The ecosystem role of macroalgal browsing fishes on coral reefs

Thesis submitted by

Andrew Scott Hoey *BSc (Hons)* James Cook University

in June 2010

for the degree of Doctor of Philosophy in Marine Biology

within the School of Marine and Tropical Biology and

the ARC Centre of Excellence for Coral Reef Studies,

James Cook University, Townsville, Queensland

Statement of Access

I, the undersigned, author of this thesis, understand that James Cook University will make this thesis available for use within the University Library and, via the Australian Digital Thesis network, for use elsewhere.

I understand that as an unpublished work, a thesis has significant protection under the Copyright Act and;

I do not wish to place any further restriction on access to this thesis.

_____ _____

Signature Date

Statement of Sources

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

Signature

Date

Electronic Copy
Declaration

I, the undersigned, the author of this work, declare that the electronic copy of this thesis provided to the James Cook University Library is an accurate copy of the print thesis submitted, within the limits of technology available.

Signature

Date

Statement on the Contribution of Others

This thesis includes some collaborative work with my supervisor Prof. David Bellwood. While undertaking these collaborations, I was responsible for the project concept and design, data collection, analysis and interpretation, and the final synthesis of results into a form suitable for publication. My collaborator provided intellectual guidance, equipment, financial support, and editorial assistance.

Financial support for the project was provided by the Ian Potter Foundation and Lizard Island Reef Research Foundation, the Australian Coral Reef Society, the Great Barrier Reef Marine Park Authority, James Cook University Graduate Research Scheme, and the Australian Research Council Centre of Excellence for Coral Reef Studies. Stipend support was provided by a James Cook University Postgraduate Research Scholarship. Financial support for conference travel was provided by the Australian Research Council Centre of Excellence for Coral Reef Studies, the Australian Coral Reef Society, and the International Union for the Conservation of Nature (IUCN) Marine Division.

Acknowledgements

Firstly I would like to thank my supervisor, David Bellwood. This thesis benefited greatly from your thought-provoking conversations, guidance and personal encouragement. Thank you for contributing so much to my personal and academic development over the past four years.

Such a field-intensive project would not have been possible without the tireless efforts of an army of field assistants. Thank you to Adam Barnett, Roberta Bonaldo, Gavin Coombes, Peter Cowman, Chris Cvitanovic, Rebecca Fox, Helena Francourt-Sims, Erin Graham, Alonso Gonzalez-Cabello, Jessica & Kiara Hoey, Jacob Johanson, Valeriya Komyakova, João Krajewski, Carine Lefèvre, Vanessa Messmer, Tony Sunderland, David Wachenfeld, Peter Wulf, and Matt Young for your assistance and enthusiasm in the field, often under very trying conditions. I am also deeply indebted to the staff of the Lizard Island Research Station, Lyle Vail, Anne Hoggett, Lance & Marianne Pearce, and Bob & Tanya Lamb. Your invaluable support, enthusiasm, and friendship made Lizard Island seem like a home away from home. I would also like to thank Pete Venables, Oliver Hentschel, Anna Beinssen, Lachin Turner, Louise Wilkins, Kylie & Robert Eddie, for field support at the Orpheus Island Research Station.

Many others have helped with various aspects of this project along the way. In particular, I would like to thank Laurence McCook and Guillermo Diaz-Pulido for invaluable help with *Sargassum* identifications, and Jess Hoey for timely and much needed assistance analysing many hours of video observations. I am grateful to Sean Connolly, Nick Graham, Mark McCormick, Morgan Pratchett, Richard Rowe, Marcus Sheaves, and Craig Syms for statistical advice. For stimulating discussions and/or comments I thank Ameer Abdulla, Andrew Baird, Adam Barnett, Roberta Bonaldo, Howard Choat, Josh Cinner, Sean Connolly, Peter Cowman, Chris Cvitanovic, Martial Depczynski, Guillermo Diaz-Pulido, Rebecca Fisher, Rebecca Fox, Chris Fulton, Monica Gagliano, Chris Goatley, Nick Graham, Adel Heenan, Jess Hoey, Tom Holmes, Charlotte Johansson, Laurence McCook, Mark McCormick, Vanessa Messmer, Phil Munday, Morgan Pratchett, Garry Russ, Tony Sunderland, Jennifer Tanner, David Wachenfeld, Peter Wainwright and Shaun Wilson. Many of these people are dear

friends and all have provided valuable advice along the way. Thank you for sharing your experiences, enthusiasm and passion for coral reefs.

This thesis would not have been possible without the generous support of many funding bodies. I would like to make a special mention of the Ian Potter Foundation and Lizard Island Reef Research Foundation who supported this research through an Ian Potter Foundation Doctoral Fellowship at Lizard Island. In particular, I want to thank Charlie Shuetrim, Ken Coles, Thomas Healy, and John Gough for their support and encouragement. Valuable funding was also provided by the ARC Centre of Excellence for Coral Reef Studies, James Cook University Internal Research Awards and Graduate Research Scheme, the Australian Coral Reef Society, the Great Barrier Reef Marine Park Authority, and the Australian Research Council through Prof. David Bellwood. I am also extremely grateful to the ARC Centre of Excellence for Coral Reef Studies, the IUCN Marine Program, and the Australian Coral Reef Society for travel funding to attend various national and international conferences. Also, to James Cook University who provided a Postgraduate Research Scholarship for the duration of my degree.

My gratitude is extended to the many people behind the scenes. In particular I would like to thank G. Bailey and V. Pullella for IT support and rescuing my computer after it ‘drank’ a cup of coffee; S. Francis, J. Webb, R. Gegg, and G. Ewels for laboratory and workshop facilities; K. Wood for travel assistance; A. Wignall and G. Jameson for assistance with purchasing; E. Coombes and T. Gough for their support and encouragement; and P. Osmond and J. Webb for boating and diving logistics. I am also extremely grateful to the anonymous reviewers of this thesis and its publications.

Finally, I thank some very special people who have provided unconditional support and encouragement for many years; my family, and extended family; ‘the Grays’ and ‘the Dons’. To my loving wife and daughter, I thank you simply for being there and the happiness you bring. Jess and Kiara your constant love, support and encouragement, through both good and trying times, made this journey so much easier. Jess, without your consistent support the walls would have fallen down around us, we all would have starved, and my sanity would have disappeared long ago. Thanks to all of you for believing in me and supporting everything I have done.

Abstract

Herbivory is a key process structuring plant communities in both terrestrial and aquatic ecosystems, with variation in herbivory often being related to shifts between contrasting groups of primary producers. On coral reefs, regional reductions in herbivores have underpinned shifts from coral-dominance to dominance by fleshy macroalgae. The capacity to remove macroalgae is, therefore, viewed as a key process in both preventing and reversing such transitions. The present study compared the role of macroalgal browsing fishes across two distinct exposure gradients, both among habitats within a single reef and across several reefs spanning the continental shelf, and among patches of differing macroalgal densities. Finally, the role of a second group of herbivorous fishes, the territorial damselfishes, in influencing macroalgal removal rates and shaping macroalgal distributions was explored.

Browsing intensity was quantified across eight habitats of varying depth and wave exposure on a mid-shelf reef in the northern Great Barrier Reef (GBR) using assays of two species of *Sargassum*. Removal rates of *Sargassum* varied significantly amongst habitats, with both species displaying broadly similar patterns. Reductions in *Sargassum* biomass were highest within the shallow habitats on the exposed aspect of the reef (81.4–91.6 $\%.d^{-1}$), lowest within the deeper exposed habitats (3.8–13.4 $\%.d^{-1}$), and intermediate within the sheltered habitats (37.9–76.5 $\% d^{-1}$). Surprisingly the rates of removal of *Sargassum* displayed no relationship with visual census estimates of the density or biomass of all roving herbivorous fishes or macroalgal browsing fishes, either collectively or independently. Stationary underwater video cameras revealed that, despite the reef supporting over fifty herbivorous fish species and six macroalgal browsing species, a single species, *Naso unicornis*, was almost solely responsible for

the removal of *Sargassum* biomass. Of the 42,246 bites taken from the *Sargassum* across all habitats, *N. unicornis* accounted for 89.8 % (37,982) of the total bites, and 94.6 % of the total mass standardized bites.

Sargassum assays revealed a distinct pattern in browsing across the continental shelf in the northern GBR, with the highest rates of removal recorded on mid-shelf reefs (55.2–79.9 $\%.d^{-1}$) and decreasing significantly on inner-shelf reefs (10.8–17.0 $\%.d^{-1}$). The low removal rates on inner-shelf reefs appeared to be directly related to the high cover of macroalgae on those reefs. Reductions in *Sargassum* biomass were also initially low on outer-shelf reefs (10.1–10.4 $\%.d^{-1}$), but increased markedly (32.1-73.4 $\%.5h^{-1}$) after the resident fishes were allowed several days to familiarize themselves with the *Sargassum*. Despite considerable cross-shelf variation in the rates of removal of *Sargassum*, there was little variation in the agents of macroalgal removal across all reefs. Feeding on the transplanted *Sargassum* was again dominated by a single browsing species. *N. unicornis* accounted for 82 % of all mass standardized bites and explained over 80 % of the total variation in the reduction in *Sargassum* biomass across all reefs and habitats. Although the majority of this feeding activity was recorded on the mid- and outer-shelf reefs, *N. unicornis* accounted for over 72 % of the recorded feeding on the inner-shelf reefs.

The territory composition and effect of resident damselfish on the removal of *Sargassum* was quantified for six common species of damselfish on a mid-shelf reef in the northern GBR. The functional composition of algal communities within territories varied markedly among species. The territories of four species were characterized by algal turfs, while the territories of two species were characterized by foliose and leathery brown macroalgae. *Sargassum*, a generally rare alga on mid-shelf reefs, was a particularly common alga within *Dischistodus prosopotaenia* territories. *D.*

prosopotaenia was the only species to retain the transplanted *Sargassum*, with only a minimal reduction in *Sargassum* biomass (1.1 $\%.d^{-1}$) being recorded within their territories. In contrast, reductions in *Sargassum* biomass were high in areas adjacent to *D. prosopotaenia* territories (83.8 $\%.d^{-1}$), and within and adjacent to the territories of the five remaining damselfish species (76.2 - 92.5 $\%.d^{-1}$). Overall, only *D. prosopotaenia* provided a refuge for leathery brown macroalgae, and may facilitate the development of this macroalgae on mid-shelf reefs of the GBR.

Habitat patches that varied in the spatial arrangement and density of macroalgae (0.25-6.23 $kg.m^{-2}$) were created on an inshore reef in the central GBR using transplanted *Sargassum*. Feeding on the *Sargassum* was dominated by two species, *Kyphosus vaigiensis* and *N. unicornis*. Both species displayed a preference for the relatively open habitat patches with low cover and biomass of *Sargassum*; only switching to the higher density patches after much of the *Sargassum* biomass within the lower density patches had been consumed. Similarly, grazing on the algal turf covered substratum within the habitat patches displayed an exponential decline with increasing *Sargassum* biomass. These feeding preferences appeared not to be related to bottom-up factors as food availability was proportional to macroalgal density for browsers and broadly comparable among habitat patches for grazers. It appears more likely that the avoidance of the higher macroalgal density patches was related to an increase in the perceived risk of predation.

Overall, the consumption rates of *Sargassum* in the present study provided strong evidence for the potential role of browsing fishes in limiting the distribution of adult *Sargassum* on mid- and outer-shelf reefs of the GBR. Browsing intensity was, however, moderated by the presence of *D. prosopotaenia* and the density of the *Sargassum* presented. These negative interactors are important and provide the

mechanistic bases through which *Sargassum* may colonize new locations, and expand and persist once established. Despite some evidence of latitudinal variation on inshore reefs, the reliance on a single species removing *Sargassum* across a range of habitats and reefs in the northern GBR was striking. This limited redundancy, both within and across local (0.1 – 40 km) scales, highlights the potential for single-species functional groups and emphasizes the importance of looking beyond biological diversity as a source of ecological stability.

Table of Contents

List of Figures

List of Tables