UNIVERSITY OF EXETER

SCHOOL OF BIOSCIENCES

MACROALGAL DYNAMICS ON CARIBBEAN CORAL FOREREEFS

Submitted by Hendrik Renken, to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biology, March 2008

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University

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This thesis is dedicated to my Mother, who after a courageous battle with cancer wasn't allowed to see the completion of this project. I will always love you and remember you fondly and will never forget the joy you brought to my life.

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ABSTRACT

Tropical coral reefs are among the most diverse ecosystems of the world but facing increasing threats to their health. Over the last thirty years, many Caribbean coral reefs have undergone dramatic changes and experienced large losses in coral cover, due to direct and indirect anthropogenic disturbances. The results of which are reefs with low rugosity, changed trophic dynamics and low fish diversity. In recent times reefs have failed to recover from disturbances due to an increase in frequency and severity of disturbances and stresses. In the Caribbean on many coral reefs this has resulted in a shift towards macroalgal dominance by species of the phylum Phaeophyta.

The processes and factors affecting the standing crop of macroalgae are many and complex. Two main hypotheses are identified in the literature as being the driving forces of algal dynamics: nutrient dynamics (availability, supply and uptake) and herbivory. However, many studies have been found to be inconclusive because of the complexity of the coral reef ecosystem, which makes it difficult if not impossible to control for all factors and processes influencing the standing crop of macroalgae such as light, water flow and sedimentation. The inherent characteristics of macroalgae, like morphology and life history, make them behave differently. Whilst herbivore characteristics, like size of mouth parts, feeding modes and preferences, will influence the amount of algal biomass removed. The spatial context (i.e. coral fore reef vs. back reef) will influence the effects of both bottom-up and top-down controls. Besides these inter-habitat differences, macroalgae within similar habitats but differing geographical locations may respond differently, for example, a forereef exposed to the open ocean or a forereef located in a sheltered bay.

This thesis attempts to provide insight into the dynamics of two dominant brown macroalgae on Caribbean coral reefs, *Dictyota* spp. and *Lobophora variegata.* This aim was addressed by developing a model for the macroalga species *Dictyota* to model the various processes and factors on a coral forereef affecting percentage cover. Further, the patch dynamics of both *Lobophora variegata* and *Dictyota* were investigated to gain an insight into their dynamics under varying environmental conditions: the windward and leeward sides of an atoll. Finally, herbivory is identified as one of the key process affecting macroalgal cover. I investigated this process by deploying cages on both the windward and leeward side of the atoll to investigate the effects of grazing pressure under varying environmental conditions.

A Bayesian Belief Network model was developed for *Dictyota* spp. to model the bottom-up and top-down processes on a coral forereef determining the percentage cover. The model was quantified using relationships identified in the scientific literature and from field data collected over a nine moth period in Belize. This is the first BBN model developed for brown macroalgae. The fully parameterized model identified areas of limited knowledge and because of its probabilistic nature it can explicitly communicate the uncertainties associated with the processes and interactions on standing crop. As such the model may be used as a framework for scientific research or monitoring programmes and it is expected that the model performance to predict macroalgal percentage cover will improve once new information becomes available.

Size-based transition matrices were developed for both *Dictyota* spp. and *Lobophora variegata* to investigate the patch dynamics under varying environmental conditions: the windward and leeward sides of an atoll. The matrices reveal that standard measures of algal percent cover might provide a misleading insight into the underlying dynamics of the species. Modelling the patch dynamics with matrices provided insight into the temporal behaviour of macroalgae. This is an important process to understand because patch dynamics are determining competitive interactions with other coral reef benthic organisms. The outcome of competitive interactions will differ with macroalgal species. This study indicate that *Dictyota* spp. responded strongly to differing environmental conditions in that it has reduced growth rates and lower percent cover on the leeward side of the atoll, whilst *Lobophora variegata* showed far less sensitivity to environmental conditions. The patch dynamics of *Dictyota* spp. also showed a higher temporal variation than *Lobophora variegata* but only on the exposed forereef.

A caging experiment was set up to investigate the response of both macroalgal species to different grazing pressure scenarios, under varying environmental conditions. *Dictyota* spp. had a significant response to environmental conditions in that a higher percentage cover was found on the exposed side of the atoll, whilst for *Lobophora variegata* the response was far less obvious. The less clear response of *Lobophora variegata* was very likely caused by competition of *Dictyota* with *Lobophora* due to the very high cover *Dictyota* obtained in the cages where all herbivores were excluded. The low grazing pressure treatments also showed an increase in cover of *Dictyota*, whilst for *Lobophora,* only a reduction in the rate of increase could be observed. The results indicate that on the leeward side of the atoll, fish grazing alone seems sufficient to control the standing crop of *Dictyota* and *Lobophora variegata*. Retrospective analysis of the experimental design showed that the limited size of the experimental set up could have confounded the results for *Lobophora* as well. In future experiments it is recommended to increase number replicates.

Management of coral reef habitats is frequently constrained by a lack of funds and resources. The BBN Model once fully parameterized can provide a useful tool for coral reef management, because the model allows exploration of different reef scenario's, which in turn can aid in prioritizing management strategies. Furthermore, the thesis provided an insight into the complexities of macroalgal dynamics. The responses of macroalgae to physiological factors and ecological processes are species specific and dependent on the location, and caution against generalizing on what controls the standing crop of macroalgae. Therefore it is argued that future investigations into algal ecology should clearly define the species, habitat and location. This can help to make informed management decisions.

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AUTHOR'S DECLARATION

I declare that all work in the co-authored papers which is not my own, has been identified correctly.

Chapter 3 consists of a paper submitted to the journal Ecological Modelling co-authored with P. Mumby. P. Mumby provided editorial advice and guidance throughout the development of the paper. H. Renken developed the concept, models, carried out the analysis and wrote the paper.

Chapter 4 consists of a paper submitted to the journal Coral Reefs co-authored with P. Mumby and H. Edwards. P. Mumby provided editorial advice and guidance throughout the development of the model, H. Edwards provided advice on the development of the matrix models. H. Renken developed the concept, models, carried out the analysis and wrote the paper.

Chapter 5 consists of a paper to be submitted to the Journal of Experimental Marine Biology and Ecology co-authored with P. Mumby. P. Mumby provided editorial advice and guidance throughout the development of the paper. H. Renken designed the experiment, carried out the analysis and wrote the paper.

All the birds in the forest they bitterly weep. Saying 'where will we shelter or where will we sleep?' For the Oak and the Ash they are all cutten down.

Lyrics from 'Bonny Portmore' a traditional Celtic folksong.

A poignant reminder that even in the olden days people were concerned with the overexploitation of natural resources.