

**STRENGTH OF SEA URCHIN HERBIVORY AND  
CONDITION FROM BIOGEOGRAPHIC TO  
ORGANISMAL SCALES**



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*Dedicated to Maria Eugenia and Mya with all my love.*

Cover image: *Heliocidaris erythrogramma* in South Australia on a limestone reef that supports high local densities. Photo in cover image: Nicholas Payne

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Juan Pablo Livore

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## ABSTRACT

Amongst the many ecological processes that can have an influence on community structure within marine ecosystems, herbivory is recognised as having an important role. Algae are not only living components of the community, they often provide a physical structure, food and protection indispensable for many other species. Therefore, understanding herbivore behaviour and their effects on the surrounding habitat is vital to further comprehend benthic marine ecosystem dynamics. Strength of herbivory is often determined by simple numbers of individual herbivores. There are however, other factors that may influence herbivore feeding behaviour such as food quantity and quality. Changes in food availability can have a strong influence on the dynamics of consumers that rely on allochthonous sources as their main supply of energy. I tested the hypothesis that a decrease in *per capita* food supply to a sedentary herbivore has a negative effect on herbivore condition and also affects the surrounding habitat through changes herbivore feeding behaviour. The reduction in food supply had a negative influence on herbivore gonad condition, whilst concomitant increases in consumer density caused greater foraging of the surrounding habitat. Poor consumer condition can be the result of food limitation and in some cases can lead to stronger herbivory. This process could help explain barrens creation across many subtidal rocky coasts.

Ecological traits may have a stronger influence on population and community dynamics than currently acknowledged; particularly sedentary herbivores that may be incapable of migrating to alternate environments. I assessed the effects of origin of food and its frequency of delivery on sea urchin behaviour and condition. Higher consumption rates and poorer condition were associated with food originating from sheltered coasts; coinciding with observations of urchin over-grazing in this type of environment. Whilst algae derived from exposed coasts caused lower consumption rates and better condition; coinciding with no urchin over-grazing on exposed reefs. Understanding such trait-mediated responses to allochthonous food may assist the

development of more comprehensive models that account for variation in strength of herbivory.

Many studies have focussed on foraging of canopy-forming algae by sea urchins associated with barrens, however, foraging effects of urchins not associated with barrens is less clear. I tested the hypothesis that the sedentary (largely site attached) sea urchin *Heliocidaris erythrogramma* has detectable effects on the canopy-forming and understory algae. In a location where densities were at the upper limits of their range of a region that lacks sea urchin barrens, algal cover was estimated beneath and immediately around sea urchins. The area under the urchins was consistently bare rock. Sea urchin removal experiments showed that canopy-forming algae were able to develop in greater covers after 16 months and approached those in areas that naturally lacked urchins. In the area immediately surrounding the sea urchins, turf-forming algae dominated the first 5-6 cm, whilst at 8 cm canopy-forming algal cover matched areas without urchins. Cover of canopy-forming algal can be reduced in the presence of non-barren forming urchins, albeit only within a few centimetres of individual urchins. This suggests that such organismal-scale effects may have an influence on the ecology of rocky coasts with dense populations of these urchins (e.g. sheltered coasts).

In conclusion, strength of herbivory can depend on many factors that vary across a broad range of scales. In this thesis, I provide knowledge on some of the factors associated with herbivory by the purple sea urchin, *Heliocidaris erythrogramma*. I show that herbivore abundance and condition which can directly affect strength of herbivory vary at regional (i.e. Eastern Australian Current v. Leeuwin Current) and local scales (i.e. sheltered v. exposed coasts). I also demonstrate that drift-algal quantity and origin can have a strong influence on sea urchin condition and feeding behaviour. Finally, the organismal scale effects (i.e. centimetres) may not only be detectable but also influential at some places and scales. Together, these results suggest that populations of herbivores, their condition and impact, may have predictable effects from local through regional scales. The integration of such dependencies to general models may contribute to a more comprehensive understanding of rocky subtidal ecosystems.





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Finding your place in a new cultural and ecological environment can be difficult, more so when trying to do fieldwork. I was very fortunate to find a friend and “guide” in John Naumann. His excitement, experience and friendship helped me cruise through what could have been a hard adaptation and helped get my project off to a good start. For that I will be forever grateful.

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## CHAPTER 1

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### GENERAL INTRODUCTION

# CHAPTER 1

## GENERAL INTRODUCTION

Consumption and resource supply can determine community structure, however, the relative roles of these two processes is often uncertain. Understanding the interacting effects of consumers and resources is becoming a growing focus of study in response to increasing human modification of ecosystems by removing consumers (Duffy 2003) and adding nutrients (Smith et al. 1999; Gorman et al. 2009). In order to comprehend and predict the consequences of these interactions it is clear that ecologists must link processes occurring at ecosystem levels (e.g. variation in resources) to community-level dynamics (e.g. population changes in interacting species) (Wootton et al. 1996).

Herbivory in marine environments has long been recognised to have strong influence on community structure. In general, fish and sea urchins are often associated with coral reef resilience by preventing a shift to macroalgal dominated states through herbivory, particularly fish on the Great Barrier Reef and urchins on Caribbean reefs (review in Bellwood et al. 2004). On temperate subtidal coasts, sea urchins have been shown to have strong influence (Chapman 1981; Sala et al. 1998; Steneck et al. 2002), whilst gastropods seem to be the predominant herbivores in the intertidal zones (Hawkins and Hartnoll 1983). Within marine ecosystems algal forests are considered to be one of the most productive marine environments (Valiela 1995). Around the temperate coasts of the world, forests of canopy-forming algae provide physical

structure for highly diverse communities. Darwin (1860) suggested that more diversity would be lost if marine forest were destroyed than if that occurred to tropical terrestrial forests. Within these forests, herbivores have wide ranging effects with sea urchins being one of the most notorious consumers. All over the world sea urchin grazing has been described to create deforested patches (i.e. sea urchin barrens) within the forests (e.g. Breen and Mann 1976; Chapman 1981; Harrold and Reed 1985; Andrew 1993; Estes et al. 1998). Many different species can be responsible for the creation and maintenance of these barren areas, which can persist for many years. However, there are algal forests in which barrens have little to no incidence although sea urchins capable of creating barrens are present (e.g. South and Western Australia; Fowler-Walker and Connell 2002; Connell and Irving 2009).

The presence of sea urchins in a forest area is a necessary but not sufficient condition for barrens to be created. In order for barrens to be created, sea urchins must engage in an active foraging mode which involves abandoning shelter and scraping the benthos free of attached macroalgae (Harrold and Reed 1985; Andrew and Underwood 1993). This feeding behaviour has been described for individuals that form part of high density aggregations suggesting this could be a necessary condition for the behaviour responsible for barrens. Increased urchin abundances as a consequence of reduced predation pressure through removal of predators have been described for barrens areas in north-eastern pacific (Estes and Duggins 1995) and New Zealand (Babcock et al. 1999). However in the Mediterranean, Sala et al. (1998) suggest that other factors such as recruitment, diseases, pollution, large-scale oceanographic features and food subsidies should also be considered in these complex community dynamics. In general, individuals that are associated to barrens have poorer gonad condition than those that

are associated to forests areas (Konar and Estes 2003). A decrease in food availability may be the cause of poor gonad condition (Harrold and Reed 1985; Konar and Estes 2003). This suggests that a poor nutritional state could be another necessary condition associated to changes in feeding behaviour.

Interactions between consumers (e.g. herbivores) and resources (e.g. nutrients) have long attracted attention from ecologists. The strength of herbivore consumers on plant communities is variable with different habitat and environmental conditions. Herbivore effect sizes appear to be greater in environments with low productivity than in highly productive ones (Chase et al. 2000). Productivity can be related to nutrient concentrations and many studies have focused on the interactive effects of nutrients and herbivory obtaining a broad range of responses. Intense herbivory, for example, has been described for herbivores that consumed plants that were nutritionally poor suggesting that herbivores were compensating the nutrient deficiencies through larger quantities of food (Cruz-Rivera and Hay 2000; Berner et al. 2005). Alternatively, other studies describe increased grazing for nutrient enriched food sources suggesting selection behaviour towards better quality food (MacKay and Elser 1998; Boyer et al. 2004). In both scenarios herbivore responses have been towards a behaviour that seeks to improve herbivore condition. It is, therefore, necessary to address these interactions with a more holistic approach that can account for large-scale variation in resources as well as local conditions that may vary within this larger framework.

Herbivores that rely on external food supply may have poor nutritional condition if food availability decreases. This may be the case for urchins that adopt a sit-and-wait feeding behaviour in which they trap pieces of algae that are loose in the water column.



These sedentary urchin populations have no control over the quantity or quality of the food material that is supplied to them (Polis and Hurd 1996). The traditional spatial subsidy theory suggests that consumer populations within a recipient habitat may have a numerical response (i.e. increased density) with an increase in the subsidy. This increase in consumer density may affect the consumer-prey dynamics in the recipient habitat to the extent where they can suppress local resources (review in Polis et al. 1997).

Sea urchins occur across all of temperate Australia and can be responsible for the patterns observed in some regions of the rocky subtidal (i.e. eastern Australia). The temperate coast of mainland Australia (~25-40°S) may be understood in reference to its two major currents, the Eastern Australian Current (i.e. eastern Australia) and the Leeuwin Current (i.e. South and Western Australia). These currents have contrasting oceanographic traits that are related to distinct subtidal ecologies (review in Connell 2007; Connell and Irving 2009). The Eastern Australian Current is associated with greater nutrient concentrations and productivity than the Leeuwin Current. Along the shallow coasts of eastern Australia sea urchin barrens are intermixed with kelp forests and occupy a substantial area of the benthic floor; whilst on the coasts of South and Western Australia (i.e. Leeuwin Current), barrens have little to no occurrence (Connell and Irving 2008). Positive associations between herbivore abundance and nutrient supply have been shown for both terrestrial (Chase et al. 2000; Haddad et al. 2000) and marine ecosystems (Bustamante et al. 1995; Wootton et al. 1996). Therefore it is important to identify if these associations exist for sea urchins in temperate Australia.

Among the sea urchin species associated with sea urchin barrens in eastern Australia is the purple sea urchin, *Heliocidaris erythrogramma*. Population densities on

open coasts vary considerably between the two regions of temperate Australia (i.e. Eastern Australian Current and Leeuwin Current), with greater densities on the eastern coasts (Connell and Irving 2008). Within these coasts (i.e. eastern Australia) it has been described to create barrens, mainly on sheltered or semi-sheltered coasts (Wright et al. 2005; Ling et al. 2010). The purple sea urchin can, nonetheless, exhibit a completely different feeding behaviour in the subtidal rocky coasts of South and Western Australia. In these waters it can be a sedentary herbivore that mainly feeds on passing algae (i.e. drift-feeding), even when attached alga is readily available in its surroundings (Vanderklift and Wernberg 2008). It is, therefore, evident that population traits of the purple sea urchin (e.g. gonad condition) could be strongly influenced by drift-algal availability and traits.

As previously mentioned, two of the main factors suggested to contribute towards a destructive grazing behaviour by sea urchins are high urchin densities and poor gonad condition. Greater densities would imply a lower per capita distribution of available food. Consequently, a reduced food intake could be expected to impoverish gonad condition, as sea urchin use gonads as storage as well as reproductive organs (Jangoux and Lawrence 1982). Along with lower quantities of food, another factor that could be considered to affect gonad condition is the origin of the drift-algae they consume. The habitat in which an alga is grown will confer traits to it that may differ from that grown in a contrasting habitat. Therefore, a comprehensive approach on the effect of drift-algal quantity and source on urchin condition and behaviour would help understand the contrasting ecologies that are described for Australian coasts.

Large areas of the rocky subtidal coasts of the world lack the presence of sea urchin barrens, and are dominated by canopy-forming algae (e.g. Western and South Australia; Connell and Irving 2008). Canopy-forming forests provide a habitat for many herbivores including urchins, however, very little research has focussed on the possible herbivory effects of urchins within these habitats. Drift-feeding sea urchins could have small-scale effects on algae that have not been previously described. Identifying and describing this small-scale interaction can be useful in the understanding of the more common but less obvious herbivore-plant interactions that may exist in large areas of rocky coasts.

In this thesis, I present research that investigates the ecology of *Heliocidaris erythrogramma* using different scales and test different factors that may mediate its effects on the surrounding algae. My research focuses on 3 main knowledge gaps:

1. The extent to which the density and condition of *H. erythrogramma* is associated to regions and coastal features (i.e. exposure);
2. Whether quantity and/or origin of drift-algae affect sea urchin condition and foraging behaviour; and
3. The potential small-scale effects of drift-feeding sea urchins on surrounding algal cover.

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

Consumers that depend on external food sources often have no control over its replenishment rate (Polis and Hurd 1996). Consumer population dynamics can consequently respond to shifts in quantities of the allochthonous resource (Anderson and Polis 2004). These shifts affect consumer condition and may result in a behavioural response that indirectly affects the surrounding species. In Chapter 2, I described patterns in *H. erythrogramma* population density and condition at a regional scale and also within contrasting habitats (i.e. forest v. barrens habitat) within a region. I test whether a reduction in drift-algae will reduce urchin gonad condition and if this will have an effect on the surrounding algae. I reduced per capita quantity of food to sea urchins by increasing urchin density and reducing food availability in a 7 month field experiment.

## Chapter 3

As observed in Chapter 2, populations of sea urchins in eastern Australia on sheltered coasts (i.e. barrens habitats) have greater densities and lower gonad condition than those on exposed coasts. In Chapter 3, I show that the observed pattern for the eastern coast of Australia is also present in the southern coast of Australia. Furthermore, only on sheltered coasts does *H. erythrogramma* have strong impacts on the algal community (Wright et al. 2005; Ling et al. 2010). A model that could explain these patterns is that food originated in sheltered coasts has a negative effect on urchin condition but, is more intensely consumed. I manipulated the origin of food (sheltered v. exposed coast) and frequency of delivery to urchins (1 v. 3 times week<sup>-1</sup>) to test their interactive effects on gonad condition and feeding rate in an aquarium experiment.

## **Chapter 4**

The effects of herbivory on ecosystems have long been recognised (Bigger and Marvier 1998). In marine habitats sea urchins have often been studied because of their important negative effects on primary producers (Chapman 1981; Harrold and Reed 1985; Tegner et al. 1995; Sala et al. 1998; Babcock et al. 1999; Steneck et al. 2002; Ling 2008). Much less attention has been directed towards sea urchins in habitats where their effects are not noticeable, although this may be the more prevalent scenario on many temperate rocky coasts. In Chapter 4, I quantified algal cover directly under and in the immediate surroundings of sea urchins to establish an area of urchin influence on algae. The results showed the strongest influence directly under urchins where there was no algal cover, hence, I experimentally tested the effects of urchins on algal cover to assess whether these patterns were caused by sea urchins.

## **Chapter 5**

In Chapter 5, I provide a 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 2-4) presents original data that has been published 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 provides information on the publication status at the time of thesis submission, and the contributions of the co-author (where relevant).

## CHAPTER 2

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### REDUCING PER CAPITA FOOD SUPPLY ALTERS URCHIN CONDITION AND HABITAT

## CHAPTER 2 PREAMBLE

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

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Collected samples, analysed and interpreted data, wrote manuscript as senior author and provided part of the funding.

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Provided funding and had input into the development of broad-scale research, data interpretation and manuscript evaluation.

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## CHAPTER 3

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### EFFECTS OF FOOD ORIGIN AND AVAILABILITY ON SEA URCHIN CONDITION AND FEEDING BEHAVIOUR

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## Effects of food origin and availability on sea urchin condition and feeding behaviour

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### ABSTRACT

The origin of food is recognised to be an important trait for sedentary consumers that have little control over the source of their food. Elevated herbivory in sea urchins is often linked to poor gonad condition as provoked by reduced food availability, but there is little recognition of the possibility that the origin of food may contribute to their poor condition and elevated feeding. This study assesses the possibility that variation in food availability and origin may together affect urchin condition and feeding rates such that they account for more intensive grazing (by *Heliocidaris erythrogramma*) on sheltered than exposed coasts (South Australia). We experimentally tested the hypothesis that reduced food availability from sheltered coasts would result in poor gonad condition and greater feeding rate; whilst enhanced food availability from exposed coasts would result in better condition and reduced feeding rates. We found that reduced food had negative effects on condition and positive effects on feeding rates independently of coastal source. Greater food availability did not equate to better condition, rather it was the delivery of more food from exposed than sheltered coasts that translated into the better gonad condition and lower feeding rates. These results suggest that plant origin and availability could help explain the greater impacts of these urchins on sheltered coasts. Whilst other factors such as water energy and sea urchin density may contribute to variation in herbivory our results suggest that origin of food may also play a role in sea urchin condition and behaviour. Understanding how such traits link to large scale features of the environment may improve models that account for variation in strength of consumer effects across landscapes.

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### 1. Introduction

Many coastal consumers depend on drift macroalgae (i.e. detritus) as their main food resource (Bustamante et al., 1995a; Harrold and Reed, 1985). The origin of this food resource may be a particularly important trait for sedentary consumers because they have little control over the origin or quantity of the detritus they depend on (Bouillon et al., 2002; Granek et al., 2009). Furthermore the population dynamics of predator and prey are decoupled which result in an absence of the usual feedback responses in density. Such variation in traits (e.g. food origin) can result in interactions that are not simple functions of density (e.g. consumer and prey density) but have profound effects on surrounding species (Werner and Peacor, 2003).

In marine ecosystems kelp forests are among the main generators of detritus and its consumption may occur in distant areas sometimes several kilometres away (Vanderklift and Wernberg, 2008). The majority of their production becomes available to consumers when it enters food webs as detritus (Mann, 1988; Newell and Field, 1983). Coastal morphology has been related to water quality and primary productivity which provide contrasting environments for community dynamics (Menge et al., 2003; Miller and Emlet, 1997; Nielsen and

Navarrete, 2004). The nutritional characteristics of the kelp detritus may vary according to its environment of origin. Varying wave exposure may be associated to contrasting water conditions that can affect the nutritional characteristics of kelps (Staeher and Wernberg, 2009). Such variations in conditions are also associated with the amount of drift algae and herbivore abundance (Bustamante et al., 1995b).

Prey preference and consumption rates of herbivores are often affected by nutrient content (Cronin and Hay, 1996; Hay and Fenical, 1988; Hay and Steinberg, 1992), as shown for fish (Barry and Ehret, 1993), crustaceans (Cruz-Rivera and Hay, 2000; Lastra et al., 2008), molluscs (Granado and Caballero, 2001; Pennings et al., 1993; Russell and Connell, 2005) and echinoids (Jacquin et al., 2006; Lyons and Scheibling, 2007). Compensatory feeding has been observed in several species when food is of low quality (Cruz-Rivera and Hay, 2000; Pennings et al., 1993), involving greater *per capita* consumption in order to counter balance the nutritional deficiency. In some cases however, food with scarce nutrients led to poor condition regardless of the feeding rate (Cruz-Rivera and Hay, 2000).

For food origin to be an attribute of ecological importance, one needs to show that it affects the strength of the consumer–prey interaction and ensuing consumer condition. Sedentary sea urchins can interact with their prey through two distinct feeding behaviours (i.e. trapping drift v. substratum scrapping). It is possible that urchins can switch from one to another; a phenomenon that has been associated to low *per capita* availability of food and poor condition of

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urchins (Dean et al., 1984; Harrold and Reed, 1985). Feeding behaviour often consists of trapping drift algae from the water column before switching to actively foraging on algae attached to the surrounding rock substratum. The consequence of the latter can be the shift in the surrounding algal habitat from a highly diverse canopy algal forest to a less productive barrens habitat devoid of standing algae. The purple sea urchin, *Heliocidaris erythrogramma*, has been associated with barren creation in sheltered and semi-sheltered waters (Ling et al., 2010; Wright et al., 2005) although it occurs on both sheltered and exposed rocky coasts. This species appears to have little effects on attached algae on exposed coasts (Vanderklift and Wernberg, 2008) where they preferentially trap unattached kelp *Ecklonia radiata* over other available drift food (Vanderklift and Kendrick, 2005).

This study assesses the general model that food origin has an effect on urchin condition and feeding behaviour, such that poor condition and greater rate of grazing is associated with sheltered coasts where barrens are more frequent. We compared condition of the sea urchin *H. erythrogramma* across multiple sites with contrasting exposure and water quality on the southern coast of Australia. These comparisons showed condition to be poorer within sheltered than exposed locations. Subsequently, we tested the interactive effect of food origin (i.e. sheltered v. exposed coast) and its frequency of delivery on sea urchin condition and feeding behaviour. We predicted that gonad condition would be greater in urchins fed algae from exposed coasts more frequently. Evidence in support of this hypothesis could assist models attempting to account for variation in condition of urchins and its possible connection to variation in foraging intensity that sometimes leads to overgrazing.

## 2. Materials and methods

Sea urchins use their gonads not only as reproductive organs but also for nutrient storage (Walker, 1982) hence gonad indices are good indicators of their condition (Meidel and Scheibling, 1999; Vadas et al., 2000). Six sites were sampled for density and gonad condition across the coast of South Australia (Fig. 1); sheltered sites ( $n=3$ ) were protected from the dominant swell (i.e. orientation, inside gulfs or bays) and exposed ( $n=3$ ) were open to the predominant swell in the area. Urchin density was estimated with  $1 \times 5$  m transects ( $n=6$  transects per site). Ten adult *Heliocidaris erythrogramma* (diameter range: 61.05–78.75 mm) were randomly collected at each site and excess water was allowed to drip on absorbent paper for 5 minutes before wet weight of individuals was recorded. Urchins

were dissected and gonads extracted, blot dried on absorbent paper and then weighed. Gonad index for each urchin was calculated as the percentage of the individual's total wet weight that was gonad. Water samples for nutrient comparison were obtained at each site at 1–2 m depth using sterile 25 ml syringes before being filtered through  $0.45 \mu\text{m}$  glass fibre filters. Filtered samples were frozen in situ and transported to the laboratory where they were analysed for dissolved inorganic nitrogen (DIN; nitrite-nitrate-ammonium) using a Lachat QuickChem 8500 Flow Injection Analyser (Hach, Loveland, Colorado, USA). Nutrient concentrations (reported as mg/L) were validated against natural seawater certified reference material. For exposure comparison, ANOVA treated 'Exposure' as fixed with 'Site' nested within it.  $\ln(x)$  transformation was used to meet assumptions of homogeneity of variances (Cochran's C-test).

If food origin can affect gonad condition and grazing rate in such a way that food from sheltered coasts causes poor gonad condition and greater rate of feeding, then we should be able to experimentally induce poorer condition and greater feeding in urchins fed algae from sheltered coasts. To test this hypothesis we provided urchins with kelp collected from sheltered coasts (Port River,  $34^{\circ}47'S$   $138^{\circ}28'E$ ) and exposed coast (Fishery Beach,  $35^{\circ}35'S$   $138^{\circ}05'E$ ). The effects of food origin and its frequency of delivery on *H. erythrogramma*'s condition (i.e. gonad index) and feeding behaviour (i.e. feeding rate) were tested in a mesocosm experiment that ran for 7.5 weeks. Sea urchins were exposed to combinations of food origin (a sheltered coast v. an exposed coast) and frequency of delivery (1 v. 3 times week<sup>-1</sup>) in a crossed design. Four replicate aquaria were used per combination of treatments, with replicate individuals in each aquaria ( $n=3$  sea urchins aquaria<sup>-1</sup>).

The kelp *Ecklonia radiata* was chosen to be the food source. The purple sea urchin has been described to prefer this kelp over other available macroalgae available in its natural habitat (Vanderklift and Kendrick, 2005). Adult kelp specimens were collected at 2–5 m depth fortnightly and placed in holding tanks with conspecifics from the same origin. Sea urchins (test diameter  $\bar{x}=69.15$  mm; range: 62.15–74.25 mm) were collected from a non-barrens forming population (Livore and Connell, 2012) situated in Victor Harbour, South Australia ( $35^{\circ}34'S$   $138^{\circ}36'E$ ) which had test sizes similar to those observed across the region (i.e. South Australia; Fig. 1). Collected urchins were maintained in 40 l aquaria with recirculated water connected to 150 l reservoirs. To maintain good water quality in all aquaria, ammonia levels were measured on alternate days and maintained below  $0.1 \text{ mg l}^{-1}$  whilst half of the reservoir's water was changed weekly regardless of ammonia levels. Temperature was kept at  $17 \pm 1^{\circ}\text{C}$  throughout the experiment. Once collected, urchins were kept for a week with *ad libitum* kelp from the same source (i.e. Victor Harbour) to reduce potential stress caused by transport and to allow them to acclimatise to the aquaria before the experiment was initiated.

Urchin response to experimental conditions was assessed through gonad index and feeding rate. Urchins were individually fed by manually placing within their spines freshly cut discs (4 cm diameter) of kelp blade to standardise effect of size and shape of food. Controls for autogenic changes were performed and no differences were detected after 24 h. Wet weights of algal discs were recorded before feeding and for any remaining pieces of algae after 24 h. Consumed kelp biomass was calculated as the difference between added and remaining wet weight ( $\pm 0.01$  g) of kelp in each aquarium. Feeding rate for each aquarium was recorded on the last day all treatments were simultaneously fed and calculated as the ratio between consumed kelp biomass and urchin biomass. Gonad index was estimated as above.

In order to nutritionally characterise the alternate origins of kelp, samples from 24 adult kelp within each food origin (i.e. exposed v. sheltered; the same sites from which kelp was collected to feed urchins throughout the experiment) were analysed for protein, carbon

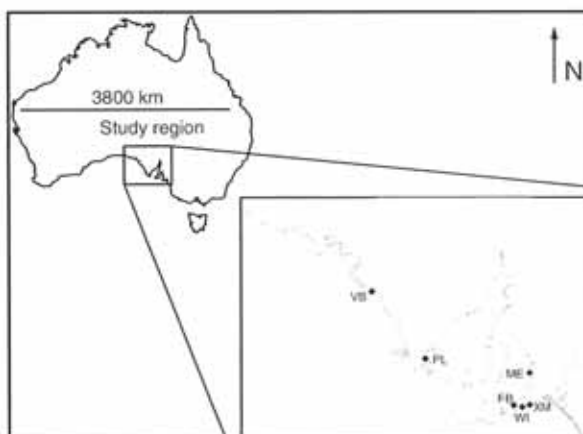


Fig. 1. Map showing the coastal sites sampled for urchin density, condition and water quality. Sheltered coasts: PL: Port Lincoln, ME: Metropolitan coast, XM: X-mark reef. Exposed coasts: VB: Venus Bay, FB: Fishery Beach, WI: West Island.

and nitrogen content. Samples were oven dried at 60 °C until constant weight and ground with mortar and pestle. Protein content was estimated following a modified Bradford's method (Duffy and Hay, 1991) using bovine albumin serum as the standard. Carbon and Nitrogen analyses were carried out using an isotope ratio mass spectrometer (Waite Campus IRMS facilities, The University of Adelaide, South Australia). For nutrient comparisons, a one-way ANOVA was performed.  $\ln(x+1)$  transformation was used on protein and nitrogen data to meet assumptions of homogeneity of variances (Cochran's C-test).

We recognise that the experimental observations between single exposed and sheltered sites provides for weak inference. For future studies, stronger evidence would require "food origin" to be derived from a number of interspersed sheltered and exposed coasts (see Hurlbert, 1984). Nevertheless, given the previously unrecognised insight into identifying additional conditions that provoke overconsumption, we believe it offers a useful perspective for those seeking to understand variation in urchin herbivory.

### 3. Results

Sea urchins collected at exposed locations had higher gonad indices than those in sheltered coasts with some variability between sites (Fig. 2a; ANOVA, Exposure,  $F_{1,4} = 13.60$ ,  $P = 0.021$ ; Site,  $F_{4,54} = 2.82$ ,  $P = 0.034$ ). Dissolved inorganic nitrogen concentrations were higher in sheltered than exposed coasts (Fig. 2b; ANOVA,  $F_{1,4} = 8.65$ ,  $P = 0.042$ ). Mean ( $\pm$ SE) sea urchin densities (urchins  $m^{-2}$ ) were greater in sheltered sites (Port Lincoln:  $1.80 \pm 0.21$ ; Metropolitan Coast:  $3.27 \pm 0.43$ ; X-mark:  $5.73 \pm 0.49$ ) than exposed sites (Venus Bay:  $0.40 \pm 0.18$ ; Fishery Beach:  $0.47 \pm 0.14$ ; West Island:  $0.60 \pm 0.07$ ) (ANOVA, Exposure,  $F_{1,4} = 11.03$ ,  $P = 0.024$ ; Site,  $F_{4,30} = 19.14$ ,  $P < 0.0001$ ).

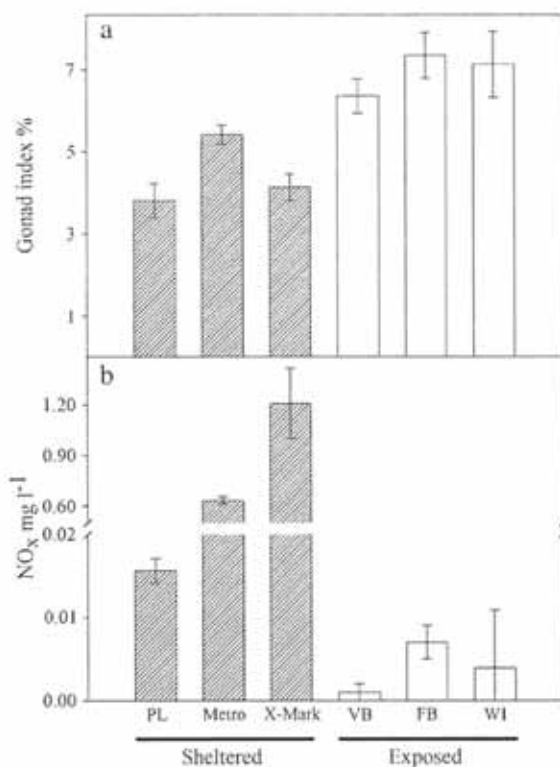


Fig. 2. Observation of mean ( $\pm$  S.E.) a) *Helicidaris erythrogramma* gonad index (%) and b) dissolved inorganic nitrogen ( $mg\ l^{-1}$ ) in water across locations with contrasting exposure (sheltered v. exposed coast) in southern Australia.

Table 1

a) Two-factor ANOVA testing for the effect of food origin (sheltered v. exposed coast) and its frequency of delivery (1 v. 3 feeds week<sup>-1</sup>) on gonad index of the sea urchin *H. erythrogramma*. b) SNK test on significant food origin  $\times$  frequency of food delivery term.

a) ANOVA				
Source	df	MS	F	P
Origin	1	3.92	11.22	<b>0.006</b>
Frequency	1	1.92	5.51	<b>0.037</b>
Origin $\times$ Frequency	1	2.39	6.83	<b>0.023</b>
Residual	12	0.35		

b) SNK tests on origin and frequency			
Sheltered coast	Less	=	More
Exposed coast	Less	<	More
Less	Sheltered	=	Exposed
More	Sheltered	<	Exposed

P values in bold are significant.  $\ln(x)$  transformation was used to meet assumptions of homogeneity of variances (Cochran's C-test).

Gonad condition in urchins under experimental condition was affected by an interaction between food origin and frequency of delivery (Table 1). Gonad indices were low when urchins were fed kelp from sheltered coast regardless of the frequency and when fed less frequently exposed kelp, whereas highest gonad indices were obtained by urchins fed more frequently exposed kelp (Fig. 3, Table 1b). Feeding rate was also affected by an interaction between the two factors (Fig. 4, Table 2a). Greater rates of feeding were observed in urchins fed less frequently and also in those fed more frequently sheltered algae, whereas low rates of feeding were only recorded for urchins fed more frequently exposed algae (Table 2b).

The standard sized pieces of algae (4 cm diameter) were similar in biomass between origins (sheltered v. exposed coasts: ANOVA,  $F_{1,78} = 0.18$ ,  $P = 0.676$ ). Whilst size and biomass were similar between these treatments, nutritional properties were anticipated to differ. Protein and nitrogen concentrations were greater in the algae collected from sheltered than exposed sites (Fig. 5, ANOVA, protein:  $F_{1,46} = 8.57$ ,  $P = 0.005$ ; nitrogen:  $F_{1,46} = 604.17$ ,  $P < 0.0001$ ), whilst carbon content did not differ (ANOVA,  $F_{1,46} = 1.35$ ,  $P = 0.252$ ).

### 4. Discussion

Variation in ecological traits can result in interactions that do not reflect density of the participants (Werner and Peacor, 2003). Food origin can be an attribute that determines condition of a consumer

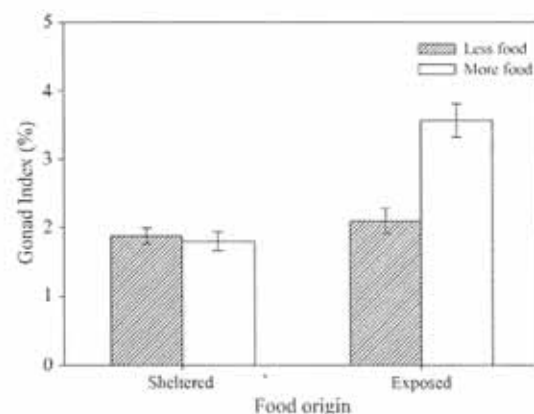


Fig. 3. Effects of food origin (sheltered v. exposed coast) and its frequency of delivery (1 v. 3 feeds week<sup>-1</sup>) on gonad condition of *H. erythrogramma* (mean  $\pm$  SE). The initial gonad index (mean  $\pm$  SE) for the urchin population was:  $\bar{x} = 3.06 \pm 0.28$ .

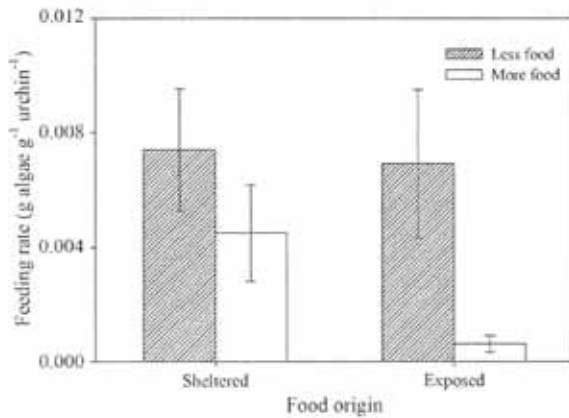


Fig. 4. Effects of food origin (sheltered v. exposed coast) and its frequency of delivery (1 v. 3 feeds week<sup>-1</sup>) on feeding rate of *H. erythrogramma* (mean  $\pm$  SE).

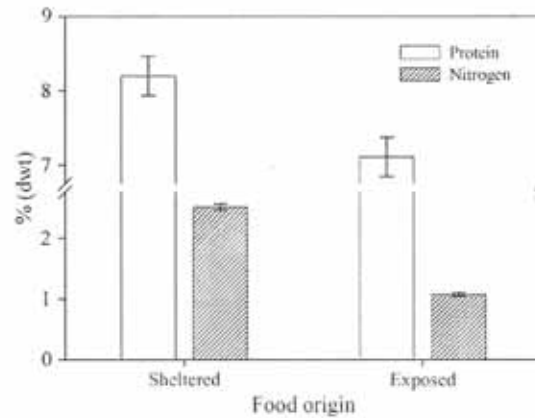


Fig. 5. Nutrient content of algal food derived from locations with contrasting exposure (sheltered v. exposed). Carbon (mean dwt.  $\pm$  S.E.) content (not shown): Sheltered coast, 32.12  $\pm$  0.37; Exposed coast, 31.55  $\pm$  0.33.

and ensuing feeding behaviour. Our results show the response of urchin condition and feeding rate to varying quantities of food was mediated by origin of food. More food did not equate to better condition, rather it was the delivery of more food from exposed than sheltered coasts that translated into the better gonad condition and lower feeding rates. These results could help explain the general pattern that urchin condition is poorer on sheltered than exposed coasts of Australia (this study, Livore, 2011) and Canada (Meidel and Scheibling, 1998).

Barrens creation by *Heliocidaris erythrogramma* has been observed on sheltered (Ling et al., 2010; Wright et al., 2005), but not exposed coasts (Connell and Irving, 2008), and such overgrazing is associated with poorer gonads in sheltered than exposed populations across much of temperate Australia (this study). Whilst the rate of food supply (i.e. quantity) may appear as an obvious driver of urchin condition, the current study suggests that the origin of the food may also affect condition. When the rate of food delivery was less, gonad condition was poor and feeding rates high regardless of food origin. However, when the rate of delivery was more, urchins discriminated between food origins by feeding at greater intensities on food from sheltered coasts. Urchins with poor condition fed at greater rates, indicating that condition can be a driving factor of sea urchin feeding behaviour as previously suggested (Harrold and Reed, 1985). Whilst food origin may not be the only driver involved in sea urchin barrens creation we have shown that this attribute may play a role, albeit

greater replication and interspersed replication is required for stronger inference and generality. We suggest that the potential for elevated rate of grazing is enhanced in the circumstances in which barrens formation is frequently observed. In certain cases, sheltered coasts may have low delivery of food of a poor quality that combine to cause elevated rates of feeding.

Over grazing by urchins is a renowned example of a major ecosystem shift (Steneck et al., 2002), but much remains to be understood as to why urchins switch behaviour from trapping drift algae to scraping of attached algae (Dean et al., 1984; Estes and Palmisano, 1974; Harrold and Reed, 1985). The switch in feeding mode is widely thought to be driven by a decrease in the supply of food; urchins that scrape the benthos at elevated rates are often in poorer condition than those that do not create barrens (Andrew, 1986; Konar and Estes, 2003).

Herbivore feeding behaviour is well known to be flexible and often respond differentially to food availability and nutritional value (review Mattson, 1980). Increased feeding can occur when food has elevated (MacKay and Elser, 1998) or reduced nutrient content (Cruz-Rivera and Hay, 2000). In the current experiment, the observation that alga with greater protein and nitrogen content did not cause better gonad condition was unexpected. One explanation is that a proportion of nitrogen be bound in biochemical forms that are unavailable for digestion and/or assimilation (review in: Steinberg and Altana, 1992). An alternate explanation suggests that reproductive output may not always be a linear response to food quality, but condition can peak at intermediate level of food quality (Joern and Behmer, 1997). The idea that 'more is not necessarily better' has been invoked to explain the impact of limiting and excess nutrient on herbivores (Zehnder and Hunter, 2009). In the marine realm, the mediating effects of nutrition may assist models account for variations in the intensity of herbivory, but the study of such nutritional processes have been emphasised to be under researched (Clements et al., 2009).

In conclusion, variation in traits of food on prey can result in interactions that are not a simple function of predator and prey density. Our results reveal a possible link between local responses (i.e. gonad condition) to large scale features of the environment (i.e. coastal morphology) through variation in traits of the primary producers. The abiotic environment can determine the strength of plant-herbivore interactions through its influence on trait-mediated effects on grazing (Cruz-Rivera and Hay, 2003). Understanding how such traits link to large scale features of the environment may improve models that account for variation in the strength of consumer effects across landscapes and their influence on the broader ecosystem.

Table 2

a) Two-factor ANOVA testing for the effect of food origin (sheltered v. exposed coast) and its frequency of delivery (1 v. 3 feeds week<sup>-1</sup>) on feeding rate of the sea urchin *Heliocidaris erythrogramma*. b) SNK test on significant food origin  $\times$  frequency of food delivery term.

a) ANOVA				
Source	df	MS	F	P
Origin	1	2.61	6.38	<b>0.027</b>
Frequency	1	6.13	14.98	<b>0.002</b>
Origin $\times$ Frequency	1	6.53	15.95	<b>0.002</b>
Residual	12	0.41		

b) SNK tests on origin and frequency			
Sheltered coast	Less	=	More
Exposed coast	Less	>	More
Less	Sheltered	=	Exposed
More	Sheltered	>	Exposed

P values in bold are significant. Ln (x) transformation was used to meet assumptions of homogeneity of variances (Cochran's C-test).

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## CHAPTER 4

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### FINE-SCALE EFFECTS OF SEDENTARY URCHINS ON CANOPY AND UNDERSTORY ALGAE

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## CHAPTER 4 PREAMBLE

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### Contributions and signatures of authors:

#### **JUAN PABLO LIVORE**

Had input into the development of ideas, assembled and ran the experiment. Collected, analysed and interpreted data, wrote manuscript as senior author.

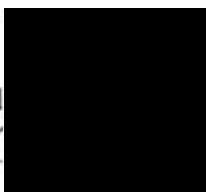
**Signed:**.....

**Date:** .....

#### **SEAN D. CONNELL**

Provided input into the development of ideas and experimental design. Also supervised development of research, data interpretation and manuscript evaluation.

**Signed**



**Date:** ..... 27.03.12



## Fine-scale effects of sedentary urchins on canopy and understory algae

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Temperate

### ABSTRACT

The effect of sea urchins on algae has often been studied when sea urchins forage over areas to create or maintain urchin barrens. The effect of sea urchins that are not associated with barrens, however, is not so clear. This study tested the hypothesis that sedentary and largely site attached sea urchins (*Heliocidaris erythrogramma*) have detectable effects on the covers of canopy-forming and understory algae, whether that be due to their mere presence or grazing. Algal cover was estimated beneath and immediately surrounding urchins in a location where they do not create barrens but attain densities at the upper end of their local range. The area immediately beneath the urchins was mostly devoid of visible algae. Experimental removal of urchins over 3 years revealed that canopy-forming algae were able to develop in more extensive covers to match those in areas naturally lacking urchins. In the presence of urchins, the immediate area (i.e. first 5–6 cm from urchins) was primarily comprised of turf-forming algae, thereafter the cover of canopy-forming algae sharply increased until at ~8 cm their cover matched areas without urchins. These data support the model that composition and cover of algae can be altered in the presence of non-barren forming urchins, albeit only within a few centimetres of individual urchins. Where populations of sedentary urchins are dense and widespread (e.g. sheltered coasts for *H. erythrogramma*) such fine-scale effects may repeat over large areas such that urchins do not need to be associated with barrens before their effects are detectable.

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### 1. Introduction

Canopy-forming algae are one of the most productive of all marine ecosystems (Valiela, 1995) and understanding variation in its cover is a persistent area of ecological research. Variation in the generation and maintenance of canopy cover may reflect a number of physical processes (e.g. storm-driven loss of canopies) and biological processes, including herbivory. Indeed, the effects of herbivory on cover of canopy and understory algae are widely reported (review: Bigger and Marvier, 1998) and variation in the abundance of herbivores is often associated with the presence or absence of canopies (Andrew and Underwood, 1989).

Sea urchins are renown for their intense herbivory on attached algae and capacity to transform complex algal habitat into more simple sea urchin barrens (review: Pinnegar et al., 2000). Much attention has been given to the creation of sea urchin barrens and the mechanisms that drive this process (Andrew, 1993; Estes and Palmisano, 1974; Sala et al., 1998; Shears and Babcock, 2002). The grazing of canopy-forming algae is often thought to centre on a process that involves urchins abandoning shelter and then scrapping virtually all algae from rock (Andrew, 1993; Dean et al., 1984; Harrold and Reed, 1985). Less emphasis, however, has been placed on the effect

of sea urchins when barren creation does not occur and urchins adopt a sit-and-wait feeding behaviour that relies on trapping drifting algae with their spines, pedicellaria and tube feet. At experimentally elevated densities such feeding can trap elevated amounts of drift algae and cause weak and ephemeral effects to attached algae (Vanderklift and Kendrick, 2005). There are many coastal areas where such sea urchins are abundant but do not create sea urchin barrens (Vanderklift and Kendrick, 2004), yet it is largely unknown whether they may affect the surrounding assemblage of algae.

The shallow subtidal rocky coast of the Leeuwin Current (i.e. South and Western Australia) is characterised by extensive forests of canopy-forming algae that lack sea urchin barrens (Connell and Irving, 2008). This absence of barrens is not due to a lack of urchins as the purple sea urchin, *Heliocidaris erythrogramma* (Valenciennes, 1846), is widely distributed across the temperate Australian coast. Their densities tend to be greater on the eastern coast of Australia compared with the southern and western coasts (Connell and Irving, 2008), except on some sheltered coasts of southern Australia (Livore, 2011; Vanderklift and Kendrick, 2004; Vanderklift and Wernberg, 2008). Although it has been observed to actively forage by scrapping algae from the rock in eastern Australian waters (Ling et al., 2010; Wright et al., 2005), this behaviour appears rare across the coasts of the Leeuwin Current (Livore and Connell, pers. obs.). Instead these latter coasts appear to be associated with passive drift-feeding mode, even when attached algae are readily available (Vanderklift and Wernberg, 2008). Whilst the relatively weak effects

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of drift-feeding urchins on canopy-forming algae is largely accepted for broad parts of Australia's Leeuwin Current (Connell and Irving, 2008; Vanderklift and Wernberg, 2008), there remains little to no recognition of their potential effects where populations are unusually dense (i.e. sheltered bays) within this broad east–west coastline.

We quantified the cover of algae directly underneath and with increasing distance from sea urchins in a sheltered bay in South Australia that lacked obvious sea urchin barrens. The present study observed that the area immediately beneath urchins was devoid of algae in all cases. Potential models that account for this pattern centre on either the direct effects of urchins on algae or by the preference of urchins for areas devoid of algae. We tested the hypothesis that the removal of sea urchins will result in (i) an increase in algal cover in the area previously occupied by the urchin; and (ii) canopy cover would increase to match that observed in areas where urchins were naturally absent. We accepted the model of urchin driven effects and then assessed the scale of their influence by estimating the distance at which algal cover returned to match that of areas without urchins.

## 2. Materials and methods

The experiment was carried out on X-mark reef in Encounter Bay, South Australia chosen for its unusually high density of *Helicidaris erythrogramma* ( $\bar{x} = 5.46 \pm 0.24$  SE urchins  $m^{-2}$ ). The limestone reef extends parallel to the shore and has an approximate depth of 2–3 m. The reef supports stands of canopy-forming algae predominantly dominated by furoids (i.e. *Cystophora* spp and *Sargassum* spp). We classed the algae into four morphological groups: (i) canopy-forming: algae that reached >30 cm height; (ii) foliose: algae with a height range between 5 and 30 cm, (iii) turfs: non-crustose algae that developed to <2 cm and (iv) articulated corallines. Manipulative experiments to test the effects of urchin removal on algae began 1st April 2008 and finished 26th July 2011 (3.3 years). Three sites separated by no less than 100 m were randomly chosen within the reef. Urchins were removed and a steel peg with an identifying plastic tag was hammered into the rock immediately beside the bare plot where the urchin had sat (i.e. present) and in areas where sea urchins were absent ( $n = 8$  plots  $treatment^{-1} site^{-1}$ ). Sites were periodically monitored to ensure that removal plots were not re-occupied. Percentage primary cover of algal species was recorded at the 0, 8, 16, 24 and 40 months of the

experiment in each plot with a 25 point quadrat (5 × 5 cm) which fitted well within the bare area found upon removal of individual urchins. In other words, this size of quadrat was chosen so that it was of similar size of the urchins themselves.

Before (0 months) and after (40 months) removal data was analysed using a three factor ANOVA that treated Time (before v. after removal) and Urchin (present v. absent) as fixed and orthogonal, whilst Sites were treated as random and orthogonal.

To quantify cover of algal groups with distance from sea urchins we sampled sea urchins' immediate surroundings. Fifteen centimetre transects from the edge of the urchin's test ( $n = 90$  urchins) were used. Transects radiated in a random direction that avoided the presence of other urchins within 50 cm. Only one transect per urchin was used in order to obtain independent data. Cover of algal species was recorded within each centimetre. To test for a serial correlation in algal assemblage structure with increasing distance from urchins the RELATE routine was used. Cover data for each cm section of transects were square root transformed. The procedures reported here were performed in the PRIMER 6 software (Clarke and Warwick, 2001) with the PERMANOVA add-on (Anderson et al., 2007).

## 3. Results

The area directly under the urchins was consistently devoid of visible algae. Urchin removal had a positive effect on algal cover with plots previously occupied by urchins reaching 100% algal cover in all plots within the first eight months. Forty months into the experiment covers of all algal groups were indistinguishable between treatments (Fig. 1). Canopy-forming algal cover was affected by a time × urchin interaction (Table 1a). Greater cover was observed after than before manipulation in both urchin present and absent plots. No differences in canopy cover between urchin present and absent plots at the end of the experiment were detected (Table 1b). Foliose algal cover was marginally affected by a Time × Urchin interaction (Table 1a), no differences were detected at the end of the experiment between urchin present and absent plots (Table 1b, Fig. 1). The ANOVA also detected time and urchin effects on articulated coralline algae, with greater cover after the experiment and in urchin absent than present plots (Table 1a, Fig. 1). The ANOVA was not able to detect differences in percentage cover of turf-forming algae (Table 1a),

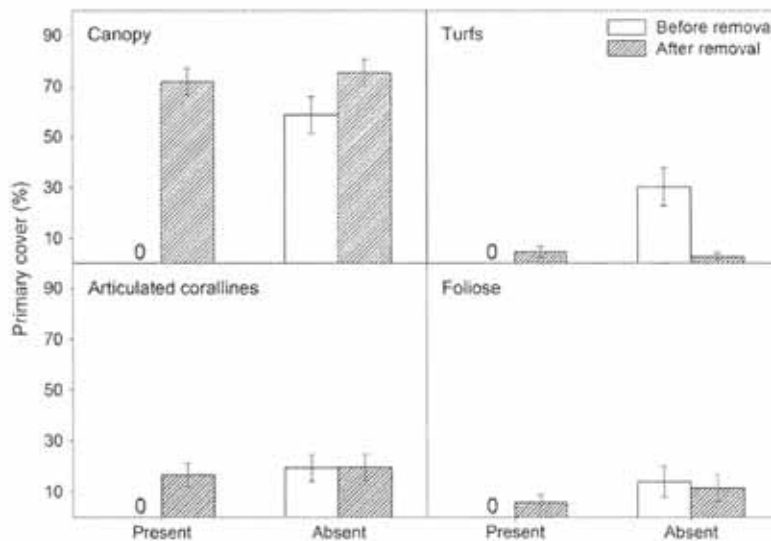


Fig. 1. Effects of time (before v. after urchin removal, 3.3 years) and urchin (presence v. absence) on mean ( $\pm$  SE) percentage cover of canopy-forming, turf-forming, articulated coralline and foliose algae.

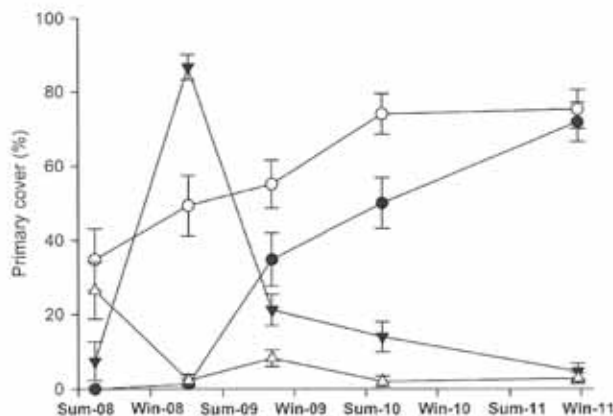
**Table 1**

a) Results of the three-way ANOVAs testing for the effects of time (before v after urchin gaps), urchin (present v absent) and Site ( $n=3$ ) in percentage cover of algal groups, and b) SNK tests on significant interaction terms for canopy and foliose algal cover. 'Time' and 'urchin presence' were treated as fixed and orthogonal, 'Site' was random and orthogonal.

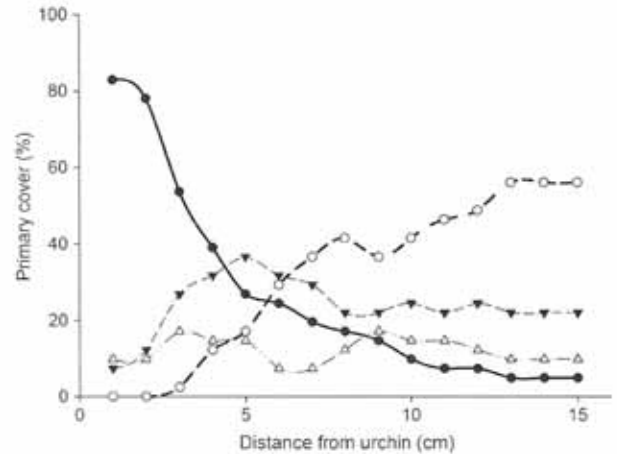
a) ANOVA							
Source	df	MS	F	P	MS	F	P
				(a) Canopy			
Time	1	46993.50	47.02	<b>0.021</b>	8.65	4.61	0.165
Urchin	1	23188.17	34.04	<b>0.028</b>	13.23	11.47	0.077
Site	2	41.17	0.06	0.941	4.22	2.08	0.131
Time × urchin	1	18260.17	567.67	<b>0.002</b>	22.23	10.84	0.081
Time × site	2	999.50	1.48	0.234	1.88	0.92	0.401
Urchin × site	2	681.17	1.01	0.369	1.15	0.57	0.569
Time × urchin × site	2	32.17	0.05	0.954	2.05	1.01	0.369
Residuals	84	675.88			2.03		
				(b) Turfs			
Time	1	1.35	1.20	0.388	1908.17	75.82	<b>0.013</b>
Urchin	1	6.69	9.03	0.095	2688.17	30.49	<b>0.031</b>
Site	2	0.09	0.05	0.948	519.50	1.06	0.350
Time × urchin	1	2.11	18.58	<b>0.049</b>	1837.50	8.99	0.096
Time × site	2	1.12	0.63	0.533	25.17	0.05	0.950
Urchin × site	2	0.74	0.42	0.659	88.17	0.18	0.835
Time × urchin × site	2	0.11	0.06	0.938	204.50	0.42	0.659
Residuals	84	1.77			488.21		
				(c) Foliose			
				(d) Articulated corallines			
b)							
SNK							
				(i) Canopy		(ii) Foliose	
Before	Present < absent			Present < absent			
After	Present = absent			Present = absent			
Present	Before < after			Before < after			
Absent	Before < after			Before < after			

df: degrees of freedom; MS: mean square. Values in bold are significant. Turfs and foliose data were  $\ln(X+1)$  and  $X^2$  transformed, respectively, to meet assumption of homogeneity of variances (Cochran's C-test).

Urchin present plots were initially dominated by turf-forming algae which after 16 months were largely replaced by canopy-forming algae, but only after 40 months was turf cover indistinguishable to urchin absent plots (Fig. 2). Whilst turf covers in urchin absent plots originally started with ~26% and decreased throughout the experiment to levels below ~10%. Cover of canopy-forming algae in urchin absent plots was relatively high throughout the experiment with a natural increase in cover observed between 16 and 24 months



**Fig. 2.** Mean ( $\pm$  SE) percentage cover of canopy-forming (circles) and turf-forming (triangles) algae throughout the experiment (0, 8, 16, 24 and 40 months) for urchin present (solid symbols) and absent plots (open symbols).



**Fig. 3.** Percentage cover of turf (solid circles), canopy (open circles), foliose (solid triangles) and articulated coralline (open triangles) algal groups in each cm of 15 cm transects that radiated away from sea urchins.

period (Fig. 2). Urchin present plots showed a constant increase of canopy-forming algal cover and converged on those covers within urchin absent plots at the end of the experiment (i.e. 3.3 years).

The similarity matrix based on algal groups cover along the 15 cm transect was well correlated with the seriation model matrix ( $\rho=0.75$ ,  $P=0.001$ ), as determined by RELATE procedure. Algal groups varied with distance from urchins. Turf-forming algae reached >80% cover near sea urchins (i.e. 1–5 cm; Fig. 3) after which they declined and canopy-forming and foliose algae gradually rose (i.e. 6–9 cm). Away from urchins (i.e. 10–15 cm) canopy-forming algae dominated (i.e. >50% cover) and turf-forming algae were practically absent (Fig. 3). Articulated coralline algae occurred in similar covers at all distances, whilst the cover of foliose algae peaked in the intermediate section but were usually sparse across all sections.

#### 4. Discussion

These results support the model that sedentary sea urchins have an effect on algal cover, particularly a negative effect on canopy-forming algae at the fine-scale of the individual urchin. The removal of sea urchins allowed canopy-forming species to establish themselves to become indistinguishable from areas where urchins were naturally absent. Whilst turf-forming algae initially increased in cover after urchin removal, they declined to occupy a small proportion of the total cover after two years and became indistinguishable from areas naturally without urchins. Other algal groups such as articulated corallines and foliose algae showed similar patterns of change.

The presence of 'urchin halos' within canopies may not be a trivial pattern where populations of drift-feeders are dense. About 12% of reef may be devoid of canopies as a consequence of dense populations (~5 individuals  $m^{-2}$ ) of urchins (i.e. 72 mm test diameter) that create halos (i.e. 50 mm clearings from edge of test). Using such general estimates, it would appear that total absence of canopy-forming algae would require ~43 individuals  $m^{-2}$  without the need for urchins to switch their feeding behaviour from a passive drift-feeder to an active forager. Such densities (i.e. ~40 individuals  $m^{-2}$ ) were experimentally observed to denude rock of all erect algae, including canopy-forming algae in eastern Australia (Wright et al., 2005). These small-scale patterns and processes (i.e. halos around an urchin) may contribute to the landscape scale features of rocky coasts that support dense populations of such urchins.

Canopy dominated areas (i.e. outside 'urchin halos') suppress turf (Irving and Connell, 2006a) however, in the near vicinity of urchins the cover of turfs was consistently extensive. This coincides with

the findings reported by Ling et al. (2010) where turf-forming algae that trapped significant amounts of sediment represented ~20% cover in areas they classified as '*Helicoidaris erythrogramma* barrens'. Such turf-forming algae (i.e. simple habitats; see review Krause-Jensen et al., 2008) can replace canopy-forming algae (i.e. high structural complexity and highly productive habitats) particularly in historically low-nutrient coastal waters (Connell et al., 2008). Furthermore, inhibitory effects of turfs on recruitment of canopy-forming algae have been shown to reduce recovery of canopy forests in many locations around the world (Airoldi et al., 2008), including temperate Australia (Gorman and Connell, 2009).

Across the Leeuwin Current, sheltered coasts that support dense populations of urchins tend to also be associated with high terrestrial discharge of nutrients that sustain turf covers (Gorman et al., 2009). Whilst nutrients can increase (Bertness et al., 2008; Russell and Connell, 2005) or decrease rates of herbivory (Chase et al., 2000), it is possible that nutrients and urchins may together enhance the cover of turfs. Where nutrients directly elevate turfs, which inhibit canopy recruitment (Gorman and Connell, 2009), dense populations of urchins can reduce canopies which would otherwise suppress turf growth (Irving and Connell, 2006b). In this way, canopies may be reduced by the indirect effect of nutrients (i.e. enhancing turfs that inhibit canopy recruitment) and direct effects of urchins (i.e. grazing of canopies) to perhaps create the pattern of more extensive covers of turfs on sheltered than exposed coasts.

Large areas of the exposed Leeuwin Current coast have few if any urchins (Connell and Irving, 2008), but sheltered coasts tend to be associated with greater densities (Livore, 2011; Vanderklift and Kendrick, 2004). Indeed, the observed and experimental densities reported here (eastern part of Leeuwin Current) are similar to comparable coasts of Western Australia (western part of Leeuwin Current; Vanderklift and Kendrick, 2004; Vanderklift and Wernberg, 2008). Despite these densities and the relatively weak to non-existent effects of urchins across much of this coast (Connell, 2007), locations with densities >40 individuals m<sup>-2</sup> are likely to be intensively grazed (see earlier discussion). Grazing by *Helicoidaris erythrogramma*, however, is probably not as substantial as that of the black sea urchin (*Centrostephanus rodgersii*) which is associated with barrens across much of the coast of the Eastern Australian Current (Andrew and Underwood, 1993; Connell and Irving, 2008). A key difference between *C. rodgersii* and *H. erythrogramma* is that black sea urchins are much larger and are more dynamic foragers that actively scrape nearly all erect algae from rock on exposed coasts where as *H. erythrogramma* only adopt this behaviour in some circumstances in sheltered coasts (e.g. Ling et al., 2010; Wright et al., 2005).

In conclusion, these results suggest that sedentary sea urchins can have an effect on algal cover at a fine-scale (centimetres). Although these urchins seldom occur in dense populations, those localities with such populations (e.g. sheltered coasts) may be more affected by urchins than currently thought. Indeed, urchins do not necessarily need to create barrens before their effects on the broader community are detectable or even perhaps substantial.

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## CHAPTER 5

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### GENERAL DISCUSSION



## CHAPTER 5

### GENERAL DISCUSSION

The effects of herbivory can vary across wide-ranging habitats and spatial scales, therefore, an integrative approach across these scales is necessary to comprehensively understand how functional dynamics of herbivores may differ. At its most basic, abundance can often determine the effect size of herbivory (Estes et al. 1998; Shears and Babcock 2002), hence, knowledge of patterns of abundance of herbivores at various spatial scales is essential.

In this thesis, I have shown that variation in abundance and condition of sea urchins may operate at two contrasting scales, namely regional and local scales. The observed patterns provide a basis to experimentally assess variables that may determine rates of algal consumption and potential consequences to the surrounding habitat. Herbivore feeding behaviour is a factor that can influence consumption and can range from very local small-scale effects (i.e. centimetres) to aggregative effects that create landscapes across entire regions (e.g. sea urchin barrens across eastern Australia; Connell and Irving 2008). Consequently, factors that mediate herbivore behaviour and are associated to the environment (e.g. quantity and quality of food) can have an influence on plant/algal communities.

Sedentary sea urchins rely on water currents to deliver food, hence, a decrease in the amount of available food (i.e. drift-algae) will lead to a deteriorated condition and a foraging behaviour that reduces standing algal biomass (Chapter 2). Urchins with poor

condition and increased foraging rates can also be the consequence of the availability and traits of food. Algae that originated in sheltered rather than exposed habitats caused sea urchins to graze more intensely, yet achieve poorer condition; this evidence is in agreement with the natural population patterns of poor condition observed on sheltered but not exposed coasts (Chapter 3). Finally, I experimentally demonstrated the effects of sea urchins on algae in the common behavioural state observed in South and Western Australia (i.e. sedentary drift-feeding) at a small-scale (i.e. centimetres) (Chapter 4).

This chapter provides a discussion of the key points of interest outlined in the introduction (Chapter 1), and how they are linked. Finally, future directions for research are suggested and final conclusions mentioned.

### **5.1 Patterns of sea urchin abundance and condition**

To understand the processes that drive variation in herbivory on coastal rocky reefs, we need to know the spatial scale at which herbivore populations fluctuate. I assessed regional to local scale relationships of sea urchin density and condition across much of the coast of temperate Australia, thus, determining the spatial scales at which these variables change. I found that the more productive coast of eastern Australia supported greater densities of the sea urchin *Heliocidaris erythrogramma* than did the other regions to the extent that sea urchin barrens were only observed in the eastern Australian region. Furthermore, within the latter region abundances were substantially higher on sheltered than exposed coasts suggesting that abundance patterns may vary at both large and local scales. The local scale pattern (i.e. more abundant in sheltered waters) was also evident in southern Australia, albeit no barrens were observed within this region. There are many mechanisms that may influence abundance patterns at each

scale. Recruitment, for example, could affect patterns of density at a local scale as bays and gulfs often have local currents that tend to facilitate larval retention. This could be the case particularly for species that have short pelagic larval phases such as *H. erythrogramma* (3.5 d; Williams and Anderson 1975). The purple sea urchin has a lecithotrophic pelagic larval stage in which it does not need to feed to survive. After this pelagic stage larvae settle on the benthos following specific cues released by certain biofilms formed by bacteria. The variation in biofilm composition and characteristics that affect larval settlement could also help explain density patterns observed for the purple sea urchin at both the regional and local scale. Hugget et al. (2006) showed that bacteria in biofilms associated to articulated coralline algae induced the settlement of *H. erythrogramma* larvae whilst other co-existing algae-biofilm associations did not. At a regional scale, Eastern Australian coasts (high sea urchin densities) have greater presence of articulated corallines than the Leeuwin Current coasts (low sea urchin densities) (Fowler-Walker and Connell 2002), suggesting that favourable conditions for larval settlement may be prevalent in the former region. Water nutrients may also cause variation in biofilms that can lead to differences in recruitment. Waters with elevated nutrients have been shown to produce biofilms that induce greater recruitment of invertebrate larvae than those in lower nutrient waters (Hung et al. 2007). At a large scale, the Eastern Australia Current has greater nutrient (Rochford 1979; Russell et al. 2005) and chlorophyll *a* (appendix A) concentration, which can be related to water column productivity, than the Leeuwin Current. At a local scale, sheltered coasts tend to have higher nutrients than exposed coasts (Chapter 3) which in combination with prevalent currents that increase larval retention may determine a higher recruitment in these areas. Whilst the relationship between nutrients and chlorophyll *a* with sea urchin

densities may not describe the mechanisms that drive it, they can still be a useful tool to help identify the conditions that are favourable for urchin populations. The individual mechanisms (i.e. larval retention, settlement cues, nutrients in water column), or a combination of them, provide possible pathways that can be contributing the observed relationship between urchin density and coastal features at both large and local scales. However there are other factors that have not been explored in this thesis that may also be linked to the observed patterns of abundance, such as juvenile and adult survival related to predation or diseases, food availability for the juvenile stages or temperature oscillation tolerance, that cannot be excluded and merit consideration for future studies.

A relationship between sea urchin gonad condition and coastal exposure (i.e. sheltered and exposed coasts) was observed for both regions; sheltered coasts consistently harboured sea urchin populations with poorer gonad condition. This is of particular relevance because *Heliocidaris erythrogramma* barrens have only been described in sheltered waters and poor condition is often associated with barren-forming urchin populations. The patterns identified for sea urchin abundance and condition across wide ranging scales provided an appropriate framework for part of the experimental research of this thesis (i.e. Chapter 3 and 4) where conditions that were considered to potentially affect urchin condition (e.g. food quantity and origin) were manipulated.

## **5.2 The influence of drift-algae on sea urchin condition and behaviour**

Sea urchins that exert strong herbivore effects on standing algae can have poor condition (e.g. Harrold and Reed 1985; Konar and Estes 2003). It has been suggested that poor condition may lead to changes in feeding behaviour which result in increased

herbivory. Purple sea urchins in South Australia mainly display a sedentary drift-feeding behaviour and therefore have no control over the quantity or quality of food that is delivered to them. It is expected that both quantity and traits of the food consumed will affect their condition. I show that a reduction in food availability not only reduced gonad condition, but also caused sea urchins to forage more actively on surrounding algae (Chapter 2). This grazing effect was intensified at higher densities which showed an interaction between the two factors (i.e. food availability and density) and caused the poorest condition.

As a drift-feeder the purple sea urchin relies on external subsidies to provide the necessary food resources. The traditional spatial subsidies theory suggests that an increment in the subsidy would allow for consumer population growth in the recipient habitat (Polis et al. 1997). The increased abundance would reduce *per capita* food for consumers which may lead to a reduction of the local resource (i.e. reduction of resource in recipient habitat) through more consumption. The case for *Heliocidaris erythrogramma* seems to go against this model as more consumption would be the result of a decrease of the subsidy. A reduction (not an increment) in the subsidy leads to impoverished condition which can trigger a switch in feeding behaviour and the ensuing overconsumption of the local resource (Chapter 2). This finding suggests that this spatial subsidies model may not always apply ubiquitously and that the ecological role of consumers in trophic webs may need to be considered independently in for each ecosystem.

The origin of the subsidy and therefore the traits the food has also seems to have an important role for *H. erythrogramma*. A negative effect on gonad condition was

observed when urchins were fed algae originated in sheltered coasts regardless of how frequently they fed (Chapter 3). When food originated on exposed coasts was delivered frequently, urchins developed better gonad condition and showed the lowest feeding rates. Therefore, sea urchin condition and foraging behaviour seems to be affected by both quantity (Chapter 2 and 3) and origin of the food source (Chapter 3).

These results provide an explanation for why *Heliocidaris erythrogramma* can have a strong impact on the algal habitat in sheltered and semi-sheltered waters (Wright et al. 2005; Ling et al. 2010). Water energy and turnover on sheltered coasts is lower than on exposed coasts, the former receive less amount of wrack than exposed coasts (Bustamante and Branch 1996), which I have shown has an effect on both urchin foraging and condition (Chapter 2 and 3). Concurrently, sea urchin densities are greater in sheltered coasts (Chapter 3) suggesting a lower *per capita* distribution of an already low amount of food when compared to exposed coasts. Also, sheltered coastal waters are often affected by human settlements through sewage and rainwater runoffs that increase nutrient concentrations (Gorman et al. 2009) and which could confer traits to algae that have a detrimental effect on urchins (Chapter 3). A comprehensive view of these results suggests that some sheltered coasts may have a set of ecological traits that when concurrently present make them the most likely type of habitat for *H. erythrogramma* to exhibit a strong herbivore effect.

### **5.3 Small-scale effects of drift-feeders**

Herbivory by sea urchins has received much attention around the world with focus set primarily on the creation of gaps devoid of algae (i.e. sea urchin barrens) within canopy-algal forests (Breen and Mann 1976; Chapman 1981; Harrold and Reed

1985; Sala et al. 1998; Konar and Estes 2003; Ling 2008). Many temperate rocky coasts while containing an abundance of sea urchins, however, lack the presence of these barrens areas and are covered with large extensions of forests (Connell 2007; Connell and Irving 2008). Yet, studies on the foraging effects of sea urchins in the absence of barrens are scarce (but see Vanderklift and Kendrick 2005; Vanderklift et al. 2009). Therefore, our understanding of sea urchin ecology is currently influenced by studies on sea urchins that have a strong and obvious herbivorous effect although this may only represent a small section of the environments they occur in.

Sea urchins often adopt a drift-feeding behaviour that does not have obvious effects on the surrounding algae on a large scale (e.g. lack of sea urchin barrens). By assessing algal assemblages on a small scale, I determined an area of influence of drift-feeding sea urchins on algae. In the vicinity of sea urchins (~ 8cm) turf-forming algae monopolized space, after which canopy-forming algae dominated primary cover (Chapter 4). Furthermore, I demonstrated that sea urchin caused an absence of algae directly underneath them. The removal of urchins allowed for turf-forming algae to immediately dominate the freed space. Turf-forming algae can have a strong influence on forest recovery as it can inhibit recruitment of canopy-forming species (Gorman and Connell 2009). Canopy recruits may have less success at recruiting to unstable substrate created by turf that trap and bind sediments (review in Airoidi 2003). Canopy-forming algae were able to reach cover indistinguishable to those in areas unaffected by urchins, within ~ 3 years (Chapter 4). Although the experiment was done at a sheltered reef with high sea urchin density, canopy-forming algae dominated the small gaps previously occupied by urchins. Consequently, for a declining forest scenario to occur in South Australia, densities of the purple sea urchin need to reach greater densities than those

described in Chapter 4, in order to magnify small scale effect of sea urchins on algal cover.

Many studies have related strong grazing to sea urchin density suggesting that the competition for food led to a destructive feeding behaviour (Harrold and Reed 1985; Shears and Babcock 2002). By demonstrating the existence of and quantifying small scale effects of urchins on surrounding algae I have added a new level of understanding to this matter. The estimation of urchin densities at which a barrens scenario could be expected even without a switch in urchin feeding behaviour is a previously unexplored alternative that may be considered in future studies. It is possible that some of the previously recorded occurrences of *H. erythrogramma* barrens (i.e. Shepherd 1974; Wright et al. 2005) may actually be a consequence of the very high densities observed at those particular sites and not of a destructive feeding behaviour.

#### **5.4 Future research**

In Chapters 2 and 3, I related sea urchin densities and condition across temperate mainland Australia across wide ranging scales in a particular time of the year. A more comprehensive assessment of this relationship would be possible if future sampling is done on several occasions within a year (e.g. seasonally) and throughout multiple years. Additional sites expanding the range of exposure in order to obtain a wide range rather than extremes would also provide valuable information on potential exposure thresholds. Along with this sampling it would be insightful to include the measurement of benthic productivity of the contrasting locations in order to relate sea urchin density and condition to local benthic food availability. Assessing recruitment throughout the same periods and across the same geographic extent would provide a further



understanding of the mechanisms driving these patterns. Furthermore, recruitment can have an influence in the contrasting urchin densities on sheltered and exposed coasts which also need verification. Anecdotal evidence suggests that spawning in *H. erythrogramma* occurs in warm waters and extremely calm seas. Understanding the mechanisms that trigger spawning, identifying which populations have spawning potential based on these mechanisms and the factors that determine larval dispersal can be useful to combine with existing settlement knowledge to predict high sea urchin density areas in Australia.

Drift-algal availability and sea urchin density were shown to have a determining influence on sea urchin condition and behaviour in a cage experiment on an exposed coast of South Australia (Chapter 2). The effect of these factors was measured on algae recruiting to urchin enclosures, which consisted mainly of turf-forming algae. This scenario is similar to what occurs after storms create gaps in temperate forests and the succession process begins. A different scenario that needs to be tested would be to determine the effect of sea urchins on an established canopy-forming community under reduced drift-algal availability and elevated densities. Future experiments could be done caging urchins directly inside forests, with appropriate controls in surrounding areas. These two factors can also be assessed in both sheltered and exposed coasts simultaneously which would incorporate a third factor (i.e. origin of food) that has also been shown to effect sea urchin behaviour and condition (Chapter 3). This would broaden the effects of drift-algae on sea urchins described so far.

Food source that originated on sheltered coasts can reduce sea urchin condition and cause a higher feeding rate than food originated on open coasts (Chapter 3). I

quantified algal protein and C:N ratios to establish if the origin of the food had biochemical differences that could explain the results. High protein food has been shown to increase gonad condition in sea urchins (Hammer et al. 2000), however, this was not observed in this experiment. Chemical compounds found in the kelps (i.e. phlorotannins) can deter herbivore consumption of the algae (Hay and Fenical 1988). Phlorotannin concentrations tend to be higher in plants with low C:N ratios (Targett and Arnold 1998), therefore, feeding rates in my experiment cannot be explained through these secondary metabolites. Identifying the physiological pathways that acted to determine such contrasting effects among habitat of origin would allow for a better understanding of habitat related traits that are of ecological importance for rocky shore communities.

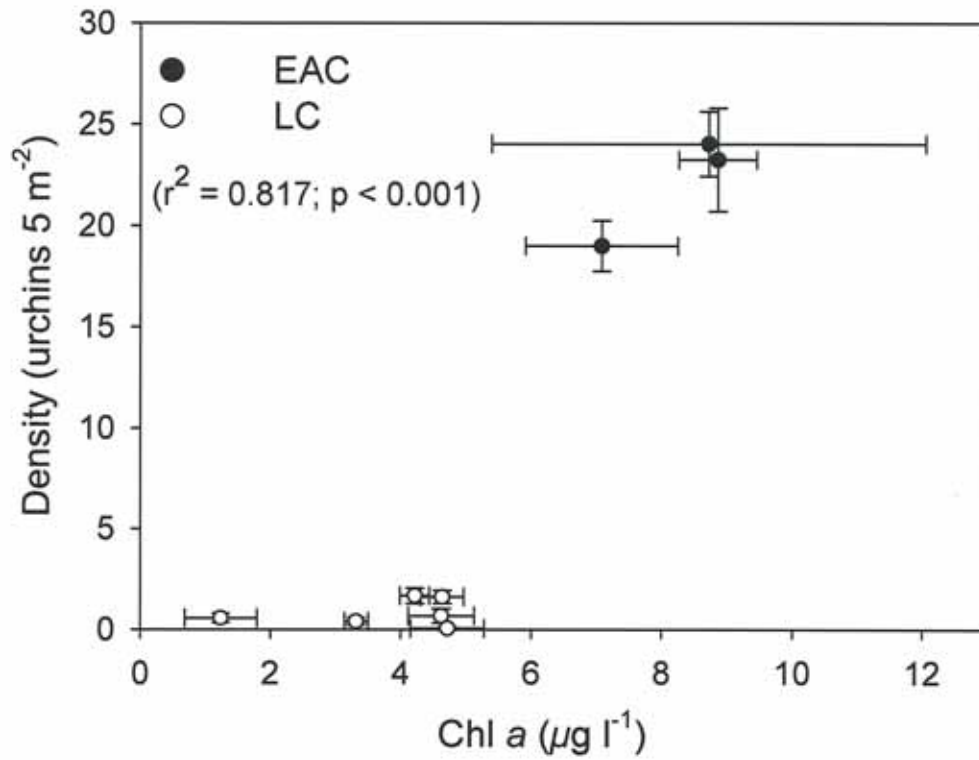
In Chapter 4, I showed that drift-feeding sea urchins can affect algal cover in their surroundings, albeit at a small scale on a sheltered South Australian rocky reef. There has been limited research done on urchin species that may have small herbivore effect sizes in marine ecosystems, however, this may be the type of herbivory that is occurring across large areas of temperate rocky coasts. Knowledge on small scale herbivory by other species would allow for a comprehensive appreciation of community dynamics.

## **5.5 Conclusions**

Herbivory can determine algal community structures, but generalisations based on herbivores that have strong effect sizes may lead to equivocal ecological interpretations and assumptions. In this thesis, I provide knowledge across a broad range of scales that allow for a more comprehensive view of *H. erythrogramma*'s

ecology. I have shown that sea urchin abundance and condition vary at a regional and local scale. I have also shown that herbivore behaviour and condition is reliant on quantity and traits (i.e. source) of food, both of which can be associated with the characteristics of the local habitat (e.g. local scale). Furthermore, I have demonstrated that on a small scale the herbivorous effects of sedentary urchins can be detectable and should be considered in rocky subtidal community studies of locations with such consumers. The strength of herbivory appears to vary widely across temperate Australia and this thesis may provide a continental and coastal morphology framework in which to understand this variation. This thesis also supports the idea that strong herbivory on subtidal coasts is not ubiquitous and is context dependent. Understanding such context-dependency, therefore, may improve the generality of models that account for the dynamics of subtidal rocky ecosystems.

## APPENDIX A



Linear regression between Chl *a* concentration (mean  $\pm$  SE) and sea urchin abundance (mean  $\pm$  SE) for *H. erythrogramma* across the 2 major currents.

## APPENDIX B

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