Kramer, Michael John (2015) ***Crustacea on coral reefs: habitat associations and trophic relationships*****. PhD thesis, James Cook University.**

Crustacea on coral reefs: habitat associations and trophic relationships

Thesis submitted by

Michael John Kramer

***BSc (Hons.)* James Cook University**

in November 2015

for the degree of Doctor of Philosophy in Marine Biology and Ecology
within the College of Marine and Environmental Sciences and
the ARC Centre of Excellence for Coral Reef Studies
James Cook University, Townsville, Queensland, Australia

Statement on the Contribution of Others

In conducting the projects within this thesis I collaborated with my supervisors, Prof. David Bellwood and Dr. Orpha Bellwood. I also worked with Dr. Christopher Fulton (Chapter 5) and Dr. Richard Taylor (Chapter 4). In these collaborations I was responsible for the conception of the project, data collection (except for Chapter 5), analysis and interpretation of data. My co-authors provided technical assistance, intellectual guidance, editorial assistance and financial support. Dr. Richard Taylor also gave field support at Leigh Marine Laboratory for Chapter 4, and Prof. David Bellwood and Dr. Christopher Fulton collected and provided the wrasse gut content data for Chapter 5.

Financial support was provided by the Australian Research Council (D. Bellwood), the ARC Centre of Excellence for Coral Reef Studies (D. Bellwood) and James Cook University Graduate Research Scheme. Stipend support was provided by an Australian Postgraduate Award Scholarship and James Cook University Tuition Fee Waiver.

Research procedures reported in this thesis were approved by the James Cook University Animal Ethics Committee (projects numbers: A650 and A2013).

Acknowledgements

To my supervisors, David and Orpha Bellwood, thank you for your excellent guidance during my years of postgraduate research at JCU. Your encouragement, enthusiasm and reminders to look at the bigger picture are greatly appreciated. I have learnt a great deal about the many facets of research and teaching from you, for this I am very grateful.

I have had some wonderful volunteers join me in this endeavour. Thank you to Simon Brandl, Chris Mirbach, Justin Rizzari, Arie Spyksma, Timo Staeudle, Tara Stephens, Richard Taylor and Justin Welsh for giving your time to help me collect and process samples, and occasionally encouraging me to have some non-research fun while at amazing field locations. Thank you to Mum and Dad, Christopher Heckathorn, Dominik Schmid and Jessica Tengvall for helping me make the data collection process more efficient.

Several staff members at James Cook University and Lizard Island Research Station have been very helpful in aiding various aspects of my projects, including obtaining field supplies, technical support and organising field paperwork. For their excellent support I thank Gordon Bailey, Debbie Berry, Glenn Ewels, Anne Hoggett, Stratis Manolis, Andrew Norton, Phil Osmond, Lyle Vail and Tammy Walsh.

To those that have taught the next generation of young biologists with me, thank you for creating many lightbulb moments for me and for the students. I would especially like to thank John Collins, Hannah Epstein, Katharine Darlington, Marnie Freckelton, Lindsay Harrington, Jessica Hopf, Mike Kingsford, Oona Lonnstedt, Janine Sheaves, Jessica Stella, Tiffany Sih and Muhammad Abdul Wahab for your inspirational enthusiasm for marine organisms (particularly the invertebrates) and the philosophical conversations.

I have had the privilege to work alongside some outstanding scientists while being a part of the Bellwood Lab. To Roberta Bonaldo, Simon Brandl, Peter and Jenn Cowman, Christopher Goatley, Sophie Gordon, Christopher Heckathorn, Jennifer Hodge, Andrew Hoey, Charlotte Johansson, James Kerry, Joanna Khan, Carine Lefèvre, Zoe Loffler, Robert Streit, Sterling Tebbett, Justin Welsh and Matthew Young, thank you for the discussions, comments on manuscripts, statistical advice, or simply being inspirational.

Finally, thank you to Mum, Dad and Kim for the love and support during my time in Townsville and encouraging me to step out of my comfort zone. It's been a long journey and I'm looking forward to spending less time on Skype and more time together.

Abstract

Crustaceans are one of the most widespread and speciose marine groups, performing key ecological roles to many ecosystems. On coral reefs they are part of one of the most diverse and complex ecosystems on Earth. It would be reasonable to expect that crustaceans are important coral reef organisms, yet the body of work concerning coral reef crustaceans pales in comparison to other popular groups, such as fishes and corals. To rectify this, I investigated the importance of crustaceans as a component of the coral reef faunal assemblage, quantifying their distribution and abundance across a range of reef microhabitats, comparing the tropical assemblage to the better-understood temperate assemblage, and examining the role of reef Crustacea as a dietary resource for fishes.

To determine the community structure, abundance, biomass and productivity of benthic Crustacea on a typical coral reef, I investigated 5 major microhabitats: dead coral, coral rubble, sand, epilithic algal matrix (EAM) and fine-branching live coral at Lizard Island, a mid-shelf reef on the Great Barrier Reef, Australia (**Chapter 2**). Crustacean communities differed significantly among habitats. Dead coral was by far the most important microhabitat type in terms of crustacean abundance (7838 ± 628 ind. 100 cm^{-2}, mean ± SE), biomass (0.75 ± 0.13 g m^{-2}, wet weight) and estimated productivity (0.92 ± 0.13 g 100 cm^{-2} yr^{-1} ash-free dry weight). These values were 2 to 3 orders of magnitude greater than those for the least important habitats (EAM and fine-branching live coral). The average crustacean body length was just 0.79 ± 0.32 mm, largely due to the dominance of relatively small harpacticoid copepods. In contrast, decapods exhibited very low abundances, but yielded the greatest biomass and productivity and were particularly abundant in dead coral and coral rubble. The results highlighted the importance of small crustaceans and dead coral microhabitats as valuable contributors to the trophic structure of coral reefs.

Although it is well established that fish, coral and algal assemblages vary across large spatial scales, very little is known of the differences in crustacean assemblages across similar scales. To determine whether crustaceans had similar spatial patterns to other reef organisms, I investigated the EAM cryptofaunal community, dominated by Crustacea, at three locations on the Great Barrier Reef: two inner shelf locations - Orpheus Island and the Turtle Island group - and a mid-shelf location, Lizard Island (**Chapter 3**). Although the EAM appears to be a relatively simple and consistent habitat, significant differences in cryptofaunal assemblages were found between locations. EAM assemblages from Orpheus Island were markedly different to those from the Turtle Island group and Lizard Island. This appears to be a function of the sediment profile (grain size >60 μm) at

Orpheus Island, as many cryptofaunal taxa displayed a positive relationship with sediment volume. However, sediment volumes did not differ significantly between the three locations, highlighting the possibility of cyclonic activity affecting the sediment profile at Orpheus Island in the months preceding the study, in addition to the nutrient input from major terrigenous sources. The results show that EAM cryptofaunal assemblages are not uniform across the Great Barrier Reef and suggest that dissolved nutrients, sediment loads and distance from river systems may be significant drivers of cryptobenthic faunal compositions.

Tropical and temperate marine habitats have long been recognised as fundamentally different systems; yet, comparative studies are rare, particularly for small organisms such as Crustacea. I investigated the ecological attributes (abundance, biomass and productivity) of benthic Crustacea in selected microhabitats from a tropical and a temperate location, revealing marked differences in the structure of crustacean assemblages (**Chapter 4**). In general, microhabitats from the tropical location (dead coral, the EAM and sand) supported high abundances of small individuals (mean size = 0.53 mm vs. 0.96 mm in temperate microhabitats), whilst temperate microhabitats (the brown seaweed *Carpophyllum* sp., coralline turf and sand) had substantially greater biomasses of crustaceans and higher estimated productivity rates. In both locations, the most important microhabitats for crustaceans (per unit area) were complex structures: tropical dead coral and temperate *Carpophyllum* sp.. It appears that the differences between microhabitats are largely driven by the size and abundance of key crustacean groups. Temperate microhabitats have a higher proportion of relatively large Peracarida (Amphipoda and Isopoda), whereas tropical microhabitats are dominated by small detrital and microalgal feeding crustaceans (i.e. harpacticoid copepods and ostracods). These differences indicate the vulnerability of tropical systems, especially to the loss of complex benthic structures and the associated crustacean assemblages as a result of habitat degradation.

Crustaceans are one of the most influential groups in aquatic trophic networks by providing a major connection between primary production and higher consumers. Although coral reefs support a high diversity and abundance of crustaceans, and crustacean predators, their trophic interrelationships remain unclear. Using predator gut content analyses, I investigated trophic relationships between Crustacea and adult fishes of the family Labridae, which are one of the most abundant and diverse families of marine crustacean predators (**Chapter 5**). Crustaceans were present within the guts of 93 % of the 30 wrasse genera investigated. I found a distinct division between micro- and macro-crustacean predators: wrasses <80 mm standard length (SL) were predominantly micro-crustacean feeders, while wrasses >90 mm SL displayed a predominantly macro-

crustacean diet. Notably, micro-crustacean predators tended to specialise on certain crustacean taxa, whereas macro-crustacean predators consumed mostly brachyurans. My findings highlight complex patterns of feeding diversity within crustacean predators that prompt a more detail-oriented approach to defining the role of crustacean-feeding fishes in coral reef trophodynamics.

Having established Crustacea as an important component in coral reef ecosystems, occupying a broad range of coral reef microhabitats, with the greatest biomass in dead coral and coral rubble, I investigated the relationship between foraging in wrasses and the major reef microhabitats occupied by Crustacea (**Chapter 6**). Although the greatest biomass of crustaceans is in dead coral and coral rubble, crustacean-feeding wrasses displayed strong selection for a broader range of microhabitats. Of the 14 macro-crustacean predators, only 6 selectively foraged in dead coral or coral rubble. The 10 micro-crustacean predators likewise displayed a wide range of microhabitat foraging associations, reflecting specific prey type preferences. The relationships between crustacean predators and their prey appear to be more complicated than previously assumed, and may be mediated by other morphological and behavioural factors.

This thesis represents an important contribution to the relatively new, emerging field of coral reef crustacean ecology. By establishing key baseline information about the contribution of crustaceans to the overall coral reef faunal assemblage, I have confirmed the long-held assumptions that crustaceans are highly abundant and potentially very important on coral reefs. However, crustacean assemblages differ considerably across large spatial scales due to local environmental factors. I also present the first tropical-temperate comparison of crustaceans within comparable microhabitats, which has given a new perspective on the trophic functioning of each ecosystem. Importantly, crustaceans are a major component of the diet of coral reef fishes; wrasses are a key example and provide evidence for a trophic division within crustacean-feeding taxa. However, the relationship between crustaceans and their fish predators appears to be complex, mediated by various factors including microhabitat, fish morphology and behaviour. Crustaceans have often been perceived as a group of organisms that are simply 'present' on coral reefs, yet this thesis demonstrates that their importance in reef trophodynamics cannot be underestimated. Crustacea have a pivotal role in coral reef ecology.

Table of Contents

List of Figures

List of Tables

General Introduction

Crustaceans are one of the most familiar and recognisable groups of organisms in aquatic ecosystems. Although they are found throughout the world in terrestrial and freshwater habitats, it is the marine environment in which they are most diverse and widespread, with over 42,000 species in habitats ranging from the upper pelagic to deep oceanic trenches, from the poles to the equator (Martin & Davis 2001, Ruppert et al. 2004). The extensive evolutionary history of crustaceans, dating back to at least the Cambrian (Walossek 1995, Wills et al. 1997), has likely contributed to their success in exploiting almost all known habitats (Martin & Davis 2001). In addition to their widespread distribution, crustaceans also have the greatest variation in size and morphological diversity of the metazoans, ranging from 94 μm (the tantulocarid *Stygotantulus stocki;* Boxshall & Huys 1989) to approximately 4 m in the giant Japanese spider crab, *Macrocheira kaempferi* (Martin & Davis 2001, Ruppert et al. 2004). Crustaceans perform an astounding variety of ecological functions. However, it is likely that their role as a link in trophic pathways may be the most influential in marine ecosystems. In this thesis I intend to bring to light a different ecological perspective of crustaceans on coral reefs, focussing on their habitat associations and their role in coral reef trophodynamics.

1.1 Trophic importance of coral reef crustaceans

Coral reefs support some of the highest abundances and greatest diversity of animal life on the planet (Connell 1978, Reaka-Kudla 1997). As such, it can be expected that crustaceans on coral reefs are a major faunal component that serve a range of ecological roles. Indeed, coral reef crustaceans are known to scavenge dead organisms (Kensley 1998), parasitise fishes (Grutter 1999), remove parasites from fishes (Becker & Grutter 2004), defend coral colonies (Pratchett 2001) and form symbiotic relationships with other phyla (Spotte 1996, Stewart et al. 2006, Karplus & Thompson 2011). Many of these well-documented roles are performed by member of the Orders Decapoda and Isopoda, which represent only a small proportion of the overall crustacean assemblage on a coral reef (approximately 10 % of Orders). A multitude of other crustacean taxa (e.g. Amphipoda, Harpacticoida and Tanaidacea) are also present on coral reefs, though they are often difficult to observe due to their small size and cryptic nature (Klumpp et al. 1988, Takada et al. 2008, Glynn & Enochs 2011). Because of the challenges associated with detecting small crustaceans, knowledge of their habitat associations on coral reefs has often been overlooked and their roles are poorly understood.

Few researchers have investigated the abundance of crustaceans on coral reefs. The information that is known, however, indicates that they are present in surprisingly high numbers on dead substrata (Klumpp et al. 1988, Takada et al. 2008, Enochs 2012) but in relatively low numbers on live coral (Abele & Patton 1976, Stella et al. 2010). However, this information is restricted to a few individual habitats (i.e. turf, live coral, dead coral and coral rubble) from different biogeographical regions. It is not completely clear what microhabitat within a coral reef ecosystem supports the greatest number of crustaceans. Previous studies from the Great Barrier Reef indicate that the abundance of crustaceans may range from approximately 200-600 individuals 100 cm^{-2} in dead coral (Klumpp et al. 1988), ~300 individuals 100 cm^{-2} in algal turfs (Zeller 1988), ~600 individuals 100 cm^{-2} in sand/coral rubble (Logan et al. 2008), to ~2-6 individuals 100 cm^{-2} in live branching coral (Stella et al. 2010). These assemblages are consistently dominated by amphipods, copepods, isopods and tanaids, whereas symbiotic decapods are characteristic of live coral. Despite the knowledge that crustaceans are generally abundant on a coral reef, no study has compared specific microhabitats on a coral reef to identify how crustacean communities differ within a reef.

In comparison to abundance studies, biomass and productivity estimates are likely to provide better indices of the relative ecological contribution that crustaceans offer to higher trophic levels within the coral reef ecosystem. However, there is very little information about crustacean biomass and even less about productivity within coral reef microhabitats on the GBR. The only known estimates are approximately 5-10 mg ash-free dry weight 100 cm^{-2} in dead coral (Klumpp et al. 1988) and ~2 mg Carbon 100 cm^{-2} in lagoonal sands (Riddle et al. 1990). Biomass data on crustaceans from other locations such as Panama (Enochs 2012) provide a point of comparison, however, these coral reefs are biogeographically separated from the GBR and likely differ in terms of benthic habitat structure. Notably, research from the Eastern Pacific suggests that invertebrates living within the coral reef matrix, including molluscs, annelids and crustaceans, may exceed the biomass of fishes within the same area of reef (Ginsburg 1983, Enochs 2012). It is possible that the biomass and productivity of crustaceans from the GBR ecosystem are equally as important. However, this remains to be determined.

Although investigations of coral reef crustaceans are extensive, studies of crustaceans from temperate systems are focussed more on their trophic ecology. Small crustaceans are characteristic of the epifauna of macroalgae (Taylor & Cole 1994) and may act as important herbivores, capable of controlling benthic algal assemblages (Duffy & Hay 2000, Berthelsen & Taylor 2014). Importantly, the biomass and productivity of crustaceans and other invertebrates has been estimated in temperate habitats (e.g. Taylor

1998, Cowles et al. 2009). As a result, crustaceans have been identified as key contributors to temperate ecosystems, particularly in terms of their trophic importance (Taylor 1998, Cowles et al. 2009). Tropical studies indicate that this importance is equally applicable to coral reef systems, although comprehensive investigations are less common (Brawley & Adley 1981, Glynn & Enochs 2011, Roff et al. 2013).

1.2 Crustaceans and fishes: trophic relationships

It is well understood that ecological communities are constructed through a network of interacting species. The movement of energy through an ecosystem commonly follows a simple pathway from primary producers to primary consumers and on to higher trophic levels (Lindeman 1942, Post 2002). In many marine and freshwater ecosystems, crustaceans play a critical link between the primary producers (i.e. algae and microbes) and higher consumers (Klumpp et al. 1989, Edgar & Shaw 1995b, Taylor 1998, Duffy et al. 2001, Shurin et al. 2006). Interestingly, the production of mesograzing crustaceans has been suggested to be the most reliable predictor of production by higher trophic levels in seagrass systems (Edgar & Shaw 1995b).

On coral reefs, the linear food chain concept becomes a highly complex web of interactions with many species consuming markedly different prey types (Kingsford 1992, Choat et al. 2002, Marnane & Bellwood 2002, Bellwood et al. 2006b) and, in some cases, bypassing whole trophic levels (Bellwood et al. 2014). Although there is pronounced variation in the trophic status of coral reef consumers (e.g. herbivores, detritivores, invertivores and piscivores), studies of fish diets have consistently identified crustaceans as a dominant prey item (Randall 1967, Hobson 1974, Williams & Hatcher 1983, Randall et al. 1997). While crustaceans display a remarkable diversity of sizes, forms and ecological roles, the exact relationship between specific crustaceans and their predators is sorely lacking (but see Randall 1967, Hobson 1974). Possibly the most influential role of crustaceans is their contribution to providing a trophic link between primary producers and higher consumers (Edgar & Shaw 1995b, Ruppert et al. 2004). However, their importance in this role on coral reefs is fragmented and requires much development.

1.3 Aims

The main goal of this thesis is to investigate the distribution and ecological aspects of crustaceans on coral reefs, particularly focussing on habitat associations and the trophic importance for higher consumers. While there is a general understanding that crustaceans are important contributors to the basic functioning of a variety of ecosystems, this information for coral reefs is largely unexplored and requires a great deal of development.

Crustaceans have the potential to be a significant influence on the overall trophic structure of a coral reef assemblage, yet the magnitude of this impact is not known. To address this knowledge gap, I ask a series of questions corresponding to each of my five data chapters. Firstly, *where are the crustaceans on coral reefs*? **Chapter 2** answers this by investigating the abundance, biomass and productivity of crustaceans in different coral reef microhabitats: live branching coral, dead coral, coral rubble, sand and the epilithic algal matrix (EAM). Following this foundational work, **Chapter 3** asks: *how do crustacean assemblages differ across large spatial scales*? This chapter focuses on the crustacean fauna of the EAM from three locations on the Great Barrier Reef. **Chapter 4** extends this spatial scale even further, addressing *how crustacean assemblages differ between tropical and temperate systems*? This chapter compares major differences in the abundance, biomass and productivity of crustacean fauna within similar structural microhabitats from Lizard Island on the GBR and the temperate rocky reef adjacent to the Leigh Marine Laboratory in New Zealand. **Chapter 5** investigates the trophic importance of crustaceans, asking: *what is the nature of crustaceans in the diet of wrasses (Labridae) on coral reefs*? Finally, in **Chapter 6**, I examine the relationship between crustaceans, the microhabitats they occupy and predatory wrasses, asking the question: *does the abundance and biomass of crustaceans influence the foraging patterns of coral reef fishes*? By examining the broad ecological role of crustaceans on coral reefs, this thesis provides answers to questions that have long been overlooked and will begin to reveal the potential importance of these diverse and intriguing organisms.

Chapter 2: Where are the benthic Crustacea on coral reefs? A quantitative survey

Published as: Kramer MJ, Bellwood DR & Bellwood O (2014) *Marine Ecology Progress Series* 511: 105-116

2.1 Introduction

Coral reefs are complex ecosystems that support a great abundance and high biomass of organisms (Ackerman & Bellwood 2000, Stella et al. 2011b, Enochs 2012). Motile invertebrates are particularly well represented, with an estimated 168,000 species described on coral reefs (Ruppert et al. 2004, Stella et al. 2011b), far surpassing the number of fish species (~5,000 species; (Bellwood et al. 2012b). Despite their abundance and diversity, however, the great majority of coral reef invertebrates are easily overlooked, as they are either small or hide within the complex structure of the reef framework (Ginsburg 1983, Enochs 2012).

Crustaceans are one of the most speciose groups on coral reefs, comprising approximately 20 % of all invertebrate species (Plaisance et al. 2011, Stella et al. 2011b). Studies that have investigated coral reef crustaceans often examined the relatively conspicuous taxa found in live corals (e.g. Abele 1976, Patton 1994, Stella et al. 2010) or those associated with fishes (Spotte 1998, Becker & Grutter 2004, Karplus & Thompson 2011). These crustaceans are almost exclusively members of the order Decapoda, which are often observed due to their relatively large size, bright colours and symbiotic relationships with fishes and corals. In addition, decapods are potentially important contributors to coral reef health, performing roles such as defending live coral from predators (Pratchett 2001) or removing parasites from fishes (Becker & Grutter 2004). Yet there are many other lesser-known crustacean taxa, such as Amphipoda, Cumacea, Cyclopoida, Harpacticoida, Isopoda, Ostracoda and Tanaidacea, which are also reported to perform important ecological roles (Klumpp et al. 1988, Preston & Doherty 1994, Takada et al. 2008, Kramer et al. 2012). Their roles in the food chain and as major prey items are particularly well documented (Edgar & Shaw 1995a, Keable 1995, Glynn & Enochs 2011, Kramer et al. 2013).

On coral reefs, crustaceans occur across all microhabitats (Ruppert et al. 2004). While decapods are known to associate with live corals (Abele & Patton 1976, Patton 1994, Stella et al. 2011b), other crustaceans are also a major faunal component of the invertebrate communities in dead coral (Klumpp et al. 1988, Preston & Doherty 1994), coral rubble (Takada et al. 2008, Enochs & Manzello 2012b), the epilithic algal matrix

(EAM; Kramer et al. 2012) and sand (Jacoby & Greenwood 1988, Danovaro & Fraschetti 2002). Despite these studies, however, there is no comprehensive overview or comparison of crustacean assemblages, abundance or biomass among coral reef microhabitats.

Crustaceans have also been suggested to be important contributors to the productivity of reefs (Edgar et al. 1994, Cowles et al. 2009). Productivity appears to be a valuable, but often overlooked, aspect of a species' role in ecosystems (Edgar & Moore 1986, Taylor 1998, Cowles et al. 2009). Estimates of productivity provide information on the relative importance of organisms as producers of organic matter for higher trophic levels (Taylor 1998). An assessment of productivity of crustaceans within various coral reef microhabitats therefore will provide a better understanding of the trophic value of Crustacea and the importance of various microhabitats in coral reef ecosystems. To date, there have been no among-habitat comparisons of crustacean productivity on coral reefs.

The overarching aim of the present study, therefore, is to provide a comprehensive overview of the community composition, abundance, biomass and productivity of crustaceans across five major benthic microhabitats (dead coral, coral rubble, sand, EAM and fine-branching live coral) on a mid-shelf coral reef of the Great Barrier Reef. The results of this study will be used to evaluate the trophic importance of crustaceans and their respective microhabitats in coral reef processes.

2.2 Methods

Study location

Samples were collected in February 2013 from Lizard Island (14° 40'40"S, 145° 26' 55"E), a mid-shelf island located in the northern Great Barrier Reef, Australia. Three sites were haphazardly selected at two semi-sheltered sampling locations (Mermaid Cove and Lagoon Entrance). The reef at each location was a typical fringing reef with a reef flat, crest, and gentle slope that reached a sandy base at approximately six metres. The chosen microhabitats (which collectively covered more than 80 % of the substratum at the selected sites) consisted of dead coral, coral rubble, EAM, sand and fine-branching live coral. Before sampling, sites were inspected to ensure that all five microhabitats were present. Samples were collected from the crest region in an area that extended no more than 5 m onto the flat or down the slope. Within each site, three replicate samples from each microhabitat were collected from as close to the crest as possible, yielding a total of 18 samples of each of the five microhabitats (90 samples overall). All samples were fixed in 4 % formaldehyde in seawater within 20 min of collection.

Microhabitat description and sample collection

Dead coral was defined as structurally intact branching coral skeletons devoid of live coral tissue but still attached to the main reef matrix. All dead coral samples were taken from *Acropora* sp. skeletons (predominantly *A. nasuta* or those of similar morphology). Dead coral protrusions (planar area: 68.0 ± 1.8 cm^2 mean ± SE, n = 18) were surrounded by a plastic bag, removed using a hammer and chisel and placed into a sampling jar, taking care to minimise loss of organisms. All samples were of a similar volume (127 ± 5 mL mean ± S.E. displacement volume, n = 18) and complexity. All dead coral samples were measured using ImageJ (see detailed description in 'Laboratory processes').

Coral rubble was defined as a loose accumulation of dead coral fragments. Due to the complex and uneven nature of coral rubble, sampling is inherently difficult. To overcome this problem, sampling was conducted by constructing wire baskets of 100 cm^2 planar surface area and 5 cm depth, which held 203.7 ± 4.7 mL (displacement volume, mean ± SE, n = 18) of coral rubble. The baskets were filled with coral rubble taken directly from a rubble field at each site and immediately placed into the depression from where the rubble was removed. Baskets were left in the site for six days to allow disturbed motile organisms to return to the coral rubble within the basket (following (Takada et al. 2007). After this re-establishment period, the basket was carefully lifted and placed into a plastic bag in a manner that prevented loss of organisms.

Sandy microhabitats were located at the base of the reef (5 m depth). Samples were collected by taking a 1 cm deep core with a 51 mm diameter corer, yielding 20.4 cm^3 of sand. The core sample was transferred into a labelled plastic bag and fixed. A 1 cm depth incorporates most sediment infauna (Coull 1970) and samples the substratum most likely to be encountered by other reef organisms (e.g. fishes).

Samples of EAM were collected from exposed, horizontal areas of EAM (following Kramer et al. 2012). Using an underwater vacuum sampler, an area of 20.4 cm^2 (defined by a plastic ring) was vacuumed for 30 seconds (Figure 2.1). Material within the sampling area was drawn into the apparatus and retained by a 60 μm filter mesh bag that was sealed underwater, placed into a labelled sample jar and fixed.

Fine-branching live coral was sampled following Stella et al. (2010). *Acropora* sp. (small corymbose form) was selected for sampling because of its abundance in the study area. Individual colonies of *Acropora* sp. were surrounded by a plastic bag to prevent resident fauna escaping, and carefully chiseled off the reef. Colonies were then transported to a boat, removed from the bag and submerged into a bucket of freshwater for one minute to extract all organisms. Care was taken to avoid immersing the dead coral (and the associated EAM) at the base of the colony. After one minute in freshwater, the coral was removed and placed into a bucket of saltwater, where it was inspected for organisms that remained within the coral. The few individuals that were detected were removed and placed into the freshwater bucket. The contents of the freshwater bucket and the collection bag were filtered through a 60 µm mesh bag and fixed. All sampled corals were approximately the same height and planar area to standardise for differences in the volume of the colony. Volumes were measured in the field using the displacement method, averaging 461 ± 22 mL (mean ± SE, n = 18) per sample. A photograph of the coral with a scale was taken to calculate the planar surface area using ImageJ (242 ±10 cm^2, mean ± SE, n = 18).

Figure 2.1 Sampling the epilithic algal matrix with a vacuum apparatus. Image credit: Robert Streit

Benthic composition

To measure the percentage benthic cover of each major microhabitat, photo transects were conducted prior to sampling. A 20 m transect tape was laid along the reef profile (i.e. from slope to outer flat). At 2 m intervals along the tape, a 1 x 1 m quadrat was placed over the reef and a photograph taken from above. Five replicate transects were conducted within each of the three sites selected for microhabitat sampling. Live coral was divided into two categories: fine-branching live coral (colonies with fine-scale complexity such as *Acropora nasuta*) and other coral (colonies with large-scale complexity, for example, massive *Porites* sp. and open branching *Acropora formosa*). The planar area of each microhabitat type was quantified from each image using ImageJ.

Laboratory processes

Dead coral and coral rubble samples were agitated within the sample jars to dislodge dead organisms from the coral skeleton. The coral skeleton was then removed from the jar and placed into a second empty vessel. The dislodged organisms in the original sample jar were poured through a 60 µm filter and retained. This washing process was repeated three times (a pilot study revealed that three washes obtained over 98 % of the organisms from the coral skeleton). Washed dead coral skeletons were then photographed with a scale to quantify the planar surface area using ImageJ.

Samples that contained large numbers of organisms or inorganic matter (i.e. dead coral, coral rubble and sand) were subsampled using the Huntsman Marine Laboratory (HML) beaker technique (van Guelpen et al. 1982). Samples were stained with eosin erythrosin and washed onto a petri dish for investigation under 40 x magnification. A grid on the base of the petri dish was followed, to avoid counting the same organism twice. Organisms were identified to the lowest practical taxonomic level (usually Order) and counted. Because of the potential loss of very small individuals (< 60 µm) from some habitats, copepod nauplii were not included in the analysis.

Data analysis

Abundances

Data from all microhabitats were standardised to 100 cm^2 before analysis. A total of 15 taxonomic units were used, 8 of which were Crustacea (Amphipoda, Cumacea, Cyclopoida, Decapoda, Harpacticoida, Isopoda, Ostracoda and Tanaidacea; details in Appendix A, Table A1). Differences in community structure between each microhabitat were investigated using a non-metric multidimensional scaling (nMDS) analysis of proportional data on a Manhattan distance matrix. The nMDS ordination and associated taxa contribution plots were constructed using the R package *vegan* (Oksanen et al. 2007). A permutational multivariate analysis of variance (PERMANOVA) was conducted in Primer 6 to test for differences between location, site and microhabitat. Pairwise comparisons, using the PERMANOVA extension in Primer 6, were used to investigate differences in assemblages between specific microhabitats.

Biomass

Wet-weight biomass of the various taxonomic groups was calculated by estimating the volumes of the first 100 organisms observed of each major crustacean taxon (Amphipoda, Cumacea, Cyclopoida, Decapoda, Harpacticoida, Isopoda, Ostracoda and Tanaidacea) following similar methods to Lawrence et al. (1987), who validated this method in micro-Crustacea (Copepoda). Decapoda within dead coral, coral rubble and fine-branching live coral varied in size, thus were grouped into their respective microhabitats for biomass estimates (ESM Table S2). Volume estimates were based on the resemblance of the taxa to simple geometric shapes (i.e. a cylinder [Amphipoda, some Decapoda, Harpacticoida and Tanaidacea], cone [Cumacea and Cyclopoida] or cuboid [some Decapoda, Isopoda and Ostracoda]). Individuals were measured for length and width (cylinder and cone) or length, width and depth (box) using an ocular micrometer in 25 μm increments. For decapod crabs, only the carapace was measured, assuming that the pereopods (which were often no longer attached) would supplement the areas of the hypothetical box that the carapace did not fill. Biomass per unit volume was estimated using the Harpacticoida, for which the volume to biomass relationship is known (Kramer et al. 2012), as a standard. To calculate the mean abundance, biomass and productivity of crustaceans within a square metre of an average semi-sheltered reef, the respective values for each crustacean taxon within each of the five microhabitats was multiplied by the mean (± 95 % CI) proportional coverage of the respective microhabitat and summed.

Productivity

Productivity of the five microhabitats was estimated based on the general allometric equation of (Edgar 1990), following McLeod et al. (2013), where $P = 0.0049 * B^{0.80}T^{0.89}$, such that P = productivity in micrograms of ash-free dry weight (AFDW) per unit area per day (μg AFDW 100cm^{-2} day^{-1}), B = biomass of an individual taxa in the microhabitat (μg AFDW 100cm^{-2}), and T = water temperature at the time of sampling, which was 29.5 °C. Productivity estimates of individual taxa from each microhabitat were then multiplied by abundance to give a total productivity estimate. Wet weight biomass estimates were converted to AFDW using published conversion factors (Ricciardi & Bourget 1998). Lizard Island Research Station sensors measured water temperature at the time of collection.

2.3 Results

Community composition

The PERMANOVA comparing the cryptofaunal assemblages found no significant differences between the factors location or site, therefore data were pooled for the remainder of the analyses. However, there was a significant difference among microhabitats ($p < 0.001$) (Appendix A, Figure A1). To account for the marked difference between fine-branching live coral and the remaining microhabitats, a second analysis was conducted, excluding fine-branching live coral. After the removal of fine-branching live coral, the significant microhabitat effect remained ($p < 0.001$) (Appendix A, Figure A2). The pairwise comparisons found no significant difference between the cryptofaunal assemblages in dead coral and coral rubble. All other pairwise comparisons were significantly different ($p < 0.01$) (Appendix A, Figure A2).

Although other invertebrates such as Polychaeta and Gastropoda were recorded and included in initial data analyses (see Appendix A, Figures A1, A2), groupings of microhabitats within ordination space were largely driven by crustacean taxa and the statistical tests based on all invertebrates were very similar to those based just on crustacean assemblages (Appendix A, Figures A1, A2, A3).

The relative contributions of each crustacean taxon to microhabitat ordinations indicated that decapods were strongly correlated with fine-branching live coral (Appendix A, Figure A3) whereas harpacticoid copepods were correlated with EAM microhabitats (Figure 2.1). Sand microhabitats displayed assemblages dominanted by the Harpacticoida and to some extent, Ostracoda and Cumacea (Figure 2.1). Dead coral and coral rubble were characterised by numerous crustacean taxa, including Amphipoda, Cumacea, Decapoda, Isopoda and Tanaidacea (Figure 2.2).

Crustacean abundance, biomass and productivity across microhabitats

Dead coral yielded the greatest numbers of crustaceans (7838 ± 662 individuals 100 cm^{-2}, mean ± S.E.), closely followed by coral rubble (6797 ± 448 ind. 100 cm^{-2}) (Figure 2.3a). In stark contrast, fine-branching live coral contained three orders of magnitude fewer Crustacea than dead coral with just 6 ± 1 ind. 100 cm^{-2} (Figure 2.3a). It is interesting to note, however, that these abundances are dominated by small harpacticoid copepods.

Biomass estimates may give a clearer view of the relative importance of the various microhabitats. Dead coral supported the greatest estimated wet-weight biomass of crustaceans (Figure 2.3b). Noticeably, the total biomass of crustaceans in dead coral (0.75 ± 0.13 g 100 cm^{-2}) was three times greater than the biomass in fine-branching live coral (0.24 ± 0.034 g 100 cm^{-2}) and 150 times greater than the EAM (0.005 ± 0.0006 g 100 cm^{-2}).

These patterns were mirrored in the productivity estimates. Dead coral was the most productive microhabitat, producing an estimated 0.92 ± 0.13 g AFDW 100 cm^{-2} $year^{-1}$, 28 times greater than the least productive microhabitat, the EAM (0.032 ± 0.004 g AFDW 100 cm^{-2} $year^{-1}$) (Figure 2.3c). Coral rubble and fine-branching live coral also had markedly different productivity values (0.55 ± 0.07 g AFDW 100 cm^{-2} $year^{-1}$ and 0.18 ± 0.03 g AFDW 100 cm^{-2} $year^{-1}$, respectively), whereas all other microhabitats (i.e. sand and the EAM) displayed values less than 0.06 g AFDW 100 cm^{-2} $year^{-1}$ (Figure 2.3c).

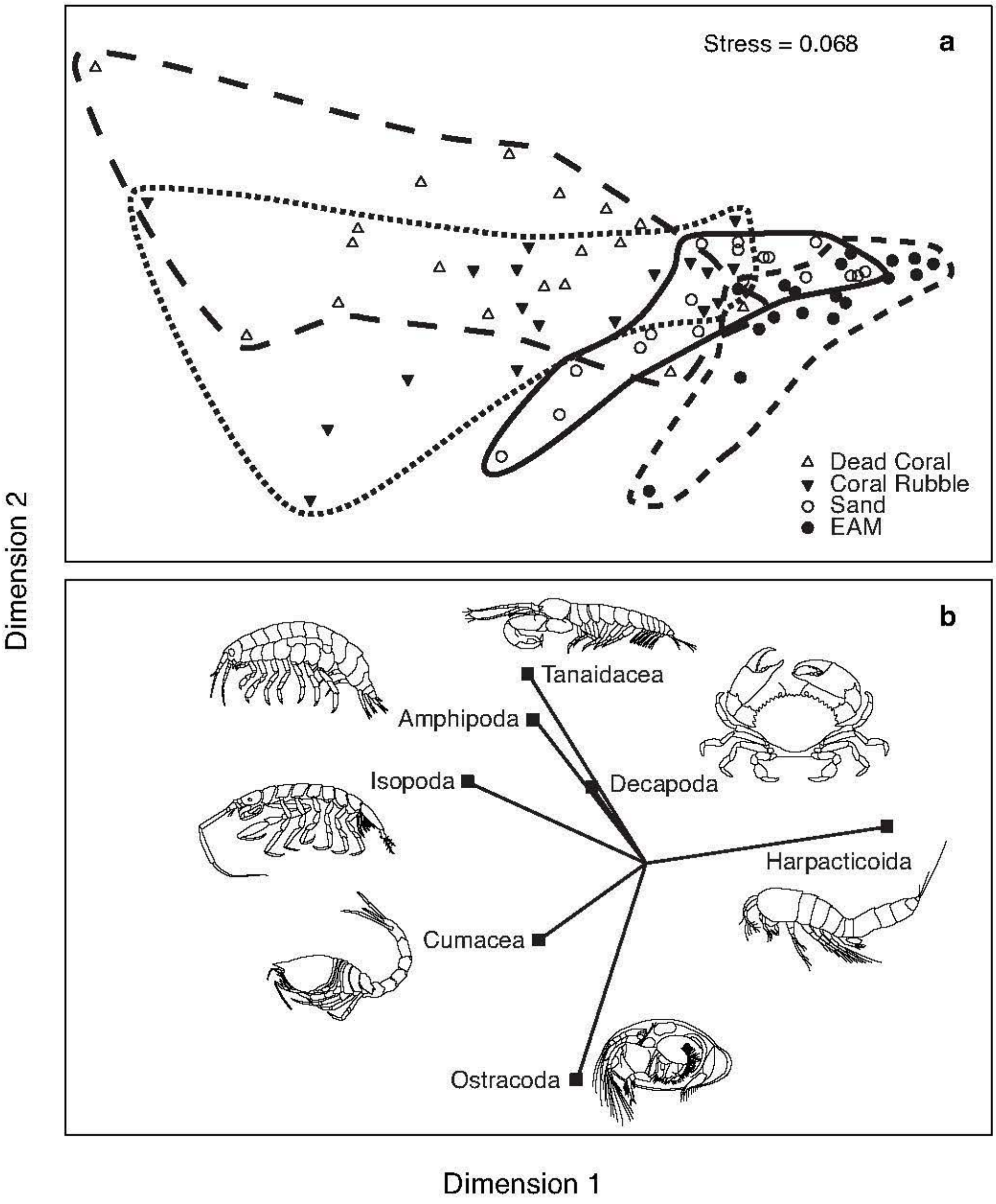

Figure 2.2 Crustacean assemblages among microhabitats, excluding fine-branching live coral. **a)** Non-metric multidimensional scaling of the abundance of crustacean taxa from dead coral, rubble, sand and epilithic algal matrix (EAM) habitats. **b)** The relative contribution of each taxon to the variation in habitat groupings is represented by the vector points. Points indicate the direction of change and strength (correlation) of taxa to each habitat. Cyclopoida is not represented as it was not significantly correlated with any microhabitat ($p > 0.05$).

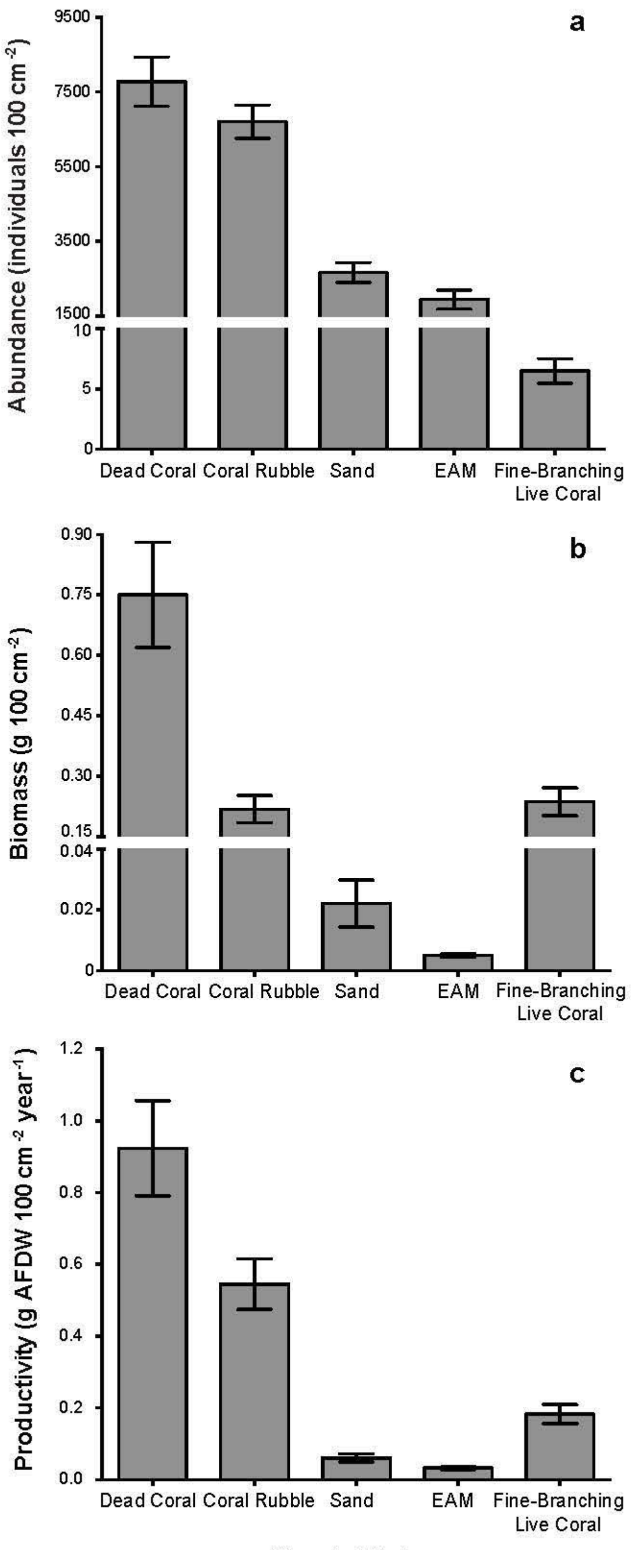

Figure 2.3 Attributes of all Crustacea within a 100 cm^2 sample of each of the five micro-habitats. **a)** Abundance, **b)** biomass and **c)** productivity. All values are expressed as mean ± standard error. Biomass units are in grams of wet weight per 100 cm^2 planar area of the micro-habitat. Productivity estimates are in grams of ash-free dry weight per 100 cm^2 sample of micro-habitat per year.

Crustacea at a reef-site scale

Benthic surveys revealed that the greatest mean (± 95 % CI) planar coverage of microhabitats in a square metre of reef was coral rubble (0.34 ± 0.06 m^2), followed by EAM (0.27 ± 0.06 m^2), other coral (0.19 ± 0.03 m^2), fine-branching live coral (0.10 ± 0.02 m^2), dead coral (0.06 ± 0.01 m^2), sand (0.03 ± 0.01 m^2) and other microhabitats such as sponges and giant clams (0.008 ± 0.003 m^{-2}) (Appendix A, Figure A4). Using these data we can estimate the ecological values of each major taxon within an average square metre of Lizard Island semi-sheltered fringing reef (Figure 2.4).

From an average square metre of the study reef, coral rubble was the most important microhabitat in terms of crustacean abundance, yielding more than three orders of magnitude more crustacean abundance than fine-branching live coral (coral rubble: 230248 ± 43114 ind. m^{-2}; fine-branching live coral: 66 ± 18 ind. m^{-2}) (Figure 2.4a). The biomass of crustaceans in coral rubble was higher than fine-branching live coral or dead coral (fine-branching live coral: 2.4 ± 0.6 g m^{-2}; dead coral: 4.4 ± 1.2 g m^{-2}; coral rubble: 7.4 ± 1.7 g m^{-2}) (Figure 2.4b), which was in part due to the prevalence of coral rubble (0.34 ± 0.06 m^2 planar surface area). Although dead coral was one of the least abundant microhabitats in the study area (0.06 ± 0.01 m^2 planar surface area), it still supported almost twice the biomass of fine-branching live coral (0.10 ± 0.02 m^2 planar surface area). In contrast, despite their area, sand (0.03 ± 0.01 m^2 planar surface area) and the EAM (0.27 ± 0.06 m^2 planar surface area) supported low biomass, with just 0.07 ± 0.04 g m^{-2} and 0.14 ± 0.03 g m^{-2}, respectively (Figure 2.4c); over 50 times less than coral rubble or dead coral. Dead coral, coral rubble and branching coral constituted a mean of 50 % of the planar surface area of the study reef, yet supported 98 % of the biomass of Crustacea.

Productivity of the microhabitats likewise revealed that coral rubble (18.5 ± 2.4 g AFDW m^{-2} $year^{-1}$) was the most productive, being greater than both dead coral (5.4 ± 0.8 g AFDW m^{-2} $year^{-1}$), fine-branching live coral (1.9 ± 0.3 g AFDW m^{-2} $year^{-1}$) and the EAM (0.9 ± 0.1 g AFDW m^{-2} $year^{-1}$) (Figure 2.4c). Despite its prevalence, the EAM contributed little to biomass or productivity.

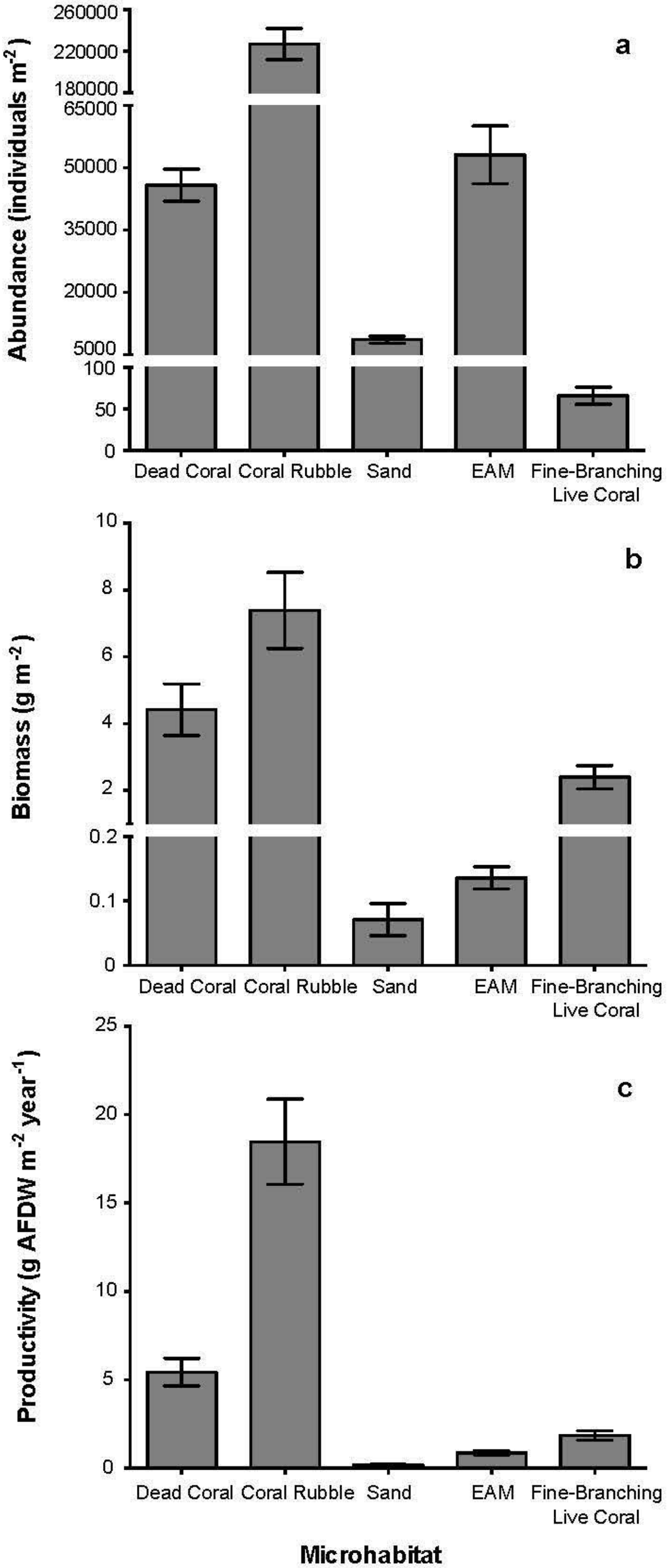

Figure 2.4 Attributes of all Crustacea within five major micro-habitats (based on the mean planar coverage of each micro-habitat) within an average square metre of the study reef. **a)** Abundance, **b)** biomass, in grams of wet-weight biomass per square metre of reef and **c)** productivity per square metre of reef in grams of ash-free dry weight per year.

Taxonomic contribution of Crustacea on reefs

Harpacticoida were, by far, the most abundant taxon on an average square metre of the study reef (293465 ± 40850 ind. m^{-2}), being seven times more abundant than all other taxa combined (Figure 2.5a). Decapoda, by comparison, had a mean abundance of just 382 ± 76 ind. m^{-2} (Figure 2.5a). Despite their very low abundance, Decapoda had the greatest biomass (12.5 ± 2.0 g m^{-2}), 18 times greater than that of the Harpacticoida (0.7 ± 0.1 g m^{-2}) (Figure 2.5b). The estimated productivity of each taxon revealed similar patterns, with Decapoda being the most productive (18.5 ± 2.5 g AFDW m^{-2} $year^{-1}$) and Cyclopoida being the least productive (0.03 ± 0.004 g AFDW m^{-2} $year^{-1}$) (Figure 2.5c).

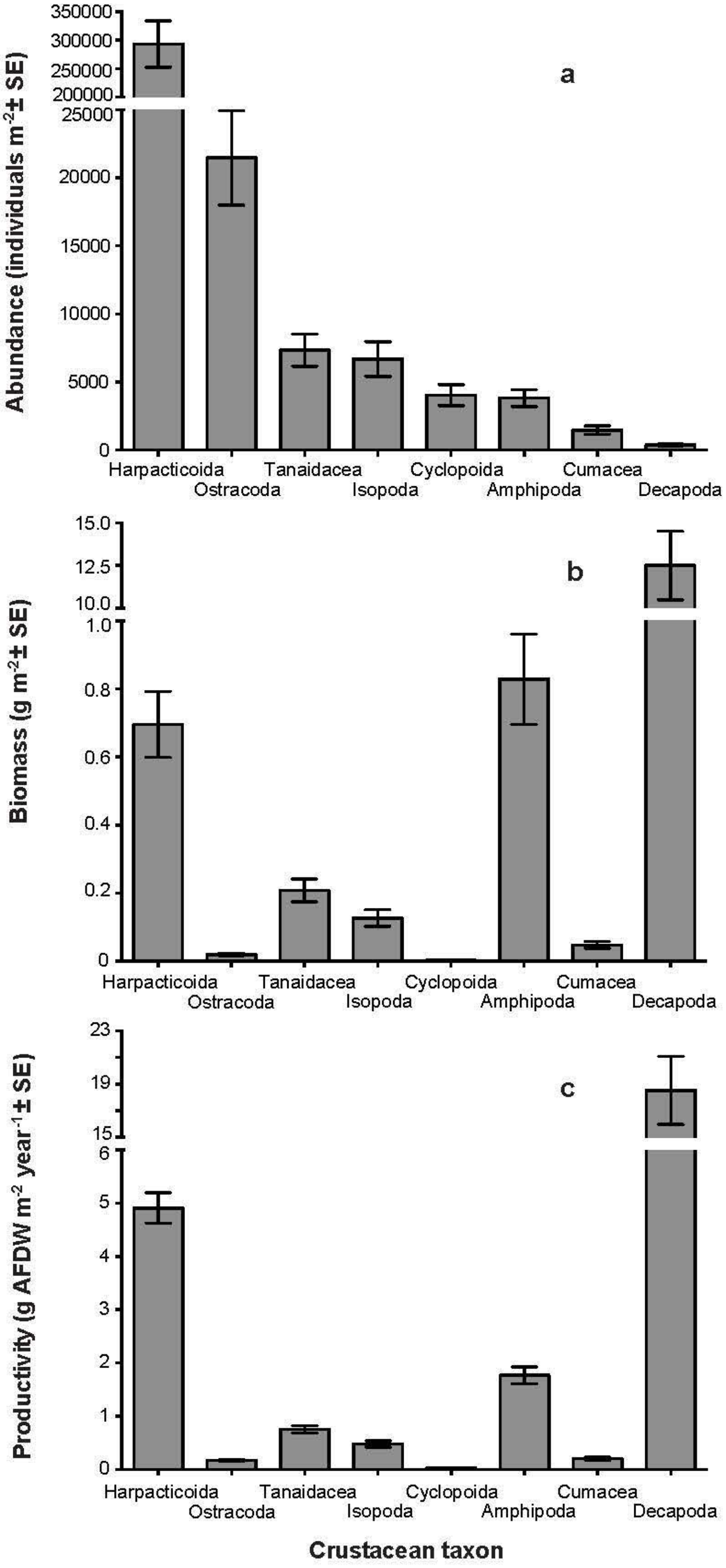

Figure 2.5. Taxonomic contribution of Crustacea taxa within a typical square metre of coral reef (values are scaled to the planar area coverage of each micro-habitat). **a)** Abundance, **b)** biomass in grams (wet weight) per square metre and **c)** estimated productivity in grams of ash-free dry weight (AFDW) per square metre per year.

2.4 Discussion

Although invertebrate assemblages within specific coral reef microhabitats have been described in a number of studies (Takada et al. 2008, Plaisance et al. 2009, Stella et al. 2011, Kramer et al. 2012), investigations that compare faunas among microhabitats are rare (but see Enochs 2012). The present study, therefore, examined the assemblages, abundance, biomass and estimated productivity of crustaceans within five major microhabitats on a coral reef. Differences between microhabitats were distinct, with dead coral and coral rubble yielding by far the greatest abundance, biomass and productivity of crustaceans. In contrast, fine-branching live coral shelters very few crustaceans. As these individuals tend to be large, the crustacean biomass in fine-branching live coral is still comparable to that found in dead coral or coral rubble. Live coral cover is often considered the most important unit of measure in determining coral reef health (Goatley & Bellwood 2011, Vroom 2011) as it is an important microhabitat for the recruitment of juvenile fishes (Jones et al. 2004), the preferred microhabitat for specific fishes and crustaceans (Stella et al. 2010, Bellwood et al. 2012a) and the foundation of coral reef structural complexity (Graham et al. 2006). However, our results suggest that the most valuable microhabitats on a coral reef, in terms of supporting the biomass and productivity of trophically valuable crustaceans, are dead coral and coral rubble. Each microhabitat on a coral reef, therefore, must be present in appropriate proportions to maintain a diverse, healthy ecosystem.

Dead coral, coral rubble and the EAM

Dead coral was a particularly important microhabitat for crustaceans, with approximately three orders of magnitude more individuals and three times more biomass than fine-branching live coral per unit area. The greater abundance and biomass of all crustaceans in dead coral is probably due to the combination of high structural complexity (Enochs et al. 2011, Enochs 2012), increased surface area of the associated EAM (Preston & Doherty 1994), and the diversity of 'nano-habitats' (i.e. filamentous algae, macro-algae, crustose coralline algae and sponges; Ginsburg 1983, Klumpp et al. 1988, Glynn & Enochs 2011) providing both shelter and trophic resources (i.e. algae, micro-algae and detritus). However, dead coral was a relatively uncommon microhabitat on the reef, comprising only 5.9 ± 1.2 % of the planar area. The lack of dead coral may be attributed to three factors. Firstly, some dead coral microhabitats may have been concealed under a canopy of live coral, particularly branching taxa, and thus, may be under-represented in the benthic surveys (Goatley & Bellwood 2011). Indeed, for some species of branching coral, live tissue may only cover the outermost 20-80 % of the branches, obscuring the dead coral skeleton that contains a diverse, abundant and different crustacean community (McCloskey 1970, Lewis & Snelgrove 1990). Secondly, bioerosion by boring organisms and parrotfishes slowly removes the skeletal structure after the death of a coral colony (Kiene & Hutchings 1994, Bellwood et al. 2003). Alternatively, physical forces may break off the dead coral, with the eroded fragments accumulating as coral rubble (Hughes 1994, Rasser & Riegl 2002).

Since dead coral is often transformed into coral rubble, these two microhabitats have similar structure and resource attributes. As a result, the crustacean assemblages of dead coral and coral rubble also remain very similar, and, interestingly, have greater dispersion in multivariate space, suggesting that investigations into crustacean diversity may benefit from focussing on these microhabitats. Likewise, the abundance and biomass of crustaceans have broadly comparable values between the two microhabitats. Although coral rubble has slightly fewer individuals, the main difference is in the biomass, with rubble having only a third of the crustacean biomass of dead coral. This decrease is probably due to the reduced complexity in coral rubble, with fragments supporting fewer large cryptic species (Enochs et al. 2011). A similar effect has been observed in live corals with less complex growth forms supporting low crustacean abundance and biomass (Vytopil & Willis 2001, Stella et al. 2010). In contrast, dead microhabitats with low environmental water flow and low porosity have been found to support higher abundance and biomass of cryptofauna than habitats with high water flow and high porosity (Enochs et al. 2011). In this context, dead coral may be considered to be of a lower porosity (i.e. smaller spaces between branches) and slightly higher water flow than coral rubble due to minimal erosion and its upright position on the reef. As such, complexity, porosity and water flow are likely to be important factors that support high abundance and biomass in dead coral.

Coral rubble covers 5.8 times the area covered by dead coral on the surveyed reefs. In terms of overall contribution to reef crustacean abundances and biomass, therefore, coral rubble may be a more important microhabitat than dead coral. The value of coral rubble has also been identified in the Pacific Gulf of Panama, where cryptofaunal biomass (i.e. all invertebrates > 2 mm) in coral rubble was estimated to be 3.5 ± 1.1 g AFDW m^{-2} (Enochs 2012). In comparison, the present study on the GBR found that in coral rubble, crustaceans alone yielded 3.5 ± 0.54 g AFDW m^{-2} (converted using factors from Ricciardi & Bourget [1998]). If crustaceans contribute approximately a third of the cryptofaunal biomass in dead substrates (Enochs 2012), this suggests that the total invertebrate biomass within a GBR coral rubble microhabitat may be three times greater than on the Eastern Pacific Panama reefs. These differences are probably due to variation in factors such as primary productivity (Hatcher 1990, Klumpp & McKinnon 1992), nutrient profiles (Fabricius 2005, Pascal et al. 2013) and, most importantly, coral species, as rubble morphology and complexity is likely to strongly influence the cryptofaunal populations at each location (Vytopil & Willis 2001, Takada et al. 2007, Enochs & Manzello 2012b).

The EAM is a ubiquitous and abundant microhabitat that is found across all dead substrates (Goatley & Bellwood 2011, Connell et al. 2014). Therefore, it is intuitive that the EAM crustacean assemblage should be a prominent component of all microhabitats in the present study, excluding live coral and sand. Indeed, the dominant EAM crustaceans, Harpacticoida, were the most abundant taxon across all microhabitats, particularly in dead coral and coral rubble. The high structural complexity of these two microhabitats presents a relatively large amount of surface area that is colonised by a variety of algal and encrusting taxa, which in turn supports the benthic micro-algae, protozoans and detrital resources on which harpacticoids feed (Buffan-Dubau et al. 1996, Buffan-Dubau & Carman 2000). The slight overlap of the nMDS groupings for dead coral, coral rubble, sand and EAM is likely due to the abundance of harpacticoid copepods in each microhabitat. It is interesting to note that harpacticoids have similar densities in EAM and sand microhabitats. Although the structure of sand and the EAM is not as complex as dead coral or coral rubble at larger scales, it is likely that sufficient micro-phytal resources exist in sand and the EAM at a micro-scale to support populations of these very small crustaceans (Montagna et al. 1995, Miller et al. 1996). Future investigations will benefit from a quantification of the precise habitable surface area or habitable volume of different microhabitats. These units of measurement may be particularly useful for estimating the capacity of a microhabitat to support crustacean biomass, particularly of very small or relatively large taxa which are likely to dominate high surface area and high porosity microhabitats, respectively.

Comparison with other marine taxa and environments

Although the present study has identified crustaceans as highly abundant reef organisms across a variety of microhabitats, it is difficult to visually appreciate Crustacea, as many individuals are either very small or very cryptic. In comparison, fishes are often conspicuous and can be quantified using relatively rapid visual censuses and ichthyocide sampling methods. The data in the present study allows the crustacean community to be compared with a representative fish assemblage from a similar habitat in the same location: Lizard Island, Great Barrier Reef, Australia (cf. Enochs 2012, Depczynski et al. 2007). In this comparison, the abundance of crustaceans on coral reefs is approximately four orders of magnitude greater than fishes (338672 ind. m^{-2} and 20 ind. m^{-2}, respectively). In contrast, the wet weight biomass of fishes (158.0 g m^{-2}; Depczynski et al. 2007) is approximately one order of magnitude greater than that of crustaceans (14.4 g m^{-2}; present study). Thus, even though crustaceans on coral reefs are generally very small organisms (mean body length of all crustacean taxa = 0.79 ± 0.32 mm, mean mass = 7.62 ± 7.59 mg), their very high abundance results in a biomass value that approaches the same order of magnitude as fishes. Furthermore, the present study did not include very large decapods such as crabs (i.e. Portunidae and Xanthidae) or lobsters (i.e. Palinuridae). These large crustaceans were not observed at the sampling locations because they shelter deep within the reef structure and only emerge at night (Frisch 2007b). Inclusion of these larger crustaceans would increase the estimated biomass of crustaceans on coral reefs and further decrease the difference between fishes and Crustacea.

The values above are based on standing stocks. The productivity of Crustacea is, perhaps, a more important metric as it provides information on the ability of this group of organisms to transfer energy to higher trophic levels (cf. Depczynski et al. 2007). Indeed, the estimated productivity of crustaceans (0.46 g wet weight m^{-2} day^{-1}) is twice the estimated productivity of fishes (0.20 g wet weight m^{-2} day^{-1}; Depczynski et al. 2007). Considering that many fishes feed on crustaceans (Hobson 1974, Edgar & Shaw 1995a, Randall et al. 1997), it is suggested that Crustacea are a major trophodynamic component of coral reefs, providing an important link in the dominant microbial- and detrital-based food webs (Arias-Gonzalez et al. 1997, Depczynski et al. 2007). In contrast, productivity of coral reef microhabitats has rarely been studied. Of the investigations that have been conducted, it is largely the primary productivity of the EAM (Hatcher 1990, Klumpp & McKinnon 1992, Russ 2003) and secondary production in lagoonal soft sediments (Riddle et al. 1990, Carleton & McKinnon 2007) that are addressed. In the present study, crustaceans in dead coral are much higher in productivity (92.3 g AFDW m^{-2} year^{-1}) to the productivity of organisms in GBR lagoonal sediments on a mid-shelf reef (19.0 g AFDW m^{-2} year^{-1}; Riddle et al. 1990). However, the present study only addressed the productivity of crustaceans. The productivity of the complete faunal assemblage of each microhabitat, however, is likely to be much greater. If this is the case, the most productive microhabitat, dead coral, may be one of the most productive microhabitats in the world, being surpassed only by Californian macrophyte detritus (~7000 g AFDW m^{-2} year^{-1}; Vetter 1995, Taylor 1998), mussel beds in the Wadden Sea (468 g AFDW m^{-2} year^{-1}; Asmus 1987, Taylor 1998) and may be of similar productivity to *Carpophyllum* forests in New Zealand (Taylor 1998).

These comparisons are interesting in light of Darwin's paradox, which questions how coral reefs can be so productive in oligotrophic tropical oceans (Sammarco et al. 1999). The abundance and high productivity of crustaceans are likely to be a contributing factor, as these organisms are capable of rapidly consuming and incorporating the available primary productivity and fine detrital material into the trophic structure of the ecosystem (Taylor 1998). Thus, the lower levels of a coral reef's trophic structure may form more of an inverse pyramid, where the biomass of consumers is greater than that of the primary producers and detritus due to rapid consumption and recycling of easily assimilated and nutritionally valuable resources (Shurin et al. 2006, Cebrian et al. 2009). This may apply at both primary and secondary consumer levels, with crustaceans rapidly assimilating primary productivity and detritus, and with their high productivity likewise supporting a high biomass of secondary consumers (i.e. fishes).

Crustaceans are an important component of all benthic coral reef microhabitats. Although abundances, biomass and productivity differed considerably among microhabitats, dead coral and coral rubble were the most important for all of these measures. The contribution of Crustacea within dead coral and coral rubble to the trophic structure of a coral reef is substantial, acting as consumers of algal and detrital material (Klumpp et al. 1988, Preston & Doherty 1994) and providing a resource to a wide variety of predatory invertebrates and fishes (Randall et al. 1997, Bellwood et al. 2006b, Kramer et al. 2013).

Coral reefs worldwide are currently experiencing a variety of environmental and anthropogenic stressors that are modifying the structure of benthic reef communities (Hughes et al. 2003, Knowlton & Jackson 2008). One of the most apparent consequences is the loss of both corals and three-dimensional structure (Graham et al. 2007, Pratchett et al. 2008). In both cases this is very likely to have a direct detrimental effect on crustacean communities, particularly for larger taxa. By understanding how different microhabitats contribute ecologically to marine ecosystems, predictions can begin to be made in terms of the future implications of habitat degradation and climate change on reef Crustacea (cf. Enochs & Manzello 2012b). Whilst fine-branching live coral is an important habitat, especially for relatively large decapods, from a crustacean perspective, its main contribution may be after the coral's death. Dead coral and coral rubble are highly dependent on the growth of live coral to sustain the structural complexity that is required to support diverse invertebrate faunas. Although fine-branching live coral may be relatively depauperate in crustacean fauna, it is an essential microhabitat that, upon death, supplies a coral reef with the necessary structure to support abundant and productive crustacean assemblages. Thus, the trophic complexity of a coral reef may not depend solely on maximising the coverage of live coral. Instead, it is the ongoing turnover of corals that produce dead substrata that are the key to supporting abundant and productive crustacean communities on coral reefs.

Chapter 3: Large-scale spatial variation in epilithic algal matrix cryptofaunal assemblages on the Great Barrier Reef

Published as: Kramer MJ, Bellwood DR & Bellwood O (2014) *Marine Biology* 161: 2183-2190

3.1 Introduction

Investigations of marine assemblages across large spatial scales often reveal distinct patterns of species distributions and community structure, particularly in latitudinal or cross-shelf studies (Stevens 1989, Bellwood & Wainwright 2001, Wismer et al. 2009). Spreading nearly 2000 km along the coastline and up to 200 km offshore, Australia's Great Barrier Reef shows clear divisions between inshore, mid- and offshore reefs. This pattern holds true for a wide variety of organisms, ranging from fishes (Bellwood & Wainwright 2001, Hoey & Bellwood 2008) and benthic macroalgae (Wismer et al. 2009), to crustose coralline algae (Fabricius & De'ath 2001) and crustaceans (Preston & Doherty 1994).

Factors that may drive the divisions in the cross-shelf distributions include wave energy (Bellwood & Wainwright 2001), benthic composition (Wismer et al. 2009), the availability of nutrients (Uthicke & Nobes 2008, Uthicke & Altenrath 2010), turbidity (Cooper et al. 2007), and sedimentation (Preston & Doherty 1994, McCook 1996, Fabricius & De'ath 2001). Relatively high rates of sedimentation on inner shelf reefs appear to be particularly influential on benthic organisms (McCook 1996, Fabricius & De'ath 2001, McCulloch et al. 2003). For example, in high sedimentation locations, crustose coralline algae cover is low (Fabricius & De'ath 2001) and crustacean communities in dead corals have distinctly different assemblages and lower abundances (Preston & Doherty 1994). Sediment, *per se*, does little to explain the large-scale community structure of Foraminifera, however, turbidity and nutrient profiles appear to have a much greater influence on these benthic organisms (Cooper et al. 2007, Uthicke & Nobes 2008, Uthicke & Altenrath 2010).

The epilithic algal matrix (EAM) is a significant, and often dominant, component of benthic assemblages on coral reefs, covering approximately 30 to 70% of the available surface area (Klumpp & McKinnon 1992, Goatley & Bellwood 2011). Within the EAM, short filamentous and crustose algal species are common (Scott & Russ 1987, Connell et al. 2014) in addition to nutrient-rich detritus (Crossman et al. 2001, Wilson et al. 2003), inorganic sediments and a community of small organisms (Kramer et al. 2012). Once thought to be exploited solely by herbivorous fishes, the EAM has progressively gained recognition as being a valuable resource for detritivorous (Wilson et al. 2003, Wilson 2004) and small carnivorous fishes (Kramer et al. 2013). Although the EAM is structurally simple, based on a short algal turf ranging from 1 to 6 mm in height (Bonaldo & Bellwood 2011) it supports a surprisingly diverse and abundant community of motile taxa (Kramer et al. 2012) that are likely to be important contributors to ecosystem function (Kennedy & Jacoby 1999, Schratzberger et al. 2000). In the present study, the term 'cryptofauna' will be used to include both meiofauna (0.06–0.5 mm; (Giere 2009) and larger taxa (up to 5 mm).

Environmental factors are capable of having both positive and negative effects on the abundance of organisms and the overall structure of a community (Fabricius et al. 2005, Takada & Shibuno 2008). One such factor is the effect of sediments, which consist of both organic and inorganic settled particulate matter. The amount of sediment is particularly important to coral reefs, as higher than normal levels are known to place corals under metabolic stress (Rogers 1990), inhibit coral settlement (Birrell et al. 2005) and suppress grazing by herbivorous fishes (Bellwood & Fulton 2008). The influence of sediment and dissolved nutrients on the abundance of small organisms is relatively well known (Preston & Doherty 1994, Cooper et al. 2007, Uthicke & Altenrath 2010, Kramer et al. 2012). However, whilst the abundance of cryptofauna is reported to remain relatively temporally consistent (Klumpp et al. 1988, Logan et al. 2008) not much is known about spatial variability. The present study aims to investigate the spatial differences in cross- and along-shelf variation of EAM cryptofauna using two inner shelf locations and a typical mid-shelf location on the GBR. In addition, sediment volumes were measured and proximity to major river systems was determined to examine the relationship between sediment, nutrients and EAM cryptofauna at these locations.

3.2 Methods

Sampling locations

Samples of EAM fauna were collected from three locations across the Great Barrier Reef: Orpheus Island, the Turtle Island group and Lizard Island (Figure 3.1). Orpheus Island is located on the inner Great Barrier Reef (18° 36’40”S, 146° 29’20”E), 16 km from the mainland. Samples were collected from four sites across the reef of Pioneer Bay, Orpheus Island. A detailed description of Pioneer Bay habitats is given in Fox and Bellwood (2007). The Turtle Island group is similarly located on the inner-shelf of the GBR, 12 km offshore and approximately 450 km north of Orpheus Island (14° 43’55”S, 145° 11’00”). Composed of nine small islands and reefs, two islands (2 sites each) were sampled for EAM cryptofauna. Lizard Island is located on the mid-shelf GBR (14° 40’40”S, 145° 26′ 55″E) 30 km offshore and on similar latitude to the Turtle Island group. Samples were collected from the reef in Mermaid Cove and the Lagoon Entrance (2 sites each). Sampling at all locations was conducted during the austral summer months (November – March) to reduce variation due to seasonal effects, although seasons usually have a minimal influence on cryptofaunal populations (Klumpp et al. 1988, Logan et al. 2008). For consistency, sampling at all locations was conducted from similar depths (2–3 m depth at high tide) on the fringing reef crest of the leeward shore where live coral and EAM were dominant and macroalgae sparse. All locations are marine protected areas where fishing is prohibited and removal of organisms is only granted for approved research. As such, the marine communities are considered to be relatively intact and include all major functional groups of herbivorous fishes (Bellwood et al. 2004, Green & Bellwood 2009), thereby subjecting the EAM to similar grazing pressure. The EAM at all sites was of a similar height (4 – 6 mm) and morphology (short, filamentous Chlorophyta and Rhodophyta). Samples were taken from open planar areas away from territorial damselfish territories that may modify EAM composition (Klumpp & McKinnon 1988). Sampling on Orpheus Island occurred one month after a tropical cyclone (Cyclone Yasi, Category 5) passed over the island (Great Barrier Reef Marine Park Authority 2011) and three months after extensive coastal flooding due to Cyclone Tasha (Hayes & Goonetilleke 2012).

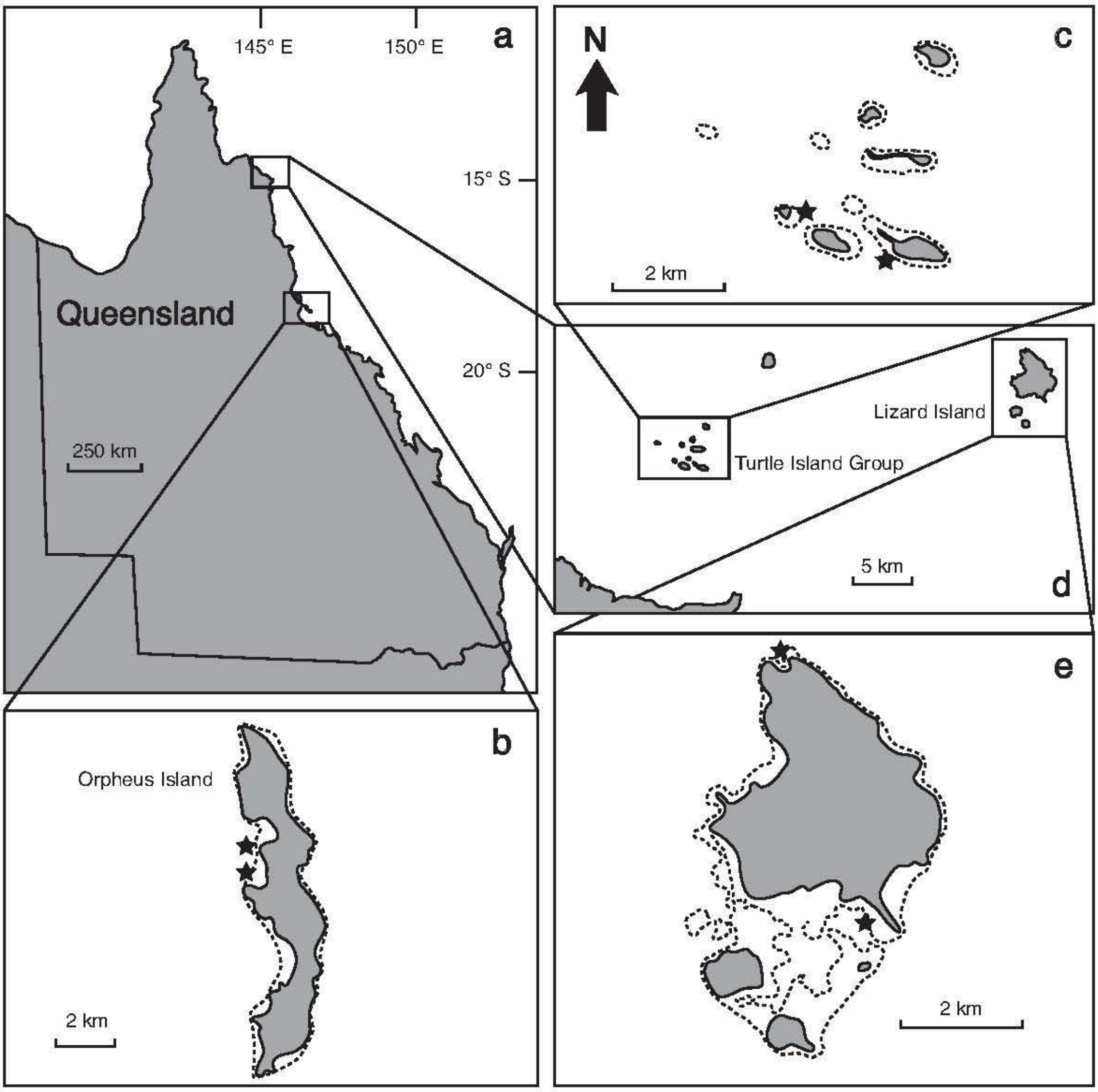

Figure 3.1 Sampling locations. **a)** Queensland, Australia, indicating regions where sampling was conducted. **b)** Orpheus Island. **c)** Turtle Island group. **d)** Northern sampling locations: Turtle Island group and Lizard Island. **e)** Lizard Island. Dashed lines indicate fringing reefs and stars are sampling sites. Two sites were sampled at each star.

Sample collection

Samples from all locations were collected using SCUBA from the reef crest zone. A total of 60 samples were obtained, consisting of five individual samples from each of the four sites at each of the three locations. An underwater vacuum apparatus based on the design described in Kramer et al. (2012) was utilised to remove all particulate material within a defined area. The sampling area was delimited by a section of PVC pipe 51 mm in diameter, representing 20.4 cm^2 of EAM. The sampling area was vacuumed thoroughly for 30 seconds, during which time the resident organisms and particulate matter were drawn into the apparatus and retained by a 60-µm plankton mesh filter bag. The filter bag was then sealed, transported to the surface and the contents fixed in 4% formaldehyde solution in seawater.

Sample and data analysis

Samples were stained with eosin erythrosin to aid in distinguishing organisms amongst the particulate matter. Collected material was washed onto a petri dish, which had a grid affixed to the bottom to prevent observing the same organism twice. Samples were examined under 40x magnification to identify taxa to the lowest functional taxonomic level (usually Order) and the abundance of the respective organisms was recorded and standardised to 100 cm^2. The sediment volume of each sample was calculated following Kramer et al. (2012). Using digital vernier calipers (accuracy: ± 0.02 mm), the depth of the settled particulates within the sample vial was measured and the volume estimated based on a calibrated vial.

The dataset used for the analysis incorporated abundant organisms and excluded those taxa with fewer than 10 individuals 100 cm^{-2}, as they made clear visualisation difficult and did not significantly affect the result of the analysis. Thus, taxa considered in the analysis were Amphipoda, Cumacea, Gastropoda, Harpacticoida, Isopoda, Polychaeta, Ostracoda and Tanaidacea. Organisms that were observed, but not included in the analysis due to low abundances, were Chaetognatha, Chironomida, Cyclopoida and Decapoda. The cryptofaunal community data were explored using a non-metric multidimensional scaling (nMDS) ordination of a Manhattan distance matrix based on standardised data, thus representing proportions rather than raw abundance and preventing the over-representation of abundant taxa. Taxa vectors were added to the ordination to aid interpretation of the data (Oksanen et al. 2007). A permutational multivariate analysis of variance (PERMANOVA) was conducted to elucidate differences in sites and locations. Spearman rank correlations were conducted to investigate the relationship between sediment and the abundance of organisms. Additionally, a one-way ANOVA was used to test the difference in sediment volume among locations. Multivariate analyses, Spearman rank correlations and ANOVA were conducted using the R packages *vegan* (Oksanen et al. 2007) and *Hmisc* (Harrell 2014). Pairwise comparisons were calculated using Primer 6 with PERMANOVA.

3.3 Results

PERMANOVA analysis found no significant difference in cryptofaunal assemblages among sites within locations, or in the interaction between sites and locations. Site data were therefore pooled within locations for the remainder of the analyses. Investigation of the nMDS revealed that each location could be separated into distinct ordination groupings. This is supported by the PERMANOVA, which indicates that locations were statistically significant (PERMANOVA, $P < 0.001$). The pairwise PERMANOVA further indicated that all locations were significantly different from each other (pairwise PERMANOVA, $P < 0.05$). From the vectors fitted to the nMDS ordination (Figure 3.2), Orpheus Island showed strong gradients for Polychaeta and Gastropoda, whereas the Turtle Islands and Lizard Island are represented by a gradient towards the Harpacticoida. Vectors also indicate that Amphipoda, Cumacea and Tanaidacea exhibit strong gradients toward the Turtle Islands. Although Orpheus Island did not exhibit any shared multivariate space with the other locations, the Turtle Islands and Lizard Island did have a small degree of overlap, indicating that some sampling locations between these two regions were somewhat similar in EAM community composition.

Data were further explored by investigating the relationship between sediment and the abundance of organisms in the EAM. The only taxon not to have a significant correlation with sediment was Isopoda (Spearman rank correlation, $r_s = 0.125$, $N = 60$, $P = 0.340$). All other taxa had a significant, positive, relationship with sediment, ranging from ($r_s = 0.571$, $N = 60$, $P < 0.001$) to ($r_s = 0.280$, $N = 60$, $P = 0.03$) for Polychaeta and Amphipoda, respectively (Figure 3.3). However, sediment volumes among locations revealed no significant difference in the volume of sediment at each location (ANOVA, $F_{(2, 57)} = 1.819$, $P = 0.171$),

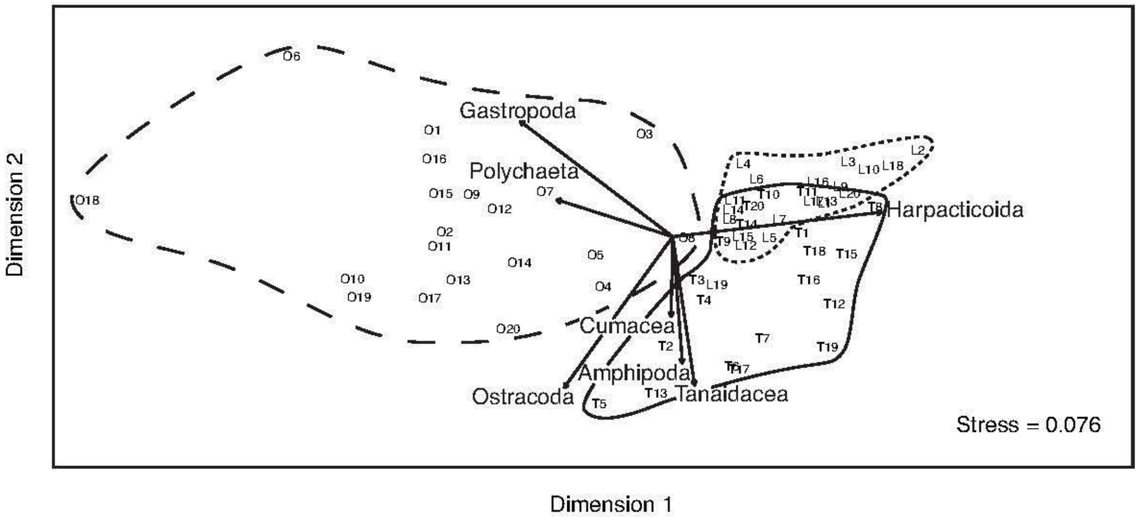

Figure 3.2 Non-metric multidimensional scaling (nMDS) ordination of epilithic algal matrix fauna from Orpheus Island (dashed line), Lizard Island (dotted line) and Turtle Island group (solid line). Vectors indicate strength and direction of taxa gradients. All locations are significantly different (pairwise PERMANOVA, $p < 0.05$).

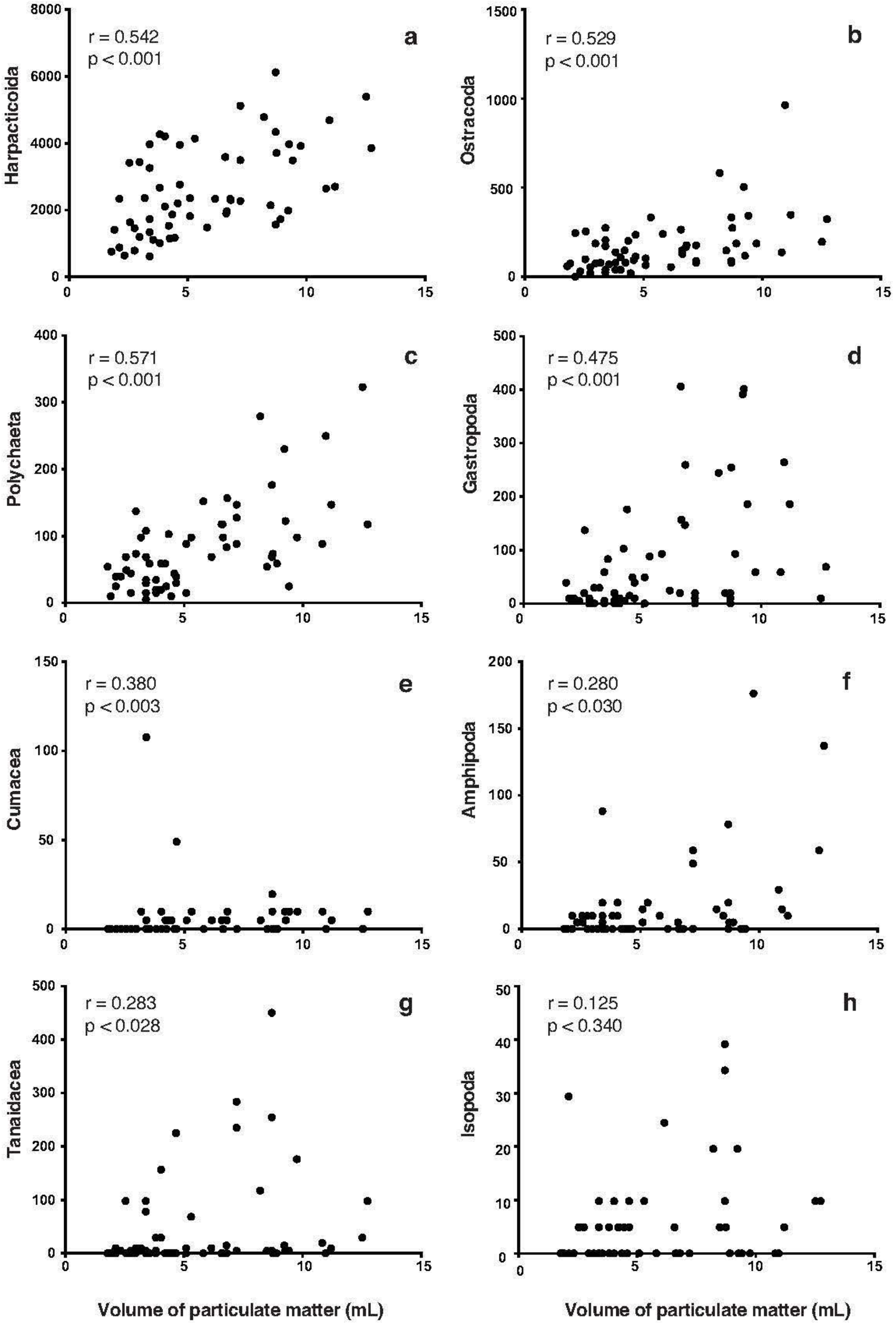

Figure 3.3 Spearman rank correlations of the relationships between sediment volume (mL 100 cm^{-2}) and abundance of cryptofaunal organisms (ind. 100 cm^{-2}). Correlation coefficients and statistical significance values for each relationship are inserted onto the respective correlations.

3.4 Discussion

Cross-shelf studies on the GBR have consistently revealed a distinct separation between inner, mid and outer shelf reefs. This pattern applies to community assemblages (Done 1982, Preston & Doherty 1994, Bellwood & Wainwright 2001), benthic composition (McCook 1996, Fabricius & De'ath 2001, Wismer et al. 2009) and ecosystem processes (Russ & McCook 1999, Hoey & Bellwood 2008). The preliminary observations in the present study suggest that not only is there a possible cross-shelf difference in EAM cryptofauna composition, but also an along-shelf separation. Somewhat surprisingly, the nMDS suggests that an inner shelf reef (Orpheus Island) differs more from another inner shelf location (Turtle Island group) than the Turtle Islands differ from a nearby mid-shelf system (Lizard Island). This result contrasts with other cross-shelf studies, which typically report that features such as hydrodynamics (Bellwood & Wainwright 2001), sediments (Preston & Doherty 1994, Fabricius & De'ath 2001), abundance of macroalgae (Wismer et al. 2009), or a combination of the above (Hoey & Bellwood 2008), drive the differences across large spatial scales. The samples of the EAM collected in the present study were taken from largely similar environments, thereby controlling for the effect of depth, reef zone, season, proximity of macroalgae and hydrodynamics. Yet, the EAM cryptofauna differed significantly among all locations.

Whilst these results were unexpected, there are indications that this variation in EAM cryptofauna may be a result of the water quality and nature of sediments at each location. The coastline adjacent to the sampling locations is subject to tropical seasonal fluctuations, namely a dry season and a wet season. During the wet season, extensive flooding is common, where large amounts of terrigenous sediments and anthropogenic contaminants are flushed into major rivers and out into coastal waters (Devlin & Brodie 2005, Brodie et al. 2010). The resulting sediment plumes typically move in a northerly direction along the Queensland coastline (McCulloch et al. 2003, Brodie et al. 2010). The catchments that are most likely to affect the locations in the present study are the Mossman-Daintree and a small section of the Northeastern Cape York catchment (Turtle Island group and Lizard Island) and the Burdekin-Haughton and Ross-Black catchments (Orpheus Island) (Neil et al. 2002, Bainbridge et al. 2012). It is important to note the difference in catchment areas that deliver floodwaters into the GBR lagoon. River catchments that affect the Turtle Island group and Lizard Island are much smaller than those that influence Orpheus Island (Neil et al. 2002). In addition, of all the rivers along the Queensland coast, the Burdekin River produces the highest volume of suspended sediments to the GBR lagoon, emitting an estimated 3×10^8 kg y^{-1} (Neil et al. 2002, McCulloch et al. 2003, Kroon et al. 2012). Although Orpheus Island is not in the direct path of the flood plume stemming from the Burdekin River, excessive nutrients and (to a lesser extent) suspended sediments from the Burdekin River have been documented at considerable distances that easily extend past, and encompass, Orpheus Island (Devlin & Brodie 2005, Devlin et al. 2008, Bainbridge et al. 2012).

In the present study, although almost all taxa displayed significant positive relationships with sediment volume, four taxa in particular appear to be influenced most strongly: Gastropoda, Harpacticoida, Ostracoda and Polychaeta (Fig. 3). Of these, Gastropoda and Polychaeta were characteristic of Orpheus Island, whereas Harpacticoida and Ostracoda were dominant taxa at the Turtle Islands and at Lizard Island. All four of these taxa are primary consumers and/or detritivores (Ruppert et al. 2004), thus it would be expected that an increase in primary productivity due to nutrient input would increase populations (Montagna et al. 1995). It is likely that the sediment composition and nutrient profile created by local terrigenous inputs (i.e. flood plumes from the Burdekin-Haughton and Ross-Black catchments) produces a distinctive EAM environment at Orpheus Island. Furthermore, it appears that Harpacticoida and Ostracoda are abundant EAM taxa in all locations, therefore it is the paucity of Gastropoda and Polychaeta at the Turtle Islands and Lizard Island locations that most clearly drove the distinctly different ordination groups.

Although the sediment volumes were not significantly different among locations, it is likely that it was the composition (i.e. particle size or nutrient profiles) rather than volume, *per se*, that most heavily influenced the abundance of certain taxa and thus, community composition. In this regard, the effect of cyclonic activity on the GBR may also be important. Cyclones subject the reef to substantial hydrodynamic action, causing resuspension and flushing of sediment from the reef, especially in shallow waters (Wolanski et al. 2005). As the majority of the fringing reef of Orpheus Island is less than 10 m depth, extensive resuspension and removal of sediment from the reef crest during cyclones is likely. Additionally, extensive flooding is often associated with cyclones, which increases the amount of terrigenous material being flushed out into the GBR lagoon. There is a strong possibility that the sediment profile at Orpheus Island observed in the present study was influenced by the combined effect of Cyclone Tasha's coastal flooding (December 2010) and Cyclone Yasi's winds (February 2011). Nutrients and sediments previously flushed into the GBR lagoon may have been resuspended and re-released by the cyclonic events (Gagan et al. 1987, Gagan et al. 1990, Russ & McCook 1999), causing an increase in the availability of primary producers and subsequently the abundance of primary consumers in the EAM cryptofauna at Orpheus Island. Furthermore, sediments that were previously established within the EAM may have been transplanted due to major wave action (Wolanski et al. 2005). Physical disturbance of the cryptofauna itself is not expected to have a great impact on the populations, as these small organisms are known to recover to pre-disturbance abundances in less than 24 hrs (Sherman & Coull 1980, Johnson et al. 2007).

While the effect of sediment and dissolved nutrients on corals, algae and cryptofauna are well documented at a taxon level, knowledge of the impact of sediment and nutrients on the EAM is in its infancy. The apparent sensitivity of most cryptofauna to sediment emphasises the potential of natural and human-induced modification of sediment and water quality to impact coastal ecosystems. Although the EAM is increasingly recognised as an important contributor to reef processes in terms of productivity of detritus and algae (Klumpp & McKinnon 1992, Wilson et al. 2003, Bonaldo & Bellwood 2011), the present study provides the first, preliminary, account of the likely existence of cross- and along-shelf variation in the cryptofauna of the EAM. Data presented herein provides a baseline by which to compare the condition of EAM communities in the respective locations and indicates that further detailed investigations are required to fully understand spatial and environmental effects on coral reef invertebrates. The present study indicates that EAM cryptofaunas are not uniform across the GBR and that particulate and dissolved nutrient input, sediment loads and position relative to catchment areas may be more important than shelf position in shaping cryptobenthic communities.

Chapter 4: Benthic crustaceans from temperate and tropical ecosystems

Ready for submission as: Kramer MJ, Bellwood DR, Taylor RB & Bellwood O

4.1 Introduction

Crustaceans are a fundamental component of almost all marine and aquatic ecosystems. The diversity of taxa and the vast range of sizes results in a variety of ecological roles, encompassing scavengers, detritivores, carnivores and herbivores (Ruppert et al. 2004). Crustaceans are, in turn, one of the most important sources of energy and nutrition for fishes (Russell 1983, Randall et al. 1997, Chapter 5 this thesis). Although crustaceans are typically cryptic and seldom observed, they are major contributors to the trophic dynamics of both tropical and temperate systems (Choat & Kingett 1982, Williams & Hatcher 1983, Edgar & Shaw 1995a).

Crustaceans have been well studied as a major faunal component of temperate macro-algal habitats (Duffy 1990, Edgar & Shaw 1995b, Taylor & Brown 2006). A range of taxonomic and ecological publications indicate that temperate crustaceans are diverse (Berthelsen et al. 2014), abundant and represent important trophic links between primary producers and fish carnivores (Edgar & Moore 1986, Edgar & Shaw 1995a, Taylor 1998).

In comparison, studies of tropical Crustacea primarily address patterns of biodiversity (Plaisance et al. 2009, Stella et al. 2011b), mutualism with live coral (Pratchett 2001, Stella et al. 2011a, Rouzé et al. 2014), habitat associations (Logan et al. 2008, Enochs 2012, Chapter 2 this thesis) and trophic importance (Klumpp et al. 1988, Carleton & McKinnon 2007, Kramer et al. 2013) from selected coral reef habitats. Recent work on coral reefs has indicated that dead coral and coral rubble harbour very high crustacean abundance, biomass and productivity relative to other reef microhabitats (Chapter 2). A comprehensive understanding of their ecological importance in tropical systems, however, is far from complete.

Despite numerous studies on benthic organisms from temperate and tropical systems, there are relatively few comparative investigations between the two systems. Of the few temperate-tropical comparisons, patterns of herbivorous fishes are relatively well known (Gaines & Lubchenco 1982, Choat 1991, Meekan & Choat 1997, Floeter et al. 2005). Herbivorous fishes decline in diversity and abundance with an increase in latitude, but the reasons are subject to discussion and may simply represent general trends in reef fish biogeography (Meekan & Choat 1997, Bellwood & Wainwright 2002, Floeter et al. 2005).

However, similar information regarding the difference between temperate and tropical benthic crustaceans, particularly their trophic and ecological importance, is lacking.

In the present study, we examine the crustacean fauna of two distinct and well-studied ecosystems: the temperate rocky coast adjacent to the Leigh Marine Laboratory in New Zealand, and the tropical coral reef surrounding Lizard Island on the Great Barrier Reef, Australia. My aim is to compare and contrast the benthic crustacean faunas in these ecosystems in terms of abundance, biomass, mean body size and estimated productivity within three major microhabitats from each location: *Carpophyllum* sp., coralline turf and sand from the temperate ecosystem, and dead coral, the epilithic algal matrix and sand from the tropical ecosystem.

4.2 Methods

Study locations

Tropical samples were collected in February 2013 from reefs around Lizard Island (14°40'40"S, 145°26'55"E), in the northern Great Barrier Reef, Australia (Figure 4.1); samples were collected at 2 – 4 m from two locations, Mermaid Cove and Lagoon Entrance, both of which have a typical fringing reef with a reef flat, crest (at approximately 2 m) and slope terminating at a sandy base at approximately 5 metres. Temperate samples were collected in January 2015 from the coast near the Leigh Marine Laboratory (36°16"09"S, 174°47'54"E) (Fig. 1). Two locations were selected (Waterfall Reef and One Spot Reef) and samples were collected from a depth and reef profile similar to that of a coral reef crest (2 – 4 m).

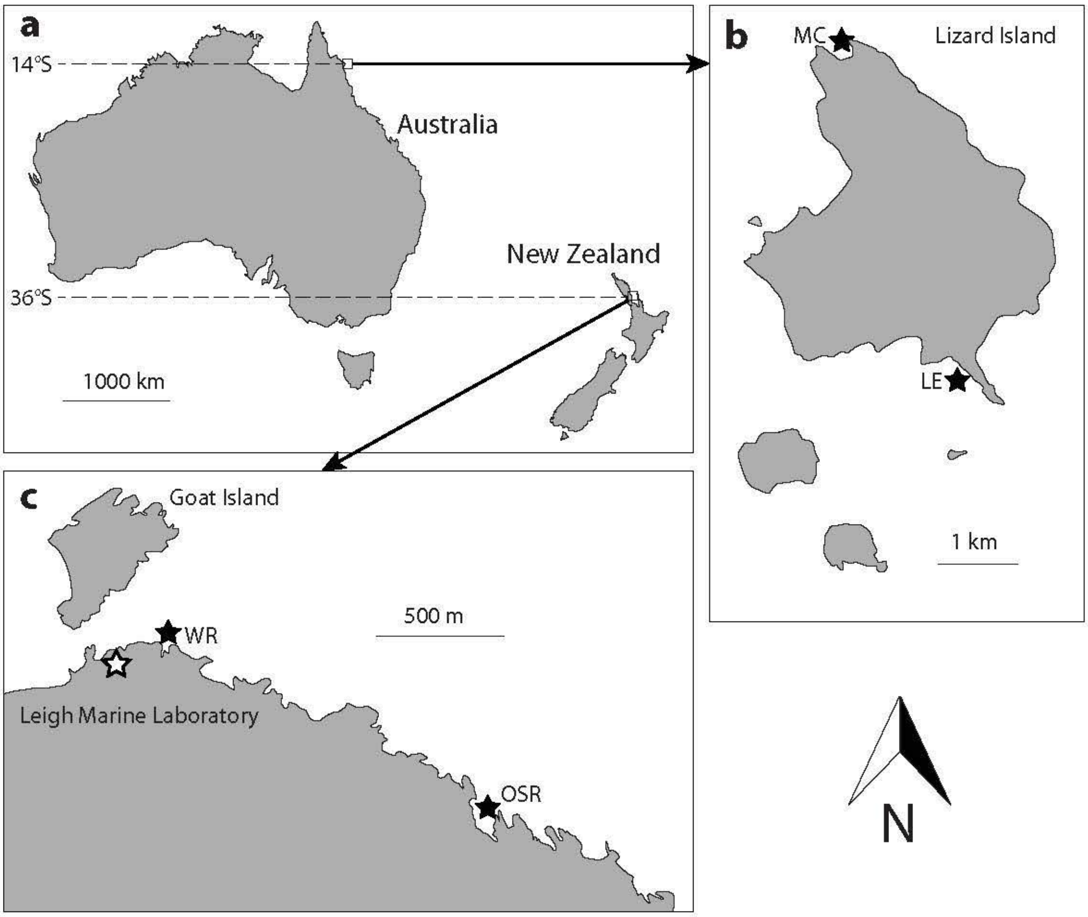

Figure 4.1 Locations from which samples were collected. **a)** Australia and New Zealand, **b)** Lizard Island with sample locations MC (Mermaid Cove) and LE (Lagoon Entrance), **c)** Leigh Marine Laboratory (depicted by open star) and adjacent coastline, with sample locations WR (Waterfall Reef) and OSR (One Spot Reef). Filled stars indicate sample locations. Three sites were sampled within each location.

Sample collection

In each of the two ecosystems, samples were collected from two locations. At each location, three sites were haphazardly selected. Within each site three replicate samples were collected for each of the three microhabitats, yielding a total of 54 samples from each ecosystem and 108 samples overall. All samples were fixed in 4 % buffered formaldehyde in seawater or GLYO-FIXX (Titford & Horenstein 2005) within 30 min of collection. All data for tropical microhabitats are taken from Chapter 2.

Three temperate and three tropical microhabitats were selected for comparison based on their broad structural attributes. Structurally complex microhabitats were represented by dead coral in the tropics and *Carpophyllum* sp. in the temperate location. Dead coral samples consisted of corymbose *Acropora* spp. skeletons that were devoid of live coral tissue but still attached to the reef matrix. These skeletons were previously found to be the primary location for tropical crustaceans (Chapter 2). Individual samples (planar area: 68.0 ± 1.8 cm^2, mean ± S.E., n= 18, measured from photographs analysed in ImageJ) were surrounded by a plastic bag, removed with a hammer and chisel and placed into a sampling jar. Dead coral samples were of a similar volume (127 ± 5 mL displacement volume, n= 18) and complexity. Individual samples were washed three times to remove organisms from the skeleton, fixed and placed into labelled sample jars following Chapter 2.

Carpophyllum sp. is a brown fucoid macroalga and the main upright, complex structure on temperate reefs at 2 – 4 m. Samples of *Carpophyllum* sp. with similar morphologies were collected by enclosing a single plant within a labelled plastic bag then cutting the plant immediately above the holdfast with a knife. The bag was sealed underwater and chilled within 30 min of collection. Samples were washed three times, concentrated on a 60 μm mesh filter and the extracted organisms were fixed, following the method for dead coral. Individual plants were standardised by measuring the circumference of the plant at the widest point to estimate planar surface area (area: 37.2 ± 7.1 cm^2; displacement volume: 257 ± 34 mL, mean ± SE).

Turf microhabitats, which were the tropical epilithic algal matrix (EAM) and temperate coralline turf, were composed of short algae (5-30 mm height) and contained trapped sediment and detritus. EAM samples were collected from horizontal areas of short, filamentous turfing algae, subject to grazing by herbivorous fishes. Similarly, coralline algae samples were collected from horizontal, open areas devoid of macroalgae and dominated by *Corallina officinalis*. For both coralline algae and the EAM, an underwater vacuum sampler was used to collect the organic and inorganic material from an area of 20.4 cm^2 following Kramer et al. (2012). Particles and organisms were drawn into the apparatus and retained on a 60 μm mesh filter that was sealed underwater, and placed into a labelled sampling jar and fixed.

The sand from both Lizard Island and Leigh Marine Reserve was comprised of relatively coarse particles (~0.06-5 mm) and samples were collected in areas of close proximity (1 – 2 m) to hard substrata. Sand from both locations was collected by taking a 10 mm deep core with a 51 mm diameter corer, yielding 20.4 mL of sand. Samples were carefully transferred into a labelled plastic bag and fixed.

Laboratory processes and data analyses

Microhabitats that contained high numbers of organisms or a large volume of inorganic matter (i.e. dead coral, sand, *Carpophyllum* sp. and coralline turf) were subsampled using the Huntsman Marine Laboratory beaker technique (van Guelpen et al. 1982). Subsamples were concentrated on a 60 μm mesh and transferred to a petri dish to be examined under 40 x magnification. A grid was affixed to the base of the petri dish to follow and to prevent counting the same organism twice. Organisms were identified to the same major taxonomic levels as Chapter 2 for comparison (i.e. Amphipoda, Cumacea, Decapoda, Harpacticoida, Isopoda, Ostracoda and Tanaidacea). Cyclopoida were omitted due to very low abundances in both ecosystems, thus having a negligible influence on abundance, biomass or productivity estimates.

The biomass of each major group of organisms was estimated by measuring appropriate dimensions (length, width at widest point and depth) of the first 100 organisms based on their similarity to geometric shapes (i.e. cone: Cumacea; cylinder: Amphipoda, Harpacticoida, Tanaidacea; or cuboid: Decapoda, Isopoda, Ostracoda). Organisms were measured to the nearest 25 μm using an ocular micrometer. Mean volumes for each group were converted to wet-weight biomass based on known density values (Lawrence et al. 1987, Kramer et al. 2012).

Biomass estimates were converted to productivity following the general allometric equation given by Edgar (1990), where $P = 0.0049 \times B^{0.80} \times T^{0.89}$, such that P is productivity (μg AFDW 100cm^{-2} day^{-1}), B is the biomass of an individual taxa in the microhabitat (μg AFDW m^{-2}) and T is water temperature at the time of sampling, which was 29.5 °C in the tropics and 19.0 °C at the temperate location. Productivity estimates of individual taxa from each microhabitat were then multiplied by abundance to give a total productivity estimate. Wet-weight estimates were converted to ash-free dry weight (AFDW) using conversion factors (Ricciardi & Bourget 1998). Water temperature was measured in the field at each location at the time of sampling.

Data from all microhabitats were standardised to 100 cm^2 planar area prior to analysis. Differences in community structure were visualised using a non-metric multidimensional scaling (nMDS) ordination of forth-root transformed data (to reduce the influence of highly abundant harpacticoid copepods) on a Bray-Curtis distance matrix. Community differences were tested using a permutational multivariate analysis of variance (PERMANOVA). Differences in abundance, biomass and productivity between ecosystems and between specific microhabitats were tested with a generalised linear model (GLM) on a negative binomial error distribution. The negative binomial distribution was chosen as data variance exceeded the mean, resulting in substantial over-dispersion. The factors were Location (fixed), Site (random) and Microhabitat (fixed). Tukey HSD multiple comparisons of means were used to compare effects of the GLM post-hoc. Statistical analyses were conducted in R (version 3.1.0) using packages *MASS*, *multcomp* and *vegan*.

4.3 Results

There was a considerable difference in the crustacean assemblages of the Leigh Marine Reserve (temperate) and Lizard Island (tropical) ecosystems (PERMANOVA, $F_{1,106} = 50.18$, $p < 0.001$) and between the different microhabitats (PERMANOVA, $F_{5,\,102} = 43.48$, $p < 0.001$). Harpacticoid copepods and ostracods were characteristic of the EAM, whereas amphipods and cumaceans were more characteristic of the coralline turf and sand (Figure 4.2). Isopods and amphipods were characteristic of *Carpophyllum* sp., whereas isopods, decapods and tanaidaceans were characteristic of dead coral (Figure 4.2). Abundances of crustacean taxa within specific microhabitats are given in the supplemental material (Appendix B, Figure B1).

The overall abundance, biomass and productivity estimates were all significantly different between the Leigh Marine Reserve and Lizard Island systems (GLM, $p < 0.001$ for abundance, $p < 0.01$ for biomass and productivity). Abundance was significantly greater in the tropical location for complex and sand microhabitats, but biomass and productivity estimates were significantly greater in the temperate location for all microhabitats (Figure 4.3a, b, c). The mean size for crustaceans from temperate and tropical locations was 307.5 ± 49.7 µg and 36.9 ± 7.9 µg (mean ± S.E.), respectively (Figure 4.3d). This can be attributed to the high abundances of small Harpacticoida at Lizard Island, and large Amphipoda and Isopoda in Leigh Marine Reserve samples. Harpacticoid copepods were the most abundant taxon in either of the temperate or tropical locations, comprising 45 % and 91 % of the crustacean fauna, respectively (Figure 4.3e).

There were marked differences between microhabitats. The GLM found significant differences amongst microhabitats for all comparisons of abundance, biomass and productivity (GLM, $p < 0.001$). Structurally complex microhabitats generally yielded the highest abundance, biomass and productivity, followed by turfs and finally sand, with few exceptions (Figure 4.3). The greatest abundance of Crustacea was found in tropical dead coral (7779 ± 657 ind. 100cm^{-2}), which were two to seven times greater than all other microhabitats (Figure 4.3a). Of the Leigh Marine Reserve microhabitats, coralline turf yielded the greatest number of crustaceans (3654 ± 216 ind. 100 cm^{-2}) (Figure 4.3a). Significant differences were found between structurally comparable microhabitats (Tukey HSD, $p < 0.001$ for dead coral vs. *Carpophyllum* sp.; $p < 0.001$ for tropical sand vs. temperate sand; $p < 0.01$ for EAM vs. coralline turf), where dead coral, coralline turf and temperate sand had the greatest abundances of crustaceans.

In contrast to abundances, the highest biomass estimates were seen in *Carpophyllum* sp. (1.23 ± 0.23 g 100 cm^{-2}) (Figure 4.3b), largely due to the high biomass of Isopoda (Appendix B, Figure B2). This was not significantly different from dead coral (Tukey HSD, $p = 0.475$), which was dominated by Decapoda (Appendix B, Figure B2). However, significant differences in biomass between microhabitats with similar structure were seen between the EAM vs. coralline turf (Tukey HSD, $p < 0.001$) and tropical vs. temperate sand (Tukey HSD, $p < 0.001$), with Leigh Marine Reserve microhabitats (i.e. coralline turf and temperate sand) having much (5 - 120 times) higher biomass estimates.

Carpophyllum sp. supported higher estimated productivity than dead coral, although this was not significant (Tukey HSD, $p = 0.103$) (dead coral: 2530 ± 364 μg AFDW 100 cm^{-2} day^{-1}, *Carpophyllum* sp.: 4230 ± 723 μg AFDW 100 cm^{-2} day^{-1}) (Figure 4.3c). This may be attributed to Isopoda yielding the highest productivity estimates (Appendix B, Figure B3). Significant differences were found between the EAM and coralline turf (Tukey HSD, $p < 0.001$) and tropical vs. temperate sand (Tukey HSD, $p < 0.001$), where coralline turf and temperate sand are, again, significantly greater. As with biomass, Leigh Marine Reserve microhabitats had 1.7 – 13.6 times higher estimated productivity, when compared to their Lizard Island counterparts.

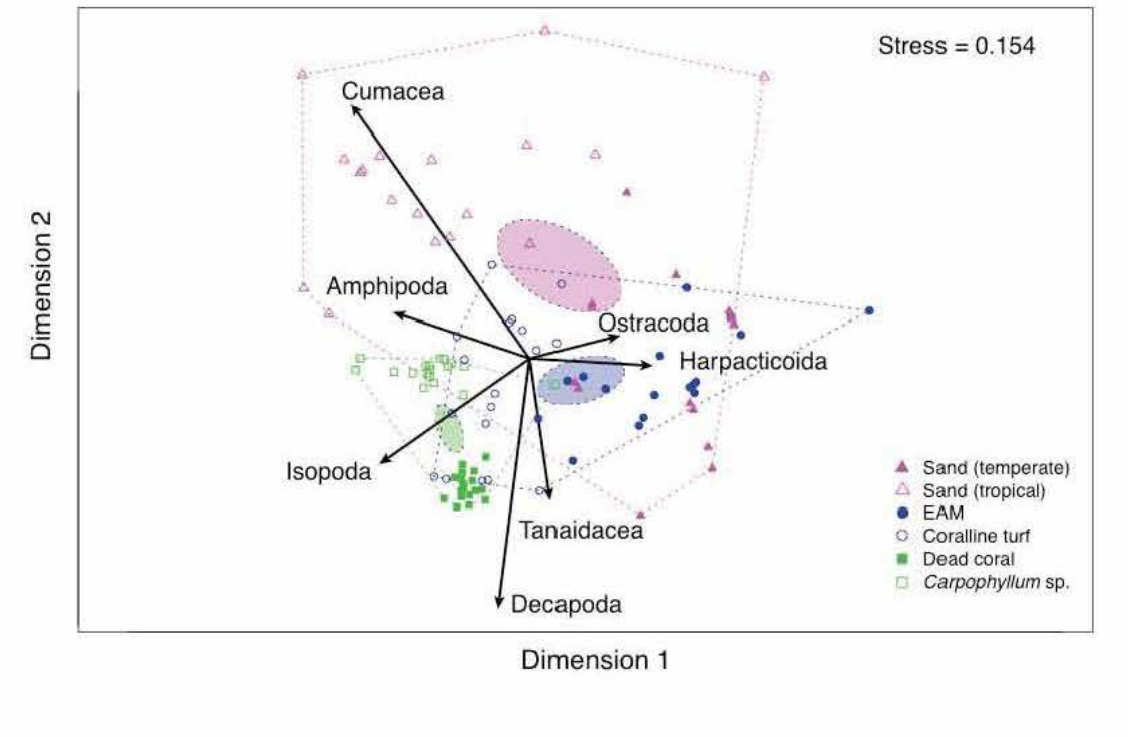

Figure 4.2 Non-metric multidimensional scaling ordination of the crustacean assemblages. Each point indicates an individual sample, and shaded sections represent 95 % confidence ellipses. The difference between tropical and temperate assemblages was significant (PERMANOVA, $F_{1,106} = 50.18$, $p < 0.001$), as was the difference between structural microhabitat groups (PERMANOVA, $F_{5,102} = 43.48$, $p < 0.001$).

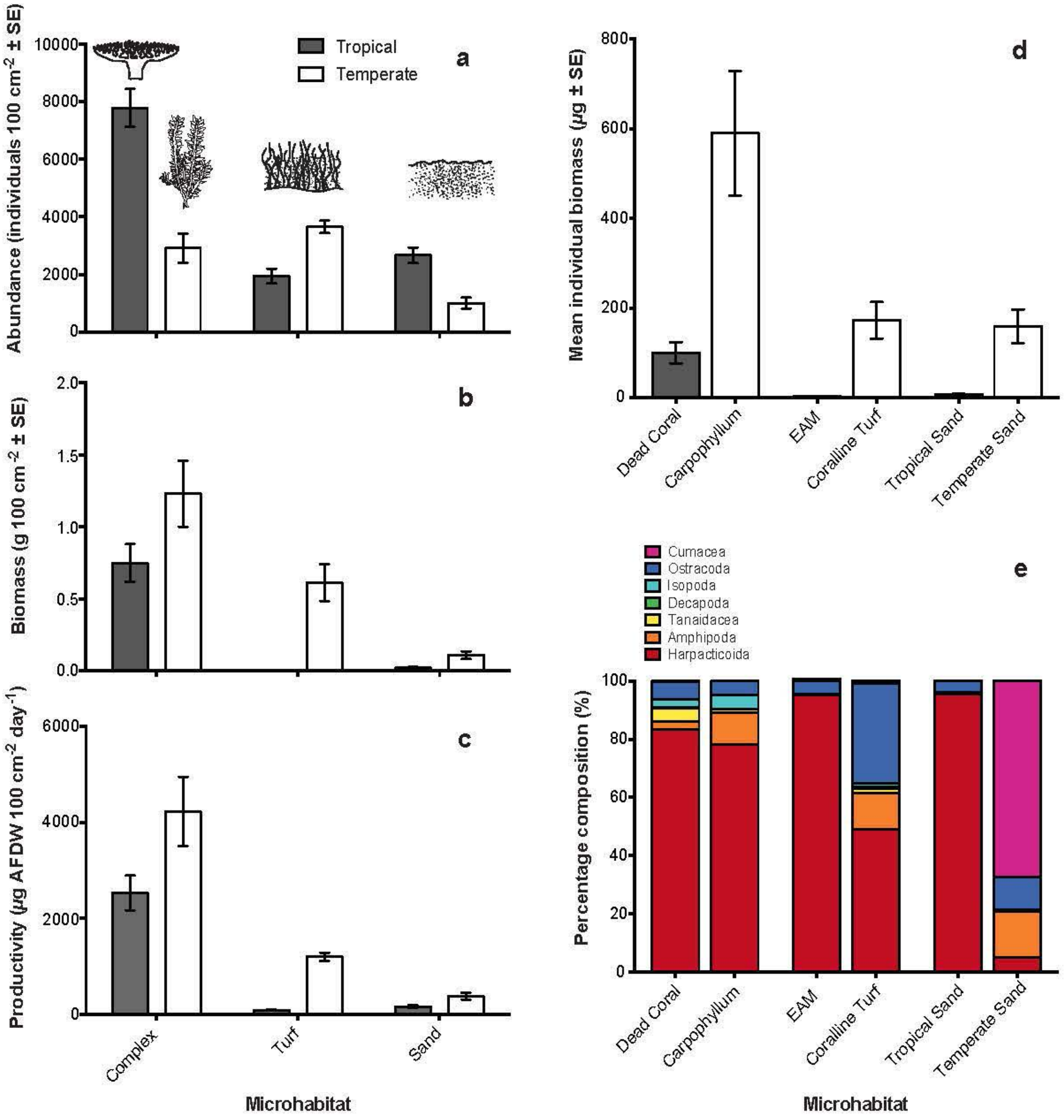

Figure 4.3 Abundance, biomass and productivity estimates along with mean body size and percentage composition of crustaceans within complex (dead coral and *Carpophyllum* sp.), turf (the EAM and coralline turf) and sand microhabitats in tropical and temperate ecosystems. All estimates are mean ± S.E. **a)** Abundance of crustaceans (individuals 100 cm^{-2}). Significant differences were found between *Carpophyllum* sp. – dead coral (Tukey HSD, $p < 0.001$), coralline turf – EAM (Tukey HSD, $p < 0.01$) and tropical sand – temperate sand (Tukey HSD, $p < 0.001$). **b)** Biomass estimates of crustaceans (g 100 cm^{-2}). Significant differences were found between the EAM – coralline turf (Tukey HSD, $p < 0.001$) and tropical sand – temperate sand (Tukey HSD, $p < 0.001$). **c)** Estimated productivity of crustaceans (μg AFDW 100 cm^{-2} day^{-1}) within Lizard Island and Leigh Marine Reserve

microhabitats. Significant differences were found between the EAM and coralline turf (Tukey HSD, $p < 0.001$), and between tropical and temperate sand (Tukey HSD, $p < 0.001$). **d)** Estimate of mean biomass of an individual crustacean from each structural microhabitat. **e)** Percentage composition of the abundance of crustacean taxa within microhabitats.

4.4 Discussion

In the present study, microhabitats of similar basic structure (complex, turf and sand) from Lizard Island and Leigh Marine Reserve supported fundamentally different crustacean communities. Although the Lizard Island microhabitats had a higher mean abundance of crustaceans, the biomass and productivity of crustaceans in Leigh Marine Reserve microhabitats were often much greater. It is likely that these broad differences are influenced in part by the Leigh Marine Reserve (temperate) crustaceans being, on average, larger than the average Lizard Island (tropical) crustacean (tropical crustacean mean size = 0.53 mm vs. 0.96 mm in temperate microhabitats). Specifically, Leigh Marine Reserve samples were characterised by relatively large amphipods and isopods, which contrast with the smaller harpacticoid copepods that dominated the Lizard Island assemblage. These differences may reflect markedly different trophic pathways and habitat characteristics in the two ecosystems.

The importance of structural complexity

In general, and with one exception, structurally complex microhabitats yielded greater crustacean abundance, biomass and productivity than turf, which in turn was greater than sand. This progression is strongly related to the diversity and scale of surface areas. Although sand may have the greatest surface area due to small particle sizes, complexity exists only on a sub-millimetre scale. Taxa associated with sand are often small and/or are capable of burrowing into the sediments (i.e. amphipods, cumaceans, harpacticoids and ostracods). In contrast, turfs present a slightly greater diversity of structure where the sediment trapped within the algae, in addition to the turfing algae, provides complexity on a scale of sub-millimetres to millimetres. More complex habitats such as dead coral and *Carpophyllum* sp., however, have a complexity that ranges from millimetres to centimetres, thus allowing more, and larger, taxa to populate these microhabitats (e.g. amphipods, decapods, isopods and tanaids). There also exists an additional element of dimensionality that should be considered: sands are 1 cm deep, turfs are ~5 – 30 mm deep and complex microhabitats stand ~5 – 35 cm above the substratum, substantially increasing the amount of living space.

In addition, highly complex habitats present a greater diversity of trophic resources for crustaceans in the form of detritus, macroalgae, microalgae and epiphytes (Edgar & Shaw 1995b, Haggitt & Babcock 2003, Glynn & Enochs 2011), whereas food in sand is often restricted to microalgae and detritus (Montagna et al. 1995, Uthicke & Klumpp 1998, Wild et al. 2005). As crustaceans are able to rapidly and efficiently consume the available primary resources (Montagna et al. 1995, Duffy & Hay 2000, Berthelsen &

Taylor 2014), this may also lead to an increase in the biomass and productivity of crustaceans within complex microhabitats. The increased availability of trophic resources in the form of both primary resources and primary consumers within complex habitats represents an important ecosystem feature supporting multiple trophic levels (including carnivorous fishes) in both tropical and temperate systems (Choat & Kingett 1982, Martin-Smith 1993, Taylor 1998, Glynn & Enochs 2011). In both systems, crustaceans appear to be a key element in this trophic pathway.

Lizard Island vs. Leigh Marine Reserve assemblages

While there is only one location within each tropical and temperate ecosystem, the locations used are broadly comparable to the ecosystems in which they are found. The prevalence of small crustaceans, particularly harpacticoids, in other locations on the GBR has also been found for algal turfs (Klumpp et al. 1988), sand (Jacoby & Greenwood 1988) and dead coral microhabitats (Preston & Doherty 1994). Similarly, crustaceans within temperate New Zealand microhabitats are dominated by relatively large amphipods and isopods (Cowles et al. 2009), particularly in coralline turfs (Berthelsen & Taylor 2014) and macroalgae (Taylor 1998). It is important to note, however, that the mesh size used to concentrate the samples in the present study (i.e. 60 μm mesh) was finer than previous tropical studies, which ranged from 100 to 250 μm; whereas in the temperate studies the typical mesh size used was 500 μm, which is likely to have resulted in the loss of smaller harpacticoids. Despite this, the abundances of crustacean taxa collected from Leigh Marine Reserve stated herein are broadly comparable to the published data, specifically pertaining to the crustaceans greater than approximately 500μm. As such, the differences observed herein, using a fine mesh, may be useful to form a basis for a more detailed latitudinal comparison.

Although structure is important, there appears to be an overriding tropical-temperate influence on crustacean communities. Regardless of the microhabitat, tropical systems are dominated by large numbers of harpacticoid copepods, whereas temperate systems contain relatively diverse proportions of all other taxa, particularly those found in turfs and sand. While there are fewer individuals in temperate microhabitats, the biomass and productivity estimates in the present study are much greater than their tropical counterparts.

Particularly noteworthy is the difference in biomass between microhabitats. Although *Carpophyllum* sp. yielded no decapods (which are the most influential contributors to coral reef biomass; Chapter 2), it still had a higher crustacean biomass per unit area than dead coral. The presence of relatively large amphipods and isopods in

Carpophyllum sp. was the major factor contributing to this difference. In comparison, dead coral does not appear to yield the same amount of large taxa, despite being a similarly complex environment with relatively large amounts of primary resources. Instead, it is dominated by numerous small harpacticoid copepods and tanaids that feed on bacteria, microalgae and detritus (Ruppert et al. 2004, Cnudde et al. 2013). It is also possible that the increased oxygen availability in the cooler temperate waters may allow the average size of crustacean taxa to be greater than their tropical counterparts, and therefore produce a higher overall biomass (Chapelle & Peck 2004).

The difference in biomass can also be seen among turf microhabitats, where coralline algae supported a higher biomass and productivity than the EAM. A number of factors may explain these differences. Firstly, coralline turf, which is composed of the calcareous alga *Corallina officinalis*, appears more structurally complex than the short, filamentous algae that characterises the EAM. Secondly, herbivorous and detritivorous fishes heavily graze the EAM, thereby removing both the algae and detritus (Fox & Bellwood 2007), and a substantial number of associated crustaceans (Kramer et al. 2013). In contrast, the structure of coralline turf is left undisturbed by temperate herbivorous fishes and is predominantly utilised by mobile carnivores (Carangidae, Cheilodactylidae, Labridae, Mullidae, Sparidae and Tripterygiidae) that forage for small invertebrates within the turf (Leum & Choat 1980, Choat & Kingett 1982, Coull & Wells 1983, Jones 1984, Taylor 1998). Despite the diversity of crustacean predators, only an estimated 15-38% of the production of crustaceans greater than 1mm in body size are consumed from coralline turf (Taylor 1998). Hence, the relatively high structural complexity of coralline turf likely provides greater protection against predation than the EAM. Finally, although coralline turf is itself unpalatable to fishes and large invertebrates because of its calcareous nature, it supports an abundance of crustaceans due to its propensity to trap detritus and host epiphytes (Berthelsen & Taylor 2014). These factors (fine-scale structure, herbivore grazing disturbance and resource availability) are likely to contribute substantially to the differences between coralline turfs and the EAM.

The sandy microhabitats also show a similar pattern of differences, where Leigh Marine Reserve sand had a lower abundance, but higher biomass and productivity of crustaceans. Again, harpacticoids were more abundant in Lizard Island sand, while cumaceans were substantially greater in Leigh Marine Reserve sand. Biomass was greater in the Leigh Marine Reserve sand for all taxa. These differences, however, are more harder to explain as the sand microhabitats were relatively consistent in terms of structure, and the crustacean inhabitants are all largely microalgal, bacterial or detrital feeders. It is possible, however, that tropical fish taxa that consume small infaunal crustaceans (e.g. the gobies *Valenciennes* spp. and *Amblygobius* spp.) may have a substantial impact on the tropical sand crustacean populations (St John et al. 1989). In contrast, the fish taxa likely to have a predatory impact on crustaceans in temperate sand are Carangidae, Cheilodactylidae, Mullidae, Sparidae and Tripterygiidae (Russell 1983, Ross et al. 2007); however, the impact from these fishes may be seasonally and spatially variable (Choat & Kingett 1982, Ross et al. 2007).

Ecological implications

The productivity estimates suggest that crustaceans from both Lizard Island and Leigh Marine Reserve microhabitats (particularly dead coral, *Carpophyllum* sp. and coralline turf) rapidly consume and convert algal and detrital biomass into useable prey biomass, which provides a highly valuable trophic resource for fishes (Russell 1983, Cowles et al. 2009, Chapter 5 this thesis). Other major invertebrate herbivores (such as echinoids and gastropods) are seldom consumed, except by fishes with specialised morphologies and/or behaviours that enable them to overcome the invertebrate's defences (Russell 1983, Bellwood et al. 2006). As such, benthic crustaceans potentially represent a very important trophic link between primary resources and secondary consumers in both temperate and tropical ecosystems.

It is interesting to note that crustacean biomass is much greater in the microhabitats of the temperate location than the tropical location, whereas herbivorous fish biomass follows the opposite trend (cf. Meekan & Choat 1997, Floeter et al. 2005). It appears that crustaceans complement other herbivorous invertebrates (i.e. echinoids and gastropods; Gaines and Lubchenco 1982) to form the dominant primary consumer assemblage on temperate reefs, whereas fishes are responsible for consuming the majority of algal biomass on tropical coral reefs (Hatcher 1983). Preliminary estimates suggest that tropical crustaceans have a standing biomass approximately 2 – 4 times less than tropical herbivorous fishes (Williams & Hatcher 1983, Depczynski et al. 2007, Chapter 2 this thesis). By contrast, in temperate systems, primary-consumer crustaceans may have 5 – 10 times greater standing biomass than herbivorous fishes (Choat 1991, Meekan & Choat 1997, Floeter et al. 2005, Cowles et al. 2009). However, these comparisons should be treated with caution, as the biomass estimates for temperate fishes are derived from general patterns rather than direct measurements and temperate herbivorous fishes typically have patchy distributions (Meekan & Choat 1997). Nevertheless, crustaceans (i.e. amphipods and isopods) in temperate systems can exert a grazing impact that exceeds fish grazing impact (per unit biomass) by a factor of 1-2 orders of magnitude (Duffy & Hay 2000), although this impact may be dependent on the nature of the local herbivore community (Poore et al. 2009). The impact of crustaceans as major temperate herbivores may be more important than previously assumed and in some cases, may be greater than their fish counterparts.

On tropical coral reefs, detritivorous fishes are an important component of the fish assemblages (Wilson et al. 2003, Goatley & Bellwood 2010). Evolutionarily, these fishes have essentially circumvented the need to consume crustaceans (a trophic link between detritus and carnivores) and instead feed directly on major tropical primary resources (Wilson et al. 2003, Bellwood et al. 2014). Although tropical reef fishes have moved down the food chain to consume microalgae and detritus directly (Bellwood et al. 2014), a similar situation is not observed on temperate reefs. Detritivorous fishes appear to be non-existent on temperate rocky reefs (Choat 1982, Russell 1983). In temperate systems crustaceans are very likely the dominant consumers of detritus and algal epiphytes, with juvenile urchins and small gastropods playing a minor role (Doropoulos et al. 2009, Gacia et al. 2009, Wing & Wing 2015). Thus, crustaceans maintain the important trophic link to higher consumers, as temperate fishes rely heavily on the consumption of crustaceans, and other invertebrates, as major trophic resources (Choat 1982, Russell 1983).

By constructing and comparing structurally similar microhabitats within tropical and temperate ecosystems, we may be able to infer the ecological importance of these microhabitats at a reef-area scale in future investigations. However, it is important to note that the natural benthic composition differs between the two ecosystems. For example, temperate reefs are primarily dominated by large stands of macroalgae, but large areas of coralline turf can be present as an alternate state when macroalgae are absent (Ayling 1981, Connell et al. 2008). In contrast, the EAM often covers the majority of hard substrates on tropical coral reefs, with dead coral being relatively rare (Goatley & Bellwood 2011, Chapter 2 this thesis). Nevertheless, the predominant temperate microhabitats (i.e. macroalgae and coralline turfs) have relatively high crustacean biomass and productivity, whereas the EAM (the dominant tropical habitat) is characterised by high abundance but low biomass. As such, this suggests that the relative availability, and possibly importance, of crustaceans as a major trophic resource in temperate systems may far outweigh that of tropical systems. An exception may occur on some coral reefs which are dominated by *Sargassum* sp., a macroalgae which is common on inshore reefs of the GBR (Wismer et al. 2009) and occasionally degraded systems (Bellwood et al. 2006a). This latitudinally-widespread macroalgae hosts a similar crustacean fauna to *Carpophyllum* sp. in the present study (cf. Martin-Smith 1993), and may, therefore, support an ecosystem driven by crustaceans and present a useful microhabitat of comparison for future studies.

The high availability of crustacean biomass across all three Leigh Marine Reserve microhabitats also suggests that temperate systems may be more robust to environmental change. The most common loss in both temperate and tropical habitats is a decrease in structurally complex microhabitats (Graham et al. 2006, Connell et al. 2008, Goatley & Bellwood 2011). In this situation, the abundance of turf algae and sand will likely ensure that crustaceans will remain a major component of a temperate system, preserving the trophic resource that supports the majority of fishes (Choat & Kingett 1982, Russell 1983). In contrast, a major change in benthic assemblage in coral reef systems, i.e. the loss of live corals (which ultimately provide dead coral structure), is likely to result in a major decrease in crustacean biomass and a potential loss of associated crustacean-feeding taxa (Jones & Syms 1998, Bellwood et al. 2012a). If all three structural types were assumed to be equally abundant, the loss of structure on coral reefs would result in an approximate 97 % drop in crustacean biomass; in temperate systems this would be a loss of just 63 %. Clearly, crustaceans on tropical reefs are highly dependent on the structural complexity provided by coral skeletons.

The crustacean fauna of key microhabitats appears to reflect the dominant primary producers of temperate and tropical ecosystems. Tropical trophic systems are often based on detritus, microalgae and filamentous algae with intensive grazing by fishes, and in such systems, the crustaceans are relatively small. Temperate primary production, however, is often in the form of macroalgae or large coralline turfs and associated epiphytes, hence the crustaceans are correspondingly larger than their tropical counterparts due to increased microhabitat complexity. Most consumption of primary productivity in temperate systems is by invertebrates, including crustaceans. These contrasting temperate and tropical ecosystems reflect substantially different ecological characteristics, particularly in terms of the overall trophic structure and the roles of crustaceans in benthic ecosystems.

Chapter 5: Refining the invertivore: diversity and specialisation in fish predation on coral reef crustaceans

Published as: Kramer MJ, Bellwood O, Fulton CJ & Bellwood DR (2015) *Marine Biology* 162: 1779-1786

5.1 Introduction

Coral reefs are considered to be one of the most productive (Reaka-Kudla 1997) and species-rich ecosystems in the world (Plaisance et al. 2009; Stella et al. 2011). To support such a diverse ecosystem, the organisms that inhabit coral reefs utilise a wide variety of nutritional resources such as algae (Choat & Clements 1998, Bellwood et al. 2004), detritus (Wilson et al. 2003), coral (Cole et al. 2008) and benthic invertebrates (Glynn & Enochs 2011). Fishes are one of the most important consumers on a coral reef, incorporating all major nutritional resources into their respective diets and, as a result, shaping ecosystem dynamics (Bellwood & Wainwright 2002; Wilson et al. 2003; Bellwood et al. 2006).

Fishes are widely considered to be major conduits for the movement of energy from benthic invertebrates to higher trophic levels in aquatic ecosystems (Marnane & Bellwood 2002, Pusey et al. 2004, Depczynski et al. 2007, Kramer et al. 2013). Of the 1,460 species of fish on the Great Barrier Reef (GBR), approximately 70 % feed predominantly on invertebrates (Williams & Hatcher 1983; Randall et al. 1997; Froese & Pauly 2014). Of these invertivores, 60 % incorporate benthic Crustacea in their diet as a primary component (Randall et al. 1997, Froese & Pauly 2014). Furthermore, broad-scale studies on the diet of reef fish assemblages have found that the most important category is crustaceans, which are consumed by over 50 % of the investigated species (Hiatt & Strasburg 1960, Randall 1967, Hobson 1974). Although the number of fish species that feed on Crustacea appears to outnumber all other groups on coral reefs (Randall 1967, Ferry-Graham et al. 2002, Depczynski & Bellwood 2003, Cowman et al. 2009), information on this trophic group is scarce, even within well-studied families such as the Labridae (but see Bellwood et al. 2006b, Ashworth et al. 2014).

Quantitative dietary information is essential in characterising the trophic level of predators, developing tractable trophodynamic models, and for ecosystem-based fisheries models (Pauly et al. 1998, Stergiou & Karpouzi 2002, Smith et al. 2011). To explore the potential role of Crustacea in the diet of reef fishes, we concentrate on one of the most abundant, speciose and widespread marine fish families: the Labridae (Randall et al. 1997; Bellwood et al. 2006). I focussed on adult specimens (i.e. above 50 % of the maximum adult size; cf. Bellwood & Choat 2011) to minimise the confounding effects of ontogenetic shifts in diet and habitat-use (Fulton & Bellwood 2002b), and to focus on the larger individuals within a species that are likely to contribute most to reef trophodynamics (cf. Bonaldo & Bellwood 2008). Our goal was to quantitatively determine the extent and nature of Crustacea in the diets of adult labrids, and to determine whether specialisation in crustacean feeding is apparent among labrid genera.

5.2 Methods

Dietary data were collected from 1,864 adult specimens of 107 species in 30 labrid genera (average of 17 ± 1 individuals per species, sample sizes are given in Appendix C, Table C1). This represents 91 % of wrasse species (Labridae, excluding parrotfishes) and 88 % of genera found on the GBR (Randall et al. 1997, Froese & Pauly 2014). The vast majority of individuals were collected using barrier nets and hand spears from the northern section of the GBR, between Orpheus and Lizard Islands. Species/genera that were uncommon or unavailable on the GBR were represented by specimens from other GBR locations (*Pseudolabrus guentheri* from Heron Island), as well as French Polynesia (*Halichoeres ornatissimus*, *Pseudojuloides cerasinus*) and Papua New Guinea (*Diproctacanthus, Pseudocheilinops, Paracheilinus*). Specimens were placed on ice shortly after capture, and then either the whole intestine or the whole fish (with the lateral abdominal wall removed) was fixed in 10 % buffered seawater formalin for a minimum of four weeks before being transferred to 70 % ethanol for storage and gut content analysis. The contents of the anterior section of the intestine (wrasses have no stomach) were carefully removed under a dissecting microscope, using irrigation to remove all particles, and evenly spread into a single layer of prey items, arranged in a square shape on a petri dish. Contents were then viewed under a dissection microscope (10-40 x magnification) through an overlayed grid of 100 squares, of which 40 random squares were open to view. Dietary items nearest to the upper-right corner of each random square (i.e., point-intersect) were identified to the lowest practical taxonomic level and translated to proportions for data analysis. We subsequently allocated each of these taxa to functional prey types for graphical representation: micro-Crustacea, macro-Crustacea and non-Crustacea (see Appendix C, Table C2 for specific prey items within each category). Micro- and macro-Crustacea are separated based on size and habitat associations: micro-crustaceans are small (< 3 mm) and highly abundant in almost all habitats, whereas macro-crustaceans are large (> 3 mm) and only found in particular habitats such as dead coral or coral rubble (Chapter 2). The standard length of each fish was recorded to the nearest mm. Collections and dissections were conducted under approval from the James Cook University Animal Ethics committee (A650).

Mean proportions (± S.E.) of all identified prey items found within the guts of species were assembled for each wrasse genus. Principal component analysis (PCA) (based on covariance with no pre-transformation) in conjunction with K-means cluster analysis was used to identify major feeding groups within the investigated wrasses (micro-Crustacea, macro-Crustacea and non-Crustacea) and the specific genera associated with each group. Locally weighted scatterplot smoothing (LOESS) regression models were conducted on the relationship between the standard length and the mean proportion of micro- and macro-Crustacea within the gut of each genus. A step function, using a tree model, was used to determine threshold values that separated genera into micro- and macro-crustacean groups (Crawley 2007). All analyses were conducted with the software R (version 3.1.0) and the package *tree.*

5.3 Results

Crustacea were found to be a significant dietary item in all labrid genera examined, except *Diproctacanthus, Labrichthys, Labropsis, Pseudodax, Pteragogus* and *Macropharyngodon* (Figure 5.1). Crustaceans comprised more than 50 % of the diet in most (17 of 30) labrid genera (Figure 5.1), with the diets of a further 7 labrid genera comprising, on average, at least 20 % Crustacea. While 8 labrid genera fed predominantly on macro-Crustacea, 14 genera fed predominantly on micro-Crustacea (Figure 5.2). *Choerodon* and *Coris* consumed similar proportions of macro- and micro-Crustacea (Figure 5.2). Limited among-species variation in the proportion of Crustacea within wrasse gut contents was apparent for most genera. *Gomphosus* and *Novaculichthys* were the greatest consumers of macro-Crustacea (69 - 85 % of prey items in the gut), whereas *Cirrhilabrus*, *Labroides*, *Pseudocoris*, *Stethojulis*, *Pseudocheilinops* and *Paracheilinus* contained the highest proportion (over 70 % of prey items in the gut) of micro-Crustacea (Figure 5.2). Molluscs, coral tissue and fish were the dominant food items in the guts of non-crustacean feeding genera. Non-identifiable material was predominantly amorphous organic matter and comprised 15.6 ± 3.5 % of the diet of all genera.

Groups of micro-, macro- and non-Crustacea predators were confirmed by K-means clustering (Figure 5.3a), against which the prey vectors provided detail of the characteristic crustaceans consumed by each group (Figure 5.3b). The only overlap that occurred between groupings was observed in *Bodianus*, which consumed a slightly greater proportion of non-Crustacea (principally molluscs) than Crustacea (Figure 5.3). Amphipoda and Harpacticoida were characteristic of micro-Crustacea predators, while

Brachyura and Stomatopoda were characteristic of macro-Crustacea predators (Figure 5.3b). Fish body size appeared to play a role in these consumption patterns, with a distinct division between consumption of micro-Crustacea and macro-Crustacea below and above a standard length threshold of 78 to 94 mm, respectively (Figure 5.4).

Crustaceans consumed by micro-crustacean feeders varied from predominantly Amphipoda (*Anampses*, *Halichoeres*, *Pseudojuloides* and *Stethojulis*), Harpacticoida (*Anampses*, *Hemigymnus* and *Stethojulis*) and Calanoida (*Cirrhilabrus*, *Paracheilinus*, *Leptojulis*, *Pseudocoris* and *Thalassoma*) to Isopoda (*Labroides*) (Figure 5.5). Of the identifiable items for macro-crustacean predators, Brachyura was the major prey item in almost all genera. Notably, over 40 % of the prey items consumed by *Gomphosus* and *Novaculichthys* were Brachyura (Figure 5.6).

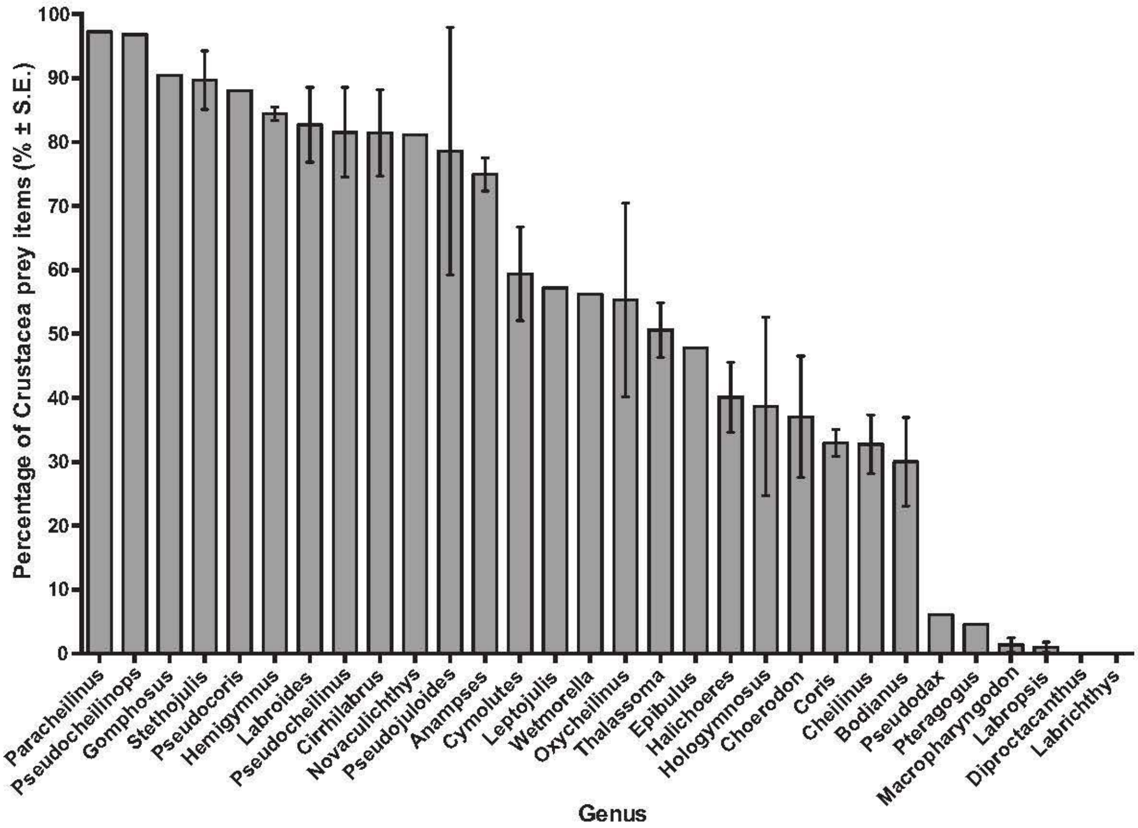

Figure 5.1 Mean percentages (± S.E.) of crustacean prey items in the diet of wrasses. Error bars indicate among-species variation within genera (none for genera with only one species examined). Number of species and individuals within genera are given in Appendix C, Table C1.

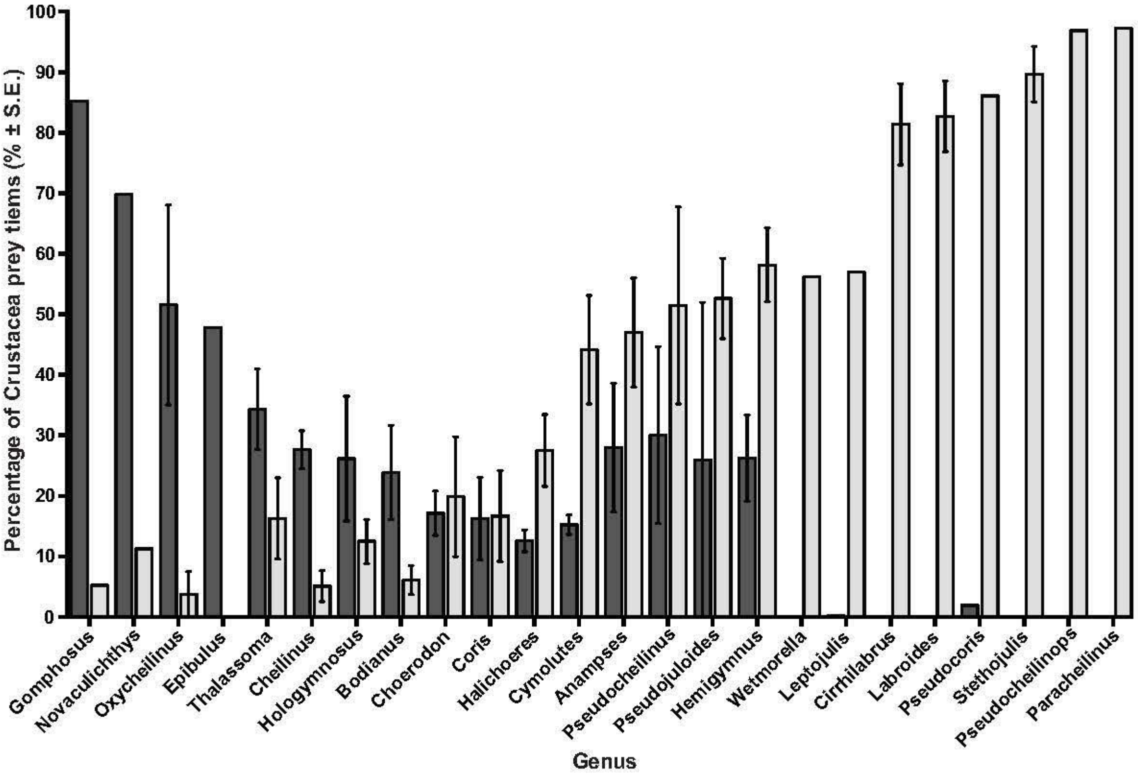

Figure 5.2 Mean percentage (± S.E.) of macro- and micro-Crustacea prey items in the diet of wrasses. Macro-Crustacea are represented by dark bars, micro-Crustacea by light bars. Only genera with > 10 % Crustacea in the diet are included (Figure 5.1).

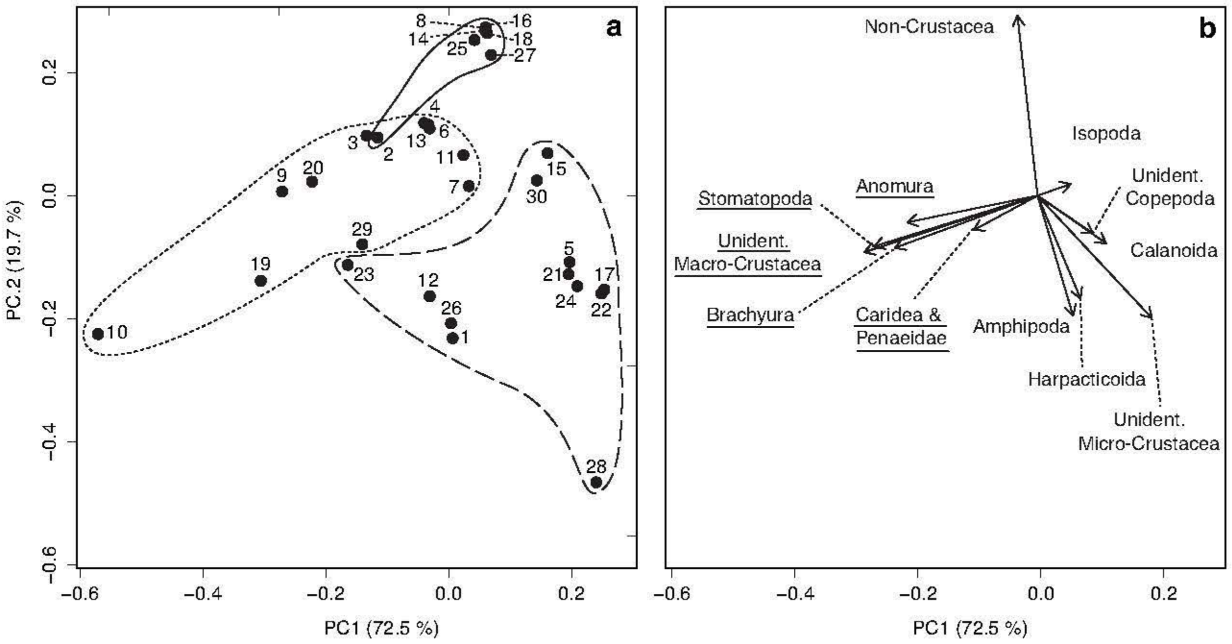

Figure 5.3 Principal components analysis (PCA) of prey items within wrasse genera indicating a) three major groups based on cluster analysis. (K-means clustering) and b) identifying the major prey items (n species and n individuals are given in in ESM Table 1). Non-Crustacea, Macro-Crustacea and Micro-Crustacea feeders are indicated by solid, dotted and dashed lines, respectively. Macro-Crustacea are underlined.

1. *Anampses* 2. *Bodianus* 3. *Cheilinus* 4. *Choerodon* 5. *Cirrhilabrus* 6. *Coris* 7. *Cymolutes* 8. *Diproctacanthus* 9. *Epibulus* 10. *Gomphosus* 11. *Halichoeres* 12. *Hemigymnus* 13. *Hologymnosus* 14. *Labrichthys* 15. *Labroides* 16. *Labropsis* 17. *Leptojulis* 18. *Macropharyngodon* 19. *Novaculichthys* 20. *Oxycheilinus* 21. *Paracheilinus* 22. *Pseudocheilinops* 23. *Pseudocheilinus* 24. *Pseudocoris* 25. *Pseudodax* 26. *Pseudojuloides* 27. *Pteragogus* 28. *Stethojulis* 29. *Thalassoma* 30. *Wetmorella*

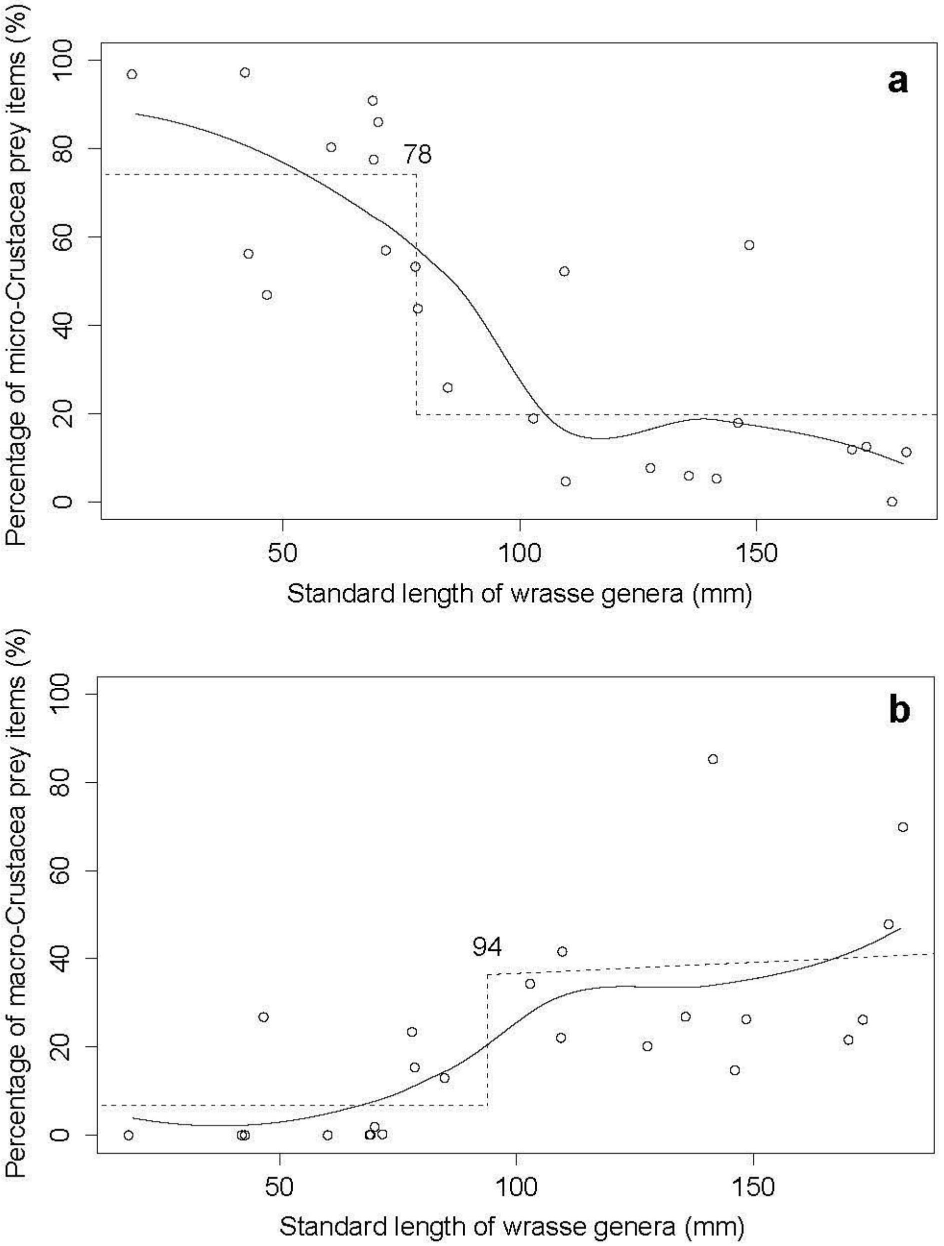

Figure 5.4 Mean percentage of prey items in the gut contents of 24 wrasse genera, separated into **a)** micro-crustacean and **b)** macro-crustacean prey items. The LOESS regression smoothing model is indicated by the solid line. The dashed line and associated number indicates the step threshold at which the data is split between high and low sections of mean percentage. Numbers indicate the standard length (mm) at which the step occurs.

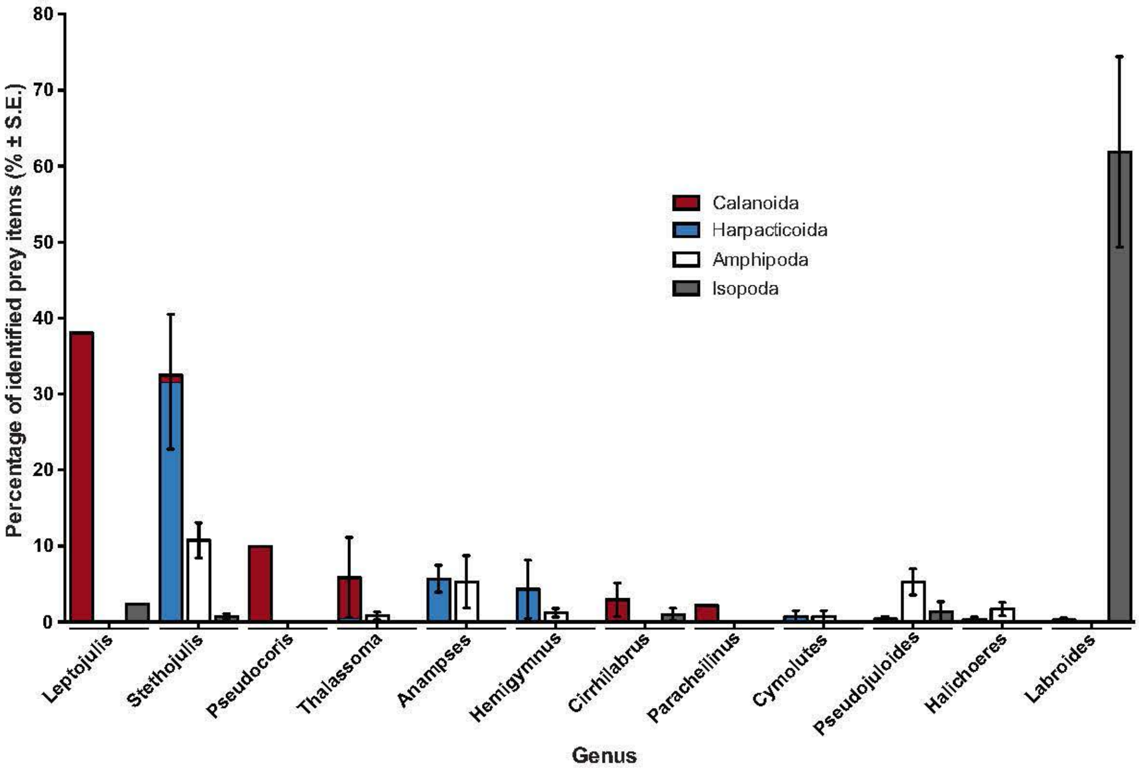

Figure 5.5 Mean percentage (± S.E.) of micro-Crustacea prey items identified in the gut contents of different wrasse genera. Only genera with > 20 % micro-Crustacea prey are included. The dietary category 'unidentified fragments' was excluded to emphasise identifiable prey items. Stacked bars indicate total Copepoda.

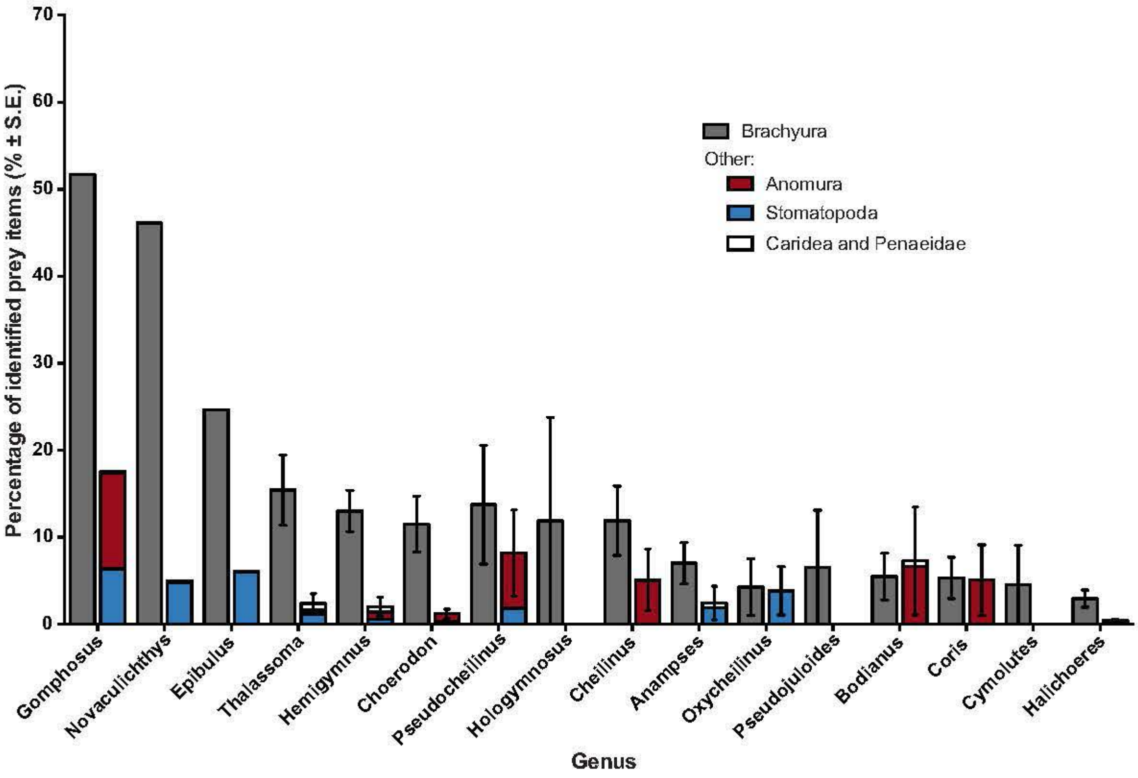

Figure 5.6 Mean percentage (± S.E.) of macro-Crustacea prey items identified in the gut contents of different wrasse genera. Only genera with > 10 % macro-Crustacea are included. The dietary category 'unidentified fragments' was excluded to emphasise identifiable prey items. Stacked bars indicate total non-Brachyura.

5.4 Discussion

Crustaceans are abundant, widespread and diverse members of marine faunas (Ruppert et al. 2004; Stella et al. 2011; Chapter 2 this thesis). They support a diverse group of predators, including the majority of fish species and genera within the diverse and abundant group of fishes in the family Labridae. In exploring the crustaceans consumed by each wrasse genus, we found three different trophic groups, with consequences for broader trophic pathways within reef ecosystems. Predator body size appears to be linked to these patterns: wrasse genera with a mean standard length above 94 mm or below 78 mm predominantly consuming brachyuran crabs or micro-Crustacea, respectively. Nuanced differences in micro-crustacean feeding were also apparent, with different wrasses tending to specialise towards the Amphipoda, Calanoida, Harpacticoida and/or Isopoda. This suggests there are at least two distinct crustacean-based trophic pathways on reefs, and that care is needed when assessing the role of crustacean feeding fishes in coral reef trophodynamics (Depczynski & Bellwood 2003; Graham et al. 2003; Ashworth et al. 2014).

Allometric trends in prey consumption are common in predatory animals, including fishes, where crustaceans appear to be the foundational diet of small fishes (e.g. Alheit & Scheibel 1982, Bellwood 1988, Wen et al. 2012). Throughout the ontogeny of predatory fish species, prey sizes have been found to correlate strongly with body size. Prey items will often progress from copepods to small shrimps, then to crabs and finally to fishes (Wainwright & Richard 1995, Morton et al. 2008, Fukuoka & Yamada 2015). Previous research of fishes from the Haemulidae, Labridae, Lutjanidae, Serranidae and Centrarchidae have found major shifts in prey type at standard lengths of approximately 70 to 100 mm (Wainwright 1988, Wainwright & Richard 1995, Morinière et al. 2003). However, these size thresholds have overwhelmingly been associated with ontogenetic shifts within species, rather than the dietary differences we find here in labrid adults of different mean sizes. Nonetheless, such congruence in predator size with prey relationships suggests an overarching mechanism is at work, such as limitations in the feeding morphology for consumption of larger prey. This may involve the gape of the oral and pharyngeal jaws, or the crushing capability of the levator posterior muscle and the pharyngeal apparatus (Wainwright 1988; Wainwright & Richard 1995). Combined with the trade-off between costs of foraging and prey consumption, and the value of larger prey (Osenberg & Mittelbach 1989, Wainwright & Bellwood 2002), there appears to be powerful selection for size-related divisions in prey consumption. Thus, most predatory species will likely progress through size-appropriate diet shifts until reaching maturity, where the adult body size will be a good indication of the predominant prey items.

Micro-crustaceans were of particularly high importance for small wrasses. The consumption of small Crustacea (i.e. amphipods, copepods and isopods) likely requires minimal foraging effort, as these prey items are highly abundant across all reef substrata, except live corals (Chapter 2). It is important to note, however, that the wrasse genera that feed on these items differ in their preferred micro-crustacean prey. For more demersal wrasses such as *Anampses, Hemigymnus, Pseudojuloides* and *Stethojulis*, benthic amphipods and harpacticoid copepods are the dominant identifiable prey item, while water-column users such as *Cirrhilabrus*, *Leptojulis, Paracheilinus* and *Pseudocoris* prey on planktonic copepods (Fulton et al. 2001, Fulton & Bellwood 2002a). *Labroides* functions as a cleaner, feeding primarily on parasitic isopods located on other fishes (as previously noted by Grutter 2000). These specialisations are likely to be due, at least in part, to the extensive morphological disparity among crustacean-consuming wrasses, which is broader than corallivorous or piscivorous wrasses (Wainwright et al. 2004). Moreover, wrasses often display different patterns of foraging behaviour and microhabitat preferences, which are likely to influence the micro-crustaceans they encounter (Bellwood & Wainwright 2001, Fulton et al. 2001, Fulton & Bellwood 2002b).

A relatively narrow group of macro-crustaceans appear to be consumed by larger wrasse genera. Although fewer wrasse genera utilise macro-crustaceans as a resource, the major predators (*Gomphosus*, *Novaculichthys* and *Epibulus*) all appear to feed predominantly on brachyurans. These genera have particular morphological or behavioural adaptations that enable them to target elusive Crustacea in crevices, coral heads or under coral rubble (Wainwright 1988, Ferry-Graham et al. 2002, Fulton & Bellwood 2002b, Wainwright et al. 2004). For example, *Gomphosus* has a prominent snout that enables it to extract prey from crevices (Fulton & Bellwood 2002b, Wainwright et al. 2004), while *Novaculichthys* is renowned for its ability to move pieces of coral rubble to uncover large, cryptic animals hiding underneath (Randall et al. 1997). Although macro-crustaceans are relatively scarce in comparison to micro-crustaceans (Chapter 2), it is likely that the effort exerted in order to capture macro-crustaceans is justified by the relatively high nutritional and energetic return. Additionally, wrasses that prey on larger crustaceans have the mechanical ability to obtain and process a wide range of hard-shelled prey items, including molluscs. Indeed, the crushing strength of the pharyngeal jaw has been suggested to be an excellent predictor for feeding abilities on hard-shelled prey; fishes with a crushing strength greater than 3-5 N consume a higher proportion of gastropods and hard decapods (Wainwright 1988). Although the relationship between standard length and pharyngeal jaw crushing strength varies between species of *Halichoeres*, it is important to note that the change in diet occurs between 65-120 mm

(Wainwright 1988). This range is consistent with the size-related step threshold between micro- and macro-Crustacea predators observed in the present study.

Coral reef fishes are often grouped into distinct trophic categories, such as herbivores, planktivores and carnivores. The present study suggests that fishes previously classed as invertivores may contain representatives from at least two separate functional pathways: micro- and macro-crustacean predators. Macro-crustacean predators have the ability to feed on a variety of resources as a result of the mechanical advantage obtained with size (e.g. raptorial dentition and large levator posterior muscles for crushing). Although some species predominantly consume micro-crustaceans as a juvenile, upon reaching adult size (> 80 mm) they are likely to feed on other large, shelled invertebrates such as gastropods (Wainwright 1987) and echinoderms (Young & Bellwood 2012) in addition to macro-Crustacea. The present study provides a differentiation within the invertivore group, not unlike the separation of grazers, browsers and excavators within coral reef herbivores (Green & Bellwood 2009). Some finer division of trophic categories is also apparent within micro-crustacean feeders where major prey items reflect feeding modes, for example, harpacticoids and amphipods in *Stethojulis* spp., isopods in *Labroides* spp. and calanoids in *Cirrhilabrus* spp. The predominant type of Crustacea consumed reflects the morphological or behavioural modifications in each genus. *Stethojulis* spp., for example, feed by taking bites from dead substrata and filtering material in the branchial basket, while *Cirrhilabrus* spp. swim above the reef, capturing pelagic copepods using well-developed eyes and a fast, low-strength jaw, and *Labroides* spp. are characteristic cleaners that remove parasitic isopods from fish hosts (Grutter 2000, Wainwright & Bellwood 2002, Wainwright et al. 2004).

Although crustaceans have been generally recognised as a major dietary category for fishes on coral reefs, the present study provides a new perspective with regard to the importance and diversity in consumption of Crustacea by fishes. Notably, there appears to be a substantial division between crustacean predators within the Labridae, with two separate trophic pathways based on micro-Crustacea and macro-Crustacea. Given an underlying connection to predator size (threshold around approximately 85 mm SL), there is potential for this division to be broadly relevant among and within a range of reef fish species. Accordingly, our understanding of invertivore trophic pathways requires a more detailed appreciation of the distinct contributions of invertivores, whereby crustacean-feeding fishes can provide very different contributions to flow of trophic biomass and energy on coral reefs.

Chapter 6: Foraging and microhabitat use by crustacean-feeding wrasses on coral reefs.

Published as: Kramer MJ, Bellwood O and Bellwood DR (2016) *Marine Ecology Progress Series* 548: 277-282

6.1 Introduction

Crustacea are one of the most widespread and abundant groups of marine invertebrates. On coral reefs, Crustacea are both diverse and abundant (Plaisance et al. 2009, Stella et al. 2011, Chapter 2 this thesis). The high diversity of coral reef Crustacea has enabled them to perform a wide range of functional roles, including scavenging dead material, cleaning fishes, clearing sediments and defending coral colonies (Keable 1995, Becker & Grutter 2004, Stewart et al. 2006, Pollock et al. 2012, Rouzé et al. 2014). However, their most influential role is arguably in trophic pathways, as prey for higher-level consumers (Glynn & Enochs 2011, Kramer et al. 2013, Chapter 5 this thesis).

Although crustaceans are abundant on coral reefs, recent work has indicated that the abundance and biomass of Crustacea vary greatly among microhabitats. Dead coral and coral rubble are particularly crustacean-rich, whereas live coral supports very low abundances (Chapter 2). As crustaceans are a valuable source of energy and nutrition for a wide range of fishes (Randall et al. 1997, Chapter 5 this thesis) it is likely that the availability of crustaceans influences the trophic relationship between microhabitats and small benthic predators (Syms & Jones 2000, Berkström et al. 2012). For a fish feeding on crustaceans, therefore, it is expected that an individual will forage primarily from dead corals where the density and biomass of Crustacea is highest (Chapter 2). Information on the relationship between coral reef microhabitats and the foraging habits of crustacean predators, however, is limited (but see Fulton & Bellwood 2002b, Layton and Fulton 2014).

Benthic crustaceans are the dominant prey item for approximately 50 % of all fish species on the Great Barrier Reef (GBR) (Froese & Pauly 2014, Chapter 5 this thesis). One family in particular, the wrasses (Labridae), contains one of the highest proportions of crustacean-feeding species, in addition to being one of the most diverse and abundant families of coral reef fishes (Randall et al. 1997, Bellwood et al. 2006). Wrasses exhibit unusual morphologies and behaviours, allowing them to exploit resources from a wide range of microhabitats (Wainwright et al. 2004, Bellwood et al. 2006). Recent studies also indicate that there is a division between micro- and macro-crustacean feeding taxa (Chapter 5). This trophic division within crustacean predators may influence their choice of microhabitat in which to forage. Foraging patterns of many fishes are governed largely by the capacity of specific microhabitats to yield the preferred prey (Berumen et al. 2005). The morphological and functional diversity within wrasses, therefore, provides an opportunity to investigate the nature of the foraging behaviour of wrasses within coral reef microhabitats, in the context of the distribution of one of their most important prey items: Crustacea.

6.2 Methods

Observations were conducted in February 2014 at Lizard Island (14° 40′ 40″S, 145° 26′ 55″E), a mid-shelf island in the Northern Great Barrier Reef, Australia. Two locations on the fringing reef were selected for surveys (Mermaid Cove and Lagoon Entrance). The present study was conducted at the same locations as Chapter 2, with no ecological disruption occurring in the time between the undertakings of the two studies. The fringing reef at each location was a typical fringing reef with a reef flat, crest and slope that reached a sandy base at approximately 6 m depth. The microhabitats that were present at each location were: live coral (branching, massive and other), dead coral, coral rubble, sand and the EAM (epilithic algal matrix); for detailed microhabitat cover data, please see Appendix A, Figure A4. Foraging surveys occurred between the hours of 0900 and 1600. Survey swims focussed on the crest region in an area that extended approximately 10 m onto the reef flat and down the slope, respectively. A non-overlapping path was swum at each location for an hour and replicated over multiple days. When a wrasse was sighted, the individual was identified to species level, and its activity and microhabitat association in the first three seconds of observation recorded. Activity was defined as either foraging (i.e. searching or feeding) or swimming. This was repeated daily until a minimum of 10 foraging observations were recorded for each species (mean number of foraging observations = 25 per species). Juveniles were not recorded to avoid shifts in diet or habitat during ontogeny (Dahlgren & Eggleston 2000) and care was taken to avoid sampling the same individuals.

Data were analysed using the Sampling Design 1 Protocol A procedure outlined by Manly et al. (2002) to determine habitat selectivity by each species. Confidence intervals (95 % CI) were constructed by applying a Bonferroni inequality adjustment ($z_{\alpha/2I}$, where: $\alpha = 0.05$ and I = number of microhabitats) to the standard error of the standardised selection ratio (Manly et al. 2002). Confidence intervals served to indicate the significance of positive or negative selection. A Chi-square test (df = 1) was also conducted to determine if the microhabitat utilisation patterns differed from random expectations based on microhabitat availability. A non-metric multidimensional scaling (nMDS) ordination was then conducted on a Bray-Curtis matrix of the standardised selection ratios (from the selection index of Manly et al. 2002) to graphically represent habitat selection. Ward's cluster analysis was used to determine clusters, of which six were identified based on a within-groups sum of squares by number of clusters scree plot (Everitt & Hothorn 2010).

6.3 Results

A total of 24 wrasse species were observed foraging during the study period. The proportion of foraging time ranged from 27.5 % in *Thalassoma lunare* to 83.6 % in *Stethojulis bandanensis* (see Appendix D, Table D1).

In terms of habitat selection, 15 (62.5 %) of the 24 species exhibited positive microhabitat selection when foraging. Of the available microhabitats, dead coral, the EAM and coral rubble were each selected for by 5, 6 and 5 species, respectively (Table 6.1). This is in marked contrast to live coral and sand, which were not selected for by any species, and both were negatively selected by 21 species (Table 6.1).

The Ward's clustering method identified six clusters, represented in the nMDS, which were largely associated with particular microhabitats (Figure 6.1). Notably, *N. taeniourus* was the only individual within its group, associating solely with coral rubble. Three species (*C. batuensis*, *H. chloropterus* and *H. trimaculatus*) appear to be grouped in a region of the ordination correlated with both sand and coral rubble, while *A. neoguinaicus*, *E. insidiator*, *H. fasciatus* and *P. hexataenia* all associate strongly with dead coral (Figure 6.1). The remaining two groups include species that appear to be relatively general, but have a tendency to associate with both the EAM and coral rubble (*C. gaimard*, *H. annularis*, *H. margaritaceus*, *H. nebulosus*, *S. bandanensis*, *S. trilineata* and *T. lunare*), and generally with dead coral (*A. geographicus, C. chlorourus, C. fasciatus, G. varius, H. hortulanus, H. melanurus, H. melapterus, T. hardwicke* and *T. jansenii* (Figure 6.1).

Notably, a number of taxa did not appear to associate with any particular microhabitat, either being part of the three central clusters on the nMDS (16 species) or displaying no positive microhabitat selection in the selection index (nine species). The eight taxa that were present in the central clusters and exhibited neutral selection indices included *A. geographicus*, *C. fasciatus*, *C. gaimard*, *G. varius*, *H. hortulanus*, *H. melanurus*, *S. trilineata* and *T. lunare*.

Table 6.1. Selection of foraging microhabitats by species of Labridae: ‘+’ indicates positive selection, ‘-‘ indicates negative selection and ‘o’ indicates neutral selection, based on the foraging index of Manly et al. (2002). The Chi-square test ($df = 1$) denotes whether the species foraging behaviour differed from random based on the abundance of microhabitats. Species are ordered based on their microhabitat selection. Potential macro-crustacean predators (species with mean standard length > 90 mm; cf. Chapter 5) are noted with an ‘M’.

	Dead coral	**Coral rubble**	**EAM**	**Sand**	**Live coral**	**Chi-square test**
Epibulus insidiator **(M)**	+	o	o	-	-	$p < 0.001$
Anampses neoguinaicus **(M)**	+	o	o	-	-	$p < 0.001$
Hemigymnus fasciatus **(M)**	+	o	o	-	-	$p < 0.001$
Pseudocheilinus hexataenia	+	-	-	-	o	$p < 0.001$
Hemigymnus melapterus **(M)**	+	-	+	-	-	$p < 0.001$
Cheilinus chlorourus **(M)**	o	+	-	-	-	$p < 0.05$
Coris batuensis	o	+	o	o	-	$p < 0.001$
Halichoeres chloropterus	o	+	o	o	-	$p < 0.02$
Novaculichthys taeniourus **(M)**	-	+	-	-	-	$p < 0.001$
Stethojulis bandanensis	o	+	o	-	-	$p < 0.002$
Halichoeres marginatus	o	o	+	-	-	$p < 0.001$
Halichoeres nebulosus	-	o	+	-	-	$p < 0.02$
Thalassoma hardwicke **(M)**	o	-	+	-	-	$p < 0.001$
Thalassoma jansenii **(M)**	o	o	+	-	-	$p < 0.01$
Halichoeres hortulanus **(M)**	o	o	o	-	-	$p < 0.005$
Halichoeres melanurus	o	o	o	-	-	$p < 0.001$
Halichoeres trimaculatus	-	o	o	o	-	$p < 0.001$
Halichoeres margaritaceus	o	o	+	-	-	$p > 0.05$ NS
Anampses geographicus **(M)**	o	o	o	-	-	$p > 0.05$ NS
Cheilinus fasciatus **(M)**	o	o	o	-	o	$p > 0.05$ NS
Coris gaimard **(M)**	-	o	o	-	-	$p > 0.05$ NS
Gomphosus varius **(M)**	o	-	o	-	o	$p > 0.05$ NS
Thalassoma lunare **(M)**	o	o	o	-	-	$p > 0.05$ NS
Stethojulis trilineata	o	o	-	-	-	$p > 0.05$ NS

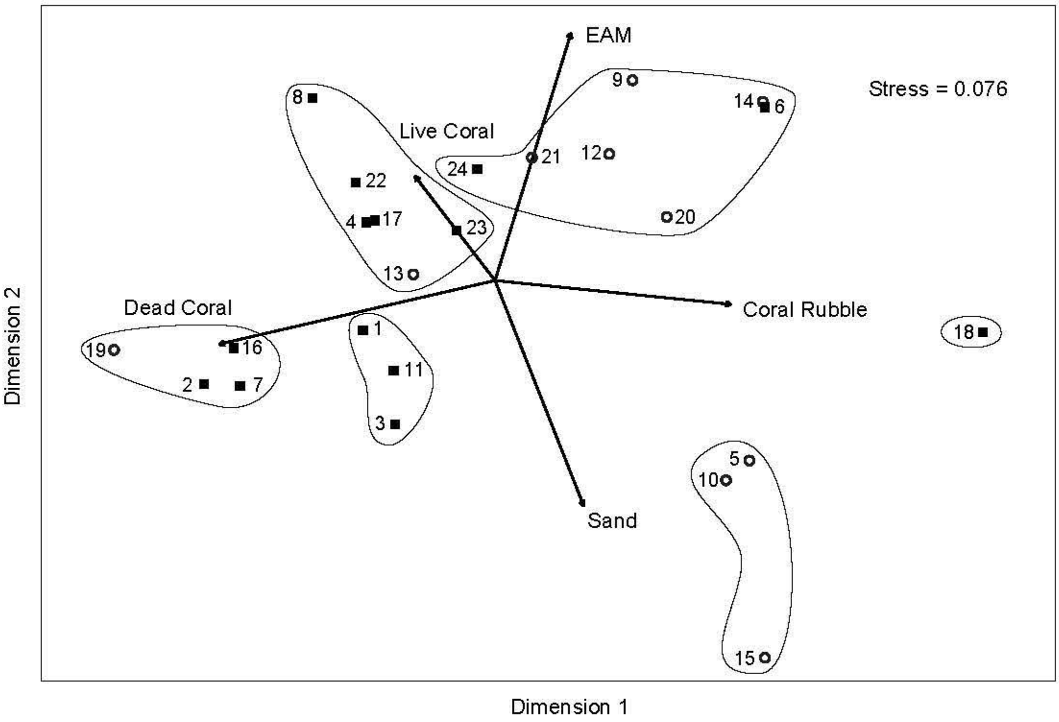

Figure 6.1 Non-Metric Multidimensional Scaling (nMDS) ordination of the microhabitat foraging exhibited by wrasse species based on the standardised selection ratio of Manly et al. (2002). Likely macro-crustacean predators are indicated by squares, micro-crustacean predators are indicated by open circles.

1. *Anampses geographicus*, 2. *Anampses neoguinaicus*, 3. *Cheilinus chlorourus*, 4. *Cheilinus fasciatus*, 5. *Coris batuensis*, 6. *Coris gaimard*, 7. *Epibulus insidiator*, 8. *Gomphosus varius*, 9. *Halichoeres marginatus*, 10. *Halichoeres chloropterus*, 11. *Halichoeres hortulanus*, 12. *Halichoeres margaritaceus*, 13. *Halichoeres melanurus*, 14. *Halichoeres nebulosus*, 15. *Halichoeres trimaculatus*, 16. *Hemigymnus fasciatus*, 17. *Hemigymnus melapterus*, 18. *Novaculichthys taeniourus*, 19. *Pseudocheilinus hexataenia*, 20. *Stethojulis bandanensis*, 21. *Stethojulis trilineata*, 22. *Thalassoma hardwicke*, 23. *Thalassoma jansenii*, 24. *Thalassoma lunare*

6.4 Discussion

Given that dead coral and coral rubble contain 2 to 3 orders of magnitude higher abundances and biomasses of crustaceans than other reef substrata, and live coral also support relatively high biomass values for crustaceans (Chapter 2), one would expect that crustacean-feeding fishes would forage preferentially in these three microhabitats. However, the results of the present study show that less than half of the crustacean-feeding wrasses exhibit positive selection for dead coral and coral rubble combined, and live coral was strongly negatively selected. There was, therefore, a clear mismatch between the microhabitats where crustaceans were most abundant and the foraging locations of their fish predators.

Of the wrasse taxa investigated in this study, 14 can be categorised as macro-crustacean predators (Chapter 5). Surprisingly, however, only 6 species (*A. neoguinaicus, C. chlorourus, E. insidiator, N. taeniourus, H. fasciatus* and *H. melapterus*) selectively forage in dead coral or coral rubble. Of these 6 species, only 2 (*E. insidiator* and *N. taeniourus*) have a diet that is composed predominantly (i.e. greater than 45 %) of macro-Crustacea (Chapter 5). Although macro-crustaceans are most abundant in dead coral and coral rubble, obtaining and consuming these crustaceans appears to be limited to wrasses that have highly modified behavioural or morphological adaptations (Ferry-Graham et al. 2002, Wainwright et al. 2004) which allow them to feed from these microhabitats. The nature of the relationship between crustacean-feeding fishes and macro-Crustacea may be more complex than expected.

Many of the remaining wrasses in this study can be classified as micro-crustacean predators (Chapter 5). However, as with the nominal macro-crustacean feeders, there is no strong selection for microhabitats where the abundance of prey items are found at their highest, i.e. dead coral and coral rubble. These taxa all displayed a broad range of microhabitat foraging associations, including the EAM, dead coral and coral rubble. Only 4 of the 10 species that are nominal micro-crustacean predators foraged from microhabitats yielding the highest abundances of crustaceans. As with the macro-crustacean feeders, there is no clear microhabitat link between crustaceans and their predators.

Wrasses, therefore, appear to be foraging in a manner that does not reflect the densities of their prey, and may be influenced by other factors such as energy expenditure, prey accessibility and predation risk. Previous studies suggest that foraging strategies vary substantially within the Labridae due to differences in behaviour and morphology (Fulton & Bellwood 2002b, 2005, Layton & Fulton 2014). For example, taxa such as *G. varius* and *H. melapterus* swim to patches of dead coral in a very direct manner, maximising their foraging yield and likelihood of encountering prey for the energy expended (Fulton & Bellwood 2002b). In contrast, *Halichoeres* spp. and *Thalassoma* spp. swim haphazardly across a variety of microhabitats that potentially yield prey items (Fulton & Bellwood 2002b). These observations are consistent with the microhabitat preferences presented herein. It appears that species that forage in a haphazard manner, across a variety of microhabitats, tend to feed opportunistically on a wide variety of prey and seldom exhibit positive selection for any single microhabitat (Fulton & Bellwood 2002b, Chapter 2 this thesis).

The relationship between predator and prey may also be moderated by the complexity of the substrata: live and dead corals are often composed of highly complex branching skeletons with relatively deep interstices (Stella et al. 2010, Enochs & Manzello 2012). Although live corals support a relatively high biomass of crustaceans, particularly macro-Crustacea (Chapter 2), no crustacean-feeding wrasses showed selection for this microhabitat, and only 3 species (*P. hexatenia, C. fasciatus,* and *G. varius*) showed neutral selection; 21 were strongly negative. It is highly likely that the complex structural morphology of corals prevents predators from extracting prey (Hixon & Jones 2005). Large crustaceans may, therefore, be present in high abundance within live or dead coral simply because wrasse predators are unable to capture them, except for those species that have specialized morphologies (e.g. *G. varius;* Wainwright et al. 2004). The distribution of large Crustacea in reef microhabitats may reflect realized variation in predation pressure, with the highest values found in areas where predation is least effective. The results of this study suggest that fish forage where predation events are likely to be most efficient, not necessarily where prey items are most abundant. This has also been demonstrated in freshwater systems, where predators are most successful at an intermediate level of habitat complexity (Crowder & Cooper 1982, Warfe & Barmuta 2004).

The risk of predation may also determine where an organism forages (Lima et al. 1985, Cowlishaw 1997). For an individual to forage actively in an open area such as bare EAM, there are few opportunities for shelter and this may represent a dangerous location in which to feed (Hay 1981, Fox & Bellwood 2007). Predation risk in open areas has been suggested as a potential limitation to herbivory (Fox & Bellwood 2007), and predator-avoidance responses amongst a range of herbivores are well documented (Nomikou et al. 2003, Heithaus et al. 2008, Valeix et al. 2009). To counter this, group formation in order to increase vigilance against predation has been suggested in mammals, birds and fishes (Elgar 1989, Magurran 1990, White & Warner 2007). In the present study, this schooling behaviour is apparent in the taxa that positively select EAM (e.g. *Halichoeres* spp.; Nunes et al. 2013).

In contrast, in complex microhabitats such as dead coral, the structural complexity, and therefore shelter, may permit solitary or pairing behaviour, particularly for small fishes (Hixon & Beets 1993, Munday & Jones 1998, Brandl & Bellwood 2014). Complex microhabitats in the form of live and dead corals have been identified as vital refuges for recruiting fishes in order to evade predation (Beukers & Jones 1998, Jones et al. 2004, Hixon & Jones 2005, Graham et al. 2006, Wilson et al. 2008). These reasons may also apply to small wrasses. Thus, for species such as *P. hexataenia* and *C. batuensis,* microhabitat complexity may represent both a profitable foraging location and protection from larger predators. Interestingly, the shelter afforded by complex microhabitats also applies to the protection of crustaceans from their fish predators. The high abundance and biomass of crustaceans in dead corals and other complex microhabitats may reflect this process. Complex microhabitats are, therefore, a refuge for both fish and Crustacea.

In conclusion, foraging behaviour in wrasses is far more complex than one might expect given the distribution of potential prey. In this regard, high diversity coral reef systems appear to reflect their freshwater and temperate counterparts, in that foraging behaviour is influenced by prey availability, the accessibility of microhabitats, and predation risk to the predators. With changing habitat complexities on coral reefs (Graham et al. 2006, Wilson et al. 2006), therefore, it is important to understand the subtleties of interactions between predators, prey and their habitats.

General Discussion

To understand how an ecosystem works, it is essential to know the functional roles of its component organisms. This thesis sheds light on one of the most important groups on coral reefs: benthic Crustacea. My overarching aim was to investigate the distribution and ecological role of coral reef crustaceans in terms of their habitat associations and their trophic importance for higher consumers. I asked five key questions corresponding to the five data chapters in this thesis: where are crustaceans on coral reefs (**Chapter 2**); how do crustacean assemblages vary across the Great Barrier Reef (**Chapter 3**), and between tropical and temperate systems (**Chapter 4**); how important are crustaceans as a dietary resource for fishes (**Chapter 5**), and does crustacean abundance influence fish foraging on coral reefs (**Chapter 6**)? My studies show that crustaceans are numerically abundant on coral reefs, particularly within dead coral and coral rubble. However, contrary to common perceptions, live coral supported very few crustaceans. In terms of spatial differences, the proximity to major riverine outputs appeared to have a strong influence on the crustacean assemblage, while a comparison between tropical and temperate systems points to a fundamental difference in trophic structure and emphasises the importance of structural complexity on coral reefs. My results also confirm that crustaceans are a major component of the diet of labrid fishes on coral reefs and demonstrate that there is a marked division between macro-crustacean and micro-crustacean feeders. However, it appears that the abundance of crustaceans within specific microhabitats is not the sole factor that governs wrasse foraging behaviour, with morphological and behavioural factors possibly contributing to subtleties in foraging patterns.

7.1 The ecological importance of benthic Crustacea

Investigating the abundance, biomass and productivity of crustaceans from different microhabitats and across various spatial scales has provided a strong base from which to investigate the trophic relationships of crustaceans with higher consumers. An important feature of the crustacean assemblages on a coral reef is the dominance of small taxa such as harpacticoids and amphipods. In contrast, 'popular' taxa (i.e. coral-obligate decapods) were the minority, and were only found in specific live branching coral microhabitats. Although coral-obligate fauna are admired for their colour, relatively large size and association with corals, they may not contribute to the trophic ecology of a coral reef to the same degree as the less colourful, smaller and more abundant taxa. Overall, it appears that the contribution of large, colourful, coral-obligate decapods in the diet of fishes is minimal (Hobson 1974), even for coral-dwelling predators such as Cirrhitidae and Caracanthidae (Leray et al. 2015).

Crustaceans are consistently the most important prey item for the majority of fishes, for probably all marine ecosystems, from the poles to the equator (Randall 1967, Targett 1981, Choat 1982, Russell 1983, Edgar & Shaw 1995a, Froese & Pauly 2014). On coral reefs, almost all of the fish families that compose the cryptofaunal community consume crustaceans as a major component of their diet (Depczynski & Bellwood 2003, Kramer et al. 2013). Most of these fishes are less than 50 mm (Ackerman & Bellwood 2000) and their productivity outweighs that of larger groups (Depczynski et al. 2007). It is very likely that the highly nutritional nature (Ajiboye et al. 2011) and ready availability of small crustaceans are influential factors that support this predatory trophic pathway, which has been suggested to be one of the most substantial conduits of energy on coral reefs (Depczynski et al. 2007).

These findings suggest that the most familiar, popular and photogenic crustaceans may not be a major component of the trophic network of a coral reef; rather, the smaller, more cryptic taxa are likely to be the most important prey items. This has trophic implications, because the majority of crustaceans that are important prey items are herbivores (amphipods and isopods), micro-herbivores (harpacticoids and tanaidaceans) or detritivores (amphipods, harpacticoids and tanaidaceans) (Brawley & Adey 1981, Duffy & Hay 1991, Ruppert et al. 2004, Cnudde et al. 2015). As such, these organisms represent an important link in the trophic pathway stemming from benthic primary producers. The rapid conversion of algae and detritus into consumable crustacean biomass is probably a major factor to the rapid assimilation and recycling of nutrients on a coral reef. The paradoxical claim that an oligotrophic coral reef environment can still support high biomass likely stems from the rapid assimilation and recycling of nutrients (Rougerie et al. 1992). Small, highly abundant crustaceans are probably one of the most important factors facilitating this phenomenon (Klumpp & McKinnon 1989, Cnudde et al. 2015).

7.2 Coral reef crustacean ecology: future directions

The most pressing issues affecting marine ecosystems worldwide are the impacts occurring as a consequence of climate change and direct anthropogenic disturbance. Frequently, a consequence of these factors includes some degree of change to the benthic assemblage, whether it is the loss of live coral (Baird & Marshall 2002, Alevizon & Porter 2015), structural complexity (Jones & Syms 1998, Graham et al. 2006), or an increase in macroalgae (Bellwood et al. 2004, Bellwood et al. 2006a) or sediment (Rogers 1990, McCulloch et al. 2003). How these changes to the habitat may affect the resident crustaceans is largely unknown, although the loss of complexity may have the greatest implications for crustacean populations on coral reefs (Chapter 4). In contrast, the loss of live coral may increase the overall crustacean population due to a greater abundance of dead coral, and thereby structural complexity and resource availability in the form of algae, microalgae and detritus. However, this scenario is not sustainable in the long term without the continual replenishment of dead coral by live coral growth, as bioerosion will eventually reduce the structural complexity and probably result in a habitat dominated by the EAM (Chapter 2). Similarly, higher levels of macroalgae and sedimentation may provide analogous short-term benefits to crustaceans. However, crustaceans are only a single component within a greater community of marine organisms. Whether higher trophic levels, particularly those taxa that feed largely on Crustacea, benefit or suffer from the combined effect of increased abundance of prey and a change to the benthic habitat remains to be determined. Current research suggests that crustacean-feeding taxa may be microhabitat generalists that are able to persist in the event of a widespread loss of live coral (Bellwood et al. 2012a, Berkström et al. 2012). The long-term effects of negative benthic impacts on crustacean and associated fish assemblages are uncertain and need to be monitored, as there is potential to produce a persistent change in the coral reef fish assemblage, regardless of the recovery of live coral (Bellwood et al. 2012a).

Coral reefs are dynamic systems that host a wide range of microhabitats. One microhabitat in particular, the macroalgae *Sargassum* spp., was not investigated in this thesis due to its absence at the study locations. However, *Sargassum* spp. is a prominent benthic component of reefs of the inner-shelf GBR (Wismer et al. 2009) and can be a characteristic feature of a degraded reef system (Bellwood et al. 2006a). Despite the association with negative impacts, *Sargassum* spp. hosts an impressive faunal assemblage, including many crustaceans (Martin-Smith 1993, Edgar & Klumpp 2003). It will be of great interest to examine the trophic structure of reefs that have high *Sargassum* spp. coverage and compare these with coral-dominated reefs. I would anticipate that there might be similarities to the tropical-temperate comparison of Chapter 4, where the dominant primary consumers are Crustacea and herbivorous and detritivorous fishes are the minority. On coral reefs with complete loss of live coral and structural complexity, the expansion of *Sargassum* spp. may provide rapid re-establishment of the necessary structural complexity for crustacean resources to maintain a functional and productive trophic network, albeit devoid of carbonate-accreting live coral; a potential scenario that would require careful and comprehensive monitoring before and after the event of a major benthic shift (Hughes 1994, Bellwood et al. 2004).

Trophic importance to higher consumers is arguably the most influential contribution that crustaceans make to coral reefs, and indeed, marine ecosystems in general. Chapters 2 and 5 provide a foundation on which to develop further research and provide comparisons with other ecosystems. However, the biomass, productivity and consumption information would benefit from future studies that directly measure (rather than estimate) the biomass, population turnover, and caloric and nutritional values of coral reef crustaceans. This improved level of detail is required to better understand the impact that crustaceans have on the overall trophic network of a coral reef, particularly in comparison to better-studied trophic groups such as herbivorous, piscivorous and detritivorous fishes. Indeed, the role of crustaceans in contributing to the detritivory and/or herbivory trophic channels may influence our understanding of the relative effects of changing the bottom-up or top-down controls in coral reef ecosystems (Ward et al. 2015). Because crustaceans are a major faunal component of coral reef microhabitats (Chapter 2) and reef fish diets (Chapter 5), this particular trophic pathway may support the most important flow of energy and nutrients for coral reef ecosystems.

7.3 Concluding remarks

Until recently, the focus of much crustacean research on coral reefs has been dominated by taxonomy and systematics. Current environmental and ecological events, however, have emphasised the need to move beyond taxonomic descriptions to begin to understand the roles and functions of each member of an ecosystem. This thesis represents a step in this direction by contributing to a growing awareness of the ecological value of coral reef crustaceans that extends beyond parasitism (Grutter 1999), coral-obligate taxa (Stella et al. 2010), commercial interests (Frisch 2007a) and commensal relationships (Karplus & Thompson 2011). Although there have been some foundational studies conducted on crustacean ecology from the GBR (Klumpp et al. 1988, Preston & Doherty 1994, Carleton & McKinnon 2007, Logan et al. 2008, Stella et al. 2011b) and Eastern Pacific (Enochs et al. 2011, Glynn & Enochs 2011, Enochs 2012, Enochs & Manzello 2012a), the recognition given to this research area does not reflect its potential value for understanding the ecology of coral reefs as a whole. It appears that although some progress is being made in the efforts to investigate coral reef ecosystems from a functional perspective, it is likely that it will take some time before the awareness of the ecology of crustaceans (and other mobile invertebrates) approaches that of the current knowledge for other coral reef groups, i.e. corals and fishes. Regardless, it is becoming increasingly apparent that crustaceans play a greater role in the functioning of coral reef ecosystems than generally perceived. Crustacea may be overlooked, but they are not to be underestimated.

References

Abele LG (1976) Comparative species composition and relative abundance of decapod crustaceans in marine habitats of Panama. *Marine Biology* 38:263-278

Abele LG, Patton WK (1976) The size of coral heads and the community biology of associated decapod crustaceans. *Journal of Biogeography* 3:35-47

Ackerman JL, Bellwood DR (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Marine Ecology Progress Series* 206:227-237

Ajiboye O, Yakubu A, Adams T, Olaji E, Nwogu N (2011) A review of the use of copepods in marine fish larviculture. *Reviews in Fish Biology and Fisheries* 21:225-246

Alevizon WS, Porter JW (2015) Coral loss and fish guild stability on a Caribbean coral reef: 1974–2000. *Environmental Biology of Fishes* 98:1035-1045

Alheit J, Scheibel W (1982) Benthic harpacticoids as a food source for fish. *Marine Biology* 70:141-147

Arias-Gonzalez JE, Delesalle B, Salvat B, Galzin R (1997) Trophic functioning of the Tiahura reef sector, Moorea Island, French Polynesia. *Coral Reefs* 16:231-246

Ashworth EC, Depczynski M, Holmes TH, Wilson SK (2014) Quantitative diet analysis of four mesopredators from a coral reef. *Journal of Fish Biology* 84:1031-1045

Asmus H (1987) Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. *Marine Ecology Progress Series* 39:251-266

Ayling AM (1981) The role of biological disturbance in temperate subtidal encrusting communities. *Ecology* 62:830-847

Bainbridge ZT, Wolanski E, Álvarez-Romero JG, Lewis SE, Brodie JE (2012) Fine sediment and nutrient dynamics related to particle size and floc formation in a Burdekin River flood plume, Australia. *Marine Pollution Bulletin* 65:236-248

Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* 237:133-141

Becker JH, Grutter AS (2004) Cleaner shrimp do clean. *Coral Reefs* 23:515-520

Bellwood DR (1988) Ontogenetic changes in the diet of early post-settlement *Scarus* species (Pices, Scaridae). *Journal of Fish Biology* 33:213-219

Bellwood DR, Baird A, Depczynski M, González-Cabello A, Hoey A, Lefèvre C, Tanner J (2012a) Coral recovery may not herald the return of fishes on damaged coral reefs. *Oecologia* 170:567-573

Bellwood DR, Choat JH (2011) Dangerous demographics: the lack of juvenile humphead parrotfishes *Bolbometopon muricatum* on the Great Barrier Reef. *Coral Reefs* 30:549-554

Bellwood DR, Fulton CJ (2008) Sediment-mediated suppression of herbivory on coral reefs: decreasing resilience to rising sea levels and climate change? *Limnology and Oceanography* 53:2695-2701

Bellwood DR, Hoey AS, Bellwood O, Goatley CHR (2014) Evolution of long-toothed fishes and the changing nature of fish–benthos interactions on coral reefs. *Nature Communications* 5:3144

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* 6:281-285

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429:827-833

Bellwood DR, Hughes TP, Hoey AS (2006a) Sleeping functional group drives coral-reef recovery. *Current Biology* 16:2434-2439

Bellwood DR, Renema W, Rosen BR (2012b) Biodiversity hotspots, evolution and coral reef biogeography: a review. In: Gower D, J., Johnson K, Richardson J, Rosen B, Rüber L, Williams S (eds) *Biotic evolution and environmental change in Southeast Asia*. Cambridge University Press, Cambridge, UK

Bellwood DR, Wainwright P (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs* 20:139-150

Bellwood DR, Wainwright PC (2002) The history and biogeography of fishes on coral reefs. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex system*. Academic Press, San Diego

Bellwood DR, Wainwright PC, Fulton CJ, Hoey AS (2006b) Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B: Biological Sciences* 273:101-107

Berkström C, Jones G, McCormick M, Srinivasan M (2012) Ecological versatility and its importance for the distribution and abundance of coral reef wrasses. *Marine Ecology Progress Series* 461:151-163

Berthelsen AK, Hewitt JE, Taylor RB (2014) Coralline turf-associated fauna are affected more by spatial variability than by host species identity. *Marine Biodiversity* doi: 10.1007/s12526-014-0270-z

Berthelsen AK, Taylor RB (2014) Arthropod mesograzers reduce epiphytic overgrowth of subtidal coralline turf. *Marine Ecology Progress Series* 515:123-132

Berumen ML, Pratchett MS, McCormick MI (2005) Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). *Marine Ecology Progress Series* 287:217-227

Beukers JS, Jones GP (1998) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50-59

Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin* 51:408-414

Bonaldo R, Bellwood D (2011) Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. *Coral Reefs* 30:381-390

Bonaldo RM, Bellwood DR (2008) Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. *Marine Ecology Progress Series* 360:237-244

Boxshall GA, Huys R (1989) New tantulocarid, *Stygotantulus stocki*, parasitic on harpacticoid copepods, with an analysis of the phylogenetic relationships within the Maxillopoda. *Journal of Crustacean Biology* 9:126-140

Brandl SJ, Bellwood DR (2014) Pair-formation in coral reef fishes: an ecological perspective. *Oceanography and Marine Biology - An Annual Review* 52:1-80

Brawley SH, Adey WH (1981) The effect of micrograzers on algal community structure in a coral reef microcosm. *Marine Biology* 61:167-177

Brodie J, Schroeder T, Rohde K, Faithful J, Masters B, Dekker A, Brando V, Maughan M (2010) Dispersal of suspended sediments and nutrients in the Great Barrier Reef lagoon during river-discharge events: conclusions from satellite remote sensing and concurrent flood-plume sampling. *Marine and Freshwater Research* 61:651-664

Buffan-Dubau E, Carman KR (2000) Diel feeding behavior of meiofauna and their relationships with microalgal resources. *Limnology and Oceanography* 45:381-395

Buffan-Dubau E, de Wit R, Castel J (1996) Feeding selectivity of the harpacticoid copepod *Canuella perplexa* in benthic muddy environments demonstrated by HPLC analyses of chlorin and carotenoid pigments. *Marine Ecology Progress Series* 137:71-82

Carleton JH, McKinnon AD (2007) Resident mysids: secondary production, consumption, and trophic role in a coral reef lagoon. *Marine Ecology Progress Series* 336:89-98

Cebrian J, Shurin JB, Borer ET, Cardinale BJ, Ngai JT, Smith MD, Fagan WF (2009) Producer nutritional quality controls ecosystem trophic structure. *PLoS One* 4:e4929

Chapelle G, Peck LS (2004) Amphipod crustacean size spectra: new insights in the relationship between size and oxygen. *Oikos* 106:167-175

Choat JH (1982) Fish feeding and the structure of benthic communities in temperate waters. *Annual Review of Ecology and Systematics* 13:423-449

Choat JH (1991) The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego

Choat JH, Clements KD (1998) Vertebrate herbivores in marine and terrestrial environments: a nutritional ecology perspective. *Annual Review of Ecology and Systematics* 29:375-403

Choat JH, Clements KD, Robbins WD (2002) The trophic status of herbivorous fishes on coral reefs I: Dietary analyses. *Marine Biology* 140:613-623

Choat JH, Kingett PD (1982) The influence of fish predation on the abundance cycles of an algal turf invertebrate fauna. *Oecologia* 54:88-95

Cnudde C, Moens T, Werbrouck E, Lepoint G, Van Gansbeke D, De Troch M (2015) Trophodynamics of estuarine intertidal harpacticoid copepods based on stable isotope composition and fatty acid profiles. *Marine Ecology Progress Series* 524:225-239

Cnudde C, Moens T, Willems A, Troch M (2013) Substrate-dependent bacterivory by intertidal benthic copepods. *Marine Biology* 160:327-341

Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* 9:286-307

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302-1310

Connell SD, Foster MS, Airoldi L (2014) What are algal turfs? Towards a better description of turfs. *Marine Ecology Progress Series* 495:299-307

Connell SD, Russell BD, Turner DJ, Shepherd SA, Kildea T, Miller D, Airoldi L, Cheshire A (2008) Recovering a lost baseline: missing kelp forests from a metropolitan coast. *Marine Ecology Progress Series* 360:63-72

Cooper TF, Uthicke S, Humphrey C, Fabricius KE (2007) Gradients in water column nutrients, sediment parameters, irradiance and coral reef development in the Whitsunday Region, central Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 74:458-470

Coull B (1970) Shallow water meiobenthos of the Bermuda Platform. *Oecologia* 4:325-357

Coull BC, Wells JBJ (1983) Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. *Ecology* 64:1599-1609

Cowles A, Hewitt JE, Taylor RB (2009) Density, biomass and productivity of small mobile invertebrates in a wide range of coastal habitats. *Marine Ecology Progress Series* 384:175-185

Cowlishaw GUY (1997) Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour* 53:667-686

Cowman PF, Bellwood DR, van Herwerden L (2009) Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. *Molecular Phylogenetics and Evolution* 52:621-631

Crawley MJ (2007) *The R Book*. John Wiley & Sons Ltd., Chichester

Crossman DJ, Choat JH, Clements KD, Hardy T, Jason M (2001) Detritus as food for grazing fishes on coral reefs. *Limnology and Oceanography* 46:1596-1605

Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802-1813

Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227-2240

Danovaro R, Fraschetti S (2002) Meiofaunal vertical zonation on hard-bottoms: comparison with soft-bottom meiofauna. *Marine Ecology Progress Series* 230:159-169

Depczynski M, Bellwood DR (2003) The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series* 256:183-191

Depczynski M, Bellwood DR (2004) Microhabitat utilisation patterns in cryptobenthic coral reef fish communities. *Marine Biology* 145:455-463

Depczynski M, Fulton C, Marnane M, Bellwood D (2007) Life history patterns shape energy allocation among fishes on coral reefs. *Oecologia* 153:111-120

Devlin MJ, Brodie J (2005) Terrestrial discharge into the Great Barrier Reef Lagoon: nutrient behavior in coastal waters. *Marine Pollution Bulletin* 51:9-22

Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1:95-107

Doropoulos C, Hyndes GA, Lavery PS, Tuya F (2009) Dietary preferences of two seagrass inhabiting gastropods: allochthonous vs. autochthonous resources. *Estuarine, Coastal and Shelf Science* 83:13-18

Duffy JE (1990) Amphipods on seaweeds: partners or pests? Oecologia 83:267-276

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 (2000) Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs* 70:237-263

Duffy JE, Macdonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82:2417-2434

Easton LM, Lewis GD, Pearson MN (1997) Virus-like particles associated with dieback symptoms in the brown alga *Ecklonia radiata*. *Diseases of Aquatic Organisms* 30:217-222

Edgar G, Moore P (1986) Macro-algae as habitats for motile macrofauna. *Monografias Biologicas* 4:255-277

Edgar GJ (1990) The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *Journal of Experimental Marine Biology and Ecology* 137:195-214

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

Edgar GJ, Shaw C (1995a) The production and trophic ecology of shallow-water fish assemblages in southern Australia II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* 194:83-106

Edgar GJ, Shaw C (1995b) The production and trophic ecology of shallow-water fish assemblages in southern Australia III. General relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology* 194:107-131

Edgar GJ, Shaw C, Watson GF, Hammond LS (1994) Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* 176:201-226

Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews* 64:13-33

Enochs IC (2012) Motile cryptofauna associated with live and dead coral substrates: implications for coral mortality and framework erosion. *Marine Biology* 159:709-722

Enochs IC, Manzello DP (2012a) Responses of cryptofaunal species richness and trophic potential to coral reef habitat degradation. *Diversity* 4:94-104

Enochs IC, Manzello DP (2012b) Species richness of motile cryptofauna across a gradient of reef framework erosion. *Coral Reefs* 31:653-661

Enochs IC, Toth LT, Brandtneris VW, Afflerbach JC, Manzello DP (2011) Environmental determinants of motile cryptofauna on an eastern Pacific coral reef. *Marine Ecology Progress Series* 438:105-118

Everitt BS, Hothorn T (2010) *A handbook of statistical analyses using R.* CRC Press, Boca Raton, Florida

Fabricius K, De'ath G (2001) Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19:303-309

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50:125-146

Fabricius K, De'ath G, McCook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin* 51:384-398

Ferry-Graham L, Wainwright P, Westneat M, Bellwood D (2002) Mechanisms of benthic prey capture in wrasses (Labridae). *Marine Biology* 141:819-830

Floeter SR, Behrens MD, Ferreira CEL, Paddack MJ, Horn MH (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology* 147:1435-1447

Fox RJ, Bellwood DR (2007) Quantifying herbivory across a coral reef depth gradient. *Marine Ecology Progress Series* 339:49-59

Frisch AJ (2007a) Growth and reproduction of the painted spiny lobster (*Panulirus versicolor*) on the Great Barrier Reef (Australia). *Fisheries Research* 85:61-67

Frisch AJ (2007b) Short- and long-term movements of painted lobster (*Panulirus versicolor*) on a coral reef at Northwest Island, Australia. *Coral Reefs* 26:311-317

Froese R, Pauly D (2014) FishBase, http://www.fishbase.org.

Fukuoka K, Yamada H (2015) Food habits of juvenile tuskfishes (*Choerodon schoenleinii* and *C. anchorago*) in relation to food availability in the shallow waters of Ishigaki Island, Southwestern Japan. *Fisheries Science* 81:331-344

Fulton CJ, Bellwood DR (2002a) Ontogenetic habitat use in labrid fishes: an ecomorpological perspective. *Marine Ecology Progress Series* 236:255-262

Fulton CJ, Bellwood DR (2002b) Patterns of foraging in labrid fishes. *Marine Ecology Progress Series* 226:135-142

Fulton CJ, Bellwood DR (2005) Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnology and Oceanography* 50:255-264

Fulton CJ, Bellwood DR, Wainwright PC (2001) The relationship between swimming ability and habitat use in wrasses (Labridae). *Marine Biology* 139:25-33

Gacia E, Costalago D, Prado P, Piorno D, Tomas F (2009) Mesograzers in *Posidonia oceanica* meadows: an update of data on gastropod-epiphyte-seagrass interactions. *Botanica Marina* 52

Gagan M, Sandstrom M, Chivas A (1987) Restricted terrestrial carbon input to the continental shelf during Cyclone Winifred: implications for terrestrial runoff to the Great Barrier Reef Province. *Coral Reefs* 6:113-119

Gagan MK, Chivas AR, Herczeg AL (1990) Shelf-wide erosion, deposition, and suspended sediment tranport during Cyclone Winifred, central Great Barrier Reef, Australia. *Journal of Sedimentary Petrology* 60:456-470

Gaines SD, Lubchenco J (1982) A unified approach to marine plant-herbivore interactions. II. Biogeography. *Annual Review of Ecology and Systematics* 13:111-138

Giere O (2009) *Meiobenthology: The microscopic motile fauna of aquatic sediments.* Springer Berlin Heidelberg, Berlin

Ginsburg RN (1983) *Geological and biological roles of cavities in coral reefs.* In: Barnes D (ed) Perspectives on Coral Reefs. Brian Clouston, Townsville, Australia

Glynn PW, Enochs IC (2011) Invertebrates and their roles in coral reef ecosystems. In: Dubinsky Z, Stambler N (eds) *Coral reefs: an ecosystem in transition.* Springer Netherlands

Goatley CHR, Bellwood DR (2010) Biologically mediated sediment fluxes on coral reefs: sediment removal and off-reef transportation by the surgeonfish *Ctenochaetus striatus. Marine Ecology Progress Series* 415:237-245

Goatley CHR, Bellwood DR (2011) The roles of dimensionality, canopies and complexity in ecosystem monitoring. *PLoS One* 6:e27307

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP, Daw TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology* 21:1291-1300

Graham NAJ, Wilson SK, Simon J, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 103:8425-8429

Great Barrier Reef Marine Park Authority (2011) *Impacts of tropical cyclone Yasi on the Great Barrier Reef: a report on the findings of a rapid ecological impact assessment, July 2011.* GBRMPA, Townsville

Green AL, Bellwood DR (2009) *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience*. IUCN working group on Climate Change and Coral Reefs, IUCN, Gland, Switzerland

Grutter AS (1999) Infestation dynamics of gnathiid isopod juveniles parasitic on the coral-reef fish *Hemigymnus melapterus* (Labridae). *Marine Biology* 135:545-552

Grutter AS (2000) Ontogenetic variation in the diet of the cleaner fish *Labroides dimidiatus* and its ecological consequences. *Marine Ecology Progress Series* 197:241-246

Haggitt TR, Babcock RC (2003) The role of grazing by the lysianassid amphipod *Orchomenella aahu* in dieback of the kelp *Ecklonia radiata* in north-eastern New Zealand. *Marine Biology* 143:1201-1211

Harrell FE (2014) *The 'Hmisc' package*. Available at https://cran.r-project.org/web/packages/Hmisc/index.html

Hatcher BG (1983) Grazing in coral reef ecosystems. In: Barnes DJ (ed) *Perspectives on coral reefs*. Brian Clouston, Australian Institute of Marine Science, pp.164-179

Hatcher BG (1990) Coral reef primary productivity. A hierarchy of pattern and process. *Trends in Ecology and Evolution* 5:149-155

Hay ME (1981) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquatic Botany* 11:97-109

Hayes J, Goonetilleke A (2012) Building community resilience - Learning from the 2011 floods in Southeast Queensland, Australia. In: Kakimoto R, Yamada F (eds) *8th Annual Conference of International Institutes for Infrastructure, Renewal and Reconstruction*: International Conference on Disaster Management, Kumamoto University, Kumamoto, Japan

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* 23:202-210

Hiatt RW, Strasburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs* 30:65-127

Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63:77-101

Hixon MA, Jones GP (2005) Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* 86:2847-2859

Hobson ES (1974) Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fishery Bulletin* 72:915-1031

Hoey A, Bellwood D (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27:37-47

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547-1551

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929-933

Jacoby CA, Greenwood JG (1988) Spatial, temporal and behavioural patterns in emergence of zooplankton in the lagoon of Heron Reef, Great Barrier Reef, Australia. *Marine Biology* 97:309-328

Johnson GEL, Attrill MJ, Sheehan EV, Somerfield PJ (2007) Recovery of meiofauna communities following mudflat disturbance by trampling associated with crab-tiling. *Marine Environmental Research* 64:409-416

Jones GP (1984) The influence of habitat and behavioural interactions on the local distribution of the wrasse, *Pseudolabrus celidotus*. *Environmental Biology of Fishes* 10:43-57

Jones GP, McCormick MI, Srinivasan M, Eagle JV, Paine RT (2004) Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences of the United States of America* 101:8251-8253

Jones GP, Syms C (1998) Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology* 23:287-297

Karplus I, Thompson AR (2011) The partnership between gobiid fishes and burrowing alpheid shrimps. In: Patzner RA, Van Tassell JL, Kovacic M, Kapoor BG (eds) *The Biology of Gobies*. Science Publishers, New Hampshire

Keable SJ (1995) Structure of the marine invertebrate scavenging guild of a tropical reef ecosystem: field studies at Lizard Island, Queensland, Australia. *Journal of Natural History* 29:27 - 45

Kennedy A, Jacoby C (1999) Biological indicators of marine environmental health: meiofauna – a neglected benthic component? *Environmental Monitoring and Assessment* 54:47-68

Kensley B (1998) Estimates of species diversity of free-living marine isopod crustaceans on coral reefs. *Coral Reefs* 17:83-88

Kiene WE, Hutchings PA (1994) Bioerosion experiments at Lizard Island, Great Barrier Reef. *Coral Reefs* 13:91-98

Kingsford MJ (1992) Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus*, Serranidae). *Coral Reefs* 11:193-198

Klumpp DW, Howard RK, Pollard PC (1989) Trophodynamics and nutritional ecology of seagrass communities. In: Larkum AWD, McComb AJ, Shepherd SA (eds) *Biology of Seagrasses*. Elsevier, Amsterdam

Klumpp DW, McKinnon AD (1989) Temporal and spatial patterns in primary production of a coral-reef epilithic algal community. *Journal of Experimental Marine Biology and Ecology* 131:1-22

Klumpp DW, McKinnon AD (1992) Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. *Marine Ecology Progress Series* 86:77-89

Klumpp DW, McKinnon AD, Mundy CN (1988) Motile cryptofauna of a coral reef - abundance, distribution and trophic potential. *Marine Ecology Progress Series* 45:95-108

Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biol* 6:e54

Kramer MJ, Bellwood DR, Bellwood O (2012) Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef. *Coral Reefs* 31:1007 - 1015

Kramer MJ, Bellwood DR, Bellwood O (2014) Benthic Crustacea on coral reefs: a quantitative survey. *Marine Ecology Progress Series* 511:105-116

Kramer MJ, Bellwood O, Bellwood DR (2013) The trophic importance of algal turfs for coral reef fishes: the crustacean link. *Coral Reefs* 32:575-583

Kramer MJ, Bellwood O, Fulton CJ, Bellwood DR (2015) Refining the invertivore: diversity and specialisation in fish predation on coral reef crustaceans. *Marine Biology* 162:1779-1786

Kroon FJ, Kuhnert PM, Henderson BL, Wilkinson SN, Kinsey-Henderson A, Abbott B, Brodie JE, Turner RDR (2012) River loads of suspended solids, nitrogen, phosphorus and herbicides delivered to the Great Barrier Reef lagoon. *Marine Pollution Bulletin* 65:167-181

Lawrence SG, Malley DF, Findlay WJ, Maclver MA, Delbaere IL (1987) Method for estimating dry weight of freshwater planktonic crustaceans from measures of length and shape. *Canadian Journal of Fisheries and Aquatic Sciences* 44:s264-s274

Layton C, Fulton C (2014) Status-dependent foraging behaviour in coral reef wrasses. *Coral Reefs* 33:345-349

Leray M, Meyer CP, Mills SC (2015) Metabarcoding dietary analysis of coral dwelling predatory fish demonstrates the minor contribution of coral mutualists to their highly partitioned, generalist diet. *PeerJ* 3:e1047

Leum LL, Choat JH (1980) Density and distribution patterns of the temperate marine fish *Cheilodactylus spectabilis* (Cheilodactylidae) in a reef environment. *Marine Biology* 57:327-337

Lewis JB, Snelgrove PVR (1990) Corallum morphology and composition of crustacean cryptofauna of the hermatypic coral *Madracis mirabilis*. *Marine Biology* 106:267-272

Lima SL, Valone TJ, Caraco T (1985) Foraging-efficiency-predation-risk trade-off in the grey squirrel. *Animal Behaviour* 33:155-165

Lindeman RL (1942) The trophic-dynamic aspect of ecology. *Ecology* 23:399-417

Logan D, Townsend KA, Townsend K, Tibbetts IR (2008) Meiofauna sediment relations in leeward slope turf algae of Heron Island reef. *Hydrobiologia* 610:269-276

Magurran AE (1990) The adaptive significance of schooling as an anti-predator defence in fish. *Annales Zoologici Fennici* 27:51-66

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) *Resource selection by animals: statistical analysis and design for field studies*. Kluwer, Nordrecht, The Netherlands

Marnane MJ, Bellwood DR (2002) Diet and nocturnal foraging in cardinalfishes (Apogonidae) at One Tree Reef, Great Barrier Reef, Australia. *Marine Ecology Progress Series* 231:261-268

Martin JW, Davis GE (2001) *An updated classification of the recent Crustacea*, Vol 39. Natural History Museum of Los Angeles County, Los Angeles

Martin-Smith KM (1993) Abundance of mobile epifauna - the role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology* 174:243-260

McCloskey LR (1970) The dynamics of the community associated with a marine scleractinian coral. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 55:13-81

McCook LJ (1996) Effects of herbivores and water quality on *Sargassum* distribution on the central Great Barrier Reef: cross-shelf transplants. *Marine Ecology Progress Series* 139:179-192

McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D (2003) Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* 421:727-730

McLeod IM, Parsons DM, Morrison MA, Van Dijken SG, Taylor RB (2013) Mussel reefs on soft sediments: a severely reduced but important habitat for macroinvertebrates and fishes in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 48:48-59

Meekan MG, Choat JH (1997) Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical reefs. *Marine Biology* 128:373-383

Miller DC, Geider RJ, MacIntyre HL (1996) Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. II. Role in sediment stability and shallow-water food webs. *Estuaries* 19:202-212

Montagna PA, Blanchard GF, Dinet A (1995) Effect of production and biomass of intertidal microphytobenthos on meiofaunal grazing rates. *Journal of Experimental Marine Biology and Ecology* 185:149-165

Morinière ECdl, Pollux BJA, Nagelkerken I, Hemminga MA, Huiskes AHL, Velde Gvd (2003) Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. *Marine Ecology Progress Series* 246:279-289

Morton J, Platell M, Gladstone W (2008) Differences in feeding ecology among three co-occurring species of wrasse (Teleostei: Labridae) on rocky reefs of temperate Australia. *Marine Biology* 154:577-592

Munday PL, Jones GP (1998) The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology - An Annual Review* 36:373-411

Neil DT, Orpin AR, Ridd PV, Yu B (2002) Sediment yield and impacts from river catchments to the Great Barrier Reef lagoon: a review. *Marine and Freshwater Research* 53:733-752

Nomikou M, Janssen A, Sabelis M (2003) Herbivore host plant selection: whitefly learns to avoid host plants that harbour predators of her offspring. *Oecologia* 136:484-488

Nunes JdC, Sampaio CS, Barros F (2013) How wave exposure, group size and habitat complexity influence foraging and population densities in fishes of the genus *Halichoeres* (Perciformes: Labridae) on tropical rocky shores. *Marine Biology* 160:2383-2394

Oksanen J, Kindt R, Legendre P, O'Hara B, Stevens MHH, Oksanen MJ, Suggests M (2007) *The vegan package*. Available at https://cran.r-project.org/web/packages/vegan/index.html

Osenberg CW, Mittelbach GG (1989) Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. *Ecological Monographs* 59:405-432

Pascal PY, Fleeger JW, Boschker HTS, Mitwally HM, Johnson DS (2013) Response of the benthic food web to short- and long-term nutrient enrichment in saltmarsh mudflats. *Marine Ecology Progress Series* 474:27-41

Patton WK (1994) Distribution and ecology of animals associated with branching corals (*Acropora* spp.) from the Great Barrier Reef, Australia. *Bulletin of Marine Science* 55:193-211

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. *Science* 279:860-863

Plaisance L, Caley MJ, Brainard RE, Knowlton N (2011) The diversity of coral reefs: what are we missing? *PLoS One* 6:e25026

Plaisance L, Knowlton N, Paulay G, Meyer C (2009) Reef-associated crustacean fauna: biodiversity estimates using semi-quantitative sampling and DNA barcoding. *Coral Reefs* 28:977-986

Pollock FJ, Katz SM, Bourne DG, Willis BL (2012) *Cymo melanodactylus* crabs slow progression of white syndrome lesions on corals. *Coral Reefs* 32:43-48

Poore AGB, Campbell AH, Steinberg PD (2009) Natural densities of mesograzers fail to limit growth of macroalgae or their epiphytes in a temperate algal bed. *Journal of Ecology* 97:164-175

Post DM (2002) The long and short of food-chain length. *Trends in Ecology and Evolution* 17:269-277

Pratchett MS (2001) Influence of coral symbionts on feeding preferences of crown-of-thorns starfish *Acanthaster planci* in the western Pacific. *Marine Ecology Progress Series* 214:111-119

Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes; ecological and economic consequences. *Oceanography and Marine Biology - An Annual Review* 46:251-296

Preston NP, Doherty PJ (1994) Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. II. Cryptofauna. *Marine Ecology Progress Series* 104:27-38

Pusey B, Kennard M, Arthington A (2004) *Freshwater fishes of north-eastern Australia*. CSIRO Publishing, Melbourne

Randall J, Allen G, Steene R (1997) *Fishes of the Great Barrier Reef and Coral Sea*. University of Hawaii Press, Honolulu, Hawaii

Randall JE (1967) *Food habits of reef fishes of the West Indies*. Institute of Marine Sciences, University of Miami

Rasser M, Riegl B (2002) Holocene coral reef rubble and its binding agents. *Coral Reefs* 21:57-72

Reaka-Kudla ML (1997) The global biodiversity of coral reefs: a comparison with rainforests. In: Reaka-Kudla ML, Wilson DE (eds) *Biodiversity II: Understanding and protecting our biological resources*. Joseph Henry Press, Washington, D.C.

Ricciardi A, Bourget E (1998) Weight-to-weight conversion factors for marine benthic macroinvertebrates. *Marine Ecology Progress Series* 163:245-251

Riddle MJ, Alongi DM, Dayton PK, Hansen JA, Klumpp DW (1990) Detrital pathways in a coral reef lagoon I: Macrofaunal biomass and estimates of production. *Marine Biology* 104:109-118

Roff G, Wabnitz CCC, Harborne AR, Mumby PJ (2013) Macroalgal associations of motile epifaunal invertebrate communities on coral reefs. *Marine Ecology* 34:409-419

Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62:185-202

Ross PM, Thrush SF, Montgomery JC, Walker JW, Parsons DM (2007) Habitat complexity and predation risk determine juvenile snapper (*Pagrus auratus*) and goatfish (*Upeneichthys lineatus*) behaviour and distribution. *Marine and Freshwater Research* 58:1144-1151

Rougerie F, Fagerstrom JA, Andrie C (1992) Geothermal endo-upwelling: a solution to the reef nutrient paradox? *Continental Shelf Research* 12:785-798

Rouzé H, Lecellier G, Mills SC, Planes S, Berteaux-Lecellier V, Stewart H (2014) Juvenile *Trapezia* spp. crabs can increase juvenile host coral survival by protection from predation. *Marine Ecology Progress Series* 515:151-159

Ruppert EE, Fox RS, Barnes RD (2004) *Invertebrate zoology: a functional evolutionary approach*. Brooks/Cole, Belmont, CA

Russ GR (2003) Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs* 22:63-67

Russ GR, McCook LJ (1999) Potential effects of a cyclone on benthic algal production and yield to grazers on coral reefs across the central Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 235:237-254

Russell BC (1983) The food and feeding habits of rocky reef fish of north‐eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 17:121-145

Sammarco P, Risk M, Schwarcz H, Heikoop J (1999) Cross-continental shelf trends in coral δ 15N on the Great Barrier Reef: further consideration of the reef nutrient paradox. *Marine Ecology Progress Series* 180:131-138

Schratzberger M, Gee JM, Rees HL, Boyd SE, Wall CM (2000) The structure and taxonomic composition of sublittoral meiofauna assemblages as an indicator of the status of marine environments. *Journal of the Marine Biological Association of the United Kingdom* 80:969-980

Scott FJ, Russ GR (1987) Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. *Marine Ecology Progress Series* 39:293-304

Shears NT, Babcock RC (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series* 246:1-16

Sherman KM, Coull BC (1980) The response of meiofauna to sediment disturbance. *Journal of Experimental Marine Biology and Ecology* 46:59-71

Shurin JB, Gruner DS, Hillebrand H (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society B: Biological Sciences* 273:1-9

Smith ADM, Brown CJ, Bulman CM, Fulton EA, Johnson P, Kaplan IC, Lozano-Montes H, Mackinson S, Marzloff M, Shannon LJ, Shin Y-J, Tam J (2011) Impacts of fishing low-trophic level species on marine ecosystems. *Science* 333:1147-1150

Spotte S (1996) Supply of regenerated nitrogen to sea anemones by their symbiotic shrimp. *Journal of Experimental Marine Biology and Ecology* 198:27-36

Spotte S (1998) "Cleaner" shrimps? *Helgoländer Meeresunters* 52:59-64

St John J, Jones GP, Sale PF (1989) Distribution and abundance of soft-sediment meiofauna and a predatory goby in a coral reef lagoon. *Coral Reefs* 8:51-57

Stella JS, Jones GP, Pratchett MS (2010) Variation in the structure of epifaunal invertebrate assemblages among coral hosts. *Coral Reefs* 29:957-973

Stella JS, Munday PL, Jones GP (2011a) Effects of coral bleaching on the obligate coral-dwelling crab *Trapezia cymodoce*. *Coral Reefs* 30:719-727

Stella JS, Pratchett MS, Hutchings PA, Jones GP (2011b) Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. *Oceanography and Marine Biology - An Annual Review* 49:43-104

Stergiou K, Karpouzi V (2002) Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries* 11:217-254

Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist* 133:240-256

Stewart H, Holbrook S, Schmitt R, Brooks A (2006) Symbiotic crabs maintain coral health by clearing sediments. *Coral Reefs* 25:609-615

Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81:2714-2729

Takada Y, Abe O, Shibuno T (2007) Colonization patterns of mobile cryptic animals into interstices of coral rubble. *Marine Ecology Progress Series* 343:35-44

Takada Y, Abe O, Shibuno T (2008) Cryptic assemblages in coral-rubble interstices along a terrestrial-sediment gradient. *Coral Reefs* 27:665-675

Targett TE (1981) Trophic ecology and structure of coastal Antarctic fish communities. *Marine Ecology Progress Series* 4:243-263

Taylor RB (1998) Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. *Marine Ecology Progress Series* 172:37-51

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

Taylor RB, Cole RG (1994) Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand. *Marine Ecology Progress Series* 115:271-282

Titford ME, Horenstein MG (2005) Histomorphologic assessment of formalin substitute fixatives for diagnostic surgical pathology. *Archives of Pathology and Laboratory Medicine* 129:502-506

Uthicke S, Altenrath C (2010) Water column nutrients control growth and C : N ratios of symbiont-bearing benthic foraminifera on the Great Barrier Reef, Australia. *Limnology and Oceanography* 55:1681-1696

Uthicke S, Klumpp DW (1998) Microphytobenthos community production at a near-shore coral reef: seasonal variation and response to ammonium recycled by holothurians. *Marine Ecology Progress Series* 169:1-11

Uthicke S, Nobes K (2008) Benthic Foraminifera as ecological indicators for water quality on the Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 78:763-773

Valeix M, Loveridge AJ, Chamaillé-Jammes S, Davidson Z, Murindagomo F, Fritz H, Macdonald DW (2009) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* 90:23-30

van Guelpen L, Markle DF, Duggan DJ (1982) An evaluation of accuracy, precision, and speed of several zooplankton subsampling techniques. *Journal du Conseil* 40:226-236

van Woesik R, Tomascik T, Blake S (1999) Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. *Marine and Freshwater Research* 50:427-440

Vetter EW (1995) Detritus-based patches of high secondary production in the nearshore benthos. *Marine Ecology Progress Series* 120:251-262

Vroom PS (2011) "Coral dominance": a dangerous ecosystem misnomer? *Journal of Marine Biology* 2011:164127. doi: 10.1155/2011/164127

Vytopil E, Willis BL (2001) Epifaunal community structure in *Acropora* spp. (Scleractinia) on the Great Barrier Reef: implications of coral morphology and habitat complexity. *Coral Reefs* 20:281-288

Wainwright PC (1987) Biomechanical limits to ecological performance: mollusc-crushing by the Caribbean hogfish, *Lachnolaimus maximus* (Labridae). *Journal of Zoology* 213:283-297

Wainwright PC (1988) Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. *Ecology* 69:635-645

Wainwright Peter C, Bellwood DR (2002) Ecomorphology of feeding in coral reef fishes. In: Sale PF (ed) *Coral reef fishes: Dynamics and diversity in a complex system*. Academic Press, San Diego

Wainwright PC, Bellwood DR, Westneat MW, Grubich JR, Hoey AS (2004) A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. *Biological Journal of the Linnean Society* 82:1-25

Wainwright PC, Richard BA (1995) Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes* 44:97-113

Walossek D (1995) The Upper Cambrian *Rehbachiella*, its larval development, morphology and significance for the phylogeny of Branchiopoda and Crustacea. *Hydrobiologia* 298:1–13.

Ward CL, McCann KS, Rooney N (2015) HSS revisited: multi-channel processes mediate trophic control across a productivity gradient. *Ecology Letters* 18:1190-1197

Warfe D, Barmuta L (2004) Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* 141:171-178

Wen C, Almany G, Williamson D, Pratchett M, Jones G (2012) Evaluating the effects of marine reserves on diet, prey availability and prey selection by juvenile predatory fishes. *Marine Ecology Progress Series* 469:133-144

White JW, Warner R (2007) Behavioral and energetic costs of group membership in a coral reef fish. *Oecologia* 154:423-433

Wild C, Rasheed M, Jantzen C, Cook P, Struck U, Huettel M, Boetius A (2005) Benthic metabolism and degradation of natural particulate organic matter in carbonate and silicate reef sands of the northern Red Sea. *Marine Ecology Progress Series* 298:69-78

Williams DM, Hatcher AI (1983) Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Marine Ecology Progress Series* 10:239-250

Wills MA, Briggs DEG, Fortey RA (1997) Evolutionary correlates of arthropod tagmosis: scrambled legs. In: Fortey RA, Thomas RH (eds) *Arthropod Relationships*. Chapman & Hall, London, pp.57-65

Wilson SK (2004) Growth, mortality and turnover rates of a small detritivorous fish. *Marine Ecology Progress Series* 284:253-259

Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanography and Marine Biology - An Annual Review* 41:279-309

Wilson SK, Burgess SC, Cheal AJ, Emslie M, Fisher R, Miller I, Polunin NVC, Sweatman HPA (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* 77:220-228

Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* 12:2220-2234

Wing SR, Wing L (2015) Ontogenetic shifts in resource use by the sea urchin *Evechinus chloroticus* across an ecotone. *Marine Ecology Progress Series* 535:177-184

Wismer S, Hoey AS, Bellwood DR (2009) Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Marine Ecology Progress Series* 376:45-54

Wolanski E, Fabricius K, Spagnol S, Brinkman R (2005) Fine sediment budget on an inner-shelf coral-fringed island, Great Barrier Reef of Australia. *Estuarine, Coastal and Shelf Science* 65:153-158

Young MAL, Bellwood DR (2012) Fish predation on sea urchins on the Great Barrier Reef. *Coral Reefs* 31:731-738

Zeller DC (1988) Short-term effects of territoriality of a tropical damselfish and experimental exclusion of large fishes on invertebrates in algal turfs. *Marine Ecology Progress Series* 44:85-93

Zeppilli D, Sarrazin J, Leduc D, Arbizu P, Fontaneto D, Fontanier C, Gooday A, Kristensen R, Ivanenko V, Sørensen M, Vanreusel A, Thébault J, Mea M, Allio N, Andro T, Arvigo A, Castrec J, Danielo M, Foulon V, Fumeron R, Hermabessiere L, Hulot V, James T, Langonne-Augen R, Le Bot T, Long M, Mahabror D, Morel Q, Pantalos M, Pouplard E, Raimondeau L, Rio-Cabello A, Seite S, Traisnel G, Urvoy K, Van Der Stegen T, Weyand M, Fernandes D (2015) Is the meiofauna a good indicator for climate change and anthropogenic impacts? *Marine Biodiversity* 45:505-535

Appendix A

Table A1. Summary of data used to construct figures and conduct analyses (mean ± SE). Columns indicate major microhabitats investigated and rows indicate data type or taxonomic group. Crustacean taxa are underlined. Estimates of abundance, biomass and productivity refer to Crustacea only.

	Dead coral	**Coral rubble**	**Sand**	**EAM**	**Fine-branching live coral**
Microhabitat cover m^2 (95% CI)	0.0589 (0.0115)	0.339 (0.0594)	0.0322 (0.0124)	0.273 (0.0607)	0.101 (0.022)
Abundance ind. 100cm^{-2} (SE)	7838 (662)	6797 (448)	2667 (267)	1964 (255)	6 (1)
Biomass µg 100 cm^{-2} (SE)	750319 (130756)	218783 (33608)	22022 (7726)	4978 (633)	236458 (34434)
Productivity g AFDW 100 cm^{-2} yr^{-1} (SE)	0.924 (0.133)	0.545 (0.071)	0.061 (0.012)	0.032 (0.004)	0.183 (0.027)
Harpacticoida	6487 (621)	5799 (450)	2543 (263)	1854 (246)	4 (1)
Amphipoda	364 (68)	149 (15)	9 (4)	4 (1)	0 (0)
Tanaidacea	80 (364)	40 (149)	14 (9)	3 (4)	1 (0)
Isopoda	213 (30)	158 (24)	0 (0)	2 (1)	0 (0)
Ostracoda	479 (53)	472 (52)	106 (27)	84 (24)	0 (0)
Cumacea	20 (5)	39 (6)	1 (1)	1 (0)	0 (0)
Cyclopoida	59 (10)	95 (15)	0 (0)	17 (3)	0 (0)
Decapoda	14 (3)	8 (2)	1 (0)	1 (0)	2 (0)
Gastropoda	53 (7)	63 (8)	113 (39)	7 (1)	0 (0)
Chaetognatha	13 (5)	48 (8)	0 (0)	1 (1)	0 (0)
Ophiuroida	2 (1)	2 (1)	0 (0)	0 (0)	0 (0)
Pycnogonida	2 (1)	1 (1)	0 (0)	0 (0)	0 (0)
Chironomida	27 (6)	15 (3)	0 (0)	1 (1)	0 (0)
Echinioida	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)
Polychaeta	428 (73)	351 (22)	251 (34)	42 (8)	0 (0)

Table A2. Information used in the calculation of biomass estimates for individual organisms of each crustacean taxon. Estimates are derived from length, width and height of taxa (measured in 25µm increments) and similarity to known geometric shapes.

	Relative shape	Mean volume mm^3 (SE)	Mean mass µg (SE)
Harpacticoida	Cylinder	0.00381 (0.0000883)	2.37 (0.0549)
Amphipoda	Cylinder	0.348 (0.0804)	216.29 (49.97)
Tanaidacea	Cylinder	0.0456 (0.00801)	28.36 (4.982)
Isopoda	Cuboid	0.0306 (0.00305)	19.03 (1.897)
Ostracoda	Cuboid	0.00152 (0.000139)	0.94 (0.086)
Cumacea	Cone	0.0527 (0.00882)	32.8 (5.489)
Cyclopoida	Cone	0.00127 (0.0000597)	0.79 (0.0371)
Decapoda (Rubble)	Cylinder/Cuboid	35.061 (6.759)	21807.616 (4204.088)
Decapoda (Dead coral)	Cylinder/Cuboid	75.094 (20.734)	46707.542 (12896.182)
Decapoda (Branching coral)	Cylinder/Cuboid	245.817 (33.666)	152895.397 (20939.836)

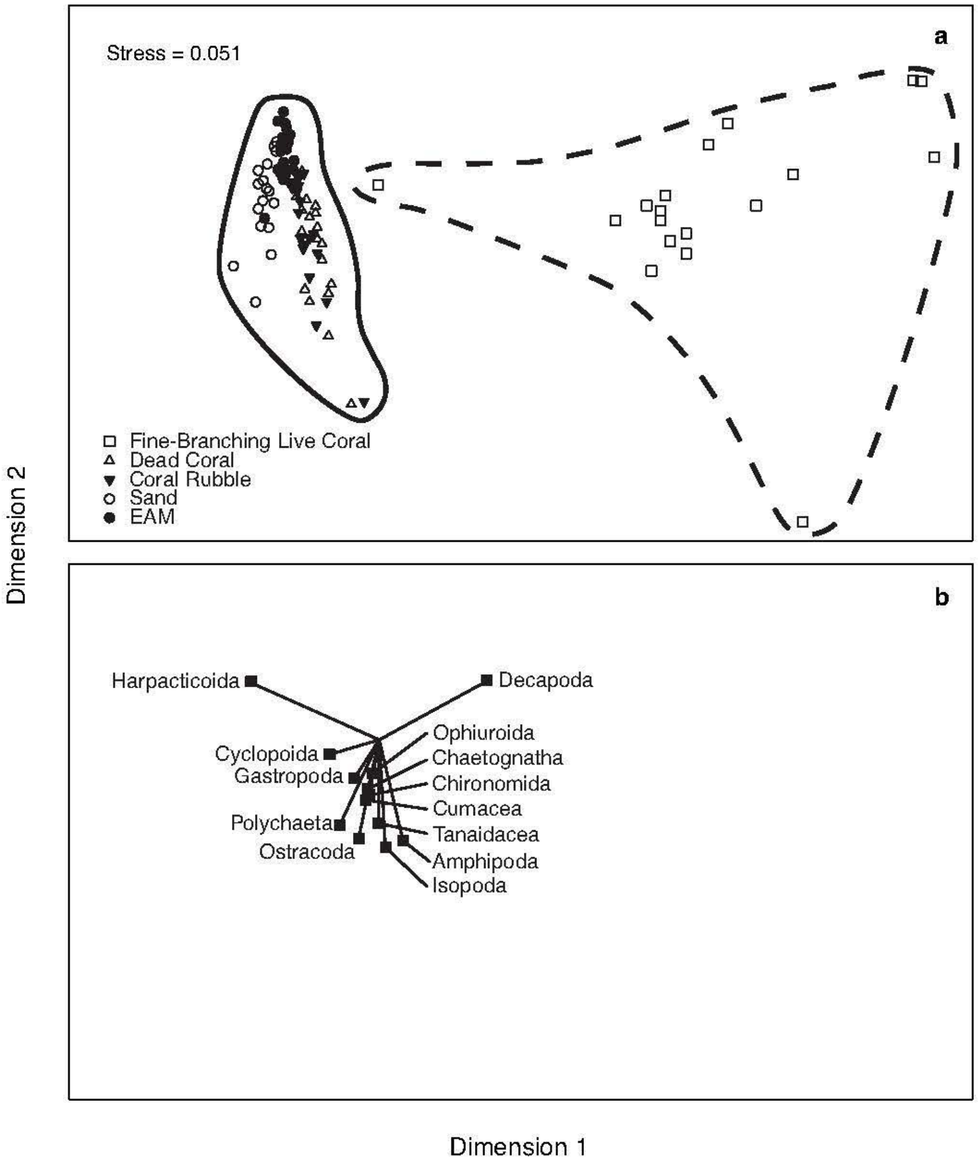

Figure A1. Assemblage structures: all taxa within all habitats, including fine-branching live coral. **a)** Non-metric multidimensional scaling of the proportional abundance of major invertebrate taxa from fine-branching live coral, dead coral, rubble, sand and epilithic algal matrix habitats. **b)** The relative contribution of each taxa to the variation in habitat groupings is represented by the vector points. Points indicate the direction of change and strength (correlation) of taxa to each habitat.

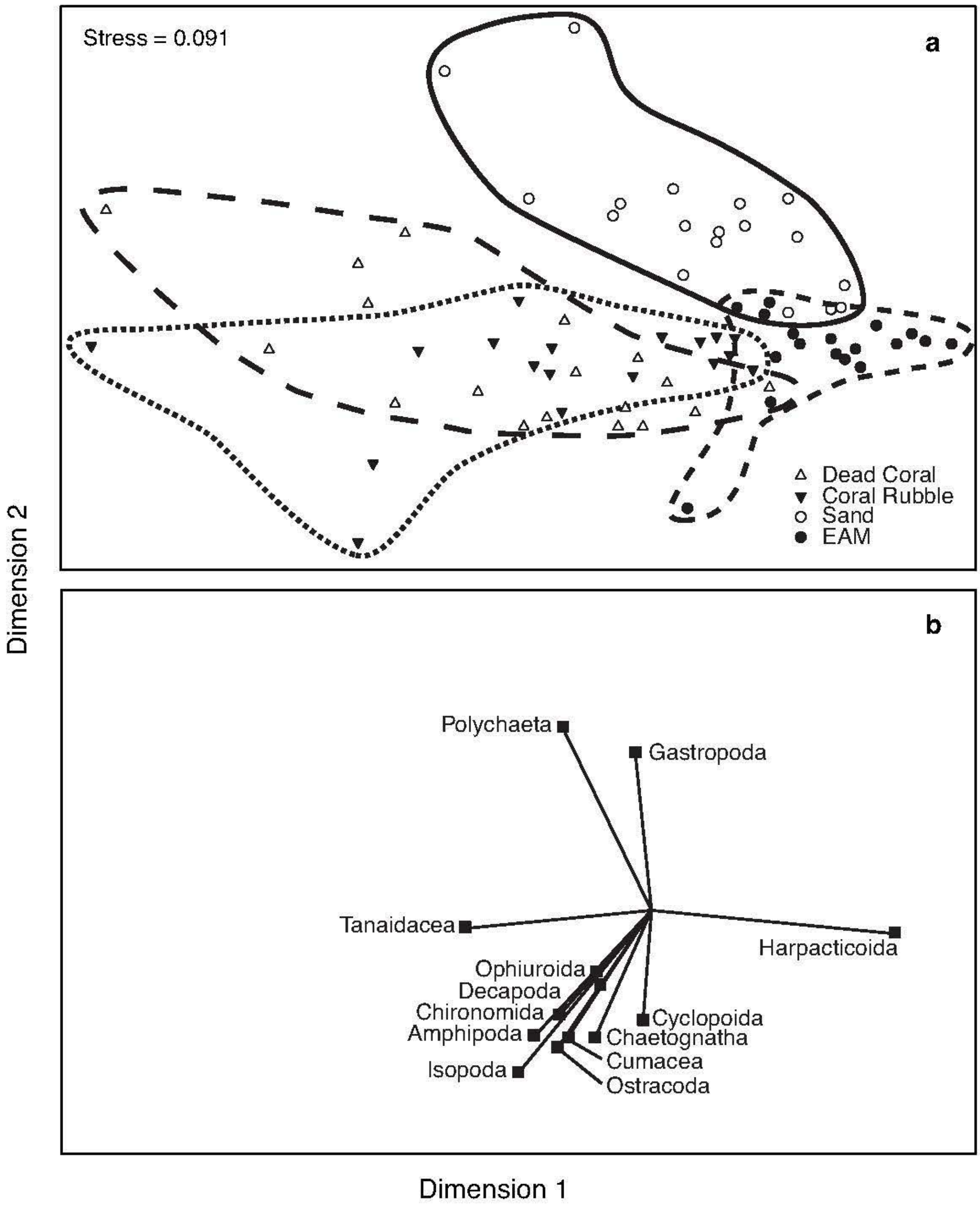

Figure A2. Assemblage structures: All taxa within all habitats, excluding fine-branching live coral. **a)** Non-metric multidimensional scaling of the proportional abundance of major invertebrate taxa from dead coral, rubble, sand and epilithic algal matrix (EAM) habitats. **b)** The relative contribution of each taxa to the variation in habitat groupings is represented by the vector points. Points indicate the direction of change and strength (correlation) of taxa to each habitat.

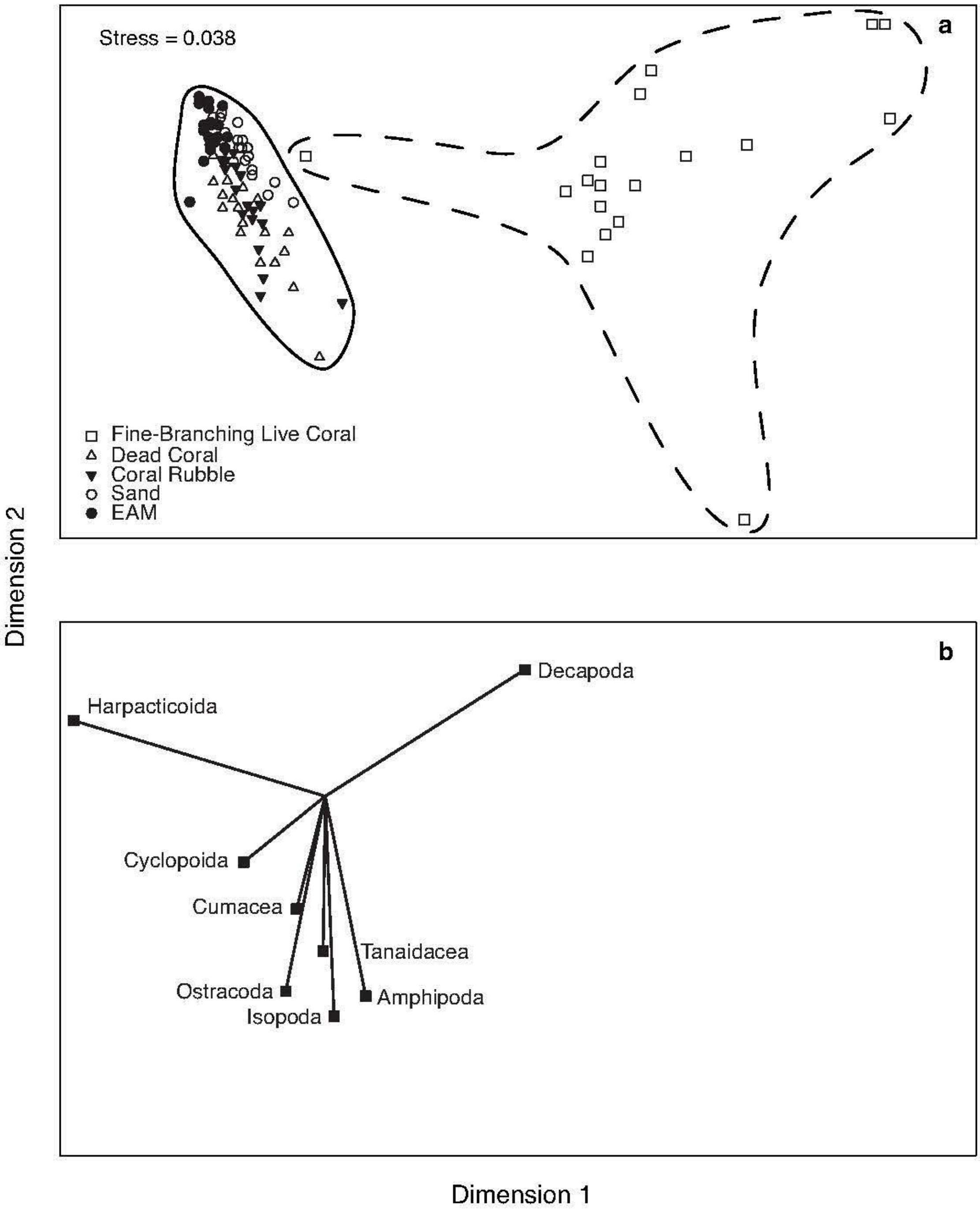

Figure A3. Assemblage structures: all Crustacea within all habitats (including fine-branching live coral). **a)** Non-metric multidimensional scaling of the proportional abundance of crustacean taxa from fine-branching live coral, dead coral, rubble, sand and epilithic algal matrix (EAM) habitats. **b)** The relative contribution of each taxon to the variation in habitat groupings is represented by the vector points. Points indicate the direction of change and strength (correlation) of taxa to each habitat.

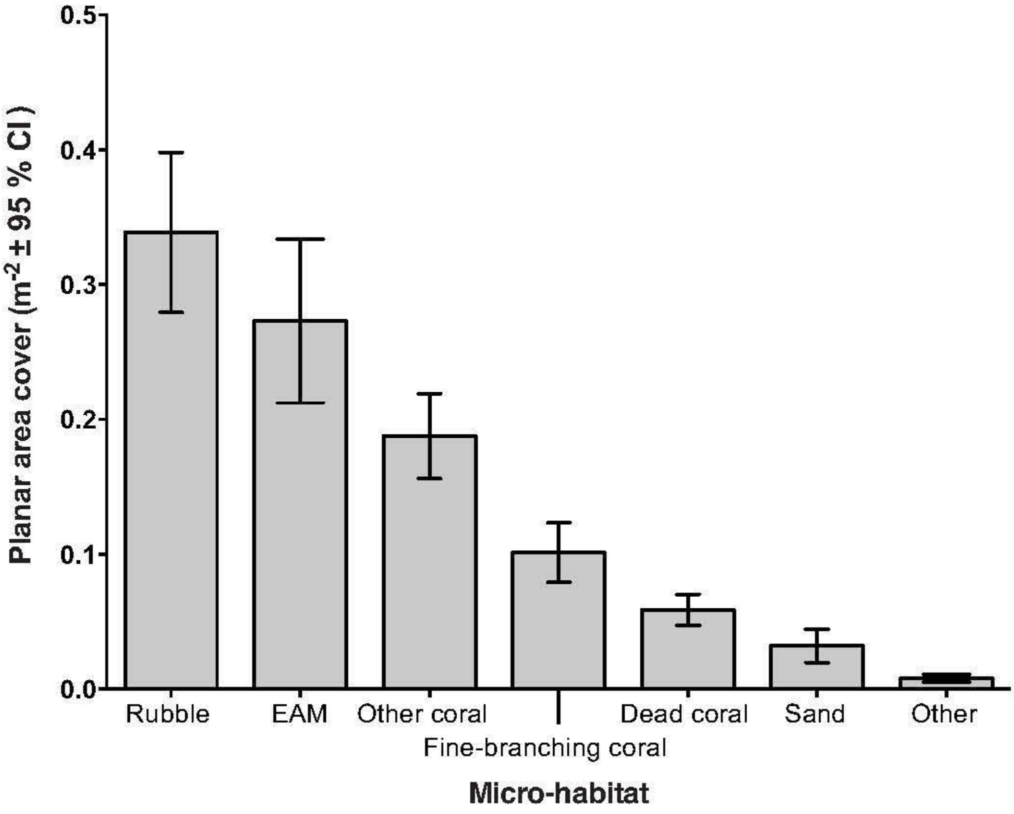

Figure A4. Planar area covered by microhabitats in the study area: a Lizard Island fringing coral reef (mean ± 95 % CI).

Appendix B

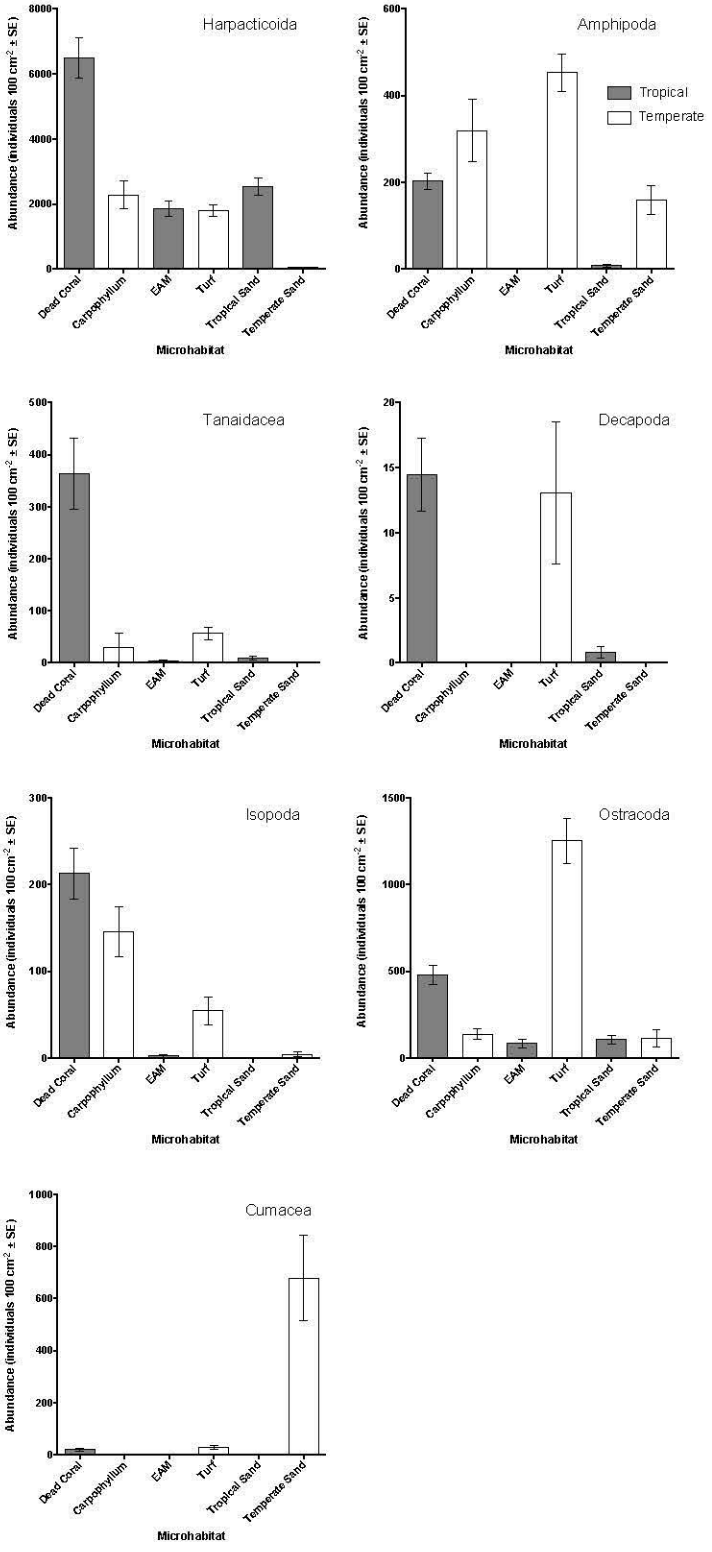

Figure B1 Abundance of crustacean taxa within specific microhabitats expressed as individuals per 100 cm^2.

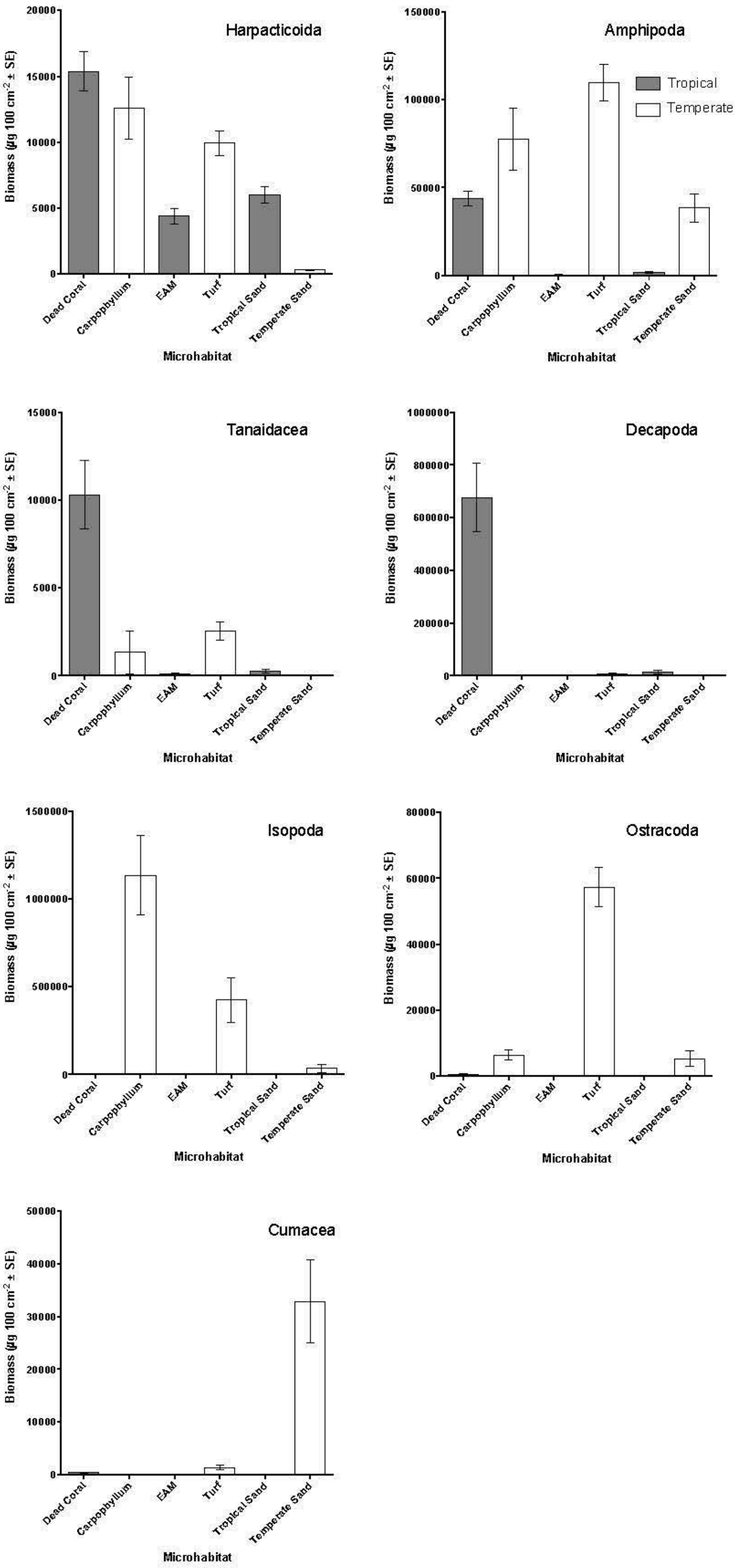

Figure B2 Biomass estimates of crustacean taxa within specific microhabitats in µg per 100 cm².

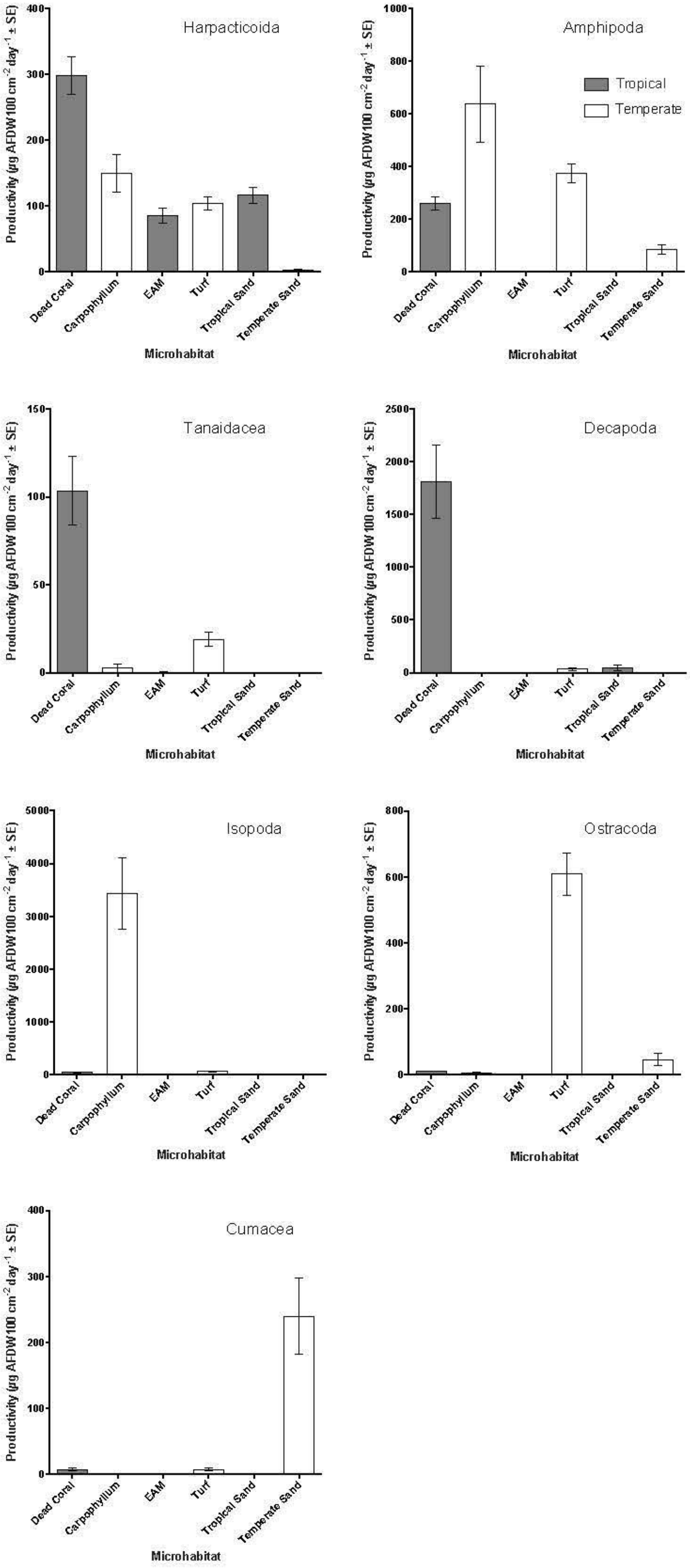

Figure B3 Productivity estimates of crustacean taxa within specific microhabitats in µg ash free dry weight per 100 cm^2 per day.

Appendix C

Table C1 Number of species and number of individuals sampled within each genus.

Genus	Number of species	Number of individuals
Anampses	5	85
Bodianus	4	69
Cheilinus	4	93
Choerodon	10	134
Cirrhilabrus	8	146
Coris	4	77
Cymolutes	2	46
Diproctacanthus	1	16
Epibulus	1	33
Gomphosus	1	22
Halichoeres	20	376
Hemigymnus	2	62
Hologymnosus	2	26
Labrichthys	1	23
Labroides	4	55
Labropsis	5	41
Leptojulis	1	14
Macropharyngodon	4	61
Novaculichthys	1	21
Oxycheilinus	4	72
Paracheilinus	1	20
Pseudocheilinops	1	8
Pseudocheilinus	5	67
Pseudocoris	1	21
Pseudodax	1	11
Pseudojuloides	2	20
Pteragogus	1	5
Stethojulis	4	79
Thalassoma	7	156
Wetmorella	1	5

Table B2 Specific prey items consumed by wrasses, grouped into broad dietary categories.

Micro-Crustacea	Macro-Crustacea	Non-Crustacea
Amphipoda	Anomura	Annelida
Calanoida	Brachyura	Anthozoa
Harpacticoida	Caridea	Ascidiacea
Isopoda (including Gnathiidae)	Cirripedia	Bivalvia
Ostracoda	Penaeidae	Bryozoa
Unidentified Copepoda	Stomatopoda	Cephalopoda
Unidentified fragments (< 3 mm)	Unidentified fragments (> 3 mm)	Echinodermata
		Foraminifera
		Gastropoda
		Polychaeta
		Porifera
		Teleostei

Appendix D

Table D1. Behavioural observations of species of Labridae expressed as a percentage of the total number of observations for each species. Foraging behaviour is the sum of both feeding and searching. A * indicates species occurring in groups and/or exhibiting occasional group foraging.

	Feeding	**Searching**	**Swimming**	**Number of observations**
Epibulus insidiator	17.4	26.1	56.5	23
Anampses neoguinacus	58.8	11.8	29.4	17
Hemigymnus fasciatus	47.1	11.8	41.2	17
Pseudocheilinus hexataenia	17.4	34.8	47.8	23
Hemigymnus melapterus	58.6	14.9	26.4	87
Cheilinus chlorourus	15.2	24.2	60.6	33
Coris batuensis	25.0	53.8	21.2	52
Halichoeres chloropterus	25.6	38.5	35.9	39
Novaculichthys taeniourus	37.5	39.6	22.9	48
Stethojulis bandanensis	83.6	0.0	16.4	61
Halichoeres marginatus *	30.0	22.0	48.0	50
Halichoeres nebulosus *	18.5	55.6	25.9	27
Thalassoma hardwicke *	9.4	20.9	69.8	139
Thalassoma jansenii *	9.1	30.3	60.6	66
Halichoeres hortulanus	22.9	37.1	40.0	35
Halichoeres melanurus *	27.4	37.1	35.5	62
Halichoeres trimaculatus *	15.4	61.5	23.1	39
Halichoeres margaritaceus *	34.8	47.8	17.4	23
Anampses geographicus	42.9	9.5	47.6	21
Cheilinus fasciatus	20.8	20.8	58.3	24
Coris gaimard	22.2	44.4	33.3	18
Gomphosus varius	10.0	31.7	58.3	60
Thalassoma lunare *	11.6	15.9	72.5	69
Stethojulis trilineata	64.7	0.0	35.3	17

Appendix E

Publications arising from this thesis:

Kramer MJ, Bellwood DR, Bellwood O (2014) Benthic Crustacea on coral reefs: a quantitative survey. *Marine Ecology Progress Series* 511: 105-116

Kramer MJ, Bellwood DR, Bellwood O (2014) Large-scale spatial variation in epilithic algal matrix cryptofaunal assemblages on the Great Barrier Reef. *Marine Biology* 161: 2183-2190

Kramer MJ, Bellwood O, Fulton CJ, Bellwood DR (2015) Refining the invertivore: diversity and specialisation in fish predation on coral reef crustaceans. *Marine Biology* 162: 1779-1786

Kramer MJ, Bellwood O, Bellwood DR (2016) Foraging and microhabitat use by crustacean-feeding fishes. *Marine Ecology Progress Series* 548: 277-282

Kramer MJ, Bellwood DR, Taylor RB, Bellwood O (ready for submission) The ecological role of benthic crustaceans: a tropical-temperate comparison

Other relevant publications:

Kramer MJ, Bellwood DR, Bellwood O (2012) Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef *Coral Reefs* 31: 1007-1015

Kramer MJ, Bellwood DR, Bellwood O (2013) Emergent fauna from hard surfaces on the Great Barrier Reef, Australia. *Marine and Freshwater Research* 64: 687-691

Kramer MJ, Bellwood O, Bellwood DR (2013) The trophic importance of algal turfs for coral reef fishes: the crustacean link. *Coral Reefs* 32: 575-583