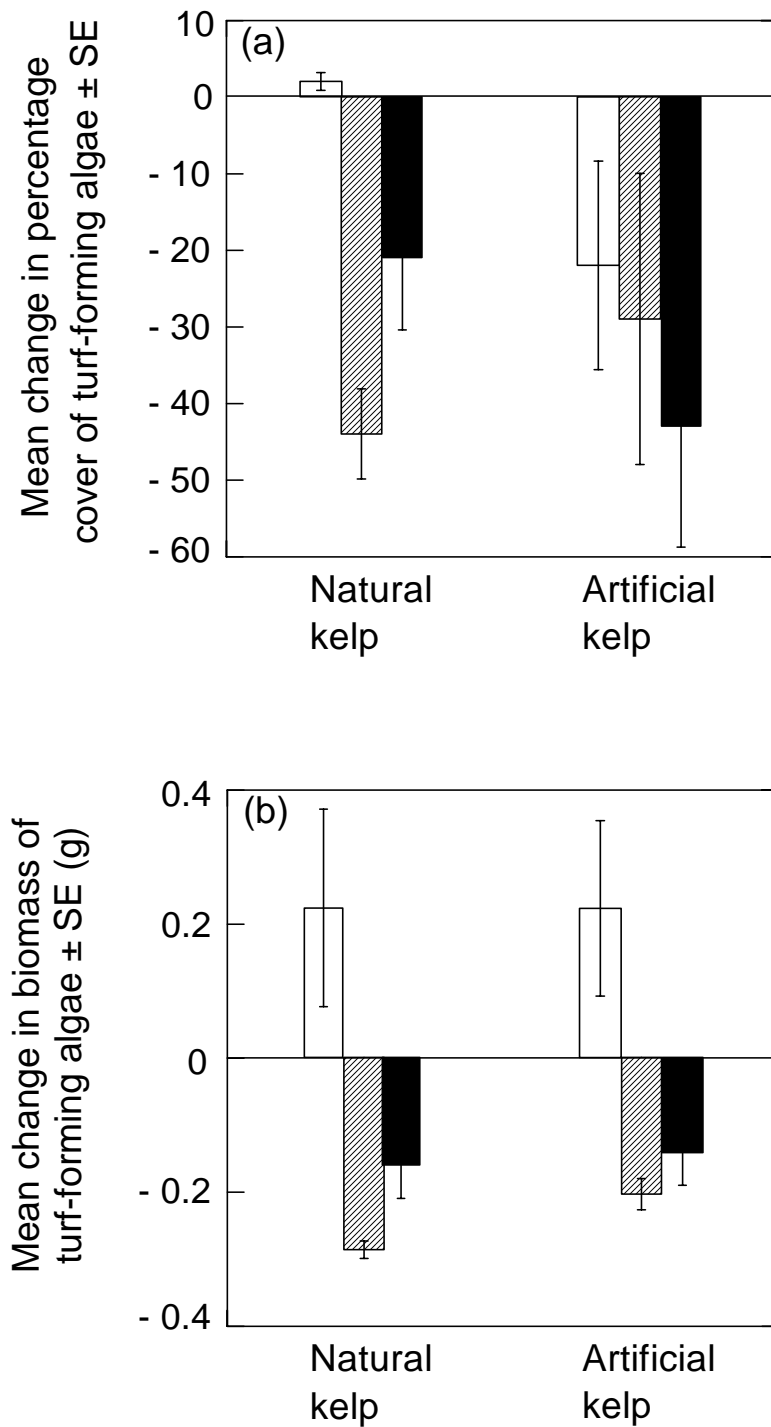


Figure 5.2 The effect of natural abrasion (absent *v.* present *v.* procedural control) and artificial abrasion (absent *v.* present *v.* procedural control) on the change in (a) percentage cover and (b) biomass of turf-forming algae on settlement plates. Treatments correspond to legend in Figure 1.

Effect of water flow and abrasion

Reduced water flow and the presence of abrasion by canopy had negative effects on the percentage cover of turf-forming algae. For the colonisation of turf-forming algae, flow and abrasion interacted so that when water flow was absent, percentage cover of algae was less when scour was present than absent (Figure 5.3a, Table 5.3a & b). There was also a significant effect of the partial cage (abrasion procedural control) when flow was absent. In contrast to percentage cover, biomass of turf-forming algae was only affected by abrasion, and was less when abrasion was present than absent (Figure 5.3b, Table 5.3a).

Water flow had a large effect on the removal of percentage cover of turf-forming algae. A greater percentage cover of turf-forming algae was lost from plates when water flow was absent than when flow was present (Figure 5.4a, Table 5.4). Both water flow and abrasion affected the removal of algal biomass. Biomass of turf-forming algae was reduced more when flow was absent than present (Figure 5.4b, Table 5.4) and reduced more when abrasion was present than absent (Figure 5.4b, Table 5.4).

Table 5.3 (a) Results of two-factor ANOVAs testing for the effects of water flow (present *v.* absent *v.* procedural control) and abrasion by artificial canopy (present *v.* absent *v.* procedural control) on the colonisation of (i) percentage cover and (ii) biomass of turf-forming algae, (b) SNK comparison of means for the significant flow \times abrasion interaction for percentage cover. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

(a) Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
		(i) Percentage cover			(ii) Biomass		
Flow	2	2907.11	3.18	0.057	0.035	1.35	0.276
Abrasion	2	2760.44	3.02	0.065	0.125	4.82	0.016
<i>F</i> \times <i>A</i>	4	3591.11	3.93	0.012	0.047	1.81	0.156
Residual	27	913.19			0.026		

(b) Pairwise comparisons for percentage cover

Flow

Present Abrasion present = Abrasion absent = Procedural control

Absent Abrasion present \ll Abrasion absent = Procedural control

Abrasion

Present Flow absent < Flow present = Procedural control

Absent Flow absent = Flow present = Procedural control

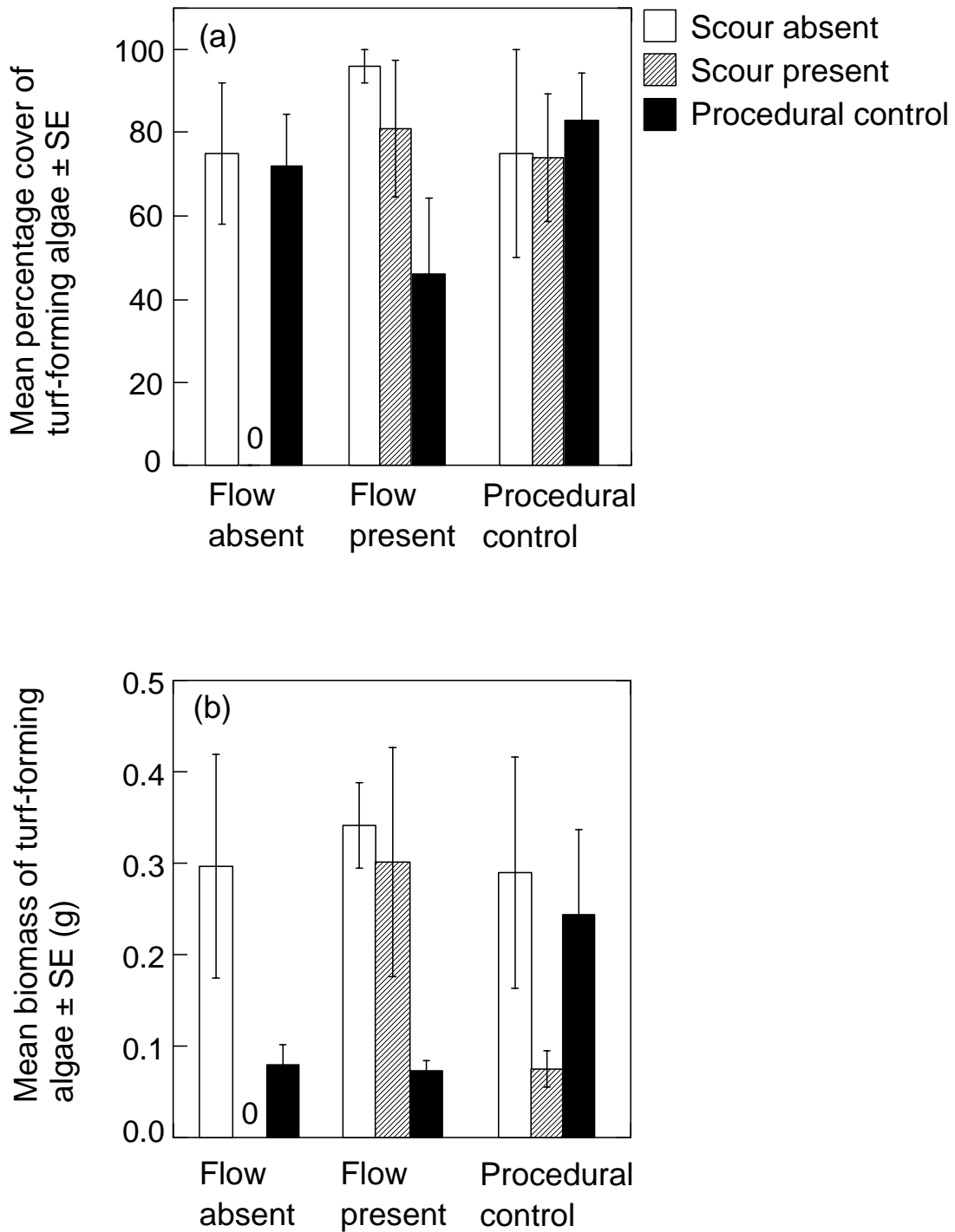


Figure 5.3 The effect of water flow (absent *v.* present *v.* procedural control) and canopy abrasion (absent *v.* present *v.* procedural control) on the colonisation of turf-forming algae on bare settlement plates. (a) percentage cover and (b) biomass of turf-forming algae. “0” indicates 0 % cover or 0 g biomass.

Table 5.4 Results of two-factor ANOVAs testing for the effects of water flow (present *v.* absent *v.* procedural control) and abrasion by artificial canopy (present *v.* absent *v.* procedural control) on the removal of turf-forming algae, (i) change in percentage cover and (ii) biomass. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

Source	<i>df</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
		(i) Percentage cover			(ii) Biomass		
Flow	2	7744.00	8.83	0.001	3.993	5.42	0.011
Abrasion	2	185.33	0.21	0.811	2.495	3.39	0.049
F × A	4	565.33	0.64	0.635	0.152	0.21	0.932
Residual	27	877.33			0.734		

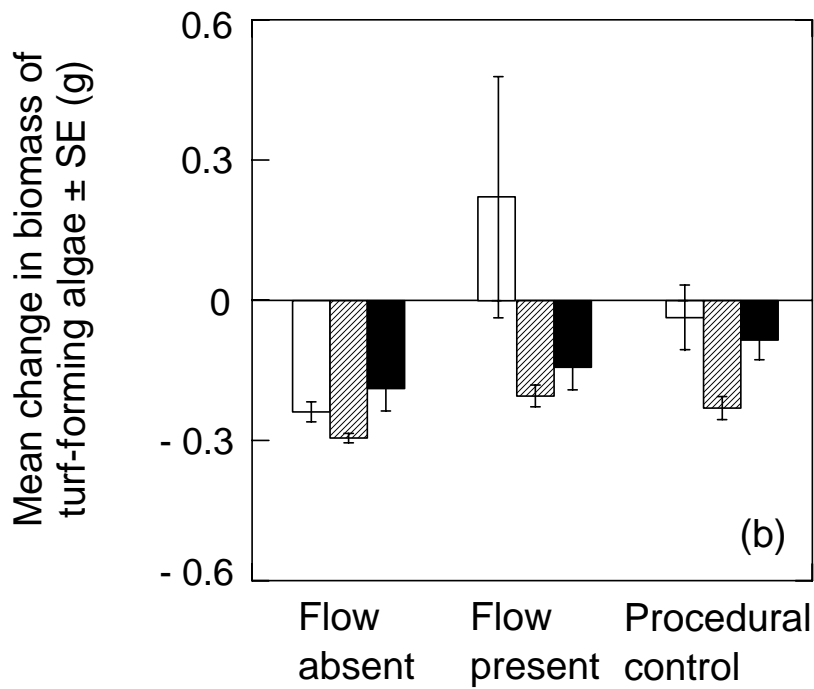
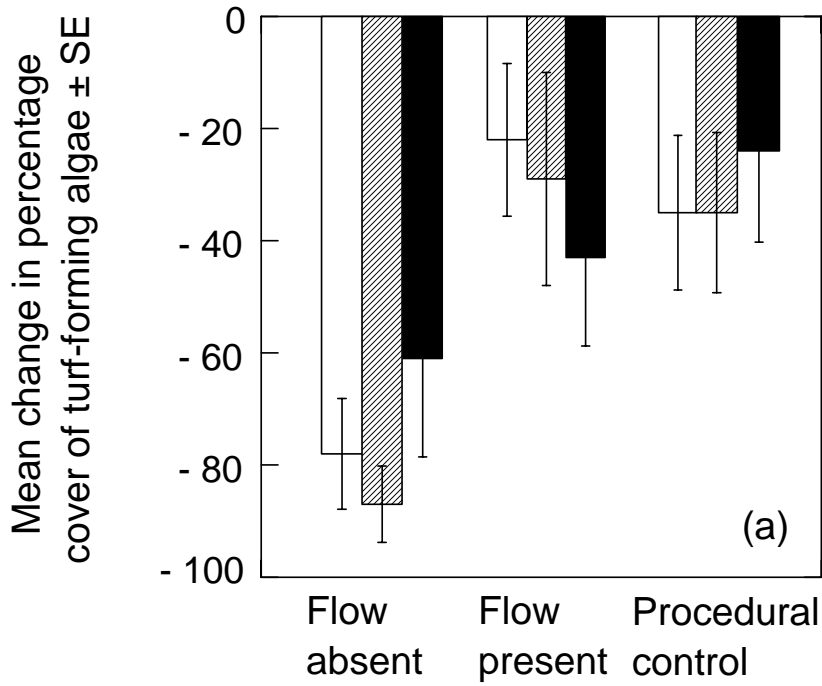


Figure 5.4 The effect of water flow (absent *v.* present *v.* procedural control) and canopy abrasion (absent *v.* present *v.* procedural control) on the change in (a) percentage cover and (b) biomass of turf-forming algae on settlement plates. Treatments correspond to legend in Figure 1.

Effect of shade

Reduced light (shade) had mixed effects on the colonisation of turf-forming algae. The percentage cover of turf-forming algae that colonised was not affected by shade (Figure 5.5a, Table 5.5). In contrast, shade had a large effect on the biomass of turf-forming algae, so that there was less biomass under shade than under full light (Figure 5.5a, Table 5.5). For the removal of turf-forming algae, the change in both percentage cover and biomass was affected by shade. In full light, both the percentage cover and biomass of algae increased, while under shade percentage cover and biomass decreased (Figure 5.5b, Table 5.6).

Tests for differences in light and flow conditions

The light intensity under artificial canopy was affected by water flow. Light intensity was much less when water flow was absent than present (mean \pm SE; flow absent $4.9 \pm 1.6 \mu\text{moles m}^{-2} \text{s}^{-1}$; flow present $52.6 \pm 2.1 \mu\text{moles m}^{-2} \text{s}^{-1}$; procedural control $22.7 \pm 1.9 \mu\text{moles m}^{-2} \text{s}^{-1}$; ANOVA: $F_{2,18} = 89.23$, $P < 0.0001$). Light intensity was much less under natural canopies ($14.0 \pm 6.2 \mu\text{moles m}^{-2} \text{s}^{-1}$) than under artificial canopies when flow was present ($52.6 \pm 2.1 \mu\text{moles m}^{-2} \text{s}^{-1}$), and was least under artificial canopies when water flow was absent ($4.9 \pm 1.6 \mu\text{moles m}^{-2} \text{s}^{-1}$) (artificial canopy flow absent *v.* flow present *v.* natural canopy; ANOVA: $F_{2,6} = 45.88$, $P < 0.001$). This difference is possibly because when water flow was absent, the artificial canopy remained motionless above settlement plates, but when water flow was present the artificial canopy would move on and off the plates in different directions, leaving the plate totally uncovered for short periods (B. Russell, pers. obs.). In contrast, even in high flow conditions, part of the natural canopy always seemed to be covering the settlement plates, leaving very little time that plates were totally uncovered.

Light intensity was different among treatments of shade (ANOVA: $F_{2,6} = 26.80$, $P = 0.001$), so that shade $<$ open = procedural control ($6.0 \pm 1.4 \mu\text{moles m}^{-2} \text{s}^{-1}$; $182.3 \pm 30.8 \mu\text{moles m}^{-2} \text{s}^{-1}$; $177.2 \pm 13.4 \mu\text{moles m}^{-2} \text{s}^{-1}$, respectively). Light intensity under shade roofs was similar to light intensity in the absence of water flow (artificial flow *v.* abrasion experiment: $4.9 \pm 1.6 \mu\text{moles m}^{-2} \text{s}^{-1}$) and under natural kelp canopies ($14.0 \pm 6.2 \mu\text{moles m}^{-2} \text{s}^{-1}$). In the presence of water flow, light intensity was greater under artificial kelp canopy ($52.6 \pm 2.1 \mu\text{moles m}^{-2} \text{s}^{-1}$) than under natural kelp

canopies ($14.0 \pm 6.2 \mu\text{moles m}^{-2} \text{ s}^{-1}$). The greater shading under artificial canopies, when water flow was absent, than under natural canopies creates problems for interpreting the effects of water flow, because any observed effect may be a result of the greater shading, and not a result of a reduction of water flow *per se*. The greater light intensity under artificial canopies, in the presence of water flow, also creates problems for comparing results between artificial and natural canopies, because the greater light intensity makes it less likely to detect an effect of canopy. However, because light intensity was not reduced as much under artificial canopies as natural canopies when water flow was present, this leads to a more conservative experimental test and a greater likelihood of rejecting the alternative hypothesis.

The percentage of mass lost from plaster clods was affected by water flow. Less mass was lost when water flow was absent ($43.6 \pm 0.6 \%$) than present ($54.3 \pm 0.6 \%$) or in the procedural control ($51.7 \pm 0.6 \%$; two-factor ANOVA flow \times abrasion: $F_{2,18} = 100.89$, $P < 0.0001$). When water flow was present, a greater percentage of mass was lost from clods under artificial canopies (flow present: $55.7 \pm 0.2 \%$) than under natural canopies ($52.4 \pm 0.8 \%$), but loss from under artificial canopies did not differ from clods in the open ($55.8 \pm 0.4 \%$; single-factor ANOVA: $F_{2,6} = 14.96$, $P < 0.005$). This result indicates that artificial canopies were not slowing water flow to the same degree as natural canopies. As with light intensity, this difference between artificial and natural canopies creates difficulties in interpretation, because the greater water flow makes it less likely to detect treatment effects, but is a more conservative test of experimental effects.

Table 5.5 Results of single-factor ANOVAs testing for the effects of reduction in light intensity (shade *v.* open *v.* procedural control) on the colonisation of (i) percentage cover and (ii) biomass of turf-forming algae. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
		(i) Percentage cover			(ii) Biomass		
Shade	2	32.89	1.27	0.310	0.117	8.20	0.004
Residual	15	25.96			0.014		

Table 5.6 Results of single-factor ANOVAs testing for the effects of reduction in light intensity (shade *v.* open *v.* procedural control) on the removal of turf-forming algae, (i) change in percentage cover and (ii) biomass. Ln (X+1) transformation was used on (i) and (ii) to remove heterogeneity, but the data remained heterogeneous, so significance was judged at the more conservative $\alpha = 0.01$ (Underwood 1997). *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
		(i) Percentage cover			(ii) Biomass		
Shade	2	896.89	8.02	0.004	0.309	7.18	0.007
Residual	15	111.82			0.043		

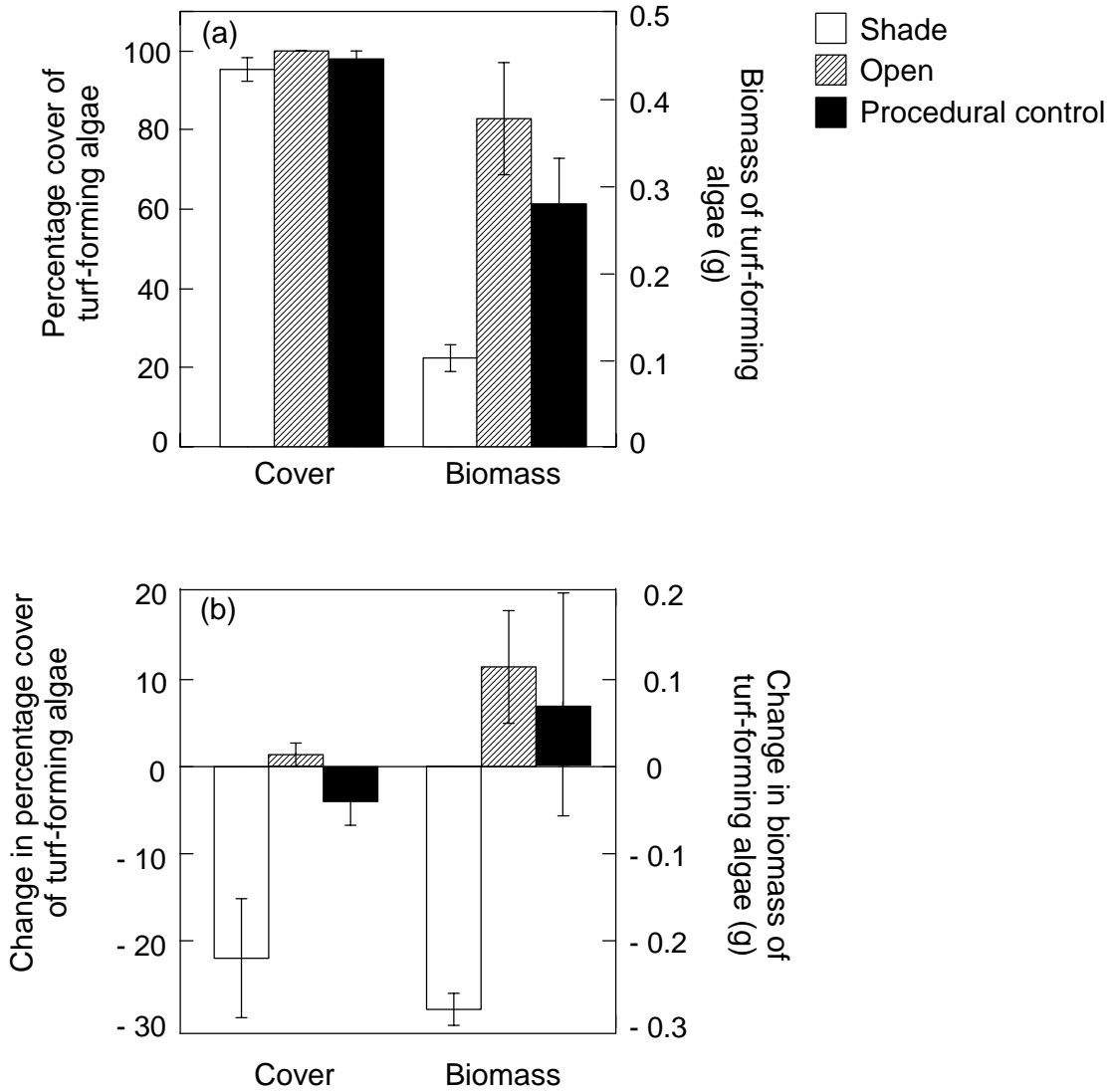


Figure 5.5 The effect of light (shade *v.* open *v.* procedural control) on (a) the colonisation of turf-forming algae, shown as percentage cover and biomass and (b) the change in percentage cover and biomass of turf-forming algae.

5.5 DISCUSSION

Effect of water flow

A key finding of this study was that water flow had a large effect on the early colonisation of turf-forming algae under canopies. The effect of physical abrasion by kelp canopies on the benthos seems to increase with increasing water flow (Kennelly 1989), so I expected that when flow was reduced, the movement of canopy across the surface of settlement plates would be less, thus reducing abrasion. This reduced abrasion should then mean that the canopy would remove less turf-forming algae. In contrast, the canopy removed a greater percentage cover and biomass of turf-forming algae when water flow was reduced. Abrasion did not remove turf-forming algae, so abrasion alone cannot account for the effect that was detected. Therefore, it is likely that other factors, such as light intensity or nutrient availability, were altered by a reduction in flow, and consequently caused the differences in algal growth.

The light intensity reaching the substrate through algal canopies is often used to explain the structuring of understory assemblages and the changes that occur when canopy is removed (Reed & Foster 1984; Kennelly 1989; Connell 2003a). In the reduced water flow treatment, the amount of light under artificial kelp canopy was an order of magnitude less than when water flow was present, and was similar to under the shade roofs. Reduced light under kelp canopies can structure understory assemblages (Reed & Foster 1984; Kennelly 1989; Connell 2003a, 2005), so the reduced light under canopies in the reduced flow treatment could account for the reduction in the biomass and percentage cover of turf-forming algae. There was, however, a greater loss of percentage cover of turf-forming algae when water flow was reduced (~ 80 % loss) than under the shade roofs (~ 20 % loss). This difference suggests that a reduction in light intensity may only account for part of the loss seen when water flow is reduced, especially given that the treatments reduced light intensity to artificially low levels compared to under natural kelp canopies.

The effect of water flow on nutrient uptake by macroalgae is not a simple relationship, but in general, uptake of nutrients is limited at slower water velocities (Wheeler 1980; Hurd et al. 1996; Williams & Carpenter 1998; Ryder et al. 2004), because at lower water velocities a boundary layer of nutrient depleted water rapidly

forms around algae (Hurd 2000). Furthermore, filamentous turf-forming algae have a physiology that is suited to quick uptake of nutrients (Hein et al. 1995; Pedersen & Borum 1996), and are more likely to be affected by any boundary layer of water that is poor in nutrients (Hurd 2000). In the present study, there was a decrease in biomass and percentage cover of turf-forming algae when water flow was reduced. Although reduced light intensities in the reduced flow treatment may account for some of the loss of percentage cover and biomass of turf-forming algae (see previous paragraph), it is possible that when water flow was reduced, the rapid uptake of nutrients by turf-forming algae caused a boundary layer of nutrient depleted water to rapidly form, and may also account for some of the reduced biomass and percentage cover that I observed.

Effect of abrasion

Physical abrasion by canopy algae is known to reduce the biomass of erect forms of benthic algae (Kennelly 1989; Kendrick 1991; but see Toohey et al. 2004). My results for natural and artificial abrasion conform to this pattern, as when I removed abrasion by canopies there was greater biomass of turf-forming algae on settlement plates. In an experiment investigating factors that affect colonisation of turf-forming algae, Kendrick (1991) found that artificial abrasion reduced percentage cover and biomass of turf-forming algae, but that there was a greater negative effect on biomass. In the present study, abrasion had a greater effect on the biomass of turf-forming algae than the percentage cover. It is possible that biomass of turf-forming algae is quickly lost to canopy abrasion, but when the algal filaments are smaller than a critical vertical height no more is lost. If this is so, biomass could be lost without a corresponding reduction in percentage cover.

To my knowledge, this is the first study to investigate the interactive effects of water flow and abrasion on algal colonisation. Other studies on water flow have concentrated on either the effects of flow on sedimentation under canopies (e.g. Eckman et al. 1989) or nutrient uptake by algae (e.g. Wheeler 1980; Hurd et al. 1996). Furthermore, other studies have successfully used artificial abrasion to experimentally assess the effects of canopies on benthic algae (e.g. Kendrick 1991; Toohey et al. 2004), but this is the first study to compare artificial and natural

abrasion, providing an estimate of the effectiveness of the artificial abrasion at mimicking natural abrasion.

I did not detect any difference between abrasion by natural and artificial kelp. However, for the colonisation of turf-forming algae, the mean percentage cover and biomass appeared to be greater for artificial kelp than natural kelp, but the large variation in samples from the artificial kelp possibly meant that no difference was detected statistically. Furthermore, water flow was also reduced by natural kelp canopy but not artificial kelp (percentage of plaster clods lost), and light intensity was almost 4 times greater under artificial kelp than natural kelp canopies. Even though no difference was detected between the effects of natural and artificial kelp canopies on turf-forming algae, it is probable that a combination of the greater water flow and greater light meant that the artificial kelp only accounted for a percentage of the effect of natural kelp. For the colonisation of turf-forming algae, it is likely that artificial canopy accounted for ~ 80 % of the effect for percentage cover, and 50 % for biomass. Furthermore, density of kelp is known to influence understory composition (Kendrick et al. 1999), and my artificial kelp may have been more consistent with sparse densities of natural kelp than used in this study. However, the greater light intensity and water flow are likely to make my interpretation of treatment effects more conservative, increasing the higher likelihood of accepting the null hypothesis.

Effect of Shade

The percentage cover of turf-forming algae that colonised settlement plates did not differ between shaded and full light treatments. In contrast, ~ 20 % more percentage cover and ~ 75 % more biomass was removed under shade than full light conditions. The difference in response suggests that turf-forming algae can show acclimation to low light levels when assembling under reduced light, but these same low light levels will cause reduction of percentage cover and biomass when the turf-forming algae have colonised under higher light conditions. Algae are known to acclimate to differences in available light by changing the concentration of photosynthetic pigments within short periods (King & Schramm 1976; Ramus et al. 1976a; Ramus et al. 1976b; Henley & Ramus 1989; Lüder & Knoetzel 2002), and some algae are

known to have higher photosynthetic rates in limited light compared to full sunlight (Irving et al. 2004a). It is unlikely, however, that acclimation would occur over longer times, because shading experiments at the same location (Connell 2003 & 2005) detected a reduction of turf-forming algae of ~ 52 % over 300 days.

Conclusion

Abrasion by kelp in southern Australia facilitates prostrate forms of encrusting coralline algae by suppressing erect forms of algae (Melville & Connell 2001) and excluding sessile invertebrates (Connell 2003b). These experimental effects match naturally occurring patterns across western and southern Australia (Fowler-Walker & Connell 2002). My experimental results are consistent with this pattern, but I have shown that the effects of abrasion are altered by the amount of water flow through a canopy. Some of the ability of canopies to suppress turf-forming algae is also due to the reduction in light intensity by a canopy (Connell 2003a), but it seems likely that shading under canopies will be greater in lower flow environments. Furthermore, I suggest that the reduction in abundance of turf-forming algae in the reduced water flow under canopies may be partly caused by nutrient limitation, an area that requires further study. To understand how canopies of algae can suppress the colonisation of turf-forming algae, and how this may reduce the frequency with which habitats switch from canopy to turf dominated, it is useful to understand the mechanisms by which canopies alter the physical environment.



An example of the artificial habitats used to test for the effects of size of neighbouring habitat and isolation of habitats on the invertebrate assemblage (top) and articulated coralline algae at the field site (bottom). Photos: author (top) and Andrew Irving (bottom).

CHAPTER SIX



PROXIMITY AND SIZE OF NEIGHBOURING HABITAT AFFECTS INVERTEBRATE DIVERSITY

CHAPTER SIX PREAMBLE

Habitat loss and fragmentation (through natural or anthropogenic disturbance) affects the fauna inhabiting habitat patches. Chapter 6 investigates the interactive effects of the size and the proximity of neighbouring turf habitat on macroinvertebrate assemblages, species richness, and abundance. The artificial habitats used in this experiment are structurally similar to the articulated coralline algae at the field site which can form large turfs.

This chapter is a co-authored paper in press in Marine Ecology Progress Series, and as such is written in plural throughout. The paper can be cited as:

Russell B.D., Gillanders B.M. and Connell S.D. 2005. Proximity and size of neighbouring habitat affects invertebrate diversity. *Marine Ecology Progress Series*, **in press**

In this paper Bronwyn Gillanders and Sean Connell had input into the development of the original idea for the experiment. They supplied part of the funding and Sean Connell helped with the fieldwork. I set up and ran the experiment, sorted the samples and identified the macrofauna, did the data analysis and wrote the paper.

Signatures of co-authors:

Signed:

Bronwyn M. Gillanders

Signed:

Sean D. Connell

CHAPTER SIX

This publication is included on pp. 111-130 in the print copy of the thesis in the University of Adelaide Library.

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The research vessel ("*Odax*") used throughout my research, viewed from West Island.
Photo: Author.

CHAPTER SEVEN



GENERAL DISCUSSION

CHAPTER SEVEN

GENERAL DISCUSSION

Massive changes to coastal habitats are forecast as a result of increasing nutrient availability from human activities (Vitousek et al. 1997a; Worm et al. 1999). Grazing by herbivores can counter the effects of nutrient enrichment on algal habitats (Lotze et al. 2001; Hillebrand 2003), yet humans continue to increase harvesting of herbivores. To enable the management of activities that are likely to have impacts on coastal habitats, we need to know the interactive effects of factors such as nutrients, grazing, and loss of algal canopies, and how these factors structure the benthos. In this thesis, I have shown that elevated nutrient concentrations cause an increase in the abundance of turf-forming algae growing on kelp on coasts of low nutrient concentration to match that of coasts of high nutrient concentration (Chapter 2). Although turf-forming algae tend to rapidly colonise and dominate available space (Melville & Connell 2001), grazers can reduce the abundance of turfs in the presence of elevated nutrients (Chapter 4), causing a shift in algal abundance (Chapter 3). This shift away from spatial monopolies of turf-forming algae is important to understand because turf-forming algae can inhibit the settlement of longer-lived, canopy-forming algae (Devlinny & Volse 1978; Sousa et al. 1981; Kennelly 1987a), and the presence of an algal canopy further reduces the abundance of turf-forming algae (Chapter 5). Finally, I experimentally demonstrated that the fragmentation of turf-like habitats has strong effects on assemblages of invertebrates that use them for habitat (Chapter 6).

This chapter provides a discussion of the key points of the individual chapters, and how they are linked. Finally, future directions for research are suggested and final conclusions mentioned.

7.1 Effects of elevated nutrients, algal canopy and grazing on turf-forming algae

To understand how to manage the impact of increasing availability of nutrients in coastal waters, we need to know both the geographical scale over which nutrients may vary, and their effects. I assessed local to regional scale relationships between

the abundance of epiphytic algae on kelp (*Ecklonia radiata*) and nutrient concentrations across much of the temperate coast of Australia, thus, assessing the spatial scales over which nutrients may affect benthic assemblages. I found that the percentage cover of epiphytes was, in general, greater at locations with higher nutrient concentrations, and that the cover of epiphytes was most extensive around the coast of Sydney, the study location with the greatest concentration of coastal nutrients (Chapter 2). Although there was some among site variation in the abundance of epiphytes (kms), the greatest differences were seen among locations (100s kms). Importantly, it is over this broader scale that we detected large differences in the ambient concentration of nutrients.

The relationship between water nutrient concentrations and epiphyte abundance observed in the broad scale study was correlative, so I took the extra step of experimentally elevating water nutrient concentrations to assess the extent to which I could match the more extensive epiphyte covers observed at more nutrient rich locations. At a location in South Australia, I was able to increase the percentage cover of turf-forming algae growing as epiphytes to be comparable to the percentage covers observed around Sydney's coastline (Chapter 2). This result was achieved despite the inability to match nutrient concentrations observed around Sydney (< 5 % of Sydney concentrations), suggesting that increases in nutrient concentrations may have disproportionately larger effects in oligotrophic waters.

Elevated nutrient concentrations are likely to affect benthic algae both directly (e.g. altering competitive dominance) and indirectly (e.g. through removal of canopy algae because of reduced health). These effects are likely to be moderated by grazing (Hillebrand et al. 2000; Lotze et al. 2001; Hillebrand 2003), but little experimental work has been done in a system that has weak grazing pressure, which is also subjected to elevated nutrients. I established that the loss of canopy-forming algae is likely to be a key precursor to nutrient driven changes of assemblages of benthic algae, because nutrients had no effect on algal assemblages in the presence of canopy-forming algae (Chapter 3), which is possibly related to the ability of canopy algae to structure the benthos (Chapter 5; Kennelly 1989; Bertness et al. 1999; Bruno 2000; Connell 2003; Irving 2005). In the absence of an algal canopy, space was

monopolised by turf-forming algae, but in the presence of elevated nutrients, grazers reduced the monopoly of turf-forming algae in favour of foliose algae (Chapter 3). It seems that in the presence of elevated nutrients, grazers can preferentially reduce the abundance of turf-forming algae to a greater extent than in the presence of ambient nutrients, thus, reducing the effect of nutrients. Furthermore, it is possible that in the presence of elevated nutrients, grazers are an important check against the possibility of habitat switches from canopy-forming to turf-forming algae that are seen in other systems (Hughes et al. 2005).

Herbivores can preferentially consume greater amounts of plants and algae containing higher nutrient content (Neckles et al. 1993; Williams & Ruckelshaus 1993; Karez et al. 2000; Silliman & Zieman 2001) and, therefore, may be able to counter the negative effects of elevated nutrients (Roll et al. 2005). This observation may be useful to understand in systems that are changing to become dominated by opportunistic algae (e.g. turf-forming algae) as a consequence of elevated nutrients. By exposing turf-forming algae to elevated concentrations, I found that molluscs consumed a greater percentage cover of nutrient rich turf-forming algae, and this translated to an increase in biomass of turf-forming algae (Chapter 4). Importantly, the greater consumption of more nutrient rich algae by grazers may be an important mechanism in countering the effects of coastal eutrophication. Furthermore, grazers with historical access to nutrient poor algae, as found on oligotrophic coasts, consumed greater amounts of nutrient rich turf-forming algae than grazers with historical access to nutrient rich algae. As increased nutrient concentrations may have a disproportionately large effect on oligotrophic coasts (Chapter 2), grazers may play a large role in countering the negative effects of elevated nutrients on these coasts.

7.2 Effects of reduced water flow and abrasion on turf-forming algae

There are predictable associations between canopies formed by algae and the benthic understorey, and these associations are maintained by the canopy altering the physical environment (Chapter 5; Kennelly 1989; Bertness et al. 1999; Bruno 2000; Connell 2003a, b; Irving et al. 2004; Irving 2005). With the increase in switches from habitats dominated by canopy-forming to turf-forming algae, it is useful to

understand how canopies of algae suppress turf-forming algae. Two physical factors that are modified by an algal canopy, and are likely to affect the abundance of turf-forming algae, are abrasion by the canopy and water flow. I expected that a reduction in water flow would cause reduced abrasion (Kennelly 1989; Toohey et al. 2004), and therefore an increase in the abundance of turf-forming algae. I found that while a reduction in abrasion increased the abundance of turf-forming algae, reducing water flow had a negative effect on the abundance of turf-forming algae (Chapter 5). It is likely that the negative effect of reduced water flow was a combination of the increased shading associated with a reduction in canopy movement, and a reduction in nutrient uptake by turf-forming algae (e.g. Wheeler 1980; Hurd et al. 1996).

Canopies of algae are able to counter the negative effects of elevated nutrients (Chapter 3), but it is likely that this ability would depend on the strength of abrasion by the canopy. Abrasion is reduced when there is less water movement (Kennelly 1989; Toohey et al. 2004), so it could be expected that the ability of canopies to counter the effects of nutrients would be less when there is less water flow. However, when water flow is reduced, the availability of nutrients for turf-forming algae will also be reduced (Hurd 2000), countering the positive effect of elevated nutrients on abundance of turf-forming algae (Chapter 2).

7.3 Effect of fragmentation of turf habitats on invertebrate diversity

Species richness and abundance of animals are often not independent of neighbouring habitats (Wiens et al. 1993; Hanski 1999). There is increasing evidence that within protected areas the size and number of harvested species increase (e.g. Roberts 1995; McClanahan & Kaunda-Arara 1996; Edgar & Barrett 1999; Halpern & Warner 2002), but concern also centres on whether changes to adjacent habitats (e.g. unprotected habitats) can affect the conservation value of protected habitats (Allison et al. 1998; Boersma & Parrish 1999; Lenihan et al. 2001). The extent to which these concerns are real may be affected by differences in dispersal mode and capacity of the target animals. I tested the interactive effects of size and isolation of neighbouring habitats on the assemblage composition, species richness and abundance of two taxonomic groups with contrasting adult dispersal modes (Chapter 6). I found that isolation of habitats had a greater negative effect on fauna with more

limited dispersal, but that richness and abundance of rapid dispersers were greater in habitats that were far from small habitats. These results suggest that impacts at greater distances from habitat will potentially have greater effects on taxa with greater dispersal capabilities, and that local impacts will be more important for taxa with limited dispersal capabilities. Importantly, these results reinforce the need to consider issues of dispersal of taxa, and proximity to neighbouring habitats, when planning protected areas to achieve conservation goals.

The size and isolation of turf habitats can be affected by a number of factors. Elevated concentrations of nutrients in the water can increase (Chapters 2), and grazing decrease (Chapters 3 & 4), the size of turf habitats. Physical removal of turf by algal canopies (Chapter 5) and other physical disturbances (e.g. trampling: Brown & Taylor 1999) can also reduce the size of turf habitats. As the species richness and abundance of macroinvertebrates within habitats is affected by the size and isolation of turf habitats (Chapter 6), it is likely that processes affecting turf habitats will also affect their inhabitants. Although there may be some direct effect of these processes on the inhabitants (i.e. mortality), it seems likely that changes in assemblages are largely due to indirect effects associated with habitat loss (e.g. Brown & Taylor 1999).

7.4 Future research

In Chapter 2, I assessed the validity of a positive correlation between water nutrient concentration and epiphyte abundance on kelp with an experiment done at one site in South Australia. To fully assess this relationship, experiments need to be done at a number of sites, across temperate Australia, which have a range of ambient nutrient concentrations. Furthermore, by using simultaneous experiments in regions with different ambient nutrient concentrations, it would be possible to determine if the effect of elevated nutrients is greater on oligotrophic coasts. This knowledge would allow greater understanding of how to structure management of nutrient inputs, and where to allocate resources, as effects may be greater on oligotrophic coasts.

It seems that in the presence of elevated nutrients, grazers can reduce the cover of turf-forming algae, allowing longer-lived algae, such as kelp, to colonise (Chapter 3).

However, turf-forming algae are ephemeral and have low abundance during winter, a period of high recruitment for the kelp *Ecklonia radiata*. Experiments assessing the interactive effects of canopy, elevated nutrients and grazing need to be done over multiple seasons to assess if the presence of elevated nutrients (and reduced grazing) allows turf-forming algae to maintain dominance over available space, or if the seasonal loss of turfs allows longer lived algae to colonise, regardless of nutrient concentration.

Grazers are able to counter the effects of elevated nutrients (Chapter 4, Hillebrand et al. 2000; Lotze et al. 2001; Hillebrand 2003), but, to my knowledge, this study is the first to show that grazers can reduce biomass of turf-forming algae that has been exposed to elevated nutrients to be less than algae exposed to ambient nutrients (Chapter 4). However, as identified in Chapter 4, the densities of grazers on experimental reefs were as high, or higher, than densities recorded on natural reefs close to the experimental site, yet still less than on other temperate coasts (up to 1000 m⁻²: Norton et al. 1990). To assess the generality of the response of grazers to elevated nutrients, this experiment needs to be done on natural reefs at a number of sites, including reefs adjacent to urbanised coasts, because these coasts are the most likely to have a reduction of herbivores and increases in nutrient concentrations.

In Chapter 4, I was unable to determine if the greater consumption of turf-forming algae in the presence of elevated nutrients was a function of increased per capita consumption or the redistribution of grazing pressure. Controlled experiments could be done in aquaria to identify the per capita grazing rates of these molluscs in the presence and absence of elevated nutrients. Furthermore, field experiments using turf-forming algae that had been grown in the presence of enriched ¹⁵N would enable isotope analysis of grazer tissue to determine the proportion of molluscs in an area (or on experimental reefs) that were consuming turf-forming algae exposed to elevated nutrients.

It is well established that algal canopies can structure the benthic understorey through positive (Bertness et al. 1999; Bruno 2000; Connell 2003a; Irving et al. 2004a) or negative interactions (Chapter 5; Reed & Foster 1984; Kennelly 1989;

Irving 2005). In Chapter 5, I showed that canopies reduce the abundance of turf-forming algae, but that this effect is modified by water flow. If a gap is created in the kelp canopy, light, water flow, sedimentation, and abrasion by the canopy are all modified. Turf-forming algae are facilitated by full light, increased sediment deposition and reduced abrasion by canopies (Kennelly 1987a; Airoidi 1998; Airoidi & Virgilio 1998; Connell 2003a, 2005), which may allow turf-forming algae to dominate newly created space within kelp canopies (e.g. Melville & Connell 2001). To understand how kelp canopies re-establish, and dominate space, it needs to be determined if kelp re-establish from the edge of patches (e.g. through the effects of abrasion and shading by surrounding canopy) or from within the gap through propagule settlement (e.g. through seasonal loss of turf-forming algae). However, even if propagules settle in the middle of gaps, the survival of propagules and recruits within gaps may determine how kelp recolonise gaps. By studying propagule settlement and recruit survival in gaps of differing sizes (from small to very large), over multiple seasons, it would be possible to identify if there is a critical size of gap in which kelp cannot re-establish, possibly leading to habitat switches.

In Chapter 6, I compared two taxonomic groups with different modes of adult dispersal, making identification to morphospecies sufficient to detect experimental effects. Although morphological “species” are useful for testing ecological hypotheses (e.g. Steneck & Dethier 1994; Oliver & Beattie 1996), identifying fauna to species would provide more specific knowledge of the treatment effects, and may provide more detailed information on the potential effects of variation due to diet, predation and reproductive modes. Furthermore, this study could be extended to test other hypotheses about movement of animals among habitats. In natural systems, fauna in a habitat are likely to have links to more than one neighbouring habitat, as similar habitats are rarely in pairs. Furthermore, the arrangement of habitats is likely to vary in configuration, such as linear (along a coast) or grouped (more offshore). Both the continuity and spatial arrangement of habitats affect community assemblages (Hanski 1999), but the effects are likely to vary with dispersal ability (Bowman et al. 2002). Turf habitats would be useful to test hypotheses on how faunal assemblages are altered by the arrangement of habitats, and position of a habitat within this arrangement (e.g. edge *vs* centre).

7.5 Conclusions

Increasing nutrient concentrations in coastal waters can cause shifts in benthic habitats from canopy dominated to turf dominated assemblages (Worm et al. 1999), and these switches can be maintained for decades (Jackson 2001; Eriksson et al. 2002). In this thesis, I have demonstrated that although it is possible to make some generalisations about the effects of elevated nutrients (e.g. increased nutrients lead to increases in epiphyte abundance), generalisations may not be possible among regions of different nutrient regimes. I have also shown that increased grazing by herbivores can reduce the negative effects of elevated nutrients, but the effectiveness of this control is likely to vary among regions of different consumer pressure. Furthermore, increases in nutrient availability are likely to occur simultaneously to other human impacts, such as increased harvesting of herbivores, reducing the ability of grazing to counter the effects of elevated nutrients. To effectively manage the effects of increasing coastal nutrient concentrations, it is useful to understand how nutrients and grazers interact in regions of different nutrient inputs and consumer pressures. Indeed, maintaining more desirable habitat states (i.e. habitat formed by canopy algae) may depend on understanding these interactions.

APPENDIX A



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CHAPTER 2

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CHAPTERS 3 AND 6

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