2007

The use of detached kelp (Ecklonia radiata) by seagrass-associated mesograzers in temperate South-Western Australia

Christopher Doropoulos
Edith Cowan University

Edith Cowan University

Copyright Warning

You may print or download ONE copy of this document for the purpose of your own research or study.

The University does not authorize you to copy, communicate or otherwise make available electronically to any other person any copyright material contained on this site.

You are reminded of the following:

- Copyright owners are entitled to take legal action against persons who infringe their copyright.

- A reproduction of material that is protected by copyright may be a copyright infringement. Where the reproduction of such material is done without attribution of authorship, with false attribution of authorship or the authorship is treated in a derogatory manner, this may be a breach of the author's moral rights contained in Part IX of the Copyright Act 1968 (Cth).

- Courts have the power to impose a wide range of civil and criminal sanctions for infringement of copyright, infringement of moral rights and other offences under the Copyright Act 1968 (Cth). Higher penalties may apply, and higher damages may be awarded, for offences and infringements involving the conversion of material into digital or electronic form.

The use of detached kelp (*Ecklonia radiata*) by seagrass-associated mesograzers in temperate south-western Australia

Christopher Doropoulos

A thesis submitted in partial fulfilment of the requirements for the awards of
Bachelor of Science (Biological Science) Honours

At the School of Natural Sciences
Faculty of Computing, Health and Science
Edith Cowan University

Supervisors:
Dr Glenn Hyndes
Professor Paul Lavery
Dr Fernando Tuya

Date of Submission: 2nd November, 2007

USE OF THESIS

The Use of Thesis statement is not included in this version of the thesis.

Abstract

The movement of nutrients and organisms between habitats provide important spatial subsidies on local and regional scales, resulting in increased primary and secondary production, especially where inputs supplement habitats of relatively low levels of comparable resources. In coastal south-western Australia, the brown kelp, *Ecklonia radiata*, is produced in large quantities on offshore reefs from where it detaches and passes through neighbouring habitats. This allochthonous resource is present in large quantities in seagrass meadows and thereby potentially influences the trophic dynamics of this habitat, providing an additional food source for grazers to those produced *in situ*. This study investigated the effects of the large detached kelp on mesograzer trophic dynamics in *Posidonia* and *Amphibolis* seagrass meadows. Laboratory choice and no-choice feeding experiments tested whether preferential consumption of the kelp occurred in comparison to autochthonous resources by two locally abundant gastropods, *Pyrene bidentata* and *Cantharidus lepidus*. Results from the feeding experiments demonstrated that both species of gastropod did not preferentially consume fresh or aged kelp, but the rates of consumption were generally similar to locally abundant periphyton and red algae that are epiphytes on seagrass leaves. In comparison, the gastropods consistently avoided consumption of seagrass leaves. Field experiments were conducted at four sites during winter to measure the effects of mesograzer consumption of kelp in different dominant seagrass habitats and at different proximities to reef to encompass a range of landscape-scale effects on seagrass meadows. There were no significant effects of any main factor in the field experiment, due to an apparent lack of grazing of the large detached kelp by the mesograzers in the seagrass meadows. High variability influenced the consistency of the results, which may have been a result of cage artefacts, bacterial decomposition, or physical abrasion. Overall, the results suggest that, although seagrass-inhabiting mesograzers are capable of consuming detached *E. radiata*, consumption was either absent or not detected, possibly due to the high availability of autochthonous resources in seagrass meadows. Thus, it is possible that this allochthonous food source provides a negligible spatial subsidy to mesograzers in a habitat where comparable food resources are relatively unlimited, matching empirical thought. However, additional studies during different seasons and at different locations are necessary to further investigate these conclusions, to assess if allochthonous resources influence seagrass meadow trophic dynamics when *in situ* food limitation occurs.

Copyright and Access Declaration

I certify that this thesis does not, to the best of my knowledge and belief:

> *(i)   incorporate without acknowledgement any material previously submitted for a degree or diploma in any institution of higher education;*

> *(ii)   contain any material previously published or written by another person except where due reference is made in the text; or*

> *(iii)   contain any defamatory material.*

I also grant permission for the Library at Edith Cowan University to make duplicate copies of my thesis as required.

Signed___

Dated___ 29/11/07

Acknowledgements

Table of Contents

List of Figures

List of Tables

1. Introduction

1.1 Spatial subsidies and trophic connectivity

Boundaries between different habitats are generally imprecise and allow for the passive and active movement of biological and physical resources, which include organisms, organic matter and nutrients (Jones & Andrew 1992, Polis & Strong 1996, Valentine & Heck 2005, Marczak et al. 2007). In general, nutrient inputs increase primary productivity, whilst detrital and prey inputs produce numerical responses in consumers (Polis et al. 1997). The movement of food and nutrients between habitats can be important where habitats of relatively low productivity are located adjacent to those of relatively higher primary productivity (Polis & Strong 1996, Valentine & Heck 2005, Wernberg et al. 2006). Strong effects of subsidies are often seen in environments that are relatively open to neighbouring ecosystems or have a large perimeter to area ratio (Polis & Strong 1996, Polis et al. 1997, Marczak et al. 2007). Most importantly, subsidy effects appear to be the greatest when they subsidise a system with low levels of comparable resources, rather than just systems of contrasting primary productivity (Marczak et al. 2007).

Understanding the trophic connections within and between habitats is essential to the understanding of trophic dynamics of food webs (Krebs 2001). The flow of energy through food webs is rarely a simple vertical process as described by linear food chains (Polis & Strong 1996, Krebs 2001); rather, most food webs are reticulate and species are highly interconnected (Polis & Strong 1996). Many species can change trophic levels depending on spatial and temporal influences, further increasing the trophic complexity of food webs (Fairweather & Quinn 1992, Polis & Strong 1996, Polis et al. 1997). The increased connectivity of food webs diffuses the direct effects of productivity and consumption throughout trophic levels, with producers and consumers both being influenced by resources at multiple trophic levels (Polis & Strong 1996, Krebs 2001). The movement between habitats of higher order consumers supports their abundances by consuming a vast array of resources from many different habitats without overexploitation (Valentine & Heck 2005). Physical and biological phenomena apparent at large geographical scales may contribute to those of small geographic scales, and *vice versa* (Jones & Andrew 1992, Anderson et al. 2005). For example, Dulvy et al. (2002) demonstrated in a coral reef habitat

that, at small scales, epifaunal density was influenced by algal biomass, but at large scales predation by fish was the main contributor structuring epifaunal communities. Therefore, understanding the mechanisms of trophic connections – in consideration of supply, trapping and consumption, and export – is essential in understanding the ecology of communities for the effective management of the marine environment for particular species, for fisheries management (Fairweather & Quinn 1992), and marine conservation (Valentine & Heck 2005).

Spatial subsidies generally increase where the physical transport agents (currents and winds) are relatively strong (Polis & Strong, 1996, Polis et al. 1997, Tanaka & Leite 2003). The intensity of their effects can change through time due to episodic or seasonal variations (Marczak et al. 2007), such as changes to the amount of input into a habitat or changes in the productivity of the recipient habitat due to seasonal weather regimes. In theory, spatial subsidies influence all aspects of food web structure and dynamics, of which some predictions match empirical patterns whilst others need assessment (Polis et al. 1997). In a recent meta-analysis of literature reviewing the effects of spatial subsidies, Marczak et al. (2007) found that subsidies inconsistently affected consumer density or biomass across habitats, trophic and functional groups.

1.2 Spatial subsidies in seagrass meadows

Traditionally, seagrass ecology has focussed on seagrass habitats independent of their surroundings (Jernakoff et al. 1996), and linkages between reefs and adjacent seagrass beds in temperate environments are poorly understood (Jones & Andrew 1992). Some studies have considered the influence of coral-inhabiting organisms on neighbouring seagrass meadows (Valentine & Heck 2005), and gradient effects of invertebrates have been studied between reef and unvegetated habitats (Barros et al. 2001). Recent trophodynamic research conducted in seagrass meadows in south-western Australia have identified that brown algae, red algae, and periphyton, contribute the majority of carbon and nitrogen to mesograzers rather than live seagrass leaves (Smit et al. 2005, 2006, Hanson et al. unpublished data). It is unresolved whether these are derived from either autochthonous or allochthonous resources, or a combination of both. A few recent studies have considered the proximity of seagrass habitats to reefs, in relation to the effects on epiphytic macroalgal

assemblages (van Elven et al. 2004), drift macroalgal and fish assemblages (Wernberg et al. 2006), and gastropod assemblages (Tuya et al., in prep.). The present study has focused on the trophic dynamics and connectivity involving large drift kelp detached from reefs and mesograzers inhabiting seagrass meadows, along gradients with proximity to reefs. These relationships may form trophic links between the communities and higher order consumers that inhabit them, thus playing an important role in food web dynamics and the management of marine ecosystems.

1.3 Grazing of macrophytes in marine habitats

Temperate rocky reefs are heterogeneous habitats, usually surrounded by vegetated (seagrass) and un-vegetated substrates, with sharp or gradual boundaries (Jones & Andrew 1992, Barros et al. 2001). Predatory fauna, such as fish and crustaceans, that inhabit temperate rocky (and coral) reefs often use seagrass beds and unvegetated areas for foraging and nurseries (Jones & Andrew 1992, Valentine & Heck 2005). Many of these organisms rely on epifaunal mesograzers as prey (Taylor 1998, Dulvy et al. 2002, Tanaka & Leite 2003, Poore & Hill 2005, Crawley et al. 2006). Within the adjacent seagrass meadows, diverse assemblages of mesograzers (grazers between 2 mm and 2.5 cm [Jernakoff et al. 1996]) are often the primary consumers of detrital and fresh macrophytes, including brown, red, and green algae, and seagrasses (Edgar 1990a, 1990b, Duffy & Hay 1991, Hyndes & Lavery 2005, Crawley & Hyndes 2007). The choice of a host plant by mesograzers may depend upon a multitude of factors including mobility and competition, host-plant nutritional value, refugia from predation, morphology, toughness, and chemistry, of which no single factor explains plant-mesograzer relations (Lubchenco & Gaines 1981).

Living seagrass is traditionally understood to be a low quality food resource for marine invertebrates (Nielsen & Lethbridge 1989, Hyndes & Lavery 2005, Heck & Valentine 2006), particularly in temperate seagrass habitats (Valentine et al. 1997, Valentine & Heck 1999), where direct consumption of seagrass by marine organisms can be <5% of the total production (Orth & van Montfrans 1984). Seagrass food webs are often considered to be based on epiphytic and periphytic material that grows on seagrass leaves, providing an important resource for grazers (Edgar 1992, Jernakoff et al. 1996, Jernakoff & Nielson 1997, Peterson & Heck 2001, Keuskamp 2004). Epiphytes also influence the species

richness and abundance of grazers through their diversity (Edgar 1990a), the provision of structural complexity (Tanaka & Leite 2003), and the increase in food availability (Bologna & Heck 1999).

Mesograzers, particularly amphipods and gastropods, are important grazers of the epiphytes, periphyton, detrital matter, and particulate organic matter (POM) found in seagrass habitats (Nielsen & Lethbridge 1989, Hutchings et al. 1990/91, Kirkman et al. 1990/91, Edgar & Shaw 1993, Jernakoff et al. 1996, Jernakoff & Nielson 1997). Their dietary preferences often overlap (Hootsmans & Vermaat 1985, Howard & Short 1986, Edgar 1990b) with epiphytes and periphyton being preferred to detrital resources (Nielsen & Lethbridge 1989, Jernakoff et al. 1996, Jernakoff & Nielsen 1997). Yet, sometimes dietary preferences are distinct, with specific assemblages of amphipods often being associated with detached macrophytes (Edgar 1990a, 1992) or POM found on the sediment surface (Edgar 1990b, Smit et al. 2005). Consumption of resources by the different size classes of mesograzers often differs (see table in Jernakoff et al. 1996), with smaller amphipods and isopods exhibiting much higher feeding rates than gastropods.

Brown algae are a conspicuous component of the temperate marine ecosystems of south-western Australia, often dominating the algal biomass (Kirkman 1984, Kendrick et al. 1999, Wernberg et al. 2003, 2006). The consumption of brown algae is a common feature amongst many temperate amphipods (Hay et al. 1990, Duffy & Hay 2000, Norderhaug et al. 2003, Taylor & Brown 2006, Crawley & Hyndes 2007), isopods (Pennings et al. 2000, Taylor & Steinberg 2005), and gastropods (Steneck & Watling 1982, Steinberg & van Altena 1992, Wakefield & Murray 1998). Brown algae are often the preferred food source by mesograzers in laboratory experiments, regardless of their nutritional value, toughness, morphology, or phlorotannin content (Duffy & Hay 1991, Wakefield & Murray 1998). Many mesograzers have adapted to the plant chemicals, sometimes as a compromise to food quality (Duffy & Hay 1991, Cox & Murray 2006), to provide protection from fish predation via association (Hay et al. 1990, Duffy & Hay 1994, Poore 2005). It has also been suggested that many mesograzers have adapted to the chemical content of brown kelps, due to its abundance in local environments as the resource would be a commonly encountered food source as well as habitat (Wakefield & Murray 1998). Mesograzers often preferentially consume the algae from which they are collected (Steinberg & van Altena

4

1992) due to evolutionary adaptations (Taylor & Steinberg 2005). The mobility and the scales of dispersal of mesograzers is limited relative to larger grazers, thus, there is a greater tendency for local adaptation to the available host species (Poore 2005), whereas larger grazers often have a wider breadth of food preferences (Taylor & Steinberg 2005).

Food limitation is not generally recognised as a major factor influencing grazers inhabiting seagrass meadows, due to the abundance of epiphytes, periphyton, and detrital resources (Orth & van Montfrans 1984, Jernakoff et al. 1996), although it has been suggested that diffuse exploitative competition is widespread (Edgar 1990b). Grazers associated with macrophytes rather than detritus have shown greater seasonal fluctuations in total populations due to the rapid changes of epiphyte biomass compared to the slowly decomposing pool of detrital resources (Edgar 1990b). Furthermore, in experiments using mesocosms, grazing by amphipods, isopods and gastropods were demonstrated to have significant impacts in reducing epiphytes and periphyton growing on seagrass leaves (Hootsmans & Vermaat 1985, Howard & Short 1986). Conversely, field experiments in southern Australian seagrass meadows using grazer exclusion cages have demonstrated that there was a relative lack of real influence in controlling periphyton or epiphytes by amphipods or gastropods despite their known high grazing rates (Jernakoff & Nielsen 1997, Keuskamp 2004). Thus, the feeding of seagrass-inhabiting mesograzers appears variable in regards to the food they consume and is highly dependent on their mobility and the availability of epiphytes, periphyton, large detrital and particulate detrital material.

1.4 Influence of detached macrophytes on seagrass trophic dynamics

Many marine herbivores consume macrophytes after they have been detached from their substrata and become drift (Steinberg 1989), which is subject to physical and microbial degradation. Amphipods (Pennings et al. 2000, Norderhaug et al. 2003) and isopods (Pennings et al. 2000) have increased feeding preferences and survivorship on degraded kelp, correlated to increases in the nutritional quality and decreases in the chemical content of the material. Norderhaug et al. (2003) suggested that bacteria on the thalli surface played a key role in transferring primary production to higher trophic levels. Furthermore, the biofilm on subsidiary coarse woody debris has been demonstrated to be the preferred food source of gastropods inhabiting inter-tidal zones (Storry et al. 2006) and invertebrate

colonisation corresponds with the development of periphytic film or algae on artificial seagrass (Edgar & Klumpp 2003).

The common brown kelp, *Ecklonia radiata*, is a major forest forming kelp found in temperate Australian reefs (Goodsell et al. 2004). Direct grazing is rarely seen on *E. radiata* growing on reefs (Kirkman 1984, Wernberg et al. 2003, Vanderklift & Kendrick 2006), but as a detrital resource it is important for primary consumers in many Australian temperate marine environments (Kirkman 1984, Steinberg 1989, Kirkman & Kendrick 1997). For example, sea urchins studied in south-west Australian reefs used detached drift kelp as their main food source, rather than attached macroalgae (Vanderklift & Kendrick 2005). Detached macroalgae and seagrasses are also a valuable detrital resource in south-west Australian unvegetated surf zones and exposed sandy beaches (Kirkman & Kendrick 1997, Hyndes & Lavery 2005, Crawley et al. 2006, Ince et al. 2007). In sub-littoral unvegetated zones, detrital material has been demonstrated to increase the abundance of amphipods, primarily the common *Allorchestes compressa* (Crawley & Hyndes 2007), resulting in the increased abundance and biomass of invertebrate eating fish (Vanderklift & Jacoby 2003, Crawley et al. 2006). *E. radiata* and *Sargassum* sp. are likely to be driving the production of *A. compressa* in these unvegetated habitats (Crawley 2006).

1.5 Significance and aims of study

Reef algae can be highly productive, and inputs of decomposing drift and live and dead organisms to adjacent seagrass meadows may provide nutrients not available in seagrass meadows distant from reefs (van Elven et al. 2004). In south-western Australia, Wernberg et al. (2006) found that the kelp, *E. radiata*, dominated the detached algae found in seagrass meadows at varying distances from the adjacent reefs. The proportion of detached kelp found in the seagrass meadows was often greater than twice the amount of attached kelp found in the adjacent reefs. Furthermore, the total biomass of the detached macrophytes was not always significantly higher closer to the reef than at distances greater than 300m away. As result, it was concluded that there are likely to be local and regional linkages between reefs and seagrass meadows (Wernberg et al. 2006), as tagged drift kelp is known to travel distances up to 2 km (Kirkman & Kendrick 1997). There was a positive correlation between densities of herbivorous fish and the rates of consumption close to the reefs, but not far from the reef (Wernberg et al. 2006), suggesting that further from the reefs other

herbivorous taxa may be consuming the detached algae. Amphipods and gastropods are significant consumers of seagrass epiphytes, periphyton and detrital material (Edgar 1992, Jernakoff & Nielson 1997), but their grazing effects on the biomass of large detached kelp in these seagrass habitats remains unknown. The high abundances of these mesograzers potentially provide a significant source of consumption of the allochthonous brown algae.

The broad aim of this study was to gain a further understanding of the flow of energy through seagrass systems, by testing the influence of an allochthonous resource on the trophic dynamics of seagrass habitats. Furthermore, I sought to test whether any influence was consistent among the different dominant seagrasses of the region. In temperate Western Australia, *Posidonia* spp. and *Amphibolis* spp. form dominant seagrass meadows (Kendrick et al. 2000, Kirkman & Kirkman 2000). *Posidonia* spp. have strap-shaped leaves which arise directly from the sediment, whilst *Amphibolis* spp. have long, wiry stems from which clusters of leaves grow at the tips (Jernakoff et al. 1996). These differences provide distinct architectural types in which meadows of *Amphibolis* spp. consist of relatively open spaces below a dense leaf canopy, whereas those of *Posidonia* spp. consist of a uniformly dense leaf canopy arising directly from the sediment (Hyndes et al. 2003). These differences in architecture affect the fish assemblages (Hyndes et al. 2003), epiphyte diversity and biomass (Lavery & Vanderklift 2002), and may also affect the hydrodynamics and retention time of detrital material in seagrass meadows (Verduin et al. 2002). Together, this may produce differences in the availability and consumption of allochthonous resources by mesograzers in *Posidonia* and *Amphibolis* spp. habitats.

Specifically, the aim of the research was to determine the degree of connectivity between temperate rocky-reefs and adjacent seagrass habitats via consumption of large detached *E. radiata* by seagrass-associated mesograzers. I predicted that:
1. Key mesograzers inhabiting seagrass habitats consume large detached *E. radiata*, and that this consumption differs between, (a) the different size classes of mesograzers, with an alteration in the magnitude of consumption, (b) between two distinct seagrass habitats, and (c) with varying proximity to reefs; and
2. Mesograzers preferentially consume large detached *E. radiata* compared with locally-produced macrophytes, and this preference is affected by the resource's state of decomposition.

2. Materials and Methods

2.1 Field experiment

2.1.1 Pilot study

A pilot study was conducted at Wanneroo Reef (Figure 2.1) from the 9/4/07 to the 19/4/07 to test potential issues with the approach and design of the field experiment. The effect of pre-experimentation handling on the biomass of detached kelp was a priority for the pilot study, as the loss of kelp biomass was the main variable being tested. Since freezing provides a convenient method of storing *Ecklonia* prior to experimentation, the effects of freezing the kelp was examined by placing frozen and fresh material *in situ* for 5 and 10 days. The frozen kelp replicates ($n = 8$) were completely absent after 5 days *in situ*, whereas all replicates ($n = 8$) of the fresh detached kelp were present after 10 days *in situ*, indicating that fresh detached kelp should be used for the experiment. The effects of fresh detached kelp being placed in a 4°C fridge in the experimental cages, in an esky, or in seawater overnight was then examined. The kelp left in cages at 4°C overnight lost a mean (± SE) biomass of 21.90 ± 1.55% ($n = 2$), the kelp left in the esky lost 9.43 ± 1.28% ($n = 2$), while there was no loss of biomass of the kelp left in seawater overnight ($n = 2$). Thus, it was decided to store the fresh detached kelp in seawater overnight and prepare it directly prior to deployment of the experiment.

The second major set of concerns of the pilot study were the effectiveness of the experimental controls and treatments, and the effect of the duration of the experimentation period for mesograzer recruitment and possible detached kelp consumption. Two controls and two treatments were tested, with three replicates of each. These were: 'closed' and 'open' controls, and '<5mm' and '<20mm' treatments (see *2.1.2 Experimental design and approach* for a detailed description). The expected differences between the experimental units were that there would be minimal biomass loss of detached kelp in the closed control, increased biomass loss of detached kelp in the <5mm treatment, further increased biomass loss of the detached kelp in the <20mm treatment, and maximum biomass loss of detached kelp in the open control. There were some expected significant ($P < 0.05$) effects between some of the controls and treatments; thus the design of the experimental controls and treatments were clarified as appropriate for the aims. A significant difference ($P < 0.05$) of

biomass loss of detached kelp between the 5 day and 10 day experimental periods was found. Mesograzer recruitment into the cages were high and similar between both time periods. The potential growth of epiphytes and/or periphyton was another concern relating to the time period of experimentation. No major growth was qualitatively noticed after the 5 day time period, but a slight amount of periphyton growth was noticed after 10 days. Thus, considering these pilot results, it was decided to deploy the experiment for a 7 day time period.

An unexpected accumulation of sand within some of the experimental cages was encountered at the end of both time periods during the pilot experiment. Thus, to counteract the accumulation of sand as a confounding factor, the cages were not placed on the edges of seagrass meadows, but were placed in areas of seagrass of similar shoot density, and were orientated in the same direction with the elongated faces parallel to the coastline (parallel to the flow of sand).

2.1.2 Experimental design and approach

The field experiment was located within Marmion Marine Park, Western Australia (31°49.4' S, 115°44.0' E) (Figure 2.1). Marmion Marine Park is characterised by intermittent lines of outer and inner aeolianite limestone reef platforms parallel to the coast, ranging from 1 to 6 km offshore (Searle & Semeniuk 1985). These reefs are typically dominated by *Ecklonia radiata*, fucalean macroalgae, and small erect red algae (Kendrick et al. 1999, Wernberg et al. 2003). Extensive meadows of the seagrasses *Posidonia* spp. and *Amphibolis* spp. are interspersed between the reefs and unvegetated patches adjacent to reefs throughout the region (Kirkman & Walker 1989, Kirkman & Kirkman 2000). Six interspersed sites were selected within the area, with three dominated by *Posidonia* spp. and three dominated by *Amphibolis* spp. The sites were generally separated by 1 km, and were the same as those used by Wernberg et al. (2006) and Tuya et al. (In prep.). Sites ranged in depth from 4 to 10 m. *Posidonia* spp. sites were located at The Lumps, Whitfords Rock SW, and Wanneroo Reef, whilst *Amphibolis* spp. sites were located at Whitfords Rock NE, Wreck Rock, and Cow Rocks (Figure 2.1).
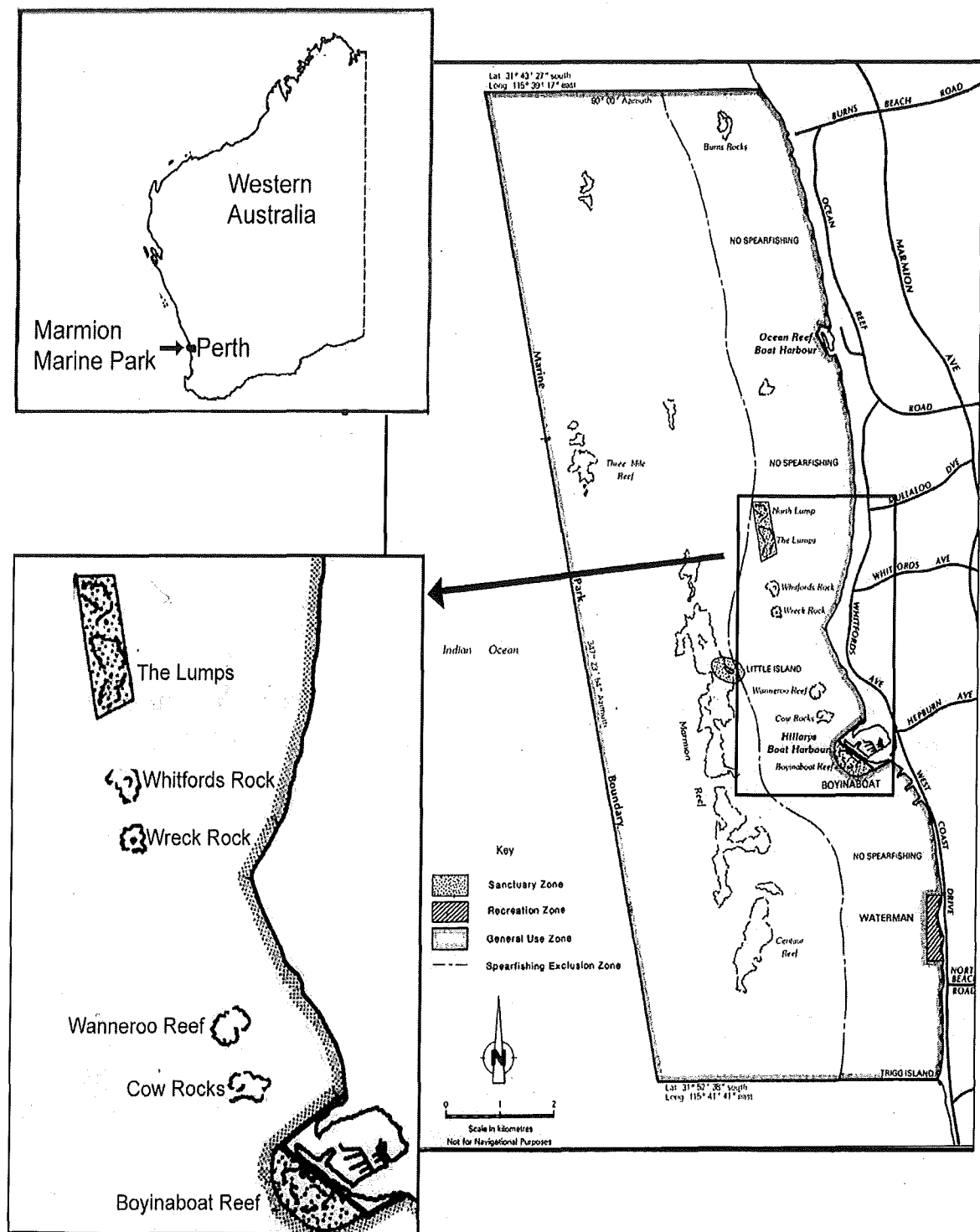
Figure 2.1 Location of Marmion Marine Park. The five reefs where the six sampling sites were located are shown in the bottom left map. *Posidonia* spp. meadows are located at The Lumps, Whitfords Rock SW, and Wanneroo Reef; *Amphibolis* spp. meadows are located at Whitfords Rock NE, Wreck Rock, and Cow Rocks (Source: Department of Conservation and Land Management, 1992 [?]).

The field experiment was conducted from the beginning of June to mid-July, 2007. During this time of year, detached *E. radiata* is present in its highest biomass in unvegetated surf zones (Kirkman 1984, Kirkman & Kendrick 1997, Crawley et al. 2006), correlating to the time of year when the frequency of storms is the highest, resulting in increased intensity of seas and swell (Lemm et al. 1999). Thus, it is assumed that the biomass of the detached kelp will also be at its highest in seagrass meadows, due to its movement from offshore reefs through seagrass beds to the unvegetated shoreline (Kirkman & Kendrick 1997). Due to logistical constraints, experimentation took place at three different times within the six week period. Two randomly selected sites were set up and collected within each two week time period. The differences in the sampling times were not considered important to the independent comparison of the six sites, thus time was not incorporated into any analysis as a factor.

Detached *E. radiata* significantly dominates the detached macroalgae accumulations at all six sites, and at distances of 0, 50 and >300 m from the reef (Wernberg et al. 2006). The greatest accumulations of detached kelp are generally found at the edge of the seagrass meadow and the reef (0 m), whereas highly variable accumulations are found >300 m away from the reef, and the lowest accumulations generally occur 50 m away from the reef (Wernberg et al. 2006). Accumulations of detached seagrass and red macroalgal seagrass epiphytes are also abundant at these sites (Wernberg, pers. comm.). In the current study, the distances with proximity from the reef were termed 'interface' (edge of seagrass-reef), 'close' (approximately 50 m into seagrass meadow) and 'far' (>300 m from reef). Experimental units comprised two treatments and two controls, which were designed to restrict access to the detached *E. radiata* depending upon the size class of the organisms. The two treatments also provided smaller organisms with protection from potential predators. The 'closed' control restricted access of fauna <0.5 mm to the detached kelp; the '<5 mm' treatment allowed access of fauna <5 mm to the detached kelp; the '<20 mm' treatment allowed access of fauna <20 mm to the detached kelp; and, the 'open' control allowed access of any fauna to the detached kelp. To evaluate the possible differences in mesograzer consumption of detached *E. radiata* at varying distances within seagrass meadows moving away from reefs, experimental units were placed in seagrass meadows at constant distances away from the reef, using similar criteria as Wernberg et al. (2006) and Tuya et al. (In prep.). Experimental distances used along each transect were located at the

12

seagrass-reef interface, close to the reef, and far from the reef. Three replicates of the two controls and two treatments were randomly located at each distance at each site (total $n =$ 216). Cages were spaced perpendicular to the transect, orientated with the elongated face parallel to the reef, with approximately 1m between every experimental unit (Figure 2.2).
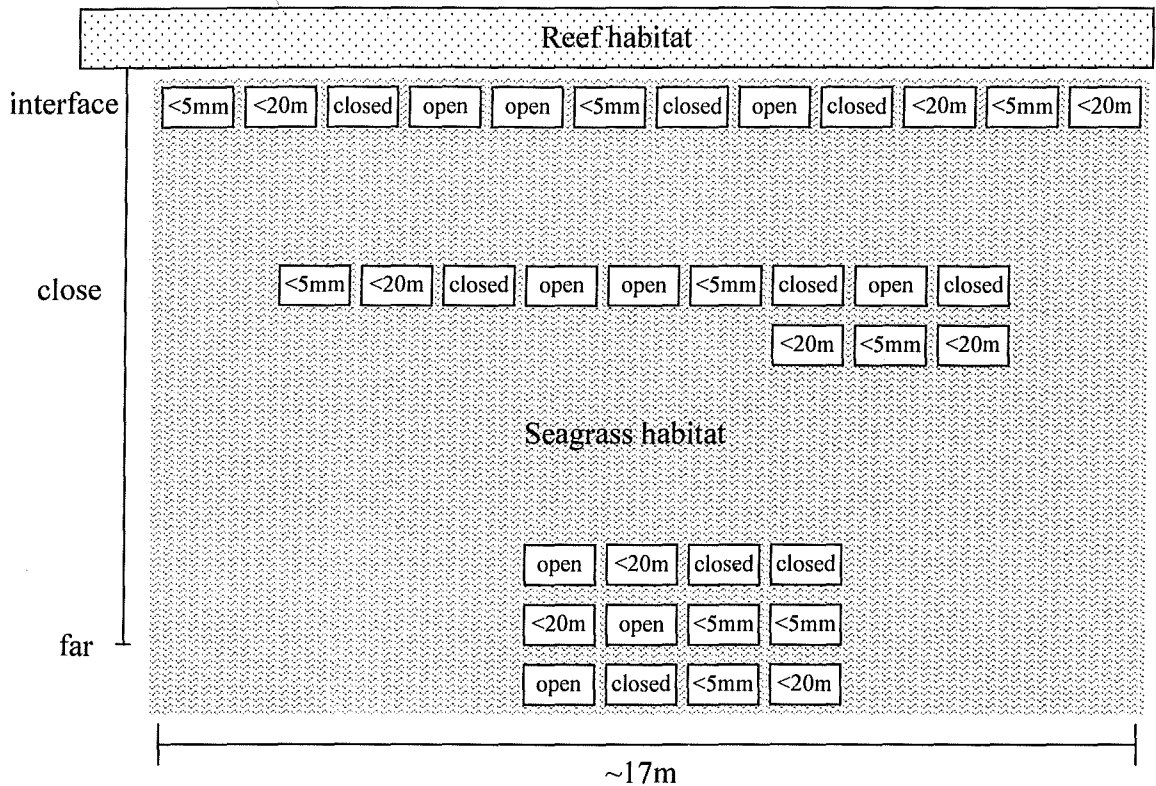
Figure 2.2 Example of the design of a single site within a seagrass meadow, indicating the sampling distances (3: interface, close, far), number of cage treatments (2: <5mm, <20mm) and controls (2: closed, open) and replicates (3) randomised at each distance ($n = 3$). Experimental units within a distance were spaced ~1m apart. Diagram is not to scale.

Metal 'bait' cages (30 cm long, 12 cm wide and 14 cm high) were used to house detached kelp for the closed, <5mm and <20mm experimental cages (Figure 2.3). Cages were covered in 0.5 mm PVC fly-screen with holes systematically cut into one of the small vertical sides, and haphazardly along the other small vertical side and the two elongated sides of the <5 mm and <20 mm treatments (Figure 2.3). This reduced any hydrodynamic variation between the two treatments and closed control (Keuskamp 2004), but still allowed mesograzer recruitment. The <5 mm treatment had 56 holes cut into one of the small faces, five holes cut into the other small side, and ten holes cut into the two elongated sides. The <20 mm treatment had nine holes cut into one of the small faces, three holes cut into the

13

other small face, and four holes cut into the elongated faces. All cages had clothes pegs attached on the inside diagonal corners to which the detached kelp was secured, thereby reducing any changes to the material from physical abrasion with the cage due to movement by currents and surge. The cages had a plastic loop on two bottom diagonal corners through which large tent pegs were inserted and hammered into the sediment to secure them to the benthos. The open controls used tethered pieces of detached kelp attached to clothes pegs. Clothes pegs were attached to both ends of the detached kelp, which were attached to small tent pegs and hammered into the benthos following Wernberg et al. (2006).
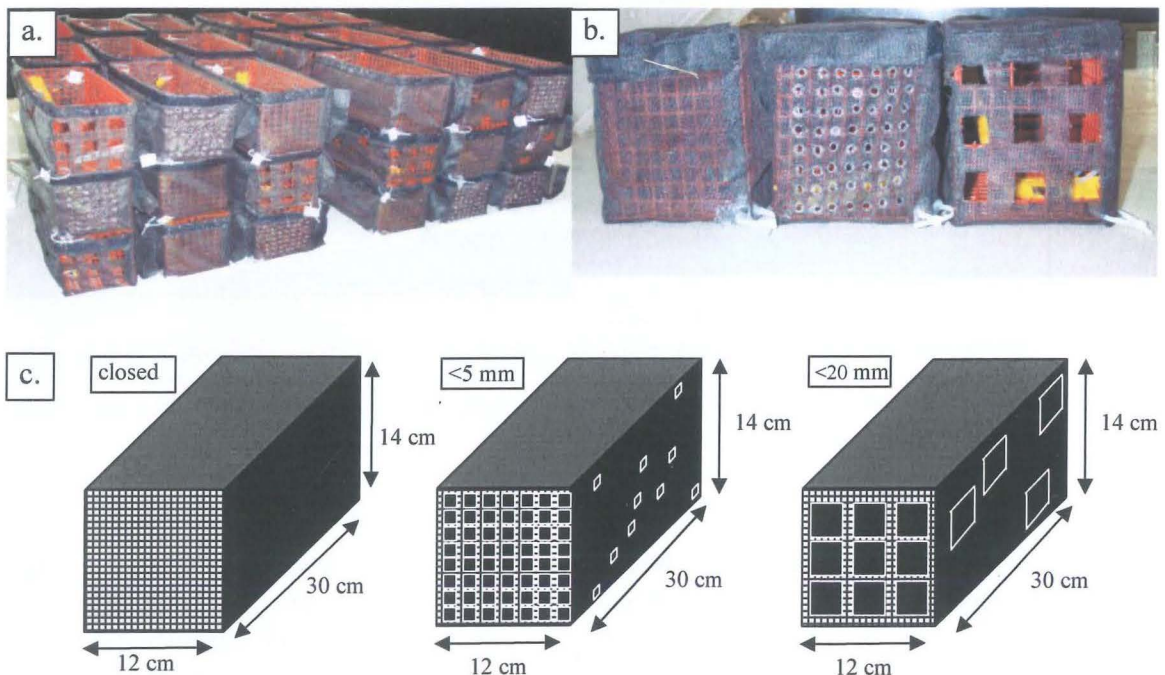
Figure 2.3 Photographs (a, b) and schematic design (c) of the closed control, <5mm and <20mm treatments used for the field experimentation. The experimental units shown in the photograph (a) are randomised for two sites. Diagrams are not to scale.

Prior to each experimental deployment, attached *E. radiata* was collected from Boyinaboat Reef (Figure 2.1). Approximately 60 mature individual plants of similar age, avoiding young plants due to their increased phenolic content (Steinberg 1989), were randomly collected and equally distributed amongst four large hessian bags in which they were aged *in situ*. The hessian bags had large holes cut into them to allow water to flow through the contents of the bag, avoiding any possibility of anoxia that could have fouled the kelp. The kelp was collected after four to nine days of aging, returned immediately to the laboratory

and placed in seawater. Approximately 100 individual secondary lamina of similar size (ranging from 6.00 to 19.00 g) were cut from the stipe, avoiding basal secondary lamina due to their increased secondary metabolite concentrations (Jennings & Steinberg 1997). Individual pieces were then scrubbed to remove any epiphytes (although these were very minimal [pers. obs.]), rinsed in fresh water, and returned to fresh seawater which was stored at 19°C overnight.

Prior to deployment of the experiment, the detached kelp was blotted to remove excess water prior to recording the wet weight (0.01 g), and was then placed in the experimental cages or prepared as an open control (Figure 2.4). The open controls were placed in an esky of seawater for transportation into the field. The experimental cages were grouped together according to site and proximity to reef, placed into a large hessian bag for transportation to the field, and constantly drenched with seawater to circumvent any possible desiccation of the kelp. On completion of each experimental period, experimental cages were collected underwater, retaining the contents of the cages for quantification in the laboratory. Calico bags were carefully placed over the cages, minimising any disturbance to the cages and fauna. Cages from each distance and site were placed into the hessian bags and continually drenched with seawater whilst on the boat. The open tethers were placed in plastic zip-lock bags containing seawater.
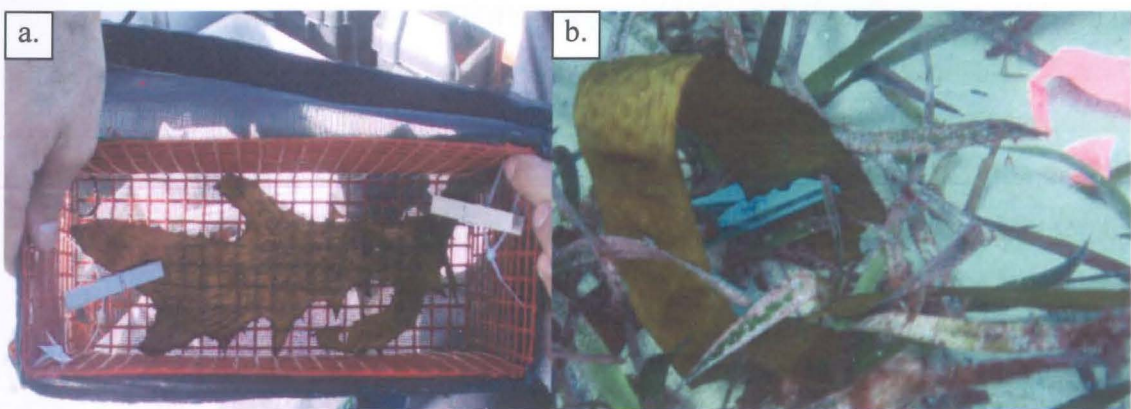
Figure 2.4 Detached *E. radiata* pegged inside a cage prior to deployment (a) and an open tether of detached *E. radiata in situ* (b).

2.1.3 Laboratory processing

On return to the laboratory, the detached kelp was immediately rinsed clean with fresh water, blotted dry, and reweighed (0.01 g). The contents of the cages were filtered through a 0.5 mm sieve to remove any sand and particulate matter, and samples were placed in 70% ethanol and stored at 4°C prior to sorting. Closed control and <20 mm treatment fauna samples were sorted using a dissecting microscope to the lowest possible taxa using Wilson (1993), Edgar (2000), and Wells & Bryce (2000), and the abundances of each group quantified (Appendix 1). The ash-free dry weight (AFDW) for each of Amphipoda, Isopoda, and Gastropoda was calculated as the difference between the dried (80°C for 48 hours) and ashed (550°C for 4 hours) weights of the animals (Appendix 2) (Edgar 1990c, Brearley & Wells 2000). A sucrose standard of 1.000 g was used to confirm combustion efficiency of the organic matter in the furnaces (Kendrick & Lavery 2001). Where 100% combustion of the sucrose did not occur (mean combustion $\pm$ SE = 98.30 $\pm$ 1.59%), the weights of the samples were corrected using the following equation: AFDW = DW (550°C) x (100/efficiency). All samples were placed in desiccators for 24 hours prior to weighing and were weighed to 0.0001 g.

2.1.4 Habitat composition

The percent cover of the physical and biological features of the benthos was quantified at each distance at each site, to verify that the *Posidonia* and *Amphibolis* spp. sites were dominated by the respective seagrass types. A 0.5 x 0.5 m quadrat was haphazardly tossed onto the benthos and at least 10 super high quality (3072 x 2304) images were taken with an Olympus μ725SW digital camera. Due to issues of image quality (e.g. bad visibility, blurring, low light), five high quality photos from each distance within each site were randomly selected for analysis. The images were analysed using Coral Point Count with Excel Extensions (Kohler & Gill 2006). The benthos was quantified by overlaying 10 x 10 grids on each image, and assessing the substrate type at each intersection point (n = 100) (Figure 2.5). Substrate was categorised using the following descriptions: *Posidonia* spp., *Amphibolis* spp., *Halophila* spp., *Heterozostera tasmanica*, brown algae, red algae, green algae, sand, rock, tape, and unknown.

16
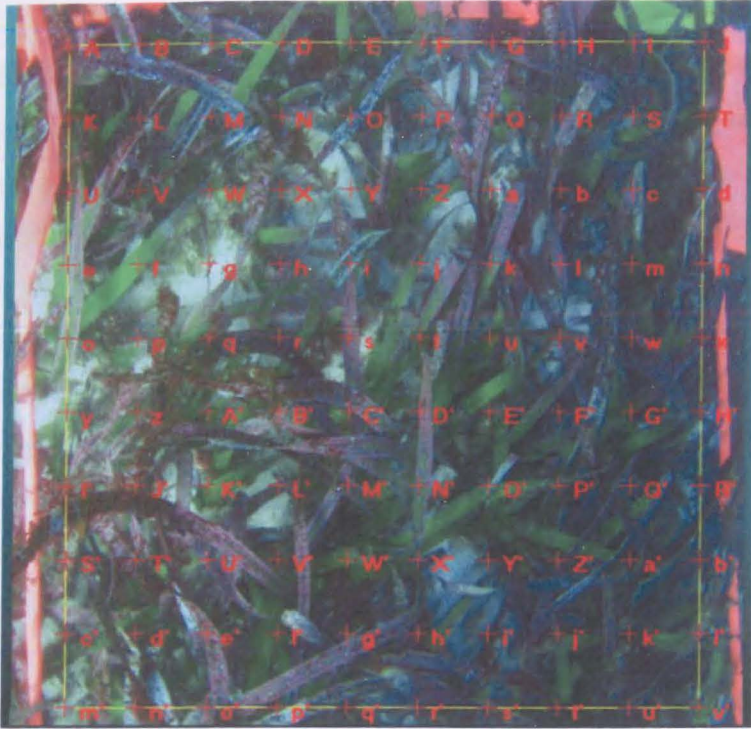
Figure 2.5 A screen-shot from Coral Point Count with Excel Extensions (Kohler & Gill 2006) displaying the 10 x 10 grid overlaid the image with the 0.25m^2 quadrat placed on the benthos.

2.1.5 Data analysis

The data from The Lumps (*Posidonia* spp.) and Cow Rocks (*Amphibolis* spp.) were not incorporated into the analyses. The interface site at The Lumps contained only 14% *Posidonia* spp. cover and was dominated by sand (65%), and therefore not representative of a seagrass habitat. Large losses of the experimental cages occurred at Cow Rocks. Of the nine cages at each distance, three were lost at the seagrass-reef interface, seven were lost at the close distance, and four were lost at the far distance. Presumably, this was due to localised hydrodynamic conditions at this site, where large surge and very strong currents were noticed during the deployment and retrieval of the experiment. At the four sites used in the study, three experimental units were lost. These were a <5mm treatment from the seagrass-reef interface and a <20mm treatment from the far distances at Whitfords Rock NE, and a <20mm treatment from the close distance at Wreck Rock. These missing values were replaced with the average of the two remaining replicate treatments from each distance at each site (Underwood 1997).

Differences between the initial and final wet weights of the detached kelp were used to calculate the amount of biomass loss. The biomass loss of the detached kelp was evaluated by testing the differences between the categories of predictive factors using univariate ANOVA. Permutational Analysis of Variance (PERMANOVA, Anderson 2005) was used to partition univariate variability, using permutations to calculate the p-values. The data were analysed using a mixed effects, four-factor ANOVA model, incorporating the factors: (1) Treatment (fixed factor with four levels: closed, <5 mm, <20 mm, open), (2) Habitat (orthogonal to treatments and fixed factor with 2 levels: *Posidonia* spp. vs *Amphibolis* spp.), (3) Distance (orthogonal to the previous factors and fixed factor with three levels: interface, close, far), and (4) Site (random factor with two levels nested in Habitat). The data were transformed prior to analysis using Ln (x + 1) to meet the requirements of homogeneity using Cochran's test, conducted in GMAV statistical package. Univariate analysis was based on Euclidean distances and the p-values were calculated from 9999 unrestricted permutations of the data. Analysis was performed using Primer & PERMANOVA+β4 statistical package.

Correlations testing the abundances and the biomass of the mesograzer groups versus the loss of the detached kelp biomass within the *Posidonia* spp. and *Amphibolis* spp. habitats were conducted by calculating the R^2 values in Microsoft Excel. The mesograzer abundances and biomass were plotted against the detached kelp biomass loss using fauna data from the closed control and <20 mm treatment cages. Mesograzers were categorised into the groups of Amphipoda, Isopoda, Gastropoda, and total mesograzers. The closed control and <20 mm treatment data were combined, and the nested sites were combined within each habitat.

2.2 Feeding preference experiments

2.2.1 Pilot study

Multiple pilot studies were conducted to test logistical problems associated with laboratory feeding experiments. Animal death was a major concern prior to experimentation, but the pilot studies indicated that death was minimal. The amount of individuals per treatment cell was tested, by using 5, 10, and 15 individuals per cell for choice feeding experiments. It

was determined that 15 individuals for choice and 5 individuals for no-choice feeding experiments was optimal. These numbers were appropriate in terms of detecting consumption without overcrowding the individual cell, which could possibly force macrophyte consumption upon individuals, aggression or competition between individuals (Peterson & Renaud 1989), but allowed the chance for individuals to encounter macrophyte material.

It was desired to have equal initial weights of all macrophytes to allow a comparison using percentage for the choice feeding trials. However, due to large differences in the density of the macrophytes used, the initial weights could not be identical between groups, as this would have provided a greater area of some material to the consumers, which may have biased results. Rather, the 2-dimensional surface area of the macrophytes were similar, allowing an equal chance for the gastropods to encounter each food source (Wakefield & Murray 1998). The gastropods commuted regularly and rapidly during the experimental periods, especially when first placed in the treatment cells with the macrophytes, thus the encounter of macrophytes was not problematic.

Starved versus satiated choice feeding trials were conducted by comparing the consumption of macrophytes by gastropods that were removed from holding tanks without food or removed from holding tanks containing a mixture of macrophytes. In the first trial, starved individuals consistently consumed more than satiated individuals, but in the second trial satiated individuals sometimes consumed more than starved individuals. Both trials were not statistically significant ($P > 0.05$). Due to the inconsistency of these results, and following the literature where starvation of gastropods in feeding trials is often used (Steinberg & van Altena 1992, Chavanich & Harris 2002, Cox & Murray 2006, Storry et al. 2006), it was determined that the starvation period of 48 hours was preferable to clear the gut contents of the gastropods and assure that consumption occurred.

2.2.2 Animal selection

The gastropods *Pyrene bidentata* (Collumbellidae) and *Cantharidus lepidus* (Trochidae) were used in the choice and no-choice feeding experiments. Both species of gastropod are common to south-western Australian coastal environments and can occur in very high

numbers (Nielsen & Lethbridge 1989, Edgar 1990a, 1990b, 2000, Tuya et al., in prep.), thus they are likely to be important in community ecology. Individuals of the two species also commonly occurred in the cages from the field experiment (Appendix 1). Furthermore, the abundances of *P. bidentata* in *Amphibolis* spp. and *Posidonia* spp. seagrass meadows tends to decrease with distance moving away from the reef, while the abundances of *C. lepidus* show the inverse pattern (Tuya et al., in prep.).

It was intended to conduct choice and no-choice feeding experiments using amphipods, due to their high abundances found in the cages from the field experiment (Appendix 1). Amphipods are also known to be very mobile and abundant in seagrass meadows and important in community dynamics throughout the region (Edgar 1990a, 1990b, Edgar 1992, Jernakoff & Nielson 1997). Multiple attempts using several different collection methods were conducted to collect amphipods, but these attempts gathered inadequate numbers of individuals of a single or multiple species. Individuals that were collected (~50) were stored in aquaria with a mixture of macrophyte resources, with the expectation that breeding may occur to supply individuals for use in experimentation. Unfortunately, breeding did not occur. Thus, amphipod feeding preference experiments were not conducted.

2.2.3 Macrophyte and gastropod collection

Macrophytes and gastropods used in the feeding preference experiments were collected and used for experimentation from the 12/7/07 to the 27/8/07. Adult *P. bidentata* and *C. lepidus* individuals were collected from *Posidonia* spp. and *Amphibolis* spp. seagrass meadows in Shoalwater Bay, located approximately 60km south of Marmion Lagoon. The body whorl of *P. bidentata* and *C. lepidus* individuals selected for experimentation ranged from 11 to 16 mm and 9 to 15 mm, respectively. Animals were transported to the laboratory where they were housed in 4.7 L (30 cm long x 16 cm wide x 19 cm high) aquaria and fed on a mixture of macrophytes (including *E. radiata*, *Sargassum* sp., *Posidonia* spp., *Amphibolis* spp., Rhodophyta spp. and Chlorophyta spp.) for a minimum of seven days prior to experimentation, which allowed them to acclimatise to laboratory conditions before use in experimental trials. To assure independence, no individual gastropod was used for more than a single feeding trial. All aquaria were aerated using air stones, housed in a laboratory

at 19°C room temperature, and illuminated with 36 W Sylvania daylight fluorescent lights, with 12 hours light and 12 hours darkness, providing ca 5 μmol m^{-2} s^{-1}.

Macrophytes used in the feeding trials included fresh *E. radiata*, aged *E. radiata*, *Posidonia australis* with no epiphytic or periphytic growth, *P. australis* with periphytic growth only, and *Hypnea* sp. These macrophytes were selected as they are readily available in the habitat frequented by *P. bidentata* and *C. lepidus*. *Ecklonia radiata* was collected from Boyinaboat reef and aged *in situ* for seven days, using the same method described for the field experiment. *Posidonia australis* and *Hypnea* sp. were collected from Shoalwater Bay. All macrophytes were collected a day prior to experimentation, placed in an esky filled with seawater, and returned to the laboratory. Macrophytes were sorted, scrubbed cleaned of epiphytes (although these were very minimal [pers. obs.]), rinsed in freshwater, and stored overnight in aerated seawater at 19°C to emulate environmental sea temperature. Periphyton found on *Posidonia* spp. leaves consists of bacteria, diatoms, cyanobacteria, crustose red algae, and other organic matter (Jernakoff et al. 1996, Smit et al. 2006). *Hypnea* sp. was used as a food source to represent red algae (Rhodophyta), which is commonly found as a seagrass epiphyte (van Elven et al. 2004).

2.2.4 Experimental design

Choice feeding experiments were conducted in aerated 1.4 L plastic containers (13 cm long x 13 cm wide x 9.5 cm high) (Figure 2.6a and c), while no-choice feeding experiments were conducted in aerated 770 mL plastic containers (15 cm long x 10 cm wide x 6.5 cm high) (Figure 2.6b and c). A treatment cell containing animals and a control cell without animals were nested within a single container (Prince et al. 2004), with 500 μm fly-screen mesh separating the two cells. This mesh width was large enough to allow water to flow between the two chambers, but small enough to restrict the animals and any food debris within their respective chamber. This nested design ensures that external and internal factors jointly affect the control and experimental foods (Prince et al. 2004).

For choice and no-choice feeding experiments, experimentation occurred over 96 hours, providing sufficient time to detect grazing effects (Crawley & Hyndes 2007) and minimise autogenic changes in macrophyte materials (Peterson & Renaud 1989). Animals were

21

starved for 48 hours prior to experimental trials to clear the gut contents of the animals, ensuring the animals would consume food during the feeding experiments and minimising the possibility that any food recently consumed would influence food choice. Two treatments were used for choice feeding trials: (1) fresh kelp, seagrass without periphyton, seagrass with periphyton, and red algae; and (2) aged kelp, seagrass without periphyton, seagrass with periphyton, and red algae. Macrophytes were randomly placed into the treatment and control cells, with 15 individuals of either *P. bidentata* or *C. lepidus* randomly selected from the housing tanks, and placed in the treatment cells. For no-choice feeding experiments, a single macrophyte type of fresh kelp, aged kelp, seagrass without periphyton, seagrass with periphyton, or red algae was placed into the treatment and control cells, with 5 individuals of either *P. bidentata* or *C. lepidus* randomly selected from the housing tanks placed in the treatment cells. There were 10 replicates for each choice and no-choice feeding experiment. The initial blotted wet weights of the macrophytes ranged between 1.00-1.50 g for fresh and aged kelp, 0.15-0.30 g for seagrass without periphyton, 0.20-0.40 g for seagrass with periphyton, and 1.00-1.50 g for red algae.
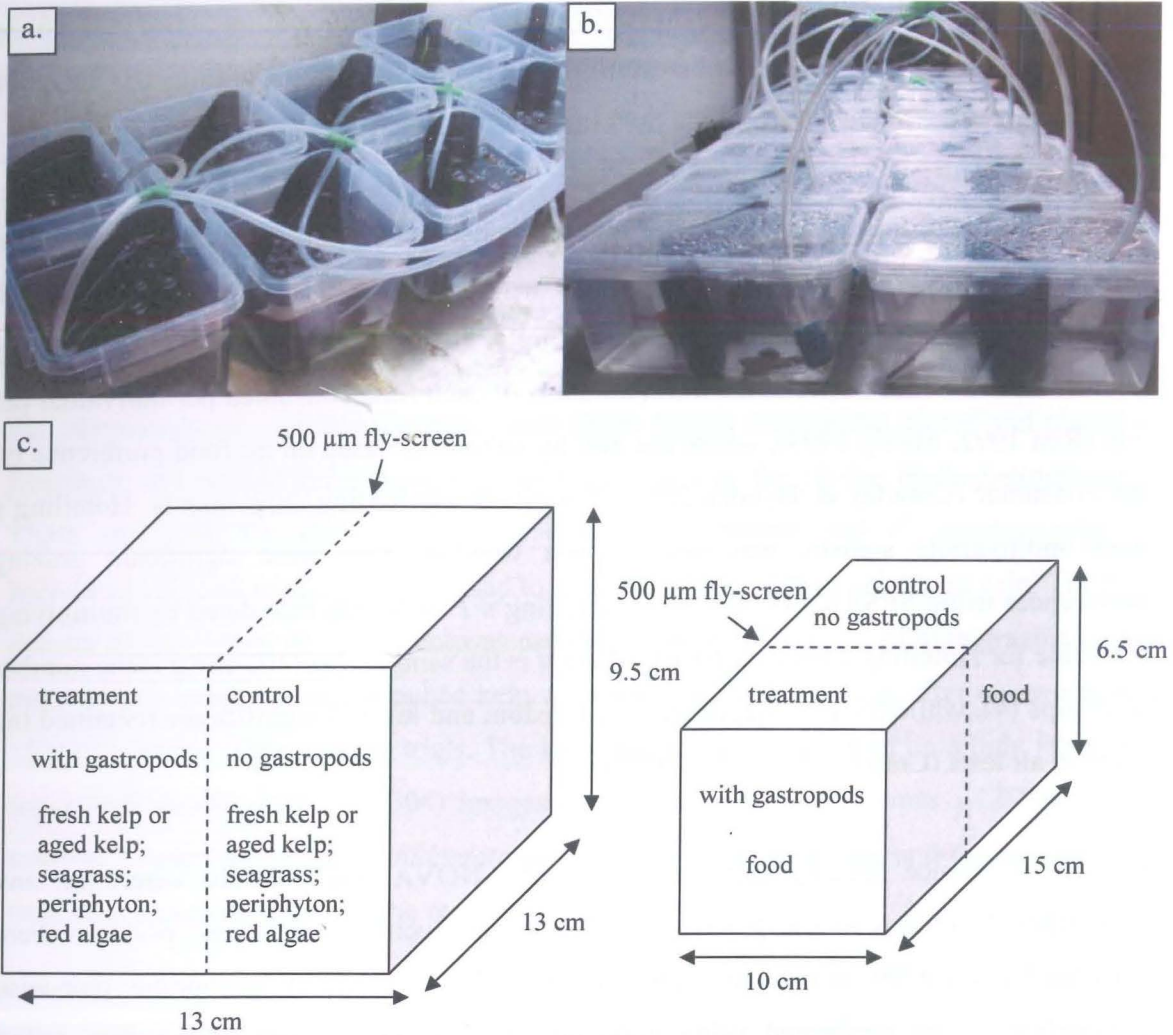
Figure 2.6 Photographs of the choice (a) and no-choice (b) feeding experiments. The nested design of the treatment and control cells of the containers used for the choice (left) and no-choice (right) feeding experiments (c). Diagrams are not to scale.

2.2.5 Data analysis

The differences between the initial and final wet weights of the different macrophytes were used to calculate the amount (mg) of material consumed, and converted to mg per individual per day. Control chambers were used to determine autogenic changes to macrophytes in the absence of mesograzers (Peterson & Renaud 1989), and the nested design avoids complications of randomly assigning controls with treatments (Roa 1992), or of comparing the means of two multivariate samples that may not have the same covariance (Manly 1993). Thus, the consumption of each macrophyte is calculated as its loss in biomass (blotted wet weight) as $(T_{pre} - T_{post}) - (C_{pre} - C_{post})$, where T is the treatment cell and

23

C is the control cell found in a single container (following Prince et al. 2004). Where the biomass loss of the control was more than the treatment, resulting in 'negative consumption', the value was replaced by 0 for statistical analysis.

For the choice feeding experiments, the amount of material consumed can not be treated as independent due to the presence of multiple macrophytes in a single cell (Peterson & Renaud 1989). Thus, a multivariate Hotelling's T^2 test was used to determine any significant difference between the mean amounts of each food consumed per individual per day (Roa 1992, Manly 1993), where the null hypothesis is based on no food preference by the consumer (Crawley & Hyndes 2007). For all choice feeding experiments, Hotelling's trace multivariate statistic was used to test whether there were significant grazing preferences using SPSS v.14.0 software. Hotelling's T^2 was then calculated by multiplying the value for Hotelling's trace by $(n–g)$, where n is the sample size (40) and g is the number of groups (4), while the F value, degrees of freedom and level of significance remained the same in all tests (Crawley & Hyndes 2007).

For the no-choice feeding experiments, PERMANOVA was used to determine any significant difference in the grazing rates based on Euclidean distances; p-values were calculated from 9999 unrestricted permutations of the data. When appropriate, pair-wise comparisons were performed using 9999 unrestricted permutations of the data, using Primer & PERMANOVA+β4 statistical package. For both choice and no-choice feeding experiments, when necessary, the data was transformed using Ln (x + 1) to meet the requirements of homogeneity using Cochran's test, conducted in GMAV statistical package.

2.3 Qualitative measures

2.3.1 Posidonia australis *with periphyton visual assessment*

A qualitative assessment was conducted to determine what the gastropods were consuming on the *Posidonia australis* with periphyton food source. Super high quality (3072 x 2304) images of sections of the seagrass leaves were taken using an Olympus SZX12 dissecting microscope with an Olympus LG-PS2 camera. Seagrass leaves from the choice feeding

trials using *P. bidentata* and *C. lepidus* were used. Images were visually assessed to determine if there was any scarring on the seagrass tissue, inferring consumption of the seagrass material, or if there was any obvious loss of periphyton due to grazing.

2.3.2 Detached Ecklonia radiata *consumption visual assessment*

A qualitative assessment was conducted to determine the effects of *P. bidentata* and *C. lepidus* grazing on detached *E. radiata*. Kelp aged for 12 days (7 days *in situ* and 5 days in the laboratory) was cut into similarly sized (9 cm long x 4 cm wide) pieces and placed in treatment and control cells, using the same containers as the choice feeding experiments. Three replicates for each gastropod species, *P. bidentata* and *C. lepidus*, with 30 individuals in each treatment, were used to determine any scarring effects on kelp. The high density of gastropods per treatment was used to increase the chances of high grazing on the macrophyte. Images of the detached kelp were taken at the beginning, after one week, and after two weeks of the feeding trials. The kelp was blotted dry, placed on a light table, and super high quality (3072 x 2304) images were taken with an Olympus µ725SW digital camera. A selection of one *P. bidentata* and one *C. lepidus* treatment and a control at each time interval are presented in the results.

3. Results

3.1 Field experimentation

3.1.1 Habitat composition

Posidonia spp. was the dominant seagrass habitat surrounding Wanneroo Reef (Figure 3.1a) and Whitfords Rock SW (Figure 3.1b), with it covering >67.0% of the area at all distances within the sites. The percent cover of *Posidonia* spp. at Wanneroo Reef was 88.5% at the interface and far from the reef, and 75.0% close to the reef. *Posidonia* spp. cover was slightly lower at Whitfords Rock SW, increasing from 67.1% at the seagrass-reef interface, to 72.4 and 77.0% close to the reef and far from the reef, respectively. At Wanneroo Reef, the cover of *Heterozostera tasmanica* was 14.0%, green algae 3.5%, and sand 2.8%, close to the reef. Sand made up 9.0% and 8.5% of the benthos at the seagrass-reef interface and far from the reef, respectively. At Whitfords Rock SW, sand covered between 17.0 and 20.0% of the benthos at all distances. The cover of red algae was 6.4% and green algae was 5.6% at the seagrass-reef interface. Green algae contributed 4.0% to the cover close to the reef.

At Whitfords Rock NE (Figure 3.1c) and Wreck Rock (Figure 3.1d), *Amphibolis* spp. was the dominant seagrass habitat, with it covering >64.0% of the total area at all distances within the sites. The *Amphibolis* spp. cover at Whitfords Rock NE was 65.0% at the seagrass-reef interface and close to the reef, and 75.0% far from the reef. At Wreck Rock, *Amphibolis* spp. cover was 70.8% at the seagrass-reef interface, 63.1% close to the reef, and 67.5% far from the reef. Red algae contributed 25.0% cover close to the reef, 8.3% far from the reef, and 4.0% at the seagrass-reef interface at Whitfords Rock NE. Green algal cover was 8.7% at the seagrass-reef interface, and 2.0% close to the reef and far from the reef. Sand covered 18.0, 5.3, and 13.5%, at the seagrass-reef interface, close to the reef, and far from the reef, respectively. The red algal cover at Wreck Rock was 28.0% close to the reef, 19.5% at the seagrass-reef interface, and 9.5% far from the reef. Sand cover was 8.0% at the seagrass-reef interface and close to the reef, and 20.5% far from the reef.
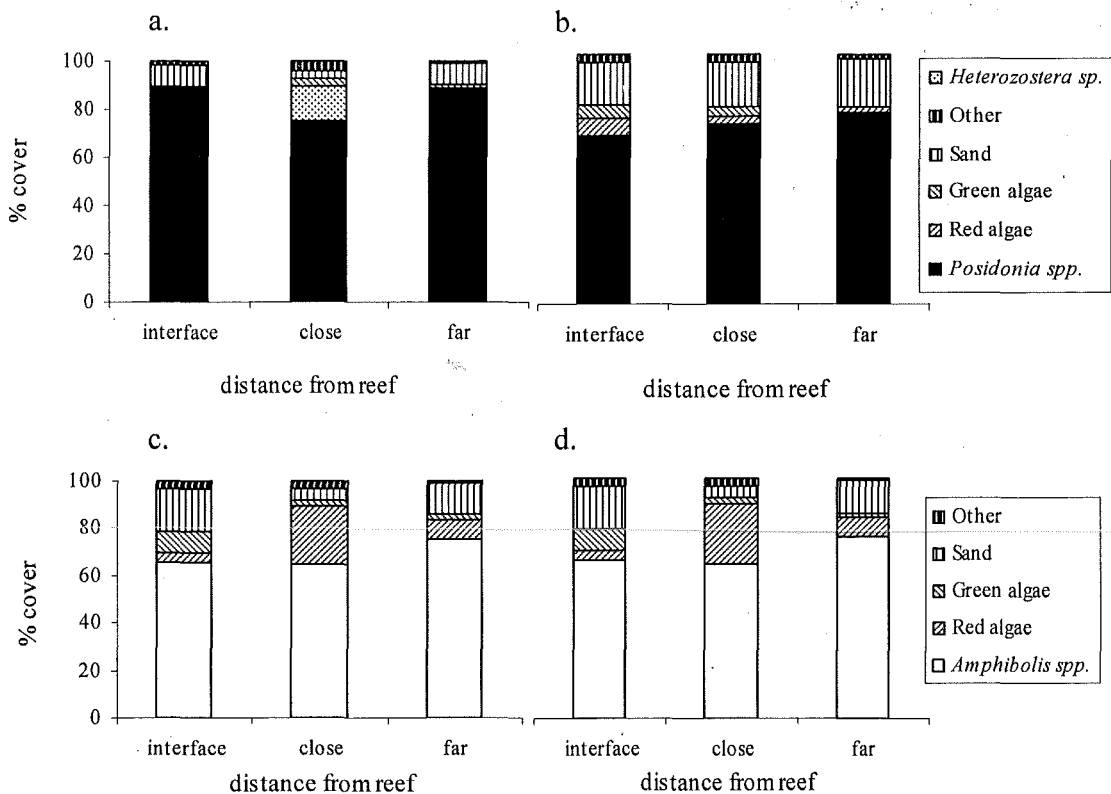
Figure 3.1 Percentage cover of the biophysical characteristics with proximity to reefs at the two *Posidonia* spp. sites: Wanneroo Reef (a) and Whitfords Rock SW (b), and the two *Amphibolis* spp. sites: Whitfords Rock NE (c) and Wreck Rock (d). Other includes rock and tape.

3.1.2 Detached kelp biomass loss

Treatments, habitats, or distances with proximity to reef had no significant effect on the biomass loss of detached *E. radiata* at any of the four sites (Table 3.1). There was a significant site within habitat effect, and an interaction between site within habitat and treatment (Table 3.1), indicating inconsistent responses to treatments from site to site. The loss of detached kelp biomass ranged between 0.00 to 9.12 g week^{-1} across all treatments, habitats, and distances with proximity to the reefs.

In all treatments and distances, the loss of the kelp biomass at the two *Posidonia* spp. sites was similar, ranging between a mean of 0.62 to 3.65 g week^{-1} at Wanneroo Reef (Figure 3.2a), and 0.46 to 2.19 g week^{-1} at Whitfords Rock SW (Figure 3.2b). Between the two *Amphibolis* spp. sites, the biomass loss of the detached kelp was different. At Whitfords Rock NE (Figure 3.2c), the biomass loss ranged between a mean of 0.25 and 1.99 g week^{-1}

across all treatments and distances, similar to the values of the two *Posidonia* spp. sites. In comparison, at Wreck Rock (Figure 3.2d), the biomass loss of detached kelp was higher across all treatments and distances at a mean of 0.83 and 5.47 g week^{-1}. These higher values at Wreck Rock are the likely cause of the significant treatment by site within habitat interaction. The overall mean detached kelp loss was much higher at Wreck Rock (2.86 g week^{-1}) than Whitfords Rock NE (1.01 g week^{-1}), or the two *Posidonia* spp. sites, Wanneroo Reef (1.45 g week^{-1}) and Whitfords Rock SW (1.02 g week^{-1}).

Table 3.1 Results of the 4-factor ANOVA of the detached *E. radiata* biomass loss (g week^{-1}) testing for differences among (1) Treatments (fixed factor, 4 levels), (2) Habitats (fixed factor, 2 levels), (3) Distances (fixed factor, 3 levels), and (4) Sites (random, 2 levels). Data was transformed using Ln (x + 1) prior to analysis. ns = ($P > 0.05$).

Source	df	MS	Pseudo-F	P (perm)
treatment	3	0.1082	0.2714	ns
habitat	1	0.7853	0.2957	ns
distance	2	0.3954	3.1146	ns
site (habitat)	2	2.6554	16.6130	0.0001
treatment x habitat	3	0.8075	2.0263	ns
treatment x distance	6	0.2031	0.7917	ns
habitat x distance	2	0.1947	1.5335	ns
treatment x site (habitat)	6	0.3985	2.4930	0.0248
distance x site (habitat)	4	0.1269	0.7942	ns
treatment x habitat x distance	6	0.2302	0.8975	ns
treatment x distance x site (habitat)	12	0.2565	1.6046	ns
Res	96	0.1598		
Total	143			
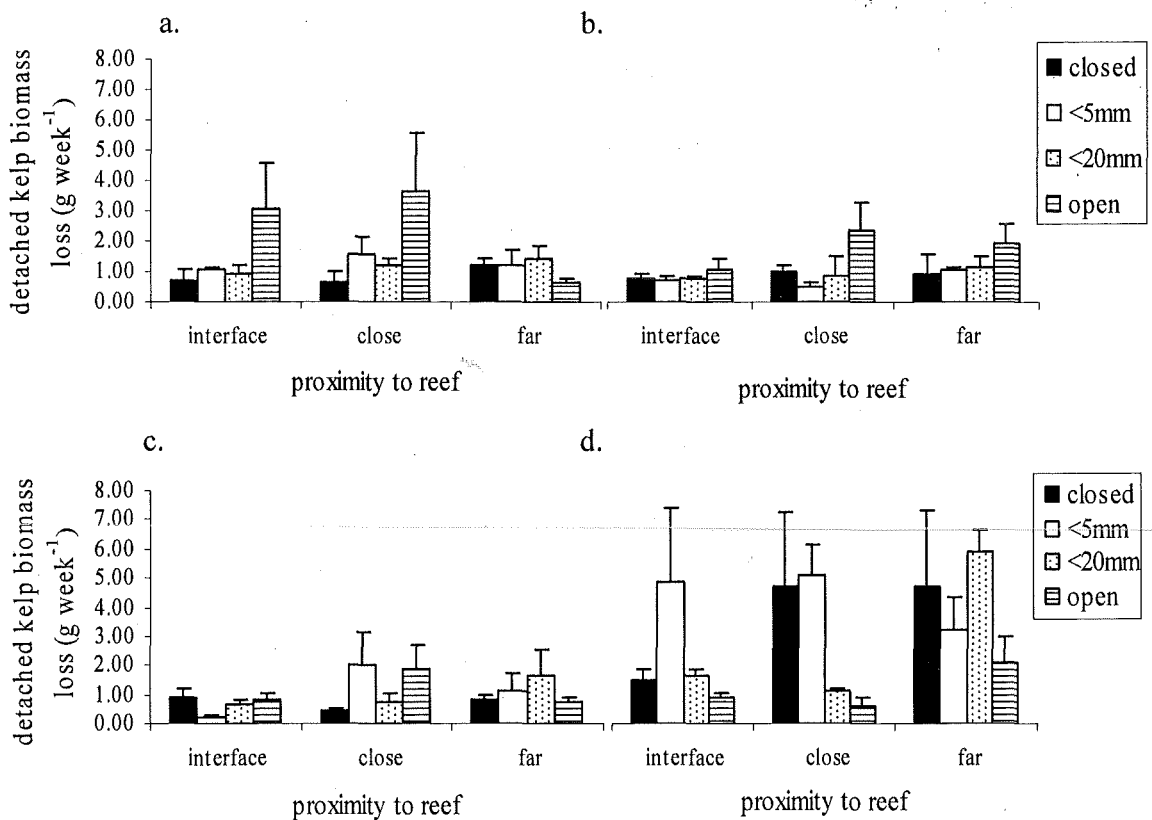
Figure 3.2 Mean (± SE, $n = 3$) biomass loss of detached *E. radiata* in *Posidonia* dominated seagrass meadows at different distances with proximity to reef at Wanneroo Reef (a) and Whitfords Rock SW (b), and in *Amphibolis* dominated seagrass meadows at Whitfords Rock NE (c) and Wreck Rock (d).

3.1.3 Mesograzer abundances and biomass relations with kelp consumption

Neither the abundances nor biomass (AFDW) of the amphipods, isopods, gastropods, and combined mesograzers, in the closed control and <20mm treatment cages, at the end of the experiment showed any correlation to the biomass loss of the detached *E. radiata* in the *Posidonia* spp. or *Amphibolis* spp. habitats, with all R^2 values less than 0.175 (Figures 3.3 and 3.4) and less than 0.1045 (Figures 3.5 and 3.6) for abundances and AFDW, respectively.
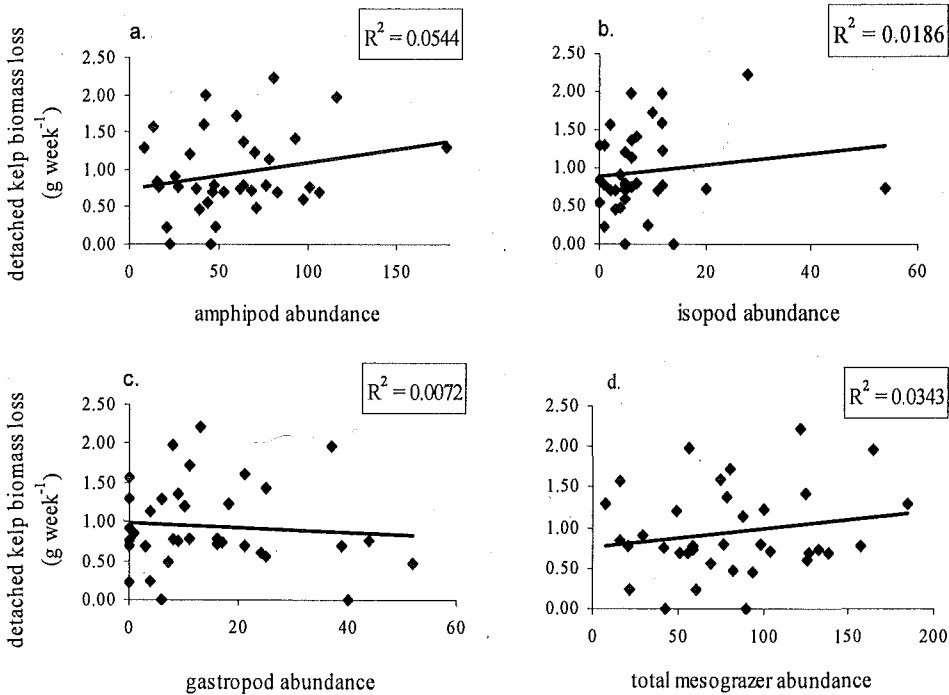
Figure 3.3 Correlation between amphipod (a), isopod (b), gastropod (c), and total mesograzer (d) abundances and the loss of detached kelp biomass (n = 36) in *Posidonia* dominated seagrass meadows.
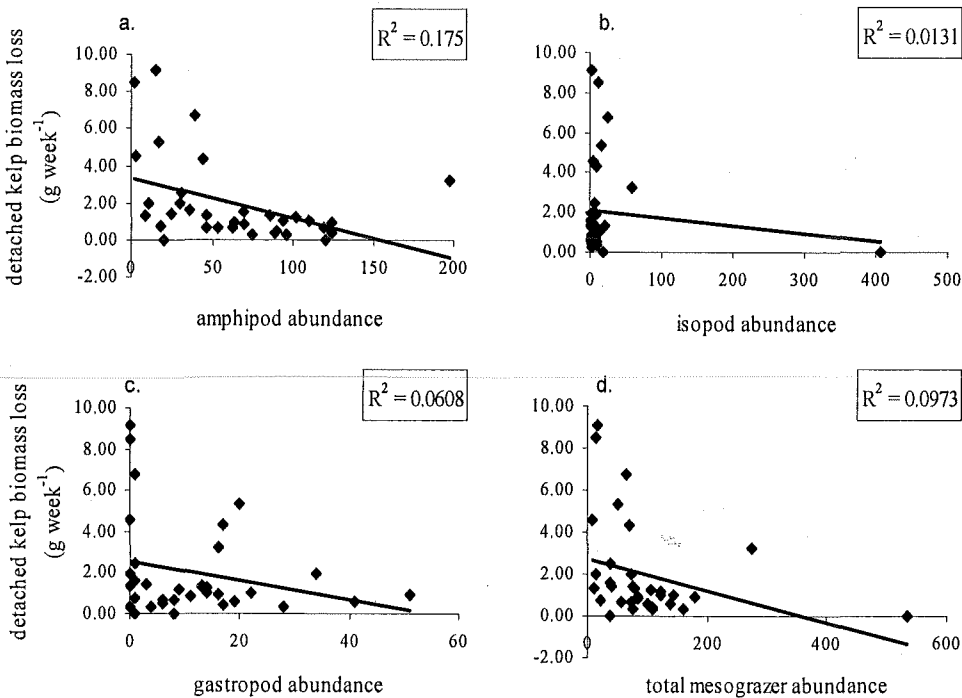
Figure 3.4 Correlation between amphipod (a), isopod (b), gastropod (c), and total mesograzer (d) abundances and the loss of detached kelp biomass (n = 36) in *Amphibolis* dominated seagrass meadows.
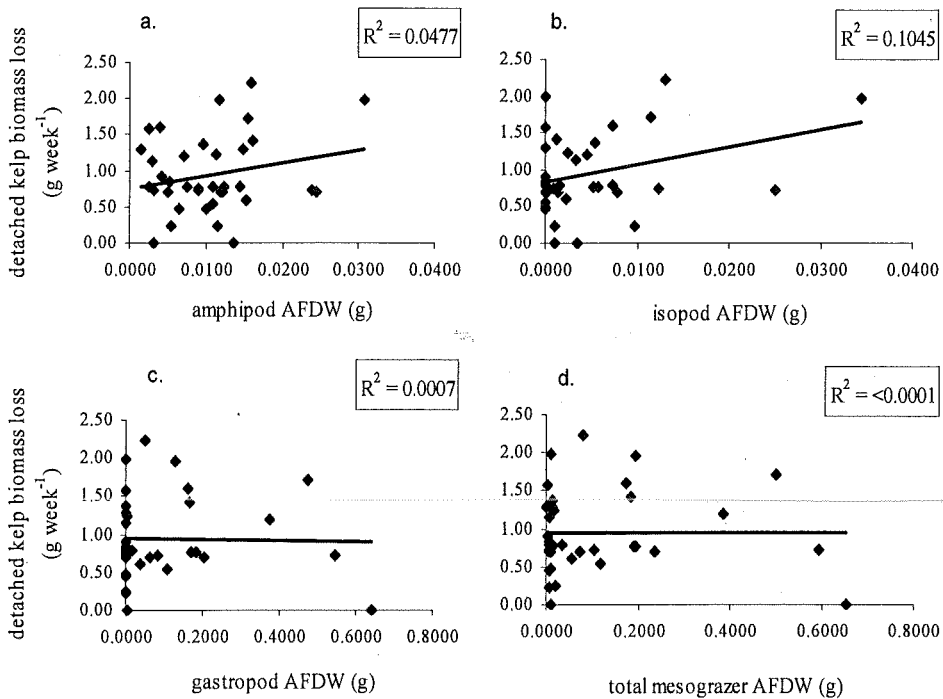
Figure 3.5 Correlation between amphipod (a), isopod (b), gastropod (c), and total mesograzer (d) AFDW (g) and the loss of detached kelp biomass (n = 36) in *Posidonia* dominated seagrass meadows.
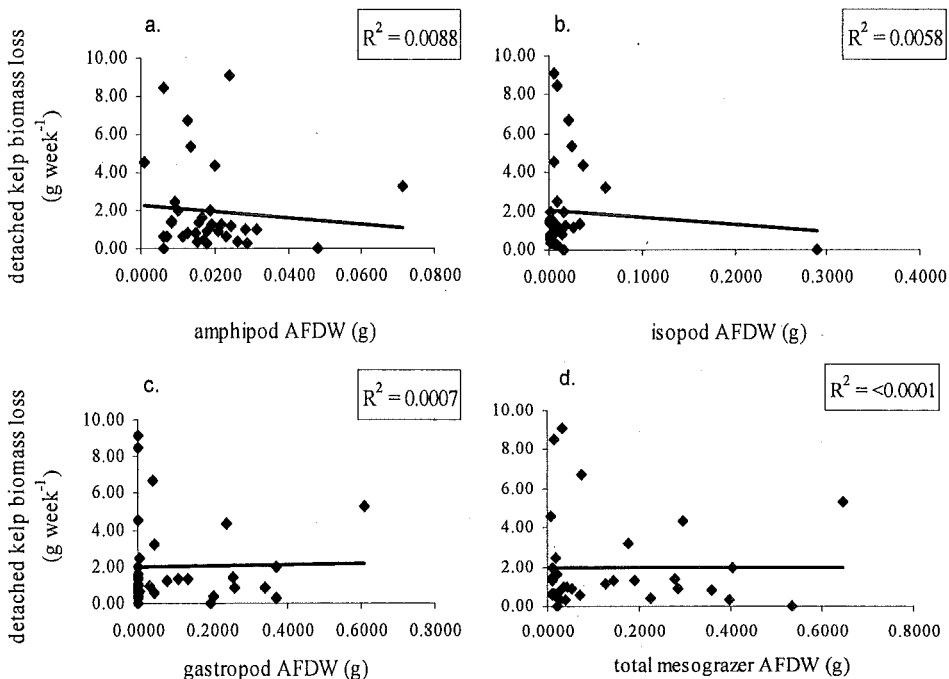
Figure 3.6 Correlation between amphipod (a), isopod (b), gastropod (c), and total mesograzer (d) AFDW (g) and the loss of detached kelp biomass (n = 36) in *Amphibolis* dominated seagrass meadows.

3.2 Feeding preference experiments

3.2.1 Pyrene bidentata *and* Cantharidus lepidus *choice feeding experiments*

In choice feeding trials, *Pyrene bidentata* displayed a significant grazing preference (Hotelling's T^2 = 1639.512, F = 68.312, P = 0.000) when provided with fresh kelp, red algae, and seagrass with and without periphyton (Figure 3.7a). Fresh kelp, seagrass with periphyton and red algae were consumed at similar mean rates of 0.53 to 0.75 mg ind^{-1} day^{-1}. There was no difference in preference among these three food sources, contrasting seagrass without periphyton, which was not consumed. Similarly, this species displayed a significant grazing preference (Hotelling's T^2 = 671.436, F = 27.976, P = 0.001) when provided with aged kelp, red algae, and seagrass with and without periphyton (Figure 3.7b). Red algae, seagrass with periphyton, and aged kelp were consumed at mean rates of 2.62, 1.27, and 0.94 mg ind^{-1} day^{-1}, respectively, whilst seagrass without periphyton was consumed at a mean of 0.17 mg ind^{-1} day^{-1}. Again, this species displayed a grazing preference towards the two macroalgal and seagrass with periphyton food sources, while they avoided the seagrass without periphyton material.

Cantharidus lepidus displayed a significant feeding preference (Hotelling's T^2 = 232.128, F = 9.673, P = 0.009) when provided with fresh kelp, red algae, and seagrass with and without periphyton in choice feeding trials (Figure 3.7c). A preference for seagrass with periphyton was observed, with a mean consumption at 1.41 mg ind^{-1} day^{-1}. Fresh kelp was consumed at a rate of 0.39 mg ind^{-1} day^{-1}, whilst there was no consumption of either seagrass without periphyton or red algae. *Cantharidus lepidus* also displayed a significant feeding preference (Hotelling's T^2 = 1185.408, F = 49.391, P = 0.000) when provided with aged kelp, red algae, and seagrass with and without periphyton in choice feeding trials (Figure 3.7d), which contrasted the trials with fresh kelp. Red algae was consumed in the highest amount at a mean of 3.64 mg ind^{-1} day^{-1}; seagrass with periphyton and aged kelp were consumed at mean rates of 1.55 and 0.95 mg ind^{-1} day^{-1}, respectively, whilst seagrass without periphyton was consumed at a mean of 0.24 mg ind^{-1} day^{-1}.

In these choice feeding trials, both *P. bidentata* and *C. lepidus* appear to feed preferentially on the two macroalgal and seagrass with periphyton food sources, whilst avoiding the seagrass without periphyton material.
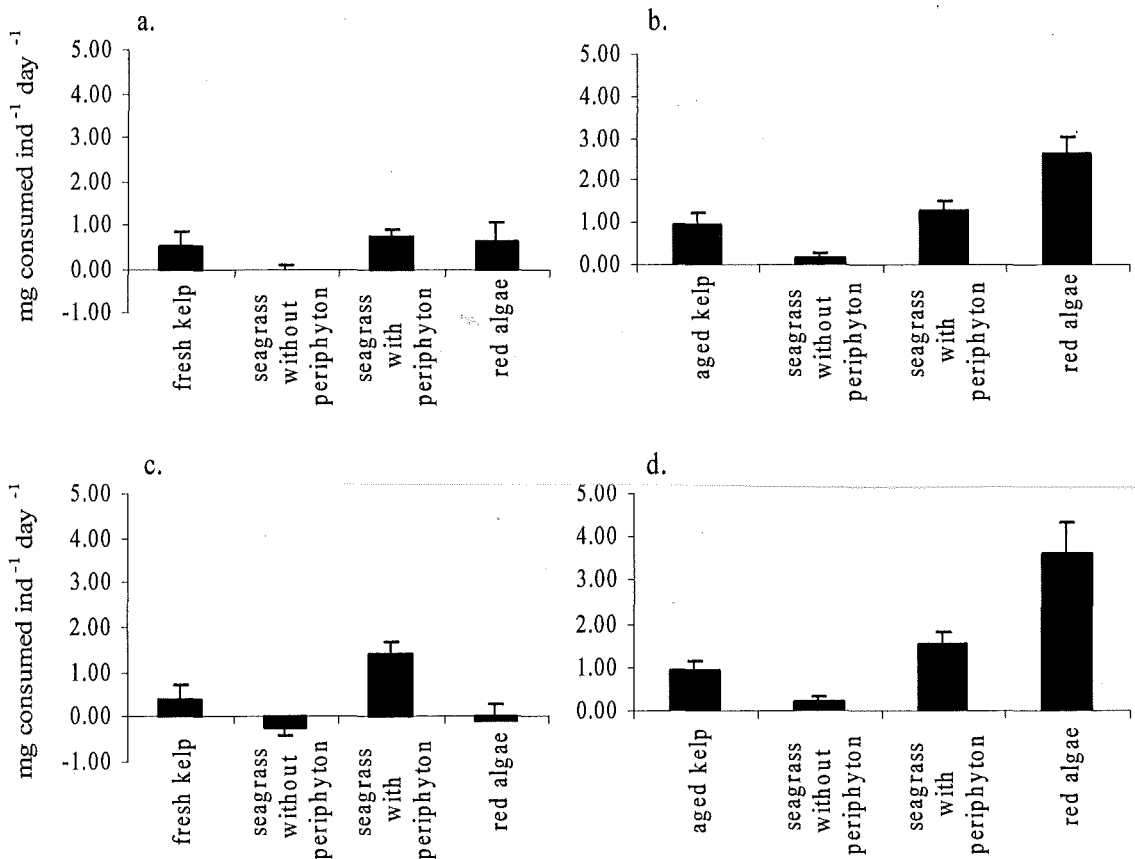
Figure 3.7 Mean (± SE, *n* = 10) *P. bidentata* (a, b) and *C. lepidus* (c, d) macrophyte consumption (mg ind^{-1} day^{-1}) after corrections for autogenic loss in choice feeding experiments conducted over a 4 day feeding period using fresh kelp (a, c) and aged kelp (b, d). Fresh kelp = fresh *E. radiata*; Aged kelp = 7 day aged *E. radiata*; Seagrass without periphyton = *P. australis* without periphyton; Seagrass with periphyton = *P. australis* with periphyton; Red algae = *Hypnea* sp.

3.2.2 Pyrene bidentata *and* Cantharidus lepidus *no-choice feeding experiments*

Pyrene bidentata displayed a significant difference in the grazing rates (F = 6.4197, P = 0.000) between the food types (Figure 3.8a). Post-hoc analysis revealed no significant differences in consumption between fresh kelp, aged kelp, seagrass with periphyton, and red algae, but did reveal a significant difference between the consumption of these four food sources and seagrass without periphyton material. Fresh and aged kelp, seagrass with periphyton, and red algae were all consumed between a mean of 2.00 to 7.21 mg ind^{-1} day^{-1}, whilst there was no consumption of seagrass without periphyton (Figure 3.8a).

Cantharidus lepidus displayed significant differences ($F = 3.5817$, $P = 0.0162$) in the grazing rates between food sources (Figure 3.8b). Post-hoc analysis revealed no significant difference between the consumption of fresh kelp, aged kelp, seagrass without periphyton, and red algae, but a significant difference between these four food sources and seagrass with periphyton. Seagrass with periphyton was consumed at a mean rate of 3.61 mg ind^{-1} day^{-1}, whilst fresh kelp, aged kelp, seagrass without periphyton, and red algae, were all consumed between a mean of 0.33 to 1.10 mg ind^{-1} day^{-1} (Figure 3.8b).
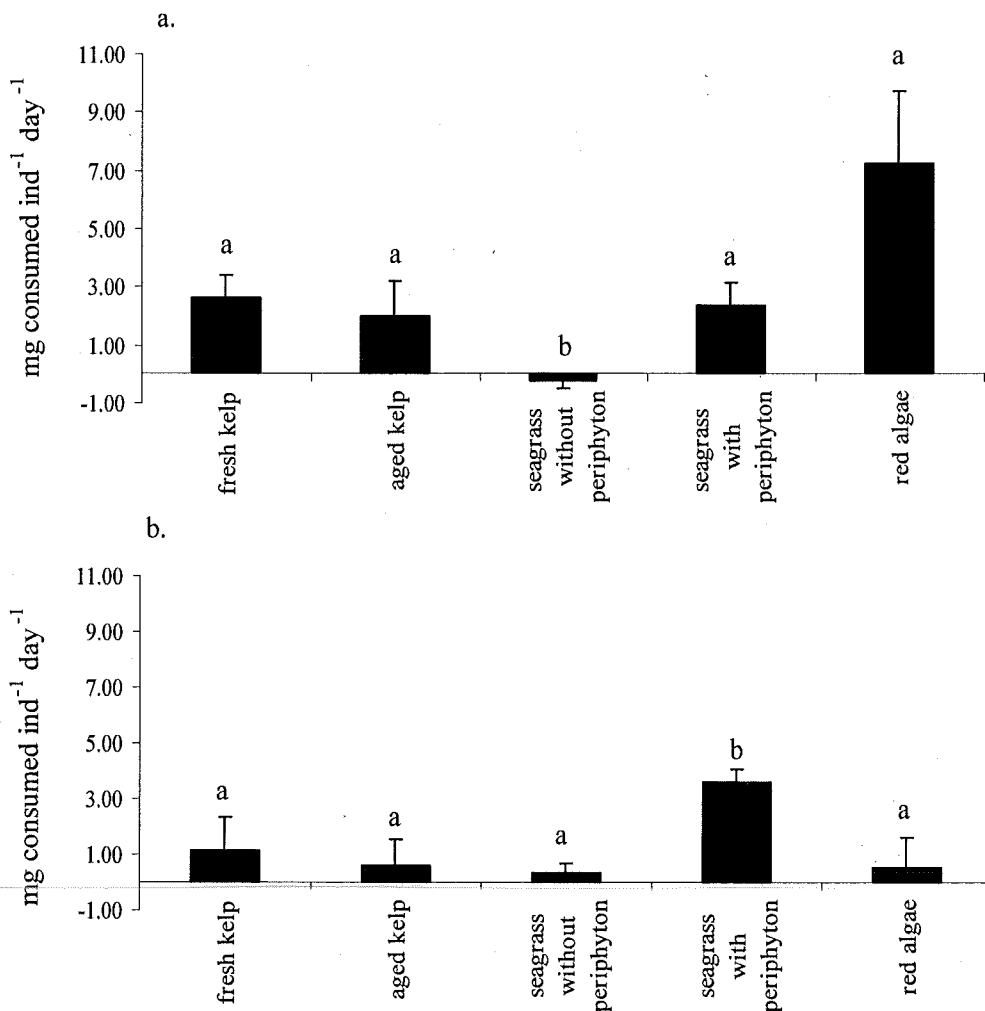
Figure 3.8 Mean ($\pm$ SE, $n = 10$) macrophyte consumption rates (mg ind^{-1} day^{-1}) by *P. bidentata* (a) and *C. lepidus* (b), corrected for autogenic loss in no-choice feeding experiments conducted over a 4 day feeding period. Data was transformed using Ln (x + 1) prior to analysis. Bars labelled with the same letter are not significantly different (post-hoc analysis P > 0.05). Fresh kelp = fresh *E. radiata*; Aged kelp = 7 day aged *E. radiata*; Seagrass without periphyton = *P. australis* without periphyton; Seagrass with periphyton = *P. australis* with periphyton; Red algae = *Hypnea* sp.

3.2.3 Posidonia australis *periphyton consumption*

The micrographs of the *Posidonia australis* segments with periphyton from the *Pyrene bidentata* and *Cantharidus lepidus* choice feeding experiments (Figure 3.9) do not show any obvious grazing scars on the seagrass tissue itself. Rather, the periphyton is patchy in distribution, possibly due to the gastropod grazing. The segments of seagrass in the *P. bidentata* trials lost 20 mg (Figure 3.9a), 50 mg (Figure 3.9b), and 30 mg (Figure 3.9c), whilst the segments of the seagrass in *C. lepidus* trials lost 90 mg (Figure 3.9d), 120 mg (Figure 3.9e), and 40 mg (Figure 3.9f). These results further support the lack of preference, or the avoidance, of seagrass material presented to the gastropods in the quantitative choice and no-choice feeding experiment results.

a. *Pyrene bidentata*   d. *Cantharidus lepidus*
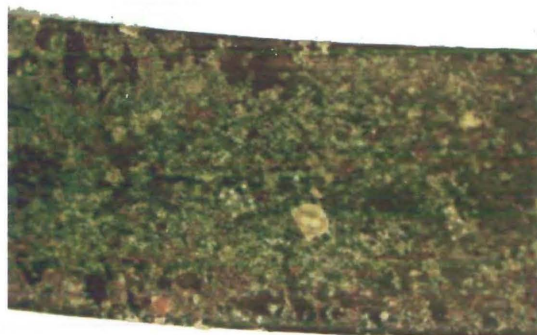
b.
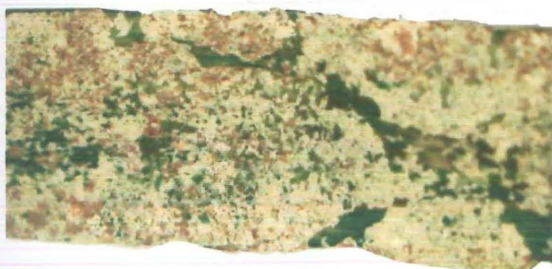
e.
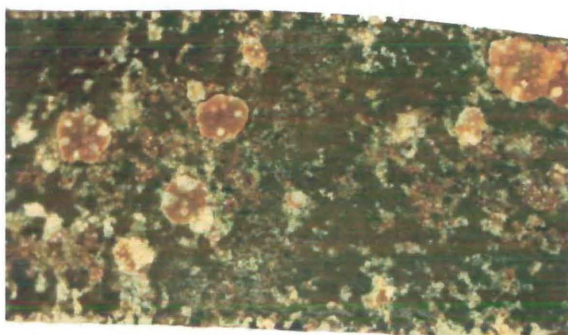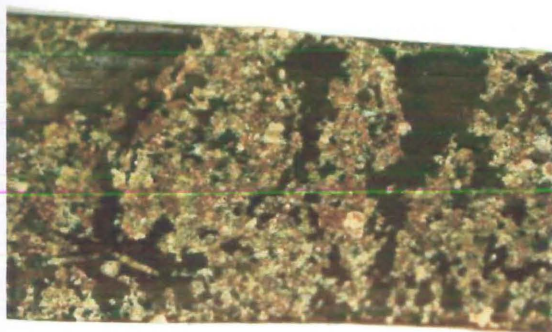
c.   f.
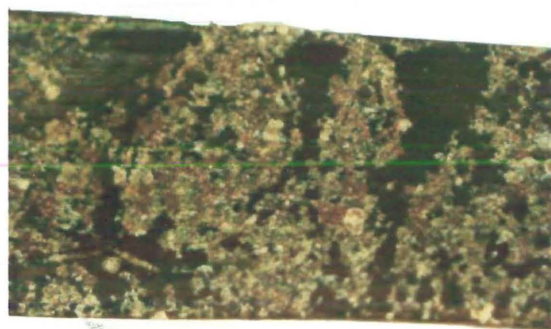
⊢————————————⊣
    1 cm

Figure 3.9 A representation of *P. australis* with periphyton segments after 4 day feeding experiments with *P. bidentata* (a – c) and *C. lepidus* (d – f).

3.2.4 Gastropod grazing on detached Ecklonia radiata

Grazing by *Pyrene bidentata* and *Cantharidus lepidus* individuals on detached *Ecklonia radiata* appears to create small circular holes through the thallus (Figure 3.10). After prior aging for 12 days, at the beginning of the experiment, the thalli had very few signs of degradation and no apparent holes or grazing scars in the epidermal layers or through the tissue (Figure 3.10a and d). After one week of experimentation in the presence of *P. bidentata* individuals (Figure 3.10b), obvious grazing marks were present, with four holes fully through the thallus and nine holes apparently through the epidermis. This increased to 16 holes fully through the thallus, and six through the epidermis, after two weeks of experimentation (Figure 3.10c).

Similar results were observed in grazing experiments with *C. lepidus* individuals. Grazing marks appeared on the detached kelp thallus with one hole fully through the thallus and nine holes through the epidermis (Figure 3.10e). After two weeks of experimentation, the number of holes fully through the thallus was two, and additionally a large portion of an edge of the thallus was removed, and 18 epidermal holes were present (Figure 3.10f). The other two *P. bidentata* and two *C. lepidus* replicates (not shown) all had similar signs of grazing scars on the thallus of the detached *E. radiata* after one and two weeks of experimentation.

The controls of detached *E. radiata* (Figure 3.11), absent of *P. bidentata* or *C. lepidus* individuals, showed no signs of grazing scars in the form of holes. Rather, the thallus degraded in a much more diffuse manner. It appears that the thalli in both controls degraded as a result of decomposition, where the tissue of the thalli has simply started to break-up and erode. Signs of degradation appeared after one week of experimentation (Figure 3.11b and d), and increased after two weeks (Figure 3.11c and e).

a. *Pyrene bidentata*   d. *Cantharidus lepidus*

b.   e.
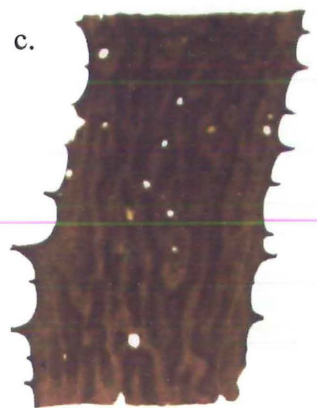
c.   f.
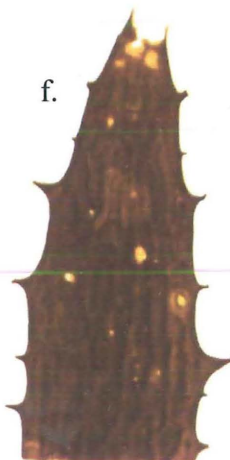
2 cm

Figure 3.10 Pieces of detached *E. radiata* in the presence of *P. bidentata* at the start (a), after 1 week (b), and after 2 weeks (c), and in the presence of *C. lepidus* at the start (d), after 1 week (e), and after 2 weeks (f) of experimentation.
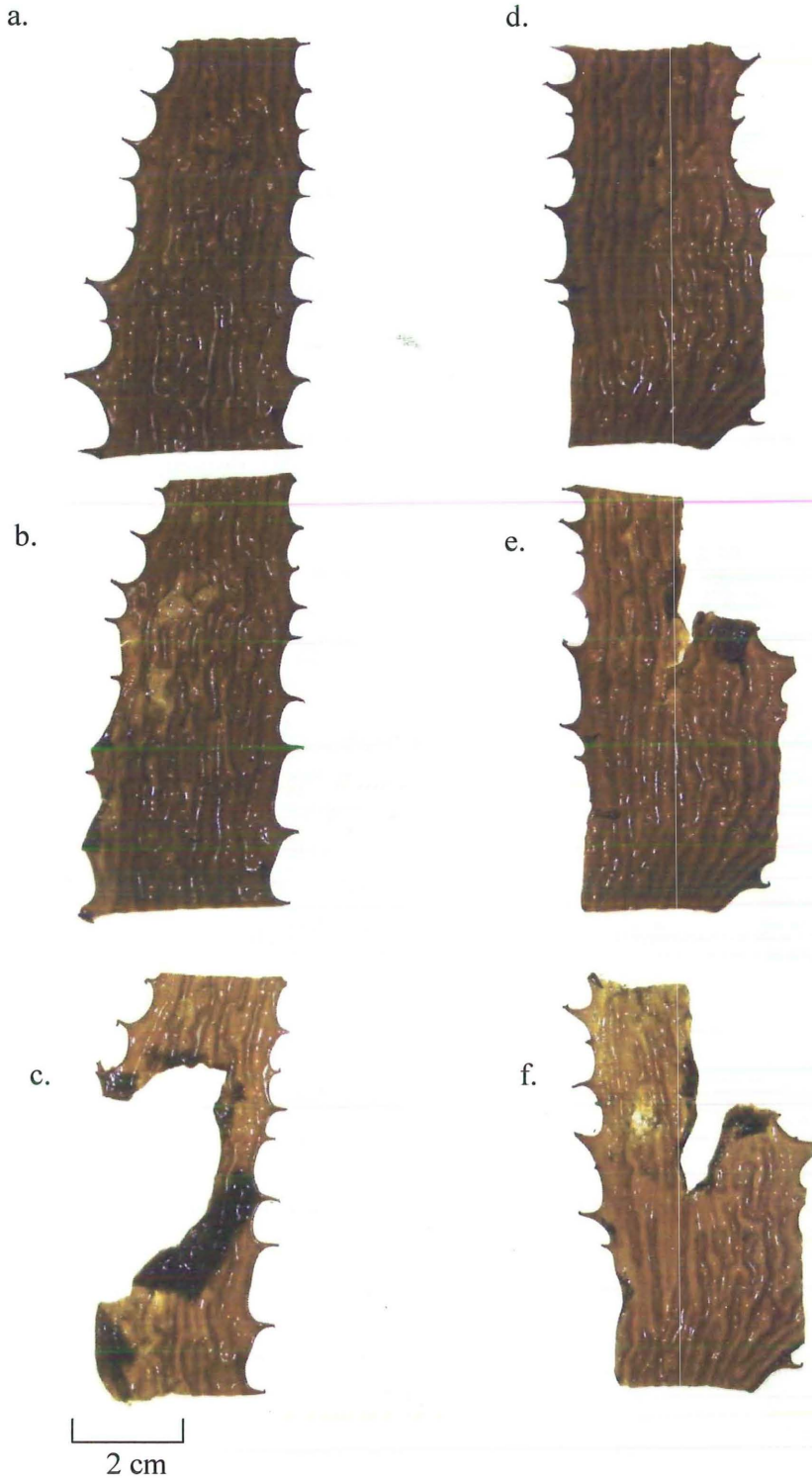
Figure 3.11 Control pieces of detached *E. radiata* in the absence of *P. bidentata* at the start (a), after 1 week (b), and after 2 weeks (c), and in the absence of *C. lepidus* at the start (d), after 1 week (e), and after 2 weeks (f) of experimentation.

4. Discussion

The aim of this research was to determine if large detached *Ecklonia radiata* provides an important trophic connection between temperate reef and seagrass habitats through its consumption via mesograzers that inhabit seagrass meadows, and to determine whether this changes between two distinct seagrass habitats and with proximity to reefs. To evaluate its importance in trophic connectivity, it was determined whether there was: (1) any potential consumption of the resource by key mesograzers that inhabit seagrass meadows through feeding preferences; and (2) any evidence of consumption by mesograzers in seagrass meadows.

4.1 Feeding preferences of mesograzers in seagrass meadows

Choice and no-choice feeding experiments showed that the gastropods *Pyrene bidentata* and *Cantharidus lepidus* both consumed the kelp *E. radiata* when it was fresh and aged. The rate of consumption for this allochthonous resource was often similar to the autochthonous resources, i.e. periphyton on seagrass leaves and epiphytic red algae, that are present in seagrass meadows. The consumption of kelp by these two gastropod species is also supported by results from the qualitative feeding experiment, which demonstrated that both of these gastropod species are capable of producing obvious large grazing scars on the thallus of the kelp. Thus, although the gastropods did not consume the allochthonous resources in a preferential manner to the autochthonous resources, they are obviously capable of consuming *E. radiata*. Given the known accumulation of detached kelp within seagrass meadows (Wernberg et al. 2006), the consumption observed in the laboratory experiments indicates that the resource has the potential to act as a spatial subsidy for *P. bidentata* and *C. lepidus* in seagrass meadows.

Since gastropods in rocky-reef habitats often exhibit preferences for brown macroalgae compared to other red and green algae (Wakefield & Murray 1998, Cox & Murray 2006, Toth et al. 2007), it was expected that *P. bidentata* would show a preference for the *E. radiata* as it is abundantly found on reefs (Tuya et al., in prep.), whereas *C. lepidus* would show a preference for autochthonous material in seagrass meadows as it is abundant in

41

seagrass meadows further from reefs (Tuya et al., in prep.). Furthermore, the rachiglossan radulae of *P. bidentata* is a robust and versatile structure for food gathering (Nielsen & Lethbridge 1989), whereas the rhipidoglossan radulae of *C. lepidus* is less capable of scraping very tough substrata (Steneck & Watling 1982). The general consumption of the macroalgal and periphytic resources by the gastropods indicates that these herbivores have low selectivity in their food choice, perhaps due to their relative low mobility compared to amphipod and isopod mesograzers, which can show selective feeding (Edgar 1992, Cruz-Rivera & Hay 2000, Crawley & Hyndes 2007), or that the nutritional quality of all these resources meets the requirements of the gastropods (Jernakoff et al. 1996, Jernakoff & Nielsen 1997).

The feeding preference experiments indicated no strong preference by the gastropods *P. bidentata* or *C. lepidus* for aged *E. radiata* over autochthonous resources. The influence of secondary metabolites, specifically phlorotannins (Steinberg 1989), was not apparent, with fresh kelp and kelp aged for seven days consumed at similar rates in both species. It has been demonstrated that some isopods and amphipods show strong feeding preferences to wrack compared to fresh brown algae (Pennings et al 2000, Taylor et al. 2002, Norderhaug et al. 2003), possibly due to the leaching out of secondary metabolites (Pennings et al. 2000, Norderhaug et al. 2003). However, generally, mesograzers do not exhibit deterred consumption as a result of phlorotannins produced by brown algae, with amphipods (Duffy & Hay 1991, 1994, 2000, Taylor & Brown 2006), isopods (Jormalainen et al. 2001), and gastropods (Wakefield & Murray 1998, Norderhaug et al. 2003) all demonstrating feeding preferences towards brown algae containing secondary metabolites. The gastropods used in the feeding experiments in this study did not have any preference towards the aged kelp compared to the fresh kelp. This may be a reflection of the general tolerance that Australian mesograzers seem to show to secondary metabolites produced by macrophytes, which are greater than those produced by macroalgae in the northern hemisphere (Taylor & Steinberg 2005).

No-choice feeding experiments showed that kelp was consumed at a higher mean rate by *P. bidentata* than *C. lepidus* (1.5 vs 0.8 mg ind^{-1} day^{-1}), possibly reflecting its much higher densities on reefs relative to seagrass meadows and the structure of its radula (see above). Allowing for the grazing rates of these two species, the gastropods would consume <0.1 g

42

m^{-2} day^{-1} of the total biomass of detached kelp in seagrass meadows, in relation to their densities (Tuya et al., in prep.) found in *Posidonia* and *Amphibolis* spp. meadows at the different proximities to the reefs. Considering this is quantified per day, and the input of detached kelp is not likely to dramatically increase on a daily basis, their consumption over time may have a higher impact, especially if the resource is retained in a small area.

Amphipods and isopods exhibit preferences for brown algae (Duffy & Hay 1991, Wakefield & Murray 1998) at much higher grazing rates than gastropods in feeding experiments (see table in Jernakoff et al. 1996). For example, the common south-western Australian gammarid amphipod *Allorchestes compressa* displays a strong preference for brown algae and is capable of consuming 3 mg ind^{-1} day^{-1} of *E. radiata* in choice feeding experiments (Crawley & Hyndes 2007). Amphipods and isopods are abundant in seagrass meadows of the region (Orth & van Montfrans 1984, Jernakoff et al. 1996), and although the grazing rates of these mesograzers were not quantified in this study, it is likely that they also consume *E. radiata* and at higher rates than the gastropods in this study. The direct quantification of seagrass inhabiting amphipods and isopod is an important area of future study for the understanding of mesograzer trophic dynamics in seagrass meadows. The higher abundances and mobility of amphipods and isopods in seagrass meadows (Hutchings et al. 1990/91, Kirkman et al. 1990/91, Edgar & Shaw 1993, Brearley & Wells 2000), relative to gastropods, may have an increased effect on the consumption of detached *E. radiata* in seagrass meadows. Kelp being transported into seagrass meadows from reefs therefore has the potential to subsidise secondary production in this habitat.

4.2 The importance of *Ecklonia radiata* for seagrass inhabiting mesograzers

In contrast to the laboratory feeding experiments, the field experiment indicated no effect of mesograzer size class, seagrass species, or proximity to reefs on the biomass loss of large detached kelp over a week. The results from the field experiment consistently displayed high variability across all treatments and sites, which may have confounded any potential effects resulting from possible detached kelp consumption. The loss of detached kelp biomass across all treatments and sites ranged from 0.00 – 9.15 g week^{-1}, with a mean (± SE) of 1.58 ± 0.14 g week^{-1}. This high degree of variability may be a result of differential

grazing by mesograzers which are heterogeneously distributed in seagrass meadows, or other biological or physical factors, such as microbial interactions or physical abrasion.

The lack of effect between the closed and open controls infers that biomass loss of kelp is due to an influence or influences of factors that equally affected the kelp regardless of mesograzers. Microbial decomposition (Kirkman & Kenrick 1997, Norderhaug et al. 2003) may have influenced the loss of kelp biomass, as partially supported by the different levels of (potential) microbial decomposition of *E. radiata* observed in the qualitative feeding experiments. The thalli of kelp in the absence of grazers showed variable degrees of degradation, whereas none of the kelp in the presence of grazers had indications of bacterial degradation, possibly due to the grazers feeding on the biofilm on the surface of the thalli, as well as the thalli itself (Storry et al. 2006). Although the pieces of kelp thalli used in the field experiment were scrubbed and washed prior to experimentation, the influence of microbial decomposition prior to and during experimentation may have influenced the variability in the loss of kelp biomass.

Physical abrasion (Kirkman 1984, Kirkman & Kenrick 1997, Lavery et al. 2007) could also influence the loss of kelp biomass. The mean loss of kelp biomass was similar between three of the four sites (1.01 – 1.45 g week^{-1}) when offshore swell and wave conditions were 1.3–1.6 m and 1.2–1.4 m, respectively (Department of Planning and Infrastructure, unpublished data). However, the mean loss of kelp biomass was much higher at Wreck Rock (2.86 g week^{-1}) when swell and wave conditions were 2.1 m and 1.2 m, respectively (Department of Planning and Infrastructure, unpublished data). Furthermore, the loss of kelp biomass was generally much higher in the cages than the open tethers at this site. Despite efforts to reduce abrasion by securing the kelp by two of its ends inside of the cage, the kelp may have been continually knocked against the sides of the cages, resulting in increased physical erosion. This suggests that the swell could have influenced the physical abrasion and, thus, the overall loss of kelp biomass.

Wernberg et al. (2006), who used the same sites and distances from reef as this study, found that tethered fresh kelp generally lost <10% biomass over a five day period at most distances at most sites. Wernberg et al. (2006) also found that at some distances at some sites there was 25 – 75% loss of kelp biomass, which was positively correlated to densities

44

of herbivorous fish at the seagrass-reef interface. Similarly, in the present study, the aged kelp open tethers lost a mean of 14% over a seven day period, while 6/36 pieces of detached kelp lost between 30 – 80% biomass, but this was not restricted to the open tethers. Of the closed control and two treatments, 11/108 replicates lost between 30 – 80%. The lack of significant difference in the loss of the kelp biomass between the closed and open controls, and the <5mm and <20mm treatments, suggests that mesograzers were not the main influence on the loss of kelp biomass in the experiment. Furthermore, since this lack of difference occurred in both open and closed treatments, grazing by fish was not influencing the results.

Evidence of large detached kelp consumption by mesograzers is further complicated by the lack of correlations between kelp biomass loss and mesograzer abundances or biomass in the cages, in the *Posidonia* or *Amphibolis* dominated seagrass meadows, indicating that the consumption of the material was limited. The abundances of amphipods, isopods, and gastropods were rarely associated with biomass loss of kelp. For example, one of the treatments had a total of 120 (0.05 g AFDW) amphipods, 407 (0.29 g AFDW) isopods, and eight (0.19 g AFDW) gastropods at the time of collection, but the weight loss of the kelp over a week was only 0.2%. Conversely, another treatment had 15 (0.02 g AFDW) amphipods, two (0.01 g AFDW) isopods, and no gastropods at the time of collection, but the weight loss of the kelp was 78.5%. Thus, it appears that large detached kelp was not greatly consumed by the mesograzers inhabiting seagrass meadows, through the correlative inference from the experimental data of detached kelp consumption by mesograzers in the experimental units. Caution must be exercised in such comparisons, since mesograzer abundances may reflect neither true abundances nor the numbers of mesograzers in the cages over the week. Biophysical factors such as predation, competition, fitness, resource availability, mobility, currents, or disturbance may have influenced the populations of taxa in the cages throughout the experimentation period, and at the conclusion of the experiment. It is also possible that the more mobile animals were residing in the cages for shelter during the day, and feeding away from the cages at night, as has been observed in some invertebrates which display diurnal feeding movement (Edgar 1992, Taylor 1998).

4.3 Pathways driving secondary production in seagrass meadows: allochthonous or autochthonous resource?

The previous discussion indicates that *E. radiata* that is transported into seagrass meadows can be consumed by key mesograzers, but the field experiment provides no evidence that this form of production contributes substantially to secondary production in these habitats. How then, can these apparently complicating results be reconciled? The lack of clarity in the results of this study may be related to the availability of alternative, autochthonous food resources, the season in which the study was conducted, or the time period of the experimentation. Seagrass meadows can be highly productive habitats with a high diversity of food resources for grazers, including seagrass, epiphytic macroalgae, periphyton and detritus (Orth & van Montfrans 1982, Jernakoff et al. 1996).

The magnitude of consumer response to allochthonous resources is not affected by recipient habitat productivity or the ratio of productivity between donor and recipient habitats, but is significantly related to the ratio of subsidy resources to equivalent resources in the recipient habitat (Polis & Strong 1996, Marczak et al. 2007). In this case, the most likely equivalent autochthonous resources are seagrass periphyton and epiphytes. Seagrass does not appear to provide a direct source of food to mesograzers, as indicated by the avoidance of this food source by the two gastropod species in the feeding experiments (seagrass leaves without periphyton), and the lack of grazing scars observed on seagrass with periphyton. This avoidance has also been shown for the amphipod *A. compressa* in the region (Crawley and Hyndes 2007), further supporting that seagrass material either can not be consumed or is avoided by mesograzers. The resource may not be able to be consumed due to physical toughness of the resource (Lubchenco & Gaines 1981, Steneck & Watling 1982, Jernakoff et al. 1996). Alternatively, it may be avoided due to the relatively poor nutritional value of the resource compared to the macroalgal and periphytic resources in the feeding experiments or those found in seagrass meadows (Lubchenco & Gaines 1981, Hootsmans & Vermatt 1985, Howard & Short 1986, Jernakoff et al. 1996). Presumably, it is the latter, as indicated by the minor consumption of seagrass leaves observed in some of the choice and no-choice feeding experiments. In temperate environments, seagrass material is rarely consumed directly by grazers (Jernakoff et al. 1996, MacArthur & Hyndes 2007), whereas in tropical habitats seagrass consumption by fish and urchins grazing can be high

(Valentine et al. 1997, Valentine & Heck 1999, Kirsch et al. 2002). The lack of grazing scars on the *P. australis* tissue and the patchy spatial distribution of the periphytic material, and the lack of grazing of the seagrass without periphyton in the choice and no-choice feeding experiments, infers that the consumption of the seagrass with periphyton was towards periphyton, rather than seagrass tissue. This is not surprising, as periphyton is known to be an important food resource for gastropods inhabiting seagrass meadows in temperate seagrass meadows (Hootsmans & Vermatt 1985, Howard & Short 1986, Nielsen & Lethbridge 1989, Jernakoff & Nielsen 1997, Nelson 1997, Keuskamp 2004, Smit et al. 2006).

The presence of periphytic and epiphytic macroalgal autochthonous resources in seagrass meadows (Jernakoff et al. 1996, Lavery & Vanderklift 2002, van Elven et al. 2004) appears to be the strongest influence in determining the lack of consumption of detached kelp by mesograzers in seagrass meadows (Figure 4.1). The non-preferential consumption by the gastropods between the fresh and aged kelp, seagrass with periphyton, and red algae, provides further explanation to the lack of consumption by mesograzers found in the field experiment. The results of the feeding experiments using gastropods, in regards to the results of field experimentation, can be extrapolated, albeit with caution, to include the other mesograzers, amphipods and isopods, as the dietary preferences of these groups often overlaps in seagrass habitats (Hootsmans & Vermatt 1985, Howard & Short 1986, Edgar 1990b, Jernakoff & Nielsen 1997, Smit et al. 2005, 2006). When considering food consumption in the field, if a grazer is able to fulfil its nutrient requirements without having to leave its host plant, thereby minimising the risk of predation (Taylor 1998), then the individual would likely graze on resources readily available to it (Lubchenco & Gaines 1981). Conversely, in habitats where autochthonous food supply limits the abundances and productivity of primary consumers, such as unvegetated habitats, the magnitude of primary consumer response to allochthonous resources is greatly increased, even with an increased risk of predation (Figure 4.1) (Kirkman & Kendrick 1997, Stapp & Polis 2003, Vanderklift & Jacoby 2003, Hyndes & Lavery 2005, Crawley et al. 2006, Crawley & Hyndes 2007, Ince et al. 2007).
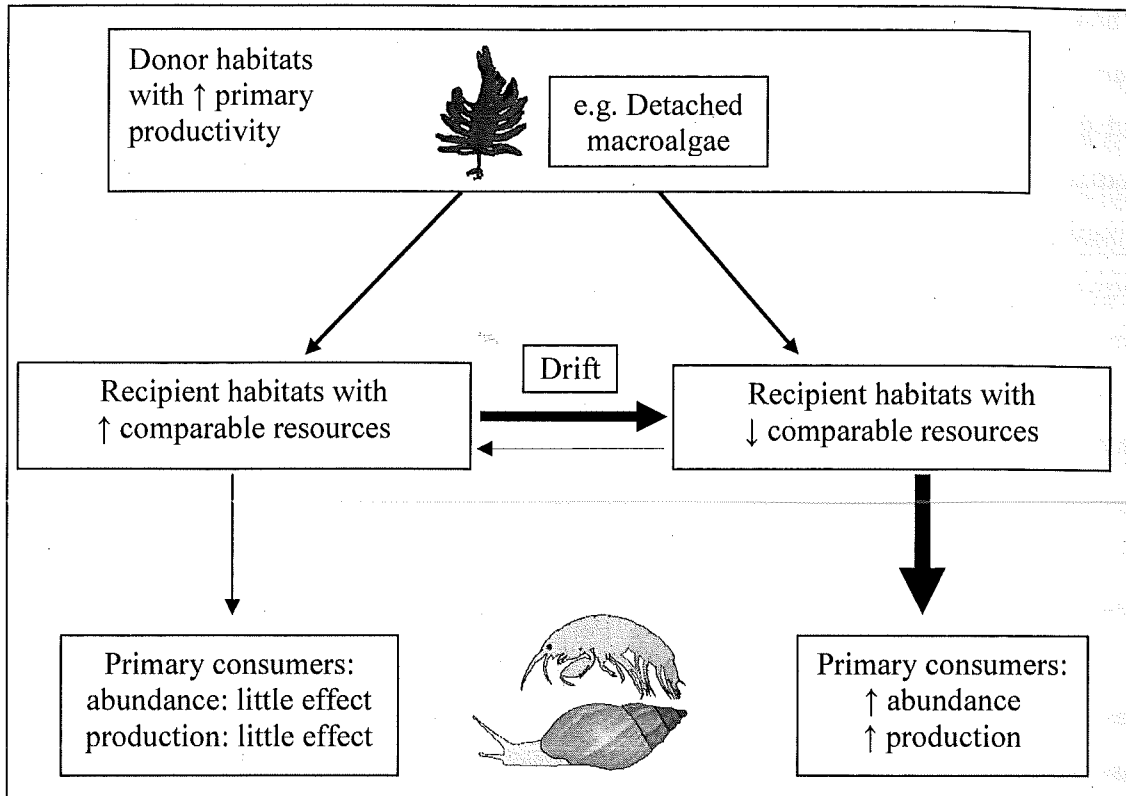
Figure 4.1 Schematic model displaying the effects of allochthonous resources on primary consumers in recipient habitats with high productivity of comparable resources (this study) and recipient habitats with low productivity of comparable resources (Kirkman & Kendrick 1997, Stapp & Polis 2003, Vanderklift & Jacoby 2003, Hyndes & Lavery 2005, Crawley et al. 2006, Crawley & Hyndes 2007, Ince et al. 2007). The weight of the lines represents the magnitude of effects.

Generally, food limitation has not been recognised as a major limiting factor for mesograzers inhabiting seagrass meadows (Jernakoff et al. 1996), most likely due to the abundance of epiphytic, periphytic, detrital and particulate material found in the habitat (Edgar 1990a, Jernakoff et al. 1996, Lavery & Vanderklift 2002, Heck & Valentine 2006). Yet, it has been found that the epifaunal populations associated with epiphytes and periphyton can be food limited (Edgar 1990b). Thus, the lack of evidence of significant consumption of the detached kelp resulting from this study may be related to there being no resource limitation for primary consumers in the seagrass habitats. The mesograzers were most likely consuming locally abundant epiphytes, periphyton, small drift, or particulate organic matter (POM) in the field, or even that which was trapped inside the cages, rather than the experimental detached kelp.

The feeding experiments with the gastropods indicated that feeding on the large detached kelp occurs, and at similar rates to other food sources. Additionally, in the field, the consumption of smaller rather than larger fragments of kelp by mesograzers may occur, due to ease of consumption. Particularly, smaller particles may be preferred by amphipods and isopods due to their smaller mouthparts. Gastropods are less mobile and often exhibit more generalist feeding than amphipods (Jernakoff & Nielsen 1997). The functional morphology of their mouthparts allows amphipods to exploit a wider variety of food types, shapes and sizes than gastropods, but they can also selectively feed on smaller and softer food due to their mobility (Jernakoff & Nielsen 1997). Edgar (1990a) found that the secondary production of invertebrate fauna, comprising predominantly two species of amphipods, was highly correlated with POM bound at the sediment surface, rather than the biomass of drift macrophytes or seagrass rhizomes. Thus, whilst this study focussed on the consumption of large detached kelp in seagrass meadows, the influence of allochthonous derived POM is an important area of further investigation.

Edgar (1992) suggested that the presence of guilds of mobile amphipods, which feed on decaying plants, are widely distributed in south-west Australian coastal habitats. Mesograzer abundances usually peaks in spring/summer, and are at their least in winter in seagrass beds, with the seasonal abundances of amphipods fluctuating over orders of magnitude (Edgar 1990a, 1990b, Jernakoff et al. 1996). Large populations of *Tethygenia* sp. amphipods have been recorded to move into *Amphibolis* seagrass beds from unvegetated habitats on two occasions in summer, which coincided with the dieback of shallow seagrass and its associated epiphytes (Edgar 1992). Thus, the magnitude of consumption of large detached kelp by amphipods inhabiting seagrass meadows may be related to the season, with increased consumption possibly occurring in spring/summer.

Spatial subsidies generally increase consumer densities or biomass in most habitats (Polis & Strong 1996, Polis et al. 1997, Crawley & Hyndes 2007, Ince et al. 2007, Marczak et al. 2007), with detritivores having the largest significant mean effect in all habitats (Marczak et al. 2007). Thus, if large detached kelp were a highly important subsidy for seagrass habitats, the immediate likely effect would be the consumption of the resource resulting in the increase in the density of detritivores, including mesograzers. Possibly, there was little indication of detached kelp consumption by mesograzers in the field experiment as a result

of other abundant food resources (Figure 4.1). During winter, the time of year the study was conducted, the amount of detached *E. radiata* is at its highest due to early winter storms which tear segments or whole plants from the substrate (Kirkman 1984). As Polis & Strong (1996) express, to examine the effect of a spatial subsidy, the analysis of the abundance of various consumers can be observed through the manipulation of detritus by its removal or addition. Thus, as well as adding an allochthonous resource to the habitat, material already found in the sites at the time of installation and throughout the experimentation period could have been removed and controlled. Conducting the research in summer when storms are rare, resulting in decreased seas and swell (Lemm et al. 1999), would likely reduce the amount of ambient detrital material that could potentially alter the amount of detached kelp consumed in experimental units. Epifaunal abundances are also highest during this season (Edgar 1990a, 1990b, Jernakoff et al. 1996). These factors may potentially lead to different results related to the loss of detached kelp biomass through the consumption by mesograzers.

4.4 Conclusions

This study has shown that, although the gastropods *P. bidentata* and *C. lepidus* can consume the brown algae *E. radiata*, there was no evidence of an influence of large detached kelp as a spatial subsidy (*sensu* Polis et al. 1997) for mesograzer trophic dynamics in the seagrass meadows in south-western Australia. These mesograzers exhibit similar preferences for kelp, red algae and periphyton. Thus, while *E. radiata* dominates the detrital macroalgae found in seagrass meadows (Wernberg et al. 2006), it is possible that this is a result of abundant autochthonous resources and POM found in the seagrass meadows studied during the time of experimentation, which may change according to location and/or season. Thus, extrapolating the lack of *E. radiata* consumption in seagrass meadows by the test species used here to all mesograzers and times should be made with caution, as this could potentially change when similar autochthonous resource are low in abundance or biomass. Further investigations are needed at different locations and times of the year to quantify any changes in the consumption of the resource. Furthermore, its importance as a contributor to the POM pool found on the sediment surface in seagrass meadows needs to be quantified, to estimate its importance to trophic dynamics of the micro- and macro-fauna who exploit this resource. Thus, the role of large detached *E.*

radiata in seagrass meadows as a food source for mesograzers is clearly possible, but whether the possibility is realised is still uncertain. It is possible that kelp contributes to the trophic dynamics of seagrass meadows through other mechanisms, or during other seasons and at other locations.

References

Anderson MJ (2005) PERMANOVA: a FORTRAN computer program for permutational analysis of variance. Department of Statistics, University of Auckland, New Zealand

Anderson MJ, Connell SD, Gillanders BM, Diebel CE, Bloms WM, Saunders JE, Landers TJ (2005) Relationships between taxonomic resolution and spatial scales of multivariate variation. J Anim Ecol 74: 636-646

Barros F, Underwood AJ, Lindegarth M (2001) The influence of rocky reefs on structure of benthic macrofauna in nearby soft-sediments. Est Coast Shelf Sci 52: 191-199

Bologna PAX, Heck Jr KL (1999) Macrofaunal associations with seagrass epiphytes: relative importance of trophic structural characteristics. J Exp Mar Biol Ecol 242: 21-39

Brearley A, Wells FE (2000) Shellsand dredging environmental management programme. Project S1: Ecological significance of seagrass invertebrates. Phase 3 Report. Unpublished report, prepared for Cockburn Cement Limited

Chavanich S, Harris LG (2002) The influence of macroalgae on seasonal abundance and feeding preference of a subtidal snail, *Lacuna vincta* (Montagu) (Littorinidae) in the Gulf of Maine. J Molluscan Stud 68: 73-78.

Cox ET, Murray SN (2006) Feeding preferences and the relationships between food choice and assimilation efficiency in the herbivorous marine snail *Lithopoma undosum* (Turbinidae). Mar Biol 148: 1295-1306

Crawley KR (2006) Detached macrophyte accumulations in surf zones: significance of macrophyte type and volume in supporting secondary production. Unpublished PhD dissertation, Edith Cowan University: Perth, Western Australia.

Crawley KR, Hyndes GA (2007) The role of different types of detached macrophytes in the food and habitat choice of a surf-zone inhabiting amphipod. Mar Biol 151: 1433-1443

Crawley KR, Hyndes GA, Ayvazian SG (2006) Influence of different volumes and types of detached macrophytes on fish community structure in surf zones of sandy beaches. Mar Ecol Prog Ser 307: 233-246

Cruz-Rivera E, Hay ME (2000) Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. Ecology 81: 201-219

Department of Conservation and Land Management (1992 [?]) Marmion marine park management plan 1992-2002. Management plan no 23. Published report prepared for the National Parks and Nature Conservation Authority, Perth, Western Australia

Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72: 1286-1298

Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75: 1304-1319

Duffy JE, Hay ME (2000) Strong impacts of grazing amphipods on the organisation of a benthic community. Ecol Monogr 70: 237-263

Dulvy NK, Mitchell RE, Watson D, Sweeting CJ, Polunin NVC (2002) Scale-dependent control of motile epifaunal community structure along a coral reef fishing gradient. J Exp Mar Biol Ecol 278: 1-29

Edgar GJ (1990a) The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. J Exp Mar Biol Ecol 137: 215-240

Edgar GJ (1990b) Population regulation, population dynamics and competition amongst mobile epifauna associated with seagrasses. J Exp Mar Biol Ecol 144: 205-234

Edgar GJ (1990c) The use of size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. J Exp Mar Biol Ecol 137: 195-214

Edgar GJ (1992) Patterns of colonisation of mobile epifauna in a Western Australian seagrass bed. J Exp Mar Biol Ecol 157: 225-246

Edgar GJ (2000) Australian marine life: the plants and animals of temperate waters (revised edition). Reed New Holland, Sydney

Edgar GJ, Shaw C (1993) Inter-relationships between sediments, seagrasses, benthic invertebrates and fishes in shallow marine habitats off south-western Australia. In: Wells FE, Walker DI, Kirkman H, Lethbridge R (eds) Proceedings of the Third International Marine Biology Workshop: The Marine Flora and Fauna of Albany, Western Australia. Western Australian Museum, Perth, pp 634.

Edgar GJ, Klumpp DW (2003) Consistencies over regional scales in assemblages of mobile epifauna associated with natural and artificial plants of different shape. Aq Bot 75: 275-291

Fairweather PG, Quinn GP (1992) Seascape ecology: the importance of linkages. In: Battershill CN, Schiel DR, Jones GP, Creese RG, MacDiarmid AB (eds) Proceedings of the Second International Temperate Reef Symposium. NIWA, Wellington, Auckland, New Zealand, pp 77-83

Goodsell PJ, Fowler-Walker MJ, Gillanders BM, Connell SD (2004) Variations in the configuration of algae in subtidal forests: implications for invertebrate assemblages. Aust J Ecol 29: 350-357

Hay ME, Duffy JE, Fenical W (1990) Host-plant specialisation decreases predation on a marine amphipod: an herbivore in plant's clothing. Ecology 71: 733-743

Heck Jr KL, Valentine JF (2006) Plant-herbivore interactions in seagrass meadows. J Exp Mar Biol Ecol 330: 420-436

Hootsmans MJ, Vermaat JE (1985) The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. Aq Bot 22: 83-88

Howard RK, Short FT (1986) Seagrass growth and survivorship under the influence of grazers. Aq Bot 24: 287-302

Hutchings PA, Wells FE, Walker DI, Kendrick GA (1990/91) Seagrass, sediment and infauna - a comparison of *Posidonia australis*, *Posidonia sinuosa* and *Amphibolis antarctica* in Princess Royal Harbour, south-western Australia. II. Distribution, composition and abundance of macrofauna. In: Wells FE, Walker DI, Kirkman H, Lethbridge R (eds) Proceedings of the Third International Marine Biology Workshop: The Marine Flora and Fauna of Albany, Western Australia. Western Australian Museum, Perth, pp 722

Hyndes GA, Lavery PS (2005) Does transported seagrass provide an important trophic link in unvegetated, nearshore areas? Est Coast Shelf Sci 63: 633-643

Hyndes GA, Kendrick AJ, MacArthur LD, Stewart E (2003) Differences in the species- and size-composition of fish assemblages in three distinct habitats with differing plant and meadow structure. Mar Biol 142: 1195-1206

Ince R, Hyndes GA, Lavery PS, Vanderklift MA (2007) Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. Est Coast Shelf Sci 74: 77-86

Jennings JG, Steinberg PD (1997) Phlorotannins versus other factors affecting epiphyte abundance on the kelp *Ecklonia radiata*. Oecologia 109: 461-473

Jernakoff P, Nielsen J (1997) The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. Aq Bot 56: 183-202

Jernakoff P, Brearley A, Nielsen J (1996) Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. Oceanogr Mar Biol Annu Rev 34: 109-162

Jones GP, Andrew NL (1992) Temperate reefs and the scope of seascape ecology. In: Battershill CN, Schiel DR, Jones GP, Creese RG, MacDiarmid AB (eds) Proceedings of the Second International Temperate Reef Symposium. NIWA, Wellington, Auckland, New Zealand, pp 63-76

Jormalainen V, Honkanen T, Heikkila N (2001) Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. Mar Ecol Prog Ser 220: 210-230

Kendrick GA, Lavery PS (2001) Assessing biomass, assessing assemblage structure and productivity of algal epiphytes on seagrasses. In: Short FT, Coles, RG, Short CA (eds) Global seagrass research methods. Elsevier, Amsterdam. pp 199-222

Kenrick GA, Lavery PS, Phillips JC (1999) Influence of *Ecklonia radiata* kelp canopy on structure of macro-algal assemblages in Marmion Lagoon, Western Australia. Hydrobiologia. 398/399: 275-283

Kendrick GA, Hegge BJ, Wyllie A, Davidson A, Lord DA (2000) Changes in seagrass cover on Success and Parmelia Banks, Western Australia between 1965 and 1995. Est Coast Shelf Sci 50: 341-353

Keuskamp D (2004) Limited effects of grazer exclusion on the epiphytes of *Posidonia sinuosa* in South Australia. Aq Bot 78: 3-14

Kirkman H (1984) Standing stock and production of *Ecklonia radiata* (C. Ag.) J. Agardh. J Exp Mar Biol Ecol 76: 119-130

Kirkman H, Walker DI (1989) Regional studies – Western Australian seagrass. In: Larkum AWD, McComb AJ, Shepherd D (eds) Biology of seagrass – a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam. pp 157-181

Kirkman H, Kendrick GA (1997) Ecological significance and commercial harvesting of drifting and beach-cast macro-algae and seagrasses in Australia: a review. J Appl Phyc 9:311-326

Kirkman H, Kirkman J (2000) Long-term seagrass meadow monitoring near Perth, Western Australia. Aq Bot 2000: 319-332

Kirkman H, Humphries P, Manning R (1990/91) The epibethic fauna of seagrass beds and bare sand in Princess Royal Harbour and King George Sound, Albany, south-western Australia. In: Wells FE, Walker DI, Kirkman H, Lethbridge R (eds) Proceedings of the Third International Marine Biology Workshop: The Marine Flora and Fauna of Albany, Western Australia. Western Australian Museum, Perth, pp 722.

Kirsch KD, Valentine JF, Heck Jr KL (2002) Parrotfish grazing on turtlegrass *Thalassia testudinum*: evidence for the importance of seagrass consumption in food web dynamics of the Florida Keys National Marine Sanctuary. Mar Ecol Prog Ser 227: 71-85

Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basiv program for the determination of coral and substrate coverage using random point count methodology. Comput Geosci 32: 1259-1269

Krebs CJ (2001) Ecology. Benjamin-Cummings, San Francisco.

Lavery PS, Vanderklift MA (2002) A comparison of spatial and temporal patterns in epiphytic macroalgal assemblages of the seagrass *Amphibolis griffithii* and *Posidonia coriacea*. Mar Ecol Prog Ser 236: 99-112

Lavery PS, Reid T, Hyndes GA, van Elven BR (2007) Effect of leaf movement on epiphytic algal biomass of seagrass leaves. Mar Ecol Prog Ser 338: 97-106

Lemm AJ, Hegge BJ, Masselink G (1999) Offshore wave climate, Perth (Western Australia), 1994-96. Mar Fresh Res 50: 95-102

Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. Annu Rev Ecol Syst 12: 405-437

MacArthur LD, Hyndes GA (2007) Varying foraging strategies of Labridae in seagrass habitats: herbivory in temperate seagrass meadows? J Exp Mar Biol Ecol 340: 247-258

Manly BFJ (1993) Comments on design and analysis of multiple-choice feeding-preference experiments. Oecologia 93: 149-152

Marczak LB, Thompson RM, Richardson JS (2007) Meta-analysis: trophic level, habitat, and productivity shape food web effects of resource subsidies. Ecology 88: 140-148

Nelson TA (1997) Epiphyte-grazer interactions on *Zostera marina* (Anthophyta: Monocotyledones): effects of density on community function. J Phycol 33: 743-752

Nielsen J, Lethbridge R (1989) Feeding and the epiphyte resources of gastropods living on the leaves of the seagrasses *Amphibolis griffithii* in south-western Australia. J Malac Soc Aust 10: 47-58

Norderhaug KM, Fredriksen S, Nygaard K (2003) Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of the bacterial degradation to food quality. Mar Ecol Prog Ser 255: 135-144

Orth RJ, van Montfrans J (1984) Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. Aq Bot 18: 43-69

Pennings SC, Carefoot TH, Zimmer M, Danko JP, Ziegler A (2000) Feeding preferences of supralittoral isopods and amphipods. Can J Zool 78: 1918-1929

Peterson BJ, Heck Jr KL (2001) Positive interactions between suspension-feeding bivalves and seagrass – a facultative mutualism. Mar Ecol Prog Ser 213: 143-155

Peterson CH, Renaud PE (1989) Analysis of feeding preference experiments. Oecologia 80: 82-86

Polis GA, Strong DR (1996) Food web complexity and community dynamics. The Amer Nat 147: 813-846

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidised food webs. Ann Rev Ecol Syst 28: 289-316

Poore AGB (2005) Scales of dispersal among hosts in a herbivorous marine amphipod. Austr J Ecol 30: 219-228

Poore AGB, Hill NA (2005) Spatial associations among palatable and unpalatable macroalgae: a test of associational resistance with a herbivorous amphipod. J Exp Mar Biol Ecol 326: 207-216

Prince JS, LeBlanc WG, Macia S (2004) Design and analysis of multiple choice feeding data. Oecologia 138:1-4

Roa R (1992) Design and analysis of multiple-choice feeding-preference experiments. Oecologia 89: 509-515

Searle DJ, Semeniuk V (1985) The natural sectors of the inner Rottnest Shelf coast adjoining the Swan Coastal Plain. J R Soc West Aust 67: 116-136

Smit AJ, Brearley A, Hyndes GA, Lavery PS, Walker DI (2005) Carbon and nitrogen stable isotope analysis of an *Amphibolis griffithii* seagrass bed. Est Coast Shelf Sci 65: 545-556

Smit AJ, Brearley A, Hyndes GA, Lavery PS, Walker DI (2006) $\delta^{15}N$ and $\delta^{13}C$ analysis of a *Posidonia sinuosa* seagrass bed. Aq Bot 84: 277-282

Stapp P, Polis GA (2003) Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. Oecologia. 134: 496-504

Steinberg PD (1989) Biogeographical variation in brown algal polyphenolics and other secondary metabolites: comparison between temperate Australasia and North America. Oecologia 78: 373-382

Steinberg PD, van Altena I (1992) Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australia. Ecol Monogr 62: 189-222

Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Mar Biol 68: 299-319

Storry KA, Weldrick CK, Mews M, Zimmer M, Jelinski DE (2006) Intertidal coarse woody debris: a spatial subsidy as shelter or feeding habitat for gastropods? Est Coast Shelf Sci 66:197-203

Tanaka MO, Leite FPP (2003) Spatial scaling in the distribution of macrofauna associated with *Sargassum stenophyllum* (Mertens) Martius: analyses of faunal groups, gammarid life habits, and assemblage structure. J Exp Mar Biol Ecol 293: 1-22

Taylor RB (1998) Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal seaweeds in northeastern New Zealand. Hydrobiologia 361: 25-35

Taylor RB, Steinberg PD (2005) Host use by Australasian seaweed mesograzers in relation to feeding preferences of larger grazers. Ecology 86: 2955-2967

Taylor RB, Brown PJ (2006) Herbivory in the gammarid amphipod *Aora typical*: relationships between consumption rates, performance and abundance across ten seaweed species. Mar Biol 149: 455-463

Taylor RB, Sotka E, Hay ME (2002) Tissue-specific induction of herbivore resistance: seaweed response to amphipod grazing. Oecologia 132: 68-76

Toth GB, Karlsson M, Pavia H (2007) Mesoherbivores reduce net growth and induce chemical resistance in natural seaweed population. Oecologia 152: 245-255

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge.

Valentine JF, Heck Jr KL (1999) Seagrass herbivory: evidence for the continued grazing of marine grasses. Mar Ecol Prog Ser 176:291-302

Valentine JF, Heck Jr KL (2005) Perspective review of the impacts of overfishing on coral reef food web linkages. Coral Reefs 24: 209-213

Valentine JF, Heck Jr KL, Busby J, Webb D (1997) Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. Oecologia 112: 193-200

Vanderklift MA, Jacoby CA (2003) Patterns in fish assemblages 25 years after major seagrass loss. Mar Ecol Prog Ser 247: 225-235

Vanderklift MA, Kendrick GA (2005) Contrasting influence of sea urchins on attached and drift macroalgae. Mar Ecol Prog Ser 299: 101-110

Vanderklift MA, Kendrick GA (2006) Variation in abundances of herbivorous invertebrates in temperate subtidal rocky reef habitats. Mar Fresh Res 55: 93-103

van Elven BR, Lavery PS, Kenrick GA (2004) Reefs as contributors to diversity of epiphytic macroalgae assemblages in seagrass meadows. Mar Ecol Prog Ser 276: 71-83

Verduin JJ, Backhaus JO, Walker DI (2002) Estimates of pollen dispersal and capture within *Amphibolis antarctica* (Labill.) Sonder and Aschers. Ex Aschers. Meadows. Bull Mar Sci 71: 1269-1277

Wakefield RL, Murray SN (1998) Factors influencing food choice by the seaweed-eating marine snail *Norrisia norrisi* (Trochidae). Mar Biol 130: 631-642

Wells FE, Bryce CW (2000) Seashells of Western Australia. Western Australia Museum, Perth

Wernberg T, Kendrick GA, Phillips JC (2003) Regional differences in kelp-associated algal assemblages on temperate limestone reefs in south-western Australia. Diver Distr 9: 427-411

Wernberg T, Vanderklift MA, How J, Lavery PS (2006) Export of detached macroalgae from reefs to adjacent seagrass beds. Oecologia 147: 692-701

Wilson B (1993) Australian marine shells: volumes 1 & 2. Odyssey Publishing, Western Australia

Appendix 1

Fauna abundance sheets from closed control and <20mm treatment cages from Wanneroo Reef, Whitfords Rock SW, Whitfords Rock NE, and Wreck Rock.

Site: Wanneroo Reef
Distance: Interface

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	3
Cnidaria	Anthozoa							
Annelida	Polychaete			1	1	1		
Other Worms			1					1
Chelicerata								
Crustacea	Ostracoda		3		2	9	8	4
	Copepoda							
	Amphipoda	Gammarid	53	21	178	93	47	97
		Caprellid						
		Cerapid						
	Isopoda		3	1	1	7	1	5
	Cumacea							
	Nebaliacea				1	1		1
	Tanaidacea				2	4	1	3
	Mysidacea							
	Decapoda		2		1	12	10	5
Mollusca	Polyplacophora							
	Gastropoda	Pyrene bidentata				1	1	2
		Cantharidus lepidus				1		
		Prothalotia lehmanni						
		Thalotia conica						
		Thalotia chlorostoma						
		Australium squamiferum				1		
		Other			6	21	10	22
	Bivalve					1	1	
	Cephalopod							
Echinodermata	Crinoidea							
	Asteroidea						8	2
	Ophuiroidea							
	Echinoidea							
	Holothuroidea			1				1
Chordata	Fish							1
Unknown								

Site: Wanneroo Reef
Distance: Close

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	3
Cnidaria	Anthozoa							
Annelida	Polychaete		1	2		1	3	2
Other Worms				2				
Chelicerata			1					
Crustacea	Ostracoda			8	1	8	25	17
	Copepoda		7					
	Amphipoda	Gammarid	78	64	23	62	70	41
		Caprellid						1
		Cerapid						
	Isopoda		6	5	14	54	12	12
	Cumacea		1					
	Nebaliacea							
	Tanaidacea		4	1		7	4	1
	Mysidacea							
	Decapoda		1	1		9	13	19
Mollusca	Polyplacophora		1			1	1	
	Gastropoda	Pyrene bidentata				6		7
		Cantharidus lepidus						
		Prothalotia lehmanni						
		Thalotia conica						
		Thalotia chlorostoma						1
		Australium squamiferum						2
		Other	4	8	6	11	18	11
	Bivalve							
	Cephalopod							
Echinodermata	Crinoidea							
	Asteroidea						10	2
	Ophuiroidea							
	Echinoidea							
	Holothuroidea						3	
Chordata	Fish					1		
Unknown								

62

Site: Wanneroo Reef
Distance: Far

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	3
Cnidaria	Anthozoa							
Annelida	Polychaete		4	6	13		1	1
Other Worms					1			
Chelicerata			2			3		
Crustacea	Ostracoda			3	14	12	12	78
	Copepoda				1			
	Amphipoda	Gammarid	16	8	14	34	27	81
		Caprellid						
		Cerapid				1	4	4
	Isopoda		5		2	5	6	28
	Cumacea							
	Nebaliacea							4
	Tanaidacea				3		1	1
	Mysidacea							
	Decapoda		1			5	1	8
Mollusca	Polyplacophora							
	Gastropoda	Pyrene bidentata						
		Cantharidus lepidus						
		Prothalotia lehmanni						
		Thalotia conica				2	1	
		Thalotia chlorostoma						
		Australium squamiferum						
		Other				8	8	13
	Bivalve							
	Cephalopod							
Echinodermata	Crinoidea							1
	Asteroidea							
	Ophuiroidea							
	Echinoidea							
	Holothuroidea							
Chordata	Fish					1		
Unknown								

63

Site: Whitfords Rock SW
Distance: Interface

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	3
Cnidaria	Anthozoa					1		
Annelida	Polychaete		14	9	12	7	9	11
Other Worms			5	32	4			
Chelicerata						1	1	1
Crustacea	Ostracoda		10				23	2
	Copepoda		2			3	1	6
	Amphipoda	Gammarid	39	25	14	79	100	70
		Caprellid						
		Cerapid			1	4	1	6
	Isopoda		3	4		5	12	7
	Cumacea					1	2	2
	Nebaliacea		2				3	
	Tanaidacea				1	1	3	2
	Mysidacea							
	Decapoda		1		1	6	11	1
Mollusca	Polyplacophora							
	Gastropoda	Pyrene bidentata				2		
		Cantharidus lepidus					1	
		Prothalotia lehmanni						
		Thalotia conica						
		Thalotia chlorostoma						
		Australium squamiferum					3	
		Other	52		1	37	40	16
	Bivalve					1	2	
	Cephalopod							
Echinodermata	Crinoidea						1	
	Asteroidea							
	Ophuiroidea					1		
	Echinoidea							
	Holothuroidea							
Chordata	Fish							
Unknown								

Site: Whitfords Rock SW
Distance: Close

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	3
Cnidaria	Anthozoa			1		1		1
Annelida	Polychaete		2	18	7	4	23	5
Other Worms				37	2		35	1
Chelicerata			1		2	4	1	
Crustacea	Ostracoda			5		13	5	5
	Copepoda			2	8	3		2
	Amphipoda	Gammarid	46	37	62	115	45	42
		Caprellid				1		
		Cerapid			2	1		2
	Isopoda		2	5	6	12	5	
	Cumacea		3	2	2			
	Nebaliacea							
	Tanaidacea		2	1			2	
	Mysidacea							
	Decapoda		1		1	4	26	8
Mollusca	Polyplacophora					1		
	Gastropoda	Pyrene bidentata					6	
		Cantharidus lepidus				4	2	2
		Prothalotia lehmanni						
		Thalotia conica						
		Thalotia chlorostoma						2
		Australium squamiferum					1	
		Other	3	17	9	32	25	21
	Bivalve					4	4	1
	Cephalopod							
Echinodermata	Crinoidea							
	Asteroidea							
	Ophuiroidea						1	
	Echinoidea					1		
	Holothuroidea					1		
Chordata	Fish							1
Unknown								

Site: Whitfords Rock SW
Distance: Far

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	3
Cnidaria	Anthozoa							
Annelida	Polychaete		10	5	8	19		3
Other Worms			7		2	29		1
Chelicerata			1	1		1		
Crustacea	Ostracoda		27	4		5	20	3
	Copepoda		3	2			5	
	Amphipoda	Gammarid	43	69	48	56	109	67
		Caprellid						
		Cerapid		2		4	7	1
	Isopoda		6	4	9	10	11	20
	Cumacea		1	5	1	1	4	1
	Nebaliacea		1					
	Tanaidacea		14	3				
	Mysidacea			4		10		1
	Decapoda		3		1	5	11	12
Mollusca	Polyplacophora							
	Gastropoda	Pyrene bidentata					3	
		Cantharidus lepidus				3		1
		Prothalotia lehmanni						1
		Thalotia conica				1	1	1
		Thalotia chlorostoma				2		2
		Australium squamiferum						
		Other	8	7	4	5	17	11
	Bivalve							
	Cephalopod							
Echinodermata	Crinoidea							1
	Asteroidea							
	Ophuiroidea				1			
	Echinoidea							
	Holothuroidea					1		1
Chordata	Fish							10
Unknown								

66

Site: Whitfords Rock NE
Distance: Interface

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	3
Cnidaria	Anthozoa				1		6	1
Annelida	Polychaete			6	8		8	3
Other Worms			3		4		32	3
Chelicerata								
Crustacea	Ostracoda		8	5	4	3	1	18
	Copepoda		2	6	7	9		7
	Amphipoda	Gammarid	45	70	63	89	66	124
		Caprellid	1			1	1	
		Cerapid	1				3	
	Isopoda		6	2	2	3	3	3
	Cumacea		3		1		1	5
	Nebaliacea							
	Tanaidacea		1		1		3	1
	Mysidacea							
	Decapoda		1		1	11	22	18
Mollusca	Polyplacophora							
	Gastropoda	Pyrene bidentata				2		
		Cantharidus lepidus				3	2	
		Prothalotia lehmanni						
		Thalotia conica						
		Thalotia chlorostoma					1	
		Australium squamiferum						
		Other	6	3	8	13	2	51
	Bivalve						2	4
	Cephalopod							
Echinodermata	Crinoidea					1		
	Asteroidea							
	Ophuiroidea							
	Echinoidea						1	
	Holothuroidea							
Chordata	Fish							
Unknown				1				

Site: Whitfords Rock NE
Distance: Close

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	3
Cnidaria	Anthozoa		2	1		6		3
Annelida	Polychaete		38	6	7	5		3
Other Worms			27	4	2	1	3	
Chelicerata					2	2		2
Crustacea	Ostracoda		14		3	3	11	11
	Copepoda		1		6		6	11
	Amphipoda	Gammarid	52	76	124	86	118	93
		Caprellid						
		Cerapid	2				1	3
	Isopoda		5	1	8	7	2	8
	Cumacea		3			1		
	Nebaliacea							
	Tanaidacea		1		1	1		
	Mysidacea							
	Decapoda				1	22	2	2
Mollusca	Polyplacophora					1		
	Gastropoda	Pyrene bidentata						
		Cantharidus lepidus					1	3
		Prothalotia lehmanni						
		Thalotia conica						
		Thalotia chlorostoma				1		1
		Australium squamiferum						
		Other	41		28	18	18	29
	Bivalve				3		2	4
	Cephalopod							
Echinodermata	Crinoidea				1	2		
	Asteroidea							
	Ophuiroidea			1	1			
	Echinoidea							
	Holothuroidea							
Chordata	Fish						1	
Unknown								

Site: Whitfords Rock NE
Distance: Far

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	NA
Cnidaria	Anthozoa					3	5	
Annelida	Polychaete		2	2	3	63	55	
Other Worms				4	1	12	1	
Chelicerata			3	1		3		
Crustacea	Ostracoda		10	3	7	21	4	
	Copepoda		1	1	2			
	Amphipoda	Gammarid	90	94	110	194	115	
		Caprellid						
		Cerapid				4	5	
	Isopoda		8	14	11	60	407	
	Cumacea		1		2			
	Nebaliacea					6		
	Tanaidacea			1	3	2	1	
	Mysidacea							
	Decapoda		1	2	1	8	10	
Mollusca	Polyplacophora				1	1	2	
	Gastropoda	Pyrene bidentata				1		
		Cantharidus lepidus				1	1	
		Prothalotia lehmanni						
		Thalotia conica						
		Thalotia chlorostoma						
		Australium squamiferum						
		Other	6	14	22	14	7	
	Bivalve					3		
	Cephalopod					1		
Echinodermata	Crinoidea					1		
	Asteroidea					11	1	
	Ophuiroidea		1		2		1	
	Echinoidea						1	
	Holothuroidea				1	2		
Chordata	Fish					1	2	
Unknown								

Site: Wreck Rock
Distance: Interface

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	3
Cnidaria	Anthozoa							
Annelida	Polychaete		3	10	1	1	9	6
Other Worms				5			15	3
Chelicerata						1	1	2
Crustacea	Ostracoda							2
	Copepoda						1	
	Amphipoda	Gammarid	18	11	9	25	30	33
		Caprellid						
		Cerapid						13
	Isopoda		2	2	1	4	10	20
	Cumacea						1	
	Nebaliacea							
	Tanaidacea							
	Mysidacea							
	Decapoda			1		32	41	19
Mollusca	Polyplacophora							
	Gastropoda	Pyrene bidentata					3	
		Cantharidus lepidus					10	3
		Prothalotia lehmanni						
		Thalotia conica						
		Thalotia chlorostoma				1		
		Australium squamiferum						
		Other	1			13	21	10
	Bivalve						1	5
	Cephalopod							
Echinodermata	Crinoidea							
	Asteroidea					1	4	
	Ophuiroidea							
	Echinoidea							1
	Holothuroidea							1
Chordata	Fish						1	
Unknown								

Site: Wreck Rock
Distance: Close

			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	NA
Cnidaria	Anthozoa			1			3	
Annelida	Polychaete		2	1		2	14	
Other Worms			2			8	32	
Chelicerata				1				
Crustacea	Ostracoda			1			6	
	Copepoda							
	Amphipoda	Gammarid	36	31	15	63	97	
		Caprellid						
		Cerapid				1	5	
	Isopoda		1	6	2	4	12	
	Cumacea						1	
	Nebaliacea					1	1	
	Tanaidacea							
	Mysidacea							
	Decapoda		3	1		16	9	
Mollusca	Polyplacophora							
	Gastropoda	Pyrene bidentata				2		
		Cantharidus lepidus				5	1	
		Prothalotia lehmanni						
		Thalotia conica						
		Thalotia chlorostoma						
		Australium squamiferum						
		Other	1	1		9	8	
	Bivalve							
	Cephalopod							
Echinodermata	Crinoidea							
	Asteroidea					6		
	Ophuiroidea		1					
	Echinoidea						1	
	Holothuroidea					1		
Chordata	Fish						2	
Unknown								

|			Abundance per cage					
			Closed reps			<20mm reps		
			1	2	3	1	2	3
Cnidaria	Anthozoa			1	1		3	3
Annelida	Polychaete		16	9	27	13	35	36
Other Worms			8	2	8	3	25	
Chelicerata			1		1	2		3
Crustacea	Ostracoda					1	11	7
	Copepoda							
	Amphipoda	Gammarid	20	2	9	17	37	43
		Caprellid		1				
		Cerapid					2	1
	Isopoda		18	4	12	15	24	9
	Cumacea						2	
	Nebaliacea						3	3
	Tanaidacea							3
	Mysidacea							
	Decapoda		2	4	2	8	12	29
Mollusca	Polyplacophora							
	Gastropoda	Pyrene bidentata						1
		Cantharidus lepidus				3	1	6
		Prothalotia lehmanni						
		Thalotia conica						
		Thalotia chlorostoma				1		1
		Australium squamiferum						
		Other		1		16		9
	Bivalve					1		
	Cephalopod							
Echinodermata	Crinoidea					1		1
	Asteroidea					5		4
	Ophuiroidea							1
	Echinoidea					2		1
	Holothuroidea					1		
Chordata	Fish							
Unknown							1	1

Appendix 2

Amphipod, isopod, and gastropod AFDW (g) from closed control and <20mm treatment cages from Wanneroo Reef, Whitfords Rock SW, Whitfords Rock NE, and Wreck Rock.
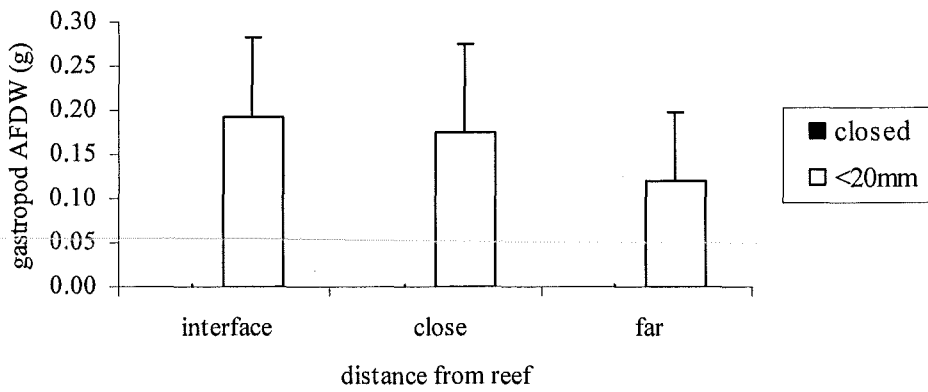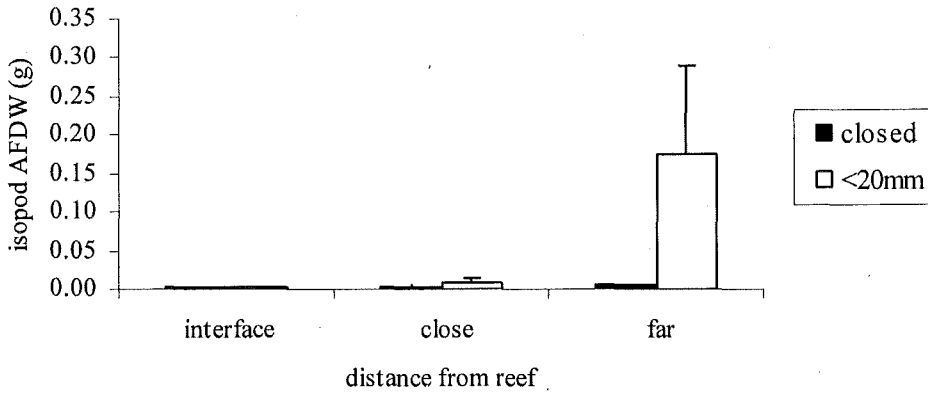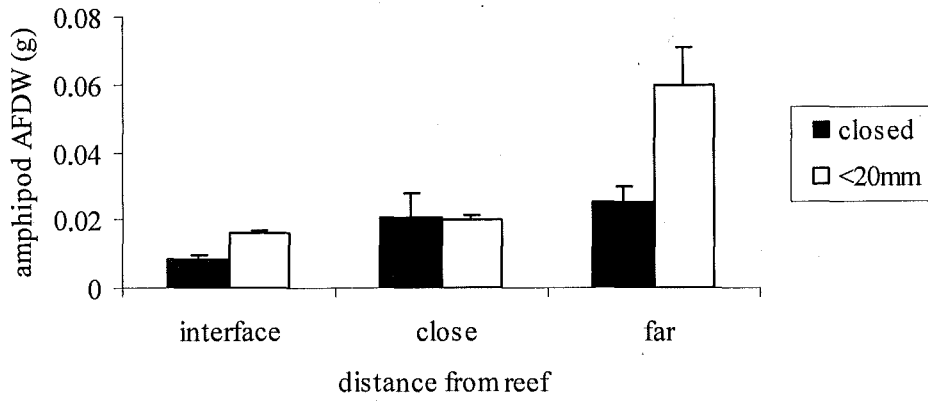
Site: Wanneroo Reef
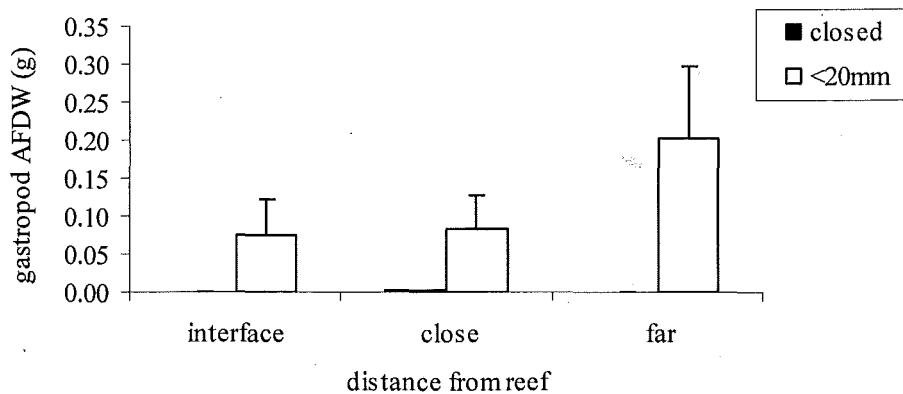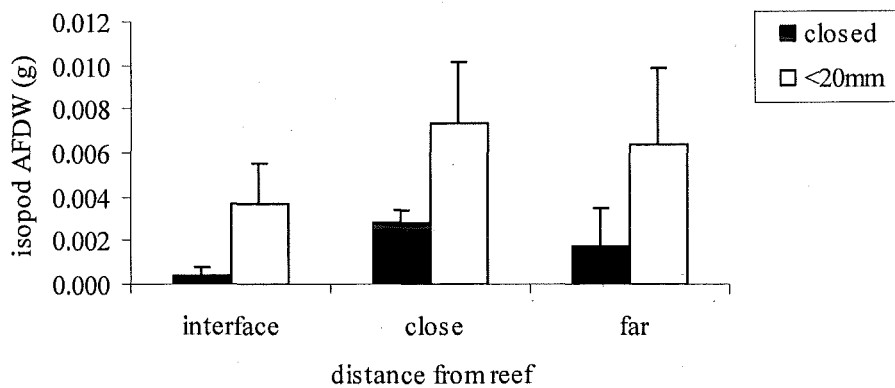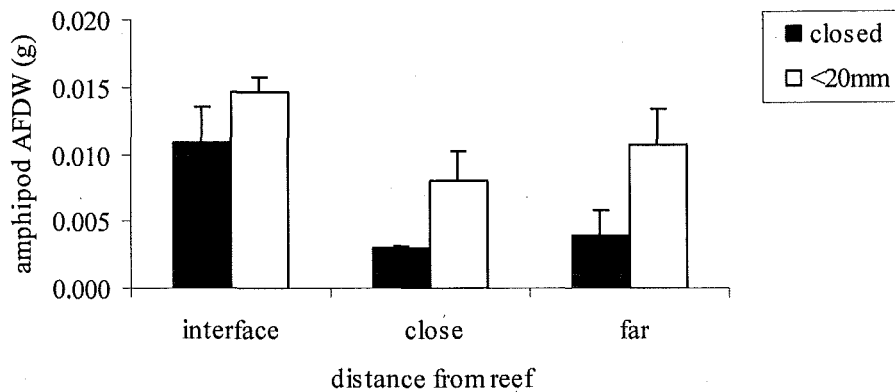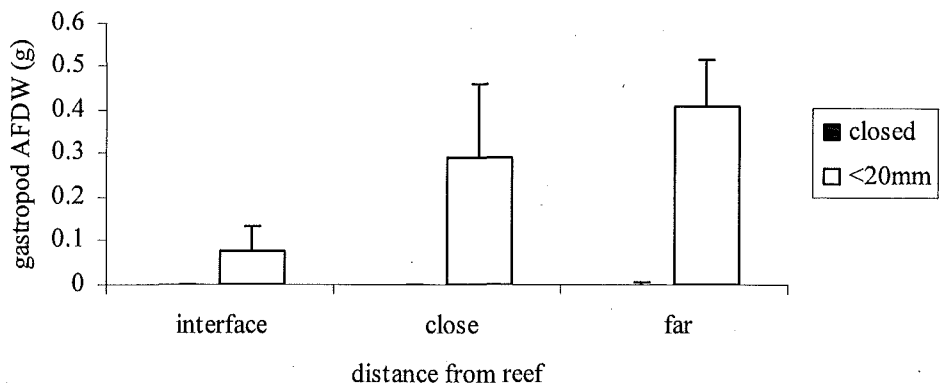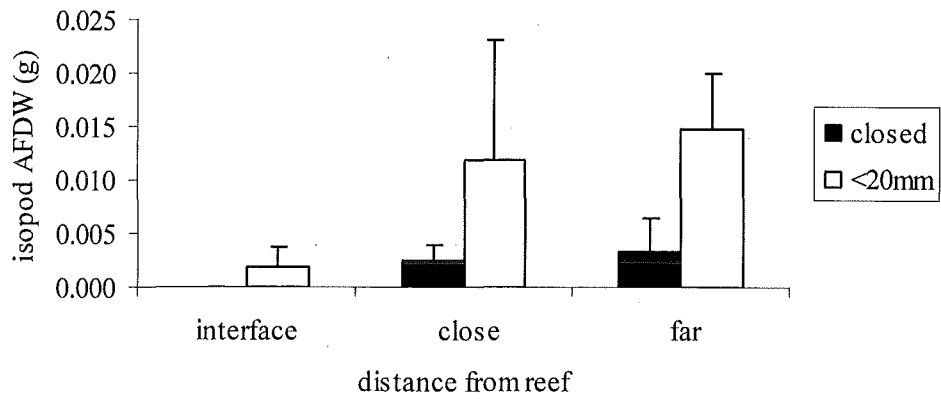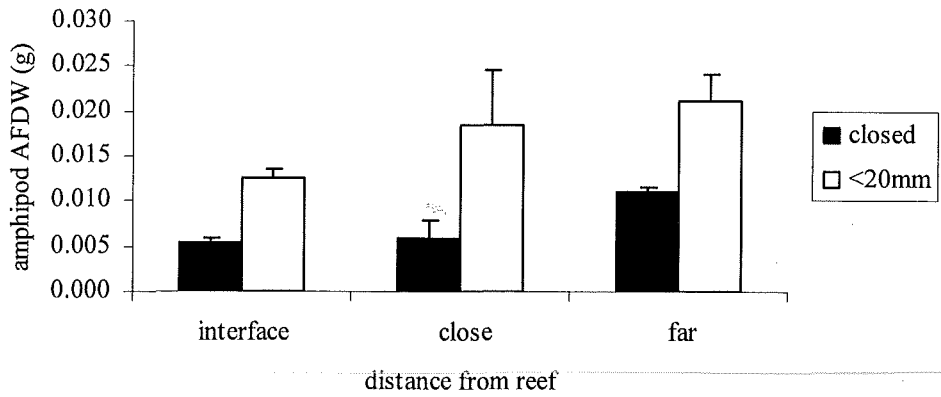
Site: Whitfords Rock NE

Site: Wreck Rock

76