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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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ACKNOWLEDGEMENT

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.

There are no words to describe the amount of love I received from my wife Ana Maria. Without her support and patience I would have never gotten to the final stage of this project. I will always love you and looking very much forward to sharing the rest of my life with you. In addition I thank my family for their love and support throughout this endeavour.

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MACROALGAL DYNAMICS ON CARIBBEAN CORAL FOREREEFS

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.

Chapter 1 Introduction

INTRODUCTION

1 THE DECLINING HEALTH OF CARIBBEAN CORAL REEFS

Tropical coral reefs are among the most diverse and productive ecosystems of the world. Although they cover less than 1% of the earth's surface, millions of people depend upon coral reefs for all or part of their livelihood (Moberg and Folke 1999, Marshall and Schuttenberg 2006). Healthy coral reefs besides having a high biodiversity sustain many ecosystem services, supporting fisheries productivity and provide coastal protection from storms and hurricanes and attract tourism to the region (Moberg and Folke 1999). In the last three decades many coral reefs have undergone dramatic changes and experienced large losses in coral cover, most notably in the Caribbean (Connell 1997, Gardner et al. 2003, Pandolfi et al. 2003, Bellwood et al. 2004). The losses of coral cover are attributed to a wide range of direct and indirect anthropogenic disturbances ranging from point source pollution, overfishing, increased sedimentation from dredging and deforestation to bleaching, diseases, hurricanes and global rises in sea temperatures (Lapointe and Matzie 1996, Aronson and Precht 2001, Wolanski et al. 2003, Hoegh-Guldberg et al. 2007). The result of which are reefs with low rugosity, low fish diversity, and changed trophic dynamics (Carpenter 1990, Tanner 1995, Adey 1998, Knowlton 2001, Hughes et al. 2003, Bellwood et al. 2004). The declining health of coral reefs is thus a major concern and urgent action is needed to reverse this trend (Bellwood et al. 2004).

The degradation of coral reefs is not a new phenomenon and coral reefs undergo changes several times in a decade and are able to recover from disturbances (Pandolfi et al. 2003, McManus and Polsenberg 2004). In recent times coral reefs have failed to regenerate after disturbances because of an increase in frequency and severity of disturbances and stresses and many coral reefs in the Caribbean have now shifted to a macroalgae dominated state (Connell 1997, Hughes et al. 2005). This process is known as a phase shift (Done 1992). A major concern is that these alternate states are stable and thus has serious consequences for the health of coral reefs (Knowlton 1992, Mumby et al. 2007).

2 MACROALGAE ON CORAL REEFS

Numerous studies have investigated the phase shift to a macroalgal dominated state to determine what the main driving forces are (Lapointe 1997, Lapointe et al. 1997, Hughes et al. 1999, Lapointe 1999, Aronson and Precht 2000, Lapointe 2004, McClanahan et al. 2004, Littler et al. 2006). In general it is believed that increased nutrients and/or reduced grazing result in a shift from a coral to a macroalgae dominated reef (Lapointe et al. 1997, Hughes et al. 1999, Lapointe 1999). These two hypotheses seem intuitive because macroalgae can show increased growth rates due to increased nutrient supply. The study of Kaneohe bay in Hawaii is a classic example of the effects of increased nutrients on macroalgal cover (Smith 1977). Here a sewage outfall increased nutrients levels significantly in an enclosed bay, which resulted in the coral reefs being overgrown by macroalgae. A subsequent relocation of the outfall resulted in a reduction of macroalgal cover. On the other hand macroalgae increased their cover rapidly as a response to a reduction in grazing, as shown for coral reefs in Jamaica (Hughes et al. 1999). Here it was shown that due to a significant reduction of grazing, attributed to overfishing and the mass mortality of a key herbivore, *Diadema antillarum*, macroalgal cover increased significantly. Recently, experimental studies have manipulated both nutrients and grazing simultaneously but results remained different (Smith et al. 2001, Belliveau and Paul 2002, Lapointe et al. 2004), although recent evidence suggests that herbivory plays a crucial role (Burkepile and Hay 2006, Mumby et al. 2007) .

A variety of reasons may have contributed to the differential outcomes of these field experiments. First, coral reefs are highly complex ecosystems and a multitude of other factors may have interacted with nutrients and herbivores, such as light, sedimentation and water motion. Secondly, the inherent characteristics of macroalgae will result in diverse responses to physical factors and ecological processes. Thirdly, experiments are of an ad-hoc nature. For example macroalgae on a coral forereef exposed to the open ocean will have a different set of environmental factors and ecological processes acting upon them compared to macroalgae growing on a forereef in a secluded bay. Responses also differ along a depth gradient, i.e. from patch reefs in a lagoon, the back reef, reef crest, shallow forereef and deep forereef (De Ruyter van Steveninck et al. 1988, Szmant 2002, McManus and Polsenberg 2004, Hwang et al. 2005).

In this thesis I investigated aspects of the dynamics of two dominant macroalgae on Caribbean coral reefs, *Lobophora variegata* (Lamouroux) and *Dictyota* spp. on different spatial scales. In practice it was difficult to distinguish patches of different species of *Dictyota* as they are often intermingled. The patches I observed were mainly represented by the species *Dictyota pulchella* (Hörnig and Schnetter), with *Dictyota humifusa* (Hörnig) and *Dictyota pfaffii* (Schnetter) often found growing in or under their canopy. Hence in the thesis I refer to *Dictyota* spp. Both macroalgae are from the same phylum, Phaeophyta and belong to the same family, Dictyotaceae, but exhibit different growth forms (Littler and Littler 2000). It might be expected they will respond differentially to the environment in which they grow.

Furthermore, I concentrated my research on the forereef habitat between depths of 5 m and 15 m, classified as the *Montastraea annularis* zone (Geister 1977). This zone is where the major reef building corals are found and shifts in this habitat from corals to macroalgae dominance have the greatest impact. I limited the investigations to the dominant macroalgal species and within this limited depth range, because the behaviour and growth form of the species may vary significantly between habitats as well as the impacts of environmental factors and ecological processes. Therefore by confining my research to the two dominant macroalgae and within a single habitat but exposed to different environmental regimes I hoped to gain a better insight in the spatial dynamics of macroalgae and thus increase our understanding of what makes these species successful on the coral reef.

3 MODELLING MACROALGAL DYNAMICS

3.1 Ecosystem models

Modelling is a useful technique to gain a better understanding and insight into complex ecosystems. Over the last 80 years or so, an overwhelming amount of modelling techniques have been developed and applied in ecology. Each of these models have there own advantages and disadvantages but they all have in common that they aim to characterize processes and dynamics in simplified and general ways that provide insight into factors that are responsible for the observed patterns (Johnson and Omland 2004).

One of the earliest and well known models are the predator-prey and competition models (Begon et. al. 1996). These models were developed by Lotka and Volterra in the 1920's and 1930's (Volterra 1926, Lotka 1932) and have since been applied to many organisms and communities (Svirezhev 2000, Spencer and Tanner 2008). The application of matrices to study population dynamics was developed by Leslie in the 1940's (Leslie 1945) and became widely used in ecology for example, plants (Bierzychudek 1982), tortoises (Doak et. al. 1994), Killer whales (Brault and Caswell 1993), Algae (Ang and De Wreede 1990), corals (Hughes 1984), and birds (Gauthier and Lebreton 2004). Another important set of models applied many times in ecology are Generalized Linear Models (GLM) and Generalized Additive Models (GAM). GLM's are mathematical extensions of linear models that do not force data into unnatural scales and thereby allow for non-linearity and non-constant variance structure in the data (Hastie and Tibshirani 1986). They are based on an assumed relationship between the mean of the response variable and the linear combination of the explanatory variables (Guisan et al 2002). GLM's are (Guisan et al 2002). GAM's are semi-parametric extensions of GLM's. A GAM uses a link function to establish a relationship between the mean of the response variable and a function of the explanatory variable(s) (Hastie and Tibshirani 1986). The strength of GAM's is their ability to deal with highly non-linear and non-monotonic relationships between the response and the set of explanatory variables. GAM's are sometimes reffered to as data- rather than model-driven (Guisan et al 2002).

With the advances in computer science and the availability of more powerful computers, models requiring high computing power such as cellular automata, individual based modelling, graph theory and Bayesian belief networks (BBN) became more widely used by ecologists. Cellular automata date back to the late 1940's but developed rapidly in the 1980's and have been applied to a wide variety of subjects, amongst others, coral reefs (Karlson and Jackson 1981, Langmead and Sheppard 2004), forests (Sato and Iwasa 1993), and human populations (Sieburg and Clay 1991). Individual based modelling techniques have been around since the 1970's and refer to simulation models that treat individuals as unique and discrete entities which have at least one property in addition to age that changes during the life cycle (Grimm 1999). Recently, modelling techniques such as graph theory and BBN's have been applied to answer ecological questions. For example, graph theory has been applied to landscape connectivity (Monor and Urban 2008) and population connectivity by ocean currents (Treml et. al. 2008), whilst BBN's have been applied to model eutrophication in estuaries (Borsuk et. al. 2004), wildlife population viability (Marcot et. al. 2001) and coral reefs (Wooldridge and Done, 2004).

Given the plethora of modelling techniques, an important question becomes then, which modelling approach to use? To answer this question a few decisions have to be made. Firstly, the data available have to be considered. The model must be able to handle the available data. Some models are better in handling missing data than others. Secondly, given the ecosystem to be modelled which model can accurately capture the dynamics? More complex models are not necessary better models, because the added complexity also adds more uncertainty and if data is lacking then this would not lead to better models.

In this thesis I have applied Bayesian Belief Networks to investigate the effects of factors and processes on the percent cover of *Dictyota* spp. Secondly, I applied Matrix Population Models to investigate the patch dynamics of both *Dictoyta* spp. and *Lobophora variegata*. The next sections will explain both modelling techniques in more detail.

3.2 Matrix Population Models

Matrix Population Models have been applied to many organisms (Caswell 2001 and references therein). Traditionally age has been used as the categorical variable, as developed by Leslie (Leslie 1945). This model has been used to analyze the growth in age-structured populations. However, for many organisms age is not correlated with demographic parameters and for such size or stage is a better categorical variable (Sauer and Slade 1987). The Leslie matrix model has been extended to stage or size structured populations by Lefkowitch (Lefkowitch 1965). See for an application example Hughes (1984). In this thesis I used a size based matrix model, also known as a transition matrix, to describe the patch dynamics of two populations of algae under varying environmental conditions. The generic form of the model is:

$$x_{t+1} = \mathbf{A} \cdot x_t$$

Here x_t is a column vector describing the population size structure at time t, and **A** is a matrix which determines the dynamics of the population. This transition matrix (Table 1.1) describes the contribution of each size class to every other class during a time interval (t, t+1). Each element in the matrix represents the probability that a patch in a size class will undergo a transition to another size class at time t+1. Elements on the diagonal of the matrix represent probabilities of remaining in the same size class during a given time interval; elements above the diagonal correspond to a reduction to smaller size classes, whereas elements below the diagonal correspond to increases to larger size classes.

Table 1.1 Generic 4 x 4 matrix. $G_{j,i}$ denotes growth from size class i to size class j, F_i is the fecundity of size class i, $L_{j,i}$ is survival from size class i to size class j, $C_{j,i}$ is fusion and $S_{j,i}$ is fragmentation.

		t			
		I	**II**	**III**	**IV**
	I	$F_1+L_{1,1}+S_{1,1}$	$F_2+S_{1,2}$	$F_3+S_{1,3}$	$F_4+S_{1,4}$
t+1	**II**	$G_{2,1}+C_{2,1}$	$L_{2,2}$	$S_{2,3}$	$S_{2,4}$
	III	$G_{3,1}+C_{3,1}$	$G_{3,2}+C_{3,2}$	$L_{3,3}$	$S_{3,4}$
	IV	$G_{4,1}+C_{4,1}$	$G_{4,3}+C_{4,2}$	$G_{4,3}+C_{4,3}$	$L_{4,4}$

An advantage of matrix models is that they provide population parameters of a single value making it easy to compare different matrices. Calculations of population parameters are performed with the Matlab software. The relevant scripts are provided.

The population growth rate

The population growth rate, known as the dominant eigenvalue λ_1 is calculated from the matrix. A population of arbitrary size structure that changes according to the transition matrix will eventually reach a stable size distribution and grow with a rate given by the dominant eigenvalue (Bierzychudek 1982). λ_1 provides a single value that enables us to compare the different matrices. Dominant eigenvalues of less than 1 indicate a long term decline in the population or that patches are becoming smaller, whilst values greater than 1 indicate an increase in the size of patches. The dominant eigenvalue can be found by solving the characteristic equation of matrix A. In general the characteristic equation of an n x n matrix is an n^{th} order polynomial with n solutions. The dominant eigenvalue is the n^{th} solution which is strictly greater in magnitude than all other eigenvalues in the vector. To calculate the dominant eigenvalue in Matlab, run the following script:

```
eig(A)
imax = find(d==max(d)
```

The first line will return a list of eigenvalues for matrix A. the second line will identify the dominant eigenvalue, which is the largest value of the list.

The damping ratio

The damping ratio (ρ). On reaching equilibrium, a population has a stable (equilibrial) size distribution (the right eigenvector w). The speed of convergence to a stable size distribution is given by the ratio of the dominant eigenvalue to the second largest eigenvalue: $\lambda_1/|\lambda_2|$, known as the damping ratio (ρ) (Caswell 2001). Convergence will be more rapid the larger λ_1 is relative to the other eigenvalues (Caswell 2001). The rate of convergence is independent of whether the population is in decline or growth. The damping ratio may be interpreted as a measure of the variation observed within the patch dynamics because it describes the oscillations produced by the subdominant eigenvalues during convergence. A species that has a high variance in its patch dynamics due to many fusion and fragmentation events and rapid growth and shrinkage will therefore have a low damping ratio. The damping ratio can be easily calculated by dividing the subdominant eigenvalue of a matrix A by the dominant eigenvalue of matrix A. These values are found running the script to calculate the eigenvalues of matrix A.

The stable size distribution

The stable size distribution is given by the right eigenvector w of the matrix. The elements of the eigenvector sum to 1 or 100, and therefore describes a vector which gives the percentage of the population in each size class. The right eigenvector w of the matrix can be calculated in Matlab by running the following script:

```
eig(A)
[W,d]= eig(A)
imax= find(d == max(d))
w = W(:, imax)
```

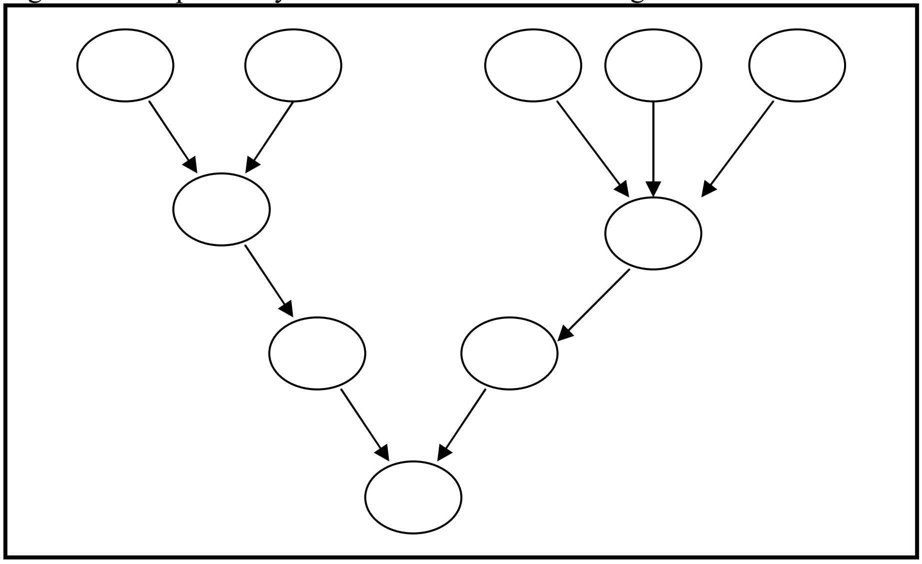
The first line will return a list of eigenvalues of the matrix A. The second line will return a matrix with right eigenvectors and corresponding eigenvalues. The third line finds the dominant eigenvalue of the matrix. The final line gives the right eigenvector w corresponding to the dominant eigenvalue. Note that this vector is not yet scaled to percentages in each size class, subsequently these values have to be scaled to 1.

3.3 Bayesian Belief Networks

Bayesian Belief Networks (BBN) are a relative new concept in ecological modelling and therefore I will provide here a more detailed introduction to the principles and practices of BBNs. However, for a very detailed introduction to the algorithms and theory behind BBNs the reader is referred elsewhere (Pearl 1988, Spiegelhalter et. al. 1993, Jensen 2001). Bayesian Belief Networks (BBN), also know as belief networks, Bayes nets, knowledge maps, or causal probabilistic networks are a method for modelling uncertain and complex domains such as ecosystems. They emerged from the artificial intelligence community and have been applied to a wide range of problems in medical diagnosis (Spiegelhalter et. al. 1989), language (Charniak and Goldman 1989), and search and rescue (sarbayes.org). Perhaps the most famous (notorious) application is the ever helpful Microsoft office assistant. BBN's are now increasingly used in environmental and ecological modelling (Varis 1997, Marcot et. al. 2001, Borsuk et. al. 2004, Wooldridge et. al. 2005). Although Bayesian theory has been around for a very long time (Reverend Bayes 1702-1761), it is only in the last years that efficient algorithms and appropriate software have become available to implement BBN's in such a way that they can solve realistic problems.

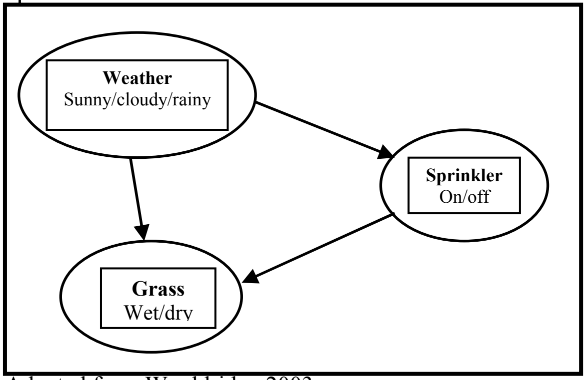
The development of a BBN begins by conceptualizing a model of interest as a graph or network of connected nodes and linkages (Fig. 1.1). A network node represents a system variable and a link from one node to another (depicted as an arrow) represents a dependency relationship between the variables. The relationship may indicate direct causal dependencies or the combined effect of more complex associations (Pearl 1988). Here the node from which an arrow is leaving is known as a parent node and the node to which an arrow enters is called the child node. To quantify the dependency links, BBN's utilize probabilistic relations, rather than deterministic expressions. The node-link structure of the model domain, in combination with probability calculus and Bayes theorem provides the basis to efficiently disseminate the evidence throughout the network, thereby updating the strength of belief in our outcome variables.

Fig. 1.1 Conceptual Bayesian Belief Network showing the node-link structure



The easiest way to understand BBN's is to imagine trying to model a situation in which dependency between variables is known to exist but where our understanding of the relationship is incomplete. We therefore need to describe the dependency probabilistically. The probabilities aim to show the fact that some states in our model will tend to occur more frequently when other conditions are also present (i.e. conditional probabilities). For example, if it is cloudy, the chances of rain are higher. Fig 1.2. gives an example adopted from Wooldrige (2003) to demonstrate these concepts. In this simple model, let us assume the weather can have three states: sunny, cloudy, or rainy, also the lawn can be wet or dry, and the sprinkler can be on or off. There are some dependence links in this model. When it rains, then the lawn will become wet directly. But, after a long sunny spell the lawn can also become wet, indirectly, because I turned on the sprinkler.

Fig 1.2. BBN describing weather, lawn and sprinkler-use-behaviour.



Adapted from Wooldridge 2003

When actual probabilities are entered into this BBN reflecting the reality of weather conditions, lawn, and sprinkler-use-behaviour, the BBN can be made to answer useful questions, like, “if the lawn is wet, what are the chances it was caused by rain or by sprinkler”, and “if the chance of rain increases, how much time do I have to allocate for watering the lawn”.

BBNs are particularly useful for making probabilistic inference about model worlds that are characterized by inherent complexity and uncertainty. This uncertainty may be due to incomplete knowledge of the model domains and its states, randomness within the behaviour of the domain, or a combination of these. Once BBNs are fully developed and parameterized, they provide a rational framework to infer whether knowledge of some event should influence our belief in other events. In addition to being able to deal with complexity problems which cannot be feasibly modelled by other approaches, BBNs offer other advantages.

BBNs are very helpful in challenging experts to clearly stipulate their understanding of what they know about the model domain. The graphical nature of the BBN facilitates this process, because the formal structure of the network, makes it easy to challenge the assumptions on dependencies in the network. Because the BBN uses probabilities as a measure of uncertainty they explicitly communicate the uncertainties to stakeholders.

The modular design of the BBN makes them easy to update once new data becomes available. Only the nodes of the network need to be updated for which new data became available. In addition, BBNs can start of small when little data is available or datasets are incomplete. New variables can be easily added once new knowledge becomes available.

There are limitations of the method one should be aware of. There is a danger to rely too heavily on expert opinion, especially where empirical data is lacking. In these cases the model is no better than the best guess and can reflect personal bias. Therefore, ideally when there is a need to rely on expert opinion, it is best to have a team of experts and then average their estimated probabilities to reflect the collective uncertainty in the beliefs.

BBN’s can become large and unmanageable. In these cases estimating conditional probabilities will become difficult and unreliable. There are two points to be aware of. First, the total number of nodes in the network and secondly the number of states each node can obtain. Research has suggested that ideally, nodes should have no more than 10 states (Uusitalo 2007).

3.3.1 An introduction to the theory of BBNs.

In order to deal with the implications of uncertainties in the entire model domain, it is necessary to calculate the probabilities correctly. For a specific model of interest we need to represent the joint probability distribution. The joint probability distribution is a table of all the probabilities of all the possible combinations of states in the model domain. These distributions can become quickly very large, because every possible state combination for every variable must be represented. As an example; assuming only binary variables, a system with 10 variables would require $2^{10} = 1024$ individual probabilities to be calculated. This number increases significantly if the variable can take on more than two states, see chapter three.

Pearl (1988) introduced BBNs as a method to make this type of calculations easier. Pearl demonstrated that by defining the behaviour of a system in terms of a succession of local conditional probabilities, BBNs were able to provide the correct framework to transmit local conditional probabilities. Critically, by using the concept of conditional independence (see next section), BBN's were able to derive the required knowledge needed from the joint probability distribution using a much smaller number of conditional probabilities.

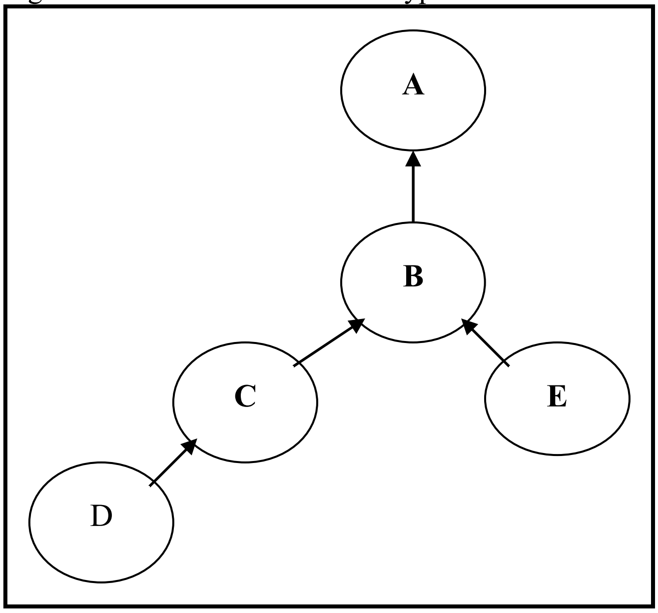
For example, a network consists of five variables (nodes) A,B,C,D,E. In not specifying the dependencies explicitly, we are assuming that all the variables are dependent on each other. Using the chain rule from probability theory, we can calculate the joint probability distribution:

$$p(A,B,C,D,E) = p(A|B,C,D,E)*p(B|C,D,E)*p(C|D,E)*p(D|E)*p(E)$$

However, if we explicitly model the dependencies as for the hypothetical BBN in Fig. 1.3, the joint probability distribution p(A,B,C,D,E) is much simplified:

$$p(A,B,C,D,E) = p(A|B)*p(B|C,E)*p(D)*p(E)$$

Fig 1.3. Node-link structure of a hypothetical BBN



Here we can see what the links in the BBN mean, and what needs to be determined to turn the graphical structure of a BBN into a probability distribution. For each node we need the conditional probability of that node (for example node B in Fig, 1.3) taking a certain value depending on the values of its parent nodes (Nodes C and E in Fig. 1.3). For discrete BBN's this involves defining a conditional probability table (CPT).

To illustrate the concept of a CPT consider node B in Fig 1.3. This requires a CPT denoting the conditional distribution p(B|C,E). Likewise, the CPTs for nodes A and C would specify p(A|B) and p(C|D). The nodes D and E have no parent node and therefore only require prior probability distributions p(D) and p(E). Keeping with the assumption that all variables in Fig. 1.3 are binary, taking on the states true or false, the CPT for node B would look like Table 1.2. Note that in a real CPT, the p(…..) probability expressions are values between 0 and 1.

Table 1.2. CPT for node B in Fig. 1.3

		B	
C	**E**	**true**	**false**
true	true	P(B=true | C=true, E=true)	P(B=false | C=true, E=true)
true	false	P(B=true | C=true, E=false)	P(B=false | C=true, E=false)
false	true	P(B=true | C=false, E=true)	P(B=false | C=false, E=true)
false	false	P(B=true | C=false, E=false	P(B=false | C=false, E=false)

An important concept in developing BBN's is the idea of conditional independence. Two sets of variables A and B, are (conditionally) independent given a third set C of variables. This can only be true when the values of the variables C are known. Therefore knowledge about the values of the variables B will provide no further information about the values of the variables A. This can be expressed as:

$$p(A|B,C) = p(A|C)$$

To better understand this concept, consider the following three events, for which the statement $p(A|B,C) = p(A|C)$ holds true:

Event A = I take an umbrella;
Event B = I observe rain clouds;
Event C = It is raining.

Notice that me taking an umbrella and observing rain clouds are not independent events. However, the event of me taking an umbrella is conditionally independent of me observing rain clouds given that it is actually raining. Once it is raining, observing rain clouds doesn't change the likelihood of me taking an umbrella. The conditional independence assumption expressed by the BBN (i.e. there is no dependency link) mean that fewer parameters need to be estimated because the probability distribution for each variable depends only on the node's parents. This independence allows us to consider each node and its parents independently from the rest of the model.

The key mathematical calculations undertaken in a BBN application are associated with probabilistic inference. Meaning, we can compute the conditional probability for some variables given knowledge on other variables. To calculate these probabilities a basic law of probability is applied, known as Bayes rule (Pearl 1988). Bayes rule for any two events, A and B, can be written as:

$$p(A|B) = p(B|A) * p(A)/p(B).$$

This rule answers the question, 'Given our beliefs about an event, how should we revise the probability assigned to the event when new evidence becomes available?' The idea is that, if we have a high degree of belief in the likelihood of event A based on past experience (i.e. $p(A)$), and we now have new data (event B) that would be likely to happen if event A happens (i.e. $p(B|A)$ then our after the evidence confidence (i.e $p(A|B)$ in event A should be strengthened.

The calculation of prior probabilities and the revised probabilities is relatively straight forward for a BBN involving only two events. However, for a BBN involving many dependencies and where nodes can take on more than two values, this is quite a different task. Therefore only recently efficient algorithms and software that make that possible were developed. Nowadays BBNs can be applied to solve more complex and realistic problems.

The data to parameterize the nodes in a BBN can come from a wide range of sources, including field data, expert opinion, or outputs from existing models such as linear regression models, or even simulation models. In the BBN three distinct categories of nodes can be identified. First, input nodes, these are the nodes that can be measured in the field, having no other nodes entering them. Each input node can have a series of prior (or unconditional) probabilities of being found in a particular state. The values for priors can be derived from existing survey data or expert opinion. Secondly, intermediate nodes, depend on input nodes or other intermediate nodes and are useful in integrating variables measured on different scales or for linking subsets of the network. These nodes are represented by a conditional probability, which is the likelihood of the state of the node given the states of input parameters affecting it. The strength or certainty of the dependency relationship among variables is summarized through a conditional probability table (CPT). Finally, the outcome nodes or query nodes being those nodes for which hypotheses are formulated.

Once the BBN is fully parameterized, there are several ways in which a BBN can be used to make inference about the model domain. There are three potential types of inference:

Diagnostic inference

Here evidence of an effect is used to infer the most likely cause. This often referred to as bottom-up reasoning, since is goes from effect to cause. For example, if we know the percentage macroalgal cover on a reef, we can query the BBN to ask what is the most likely cause of having a particular percentage macroalgal cover.

Causal inference

Here evidence is used to identify the most likely effect of a cause. This is often referred to as top-down reasoning, since it goes from cause to effect. This type of inference is mostly used in ecological modeling, giving evidence of past events, running it through the model to find the most likely future outcome. Fore example, if we know the amount of grazing on a coral reef, what will be the most likely percentage cover of macroalgae.

Inter-causal inference

Here we try to explain away potentially competing causes of a shared effect. For example, the causes of a high percentage cover of macroalgae could be partially explained by high nutrients or low grazing. The most important thing to be remembered is that whatever form of inference is used, the output for the hypothesis (outcome node) is a probability distribution representing the degrees-of-belief in each state, rather than a simple scalar.

4 This thesis

The main aim of the thesis was to provide insight in the dynamics of *Dictyota* spp. and *Lobophora variegata* on Caribbean coral forereefs. This thesis attempts to provide insight into this process by addressing the following objectives:

1. To develop a model incorporating both top-down and bottom-up processes influencing the percentage cover of the macroalga genus *Dictyota*.
2. To investigate the responses of individual patches of *Dictyota* spp. and *Lobophora variegata* under differing environmental conditions.
3. To investigate the responses of *Dictyota* spp. and *Lobophora variegata* to varying levels of grazing pressure under differing environmental conditions.

To answer these three objectives I first undertook a comprehensive literature review, which is presented in Chapter 2. The literature review investigated factors determining the standing crop of tropical brown macroalgae (Phaeophyta). This chapter starts with an overview of the two main hypotheses proposed to control the standing crop of macroalgae. Studies investigating these hypotheses remain largely inconclusive to what the main driving force is. I continue to describe what other factors may contribute to the success of Phaeophyta on coral reefs and draw conclusions, part of which are further explored in the next chapters of the thesis.

Chapter 3 comprises a paper modelling the dynamics of *Dictyota* spp. on coral forereefs applying a relatively new method in coral reef ecology: Bayesian Belief Networks (BBN). A BBN model can be described as a form of influence diagram depicting the causal relationships among physical and ecological factors influencing the outcome states of variables of interest, in this case percent cover of *Dictyota* spp. The BBN was developed based on factors and processes determining macroalgal standing crop identified in the literature review.

To my knowledge this is the first model integrating the main factors affecting the percent cover of a macroalgal species using a Bayesian Belief Network approach. Here I describe the development of the model and analyse the accuracy of the model in predicting the cover of *Dictyota* spp. This model can be seen as a work in progress and the main contribution of the work is that it provides a useful tool in integrating many bottom-up and top-down processes on coral reefs to predict the standing crop of *Dictyota* spp. Because the outcomes of the model are expressed as probabilities, it can explicitly communicate the uncertainties associated with the factors and processes influencing the standing crop of *Dictyota* spp. Certainly the model is in need of improvement (to include a wider range of coral reef habitats) but the first results are promising and therefore the model can be used to further our understanding of the processes affecting macroalgal standing crop. The model identified gaps in our understanding in need of further experimental studies or better it can be used as a unifying framework in research on macroalgal dynamics.

Chapter 4 describes the patch dynamics for both *Dictyota* spp. and *Lobophora variegata* under different environmental conditions, i.e. the windward and leeward side of a coral reef atoll. I characterize the dynamics of these two dominant species on forereefs, using size-based transition matrices. Consequently two spatial dynamics processes; fusion and fragmentation needed to be incorporated explicitly into the matrices. Fragmentation is where patches of macroalgae are broken up into smaller units through a variety of processes. Fusion is where two or more patches combine together to form a larger patch.

The main contribution of this chapter is that it provided insight in the complex patch dynamics of two dominant macroalgal species on Caribbean forereefs. Here, I modelled the dynamics of both *Dictyota* spp. and *Lobophora variegata* on the scale of individual patches. The advantage of this detail compared with percent cover is that many interactions occur at this small scale. Dynamics which might otherwise not have been detected only looking at percent cover. I used a size based matrix approach and therefore had to incorporate two important processes; fusion and fragmentation. To my knowledge this has not been done before in matrix models. I also introduced a simple metric in matrix analysis: the matrix entry ratio. This metric can aid in the interpretation of complex dynamics as it defines the degree of complexity.

Chapter 5 is an experimental study investigating the differential effects of one of the key ecosystem processes on coral reefs, grazing. In this study I used cages to exclude various herbivore guilds from grazing certain areas. Caging experiments have been applied to study this process many times (Sammarco 1980, Carpenter 1986, Lewis 1986, McClanahan et al. 2003, Hughes et al. 2007). The main contribution of this study was that I investigated the effects of grazing pressure under different environmental conditions, by comparing a forereef on the windward side of the atoll with one located on the leeward side of the atoll and under the virtual absence of the key herbivore *Diadema antillarum*.

Chapter 6 summarizes the major findings on the dynamics of *Dictyota* spp. and *Lobophora variegate.* These findings and the potential advantages and disadvantages of the approaches are further discussed. Subsequently future research areas are identified and the major conclusions of the thesis are given.

5 References

Adey WH. 1998. Coral reefs: Algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. Journal of Phycology 34:393-406.

Ang PO, De Wreede RE. 1990. Matrix models for algal life history stages. Marine Ecology Progress Series 59:171-181.

Aronson RB, and Precht WF. 2000. Herbivory and algal dynamics on the coral reef at discovery bay, Jamaica. Limnology and Oceanography 45:251-255.

Aronson RB, and Precht WF. 2001. White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460:25-38.

Begon M, Harper JL, and Townsend CR. 1996 Ecology: individuals, populations and communities. 3rd edition. Blackwell Publishing. Oxford. pp 1068.

Belliveau SA, and Paul VJ. 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. Marine Ecology Progress Series 232:105-114.

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

Bierzychudek P. 1982. The demography of Jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335-351.

Borsuk ME, Stow CA, Reckhow KH. 2004. A bayesian network of eutrophication models for synthesis, prediction and uncertainty analysis. Ecological Modelling 173:219-239.

Brault S, Caswell H. 1993. Pod-specific demography of killer whales (Orcinus orca). Ecology 74:1444-1454.

Burkepile DE, and Hay ME. 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128-3139.

Carpenter RC. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs 56:345-363.

Carpenter RC. 1990. Mass mortality of Diadema antillarum. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. Marine Biology 104:67-77.

Caswell H, and Werner PA. 1978. Transient behavior and life history analysis of teasel (Dipsacus sylvestris). Ecology 59:53-66.

Caswell H. 2001. Matrix population models. 2nd edition. Sinauer Associates. Sunderland. pp 722.

Charniak E, and Goldman R. 1989. Plan recognition in stories and in life. Proceedings of the 5th workshop on uncertainty in artificial intelligence. California. pp 54-60.

Connell JH. 1997. Disturbance and recovery of coral assemblages. Coral Reefs 16:S101-S113.

De Ruyter van Steveninck ED, Kamermans P, and Breeman AM. 1988. Transplant experiments with two morphological growth forms of Lobophora variegata (Phaeophyceae). Marine Ecology Progress Series 49:191-194.

Doak D, Kareiva P, Klepetka B. 1994. Modeling population viability for the desert tortoise in the western Mojave desert. Ecological Applications 4:446-460.

Done TJ. 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121-132.

Gardner TA, Cote IM, Gill JA, Grant A, and Watkinson AR. 2003. Long-term region-wide declines in Caribbean Corals. Science 301:958-960.

Gaulthier G, Lebreton J-D. 2004. Population models for Greater Snow Geese: a comparison of different approaches to assess potential impacts of harvest. Animal Biodiversity and Conservation 27:503-514.

Geister J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Proceedings of the 3rd International Coral Reef Symposium 1:23-30.

Grimm V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecological Modelling 115:129-148.

Guisan A, Edwards TC, and Hastie T. 2002.Generalized linear and generalized added models in studies of species distributions: setting the scene. Ecological Modelling 157:89-100.

Hastie TJ, and Tibshirani RJ. 1986. Generalized Additive Models. Statistical Science 1:297-318

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, and Hatziolos ME. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318:1737-1742.

Hughes TP. 1984. Population dynamics based on individual size rather than age: A general model with a reef coral example. American Naturalist 123:778-795.

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

Hughes TP, Bellwood DR, Folke C, Steneck RS, and Wilson JA. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology and Evolution 20:380-386.

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli DM, Hoegh-Guldberg O, McCook LJ, Moltschaniwskyj NA, Pratchett MS, Steneck RS, and Willis BL. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology 17:360-365.

Hughes TP, Szmant AM, Steneck RS, Carpenter RC, and Miller S. 1999. Algal blooms on coral reefs: what are the causes? Limnology and Oceanography 44:1583-1586.

Hwang I.-K, Kim H-S, and Lee WJ. 2005. Polymorphism in the brown algal Dictyota dichotoma (Dictyotales, Phaeophyceae) from Korea. Marine Biology 147:999-1015.

Jensen FV. 2001. Bayesian Networks and decision graphs. 1st edition. Springer. New York. pp 268.

Johnson JB, Omland KS. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101-108.

Karlson RH, Jackson JBC. 1981. Competitive networks and community structure: A simulation study. Ecology 62:670-678.

Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist 32:674-682.

Knowlton N. 2001. The future of coral reefs. Proceedings of the National Academy of Sciences of the United States of America 98:5419-5425.

Langmead O, Sheppard C. 2004. Coral reef community dynamics and disturbance: a simulation model. Ecological Modelling 175:271-290.

Lapointe BE. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography 42:1119-1131.

Lapointe BE. 1999. Simultaneous top-down and bottom up forces control macroalgal blooms on coral reefs (reply to the comment by Hughes et al.). Limnology and Oceanography 44:1568-1592.

Lapointe BE. 2004. Phosphorus-rich waters at Glovers Reef, Belize? Marine Pollution Bulletin 48:193-195.

Lapointe BE, Barile PJ, Yentsch CS, Littler MM, Littler DS, and Kakuk B. 2004. The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman's Pond Cay, Exumas Cays, Bahamas: a "natural" enrichment experiment. Journal of Experimental Marine Biology and Ecology 298:275-301.

Lapointe BE, Littler MM, and Littler DS. 1997. Macroalgal overgrowth of fringing coral reefs at discovery bay, Jamaica: Bottom-up versus top-down control. Proceedings of the 8th International Coral Reef Symposium 1:927-932.

Lapointe BE, and Matzie WR. 1996. Effects of stormwater nutrient discharges on eutrophication processes in nearshore waters of the Florida Keys. Estuaries 19:422-435.

Lefkovitch LP. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1-18.

Lek S, Delacoste M, Baran P, Dimopoulos I, Lauga J, and Aulagnier S. 1996. Application of neural networks to modelling nonlinear relationships in ecology. Ecological Modelling 90:39-52.

Leslie PH. 1945. On the use of matrices in certain population mathematics. Biometrika 35:213-245.

Lewis SM. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecology Monographs 56:183-200.

Littler DS, and Littler MM. 2000. Caribbean Reef Plants, 1st edition. OffShore Graphics Inc., Washington D.C.

Littler MM, Littler DS, Brooks BL. 2006. Harmful algae on tropical coral reefs: Bottum-up eutrophication and top-down herbivory. Harmful Algae 5:565-585.

Lotka AJ. 1932. The growth of mixed populations: two species competing for a common food supply. Journal of the Washington Journal of Science 24:199-216.

Mac Nally R. 2002 Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. Biodiversity and Conservation 11:1397-1401.

Marcot BG, Holthausen RS, Raphael MG, Rowland MM, Wisdom MJ. 2001. Using Bayesian belief networks to evaluate fish and wildlife population viability under land management alternatives from an environmental impact statement. Forest Ecology and Management 153:29-42.

Marshall PA, and Schuttenberg H. 2006. A reef managers's guide to coral bleaching. Great Barrier Reef Marine Park Authority, Townsville.

McClanahan TR, Sala E, Mumby PJ, and Jones S. 2004. Phosphorus and nitrogen enrichment do not enhance brown frondose "macroalgae". Marine Pollution Bulletin 48:196-199.

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, and Jones SHI. 2003. Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Marine Ecology Progress Series 261:135-147.

McManus JW, and Polsenberg JF. 2004. Coral-algal phase shifts on coral reefs: ecological and environmental aspects. Progress in Oceanography 60:263-279.

Minor ES, Urban DL. 2008. A graph-theory framework for evaluating landscape connectivity and conservation planning. Conservation Biology 22:297-307.

Moberg F, and Folke C. 1999. Ecological goods and services of coral reef ecosystems. Ecological economics 29:215-233.

Mumby PJ, Hastings A, and Edwards HJ. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98-101.

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenechan L, Newman MJH, Paredes G, Warner RR, and Jackson JBC. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955-958.

Pearl J. 1988. Probabilistic reasoning in intelligent systems: Networks of plausible inference. 2nd edition. Morgan Kaufmann Publishers. San Fransisco. pp 552.

Sammarco PW. 1980. Diadema and its relationship to coral spat mortality: grazing, competition, and biological disturbance. Journal of Experimental Marine Biology and Ecology 45:245-272.

Sato K, Iwasa Y. 1993. Modeling of wave regeneration in subalpine Abies forests: Population dynamics with spatial structure. Ecology 74:1538-1550.

Sauer JR, Slade NA. 1987 Size-based demography of vertebrates. Annual review of ecology and systematics 18:71-90.

Smith JE, Smith CM, and Hunter CL. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332-342.

Smith SV. 1977. Kaneohe Bay: A preliminary report on the responses of a coral reef/estuary ecosystem to relaxation of sewage stress. Proceedings of the 3rd International Coral Reef Symposium:577-583.

Spencer M, Tanner JE. 2008. Lotka-Volterra competition models for sessile organisms. Ecology 89:1134-1143.

Spiegelhalter D, Franklin R, Bull K. 1989. Assessment criticism and improvement of imprecise subjective probabilities for a medical expert system. Proceedings of the 5th workshop on uncertainty in artificial intelligence. California. pp 335-342.

Spiegelhalter D, Dawid AP, Lauritzen SL, Cowell RG. 1993. Bayesian analysis in expert systems. Statistical Science 8:219-247.

Svirezhev Y. 2000. Lotka-Volterra models and the global vegetation patteren. Ecological Modelling 135:135-146.

Szmant AM. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries 25:743-766.

Tanner JE. 1995. Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. Journal of Experimental Marine Biology and Ecology 190:151-168.

Treml EA, Halpin PM, Urban DL, Pratson LF. 2008. Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. Landscape Ecology 23:19-36.

Varis O. 1997. Bayesian decision analysis for environmental and resource management. Environmental modelling and Software 12: 177-185.

Volterra V. 1926. Variations and fluctuations of the numbers of individuals in animal species living together. (Reprinted in 1931. in Chapman RN, animal ecology New York).

Wolanski E, Richmond L, McCook LJ, and Sweatman H. 2003. Mud, marine snow, and coral reefs. American Scientist 91:44-51.

Wooldridge S, Done T. 2004. Learning to predict large-scale coral bleaching from past events: A bayesian approach using remotely sensed data, in-situ data, and environmental proxies. Coral reefs 23:96-108.

Wooldridge S, Done T, Berkelmans R, Jones R, Marshall P. 2005. Precursors for resilience in coral communities in a warming climate: a belief network approach. Marine Ecology Progress Series 295:157-169.

Chapter 2 Factors determining the standing crop of tropical brown macroalgae (Phaeophyta) on coral forereefs

FACTORS DETERMINING THE STANDING CROP OF TROPICAL BROWN MACROALGAE (PHAEOPHYTA) ON CORAL FOREREEFS

Henk Renken

1 INTRODUCTION

Tropical coral reefs are among the most diverse and highly productive ecosystems in the world. In the last three decades many coral reefs in the Caribbean have undergone dramatic changes, and experienced loss of coral cover from around 50% to <10% (Gardner et al. 2003) because of a variety of direct and indirect anthropogenic factors (Hughes and Connell 1987, Hughes et al. 1987, Hughes 1994, Shulman and Robertson 1996, Lapointe 1997, McClanahan and Muthinga 1998, McClanahan et al. 1999b, Stimson et al. 2001, Pandolfi et al. 2003). Indirect causes most frequently cited are bleaching (Brown 1997), coral disease (Aronson and Precht 2001), hurricanes (Hughes 1994, Gardner et al. 2005) and mass die-off of the urchin *Diadema antillarum* (Hughes 1994). Direct anthropogenic causes generally cited are over fishing of grazers (Hughes 1994), destructive extraction, direct sewage inputs and indirectly by increased sedimentation due to deforestation, and nutrients runoff from the land (Lapointe et al. 1997, Wolanski et al. 2003).

In recent times many reefs in the Caribbean have failed to regenerate after direct and indirect human disturbances, causing a shift in the balance between coral and algal cover. This shift is known as a phase shift (Done 1992). These shifts can either be reversible or form and alternate stable state (Knowlton 1992, Mumby et al. 2007b) and if the latter, will have serious deleterious consequences for fishery productivity, biodiversity and the ability of the reefs to provide coastal protection from tropical storms (Hughes 1994, Moberg and Folke 1999, Knowlton 2001). In many instances in the Caribbean the alternate state is dominated by macroalgae (Connell 1997). The high abundance of macroalgae prevents the forereefs from recovering after disturbances because they inhibit coral recruitment through pre-emption of space (Miller and Hay 1996) and undertake direct competitive interactions with corals through overgrowth, shading, abrasion and allelopathy (De Ruyter van Steveninck et al. 1988b, Tanner 1995, Jompa and McCook 2002, 2003). The outcomes of such competition include a decline in coral recruitment (Carpenter and Edmunds 2006, Mumby et al. 2007a), a decline in growth rates of both the alga and coral (De Ruyter van Steveninck et al. 1988b, Jompa and McCook 2002, Nugues and Bak 2006, Box and Mumby 2007), a reduction in the fecundity of corals (Tanner 1995) and even coral mortality (Lewis 1986, Hughes and Tanner 2000, Lirman 2001b, Hughes et al. 2007).

The distribution, abundance and standing crop of macroalgae are determined by the interactive effects of herbivory, competition and physical disturbances or stresses (Hay 1997). Numerous experiments have been carried out to determine what the controlling forces are on the dynamics of macroalgal standing crop. Two main hypotheses have been put forward; reduced herbivory or increased nutrients. The subject remains controversial (Lapointe 1997, Hughes et al. 1999, Lapointe 1999, Aronson and Precht 2000, Lapointe 2004, Lapointe et al. 2004b, McClanahan et al. 2004, Littler et al. 2006a), but there is an increasing awareness that they are not mutually exclusive (Burkepile and Hay 2006).

Recently there has been a number of experimental studies investigating the relative roles of herbivory and nutrients on macroalgal dynamics (Stimson et al. 2001, Belliveau and Paul 2002, Diaz-Pulido and McCook 2003, McClanahan et al. 2003, Lapointe et al. 2004b). These studies are also largely inconclusive (see section 2). Due to the complexity of coral reef ecosystems many experimental designs have failed to control for other physical and ecological factors driving the production of macroalgae and interacting with nutrients and herbivores such as light, topography, sedimentation, water flow, and temperature. The interpretation of the experimental studies is further complicated by the inherent characteristics of macroalgae (ephemeral or perennial life history, seasonality, heteromorphic life forms, size) and herbivores (size, seasonality, feeding preferences, feeding mechanisms) and it has to be put in a spatial (fore reef, back reef, patch reef) and temporal (winter vs. summer) context. The complexity of interacting factors complicates the interpretation of results of experiment, focussing mainly on herbivory, nutrients or a combination of both factors.

This review focuses on the factors determining the standing crop of brown macroalgae (Phaeophyta) in the shallow (up to 20 m depth) coral forereef habitat. The Phaeophyta or brown algae are named after their characteristic color from large amounts of the carotenoid fucoxanthin in their chloroplast as well as from tannins that might be present (Lee 1999). The Phaeophyta are divided in seven orders, which are all found in tropical waters, with the exception of the order of Laminariales (which contains the kelps) (Lee 1999). Standing crop is defined as the balance between two dynamic processes: net algal production and the removal of algal biomass by herbivory, wave action, senescence and reproductive losses (Carpenter 1985b). The focus is on macroalgal standing crop (biomass per unit area) rather than algal production (biomass per unit time) because many of the reasons why macroalgae seem to compete so successfully with corals are because of spatial considerations (pre-emption, abrasion, overgrowth and shading) rather than temporal interactions. Also increased growth does not necessarily result in increased standing crop, as standing crop is determined by the amount of biomass accumulated minus the biomass removed.

The reasons for focussing on the coral forereef and brown macroalgae (Phaeophyta) such as *Dictyota* spp., *Lobophora variegata, Sargassum* spp. and *Turbinaria* spp. are that firstly, they are frequently cited as being the dominant macroalgae on coral forereefs (Steneck 1993, Hughes 1994, Bak and Nieuwland 1995, Shulman and Robertson 1996, Diaz-Pulido and Diaz 1997, Lapointe et al. 1997, McClanahan et al. 1999a, Jompa and McCook 2002, McClanahan et al. 2003, McClanahan et al. 2004, Mumby et al. 2005, Beach et al. 2006) and the phase shift mentioned in numerous papers (Done 1992, Hughes 1994, Lapointe 1997, McCook et al. 2001, Belliveau and Paul 2002) mainly refers to changes in this habitat, which is a major concern as this zone often has the highest biodiversity and fish biomass (Mumby et al 2008). The phase shift towards macroalgal domination has a strong impact on the major carbonate producing organisms, i.e. scleractinian corals and coralline algae, resulting in reduced structural complexity, changed trophic dynamics and a loss in biodiversity (Tanner 1995, Adey 1998). Secondly, in “undisturbed” coral reef ecosystems macroalgae are abundant on reef flats (Connor and Adey 1977), unstructured sand plains (Hay 1981a) or deeper fore reefs (>20 m) (Littler and Littler 1984a, Lewis 1986) and not on shallow forereefs (McManus and Polsenberg 2004). The reason often cited to explain why macroalgae are not nearly as abundant on “pristine” shallow forereefs are that herbivores and omnivores concentrate their foraging on topographically complex areas such as the shallow forereef where the branching corals provide shelter from predators (Randall 1965, Littler and Littler 1980, Hay 1997, Stimson et al. 2001).

This review does not intend to discuss the various factors contributing to macroalgal growth and standing crop, such as nutrients, water flow, herbivory, in detail as many excellent reviews have been written on these factors amongst others; reproduction, dispersal and recruitment (Santelices 1990), water flow on settlement (Abelson and Denny 1997) and physiology and production (Hurd 2000), herbivory on populations and communities (Lubchenco and Gaines 1981), biogeography (Gaines and Lubchenco 1982) and ecology and evolution (Hay 1997), nutrients (McCook 1999, Szmant 2002) and competition (Carpenter 1990, McCook et al. 2001). Rather I focus on what is known about the interactions among factors determining macroalgal standing crop on coral forereefs and how they relate to nutrients and herbivory, where appropriate.

The review will start with the two main hypotheses cited in the literature for bottom-up versus top-down control of algae. Determination of macroalgal standing crop is not so much a bottom-up versus top-down strategy as pointed out in many papers (Lapointe et al. 1997, McCook 1999, Smith et al. 2001, Diaz-Pulido and McCook 2003, Lapointe 2004, Lapointe et al. 2004b), but a rather more complex set of interactions. Next I will discuss what is known about physiological and biological factors, and how they potentially interact with nutrients and herbivory. Finally I draw conclusions on how we might gain a better understanding of the complexity of macroalgal standing crop on coral reefs.

2 THE NUTRIENT AND HERBIVORY HYPOTHESES

In terrestrial ecosystems, such as forests, it has been suggested that bottom-up processes generally outweigh top-down processes in driving plant biomass, but the relative contributions of both can vary in space and time and with the species or ecosystems involved (Hairston et al. 1960). Similarly on coral reefs a complex set of interactions of bottom-up and top-down controls are important (Diaz-Pulido and McCook 2003). Many of the observed patterns seem to be generated by competition mediated by the interaction of variations in nutrient availability and disturbances by herbivores and wave action (Littler and Littler 1984, Littler and Littler 1988, Littler et al. 2006a). Most evidence suggests that macroalgal standing crop is controlled by grazing (top down) and the rate of production is controlled by nutrient supply (bottom up) (Gaines and Lubchenco 1982, Belliveau and Paul 2002, Russ 2003). In this section I will discuss the current knowledge of the roles of nutrients and herbivory in promoting macroalgal standing crop.

2.1 The nutrient hypothesis

The nutrient hypothesis states that with an increase in nutrients, mainly due to anthropogenic enrichment, macroalgal biomass will increase and therefore is said to be the main driving force in determining macroalgal standing crop. Conceptual models suggest that corals will dominate under low (oligotrophic) nutrient conditions, with the competitive advantage shifting towards macroalgae as nutrients increase (Littler and Littler 1984a, Steneck and Dethier 1994, McManus and Polsenberg 2004), assuming that macroalgae are nutrient limited. The widespread view that oversupply of nutrients will lead to macroalgal overgrowth seems logical and is supported by various studies (Lapointe and Tenore 1981, Delgado and Lapointe 1994, Lapointe 1997, Lapointe et al. 1997, Schaffelke and Klumpp 1997b, 1998, Lapointe et al. 2004a). However, one study showed evidence that brown macroalgae are actually inhibited by high nutrient levels (PO_4: 0.76 µM and NO_3: 2.10 µM) due to competitive inability with filamentous turf algae (McClanahan et al. 2003).

Whilst nutrients may play a role in the phase shift towards macroalgal dominance, their roles are still unclear (Szmant 1997, McCook 1999, Koop et al. 2001), because field experiments are not conclusive (Table 1) with some studies showing increased macroalgal standing crops (Lapointe

1987, Delgado and Lapointe 1994, Schaffelke and Klumpp 1997b) and others not (Larkum and Koop 1997, McClanahan and Muthinga 1998, Belliveau and Paul 2002, McClanahan et al. 2003) . Some of these studies were criticised recently (Littler et al. 2006b) for inappropriate length of experiment (Belliveau and Paul 2002), inadequate nutrient analysis and ambient nutrient concentrations that already exceeded proposed critical levels for increased macroalgal growth (Larkum and Koop 1997). The simplest model suggests that increased nutrients lead to increased macroalgal growth and increased growth will lead to an increase in macroalgal standing crop (McCook 1999). However, increased growth does not automatically result in increased macroalgal standing crop, because macroalgal standing crop is the balance of macroalgal production minus the removal of biomass due to herbivory, senescence and wave action. When discussing the role of nutrients we therefore have to look at how nutrients enhance growth of macroalgae rather than standing crop (Russ 2003).

An overview of studies measuring the effects of nutrients on macroalgal growth (Table 2.1), demonstrates that 9 conclude that nutrients enhance growth, 8 stated they do not and 3 are inconclusive. Traditionally, nutrient availability has been estimated by monitoring water column nutrient concentrations (Fong et al. 2001). However, field studies in tropical regions suggest there is little correlation between ambient water column nitrogen (N) and Phosphorous (P) concentrations and abundance of macroalgae (reviewed in McCook (1999), see also Table 2.1). This low correlation may be due to a variety of processes and factors and include: (1) nutrient supplies that are spatially and temporally variable (Pedersen and Borum 1997, Schaffelke and Klumpp 1997a, Szmant 1997, Schaffelke and Klumpp 1998, Schaffelke 1999, Fong et al. 2003, McClanahan et al. 2003), (2) nutrient uptake rate by macroalgae (Fong et al. 2001), (3) tight coupled recycling between reef organisms (Schaffelke and Klumpp 1998), (4) initial macroalgal tissue nutrient status (Pedersen and Borum 1997, Fong et al. 2003), (5) macroalgal morphology and life history (O'Neal and Prince 1988, Creed et al. 1997, Pedersen and Borum 1997, Schaffelke 1999, McClanahan et al. 2004), (6) water motion (Atkinson and Bilger 1992b, Bilger and Atkinson 1995, Hurd 2000), (7) topographic structure (Szmant 1997) and (8) ambient light (Lapointe and Tenore 1981, Lapointe and O'Connell 1989, Creed et al. 1997). These interacting factors will be discussed in the next section. Because of this lack of correlation, water column nutrients alone may not always provide an adequate indicator of nutrient availability on tropical coral reefs (McCook 1999). Therefore, nutrient availability might be a better indicator in controlling the growth of macroalgae (Hatcher and Larkum 1983, Pedersen and Borum 1997). Nutrient availability is made up of three components; (1) ambient water concentration, discussed here, (2) supply of nutrients and (3) nutrient uptake. I differentiate between supply and uptake in that by supply I refer to the amount of nutrients delivered to the alga across the diffusive boundary layer formed around the macroalgae, and hence its main influence will be water motion. Nutrient uptake is the amount of nutrients delivered through metabolic processes and subsequent storage in the alga cells, hence its close association with morphology. These two aspects will be discussed in the relevant sections. I acknowledge that these are not necessary three additive components but for ease of discussion I treat them separately.

Very low nutrient thresholds of ~ 1 μM dissolved inorganic nitrogen (DIN = NH_4^+ + NO_3^- + NO_2^-) and ~ 0.1 – 0.2 μM soluble reactive phosphorus (SRP = PO_4^{3-}) have been hypothesized as contributing to the shift from coral dominated reef habitats to those dominated by macroalgae. A nutrient threshold model based on nutrient concentrations (rather than on nutrient supply and uptake) is suggested to be the best index of nutrient status on a coral reef relative to macroalgal growth demands (Lapointe 1999). However, those threshold levels once proposed (Lapointe 1997, Lapointe et al. 1997), beyond which coral reefs are assumed eutrophic seems very difficult to uphold (Thacker et al. 2001) as shown in the variability in outcomes of various nutrient enrichment studies (Table 1). Also some investigators have pointed out that a large proportion of the worlds coral reefs have developed and persisted in coastal areas with naturally turbid water and high nutrient concentrations (Szmant 1997, McCook 1999, Szmant 2002). On the other hand it has been argued that most experiments on the effects of nutrients on macroalgal overgrowth were conducted in environments where ambient nutrient concentrations were already exceeding levels which limit macroalgal overgrowth thus the effects of additional nutrients on macroalgae could not be effectively measured (Littler et al. 2006a).

Both nutrient concentrations and dynamics typically vary greatly at a variety of temporal and spatial scales (Table 2.1), therefore point measurements of dissolved nutrient levels are unlikely to be representative unless it is based on extensive sampling (Szmant 1997, Thacker et al. 2001). However, ambient nutrient concentrations represent the net sum of internal nutrient cycling, macroalgal assimilation, and external inputs. Ambient nutrient concentrations are the most direct method to assess nutrient adequacy for macroalgal growth (Lapointe 1999). Also, it is relatively simple and inexpensive compared to that of estimating the hydrodynamic parameters needed to calculate fluxes (supply and uptake) (Szmant 1997). Therefore, it probably remains the best method to measure nutrient effects on macroalgal growth, especially for long term monitoring programmes. Carpenter and Williams (1993) found water flow to strongly influence algal turf canopy and they suggest that water flow will be a better predictor of macroalgal dominance then nutrients, whilst Fong et. al. (1994, 2001) suggested the concentration of nutrients within the tissue of macroalgae may be a more useful indicator (see, next section).

Table 2.1: Overview of the effects of nutrient concentrations on macroalgal species and study locations.

Reference	**Location**	**Species**	**Nutrient Concentration**	**Effect on Growth**
Belliveau and Paul 2002	Guam	Crustose Coralline Algae and fleshy algae	NO_3-: 0.59-1.55 PO_4^{3-}: n.d	Nutrients no significant effect on fleshy algae
Cronin and Hay 1996	North Carolina	*Sargassum filipendula, Dictyota ciliolata*		Nutrients were not limiting growth
Delgado and LaPointe 1994	Florida	*Halimeda, opuntia, Penicillus dumetosus, Penicillus capitatus, Ulva spp., Laurencia intricata, Hydroclathrus clathratus, Dictyota cervicornis*	NO_3-: 0.29-0.30 SRP: 0.07-0.11	Nutrient enrichment enhances productivity of fleshy algae
Fong et al 2003	Puerto Rico	*Acanthophora spicifera, Dictyota cervicornis, Hypnea musciformis*	DIN: 3.93-15	Variable. Depending on initial nutrient content of algae
Kuffner and Paul 2001	Guam	*Halimeda incrassata, Padina tenuis, Dictyota bartayresiana* and three cyanobacteria	NO_3-: 0.23 PO_4^{3-}: <0.03	No nitrogen and Phosphate limitation except maybe in Padina
LaPointe 1987	Florida Keys	*Gracilaria tikvahiae*	DIN: 1.14-2.42 PO_4^{3-}: 0.08-0.14	Phosphorus yearly and nitrogen seasonal limited growth
LaPointe 1997	Jamaica and Florida	*Dictyota dichotoma, Chaetomorpha linum, Lobophora variegata, Sargassum polyceratum, Codium isthmocladum, Laurencia poiteaui, Padina sanctae-crusis, Acanthophora spicifera Sargassum hystrix, Gracilaria ferox*	J: NH_4^+: 0.19-0.49 DIN: 4.62-28.10 SRP: 0.10-0.33 F: NH_4^+: 0.20-2.42 DIN: 0.75-3.44 SRP: 0.13-0.32	Nutrients enhance algal growth
LaPointe 2004	Caribbean	Macroalgae	NH_4^+: 0.23-0.64 NO_3^-: 0.15-0.55 DIN: 0.63-1.18 PO_4^{3-}: 0.04-0.09	Nutrient enhance algal growth
LaPointe and Tenore 1981	USA	*Ulva fasciata*		Growth not affected by nutrients under low light but increased under high light
LaPointe and O'Connell 1989	Bermuda	*Cladophora prolifera*	NO_3-: 0.73 NH_4^+: 0.53 PO_4^{3-}: 0.14	Nutrients enhanced algal growth
LaPointe et al 1997	Jamaica	*Dictyota* spp, *Sargassum* spp, *Chaetomorpha linum, Lobophora variegata, Codium isthmocladum, Laurencia poiteaui, Padina sanctae-crucis, Acanthophora spicifera*	DIN: 4.5-9 SRP: 0.09-0.15	Nutrient driven algal growth
LaPointe et al 2004	Bahamas	*Microdictyon marinum, Cladophora catenata, Laurencia intricate, Digenea simplex* and others	DIN: 0.49-0.80 NH_4^+: 0.14-0.44 NO_3^- + NO_2^-: 0.07-0.39 SRP: 0.01-0.018	Nutrient driven but grazing does play a role
Larkum and Koop 1997	Great Barrier Reef	Epilithic Algal Community		Not nutrient driven
McClanahan et al 2004	Belize, Glovers reef	Brown frondose macroalgae	PO_4^{3-}: 0.3	P and N do not enhance growth of frondose macroalgae
McCook 2001	Great Barrier Reef	*Sargassum* spp	DIN: 0.09-0.59 NH_4^+: 0.06-0.17 NO_3^- + NO_2^-: 0.02-0.21 PO_4^{3-}: 0.03-0.15	Not driven by nutrients

Table 2.1 continued

McCook et al 1997	Great Barrier Reef	*Sargassum* spp and *Padina* spp		Enhanced nutrients inhibited growth
Russ and McCook 1999	Great Barrier Reef	Epilithic Algal Community		Not nutrient driven
Schaffelke 1999	Great Barrier Reef	Macroalgae	DIN: 0.3 PO_4^{3-}: 0.04	Mixed results. Different species have different responses
Schaffelke and Klumpp 1997	Great Barrier Reef	*Sargassum baccularia*	DON: 2-5 DIN: n.d-1.7	Growth is stimulated by enhanced nutrients
Schaffelke and Klumpp 1998	Great Barrier Reef	*Sargassum baccularia*	DIN: 0.3 PO_4^{3-}: 0.02	Nutrients significantly increase productivity

DIN = Dissolved Inorganic Nitrogen, DON = Dissolved Organic Nitrogen, SRP = Soluble Reactive Phosphorous, n.d. = not detected. Units in µM.

2.1.1 Relative roles of nitrogen and phosphorous

Quantifying the relative roles of nitrogen (N) and phosphorous (P) limitation has also become an important focus (Fong et al. 2003). Algal growth can be limited by only one nutrient at a time (Lobban and Harrison 1994). Whether the growth-limiting nutrient is N or P can be gauged roughly from the ambient and cellular N:P ratios (Borchart 1996). The optimal ratio of N:P varies among species, with typical ratios of 30:1 in macroalgae (Atkinson and Smith 1983). Low ratios of N:P (usually < 10:1) may indicate N-limitation, whereas higher values (20-30:1) may indicate P-limitation.

Several studies found P to limit productivity and growth more frequently than N on tropical coral reefs (Atkinson and Smith 1983, Hatcher and Larkum 1983, Littler and Littler 1984b, Lapointe 1987, Lapointe and O'Connell 1989, Delgado and Lapointe 1994, Schaffelke and Klumpp 1997a, Schaffelke and Klumpp 1998, Belliveau and Paul 2002). However, these studies did find N to be important, at least seasonally (Lapointe 1987). Others found stimulation by both N and P in summer for *Sargassum baccularia* on the Great Barrier Reef (Schaffelke and Klumpp 1998) and in winter for *Gracilaria tikvahiae* in Florida (Lapointe 1987).

Various explanations have been proposed for the spatial and temporal variability in the relative importance of N and P limitation in reefs. Firstly, the strength of P limitation has been related to the amount of P-adsorbing carbonate in the substrate. Higher levels of carbonate will result in more P being adsorbed to the substrate and is thus not available for the alga and P limitation will occur (Littler and Littler 1984a, Littler and Littler 1988, Lapointe and O'Connell 1989, Lapointe et al. 1992a, Delgado and Lapointe 1994). Secondly, the relative importance of N and P limitation vary across a nutrient supply gradient, with N increasing in importance in more eutrophic systems due to high denitrification rates (Delgado and Lapointe 1994, Pedersen and Borum 1997, Schaffelke and Klumpp 1997a, Schaffelke 1999) and thirdly, species specificity in nutrient requirements and initial tissue status (O'Neal and Prince 1988, Pedersen and Borum

1997, Schaffelke and Klumpp 1998, Fong et al. 2003, McClanahan et al. 2004). Different growth forms of algae require different amount of nutrients to sustain their growth. In general filamentous algae will require less nutrients compared with macroalgae due to higher surface to volume ratios. Initial nutrient status partly determines when an alga becomes nutrient limited, because alga can utilize stored nutrients during times when nutrients are limited.

Three approaches have been used to determine whether N and/or P limit productivity of marine macroalgae. (1) N:P ratios of dissolved inorganic nutrients in the water column have been used as a measure of nutrient availability (Atkinson 1988), (2) N:P ratios of algal tissue have been used to predict nutrient limitation (Lapointe et al. 1992b) and (3) factorial enrichment experiments adding N and P alone and in combination, and quantifying response variables such as photosynthesis, growth and changes in tissue and water column N and P content. When addition of a nutrient increased photosynthesis or growth, it was considered to be limiting (Larned 1998).

N:P ratios of dissolved inorganic nutrients in the water column

This method involves comparing water column N:P ratios with nutrient requirements of the algae. The problem with this method is that different functional forms of algae may require nutrients in different proportions (Fong et al. 2003). In addition water column measures only provide a snapshot in time and may not adequately characterize availability in many tropical areas where nutrients are supplied in pulses (Szmant 1997, McCook 1999, McClanahan et al. 2003, Beach et al. 2006).

N:P ratios of algal tissue

This method has its shortcomings in the fact that the different functional forms of macroalgae have different uptake and storage capabilities and this confounds the relationship (see next chapter). For example, if both N and P are abundant in the water, and the macroalgae has greater uptake ability and storage capability for N than P, the resultant high tissue N:P ratio would indicate P limitation when limitation by nutrients in effect was not occurring (O'Neal and Prince 1988, Schaffelke 1999, Fong et al. 2003).

Factorial enrichment experiments

This approach has the advantage that it provides direct rather than indirect evidence of limitation (Fong et al. 2003). However some problems are associated with in situ nutrient enhancement experiments, such as high or variable background nutrient levels or the possibility that the added nutrients are lost by tidal flushing or taken up by reef biota other than macroalgae (Schaffelke and Klumpp 1998). Further, nutrient enrichment experiments are usually done with concentrations well above ambient nutrient levels and therefore set unrealistically high levels which normally will not occur under natural conditions, even where eutrophication is taking place and the duration of the experiments were too short (Littler et al. 2006b).

2.2 The herbivory hypothesis

The herbivory hypothesis states that due to a reduction in herbivory caused by diseases (i.e. the mass mortality of *Diadema antillarum* in the Caribbean) and overfishing, macroalgal standing crop increased on many forereefs (Hughes et al. 1987, Hughes and Connell 1999, Hughes et al. 2007) and forereefs have shifted from a coral dominated habitat to a macroalgae dominated habitat. Although macroalgal distribution and standing crop are determined by the effects of competition and physical disturbances or stresses (see later) and herbivory (Hatcher and Larkum 1983, Littler and Littler 1984b, Steneck and Dethier 1994, Hay 1997), numerous studies have described the importance of herbivory (Hay 1981a, Sammarco 1982, Steneck and Watling 1982, Carpenter 1986, Lewis 1986, De Ruyter van Steveninck and Breeman 1987, Foster 1987, Lessios 1988, Morrison 1988, Hughes 1994, Aronson and Precht 2000, Belliveau and Paul 2002, Mumby et al. 2006a, Hughes et al. 2007, Mumby et al. 2007b). In the Caribbean, herbivory can account for a distinct pattern in algal distribution between different habitats (Hay 1981a, b, Lubchenco and Gaines 1981, Hay et al. 1983, Lewis 1986, Hay 1997) and along a depth gradient (reviewed by Lubchenco and Gaines (1981). The notable absence of brown macroalgae on “undisturbed” fore reefs is thought to be due to the high numbers of herbivores in these habitats. The proportionally large numbers of herbivores on the fore reef are thought to be attributed to the high topographic complexity providing shelter for herbivores against predators (Randall 1961, Wanders 1976a, Lubchenco and Gaines 1981, Russ 2003).

Herbivory influences macroalgal distribution and standing crop on the coral reef by three mechanisms;

Grazing intensity varies spatially on the reef
Herbivores can be restricted from grazing on the reef crest due to high wave action, turbidity and the absence of refuges from predation (Randall 1961, Hay 1981b, Lubchenco and Gaines 1981, Hay et al. 1983, Foster 1987) and they are often less abundant on the deeper forereef (>20 m) due to reduced trophic carrying capacity as a function of lowered benthic productivity (Steneck 1983, Littler and Littler 1984a, Steneck and Dethier 1994). As a result, grazing intensity is lower in these habitats than on the shallow fore reef (Hay 1981a, b, Steneck 1983). Therefore the deeper reef and reef crest may be spatial refuges from grazers for large brown macroalgae.

Selectivity of herbivores in feeding

Herbivores preferentially feed on turf and crustose coralline algae and tend to avoid macroalgae, as a consequence a mosaic of patches of different algal assemblages develops at low to moderate rates of herbivory, with grazing concentrated in areas dominated by more palatable algal groups (Lubchenco and Gaines 1981, Steneck and Dethier 1994, Williams and Polunin 2001).

Herbivore composition (species and/or relative abundance)

Herbivore composition differs among reef habitats (Hay 1981a, Hay et al. 1983, Hay 1984), which when coupled with the differential effectiveness of algal defences against different herbivores (Coen and Tanner 1989, Cronin and Hay 1996a) could result in brown macroalgae being abundant in some habitat but not others.

The herbivore guild on Caribbean coral reefs is mainly composed of fish grazers, represented by Scaridae and Acanthuridae and the main invertebrate grazer is *Diadema antillarum*. The grazing intensity, foraging range and feeding mode of fishes and urchins vary and thus the effect they will have on macroalgae standing crop.

Fish grazers

Scaridae and Acanthuridae graze hap hazardously within their territories and leave significant parts of the algae untouched and these patches will continue to grow (De Ruyter van Steveninck and Breeman 1987). It is suggested that an upper threshold of benthic space exists in which herbivores are able to effectively control macroalgal growth, because herbivorous fishes are not limited by their food supply on coral reefs (Williams and Polunin 2001). Especially in the absence of *Diadema antillarum* it seems that herbivorous fish alone are not able to graze sufficiently the macroalgae. Data from the study of Williams and Polunin (2001) suggested an upper limit of about 60% of the benthos that could be grazed by fishes alone in relatively flat habitats, whilst recent studies suggested this to be only 40% in more structurally-complex habitats (Mumby et al. 2006b, Mumby et al. 2007b). The above suggests that the upper limit of benthos grazed is related to the rugosity of the reef, in that the upper limit increases with a decrease in rugosity. The suggested upper threshold seems to be supported by other investigators who found that fish continued to graze on *Lobophora variegata* but that total grazing pressure was lower than before the *Diadema antillarum* mortality in Curacao (De Ruyter van Steveninck and Bak 1986).

Diadema antillarum

Studies on grazing intensity have shown that *D. antillarum* is much more effective in removing algae than herbivorous fishes (Carpenter 1986, De Ruyter van Steveninck and Breeman 1987, Foster 1987, Adey 1998). On the other hand their grazing range is limited to 0.5 – 1 m^2 (Carpenter 1986) as compared to fishes, which have ranges of hundreds of meters (Mumby and Wabnitz 2002, Russ 2003). Therefore very low densities of *Diadema antillarum* (< 1 m^{-2}) will not be able to control macroalgal growth on the coral reef, because large areas will not be grazed upon (i.e. outside their feeding range). However within their feeding range, *D. antillarum* scrapes the surface very systematically and remove completely areas of algae including germlings and sporelings of otherwise avoided brown macroalgae (Adey 1998).

When both herbivorous fishes and *Diadema antillarum* are excluded from the forereef, rapid increases in macroalgae percentage cover have been widely documented, with increases reported of 1.5 to 15 times (Hatcher and Larkum 1983, Littler and Littler 1984a, Lewis 1986, Coen and Tanner 1989, Steneck and Dethier 1994, Jompa and McCook 2002, Hughes et al. 2007). Recent modelling of grazing on coral reefs also showed that the loss of the urchin *Diadema antillarum* resulted in the emergence of two stable states, once grazing became dominated by parrotfishes. Here it was shown that reefs in an unstable equilibrium could either become stable at a high coral cover or follow a trajectory towards a stable macroalgal dominated state. The trajectory depended heavily on the amount of grazing (Mumby et al. 2007b). The models suggest that on macroalgal dominated coral reefs removal of one of the herbivore guilds might be enough to keep the reef in a state of macroalgal dominance.

2.2.1 Algal-herbivore interactions

To persist on coral reefs, brown macroalgae must escape, tolerate, or deter herbivory (Gaines and Lubchenco 1982, Hay 1997). Brown macroalgae have developed several strategies to do so. More than one of these strategies are often expressed by a given species (Littler and Littler 1980, Littler et al. 1983, Hay 1997) and may include: (1) occupation of refuge habitats that are physically unfavourable or unavailable to herbivores (Wanders 1976b, Hay 1981b, Hay et al. 1983, Hay 1997, Hughes et al. 1999), (2) rapid growth involving the replacement of vegetative and reproductive tissues while simultaneously satiating the appetites of herbivores (Littler and Littler 1980, 1984a, De Ruyter van Steveninck and Breeman 1987) and (3) allocation of materials and energy towards herbivore defences. The last strategy has several components that encompass: (a) toxins, digestion-inhibitors or unpalatable secondary metabolites (Cronin and Hay 1996c, a, Hay 1997), (b) reduced calorific content (Steneck and Dethier 1994), (c) morphological shapes and sizes that minimize accessibility (Hay 1981a, Lubchenco and Gaines 1981, Steneck and Watling 1982, Lewis et al. 1987, Hay 1997) and (d) structural materials such as $CaCO_3$ that decrease palatability or nutritional value (Littler and Littler 1984b, Padilla 1985, De Ruyter van Steveninck et al. 1988a).

Susceptibility of brown macroalgae to grazing not only depends on macroalgal characteristics, but also on herbivore characteristics such as feeding mode and behaviour (Lubchenco and Gaines 1981, Gaines and Lubchenco 1982, Padilla 1985, De Ruyter van Steveninck and Bak 1986, Cronin and Hay 1996b). The susceptibility to grazing (Table 2.2) of brown macroalgal species varies highly per species and even within the same species and seems to be dependent on multiple factors. Firstly, tissue nutrient status of the species. Species with higher tissue nutrients seem to be preferred by herbivores (De Ruyter van Steveninck and Bak 1986, Cronin and Hay 1996a, Miller et al. 1999, Diaz-Pulido and McCook 2003, McClanahan et al. 2003). Secondly, preference of herbivores for certain parts of the plant such as apices as a function of the defence mechanism (Morrison 1988, Cronin and Hay 1996a, McClanahan et al. 2003). For example, Scaridae were deterred by chemical defences (for example dictyoal E and pachydictyoal A) found in reproductive and growth parts of the algae, but not to the structural defence of $CaCO_3$, which forms crystals in the tissue of algae. While Acanthuridae were deterred by $CaCO_3$ but not chemicals (Hay 1997). Thirdly, mobility and feeding strategy of herbivores. The tolerance of *Diadema antillarum* to chemicals identified as fish toxins is possibly due to the relatively limited feeding range of *D. antillarum* and therefore *D. antillarum* cannot afford to be very selective in the species it consumes (Littler et al. 1983). Fourthly, life history stage of the macroalgal species. Young germlings or sporelings may be preferred by grazers due to increased palatability as a function of less developed structural and chemical defences in the recruits (Thacker et al. 2001, Diaz-Pulido and McCook 2003). Lastly, herbivores may become less selective when food resources are limited will consume species with high levels of secondary metabolites that normally would deter them (Cronin and Hay 1996b).

Table 2.2: Susceptibility to grazing of different brown macroalgal species, herbivore type and location of study

Species	Location	Susceptibility	Herbivore type	Reference
Dictyota cervicornis	Belize	high	Scaridae, *Diadema antillarum*	Littler et al 1983, Lewis 1986
Dictyota cervicornis	Belize	low	Scaridae, Acanthuridae	Hay 1981, Littler et al 1983,
Dictyota ciliolata	North Carolina	medium	*Arbacia punctulata*, *Ampithoe longimana*	Cronin and Hay 1996a,b
Dictyota divaricata	Jamaica	high	*Diadema antillarum*	Morrison 1988
Dictyota menstrualis	North Carolina	medium	*Arbacia punctulata*, *Ampithoe longimana*	Cronin and Hay 1996b
Lobophora variegata, ruffled form	Belize, Jamaica	low	Scaridae, Acanthuridae	Hay 1981, Morrison 1988
Lobophora variegata, decumbent form	Jamaica, Belize, Curacao	high	*Diadema antillarum*, fishes	De Ruyter van Steveninck and Breeman 1987, Morrison 1988, Coen and Tanner 1989
Sargassum polyceratium	Belize	low	Scaridae, Acanthuridae	Hay 1981, Littler et al 1983
Turbinaria turbinata	Belize	high	Scaridae	Lewis 1986
Turbinaria turbinata	Belize, Southwest Caribbean	low	Scaridae, Acanthuridae, *Diadema antillarum*	Littler et al 1983, Diaz-Pulido and Diaz 1997

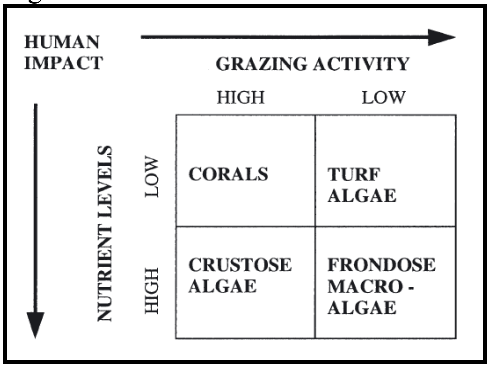
Herbivores may indirectly determine the success of a given macroalga because the algae have to allocate resources between chemical defences and structural materials. The production of chemical defences is thought to be costly because defences utilize resources that could have been allocated toward growth or reproduction (Littler et al. 1983). Species that rely primarily on chemical defences (i.e. *Dictyota cervicornis*, *Stypopodium zonale*) are able to maintain high photosynthetic rates, but remain susceptible to physical forces such as wave shear and sand scour (Littler et al. 1983, Hay 1997). In contrast, the tougher species such as thick fleshy algae (i.e. *Sargassum* spp*., Turbinaria* spp.) resist both grazing and physical forces by means of relatively high proportions of structural materials, but at the cost of lower photosynthetic and growth rates (Littler et al. 1983, Littler and Littler 1984b, Hay 1997). How macroalgae will allocate their resources will very much depend on the local environmental circumstances and the dominant herbivores present (Hay 1981a, Steneck 1986, Thacker et al. 2001).

Herbivores not only reduce algal biomass but may actually enhance algal distribution and standing crop if their grazing activity stimulates spore release (Santelices 1990) or generates fragments (Herren et al. 2006). Quantification of the process of spore release through grazing activity indicated that the quantities of macroalgal propagules produced in certain macroalgal species compared well with the recorded abundance of propagules settling in experimental plots in the field (Santelices 1990). Whilst a recent study in *Dictyota* spp. identified the generation of fragments by grazing activities of fishes as a mechanism by which this species could successfully reproduce (Herren et al. 2006). But whether this mechanism outweighs the ability of herbivorous fishes to reduce macroalgal cover is not clear.

2.3 Nutrient-herbivore interaction studies

The review of existing studies demonstrates how the interactions between macroalgae, nutrients, and herbivores are complex (Hughes 1994, Lapointe et al. 1997, Hughes et al. 1999, Lapointe 2004, McClanahan et al. 2004). In general it is believed that nutrient levels may set limits on macroalgal standing crop, but that herbivores can limit macroalgal standing crop to levels well below the constraints imposed by low nutrients. As a result, macroalgae are only abundant when herbivory is reduced and nutrient levels are high (Gaines and Lubchenco 1982, Hatcher and Larkum 1983, Belliveau and Paul 2002). This concept was developed in a model, known as the Relative Dominance Model (RDM) (Fig. 2.1), to predict interactions between nutrients and herbivores and their effects on coral reef communities (Littler and Littler 1984a, Aronson and Precht 2000, Littler et al. 2006a). This proved to be a simple and useful model to test nutrient and herbivore effects. The RDM predicts that the dominance of 4 major coral reef functional groups (1) reef building corals, (2) crustose coralline algae, (3) turf algae and (4) macroalgae, can be predicted by levels of herbivory and nutrients, but results have not always been in accordance with the model (McClanahan et al. 2003).

Fig. 2.1. The Relative Dominance Model



Reproduced from (Littler and Littler 1984a)

Recently a number of studies have been published investigating the effects of nutrients and herbivores simultaneously. These studies show that the results were variable (Table 2.3), with five studies stating that macroalgal dynamics were driven by herbivory, three studies emphasizing the role of herbivory but acknowledge the importance of nutrients, one study concluded it was nutrient driven but grazing plays a role and four studies are inconclusive in that both herbivory and nutrients play a role. Reasons for these varying results were discussed earlier, but it highlights the difficulty of interpreting the results as responses can be complex and not always consistent between experimental methods, habitats and regions. The majority of these studies seem to show that herbivory is a stronger factor than nutrients in controlling algal biomass (Vadas et al. 1992, McClanahan et al. 2003).

Table 2.3. Outcomes of herbivory-nutrient interaction studies, algal species and location

Reference	**Algal species**	**Location**	**Conclusion**
Hatcher and Larkum 1983	Epilithic Algal Community	Australia, GBR	Within limited temporal and spatial scales, grazing intensity alone is an adequate predictor of benthic algal standing crop
McCook 1996	*Sargassum* spp.	Australia, GBR	Herbivory driven
Miller et al 1999	*Laurencia poitei* , *Dictyota* spp, *Chondria* spp, *Neomeris annulata*, *Scytonema* spp, others	USA, Florida	Strong effects of herbivore exclusion and negligible effects of nutrient enrichment
Belliveau and Paul 2002	Crustose Coralline Algae and fleshy algae	Guam	Herbivory marked effect on algae. Nutrients no significant effect on fleshy algae
McClanahan et al 2003	Frondose, Crustose coralline, geniculated coralline, Turf algae	Belize, Glovers Reef	Herbivory driven, and coral mortality
Stimson et al 2001	*Dictyosphaeria cavernosa*	USA, Hawaii	Mainly grazing controlled
Thacker et al 2001	*Dictyota bartayresiana*, *Padina tenuis*, *Halimeda* spp, *Caulerpa* spp and cyanobacteria	Guam	Herbivory critical role in determining coral reef community structure, although nutrients do play a role
Diaz-Pulido and McCook 2003	*Sargassum fissifolium*, *Lobophora variegata*	Australia, GBR	Dominance of herbivory over nutrient effects, but emphasize the importance of herbivores

Table 2.3 continued

LaPointe et al 2004	*Microdictyon marinum*, *Cladophora catenata*, *Laurencia intricata*, *Digenea simplex* and others	Bahamas	Nutrient driven but grazing does play a role
Littler et al 2006	*Dictyota* spp, *Acanthophora* spp, *Caulerpa* spp, *Gracilaria* spp, *Halimeda* spp, *Porolithon* spp, *Neogoniolithon* spp, calcified crustose, *Peyssonnelia* spp	Belize	Complex interaction between nutrients and herbivory having direct/indirect and stimulating/limiting effects on macroalgae
Miller and Hay 1996	*Sargassum* spp., *Dictyopteris*, *Zonaria* spp, *Dictyota* spp.	USA, North Carolina	Competition, nutrients and herbivory interact
Russ and McCook 1999	Epilithic Algal Community	Australia, GBR	Not nutrient driven
Smith et al 2001	Fleshy algae and Crustose Coralline algae	USA, Hawaii	Both nutrients and herbivory play a role

3 FACTORS INTERACTING WITH NUTRIENTS AND HERBIVORY

The focus on nutrients and herbivory in determining macroalgal standing crop mainly reflects concerns about eutrophication and overfishing leading to a phase shift on coral reefs (McCook 1999, McCook et al. 2001, Scheffer et al. 2001, Hughes et al. 2003, Bellwood et al. 2004). However, as became clear from the previous section, many other processes (species interaction) and factors (light, water motion) combined with nutrients and herbivory determine the standing crop of macroalgae on coral reefs (McClanahan et al. 2002a, Diaz-Pulido and McCook 2003). In this section alternative factors identified in the literature, which contribute to the dynamics of macroalgal standing crop are discussed, focusing on their interactions with nutrients and herbivory.

3.1 Macroalgae morphology and life history

Brown macroalgae display a wide range of growth forms between species, ranging from filamentous algae, through corticated foliose algae to leathery macrophytes (Sensu Steneck and Watling 1982) (Fig 2.2). Also within the same species different growth forms can be found, known as polymorphism (Hanisak et. al. 1988). A well known example of a species showing polymorphism is *Lobophora variegata*, displaying three distinct growth forms; decumbent, crust and ruffled (Littler and Littler 2000) depending on the environment in which they grow (De Ruyter van Steveninck et. al. 1988). In order to identify broad patterns in macroalgal responses, a functional group or functional form model was proposed (Littler and Littler 1980, Steneck and Watling 1982). Based on there overall form, the algal functional groups behave in similar ways and display characteristic rates of mass-specific productivity, thallus longevity and canopy height.

Fig. 2.2. Examples of functional forms of brown macroalgae (Phaeophyta). A: filamentous algae, *Sphacelaria* spp., B: corticated foliose (branching), *Dictyota menstrualis*, C: Corticated foliose (Sheet), *Lobophora variegata*, D: Leathery macrophytes, *Turbinaria turbinata*

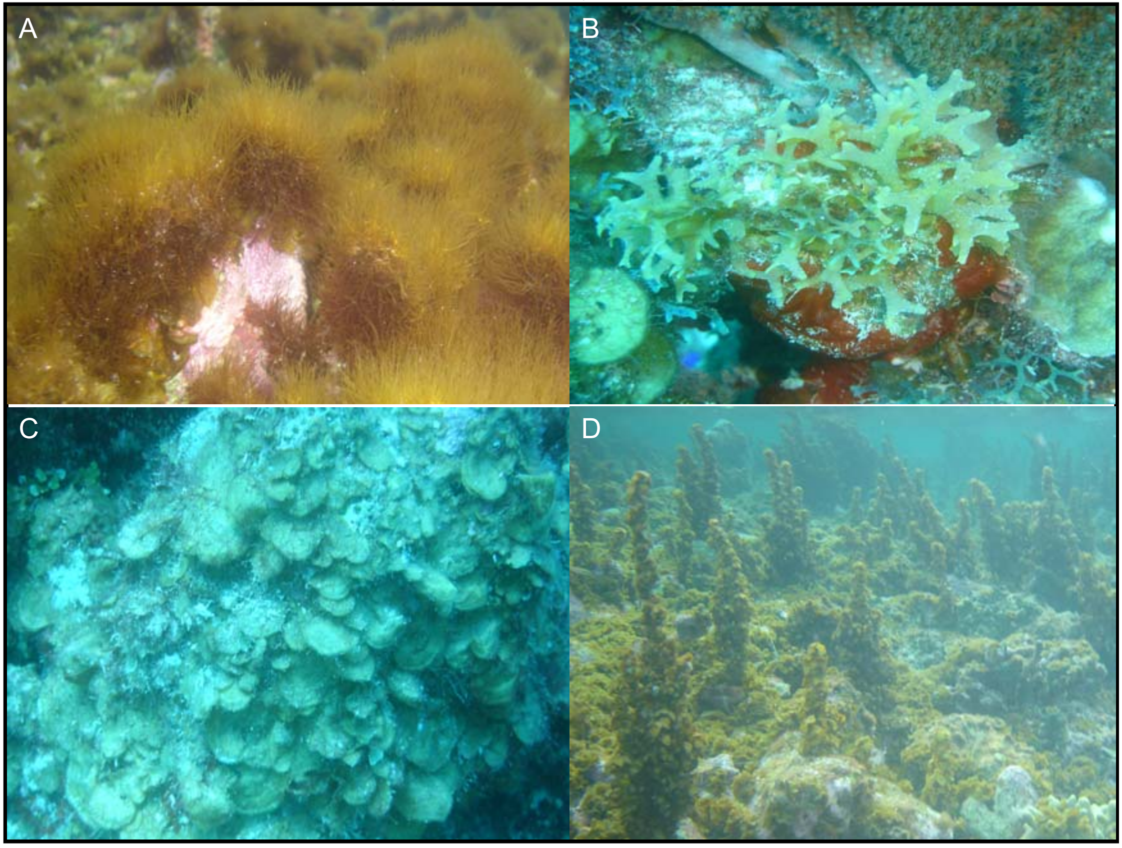


Photo: Hendrik Renken.

The species implicated in the overgrowth of coral reefs such as *Dictyota* spp. and *Lobophora variegata* (Bak et al. 1984, Steneck 1993, Hughes 1994, Shulman and Robertson 1996, Diaz-Pulido and Diaz 1997, Lapointe et al. 1997, McClanahan et al. 1999a, Lirman 2001a, McClanahan et al. 2003, McClanahan et al. 2004) are mainly from the corticated foliose and leathery macrophyte algal functional group (sensu Steneck and Watling 1982). These species are characterized by having a thallus, which is differentiated into an outer layer of small, often thick-walled cells called a cortex and a central region of larger thin-walled cells called the medulla. The leathery macrophytes are morphologically the most complex with multiple thick walled cells for structural strength (Steneck and Watling 1982). The success of these species in maintaining high standing crops once they are established is partly due to their morphology and life history characteristics.

3.1.1 Macroalgal morphology

Resistance to grazing and nutrient uptake is closely related to thallus morphology because total plant surface area, stature and form influences the susceptibility to grazing and nutrient uptake efficiency as well as many other crucial processes such as photosynthetic capacity, light reception and resistance to physical forces (wave action and sand scour) (Littler and Littler 1980, Steneck and Watling 1982, Lewis et al. 1987, Coen and Tanner 1989, Steneck and Dethier 1994, Hurd 2000, Padilla and Allen 2000). Brown macroalgae have two morphological strategies in order to maximise their survival and the favoured strategy depends upon the local environmental conditions and grazing intensity (Russel 1973, Santelices 1990a). The first strategy is for selection for more delicate sheet-like or (corticated) foliose thalli in loose aggregations with high productivity (for example *Dictyota cervicornis*) and the second is a selection for tougher coarsely branched morphologies (for example *Sargassum* spp. and *Turbinaria* spp.), having lower photosynthetic rates due to greater proportions of structural/non photosynthesising tissue (Littler and Littler 1984b, Hanisak et al. 1988, Enriquez et al. 1994, Hay 1997). Both strategies involve a cost for the particular macroalga. Energy used for environmental resistance or morphological defensive systems is not available for other uses and materials that are assigned for structural strength are not available as reproductive tissue (Littler and Littler 1980, Lubchenco and Cubit 1980, Littler and Littler 1984b, Hanisak et al. 1988, Cronin and Hay 1996a).

Nutrients - The process of nutrient uptake, which I defined earlier as the amount of nutrients delivered through metabolic processes and subsequent storage in the plant cells, as opposed to nutrient supply (the delivery to the algae across the diffuse boundary layer) is closely associated with macroalgal morphology. Uptake of nutrients and storage capacity is species-specific but some generalisations can be made. The rate at which algae take up nutrients depends largely on their nutritional history (Lobban and Harrison 1994), with nutrient starved macroalgae showing higher uptake rates than those that are not initially nutrient-limited. When grown under nutrient-saturated conditions, the uptake rate is equal to the growth rate (Fong et al. 1994). When cells become nutrient-limited and then encounter a nutrient pulse, high uptake rates permit rapid replenishment of internal nutrient stores, a process known as luxury uptake. Luxury uptake allows algae to store nutrients beyond the immediate metabolic requirements of the cells. It is this surplus that allows algae to grow when external concentrations later become limiting.

Macroalgae that form more delicate thalli have a greater ability to uptake nutrients than the tougher algae. Their thallus is usually only a few cells thick and therefore the ratio of exposed surface to internal volume of the alga is greater than in macroalgae with tougher morphologies. Thus, potentially higher growth rates can be achieved through more rapid assimilation of nutrients and higher light harvesting (Russel 1973, King and Schramm 1976, Wanders 1976a, Ramus et al. 1977, Lubchenco and Cubit 1980, Dudgeon et al. 1995, Pedersen and Borum 1997, Schaffelke 1999, Diaz-Pulido and McCook 2003). On the other hand species with more complex thalli have more storage capacity and may have a competitive advantage because they can utilize stored nutrients during periods of low nutrient availability (Pedersen and Borum

1997, Schaffelke and Klumpp 1997a, Schaffelke and Klumpp 1998). Whether one strategy is competitively superior depend on the species-specific requirements for growth (O'Neal and Prince 1988, Pedersen and Borum 1997, Schaffelke 1999, McClanahan et al. 2004).

Initial tissue nutrient status has a strong affect on nutrient uptake. If the internal N and P reserves are already above the critical tissue nutrient level, the growth enhancement by nutrient uptake was found to be comparably weak (Schaffelke and Klumpp 1997a, Schaffelke and Klumpp 1998, Miller et al. 1999). Also with highly variable levels of water column nutrients ranging from non detectable to concentrations indicating eutrophication, species from the same macroalgal functional group responded remarkably differently (Schaffelke and Klumpp 1997a). *Sargassum baccularia* showed production increases of 30% after a single nutrient pulse while *Turbinaria ornata* did not respond to a nutrient addition. The reasons Schaffelke and Klumpp (1997) cited for these differences were that initial tissue nutrient status for *Sargassum* spp. was very low and thus showed an increase in production and the form of *Sargassum* spp. is different from that of *Turbinaria ornata. Sargassum* spp. with its flattened thalli and complex branching allowed for a larger photosynthetic surface area and hence higher production rate (Wanders 1976b).

Herbivory - Thallus form is a very important factor in influencing the impact of herbivores on macroalgae (Gaines and Lubchenco 1982, Littler and Littler 1984a, Padilla 1985). For example in *Padina jamaicensis* and *Lobophora variegata* it has been suggested that the different growth forms represent responses to fundamentally different environmental conditions associated with spatial variation in herbivore grazing (Russel 1973, De Ruyter van Steveninck and Breeman 1987, Lewis et al. 1987, De Ruyter van Steveninck et al. 1988a, Coen and Tanner 1989). The upright foliose forms are highly susceptible to grazing but provide increased canopy height and a broad-leafed morphology, both of which may be advantageous under light competitive conditions. The foliose form also exhibits rapid growth to reproductive maturity as well as high reproductive output (De Ruyter van Steveninck and Breeman 1987, Lewis et al. 1987, Hay 1997). The upright form of *L. variegata* was observed only in habitats with predictable low levels of fish grazing or spatial refuges in areas of high fish grazing (Coen and Tanner 1989). Transplant experiments also supported this hypothesis in that after transplantation differences in morphology decreased. Two distinct growth forms of *Lobophora variegata* (decumbant and ruffled) once transplanted to each respective habitat took on the exhibited growth form associated with the habitat, an indication of the functional importance of each morphology in its respective habitat (De Ruyter van Steveninck et al. 1988a).

It seems that under low levels of herbivory macroalgae favor upright growth forms above any other growth strategy to promote higher growth rates. Adaptations of upright macroalgae that contribute to higher growth rates at the expense of herbivory are (1) most of the surface of an upright thallus neither adheres to the substratum or is buried in it, and the thallus being only a few cells thick, the ratio of exposed surface to internal volume of the plant is greater than in non upright forms. This allows for potentially higher growth rates through more rapid assimilation of nutrients and higher rates of light harvesting per unit biomass (Hay 1997), (2) Upright forms presumably allocate less energy and material for attaching themselves to the substratum or burrowing through it and with small points of attachment the upright macroalgae requires less space per unit biomass than crustose forms (Lubchenco and Cubit 1980, Hay 1981a, b).

3.1.2 Life history

Three basic life histories occur in the brown algae:

1) Predominantly diploid life history, with meiosis occurring before the formation of gametes. Thus the gametes are the only haploid part of the life cycle and fuse to form the diploid zygote. Growth is by an apical cell division (Fig. 2.3). A typical example of this type of life history on coral reefs is *Sargassum hystrix* (Fig. 2.4).
2) Isomorphic alternation of generations, consisting of the alternation of haploid (gametophytic) plants bearing gametes with structurally identical diploid (sporophytic) plants bearing spores. Growth is by an apical cell. A typical example of this type of life history on coral reefs is *Dictyota cervicornis* (Fig. 2.5).
3) Heteromorphic alternation of generations, consisting of the alternation of small haploid plants bearing gametes with large diploid plants bearing spores. This type is not found on coral reefs but a well known example is *Laminaria japonica* (Fig. 2.6).

Fig. 2.3. Apical cell division

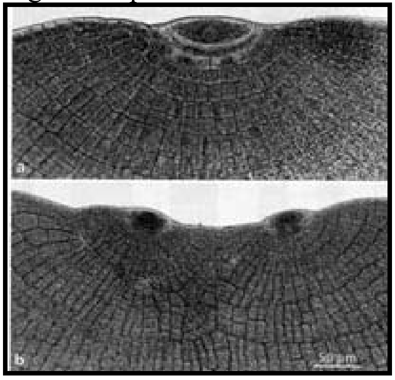


Photo: Frank Lochem, Florida International University

Fig. 2.4. Life history of a *Sargassum* spp.

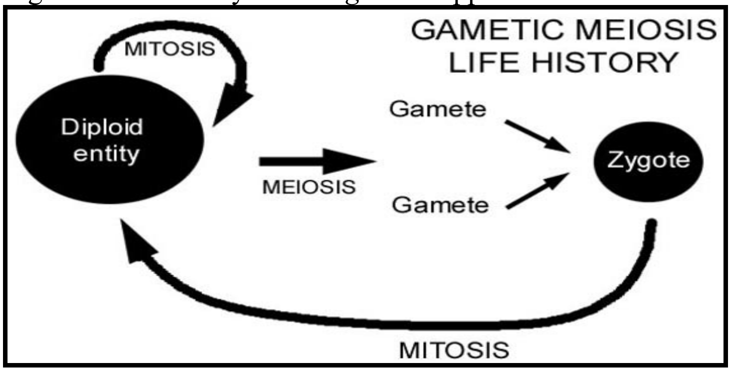


Photo: Celia Smith, University of Hawaii

Fig. 2.5. Life history of *Dictyota* spp.

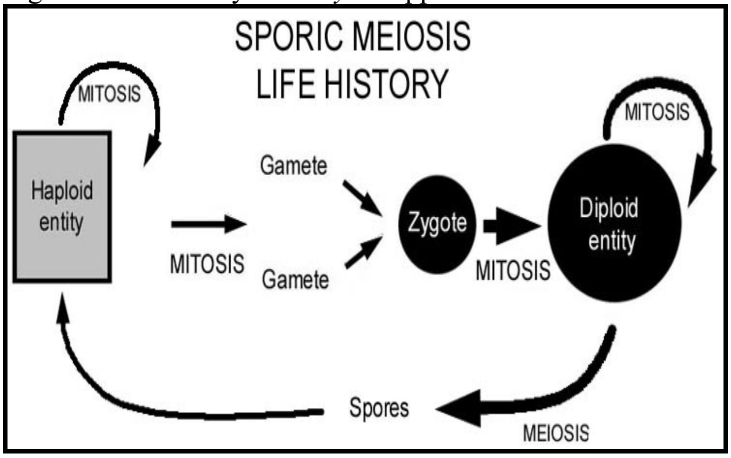


Photo: Celia Smith, University of Hawaii

Fig. 2.6. Life history of *Laminaria* spp.

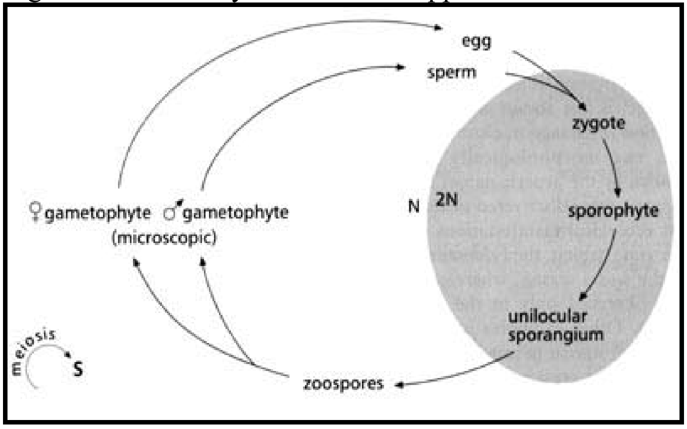


Photo: Frank Lochem, Florida International University

Many species (*Dictyota* spp. *Lobophora variegata* and *Sargassum* spp.) are also capable of asexual reproduction through fragmentation and subsequent growth of the fragments into adult plants. This ability is thought to be one of the reasons why brown macroalgae are able to dominate coral reef habitats (Herren et. al. 2006).

The debate over the relative contributions of reduced herbivory and eutrophication to macroalgal overgrowth has largely focussed on established mature macroalgae and ignored processes that affect earlier life history stages (Schaffelke and Klumpp 1997b). It is likely that herbivory and nutrient supply act differently on recruits and adults. For example, nutrient competition between propagules is probably far more intense than competition for light, as shading effects are minimal, but under a canopy of adult plants, juveniles may be highly light limited (Creed et al. 1997) and herbivores may preferentially feed on turfalgae including the propagules and germlings of macroalgae (Thacker et al. 2001). However, a study on the effect of both herbivory and nutrients on recruitment did not show any significant difference on recruits and adults (Diaz-Pulido and McCook 2003).

The most common sequence of life history transitions for macroalgae include four stages: spores or zygotes, germlings, juveniles and adults (Vadas et al. 1992). Each stage may respond differently to biotic and abiotic pressures (Vadas et al. 1992, Steneck and Dethier 1994, Diaz-Pulido and McCook 2003). The first stage in the life cycle of an alga is the production and subsequent release of propagules (spores or zygotes) in the water column and dispersal through a pelagic phase. The number of propagules produced by an alga and the timing of discharge depend mainly on, (1) the physiological state of the parent plant and especially the reproductive tissues (Umar et al. 1998), (2) the degree of maturation of the developing propagule (Creed et al. 1997) and (3) the effects of environmental factors triggering the reproductive process. Temperature, irradiance, light quality, emersion, salinity and nutrient enrichment or depletion, all have been experimentally shown to influence propagule release in macroalgae (Santelices 1990, Vadas et al. 1992, Kendrick 1994, Abelson and Denny 1997).

Recruitment to the macroalgal community is highly variable in space and time (Wright and Steinberg 2001) and macroalgal propagules are in general short-lived and have poor dispersal capacities (Norton 1992, Schaffelke and Klumpp 1997a) because of various factors and processes such as floating and sinking capacities due to the composition and size of a macroalgal propagule, and the height of release above substratum of propagules as a factor of macroalgal size. Furthermore, many propagules exhibit passive transport, because they lack motility. Lastly, water movement and grazing will affect where and when a propagule can successfully settle. However, other mechanisms such as detachment of parts of macroalgal or whole macroalga caused by a disturbance (wave action, storms, grazing) can contribute to wide dispersal, as these parts or whole alga can survive for long periods and subsequent become fertile or attach rapidly (Norton 1992, Herren et al. 2006).

Adult macroalgal thalli may interfere with recruitment and distribution by a variety of processes as a function of density (Kendrick 1994, Creed et al. 1997). The height of adult macroalgae has been suggested to limit dispersal ranges of propagules (Stiger and Payri 1999), adult macroalgae take up nutrients which otherwise would be available for recruits (Creed et al. 1997), the adult macroalgal canopy reduces illumination of germlings and thus inhibits their development into adults (Kirkman 1981, Reed 1990, Creed et al. 1997), and adult macroalgae interrupt water movement and could negatively influence the settlement of recruits and subsequent development (Steneck and Dethier 1994, Creed et al. 1997).

The recruitment process consists of a settlement phase and a development phase into germlings, juveniles and finally adults. Settlement can be divided in two stages: the delivery of propagules to the substratum, and the subsequent establishment of the propagules, a stage that includes both attachment and metamorphosis (Abelson and Denny 1997). The delivery of the propagule to the substratum is either active or passive. Various environmental factors are significant in the process, such as chemical cues, substratum heterogeneity and flow patterns (Santelices 1990, Abelson et al. 1994, Kendrick 1994). Once the propagule becomes fixed to the substratum means having no possibilities of habitat change under adverse conditions. Therefore propagule mortality is high and may determine the observed pattern of species distribution in the field. The mortality factor may be biotic, abiotic or an interaction of both (Coen and Tanner 1989, Santelices 1990).

Many macroalgae show distinct seasonal trends in abundance and growth, even in tropical regions where seasonal differences are less distinct compared with temperate climates (McCourt 1984). In general brown macroalgae have peak abundances in the summer (Table 2.4) and a reduction of biomass throughout the winter season, but exceptions are plentiful, for example in the study carried out by De Wreede (1976) for three species of *Sargassum* in Hawaii and in the Red Sea for *Dictyota cervicornis* (Ateweberhan et al. 2005) and *Lobophora variegata* (Quan-Young et al. 2004) . The seasonality in tropical regions seems little correlated with seasonal trends in temperature, salinity or nutrient levels. For example, off the North Carolina coast, *Lobophora variegata* has the highest rates of photosynthetic performance during the time period when ambient water temperatures where the coolest (Peckol 1983). Luxury uptake is also thought to cause a lack of correlation between seasonal changes in temperature and algal growth. The lack of a direct response to a change in temperature is believed to be caused by the ability of macroalgae to utilise stored nutrients under adverse conditions maintaining high growth rates (Fong et. al. 1994).

Table 2.4. Peak abundance of selected brown macroalgae in various locations

Reference	Species	Months	Location
Airoldi 1998	*Dictyota dichotoma*	July	Italy
Ateweberhan et al 2004	*Dictyota cervicornis*	December to January	Eritrea
Diaz-Pulido and Garzon-Ferreira 2002	*Dictyota* spp.	February and August	Colombia, Caribbean
De Wreede 1976	*Sargassum polyphyllum*	October	Hawaii
De Wreede 1976	*Sargassum oligocystum*	August	Hawaii
Espinoza and Rodriguez 1987	*Sargassum sinicola*	April	Gulf of California
Lirman and Biber 2000	*Dictyota* spp.	August	Florida
McCourt 1984	*Sargassum Johnstonii*	February	Gulf of California
Schaffelke and Klummp 1997	*Sargassum baccularia*	March	Great Barrier Reef
Schaffelke and Klummp 1997	*Turbinaria* spp.	February	Great Barrier Reef
Quan-Young et al 2004	*Lobophora variegata*	February and June	Yucatan

3.2 Resource availability

3.2.1 Light

One of the primary resource requirements for macroalgae is light and its quantity and quality largely determine the type and occurrence of algae (Wheeler 1980, Lee 1999). The important part of the light spectrum for algal growth is the Photosynthetically Active Radiation (PAR), which is the part of the visible light spectrum ranging from 300 to 700 nm (Carr et al. 1997). The PAR will fluctuate during the day and shows an asymmetry, due to the variability of the strength of the sun (Lapointe and Tenore 1981). Typically, photosynthesis reaches a maximum in the morning and decreases in the afternoon (Wanders 1976a, Ramus and Rosenberg 1980). As much as 70% of the daily photosynthesis can occur in the first half of the day (Ramus and Rosenberg 1980).

The quantity and quality of the light reaching the reef are determined by the amount of back-reflectance at the surface of the water, which varies over a day with the degree of cloud cover, angle of incidence of the sun and wave action (Carr et al. 1997). Also water depth, in general it is assumed that the photic depth corresponds to the limit where irradiance is 1% of surface light and together with herbivory determines the maximum depth where macroalgae grow (Norton 1977, Ramus et al. 1977, Calado and Duarte 2000), although studies of *Laminaria hyperborea* have indicated that there is often less change in growth rate with depth than might be expected to result from the decrease in irradiance (Kain 1976). Furthermore, turbidity; the amount of particulate matter in the water, determines to what depth light effectively can penetrate (Umar et al. 1998). Colored Dissolved Organic Matter (CDOM) diminishes light as it penetrates water and affects both availability and spectral quality of light (Kowalczuk et al 2005). Substratum orientation (Carpenter 1990) and the relative proximity of neighbouring organisms that shade the thallus of macroalgae both play a role (Lapointe and Tenore 1981, Carpenter 1985, Carpenter 1990, Rivers and Edmunds 2001).

Aspects of algal morphology such as, thallus composition (photosynthetic tissue and structural tissue) play a role in the amount of light captured by the macroalgae. Thallus composition resulting in the efficient capture of light energy will determine the total amount of energy that can be allocated to growth, reproduction, defences and other metabolic processes and thereby will influence the potential success of the alga (Ramus and Rosenberg 1980, Carpenter 1985, Carpenter 1990, Santelices 1990, Enriquez et al. 1994). It is thought that photosynthetic capacity should be greater for thin macroalgae because the ratio of photosynthetic tissue to structural tissue is greater for thin macroalgae (Ramus et al. 1977, Lubchenco and Cubit 1980, Steneck and Dethier 1994, Dudgeon et al. 1995). Therefore thick macroalgae should be able to support lower maximal growth rates and have higher minimum light requirements for growth than thin macroalgae. Increasing thickness reduces the efficiency of light capture for growth and sets limits to the capacity to improve the photosynthetic yield (Enriquez et al. 1994), but this might be partially compensated by increasing the light harvesting pigment concentration in growth cells (Ramus et al. 1977), which might also have explained the results of the study on *Laminaria hyperborea*.

Tropical macroalgae growing in shallow waters are usually subjected to high light intensities and have evolved adaptations to prevent damage by high light levels and ultraviolet radiation. Tropical oceanic waters typically contain little particulate matter that would absorb and scatter UV wavelengths and transmittance of these wavelengths is assumed to be high, especially in the upper 5 m of the water column (Jokiel and York 1984). This suggests that macroalgal growth on shallow coral reefs may be limited by more than nutrient availability alone and most likely will be a combination of light intensity and nutrient availability (Carpenter 1985, Creed et al. 1997). This is supported by Lapointe and O’Connell (1989) for *Cladophora* spp. and in *Ulva fasciata* (Lapointe and Tenore 1981). In these studies they found a strong interaction between irradiance and nutrient availability in regulating macroalgal growth. Nutrient-limitation of macroalgal productivity is of primary importance when irradiance is high, whereas light-limitation of macroalgal productivity is of primary importance when nutrient availability is non-limiting. This relationship is by no means linear, because the nature of these interactions continuously changes over time due to variations in self-shading, water transparency, local weather patterns and seasonal differences in nutrient availability (Lapointe and Tenore 1981, Lapointe and O'Connell 1989, Enriquez et al. 1994).

3.2.2 Substrate and topography

The extent and type of substrate available for settlement of macroalgae is an important factor determining the settlement success of a macroalga, as well as micro- and reef topography (Dahl

1973, Harlin and Lindbergh 1977, Norton and Fetter 1981, Norton 1983, Carpenter and Williams 1993, Abelson et al. 1994, Szmant 1997, McClanahan et al. 2002b). A macroalgal propagule must assess the suitability of the substratum for adult requirements by using a variety of settlement cues, which may include surface contour, substrate type, chemistry, the presence of a microbial film and flow conditions. Finally the macroalgal propagule must be able to effectively attach (Abelson and Denny 1997). A fixed point attachment is one of the scarcest but most desired resource for many macroalgae, particularly in the photic zone. For macroalgae it provides a stable location and orientation with respect to the incoming light energy and the more substrate surface available (i.e. with increasing rugosity), the greater the potential efficiency of macroalgae in using the energy available in light and water motion (Dahl 1973). Brown macroalgae preferentially settle on hard substrate, i.e. dead coral and/or bare rock. Various studies have shown that macroalgae cannot establish themselves on live coral via propagule dispersal (Diaz-Pulido and McCook 2003) or in environments with a substantial sediment cover. For example Prince and O'Neal (1979) found that for *Sargassum pteropleuron,* the seaward extension of the population was limited by sandy sediments greater than 0.25 cm depth and Hay (1981b) concluded that for the sand plain the macroalgal community was limited over 96% of the surface by lack of adequate attachment sites. The other 4% comprised of hard substrate and supported 93% of the biomass and 88% of the individuals occurring on the sand plain. Wherever water movement conditions are most suitable for algal propagule settlement they are also likely to be favourable for sediment settling (Santelices 1990). Hence propagules that settle on sediment particles are likely to be moved away especially in faster moving waters and is a likely explanation why macroalgae propagules favor hard substrata for settlement.

The micro relief of benthic substrata plays an important role in the initial establishment of macroalgal recruits (Harlin and Lindbergh 1977, Norton and Fetter 1981, Santelices 1990). Rougher textures and porous materials (for example dead coral skeletons) have been suggested to protect macroalgal recruits from dislodgement by wave action, water currents and grazing activity and to increase the surface area available for settlement and recruitment. For example in *Sargassum muticum* settlement density increased with substratum roughness up to an optimum roughness with depressions averaging 800 µm deep (Norton and Fetter 1981). Larger depressions (> 800 µm) can adversely affect settlement, because depending on the shape, size and a given water velocity macroalgal propagules can dislodge easily (Harlin and Lindbergh 1977). Diaz-Pulido and McCook (Diaz-Pulido and McCook 2003) observed a similar pattern for *Lobophora variegata* where the density of recruits was significantly different on ceramic and coral plates, with ceramic plates having less recruits although it was not clear whether this was due to physical or chemical differences in the plates.

3.3 Disturbance regimes and physical stress

3.3.1 Periodic disturbances

Disturbance usually refers to mechanisms causing partial or total removal of organisms. Disturbances vary in their intensity, scale and effects on the species, as well as on the local physical and biological environment (Airoldi 1998). This variation has important effects on the process of community recovery after disturbance (Connell et al. 1997). On coral reefs, disturbances have been recognised as a primary mechanism that creates open space (Airoldi 1998, McCook et al. 2001, McManus and Polsenberg 2004, Aronson and Precht 2006). Disturbances can be classified according to their severity, the extent of the area, or the frequency with which they occur. Hurricanes are stochastic in nature but can cause massive coral mortality over large areas, subsequently creating space for settlement by macroalgae (Hughes and Connell 1999, Wright and Steinberg 2001). In contrast, herbivory is a chronic disturbance that generates small patches of grazed substrate. The size of herbivore mouthparts, feeding rate, and specific foraging behaviours affect the size of patch created. The frequency that a particular area is grazed depends on the mobility of herbivores, abundance and the size and constancy of the foraging range (Carpenter 1986, Mumby and Wabnitz 2002). For example in Jamaica, macroalgae have colonised free space generated by hurricanes in the early eighties, (Hughes 1994, Hughes and Connell 1999). Subsequently a few years later mass mortality of *Diadema antillarum* and overfishing, prevented the coral reefs to recover to a coral dominated reef (Hughes 1994). In the Mediterranean Sea on a smaller time scale, plots were cleared of *Dictyota dichotoma* at different times of the year. Here it was reported that recruitment was more abundant in plots cleared in the summer compared to those cleared in the winter (Airoldi 1998). This could be indicative that the timing of an event creating space will be of benefit to the alga if it co-occurs with recruitment of the alga.

Trade-offs in species-specific reproductive and growth abilities often have been cited to explain differential recovery patterns following disturbances, creating patches of different sizes. The importance of life histories in mediating spatial dominance is beginning to be appreciated in marine ecosystems and growth patterns have been suggested to be as important as the disturbance regime in determining community structure (Airoldi 1998).

Coral reef habitats with unstable conditions (e.g. exposed to frequent and unpredictable changes) are often dominated by macroalgae with the ability to produce abundant offspring (for example *Sargassum* spp.). This ability seems to be more important than competing with other benthic organisms (Santelices 1990). In such variable habitats mortality of juvenile and adult algae tends to be high. The abundant and frequent propagule production permits the colonisation and survival of such species in unstable habitats. In contrast macroalgae (for example *Lobophora variegata*) dominating in more stable environments devote relatively less energy and materials to reproduction and more to vegetative growth, competing for resources with the nearest organisms (Santelices 1990).

The sequence of replacement of species after a disturbance depends on environmental stress, availability of resources, and the adaptive, competitive and reproductive abilities of the main space occupiers (Airoldi 1998). Coral and algal turf-rich reefs can quickly (months to years) be transformed, by storm disturbance, increasing nutrients, or overfishing, to a high standing crop macroalgal-dominated community (Adey 1998), which seems to be supported by a report of Hatcher and Larkum (1983). They found that in subtidal habitats, 4 months is sufficient time for recolonization of new coral rock surface. Algal colonization of newly killed corals in the Red Sea took from 14 to 198 days (Hatcher and Larkum 1983).

3.3.2 Water motion

Water motion is a key determinant of marine macroalgal production, influencing directly or indirectly, thallus morphology, physiological rates and community structure (Leigh et al. 1987, Hurd 2000). For example the under water light climate is partly determined by seawater turbidity as a function of water motion (Umar et al. 1998). Rates of nutrient supply to macroalgae depend on mainstream seawater velocity and the water movements in the direct vicinity of the macroalgae (Atkinson and Bilger 1992b).

The thallus morphology of macroalgae varies with the hydrodynamic environment in which they grow because of mechanical constraints to resist hydraulic forces, which can dislodge or break them. The hydraulic forces on macroalgae induced by water currents can be explained in terms of three factors; shoot size, current velocity and an arbitrary but species-specific factor describing roughness, flexibility and shape (Schutten and Davy 2000). In general thalli of macroalgae subjected to slow flows are wide, thin and often have undulate (ruffled) margins compared with wave exposed specimens of the same species which have narrow, thick thalli and increased branching or dissection (for example, the ruffled and crust form of *Lobophora variegata*) (Hurd 2000). On the other hand, a major benefit for macroalgae in living in moving water is that the thickness of the stagnant layer of water surrounding an organism, the diffusive boundary layer (dbl), is reduced as flow speed increases and the thickness of the momentum boundary layer is reduced (Carpenter 1986, Bilger and Atkinson 1995). The dbl presents a resistance to the diffusive exchange of nutrients and other materials to the surface of an alga from the surrounding water and is an important factor limiting the metabolism (Bilger and Atkinson 1992, Carpenter and Williams 1993, Bilger and Atkinson 1995, Hurd 2000). The rate of supply across the dbl is known as mass transfer. Mass transfer limitation refers to the condition whereby macroalgal productivity is limited by the supply of an essential nutrient (e.g. nitrogen or phosphorous). The degree to which mass transfer limitation occurs will depend in part on the dbl thickness, the concentration gradient across the dbl and turbulence close to the macroalgal thallus surface (Carpenter et al. 1991).

In regions or seasons where ambient inorganic nutrient concentrations (N and P) limit macroalgal growth, the potential for mass transfer limitation is greater than at nutrient-rich sites because the concentration gradient between the mainstream seawater and thallus is much reduced (Atkinson and Bilger 1992a, Bilger and Atkinson 1995, Hurd 2000). Therefore, the slow growth rates in slow-flowing water are typically attributed to a reduction in the mass transfer of inorganic nutrients to the macroalgal surface due to the presence of thick dbl's (Hurd 2000). However, many macroalgae have other nutrient sources besides the mainstream seawater which may alleviate nutrient limitation even in slow flows. For example, tropical *Sargassum* spp. growing in seawater with low levels of dissolved inorganic nutrients, obtain nutrients from particulate matter that deposits on their surfaces (Hurd 2000) and in *Caulerpa cupressoides* and *Dictyosphaeria cavernosa* through nutrient uptake from the sediment (Williams 1984, Larned and Stimson 1996). Therefore even in slow-flowing water where the possibility of mass transfer limitation is greatest, nutrient sources other than those from the mainstream seawater may reduce or alleviate mass transfer limitation (Hurd 2000).

The scale at which water motion is measured is another issue potentially affecting the outcomes of studies of nutrient enrichment. Coral reefs will have very complex water flow patterns due to the redirection of the flow when it encounters obstacles of varying shape and height (Carpenter and Williams 1993). Carpenter and Williams (1993) showed the small scale differences in flow velocities. For example within grazed algal turf communities, seawater velocities 2 mm above the seabed were considerably faster (15 cm/s) than those 2 cm above the seabed (< 2 cm/s). They suggest that the local flow speeds affecting a particular area of substratum will not be predictable from large-scale, long term data without corresponding data on profiles of flow speed over various substrata on smaller spatial scales. They emphasize the importance of measuring velocities at the surface of macroalgae or within turf-forming vegetation rather than using mainstream velocities as suggested by Hurd (2000) (Carpenter and Williams 1993). Atkinson and Bilger (1992b) however, take an opposite view. They state that the roughness of the bottom creates turbulence in the flowing water, which extends fully to the surface of the water column. The diffusive boundary layer formed around objects or organisms on a rough bottom are considered part of the roughness layer, which conceptually replaces the diffusive boundary layer. Thus individual macroalgal thalli on a coral reef reside in turbulent flow with their individual boundary layers fluctuating in thickness through time. Atkinson and Bilger

(1992b) suggested that a large scale view of the supply of nutrients to the coral reef community as a whole should yield a simplified approach to a problem that is very complex from a small scale viewpoint.

3.3.3 Sediment deposition and turbidity

Sedimentation is considered a major cause of coral reef degradation world wide (Rogers 1990, Wesseling et al. 1999, Nugues and Roberts 2003). Sedimentation and turbidity may act directly on macroalgae either positively or negatively.

Positive effects

The effects include enhancing macroalgal recruitment or survival (Kennelly 1983), increasing the supply of nutrients (Williams 1984, Schaffelke and Klumpp 1997a, Szmant 1997, Stimson and Larned 2000), and reducing herbivory (Hay 1981b, Lubchenco and Gaines 1981, Kennelly 1983).

Negative effects

Sedimentation reduces settlement rates (Santelices 1990), and reduces ambient light levels (Umar et al. 1998). Sediments can smother or bury the macroalgae and casues scouring (De Ruyter van Steveninck et al. 1988a, Vadas et al. 1992, Airoldi 1998, Fabricius and De'ath 2001, McClanahan et al. 2002a).

Indirectly sedimentation affects macroalgae by inhibiting its competitors (i.e. corals) or herbivores (Umar et al. 1998, Nugues and Roberts 2003). Both direct and indirect impacts involve effects of either suspended sediment (turbidity) or sediment deposition on the substratum and effects of either are difficult to distinguish in field experiments (McCourt 1984, Abelson and Denny 1997).

Sedimentation will have different effects on different life history stages. Outcomes on recruitment likely include effects on settlement and attachment of new propagules and on growth of already settled recruits into adult populations (Santelices 1990, Vadas et al. 1992, Umar et al. 1998). Results of a study on the Great Barrier Reef showed that recruitment, growth, survival and seasonal regeneration of *Sargassum microphyllum* were significantly affected by an increase in sediment load and involved smothering short fronds and recruits, and preventing attachment of new recruits (Umar et al. 1998). In contrast, the effects of sediment removal were rarely significant and it was suggested that the abundance of *S. microphyllum* is not significantly affected by current sediment levels at the study site (Umar et al. 1998). However, another study on the Great Barrier Reef showed that *Sargassum* spp. are more abundant in reef areas with relatively high sedimentation (McCook 1997). Taken together, these studies suggest that abundant *Sargassum* spp. in areas with higher sediment load is not due to direct effects of sediments, but are likely caused by other factors correlated with sediments (e.g. increased nutrients, (Williams 1984, Schaffelke and Klumpp 1997a, Stimson and Larned 2000) or indirectly by the effects of sediments on other organisms (Nugues and Roberts 2003). Espinoza and Rodriguez (1987) also found a reduction in thallus size and reproductive capacity of *Sargassum sinicola* in the Gulf of California when comparing different sites. Sediment deposition was found on *Sargassum* spp. thalli after periods of high water movement, but the authors did not find any correlation with nutrient concentrations and concluded that very likely sediment deposition and turbid waters causing a reduction in light levels was the most likely explanation of reduction in thallus size and reproductive capacity.

Indirect effects of sedimentation may strongly facilitate macroalgal colonisation (Rogers 1990, Nugues and Roberts 2003). Sedimentation kills other species such as hard corals (Wesseling et al. 1999) and subsequently the space created for macroalgae may increase considerably. For example, *Sargassum* spp. does not seem to be dependent on the physical/chemical environmental conditions on the inshore reef flats, where it is normally abundant (McCook 1996, 1997). Thus macroalgae such as *Sargassum* spp. may be opportunistic beneficiaries of the negative effect of sediments on other organisms, rather than being favoured by high sediment loads (Umar et al 1998). Nugues and Roberts (2003) suggested that for the coral *Siderastrea siderea* to survive in areas under high sediment loads it may allocate energy towards vertical growth at the expense of horizontal growth as a means to escape in height against sediment smothering and burial and may explain the success of this species under these conditions (Nugues and Roberts 2003). This strategy might also explain why macroalgae are so successful in areas of relatively high sediment loads and turbidity.

3.3.4 Temperature

Many macroalgae on coral reefs are highly seasonal and this seasonality is thought to be related to changes in water temperature (Naim 1993, Stimson et al. 1996, McCook et al. 1997). In the southern Caribbean upwelling brings cooler and nutrient rich waters to the coral reef, promoting macroalgal growth (Diaz-Pulido and Garzon-Ferreira 2002). The authors found a significant inverse correlation between water temperature and macroalgal cover. For example, the cover of *Dictyota* spp. declined from about 34 % to 5 % in the non-upwelling season having higher water temperatures. Diaz-Pulido and Garzon-Ferreira (2002) concluded that the reductions in macroalgal cover were likely to be related to water temperature rather than changes in salinity or turbidity. However, it cannot be clearly determined whether the effects of temperature have a direct effect on macroalgae or whether they simply covary with other seasonal factors, such as nutrients, that then trigger processes in the life history of the macroalgae.

Temperature affects growth rates, and reproduction of macroalgae (Gaines and Lubchenco 1982). Studies on *Sargassum polyphyllum* in Hawaii showed that possibly changes in temperature regimes brings on fertility. Thallus height and fertility all occurred at a time of lower seawater temperatures and growth occurred during the preceding warmer months (De Wreede 1976).

Indirectly temperature can have a large effect on macroalgal standing crop. Temperature induced coral bleaching is a major cause of coral reef decline world wide (Brown 1997, McWilliams et al. 2005, Bellwood et al. 2006). Space created on dead corals by coral bleaching is rapidly colonised by macroalgae. This process is likely to become more frequent with global warming (Hughes et al. 2003, Bellwood et al. 2004).

3.4 Species interactions

The relative dominance model identifies four major space-occupying groups of benthic photosynthetic organisms on the coral reef as a function of long-term nutrient levels and herbivore activity: (1) corals, (2) coralline algae, (3) filamentous algae and (4) macroalgae (Littler and Littler 1984a, c, Littler et al. 2006a). All of these benthic organisms compete strongly for space and light and each group can predominate under specific environmental conditions. Variations in the levels of grazing, limiting or toxic nutrient levels and wave action, could lead to spatial separation of these four communities between or within habitats (Littler and Littler 1984a).

Various mechanisms for competition between macroalgae and corals have been identified and include: overgrowth, shading, abrasion, allelopathy and pre-emption (reviewed in (McCook et. al. 2001). The outcome of competition between macroalgae and corals include, declined growth rates of both species (De Ruyter van Steveninck et al. 1988b, Jompa and McCook 2002, Box and Mumby 2007), reductions in the fecundity of corals (Tanner 1995, Adey 1998) and even mortality of corals (Lewis 1986, Hughes and Connell 1999, Hughes and Tanner 2000). Contact interactions between macroalgae and corals can be common along the margins of coral colonies. For example on the northern Florida reefs, coral colonies had more than 50% of their basal perimeter in contact with macroalgae during the peak of macroalgal abundance (Lirman 2001a). This high encounter rate between corals and macroalgae will have a negative effect on both the macroalgae and coral colony (Tanner 1995). For example the macroalga *Lobophora variegata* was able to overgrow and kill live tissue of the coral *Porites cylindrica*, but the coral was also able to inhibit the growth of the macroalga, although to a lesser degree. The inhibition of *L. variegata* by *P. cylindrica* was substantially less (<25%) than that of the macroalga on the coral (up to 100%) (Jompa and McCook 2002). Nugues and Bak (2006) found similar results for the coral *Agaricia agaricites* when in contact with *Lobophora variegata*. Several factors play a role in the success of a macroalga in overgrowing live corals. The growth form of the macroalga determines its ability to overgrow live corals, with species having an upright bushy form such as *Dictyota cervicornis* not being as successful compared to creeping foliose forms such as *Lobophora variegata*. Secondly, the shape of the coral colony will affect its ability to resist overgrowth by algae. Low growing forms like *Agaricia* spp. and *Porites* spp. are more likely to be overgrown than large dome-shaped coral colonies like *Montastraea annularis*. Thirdly, small coral colonies such as recruits and juvenile corals are more susceptible to overgrowth than adult colonies. Finally the duration of contact between the macroalgae and coral will determine the success rate of macroalgae overgrowing corals with longer contact duration being advantageous for the macroalgae.

A recent study found strong effects of shading of *Dictyota pulchella* by reducing the growth rate of juvenile *Agaricia* corals whilst shading by *Lobophora variegata* caused substantial mortality of up to 50% after 6 months (Box and Mumby 2007). The authors also found that abrasion by *Dictyota pulchella* reduced growth rates of the coral and was linked to physical mechanisms rather than allelochemical inhibition, because a synthetic mimic of *D. pulchella* caused a similar reduction in growth rate (Box and Mumby 2007). Similar results were found for *Sargassum hystrix* on the coral *Porites porites* (River and Edmunds 2001). These mechanisms (pre-emption, overgrowth, shading, abrasion) will eventually lead to a reduction in growth rate of corals, partial or even whole colony mortality. Subsequently this creates space for macroalgae to occupy and hence increase their standing crop.

Larger erect macroalgae such as *Dictyota* spp., *Padina* spp., *Sargassum* spp. and *Turbinaria* spp. may provide refuges for opportunistic delicate algae under their canopies because they are unpalatable or provide a physical barrier to grazing fishes (Littler and Littler 1984a, Diaz-Pulido and Diaz 1997). For example *Turbinaria* spp. seems to be little grazed by herbivores, as shown by the lush populations observed (21% cover at 1 m depth, (Diaz-Pulido and Diaz 1997). This is however, in contrast with results of Lewis (1986) in Belize, who found that *Turbinaria* spp. was readily consumed by herbivorous fishes on the back reef.

One other potentially important interaction between species is that of epiphytes on macroalgae (Capone 1977, Littler and Littler 1999, Russell et al. 2005). Studies have shown epiphytes interact with various factors influencing macroalgal growth (Littler and Littler 1999). The effects of epiphytes on their host macroalgae can be beneficial (i.e. allowing grazers to consume the epiphyte rather than the macroalga itself), but are more often harmful particularly at high epiphyte densities. The negative effects of epiphytes include increased hydrodynamic drag leading to breakage, smothering effects due to interference in the diffuse boundary layer, and lower light levels at host macroalgal surfaces. Finely branched epiphytes out-compete their coarser hosts for nutrients and potentially leading to lethal anoxic conditions for the macroalgal host (Schaffelke and Klumpp 1997a, Littler and Littler 1999, Airoldi 2000).

4 CONCLUSIONS

Many factors have contributed to the observed declines in the health of coral reefs and the subsequent dominance of macroalgae, including large-scale perturbations such as hurricanes and coral bleaching. It is clear that many factors contribute towards macroalgal dominance and that the effects can vary from reef to reef. The disparate results found in the literature regarding nutrients and herbivory only shows that generalizations drawn from small scale experiments are difficult to uphold for a number of reasons.

Experiments are region or habitat specific and nutrient enhancement, for example, will have a different effect depending where the experiment is located, i.e. on a forereef exposed to the wide ocean or a forereef situated in a sheltered bay where nutrient build-up can be rapid. Herbivore abundance and composition can vary significantly between the backreef, reef flat or forereef or even from site to site within the same reef habitat. The differential effects of both herbivory and nutrients on individual macroalgal species also make generalizations very difficult. Nutrients might certainly increase growth in one species but not in others or outcomes for the same species can be different, depending on initial nutrient content, and morphology and herbivores have preferences for certain algal species (fishes in general) or are indiscriminate (urchins).

The difficulty of carrying out experiments controlling for all factors usually means a focus on either nutrients, herbivores or a combination of both as they are widely claimed to be the driving forces behind the phase shift towards macroalgal dominance. Small scale experiments are useful in determining which processes or mechanisms are involved in promoting macroalgal standing crop and carefully designed multi-factorial experiments should continue to be carried out. But such experiments need to be repeated in different geographic areas to determine whether effects of factors are habitat specific and over a long period. For example, the effects of nutrient enrichment might only become noticeable after 6 months and thus shorter nutrient enrichment experiments will not detect a significant effect. While the functional group approach to categorising algae (sensu Steneck and Watling (1982, 1994) and Steneck and Dethier (1994)) is easy to implement, it should ideally be complemented with a clarification of the phylum (i.e. Phaeophyta or Rhodophyta) or even perhaps the order, to relate species specific responses to experimental conditions. On the other hand a useful approach was suggested by Padilla and Allen (2000) in that functional groups should be based on specific functions, i.e. nutrient uptake rates, photosynthesis, herbivore resistance, etc). Here it should be clarified though at which scale the properties of macroalgal community are evaluated.

Small scale experiments or even whole reef manipulations might not be able to elucidate all effects controlling macroalgal standing crop because of difficulties in controlling for all potential factors. Thus a combination of field experiments and modelling may provide greater insights in the future. For example, Bayesian Belief Networks (BBN) recently gained popularity in the field of ecology (Marcot et al. 2001, Borsuk et al. 2004, Wooldridge et al. 2005). BBN's are a form of influence diagram that depict the causal or logical relations amongst physical and ecological factors. The application of BBNs to understanding the factors driving macroalgal cover is studied in greater detail in the next chapter.

5 REFERENCES

Abelson A, and Denny MW. 1997. Settlement of marine organisms in flow. Annual review of ecology and systematics 28:317-339.

Abelson A, Weihs D, and Loya Y. 1994. Hydrodynamic impediments to settlement or marine propagules, and adhesive-filament solutions. Limnology and Oceanography 39:164-169.

Adey WH. 1998. Coral reefs: Algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. Journal of Phycology 34:393-406.

Airoldi L. 1998. Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. Ecology 79:2759-2770.

Airoldi L. 2000. Effects of disturbance, life histories, and overgrowth on coexistence of algal crusts and turfs. Ecology 81:798-814.

Aronson RB, and Precht WF. 2000. Herbivory and algal dynamics on the coral reef at discovery bay, Jamaica. Limnology and Oceanography 45:251-255.

Aronson RB, and Precht WF. 2001. White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460:25-38.

Aronson RB, and Precht WF. 2006. Conservation, precaution, and Caribbean reefs. Coral Reefs 25:441-450.

Ateweberhan M, Bruggemann JH, and Breeman AM. 2005. Seasonal patterns of biomass, growth and reproduction in Dictyota cervicornis and Stoechospermum polypodioides

(Dictyotales, Phaeophyta) on a shallow reef flat in the southern Red Sea (eritrea). Botanica Marina 48:8-17.

Atkinson MJ. 1988. Are coral reefs nutrient-limited. Proceedings of the 6th international Coral Reef Symposium 1:157-166.

Atkinson MJ, and Bilger RW. 1992a. Effects of water velocity on phosphate uptake in coral reef-flat communities. Limnology and Oceanography 37:273-279.

Atkinson MJ, and Bilger RW. 1992b. Effects of water velocity on phosphate uptake on coral reefs. Limnology and Oceanography 37:261-272.

Atkinson MJ, and Smith SV. 1983. C:N:P Ratios of benthic marine plants. Limnology and Oceanography 28:568-574.

Bak RPM, Carpay MJE, and De Ruyter van Steveninck ED. 1984. Densities of the sea urchin Diadema antillarum before and after mass mortalities on the coral reefs of Curacao. Marine Ecology Progress Series 17:105-108.

Bak RPM, and Nieuwland G. 1995. Long-term change in coral communities along depth gradients over leeward reefs in the Netherlands Antilles. Bulletin of Marine Science 56:609-619.

Beach KS, Walters LJ, and Borgeas HB. 2006. Irradiance and nutrient limitation of Dictyota spp. populations on Conch Reef, Florida Keys, USA. Journal of Experimental Marine Biology and Ecology 329:101-112.

Belliveau SA, and Paul VJ. 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. Marine Ecology Progress Series 232:105-114.

Bellwood DR, Hoey AS, Ackerman JL, and Depczynski M. 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Global Change Biology 12:1587-1594.

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

Bilger RW, and Atkinson MJ. 1992. Anomalous masss transfer of phosphate on coral reefs. Limnology and Oceanography 37:261-272.

Bilger RW, and Atkinson MJ. 1995. Effects of nutrient loading on mass transfer rates to a coral reef community. Limnology and Oceanography 40:279-289.

Borsuk ME, Stow CA, and Reckhow KH. 2004. A bayesian network of eutrophication models for synthesis, prediction and uncertainty analysis. Ecological Modelling 173:219-239.

Box SJ, and Mumby PJ. 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Marine Ecology Progress Series 342:139-149.

Brown BE. 1997. Coral bleaching: Causes and consequences. Coral Reefs 16:S129-S138.

Burkepile DE, and Hay ME. 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128-3139.

Calado G, and Duarte P. 2000. Modelling growth of Ruppia cirrhosa. Aquatic Botany 68:29-44.

Capone D. 1977. N2(C2H2) fixation by macroalgal epiphytes. Proceedings of the 3rd International Coral Reef Symposium:337-342.

Carpenter RC. 1985. Relationships between primary production and irradiance in coral reef algal communities. Limnology and Oceanography 30:784-793.

Carpenter RC. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs 56:345-363.

Carpenter RC. 1990. Competition among marine macroalgae: A physiological perspective. Journal of Phycology 26:6-12.

Carpenter RC, and Edmunds PJ. 2006. Local and regional scale recovery of Diadema promotes recruitment of scleractinian corals. Ecology Letters 9:271-280.

Carpenter RC, Hackney JM, and Adey WH. 1991. Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. Limnology and Oceanography 36:40-49.

Carpenter RC, and Williams SL. 1993. Effects of algal turf canopy heights and microscale substratum topography on profiles of flow speed in a coral forereef environment. Limnology and Oceanography 38:687-694.

Carr GM, Duthie HC, and Taylor WD. 1997. Models of aquatic plant productivity: a review of the factors that influence growth. Aquatic Botany 59:195-215.

Coen LD, and Tanner CE. 1989. Morphological variation and differential susceptibility to herbivory in the tropical brown alga Lobophora variegata. Marine Ecology Progress Series 54:287-298.

Connell JH. 1997. Disturbance and recovery of coral assemblages. Coral Reefs 16:S101-S113.

Connell JH, Hughes TP, and Wallace CC. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67:461-488.

Connor JL, and Adey WH. 1977. The benthic algal composition, standing crop, and productivity of a Caribbean algal ridge. Atoll Research Bulletin 211:1-39.

Creed JC, Norton TA, and Kain JM. 1997. Intraspecific competition in Fucus serratus germlings: The interaction of light, nutrients and density. Journal of Experimental Marine Biology and Ecology 212:211-223.

Cronin G, and Hay ME. 1996a. Chemical defenses, protein content, and susceptibility to herbivory of diploid vs haploid stages of the isomorphic brown alga Dictyota ciliolata (Phaeophyta). Botanica Marina 39:395-399.

Cronin G, and Hay ME. 1996b. Susceptibility to herbivores depends on recent history of both the plant and animal. Ecology 77:1531-1543.

Cronin G, and Hay ME. 1996c. Within-plant variation in seaweed palatability and chemical defenses: optimal defense theory versus the growth-differentiation balance hypothesis. Oecologia 105:361-368.

Dahl AL. 1973. Surface area in ecological analysis: Quantification of benthic coral-reef algae. Marine Biology 23:239-249.

De Ruyter van Steveninck ED, and Bak RPM. 1986. Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin Diadema antillarum. Marine Ecology Progress Series 34:87-94.

De Ruyter van Steveninck ED, and Breeman AM. 1987. Deep water populations of Lobophora variegata (Phaeophyceae) on the coral reef of Curacao: influence of grazing and dispersal on distribution patterns.

De Ruyter van Steveninck ED, Kamermans P, and Breeman AM. 1988a. Transplant experiments with two morphological growth forms of Lobophora variegata (Phaeophyceae). Marine Ecology Progress Series 49:191-194.

De Ruyter van Steveninck ED, Mulekom LL, and Breeman AM. 1988b. Growth inhibition of Lobophora variegata (Lamouroux) Womersley by scleractinian corals. Journal of Experimental Marine Biology and Ecology 115:169-178.

De Wreede RE. 1976. The phenology of three species of Sargassum (Sargassaceae, Phaeophyta) in Hawaii. Phycologia 15:175-183.

Delgado O, and Lapointe BE. 1994. Nutrient-limited productivity of calcareous versus fleshy macroalgae in a eutrophic, carbonate-rich tropical marine environment. Coral Reefs 13:151-159.

Diaz-Pulido G, and Diaz JM. 1997. Algal assemblages in lagoonal reefs of Caribbean oceanic atolls. Proceedings of the 8th International coral reef symposium 1:827-832.

Diaz-Pulido G, and Garzon-Ferreira J. 2002. Seasonality in algal assemblages on upwelling-influenced coral reefs in the Colombian Caribbean. Botanica Marina 45:284-292.

Diaz-Pulido G, and McCook LJ. 2003. Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology 84:2026-2033.

Done TJ. 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121-132.

Dudgeon SR, Kubler JE, Vadas RL, and Davison IR. 1995. Physiological responses to environmental variation in intertidal red algae: does thallus morphology matter? Marine Ecology Progress Series 117:193-206.

Ekebom J, Laihonen P, and Suominen T. 2003. A GIS-based step-wise procedure for assessing physical exposure in fragmented archipelagos. Estuarine, Coastal and Shelf Science 57:887-898.

Enriquez S, Agusti S, and Duarte CM. 1994. Light absorption by marine macrophytes. Oecologia 98:121-129.

Espinoza J, and Rodriguez H. 1987. Seasonal phenology and reciprocal transplantation of Sargassum sinicola Setchell et Gardner in the southern Gulf of California. Journal of Experimental Marine Biology and Ecology 110:183-195.

Fabricius K, and 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.

Fong P, Foin, TC, Zedler JB. 1994. A simulation model of lagoon algae based on nitrogen competition and internal storage. Ecological Monographs 64:225-247.

Fong P, Boyer KE, Kamer K, and Boyle KA. 2003. Influence of initial tissue nutrient status of tropical marine algae on response to nitrogen and phosphorus additions. Marine Ecology Progress Series 262:111-123.

Fong P, Kamer K, Boyer KE, and Boyle KA. 2001. Nutrient content of macroalgae with differing morphologies may indicate sources of nutrients for tropical marine systems. Marine Ecology Progress Series 220:137-152.

Foster SA. 1987. The relative impacts of grazing by Caribbean coral reef fishes and Diadema: effects of habitat and surge. Journal of Experimental Marine Biology and Ecology 105:1-20.

Gaines SD, and Lubchenco J. 1982. A unified approach to marine plant-herbivore interactions. II. Biogeography. Annual review of ecology and systematics 13:111-138.

Gardner TA, Cote IM, Gill JA, Grant A, and Watkinson AR. 2003. Long-term region-wide declines in Caribbean Corals. Science 301:958-960.

Gardner TA, Cote IM, Gill JA, Grant A, and Watkinson AR. 2005. Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. Ecology 86:174-184.

Hairston N, Smith FE, and Slobodkin LB. 1960. Community structure, population control, and competition. The American Naturalist 94:421-425.

Hanisak MD, Littler MM, and Littler DS. 1988. Significance of macroalgal polymorphism: intraspecific tests of the functional-form model. Marine Biology 99:157-165.

Harlin MM, and Lindbergh JM. 1977. Selection of substrata by seaweeds: Optimal surface relief. Marine Biology 40:33-40.

Hatcher BG, and Larkum AWD. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. Journal of Experimental Marine Biology and Ecology 69:61-84.

Hay ME. 1981a. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. American Naturalist 118:520-540.

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

Hay ME. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: Are previous results typical? Ecology 65:446-454.

Hay ME. 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs 16:S67-S76.

Hay ME, Colburn T, and Downing D. 1983. Spatial and temporal patterns in herbivory on a caribbean fringing reef: the effects on plant distribution. Oecologia 58:299-308.

Herren LW, Walters LJ, and Beach KS. 2006. Fragment generation, survival, and attachment of Dictyota spp. at Conch Reef in the Florida Keys, USA. Coral Reefs 25:287-295.

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 RM, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas JA, Lough J, Marshall PA, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, and Rougharden J. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929-933.

Hughes TP, and Connell JH. 1987. Population dynamics based on size or age? A Reef-Coral analysis. American Naturalist 129:818-829.

Hughes TP, and Connell JH. 1999. Multiple stressors on coral reefs: A long-term perspective. Limnology and Oceanography 44:932-940.

Hughes TP, Reed DC, and Boyle M. 1987. Herbivory on coral reefs: community structure following mass mortalities in sea urchins. Journal of Experimental Marine Biology and Ecology 113:39-59.

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli DM, Hoegh-Guldberg O, McCook LJ, Moltschaniwskyj NA, Pratchett TA, Steneck RS, and Willis BL. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology 17:360-365.

Hughes TP, Szmant AM, Steneck RS, Carpenter R, and M. S. 1999. Algal blooms on coral reefs: what are the causes? Limnology and Oceanography 44:1583-1586.

Hughes TP, and Tanner JE. 2000. Recruitment failure, life histories and long-term decline of Caribbean corals. Ecology 81:2250-2263.

Hurd CL. 2000. Water motion, marine macroalgal physiology, and production. Journal of Phycology 36:453-472.

Jokiel PL, and York RHJ. 1984. Importance of ultraviolet radiation in photoinhibition of microalgal growth. Limnology and Oceanography 29:192-199.

Jompa J, and McCook LJ. 2002. Effects of competition and herbivory on interactions between a hard coral and a brown alga. Journal of Experimental Marine Biology and Ecology 271:25-39.

Jompa J, and McCook LJ. 2003. Coral-algal competition: macroalgae with different properties have different effects on corals. Marine Ecology Progress Series 258:87-95.

Kain JM. 1976. The biology of Laminaria hyperborea. VIII. Growth on cleared areas. Journal of the Marine Biological Association of the UK 56:267-290.

Kendrick GA. 1994. Effects of propagule settlement density and adult canopy on survival of recruits of saegassum spp. (Sargassaceae: Phaeophyta). Marine Ecology Progress Series 103:129-140.

Kennelly SJ. 1983. An experimental approach to the study of factors affecting algal colonization in a sublittoral kelp forest. Journal of Experimental Marine Biology and Ecology 68:257-276.

King RJ, and Schramm W. 1976. Photosynthetic rates of benthic marine algae in relation to light intensity and seasonal variations. Marine Biology 37:215-222.

Kirkman H. 1981. The first year in the life history and survival of the juvenile marine macrophyte, Ecklonia radiata (Turn.) J. Agardh. Journal of Experimental Marine Biology and Ecology 55:243-254.

Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist 32:674-682.

Knowlton N. 2001. The future of coral reefs. Proceedings of the National Academy of Sciences of the United States of America 98:5419-5425.

Koop K, Booth D, Broadbent A, Brodie J, Bucher D, Capone D, Coll J, Dennison WC, Erdmann M, Harrison P, Hoegh-Guldenberg O, Hutchings P, Jones GB, Larkum AWD, O'Neil J, Steven A, Tentoris E, Ward S, Williamson J, and Yellowlees D. 2001. ENCORE: The effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. Marine Pollution Bulletin 42:91-120.

Kowalczuk P, Ston-Egiert J, Cooper WJ, Whitehead RF, and Durako MJ. 2005. Characterization of chromophoric dissolved organic matter (CDOM) in the Baltic Sea by excitation emission matrix fluorescence spectroscopy. Marine Chemistry 96:273-292.

Lapointe BE. 1987. Phosphorus- and nitrogen-limited photosynthesis and growth of Gracilaria tikvahiae (Rhodophyceae) in the Florida Keys: an experimental field study. Marine Biology 93:561-568.

Lapointe BE. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography 42:1119-1131.

Lapointe BE. 1999. Simultaneous top-down and bottom up forces control macroalgal blooms on coral reefs (reply to the comment by Hughes et al.). Limnology and Oceanography 44:1568-1592.

Lapointe BE. 2004. Phosphorus-rich waters at Glovers Reef, Belize? Marine Pollution Bulletin 48:193-195.

Lapointe BE, Barile PJ, and Matzie WR. 2004a. Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys: discrimination of local versus regional nitrogen sources. Journal of Experimental Marine Biology and Ecology 308:23-58.

Lapointe BE, Barile PJ, Yentsch CS, Littler MM, Littler DS, and Kakuk B. 2004b. The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman's Pond Cay, Exumas Cays, Bahamas: a "natural" enrichment experiment. Journal of Experimental Marine Biology and Ecology 298:275-301.

Lapointe BE, Littler MM, and Littler DS. 1992a. Modification of benthic community structure by natural eutrophication: the Belize Barrier Reef. Proceedings of the 7th International Coral Reef Symposium 1:323-334.

Lapointe BE, Littler MM, and Littler DS. 1992b. Nutrient availability to marine macroalgae in siliclastic versus carbonate-rich coastal waters. Estuaries 15:75-82.

Lapointe BE, Littler MM, and Littler DS. 1997. Macroalgal overgrowth of fringing coral reefs at discovery bay, Jamaica: Bottom-up versus top-down control. Proceedings of the 8th International coral reef symposium 1:927-932.

Lapointe BE, and O'Connell J. 1989. Nutrient-enhanced growth of Cladophora prolifera in Harrington Sound, Bermuda: Eutrophication of a confined, phosphorus limited marine system. Estuarine, Coastal and Shelf Science.

Lapointe BE, and Tenore KR. 1981. Experimental outdoor studies with ulva fasciata Delile. I. Interaction of light and nitrogen on nutrient uptake, growth, and biochemical composition. Journal of Experimental Marine Biology and Ecology 53:135-152.

Larkum AW, and Koop K. 1997. ENCORE, Algal productivity and possible paradigm shifts. Proceedings of the 8th International Coral Reef Symposium 1:881-884.

Larned ST. 1998. Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. Marine Biology 132:409-421.

Larned ST, and Stimson J. 1996. Nitrogen-limited growth in the coral reef chlorophyte Dictyosphaeria cavernosa, and the effect of exposure to sediment-derived nitrogen on growth. Marine Ecology Progress Series 145:95-108.

Lee RE. 1999. Phycology, third edition. Cambridge University Press, Cambridge.

Leigh EG, Paine RT, Quinn JF, and Suchanek TH. 1987. Wave energy and intertidal productivity. Proceedings of the National Academy of Sciences of the United States of America 84:1314-1318.

Lessios HA. 1988. Population dynamics of Diadema antillarum (echinodermata: Echinoidea) following mass mortality in Panama. Marine Biology 99:515-526.

Lewis SM. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecology Monographs 56:183-200.

Lewis SM, Norris JN, and Searles RB. 1987. The regulation of morphological plasticity in tropical reef algae by herbivory. Ecology 68:636-641.

Lirman D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs:392-399.

Littler MM, and Littler DS. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. American Naturalist 116:25-44.

Littler MM, and Littler DS. 1984a. Models of tropical reef biogenesis: The contribution of algae. Progress in Phycological Research 3:323-364.

Littler MM, and Littler DS. 1984b. Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. Journal of Experimental Marine Biology and Ecology 74:13-34.

Littler MM, and Littler DS. 1984c. A relative-dominance model for biotic sciences. Proceedings of the joint meeting of the Atlantic Reef Committe Society of reef studies:2.

Littler MM, and Littler DS. 1988. Structure and role of algae in tropical reef communities. Pages 29-55 *in* J. R. Waaland, editor. Algae and human affairs. Cambridge University Press.

Littler MM, and Littler DS. 1999. Blade abandonment/proliferation: A novel mechanism for rapid epiphyte control in marine macrophytes. Ecology 80:1736-1746.

Littler MM, Littler DS, and Brooks BL. 2006a. Harmful algae on tropical coral reefs: Bottom-up eutrophication and top-down herbivory. Harmful Algae 5:565-585.

Littler MM, Littler DS, Brooks B L, and LaPointe BE. 2006b. Nutrient manipulation methods for coral reef studies: A critical review and experimental field data. Journal of Experimental Marine Biology and Ecology 336:242-253.

Littler MM, Taylor PR, and Littler DS. 1983. Algal resistance to herbivory on a Caribbean barrier reef. Coral Reefs 2:111-118.

Lubchenco J, and Cubit JD. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. Ecology 61:676-687.

Lubchenco J, and Gaines SD. 1981. A unified approach to marine plant-herbivore interactions. I. populations and communities. Annual review of ecology and systematics 12:405-437.

Marcot BG, Holthausen RS, Raphael MG, Rowland MM, and Wisdom MJ. 2001. Using Bayesian belief networks to evaluate fish and wildlife population viability under land management alternatives from an environmental impact statement. Forest Ecology and Management 153:29-42.

McClanahan TR, Aronson RB, Precht WF, and Muthinga NA. 1999a. Fleshy algae dominate remote coral reefs of Belize. Coral Reefs 18:61-62.

McClanahan TR, Cokos BA, and Sala E. 2002a. Algal growth and species composition under experimental control of herbivory, phosphorous and coral abundance in Glovers reef, Belize. Marine Pollution Bulletin 44:441-451.

McClanahan TR, Hendrick VJ, Rodrigues MJ, and Polunin NVC. 1999b. Varying responses of herbivorous and invertebrate-feeding fishes to macroalgal reduction on a coral reef. Coral Reefs 18:195-203.

McClanahan, TR, and Muthinga NA. 1998. An ecological shift in a remote coral atoll of Belize over 25 years. Environmental Conservation 25:122-130.

McClanahan TR, Polunin NVC, and Done TJ. 2002b. Ecological states and the resilience of coral reefs. Conservation Biology 6.

McClanahan TR, Sala E, Mumby PJ, and Jones S. 2004. Phosphorus and nitrogen enrichment do not enhance brown frondose "macroalgae". Marine Pollution Bulletin 48:196-199.

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, and Jones SHI. 2003. Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Marine Ecology Progress Series 261:135-147.

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.

McCook LJ. 1997. Effects of herbivory on zonation of Sargassum spp. within fringing reefs of the central Great Barrier Reef. Marine Biology 129:713-722.

McCook LJ. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the great barrier reef. Coral Reefs 18:357-367.

McCook LJ, Jompa J, and Diaz-Pulido G. 2001. Competition between corals and algae on reefs: A review of evidence and mechanisms. Coral Reefs 19:400-417.

McCook LJ, Price IR, and Klumpp DW. 1997. Macroalgae on the GBR: Causes or consequences, indicators or models of reef degradation. Proceedings of the 8th International Coral Reef Symposium 2:1851-1855.

McCourt RM. 1984. Seasonal patterns of abundance, distribution, and phenology in relation to growth strategies of three Sargassum species. Journal of Experimental Marine Biology and Ecology 74:141-156.

McManus JW, and Polsenberg JF. 2004. Coral-algal phase shifts on coral reefs: ecological and environmental aspects. Progress in Oceanography 60:263-279.

McWilliams JP, Cote IM, Gill JA, Sutherland WJ, and Watkinson AR. 2005. Accelerating impacts of temperature-induced coral bleaching in the Caribbean. Ecology 86:2055-2060.

Miller MW, Hay ME, Miller SL, Malone D, Sotka E, and Szmant AM. 1999. Effects of nutrients versus herbivores on reef algae: A new method for manipulating nutrients on coral reefs. Limnology and Oceanography 44:1847-1861.

Moberg F, and Folke C. 1999. Ecological goods and services of coral reef ecosystems. Ecological economics 29:215-233.

Morrison D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology 69:1367-1382.

Mumby PJ, Broad K, Brumbaugh DR, Dahlgren CP, Harborne AR, Hastings A, Holmes KE, Kappel CV, Micheli F, and Sanchiroco JN. In Press. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. Conservation Biology.

Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, and Gill AB. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98-101.

Mumby PJ, Foster NL, and Glynn Fahy EA. 2005. Patch dynamics of coral reef macroalgae under chronic and acute disturbance. Coral Reefs 24:681-692.

Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, and Blackwell PG. 2007a. Trophic cascade facilitates coral recruitment in a marine reserve. Proceedings of the National Academy of Sciences of the United States of America 104:8362-8367.

Mumby PJ, Hastings A, and Edwards HJ. 2007b. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98-101.

Mumby PJ, Hedley JD, Zychaluk K, Harborne AR, and Blackwell PG. 2006b. Revisiting the catastrophic die-off of the urchin Diadema antillarum on Caribbean coral reefs: Fresh insights on resilience from a simulation model. Ecological modelling 196:131-148.

Mumby PJ, and Wabnitz CCC. 2002. Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. Environmental Biology of Fishes 63:265-279.

Naim O. 1993. Seasonal responses of a fringing reef community to eutrophication (Reunion Island, Western Indian Ocean). Marine Ecology Progress Series 99:135-151.

Norton TA. 1977. Ecological experiments with Sargassum muticum. Journal of the Marine Biological Association of the UK 57:33-43.

Norton TA. 1983. The resistance to dislodgement of Sargassum muticum germlings under defined hydrodynamic conditions. Journal of the Marine Biological Association of the UK 63:181-193.

Norton TA. 1992. Dispersal by macroalgae. British Phycology Journal 27:293-301.

Norton TA, and Fetter R. 1981. The settlement of Sargassum muticum propagules in stationary and flowing water. Journal of the Marine Biological Association of the UK 61:929-940.

Nugues MM, and Bak RPM. 2006. Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. Marine Ecology Progress Series 315:75-86.

Nugues MM, and Roberts CM. 2003. Coral mortality and interaction with algae in relation to sedimentation. Coral Reefs 22:507-516.

O'Neal SW, and Prince JS. 1988. Seasonal effects of light, temperature, nutrient concentration and salinity on the physiology and growth of Caulerpa paspaloides (Chlorophyceae). Marine Biology 97:17-24.

Padilla DK. 1985. Structural resistance of algae to herbivores: A biomechanical approach. Marine Biology 90:103-109.

Padilla DK, and Allen BJ. 2000. Paradigm lost: reconsidering functional form and group hypotheses in marine ecology. Journal of Experimental Marine Biology and Ecology 250:207-221.

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenechan L, Newman MJH, Paredes G, Warner RR, and Jackson JBC. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955-958.

Peckol P. 1983. Seasonal physiological responses of two brown seaweed species from a North Carolina continental shelf habitat. Journal of Experimental Marine Biology and Ecology 72:147-155.

Pedersen MF, and Borum J. 1997. Nutrient control of estuarine macroalgae: growth strategy and the balance between nitrogen requirements and uptake. Marine Ecology Progress Series 161:155-163.

Prince JS, and O'Neal SW. 1979. The ecology of Sargassum pteropleuron Grunow (Phaeophyceae, Fucales) in the waters off South Florida. I. Growth, reproduction and population structure. Phycologia 18:109-114.

Quan-Young LI, Diaz-Martin MA, and Espinoza-Avalos J. 2004. Floristics, cover, and phenology of marine macroalgae from Bajo Pepito, Isla Mujeres, Mexican Caribbean. Bulletin of Marine science 75:11-25.

Ramus J, Lemons F, and Zimmerman C. 1977. Adaptation of light-harvesting pigments to downwelling light and the consequent photosynthetic performance of the eulittoral rockweeds Ascophyllum nodosum and Fucus vesiculosus. Marine Biology 42:293-303.

Ramus J, and Rosenberg G. 1980. Diurnal photosynthetic performance of seaweeds measured under natural conditions. Marine Biology 56:21-28.

Randall JE. 1961. Overgrazing of algae by herbivorous marine fishes. Ecology 42:812.

Randall JE. 1965. Grazing effects on sea grasses by herbivorous reef fishes in the West Indies. Ecology 46:255-260.

Reed DC. 1990. An experimental evaluation of density dependence in a subtidal algal population. Ecology 71:2286-2296.

Rivers GF, and Edmunds PJ. 2001. Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. Journal of Experimental Marine Biology and Ecology 261:159-172.

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

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.

Russel G. 1973. The Phaeophyta: A synopsis of some recent developments. Oceanography and Marine Biology Annual Review 11:45-88.

Russell BD, Elsdon TS, Gillanders BM, and Connell SD. 2005. Nutrients increase epiphyte loads: broad-scale observations and an experimental assessment. Marine Biology 147:551-558.

Sammarco PW. 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. Journal of Experimental Marine Biology and Ecology 61:31-55.

Santelices B. 1990. Patterns of reproduction, dispersal and recruitment in sea weeds. Oceanography and Marine Biology Annual Review 28:177-276.

Schaffelke B. 1999. Short-term nutrient pulses as tools to assess responses of coral reef macroalgae to enhanced nutrient availability. Marine Ecology Progress Series 182:305-310.

Schaffelke B, and Klumpp DW. 1997a. Biomass and productivity of tropical macroalgae on three nearshore fringing reefs in the central Great Barrier Reef, Australia. Botanica Marina 40:373-383.

Schaffelke B, and Klumpp DW. 1997b. Growth of germlings of the macroalga Sargassum baccularia (Phaeophyta) is stimulated by enhanced nutrients. Proceedings of the 8th International Coral Reef Symposium 2:1839-1842.

Schaffelke B, and Klumpp DW. 1998. Short-term nutrient pulses enhance growth and photosynthesis of the coral reef macroalga Sargassum baccularia. Marine Ecology Progress Series 170:95-105.

Scheffer M, Carpenter S, Foley JA, Folke C, and Walker B. 2001. Catastrophic shifts in ecosystems. Nature 413:591-596.

Schutten J, and Davy AJ. 2000. Predicting the hydraulic forces on submerged macrophytes from current velocity, biomass and morphology. Oecologia 123:445-452.

Shulman MJ, and Robertson DR. 1996. Changes in the coral reefs of San Blas, Caribbean Panama: 1983-1990. Coral Reefs 15:231-236.

Smith JE, Smith CM, and Hunter CL. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332-342.

Steneck RS. 1983. Quantifying herbivory on coral reefs: Just scratching the surface and still biting off more than we can chew. Pages 103-112 *in* M. L. Reaka, editor. The ecology of deep and shallow coral reefs. NOAA.

Steneck RS. 1986. The ecology of coralline algal crusts: Convergent patterns and adaptive strategies. Annual review of ecology and systematics 17:273-303.

Steneck RS. 1993. Is herbivore loss more damaging to reefs than hurricanes? Case studies from two caribbean reef systems (1978-1988).

Steneck RS, and Dethier MN. 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69:476-498.

Steneck RS, and Watling L. 1982. Feeding capabilities and limitation of herbivorous molluscs: A functional group approach. Marine Biology 68:299-319.

Stiger V, and Payri CE. 1999. Spatial and temporal patterns of settlement of the brown macroalgae Turbinaria ornata and Sargassum mangarevense in a coral reef on Tahiti. Marine Ecology Progress Series 191:91-100.

Stimson J, and Larned ST. 2000. Nitrogen efflux from the sediments of a subtropical bay and the potential contribution to macroalgal nutrient requirements. Journal of Experimental Marine Biology and Ecology 252:159-180.

Stimson J, Larned ST, and Conklin E. 2001. Effects of herbivory, nutrient levels and introduced algae on the distribution and abundance of invasive macroalga Dictyospaeria cavernosa in Kaneohe Bay, Hawaii. Coral Reefs 19:343-357.

Stimson J, Larned ST, and McDermid K. 1996. Seasonal growth of the coral reef macroalga Dictyosphaeria cavernosa (Forskal) Borgesen and the effects of nutrient availability, temperature and herbivory on growth rate. Journal of Experimental Marine Biology and Ecology 196:53-77.

Szmant A M. 1997. Nutrient effects on coral reefs: A hypothesis on the importance of topographic and trophic complexity to reef nutrient dynamics. Proceedings of the 8th International coral reef symposium 2:1527-1532.

Szmant AM. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries 25:743-766.

Tanner JE. 1995. Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. Journal of Experimental Marine Biology and Ecology 190:151-168.

Thacker RW, Ginsburg DW, and Paul VJ. 2001. Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. Coral Reefs 19:318-329.

Umar MJ, McCook LJ, and Price IR. 1998. Effects of sediment deposition on the seaweed Sargassum on a fringing coral reef. Coral Reefs 17:169-177.

Vadas RL, Johnson S, and Norton TA. 1992. Recruitment and mortality of early post-settlement stages of benthic algae. British Phycology Journal 27:331-351.

Wanders JBW. 1976a. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles) I: Primary productivity in the coral reef. Aquatic Botany 2:235-270.

Wanders JBW. 1976b. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles) II: Primary productivity of the Sargassum beds on the North-East coast submarine plateau. Aquatic Botany 2:327-335.

Wesseling I, Uychiaoco AJ, Alino PM, Aurin T, and Vermaat JE. 1999. Damage and recovery of four Philippine corals from short-term sediment burial. Marine Ecology Progress Series 176:11-15.

Wheeler WN. 1980. Effect of boundary layer transport on the fixation of carbon by the giant kelp Macrocystis pyrifera. Marine Biology 56:103-110.

Williams ID, and Polunin NVC. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19:358-366.

Williams SL. 1984. Uptake of sediment ammonium and translocation in a marine green macroalga Caulerpa cupressoides. Limnology and Oceanography 29:374-379.

Wolanski E, Richmond L, McCook LJ, Sweatman H. 2003. Mud, marine snow, and coral reefs. American Scientist 91:44-51.

Wooldridge S, Done T, Berkelmans R, Jones R, and Marshall P. 2005. Precursors for resilience in coral communities in a warming climate: a belief network approach. Marine Ecology Progress Series 295:157-169.

Wright JT, and Steinberg PD. 2001. Effect of variable recruitment and post-recruitment herbivory on local abundance of marine alga. Ecology 82:2200-2215.

Chapter 3 Modelling the dynamics of coral reef macroalgae using a Bayesian Belief Network approach

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MODELLING THE DYNAMICS OF CORAL REEF MACROALGAE USING A BAYESIAN BELIEF NETWORK APPROACH

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1 ABSTRACT

Macroalgae are a major benthic component of coral reefs and their spatial and temporal behaviour influence the resilience of coral reefs to disturbance. The relative importance of physical and ecological processes in driving macroalgal dynamics are poorly understood. Here we develop a Bayesian Belief Network model (BBN) to integrate many of these processes and predict the growth of coral reef macroalgae. Bayesian Belief Networks use probabilistic relationships rather than deterministic rules to quantify the cause and effect assumptions. The model was developed using both new empirical data and quantified relationships elicited from the scientific literature. We demonstrate the efficacy of the BBN to predict the dynamics of a common Caribbean macroalgal genus: *Dictyota*. Predictions of the model have an average accuracy of 55% (implying that 55% of the predicted categories of *Dictyota* cover were assigned to the correct class). Sensitivity analysis suggested that macroalgal dynamics were primarily driven by top-down processes of grazing rather than bottom-up nutrification. BBN's provide a useful framework for modelling complex systems, identifying gaps in our scientific understanding and communicating the complexities of the associated uncertainties in an explicit manner to stakeholders. We anticipate that accuracies will improve as new data are added to the model.

Keywords

Bayesian Belief Network, *Diadema antillarum*, *Dictyota* spp, grazing pressure, macroalgal dynamics, nutrients, Scaridae

2 INTRODUCTION

Caribbean coral reefs have experienced a bewildering array of disturbances during recent times including overfishing, catastrophic mortality of the urchin *Diadema antillarum*, mass coral bleaching and coral diseases (Lessios 1988, Hughes et al. 2003). These processes potentially exacerbate the perpetual disturbance phenomena, such as hurricanes, which play an integral role in the dynamics of reef communities (Done 1999, Done et al. 2003, Gardner et al. 2005). As a result, many Caribbean reefs have shown dramatic declines in a variety of taxa, including corals, prompting grave concern about the resilience of reef ecosystems (Hoegh-Guldberg et al. 2007). Dead corals may be colonised by large fleshy macroalgae, many of which are fairly unpalatable to herbivores (Coen and Tanner 1989, Steneck and Dethier 1994, Cronin and Hay 1996). Not only do these macroalgae pre-empt settlement space for corals (thereby reducing the chances of successful coral recovery) (Tanner 1995), but they may form a stable alternative community state (Done 1992, Mumby et al. 2007). Such shifts from coral-rich to algal-rich community states have serious deleterious consequences for biodiversity and the ability of reefs to provide coastal protection from tropical storms (Done et al. 1996, Moberg and Folke 1999).

The physical and ecological controls of macroalgal dynamics are poorly understood. Specifically, the relative importance of bottom-up processes, such as eutrophication, and top-down mechanisms such as grazing remains controversial (Hughes 1994, Hughes and Connell 1999, Lapointe 1999, McCook 1999, Diaz-Pulido and McCook 2003, McClanahan et al. 2003). For example, nutrients may be important in some environments (Lapointe 1997, Lapointe et al. 2004) but much less so in others (Belliveau and Paul 2002, McClanahan et al. 2004). The lack of synthesis stems from the ad-hoc geographic nature of the research, choice of study species, that many of the interactions are species- and habitat specific, and that empirical studies rarely control for all factors determining macroalgal cover. In order to work towards a more holistic perspective we have modelled the dynamics of one of the dominant macroalgae genera on Belizean coral reefs, *Dictyota* spp (Mumby et al. 2005). The model incorporates both physical parameters and ecological processes and is therefore able to represent a wide variety of environments. We use a Bayesian Belief Network (BBN) modelling approach (Pearl 1988) because it explicitly communicates the uncertainty associated with predictions (and therefore our understanding of the mechanisms) and can easily be revised once new data and experiments are available.

A BBN is a form of influence diagram which depicts the logical or causal relationships among physical and ecological factors influencing the probability of outcomes states of parameters of interest, such as percent algal cover (Marcot et al. 2001). This type of modelling has gained popularity in the field of ecology (Marcot et al. 2001, Borsuk et al. 2004, Wooldridge and Done 2004, Wooldridge et al. 2005) because of its great flexibility due to its probabilistic rather than deterministic nature. Probabilities in the model can be quantified using 1) empirical data, 2) statistical associations derived from existing data sources, 3) mathematical representations and 4) probabilistic quantities obtained from experts or a combination of the above (Marcot et al. 2001, Wooldridge et al. 2005).

The purpose of this paper is to describe the development of the model and its components, to provide an analysis of its behaviour and discuss its efficacy in structuring our understanding of macroalgal dynamics under inherent uncertainty and incomplete knowledge of the system.

3 METHODS

We developed a model called Algalnet using the BBN software Netica, commercially available from http://www.norsys.com. The inference algorithms used by Netica are described elsewhere (Spiegelhalter et al. 1993). For a detailed theory behind Bayesian Belief Networks the reader is referred elsewhere (Pearl 1988, Jensen 2001).

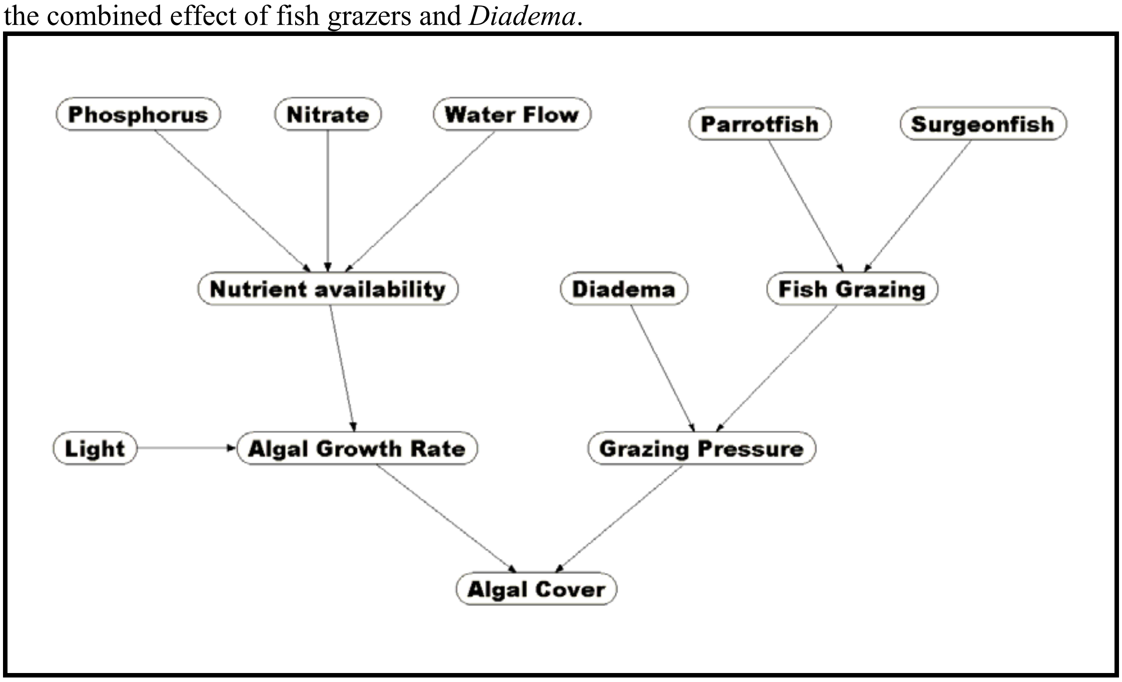
3.1 Overview of Bayesian Belief Network

The model represents the dynamics of the algal genus *Dictyota* (principally the species *pulchella*) on structurally complex forereefs in the Caribbean at depths of 5 m to 15 m. The model was designed using new empirical data and previous studies in the literature. All new empirical data on *Dictyota* spp, together with additional ecological and environmental data were collected over a period of 8 months at Glovers Reef (87^0 48’W, 16^0 50’N) an atoll about 45 km from the mainland of Belize, Central America. Six sites were monitored on the forereef between a depth of 5 m and 15 m.

The BBN approach begins by conceptualising a model of interest as a graph or network of connected nodes and linkages (Fig. 3.1). A network node represents important system variables (*Diadema*, Light, Grazing Pressure, Algal Cover, etc) and a link from one node to another (depicted as an arrow) represents a dependency relationship between the variables. The relationships may indicate direct causal dependencies or the combined effect of more complex associations (Pearl 1988). The extent of possible outcomes for a node is expressed by a probability distribution (Wooldridge et al. 2005).

Where there is no link between nodes they are said to be conditionally independent. The concept of conditional independence helps in simplifying a complex system by deconstructing it into subsets, which suggests the fact that some states in our model will likely occur more frequently when other states are present (Wooldridge et al. 2005). Input parameters are those nodes that can be measured in the field, having no other nodes entering them. Examples of these nodes are *Diadema*, Light and Parrotfish (Fig. 3.1). Each node can have a series of prior (or unconditional) probabilities of being found in a particular state. The values for priors can be derived from existing survey data or expert opinion. In the development of the model presented here, we did not rely on expert opinion and all prior values are based on field data or, if unknown, left as uninformative. For example the Parrotfish node has prior probabilities of being found in a particular biomass category, the range of each category can be found in Table 3.2 (very low: 23.7%, low: 31.8%, medium: 25.8%, high: 11.6% and very high: 7.07%) meaning that a site chosen at random (in our case at Glovers Reef, Belize) will fall into the "high" biomass category with a probability of 11.6%.

Fig. 3.1. Graphical representation of the Bayesian Belief Network Algalnet. Parrotfish and Surgeonfish represent biomass of the fish grazers, *Diadema* denotes abundance of the urchin, Nitrate and Phosphorus represent respective nutrient concentrations, Water Flow represents water motion on the reef, Light represents Photosynthetic Active Radiation measurements (PAR), Nutrient availability represents the interaction of nutrients and water flow, Algal Growth Rate corresponds to algal growth as a function of nutrient availability and light, Fish grazing represents the total biomass of Scaridae and Acanthuridae, whilst Grazing pressure represents the combined effect of fish grazers and *Diadema*.



Intermediate nodes depend on input nodes or other intermediate nodes, and are useful for integrating variables measured on different scales and for linking subsets of the network. Intermediate nodes in Algalnet include Algal Growth Rate, Fish Grazing, Grazing Pressure and

Nutrient Availability (Fig. 3.1). These nodes are represented by a conditional probability, which is the likelihood of the state of the node given the states of input parameters affecting it, such as algal growth rate being high given that nutrient availability is high and light is medium (Table 3.1). The strength or certainty of the dependency relationship among variables is summarized through a conditional probability table (CPT). The CPT specifies the conditional probability of, for example, the node Algal Growth Rate (Table 3.1) being in a certain state given both the states of the input nodes Light and Nutrient Availability. For example in Table 5, given Nutrient availability = high and Light = medium, the resulting probability of algal growth rate levels are: very low = 0%, low = 10%, medium = 10%, high = 30% and very high = 50%. In other words given the particular combination of input nodes (also known as parent nodes), the likelihood of algal growth rate being "very high" is 50% and being "high" is 30%, etc. The CPTs therefore can explicitly represent the uncertainty associated with the relationship of the variables. To avoid bias in our own beliefs on macroalgal dynamics we did not use our own opinion to determine conditional probabilities, although this approach is often used (Uusitalo 2007); rather we used our empirical data, the literature, or if no data were available at all, left each outcome with uninformative equal probability.

Table 3.1. Conditional Probability Table (CPT) of the node Algal Growth Rate

Parent nodes		**Categories of the node Algal growth rate**				
Nutrient Availability	**Light**	**Very low**	**Low**	**Medium**	**High**	**Very high**
Low	Low	20	20	20	20	20
Low	Medium	20	20	20	20	20
Low	High	20	20	20	20	20
Low	Very high	20	20	20	20	20
Medium	Low	20	20	20	20	20
Medium	Medium	50	50	0	0	0
Medium	High	20	20	20	20	20
Medium	Very high	20	20	20	20	20
High	Low	0	0	0	50	50
High	Medium	0	10	10	30	50
High	High	0	27.3	27.3	36.4	9
High	Very high	50	50	0	0	0
Very high	Low	75	25	0	0	0
Very high	Medium	91.7	8.3	0	0	0
Very high	High	20	20	20	20	20
Very high	Very high	20	20	20	20	20

3.2 Parameterisation of the Bayesian Belief Network

The categorization of model nodes (Fig. 3.1) was based on data collected at Glovers reef (Table 3.2). The model has 12 nodes of which 7 are input nodes, 4 are intermediate nodes and 1 is the final predicted outcome, macroalgal cover of a given species (Table 3.2). Here we provide a description of the intermediate nodes and the method used to quantify the conditional probabilities.

3.2.1 Algal cover: Parent nodes - Algal Growth Rate and Grazing Pressure

Macroalgal cover can be defined as a balance between two dynamic processes: net algal production (colonization and growth) and removal of algal biomass by herbivores, senescence, wave action and reproduction (Carpenter 1985). In general it is believed that nutrient flux may set limits on the total size (and thus biomass) of algae (Hatcher and Larkum 1983, Lapointe 1987, Lapointe et al. 1987, Lapointe and O'Connell 1989, Schaffelke and Klumpp 1997, 1998), but herbivorous fish and urchins can limit algal size and biomass to levels below the constraints imposed by low nutrients (Hay 1981, Steneck and Watling 1982, Carpenter 1986, Lewis 1986, Hughes 1994, Aronson and Precht 2000). As a result, macroalgae are only dominant when herbivory is reduced and/or ambient nutrient levels are high (Gaines and Lubchenco 1982, Hatcher and Larkum 1983, Belliveau and Paul 2002, McClanahan et al. 2003).

Quantification of the CPT (Appendix A, Table 1) governing this balance is based on field data from Glovers Reef. For each combination of parent nodes the probability of algal cover being in a certain algal cover category is calculated from the frequency a particular algal cover occurs in the dataset given the combination of the parent nodes. For example in Table 3.1, given the combination of Algal growth rate = very low and Grazing pressure = medium, there is a 75% likelihood of algal cover being 0-5% and a 25% likelihood it is 5-10% respectively.

Table 3.2. Overview of model nodes, categories, data collection and quantification of probabilities

Node	Node Type	Categories		Justification	Quantification	Data collection
Algal cover Input: 1) Algal growth rate 2) Grazing pressure	Predicted outcome of BBN	0 – 5% 5 – 10% 10 – 20% 20 - 50% >= 50%		Continuous data discretized to optimise frequency of occurrence in each category. Represents a sufficiently fine descritization and is ecological relevant	Quantification of the CPT is based on empirical data from Glovers Reef. See main text for a description of method.	Average percent cover of *Dictyota spp* was obtained monthly from video stills of 120 permanent quadrats (0.5 x 0.5 m) at 6 sites on Glovers Reef.
Algal growth rate Input: 1) Nutrient availability 2) Light	Intermediate node	Very low	0 – 0.05 cm^{-2}.day^{-1}	Continuous data discretized to equal width (0.05 cm^{-2}.day^{-1}). Represents a sufficiently fine descritization and is ecological relevant	Quantification of the CPT is based on field data from Glovers Reef. See main text for a description of method.	Growth rates are calculated as the increase in size of individual patches of *Dictyota* spp over a 30 day period, averaged for each quadrat. Growth rates are expressed in cm^{-2}.day^{-1}
		Low	0.05 – 0.1 cm^{-2}.day^{-1}			
		Medium	0.1 – 0.15 cm^{-2}.day^{-1}			
		High	0.15 – 0.2 cm^{-2}.day^{-1}			
		Very high	>= 0.2 cm^{-2}.day^{-1}			
Grazing pressure Input: 1) Diadema 2) Fish Grazing	Intermediate node	Very low	1-20%	Grazing carried out by different taxa, yet they fulfil the same function. Node integrates taxa in categories of percent grazed area.	Quantification of the CPT is based on relationships derived from the literature. See main text for a description of method. Carpenter 1984, Mumby 2006, Mumby et al 2006b.	Normalised probabilities based on calculations from density data of *Diadema* urchins and fish grazer biomass on Glovers Reef
		Low	20-40%			
		Medium	40-60%			
		High	60-80%			
		Very High	80-100%			
Fish grazing Input: 1) Parrotfish 2) Surgeonfish	Intermediate node	Very low	0 – 4 g.m^{-2}	Continuous data discretized to equal width (5 g.m^{-2}) Represents a sufficiently fine descritization of biomass data of Scaridae and Acanthuridae at Glovers Reef.	Quantification of the CPT is based on field data from Glovers Reef. See main text for a description of method.	Normalised probabilities based on mathematical calculations of biomass data for Scaridae and Acanthuridae.
		Low	5 – 9 g.m^{-2}			
		Medium	10 – 14 g.m^{-2}			
		High	15 – 19 g.m^{-2}			
		Very high	>= 20 g.m^{-2}			
Parrotfish	Input node	Very low	0 – 4 g.m^{-2}	Continuous data discretised to equal width (5 g.m^{-2}) based on biomass values for Scaridae at Glovers Reef.	Quantification of prior probabilities is based on frequency distribution of all transect data for Glovers Reef.	Average biomass of Scaridae surveyed monthly on eight 4 x 30 m transects at each site. Length converted to biomass using allometric relationships from fishbase (Froese and Pauly 2006), expressed in g.m^{-2}.
		Low	5 – 9 g.m^{-2}			
		Medium	10 – 14 g.m^{-2}			
		High	15 – 20 g.m^{-2}			
		Very high	>= 20 g.m^{-2}			

Table 3.2 continued

Surgeonfish	Input node	Very low	0 – 4 g.m^{-2}	Continuous data discretized to equal width (5 g.m^{-2}) based on biomass values for Acanthuridae at Glovers Reef.	Quantification of prior probabilities is based on frequency distribution of all transect data for Glovers Reef.	Average biomass of Acanthuridae surveyed monthly on eight 4 x 30 m transects at each site. Length converted to biomass using allometric relationships from fishbase, expressed in g.m^{-2}
		Low	5 – 9 g.m^{-2}			
		Medium	10 – 14 g.m^{-2}			
		High	15 – 20 g.m^{-2}			
		Very high	>= 20 g.m^{-2}			
Diadema	Input node	Low	0.01 – 0.50 m^{-2}	Continuous data discretized to equal width (0.50 m^{-2}) based on abundance data for *Diadema antillarum* at Glovers Reef.	Quantification of prior probabilities is based on frequency distribution of all transect data for Glovers Reef.	Average density of *Diadema antillarum* surveyed monthly on five 2 x 50 m transects at each site, expressed in nr.m^{-1}.
		Medium	0.51 – 0.99 m^{-2}			
		High	>= 1 m^{-2}			
Nutrient availability Input: 1) Nitrate 2) Phosphorus 3) Water flow	Intermediate node	Low Medium High Very high		Node integrates different parameters using simple discrete categories.	Quantification of the CPT is based on quantified published relationships. See main text for a description of method. Bilger and Atkinson 1995, Carr et al 1997, Hearn et al 2001.	Normalised probabilities derived from published studies.
Water flow	Input node	Low	0 – 0.09 g.h^{-1}	Continuous data discretized to equal width (0.1 g.h^{-1}) based on all values recorded at Glovers Reef.	Quantification of prior probabilities is based on frequency distribution of all clod card data for Glovers Reef.	Difference in weight of plaster of paris clod cards after 48 hrs submersion on the reef at each site, expressed in g.h^{-1} weight loss.
		Medium	0.1 – 0.19 g.h^{-1}			
		High	0.2 – 0.29 g.h^{-1}			
		Very high	>= 0.3 g.h^{-1}			
Nitrate	Input node	Low	0 – 0.9 µM	Continuous data discretized to equal width (1 µM) based on all values recorded at Glovers Reef.	Quantification of prior probabilities is based on frequency distribution of all water sample data for Glovers Reef.	Spectrophotometer analysis of water samples collected from the reef, expressed in µ M
		Medium	1 – 1.9 µM			
		High	2 – 2.9 µM			
		Very high	>= 3 µM			
Phosphorus	Input node	Low	0 – 0.09 µM	Continuous data discretized to equal width (0.1 µM) based on all values recorded at Glovers Reef.	Quantification of prior probabilities is based on frequency distribution of all water sample data for Glovers Reef.	Spectrophotometer analysis of water samples collected from the reef, expressed in µ M
		Medium	0.1 – 0.19 µM			
		High	0.2 – 0.29 µM			
		Very high	>= 0.3 µM			
Light	Input node	Low	0 – 39 W.m^{-2}	Continuous data discretized to equal width (40 W.m^{-2}) based on values recorded at Glovers Reef.	Quantification of prior probabilities is based on frequency distribution of all irradiance values for Glovers Reef.	PAR readings at depth converted from average daily irradiance measurements expressed in W.m^{-2}
		Medium	40 – 79 W.m^{-2}			
		High	80 – 119 W.m^{-2}			
		Very high	>= 120 W.m^{-2}			

When it was not possible to calculate the probability because the combination of parent nodes did not occur in the dataset (e.g. Algal growth rate = low and Grazing pressure = highest, Appendix A, Table 1) uninformed priors were assigned to each category of the node algal growth rate. Equally, where insufficient data were available for a certain combination of parent nodes (e.g. a single observation for a given pair of parent nodes) we opted to assign only 60% to the category (i.e. a little over half) and divided the remaining 40% equally among other categories. This is because we lacked the confidence necessary to assign the full weight to a single category and this approach downweighted potential biases because of overconfidence. Research in estimation processes has shown that regardless of the method used, human estimators are likely to be overconfident, that is, giving estimates that are too near to zero or one (Morgan and Henrion 1990).

3.2.2 Algal Growth Rate: Parent nodes - Nutrient Availability and Light

Both nutrients and light have a strong influence on algal growth rates and the combination of these two factors may determine maximum coral reef algal production (Carpenter 1985, Creed et al. 1997) .The interaction of the two factors on growth rate is complex and influenced by morphological properties of the specific alga and physiological processes (Littler and Littler 1980, Pedersen and Borum 1997) and continuously changes over time (Lapointe and Tenore 1981, Lapointe and O'Connell 1989, Enriquez et al. 1994) . However, nutrient additions are usually found to enhance growth more under high rather than low light conditions (Lapointe and Tenore 1981). A recent study indicated that growth of *Dictyota menstrualis* was nutrient-limited at certain times of the year possibly associated with local upwelling events (Leichter et al. 1996, Leichter et al. 2003). This species was found to be light limited only at depths of over 32 m (Beach et al. 2006), which is well beyond the depth range of our model. Thus, we made the assumption that macroalgal growth on reefs is not light limited. In general, where the species is not light or nutrient limited both factors will positively contribute to growth rate and only at the extreme ends of light and nutrient levels will limitation occur (Lapointe and Tenore 1981, Dawes and Kovach 1992).

Quantification of the CPT (Table 3.1) governing the interactions between light and nutrients followed the same method as that used for the Algal Cover node. Even though previous studies allude to relationships between nutrients, light and algal growth rates (Lapointe and Tenore 1981) we did not quantify these for combinations of parent nodes for which we did not have empirical data. These categories have uninformed priors.

3.2.3 Nutrient Availability: Parent nodes - Nitrate, Phosphorous and Water Flow

Nutrients are undoubtedly an important resource for algae but whether natural fluctuations influence algal growth rate remains controversial (reviewed in McCook 1999), partly because nutrient concentrations fluctuate over time and space (Andrews and Muller 1983) and uptake by macroalgae is species specific (Fong et al. 2001). A recent study on *Dictyota* spp provided evidence for this (Beach et al. 2006). Their experiments showed differential response of *Dictyota menstrualis* in natural vs. artificial nutrient enrichment and the authors' suggested that the differences related directly to the time spent in cool nutrient-enriched water from local upwelling prior to the experiments. On patch reefs at Glovers Reef, it was found that the addition of nutrients does not enhance the growth of macroalgae (McClanahan et al. 2004), although background concentrations of phosphorous were relatively high (0.38 µM ±0.009).

Nutrient availability (Hatcher and Larkum 1983, Pedersen and Borum 1997) is determined by ambient nutrient concentration of the surrounding waters and the uptake rate by the algae. Water flow plays a key role in this process (Williams and Carpenter 1998, Hurd 2000) and might explain why macroalgal cover shows such variability over time and space. Experimental studies reveal that nutrient uptake is proportional to the current speed to the 0.8 root and decreasing to 0.4 under high current conditions (Hearn et al. 2001). In short, water flow enhances nutrient uptake until a threshold is reached (Carr et al. 1997). When high ambient nutrient concentrations are present the uptake rate will be reduced as it has been found that the mass-transfer exponents are inversely related to nutrient loading (Bilger and Atkinson 1995). The aforementioned study found that the uptake rate constant, for real surface reactivity decreases following high nutrient loading. Very low flow rates impede nutrient uptake as the boundary layer surrounding the algae will not be broken down and serves as a barrier (Carr et al. 1997, Hurd 2000), whilst very high flow rates will impede uptake because it might cause structural damage or even dislodgement of the algae from the reef (Schutten and Davy 2000).

Quantification of the CPT (Appendix A, Table 2) among nutrients and water flow utilised results from published studies. Nutrient uptake is considered mass transfer limited under field conditions of low nutrients and high water velocities (Bilger and Atkinson 1995). Where higher nutrient concentrations are found the uptake rate of nutrients will be reduced (Bilger and Atkinson 1995). The CPT made the following assumptions: 1) Where low nutrient concentrations are present water flow will determine the nutrient availability and 2) Where nutrient concentrations are higher, nutrient availability will be slightly reduced. In the CPT this relates to assigning the proportional relationships of water flow and nutrient uptake to the highest category of nutrient availability. Here we assigned an 80% probability to the highest category of nutrient availability under medium water flow, reducing to 40% under very high water flow. The remaining percentages were divided equally among other categories. When nutrient concentrations increased we assigned the same proportional relationships of nutrient uptake and water flow but to a lower category of nutrient availability, with the remaining percentages divided equally among other categories.

Under low water flow conditions nutrient uptake rates are thought to be impeded (Carr et al. 1997) but because this relationship has not been quantified the most parsimonious approach at this stage is to assign equal weight to each category of the node nutrient availability. For example in Table 3.1 where Water flow = low, Nitrate = low and Phosphorous = low.

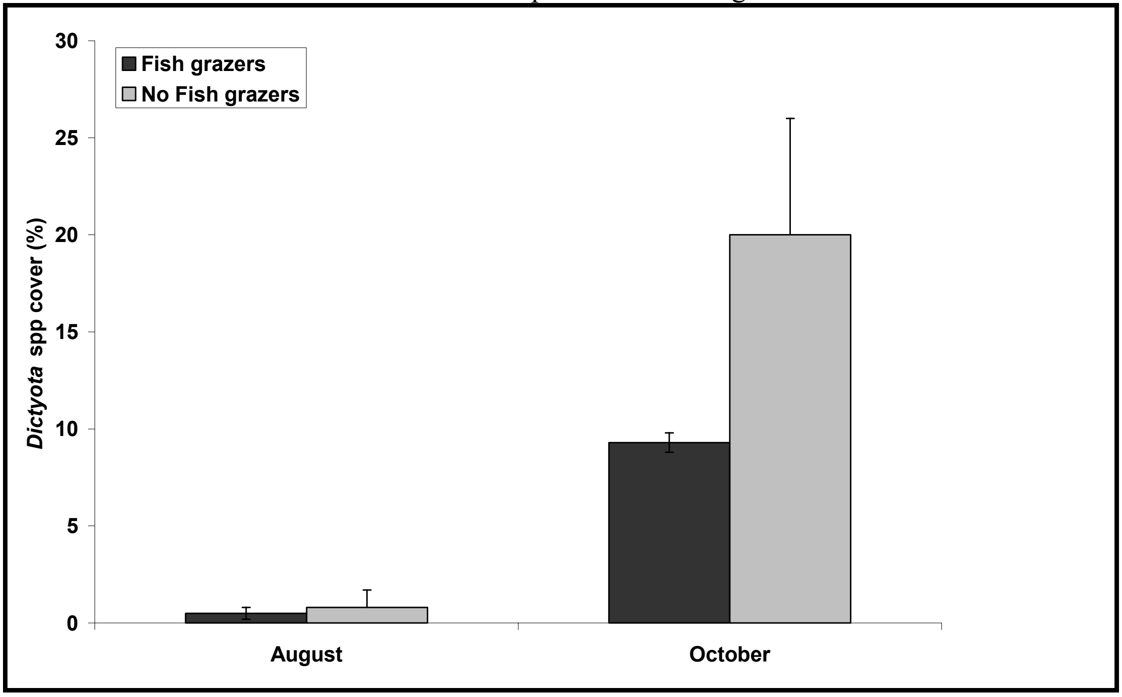
The model does not distinguish between the effects of nitrate and phosphorous on macroalgal growth rate, because the results of studies comparing N and P are equivocal. In oligotrophic reef waters studies showed that phosphorus availability limits productivity (Lapointe et al. 1987, Littler et al. 1991, Lapointe et al. 1992), whilst nitrogen limitation is not uncommon (Lapointe 1987, Delgado and Lapointe 1994, Larned 1998). Experiments on patch reefs at Glovers Reef did not find increased growth when phosphorous was added (McClanahan et al. 2002, McClanahan et al. 2004) but levels of phosphorus are already high at this atoll (0.38 μM ± 0.009). The node Phosphorous was included in the model for completeness and future updating purposes though its inclusion now does not influence model behaviour. Therefore, only the nitrate node was combined with water flow to define the probabilities for each category of nutrient availability. Two levels of nitrate concentration were assigned probabilistic relationships but other categories cannot be parameterised at this stage because of an absence of information on effects of different nitrogen concentrations on algal growth rate.

3.2.4 Fish Grazing: Parent nodes - Parrotfish and Surgeonfish

In the absence of the urchin *Diadema antillarum*, parrotfishes (Scaridae) are the most important grazers on most mid-depth (5-15 m) Caribbean forereefs (Mumby et al. 2006a), with surgeonfishes (Acanthuridae) being a secondary herbivore (Robertson et al. 2005). Many studies have documented the impact of fish grazers through exclusion experiments (Lewis 1986, Morrison 1988, McClanahan et al. 2003) and found that algal biomass generally increased. On Glovers Reef a caging experiment revealed a doubling of algal cover over a 2 month time period during which fish grazers were excluded from areas of 0.5 m x 0.5 m compared to uncaged and partially-caged controls that were accessible to fish grazers (Fig.

3.2). Note that full results of these experiments including cage controls will be reported in chapter 5. Quantification of the CPT (Appendix A, Table 3) governing the combined effect of parrotfish and surgeonfish is based on field data from Glovers Reef. The nodes within this subset of the BBN assume that the total grazing contribution of fishes scales linearly with total biomass.

Fig. 3.2. Mean cover (±SE) of *Dictyota* spp. after 2 months of a caging experiment on the seaward forereef of Glovers Reef. Start of experiment was August 2005.



3.2.5 Grazing Pressure: Parent nodes - Diadema and Fish Grazing

Prior to the disease-induced mass mortality of the urchin *Diadema antillarum* in the mid 1980s, urchins were considered one of the most important grazers on Caribbean reefs (Carpenter 1986, Carpenter 1988, Lessios et al. 2001) occasionally attaining extremely high densities in shallow waters (71 m^{-2} (Sammarco 1982). Mass mortalities have reduced their numbers throughout the Caribbean by up to 97% of earlier population densities (Lessios et al. 2001). Today localized recoveries have been reported (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006) but have not reached the pre-mortality densities in much of the Caribbean and numbers remain very low (< 1 m^{-2}, Kramer 2003).

Here we used *D. antillarum* densities rather than biomass as a measurement of grazing pressure on the assumption that *Diadema* are very efficient grazers and are able to control macroalgae within their territory (hence higher densities of *Diadema* in an area will exert more grazing pressure). The CPT of combined grazing between urchins and fishes (Appendix A, Table 4) was based on previous comparisons of the grazing of these taxa (Table 3.2). Densities of 1 m^{-2} are able to control macroalgae (Craig Dahlgren, pers. comm.), having an average territory size of 2.25 m^2 (Carpenter 1984). Densities of *Diadema* on Glovers Reef are much lower at with an average of 0.05 m^{-2}. We linearly scaled the proportion of reef grazed to observed urchin densities assuming that 100% of the reef would be grazed at a density of 1 m^{-2} and 0% when *Diadema* is absent.

To combine urchin and fish grazing, we modified the method used in a simulation model of Caribbean reefs (Mumby 2006). At their highest levels, fish grazers are able to maintain 40% of the reef in a grazed state. In contrast, urchin densities of ≥ 1 m^{-2} are needed to maintain the reef in 100% grazed state. Total grazing can exceed 100% when urchins and fish re-graze the same algal turfs and exclude macroalgae. Therefore, the combination of classes for grazing followed equation (1)

$$\text{Combined grazing}, G(\%) = \left[\frac{\text{Fish class}}{5} \times 40\right] + \left[\frac{\text{Urchin class}}{5} \times 100\right] \qquad (1)$$

Where a fish class of 'very low' = 1 and 'very high' = 5, an urchin class of 'none' or 0 represents densities of 0 m^{-2}, 'very low' or '1' represents densities of 0.01-0.20 m^{-2}, 'low / 2' of 0.21-0.50 m^{-2} , 'medium / 3 of 0.51-0.99 m^{-2} and 'high / 4' of > 1 m^{-2}, and where any value of G that exceeds 100% is truncated at 100%. Values of total grazing in CPT (Table 3.2) were discretized into 20% bands representing a total grazing of 'very low' (1-20%) to 'very high' (80-100%). Corresponding values of G were assigned as follows: if G fell within the two central quartiles of a total grazing class (e.g. in the range 26-35% for the class 'low' which ranges from 21-40%), then it was assigned to the corresponding total grazing class with 100% probability. If the value for G fell into the lower quartile of a class (e.g. G = 21-25%) which is the lower quartile for the class 'low'), it was given 50% likelihood of being in the corresponding class and 50% likelihood of being in the class below. The exception was the class 'very low' (1-20%) for which no lower class exists, in which case the class designation was left at 100%. Finally, if the value for G fell in the upper quartile of a class, its membership was again divided equally between the corresponding class of total grazing and the class above. Once again, an exception was made for the 'very high' class because no greater class exists.

3.3 Model Accuracy and Sensitivity

Field data acquired at Glovers Reef generated a total of 370 cases of algal cover and associated levels for each node. All but 150 cases were used to determine prior probabilities of the model. The remaining subset of 150 cases (selected at random) were used to undertake a test of the BBN accuracy. Accuracy was determined as the proportion of predicted algal cover classes correctly identified where the predicted class was taken to be the category with the highest predicted probability). Accuracy results were then presented using error matrices (Congalton 1991). Further investigation of the accuracy was undertaken by plotting the cumulative relative frequency of absolute errors, where absolute error was defined as the absolute difference between observed algal cover (e.g. 8%) and the central value of each predicted category (e.g. for 10-20%, it would be 15%, yielding an absolute error of 7%).

A sensitivity analysis was undertaken to identify the relative influence of different nodes on the output categories of algal cover. The analysis was conducted by systematically varying the values of individual node categories from their prior value to 100% whilst (1) all other prior values for levels of that node were set to zero and (2) all other nodes were held constant (e.g. for the node parrotfish changing the category “very low” from 23.7% to 100%, next the category “low” from 31.8% to 100%, etc) to determine how they affect the absolute change in probability of output algal cover category ‘0-5%’ as a result of adjusting the parrotfish level ‘very low’.

Second, a sensitivity analysis was done for all the intermediate nodes to explore the effects of change in the conditional probabilities on the outcome of the model. We adapted the approach of Fong et al (1994) to suit our model. The conditional probabilities associated with each intermediate node were randomly changed by ± 10% and quantified the changes for the algal cover category ‘0-5%’. The sensitivity analysis described above, subsequently referred to as the baseline, will give a value for the range over which the algal cover category 0-5% will change for each respective input node (Fig 3.5). For example in Fig 3.5 the input node Diadema has a range from 0.281 to 0.404 giving a value of 0.404 – 0.281 = 0.123. The relative change for each input node was then calculated as:

$$\textit{Relative change} = ((\textit{rerun} - \textit{baseline})/\textit{baseline}) \times 100,$$

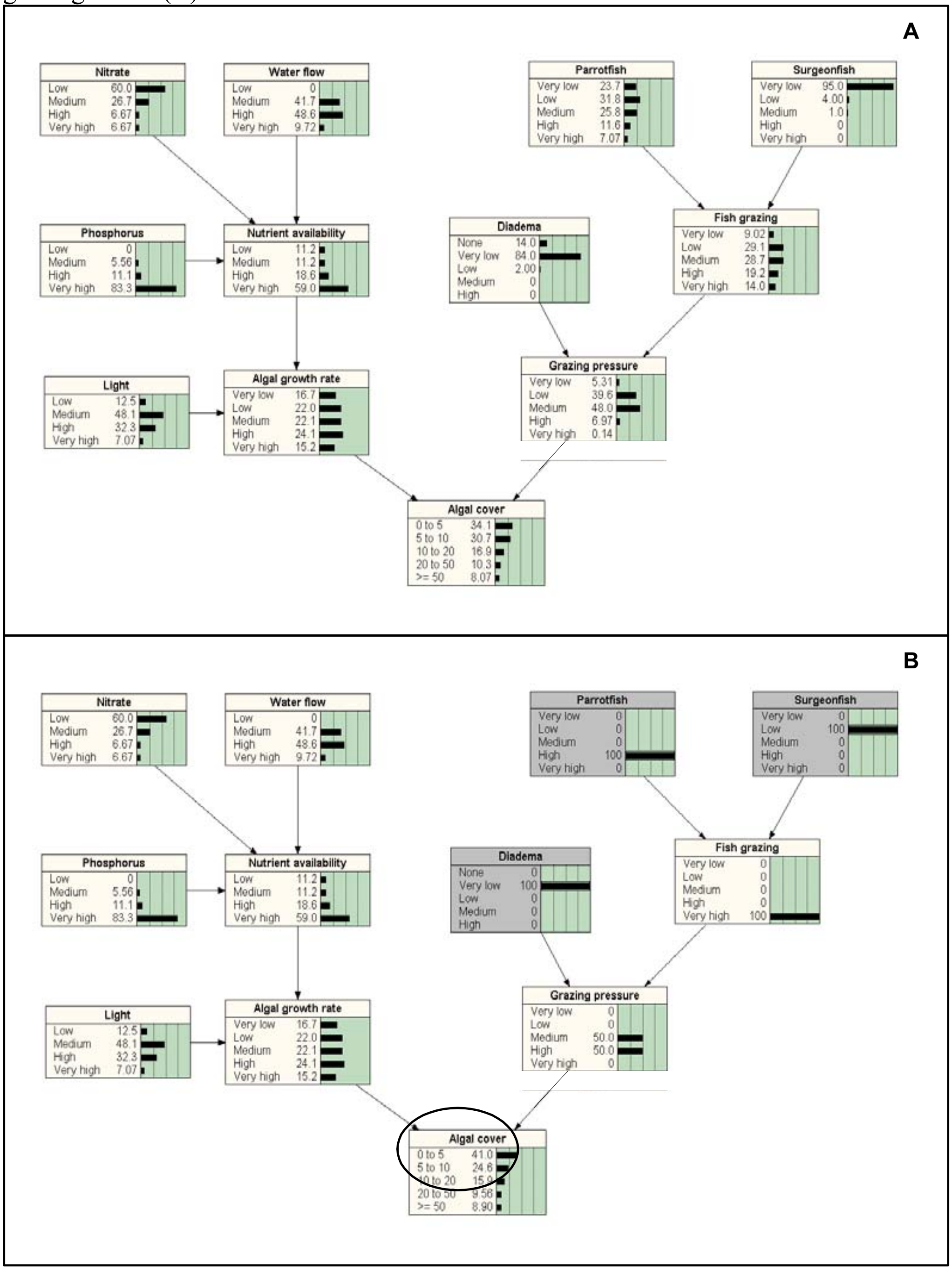
Where the rerun is the sensitivity analysis carried out with a ±10% to the probabilities in the CPTs of the respective intermediate node. The intermediate nodes tested are, Nutrient Availability, Algal Growth Rate, Fish Grazing and Grazing Pressure. The relative changes can be both negative and positive. Negative values mean a reduction in the sensitivity of an input node to changes in the conditional probabilities of the intermediate node, whilst a positive values indicates an increase in sensitivity.

4 RESULTS AND DISCUSSION

4.1 Overall Model Behaviour

To demonstrate the behaviour of the model, a comparison is given between the uninformed state, where all nodes adopt their prior values and the informed state after which new information has been added. For example, in the uninformed state there is a 34.1% chance that algal cover lies between 0 and 5% at a site chosen at random, which represents the distribution of algal cover from our sample sites from Glovers Reef, Belize (Fig. 3.3A). In the informed case (Fig. 3.3B) specific information on grazing pressure from a particular site on the eastern reef of the atoll has been entered, as shown by the colour of the nodes changing to grey and the associated states taking on a probability of 100%. Entering specific information changes the node algal cover (circled in black, Fig. 3.3B) which has now taken on new values for each of the categories. Adding this new information has increased the belief that algal cover lies somewhere between 0 and 5% by 6.9 % (i.e. from 34.1% - 41%).

Fig. 3.3. Examples of a non informed BBN (A) and the informed case with data on grazing levels (B)



4.2 Accuracy Assessment

Over the 150 independent data points the BBN predicted the correct algal cover category 55% of the time (Table 3.3). The accuracy rose to 72% if the scale was subsumed to equal sized categories of 10% intervals (Table 3.4). Whilst this appears to be a substantial increase in accuracy, it is driven by one category with an accuracy rate of 97%. Other categories had very poor predictive rates (Table 3.4). It must be born in mind that errors can be accentuated by the use of discrete cover categories. For example, an observed algal cover of 21% would be treated as incorrect if the predicted (i.e. most likely) cover class was 10-20%, yet the absolute error is small. Many conditional relationships were uninformed (e.g. uniform probabilities for each category in a node given the combination of parent nodes), adding to the poor predictive rates in certain categories.

Table 3.3. Error matrix of 150 cases.

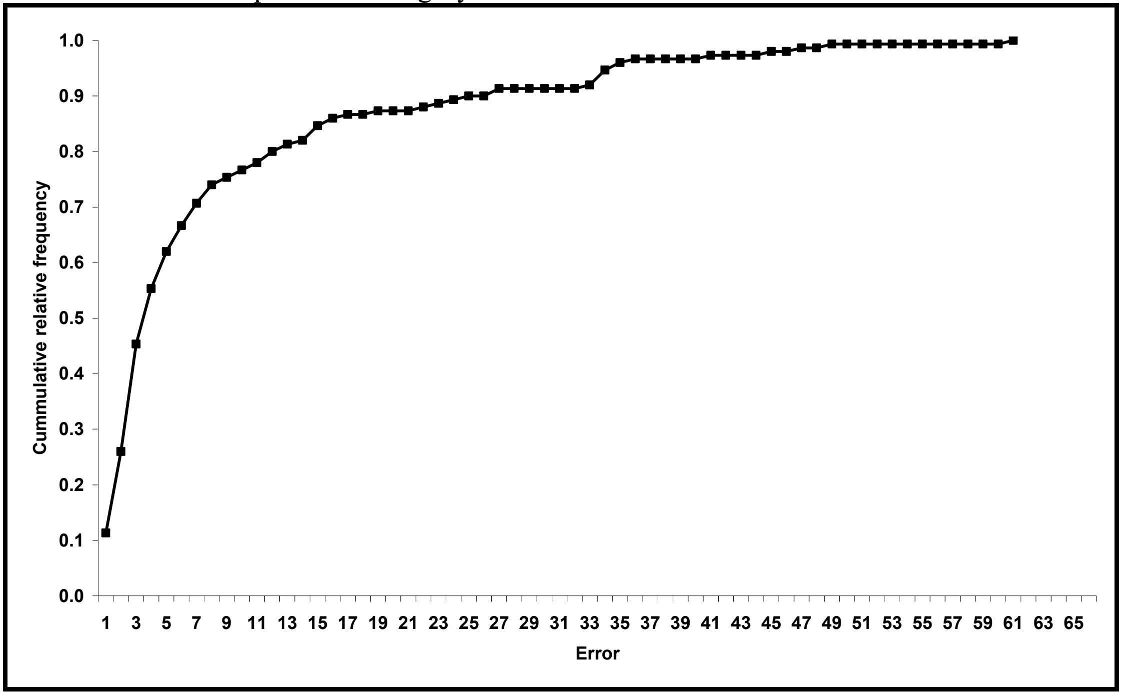
Predicted value category							
Actual value category	**0-5**	**5-10**	**10-20**	**20-50**	**50-100**	**Total of Rows**	**Accuracy**
0-5	41	15	0	3	0	59	0.69
5-10	10	35	0	0	0	45	0.78
10-20	6	14	0	1	0	21	0
20-50	0	13	0	6	0	19	0.32
50-100	0	4	0	2	0	6	0
Total of columns	57	81	0	12	0	150	0.55

Table 3.4. Error matrix of 150 cases, subsumed categories

Predicted value category											
Actual value category	**0-10**	**10-20**	**20-30**	**30-40**	**40-50**	**50-60**	**60-70**	**70-80**	**80-90**	**90-100**	**Total of rows**	**Accuracy**
0-10	101	3	0	0	0	0	0	0	0	0	104	0.97
10-20	18	2	0	0	0	0	0	0	0	0	20	0.10
20-30	8	0	1	0	0	0	0	0	0	0	9	0.11
30-40	4	0	0	0	0	0	0	0	0	0	4	0
40-50	8	0	0	0	0	0	0	0	0	0	8	0
50-60	4	0	0	0	0	0	0	0	0	0	4	0
60-70	1	0	0	0	0	0	0	0	0	0	1	0
70-80	--	--	--	--	--	--	--	--	--	--	--	--
80-90	--	--	--	--	--	--	--	--	--	--	--	--
90-100	--	--	--	--	--	--	--	--	--	--	--	--
Total of columns	144	5	1	0	0	0	0	0	0	0	150	0.72

The cumulative frequency of absolute errors revealed that 77% of predictions had an error of <10% and 85% of predictions were within 15% of the observed value (Fig 3.4). There was, however, a large tail of poor classifications. This was likely caused by the uninformed conditional relationships rather than any natural phenomena recorded on the coral reef.

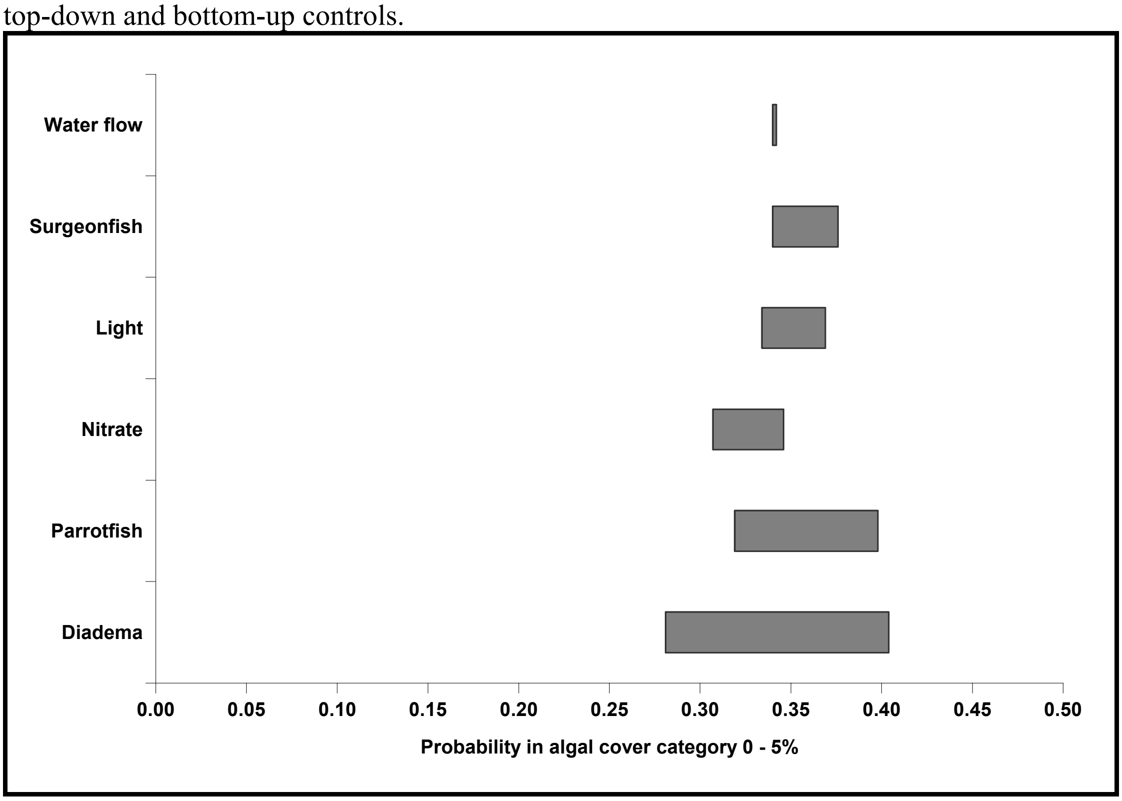
Fig. 3.4. Model accuracy showing the cumulative relative frequency of absolute errors, absolute error is defined as the absolute difference between observed algal cover and the central value of each predicted category



4.3 Sensitivity Analysis

Grazing by *Diadema* was found to exert the greatest influence on macroalgal cover (Fig. 3.5) followed by parrotfish grazing. This conclusion supports the contention of several other studies that algal dynamics are generally more heavily influenced by top-down processes than bottom-up (environmental) processes (Morrison 1988, Carpenter 1990, Hughes et al. 1999, Belliveau and Paul 2002, Diaz-Pulido and McCook 2003, McClanahan et al. 2003, Mumby et al. 2006b). Of the environmental parameters light and nutrients were found to exert the greatest influence for our data (Fig. 3.5). Light and nutrients are both important factors in determining growth rates of macroalgae. The lack of sensitivity between the two parameters is very likely to be caused by the large amount of uninformed probabilities.

Fig. 3.5. Sensitivity analysis for the Node Algal Cover, category 0-5% cover to changes in top-down and bottom-up controls.



The sensitivity analysis on the effects of changes in the conditional probabilities of the intermediate nodes (Table 3.5) strengthened the results of the sensitivity analysis shown in Fig 3.5. The relative change of the input node Water flow seems very large, but looking at Fig 3.5 it becomes clear. Here it is shown that the probabilities in the algal cover category 0-5% was the least sensitive to the input node Water flow, with a range of only 0.002% as compared for example to the node Diadema with a range of 0.123. It can thus be expected that changes in the intermediate nodes associated with the input node water flow are relatively large. Over all the results the sensitivity analysis confirmed that the model will be most sensitive to the intermediate nodes which have a relatively large number of uninformed conditional probabilities associated with them, viz. Nutrient Availability and Algal Growth Rate.

The negative relative changes of the input nodes Parrotfish, Surgeonfish and Diadema to changes in the intermediate nodes Nutrient Availability and Algal Growth Rate would be expected because of the positive relative changes of the input nodes Nitrate, Water flow and Light. The negative relative changes of Parrotfish and Surgeon fish to changes in the intermediate node Fish Grazing may seem surprising but this effect can be explained by the fact that Fish biomass was very high on Glovers atoll and any effects of changes to the intermediate Fish grazing will reduce the sensitivity of these input nodes. The positive relative change of the input node *Diadema* to changes in the node fish grazing is expected as the relative grazing capacity of *Diadema* compared with fish grazing would have increased with a reduction in fish grazing.

Overall the sensitivity analysis highlights the importance of being able to quantify correctly the relationships of nodes and its effects on algal cover. The analysis showed that changes in intermediate nodes with a high proportion of uninformed probabilities will have the greatest effect and hence it is important that these relationships are quantified as accurately as possible.

Table 3.5. Sensitivity analysis of the effects of change (±10%) in the conditional probabilities of the intermediate nodes; nutrient availability, algal growth rate, fish grazing and grazing pressure, shown for the algal cover category 0 – 5%. Values are relative change compared with the base line scenario as shown in Fig 3.5.

	Intermediate Nodes			
Input nodes	**Nutrient Availability**	**Algal Growth Rate**	**Fish Grazing**	**Grazing Pressure**
Water flow	100.0	150.0	0.0	0.0
Surgeonfish	-8.3	11.1	-2.8	-16.7
Light	22.9	20.0	0.0	-2.9
Nitrate	17.9	33.3	-2.6	-10.3
Parrotfish	-10.1	7.6	-13.9	-17.7
Diadema	-7.3	8.9	2.4	-1.6

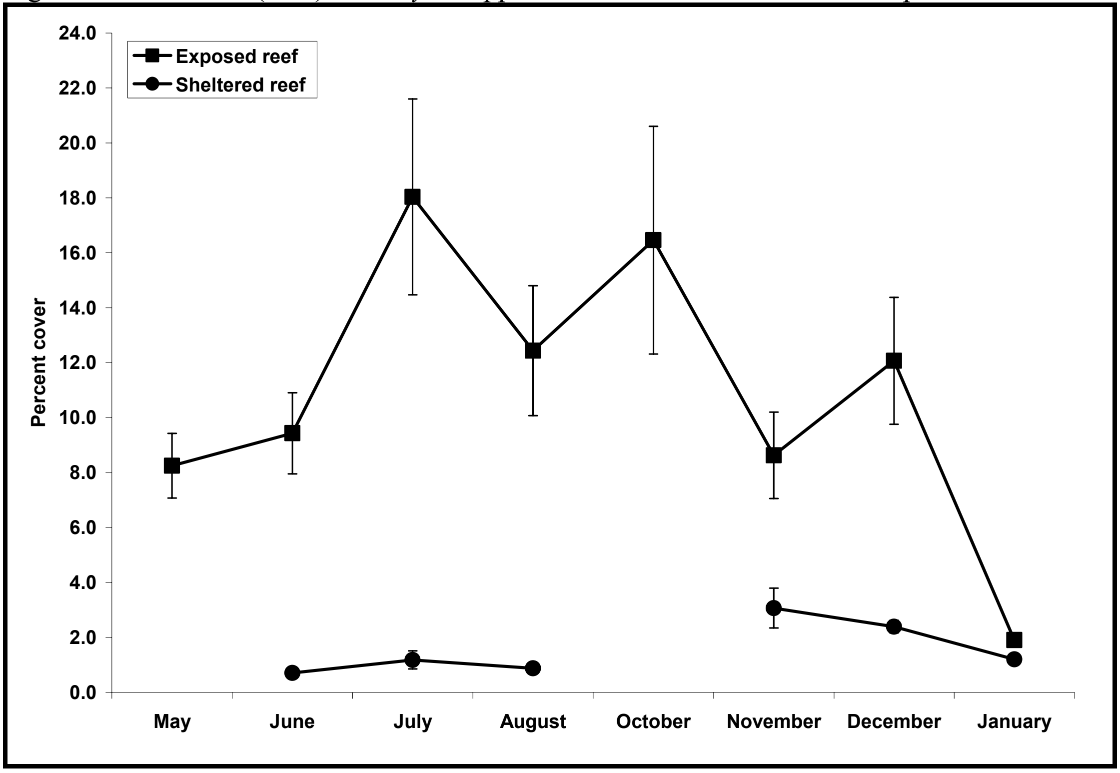
4.4 Model Limitations

The creation of the BBN was constrained by the availability of data from the literature and range of biophysical conditions around Glovers Atoll. The low sensitivity of the model to a given node or subset partly reflects the limited state of knowledge of the dynamics of coral reef macroalgae. Quantifying the relationships in the model objectively identified knowledge gaps, indicated by the relatively large number of uninformed probabilities assigned to intermediate nodes. The modelling approach therefore is very suitable in identifying key nodes in the model and helps to clearly specify our understanding of the dynamics of macroalgae on coral reefs.

The accuracy of predictions for each algal cover category was variable ranging from 0 – 78% (Table 3.3). Part of this variability can be explained in the discretization of the categories which can accentuate errors. Whilst using narrower discrete categories (e.g. 10% intervals as opposed to the current variable category width used) would reduce this problem, there is a necessary trade off between uncertainty and accuracy. Too large categories may not be able to capture subtle dynamics within a system whereas too small categories might be infeasible given the uncertainty and lack of data to define accurately the conditional probabilities for each possible combination of levels.

A recent study of the dynamics of *Dictyota pulchella* (Mumby et al. 2005) found that populations were highly variable both in space and time. Indeed, the cover of *Dictyota* spp. fluctuated greatly on a monthly basis (Fig. 3.6). Therefore, the relatively modest accuracy of the model may be partly explained by the choice of alga: *Dictyota* dynamics appear to be more complex than those of some other phaeophytes such as *Lobophora variegata* (Mumby et al. 2005) and the modelling approach may perform better for such species.

Fig. 3.6. Mean cover (±SE) of *Dictyota* spp. at Glovers Reef over a 9 month period.



Once the model is fully parameterized, i.e. the number of uninformed probabilities are reduced, it can be a useful management tool. The ability of the model to perform diagnostic analysis of reef scenario's can aid the reef manager by informing what management strategies are most likely to have the best outcome for reef health. Here the model can perform top-down and bottom-up reasoning, i.e. given a certain algal cover, what is the most likely source causing the high cover of algae or vice versa, given my monitoring data on nutrients, herbivory, light, etc, what is the likely algal cover category? Because the model has a graphical interface it aids in visualizing the complexities and uncertainties associated with algal dynamics and hence can communicate these to managers and decision makers.

5 CONCLUSIONS

The Bayesian Belief Network helped to structure our understanding of macroalgal dynamics. Building the model from empirical data and relationships identified in the literature allowed for an unbiased approach without letting untested hypotheses influence the outcomes. The model appeared to support the notion that grazing exerts a stronger influence on the dynamics of *Dictyota* spp. than nutrient input per se (Burkepile and Hay 2006) at least for Glovers Reef. However, the model also identified gaps in our understanding of mechanisms influencing algal dynamics. For example more quantitative studies are needed on the interactive effects of water flow, nutrients and light on growth rates over a range of ecological relevant values.

Our intention was to generate a first BBN for this dominant alga on coral reefs. The great flexibility of the BBN approach, however, is that the model can be continually improved as new data become available. Importantly, the acquisition of new data is not confined to experimental results. Routine monitoring programmes, often carried out by government departments, generate vast datasets that are often analysed periodically and rarely disseminated. The BBN model provides a vehicle to integrate these diverse monitoring sets and extend their use. Incorporating new data, from a more diverse set of biophysical environments will lead to quantifiable improvement in our understanding of the processes governing algal blooms. Such improvements will be manifest as a gradual reduction in the uncertainty of the model predictions. To that end, the BBN model is freely available from the authors. We anticipate that the accuracy of model predictions will improve as new data are added.

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6 REFERENCES

Andrews JC, Muller HR. 1983. Space-time variability of nutrients in a lagoon patch reef. Limnology and Oceanography 28:215-227.

Aronson RB, Precht WF. 2000. Herbivory and algal dynamics on the coral reef at discovery bay, Jamaica. Limnology and Oceanography 45:251-255.

Beach KS, Walters LJ, Borgeas HB. 2006. Irradiance and nutrient limitation of Dictyota spp. populations on Conch Reef, Florida Keys, USA. Journal of Experimental Marine Biology and Ecology 329:101-112.

Belliveau SA, Paul VJ. 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. Marine Ecology Progress Series 232:105-114.

Bilger RW, Atkinson MJ. 1995. Effects of nutrient loading on mass transfer rates to a coral reef community. Limnology and Oceanography 40:279-289.

Borsuk ME, Stow CA, Reckhow KH. 2004. A bayesian network of eutrophication models for synthesis, prediction and uncertainty analysis. Ecological Modelling 173:219-239.

Boyer KE, Fong P, Armitage AR, Cohen RA. 2004. Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass, and mangrove habitats. Coral Reefs 23:530-538.

Burkepile DE, Hay ME. 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128-3139.

Carpenter RC. 1984. Predator and population density control of homing behavior in the Caribbean echinoid Diadema antillarum. Marine Biology 82:101-108.

Carpenter RC. 1985. Relationships between primary production and irradiance in coral reef algal communities. Limnology and Oceanography 30:784-793.

Carpenter RC. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs 56:345-363.

Carpenter RC. 1988. Mass mortality of a Caribbean sea urchin: Immediate effects on community metabolism and other herbivores. Proceedings of the National Academy of Sciences of the United States of America 85:511-514.

Carpenter RC. 1990. Mass mortality of Diadema antillarum. II. Effects on population densities and grazing intensity of parrot fishes and surgeonfishes. Marine Biology 104:79-86.

Carpenter RC, Edmunds PJ. 2006. Local and regional scale recovery of Diadema promotes recruitment of scleractinian corals. Ecology Letters 9:271-280.

Carr GM, Duthie HC, Taylor WD. 1997. Models of aquatic plant productivity: a review of the factors that influence growth. Aquatic Botany 59:195-215.

Coen LD, Tanner CE. 1989. Morphological variation and differential susceptibility to herbivory in the tropical brown alga Lobophora variegata. Marine Ecology Progress Series 54:287-298.

Congalton RG. 1991. A review of assessing the accuracy of classifications of remotely sensed data. Remote Sensing of Environment 37:35-46.

Creed JC, Norton TA, Kain JM. 1997. Intraspecific competition in Fucus serratus germlings: The interaction of light, nutrients and density. Journal of Experimental Marine Biology and Ecology 212:211-223.

Cronin G, Hay ME. 1996. Chemical defenses, protein content, and susceptibility to herbivory of diploid vs haploid stages of the isomorphic brown alga Dictyota ciliolata (Phaeophyta). Botanica Marina 39:395-399.

Dawes CJ, Kovach CW. 1992. Ecology of the algae of a Florida key II. Effects of irradiance, salinity and desiccation on intertidal and subtidal populations of seven macroalgae. Bulletin of Marine Science 50:165-170.

Delgado O, Lapointe BE. 1994. Nutrient-limited productivity of calcareous versus fleshy macroalgae in a eutrophic, carbonate-rich tropical marine environment. Coral Reefs 13:151-159.

Diaz-Pulido G, McCook LJ. 2003. Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology 84:2026-2033.

Done TJ. 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121-132.

Done TJ. 1999. Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. American Zoologist 39:66-79.

Done TJ, Ogden JC, Wiebe WJ, Rosen B. 1996. Biodiversity and ecosystem function of coral reefs. *in* Mooney H, Cushman JH, Medina E, Sala E, Schulze E-D, editor. Functional roles of biodiversity: A global perspective. John Wiley & Sons.

Done TJ, Whetton P, Jones R, Berkelmans R, Lough J, Skirving W, Wooldridge S. 2003. Global climate change and coral bleaching on the Great Barrier Reef.

Edmunds PJ, Carpenter RC. 2001. Recovery of Diadema antillarum reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proceedings of the National Academy of Sciences of the United States of America 98:5067-5071.

Enriquez S, Agusti S, Duarte CM. 1994. Light absorption by marine macrophytes. Oecologia 98:121-129.

Fong P, FOin TC, Zedler JB. 1994. A simulation model of lagoon algae based on nitrogen competition and internal storage. Ecological Modelling 64:225-237.

Fong P, Kramer K, Boyer KE, Boyle KA. 2001. Nutrient content of macroalgae with differing morphologies may indicate sources of nutrients for tropical marine systems. Marine Ecology Progress Series 220:137-152.

Gaines SD, Lubchenco J. 1982. A unified approach to marine plant-herbivore interactions. II. Biogeography. Annual review of ecology and systematics 13:111-138.

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR. 2005. Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. Ecology 86:174-184.

Hatcher BG, Larkum AWD. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. Journal of Experimental Marine Biology and Ecology 69:61-84.

Hay ME. 1981. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. American Naturalist 118:520-540.

Hearn CJ, Atkinson MJ, Falter JL. 2001. A physical derivation of nutrient uptake in coral reefs: effects of roughness and waves. Coral Reefs 20:347-356.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318:1737-1742.

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 RM, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas JA, Lough J, Marshall PA, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Rougharden J. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929-933.

Hughes TP, Connell JH. 1999. Multiple stressors on coral reefs: A long-term perspective. Limnology and Oceanography 44:932-940.

Hughes TP, Szmant AM, Steneck RS, Carpenter RC, Miller S. 1999. Algal blooms on coral reefs: what are the causes? Limnology and Oceanography 44:1583-1586.

Hurd CL. 2000. Water motion, marine macroalgal physiology, and production. Journal of Phycology 36:453-472.

Jensen FV. 2001. Bayesian Networks and Decision Graphs, 1st edition. Springer, New York.

Kramer PA. 2003. Synthesis of coral reef health indicators for the Western Atlantic: results of the AGGRA program (1997-2000). Atoll Research Bulletin 496:1-58.

Lapointe BE. 1987. Phosphorus- and nitrogen-limited photosynthesis and growth of Gracilaria tikvahiae (Rhodophyceae) in the Florida Keys: an experimental field study. Marine Biology 93:561-568.

Lapointe BE. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography 42:1119-1131.

Lapointe BE. 1999. Simultaneous top-down and bottom up forces control macroalgal blooms on coral reefs (reply to the comment by Hughes et al.). Limnology and Oceanography 44:1568-1592.

Lapointe BE, Barile PJ, Yentsch CS, Littler MM, Littler DS, Kakuk B. 2004. The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman's Pond Cay, Exumas Cays, Bahamas: a "natural" enrichment experiment. Journal of Experimental Marine Biology and Ecology 298:275-301.

Lapointe BE, Littler MM, Littler DS. 1987. A comparison of nutrient-limited productivity in macroalgae from a Caribbean barrier reef and from a mangrove ecosystem. Aquatic Botany 28:243-255.

Lapointe BE, Littler MM, Littler DS. 1992. Modification of benthic community structure by natural eutrophication: the Belize Barrier Reef. Proceedings of the 7th International Coral Reef Symposium 1:323-334.

Lapointe BE, O'Connell J. 1989. Nutrient-enhanced growth of Cladophora prolifera in Harrington Sound, Bermuda: Eutrophication of a confined, phosphorus limited marine system. Estuarine, Coastal and Shelf Science.

Lapointe BE, Tenore KR. 1981. Experimental outdoor studies with ulva fasciata Delile. I. Interaction of light and nitrogen on nutrient uptake, growth, and biochemical composition. Journal of Experimental Marine Biology and Ecology 53:135-152.

Larned ST. 1998. Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. Marine Biology 132:409-421.

Leichter JJ, Stewart HL, Miller SL. 2003. Episodic nutrient transport to Florida coral reefs. Limnology and Oceanography 48:1394-1407.

Leichter JJ, Wing SR, Miller SL, Denny MW. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. Limnology and Oceanography 41:1490-1501.

Lessios HA. 1988. Mass mortality of Diadema Antillarum in the Caribbean: What have we learned? Annual review of ecology and systematics 19:371-393.

Lessios HA, Garrido MJ, Kessing BD. 2001. Demographic history of Diadema antillarum, a keystone herbivore on Caribbean reefs. Proceedings of the Royal Society of London Series B Biological Sciences 268:2347-2353.

Lewis SM. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecology Monographs 56:183-200.

Littler MM, Littler DS. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. American Naturalist 116:25-44.

Littler MM, Littler DS, Titlyanov EA. 1991. Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: a test of the relative-dominance paradigm. Coral Reefs 10:199-209.

Marcot BG, Holthausen RS, Raphael MG, Rowland MM, Wisdom MJ. 2001. Using Bayesian belief networks to evaluate fish and wildlife population viability under land management alternatives from an environmental impact statement. Forest Ecology and Management 153:29-42.

McClanahan TR, Cokos BA, Sala E. 2002. Algal growth and species composition under experimental control of herbivory, phosphorous and coral abundance in Glovers reef, Belize. Marine Pollution Bulletin 44:441-451.

McClanahan TR, Sala E, Mumby PJ, Jones S. 2004. Phosphorus and nitrogen enrichment do not enhance brown frondose "macroalgae". Marine Pollution Bulletin 48:196-199.

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Jones S. 2003. Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Marine Ecology Progress Series 261:135-147.

McCook LJ. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the great barrier reef. Coral Reefs 18:357-367.

Moberg F, Folke C. 1999. Ecological goods and services of coral reef ecosystems. Ecological economics 29:215-233.

Morgan MG, Henrion M. 1990. Uncertainty: A Guide to dealing with uncertainty in quantitative risk and policy analysis. Pages 112-116 *in* A Guide to dealing with uncertainty in quantitative risk and policy analysis. Cambridge University Press, Cambridge.

Morrison D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology 69:1367-1382.

Mumby PJ. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecological Applications 16:747-769.

Mumby PJ, Dahlgren CP, Harborne AR, Kappel, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB. 2006a. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98-101.

Mumby PJ, Foster NL, Glynn Fahy EA. 2005. Patch dynamics of coral reef macroalgae under chronic and acute disturbance. Coral Reefs 24:681-692.

Mumby PJ, Hastings A, Edwards HJ. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98-101.

Mumby PJ, Hedley JD, Zychaluk K, Harborne AR, Blackwell PG. 2006b. Revisiting the catastrophic die-off of the urchin Diadema antillarum on Caribbean coral reefs: Fresh insights on resilience from a simulation model. Ecological Modelling.

Pearl J. 1988. Probabilistic reasoning in intelligent systems: Networks of Plausible Inference, 2nd edition. Morgan Kaufmann Publishers, Inc, San Fransisco.

Pedersen MF, Borum J. 1997. Nutrient control of estuarine macroalgae: growth strategy and the balance between nitrogen requirements and uptake. Marine Ecology Progress Series 161:155-163.

Pillans RD, Franklin CE, Tibbetts IR. Food choice in Siganus fuscescens: influence of macrophyte nutrient content and availability. Journal of Fish Biology 64:297-309.

Robertson DR, Ackerman JL, Choat JH, Posada JM, Pitt J. 2005. Ocean surgeonfish Acanthurus bahianus I. The geography of demography. Marine Ecology Progress Series 295:229-224.

Sammarco PW. 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. Journal of Experimental Marine Biology and Ecology 61:31-55.

Schaffelke B, Klumpp DW. 1997. Growth of germlings of the macroalga Sargassum baccularia (Phaeophyta) is stimulated by enhanced nutrients. Proceedings of the 8th International Coral Reef Symposium 2:1839-1842.

Schaffelke B, Klumpp DW. 1998. Short-term nutrient pulses enhance growth and photosynthesis of the coral reef macroalga Sargassum baccularia. Marine Ecology Progress Series 170:95-105.

Schutten J, Davy AJ. 2000. Predicting the hydraulic forces on submerged macrophytes from current velocity, biomass and morphology. Oecologia 123:445-452.

Spiegelhalter DJ, Dawid AP, Lauritzen SL, Cowell RG. 1993. Bayesian analysis in expert systems. Statistical Science 8:219-247.

Steneck RS, Dethier MN. 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69:476-498.

Steneck RS, Watling L. 1982. Feeding capabilities and limitation of herbivorous molluscs: A functional group approach. Marine Biology 68:299-319.

Tanner JE. 1995. Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. Journal of Experimental Marine Biology and Ecology 190:151-168.

Uusitalo L. 2007. Advantages and challenges of Bayesian networks in environmental modelling. Ecological Modelling:In Press.

Williams SL, Carpenter RC. 1998. Effects of unidirectional and oscillatory water flow on nitrogen fixation (acetylene reduction) in coral reef algal turfs, Kaneohe Bay, Hawaii. Journal of Experimental Marine Biology and Ecology 226:293-316.

Wooldridge S, Done T. 2004. Learning to predict large-scale coral bleaching from past events: A bayesian approach using remotely sensed data, in-situ data, and environmental proxies. Coral Reefs 23:96-108.

Wooldridge S, Done T, Berkelmans R, Jones R, Marshall P. 2005. Precursors for resilience in coral communities in a warming climate: a belief network approach. Marine Ecology Progress Series 295:157-169.

Chapter 4 Effects of Physical Environmental Conditions on the Patch Dynamics of *Dictyota* spp. and *Lobophora variegata* on Caribbean Coral Reefs

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EFFECTS OF PHYSICAL ENVIRONMENTAL CONDITIONS ON THE PATCH DYNAMICS OF *DICTYOTA* SPP. AND *LOBOPHORA VARIEGATA* ON CARIBBEAN CORAL REEFS

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1 ABSTRACT

The patch dynamics of two common macroalgae in the Caribbean, *Dictyota* spp. and *Lobophora variegata* were quantified over a 9 month period and described using transition matrices. Size-based matrices were constructed for both species from forereef habitats subjected to contrasting levels of wave exposure. The matrices reveal that standard measures of algal percent cover might provide a misleading insight into the underlying dynamics of the species. The dynamics of *Dictyota* spp. are highly sensitive to the physical environment whilst *Lobophora variegata* is far less sensitive. The patch dynamics of *Dictyota* spp. showed a higher temporal variation than *Lobophora variegata*, but only on the exposed forereef. *Dictyota* spp. virtually disappeared in January at both the exposed and sheltered sites whereas *Lobophora variegata* exhibited a continuing increase in patch size irrespective of exposure. Our results demonstrate the need to investigate patch dynamics of macroalgae at the individual species level, whilst taking into account environmental conditions.

Keywords

Dictyota spp., *Lobophora variegata*, patch dynamics, transition matrices

2 INTRODUCTION

Macroalgae are major components of the benthic community of coral reefs and dominate many reefs in the Caribbean (McClanahan and Muthiga 1998, Lirman and Biber 2000, Beach et al. 2003). Indeed, macroalgae have bloomed on many Caribbean reefs during the past 30 years (Gardner et al. 2003) and many processes may have contributed to such shifts. These include mass mortalities of the urchin *Diadema antillarum* (Carpenter 1990, Hughes 1994, McClanahan et al. 1996, Lessios et al. 2001), overfishing of herbivorous fish (Hughes 1994, McClanahan 1997, Hughes et al. 2006), coral mortality from mass bleaching (Diaz-Pulido and McCook 2002, Bellwood et al. 2006) and diseases (Garzon-Ferreira et al 2001) and increasing nutrients from land-based sources (Littler et al. 1992, Lapointe et al. 1997, Lapointe et al. 2004). Although the processes driving algal dynamics have intrinsic importance, they have received renewed interest because of the deleterious consequences of algal blooms to corals (Nugues and Bak 2006). Macroalgae inhibit coral recruitment through pre-emption of space (Miller and Hay 1996) and undertake direct competitive interactions with corals (De Ruyter van Steveninck et al. 1988b, Tanner 1995, Jompa and McCook 2002a, 2003). The outcomes of such competition include a decline in coral recruitment (Carpenter and Edmunds 2006, Mumby et al. 2007), a decline in growth rates of both competitors (De Ruyter van Steveninck et al. 1988b, Jompa and McCook 2002a, Nugues and Bak 2006, Box and Mumby 2007), a reduction in the fecundity of corals (Tanner 1995) and even coral mortality (Lewis 1986, Hughes and Tanner 2000, Lirman 2001, Hughes et al. 2007).

Most studies investigating the dynamics of macroalgae have used static measures such as average percent cover (Lirman and Biber 2000, Diaz-Pulido and Garzon-Ferreira 2002). However, while measures of average percent cover undoubtedly have great utility, they reveal little of the underlying patch dynamics of macroalgae at scales smaller than individual sampling units (Mumby et al. 2005). Given that many competitive interactions occur at fine, individual-patch scales, a failure to appreciate the dynamic nature of the substratum could result in misleading conclusions being reached. For example, while overall cover in a quadrat may be stable over time, individual patches of substrate within the quadrat could undergo rapid algal colonization and extinction, which may have profound consequences for algal competitors.

We define patch dynamics as changes over time in the size and number of individual patches at a given locality. To investigate patch dynamics we focused on the two dominant macroalgae on Caribbean forereefs: *Lobophora variegata* (Lamouroux) and the genus

Dictyota (hereafter referred to as *Lobophora* and *Dictyota* respectively). In practice it was difficult to distinguish patches of the different species of *Dictyota* as they often overlap. The patches we observed were dominated by the species *Dictyota pulchella* (Hörnig and Schnetter), with *Dictyota humifusa* (Hörnig) and *Dictyota pfaffii* (Schnetter) found interwoven or under their canopy. Both *Dictyota* and *Lobophora* are from the same family, Dictyotaceae, but exhibit different growth forms. *Dictyota* displays a creeping interwoven to bushy growth form with dichotomous branching up to 10 cm in height (Littler and Littler 2000) and was the most common brown macroalga on the reef with an average overall cover of 11%. *Lobophora* has three life forms; decumbent, crust, and ruffled, whose distribution depends on depth, the level of grazing and upon the habitat (Lewis et al. 1987). This study focused on the decumbent form, which has flat blades up to 15 cm in diameter (Littler and Littler 2000) and was the second most common brown macroalga on the reef with an average cover of 2.2%. In total both species make up on average 13% of the benthic reef community.

Previous studies have indicated that the dynamics of *Dictyota* show seasonality (Neto 2000, Diaz-Pulido and Garzon-Ferreira 2002, Ateweberhan et al. 2005, Mumby et al. 2005), which in general is thought to be attributed to seasonal changes in major environmental factors such as nutrients, temperature, light intensity, and water movement (Chapman 1974, Ateweberhan et al. 2005). The seasonal patterns for *Lobophora* seem to be less clearly defined (Peckol and Searles 1984, De Ruyter van Steveninck and Breeman 1987a, Mumby et al. 2005). The temporal dynamics of these macroalgal species are very complex for three reasons: (1) patches of macroalgae fragment frequently due to the activities of herbivores, and physical stress, (2) rapid lateral growth causes patches to fuse together and (3) the environment in which they grow can influence their abundance and productivity (De Ruyter van Steveninck et al. 1988a, Costa et al. 2001, Aguilar-Rosas et al. 2002, Quan-Young et al. 2004).

Patch dynamics of coral reef macroalgae have rarely been investigated on the scale of individual patches though exceptions include, De Ruyter van Steveninck and Breeman (1987a, 1987b), De Ruyter van Steveninck et al (1988a), Stiger and Payri (1999) and Mumby et al (2005). Here we apply transition matrices (Caswell 2001) to investigate the patch dynamics of *Dictyota* and *Lobophora.* Transition matrices divide populations into categories, usually either by age (Leslie 1945) or by life-stage (Vandermeer 1978). Entries of the matrix describe probabilities of transitions between categories in a fixed time interval. The matrix itself can be thought of as a method of describing the changes that occur in the population's structure during this time interval. Transition matrices have been applied to many organisms, such as, corals (Hughes 1984, Hughes and Tanner 2000), killer whales (Brault and Caswell 1993), terrestrial plants (Caswell and Werner 1978, Hoffmann 1999, Brys et al. 2004, Nordbakken et al. 2004), tortoises (Doak et al. 1994), sea turtles (Crouse et al. 1987) and macroalgae (Ang and De Wreede 1990, Aberg 1992).

For many marine algae age is not a practical categorical variable since it is impossible to reliably age macroalgae, with the exception of large kelps (Ang and De Wreede 1990). Further, for many organisms individual age is not correlated with demographic parameters and therefore size or life stage is a better categorical variable (Sauer and Slade 1987). Here we develop matrices describing transitions between different sized patches of algae. Using these matrices we describe the temporal behaviour of *Dictyota* and *Lobophora* populations under varying environmental conditions on a forereef and test the following hypotheses:

H_1: Macroalgae dynamics differ between contrasting physical environments with greater variability on more exposed (disturbed) seaward systems.
H_2: Based on its branching morphology and high susceptibility to fragmentation, *Dictyota* exhibits greater temporal variation in patch dynamics than *Lobophora*.

3 METHODS

3.1 Study site

The study was undertaken on Glovers Reef (87^0 48'W, 16^0 50'N), an atoll approximately 45 km from the mainland of Belize. Glovers reef presents an ideal study site as both the East and West side of the atoll (hereafter referred to as the exposed and sheltered side respectively) have varying environmental conditions. The east side is exposed to prevailing north-easterly winds (Koltes et al. 1998) and therefore has higher wave energy and water flow (see also clod card data below). The horizontal visibility for the exposed side is approximately 25 m looking along a transect line at approximately 8 meters depth, whereas on the sheltered side it rarely exceeds 10 m (Renken, personal observation).

3.2 Data collection

Data were collected from May 2005 to January 2006. Patch sizes were measured at three sites, each at least 500 meters apart, on the exposed side and a further three sites on the sheltered side. At each site ten permanent 0.5 m x 0.5 m quadrats were randomly placed at a depth of around 8 m. Each site was visited on a monthly basis (excluding September) and video surveys of the quadrats, divided into four 25 x 25 cm squares were conducted. The video camera was held perpendicular to the reef substratum at a height of 50 cm to avoid parallax error. The videos were analyzed using the software VidAna[1] which allows the size of individual patches to be measured. The accuracy of the method has been found to be high (Mumby et al. 2005). The percent cover for each species was also determined to obtain the monthly average percent cover for each species.

The biomass and density of herbivores were sampled at each site over the study duration using visual census. The density of Scarids was sampled at each site using at least 4 replicate 30x4 m transects, whilst *Diadema antillarum* densities were assessed on at least 4 replicate 50 x 2 m transects. The lengths of fishes were converted to biomasses using allometric relationships from Fishbase (Froese and Pauly 2007). The differences in biomass and density were analysed using a repeated measures ANOVA with exposure and time. All data for *Diadema* density and scarid biomass was square root transformed to meet the assumptions of normality (Ryan-Joiner test).

Water flow was measured using clod cards (Doty 1971). The clods were made from plaster of paris, sun dried and glued with epoxy to plastic cards. Clods were weighed before submersion and after 48hrs collected, air-dried and re-weighed. Six clod cards were randomly placed at each site at each time interval. Water flow was greatest on the exposed side as denoted by an average weight loss over 48 hrs of 27.2 ± 6.03 g (from an initial weight of 61.2 g, i.e. a 44.4% decline) which exceeds the dissolution of plaster on the sheltered side by an average of 21.4 ± 5.76 g (*t*-test $P < 0.01$, n = 65) which was from an initial weight of 60.5 g to 39.1 g (i.e. a 35.4 % decline).

3.3 Transition matrices

We constructed size-based transition matrices (Caswell 2001) for each species (Appendix 1). To determine appropriate size classes we considered the frequency distribution of all patch sizes recorded during the sampling period. We applied the same method as Hughes (1984) to determine the patch size categories. Patch sizes were discretized so that each size class is represented by at least 50 patches. This resulted in seven size classes (denoted with roman numbers I….VII): 0.1-0.9, 1-1.9, 2-3.9, 4-9.9, 10-24.9, 25-49.9 and ≥ 50 cm^2.

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[1] This software is available free of charge from http://www.ex.ac.uk/msel

The transition matrix describes the contribution of each size class to every other class during a time interval (t, t+1) (Table 4.1). The time interval used was 30 ± 2 days, which is a small enough time period to capture the fluctuations in the cover of *Dictyota* and *Lobophora* (Mumby et al. 2005). Each element in the matrix represents the probability that a patch in a size class will undergo a transition to another size class at time t+1. Elements on the diagonal of the matrix represent probabilities of remaining in the same size class during a given time interval; elements above the diagonal correspond to a reduction to smaller size classes, whereas elements below the diagonal correspond to increases to larger size classes. Where there was not enough information for a given month, no matrices were constructed.

Table 4.1. Generic transition matrix. $G_{j,i}$ denotes growth from size class *i* to size class *j*, F_i is the fecundity of size class *i*, $L_{j,i}$ is survival from size class *i* to size class *j*, $C_{j,i}$ is fusion and $S_{j,i}$ is fragmentation.

		t						
		I	**II**	**III**	**IV**	**V**	**VI**	**VII**
t+1	**I**	$F_1+L_{1,1}+S_{1,1}$	$F_2+S_{1,2}$	$F_3+S_{1,3}$	$F_4+S_{1,4}$	$F_5+S_{1,5}$	$F_6+S_{1,6}$	$F_7+S_{1,7}$
	II	$G_{2,1}+C_{2,1}$	$L_{2,2}$	$S_{2,3}$	$S_{2,4}$	$S_{2,5}$	$S_{2,6}$	$S_{2,7}$
	III	$G_{3,1}+C_{3,1}$	$G_{3,2}+C_{3,2}$	$L_{3,3}$	$S_{3,4}$	$S_{3,5}$	$S_{3,6}$	$S_{3,7}$
	IV	$G_{4,1}+C_{4,1}$	$G_{4,2}+C_{4,2}$	$G_{4,3}+C_{4,3}$	$L_{4,4}$	$S_{4,5}$	$S_{4,6}$	$S_{4,7}$
	V	$G_{5,1}+C_{5,1}$	$G_{5,2}+C_{5,2}$	$G_{5,3}+C_{5,3}$	$G_{5,4}+C_{5,4}$	$L_{5,5}$	$S_{5,6}$	$S_{5,7}$
	VI	$G_{6,1}+C_{6,1}$	$G_{6,2}+C_{6,2}$	$G_{6,3}+C_{6,3}$	$G_{6,4}+C_{6,4}$	$G_{6,5}+C_{6,5}$	$L_{6,6}$	$S_{6,7}$
	VII	$G_{7,1}+C_{7,1}$	$G_{7,2}+C_{7,2}$	$G_{7,3}+C_{7,3}$	$G_{7,4}+C_{7,4}$	$G_{7,5}+C_{7,5}$	$G_{6,7}+C_{6,7}$	$L_{7,7}$

The rate at which algae grow may be size-dependent (Ang 1985, Ang and De Wreede 1990). Individual patches may increase by more than one size class within a given period. Rapid growth of algal patches in close proximity may also cause them to fuse to form a larger patch. Algae may reduce their size (potentially returning to smaller size classes) as a result of dislodgement from waves, grazing activities of herbivores and die back after reproductive periods. We present selected matrices in the main paper to highlight dynamics of interest, but all other matrices can be found in Appendix B.

Since fragmentation and fusion of algal patches was observed to occur frequently we devised a novel method to incorporate these demographic events into the matrices explicitly. Fragmentation $S_{j,i}$ from size class i to size class j (Table 4.1) may occur in a number of possible ways. As a simplified example, a patch in size class IV may fragment into smaller size categories as follows: I, I, I, I with a probability of p_1; I, I, II, with probability p_2; I, III, with probability p_3; and II, II with probability p_4. The total probability with which a member of size class IV will become a member of size class I, $S_{1,4}$, is $4p_1 + 2p_2 + p_3$; size class II $S_{2,4} = p_2 + 2p_4$ and size class III $S_{3,4} = p_3$. The probabilities p_x are calculated as the number of events

occurring out of the total number of patches in the size class that is fragmenting (size class IV in the above example).
Similarly, fusion involves several potential combinations of patches in different size classes. Fusion events, however, are more difficult to incorporate, since an element of the matrix considers only the relationship between a pair of size classes, whereas the process of fusion could involve algal patches from more than two size classes. The fusion terms $C_{j,i}$ (Table 4.1) are therefore not independent and the method of incorporating fusion events differs slightly to that for fragmentation. When a fusion event occurred we made the simplifying assumption that the smaller of the two patches "died" and that the larger fused into a patch in a larger size class (similar to a growth event). For example, the fusion term denoted as $C_{4,3}$ results from patches in size class III fusing with patches in smaller size classes (I and II) to form a patch in size class IV.

Fusion differs from fragmentation in that the probability of patches fusing has a strong spatial dependency: two patches growing close together have a higher probability of fusing than two patches further apart. Whilst a fragmentation event involves a single patch fragmenting, fusion requires the simultaneous presence of more than one patch (of potentially different size class categories). The probability of occurrence of a given fusion event is therefore dependent upon the frequency of patches as well as upon their proximity. This makes determining the probability of occurrence difficult even for a single combination of patches, let alone for all combinations of 7 different size classes.

To simplify this problem we calculated the probability of a given fusion event for each side of the atoll by determining the total number of times that event occurred in all quadrats on that side of the atoll, thereby ignoring the size-distribution of patches at the time of the event. On the exposed side we collected data from a total of 25 quadrats. Thus the probability $C_{4,3}$ will be 0.04 (1/25) multiplied by the total number of times a patch of size III fused with a smaller patch to become a patch of size IV.

Three statistics were generated from the matrices to describe population behaviour over time.
1) Dominant eigenvalue, λ_1: A population of arbitrary size structure that changes according to the transition matrix will eventually reach a stable size distribution and grow with a rate given by the dominant eigenvalue (Bierzychudek 1982), provided that the environment does not change (Caswell and Trevisan 1994, Caswell 2001). λ_1 provides a single value that enables us to compare the different matrices. Dominant eigenvalues of less than 1 indicate a long term decline in the population or that patches are becoming smaller, whilst values greater than 1 indicate an increase in the size of patches.

2) Damping ratio (ρ): On reaching equilibrium, a population has a stable (equilibrial) size distribution. The speed of convergence to a stable size distribution is given by the ratio of the dominant eigenvalue to the second largest eigenvalue: $\lambda_1/|\lambda_2|$, known as the damping ratio (ρ) (Caswell 2001). Convergence will be more rapid the larger λ_1 is relative to the other eigenvalues (Caswell 2001). The rate of convergence is independent of whether the population is in decline or growth. The damping ratio may be interpreted as a measure of the variation observed within the patch dynamics because it describes the oscillations produced by the subdominant eigenvalues during convergence. A species that has a high variance in its patch dynamics due to many fusion and fragmentation events and rapid growth and shrinkage will therefore have a low damping ratio.

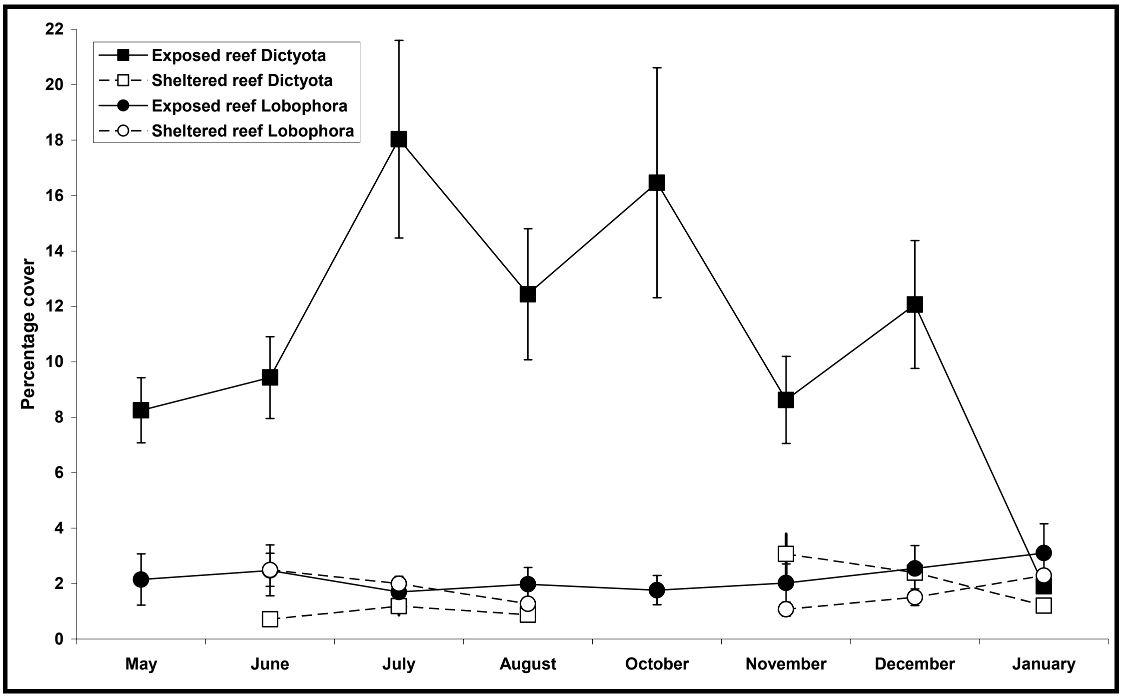
3) Matrix entry ratio: Factors influencing the damping ratio in stage or size classified models are poorly understood (Caswell 2001). To aid our interpretation of the damping ratio we used a novel measure to indicate complex patch dynamics. We define the matrix entry ratio as the number of non-zero entries in the matrix divided by the total number of entries in the matrix (in this case each 7 x 7 matrix has 49 entries, see Table 4.1). This measure follows from the fact that species exhibiting complex patch dynamics will have more non-zero entries (probabilities of transitions) in the matrix. The maximum matrix entry ratio is 1, corresponding to a matrix with no non-zero entries; The closer the matrix entry ratio is to 1 the greater the variability in patch dynamics.

4 RESULTS

4.1 Patterns of percentage cover and herbivory

At just 2.2%, the mean percentage cover of *Lobophora* was lower than that of *Dictyota* (10.8%) on the exposed reef (Fig 4.1). However the percentage covers for *Dictyota* and *Lobophora* were similar - and consistently low - on the sheltered side of the atoll with a mean of 1.6% and 1.8 % respectively (Fig 4.1). On the exposed reef, the percent cover of *Dictyota* fluctuated greatly over time from a minimum of 1.3% to a maximum of 32.3%. Peaks in cover were observed in July and October. The range of fluctuations in *Lobophora* was smaller with a minimum of 0.8%, a maximum of 5.4% and peaks in cover in June and January. Variation in cover was less dramatic on the sheltered side of the reef with a minimum of 0.2% and maximum of 5.4% for *Dictyota* that occurred in November. *Lobophora* showed a minimum of 0.7% to a maximum of 3.7% with peaks in cover in June and January.

Fig. 4.1. Percentage cover of *Dictyota* spp. and *Lobophora variegata* on the exposed and sheltered sides of Glovers Reef. Error bars denote standard error.

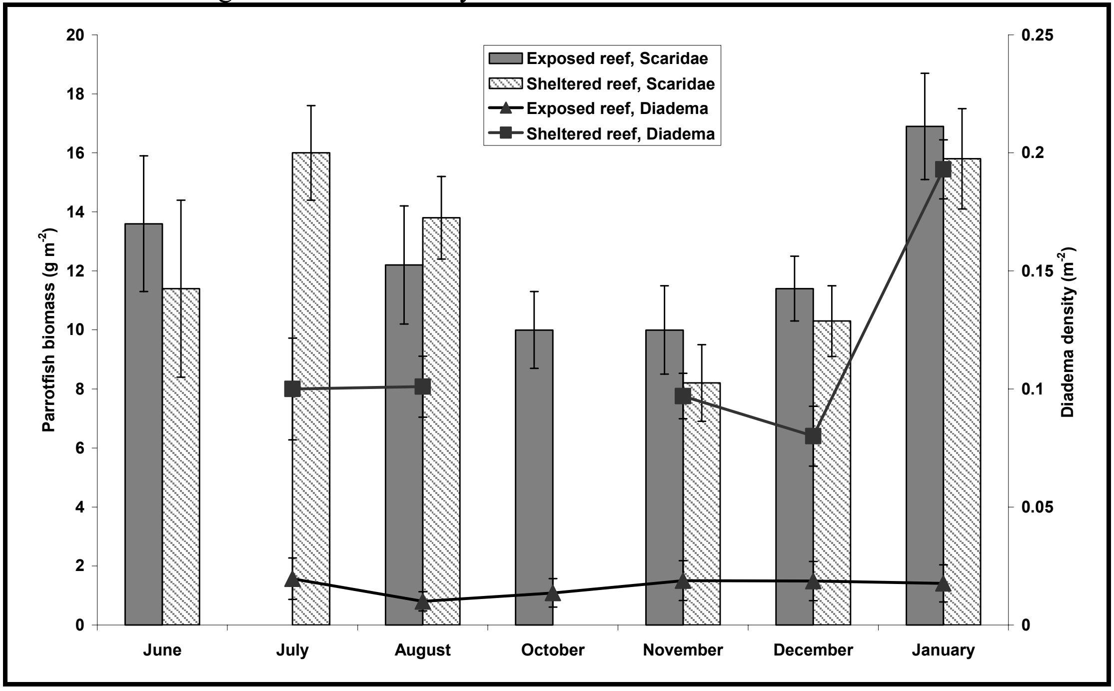


Significant differences in *Diadema antillarum* densities were observed, being on average 0.02 ± 0.01 m^{-2} for the exposed side and 0.09 ± 0.04 m^{-2} for the sheltered side (Table 4.2, Fig. 4.2). However, no significant difference in scarid biomass was observed, but over time a significant relationship was found (Table 4.2, Fig 4.2). There was no significant relationship between parrotfish biomass and algal percent cover of *Lobophora variegata* and *Dictyota* spp. (Pearson's correlation coefficient, R = 0.57, *P* = 0.054 and R = -0.41, *P* = 0.192, respectively). The relationship between algae percent cover and *Diadema* densities was not further investigated, because the densities of *Diadema* were extremely low and it is believed that this species is functionally redundant at densities lower than 1 m^{-2} (Craig Dahlgren pers. comm.).

Table 4.2. Repeated measures ANOVA results for *Diadema antillarum* densities and scarid biomass for Glovers Reef Atoll. Significant results are in bold.

Factor	**df**	***Diadema antillarum***		**Scaridae**	
		F	***P***	**F**	***P***
Exposure	1	185.53	**<0.001**	0.13	0.72
Time	6	8.70	**<0.001**	30.59	**<0.001**
Exposure x Time	6	7.75	**<0.001**	42.89	**<0.001**

Fig 4.2. Scaridae biomass and *Diadema antillarum* densities from June 2005 to January 2006. Left axis: Bars. Right axis: Lines and symbols. Error bars denote standard errors.



4.2 Growth rates of patch populations (λ_1)

The growth rates λ_1 calculated from matrices on the exposed reef ranged from 0.67 to 1.19 for *Dictyota* and from 0.89 to 1.17 for *Lobophora* (appendix 1 and Table 4.3). Corresponding values from the sheltered side were 0.83 to 1.74 for *Dictyota* which is higher than on the exposed reef and 0.81 to 1.18 for *Lobophora* respectively, showing no obvious difference in growth rates. The highest growth rate for *Dictyota* on the exposed side occurred during the period November-December with a λ_1 of 1.19, whilst on the sheltered side the highest growth rate occurred in June-July with a λ_1 of 1.74. For *Lobophora* the highest growth rates were observed in the period July-August for both sides of the atoll (1.14 and 1.18 respectively).

Table 4.3. Growth rates (dominant eigenvalue λ_1) for *Dictyota* spp. and *Lobophora variegata*. n.d = no data

	***Dictyota* spp.**		***Lobophora variegata***	
Months	**Exposed**	**Sheltered**	**Exposed**	**Sheltered**
May-June	1.03	n.d	1.00	n.d
June-July	1.07	1.74	1.07	1.11
July-August	1.06	1.10	1.14	1.18
Oct-Nov	1.07	n.d	1.04	n.d
Nov-Dec	1.19	1.06	1.07	1.01
Dec-Jan	0.67	0.83	0.89	0.81

Patterns observed in *Dictyota* population growth rates were inconsistent with those of percentage cover. For example, *Dictyota* showed a decrease in cover from July to August and from October to November on the exposed side whilst growth rates revealed that the population was actually increasing. *Dictyota* on the sheltered reef had a lower percentage cover but maintained high growth rates. The most striking difference between percentage cover and population growth rates in *Lobophora* occurred from December to January where cover displayed an increase whilst the patch population was in decline.

4.3 Dynamics of *Dictyota* and *Lobophora* under varying environmental conditions

Comparison of the matrices for *Dictyota* on the exposed and sheltered sides of the atoll reveals marked differences (Table 4.4). On the exposed side *Dictyota* grew to the largest size class category (VII), whereas patches never grew larger than size class V on the sheltered side. The proportion of patches in each size category varied throughout the year. A significant decrease in the size of patches, for example, was observed on both sides of the atoll from December to January, when the majority of patches were restricted to size class categories I and II. For the period June-July on the sheltered reef *Dictyota* patches increased in size, changing from a maximum size category of III to category IV. Again patches were larger on the exposed reef as the maximum size class (VII) had already been reached by July on this side of the atoll.

Patch population growth rates in *Lobophora* did not vary consistently with exposure (Table 4.4). The maximum size of patches on the exposed reef declined from May-June (class VII) to August (class V) and then increased to include category VII by January. The latter increase was also observed on the sheltered reef, but to a lesser extent. The most striking difference between the algal species occurred in the period December to January; whilst *Dictyota* showed a rapid decline in patch sizes, *Lobophora* patches continued to grow into the larger size classes reaching categories VI and VII.

Table 4.4. Transition matrices for *Dictyota* spp. and *Lobophora variegata* for selected time periods. Roman numbers indicate size classes, I (0-0.9 cm^2), II (1-1.9 cm^2), III (2-3.9 cm^2), IV (4-9.9 cm^2), V (10-24.9 cm^2), VI (25-49.9 cm^2), VII (≥ 50 cm^2). ---: no entries for the particular matrix.

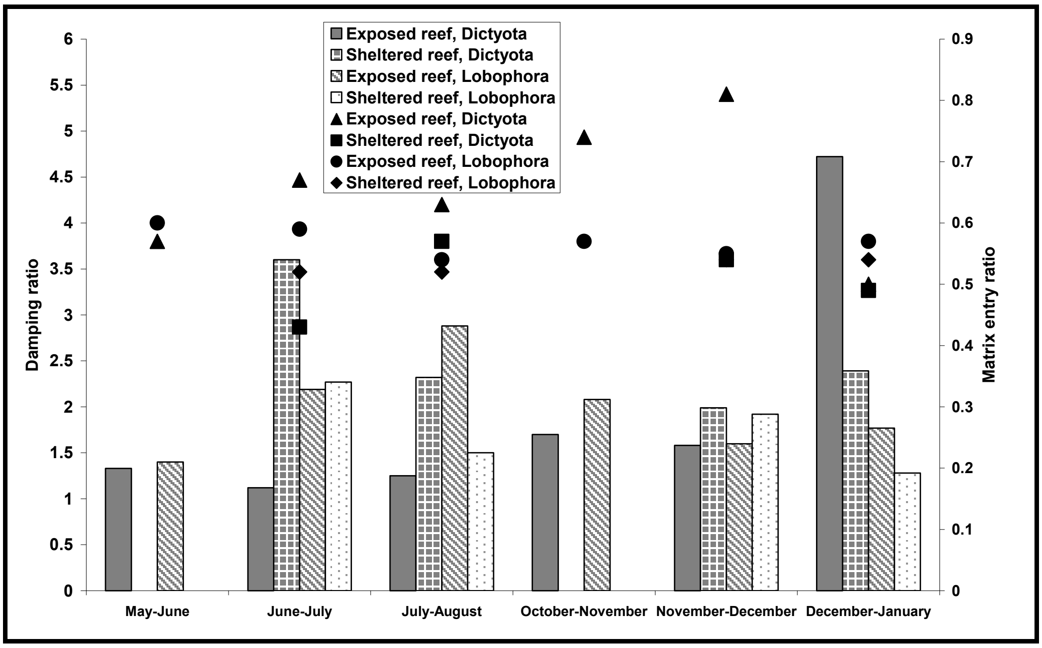
EXPOSED SIDE																
		Dictyota								***Lobophora***						
		October								**October**						
N		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
o	**I**	0.40	0.26	0.06	0.03	---	0.06	---	**I**	0.32	0.18	0.13	0.03	---	---	---
v	**II**	0.31	0.26	0.10	0.10	0.05	---	---	**II**	0.21	0.16	0.18	0.13	---	---	---
e	**III**	0.12	0.21	0.26	0.05	0.08	0.17	0.11	**III**	0.05	0.34	0.29	0.23	0.22	---	---
m	**IV**	0.02	0.11	0.48	0.48	0.39	0.17	0.52	**IV**	0.15	0.17	0.51	0.55	0.56	---	---
b	**V**	---	0.11	0.06	0.15	0.38	0.39	0.51	**V**	---	0.07	0.09	0.15	0.22	0.50	---
e	**VI**	---	---	---	0.26	0.28	0.33	0.41	**VI**	---	---	---	---	---	0.50	---
r	**VII**	---	---	---	---	0.03	---	0.23	**VII**	---	---	---	---	---	---	---
		November								**November**						
D		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
e	**I**	0.41	0.07	0.04	0.01	---	---	---	**I**	0.45	0.09	0.20	0.08	---	---	---
c	**II**	0.15	0.37	0.07	0.04	0.02	0.03	---	**II**	0.20	0.30	0.11	0.06	---	---	---
e	**III**	0.26	0.26	0.14	0.06	0.04	0.05	---	**III**	0.05	0.39	0.38	0.27	---	---	---
m	**IV**	0.15	0.19	0.18	0.29	0.23	0.08	0.11	**IV**	0.10	0.21	0.37	0.55	0.42	---	---
b	**V**	---	0.23	0.33	0.31	0.27	0.59	0.11	**V**	---	0.04	0.03	0.18	0.67	0.50	---
e	**VI**	---	---	0.04	0.27	0.31	0.32	0.11	**VI**	---	---	---	---	---	0.50	---
r	**VII**	---	---	---	0.05	0.31	0.05	0.98	**VII**	---	---	---	---	---	---	---
		December								**December**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
a	**I**	0.60	0.47	0.52	0.21	0.18	0.19	0.42	**I**	0.24	---	---	0.02	---	---	---
n	**II**	0.07	0.21	0.24	0.47	0.31	0.39	0.89	**II**	0.19	0.05	0.12	0.02	---	---	---
u	**III**	---	---	0.03	0.13	0.39	0.36	0.79	**III**	0.05	0.26	0.18	0.08	0.06	---	---
a	**IV**	---	---	---	0.06	0.11	0.12	0.32	**IV**	---	0.20	0.38	0.54	0.06	---	---
r	**V**	---	---	---	---	0.01	0.03	0.16	**V**	---	---	0.16	0.47	0.72	---	---
y	**VI**	---	---	---	---	---	---	---	**VI**	---	---	0.14	0.02	0.24	0.50	---
	VII	---	---	---	---	---	---	---	**VII**	---	---	---	---	0.10	0.54	---
SHELTERED SIDE																
		November								**November**						
D		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
e	**I**	0.60	0.13	---	---	---	---	---	**I**	0.39	0.23	0.03	---	---	---	---
c	**II**	0.10	0.63	0.53	0.36	---	---	---	**II**	0.42	0.29	0.10	0.23	0.33	---	---
e	**III**	0.20	0.25	0.18	0.36	---	---	---	**III**	0.06	0.43	0.38	0.31	0.33	---	---
m	**IV**	---	0.13	0.24	0.21	0.67	---	---	**IV**	---	0.03	0.45	0.46	0.33	---	---
b	**V**	---	---	0.06	0.07	0.33	---	---	**V**	---	---	0.07	---	0.33	---	---
e	**VI**	---	---	---	---	---	---	---	**VI**	---	---	---	---	---	---	---
r	**VII**	---	---	---	---	---	---	---	**VII**	---	---	---	---	---	---	---
		December								**December**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
a	**I**	0.79	0.40	0.24	0.23	0.17	---	---	**I**	0.47	0.12	---	---	---	---	---
n	**II**	0.07	0.17	0.35	0.41	0.17	---	---	**II**	0.41	0.21	0.07	---	---	---	---
u	**III**	---	0.05	0.22	0.27	0.33	---	---	**III**	0.17	0.24	0.54	0.03	---	---	---
a	**IV**	---	---	0.05	0.09	0.33	---	---	**IV**	0.03	0.12	0.36	0.67	0.14	---	---
r	**V**	---	---	---	---	---	---	---	**V**	---	0.09	0.02	0.39	0.14	---	---
y	**VI**	---	---	---	---	---	---	---	**VI**	---	---	---	---	0.55	---	---
	VII	---	---	---	---	---	---	---	**VII**	---	---	---	---	---	---	---

4.4 Temporal variation in patch dynamics

Damping ratios for *Dictyota* on the exposed reef ranged from 1.12 to 4.72, but exhibited a more restricted range on the sheltered site at 1.99 to 3.60 (Fig 4.3). Similarly, the matrix entry ratio (Fig. 4.3) varied from 0.50 to 0.81 on the exposed side and from 0.43 to 0.54 on the sheltered side. Thus, the patch dynamics of *Dictyota* were highly variable over time on the exposed reef.

The overall variation in damping ratio in *Lobophora* was lower than that of *Dictyota* ranging from 1.40 to 2.88 on the exposed side and 1.28 to 2.28 on the sheltered side. The matrix entry ratio was also much less variable than that in Dictyota: 0.55 to 0.60 and 0.52 to 0.54 for the exposed and sheltered sides respectively.

Fig. 4.3. Damping ratios (left axis and bars) and the matrix entry ratios (right axis and symbols) for *Dictyota* spp. and *Lobophora variegata.* No bars means no data on damping ratio.



The number of fragmentation and fusion events in *Dictyota* were much greater on the exposed side of the atoll: 68 fragmentation and 42 fusion events (exposed) versus 5 and 0 events (sheltered) respectively (Table 4.5). Exposure-based differences in fragmentation and fusion were less marked in *Lobophora* (Table 4.5): fragmentation and fusion events occurred 8 and 37 times for the exposed and 4 and 17 for the sheltered sides respectively. A striking difference between the two algal species was found in that fragmentation events outnumbered the fusion events in *Dictyota* whilst the opposite pattern occurred in *Lobophora*.

Table 4.5. Fragmentation and fusion events recorded for *Dictyota* spp. and *Lobophora variegata*. frag = fragmentation event, fus = fusion event

	Dictyota				***Lobophora***			
	Exposed reef		**Sheltered reef**		**Exposed reef**		**Sheltered reef**	
Month	**frag**	**fus**	**frag**	**fus**	**frag**	**fus**	**frag**	**fus**
June	2	0	0	0	0	2	0	0
July	3	9	0	0	3	1	2	2
August	9	0	0	0	3	4	1	1
November	39	9	0	0	4	8	0	0
December	7	24	3	0	7	5	1	3
January	18	0	2	0	1	17	0	11
Total	**68**	**42**	**5**	**0**	**18**	**37**	**4**	**17**

4.5 Influence of fusion and fragmentation events on growth rates and damping ratios

To gain insight into the importance of considering fusion and fragmentation, matrices were compared both with and without these processes (Table 4.6). For both algal species, exclusion of fragmentation and fusion resulted in both the dominant eigenvalue and damping ratio being reduced. In *Dictyota* the dominant eigenvalue was reduced from 1.07 to 0.99 and for *Lobophora* it was reduced from 1.04 to 0.98. The damping ratio in *Dictyota* was reduced from 1.70 to 1.59 and in *Lobophora* it declined from 2.08 to 1.95. Therefore, in the absence of explicit incorporation of fragmentation and fusion events, population behaviour of both species was characterized by a slight decline (rather than growth), the time taken to reach a stable size distribution having increased.

Table 4.6. Comparison of transition matrices including fragmentation and fusion events with matrices excluding both fragmentation and fusion for *Dictyota* spp. and *Lobophora variegata* on the Exposed reef. λ_1 = dominant eigenvalue, ρ = damping ratio

								DICTYOTA								
		Fragmentation and fusion								**No fragmentation and fusion**						
		October								**October**						
N		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
o	**I**	0.41	0.26	0.06	0.03	---	0.06	---	**I**	0.41	0.29	0.04	0.03	---	---	---
v	**II**	0.31	0.26	0.10	0.10	0.05	---	---	**II**	0.32	0.18	0.04	0.11	0.03	---	---
e	**III**	0.12	0.21	0.26	0.05	0.08	0.17	0.11	**III**	0.12	0.24	0.28	0.06	0.03	0.12	---
m	**IV**	0.02	0.11	0.48	0.48	0.39	0.17	0.52	**IV**	0.02	0.12	0.56	0.44	0.38	0.18	---
b	**V**	---	0.11	0.06	0.15	0.38	0.39	0.52	**V**	---	0.12	0.08	0.17	0.35	0.35	0.31
e	**VI**	---	---	---	0.26	0.28	0.33	0.41	**VI**	---	---	---	0.19	0.18	0.35	0.44
r	**VII**	---	---	---	--	0.03	---	0.23	**VII**	---	---	---	---	0.03	---	0.25
	λ_1	1.07							**λ_1**	0.99						
	ρ	1.70							**ρ**	1.59						
								LOBOPHORA								
		October								**October**						
N		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
o	**I**	0.32	0.18	0.13	0.03	---	---	---	**I**	0.38	0.21	0.10	0.03	---	---	---
v	**II**	0.21	0.16	0.18	0.13	---	---	---	**II**	0.25	0.18	0.18	0.08	---	---	---
e	**III**	0.05	0.34	0.29	0.23	0.22	---	---	**III**	0.06	0.39	0.23	0.19	0.22	---	---
m	**IV**	0.15	0.17	0.51	0.55	0.56	---	---	**IV**	0.13	0.15	0.44	0.54	0.56	---	---
b	**V**	---	0.07	0.09	0.15	0.22	0.50	---	**V**	---	0.03	0.05	0.16	0.22	0.50	---
e	**VI**	---	---	---	---	---	0.50	---	**VI**	---	---	---	---	---	0.50	---
r	**VII**	---	---	---	---	---	---	---	**VII**	---	---	---	---	---	---	---
	λ_1	1.04							**λ_1**	0.98						
	ρ	2.08							**ρ**	1.95						

5 DISCUSSION

5.1 Patterns of cover and population growth rates of *Dictyota* and *Lobophora*

Patterns of overall percentage cover in space and time mask important differences in the underlying patch-level dynamics of algal species. For example, a decline in cover of *Dictyota* was observed on the exposed side of the atoll from October to November although growth rates generated using transition matrices indicate an increase in the population. This discrepancy can be explained by the fact that a population may be increasing in size (number of patches) even though the patches themselves are becoming smaller (which would be recorded as a reduction in cover).

The most striking difference in patch dynamics between the two algal genera was found in December to January. During these months *Dictyota* patches showed a rapid decline in size, whilst *Lobophora* patches continued to grow. The decline in the size of patches of *Dictyota* was observed on both sides of the atoll which might indicate a life history-related event, such as sexual reproduction, rather than an environmental cause. Studies of *Dictyota* spp. have shown periodicity in sexual reproduction (Lewis 1910, Hoyt 1927), with gamete production related to tidal levels on fortnightly or monthly intervals, but this does not necessary correlate with changes in the season (Neto 2000). However, a study of *Dictyota dichotoma* (Hudson) suggested that individual algae may survive winter months by remaining at an early developmental stage (Richardson 1979).

As we did not survey throughout an entire year, we cannot ascertain whether *Lobophora* exhibits the dramatic die-back observed in *Dictyota*. While the transition matrices and percentage cover data do imply a reduction in the maximum sizes of patches to a minimum in August, previous studies of *Lobophora* on dead coral substrate found no evidence of seasonal die-backs in Belize (Mumby et al. 2005) and in North Carolina *Lobophora* also continued to increase in cover for almost two years before a significant reduction in cover (Peckol and Searles 1984). At Curacao, no evidence was found for seasonality in *Lobophora* (De Ruyter van Steveninck and Breeman 1987a). However, *Lobophora* did show seasonal variation in size and reproductive status in Mexico, but this was not related to cover or dynamics and was measured in a very different, shallow habitat (Quan-Young et al. 2004).

Investigating the patch dynamics will provide insight into two important processes on the coral reef, contact interactions and pre-emption of space. Contact interactions between macroalgae and corals are common along the margins of coral colonies (Lirman 2001). This high encounter rate between coral and algae will have a negative effect on both the macroalgae and coral (Tanner 1995). Although it seems that the negative effects of algae on coral outweigh the negative effects of coral on algae (Jompa and McCook 2002a,b, Nugues and Bak 2006, Box and Mumby 2007). In these interactions therefore the time particular algae are in contact with corals plays an important role, because corals may easily avert the negative effects of macroalgae in the form of abrasion, shading and overgrowth, when the duration of contact is short. The patch dynamics of algae will provide an insight in the dynamics and potential contact time of algae with corals, information which cannot be deduced from measuring overall percent cover.

Pre-emption of space is one of the key factors why algae are successful in colonizing coral reefs after a disturbance (Mumby et al 2005). Space covered by macroalgae is not available for coral recruits for settlement and hence macroalgae become the dominant organism. The patch dynamic behaviour over time of both species provided insight into the colonization capabilities each respective species, which also cannot be deduced from overall percent cover.

5.2 Size categories and growth rates

When interpreting the dominant eigenvalues for the exposed and sheltered sides of the atoll we must account for the properties of the corresponding matrices. For example, *Dictyota* on the exposed side of the atoll have a λ_1 of 1.06 for the period July-August and a λ_1 of 1.10 on the sheltered side, suggesting that *Dictyota* grows more rapidly on the sheltered side of the atoll. However, on the exposed side of the atoll, *Dictyota* reaches larger patch sizes as demonstrated by the entries in the transition matrix in size class category VII, whilst on the sheltered side *Dictyota* only reaches patches with a maximum size category of IV. Thus, comparing only the dominant eigenvalues might be misleading, as growth rates are similar for both the exposed and sheltered sides. When interpreting these values, one has to be aware that the dominant eigenvalue represents the long term growth rate of the whole population once it has converged to a stable size distribution (a vector which describes the proportion of patches in each size category), which on the exposed side incorporates seven categories in total and on the sheltered side four categories. Thus populations with similar dominant eigenvalues may have significantly different stable size distributions and thus different overall cover. Moreover, fusion and fragmentation events occur frequently in the patch dynamics of macroalgae and ignoring these events might lead to incorrect conclusions being drawn about population dynamics.

5.3 H_1: Macroalgal dynamics differ between contrasting physical environments with greater variability on more exposed (disturbed) seaward systems

We accept the hypothesis that the environment has a strong influence on the patch dynamics of *Dictyota*, but data from the transition matrices does not support this hypothesis for *Lobophora*. Previous studies have used temporal variation in some physical factors (temperature, nutrient supply, light intensity and water motion) to explain seasonal patterns of reef algal abundance (Chapman 1974, Ateweberhan et al. 2005), but their importance in driving spatial patterns has received little attention. Here we have found significant spatial variation in the dynamics of *Dictyota* which are strongly associated with exposure but we cannot yet identify specific mechanisms. Both nutrient flux and light intensity have a strong influence on algal growth rates and the combination of these factors may determine maximum coral reef algal production (Carpenter 1985, Creed et al. 1997). Although background dissolved inorganic nitrate, ammonium and phosphate concentrations are similar on both sides of the atoll (Mumby, unpublished data), higher water flow rates on the exposed side will increase nutrient flux and are likely to have fostered higher productivity. *Dictyota* may also have been light limited on the sheltered side where wind-driven sediment transport reduces light penetration throughout most of the year (Gischler 1994). A recent study found that *Dictyota menstrualis* was light limited, but only at depth of over 32 m (Beach et al. 2006). In shallower, but more turbid water this may be a possible mechanism causing a reduction in productivity.

Recent studies have shown that members of the genus *Dictyota* can successfully reproduce through vegetative fragmentation (Beach et al. 2003, Herren et al. 2006). Fragments, generated mainly by the grazing activities of fish, have the ability to re-attach within 24 h in the field (Herren et al. 2006). Higher water flow rates found on the exposed side may have facilitated the spread of these fragments and thus enabled *Dictyota* to colonise available space rapidly. In June-July a large difference in the growth rates for *Dictyota* was observed for the exposed and sheltered sides. This difference is likely to be caused by the very high transition rate in the matrix entry $F_{1}+L_{1,1}$ (describing recruits to and survivors in the smallest size class) for the sheltered side, indicating a recruitment event. Similarly, the transition rates $F_{1}+L_{1,1}$ in the other matrices for the sheltered side are higher than those on the exposed side. *Dictyota* may therefore be relying mainly on sexual reproduction on the sheltered side. The number of fragmentation events supports this, since few were recorded for *Dictyota* on the sheltered side, whereas fragmentation events regularly contributed to the smaller size classes on the exposed side. We lack data on sexual reproduction at our study site, but tentatively hypothesize from the matrices that *Dictyota* may rely more heavily on sexual reproduction under the calmer environmental conditions of the sheltered side which seem to limit production.

The observed lack of response to the environment by *Lobophora* is difficult to explain. Whilst being a relatively unpalatable alga (Paul and Hay 1986), several studies have documented growth inhibition by herbivores (De Ruyter van Steveninck et al. 1988b, Jompa and McCook 2002b). However, scarid biomass was not significantly different between the exposed and sheltered sides. Whilst *Diadema antillarum* densities were significantly different between the two sides of the atoll, they remain very low (< $1.m^{-2}$) and it is doubtful that densities are high enough to control macroalgae cover. Morphological variability in response to different environmental conditions is a common phenomenon in seaweeds (Norton et al. 1982, Fowler-Walker et al. 2006) so it is feasible that subtle morphological adaptations enable the alga to maintain growth in quite different physical environments.

5.4 H_2: Based on its branching morphology and high susceptibility to fragmentation, *Dictyota* exhibits greater temporal variation in patch dynamics than *Lobophora*

Our evidence supports the hypothesis that *Dictyota* exhibits higher temporal variation in its patch dynamics than *Lobophora*, but only on the exposed side of the atoll. Fragmentation events are a major cause of the high temporal variance in *Dictyota* dynamics and these occur more frequently on the exposed side of the atoll (68 as opposed to 5). The cause of higher fragmentation is not clear but could involve selective foraging by herbivores such that they focus on larger patches of food (Bruggemann et al. 1994) and these are more abundant on the exposed reef because of higher growth rates. Increased rates of fusion will also contribute to more variable dynamics and fusion rates are also likely to be greater on the exposed reef because of high primary production, which increases growth rate of individual patches. *Lobophora* shows an opposite trend in that fusion rates exceed fragmentation irrespective of exposure. A plausible explanation for this might be that *Lobophora* being a less palatable species (Paul and Hay 1986) is less likely to be disturbed by grazers resulting in less fragmentation. The higher number of fusion events may be partly explained by the limited dispersal range of the species (De Ruyter van Steveninck and Breeman 1987a) and thus newly formed patches will grow relatively close together, thereby increasing the chance of fusion.

In conclusion, we provide evidence that for *Dictyota* the environment in which it grows plays an important role in its patch dynamics and demography. In contrast, the environment displayed a remarkable lack of influence on the patch dynamics and demography of

Lobophora, which is observed to perform equally well under varying conditions. Unraveling these subtleties in patch dynamics of both species requires further exploration of the transition matrices and experimental studies to test specific hypothesis on sexual reproduction and morphological adaptability.

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6 REFERENCES

Aberg P. 1992. A demographic study of two populations of the seaweed Ascophyllum Nodosum. Ecology 73:1473-1487.

Aguilar-Rosas LE, Aguilar-Rosas R, Mateo-Cid LE, and Mendoza-Gonzalez AC. 2002. Marine algae from the Gulf of Santa Clara, Sonora, Mexico. Hydrobiologia 477:231-238.

Ang PO. 1985. Phenology of Sargassum siliquosum J. Ag. and S. paniculatum J. Ag. (Sargassaceae, Phaeophyta) in the reef flat of Balibago (Calatagan, Philippines). Proceedings of the 5th International Coral Reef Congress 5:51-57.

Ang PO, and De Wreede RE. 1990. Matrix models for algal life history stages. Marine Ecology Progress Series 59:171-181.

Aronson RB, and Precht WF. 2006. Conservation, precaution, and Caribbean reefs. Coral Reefs 25:441-450.

Ateweberhan M, Bruggemann JH, and Breeman AM. 2005. Seasonal patterns of biomass, growth and reproduction in Dictyota cervicornis and Stoechospermum polypodioides (Dictyotales, Phaeophyta) on a shallow reef flat in the southern Red Sea (Eritrea). Botanica Marina 48:8-17.

Beach KS, Walters LJ, Borgeas HB, Smith C, Coyer J, and Vroom P. 2003. The impact of Dictyota spp. on Halimeda populations of Conch Reef, Florida Keys. Journal of Experimental Marine Biology and Ecology 297:141-159.

Beach KS, Walters LJ, and Borgeas HB. 2006. Irradiance and nutrient limitation of Dictyota spp. populations on Conch Reef, Florida Keys, USA. Journal of Experimental Marine Biology and Ecology 329:101-112.

Bellwood DR, Hoey AS, Ackerman JL, and Depczynski M. 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Global Change Biology 12:1587-1594.

Bierzychudek P. 1982. The demography of Jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335-351.

Box SJ, Mumby PJ. 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Marine Ecology Progress Series 342:139-149.

Brault S, and Caswell H. 1993. Pod-specific demography of killer whales (Orcinus orca). Ecology 74:1444-1454.

Bruggemann JH, van Oppen JH, and Breeman AM. 1994. Foraging by the stoplight parrotfish Sparisoma viride.I. Food selection in different, socially determined habitats. Marine Ecology Progress Series 106:41-55.

Brys R, Jacquemyn H, Endels P, Blust de G, and Hermy M. 2004. The effects of grassland management on plant performance and demography in the perennial herb Primula veris. Journal of applied ecology 41:1080-1091.

Carpenter RC. 1985. Relationships between primary production and irradiance in coral reef algal communities. Limnology and Oceanography 30:784-793.

Carpenter RC. 1990. Mass mortality of Diadema antillarum. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. Marine Biology 104:67-77.

Carpenter RC, and Edmunds PJ. 2006. Local and regional scale recovery of Diadema promotes recruitment of scleractinian corals. Ecology Letters 9:271-280.

Caswell H. 2001. Matrix population models, 2nd edition. Sinauer Associates, Sunderland.

Caswell H, and Trevisan MC. 1994. Sensitivity analysis of periodic matrix models. Ecology 75:1299-1303.

Caswell H, and Werner PA. 1978. Transient behavior and life history analysis of Teasel (Dipsacus sylvestris Huds.). Ecology 59:53-66.

Chapman ARO. 1974. The ecology of macroscopic marine algae. Annual review of ecology and systematics 5:65-80.

Costa OS, Attrill MJ, Pedrini AG, and De-Paula JC. 2001. Benthic macroalgal distribution in coastal and offshore reefs at Porto Seguro Bay, Brazilian Discovery Coast. Proceedings of the 9th International Coral Reef Symposium 1:499-508.

Creed JC, Norton TA, and Kain JM. 1997. Intraspecific competition in Fucus serratus germlings: The interaction of light, nutrients and density. Journal of Experimental Marine Biology and Ecology 212:211-223.

Crouse DT, Crowder LB, and Caswell H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412-1423.

De Ruyter van Steveninck ED, and Breeman AM. 1987a. Deep water populations of Lobophora variegata (Phaeophyceae) on the coral reef of Curacao: influence of grazing and dispersal on distribution patterns. Marine Ecology Progress Series 38:241-250.

De Ruyter van Steveninck ED, and Breeman AM. 1987b. Deep water vegetations of Lobophora variegata (Phaeophyceae) in the coral reef of Curacao: population dynamics in relation to mass mortality of the sea urchin Diadema antillarum. Marine Ecology Progress Series 36:81-90.

De Ruyter van Steveninck ED, Kamermans P, and Breeman AM. 1988a. Transplant experiments with two morphological growth forms of Lobophora variegata (Phaeophyceae). Marine Ecology Progress Series 49:191-194.

De Ruyter van Steveninck ED, Mulekom LL, and Breeman AM. 1988b. Growth inhibition of Lobophora variegata (Lamouroux) Womersley by scleractinian corals. Journal of Experimental Marine Biology and Ecology 115:169-178.

Diaz-Pulido G, and Garzon-Ferreira J. 2002. Seasonality in algal assemblages on upwelling-influenced coral reefs in the Colombian Caribbean. Botanica Marina 45:284-292.

Diaz-Pulido G, and McCook LJ. 2002. The fate of bleached corals: patterns and dynamics of algal recruitment. Marine Ecology Progress Series 232:115-128.

Doak D, Kareiva P, and Klepetka B. 1994. Modeling population viability for the desert tortoise in the western Mojave desert. Ecological Applications 4:446-460.

Doty M S. 1971. Measurement of water movement in reference to benthic algal growth. Botanica Marina 14:32-35.

Fowler-Walker MJ, Wernberg T, and Connell SD. 2006. Differences in kelp morphology between wave sheltered and exposed localities: morphologically plastic or fixed traits? Marine Biology 148:755-767.

Froese R, and Pauly D. 2007. Fishbase. World Wide Web electronic publication. *in*.

Gardner TA, Cote IM, Gill JA, Grant A, and Watkinson AR. 2003. Long-term region-wide declines in Caribbean Corals. Science 301:958-960.

Garzon-Ferreira J, Gil-Agudelo DL, Barrios LM, and Zea S. 2001. Stony coral diseases observed in southwestern Caribbean reefs. Hydrobiologia 460:65-69.

Gischler E. 1994. Sedimentation on three Caribbean atolls: Glovers Reef, Lighthouse Reef and Turneffe Islands, Belize. Facies 31:243-254.

Herren LW, Walters LJ, and Beach KS. 2006. Fragment generation, survival, and attchement of Dictyota spp. at Conch Reef in the Florida Keys, USA. Coral Reefs 25:287-295.

Hoffmann WA. 1999. Fire and population dynamics of woody plants in a neotropical savanna: Matrix model projections. Ecology 80:1354-1369.

Hoyt WD. 1927. The periodic fruiting of Dictyota and its relation to the environment. American Journal of Botany 14:592-619.

Hughes TP. 1984. Population dynamics based on individual size rather than age: A general model with a reef coral example. American Naturalist 123:778-795.

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

Hughes TP, Bellwood DR, Folke C, McCook LJ, and Pandolfi JM. 2006. No-take areas, herbivory and coral reef resilience. Trends in Ecology and Evolution 22:1-3.

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli DM, Hoegh-Guldberg O, McCook LJ, Moltschaniwskyj NA, Pratchett MS, Steneck RS, and Willis BL. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology 17:360-365.

Hughes TP, and Tanner JE. 2000. Recruitment failure, life histories and long-term decline of Caribbean corals. Ecology 81:2250-2263.

Jompa J, and McCook LJ. 2002a. Effects of competition and herbivory on interactions between a hard coral and a brown alga. Journal of Experimental Marine Biology and Ecology 271:25-39.

Jompa J, and McCook LJ. 2002b. The effects of nutrients and herbivory on competition between a hard coral (Porites cylindrica) and a brown alga (Lobophora variegata). Limnology and Oceanography 47:527-534.

Jompa J, and McCook LJ. 2003. Coral-algal competition: macroalgae with different properties have different effects on corals. Marine Ecology Progress Series 258:87-95.

Koltes K, Tschirky J, and Feller IC. 1998. Carrie Bow Cay, Belize. Pages 79-94 *in* B. Kjerfve, editor. CARICOMP- Caribbean Coral Reef, Seagrass and Mangrove Sites. UNESCO, Paris.

Lapointe BE, Barile PJ, and Matzie WR. 2004. Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys: discrimination of local versus regional nitrogen sources. Journal of Experimental Marine Biology and Ecology 308:23-58.

Lapointe BE, Littler MM, and Littler DS. 1997. Macroalgal overgrowth of fringing coral reefs at discovery bay, Jamaica: Bottom-up versus top-down control. Proceedings of the 8th International Coral Reef Symposium 1:927-932.

Leslie PH. 1945. On the use of matrices in certain population mathematics. Biometrika 35:213-245.

Lessios HA, Garrido MJ, and Kessing BD. 2001. Demographic history of Diadema antillarum, a keystone herbivore on Caribbean reefs. Proceedings of the Royal Society of London Series B Biological Sciences 268:2347-2353.

Lewis IF. 1910. Periodicity in Dictyota at Naples. Botanical Gazette 50:59-64.

Lewis SM. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecology Monographs 56:183-200.

Lewis SM, Norris JN, and Searles RB. 1987. The regulation of morphological plasticity in tropical reef algae by herbivory. Ecology 68:636-641.

Lirman D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs 19:392-399.

Lirman D, and Biber PD. 2000. Seasonal Dynamics of macroalgal communities of the Northern Florida Reef Tract. Botanica Marina 43:305-314.

Littler DS, and Littler MM. 2000. Caribbean Reef Plants, 1st edition. OffShore Graphics Inc., Washington D.C.

Littler MM, Littler DS, and Lapointe BE. 1992. Modification of tropical reef community structure due to cultural eutrophication: the southwest coast of Martinique. Proceedings of the 7th International Coral Reef Symposium 1:335-343.

McClanahan TR. 1997. Primary succession of coral reef algae: differing patterns on fished versus unfished reefs. Journal of Experimental Marine Biology and Ecology 218:77-102.

McClanahan TR, Kamukuru AT, Muthiga NA, Gilagabher Yebio M, and Obura D. 1996. Effects of sea urchin reductions on algae, coral and fish populations. Conservation Biology 10:136-154.

McClanahan TR, and Muthiga NA. 1998. An ecological shift in a remote coral atoll of Belize over 25 years. Environmental Conservation 25:122-130.

Miller MW, and Hay ME. 1996. Coral seaweed grazer nutrient interactions on temperate reefs. Ecological Monographs 66:323-344.

Mumby PJ, Foster NL, and Glynn Fahy EA. 2005. Patch dynamics of coral reef macroalgae under chronic and acute disturbance. Coral Reefs 24:681-692.

Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, and Blackwell PG. 2007. Trophic cascade facilitates coral recruitment in a marine reserve. Proceedings of the National Academy of Sciences of the United States of America 104:8362-8367.

Neto AI. 2000. Observations on the biology and ecology of selected macroalgae from the littoral of Sao Miguel (azores). Botanica Marina 43:483-498.

Nordbakken J.-F, Rydgren K, and Okland RH. 2004. Demography and population dynamics of Drosera angelica and D. rotundifolia. Journal of Ecology 92:110-121.

Norton TA, Mathieson AC, and Neushul M. 1982. A review of some aspects of form and function in seaweeds. Botanica Marina 25:501-510.

Nugues MM, and Bak RPM. 2006. Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. Marine Ecology Progress Series 315:75-86.

Paul VJ, and Hay ME. 1986. Seaweed susceptibility to herbivory: chemical and morphological correlates. Marine Ecology Progress Series 33:255-264.

Peckol P, and Searles RB. 1984. Temporal and spatial patterns of growth and survival of invertebrate and algal populations of a North Carolina continental shelf community. Estuarine, Coastal and Shelf Science 18:133-143.

Quan-Young LI, Diaz-Martin MA, and Espinoza-Avalos J. 2004. Floristics, cover, and phenology of marine macroalgae from Bajo Pepito, Isla Mujeres, Mexican Caribbean. Bulletin of Marine science 75:11-25.

Richardson JP. 1979. Overwintering of Dictyota dichotoma (Phaeophyceae) near its northern distribution limit on the east coast of north America. Journal of Phycology 15:22-26.

Sauer JR, and Slade NA. 1987. Size-based demography of vertebrates. Annual review of ecology and systematics 18:71-90.

Stiger V, and Payri CE. 1999. Spatial and temporal patterns of settlement of the brown macroalgae Turbinaria ornata and Sargassum mangarevense in a coral reef on Tahiti. Marine Ecology Progress Series 191:91-100.

Tanner JE. 1995. Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. Journal of Experimental Marine Biology and Ecology 190:151-168.

Vandermeer J. 1978. Choosing category size in a stage projection matrix. Oecologia 32:79-84.

Chapter 5 Grazing Effects of Parrotfishes on Coral Forereefs Vary with Physical Exposure and Macroalgal Species

This chapter comprises a paper to be submitted to the Journal of Experimental Marine Biology and Ecology

FFECTS OF PARROTFISHES ON CORAL FOREREEFS VARY WITH PHYSICAL EXPOSURE AND MACROALGAL SPECIES

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1 ABSTRACT

Grazing is one of the key processes driving the resilience of coral reefs to disturbance. The effects of grazing by *Diadema antillarum* and parrotfishes on the dominant macroalgal species *Dictyota* spp. and *Lobophora variegata* were investigated on a Caribbean forereef under different physical exposures. Herbivore exclusion experiments were set up on the windward side (exposed) and leeward side (sheltered) of an atoll to investigate different herbivore grazing scenarios. Four cage types were constructed, (1) open plots exposed to all grazers, (2) exclusion of both parrotfishes and urchins, (3) urchin exclusion, and (4) a cage control. The effects of *Diadema antillarum* grazing could not be isolated because of feeding habits of large parrotfishes. The results of the caging experiment were therefore interpreted as differences in grazing pressure. The results revealed a significant effect of physical exposure on the cover of *Dictyota* spp., with the exposed side having a higher average percent cover. Physical exposure also had a significant effect on *Lobophora variegata* albeight opposite to *Dictyota* spp. The experiments revealed a significant increase in cover of both *Dictyota* spp. and *Lobophora variegata* on the no grazing plots. However, on the sheltered side of the atoll it seems that small-bodied parrotfishes alone are sufficient to control the cover of *Dictyota* spp., whilst for *Lobophora variegata* this was not clearly established and only a reduction in the rate of increase can be seen. This study highlighted the complexities of the effects of physical exposure and grazing on macroalgal species and the need to investigate the biological and physical factors controlling macroalgal cover on the species level.

Key words
caging experiment, *Diadema antillarum*, *Dictyota* spp., grazing pressure, *Lobophora variegata,* parrotfishes

2 INTRODUCTION

Many Caribbean coral reefs have undergone a shift from coral dominated states to macroalgal domination because of a wide variety of human and natural disturbances, including, eutrophication, overfishing, mass mortality of *Diadema antillarum*, coral bleaching, and coral diseases (Gardner et al. 2003, Hughes et al. 2003, Pandolfi et al. 2003, Bellwood et al. 2004). Healthy coral reefs provide a range of ecosystem goods and services, that are compromised by a shift towards macroalgae dominance (Moberg and Folke 1999). Furthermore, macroalgal dominated reefs are characterized by reduced rugosity, altered trophic dynamics, and a loss of biodiversity (Tanner 1995, Adey 1998). Grazing is a key process supporting the resilience of Caribbean reefs to disturbance (Hughes et al. 2007). Several species of macroalgae compete with corals (De Ruyter van Steveninck et al. 1988b, Tanner 1995, Jompa and McCook 2002) causing reduced settlement space for coral larvae (Steneck 1997), reduced coral growth rate (Tanner 1995), fecundity (Tanner 1995), and both direct and indirect coral mortality (Nugues and Bak 2006, Box and Mumby 2007). One consequence of algal blooms is a reduction in net coral recruitment (Mumby et al. 2007). Despite a wealth of studies on the effects of grazing on coral reefs (Sammarco 1980, 1982, Steneck 1983, Carpenter 1986, Lewis 1986, Foster 1987, Morrison 1988, McClanahan et al. 1996, McClanahan et al. 2002, McClanahan et al. 2003, Hughes et al. 2007), many issues remain unclear. Here we examine the effects of physical environmental setting on the outcome of grazer manipulations. We also attempt to compare the relative importance of parrotfish and urchin grazing in sheltered forereef systems of low productivity.

Physical exposure can have a profound influence on macroalgal production, influencing thallus morphology, physiological rates, and community structure (Leigh et al. 1987, Hurd 2000). Furthermore, exposure interacts with various biophysical processes and factors to determine macroalgal standing crop. These processes and factors include nutrient uptake, light, water motion, and sedimentation, along with grazing (McManus and Polsenberg 2004). For example, nutrient uptake rates of macroalgae will vary depending on the location of the reef. A forereef exposed to the open ocean will have different uptake rates compared to a forereef in a sheltered bay, because of differences in water flow rates, CDOM and turbidity (Szmant 2002). In general, macroalgal productivity is higher in moving than in still water (Leigh et al. 1987). Moderate water movement generated by waves promotes macroalgal productivity by removing the diffusive boundary layer from macroalgae, and thereby increasing nutrient uptake (Carpenter 1986, Bilger and Atkinson 1995). Wave action also influences the amount of light reaching macroalgae because they create light flecks influencing photon acquisition (Hurd 2000) and, together with turbidity and depth, determines how far light can penetrate, thereby influencing productivity (Umar et al. 1998). Severe wave disturbance from storms or hurricanes can change macroalgal community structure by removing macroalgae from the reef, and inhibit feeding of herbivores (Denny 1985, Denny et al. 1985, Foster 1987).

Natural populations of both urchins and fishes can decrease macroalgal cover, although their relative roles and the degree of inter-specific competition remains unclear (Ogden et al. 1973, Hay 1981, Sammarco 1982, Foster 1987). However, since the mass mortality of the urchin *Diadema antillarum* on Caribbean coral reefs (Lessios et al. 1984), parrotfishes (Scaridae) have become the most important grazer, and if not heavily exploited, are able to limit macroalgal cover (Carpenter 1986, Williams et al. 2001, Mumby et al. 2006, Mumby et al. 2007). Limited recovery of this urchin has occurred on some shallow water reefs in the region (Edmunds and Carpenter 2001, Lee 2006) but recovery has been limited on many mid-shelf forereefs at a depth of around 7-12 m. This may be partly because urchins prefer shallower habitats, but the recovery is limited nonetheless. It remains unclear whether such low densities ($< 1\ m^{-2}$) have a functionally-important role in limiting macroalgae. We would expect that any top-down control of algae from low urchin densities will be strongest where algal production is most limited (i.e. in sheltered environments).

We test two hypotheses concerning the dominant brown macroalgal groups *Dictyota* spp. (hereafter simply *Dictyota*) and *Lobophora variegata*.
H_1: Contrasting levels of physical wave exposure will drive differences in the cover of *Dictyota* and *Lobophora variegata* such that cover increases more rapidly on exposed (productive) systems.
H_2: The full grazing community are able to exert measurable top-down control on macroalgal cover.

Note that failure to enhance urchin density on the exposed side prevented us carrying out a full crossed experimental design between exposure and grazing.

3 MATERIALS AND METHODS

3.1 Study site and categorisation of physical environment

This study was conducted from August 2005 to January 2006 at Glovers Reef (87^0 48'W, 16^0 50'N, Fig. 5.1), an atoll approximately 45 km east of the mainland of Belize. The prevailing wind in Belize is from the north-east (Koltes et al. 1998), so that the eastern and western sides of the atoll experience different physical regimes. The windward eastern side (sites 1, 2 and 3; subsequently referred to as exposed sites) has higher wave energy. In contrast the western side (sites 4, 5, and 6; subsequently referred to as sheltered sites) is more protected from the prevailing winds, and wave energy is lower. The study sites were located on the fore reef within the *Montastraea* habitat that is visually-dominated by corals of the species *Montastraea annularis* (Geister 1977). This habitat is particularly important because it has the highest biomass and diversity of reef organisms (Mumby et al. In press). On both the windward and leeward sides of the atoll the study sites were separated by at least 1 km, and were located at a depth of 7-8 m.

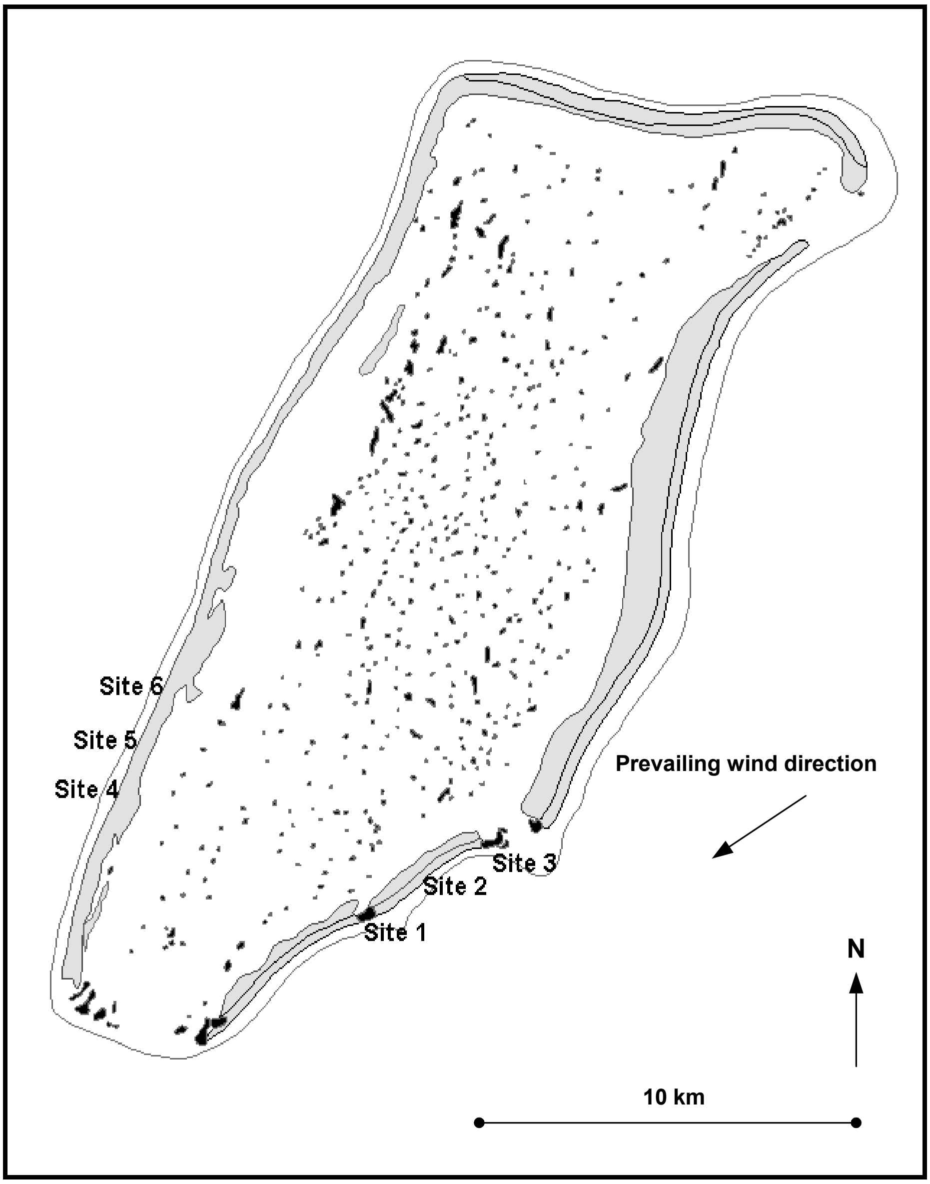
To quantify the variable wave energy among sites, water motion was measured using clod cards (Doty 1971). The clods were made from plaster of Paris, sun dried and glued with epoxy to plastic cards. Clods were weighed before submersion and after 48 hrs collected, air-dried and re-weighed. Clod cards in environments with higher water motion lose more weight than those in calmer areas. Three clod cards were randomly placed at each site at each time interval. Furthermore, in order to quantify any changes in turbidity, horizontal visibility was assessed by looking along a transect line at a depth of approximately 8 m.

3.2 Quantification of Parrotfish and *Diadema* populations

Previous surveys of parrotfish biomass across the atoll, conducted in the summers of 1998 to 2005, indicated that biomass did not vary in contrasting physical conditions (Mumby, unpublished data). To examine seasonal differences in parrotfish biomass during the experiment, visual censuses were carried out on a monthly basis. Fish were counted and sized (to the nearest cm) along at least five replicate 30 x 4 m transects. The length of fishes was converted to biomass using allometric relationships from Fishbase (Froese and Pauly 2007) and Bohnsack and Harper (1988). Replicate transects were combined to provide a mean biomass per species per site, which was standardised to an area of 1 m^2.

Diadema antillarum densities were assessed by counting individuals along four replicate 50 x 2 m transects. The test size of each urchin was estimated using a ruler and rounded to the nearest 0.5 cm.

Fig. 5.1. Map of Glovers Reef Atoll showing study sites and prevailing wind direction

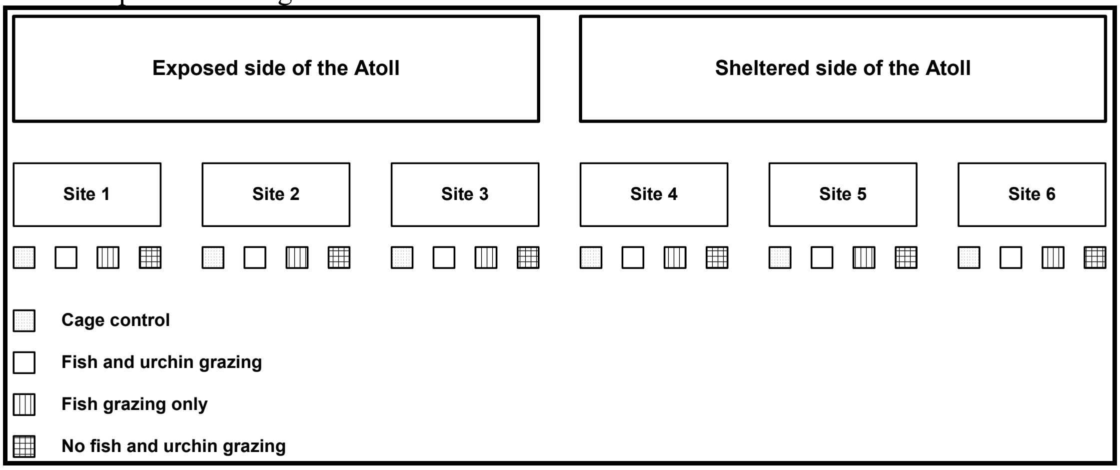


3.3 Caging experiment

The caging experiment consisted of four cage treatments: (1) an open plot with no cage where all herbivores (urchins and herbivorous fishes) could graze freely, (2) a herbivore exclusion cage in which all herbivores were excluded, (3) a partial cage with an open top allowing fish to graze freely inside the cage, but excluding urchins, and (4) a control cage with two of the sides of the cage removed to allow both urchins and fish to graze uninhibited, and acting as a control for potential caging effects (Fig. 5.2). On both the exposed and sheltered sides of the atoll, the set of four cage treatments were replicated three times, (sites 1 to 6: Figs. 5.1 and 5.2). The cages measured 0.50 x 0.50 x 0.25 m and were constructed from PVC, covered with plastic mesh (mesh size of 2.5 x 2.5 cm). This mesh size allows small and juvenile fishes to enter the cages, but does not affect the overall results of treatments (Lewis 1986). The cages were fixed to the reef substratum with iron bars (which were shielded in plastic to prevent metal contamination) to which the cages were fixed with cable ties. Before the placement of cages, an area of 0.50 x 0.50 m was cleared of all algae by scrubbing the area with wire brushes. At regular intervals, the cages were removed briefly and cleaned to prevent fouling. Scrubbing was conducted down current of the experimental plots. At each site of the caging experiment ten untreated plots of 0.5 x 0.5 m were monitored during the time of the caging experiment. Each cage and untreated plots were videoed at monthly intervals using a high-resolution digital video camera, and filming was initiated two months after the establishment of the experiment.

We did not include a cage treatment to investigate the final possible scenario of including urchins but excluding fish grazers. This study was investigating the effects of grazers under very low *Diadema antillarum* densities (< 1 m^{-2}) as opposed to the pre *Diadema* mortality studies (Sammarco 1980, 1982, Foster 1987, Morrison 1988). This would require the use of very large cages in order to get, for example, 0.5 urchins per m^2 and this was impractical in exposed environments. Moreover, attempts to enhance natural densities of urchins on the exposed side were unsuccessful and resulted in rapid urchin predation.

Fig. 5.2. Experimental design. Each side of atoll has three sites and each site has one full set of four experimental cages



3.4 Data analysis

Differences in univariate metrics on each side of the atoll (weight loss of clod cards, differences in biomass and density of herbivores, and percentage cover) were tested using a repeated measures ANOVA design with exposure and time. The data for weight loss of clod cards were normally distributed, whilst the data on biomass and density of herbivores were square root transformed to meet the assumptions of normality (Ryan-Joiner test). Videos were analysed with the VidAna[2] software to calculate percentage cover of the two dominant brown macroalgae: *Dictyota* and *Lobophora variegata*. Data on percentage cover each month were arc-sin transformed. Differential effects of physical exposure was tested using repeated measures ANOVA on percent cover across the study duration. The effects of grazing intensity was tested using a regression analysis and where significant effects were found, post hoc pairwise comparisons with Bonferroni corrections were carried out to test for significant effects of the different herbivore exclusion treatments. Because the caging experiment had a relatively limited replication, we tested the effects of sample size on our outcomes with a retrospective power analysis. Future caging experimental design should take these results into account.

4 RESULTS

4.1 Site characteristics

Clod card measurements showed a significant difference between the two sides of the atoll, with the exposed side (site 1, 2, and 3) having an average weight loss over 48 hrs of 27.2 ± 6.03 g (from an initial weight of 61.2 g, i.e. a 44.4% decline) compared with an average loss of 21.4 ± 5.76 g for the sheltered side, which is a 35.4% decline from an initial weight of 60.5 g (site 4, 5, and 6) (Table 5.1). The horizontal visibility for the exposed side of the atoll is at least 2.5 times higher than for the sheltered side, averaging about 25 m.

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[2] The software is available free of charge from http://www.ex.ac.uk/msel

Table 5.1 Repeated measures ANOVA results for clod card measurements during the experiment. Significant results are in bold

Factors	**df**	**F**	***P***
Exposure	1	12.92	**<0.001**
Time	2	0.08	0.92
Exposure x Time	2	4.47	**<0.05**

There is a significant difference in mean percentage cover of *Dictyota* between the exposed (mean percentage cover 10.3 ± 2.1 %) and sheltered sides (mean percentage cover 1.9 ± 0.3 %) of the atoll on non treated plots (Table 5.2). The interaction term exposure*time for *Lobophora variegata* did not show a significant difference in cover on non treated plots between the exposed (mean percentage cover 2.5 ± 0.6 %) and sheltered sides (mean percentage cover 1.6 ± 0.3 %) of the atoll (Table 5.2). However for exposure alone and time alone the results were significant.

Table 5.2. Repeated measures ANOVA results for *Dictyota* spp and *Lobophora variegata* during the experiment for non treated plots. Significant results are in bold

Factors	**df**	***Dictyota* spp.**		***Lobophora variegata***	
		F	***P***	**F**	***P***
Exposure	1	80.29	**<0.001**	13.98	**<0.001**
Time	4	5.48	**<0.001**	4.26	**<0.05**
Exposure x Time	4	7.10	**<0.001**	0.27	0.90

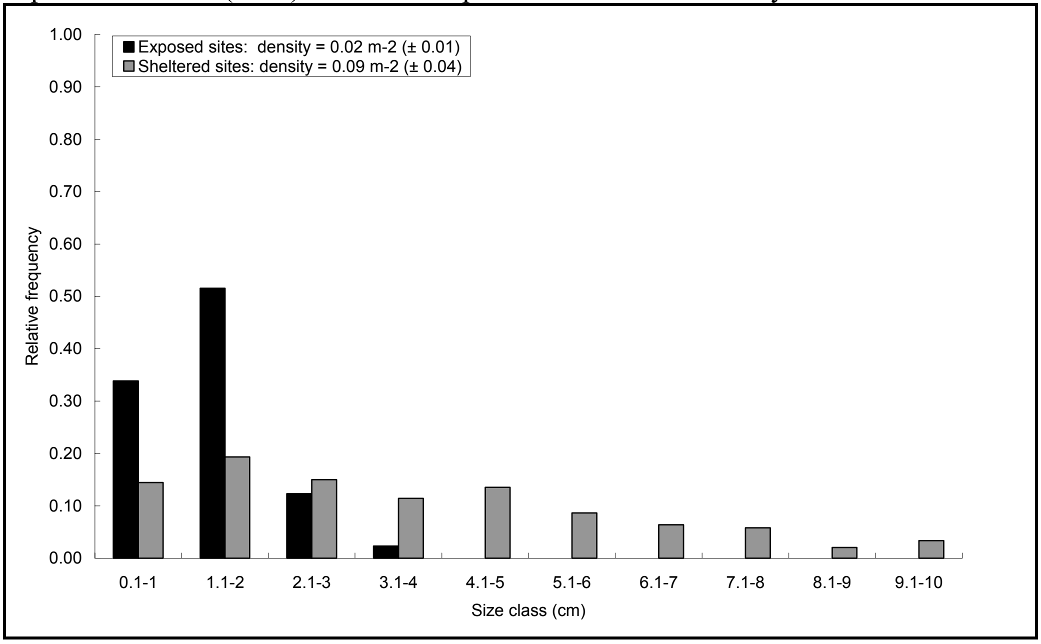
Parrotfish and Diadema populations

Densities of *Diadema* varied significantly across the atoll. Mean density was 0.02 ± 0.01 m^{-2} on the exposed side, and 0.09 ± 0.04 m^{-2} on the sheltered side (Table 5.3). *Diadema antillarum* also showed a marked difference in its size frequency distribution (Fig. 5.3). The exposed side of the atoll had only urchins in the smallest test-size categories (1-4 cm), whereas all size classes (1-10 cm) were found on the sheltered side.

Table 5.3. Repeated measures ANOVA results for *Diadema antillarum* densities recorded on Glovers Reef Atoll. Significant results are in bold.

Factors	**df**	**F**	***P***
Exposure	1	185.53	**<0.001**
Time	5	8.70	**<0.001**
Exposure x Time	5	7.75	**<0.001**

Fig. 5.3. *Diadema antillarum* relative size frequency distribution on the exposed and sheltered sides of Glovers Reef Atoll. Densities are means across all experimental sites (± SE). Data for the period June 2005 – January 2006.

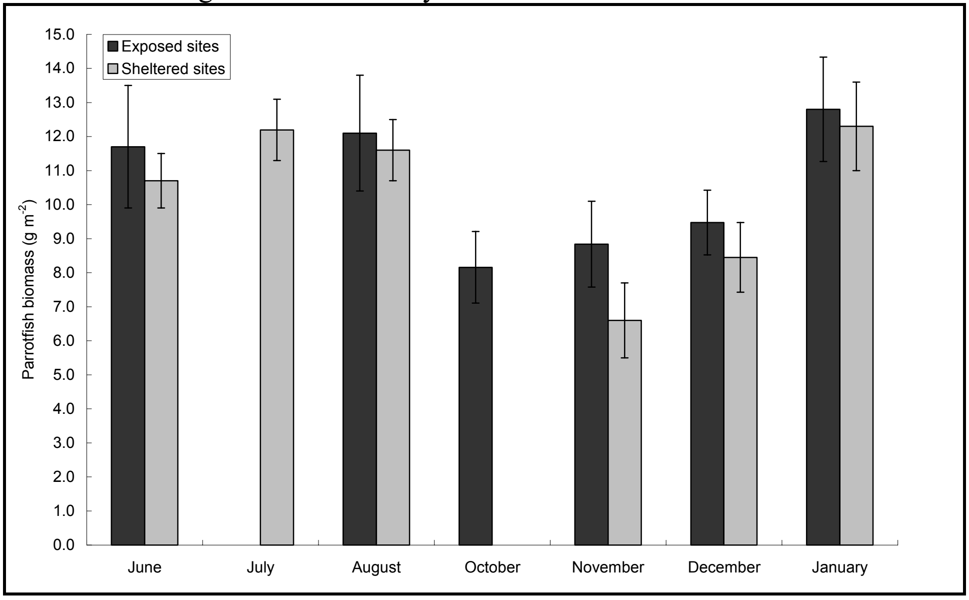


There was no significant difference in parrotfish biomass between the exposed and sheltered sides. However, significant seasonal variations were observed on both sides of the atoll (Table 5.4). Parrotfish biomass was lower for the winter months of October to December on both sides of the atoll, with an increase in biomass in January to recorded summer levels (Fig. 5.4).

Table 5.4. Repeated measures ANOVA results for parrotfish biomass recorded at Glovers Reef Atoll. Significant results are in bold.

Factors	**df**	**F**	***P***
Exposure	1	0.13	0.72
Time	6	30.59	**<0.001**
Exposure x Time	6	42.89	**<0.001**

Fig.5.4. Mean parrotfish biomass from all sites on exposed and sheltered sides of Glovers Reef Atoll throughout the duration of the caging experiment. Error bars are ± SE. Missing data means surveys were not conducted.



4.2 Caging experiment

The relative importance of parrotfish and urchin grazing could not be examined using the caging treatments. The control cage partially excluded large parrotfishes (30 ± 5 cm) from grazing inside the cage, whilst the urchin exclusion cage also prevented large parrotfish from grazing inside the cage (pers. observation). The largest sized parrotfishes could not access the entire control cage plot (due to their body height) and therefore this plot is not grazed by the full grazing community (urchins, small, and large parrotfishes). Large parrotfishes may be prevented from grazing inside the urchin exclusion cage because they approach the feeding area from the side rather than the top, and the cage would have effectively excluded them from grazing inside the cage. Therefore the grazing effects of urchins could not be isolated. The caging treatments did show interesting effects of grazing pressure and the different cage treatments (Fig. 5.2) are relabeled to investigate effects of grazing pressure on reefs with different exposure and not differentiating between urchin and parrotfish grazing. (1) The open plot with both fish and urchin grazing is relabeled as high grazing, (2) the plot where all grazers were excluded is labeled as no grazing, (3) the plot which excluded urchins and large parrotfish is relabeled as low grazing (only small-bodied parrotfish), and (4) the control cage (which partially excluded the largest parrotfishes) is labeled as medium grazing.

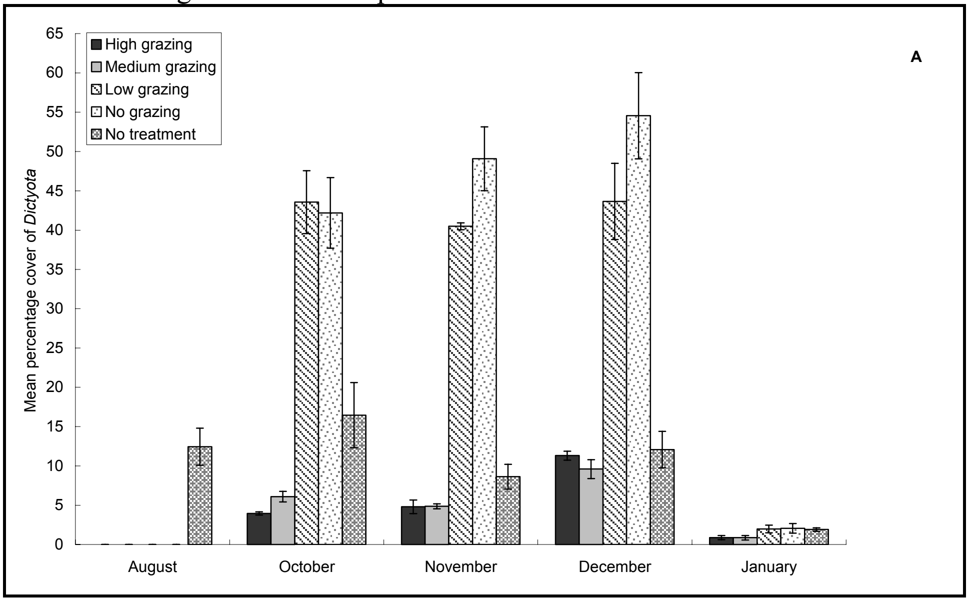
4.3 H_1: Contrasting levels of physical wave exposure will drive differences in the cover of *Dictyota* and *Lobophora variegata* such that cover increases more rapidly on exposed (productive systems).

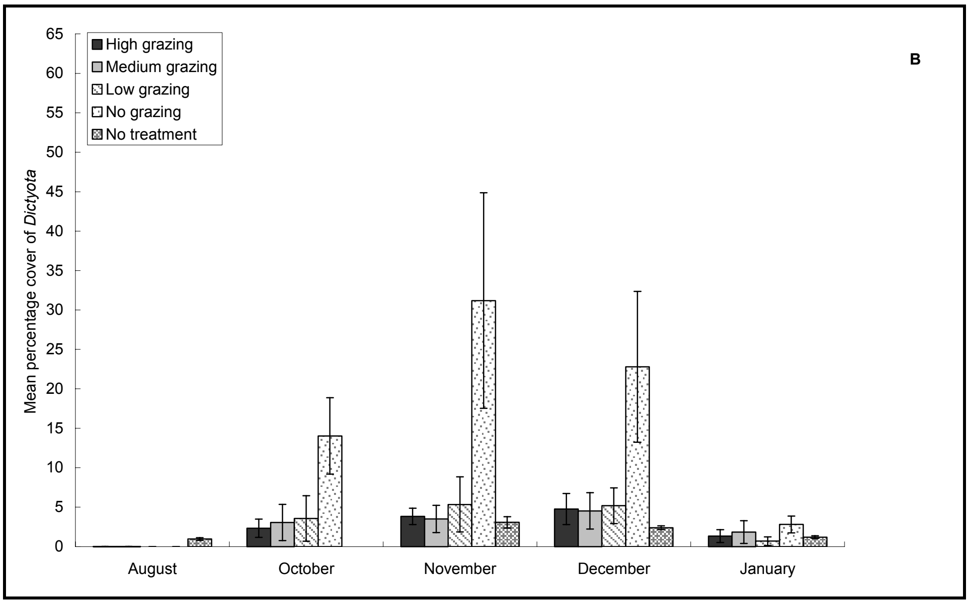
Dictyota cover increased rapidly after the start of the experiment (Figs. 5.5A and B). After 6 months, physical exposure significantly affected the cover of *Dictyota* (Table 5.5). *Dictyota* cover was higher on the exposed side of the atoll (mean of 37.0 ± 3.7 %, all data pooled), compared with the sheltered side (17.7 ± 7.3 %). *Lobophora variegata* cover did not show a significant difference across the atoll (Table 5.5) Here the cover of *Lobophora variegata* was slightly higher on the sheltered side of the atoll (mean of 2.7 ± 1.2%), compared with the exposed side (1.0 ± 0.4%). A significant decrease in cover of *Dictyota* can be observed from December to January on both sides of the atoll for all cage treatments (one way ANOVA for exposed side, df = 1, F = 91.90, $P < 0.01$ and for the sheltered side, df = 1, F = 7.76, $P < 0.05$, Figs. 5.5A and B). This pattern was also observed for the non treated plots of *Dictyota* (Figs. 5.5A and B). In contrast, the cover of *Lobophora variegata* continued to increase in all cage treatments and non treated plots (Figs. 5.6A and B).

Table 5.5. Repeated measures ANOVA results for the cover of *Dictyota* spp. and *Lobophora variegata* in the caging experiment. Significant results in bold.

Factors	**df**	***Dictyota* spp.**		***Lobophora variegata***	
		F	***P***	**F**	***P***
Exposure	1	40.73	**<0.001**	1.26	0.27
Treatment	3	30.42	**<0.001**	4.20	**<0.05**
Month	3	18.11	**<0.001**	11.73	**<0.001**
Exposure x Treatment	3	10.28	**<0.001**	5.70	**<0.001**
Exposure x Time	3	5.99	**<0.001**	0.11	0.96

Fig. 5.5. Mean percentage cover of *Dictyota* spp. in each caging treatment and on no treatment plots on (A) the exposed side and (B) the sheltered side of Glovers Reef Atoll. August is start of experiment. Error bars are ± SE





4.4 H_2: The full grazing community are able to exert measurable top-down control on macroalgal cover

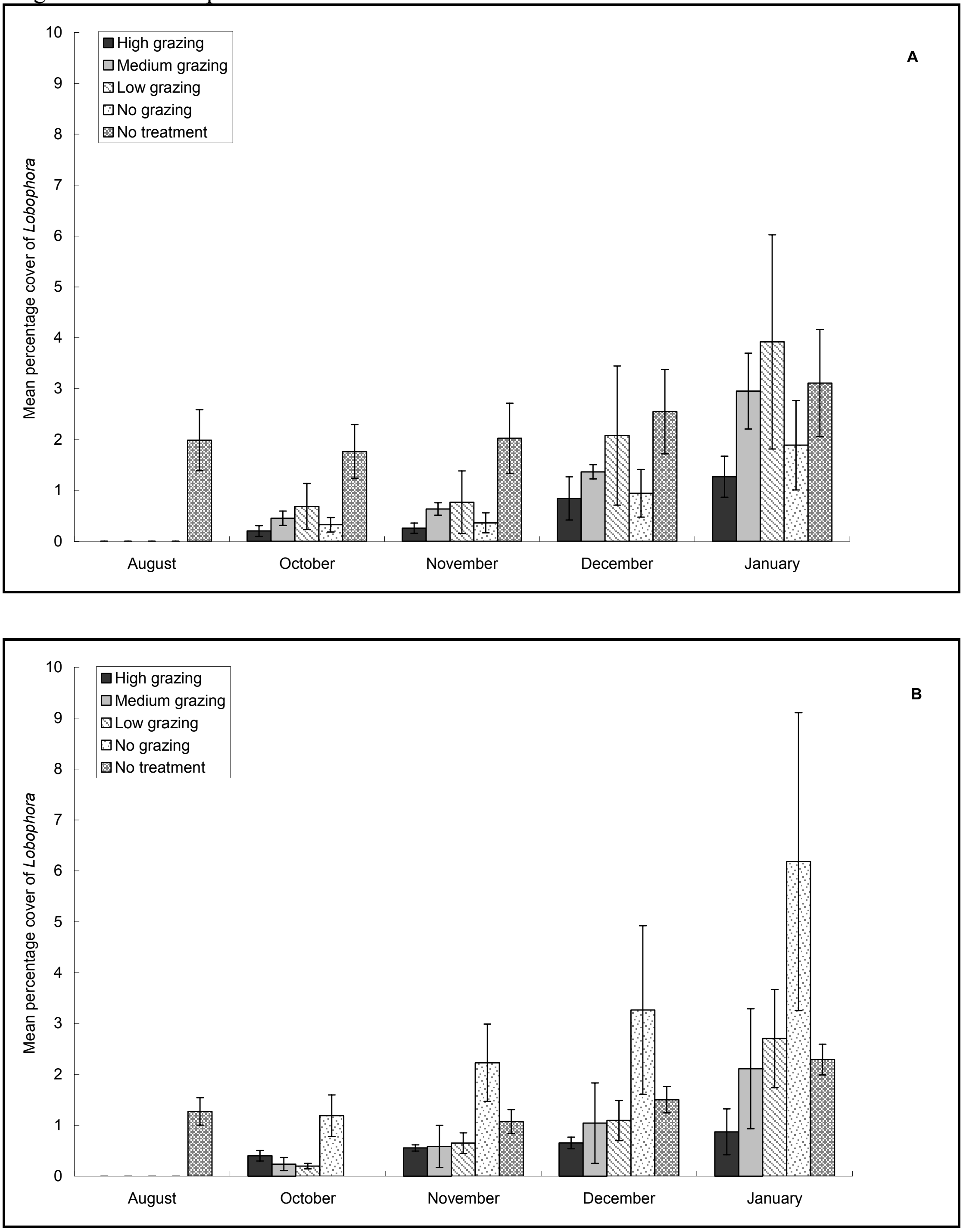
Grazing pressure exerted a significant influence on *Dictyota* percentage cover for the exposed and sheltered side of the atoll (F = 131.66, $P < 0.001$, R-sq = 78.9 and F = 15,27, $P < 0.001$, R-sq = 29 respectively), although the relationship was relatively weak for the sheltered side. There was a significant increase in cover of *Dictyota* on both sides of the atoll on plots where both parrotfishes and *Diadema antillarum* were excluded (no grazing) compared to the medium grazing and high grazing plots (Table 5.1 and Figs. 5.5A and B). *Dictyota* spp. reached a maximum mean percentage cover of 54.6 ± 5.5 % in the no grazing plots at the exposed sites, and a mean percentage cover of 31.2 ± 13.7 % in the no grazing plots at the sheltered sites (Figs. 5.5A and B). At the exposed sites there was no significant effect between the no grazing and low grazing plots (Table 5.1 and Fig. 5.6A). At the sheltered sites there was a significant effect in that more algae was present on the no grazing plots (Table 5.1 and Fig. 5.5B).

Grazing pressure exerted no significant influence on *Lobophora* percentage cover on the exposed side of the atoll (F = 0.39, $P = 0.54$, R-sq 0.0). On the sheltered side the grazing pressure was significant although weak (F = 10.74, $P < 0.05$, R-sq= 17.2). *Lobophora variegata* cover did not vary significantly at the exposed sites between the no grazing plots and the medium and high grazing plots (Table 5.6 and Figs. 5.6A and B). *Lobophora variegata* reached a maximum mean percentage cover of 1.9 ± 0.9 % on the no grazing plots at the exposed sites (Fig. 5.6A). On the sheltered side there was a significant increase in cover on no grazing plots compared to the medium and high grazing plots, where *Lobophora variegata* reached a maximum mean percentage cover of 6.2 ± 2.9 % (Table 5.6 and Fig. 5.6B) on the no grazing plots.

Table 5.6. Pair wise multiple comparison with Bonferroni corrections of Experimental treatments for (a) *Dictyota* spp. and (b) *Lobophora variegata*. Values are *P*-values. ns = not significant ($P > 0.05$)

(a) *Dictyota* spp.			
Exposed side			
Treatment	High grazing	Medium grazing	Low grazing
Medium grazing	ns		
Low grazing	<0.01	<0.01	
No grazing	<0.01	<0.01	ns
Sheltered side			
Treatment	High grazing	Medium grazing	Low grazing
Medium grazing	ns		
Low grazing	ns	ns	
No grazing	0.001	0.001	0.001
(b) *Lobophora variegata*			
Sheltered side			
Treatment	High grazing	Medium grazing	Low grazing
Medium grazing	ns		
Low grazing	ns	ns	
No grazing	0.004	0.02	0.03

Fig. 5.6. Mean percentage cover of *Lobophora* in each caging treatment and on no treatment plots (A) the exposed side and (B) the sheltered side of Glovers Reef Atoll.
August is start of experiment. Error bars are ± SE



At the exposed sites, in plots of low grazing, a significant increase in *Dictyota* cover was found (Table 5.6 and Fig. 5.5A), compared to the high and medium grazing plots. In contrast, at the sheltered sites there was no significant difference in *Dictyota* cover between these treatments (Table 5.6 and Fig. 5.5B). Comparing the low grazing with no grazing plots, there was no significant difference in cover between these plots on the exposed sites (Table 5.6 and

Fig. 5.5A). *Dictyota* reached a maximum mean percentage cover of 43.6 ± 8.4 % on the low grazing plots. At the sheltered sites however, there was a significant difference in cover between the low grazing (maximum mean percentage cover of 5.3 ± 3.9 %) and no grazing plots, in that percentage cover was higher in the no grazing plots (Table 5.6 and Fig. 5.5B).

There was no significant difference in *Lobophora variegata* cover between the low grazing plots and the high and medium grazing plots on the sheltered side of the atoll (Table 5.6 and Fig 5.6B). At the sheltered sites however, there was a significant difference in cover between the low grazing (maximum mean percentage cover of 2.7 ± 1.7 %) and no grazing plots, in that percentage cover was higher in the no grazing plots (Table 5.6 and Fig. 5.6B).

Results from the statistical power analysis indicated that the relative small sampling size of the caging experiment could have played a role in the non significant and results for *Lobophora variegata* on the exposed side of the atoll and the weak relationships for *Dictyota* (Table 5.7).

Table 5.7. Results of the retrospective power analysis to determine correct sample size for future studies. Alpha = 0.05, Number of levels = 4. Sample size 3 = is current study.

	Power			
	***Dictoyta* spp.**		***Lobophora variegata***	
Sample size	**Exposed**	**Sheltered**	**Exposed**	**Sheltered**
3	1.00	0.78	0.22	0.53
4	1.00	0.94	0.32	0.74
5	1.00	0.99	0.42	0.87
6	1.00	1.00	0.52	0.94
7	1.00	1.00	0.60	0.97
10	1.00	1.00	0.80	1.00
15	1.00	1.00	0.95	1.00

5 DISCUSSION

5.1 H_1: Contrasting levels of physical wave exposure will drive differences in the cover of *Dictyota* spp. and *Lobophora variegata* such that cover increases more rapidly on exposed (productive systems).

This study revealed a significant effect of physical exposure on the cover of *Dictyota.* Several reasons may explain this result. Both nutrients and light intensity have a strong influence on algal growth rates, and the combination of these two factors may determine maximum macroalgal production (Carpenter 1985, Creed et al. 1997). Although background nutrient levels for the exposed and sheltered sides are similar (Mumby, unpublished data), higher water flow rates on the exposed side will increase nutrient flux and may, therefore, have contributed to higher productivity. *Dictyota* may also have been light limited on the sheltered side, where poor visibility occurs throughout the year. A recent study found that *Dictyota menstrualis* was light limited, but only at depths of over 32 m (Beach et al. 2006). In shallower, but more turbid, water this may be a possible mechanism causing a reduction in growth. The physical removal of algal biomass through wave action is often cited as a mechanism by which macroalgal biomass is removed in the intertidal region (Denny 1985, Denny et al. 1985, Hurd 2000). However, for *Dictyota*, growing at depths of 8 m as in this study, this seems to be unlikely because they will not experience the full force of breaking waves, and water flow velocities will typically be lower than those of intertidal sites (Hurd 2000). An exception will be during tropical storm or hurricanes conditions, when mechanical damage will be significant.

The significant decline in cover of *Dictyota* from December to January was observed on both the exposed and sheltered sides of the atoll, and might be because of a life history event such as a decline of the population following sexual reproduction, rather than being environmentally driven. Studies of *Dictyota* have shown periodicity in sexual reproduction (Lewis 1910, Hoyt 1927). Gamete production appears to be related to tidal levels on fortnightly or monthly intervals, but this does not necessary correlate with changes in the season (Neto 2000). However, *Dictyota dichotoma* (Hudson) may survive the cooler months by remaining in an early developmental stage (Richardson 1979).

Lobophora variegata showed a significant difference in cover between the exposed and sheltered sites. Unexpectedly, the cover of *Lobophora variegata* was higher on the sheltered side, rather than the exposed side as was observed for *Dictyota.* A likely explanation for this might be that there was a competitive interaction between *Dictyota* and *Lobophora variegata*. Percentage cover of *Dictyota* was very high in the no grazing plots on the exposed side and this might have reduced the growth rate of *Lobophora* in the no grazing plots on the exposed side due to shading and overgrowth by *Dictyota*. On the sheltered side of the atoll, *Dictyota* cover in the no grazing plots was much lower than that of the no grazing plots on the exposed side (by a factor of 2). Competitive interaction between *Dictyota* and *Lobophora variegata* may have been lower, allowing *Lobophora variegata* to increase to a higher percentage cover on the no grazing plots on the sheltered side. Percentage cover of *Lobophora variegata* on untreated plots was also slightly higher on the sheltered side of the atoll, albeight not significantly. The higher percentage cover of *Lobophora variegata* may have been an effect of increased recruitment and colonization as a consequence of a higher initial percentage cover on the sheltered side of the atoll.

Finally, *Lobophora* might be able to adjust its morphology to optimize production under more benign conditions, such as lowered light and nutrient fluxes. For example, the species can adjust its morphology, in response to gradients in depth, grazing, and wave exposure (De Ruyter van Steveninck et al. 1988a, Coen and Tanner 1989). However, morphological changes of populations of *Lobophora* at similar depths, but differing physical exposure, were not readily visible.

5.2 H_2: The full grazing community are able to exert measurable top-down control on macroalgal cover

There was a significant increase in cover of *Dictyota* on both sides of the atoll on no grazing plots. *Lobophora variegata* showed a significant increase in cover but only on the sheltered side of the atoll, whilst on the exposed side it seems that the full grazing community can only reduce the rate of increase for *Lobophora variegata*. This effect has been well documented in other studies, where exclusion of herbivores lead to an increase in the cover of macroalgae (Sammarco 1982, Foster 1987, Carpenter 1990, Thacker et al. 2001, McClanahan et al. 2002, McClanahan et al. 2003, Hughes et al. 2007). The results seem to show that low levels of grazing is enough to control the cover of *Dictyota* on the sheltered side of the atoll but they can only reduce the rate of increase in cover on the exposed side. A similar pattern was observed for *Lobophora variegata* however it seems that low levels of grazing can only reduce the rate of increase on the sheltered side and for the exposed side no clear patterns in grazing pressure can be observed but this was very likely caused by the competitive interactions of *Dictyota* with *Lobophora*.

Competitive interactions of *Dictyota* may explain the effects on the cover of *Lobophora variegata*. *Dictyota* achieved a much higher percentage cover on the no grazing plots on the exposed side of the atoll, compared to the same plots on the sheltered side. Therefore, it is likely that *Dictyota* suppressed the growth of *Lobophora variegata* in the no grazing plots on the exposed side by over growing *Lobophora* or prevented *Lobophora* recruits from settling by pre-emption of space.

The full grazing community consists of both Parrotfishes and *Diadema antillarum*. The densities of *D. antillarum* recorded on the sheltered side of the atoll are significantly higher than those of the exposed side of the atoll. However, the densities of *D. antillarum* on both the sheltered and exposed side of the atoll are extremely low, equivalent to 1 urchin per 11 m^2 on the sheltered and 1 per 50 m^2 on the exposed side of the atoll. Both these areas are much larger than the average *D. antillarum* territory (2.25 m^{-2}; (Carpenter 1984). Also, these values are well below the densities at which this species is considered functional redundant (< 1 m^{-2}) (C. Dahlgren, pers. comm.). Therefore it seems highly unlikely that *D. antillarum* has a significant impact as grazer on macroalgal cover. This indicates that Parrotfishes are the most important herbivore guild on both the exposed and sheltered sides of the atoll (Mumby et al. 2006, Mumby et al. 2007).

Dictyota responded in the same way on both sides of the atoll, by considerably increasing its cover in the no grazing plots. *Lobophora variegata* on the other hand only significantly increased in cover on the no grazing plots on the sheltered side of the atoll, whilst on the exposed side it seems that grazers only reduced the rate of increase in cover of *Lobophora variegata*. This unexpected effect may be attributed to the fact that, there is relatively more *Lobophora variegata* compared to *Dictyota* on the sheltered side than on the exposed side of the atoll. Grazers will feed on a broad range of algae but, given that there is relatively more *Lobophora variegata* to feed on at the sheltered side, this species may be grazed more intensively at the sheltered sites than the exposed sites. Furthermore, *Lobophora variegata* uses chemical deterrents to resist grazing (Paul and Hay 1986, Arnold and Targett 2000). It might be that *Lobophora variegata* on the sheltered side has lower chemical defences. There is a trade off amongst investing energy in maintaining growth rates, reproductive processes, and chemical defences against herbivory (Littler and Littler 1980, Cronin and Hay 1996). Thus it might be that by investing more energy in maintaining growth rates under adverse environmental conditions *Lobophora variegata* has become more susceptible to grazing.

Dictyota production rates seem to be closely related to the physical environment and it seems likely that *Dictyota* could compensate the amount of biomass lost to grazing on the exposed side of the atoll and small-bodied parrotfishes could only reduce the rate of increase. On the sheltered side production rates seem to be a lot lower and low grazing pressure is seemingly sufficient to control *Dictyota* cover. The effects on *Lobophora variegata* are more difficult to explain because the results of differential grazing pressure on the exposed side are highly variable, but on the sheltered side it seems that low grazing pressure is sufficient to at least reduce the rate of increase.

The results indicated a strong effect of both the physical environment and grazing on *Dictyota* but these trends were far less clear for *Lobophora variegata*. Although a trend was shown for *Lobophora*, the results were not significant. This could have been attributed to the experiment having a small sample size. The results for *Dictyota* and *Lobophora* were quite variable and indicated that for *Dictyota* the sample size was sufficient, but for *Lobophora* it should be increased. In practice the sample size not only depends on the statistical power, but also on logistics of carrying out the experiment. Based on both it is recommended that a doubling in sample size, i.e. from 3 sets of experimental treatments on each side of the atoll, to 6 sets would be adequate for future caging experiments.

6 CONCLUSION

In summary, results of this study demonstrate that physical exposure plays an important role in controlling the cover of *Dictyota* and *Lobophora variegata*. The caging experiment could not isolate the effects of urchin grazing. Therefore only different levels of grazing pressure were investigated to show the importance and differential effects of grazing pressure on the cover of *Dictyota* and *Lobophora variegata.*

It appears that on the sheltered side of the atoll parrotfish grazing is sufficient to control the populations of *Dictyota* and *Lobophora variegata* at least within 6 months. This study highlighted the complexities of the effects of physical exposure and grazing on macroalgal species. However, future caging experiments should increase sample size by doubling the amount of cages presently used. Future research will address the questions of what biological and physical factors are controlling the cover of *Dictyota* and *Lobophora variegata*, and the densities at which *Diadema antillarum* start to play a significant role as grazer.

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7 REFERENCES

Adey WH. 1998. Coral reefs: Algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. Journal of Phycology 34:393-406.

Arnold TM., and Targett NM. 2000. Evidence for metabolic turnover of polyphenolics in tropical brown algae. Journal of Chemical Ecology 26:1393-1410.

Beach KS, Walters LJ, and Borgeas HB. 2006. Irradiance and nutrient limitation of Dictyota spp. populations on Conch Reef, Florida Keys, USA. Journal of Experimental Marine Biology and Ecology 329:101-112.

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

Bilger RW, and Atkinson MJ. 1995. Effects of nutrient loading on mass transfer rates to a coral reef community. Limnology and Oceanography 40:279-289.

Bohnsack JA, and Harper DE. 1988. Length-weight relationships of selected marine fishes from the southeastern United States and the Caribbean. National Fish and Wildlife Service, Miami.

Box SJ, and Mumby PJ. 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Marine Ecology Progress Series 342:139-149.

Carpenter RC. 1984. Predator and population density control of homing behavior in the Caribbean echinoid Diadema antillarum. Marine Biology 82:101-108.

Carpenter RC. 1985. Relationships between primary production and irradiance in coral reef algal communities. Limnology and Oceanography 30:784-793.

Carpenter RC. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs 56:345-363.

Carpenter RC. 1990. Mass mortality of Diadema antillarum. II. Effects on population densities and grazing intensity of parrot fishes and surgeonfishes. Marine Biology 104:79-86.

Coen LD, and Tanner CE. 1989. Morphological variation and differential susceptibility to herbivory in the tropical brown alga Lobophora variegata. Marine Ecology Progress Series 54:287-298.

Creed JC, Norton TA, and Kain JM. 1997. Intraspecific competition in Fucus serratus germlings: The interaction of light, nutrients and density. Journal of Experimental Marine Biology and Ecology 212:211-223.

Cronin G, and Hay ME. 1996. Chemical defenses, protein content, and susceptibility to herbivory of diploid vs haploid stages of the isomorphic brown alga Dictyota ciliolata (Phaeophyta). Botanica Marina 39:395-399.

De Ruyter van Steveninck ED, Kamermans P, and Breeman AM. 1988a. Transplant experiments with two morphological growth forms of Lobophora variegata (Phaeophyceae). Marine Ecology Progress Series 49:191-194.

De Ruyter van Steveninck ED., Mulekom LL, and Breeman AM. 1988b. Growth inhibition of Lobophora variegata (Lamouroux) Womersley by scleractinian corals. Journal of Experimental Marine Biology and Ecology 115:169-178.

Denny MW. 1985. Wave forces on intertidal organisms: A case study. Limnology and Oceanography 30:1171-1187.

Denny MW, Daniel TL, and Koehl MAR. 1985. Mechanical limits to size in wave-swept organisms. Ecological Monographs 55:69-102.

Doty MS. 1971. Measurement of water movement in reference to benthic algal growth. Botanica Marina 14:32-35.

Edmunds PJ, and Carpenter RC. 2001. Recovery of Diadema antillarum reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proceedings of the National Academy of Sciences of the United States of America 98:5067-5071.

Foster SA. 1987. The relative impacts of grazing by Caribbean coral reef fishes and Diadema: effects of habitat and surge. Journal of Experimental Marine Biology and Ecology 105:1-20.

Froese R, and Pauly D. 2007. Fishbase. World Wide Web electronic publication. *in*.

Gardner TA, Cote IM, Gill JA, Grant A, and Watkinson AR. 2003. Long-term region-wide declines in Caribbean Corals. Science 301:958-960.

Geister J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Proceedings of the 3rd International Coral Reef Symposium 1:23-30.

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

Hoyt WD. 1927. The periodic fruiting of Dictyota and its relation to the environment. American Journal of Botany 14:592-619.

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

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli DM, Hoegh-Guldberg O, McCook LJ, Moltschaniwskyj NA, Pratchett MS, Steneck RS, and Willis BL. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology 17:360-365.

Hurd CL. 2000. Water motion, marine macroalgal physiology, and production. Journal of Phycology 36:453-472.

Jompa J, and McCook LJ. 2002. Effects of competition and herbivory on interactions between a hard coral and a brown alga. Journal of Experimental Marine Biology and Ecology 271:25-39.

Koltes K, Tschirky J, and Feller IC. 1998. Carrie Bow Cay, Belize. Pages 79-94 *in* B. Kjerfve, editor. CARICOMP- Caribbean Coral Reef, Seagrass and Mangrove Sites. UNESCO, Paris.

Lee SC. 2006. Habitat complexity and consumer-mediated positive feedbacks on a Caribbean coral reef. OIKOS 112:442-447.

Leigh EG, Paine RT, Quinn JF, and Suchanek TH. 1987. Wave energy and intertidal productivity. Proceedings of the National Academy of Sciences of the United States of America 84:1314-1318.

Lessios HA, Robertson DR, and Cubit JD. 1984. Spread of Diadema mass mortality through the Caribbean. Science 226:335-337.

Lewis IF. 1910. Periodicity in Dictyota at Naples. Botanical Gazette 50:59-64.

Lewis SM. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecology Monographs 56:183-200.

Littler MM, and Littler DS. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. American Naturalist 116:25-44.

McClanahan TR, Cokos BA, and Sala E. 2002. Algal growth and species composition under experimental control of herbivory, phosphorous and coral abundance in Glovers reef, Belize. Marine Pollution Bulletin 44:441-451.

McClanahan TR, Kamukuru AT, Muthinga NA, Gilagabher Yebio N, and Obura D. 1996. Effects of sea urchin reductions on algae, coral and fish populations. Conservation Biology 10:136-154.

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, and Jones SHI. 2003. Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Marine Ecology Progress Series 261:135-147.

McManus JW, and Polsenberg JF. 2004. Coral-algal phase shifts on coral reefs: ecological and environmental aspects. Progress in Oceanography 60:263-279.

Moberg F, and Folke C. 1999. Ecological goods and services of coral reef ecosystems. Ecological economics 29:215-233.

Morrison D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology 69:1367-1382.

Mumby PJ, Broad K, Brumbaugh DR, Dahlgren CP, Harborne AR, Hastings A, Holmes KE, Kappel CV, Micheli F, and Sanchirico JN. In press. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. Conservation Biology.

Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, and Gill AB. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98-101.

Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, and Blackwell PG. 2007. Trophic cascade facilitates coral recruitment in a marine reserve. Proceedings of the National Academy of Sciences of the United States of America 104:8362-8367.

Neto AI. 2000. Observations on the biology and ecology of selected macroalgae from the littoral of Sao Miguel (azores). Botanica Marina 43:483-498.

Nugues MM, and Bak RPM. 2006. Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. Marine Ecology Progress Series 315:75-86.

Ogden JC, Brown RA, and Salesky N. 1973. Grazing by the echinoid Diadema antillarum Philippi: Formation of halos around West Indian patch reefs. Science 182:715-717.

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenechan L, Newman MJH, Paredes G, Warner RR, and Jackson JBC. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955-958.

Paul VJ, and Hay ME. 1986. Seaweed susceptibility to herbivory: chemical and morphological correlates. Marine Ecology Progress Series 33:255-264.

Richardson JP. 1979. Overwintering of Dictyota dichotoma (Phaeophyceae) near its northern distribution limit on the east coast of north America. Journal of Phycology 15:22-26.

Sammarco PW. 1980. Diadema and its relationship to coral spat mortality: grazing, competition, and biological disturbance. Journal of Experimental Marine Biology and Ecology 45:245-272.

Sammarco PW. 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. Journal of Experimental Marine Biology and Ecology 61:31-55.

Steneck RS. 1983. Quantifying herbivory on coral reefs: Just scratching the surface and still biting off more than we can chew. Pages 103-112 *in* M. L. Reaka, editor. The ecology of deep and shallow coral reefs. NOAA.

Steneck RS. 1997. Crustose corallines, other algal functional groups, herbivores and sediments: complex interaction along reef productivity gradients. Proceedings of the 8th International coral reef symposium 1:695-700.

Szmant AM. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries 25:743-766.

Tanner JE. 1995. Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. Journal of Experimental Marine Biology and Ecology 190:151-168.

Thacker RW, Ginsburg DW, and Paul VJ. 2001. Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. Coral Reefs 19:318-329.

Umar MJ, McCook LJ, and Price IR. 1998. Effects of sediment deposition on the seaweed Sargassum on a fringing coral reef. Coral Reefs 17:169-177.

Williams ID, Polunin NVC, and Hendrick VJ. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. Marine Ecology Progress Series 222:187-196.

Chapter 6 Synthesis and Conclusion

SYNTHESIS AND CONCLUSION

1 SYNTHESIS

1.1 Introduction

The degradation of Caribbean coral reefs is of a major concern, not only in terms of intrinsic values such as loss of biodiversity, but also because millions of people are directly dependent on the coral reef for their livelihood (Marshall and Schuttenberg 2006). Besides the direct benefits derived from the coral reef, reefs also provide important functions such as coastal protection from storms and hurricanes (Moberg and Folke 1999). The causes of the declining health of coral reefs are numerous, ranging from hurricanes, bleaching and diseases to direct anthropogenic impacts such as nutrification from point sources and runoff, increased sedimentation from deforestation and dredging, mining of corals, destructive fishing techniques and overfishing (Lapointe and Matzie 1996, Aronson and Precht 2001, Hughes et al. 2003). With the now widely accepted hypothesis of climate change, these impacts on the reef may be even more enhanced and makes it very difficult for reefs to recover from disturbances (Hoegh-Guldberg et al. 2007).

A consequence of these impacts is that many coral reefs in the Caribbean have now changed from a coral dominated to a macroalgal dominated habitat. This alternate state may be stable (Knowlton 1992, Mumby et al. 2007). Macroalgal dominated coral reefs are generally characterized by low rugosity, changed trophic dynamics, a reduction in biodiversity and reduces the ability of coral reefs to provide coastal protection from storms and hurricanes. In general two hypotheses were suggested as being the main factors in determining the standing crop of macroalgae. Many studies have indicated the important role nutrients play in enhancing macroalgal growth and is frequently cited as the primary cause for macroalgal dominance (Lapointe 1987, Delgado and Lapointe 1994, Lapointe 1997, Schaffelke and Klumpp 1997, 1998, Lapointe et al. 2004, Littler et al. 2006). Other studies, however, have indicated grazing as being the main process in determining macroalgal standing crop (Sammarco 1982, Carpenter 1986, Hughes 1994, Belliveau and Paul 2002, Mumby et al. 2006, Hughes et al. 2007). It remains controversial to which is the main cause and subsequent studies which combined both grazing and nutrients were also largely inconclusive (McCook 1996, Smith et al. 2001, Belliveau and Paul 2002, Lapointe et al. 2004). The differential results are mainly caused because of the inherent characteristics of macroalgae and herbivores, differences in environmental conditions of habitats in which experiments were carried out or because the duration of the experiment was too short. Therefore, it is clear that generalizations of responses of macroalgae to changes in the environment and ecological processes are difficult to make.

In the Caribbean many coral reefs are dominated by two macroalgae, *Dictyota* spp. and *Lobophora variegata* (Lamaroux). Both macroalgae are from the same family, Dictyotaceae, but exhibit different growth forms. *Dictyota* spp. displays a creepy interwoven to bushy growth form with dichotomous branching. *Lobophora variegata* on the other hand has flat blades displaying three distinct growth forms, decumbent, crust, and ruffled. The distribution of these growth forms depends on depth, the level of grazing and upon the habitat (Lewis et al. 1987, Littler and Littler 2000). Understanding the dynamics of these dominant macroalgal species is important, because of the key role they play in the resilience of coral reefs.

This thesis has focussed on the spatial dynamics of the two dominant macroalgal species. Emphasising on spatial dynamics is justifiable since most processes of interaction with corals on the coral reef have a spatial character, such as pre-emption, abrasion, overgrowth and shading. The studies concentrated on the forereef habitat classified as the *Montastraea annularis* zone (Geister 1977). The focus is on this habitat, because this area generally has the highest biodiversity of reef organisms and the major reef building corals are found in this zone (Mumby et al. 2008), therefore, potential disturbances can have the greatest impact on this habitat in terms of resilience and modification of the reef habitat. Also, previous investigations indicated the importance of inter habitat differences in responses of macroalgae to disturbances (Foster 1987).

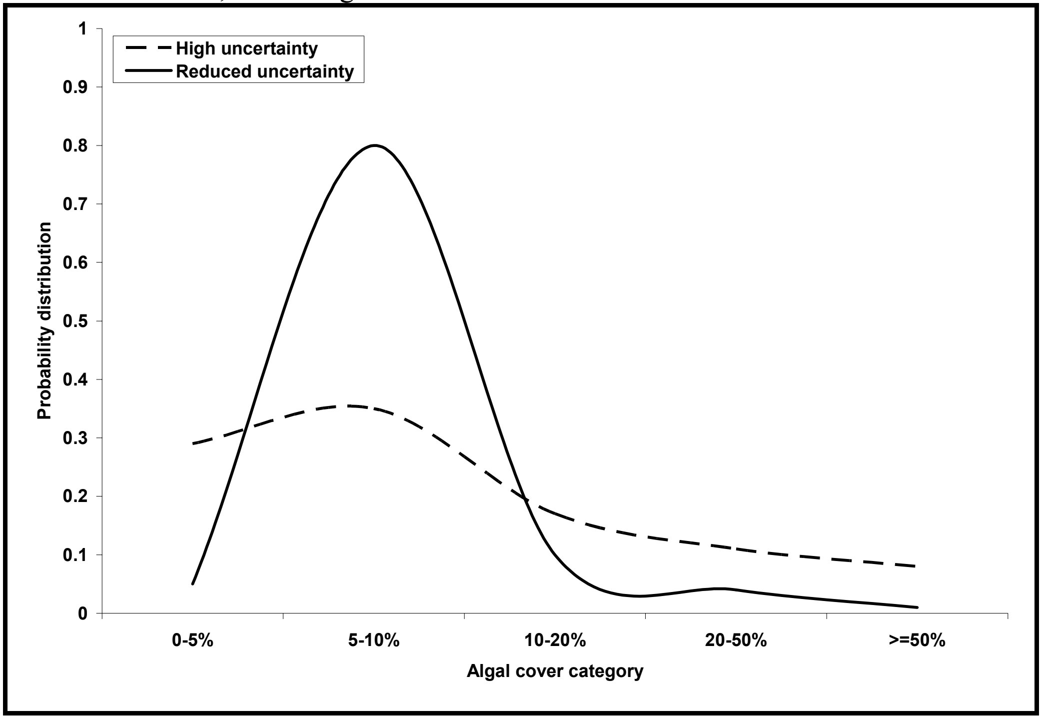
1.2 Bayesian Belief Network modelling of macroalgal dynamics

A Bayesian Belief Network (BBN) modelling approach was used to model macroalgal dynamics using *Dictyota* spp. as the model genera. I chose to focus only on one genera to try to keep the modelling simple, because this is a first BBN model developed for any macroalgal species. A BBN model can be described as a form of influence diagram depicting the causal relationships among physical and ecological factors influencing the outcome states of parameters of interest, here the percent cover of *Dictyota* spp. BBN models have gained popularity in recent years in ecology (Marcot et al. 2001, Borsuk et al. 2004, Wooldridge et al. 2005), but to my knowledge, no previous BBN models have been developed investigating the dynamics of macroalgae on coral reefs. The interactions of factors and processes determining macroalgal standing crop are complex and manifold. A BBN is ideally suited to modelling these complex systems. Overall the model behaves accordingly to recent thinking in what drives macroalgal dynamics on coral reefs. It has to be kept in mind that the model was based on data from one particular site (Glovers Reef) and as such is not suitable to use for other locations. The model indicates that the main controlling factor is herbivory, which was recently found as well (Burkepile and Hay 2006, Mumby et al 2007), although the influence of nutrients cannot be discarded as insignificant. The relative lack of sensitivity of algal cover to nutrients in our model is likely caused by the large amount of uninformed conditional probabilities, because of a lack of data to accurately define the relationships at all combinations of levels in the CPT's. The lack of data needs to be addressed in future experimental studies by addressing macroalgal responses at physiological levels.

The model had a modest accuracy, which can be explained by a few important points. The discretization of the categories in the model nodes can have a strong influence on the accuracy and can accentuate errors. Narrower categories, (e.g. 10% intervals as opposed to 25%) would reduce this problem, but there is a necessary trade off between accuracy and uncertainty. Large categories may not be able to capture subtle dynamics, whereas too small categories might be infeasible given the uncertainty and lack of data to define accurately the conditional probabilities for each combination of levels. This was already shown in our model by the relatively large amount of uninformed conditional probabilities in parts of the model. However, this highlighted an important aspect of the model development. The data for determining the conditional probabilities came from the literature and field data and thus identified gaps where we could not accurately define the conditional probabilities. In BBN development it is a common procedure to use expert opinion where data is lacking. However we did not want to rely on expert opinion to avoid bias in our model development. Secondly, errors in the model can be accentuated because the model would treat an observed algal cover of 21% as incorrect if the predicted cover (i.e. the most likely) was 10-20%, yet the absolute error is small. This was highlighted by the graph of cumulative frequency of absolute errors, where 77% of predictions had an error of < 10%.

BBNs have some major advantages in modelling ecosystems. Algalnet is the first BBN model for macroalgal dynamics on coral reef. The modest accuracy of the current model should not be seen as the modelling technique being unsuitable for modelling algal dynamics, but it rather reflects our poor understanding of the system as a whole. A major advantage of using this type of modelling is that, because of its probabilistic nature it represents the interactions as likelihoods of outcomes given a certain scenario of physical and ecological parameters. Since a BBN explicitly shows the inherent uncertainties of the system modelled through a probability distribution, they can communicate the uncertainties associated with complex systems in a clear manner. Once new information becomes availably, the uncertainty will be reduced, shown by a narrowing of the probability distribution curve (Fig 6.1).

Fig 6.1. Hypothetical graph showing a narrowing of the probability distribution curve, due to an increase in certainty after new information on system variables and their interactions becomes available, increasing our belief in an outcome state of a variable of interest.



The BBN has a modular design, that is, a complex system of interacting factors can be deconstructed into smaller units or sub-models. This modular design makes it easy to update once new information becomes available. In addition new links and nodes can be added as well, if necessary, which allows for easy updating and there is no need to re-parameterize the complete model domain, saving time and effort.

BBN's are ideally suited to force experts involved in the development of the model to state their understanding clearly and translate the dependencies of factors in the model domain into a link-node structure. By making the subjective opinions of experts explicit in a formal model, they can be easily challenged and revised, if necessary. Therefore the BBN can also be used as a framework for research or monitoring programmes. New data from either experimental research or different geographical areas can be used to continuously update the BBN and improve its accuracy in predicting the standing crop of *Dictyota* spp., given a specific scenario of bottom-up and top-down processes, which will eventually show in the narrowing of the probability distribution curve (Fig. 6.1).

Finally, the graphical design of the BBN makes it easy to communicate the complex interactions and effects of physical and ecological processes on macroalgal dynamics to a wide variety of stakeholders.

1.3 Patch dynamics of *Dictyota* spp. and *Lobophora variegata*

Understanding the patch dynamics of *Dictyota* spp. and *Lobophora variegata* at levels smaller than individual sampling units provides important information on the interactions with competitors. Static measures such as percent cover may provide valuable but potentially misleading information. It might reveal that overall percent cover is fairly stable over time but the dynamics on the scale of individual patches can show great temporal fluctuations. Understanding these small-scale interactions is important because many interactions occur at the scales of individual patches. Contact interactions between macroalgae and corals are common along the margins of coral colonies (Lirman 2001). This high encounter rate between coral and algae will have a negative effect on both the macroalgae and coral (Tanner 1995). Although it seems that the negative effects of algae on coral outweigh the negative effects of coral on algae (Jompa and McCook 2002, Nugues and Bak 2006, Box and Mumby 2007). In these interactions therefore the length of time particular algae are in contact with corals plays an important role. Corals may easily avert the negative effects of macroalgae in the form of abrasion, shading and overgrowth, when the duration of contact is short. Hence it is important to investigate the patch dynamics of algae as this will provide an insight in the dynamics and potential contact time of algae with corals. This information cannot be deduced from overall percent cover. Percent cover cannot provide information on patch sizes and stability of individual patches, which will have an influence on contact interactions with corals.

Pre-emption of space is one of the key factors why algae are successful in colonizing coral reefs after a disturbance. Space covered by macroalgae is not available for coral recruits for settlement and hence macroalgae become the dominant organism. The patch dynamics behaviour over time of both species provided insight into the colonization of empty space of each respective species. The different approaches to colonization of *Dictyota* and *Lobophora* can be described in terms of guerrilla and phalanx growth froms (Collado-Vides 1999). Guerrilla growth forms strategies can be likened to highly mobile units, constantly moving, disappearing from areas and appearing in new ones. This behaviour is shown very much in

Dictyota spp., which showed high temporal variation in the dynamics on the exposed side of the atoll and to a lesser extent on the sheltered side. The differences between these sides can be explained by other factors, discussed later. Besides the temporal variation, *Dictyota* also showed a high degree of fragmentation and had few fusion events. Fragmentation is shown to aid in the rapid colonization of new areas (Herren et. al. 2006). On the other hand, *Lobophora variegata* showed a phalanx growth form, which can be likened to tightly packed units, slowly moving, retaining their original site for long periods, neither penetrating readily neighbouring areas nor are easily penetrated by other organisms. This strategy was clearly demonstrated by *Lobophora,* having fewer fragmentation events and more fusion events, indicative of patches growing close together. It is not clear which strategy is more successful because both species are the most dominant macroalgae on many Caribbean coral reefs. It is however, recognised that both these growth forms are a very effective means of dispersal in aquatic environments (Begon 1996).

Comparing the patch dynamics in similar habitats located at different physical exposures, for example a forereef on the windward and leeward sides of an atoll, provides an experimental set up to investigate the influence of different physical exposures on the patch dynamics of macroalgae. To analyse patterns in macroalgal patch dynamics, size-based transition matrix models were applied. Using a size-based approach, two aspects of spatial dynamics were important and needed to be incorporated explicitly into the matrices; fusion and fragmentation. Fusion happens when two or more patches grow close together and combine to form a large patch, whilst fragmentation entails the break up of a larger patch into smaller patches. Incorporating these processes explicitly has never been done before, but results showed they have a significant effect on the matrix model parameters. Ignoring fusion and fragmentation could significantly change the outcome of the matrix parameters to such an extent that a population which was shown by field data to be increasing in size would be identified by the matrices to be decreasing in size. The main two parameters to describe the matrices are the growth rate and damping ratio. The growth rate identifies the rate a macroalgal patch population can grow or decline, whilst the damping ratio identifies the speed with which a population of patches reaches a stable size distribution. The damping ratio is an indication of how much a population fluctuates in size. To support the interpretation of the growth rates and damping ratios, a novel parameter was introduced to indicate complex patch dynamics, the matrix entry ratio. This ratio is defined as the number of non-zero entries divided by the total number of entries in the matrix. The closer the ratio is to 1 (the maximum entry ratio) the greater the variability in patch dynamics.

The matrices illustrated that patch dynamics of *Lobophora variegata* and *Dictyota* spp. are very different, albeight both species belonging to the same family, Dictyotaceae. The patch dynamics of *Dictyota* spp. are highly sensitive to the physical environment, whilst *Lobophora* is far less sensitive. Also the patch dynamics of *Dictyota* spp. showed greater fluctuations over time on the exposed forereef compared to *Lobophora*. In January, the clearest difference in patch dynamics was shown. *Dictyota* spp. virtually disappeared on both the windward and leeward sides of the atoll, whereas *Lobophora variegata* continued to increase in size, irrespective of the side of the atoll. The distinctive decline of *Dictoyta* on both sides of the atoll is very likely related to a life history event, such that after reproduction, the reproductive tissue might have been lost and the alga survives the cooler period as a holdfast only, for which some evidence was found in North Carolina (Richardson 1979). Seasonality in abundance, biomass, growth and reproduction have been found in many macroalgal species (McCourt 1984, Diaz-Pulido and Garzon-Ferreira 2002, Ateweberhan et al 2005, Diaz-Villa et al 2005). Although these patterns were found, they might not always match patterns in temperature, salinity and light regimes, which might have to do with a lag in response time to environmental changes (the alga has to play catch-up) or it is an effect of nutrient luxury-uptake. Nutrient luxury uptake is the process of storing excess nutrients in time of plenty and is subsequently utilized when nutrients are limiting and hence the alga can maintain its growth during adverse periods.

The difference in fragmentation events between *Dictyota* spp. and *Lobophora variegata* may be explained by the selective foraging behaviour of herbivorous fishes. In general the average size of patches of *Dictyota* spp. were larger and more abundant than those of *Lobophora* and therefore may have been more easily spotted. Also *Dictyota* was more frequently consumed in a ration of 3:1 compared with *Lobophora* (pers. observ.).

A distinct difference in cover was observed in *Dictyota* spp. when the exposed and sheltered sides of the atoll were compared, with the exposed side having a higher cover, whilst for *Lobophora variegata* the cover was fairly similar. The differences in cover between *Lobophora* and *Dictyota* can be explained by their respective growth forms, i.e. a bushy branching form for *Dictyota* compared with a flat blade like form for *Lobophora*, which adheres closely to the substratum. These distinct differences will have resulted in different surface to volume ratios, which is an important aspect in nutrient uptake dynamics of algae. The higher surface to volume ratio of *Dictyota* will result in higher uptake rates and hence promote higher growth rates.

The differences in cover of *Dictyota* spp. between the two sides of the atoll can be explained by the fact that *Dictyota* obtained higher growth rates on the exposed side. Three factors play a role here: ambient nutrient concentrations, water flow and light. Ambient nutrients concentrations are similar on both sides of the atoll and this is unlikely to explain the difference. However, water flow rates were significantly different, with higher rates on the exposed side. Water flow is an important factor in increasing the nutrient uptake rates for algae and this might have explained the differences in cover. Light is one of the key requirements for algae. The exposed side due to the fact of having higher water flow rates has greater visibility compared with the sheltered side. Therefore algae growing on this side of the atoll will receive higher levels of light enhancing photosynthesis and ultimately growth rates. The combination of higher water motion and light levels could very easily have explained the differences, and this should be explored in the future (see next section).

Many macroalgae show a high degree of polymorphism (De Ruyter van Steveninck et al 1988, Hanisak et al 1988, Hwang et al 2005, Fowler-Walker et al 2006). Polymorphism is thought to be a strategy to help organisms to adapt to their respective environments and thus create a competitive advantage (Begon et al 1996). Polymorphism will provide an alga with advantages to overcome adverse conditions. The alga might adapt to increase the surface to volume ratio, which increases their photosynthetic capacity and nutrient uptake ability because relative more cells in the plant are available for this process. In more complex forms, part of the cells will be dedicated to maintain structure and these cells are not available for metabolic functions. Secondly, the algae adapts to a more closely adhering from to the substrate to reduce sheer stress from waves and sediment scouring. The lack of significant difference in patch dynamics and cover of *Lobophora variegata* between the two sides of the atoll might be explained by polymorphism because *Lobophora variegata* displays three distinct growth forms depending on the environment in which they grow (De Ruyter van Steveninck et al 1988, Littler and Littler 2000). Although there was no obvious difference in their respective growth forms, they were able to maintain similar growth rates and patch dynamics, in considerable different environments. The levels of herbivory were very similar on both sides and hence the growth forms might not have shown a great deal of difference as *Lobophora* is thought to be very well chemically defended against herbivory (Arnold and Targett 2000). The degree of polymorphism might be of a more subtle nature in terms of cell and pigment concentrations adaptations. This needs further exploration in the future.

1.4 Effects of grazing pressure and physical exposure

Grazing is one of the key processes on coral reefs and has a large influence on the ability of reefs to withstand disturbances and aid in recovery of reefs (Mumby 2006). Grazing will in part determine the maximum amount of macroalgal biomass and has direct and indirect effects on coral-algal interactions. Similarly, physical exposure can have a pronounced effect on the cover of macroalgae. The effects of grazing on the cover of *Dictyota* spp. and *Lobophora variegata* were investigated by using experimental cages which allowed for different grazing scenarios, (1) both fish and urchin grazers, (2) fish grazing only and (3) no fish grazing at all, which was completed with (4) a cage control. The experimental treatments were set up on forereefs with different wave exposures. The grazing effects of urchins could not be isolated and therefore the results were analysed as differences in grazing pressure rather than by herbivore guild.

The results of this experiment partly supported the outcomes of the patch dynamics investigated with size based transition matrices. For *Dictyota* spp. the percent cover was significantly higher for the exposed side of the atoll compared with the sheltered side, whereas for *Lobophora* no significant differences were found. In plots where both fish and urchins were excluded from grazing, macroalgal cover of both species rapidly increased compared to the experimental plots where grazing was allowed. Although on the exposed side the cover of *Lobophora* did not increase significantly and actually on plots where there was low grazing, the cover of *Lobophora* was even higher although not significantly. This effect can be explained by interspecific competition with *Dictyota*. Overall the results are what we would expect given previous herbivore exclusion studies. In addition, the results showed that even grazing by small parrotfishes alone was sufficient to control the cover of *Dictyota* spp. and *Lobophora variegata*, at least on the sheltered side of the atoll, whilst on the exposed reefs small parrotfishes were only able to reduce the rate of increase in percentage cover. On the sheltered side the seemingly control of macroalgal cover by even low grazing can be attributed to the slower growth rates of macroalgae on this side, which I attribute to the differences in the physical environment.

Diadema antillarum is thought to be a key stone species on Caribbean coral reefs (Hughes 1994, Lessios et al 2001), although some argued otherwise (Jackson and Kaufmann 1987) and received a lot of attention. Studies have shown that recovery is occurring and this has aided the recruitment of corals (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006). After the mass mortality of this urchin, studies showed a rapid increase in cover of macroalgae, which supported the notion that herbivory is a key process on coral reefs. In this experiment the effects of grazing by *Diadema antillarum* could not be isolated from the effects of parrotfish grazing. Besides this, the density of this urchin was very low on both sides (< 1 m^{-2}) of the atoll and at these densities it is believed that they cannot control the cover of macroalgae in the reef. However, urchins may be able to control the cover in there territories, which are only on average 1.5 m^2.

Interspecific competition has been studied intensively as it is one of the key processes in population dynamics and the structuring of ecological communities (see Begon et al 1996 and references herein). In short interspecific competition will lead to individuals of one species suffering a reduction in fecundity, survivorship or growth as a result of resource exploitation or interference by individuals of another species. Interspecific competition between *Dictyota* and *Lobophora* most likely explained the unexpected results of the caging experiment. Whilst there was a significant difference in cover if *Dictyota* between the exposed and sheltered side of the atoll for the cages where all grazers were excluded, this was not found for *Lobophora.* In fact, in the grazer exclusion cages on the exposed side of the atoll *Lobophora* cover was lower than in the cages where grazing was permitted. This effect may be explained by competition with *Dictyota*. At the start of the experiment all algae were removed to create similar conditions for both *Dictyota* and *Lobophora*. After two months *Dictyota* cover about 42% and increased to an average of 55%. *Lobophora* on the other hand showed an average of only 0.8% after two months and 2% at the end of the experiment on the exposed side of the atoll. Comparing this to the sheltered side the average cover for *Dictyota* was 13% after two months and a maximum of 30%. *Lobophora* showed an average of 1.2 % at two months and an average of 6% at the end of the experiment. This may be indicative of a competitive advantage of *Dictyota* over *Lobophora*. *Dictyota* competes for resources and space with *Lobophora* and owing to higher growth rates has overwhelmed *Lobophora* on the exposed side of the atoll. Whilst on the sheltered side *Dictyota* grew slower and *Lobophora* managed to increase its cover relatively more than on the exposed side of the atoll. This competitive advantage of *Dictyota* was also demonstrated by comparing the cages with low grazing.

Lobophora variegata however seems to be able to cope with the overgrowth of *Dictyota*. *Dictyota* shows more fluctuations over time and at the end of the experiment virtually disappeared from all treatments, whilst *Lobophora* was increasing in cover on all treatments. This scenario abides well with the phalanx and guerrilla type growth strategies both algae are displaying. This needs to be further investigated on a long term experiment with more repetition.

2 FUTURE RESEARCH

2.1 Bayesian Belief Network modelling

The results from the Bayesian Belief Network (BBN) are very encouraging, although having a modest accuracy. The modest accuracy was caused by the large numbers of uninformed conditional probabilities and not because BBN modelling is unsuitable for our purpose. The BBN relied only on data and processes identified from the literature and complemented by field data. Therefore, the BBN was useful in identifying gaps in our understanding of bottom-up and top-down processes acting on the standing crop macroalgae.

There was little information on the interactive effects of water motion and nutrients and interactive effects of light and nutrients. Certainly the relationship between water motion and nutrients has been investigated in the past (Atkinson and Bilger 1992, Bilger and Atkinson 1995, Hearn et al. 2001) as well as the interactive effects of light and nutrients (Lapointe and Tenore 1981, Littler et al. 1988, Creed et al. 1997, Cronin and Lodge 2003), but to fully substantiate the effects more research is needed. Many nutrient manipulation experiments are done with nutrient levels well above the ambient levels recorded on the reef. Mainly this is done to show the effects of nutrient enrichment on macroalgal growth and where no response was noted, the conclusions was that the alga was not nutrient limited.

The BBN modelled the bottom-up and top-down processes on *Dictyota* spp. and the results from previous experiments might not be applicable to *Dictyota* spp. because they investigated other macroalgal species, which may respond differently. To investigate the effects of nutrients, light, water motion and their interactive effects, future research should have a more systematic approach to manipulation experiments using ecological relevant levels of nutrients, light and water flow under preferable natural conditions and targeting macroalgal species most likely to be involved in the overgrowth of coral reefs. The field experiments could be supplemented with laboratory experiments, if it is shown that certain relationships are difficult to fully quantify under natural conditions. The BBN is helpful in this respect, because of the modular design it identifies the smallest sub units at which experiments should be undertaken and may proof to be easier to quantify.

The BBN was developed modelling one type of macroalga (*Dictyota* spp.). If the model is to be more representative of a wider environment and the algal community as a whole, then it might be more useful to use a functional group approach (sensu Steneck and Watling 1982 and Steneck and Dethier 1994). Combining groups of algae with similar growth forms may provide a better insight. The cover of *Dictyota* spp. is highly variable over time and therefore might have affected the accuracy of the model unduly. Combining several algae of the same morphological group may give a better performance because the variability over time may be smoothed. Cover of individual algae may fluctuate but the overall cover is more stable over time and only the species composition within the overall cover will vary.

The BBN was parameterized in part with data collected from a particular environment, i.e. Glovers Reef Atoll. Here nutrient levels are not particularly high and do not seem to enhance macroalgal overgrowth (McClanahan et al. 2004) and biomass levels of fish grazers are amongst the highest recorded in the Caribbean (Mumby 2006). Clearly, new information from other parts of the Caribbean where nutrification and/or overfishing take place might result in different outcomes. This leads on to another important aspect of BBNs. The BBN can be used as a framework for research and monitoring, because relying only on data, will require large datasets. The potential to use the BBN for cooperative monitoring programmes is large, because BBNs are flexible in nature and can be very easy updated once new information becomes available.

A Caribbean wide monitoring programme needs careful planning but is feasible. Certain monitoring programmes, such as AGGRA, are already collecting most of the data from many locations, however not all data is published. Secondly, many volunteer based organizations are operating in the Caribbean, like Coral Cay Conservation and Global Vision and they may help in data collection. The data collection methods utilized to parameterize the model are simply and easy to undertake, with limited logistical means.

If the model is to be used on a Caribbean wide scale, incorporating various coral reef habitats it would very likely be necessary to incorporate additional nodes to differentiate between coral forereef habitats such as back reef habitats or coral reef flats, as we can expect algal dynamics to be different between these habitats. In addition certain nodes might be added to incorporate other interactions, for example a node covering the direct contact of the algae with corals. Recent studies have shown the effects of both algae on corals and vice versa (Jompa and McCook 2003, Nugues and Bak 2006, Box and Mumby 2007). The flexibility of the BBN's in incorporating new nodes will make this fairly easy to do.

Finally, there is always a possibility to use expert opinion to develop parts of the model when data is difficult to come by. I did not use this approach because I both developed the model network and determined the prior and conditional probabilities based on literature. If I relied on my own judgement to define conditional probabilities of combinations of levels of nodes, the potential for bias is huge and the development of the exercise becomes nothing more than an exercise in organizing my thoughts (however useful that may be!). If relying also on expert opinion a slightly different approach needs to be followed. The determining of the conditional probabilities will have to be done by a group of experts, which ideally will be independent from those who developed the network structure. This group of experts will each be asked the same questions regarding the particular conditional probabilities. For example in my model the conditional probabilities of the node Algal Growth Rate will depend on the node Nutrient Availability and the node Light. Fore the node Algal growth rate, the following questions could be asked to each individual member of the panel of experts:

- Given that the amount of light is high and the level of nutrient availability is low, what is the probability of Algal growth rate being high?
- Given that the amount of light is high and the level of nutrient availability is low, what is the probability of Algal growth rate being low?
- Etc.

Subsequently the answers to these questions will be averaged for each level of combinations in the node Algal growth rate. This will then give you a reasonable good conditional probability for the respective node. Research has shown that human estimators are prone to overconfidence, that is giving estimates that are too near zero or one (Uusitalo 2008), but averaging the opinions of a group of experts will reduce error in the estimation process.

2.2 Patch dynamics of *Dictyota* spp. and *Lobophora variegata*

Patch dynamics of macroalgae are an important ecological process, because many interactions between organisms are of a spatial nature. Different species may therefore have differential outcomes of interactions with potential competitors. Static measures such as percent cover may not always reveal the underlying dynamics of macroalgae at scales smaller than individual sampling units. Besides, the differential impacts of macroalgal species, the environment can have a pronounced influence on the dynamics of a given species. Sized based transition matrices provided insight into the dynamics of both *Dictyota* spp. and *Lobophora variegata* and revealed significant differential behaviour.

Size based transition matrices proved to be a useful tool investigating the patch dynamics of macroalgae. The matrices developed for both species could be further investigated, using for example elasticity analysis. Elasticity is defined as the proportional perturbation. For example, the response of growth rate (dominant eigenvalue λ_1) to a 10% change in survival, reproduction or growth. Elasticity analysis can be used to identify to what part of the life history a macroalgae is most sensitive. To determine the elasticity we first need to determine the sensitivity. The sensitivity of λ_1 to small changes in matrix entries can be calculated. Caswell (1978) introduced a general approach and showed that:

$$\Delta\lambda_1/\delta\lambda a_{ij} = v_i\, w_j/ \langle w,v \rangle$$

Where $\langle w,v \rangle$ is the scalar product of w and v. This means that the sensitivity of λ_1 to changes in a_{ij} is proportional to the product of the i^{th} element of the reproductive value vector v and the j^{th} element of the stable size distribution w (Caswell 2001). The elasticity of λ_1 with respect to a_{ij} is defined as:

$$E_{ij} = (a_{ij}/\lambda_1).(\Delta\lambda_1/\delta\lambda a_{ij})$$

Which gives the proportional change in λ_1 resulting from a proportional change in a_{ij}. The elasticities of $\lambda 1$ may also be used as an estimate of the contribution of each element a_{ij} to λ_1 These metrics can be easily calculated with the Matlab software once the matrices are constructed. The following one line scripts need to be run to determine the sensitivity:

```
senmat=v*w′
```

And for elasticity the script is:

```
emat=senmat.*A/max(eig(A))
```

Both these scripts will return a matrix giving the sensitivities and elasticities associated with matrix A.

Many environments are variable and disturbances can lead to substantial changes in a population’s size distribution. In these situations the long-term growth rate (λ_1) may not accurately describe the population growth in the short-term (transient). Small damping ratios indicate that transient dynamics are important in the life history of the species. Metrics have been developed to investigate transient dynamics (Townley et al. 2007).

The differences in patch dynamics of *Dictyota* spp. for both sides of the atoll needs to be explored in terms of the effects of water motion and light on the growth of *Dictoyta*. In water experimental plots could be set up to allow detailed water motion studies using water flow meters and the light environment can collected in situ using a pulse-amplitude modulated fluorometry. Clear differences were shown and is likely to be associated with the effects of water flow and light or a combination of both factors. Experimental studies need to be undertaken to clarify these.

There seems to be very limited information on recruitment and reproduction of *Lobophora variegate*, although past studies have revealed the limited dispersal range of this species. There is an urgent need to investigate these parts of the life history of *Lobophora*. Results from the matrix models revealed that *Lobophora* is relatively insensitive to the environment. To elucidate what might make this species so competitive information on reproduction, recruitment, physiological rates and morphology is urgently needed. Very likely the success of *Lobophora* is related to its morphology and simple collections over a wide range of similar habitats but different physical exposures could be carried out to compare its morphology in terms of cell wall thickness, multiple layers of cells, and surface to volume ratios can be calculated.

2.3 Effects of grazing pressure and physical exposure

Grazing is considered to be one of the key processes on coral reefs and herbivores play an important role in the resilience of coral reefs to disturbances (Mumby et al. 2006). In the past numerous herbivore manipulation experiments have been carried out and these studies indicated a strong effect of herbivores on macroalgal standing crop (Sammarco 1982, Carpenter 1986, Lewis 1986, Foster 1987, Hughes et al. 2007). The caging experiment also confirmed a significant effect on macroalgal cover in that the cover of both *Dictyota* spp. and *Lobophora variegata* increased when both fish and urchin grazers were excluded irrespective of exposure. The caging experiment also attempted to differentiate the effects of the herbivore guilds by excluding or including urchins as grazers. However the caging experiment could not isolate the effects of urchins grazing. It proved difficult to increase the densities of urchins on the exposed forereef due to high predation and the need to construct very large cages to attain a sufficiently large urchin density.

Diadema antillarum densities were extremely low and future research should be aimed at investigating at what levels *Diadema antillarum* becomes a significant contributor to grazing through the use of transplant experiments. These transplant experiments should apply different urchin densities to elucidate at what densities they may significantly start to affect macroalgal cover. Transplant experiments should be done with sufficient numbers of *Diadema*. The *Diadema* urchin is heavily predated on by fish predators and Octopus. This was the reason I had to abandon the experiment as none of the *Diadema* survived once they were discovered by predators. Alternatively, caging experiments should have an additional cage treatment in which urchins are incorporated but fish grazers excluded, may provide more inside into the effects of urchin grazers. Although these cages need to be of sufficient size to avoid artificially increasing the grazing pressure on algae because the feeding area is constrained by the cage, i.e. it is smaller than the average *Diadema* territory.

Further, since it seems that interspecific competition played an important role in the dynamics of *Dictyota* and *Lobophora* in the all grazer exclusion cages, additional experiments need to be undertaken to establish these competitive interactions. A long term experiment using the same set up as was applied in my grazer exclusion experiment should be undertaken for at least a year incorporate seasonal effects on both *Dictyota* and *Lobophora*. Seemingly both growth strategies are very successful for algae in becoming the dominant macroalgae on these reefs. These experiments can elucidate the competitive interactions between these species.

Finally, the retrospective statistical analysis of the caging experiment indicated that the variable results of the caging experiment for *Lobophora* may have been an effect of the limited replication in the experiment. Future caging experiments should at least double the amount of cages that were used in the experiment here.

3 MANAGEMENT CONSIDERATIONS OF THE RESEARCH

Once the BBN is fully specified and updated it can be very useful for coral reef management. First of all, predicted outcomes are expressed as likelihood's, making the BBN amenable to risk-analysis. The risk analysis then forms a basis for rational decision making based on precautionary principles. Secondly, the BBN is an ideal framework for testing future scenarios. For example, scenarios could be run with a reduction of herbivores on the reef, a significant increase in nutrients in the coral reef environment or various combinations of both scenarios, which will be shown in changes in algal percentage cover. BBN's can also be used as a diagnostic tool to investigate what are the most likely causes of a high algal cover. This will aid coral reef management in prioritizing management strategies, especially when resources are limited.

Matrix models are a useful tool for conservation management. Matrix models can be used to investigate the behaviour of species under different management scenarios. For example, Brys et al (2004) studied the effects of different management strategies of grassland on the demography of *Primula veris*. Crouse et al (1987) investigated which life history stages of

loggerheads turtles are most sensitive to impacts and hence conservation strategies can be focussed on this stage. For example, rather than focussing on nesting sites, it proves more effective to focus efforts on adult populations, to ensure the species survival.
Diadema antillarum is considered a key stone species in the Caribbean and attempts need to be made to enhance this species. Management strategies have focussed on enhancement of this species in areas through transplanting adult from nearby areas to form aggregates or transplanting laboratory reared juveniles to the reef. The results of these experiments were mixed, mainly due to predation and more research is needed to understand the ecology and biology to make such attempts successful.

4 CONCLUSIONS

1. *Dictyota* spp. seems to be highly sensitive to physical exposure in that the highest percent cover is found on forereefs on the windward side of the atoll compared to the leeward side of the atoll, whilst *Lobophora variegata* does not show a significant difference in cover.

2. Patch dynamics of *Dictyota* spp. showed larger fluctuations compared to *Lobophora variegata*. The fluctuations in cover and patch dynamics in *Dictyota* spp. seem to be more pronounced on the windward side of the atoll. *Lobophora variegata* on the other hand does not show large fluctuations but a steady increase in cover, on either side of the atoll likely related to physiological responses of this species .

3. Herbivores seemingly have a significant effect on the cover of both *Dictyota* spp. and *Lobophora variegata* in that the cover of both species increased significantly where herbivores are not present, irrespective of physical exposure.

4. Fish grazing alone is sufficient to control the cover of *Dictyota* spp. and *Lobophora variegata* on the leeward side of the atoll, whilst for the windward side fishes could only reduce the rate of increase.

5. The Bayesian Belief Network model showed a modest accuracy in predicting the cover of *Dictyota* spp. However, this modest accuracy is largely attributed to the uninformed probabilities of the model and perhaps being developed for a single location.

6 The Bayesian Belief Network identified gaps in our understanding of the bottom-up and top-down processes determining the standing crop of macroalgae, such as the interaction of nutrients and water flow and nutrients and light on ecological relevant levels.

7 Future research experiments and monitoring programmes could provide more insight in the bottom-up and top-down processes and it is anticipated once this information becomes available the BBN model will improve significantly in accuracy. Once fully updated, the BBN could become a useful tool in management and research for investigating the effects of different scenarios of bottom-up and top-down processes on macroalgal standing crop.

8 The behaviour of macroalgae is seemingly strongly related to localised circumstances and therefore future research should ideally have a species specific approach, defined clearly by habitat, to investigate the controlling factors on macroalgal standing crop.

4 REFERENCES

Aronson RB, and Precht WF. 2001. White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460:25-38.

Atkinson MJ, and Bilger RW. 1992. Effects of water velocity on phosphate uptake on coral reefs. Limnology and Oceanography 37:261-272.

Ateweberhan M, Bruggemann JH, Breeman AM. 2005 Seasonal patterns of biomass, growth and reproductoin in Dictyota cervicornis and Stoechospermum polypodioides (Dictyotales, Phaeophyta) on a shallow reef flat in the southern Red Sea (Eritrea). Botanica Marina 48:8-17

Begon M, Harper JL, and Townsend CR. 1996 Ecology: individuals, populations and communities, Blackwell Publishers. pp 1068.

Belliveau SA, and Paul VJ. 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. Marine Ecology Progress Series 232:105-114.

Bilger RW, and Atkinson MJ. 1995. Effects of nutrient loading on mass transfer rates to a coral reef community. Limnology and Oceanography 40:279-289.

Borsuk ME, Stow CA, and Reckhow KH. 2004. A bayesian network of eutrophication models for synthesis, prediction and uncertainty analysis. Ecological Modelling 173:219-239.

Box SJ, and Mumby PJ. 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Marine Ecology Progress Series 342:139-149.

Brys R, Jacquemyn H, Endels P, Blust de G, Hermy M. 2004. The effects of grassland management of plant performance and demography in the perennial herb Primula veris. Journal of Applied ecology 41:1080-1091.

Burkepile DE, and Hay ME. 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128-3139

Carpenter RC. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs 56:345-363.

Carpenter RC, Edmunds PJ. 2006. Local and regional scale recovery of Diadema promotes recruitment of scleractinian corals. Ecology Letters 9: 271-280.

Collado-Vides L. 1999. Morphology and photosynthesis of Caulerpa (Chlorophyta) in relation to growth form. Journal of Phycology 35:325-330

Creed JC, Norton TA, and Kain JM. 1997. Intraspecific competition in Fucus serratus germlings: The interaction of light, nutrients and density. Journal of Experimental Marine Biology and Ecology 212:211-223.

Crouse DT, Crowder LB, Caswell H. 1987. A stage-based population model for loggerhead turtles and implicatoins for conservation. Ecology 68:1412-1423.

Cronin G, and Lodge DM. 2003. Effects of light and nutrient availability on the growth, allocation, carbon/nitrogen balance, phenolic chemistry and resistance to herbivory of two freshwater macrophytes. Oecologia 137:32-41.

De Ruyter van Steveninck ED, Kamermans P, Breeman AM. 1988. Transplant experiments with two morphological griwth forms of Lobophora variegata (Phaeophyceae). Marine Ecology Progress Series 49:191-194.

Delgado O, and Lapointe BE. 1994. Nutrient-limited productivity of calcareous versus fleshy macroalgae in a eutrophic, carbonate-rich tropical marine environment. Coral Reefs 13:151-159.

Diaz-Pulido G, Garzon-Ferreira J. 2002. Seasonality in algal assemblages on upwelling-influenced coral reefs in the Colombian Caribbean. Botanica Marina 45:284-292.

Diaz-Villa T, Sanson M, Afonso-Carillo J. 2005. Seasonal variations in growth and reproduction of Sargassum orotavicum (Fucales, Phaeophyceae) from the Canary Islands. Botanica Marina 48:18-29.

Edmunds PJ, Carpenter RC. 2001. Recovery of Diadema antillarum reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proceedings of the National Academy of Sciences of the United States of America 98:5067-5071.

Foster SA. 1987. The relative impacts of grazing by Caribbean coral reef fishes and Diadema: effects of habitat and surge. Journal of Experimental Marine Biology and Ecology 105:1-20.

Fowler-Walker MJ, Wernberg T, Connell SD. 2006. Differences in kelp morphology between wave sheltered and exposed localities: morphologically plastic or fixed traits? Marine Biology 148:755-767.

Geister J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Proceedings of the 3rd International Coral Reef Symposium 1:23-30.

Hanisak MD, Littler MM, Littler DS. 1988. Significane of macroalgal polymorphism: intraspecific tests of the functional-form model. Marine Biology 99:157-165.

Hearn CJ, Atkinson MJ, and Falter JL. 2001. A physical derivation of nutrient uptake in coral reefs: effects of roughness and waves. Coral Reefs 20:347-356.

Herren LW, Walters LJ, and Beach KS. 2006. Fragmentation generation, survival, and attachment of Dictyota spp. At Conch Reef in the Florida Keys, USA. Coral Reefs 25:287-295.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, and Hatziolos ME. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318:1737-1742.

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 RM, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas JA, Lough J, Marshall PA, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, and Rougharden J. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929-933.

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli DM, Hoegh-Guldberg O, McCook LJ, Moltschaniwskyj NA, Pratchett MS, Steneck RS, and Willis BL. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology 17:360-365.

Hwang I-K, Kim H-S, Lee WJ. 2005. Polymorphism in the brown alga Dictyota dichotoma (Dictyotales, Phaeophyceae) from Korea. Marine Biology 147:999-1015.

Jackson JBC, Kaufmann KW. 1987. Diadema antillarum was not a keystone predator in cryptic reef environments. Science 235:687-689.

Jompa J, McCook LJ. 2002. Effects of competition and herbivory on interactions between a hard coral and a brown alga. Journal of Experimental Marine Biology and Ecology 271:25-39.

Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist 32:674-682.

Lapointe BE. 1987. Phosphorus- and nitrogen-limited photosynthesis and growth of Gracilaria tikvahiae (Rhodophyceae) in the Florida Keys: an experimental field study. Marine Biology 93:561-568.

Lapointe BE. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography 42:1119-1131.

Lapointe BE, Barile PJ, Yentsch CS, Littler MM, Littler DS, and Kakuk B. 2004. The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman's Pond Cay, Exumas Cays, Bahamas: a "natural" enrichment experiment. Journal of Experimental Marine Biology and Ecology 298:275-301.

Lapointe BE, and Matzie WR. 1996. Effects of stormwater nutrient discharges on eutrophication processes in nearshore waters of the Florida Keys. Estuaries 19:422-435.

Lapointe BE, and Tenore KR. 1981. Experimental outdoor studies with Ulva fasciata Delile. I. Interaction of light and nitrogen on nutrient uptake, growth, and biochemical composition. Journal of Experimental Marine Biology and Ecology 53:135-152.

Lessios HA, Garrido MJ, Kessing BD. 2001. Demographic history of Diadema antillarum, a keystone herbivore on Caribbean reefs. Proceedings of the Royal Society of London Series B: Biological Sciences 268:2347-2353.

Lewis SM. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecology Monographs 56:183-200.

Lewis SM, Norris JN, and Searles RB. 1987. The regulation of morphological plasticity in tropical reef algae by herbivory. Ecology 68:636-641.

Lirman D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivalship and growth. Coral reefs 19: 392-399.

Littler DS, and Littler MM. 2000. Caribbean Reef Plants, 1st edition. OffShore Graphics Inc., Washington D.C.

Littler MM, Littler DS, Brooks BL, and LaPointe BE. 2006. Nutrient manipulation methods for coral reef studies: A critical review and experimental field data. Journal of Experimental Marine Biology and Ecology 336:242-253.

Littler MM, Littler DS, and Lapointe BE. 1988. A comparison of nutrient- and light-limited photosynthesis in psammophytic versus epilithic froms of Halimeda (Caulerpales, Halimedaceae) from the Bahamas. Coral Reefs 6:219-225.

Marcot BG, Holthausen RS, Raphael MG, Rowland MM, and Wisdom MJ. 2001. Using Bayesian belief networks to evaluate fish and wildlife population viability under land management alternatives from an environmental impact statement. Forest Ecology and Management 153:29-42.

Marshall PA, and Schuttenberg H. 2006. A reef managers's guide to coral bleaching. Great Barrier Reef Marine Park Authority, Townsville.

McClanahan TR, Sala E, Mumby PJ, and Jones S. 2004. Phosphorus and nitrogen enrichment do not enhance brown frondose "macroalgae". Marine Pollution Bulletin 48:196-199.

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.

McCourt RM. 1984. Seasonal patterns of abundance, distribution, and phenology in relation to growth strategies of three Sargassum species. Journal of Experimental Marine Biology and Ecology 74:141-156.

Moberg F, and Folke C. 1999. Ecological goods and services of coral reef ecosystems. Ecological economics 29:215-233.

Mumby PJ. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecological Applications 16:747-769.

Mumby PJ, Broad K, Brumbaugh DR, Dahlgren CP, Harborne AR, Hastings A, Holmes KE, Kappel CV, Micheli F, and Sanchirico JN. In press. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. Conservation Biology.

Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes K, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle R, and Gill AB. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98-101.

Mumby PJ, Hastings A, and Edwards HJ. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98-101.

Nugues MM, and Bak RMP. 2006. Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. Marine Ecology Progress Series 315:75-86.

Richardson JP. 1979. Overwintering of Dictyota dichotoma (Phaeophyceae) near its northern distribution limit on the east coast of north America. Journal of Phycology 15:22-26.

Sammarco PW. 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. Journal of Experimental Marine Biology and Ecology 61:31-55.

Schaffelke B, and Klumpp DW. 1997. Growth of germlings of the macroalga Sargassum baccularia (Phaeophyta) is stimulated by enhanced nutrients. Proceedings of the 8th International Coral Reef Symposium 2:1839-1842.

Schaffelke B, and Klumpp DW. 1998. Short-term nutrient pulses enhance growth and photosynthesis of the coral reef macroalga Sargassum baccularia. Marine Ecology Progress Series 170:95-105.

Smith JE, Smith CM, and Hunter CL. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332-342.

Steneck RS, and Watling L. 1982. Feeding capabilities and limitation of herbivorous molluscs: A functional group approach. Marine Biology 68: 299-319

Steneck RS, and Dethier MN. 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69:476-498.

Tanner JE. 1995. Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. Journal of Ecperimental Marine Biology and Ecology 190:151-168.

Townley S, Carslake D, Kellie-Smith O, McCarthy D, and Hodgson D. 2007. Predicting transient amplification in perturbed ecological systems. Journal of Applied Ecology In press.

Uusitalo L. 2007. Advantages and challenges of Bayesian networks in environmental modelling. Ecological Modelling: In Press.

Wooldridge S, Done T, Berkelmans R, Jones R, and Marshall P. 2005. Precursors for resilience in coral communities in a warming climate: a belief network approach. Marine Ecology Progress Series 295:157-169.

APPENDICES

APPENDIX A - Conditional Probability Tables of the Bayesian Belief Network Algalnet

Conditional Probability Tables (CPT) for the nodes Algal cover, Nutrient Availability, Fish Grazing and Grazing Pressure.

Table 1. CPT of the node Algal Cover

Parent nodes		**Categories of the node algal cover**				
Algal growth rate	**Grazing pressure**	**0-5**	**5-10**	**10-20**	**20-50**	**50-100**
Very low	Very low	10	60	10	10	10
Very low	Low	64	23	13	0	0
Very low	Medium	75	25	0	0	0
Very low	High	60	10	10	10	10
Very low	Very high	20	20	20	20	20
Low	Very low	36	17	25	22	0
Low	Low	50	38	12	0	0
Low	Medium	25	50	25	0	0
Low	High	20	20	20	20	20
Low	Very high	20	20	20	20	20
Medium	Very low	19	23	19	31	8
Medium	Low	10	36	27	22	5
Medium	Medium	25	35	22	12	6
Medium	High	65	21	14	0	0
Medium	Very high	20	20	20	20	20
High	Very low	20	11	15	21	33
High	Low	20	11	15	21	33
High	Medium	38	30	16	8	8
High	High	60	10	10	10	10
High	Very high	20	20	20	20	20
Very high	Very low	20	20	20	20	20
Very high	Low	20	20	20	20	20
Very high	Medium	20	20	20	20	20
Very high	High	20	20	20	20	20
Very high	Very high	20	20	20	20	20

Table 2. CPT of the Node Nutrient Availability

Parent nodes		**Categories for the node Nutrient availability**				
Water flow	**Nitrate**	**Phosphorous**	**Low**	**Medium**	**High**	**Very high**
Low	Low	Low	25	25	25	25
Low	Low	Medium	25	25	25	25
Low	Low	High	25	25	25	25
Low	Low	Very high	25	25	25	25
Low	Medium	Low	25	25	25	25
Low	Medium	Medium	25	25	25	25
Low	Medium	High	25	25	25	25
Low	Medium	Very high	25	25	25	25
Low	High	Low	25	25	25	25
Low	High	Medium	25	25	25	25
Low	High	High	25	25	25	25
Low	High	Very high	25	25	25	25
Low	Very high	Low	25	25	25	25
Low	Very high	Medium	25	25	25	25
Low	Very high	High	25	25	25	25
Low	Very high	Very high	25	25	25	25
Medium	Low	Low	6.67	6.67	6.67	80
Medium	Low	Medium	6.67	6.67	6.67	80
Medium	Low	High	6.67	6.67	6.67	80
Medium	Low	Very high	6.67	6.67	6.67	80
Medium	Medium	Low	6.67	6.67	6.67	80
Medium	Medium	Medium	6.67	6.67	6.67	80
Medium	Medium	High	6.67	6.67	6.67	80
Medium	Medium	Very high	6.67	6.67	6.67	80
Medium	High	Low	6.67	6.67	80	6.67
Medium	High	Medium	6.67	6.67	80	6.67
Medium	High	High	6.67	6.67	80	6.67
Medium	High	Very high	6.67	6.67	80	6.67
Medium	Very high	Low	6.67	6.67	80	6.67
Medium	Very high	Medium	6.67	6.67	80	6.67
Medium	Very high	High	6.67	6.67	80	6.67
Medium	Very high	Very high	6.67	6.67	80	6.67
High	Low	Low	13.33	13.33	13.33	60
High	Low	Medium	13.33	13.33	13.33	60
High	Low	High	13.33	13.33	13.33	60
High	Low	Very high	13.33	13.33	13.33	60
High	Medium	Low	13.33	13.33	13.33	60
High	Medium	Medium	13.33	13.33	13.33	60
High	Medium	High	13.33	13.33	13.33	60
High	Medium	Very high	13.33	13.33	13.33	60
High	High	Low	13.33	13.33	60	13.33
High	High	Medium	13.33	13.33	60	13.33
High	High	High	13.33	13.33	60	13.33
High	High	Very high	13.33	13.33	60	13.33
High	Very high	Low	13.33	13.33	60	13.33
High	Very high	Medium	13.33	13.33	60	13.33
High	Very high	High	13.33	13.33	60	13.33
High	Very high	Very high	13.33	13.33	60	13.33
Very high	Low	Low	20	20	20	40
Very high	Low	Medium	20	20	20	40
Very high	Low	High	20	20	20	40
Very high	Low	Very high	20	20	20	40
Very high	Medium	Low	20	20	20	40
Very high	Medium	Medium	20	20	20	40
Very high	Medium	High	20	20	20	40
Very high	Medium	Very high	20	20	20	40
Very high	High	Low	20	20	40	20
Very high	High	Medium	20	20	40	20
Very high	High	High	20	20	40	20
Very high	High	Very high	20	20	40	20
Very high	Very high	Low	20	20	40	20
Very high	Very high	Medium	20	20	40	20
Very high	Very high	High	20	20	40	20
Very high	Very high	Very high	20	20	40	20

Table 3. CPT of the node Fish grazing

Parent nodes		Categories for the node fish grazing				
Parrotfish	**Surgeonfish**	**Very low**	**Low**	**Medium**	**High**	**Very high**
Very low	Very low	40	60	0	0	0
Very low	Low	0	50	50	0	0
Very low	Medium	0	0	50	50	0
Very low	High	0	0	0	50	50
Very low	Very high	0	0	0	0	100
Low	Very low	0	50	50	0	0
Low	Low	0	0	60	40	0
Low	Medium	0	0	0	60	40
Low	High	0	0	0	0	100
Low	Very high	0	0	0	0	100
Medium	Very low	0	0	50	50	0
Medium	Low	0	0	0	60	40
Medium	Medium	0	0	0	0	100
Medium	High	0	0	0	0	100
Medium	Very high	0	0	0	0	100
High	Very low	0	0	0	50	50
High	Low	0	0	0	0	100
High	Medium	0	0	0	0	100
High	High	0	0	0	0	100
High	Very high	0	0	0	0	100
Very high	Very low	0	0	0	0	100
Very high	Low	0	0	0	0	100
Very high	Medium	0	0	0	0	100
Very high	High	0	0	0	0	100
Very high	Very high	0	0	0	0	100

Table 4. CPT of the node Grazing Pressure

Parent nodes		Categories for the node Grazing pressure				
Diadema	**Fish grazing**	**Very low**	**Low**	**Medium**	**High**	**Very high**
None	Very low	100	0	0	0	0
None	Low	50	50	0	0	0
None	Medium	50	50	0	0	0
None	High	0	100	0	0	0
None	Very high	0	50	50	0	0
Very low	Very low	0	100	0	0	0
Very low	Low	0	50	50	0	0
Very low	Medium	0	50	50	0	0
Very low	High	0	0	100	0	0
Very low	Very high	0	0	50	50	0
Low	Very low	0	0	100	0	0
Low	Low	0	0	50	50	0
Low	Medium	0	0	50	50	0
Low	High	0	0	0	100	0
Low	Very high	0	0	0	50	50
Medium	Very low	0	0	0	100	0
Medium	Low	0	0	0	50	50
Medium	Medium	0	0	0	50	50
Medium	High	0	0	0	0	100
Medium	Very high	0	0	0	0	100
High	Very low	0	0	0	0	100
High	Low	0	0	0	0	100
High	Medium	0	0	0	0	100
High	High	0	0	0	0	100
High	Very high	0	0	0	0	100

Appendix B - Matrices for *Dictyota* spp. and *Lobophora variegata* for the period May 2005 until January 2006 on the exposed and sheltered sides of Glovers Reef Atoll, Belize.

Matrices are given for four different scenarios. The first scenario consists of matrices in which both fragmentation and fusion events are incorporated explicitly into the matrices. Scenario two consists of matrices where only fragmentation is incorporated. The third scenario consists of matrices where only fusion is incorporated, and finally scenario four consists of matrices not including fragmentation and fusion events. Blank matrices are not constructed due to a lack of data.

Matrices for *Dictyota* spp. on the exposed side, including fragmentation and fusion events

		May									**October**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**N**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.17	0.65	---	---	---	0.08	---	**o**	**I**	0.40	0.26	0.06	0.03	---	0.06	---
n	**II**	0.49	0.32	0.15	0.03	---	---	---	**v**	**II**	0.31	0.26	0.10	0.10	0.05	---	---
e	**III**	0.29	0.55	0.32	0.11	0.15	---	---	**e**	**III**	0.12	0.21	0.26	0.05	0.08	0.17	0.11
	IV	0.10	0.16	0.46	0.33	0.04	0.08	---	**m**	**IV**	0.02	0.11	0.48	0.48	0.39	0.17	0.52
	V	---	---	0.07	0.53	0.59	0.23	---	**b**	**V**	---	0.11	0.06	0.15	0.38	0.39	0.51
	VI	---	---	---	---	0.22	0.38	0.29	**e**	**VI**	---	---	---	0.26	0.28	0.33	0.41
	VII	---	---	---	---	---	0.23	0.71	**r**	**VII**	---	---	---	---	0.03	---	0.23
		July									**November**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**D**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.50	0.22	0.10	0.02	---	---	---	**e**	**I**	0.41	0.07	0.04	0.01	---	---	---
l	**II**	0.40	0.35	0.20	0.11	0.02	---	---	**c**	**II**	0.15	0.37	0.07	0.04	0.02	0.03	---
y	**III**	0.20	0.32	0.31	0.24	0.02	---	---	**e**	**III**	0.26	0.26	0.14	0.06	0.04	0.05	---
	IV	0.10	0.05	0.22	0.33	0.15	---	---	**m**	**IV**	0.15	0.19	0.18	0.29	0.23	0.08	0.11
	V	---	0.03	0.14	0.20	0.51	0.08	---	**b**	**V**	---	0.23	0.33	0.31	0.27	0.59	0.11
	VI	---	---	0.04	0.02	0.17	0.08	0.13	**e**	**VI**	---	---	0.04	0.28	0.31	0.32	0.11
	VII	---	---	---	0.08	0.09	0.85	0.96	**r**	**VII**	---	---	---	0.05	0.31	0.05	0.98
		July									**December**						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**J**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.55	0.22	0.05	0.03	---	---	---	**a**	**I**	0.60	0.47	0.52	0.21	0.17	0.13	0.17
g	**II**	0.35	0.31	0.18	0.03	---	---	---	**n**	**II**	0.07	0.21	0.24	0.47	0.31	0.37	0.33
u	**III**	0.10	0.44	0.43	0.11	---	---	--	**u**	**III**	---	---	0.03	0.13	0.38	0.33	0.33
s	**IV**	---	---	0.18	0.54	0.18	0.09	0.11	**a**	**IV**	---	---	---	0.06	0.11	0.13	---
t	**V**	---	---	0.11	0.26	0.69	0.18	---	**r**	**V**	---	---	---	---	0.01	0.03	0.17
	VI	---	---	---	0.03	0.10	0.55	0.21	**y**	**VI**	---	---	---	---	---	---	---
	VII	---	---	---	---	0.03	0.18	0.68		**VII**	---	---	---	---	---	---	---

Matrices for *Dictyota* spp. on the exposed side, including fragmentation events

		May									**October**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**N**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.17	0.06	---	---	---	0.07	---	**o**	**I**	0.41	0.29	0.07	0.03	---	---	---
n	**II**	0.49	0.32	0.15	0.03	---	---	---	**v**	**II**	0.32	0.18	0.11	0.11	0.05	---	---
e	**III**	0.29	0.55	0.32	0.11	0.15	0.07	---	**e**	**III**	0.12	0.24	0.30	0.06	0.08	0.11	0.11
	IV	0.10	0.16	0.46	0.33	0.04	0.27	---	**m**	**IV**	0.02	0.12	0.52	0.44	0.42	0.17	0.43
	V	---	---	0.07	0.53	0.59	0.20	---	**b**	**V**	---	0.12	0.07	0.17	0.36	0.44	0.59
	VI	---	---	---	---	0.22	0.33	0.29	**e**	**VI**	---	---	---	0.19	0.17	0.33	0.41
	VII	---	---	---	---	---	0.20	0.71	**r**	**VII**	---	---	---	---	0.03	---	0.19
		June									**November**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**D**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.50	0.22	0.10	0.02	---	---	---	**e**	**I**	0.48	0.09	0.05	0.02	---	---	---
l	**II**	0.40	0.36	0.20	0.12	0.03	---	---	**c**	**II**	0.18	0.43	0.10	0.05	0.02	0.03	---
y	**III**	0.20	0.33	0.33	0.26	0.03	---	---	**e**	**III**	0.30	0.30	0.20	0.08	0.04	0.05	---
	IV	0.10	0.06	0.22	0.35	0.16	---	---	**m**	**IV**	0.17	0.22	0.20	0.31	0.24	0.08	---
	V	---	0.03	0.10	0.23	0.58	0.09	---	**b**	**V**	---	0.17	0.35	0.39	0.29	0.62	0.11
	VI	---	---	0.04	0.02	0.19	0.09	0.13	**e**	**VI**	---	---	0.05	0.15	0.24	0.30	0.11
	VII	---	---	---	0.05	0.05	0.82	0.88	**r**	**VII**	---	---	---	0.02	0.16	0.05	0.78

		July									December						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**J**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.55	0.22	0.05	0.03	---	---	---	**a**	**I**	0.60	0.47	0.52	0.21	0.18	0.19	0.42
g	**II**	0.35	0.31	0.18	0.03	---	---	---	**n**	**II**	0.07	0.21	0.24	0.47	0.31	0.39	0.89
u	**III**	0.10	0.44	0.43	0.17	0.07	---	---	**u**	**III**	---	---	0.03	0.13	0.39	0.36	0.79
s	**IV**	---	---	0.18	0.50	0.28	0.17	0.09	**a**	**IV**	---	---	---	0.06	0.11	0.12	0.32
t	**V**	---	---	0.11	0.28	0.67	0.25	0.14	**r**	**V**	---	---	---	---	0.01	0.03	0.16
	VI	---	---	---	0.03	0.09	0.55	0.28	**y**	**VI**	---	---	---	---	---	---	---
	VII	---	---	---	---	0.02	0.17	0.64		**VII**	---	---	---	---	---	---	---

Matrices for *Dictyota* spp. on the exposed side, including fusion events

		May									October						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**N**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**								**o**	**I**	0.40	0.26	0.03	0.03	---	---	---
n	**II**								**v**	**II**	0.31	0.26	0.03	0.11	0.03	---	---
e	**III**								**e**	**III**	0.12	0.21	0.24	0.05	0.03	0.06	0.05
	IV								**m**	**IV**	0.02	0.11	0.52	0.47	0.36	0.18	0.10
	V								**b**	**V**		0.11	0.07	0.16	0.37	0.41	0.33
	VI								**e**	**VI**	---	---	---	0.21	0.31	0.35	0.24
	VII								**r**	**VII**	---	---	---	---	0.03	---	0.33

		June									November						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**D**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.50	0.22	0.10	0.02	---	---	---	**e**	**I**	0.41	0.07	0.04	0.01	---	---	---
l	**II**	0.40	0.35	0.20	0.09	---	---	---	**c**	**II**	0.15	0.37	0.07	0.04	0.02	0.03	---
y	**III**	0.20	0.32	0.32	0.21	---	---	---	**e**	**III**	0.26	0.26	0.14	0.07	0.04	0.03	---
	IV	0.10	0.05	0.22	0.33	0.15	---	---	**m**	**IV**	0.15	0.19	0.18	0.24	0.24	0.03	---
	V	---	0.03	0.14	0.23	0.53	0.08	---	**b**	**V**	---	0.23	0.37	0.32	0.25	0.47	---
	VI	---	---	0.04	0.02	0.18	0.08	0.13	**e**	**VI**	---	---	0.04	0.28	0.32	0.36	0.13
	VII	---	--	---	0.09	0.09	0.86	0.96	**r**	**VII**	---	---	---	0.05	0.32	0.06	1.08

Matrices for *Dictyota* spp. on the exposed side, fragmentation and fusion not included

		May									October						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**N**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.17	0.65	---	---	---	0.08	---	**o**	**I**	0.41	0.29	0.04	0.03	---	---	---
n	**II**	0.49	0.32	0.15	0.03	---	---	---	**v**	**II**	0.32	0.18	0.04	0.11	0.03	---	---
e	**III**	0.29	0.55	0.32	0.11	0.15	---	---	**e**	**III**	0.12	0.24	0.28	0.06	0.03	0.12	---
	IV	0.10	0.16	0.46	0.33	0.04	0.08	---	**m**	**IV**	0.02	0.12	0.56	0.44	0.38	0.18	---
	V	---	---	0.07	0.53	0.59	0.23	---	**b**	**V**	---	0.12	0.08	0.17	0.35	0.35	0.31
	VI	---	---	---	---	0.22	0.38	0.29	**e**	**VI**	---	---	---	0.19	0.18	0.35	0.44
	VII	---	---	---	---	---	0.23	0.71	**r**	**VII**	---	---	---	---	0.03	---	0.25

		June									November						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**D**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.50	0.22	0.10	0.02	---	---	---	**e**	**I**	0.48	0.09	0.05	0.02	---	---	---
l	**II**	0.40	0.36	0.20	0.10	---	---	---	**c**	**II**	0.17	0.43	0.10	0.05	0.02	0.03	---
y	**III**	0.20	0.33	0.33	0.24	---	---	---	**e**	**III**	0.30	0.30	0.20	0.08	0.04	0.03	---
	IV	0.10	0.06	0.22	0.32	0.17	---	---	**m**	**IV**	0.17	0.22	0.20	0.28	0.24	0.03	---
	V	---	0.03	0.10	0.24	0.58	0.09	---	**b**	**V**	---	0.17	0.35	0.39	0.29	0.50	---
	VI	---	---	0.04	0.02	0.19	0.09	0.13	**e**	**VI**	---	---	0.05	0.15	0.24	0.34	0.13
	VII	---	---	---	0.05	0.06	0.82	0.88	**r**	**VII**	---	---	---	0.02	0.16	0.06	0.88

		July									December						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**J**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.55	0.22	0.05	0.03	---	---	---	**a**	**I**	0.60	0.47	0.52	0.21	0.17	0.13	0.17
g	**II**	0.35	0.31	0.18	0.03	---	---	---	**n**	**II**	0.07	0.21	0.24	0.47	0.31	0.37	0.33
u	**III**	0.10	0.44	0.43	0.11	---	---	---	**u**	**III**	---	---	0.03	0.13	0.38	0.33	0.33
s	**IV**	---	---	0.18	0.54	0.18	0.09	0.11	**a**	**IV**	---	---	---	0.06	0.11	0.13	---
t	**V**	---	---	0.11	0.26	0.69	0.18	---	**r**	**V**	---	---	---	---	0.01	0.03	0.17
	VI	---	---	---	0.03	0.10	0.55	0.21	**y**	**VI**	---	---	---	---	---	---	---
	VII	---	---	---	---	0.03	0.18	0.68		**VII**	---	---	---	---	---	---	---

Matrices for *Dictyota* spp. on the sheltered side, including fragmentation and fusion events

		July						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	1.61	0.44	0.33	---	---	---	---
l	**II**	0.25	0.39	0.44	---	---	---	---
y	**III**	0.11	0.22	0.17	---	---	---	---
	IV	---	---	---	---	---	---	---
	V	---	---	---	---	---	---	---
	VI	---	---	---	---	---	---	---
	VII	---	---	---	---	---	---	---

		November						
D		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
e	**I**	0.60	0.13	---	---	---	---	---
c	**II**	0.10	0.63	0.53	0.36	---	---	---
e	**III**	0.20	0.25	0.18	0.36	---	---	---
m	**IV**	---	0.13	0.24	0.21	0.67	---	---
b	**V**	---	---	0.06	0.07	0.33	---	---
e	**VI**	---	---	---	---	---	---	---
r	**VII**	---	---	---	---	---	---	---

		July						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.60	0.17	0.17	---	---	---	---
g	**II**	0.26	0.83	0.33	---	---	---	---
u	**III**	0.21	0.33	0.08	---	---	---	---
s	**IV**	0.05	0.08	0.50	---	---	---	---
t	**V**	---	---	---	---	---	---	---
	VI	---	---	---	---	---	---	---
	VII	---	---	---	---	---	---	---

		December						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
a	**I**	0.79	0.40	0.24	0.23	0.17	---	---
n	**II**	0.07	0.17	0.35	0.41	0.17	---	---
u	**III**	---	0.05	0.22	0.27	0.33	---	---
a	**IV**	---	---	0.05	0.09	0.33	---	---
r	**V**	---	---	---	---	---	---	---
y	**VI**	---	---	---	---	---	---	---
	VII	---	---	---	---	---	---	---

Matrices for *Dictyota* spp. on the sheltered side, including fragmentation events

		June						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**							
l	**II**							
y	**III**							
	IV							
	V							
	VI							
	VII							

		November						
D		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
e	**I**	0.60	0.13	---	0.07	---	---	---
c	**II**	0.10	0.63	0.53	0.40	0.25	---	---
e	**III**	0.20	0.25	0.18	0.33	0.13	---	---
m	**IV**	---	0.13	0.24	0.20	0.63	---	---
b	**V**	---	---	0.06	0.67	0.25	---	---
e	**VI**	---	---	---	---	---	---	---
r	**VII**	---	---	---	---	----	---	---

		July						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**							
g	**II**							
u	**III**							
s	**IV**							
t	**V**							
	VI							
	VII							

		December						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
a	**I**							
n	**II**							
u	**III**							
a	**IV**							
r	**V**							
y	**VI**							
	VII							

Matrices for *Lobophora variegata* on the exposed side, including fragmentation and fusion events

		May									**October**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**N**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.72	0.08	0.03	0.05	---	---	---	**o**	**I**	0.32	0.18	0.13	0.03	---	---	---
n	**II**	0.56	0.33	0.07	0.05	---	---	---	**v**	**II**	0.21	0.16	0.18	0.13	---	---	---
e	**III**	0.11	0.46	0.40	0.24	---	---	---	**e**	**III**	0.05	0.34	0.29	0.23	0.22	---	---
	IV	---	0.42	0.40	0.43	---	---	---	**m**	**IV**	0.15	0.17	0.51	0.55	0.56	---	---
	V	---	---	0.03	0.14	0.71	---	---	**b**	**V**	---	0.07	0.09	0.15	0.22	0.50	---
	VI	---	---	---	0.05	0.18	---	---	**e**	**VI**	---	---	---	---	---	0.50	---
	VII	---	---	---	---	0.14	---	---	**r**	**VII**	---	---	---	---	---	---	---
		July									**November**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**D**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.79	0.33	0.23	0.04	0.08	0.33	---	**e**	**I**	0.45	0.09	0.20	0.08	---	---	---
l	**II**	0.26	0.39	0.19	0.18	---	0.33	---	**c**	**II**	0.20	0.30	0.11	0.06	---	---	---
y	**III**	0.11	0.22	0.31	0.32	0.23	0.33	---	**e**	**III**	0.05	0.39	0.38	0.27	---	---	---
	IV	0.05	0.06	0.12	0.39	0.38	0.67	0.50	**m**	**IV**	0.10	0.21	0.37	0.55	0.42	---	---
	V	---	---	---	---	0.46	0.33	0.50	**b**	**V**	---	0.04	0.03	0.18	0.67	0.50	---
	VI	---	---	---	---	---	0.33	---	**e**	**VI**	---	---	---	---	---	0.50	---
	VII	---	---	---	---	---	---	---	**r**	**VII**	---	---	---	---	---	---	---
		July									**December**						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**J**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.16	---	---	0.05	0.33	---	---	**a**	**I**	0.24	---	---	0.02	---	---	---
g	**II**	0.19	0.43	0.22	0.05	---	---	---	**n**	**II**	0.19	0.06	0.12	0.02	---	---	---
u	**III**	0.34	0.35	0.37	0.23	0.50	---	---	**u**	**III**	0.05	0.26	0.18	0.08	0.06	---	---
s	**IV**	0.09	0.26	0.37	0.54	0.33	---	---	**a**	**IV**	---	0.20	0.38	0.54	0.06	---	---
t	**V**	---	---	---	0.22	0.67	---	---	**r**	**V**	---	---	0.16	0.47	0.72	---	---
	VI	---	---	---	---	---	---	---	**y**	**VI**	---	---	0.14	0.02	0.25	0.50	---
	VII	---	---	---	---	---	---	---		**VII**	---	---	---	---	0.10	0.54	---

Matrices for *Lobophora variegata* on the exposed side, including fragmentation events

		May									**October**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**N**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**								**o**	**I**	0.38	0.21	0.13	0.03	---	---	---
n	**II**								**v**	**II**	0.25	0.18	0.18	0.13	---	---	---
e	**III**								**e**	**III**	0.06	0.39	0.25	0.23	0.22	---	---
	IV								**m**	**IV**	0.13	0.15	0.43	0.55	0.56	---	---
	V								**b**	**V**	---	0.03	0.05	0.15	0.22	0.50	---
	VI								**e**	**VI**	---	---	---	---	---	0.50	---
	VII								**r**	**VII**	---	---	---	---	---	---	---
		June									**November**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**D**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.79	0.35	0.23	0.04	0.08	0.33	---	**e**	**I**	0.53	0.10	0.20	0.08	---	---	---
l	**II**	0.26	0.41	0.19	0.18	---	0.33	---	**c**	**II**	0.24	0.33	0.11	0.06	---	---	---
y	**III**	0.11	0.24	0.31	0.32	0.23	0.33	---	**e**	**III**	0.06	0.38	0.34	0.26	---	---	---
	IV	0.05	0.06	0.12	0.39	0.38	0.67	0.50	**m**	**IV**	0.12	0.19	0.37	0.48	0.42	---	---
	V	---	---	---	---	0.46	0.33	0.50	**b**	**V**	---	0.05	0.03	0.18	0.67	0.50	---
	VI	---	---	---	---	---	0.33	---	**e**	**VI**	---	---	---	---	---	0.50	---
	VII	---	---	---	---	---	---	---	**r**	**VII**	---	---	---	---	---	---	---
		July									**December**						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**J**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.16	---	---	0.05	0.33	---	---	**a**	**I**	0.31	---	---	0.03	---	---	---
g	**II**	0.19	0.48	0.22	0.05	---	---	---	**n**	**II**	0.25	0.08	0.14	0.03	---	---	---
u	**III**	0.35	0.38	0.37	0.24	0.50	---	---	**u**	**III**	0.06	0.42	0.21	0.10	0.05	---	---
s	**IV**	0.10	0.29	0.33	0.52	0.33	---	---	**a**	**IV**	---	0.25	0.45	0.60	0.05	---	---
t	**V**	---	---	---	0.14	0.67	---	---	**r**	**V**	---	---	0.14	0.23	0.67	---	---
	VI	---	---	---	---	---	---	---	**y**	**VI**	---	---	0.07	0.03	0.17	0.50	---
	VII	---	---	---	---	---	---	---		**VII**	---	---	---	---	0.06	0.50	---

Matrices for *Lobophora variegata* on the exposed side, including fusion events

		May									**October**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**N**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**								**o**	**I**	0.32	0.16	0.10	0.03	---	---	---
n	**II**								**v**	**II**	0.21	0.16	0.18	0.08	---	---	---
e	**III**								**e**	**III**	0.05	0.34	0.27	0.18	0.11	---	---
	IV								**m**	**IV**	0.19	0.17	0.52	0.60	0.67	---	---
	V								**b**	**V**	---	0.07	0.09	0.16	0.22	0.50	---
	VI								**e**	**VI**	---	---	---	---	---	0.50	----
	VII								**r**	**VII**	---	---	---	---	---	---	---
		June									**November**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**D**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.79	0.33	0.23	0.04	---	---	---	**e**	**I**	0.45	0.09	0.09	0.02	---	---	---
l	**II**	0.26	0.39	0.19	0.18	---	---	---	**c**	**II**	0.20	0.30	0.12	0.04	---	---	---
y	**III**	0.11	0.22	0.31	0.32	0.25	---	---	**e**	**III**	0.05	0.39	0.43	0.23	---	---	---
	IV	0.05	0.06	0.12	0.39	0.25	---	---	**m**	**IV**	0.10	0.21	0.36	0.57	0.36	---	---
	V	---	---	---	---	0.50	0.50	---	**b**	**V**	---	0.04	0.03	0.19	0.64	0.50	---
	VI	---	---	---	---	---	0.50	---	**e**	**VI**	---	---	---	---	---	0.50	---
	VII	---	---	---	---	---	---	---	**r**	**VII**	---	---	---	---	---	---	---
		July									**December**						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**J**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.16	---	---	0.05	---	---	---	**a**	**I**	0.24	---	---	0.02	---	---	---
g	**II**	0.19	0.43	0.22	0.05	---	---	---	**n**	**II**	0.19	0.05	0.06	0.02	---	---	---
u	**III**	0.34	0.35	0.37	0.23	---	---	---	**u**	**III**	0.05	0.26	0.18	0.08	0.06	---	---
s	**IV**	0.09	0.26	0.37	0.54	0.50	---	---	**a**	**IV**	---	0.20	0.38	0.54	0.06	---	---
t	**V**	---	---	---	0.22	0.50	---	---	**r**	**V**	---	---	0.16	0.47	0.72	---	---
	VI	---	---	---	---	---	---	---	**y**	**VI**	---	---	0.14	0.02	0.25	0.50	---
	VII	---	---	---	---	---	---	---		**VII**	---	---	---	---	0.10	0.54	---

Matrices for *Lobophora variegata* on the exposed side, fragmentation and fusion not included

		May									**October**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**N**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.76	0.08	0.04	0.05	---	---	---	**o**	**I**	0.38	0.21	0.10	0.03	---	---	---
n	**II**	0.59	0.33	0.07	0.05	---	---	---	**v**	**II**	0.25	0.18	0.18	0.08	---	---	---
e	**III**	0.12	0.42	0.43	0.25	---	---	---	**e**	**III**	0.06	0.39	0.23	0.19	0.22	---	---
	IV	---	0.42	0.43	0.45	---	---	---	**m**	**IV**	0.13	0.15	0.44	0.54	0.56	---	---
	V	---	---	0.04	0.15	0.71	---	---	**b**	**V**	---	0.03	0.05	0.16	0.22	0.50	---
	VI	---	---	---	0.05	0.14	---	---	**e**	**VI**	---	---	---	---	---	0.50	---
	VII	---	---	---	---	0.14	---	---	**r**	**VII**	---	---	---	---	---	---	---
		June									**November**						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**D**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.79	0.35	0.23	0.04	---	---	---	**e**	**I**	0.53	0.10	0.09	0.04	---	---	---
l	**II**	0.26	0.41	0.19	0.18	---	---	---	**c**	**II**	0.24	0.33	0.12	0.02	---	---	---
y	**III**	0.11	0.24	0.31	0.32	0.25	---	---	**e**	**III**	0.06	0.38	0.36	0.24	---	---	---
	IV	0.05	0.06	0.12	0.39	0.25	---	0.50	**m**	**IV**	0.12	0.19	0.39	0.50	0.36	---	---
	V	---	---	---	---	0.50	0.50	0.50	**b**	**V**	---	0.05	0.03	0.20	0.64	0.50	---
	VI	---	---	---	---	---	0.50	---	**e**	**VI**	---	---	---	---	---	0.50	---
	VII	---	---	---	---	---	---	---	**R**	**VII**	---	---	---	---	---	---	---
		July									**December**						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**J**		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.17	---	---	0.05	---	---	---	**a**	**I**	0.31	---	---	0.03	---	---	---
g	**II**	0.19	0.48	0.22	0.05	---	---	---	**n**	**II**	0.25	0.08	0.07	0.03	---	---	---
u	**III**	0.35	0.38	0.37	0.24	---	---	---	**u**	**III**	0.06	0.42	0.21	0.10	0.06	---	---
s	**IV**	0.10	0.29	0.33	0.52	0.50	---	---	**a**	**IV**	---	0.25	0.46	0.60	0.06	---	---
t	**V**	---	---	---	0.14	0.50	---	---	**R**	**V**	---	---	0.14	0.23	0.67	---	---
	VI	---	---	---	---	---	---	---	**y**	**VI**	---	---	0.07	0.03	0.17	0.50	---
	VII	---	---	---	---	---	---	---		**VII**	---	---	---	---	0.06	0.50	---

Matrices for *Lobophora variegata* on the sheltered side, including fragmentation and fusion events

		June						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.91	0.24	0.14	0.13	---	---	---
l	**II**	0.36	0.36	0.33	0.16	0.21	---	---
y	**III**	---	0.12	0.29	0.38	0.07	0.40	---
	IV	---	0.08	0.05	0.41	0.29	0.20	---
	V	---	---	---	---	0.33	0.40	---
	VI	---	---	---	---	---	---	---
	VII	---	---	---	---	---	---	---

		November						
D		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
e	**I**	0.39	0.23	0.03	---	---	---	---
c	**II**	0.42	0.29	0.10	0.23	0.33	---	---
e	**III**	0.06	0.43	0.38	0.31	0.33	---	---
m	**IV**	---	0.03	0.45	0.46	0.33	---	---
b	**V**	---	---	0.07	---	0.33	---	---
e	**VI**	---	---	---	---	---	---	---
r	**VII**	---	---	---	---	---	---	---

		July						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	1.00	0.36	0.14	0.04	---	---	---
g	**II**	0.29	0.24	0.21	0.07	---	---	---
u	**III**	0.06	0.28	0.39	0.15	0.50	---	---
s	**IV**	---	0.12	0.25	0.59	0.13	---	---
t	**V**	---	---	---	0.07	0.50	---	---
	VI	---	---	---	---	---	---	---
	VII	---	---	---	---	---	---	---

		December						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
a	**I**	0.52	0.15	---	---	---	---	---
n	**II**	0.41	0.21	0.07	---	---	---	---
u	**III**	0.19	0.30	0.51	0.04	---	---	---
a	**IV**	0.04	0.15	0.37	0.71	0.20	---	---
r	**V**	---	0.06	0.02	0.25	0.20	---	---
y	**VI**	---	---	---	---	0.60	---	---
	VII	---	---	---	---	---	---	---

Matrices for *Lobophora variegata* on the sheltered side, including fragmentation events

		June						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.90	0.25	0.15	0.13	---	---	---
l	**II**	0.36	0.38	0.35	0.16	0.21	---	---
y	**III**	---	0.13	0.30	0.38	0.07	0.40	---
	IV	0.09	0.04	0.05	0.41	0.29	0.20	---
	V	---	---	---	---	0.29	0.40	---
	VI	---	---	---	---	---	---	---
	VII	---	---	---	---	---	---	---

		November						
D		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
e	**I**	0.44	0.23	0.04	---	---	---	---
c	**II**	0.41	0.30	0.11	0.23	0.33	---	---
e	**III**	0.06	0.40	0.39	0.31	0.33	---	---
m	**IV**	---	0.03	0.43	0.46	0.33	---	---
b	**V**	---	---	0.04	---	0.33	---	---
e	**VI**	---	---	---	---	---	---	---
r	**VII**	---	---	---	---	---	---	---

		July						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	1.06	0.36	0.14	0.04	---	---	---
g	**II**	0.31	0.24	0.21	0.07	---	---	---
u	**III**	0.06	0.28	0.39	0.15	0.50	---	---
s	**IV**	---	0.08	0.25	0.59	0.13	---	---
t	**V**	---	---	---	0.07	0.50	---	---
	VI	---	---	---	---	---	---	---
	VII	---	---	---	---	---	---	---

		December						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
a	**I**							
n	**II**							
u	**III**							
a	**IV**							
r	**V**							
y	**VI**							
	VII							

Matrices for *Lobophora variegata* on the sheltered side, including fusion events

		June						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.91	0.24	0.14	0.10	---	---	---
l	**II**	0.36	0.36	0.33	0.13	0.21	---	---
y	**III**	---	0.12	0.29	0.37	0.07	0.40	---
	IV	0.09	0.08	0.05	0.40	0.29	0.20	---
	V	---	---	---	---	0.33	0.40	---
	VI	---	---	---	---	---	---	---
	VII	---	---	---	---	---	---	---

		November						
D		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
e	**I**	0.39	0.23	0.03	---	---	---	---
c	**II**	0.42	0.29	0.10	0.23	---	---	---
e	**III**	0.06	0.43	0.38	0.31	0.33	---	---
m	**IV**	---	0.03	0.45	0.46	0.33	---	---
b	**V**	---	---	0.07		0.33	---	---
e	**VI**	---	---	---	---	---	---	---
r	**VII**	---	---	---	---	---	---	---

		July						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	1.00	0.36	0.14	0.04	---	---	---
g	**II**	0.29	0.24	0.21	0.07	---	---	---
u	**III**	0.06	0.28	0.39	0.15	0.29	---	---
s	**IV**	---	0.12	0.25	0.59	0.15	---	---
t	**V**	---	---	---	0.07	0.57	---	---
	VI	---	---	---	---	---	---	---
	VII	---	---	---	---	---	---	---

		December						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
a	**I**	0.47	0.12	---	---	---	---	---
n	**II**	0.41	0.21	0.07	---	---	---	---
u	**III**	0.17	0.24	0.54	0.03	---	---	---
a	**IV**	0.03	0.12	0.36	0.67	0.14	---	---
r	**V**	---	0.09	0.02	0.39	0.14	---	---
y	**VI**	---	---	---	---	0.55	---	---
	VII	---	---	---	---	---	---	---

Matrices for *Lobophora variegata* on the sheltered side, fragmentation and fusion not included

		June						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	0.91	0.25	0.15	0.10	---	---	---
l	**II**	0.36	0.38	0.35	0.13	0.21	---	---
y	**III**	---	0.13	0.30	0.37	0.07	0.40	---
	IV	0.09	0.04	0.05	0.40	0.29	0.20	---
	V	---	---	---	---	0.29	0.40	---
	VI	---	---	---	---	---	---	---
	VII	---	---	---	---	---	---	---

		November						
D		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
e	**I**	0.44	0.23	0.04	---	---	---	---
c	**II**	0.41	0.30	0.11	0.23	---	---	---
e	**III**	0.06	0.40	0.39	0.31	0.33	---	---
m	**IV**	---	0.03	0.43	0.46	0.33	---	---
b	**V**	---	---	0.04	---	0.33	---	---
e	**VI**	---	---	---	---	---	---	---
r	**VII**	---	---	---	---	---	---	---

		July						
A		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
u	**I**	1.06	0.36	0.14	0.04	---	---	---
g	**II**	0.31	0.24	0.21	0.07	---	---	---
u	**III**	0.06	0.28	0.39	0.15	0.29	---	---
s	**IV**	---	0.08	0.25	0.59	0.14	---	---
t	**V**	---	---	---	0.07	0.57	---	---
	VI	---	---	---	----	---	---	---
	VII	---	---	---	---	---	---	---

		December						
J		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
a	**I**							
n	**II**							
u	**III**							
a	**IV**							
r	**V**							
y	**VI**							
	VII							