Predicting the effects of climate change and disturbance on marine sessile communities

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by

Cheryl Anne Knowland

September 2011

UNIVERSITY OF
LIVERPOOL

In memory of
my Nan,
Phyllis Hutton
(1933-2011)

Acknowledgements

I would like to thank both of my supervisors, Dr. Matt Spencer and Prof. Chris Frid, for their advice and guidance throughout this project. I would also like to thank my examiners, Dr. Leonie Robinson and Dr. Mike Burrows for their comments and suggestions. Thanks must also go to NERC for funding this studentship.

I was assisted in the docks fieldwork by a number of people. I am extremely grateful to Keith Hatton for his input in the experimental design experiment, and help with the sampling. Thanks must also go to Carl Wright, Tony Tollitt, and other technicians from the School of Biological Sciences. I would like to thank British Waterways for their assistance with this project, especially Bill Broadbent and Andrew Goudie.

The Heron Island fieldwork could not have gone ahead without the assistance of Dr. Jason Tanner, who also gave advice on coral biology and modelling. I would also like to thank Heron Island Research Station for their assistance with the fieldwork.

Thanks to all in the Department of Ecology for your support, advice, and cake! A big thanks must go to all of the PhD students, especially Katherine, Louise, Hannah, and Jack, for providing laughs, support, and copious amounts of tea.

Special thanks must go to my mum and dad for their support, wise words, and unfailing belief in me.

Finally, thanks to Ian, for everything.

Table of Contents

Abstract

This study aims to evaluate and advance our ability to predict the effects of disturbance on communities using statistical models. This is important because climate change is likely to alter the patterns of disturbance experienced by ecosystems.

In the first chapter, I review the evidence for effects of climate change on the disturbance regimes experienced by marine ecosystems, particularly coral reefs. I also outline theories about how disturbance affects communities, and give background information on two field sites: Heron Island in the Great Barrier Reef, and Salthouse Dock in Liverpool.

Chapter 2 is a comparison of four models for coral community dynamics at Heron Island; a discrete-time Markov model and a nonlinear continuous-time model, each with and without the effects of cyclones. The models are fitted using Bayesian methods. The addition of cyclones improved the fit of the model, with cyclones causing some coral mortality, although recovery was rapid. Recruitment appeared less important than the growth and mortality of existing corals.

In Chapter 3, I use the best model from Chapter 2 to examine how different the dynamics at Heron Island for the years 1962-1992 might have been under a range of cyclone frequency scenarios. Under current or slightly increased cyclone frequency, coral cover could be either high or low, depending on the timing of cyclones. With increasing cyclone frequency, there was a transition from the outcome being contingent on chance events to being almost certain about the outcome.

In Chapter 4, we take the two models with cyclone effects from Chapter 2, and run them forwards in time until the year 2008. We then compare the predictions with newly collected field data using Bayesian methods. The continuous-time model predicted significantly less coral than was observed in 2008. Conversely, the discrete-time model predicted significantly more coral than was observed. Overall, the predictions made by the continuous-time model are closer to the observations.

Chapter 5 is a two-year experimental study on the effects of disturbance on marine sessile communities. A two-year study was carried out at the Salthouse Dock site to determine whether a disturbance regime would cause persistent changes in community composition. Recovery was rapid. A simple mathematical model suggests that recovery is almost inevitable in systems of this kind, especially for species with planktonic larval stages.

Comparing the Heron Island and Salthouse Dock results highlights the importance of external recruitment in recovery from disturbance. I discuss the advantages and disadvantages of alternative modelling strategies, and argue that simple models based on extensive data may be useful.

Chapter One: Introduction

There is increasing evidence that climate change is happening and that these prospective changes will impact on ecosystems on local and global scales (Harris *et al.* 2006). Climate change predictions include increases in mean temperatures, sea level, and the incidence of extreme climatic events, along with changes in patterns of weather and precipitation (Harris *et al.* 2006). In marine systems, the indirect effects of climate change appear to be the most widespread (Walther *et al.* 2002). Climate change will not only cause responses in individual species (Mieszkowska *et al.* 2006), but may also disrupt their interactions with other species on varying trophic levels (Walther *et al.* 2002). Thackeray *et al.* (2010) found that most life history events are occurring earlier in the year, although this has been less pronounced for secondary consumers than for producers or primary consumers; these results are consistent with warming trends. Furthermore, the combined effects of multiple stressors increase the sensitivity of species to extinction (Travis 2003). We can quantify the sensitivity of a species to extinction using Quasiextinction risk (QER) (Ginzburg *et al.* 1982) and use this to examine the effects of climate change predictions on communites.

Rapid climate change or extreme climatic events can change community composition (Walther *et al.* 2002). Long-term changes in the physical environment (e.g. climate change) can have effects on long-lived communities over large regions (Connell *et al.* 1997). For example, during periods of warmer water temperatures, substantial impacts have been observed on coral reef community structure (Walther *et al.* 2002).

Thus, it seems likely that climate change will result in large changes to ecosystems. The ability to predict these changes and their subsequent effects on marine communities will aid the management and possible restoration of these communities.

White and Pickett (1985) defined a disturbance as any discrete event in time that disrupts ecosystem, community, or population structure, and changes resource availability. Succession can be defined as the changes in an ecological community following a disturbance (Connell and Slatyer 1977). Connell (1978) suggested that the rate of succession is often much slower than the rate at which disturbance events occur. Thus, frequent disturbances can prevent a system from reaching the endpoint of succession. Connell also argued that diversity will tend to be highest when disturbance is sufficiently frequent to prevent dominant competitors from eliminating other species, but not so common that few species have an opportunity to colonise a habitat before the next disturbance event. This is known as the intermediate disturbance hypothesis. Connell suggested that this mechanism might be responsible for the high diversity observed in coral reefs and tropical rainforests. Historically, cyclones have always been present in tropical climates. However, an increase in the severity and frequency of cyclones due to anthropogenic climate change may cause a reduction in the abundance and diversity of corals. The frequency and severity of disturbances create a regeneration niche that will be occupied by species that have regeneration times that are shorter than the disturbance period (McClanahan 2002).

Coral reefs are one of the most biologically diverse and economically important ecosystems (Diaz-Pulido *et al.* 2009). They are also one of the most vulnerable marine ecosystems and there would be dire consequences if coral reefs were lost

(Hoegh-Guldberg 1999). A new disturbance regime on a reef can cause the ecosystem to fundamentally change its species composition from previous ecological states (McClanahan 2002). We will apply a disturbance regime to experimental communities to determine whether alternative ecological states can be stimulated or whether the intermediate disturbance hypothesis would apply.

Dudgeon *et al.* (2010) defines a phase shift as a change in the community equilibrium in response to a persistent change in environmental conditions. However, there are varying definitions of what actually constitutes a phase shift (Lees *et al.* 2006). There is evidence that some reefs have undergone a phase shift from a coral-dominated system to a system that is dominated by algae (Hughes 1994). Phase shifts occurred on Caribbean reefs as a consequence of cyclones, overfishing, and the loss of a key grazer (Tanner *et al.* 1994). Whilst these case studies are not currently representative of reefs worldwide, they serve as a warning of the consequences of multiple disturbances on reef communities (Bruno *et al.* 2009).

An increase in the frequency of tropical storms has increased the need to understand the ecological disturbances of these disasters. Phase shifts have been documented in a range of different ecosystems, including oceans, forests, and lakes (Scheffer *et al.* 2001). Dudgeon *et al.* (2010) defines alternative stable states as more than one community configuration that can occur in the same space and under the same environmental conditions at different times. The influence of scale and the possible existence of dynamic equilibria make it difficult to distinguish phase shifts from alternative stable states (Dudgeon *et al.* 2010).

In this study, models of coral reef dynamics were developed to enable predictions about the future trajectory of coral reef system diversity to be made, and to further our understanding of the dynamics of the system. Models may be empirical, that is based on observations, or mechanistic, which are based on actual processes within the system. There are also models of varying complexity, with a simple model being the ideal, whereas a more complex model may be required to adequately simulate the system dynamics.

There are three attributes of a model that we wish to maximise; generality, precision, and realism (Levins 1966). Generality is the ability to take a model that is based at one location, and apply it to another ecosystem at a separate location. Precision is the ability of the model to make accurate quantitative predictions. Realism is how well the model's structure and processes mimic those of the natural system. In reality, it is impossible to find a model that maximises these three attributes, and we must sacrifice one to reach our goal (Levins 1966).

We can also describe a model along two axes: its realism, and its complexity (Fig. 2.1.). An empirical model may sometimes be realistic only over a limited domain (e.g. the current set of environmental conditions). It may not necessarily be the case that this limited domain covers all observable conditions. Mechanistic models can be realistic, but are usually also complicated, which reduces their generality.

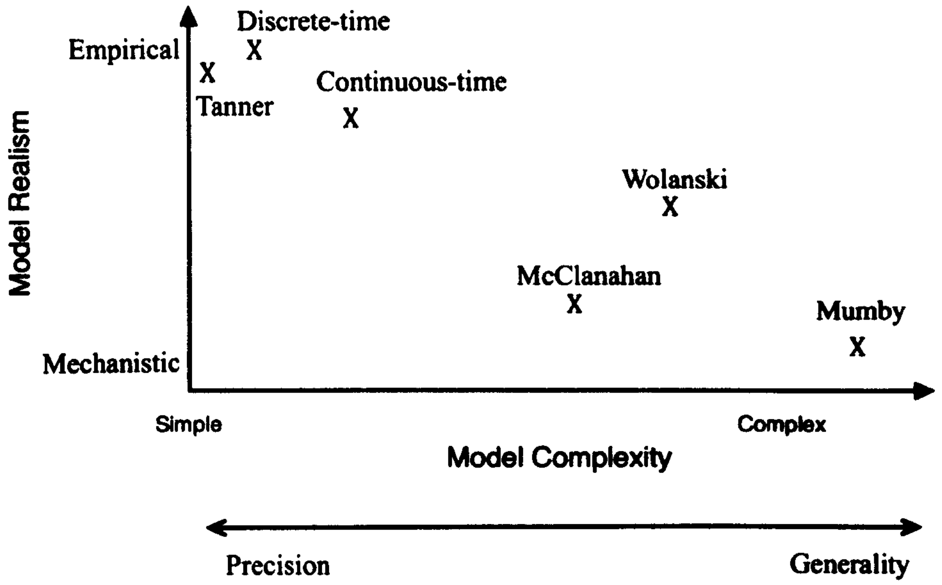

Figure 1.1 Diagram to represent trade-offs in model attributes. Illustrated with our discrete-time and continuous-time models, and models from Tanner *et al.* (1994), McClanahan (1995), Wolanski *et al.* (2004), and Mumby *et al.* (2006).

Previous models of coral reef dynamics have tended to be complicated. McClanahan (1995) described an energy-based coral reef fisheries model that simulates the entire ecosystem including fishing pressure. Fulton *et al.* (2004) described a very complicated biogeochemical ecosystem model, with over 750 parameters. Blackwood *et al.* (2010) described a model of the effect of fishing on coral reefs. They add the effects of parrotfish into an existing model, which makes the model more complicated and more realistic. However, because the values of the new parameters are unknown, the model does not become more precise.

In this study we produced a number of simple statistical models. We developed simple and more empirical models because they are realistic and precise. In accordance with Levins's (1966) theory, we sacrificed generality, so therefore we are making models for a specific ecosystem that may have restricted applicability to other systems.

Testing a model against real data is important, with different kinds of models requiring different levels of testing. Qualitative testing can be relatively easy (e.g. visual comparison of plots of model output), whereas quantitative testing is more difficult. Quantitative testing involves choosing a suitable measure of discrepancy, calculating this for a suitable data set, and then comparing this with that of the model output. For qualitative testing, parameters can come from the literature, or be chosen to make the model look like the data. Plausible parameters for quantitative testing can be determined using the discrepancy measure.

Model testing, or validation, is an important and ongoing feature of model development. Validation can be defined as a demonstration that a model possesses a satisfactory level of accuracy for the intended use of the model (Rykiel 1996). Specific methods of model validation, and their relative advantages and disadvantages will be discussed. Models will be assessed using both quantitative and qualitative means, and recommendations for model validation will be made.

Field sites

I will study the effects of disturbance on the dynamics of two contrasting communities: the Heron Island coral reef, and the fouling community in Salthouse Dock, Liverpool.

The Great Barrier Reef is the world's largest continuous reef system. It is home to most of Australia's marine biodiversity and provides a breeding ground for seabirds and marine mammals (Hennessy *et al.* 2007). Marine substrates, such as corals, are vital to the functioning of the ecosystem as a whole (Connell *et al.* 1997).

Our main study site, Heron Island, is a platform reef near the southern end of the Great Barrier Reef (Connell *et al.* 2004). A series of permanent quadrats were established on three sites on Heron Island in the early 1960's (Tanner *et al.* 1994). The quadrats have been sampled at regular intervals (~2 years) since, making it one of the longest available time series of coral community data. We use data from the Protected Crest site, which is on the southwestern rim of the island. The crest is protected from waves by the Wistari reef, which lies to the West of Heron Island.

A long-term study of coral community dynamics at the Protected Crest site (Connell *et al.* 1997) will be used. Historically, coral cover at this site has experienced large losses (>40%) during cyclone events (Connell *et al.* 1997), with recovery times ranging from 3 to 25 years (Connell *et al.* 2004).

The Liverpool South Dock chain was started in 1753 with the building of Salthouse Dock (Jones 2004, p92). They were built because the strong tides and shifting mud banks of the Mersey Estuary were major restrictions to the growth of the shipping trade in the 17th century (Hawkins *et al.* 1999). Later, the increasing size of boats necessitated using larger docks, and after 1920 the Docks were no longer used commercially (Jones 2004, p25). The South Docks were closed in 1972 and their gates were left open; this led to the docks filling with large quantities of silt (Jones 2004, p30). The Liverpool South Docks were restored for the International Tall Ships race in August 1984; the restoration involved removing 12 feet of silt, dredging the docks, and repairing the walls (Jones 2004, pp34-35).

The South Liverpool Dock chain is dominated by benthic filter feeders, and relatively diverse fish communities (Fielding 1997). This dock system will be used as a secondary study site to further inform potential models of sessile community dynamics.

Study Objectives

This study aims to advance our ability to predict the dynamics of marine communities using statistical models. This involves: adding environmental data to models, investigating the impact of climate change on disturbances, evaluating predictions using new data, and investigating the methodology used in making these predictions. These aims are addressed in five chapters:

Chapter 2 is a comparison of four models for community dynamics at Heron Island. Markov models are used to describe systems where a future event is only dependent on the current status and not on any previous states (Renshaw 1995). In the study of sessile community dynamics, it has been demonstrated that simple Markov models can be applied to organisms as diverse as forests and corals (Tanner *et al.* 1996). However, recent work has suggested that nonlinear models may be more appropriate in some cases (Spencer and Tanner 2008). I compare four models, a discrete-time Markov model and a nonlinear continuous-time model, each with and without the effects of cyclones. The models are fitted to data and are compared to one another using Bayesian methods.

Chapter 3 examines the effect of different climate change scenarios on cyclones, and therefore coral reefs. Using the best model from Chapter 2, we examine how different the dynamics at Heron Island for the years 1962-1992 might have been under a range of cyclone frequency scenarios from the literature.

Chapter 4 is an assessment of the predictions made using current models for coral reef dynamics tested against recent data. We take the two models with cyclone effects from Chapter 2, and run them forwards in time from the end of the observation period until the year 2008. We then compare the predictions with newly collected field data, using Bayesian methods.

Chapter 5 is an experimental study on the effects of different disturbance regimes on marine sessile communities. A two-year study was carried out at the Salthouse Dock site to determine whether a disturbance regime would cause changes in community composition. The disturbance regime was implemented after a period of settlement.

Chapter 6 is a general discussion of all of the previous chapters. Recommendations for further work are made, along with suggestions for model improvements. The need for synergy between ecological theory and data is discussed, as is the use of simple statistical models.

Chapter Two: Predicting the effects of cyclones on coral reefs

Introduction

Coral reefs are one of the most biologically diverse ecosystems on the planet, and are also important economically (Diaz-Pulido *et al.* 2009). There is clear evidence of a global decline in both the abundance of coral and quality of reefs due to the cumulative effects of a number of anthropogenic pressures including warming oceans, ocean acidification, coral disease, declining water quality, eutrophication, physical damage and fishing overexploitation (Hughes 2003, Bellwood *et al.* 2004, Bruno and Selig 2007, Graham *et al.* 2008). In many parts of the world coral bleaching has resulted in significant declines of live coral (Hoegh-Guldberg 1999). Coral bleaching occurs when corals lose their symbiotic zooxanthellae, and is a result of the corals being stressed (e.g. thermal stress) (Hughes 2003).

Species diversity in coral systems is critically dependant on natural mortality in the reef system and the continual mortality of the competitive dominants is essential to promoting diversity (Connell 1978). Natural coral mortality can occur as a direct result of storm events, such as cyclones. A cyclone is a ‘non-frontal synoptic scale cyclonic rotational low pressure system of Tropical origin, in which 10 minute mean winds of at least 17.5 m s^{-1} occur with the belt of maximum winds being in the vicinity of the system’s centre’ (Australian Bureau of Meteorology (ABM) 2011a). Cyclones are generated by high wind speeds, low pressures, and a sea surface temperature (SST) above 26 °C and are therefore strongly influenced by SST (Webster 2005). Increasing SST has led to an increase in cyclone frequency (Webster 2005). Cyclones have also increased in power over the last 50 years (Emanuel 2005). Cyclones cause coral mortality by sediment scouring, direct mechanical breakage, and the removal of substratum (Mumby 1999).

An ecological disturbance has been defined as a departure, relative to a normal state, or trajectory (White and Pickett 1985). The intermediate disturbance hypothesis (Connell 1978) states that high diversity is maintained in coral reef systems through disturbances at intermediate intervals. Cyclones have always been present in tropical climates but the increased severity and frequency of cyclones, due to anthropogenic climate change, may result in a reduction in the abundance and diversity of corals.

The frequency and severity of disturbances create a regeneration niche that will be occupied by species that have regeneration times that are shorter than the disturbance period (McClanahan 2002). Algae have the fastest regeneration times in coral reef systems (McClanahan 2002). A new disturbance regime on a reef can cause the ecosystem to fundamentally change its species composition from previous ecological states (McClanahan 2002). Dudgeon *et al.* (2010) define a phase shift as a change in the community equilibrium in response to a persistent change in environmental conditions. Coral reefs are potentially susceptible to such phase shifts as there is some evidence that some reefs have undergone a phase shift from a coral-dominated system to a system that is dominated by algae in response to changes in nutrient and sediment inputs, due to eutrophication (Hughes *et al.* 2007).

One of the longest time series of coral reef community data is from Heron Island. It is a platform reef near the southern end of the Great Barrier Reef (Connell *et al.* 2004). Historically, coral cover has experienced large losses (>40%) during cyclone events (Connell *et al.* 1997), with recovery times ranging from 3 to 25 years (Connell *et al.* 2004). A series of permanent quadrats were established on three sites on Heron Island in the early 1960s (Tanner *et al.* 1994) and have been sampled every 1-3 years since.

Several models have been created to describe the dynamics of this system (Tanner *et al.* 1994, Tanner *et al.* 1996, Spencer and Susko 2005, Spencer 2006, Spencer and Tanner 2008). Tanner *et al.* (1994) is a discrete-time Markov model, whereas Tanner *et al.* (1996) is a semi-Markov model where transitions depend on how long a point has spent in its current state. Spencer & Susko (2005) is a continuous-time version of a Markov model. In this context, Markov models describe the dynamics of discrete states (in these cases, groups of species) at fixed points in space. The probabilities of transitions between states are assumed to depend only on the current state. Markov models are generally used because they are relatively easy to parameterise from field data, and have a relatively simple structure, compared to many other models of community dynamics. Markov models can be used to quantify the structure of a community (e.g. succession, Hill *et al.* 2004), or to predict the outcome of a disturbance event (Wootton 2004). In contrast, Spencer & Tanner (2008) is a continuous-time Lotka-Volterra competition model. It fits the data significantly better than the other simple models because the transition rates are dependent on density. However, a goodness-of-fit test shows that there is still a large amount of unexplained variability in the model. The model does not include cyclones, or other environmental parameters, which may explain this variability. There are other models which incorporate cyclones (e.g. Massel and Done 1993, Wolanski *et al.* 2004) but these are mostly mechanistic and have not been rigorously evaluated against data.

In this chapter, we aim to develop statistical models that can be used to predict the consequences of future cyclone events on the coral reef system. These will consist of a linear discrete-time Markov model, and a nonlinear continuous-time model based on Spencer & Tanner (2008). These models will be tested using the Heron Island dataset. More generally, these models will act as a framework for adding environmental variables into statistical models of community dynamics.

Methods

Data

Information on the study site is given in Chapter 1. At 17 unequally spaced times, between 1962 and 1989, the states (coral, algae, free space) of at least 1249 fixed points in space were recorded (Tanner *et al.* 1994). The 1249 fixed points were from across all six quadrats and the data from the quadrats were pooled. For each pair of observations at consecutive times, t_1 and t_2, a matrix of transition counts was calculated, whose entries were the number of times that we saw state i at t_2 given state j at t_1.

Discrete-time model

We make the following assumptions: all time intervals are equal in length, in reality this is not exactly true (mean time interval = 1.60, with a standard error of ± 0.18 years); transition probabilities are constant over every time interval that has the same environmental conditions; that the true matrix of transition probabilities is irreducible and primitive, as it ensures that the model has a unique stationary distribution (Caswell 2001); and that all intervals that include one or more cyclones are affected equally; in reality this depends on when in the interval cyclone/s occur.

We used a Bayesian approach to estimate the model parameters, using Bayes' theorem (Equation 2.1). The output was the posterior distribution ($p(\theta|y)$) of the unknown (possibly multidimensional) parameter θ given data y, which was dependent on the prior, $p(\theta)$, and the data distribution, $p(y|\theta)$. The prior expresses our knowledge of the system, and the data distribution is the probability of these data given parameter θ.

$$p(\theta \mid y) \propto p(\theta) p(y \mid \theta) \tag{2.1}$$

(Gelman *et al.* 2004, p8)

We derived transition counts for the discrete-time model by separating the observed transition counts into intervals with and without cyclones. These were then summed to create two sets of transition counts: cyclone, and nocyclone. Intervals are included in the cyclone transition counts if there is at least one cyclone at any time during that interval.

A uniform Dirichlet prior on transition probabilities out of a given state is used, as we do not have strong prior knowledge about the transition probabilities. This prior makes any set of transition probabilities equally likely. The Dirichlet distribution has all α_j set to a value of one for the uniform case.

The Dirichlet density function is

$$p(\theta \mid \alpha) \propto \prod_{j=1}^{k} \theta_j^{\alpha_j - 1}$$

where k is the number of possible outcomes (Gelman *et al.* 2004, p83).

Using this Dirichlet prior, and assuming a multinomial model for the counts of transitions out of a given state, the posterior distribution is also Dirichlet:

$$p(y \mid \theta) \propto \prod_{j=1}^{k} \theta_j^{\alpha_j + y_j - 1},$$

where y is the vector of counts of the number of observations of each outcome (Gelman *et al.* 2004, p83). A similar prior was used on the initial probabilities of each state, resulting in a similar Dirichlet posterior distribution.

We were able to sample directly from the posterior distribution of transition probabilities. Random samples were taken from a set of gamma distributions with scale parameter = 1, and shape vector =Y+1, where Y is the matrix of transition counts. The gamma samples were then transformed into Dirichlet samples as described in Gelman *et al.* (2004, p582).

Continuous-time model

An existing continuous-time Lotka-Volterra competition model was used as the basis for a new model incorporating cyclone effects (Spencer and Tanner 2008, 2.). The basic model is a system of nonlinear differential equations, and does not include any environmental variables.

$$\frac{dx}{dt} = (\mathbf{XA} - \mathbf{C})\mathbf{x} \tag{2.2}$$

Here, **A** is a matrix whose off-diagonal elements are the interaction coefficients a_{ij}, which specify the transition rate from state j to state i, and have dimensions time^{-1}. The diagonal elements are zero. **X** is a diagonal matrix with entries x_i if $i \neq e$, and 1 if $i = e$, where e is empty space. **C** is a diagonal matrix of column sums of **XA**. **x** is a column vector of probabilities of each state.

Modelling cyclone effects

The simplest approach to add cyclone effects to the model is a step change in coral mortality sustained for a period of time after the cyclone hits (t_c). We assume that all cyclones cause the same increase in mortality. We also assume that more than one cyclone in quick succession does not cause a further increase in the rate of mortality, only an increase in the duration of the increased mortality. Added parameters were the increased mortality due to cyclones and the duration of increased mortality after a cyclone occurs, which we assume to be fixed and constant. We believe that coral mortality is sustained due to the mortality caused by coral fragments and smothering caused by sediment (Mumby 1999). The original model used a matrix of transition rates, A. The new model (Equation 2.3) uses two matrices of transition rates.

$$\frac{dx}{dt} = \begin{cases} (\mathbf{XA} - \mathbf{C})\mathbf{x} & \text{when time since last cyclone} > t_c, \\ (\mathbf{XA}_c - \mathbf{C}_c)\mathbf{x} & \text{when time since last cyclone} \leq t_c \end{cases} \qquad (2.3)$$

where $\mathbf{C}_c$ is a diagonal matrix of column sums of $\mathbf{XA}_c$.

Three new parameters were also added to the model. The original matrix, **A**, is used when cyclones are not determined to be causing mortality. A new transition matrix, $\mathbf{A}_c$ differs only from **A** in one term, the transitions of corals to empty space (a_{31}), which has been multiplied by c in $\mathbf{A}_c$. We assume that the duration of increased mortality after a cyclone occurs is fixed and constant.

The parameter c is a measure of increased mortality, which is the change in transitions from coral to empty space. When c=1 there is no change to mortality (i.e. cyclones are not causing increased mortality). $\mathbf{A}_c$ is used when cyclonic effects were known to be occurring. These occurrences were determined using the dates of known cyclones and the duration of their effects. A vector of dates when cyclones caused coral mortality at the study site on Heron Island was used (Connell *et al.* 1997). t_c is the duration of cyclone mortality. This was estimated at six months after a range of two months to two years was obtained from the primary literature (e.g. Emslie *et al.* 2008, Gardner *et al.* 2005, Guillemot *et al.* 2010). We do not estimate t_c from the data because we want to estimate as few parameters as possible, as the number of observations is fairly small. There are also potential identifiability problems because c has no effect as t_c approaches zero.

Parameter Estimation

Markov Chain Monte Carlo (MCMC) analysis is a method of estimating the posterior distribution of model parameters in a Bayesian analysis. The posterior distribution of a parameter contains all the information we have about the value of a parameter, both from prior knowledge or beliefs and from the current data. We define a Markov chain whose stationary distribution is the required posterior. We then simulate this chain. After an initial period, which is discarded (the burnin), the simulated sample is approximately a sample from the posterior distribution.

The priors used for most of the parameters were vague. We thought that an informative prior for coral mortality was important because we did not believe that the estimate of coral mortality in the original model was biologically plausible as it was too low (Clancy *et al.* 2010). To generate an informative prior, data for coral mortality were obtained from searching electronic journals for ‘coral mortality’. The data were the survival of colonies over time. Survival rates were obtained for varying lengths of time (Table 2.1). It was assumed that the rate of mortality was constant over the time period. Studies that focused on a disturbance event (e.g. tsunami, cyclone, storm) were excluded as we are trying to assess the background level of coral mortality. Where a study used an experimental treatment the control group was used. We ended up with information from four papers covering at least thirteen different coral species. For each species in each study the instantaneous rate of coral mortality was calculated using the exponential growth equation

$$N_t = N_0 e^{rt} \tag{2.4}$$

Here, N_t is the proportion alive at time t, N_0 is proportion alive at time 0 ($N_0 = 1$), r is the instantaneous mortality rate, and t is time. Equation 2.4 was rearranged to give the instantaneous growth rate (r) for each coral mortality value (Table 2.1):

$$r = -\frac{\ln N_t}{t} \tag{2.5}$$

Table 2.1. Instantaneous rates of coral mortality (r) from the literature, calculated using equation 2.5. Mortality rates were assumed to be constant over time. Original data were over varying lengths of time (t).

Reference	Reef Location	Species	r (years^{-1})	t (years)
Bak & Luckhurst (1980)	Curacao	*Agaricia agaricites*	0.204	5.00
		A. lamarcki	0.023	5.00
		Montastrea annularis	0.030	5.00
		M. cavernosa	0.030	5.00
		Meandrina meandrites	0.096	5.00
		Other coral	0.109	5.00
Harriott (1985)	Lizard Island	*Favia favus*	0.038	1.33
		Porites spp.	0.122	1.33
		Lobophyllia corymbosa	0.167	1.33
		Pocillopora damicornis	0.435	1.33
Tanner (1997)	Heron Island	*Acropora hyacinthus*	0.199	1.25
		Pocillopora damicornis	0.497	2.00
Babcock (1991)	Geoffrey Bay	*Goniastrea aspera*	0.278	1.00
		G. aspera	0.148	1.00
		G. favulus	0.251	1.00
		G. favulus	0.171	1.00
		Platygyra sinensis	0.196	1.00
		Platygyra sinensis	0.218	1.00
		G. aspera	0.209	1.00
		G. aspera	0.223	1.00
		G. favulus	0.167	1.00
		G. favulus	0.178	1.00
		Platygyra sinensis	0.128	1.00
		Platygyra sinensis	0.232	1.00

Once calculated, the values of r were plotted as a histogram (Fig. 2.2). A gamma distribution (Evans *et al.* 2000) was appropriate as a model for these data as mortality rate is non-negative, and the gamma distribution has a flexible shape. The parameters of the gamma distribution, shape and rate, were determined using the function 'fitdistr' in the MASS package in R (Venables and Ripley 2002). Figure 2.1 shows the fitted gamma distribution plotted against a histogram generated from the data in table 2.1.

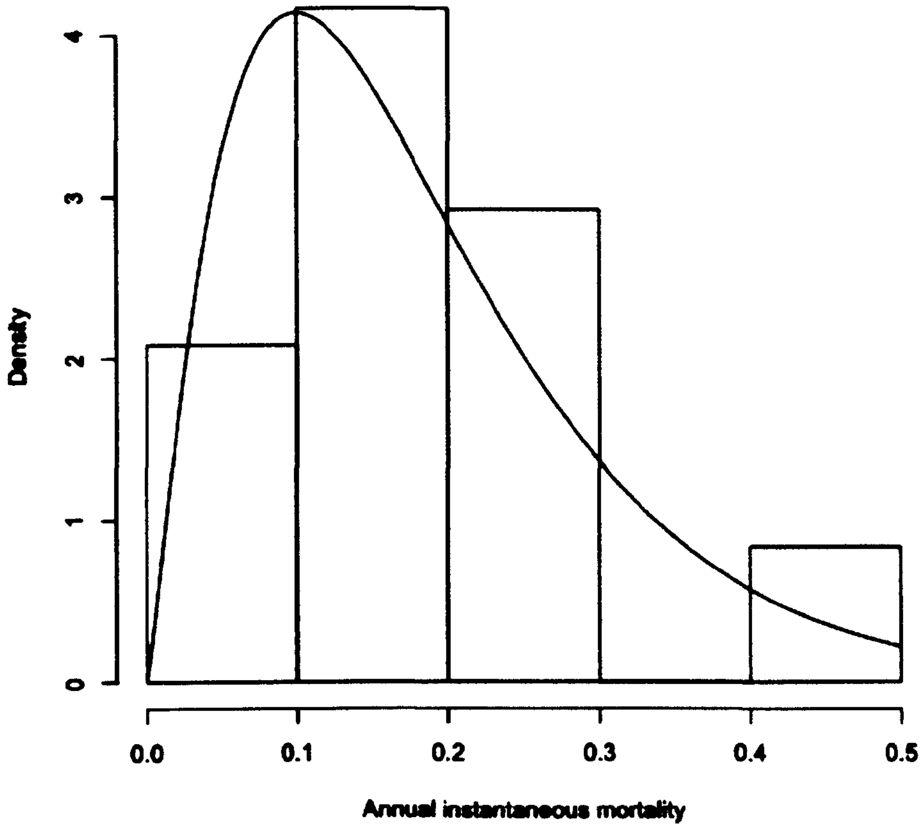

Figure 2.1. Histogram of instantaneous coral mortality rates (r) from the literature. Line represents a gamma distribution fit to the data using the function 'fitdistr' in the MASS package in R.

The estimated gamma distribution (Evans *et al.* 2000), with parameters of scale = 2.2166 and shape = 0.0818 was used as a prior for coral mortality. The model was implemented in Matlab R2009a (Mathworks 2009) and was run twice for 1 x 10^7 iterations to check for convergence on a Debian Lenny linux server with a 3 GHz Intel Xeon processor and 4G RAM, using a burnin length of 1 x 10^6. Models were compared using Bayes' factors (Gelman *et al.* 2004, p184) based on harmonic means (Newton and Raftery 1994).

Results

Discrete-time Model

The discrete-time model without the effect of cyclones quickly approaches equilibrium (Fig. 2.2.). The equilibrium state probability for empty space is highest at approximately 0.6, whereas coral is approximately 0.38, and algae is 0.02. Initially uncertainty decreases; the effect of initial conditions decays as equilibrium was approached (Fig. 2.2.). However, the uncertainty did not disappear; uncertainty in the transition probabilities was reflected in the uncertainty in where the equilibrium lies. This model approaches equilibrium too quickly and does not capture the trends in real data.

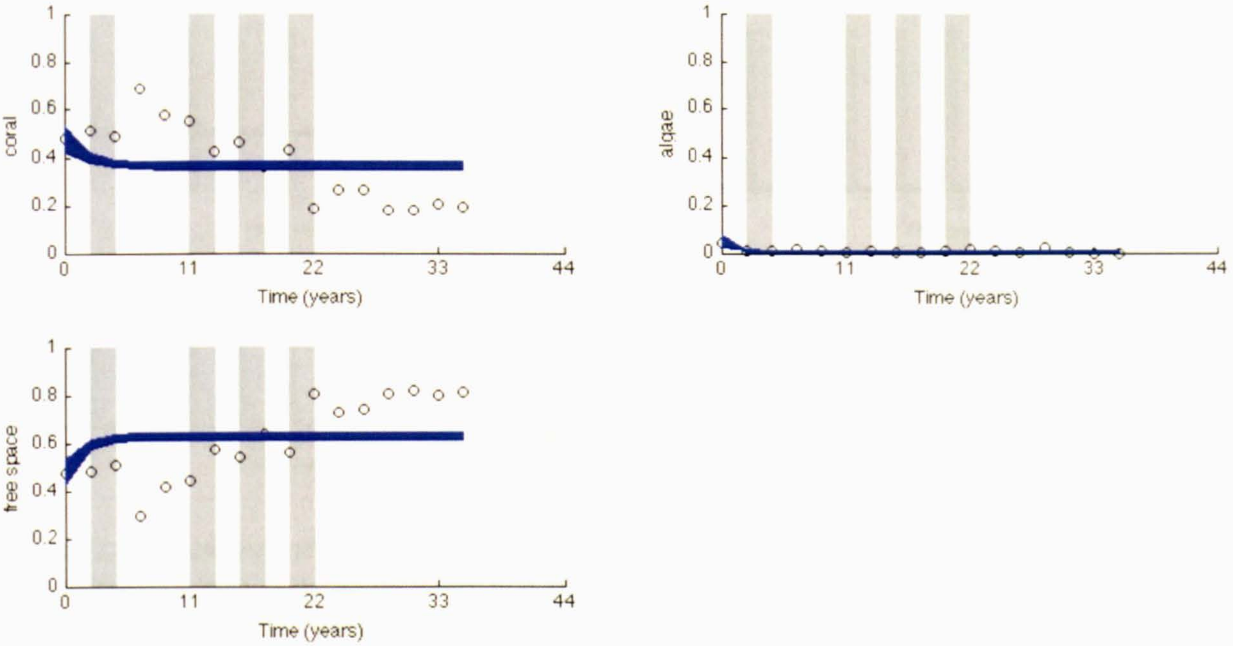

Figure 2.2. Posterior of discrete-time model without cyclones. Circles are observed proportions of each state. Each solid line represents an iteration of the model from the posterior parameter distribution, where thick solid lines represent a number of overlapping iterations. Vertical bars represent intervals with cyclones. Time is measured in years since 1963.

The discrete-time model with the effect of cyclones showed short-term fluctuations caused by cyclones around a long-term mean. When a cyclone hits, the state probabilities of empty space and algae increase, whereas the state probability of coral decreases, where cyclones cause mortality of corals (Fig. 2.3). As with the model without cyclones, the effect of uncertainty in initial conditions decays over time (Fig. 2.3). Uncertainty is higher, especially in algae, when cyclones occur. This model does not capture the overall trends in the data but it does capture the apparent effect of cyclones. For example, in the real data, the proportion of empty space increases in 4/4 time intervals with cyclones but only 7/12 time intervals without cyclones. In the model, the proportion of empty space increases over every cyclone interval.

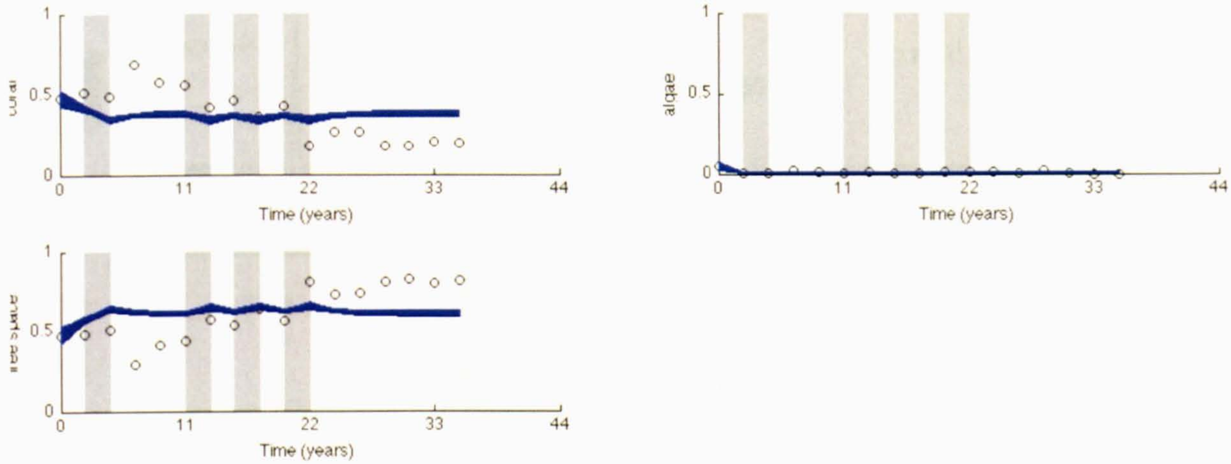

Figure 2.3. Posterior of discrete-time model with cyclones. Circles are observed proportions of each state. Each solid line represents an iteration of the model from the posterior parameter distribution, where thick solid lines represent a number of overlapping iterations. Vertical bars represent intervals with cyclones. Time is measured in years since 1963.

There are two key differences between the transition probabilities for time intervals with and without cyclones. Intervals with cyclones have higher transitions from coral to free space, and lower coral persistence (Fig. 2.4,2.5). Intervals with cyclones also have higher uncertainty in transition probabilities out of the algal state due to smaller sample sizes (Fig. 2.4,2.5). The transition probability from coral to free space in intervals when there is not a cyclone occurring has a posterior mode of approximately 0.4 (Fig. 2.4G).

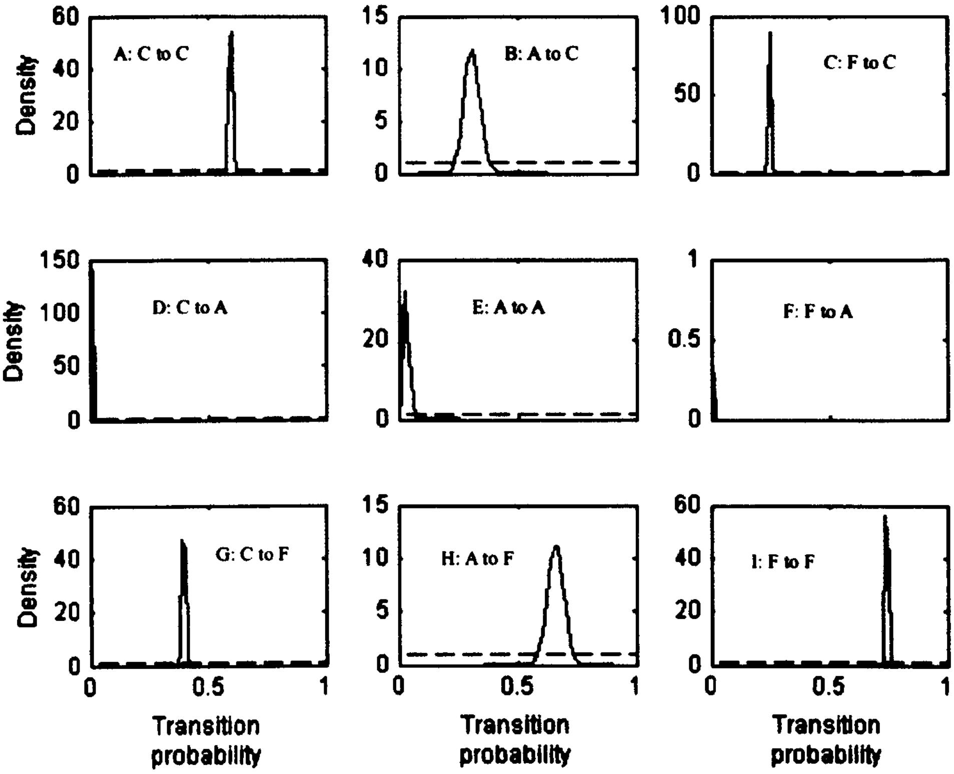

Figure 2.4. Probability density functions for posterior transition probabilities for discrete-time model with cyclones when a cyclone is not occurring. C to C is coral persistence, A to C is algae to coral, F to C is free space to coral, C to A is coral to algae, A to A is algal persistence, F to A is free space to algae, C to F is coral mortality, A to F is algal mortality, and F to F is persistence as empty space.

The probability of a coral to free space transition when there is a cyclone occurring has a posterior mode of just above 0.5 (Fig. 2.5G), which is higher than when a cyclone is not occurring (Fig. 2.4G). The probability of coral surviving decreases from approximately 0.6 when a cyclone is not occurring (Fig. 2.4A) to approximately 0.5 when a cyclone is occurring (Fig. 2.5A). This decrease is because the transition probabilities in any column must sum to one. Thus, a change in one transition probability must be balanced by changes in other transitions in the same column.

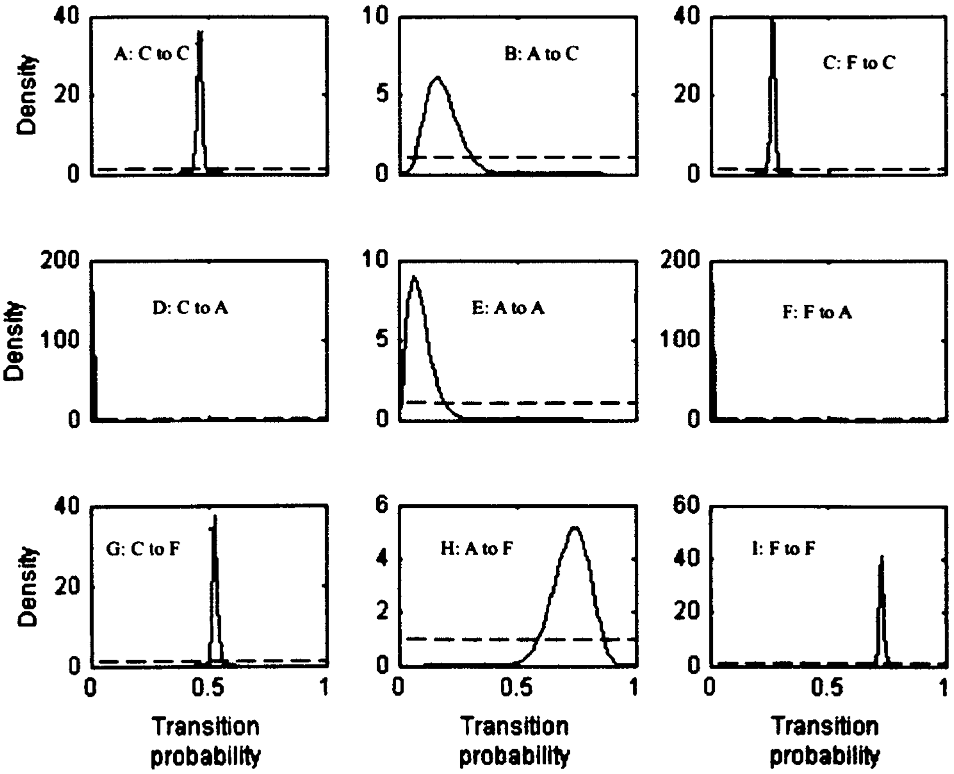

Figure 2.5. Probability density functions for posterior transition probabilities for discrete-time model with cyclones when a cyclone is occurring. C to C is coral persistence, A to C is algae to coral, F to C is free space to coral, C to A is coral to algae, A to A is algal persistence, F to A is free space to algae, C to F is coral mortality, A to F is algal mortality, and F to F is persistence as empty space.

A Bayes factor was calculated comparing the discrete-time model with cyclones to the discrete-time model without cyclones. The Bayes factor was 112.7, which is 'strong' evidence that the discrete-time model with cyclones is better than the discrete-time model without cyclones (Raftery 1996).

Continuous-time Model

Continuous-time model without cyclones

Figure 2.6 shows the marginal posteriors for one run of the continuous-time model without cyclones. The other, not shown, was very similar. Transitions from coral to algae, algae to free space, and empty space to algae were all large (Fig. 2.6). The values were similar to those in Clancy *et al.* (2010), which shows that having different priors made little difference. The rate of transitions from coral to empty space (a_{31}) is too small; even with a strong prior (Fig. 2.1) for this model the data suggest a smaller coral mortality than is biologically plausible (Fig. 2.6).

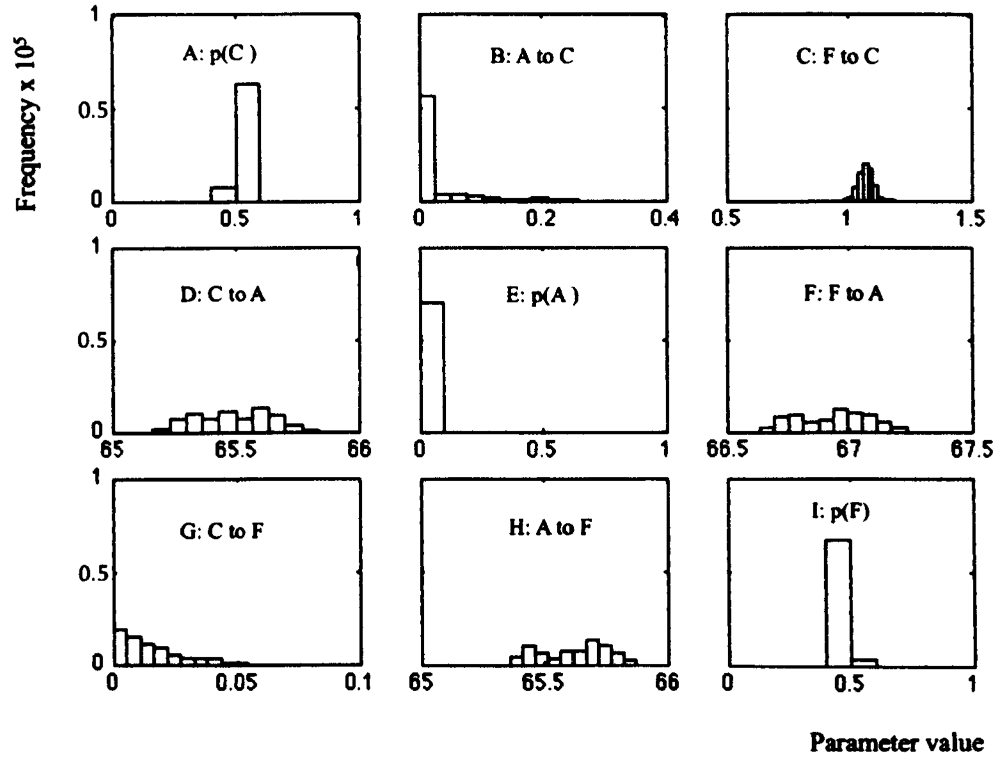

Figure 2.6. Probability density functions for marginal posteriors of continuous-time model without cyclones (one of two similar runs shown). The diagonal components are initial state probabilities of coral p(C), algae p(A), and free space p(F). The off-diagonal components are rates of transitions where C=coral, A=algae, and F=free space (years^{-1}). Run for 1 x 10^7, burnin was 1 x 10^6.

Figure 2.7 shows one run of the continuous-time model without the effect of cyclones. The other, not shown, was very similar. It approaches equilibrium after about 30 years (Fig. 2.7). The equilibrium state probability for empty space is highest at almost 1, whereas coral is approximately 0, and algae is 0.02. Initially uncertainty decreases for coral and empty space (Fig. 2.7). Uncertainty is higher in the algal state (Fig. 2.7). The model captures the overall trend in coral and free space, but there is some scatter of the data around the model predictions.

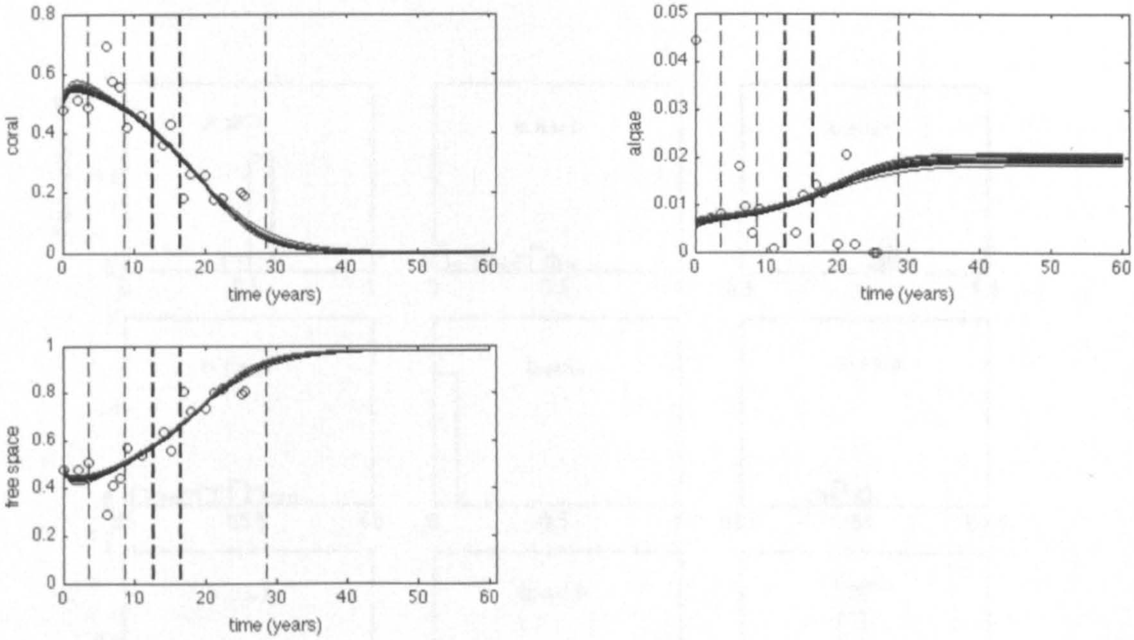

Figure 2.7. Posterior of continuous-time model without cyclones (one of two similar runs shown). Circles are observed proportions of each state. Each solid line represents one of 1000 iterations of the model from the posterior parameter distribution where thick solid lines indicate a number of overlapping iterations. Vertical dashed lines represent dates of cyclones, where thick dashed lines indicate more than one cyclone in quick succession. Time is measured in years since 1963.

Continuous-time model with cyclones

Log likelihoods for both runs (Appendix I) seemed to converge after c. 5×10^5 iterations. The key difference between the two runs of the model with cyclones is in the estimates of coral mortality parameters. The second run has higher coral mortality in the absence of cyclones (a_{31} is between 1 and 1.8×10^{-4} in the first run, Figure 2.8G, and 0.005 to 0.01 in the second run, Figure 2.9G). The real difference in model behaviour is not that great, in that in both runs, almost all coral mortality occurs after cyclones.

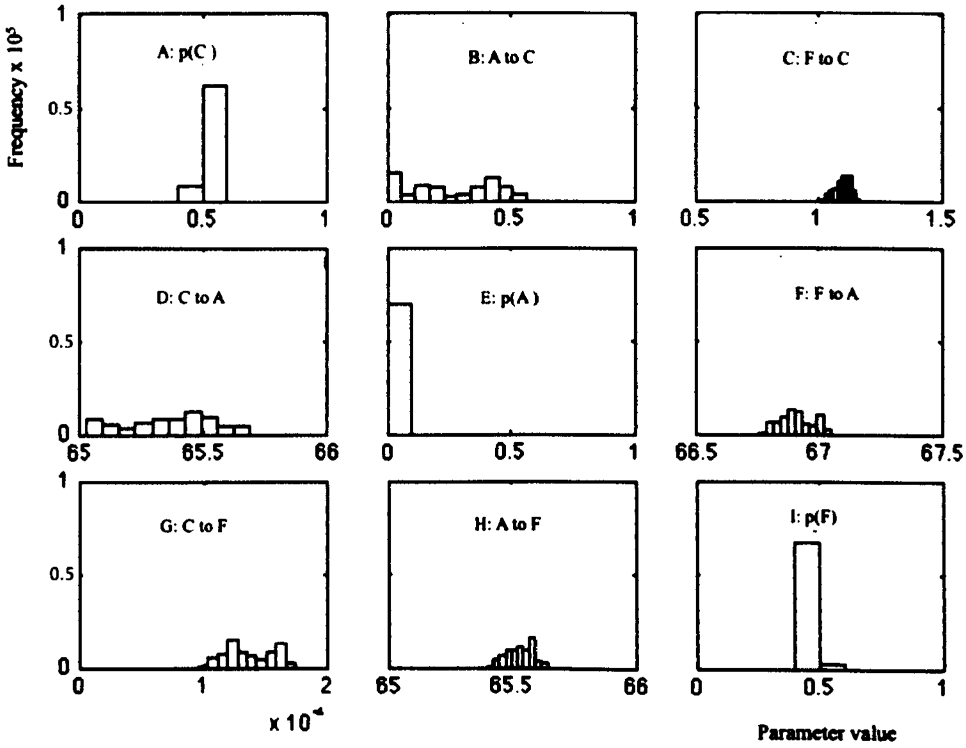

Figure 2.8. Probability density functions for marginal posteriors for continuous-time model with cyclones (first run). The diagonal components are initial state probabilities of coral p(C), algae p(A), and free space p(F). The off-diagonal components are rates of transitions where C=coral, A=algae, and F=free space (years^{-1}). Run for 1×10^7, burnin was 1×10^6.

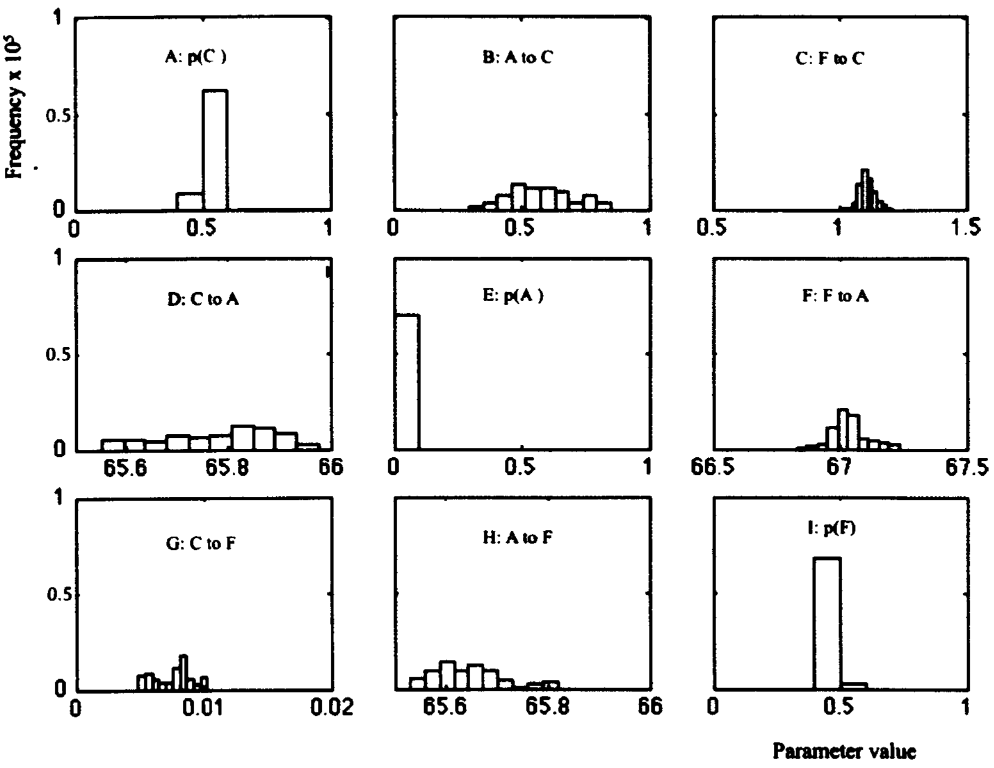

Figure 2.9. Probability density functions for marginal posteriors for continuous-time model with cyclones (second run). The diagonal components are initial state probabilities of coral p(C), algae p(A), and free space p(F). The off-diagonal components are rates of transitions where C=coral, A=algae, and F=free space (years^{-1}). Run for 1 x 10^7, burnin was 1 x 10^6.

However, the 95% credible interval for the increase in coral mortality during cyclone periods (*c*) was higher in the first than the second run (4769-8286 for the first run, and 82.4-156.6 for the second). As a result, mortality of coral during a cyclone (the product of *c* and transitions from coral to empty space) is within one order of magnitude for both runs (Fig. 2.10), while mortality of coral outside cyclone periods is very low in both runs. There seems to be a strong trend in coral mortality during cyclones in the first run, and in both runs, it looks like there are some fairly long-term changes (Fig. 2.10). This is evidence that the MCMC is having difficulty converging, even though the biological conclusions are similar in both runs.

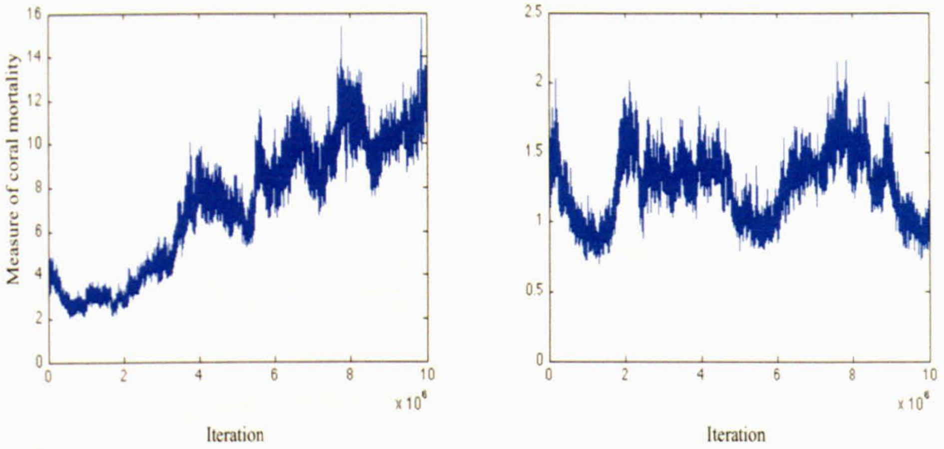

Figure 2.10. Coral mortality during a cyclone for both runs. Mortality = $a_{31} * c$ for both runs, where a_{31} is transitions from coral to empty space and c is the increase in mortality due to cyclones.

The posterior trajectories for both runs of the continuous-time model with cyclones (Fig. 2.11,2.12) are the closest match to the observed patterns out of all the models considered so far. Coral cover (Fig. 2.11,2.12) shows a strong overall downward trend, with sharp decreases when cyclones hit, followed by fairly rapid partial recovery. The patterns in free space (Fig. 2.11,2.12) are more or less a mirror image of the patterns in coral cover; with a strong upward trend overall, accompanied by sharp short-term increases after cyclones. The posterior trajectories for algal cover (Fig. 2.11,2.12) are not a particularly close match to the observations, but this is likely to be a consequence of the very low algal cover throughout the time series. For all three states, the uncertainty in the posterior trajectories is relatively low.

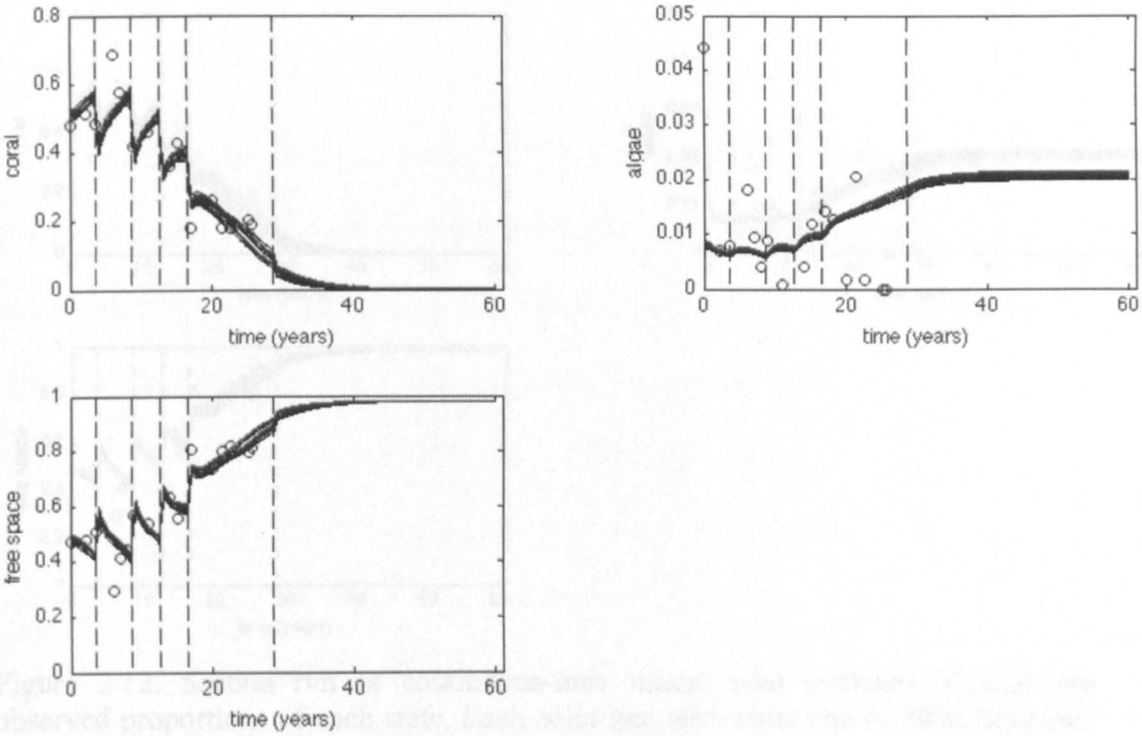

Figure 2.11. First run of continuous-time model with cyclones. Circles are observed proportions of each state. Each solid line represents one of 1000 iterations of the model from the posterior parameter distribution, where thick solid lines indicate a number of overlapping iterations. Vertical dashed lines represent dates of cyclones, where thick dashed lines indicate more than one cyclone in quick succession.

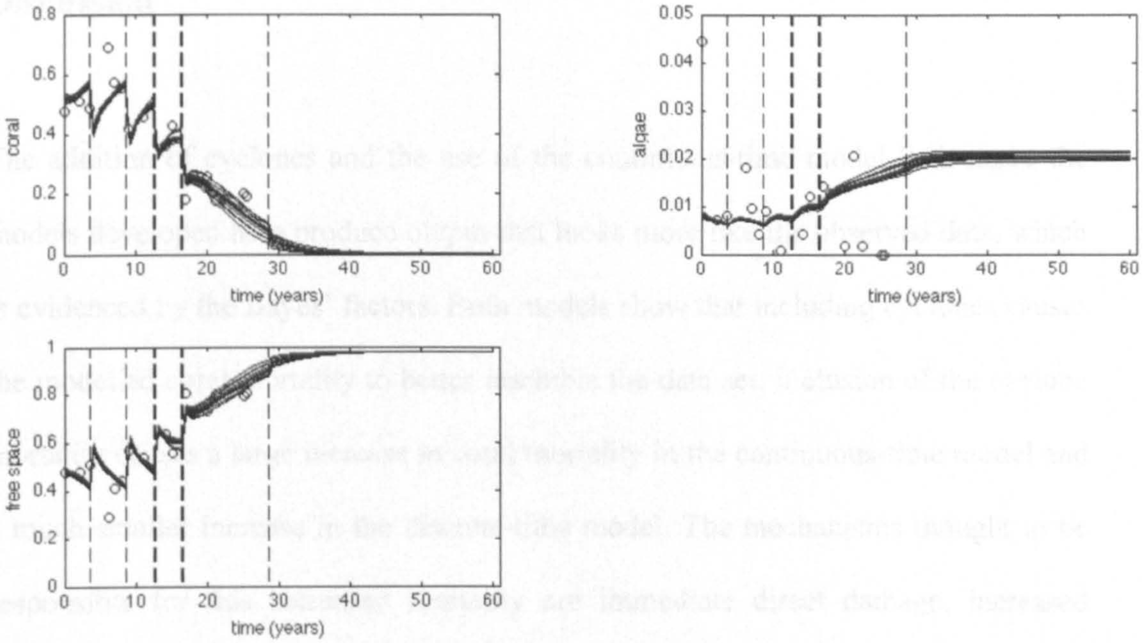

Figure 2.12. Second run of continuous-time model with cyclones. Circles are observed proportions of each state. Each solid line represents one of 1000 iterations of the model from the posterior parameter distribution, where thick solid lines indicate a number of overlapping iterations. Vertical dashed lines represent dates of cyclones, where thick dashed lines indicate more than one cyclone in quick succession.

Bayes factors were calculated comparing both runs of the continuous-time model with cyclones, with both runs of the continuous-time model without cyclones. The first run of the continuous-time model with cyclones, when compared to both runs of the continuous-time model without cyclones, produced a Bayes' factor of 44.2. This is 'strong' evidence that the continuous-time model with cyclones is better than either of the continuous-time models without cyclones (Raftery 1996). The second run of the continuous-time model with cyclones, when compared to both runs of the continuous-time model without cyclones, produced a Bayes' factor of 11.4. This is 'positive' evidence that the continuous-time model with cyclones is better than either of the continuous-time models without cyclones (Raftery 1996).

Discussion

The addition of cyclones and the use of the continuous-time model both make the models developed here produce output that looks more like the observed data, which is evidenced by the Bayes' factors. Both models show that including cyclones causes the modelled coral mortality to better resemble the data set. Inclusion of the cyclone mortality causes a large increase in coral mortality in the continuous-time model and a much smaller increase in the discrete-time model. The mechanisms thought to be responsible for this increased mortality are immediate direct damage, increased sedimentation, and delayed damage from rubble in the water (Mumby 1999). Our model does not explicitly include these mechanisms but it does generate the patterns we would expect these mechanisms to produce.

Visually, the continuous-time model produces output that is a better match for the observations than the discrete-time. This may be because the continuous-time model is nonlinear, with transition rates that depend on local abundances. In contrast, the discrete-time model is linear, and can be viewed as describing an open system with a constant input of recruits. It has been suggested that Lotka-Volterra and similar models may not be appropriate for marine invertebrates such as corals that have sessile, space-limited adults and pelagic larvae (Roughgarden *et al.* 1985). Roughgarden *et al.* (1985) used a "supply-side" model whose basic formulation is a linear Markov model. In practice, both local growth and dispersal are likely to be important. The growth rate of an existing coral population seems inherently likely to depend on coral cover. For example, under the simple assumption that each unit of cover has a constant growth rate, a unit of free space will be filled more quickly when coral cover is high than when it is low. Other, more complicated, scenarios such as size limitation and density dependence (Artzy-Randrup *et al.* 2007) will give different growth rates, but are not likely to remove the qualitative dependence of growth rate on coral cover. However, since the continuous-time model looks more like the data it could be argued that recruitment is not as important as the growth and mortality of existing corals. However, coral reefs have been shown to have high spatial variability in recruitment (Connell *et al.* 1997) therefore for some reefs recruitment will be important.

Uncertainty still remains about the rates of some transitions in the continuous-time model. This is especially true for transitions that involve algae as they have fast dynamics. Algae have been shown to be capable of undergoing a complete growth cycle in four to six months (Jompa and McCook 2003). Since observations are taken at time intervals much longer than this, it will be difficult to reconstruct algal dynamics from the data. Discrete-time models are much easier to fit to such data because they make no predictions about what happens between observations (e.g. coral to free space followed by colonization by algae becomes coral being overgrown by algae). The uncertainty about what happens to algae in the model may in part be due to cyclones both causing instantaneous mortality, and stimulating growth by the production of bare substrate. The time resolution in the data is insufficient to pick up algal dynamics. Any large changes in algae are dampened by the relatively low frequency of algae in the dataset. Algae are not a major ecosystem component at this site but are at other sites (e.g. in the Caribbean). Some reefs that have undergone recurrent disturbances (e.g. cyclone, disease, bleaching) have undergone a phase shift from a coral dominated system to one that is dominated by macroalgae (Bruno *et al.* 2009).

Coral mortality due to cyclones is not large, and recovery is fast. In our case, this short-term recovery is superimposed on a longer-term decline. Thus disturbance should be thought of as moving the system temporarily away from a trajectory towards an equilibrium (which may be changing over time), and recovery as a return to the initial trajectory (Jeffries 1976). Corals have been shown to be suppressed by cyclones and recover comparatively slowly between recurrent events (Hughes *et al.* 2010).

Related to this, our estimates of background coral mortality from the continuous-time model appear implausibly low, even after supplying strong prior information (Fig. 2.2). Again, this may be due to widely-spaced observations. In such cases, coral death followed by algal overgrowth may be attributed to direct algal overgrowth rather than to coral mortality.

It seems possible that there is not enough information in the data to reliably estimate all the parameters of a nonlinear model. This may be the cause of our convergence problems with the MCMC despite our efforts, and is a problem associated with modern, complex models (Lavine 2010). The model can not be made more complicated by adding additional parameters, as the data to support it are not available. We may be able to solve this problem simply by having a longer time series.

Returning to the ideas of generality, precision, and realism (Levins 1966) mentioned in Chapter One, the choice of model depends on whether the purpose is to understand a system or be able to make predictions. Using the discrete-time model, we could test hypotheses about impacts of stressors such as cyclones, and possibly other factors such as SST. We had at least qualitative agreement with the continuous-time model, while being much easier to work with. The data requirements are less restrictive for the discrete-time model; we don't run into problems with processes that occur on much shorter time scales than the observation interval. Predictions made using the discrete-time model might be a bit risky because it does not fit the data well, so would be unlikely to be accurate in the future. Our continuous-model would be more appropriate to use for quantitative predictions. We could also test whether the addition of data for other environmental variables could further improve the continuous-time model. With the current model, there is still some uncertainty in the predictions, which would need to be addressed. Despite our uncertainties, there are much less well-studied models that are used for predictions at much larger scales (e.g. McClanahan 1995, Mumby *et al.* 2006, Wolanski *et al.* 2004). It has been demonstrated that, beyond a threshold, as model complexity increases, model effectiveness decreases (Fulton *et al.* 2003).

In conclusion, although the effects of cyclones on coral cover are well known (Tanner *et al.* 1994, Connell 1997), it is surprisingly complicated to fit a quantitative model of cyclone effects to a time series of coral and algal reef states at points in space. It is important that we can make quantitative, rather than qualitative, predictions about the consequences of environmental change on coral reefs and we need a framework for models of such effects on ecosystems in general. Fitting models to community time series is difficult because of the often large numbers of parameters, strong nonlinearities, and range of time scales for the underlying processes. Such fitting is therefore rarely attempted. Nevertheless, the reasonable performance of the simple continuous-time model that we used suggests that our approach has some potential.

Chapter Three: Effects of increased frequency of cyclones on coral reefs

Introduction

Cyclones are predicted to increase in power and frequency due to global warming (Chapter 2 and references therein). Severe cyclones (those in categories 4 and 5 on the Saffir-Simpson scale) have been increasing since the 1970s and are predicted to increase further (Webster 2005). Severe cyclones have been shown to cause extensive damage to adult corals and recruits (Mumby 1999).

We cannot carry out experiments to simulate the effects of cyclones on coral reefs because of practical and ethical difficulties. An observational, 'natural experiment' type, study would require a large number of reefs with different cyclone regimes and community structures. There are observational studies that attempt to estimate cyclone effects; most of these are not quantitative or predictive. One such example of an observational study, by Adjeroud *et al.* (2005) described the effect of cyclones and other natural disturbances on coral reefs in French Polynesia. Whilst sites on 13 islands were monitored over a 10-year period, cyclones only occurred in one of these years. As a consequence the study was largely descriptive, and as the responses to disturbances were varied and causal relationships were not clear, conclusions could not be made about the future effects of cyclones.

To predict coral reef dynamics under future cyclone scenarios using a model, we would need to make predictions about how each of the model parameters would change in the future. Each of those predictions would have an associated uncertainty, and the combination of uncertainty in many parameters would result in high overall uncertainty in the model output.

Instead we model 'alternative pasts'; we use the current model parameters with different cyclone scenarios to see how changes in cyclone frequency would have changed the community structure at Heron Island over the years 1963-1993. This has the advantage that we already have estimates of uncertainty in all the relevant parameters, and have shown that the model is a good description of the data for these years. Alternative pasts have previously been used in conservation biology to determine which of a number of climate scenarios fit historical ecological data (Kirkpatrick and Fowler 1998).

After modelling the effects of an environmental change scenario, we need a way of summarizing these effects that incorporates uncertainty. Quasiextinction risk (QER) is the risk of a population falling below a set threshold at any point within a given timeframe (Ginzburg *et al.* 1982). The threshold is chosen to be relevant to the question. For example, it could be a level below which the population is at high risk of stochastic extinction, or a level below which we do not want the population to fall for economic or aesthetic reasons (Burgman *et al.* 1993). Predictions about future increases in cyclone frequency are translated into decreases in mean waiting times (time intervals between events of a given type: (Raup 1991)). We carried out an ecological risk analysis for the effects of changes in cyclone frequency on coral cover. Such analyses are often done at the population level, treating the dynamics of a single species in isolation (e.g. Brook et al. 2000, Bacelar et al. 2009, Keith 2009), but here we use quasiextinction risk for coral embedded within a model of community dynamics. Ecological risk is also frequently assessed at the individual level, largely because this avoids the complexity of constructing a population dynamics model. It is sometimes hoped that if we protect individual organisms, then we are probably protecting the population as well (Demott *et al.* 2005), although this may not be the case when interspecific interactions are accounted for. In addition, individual-level risk assessment may be less relevant than population or community level assessment, if the population or community is the level at which we want to protect the system.

Here, we used our semi-mechanistic continuous-time model with cyclones from Chapter 2 to look at alternative pasts under three different cyclone scenarios. We assessed the consequences of these scenarios using quasiextinction risk for corals embedded within a community dynamics model to test the hypothesis that scenarios with a larger cyclone frequency would result in communities with lower coral cover.

Method

Simulating cyclones

The simplest model for occurrence of cyclones is to assume that they have a constant rate per unit time and are independent of each other. This leads to an exponential distribution of waiting times between successive cyclones (Evans *et al.* 2000). Waiting times of 35 severe cyclones affecting the Eastern coast of Australia between 1970 and 2011 were used to create an exponential probability plot (ABM 2011b, Fig. 3.1) Waiting times would form a straight line if they came from an exponential distribution.

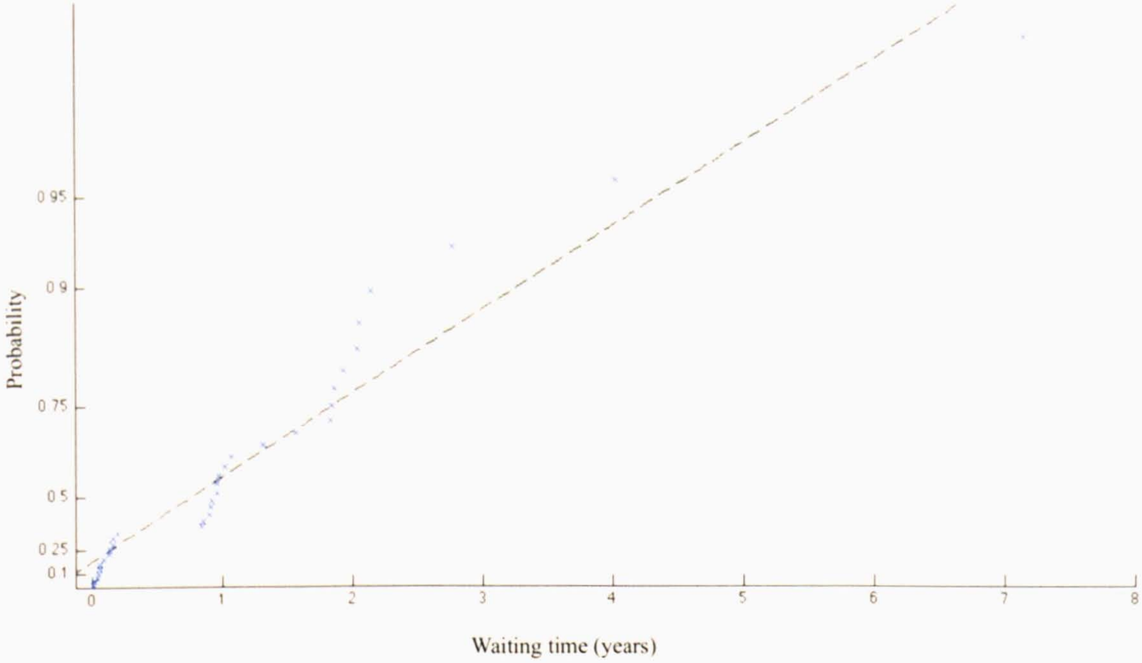

Figure 3.1. Exponential probability plot of observed cyclone waiting times between 1970 and 2011 for the Eastern coast of Australia. Dashed line is a reference line for an exponential distribution. n=35 (ABM 2011b).

Cyclones were found to only occur between the months of November and April during this period (ABM 2011b), which demonstrates that cyclones are highly seasonal (Fig. 3.2). As a result, the exponential probability plot (Figure 3.1) is far from a straight line and the exponential distribution is not a plausible model for the waiting times between cyclones.

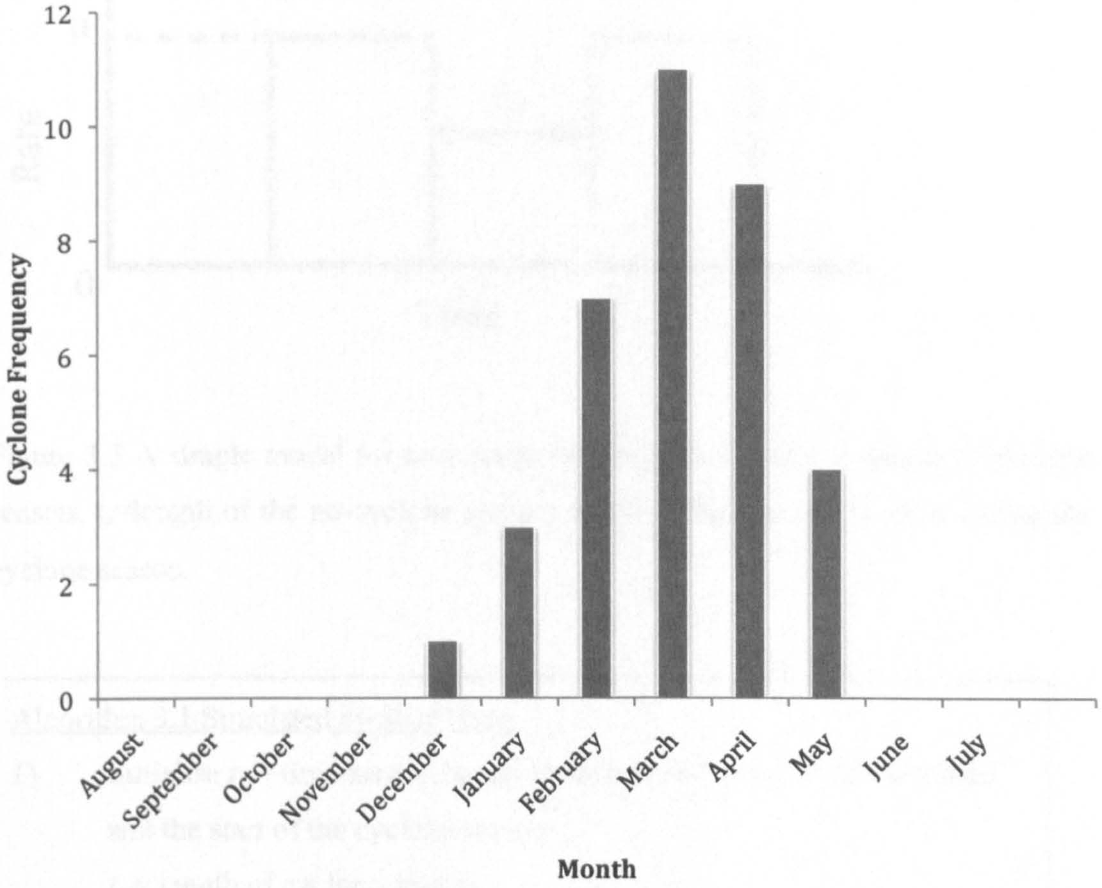

Figure 3.2 Cyclone frequency per calendar month, over 41 years (ABM 2011b) for the Eastern coast of Australia.

We therefore considered the next simplest model. We assumed that the rate of cyclones is zero outside of the observed cyclone season, and constant within this season (Fig. 3.3). Simulated waiting times under this model were obtained using Algorithm 3.1.

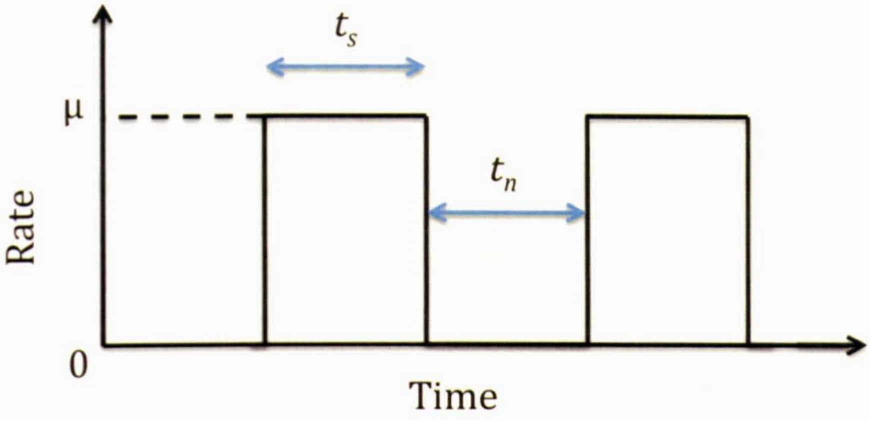

Figure 3.3 A simple model for seasonality of cyclones where t_s = length of cyclone season, t_n=length of the no-cyclone season, and μ is the rate of cyclones during the cyclone season.

```
Algorithm 3.1 Simulated cyclone times
1)  Initialise $t_0$ = time zero in model (time between the start of the model and the start of the cyclone season)
    $t_s$ = length of cyclone season
    $t_n = 1-t_s$, where $t_n$=length of the no-cyclone season
    $t_{\max}$ = total length of simulation
    $\mu$=mean waiting time between consecutive cyclones during the season
2)  Until $t>t_{\max}$,
        i) Sample a waiting time, $w$, from an exponential distribution with mean $\mu$
        ii) Set $t=t+w$.
        iii) If $t$ is outside of the current cyclone season, move it to the next one:
            while $t \bmod 1 > t_s$
                $t= t+t_n$
            (where $t \bmod 1$ is the fractional part of $t$)
3)  $i$th waiting time = $t_{i+1} - t_i - t_0$
```

Figure 3.4 shows a simulated probability plot under this model with parameters estimated from the data in Figure 3.1. The overall pattern is similar to the probability plot of the actual data, in that it shows the same characteristic steps. We therefore used this model to simulate cyclone times.

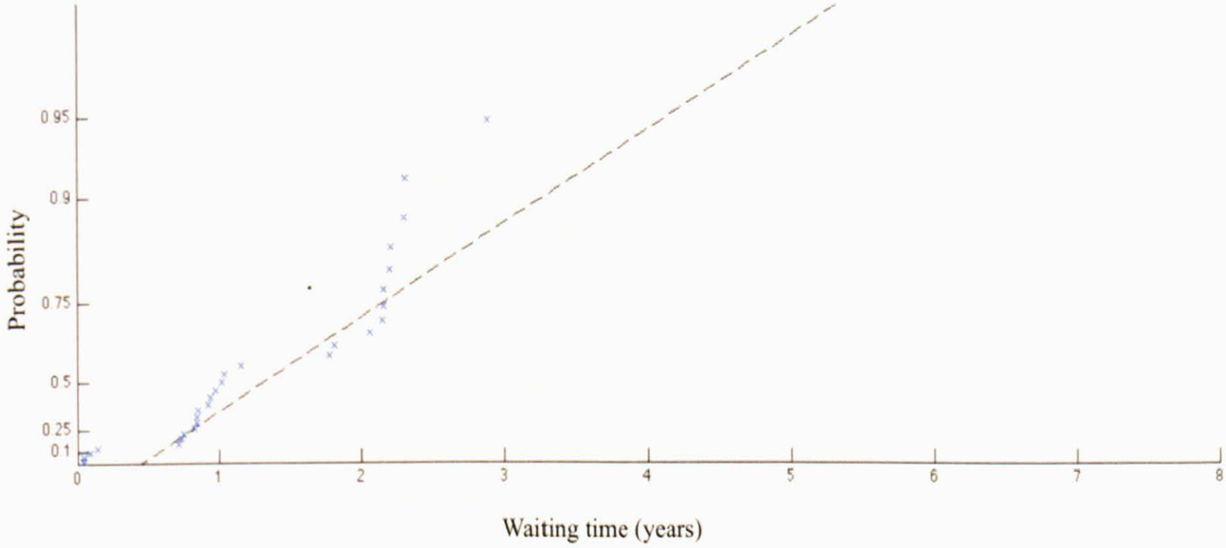

Figure 3.4. Exponential probability plot of simulated cyclone waiting times. Parameters estimated from the data in Figure 3.1. Dashed line is a reference line for an exponential distribution.

Three scenarios were chosen for the analysis; one with current cyclone waiting times, and two scenarios with increased cyclone frequency (decreased waiting time), based on studies by Leslie *et al.* (2007) and Walsh *et al.*, (2004). Leslie *et al.* (2007) predicted a 22% increase, whereas Walsh *et al.*, (2004) predicted a 56% increase in cyclones, both by 2050. Walsh *et al.* (2004) used a horizontal resolution of 30 km, 18 vertical levels, and a wind speed threshold of 17 ms^{-1}, whereas Leslie *et al.* (2007) used a resolution of 50 km, 24 vertical levels, and a wind speed threshold of 15 ms^{-1}. Walsh *et al.* (2004) compared early simulated results with observations from the Joint Typhoon Warning Center's best track data, whereas Leslie *et al.* (2007)

compared observations with data from the World Meterological Organization. Also, the area modelled in Walsh *et al.* (2004) was described as Eastern Australia, whereas Leslie *et al.* (2007) described the area modelled as the Southwest Pacific Ocean. These scenarios were used to simulate cyclone waiting times (Algorithm 3.1). For each of these scenarios, a sample of 1000 simulated trajectories were taken from the coral community dynamics model, using Algorithm 3.2.

Algorithm 3.2 Coral dynamics with simulated cyclone times

```
1)  Use Algorithm 3.1 to generate 1000 sets of waiting times for each given future cyclone scenario
2)  For each simulated set of waiting times,
        i) Sample the parameters of the coral dynamics model from the posterior distribution estimated in Chapter 2.
        ii) Solve the differential equation 2.2 to obtain the proportions of coral, algae, and free space at regularly spaced time points.
3)  Use the sample mean of each state probability at each time as an estimate of the posterior mean probability of that state.
4)  Calculate 50% and 95% Highest Posterior Density (HPD) regions, where the HPD is the smallest region (not necessarily continuous) that contains a given proportion of the distribution.
```

Preliminary analysis suggested that the posterior distributions of coral cover and free space for some time points and some cyclone frequency scenarios were bimodal. Equal-tailed credible intervals can obscure the locations of the modes in multimodal distributions. We therefore summarized the results of simulations using Highest Posterior Density (HPD) regions (Hyndman 1996, Fig 3.5). An HPD region is the smallest region that contains a specified proportion of the distribution, and is not necessarily continuous. We calculated both 50% and 95% HPD regions.

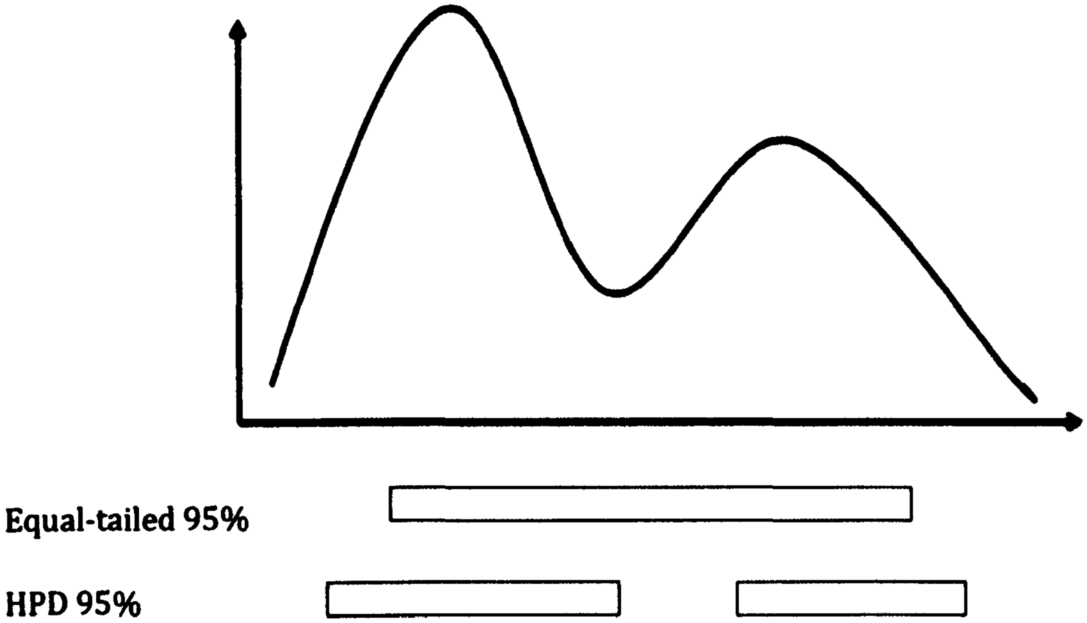

Figure 3.5 Comparison of equal-tailed intervals with highest posterior density (HPD). adapted from Hyndman (1996).

The outcomes of each scenario were also summarized by calculating the quasiextinction risk. Quasiextinction risk is usually defined as the probability of a population falling below a set threshold at any time during a set time period (Ginzburg *et al.* 1982). Here, we apply the concept to community dynamics. In this case, the quasiextinction risk is calculated as the proportion of trajectories whose coral cover falls below the threshold within the time period. A time period of 41 years was used, as this was the timeframe of the original model. The decline threshold of 50% of initial coral cover was used because it represents a substantial loss of coral cover; declines do not have to be to some critical level (Burgman *et al.* 1993). Quasiextinction risk was calculated for a range of waiting times to determine its relationship with mean waiting times. A range of waiting times, 0.1-10 was used as this covered the quasiextinction risk from 0.1-1. We then expressed these waiting times relative to the actual waiting time. The results were summarized by plotting quasiextinction risk against the ratio of scenario waiting time to actual waiting time.

We also ran simulations with very short and very long mean waiting times to determine whether the observed bimodality in coral cover was caused by parameter uncertainty, alternative stable states, or the sequence of waiting times. If these simulations do not show bimodality then the observed bimodality is due to the sequence of waiting times. If these simulations do show bimodality then this may be due to either uncertainty in our parameter estimations or the presence of alternative stable states.

In a stochastic system, the trajectory of a single reef is unlikely to display the full range of possible patterns of coral cover. We therefore compared the posterior distributions of coral cover under the current cyclone frequency with the recent distribution on 69 reefs in the Great Barrier Reef. We obtained these data from Bruno *et al.* (2009). Hard coral cover on these reefs was estimated using a variety of methods. We used the most recent coral cover recorded for each reef.

Results

Figure 3.6 shows five example trajectories from the model, using the observed mean waiting time; each line on the graph is an iteration, where each iteration has a different set of waiting times. When a cyclone hits, coral cover decreases, proportion of free space increases, and algae are not greatly affected.

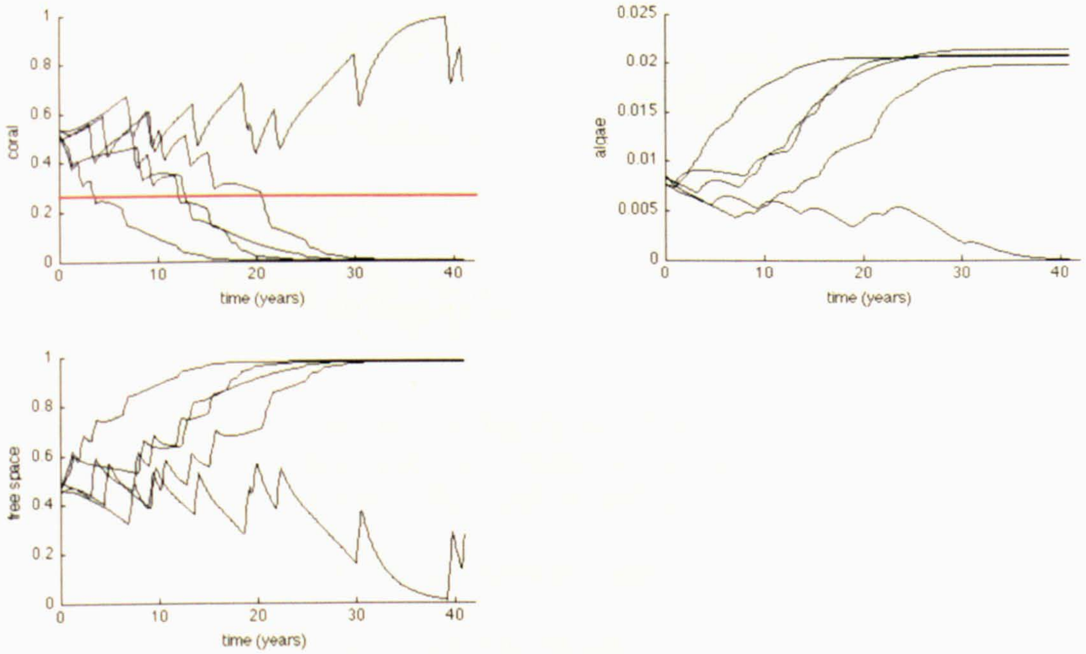

Figure 3.6. Example trajectories of the nonlinear model with simulated cyclones for (a) coral, (b) algae, and (c) free space, on varying vertical axis scales. Red horizontal line indicates an extinction threshold of 50% of original coral cover. Mean waiting time is estimated from observed cyclone data from Heron Island, Australia. 5 iterations.

Because the times at which cyclones occur are stochastic, a series of closely-spaced cyclones can reduce coral cover down to a very low level, while a long interval without cyclones can allow coral cover to become high. In the set of 1000 trajectories sampled from the posterior distribution, using the observed mean waiting time, we do not see as large steps in the boundaries of the HPD regions as we do in individual trajectories, because cyclones hit at different times in different replicates (Fig. 3.7). After about 30 years, the 50% highest posterior density (HPD) region contains almost 100% free space, and almost 0% coral (Fig. 3.7). The 95% HPD region is strongly bimodal, with low coral cover being most likely, but high coral cover also being possible (Fig. 3.7).

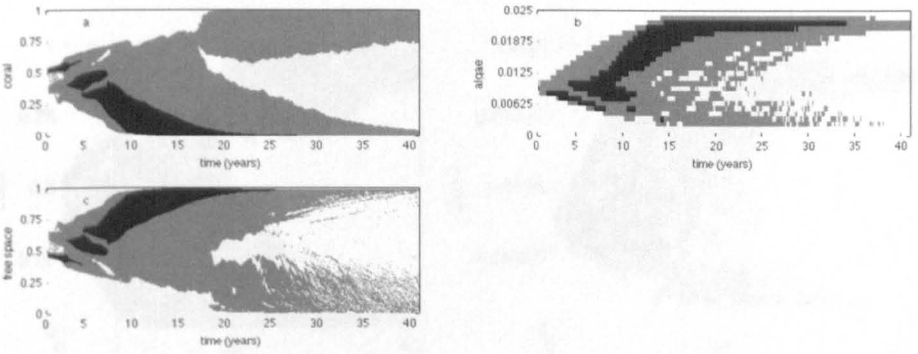

Figure 3.7 Highest posterior density regions for observed cyclone frequency for (a) coral, (b) algae, and (c) free space, with algae on a much smaller vertical axis scale. 1000 iterations. Black is the 50% HPD region, and grey is the 95% region.

With an increase of 22% in cyclone frequency, after about 25 years, the 50% highest posterior density (HPD) region contains almost 100% free space, and almost 0% coral (Fig. 3.8). The 95% HPD region is again bimodal, with low coral cover being more likely than at current cyclone rates (Fig 3.7, 3.8).

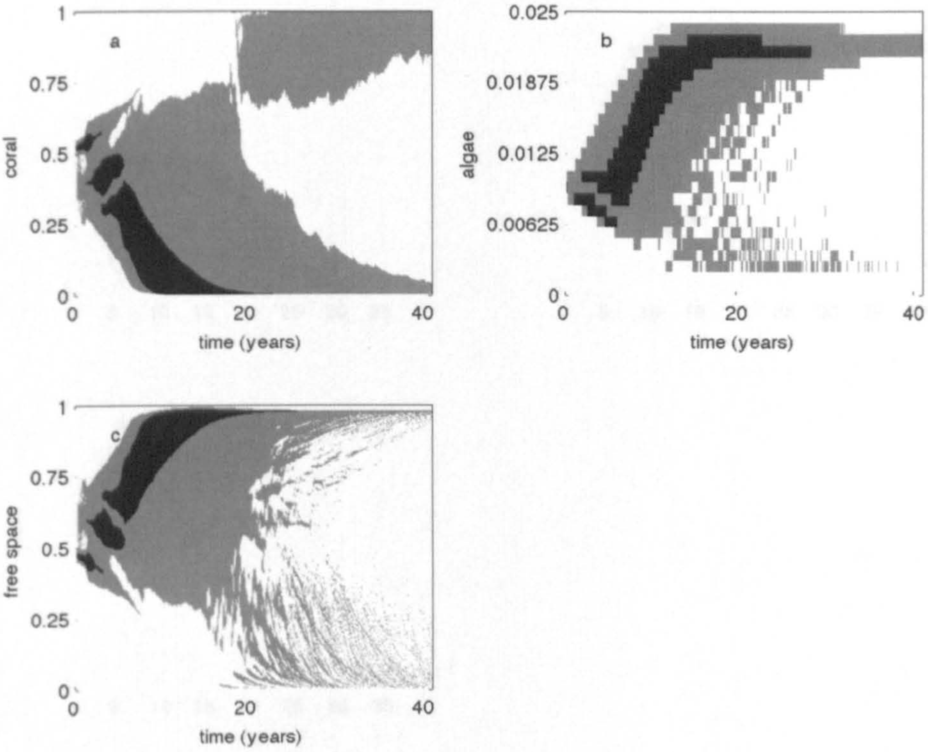

Figure 3.8 Highest posterior density regions for an increase of 22% in cyclone frequency for (a) coral, (b) algae, and (c) free space, with algae on a much smaller vertical axis scale. 1000 iterations. Black is the 50% HPD region, and grey is the 95% region.

After about 20 years, the 50% highest posterior density (HPD) region contains almost 100% free space, and almost 0% coral (Fig. 3.9). The 95% HPD region is no longer bimodal; low coral cover is now the only outcome (Fig. 3.9). So, as cyclone frequency increases, a state of low coral cover becomes the most likely outcome (Fig. 3.7-3.9).

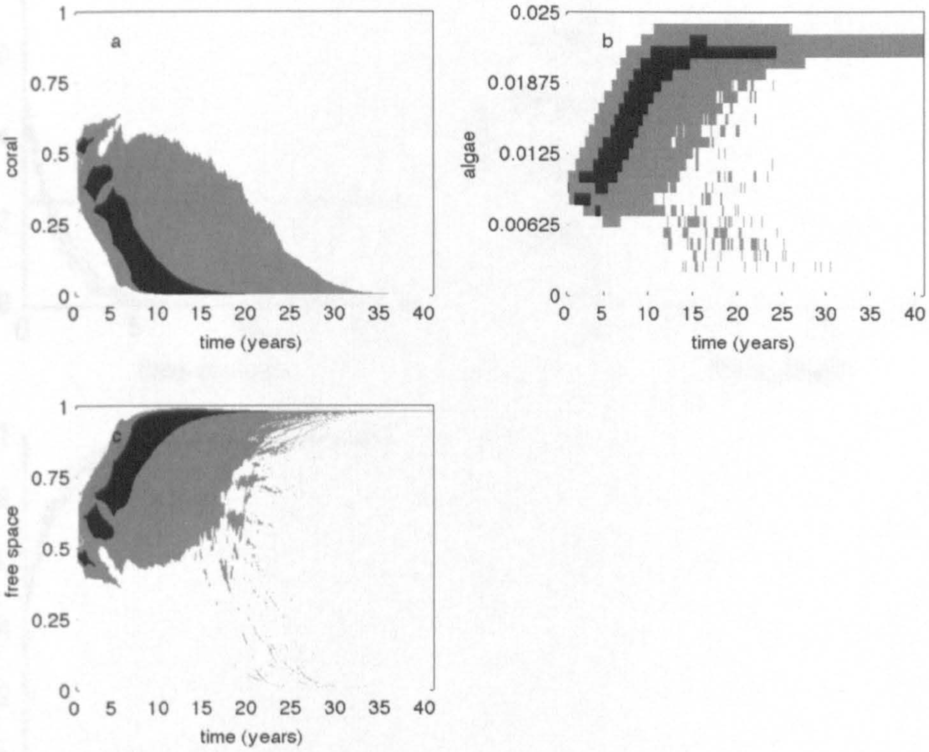

Figure 3.9 Highest posterior density regions for an increase of 56% in cyclone frequency for (a) coral, (b) algae, and (c) free space. 1000 iterations. Black is the 50% HPD region, and grey is the 95% region.

When we use a very low mean waiting time (e.g. one cyclone every 1/1000 years), cyclones are very frequent. This causes coral cover to decline rapidly in all replicates; coral approaches 0% cover whilst free space approaches 100% cover after about five years (Fig. 3.10). As there is no evidence of bimodality for these conditions, we can use equal-tailed intervals. Algal cover increases slightly under a frequent cyclone regime (Fig. 3.10).

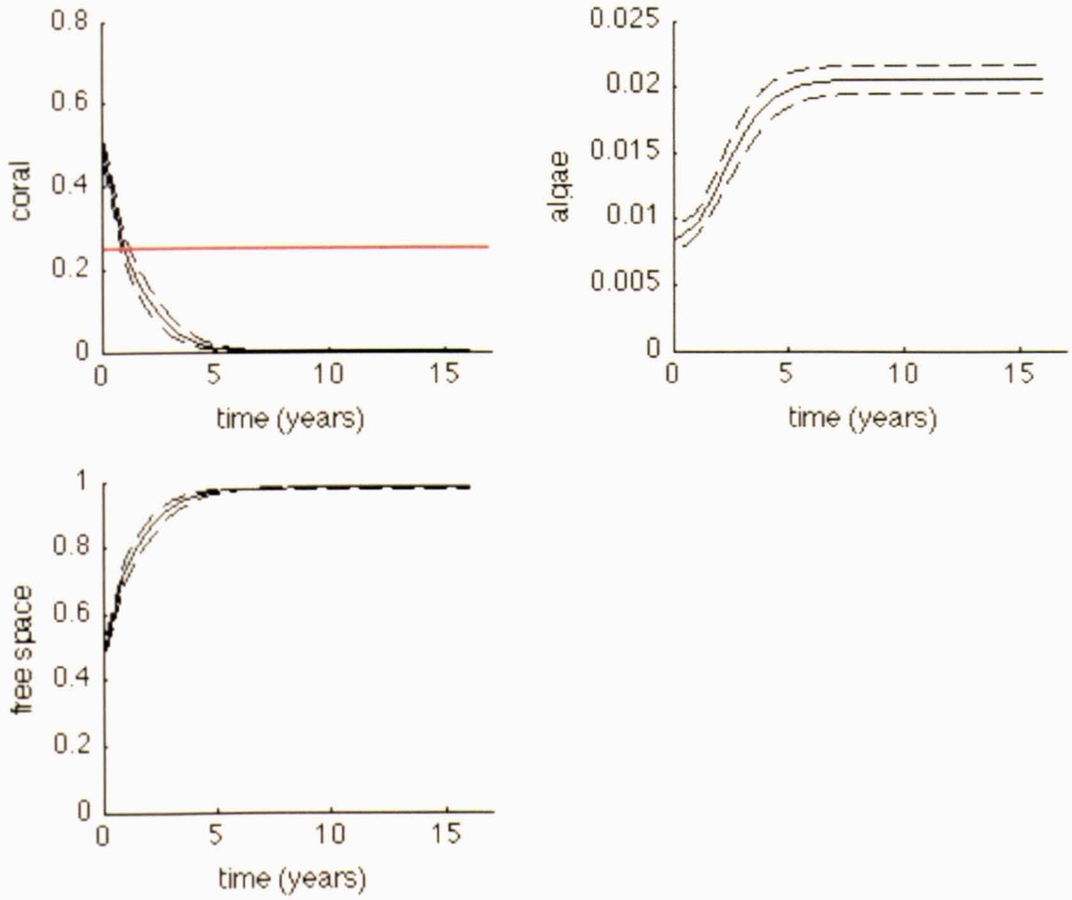

Figure 3.10 Mean and equal-tailed 95% credible intervals for 1000 iterations at a mean waiting time of 0.001 years. Red horizontal line indicates an extinction threshold of 50% of original coral cover.

When we use a very high mean waiting time (e.g. one cyclone every 2000 years), cyclones are very rare. This allows coral to grow, and increase in cover in all replicates, up to almost 100% after 15 years (Fig. 3.11). Again, equal-tailed intervals are appropriate because there is no evidence of bimodality. Algal cover decreases to almost 0% cover after 15 years of a cyclone-free regime (Fig. 3.11). This suggests that the bimodality seen in Figures 3.7-3.9 is due to moderate waiting times allowing two eventualities, rather than alternative stable states or parameter uncertainty.

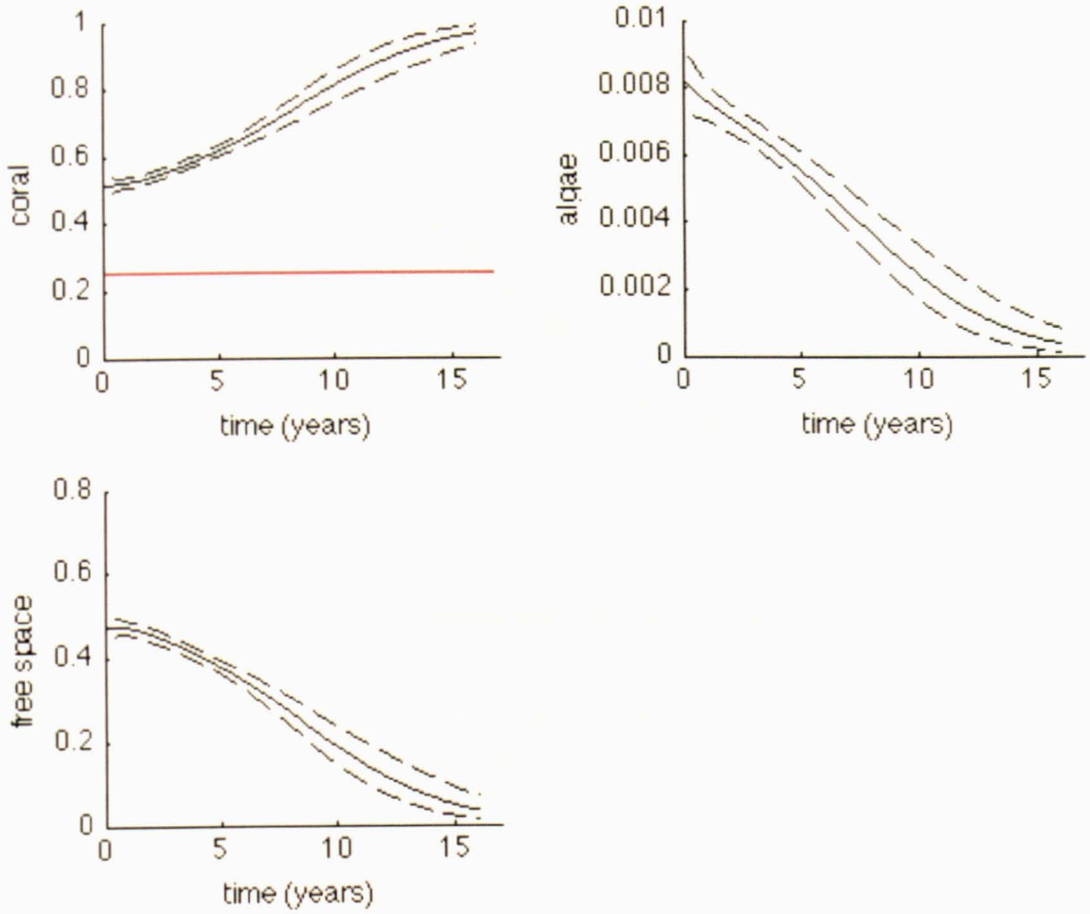

Figure 3.11 Mean and equal-tailed 95% credible intervals for 1000 iterations at a mean waiting time of 2000 years. Red horizontal line indicates an extinction threshold of 50% of original coral cover.

Quasiextinction risk increases as mean waiting time decreases (Fig. 3.12). When the mean waiting time is very short, coral cover is almost certain to drop below 50% of the observed initial value by the end of the simulation (Fig. 3.12). When the mean waiting time is very long, the risk is only 10.2% (Fig. 3.12). The observed waiting time is between these two, which is why we see bimodality (Fig. 3.7). As mean waiting time increases about the current value, the slope gets steeper (Fig. 3.12). This shows that small increases in waiting time will have large effects on quasiextinction risk (Fig. 3.12). Therefore, a small uncertainty in waiting time estimates translates into a larger uncertainty about the corresponding quasiextinction risk.

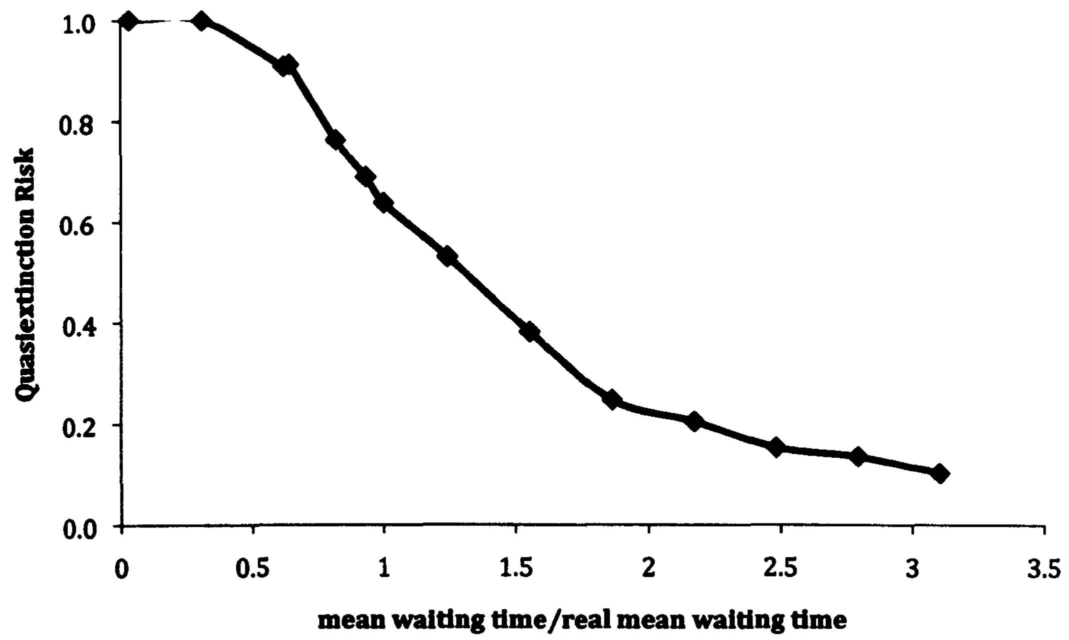

Figure 3.12 Quasiextinction risks for varying mean waiting time ratios, where 1 is the current cyclone waiting time, with a threshold of a 50% reduction in initial coral cover, for 1000 iterations over 41 years.

In order to determine whether this bimodality occurs in real reefs on the GBR, the distribution of hard coral cover from 69 different reefs was examined (Bruno *et al.* 2009, Fig. 3.13). Some bimodality is possible in these data, although the sample size is not large. Nevertheless, it is clear that the modelled distribution for Heron Island with the current cyclone frequency occupies the extremes of the range for the broader GBR data. Although the coral category in our model includes both hard and soft corals, soft corals were only abundant in the late 1980s and early 1990s, when hard coral cover was very low (Connell *et al.* 2004). This was the result of the habitat drying due to environmental changes caused by a boat running aground (Connell *et al.* 1997). Thus, differences in categories do not explain the difference between the model output and the broader GBR data.

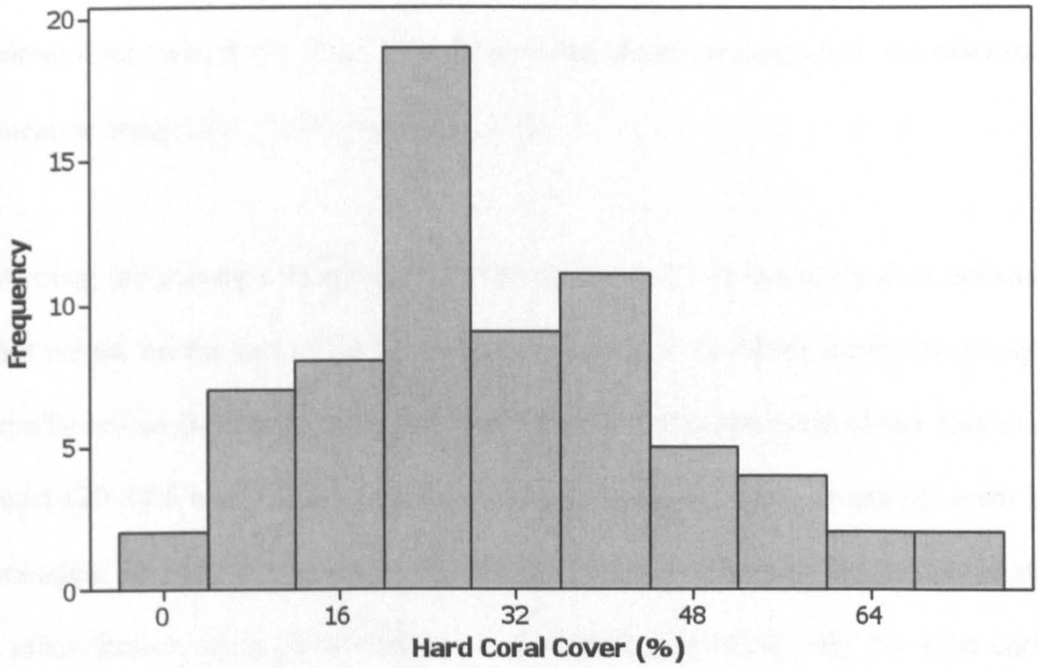

Figure 3.13 Hard coral cover percentage cover for 69 sites on the Great Barrier Reef, using the most recent data for each site (data from Bruno *et al.* 2009).

Discussion

We used a model for cyclone waiting times coupled to our coral community dynamics model to see how the coral cover over the period we modelled would have varied had the cyclone regime been different. Under current or slightly increased frequency one of two things can occur depending on when cyclones occur in the time series. When corals have a long period where they are not disturbed by cyclones, they increase their cover to a level (>50%) that is able to withstand subsequent losses due to cyclones. When cyclones hit early on in the model, the coral is unable to recover between subsequent disturbances, and cover drops to low levels (<50%). With increasing cyclone frequency, there is a transition from the outcome being contingent on chance events, at a mean waiting time of ≥ 2.64 years, or a mean waiting time ratio of ≥ 1 (Fig. 3.7-3.8), to being almost certain about the outcome at a mean waiting time of 2.07 years (Fig. 3.9).

However, the posterior distribution for the current cyclone frequency does not match what we see on the rest of the Great Barrier Reef (GBR). While coral cover may be bimodal on the GBR (Fig. 3.12), the two possible modes are much closer than in our model (20-28% and 36-44%, versus <25% and >75%). These outcomes seem less contingent on chance events than our model suggests. This may be due to variation in other factors, such as the Bruno *et al.* (2009) data being only for hard corals, whereas our model uses all types of corals grouped together. Differences in community structure and biodiversity may also make this environment differ from the rest of the GBR. The physical environment on Heron Island was so drastically changed by the effects of some cyclones that it was not suitable for colonization by corals for some time (Connell *et al.* 2004); this may explain why coral cover drops much lower in the Heron Island model than on other reefs.

The Heron Island model is currently at the steepest part of the quasiextinction risk (QER) curve (Fig. 3.11). The consequence of a steeply sloped QER curve is that an accurate estimate of QER depends on an accurate estimate of the mean waiting time (μ). There is uncertainty associated with the predictions of how μ will change in the future, as suggested by different predictions of increases in cyclone frequency. This uncertainty is likely to be mainly due to model uncertainty, but will also include lesser effects from the other five types of epistemic uncertainty, as discussed in Regan *et al.* (2002). The uncertainty in the model predictions may be due to different areas being modelled, different numbers of vertical levels, varying resolution, and different threshold wind speeds (Walsh *et al.* 2004, Leslie *et al.* 2007). The other types of epistemic uncertainty are measurement error, systematic error, natural variation, inherent randomness, and subjective judgement (Regan *et al.* 2002). There is also uncertainty in how accurate our estimates of risk are. For this reason, it has been suggested that modelled risks should not be interpreted quantitatively but should instead be interpreted relative to a standard of current conditions (Beissinger and Westphal 1998). This method allows the comparison of different risks or management scenarios, without necessitating precise quantitative risk assessment (Beissinger and Westphal 1998). This approach has previously been used to compare the risk of different timber harvesting regimes to vulnerable bird and mammal populations (Liu *et al.* 1995, Lindenmayer and Possingham 1996). Relative to current conditions, QER will increase as we decrease mean cyclone waiting time relative to current mean waiting time.

The inclusion of cyclones into the model does not make the model output resemble algal dynamics better (Fig. 3.7-3.9). There are no direct effects of cyclones on algae in our model, although cyclones do indirectly affect algae by increasing free space available for colonization. Algae are not limited by competition with corals in the model, as they reach a similar equilibrium with and without coral cover. Instead, it appears that in our model, algal cover is limited by sources of mortality that are not strongly affected by coral cover. Algae also have very high turnover rates, often in the order of weeks (Mumby *et al.* 2005). The resolution of the model may be too low to detect these frequent transitions; algal colonization events have been shown to be underestimated by quarterly observations (Mumby *et al.* 2005). Algal cover has historically been low at this site (<5% cover), whereas free space has remained high (>25% cover) (Connell *et al.* 1997).

In general, it is likely that indirect effects will be important for the assessment of ecological risk at the community level. For example, Yodzis (2000) studied a 29-species community and concluded that the predicted effect of a fur seal cull on the hake population was noticeably affected by using the entire food web rather than just the predator-prey interaction between the seals and hake. This shows that in complex community models, indirect effects can be important (Yodzis 2000). There are only three state variables in the model, so there is not much scope for long chains of indirect effects. Separation of our, rather coarse, categories would change this, but this would increase the number of parameters in our model. Number of parameters increases approximately with the square of the number of categories and we would quickly reach a point where we would be unable to estimate the parameters accurately enough to make the model useful. The coarse groupings do inherently introduce potential biases, but have the advantage of reducing variability.

The model was a good description of what has happened over the years 1963-1993. Thus, it provides a plausible baseline against which we can assess alternative past scenarios, in which we can examine the effect of a single factor such as cyclone frequency. It is likely that we can be more confident about alternative past studies than about predictions under future scenarios, because any number of factors could change in the future. The scenarios only concern changes in cyclone frequency. Cyclone intensity is also predicted to increase in the future (Emanuel 2005). If cyclone intensity does increase, then our model is likely to underestimate the impact of future climate change. In the next chapter we will see whether the model is any good at predicting future observations.

Chapter Four: Evaluation of long-term predictions made using statistical models

Introduction

Models are often assessed by comparing a number of different models of the same system to choose which is 'best' (George and McCulloch 1996). However, this only determines which of the candidate models best represents the system, and does not assess how close the model output is to the actual system. Validation is defined as a demonstration that a model possesses a satisfactory level of accuracy consistent with the intended application of the model (Rykiel 1996). A model can be validated by comparison with new data (Hilborn and Mangel 1997). Validation of a model demonstrates that it provides testable hypotheses that are relevant to important problems (Levins 1966).

Models can be evaluated qualitatively, by comparing graphical data to see if patterns match, or quantitatively, by comparison with new data. Rykiel (1996) lists 13 different methods of model validation. The most relevant here are face validity, visualization techniques, comparison to other models, statistical validation, historical data validation, and predictive validation.

Face validity is where knowledgeable people decide whether the structure and behaviour of the model are reasonable (Rykiel 1996). This forms an important part of model acceptance, as the model must be believable, however it is difficult for this to be objective.

Visualisation techniques involve comparing the system and the model using plots (Rykiel 1996). This is also a subjective method of validating models; different visualization techniques can suggest different conclusions. Tufte (1993) states that graphics are instruments for reasoning about quantitative information. The ease with which misleading graphics can be produced demonstrates that visualization is not trivial (Tufte 1993). Validation is often determined subjectively by a statement that praises the visual goodness of fit (Rykiel 1996).

Comparison to other models involves evaluating the output of different models against one another (Rykiel 1996). The model that fits the existing data best is the one with the highest belief attached to it (Hilborn and Mangel 1997). Twenty years ago, Agren *et al.* (1991) stated that comparisons of ecological models are just beginning to occur; model comparison is now much more widespread (e.g. Hanson and Stark 2011, Loo *et al.* 2007).

Statistical validation includes a variety of tests that can be performed on the model, either during model calibration or on the finished model (Rykiel 1996). This can be used to compare the model to data from the real system, compare several models, or determine whether variation in output variables from the model fall within acceptable limits (Rykiel 1996).

Historical data validation is where part of a historical dataset is used to build the model and another part is used to test the model to see if the model and system behaviour correlate (Rykiel 1996). This requires a method of splitting the data into two distinct sets; in time-series data the sets are usually divided by time (Power 1993).

Predictive validation involves using the model to make predictions about future behaviour of the system; these are then compared to other data or future observations (Rykiel 1996). This is the most robust method for evaluating predictive models but is not widely used, as collecting new data is not possible for many ecological models (Power 1993).

The models in Chapter 2 were constructed using a long-term data set from 1963-1993. As discussed in Chapter 3, using those models to make predictions would inherently and explicitly make a number of assumptions about the system since 1993. Here, we test the predictions made using the models with cyclones from Chapter 2 against new field data obtained in 2008 with data on recent cyclones to assess if the model is valid past the end of the dataset upon which it is based. We will also discuss the validity of such predictions given that other temporal changes may be occurring in these communities.

Temporal change in communities is the composite of processes over time (Glasser 1982). These processes are due to abiotic factors, such as current and wave action, and changes in temperature, or biotic interactions, such as predation, competition, disease, and parasitism (Dobson and Frid 1998). These processes can either affect colonization or the survival of species (Glasser 1982), depending on the frequency with which a particular level of a factor occurs (Dobson and Frid 1998). The outcome of these combined processes can take many different forms. For example, changes in marine communities in the UK have mainly been gradual trends over the last 20-30 years, although discontinuous step changes have also been found (Spencer *et al.* 2011).

In this chapter, the predictions made by the continuous-time model with cyclones and the discrete-time model with cyclones are compared to new data obtained in 2008. This study aims to assess how well these model predictions match the current state of the reef.

Method

Photographs were taken in August 2008 of the six permanent quadrats set up on the Protected Crest site (Connell *et al.* 2004) at Heron Island, in the Great Barrier Reef. The quadrats are permanently marked by the presence of steel stakes in each corner, to minimize movement (Tanner *et al.* 1996). At each quadrat, a plastic 1 m^2 quadrat frame was placed over the steel stakes (Fig. 4.1) and a photograph was taken from directly overhead using a hand-held camera without a tripod.

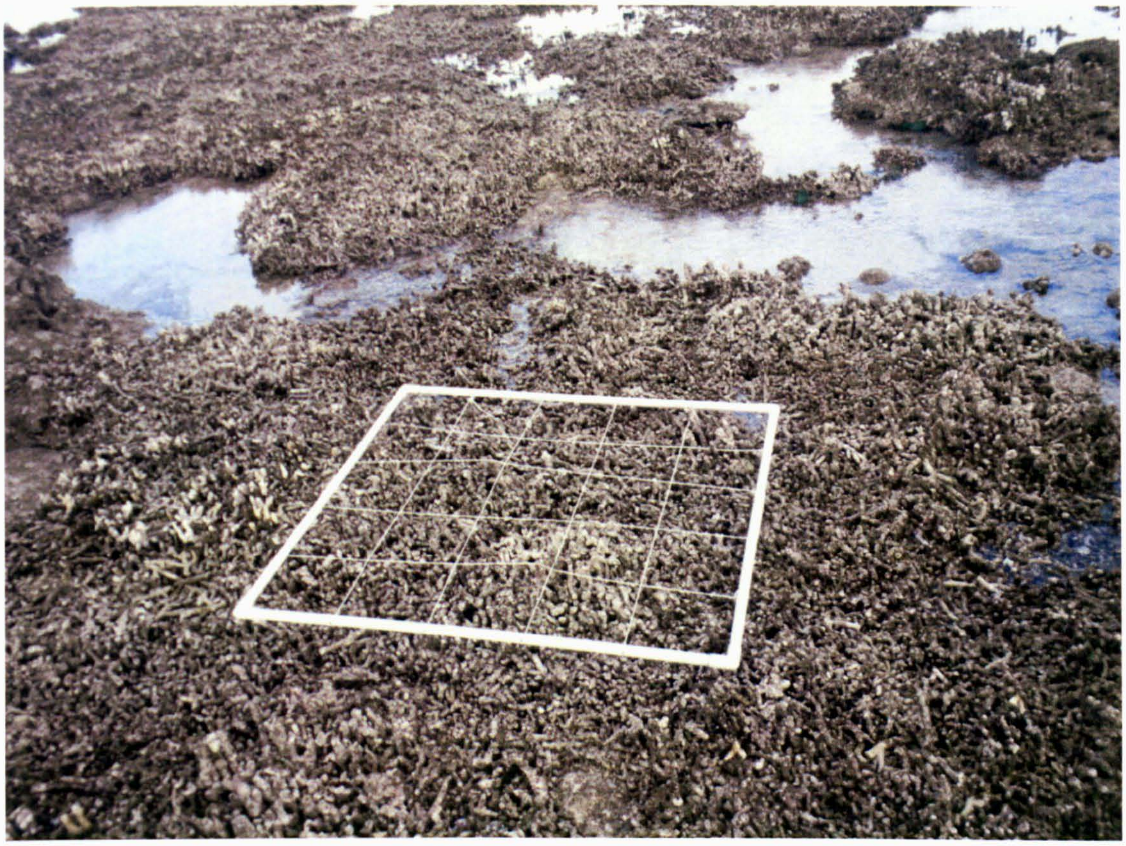

Figure 4.1 Photo of $1m^2$ quadrat on the reef flat at Heron Island, on the Great Barrier Reef, August 2008.

Photographs were taken from a height of approximately 1.5 m. Locations were recorded using a handheld GPS. Sketches of live coral colonies were made in the field to assist identification (Fig. 4.2 shows one example).

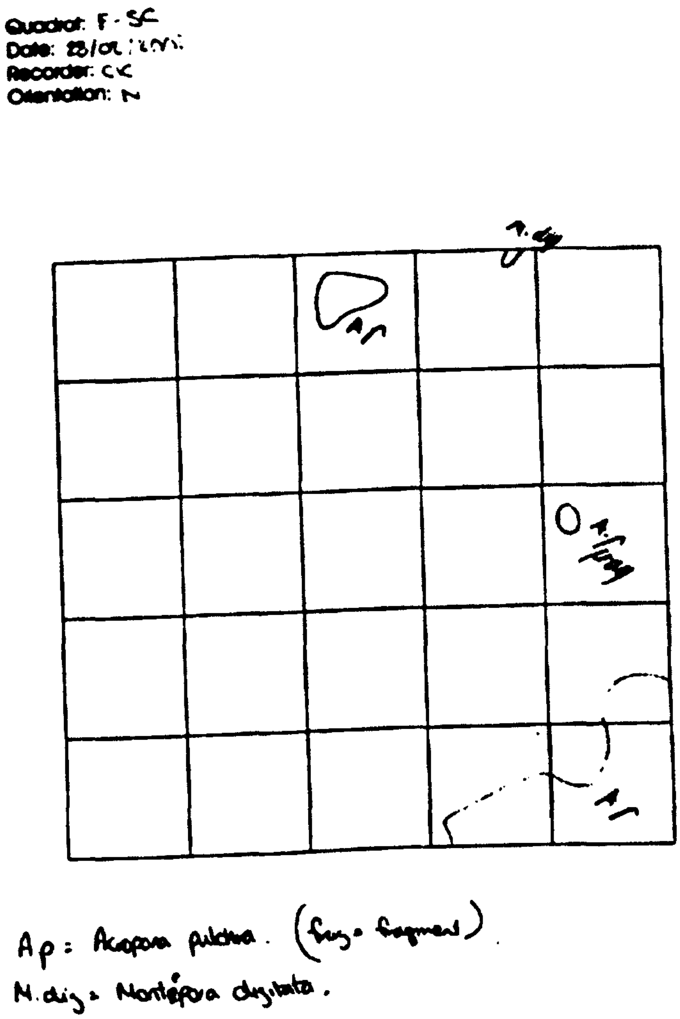

Figure 4.2 Sketch map of coral colonies within quadrat F at the Protected Crest site, Heron Island, on the Great Barrier Reef, August 2008.

Perspective distortions were removed from the photographs using Rectilinear Panorama Pro v.1.2.2, within ArcGIS 10. This programme returns the quadrat frame to a square by tagging the corners and making the sides of equal length. The six photographs were digitized by drawing around colonies using a Wacom Bamboo Fun graphics tablet and converted into polygons. ArcGIS was then used to calculate area for each species. Polygon areas were summed by species for the three categories of coral, algae, and free space. ArcGIS was used to calculate the polygon areas, and these were summed for coral and algae, and used to calculate free space.

Observed coral cover was compared to the predictions of the discrete-time model with cyclones, and the continuous-time model with cyclones, as described in Chapter 2. The dates of cyclones passing within 200 km of Heron Island from 1993-2007 were obtained from the Australian Bureau of Meterology's Tropical Cyclone Tracking Information tool (ABM 2011b). Cyclone dates for the 2007/2008 season were obtained by studying individual cyclone reports during that period, from the Australian Bureau of Meterology (ABM 2011b). Only one cyclone was found to meet these criteria during the period 1993-2008; it was added to cyclone dates for the period 1963-1993 (Chapter 2.) and the model run was extended by 16 years.

Model comparison compared the data to the posterior predictive distributions of the models (Equation 4.1; Gelman *et al.* 2004, p161). In general terms, the model output was the posterior predictive distributions of coral cover in 2008, $p(y^{rep}|y)$, where y^{rep} is defined as the predicted data that would be obtained using the same model and value of θ that produced the observed data (Gelman *et al.* 2004, p161). The model predictions for given parameters θ, $p(y^{rep}|\theta)$, were integrated over posterior distribution of parameters y, $p(\theta|y)$.

$$p(y^{rep} \mid y) = \int p(y^{rep} \mid \theta) p(\theta \mid y) d\theta \qquad (4.1)$$

We then define a discrepancy measure $T(y, \theta)$ which summarises the difference between the model predictions of the new data (in our case, the difference between observed and predicted coral cover). By analogy with classical *p*-values, we then define a posterior predictive *p*-value, the probability of a discrepancy at least as extreme as observed if the new data really came from the model, Bayes p-value = $\Pr(T(y^{rep}, \theta) \geq T(y, \theta)|y)$. The p-values were estimated from samples of size 1000 from the MCMC output described in Chapter 2. The one-sided p-values generated by this procedure were doubled to form two-sided p-values.

Results

A total of seven coral species were found in 2008; four of these were found at the last survey in 2005. The 2005 survey also found seven different coral species. In 2008, these mainly comprised of staghorn corals from the family *Acroporidae* (Fig. 4.3).

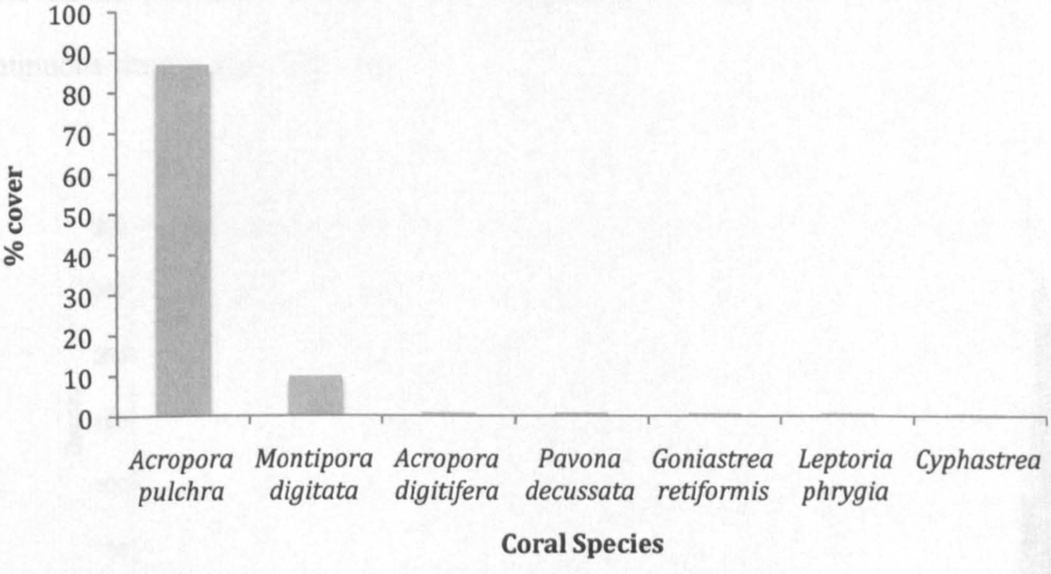

Figure 4.3 Percentage of coral cover of species, summed over all six quadrats, found at the Protected Crest study site, on Heron Island, on the Great Barrier Reef, in August 2008.

In the 2008 sampling, coral covered 5.12% of the six quadrats. No algae were found in the quadrats. The continuous-time model predicted significantly less coral than was observed ($p<0.00001$, Fig. 4.4).

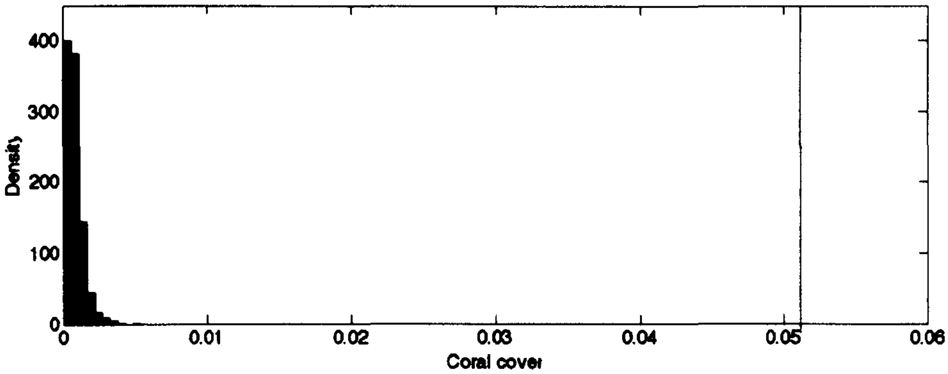

Figure 4.4 Histogram of 1000 iterations of coral cover from the continuous-time model with cyclones for 2008. Vertical line indicates observed coral cover.

The discrete-time model predicted significantly more coral than was observed (p<0.00001, Fig. 4.5). In absolute terms, the difference between predictions and observations was much larger for the discrete–time model (Fig. 4.5) than for the continuous-time model (Fig. 4.4).

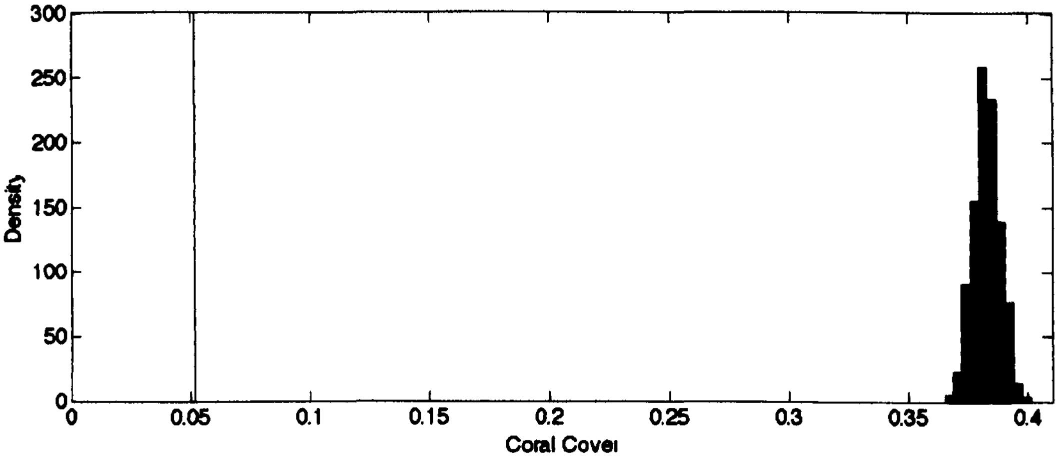

Figure 4.5 Histogram of 1000 iterations of coral cover from the discrete-time model with cyclones for 2008. Vertical line indicates observed coral cover.

To compare the predictions of the continuous-time and discrete-time model, we use a ternary graph (Fig. 4.6). The continuous-time model prediction is closer to the observed community structure than the discrete-time model prediction in axis space (Fig. 4.6).

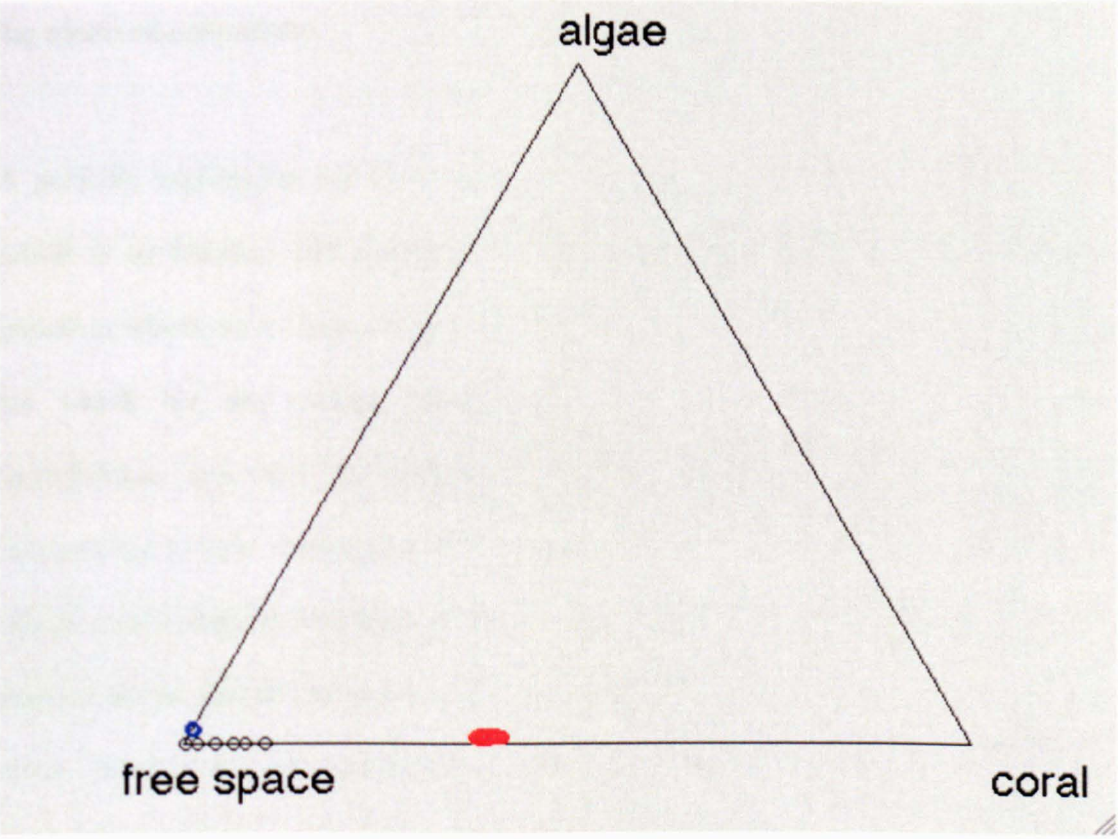

Figure 4.6. Ternary diagram of observed data (black), continuous-time model output (blue), and discrete-time model output (red). Coral cover runs from 0 at the free space-algae edge to 1 at the coral vertex, algae runs from 0 at the free space-coral edge to 1 at the algae vertex, and free space runs from 0 at the coral-algae edge to 1 at the free space vertex.

Discussion

The continuous-time model predicts significantly less coral than was observed in 2008, whereas the discrete-time model predicts significantly more coral than was observed. Overall, the predictions made by the continuous-time model are closer to the observed community.

A possible explanation for the overestimate of coral cover from the discrete-time model is as follows. The discrete-time model was constructed using data from a period in which, on average, coral cover was much higher than it was over the period for which we are making predictions. This model assumes that transition probabilities, and also the underlying rates of transitions between states, are independent of state abundances. However, it was argued in chapter 2 that the rate at which coral colonizes free space is likely to be higher when coral cover is high than when it is low (hence the success of the continuous-time, nonlinear model). Thus a linear Markov model constructed under high coral conditions will tend to overestimate the rate at which coral colonizes free space when coral cover is low. As a result, such a model will predict faster recovery from low coral cover than will occur in the real system.

A possible explanation for the underestimate of coral cover in the continuous-time model is the assumed absence of external recruitment. This model idealises the Heron Island reef as a completely closed system (in the sense of having no external inputs: (Loreau 2010, p2). The reality is that there is external recruitment, which is likely to be highly variable, especially in species that broadcast gametes (Connell *et* *al.* 1997). This input may be quantitatively unimportant when coral cover is high, but could substantially increase the rate of recovery from low coral cover.

Caswell (1988) states that we should find the simplest model that is able to generate an observed pattern. Neither of our models is able to generate the observed pattern, so we need something different and probably more complex. As the continuous-time model is closer to the observations, then that would be an obvious starting point. Adding coral recruitment into the continuous-time model would make its predictions closer to the observed value and would still result in a relatively simple model.

The study site was dominated by the branching coral, *Acropora pulchra*, in the 2008 sampling. The growth of corals from fragments is an important recruitment process in some branching corals (Wallace 1985). Coral fragments were commonly found in post-cyclone samplings at the study site (Connell *et al.* 1997). Soong and Chen (2003) have shown that under experimental conditions, *Acropora pulchra* fragments of just 4 cm long were able to transplant and survive. The dominance of this branching coral at the study site may be due to the transplantation of coral fragments produced by cyclones.

We used visualization techniques as one of our methods of model validation. The histograms of the individual models show a relatively large distance between the model outputs and the 2008 sampling, whereas the ternary diagram shows that the 2008 sampling and the model outputs are relatively close in axis space. Both methods of visualization use the same data, but different conclusions can be drawn from each. This demonstrates Tufte's (1993) view that visualization techniques are highly subjective. We would therefore recommend that one of the more quantitative validation techniques (e.g. statistical validation, predictive validation) was used in conjunction with visualization techniques to present more objective results.

There may be some variation in the coral cover between quadrats that is causing the difference between the model outputs and the observed value. We could test the heterogeneity of the quadrats, possibly by comparison with a Dirichlet distribution, to see if variability between the quadrats is larger than expected. A Dirichlet distribution is the simplest distribution that describes a composition (where the parts are non-negative and sum to one) (Gelman *et al.* 2004, p582). We could fit a Dirichlet distribution to the quadrat data, and ask whether there is more variability among the quadrats than would be expected among six samples from the Dirichlet distribution. If there is, then we would expect that there is important heterogeneity between the quadrats.

It is possible that our 2008 sampling was atypical of the dynamics of the reef over a longer period. In linear regression, 15-20 new observations are recommended for evaluating a model (Montgomery and Peck 1982). Our evaluation is based on just one new time point. Between 1993 and 2008 there were several unusual events that reduced coral cover on the Great Barrier Reef, including widespread bleaching in 1998 and 2002, and subregional outbreaks of the crown-of-thorns starfish *Acanthaster planci* (Osborne *et al.* 2011). Nevertheless, the changes in coral cover on individual reefs may be quite different from the average change at the subregional level (Sweatman *et al.* 2011), so it is not possible to conclude that the time interval between 1993 and 2008 was necessarily an unusual one on Heron Island.

There is a 16-year period between the last data point that was used to generate the models in Chapter 2, and the new data from the 2008 sampling. This is over half the length of the original time series used to develop the model. We are trying to predict quite far beyond our data, in relative terms. There may be temporal changes in the system over this time period that are not related to disturbances that are causing the differences between the models and the new observations. For comparison, Saether et al. (2002) had over 40 years of data on a single bird species and a sophisticated analysis, and were still only able to make reliable predictions a few years into the future. Their model fitted the data well, but the uncertainty in predictions increased quickly as they looked further into the future. Our models are attempting to describe a more complicated system, based on fewer data and less sophisticated functional forms than those of Saether et al. (2002). They are therefore likely to have relatively low uncertainty but high bias, exactly as seen in Figure 4.6.

In conclusion, our models were not outstandingly successful at making predictions far beyond the data on which they were developed. Nevertheless, the ways in which they failed can give us some insight into what may be missing from them, and into what might be reasonable expectations about the performance of predictive models in community ecology.

Chapter Five: Effects of experimental disturbance on fouling communities

Introduction

Succession has many controversial definitions in ecology, but here can be defined as a directional change over time at a site as a result of the processes of colonization and local extinction (Dobson and Frid 1998, page 208). Ecological succession usually occurs when a disturbance has caused some change in localized species composition (Connell 1975).

The frequency and severity of disturbances create a regeneration niche that will be occupied by species that have regeneration times that are shorter than the disturbance period (McClanahan 2002). A new disturbance regime can cause an ecosystem to fundamentally change its species composition from previous ecological states (McClanahan 2002). Such fundamental changes are sometimes referred to as phase shifts, defined by Dudgeon *et al.* (2010) as changes in the community equilibrium in response to a persistent change in environmental conditions.

In some cases, human activity such as overfishing has resulted in unintended phase shifts. For example, Daskalov *et al.* (2007) found that in the Black Sea a shift to a jellyfish-dominated state was triggered by intense fishing pressure. However, it is not always easy to distinguish between permanent phase shifts and large-scale but transient changes in ecosystem structure, given observations on the state of a natural ecosystem over time. For example, Frank et al. (2011) argued that in the case of the Scotian Shelf ecosystem off the east coast of Canada, an apparent phase shift that has been sustained for two decades is in fact a transient state, and that the ecosystem will eventually return to its original structure. For this reason, experiments have an important role in the study of phase shifts. Connell and Sousa (1983) discuss methods of determining whether community structures are stable, whereas Petraitis and Dudgeon (2004) reviewed experimental designs for detecting alternative stable states.

In addition, there are some cases in which humans have deliberately caused phase shifts. One example is the management and regeneration of docks in the UK. Much of this work has focused on the restoration of docks at Liverpool, Salford, and Preston (Allen 1992, p17). Various studies have been carried out on the Merseyside dock systems, with relation to hydrography, ecology, and water quality management (e.g. Allen 1992, Fielding 1997). Allen (1992) found that salinity and water quality caused considerable variation in the diversity of biota on dock walls. The restoration processes in the Liverpool South dock chain resulted in a phase shift from a plankton-dominated system, to an ecosystem dominated by filter feeders (Allen 1992, p188). The existence of two alternative stable states was evidenced by a sudden change from turbid to clear water conditions (Allen 1992, p193). Fielding (1997) found that docks in the Liverpool South Dock chain that had had *Mytilus edulis* settlements were now dominated by them and had relatively low plankton densities, whereas docks with an absence of benthos still maintained high number of zooplankton.

Here, I will study the effects of disturbance on the post-restoration fouling community in Salthouse Dock, Liverpool, UK. Specifically, I applied different types of disturbance to communities on experimental panels, with the aim of determining whether they are resilient to disturbance, or whether they have alternative stable states. Two of the treatments were selective, and targeted the species that was dominant after a year; this would be analogous to predation or a disease outbreak affecting a single species. The other treatments were non-selective, and were analogous to physical disturbances, such as storms and volcanic activity, that remove almost all organisms from affected areas. Two different levels of each removal type were used, to determine whether there were thresholds beyond which the system would undergo a change, along with a control treatment.

Method

The sample sites were located in the Salthouse Dock (53° 24' 6.13"N, 2° 59' 24.73"W), in the Liverpool South Docks chain (Fig. 5.1.)

Figure 5.1. Salthouse Dock in the Liverpool South Docks Chain. Study site is the floating pontoons, which follow an 'L' shape around the dock.

Epibenthic communities on experimental panels were monitored for 24 months. In early April 2008, 36 textured expanded polystyrene panels (0.25 m^2 each) were attached to sheets of 12 mm marine plywood (0.37 m^2) using Geocel® Aquaria Sealant (Fig. 5.2). All experimental set-ups were pre-leached in holding tanks before use. The set-ups were attached to permanently moored pontoons in Salthouse Dock, and submerged at approximately 0.5m below water level, weighted so that the panels hung vertically

Figure 5.2. Experimental set-up. The green plastic container is filled with sand to act as a weight.

Monthly sampling consisted of removing each setup from the water, overlaying with a purpose built frame, and obtaining a digital photograph of each polystyrene panel. The frame, made of wood and metal, slotted into holes in the setup to ensure that the photographs were taken from the same position relative to the panels each time. After sampling, the panels were resubmerged, making it a nondestructive technique.

After a year, a disturbance regime was initiated on the panels. There were four disturbance treatments, each applied to four patches of 78 cm^2 each (which together summed to half the sampling area on the panel, Figure 5.3). There was only one treatment type on each panel. The treatments were 100% removal of all erect organisms (Total Erect), 50% removal of all erect organisms (Low Erect), 100% removal of *Ciona intestinalis* (the most abundant organism on the panels at the end of the first year) (Total Selective), and 50% removal of *C. intestinalis* (Low Selective). There were 7 panels of each treatment, along with 8 that were not disturbed (Control).

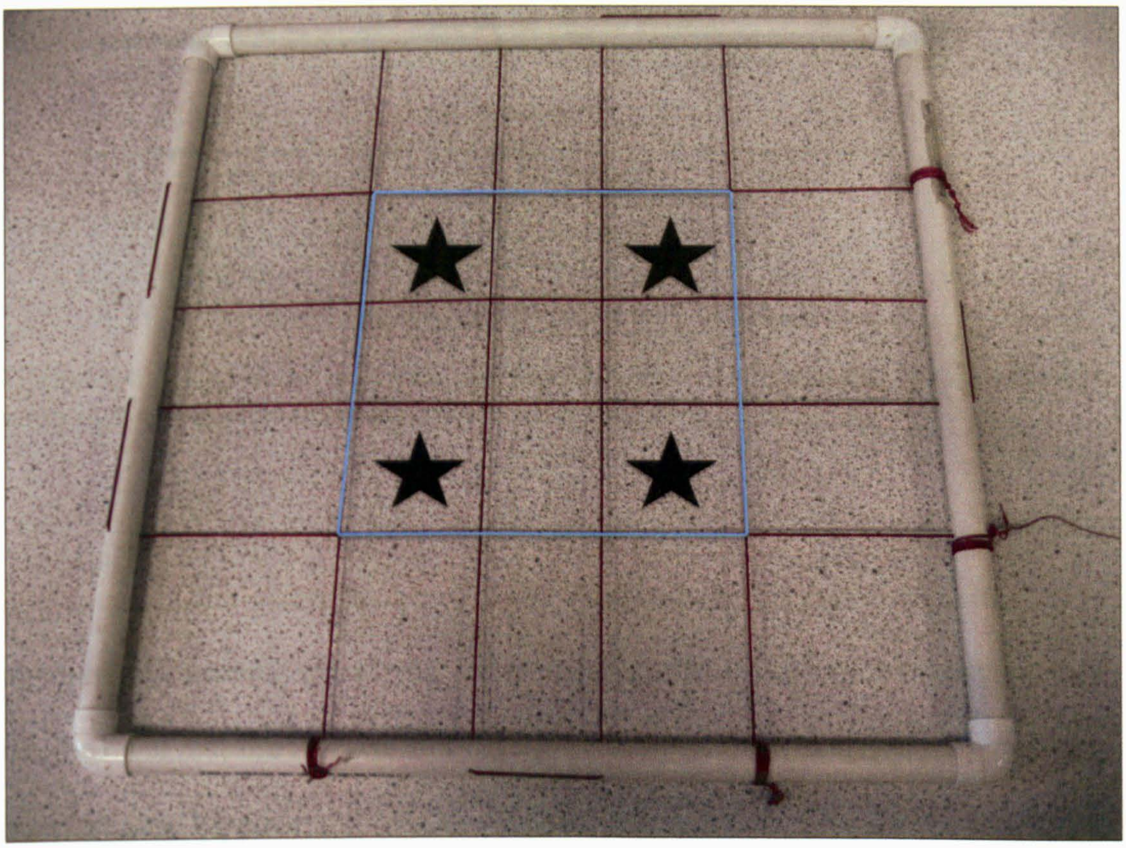

Figure 5.3. Quadrat used for disturbance regime. Blue lines illustrate sampling area. Black stars show disturbed patches.

Disturbance was carried out every four weeks, a total of six times. After the end of the disturbance regime, panels were sampled for a further six months to monitor recovery. The sampling area (Fig. 5.3) was used to collect abundance data., the rest of the panel was not sampled to avoid edge effects. Samples from before the disturbance regime and after the recovery period are analyzed here (Fig. 5.4).

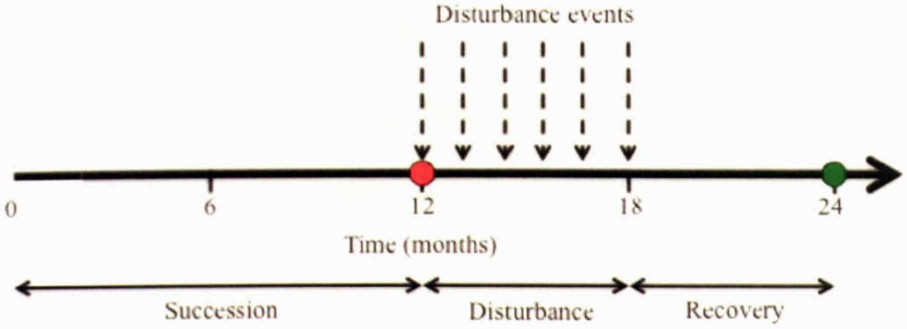

Figure 5.4. Diagram of experimental timeline. Red circle denotes pre-disturbance sampling; green circle denotes post-recovery sampling.

At the end of the study, the boards were removed and all of the organisms were removed by scraping all of the living material from the panels. Samples were weighed wet and then placed in a drying oven at 90°C for seven days. After this, samples were weighed and then re-weighed after a further 24 hours in the drying oven to ensure that no more water was lost.

Digital images from each sample date were analysed using Corel Paintshop Pro X. Photographs were cropped and scaled to uniform size, before being overlain with a grid. The grid covered the central 0.0625 m^2 of the board, and had 100 points at intervals of 2.5 cm. Transitions were recorded by creating a three layered image consisting of the previous sample, the current sample, and the grid itself. At each point on the grid, the organism present was identified to species level. The transition between the two sampling dates was recorded and placed into a matrix.

Statistical analysis

Biomass

One-way ANOVAs, in Minitab 16, were used to determine whether mean final weights (both wet and dry) differed between treatments. Both wet weights and dry weights were used as dry weights can be strongly influenced by organisms with shells.

Diversity indices

Species richness, abundance, Shannon-Weiner diversity and Berger-Parker dominance indices were calculated for each panel for the pre and post-disturbance time intervals. Species richness is the number of species recorded, whereas abundance is the total number of individuals in the sample (Magurran 2004, p76). Shannon-Weiner is widely used as a measure of biological diversity (Magurran 2004, p101). The Berger-Parker index is a measure of dominance (Magurran 2004, p117). One-way ANOVAs were carried out in Minitab 16 to determine whether the difference between pre and post disturbance values of these indices depended on treatment.

Perturbations

We denote the pre and post-disturbance compositions on a given panel by the vectors $\mathbf{x}(0)$ and $\mathbf{x}(t)$ respectively, where for D species (excluding free space), $\mathbf{x}=[x_1, x_2, \ldots, x_D]$, and $\sum_{i=1}^{D} \mathbf{x}_i = 1$. We assume that $0<x_i<1$ for each i. Here, we outline two measures of change in composition from pre to post-disturbance, the overall change, and the net change excluding the direct effects of disturbance.

We first define the closure operation (Aitchison 1986, p31) $\mathcal{C}[\mathbf{w}] = \mathbf{w} / \sum_i w_i$, which converts a vector **w** of positive numbers into a composition. Then we can define a perturbation **p** that transforms the pre-disturbance composition to its post-disturbance value:

$$
\begin{aligned}
\mathbf{x}(t) &= \mathbf{x}(0) \oplus \mathbf{p} \\
&= \mathcal{C}[\mathbf{x}_1(0)\mathbf{p}_1, \mathbf{x}_2(0)\mathbf{p}_2, \ldots, \mathbf{x}_D(0)\mathbf{p}_D]
\end{aligned}
$$

Here, $\oplus$ is the perturbation operator (Aitchison 2003, p4) (analogous to addition), and **p** is the overall change in composition between times 0 and t.

If we know $\mathbf{x}(0)$ and $\mathbf{x}(t)$, then we can find the perturbation **p** as follows:

$$
\begin{aligned}
\mathbf{p} &= \mathbf{x}(t) \ominus \mathbf{x}(0) \\
&= \mathcal{C}[\frac{x_1(0)p_1}{x_1(0)}, \frac{x_2(0)p_2}{x_2(0)}, \ldots, \frac{x_D(0)p_D}{x_D(0)}. \\
&= \mathcal{C}[\frac{x_1(t)}{x_1(0)}, \frac{x_2(t)}{x_2(0)}, \ldots, \frac{x_D(t)}{x_D(0)}]
\end{aligned} \qquad (5.1)
$$

Here, $\ominus$ denotes the inverse of $\oplus$, and is analogous to subtraction (Aitchison 2003, p3).We require that none of the components of $\mathbf{x}(0)$ is equal to zero, otherwise the result would be undefined. We suggest a solution to this restriction later.

It may also be useful to remove the direct effects of disturbance from the measure of change. Each treatment involves a series of disturbances that result in known proportional changes in abundance of each species, along with natural change in between (Figure 5.5). Using the notation above, we can write

$$\mathbf{x}(t) = \mathbf{x}(0) \oplus \mathbf{a}(1) \oplus \mathbf{b}(1) \oplus \mathbf{a}(2) \oplus \mathbf{b}(2) \oplus \ldots \oplus \mathbf{a}(k) \oplus \mathbf{b}(k),$$

where $\mathbf{a}(1),\ldots,\mathbf{a}(k)$ are disturbances, $\mathbf{b}(1),\ldots,\mathbf{b}(k)$ are natural change, and k is the number of disturbance events.

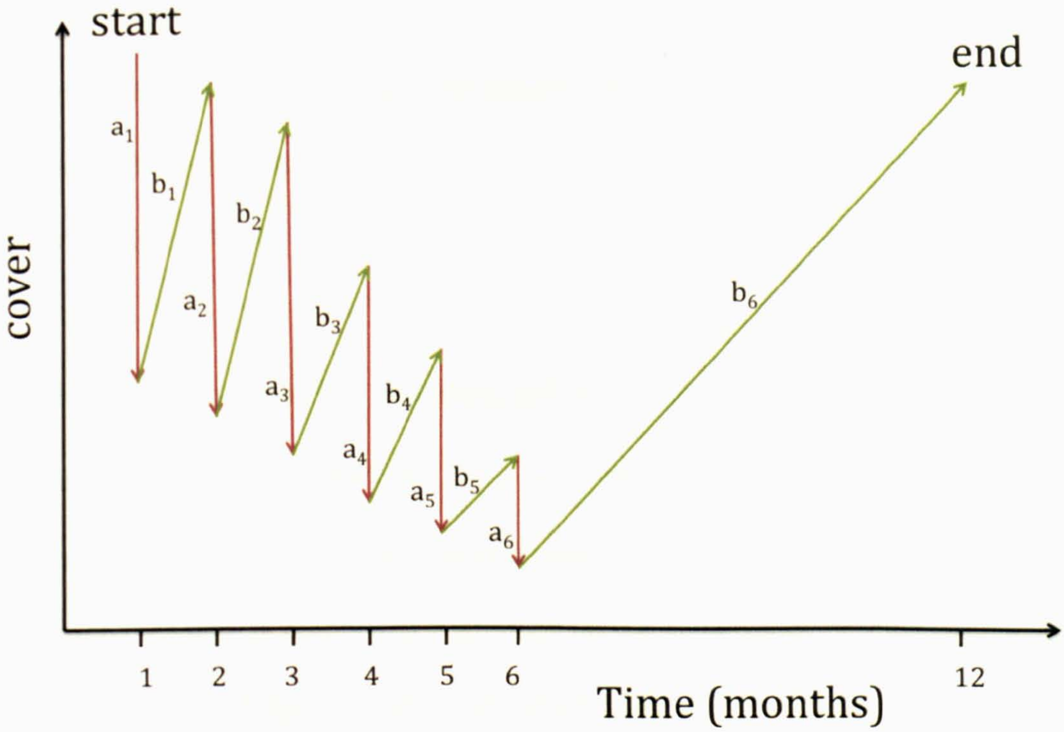

Figure 5.5 Disturbance and recovery in the experiment. The horizontal axis represents time, and the vertical axis represents community composition (which in reality is multivariate, but is shown in univariate form for simplicity). Six disturbance events (a_1-a_6) remove equal proportions of organisms, and six recovery events (b_1-b_6) occur in the five periods between disturbances and a six-month recovery period. The overall change **p** is the perturbation required to get from the start point to the end point. The net change **c** excluding the direct effects of disturbances removes the known events a_1-a_6.

As $\oplus$ is a commutative operator, the order of the disturbances and natural changes does not matter, so

$$\begin{aligned}\mathbf{x}(t) &= \mathbf{x}(0) \oplus \{\mathbf{a}(0) \oplus \mathbf{a}(1) \oplus \ldots \oplus \mathbf{a}(k)\} \oplus \{\mathbf{b}(0) \oplus \mathbf{b}(1) \oplus \ldots \oplus \mathbf{b}(k)\} \\ &= \mathbf{x}(0) \oplus \{\mathbf{a}(0) \oplus \mathbf{a}(1) \oplus \ldots \oplus \mathbf{a}(k)\} \oplus \mathbf{c}\end{aligned},$$

where $\mathbf{c} = \mathbf{b}(0) \oplus \mathbf{b}(1) \oplus \ldots \oplus \mathbf{b}(k)$ is the net natural change from time zero to time t excluding the direct effects of disturbances. If we apply the same proportional disturbance each time, then $\mathbf{a}(0) = \mathbf{a}(1) = \ldots = \mathbf{a}(k) = \mathbf{a}$. If we define the power operation (Aitchison 2003, p4) (analogous to multiplication)

$k \otimes \mathbf{w} = \mathcal{C}[a_1^{\,k}, a_2^{\,k}, \ldots, a_D^{\,k}]$ for a scalar k and a composition $\mathbf{w}$, then we can write

$$\mathbf{x}(t) = \mathbf{x}(0) \oplus (k \otimes \mathbf{a}) \oplus \mathbf{c} \quad .$$

Finally, because $\mathbf{x}(0)$, $\mathbf{x}(t)$, k, and $\mathbf{a}$ are known, we can find the net change excluding the direct effect of disturbance:

$$\mathbf{c} = \mathbf{x}(t) \ominus (\mathbf{x}(0) \oplus k \otimes \mathbf{a}) \tag{5.2}$$

The disturbances $\mathbf{a}$ depend on treatment, and will be described in detail in the Results section. In general terms, $\mathbf{a} = \mathcal{C}[d_1, d_2, \ldots, d_D]$, where d_i is the proportion of species i removed in a disturbance event. It is necessary to exclude empty space, because the proportional change in empty space depends on the abundances of other species, not just on the current proportion of empty space. The closure operator can in fact be dropped here, because it can be applied once at the end of the sequence of calculations.

We now discuss a solution to the problem that all parts of the composition are assumed strictly positive. We do not believe that if we did not see a species on a given panel at a given time, there was zero chance of it appearing. Therefore, we use add-one pseudocount estimates $x_i = \dfrac{n_i + 1}{\sum_i (n_i + 1)}$, where n_i is the sample count of the ith species. Then a zero count becomes $\dfrac{1}{100 + D}$. This is a Bayesian estimator under the assumption of a uniform prior over the D categories, which is sensible as there is only a small number of categories (Manning and Schutze 2002, p202).

Multi-dimensional scaling

Non-metric multi-dimensional scaling (MDS, Kruskal 1964) was carried out in Primer 6 using Euclidean distances. MDS was used on the pre and post-disturbance assemblages, both separately and together to determine if there was variation within the pre and post-disturbance communities, and if there were overall changes in community composition over time. MDS was also carried out on the perturbation measures **p**, and **c**, to determine if there were differences in the overall and net community change between treatments. ANOSIM (Warwick and Clarke 1993) was used to determine whether there were significant differences in net change over the sampling period among the different treatments. Post-hoc pairwise tests were also carried out to determine which treatments resulted in different community compositions.

Transition probabilities

Transition counts were calculated by counting the number of points undergoing each possible transition from one state (all species, plus empty space) to another (including persisting in the same state). These counts were then pooled over replicates for each treatment. We then calculated a p-value from a likelihood ratio test of the null hypothesis that the count matrices for all treatments are generated by the same discrete-time Markov chains, against the alternative hypothesis that they are generated by different discrete-time Markov chains, as described in Tanner et al (1994).

Results

Biomass

There was little evidence for differences in mean wet (Figure 5.6; One-way ANOVA, df=4,31, F=0.60, p=0.666) or dry (Figure 5.7; One-way ANOVA, df=4,31, F=0.38, p=0.819) weights between treatments.

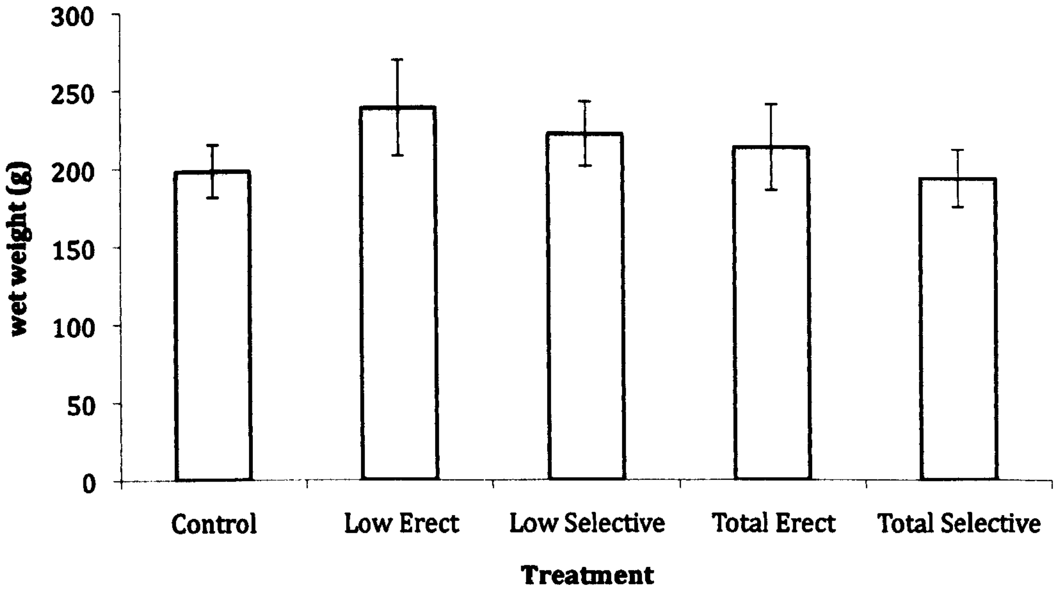

Figure 5.6. Comparison of means (± standard error) for wet weights across treatments on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Sample size n=7 except for control (n=8).

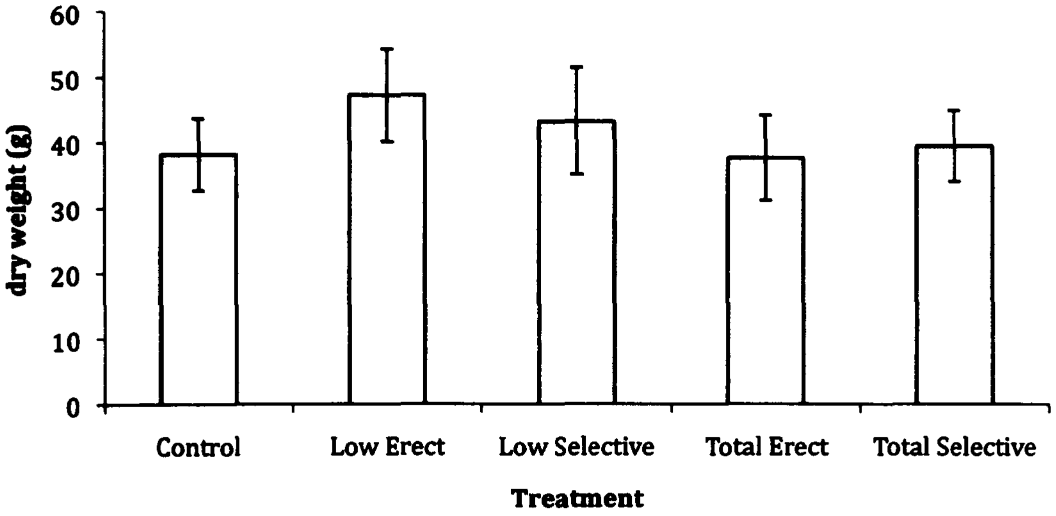

Figure 5.7. Comparison of means (± standard error) for dry weights across treatments on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Organisms were dried at at 90°C for seven days. Sample size n=7 except for control (n=8).

Scalar indices

Species richness decreased in all five treatments over the time interval (Fig. 5.8). The decreases were not significantly different from one another (One-way ANOVA, df=4,31, F=0.40, p=0.810).

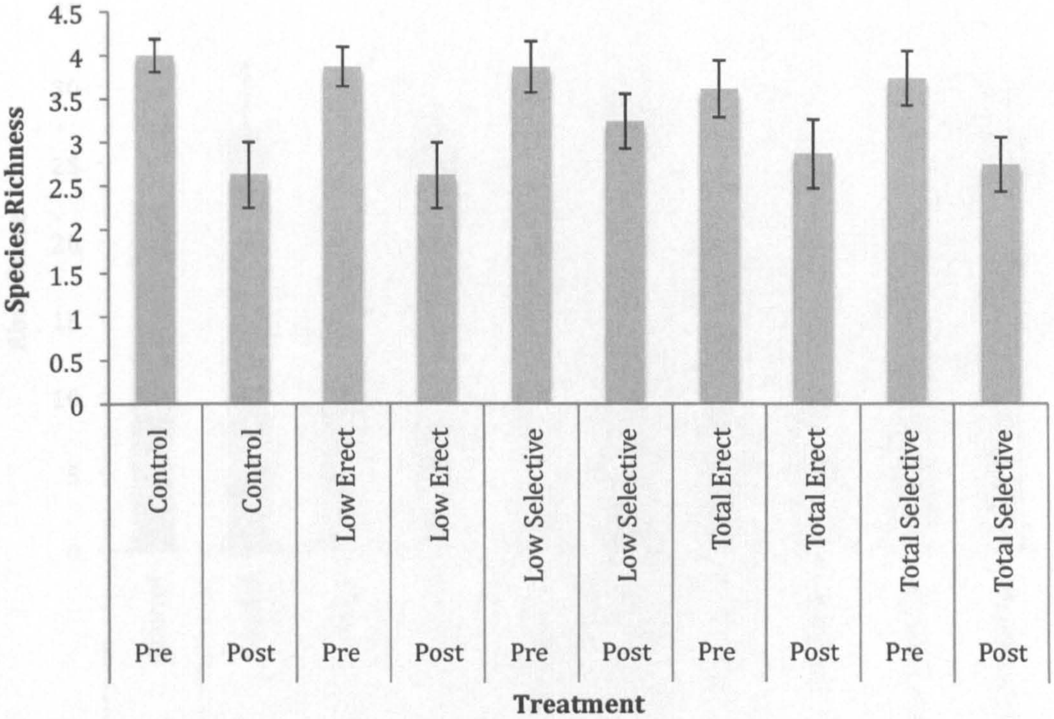

Figure 5.8. Comparison of means (± standard error) of species richness across treatments on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Pre values are from before a disturbance regime; post values are from 6 months after the end of disturbance. Sample size n=7 except for control (n=8).

Abundance increased in all five treatments over the time interval (Fig. 5.9). The increases were not significantly different from one another (One-way ANOVA, df=4,31, F=0.15, p=0.960).

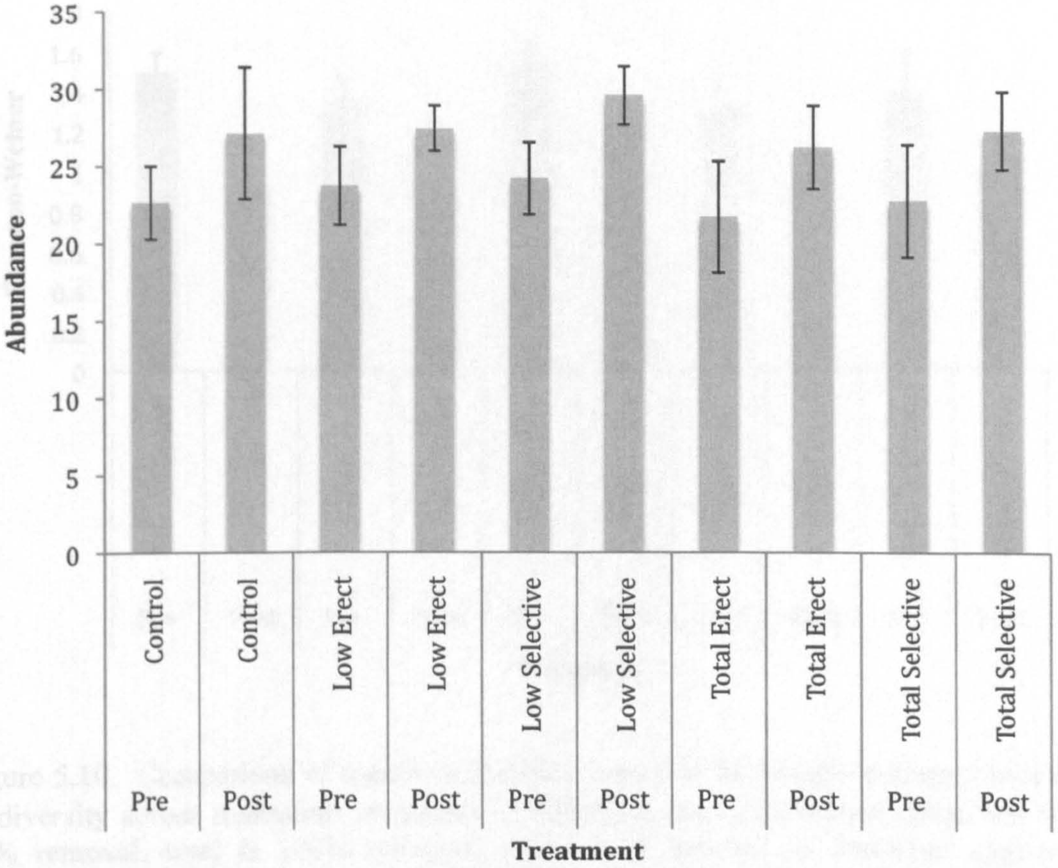

Figure 5.9. Comparison of means (± standard error) of abundance across treatments on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Abundance is measured as the number of points (out of 100). Pre values are from before a disturbance regime; post values are from 6 months after the end of disturbance Sample size n=7 except for control (n=8).

Diversity (Shannon-Weiner) decreased in all five treatments over the time interval (Fig. 5.10). The decreases were not significantly different from one another (One-way ANOVA, df=4,31, F=0.65, p=0.634).

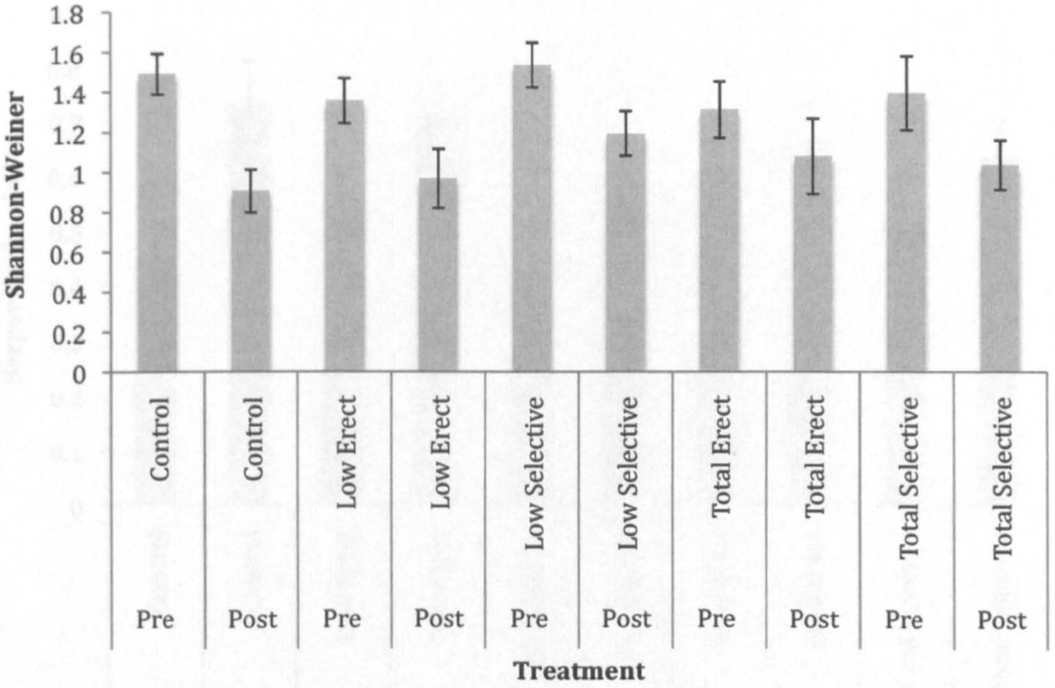

Figure 5.10. Comparison of means (± standard error) of the Shannon-Weiner index of diversity across treatments on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Pre values are from before a disturbance regime; post values are from 6 months after the end of disturbance. Sample size n=7 except for control (n=8).

Dominance (Berger-Parker) increased in all five treatments over the time interval (Fig. 5.11). The decreases were not significantly different from one another (One-way ANOVA, df=4,31, F=0.94, p=0.456).

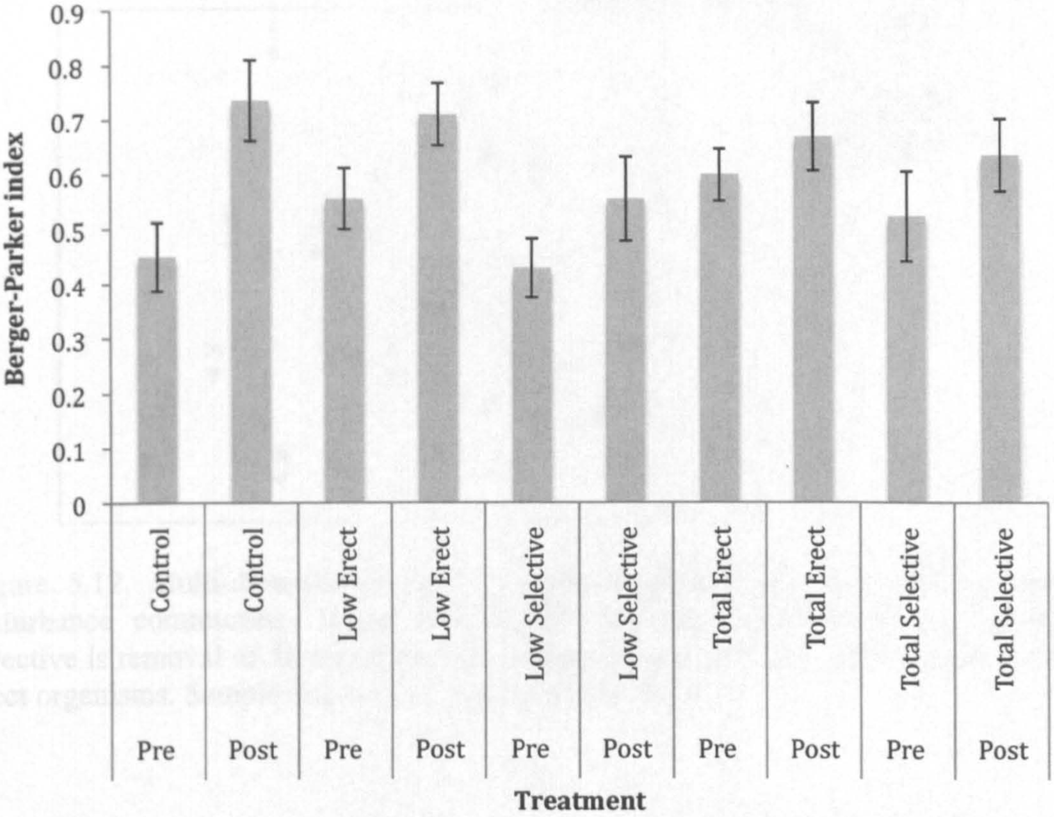

Figure 5.11. Comparison of means (± standard error) of the Berger-Parker index of dominance across treatments on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Pre values are from before a disturbance regime; post values are from 6 months after the end of disturbance. Sample size n=7 except for control (n=8).

Multi-dimensional scaling

The pre-disturbance communities were highly variable (Fig. 5.12).

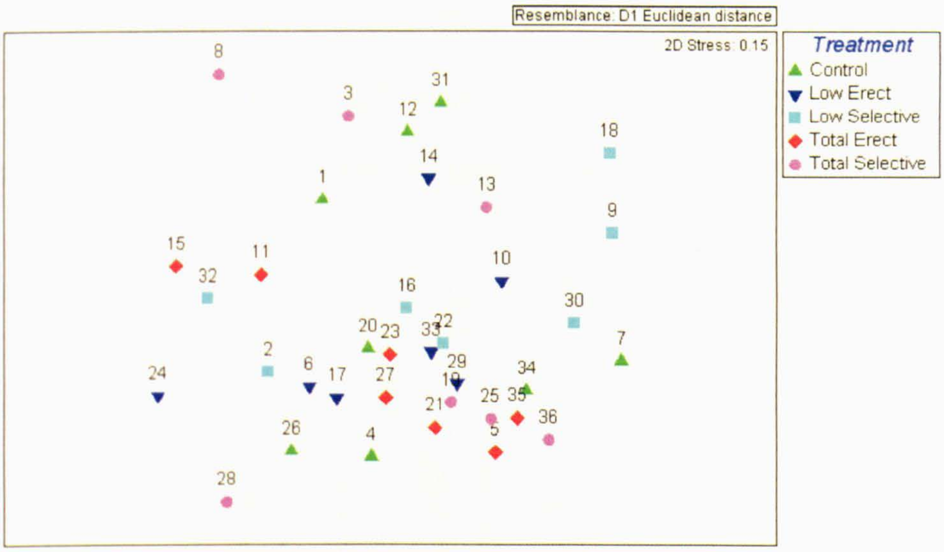

Figure 5.12. Multi-dimensional scaling, using Euclidean distances, for the pre-disturbance communities where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Sample size n=7 except for control (n=8).

The post-disturbance communities were also highly variable (Fig. 5.13).

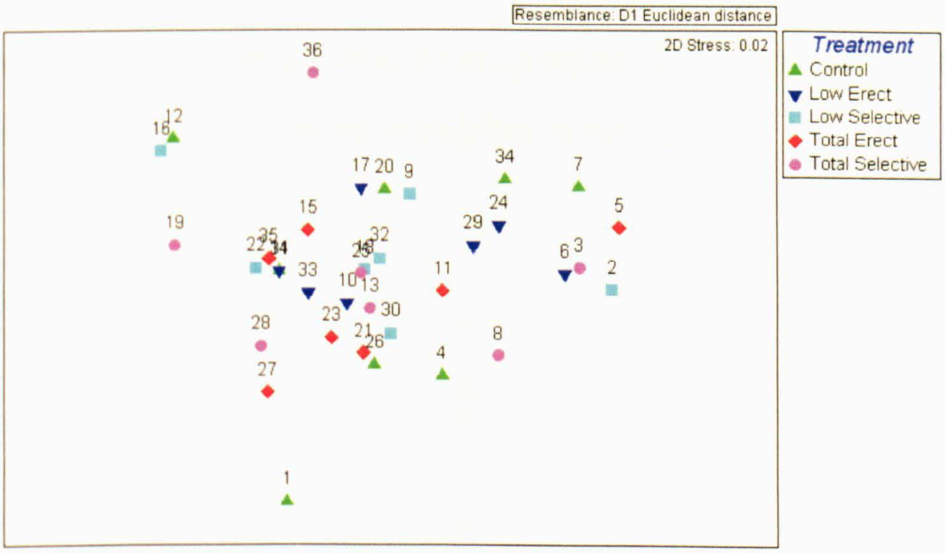

Figure 5.13. Multi-dimensional scaling, using Euclidean distances, for the post-disturbance communities, values are from 6 months after the end of disturbance. Low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Sample size n=7 except for control (n=8).

When plotted together on a single MDS plot, the pre and post-disturbance communities formed reasonably distinct groups (Fig. 5.14). This implies that there was substantial change in community composition over time.

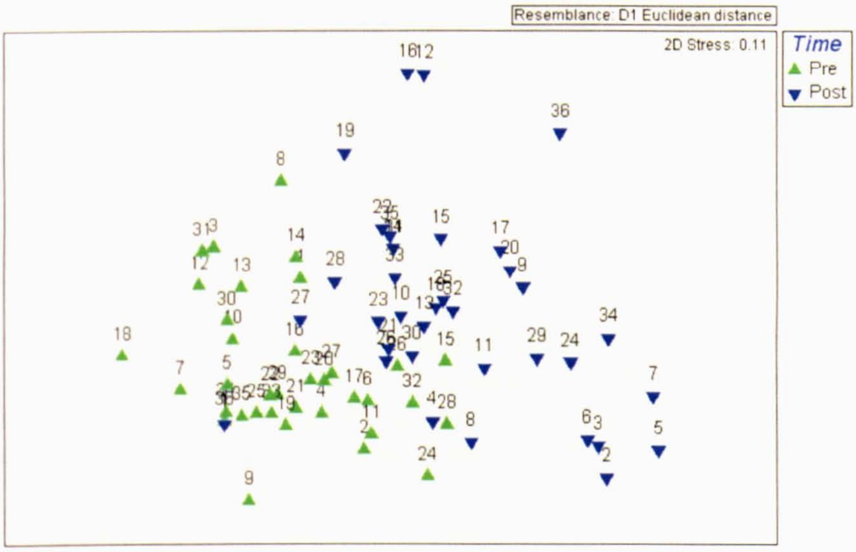

Figure 5.14. Multi-dimensional scaling, using Euclidean distances, for the pre and post-disturbance communities, where post values are from 6 months after the end of disturbance. Sample size n=7 except for control (n=8).

A measure of the overall change over the sampling period, **p** (Equation 5.1), did not show any difference between the treatments (Fig. 5.15).

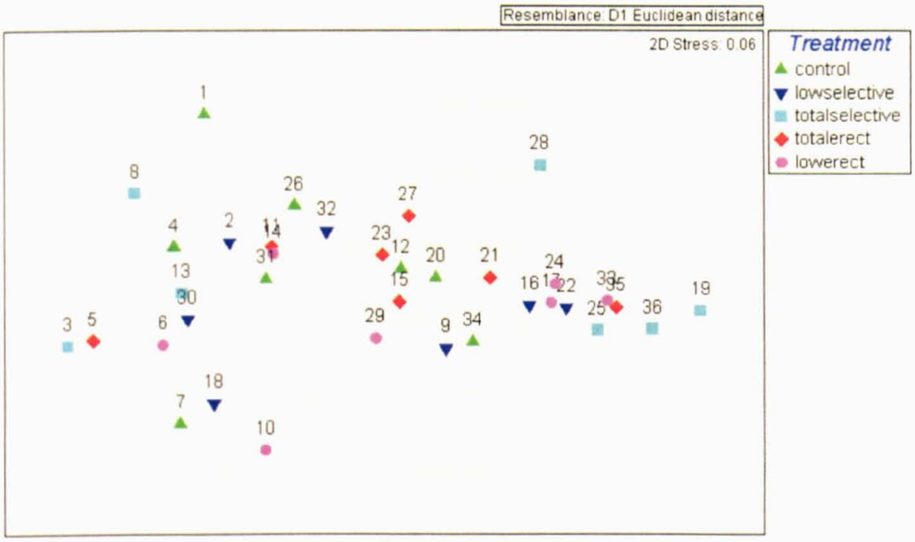

Figure 5.15. Multi-dimensional scaling, using Euclidean distances, for the overall difference in communities prior to and 6 months after a disturbance regime (**p**). Low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Sample size n=7 except for control (n=8).

Disturbance vectors

As total removal is 100% removal of half of the area, this is equal to a 50% removal over the whole sampling area. Similarly, low removal is 50% removal of half the area, which is equal to a 25% removal overall. Selective removal only affects *Ciona intestinalis*, and erect removal affects all species except *Botryllus schlosseri*, which forms flat colonies (Hiscock 2008). We can calculate the disturbance vector **a** for different treatments where the elements of the vector **a** represent effects of the treatment on *Ciona intestinalis*, *Styela clava*, *Botryllus schlosseri*, *Mytilus edulis*, and *Dendrodoa grossularia*; $\mathbf{a}_{\text{control}}=[1,1,1,1,1]$, $\mathbf{a}_{\text{low erect}}=[0.75,0.75,1,0.75,0.75]$, $\mathbf{a}_{\text{total erect}}=[0.5,0.5,1,0.5,0.5]$. $\mathbf{a}_{\text{low Selective}}=[0.75,1,1,1,1]$, and $\mathbf{a}_{\text{total selective}}=[0.5,1,1,1,1]$.

A measure of the net change over the sampling period, **c** (Equation 5.2), had separated groups with some overlap for the low selective and total selective treatments (Fig. 5.16). There were high levels of similarity between the groups

(ANOSIM, *R*=0.443). Post-hoc pairwise tests showed high similarity between the control and low selective (ANOSIM pairwise, *R*=0.547), the control and total selective (ANOSIM pairwise, *R*=0.907), low selective and total selective (ANOSIM pairwise, *R*=0.254), low selective and total erect (ANOSIM pairwise, *R*=0.568), low selective and low erect (ANOSIM pairwise, *R*=0.363), total selective and total erect (ANOSIM pairwise, *R*=0.822), and total selective and low erect (ANOSIM pairwise, *R*=0.720) treatments. There was lower similarity between the control and total erect, control and low erect, and total erect and low erect treatments.

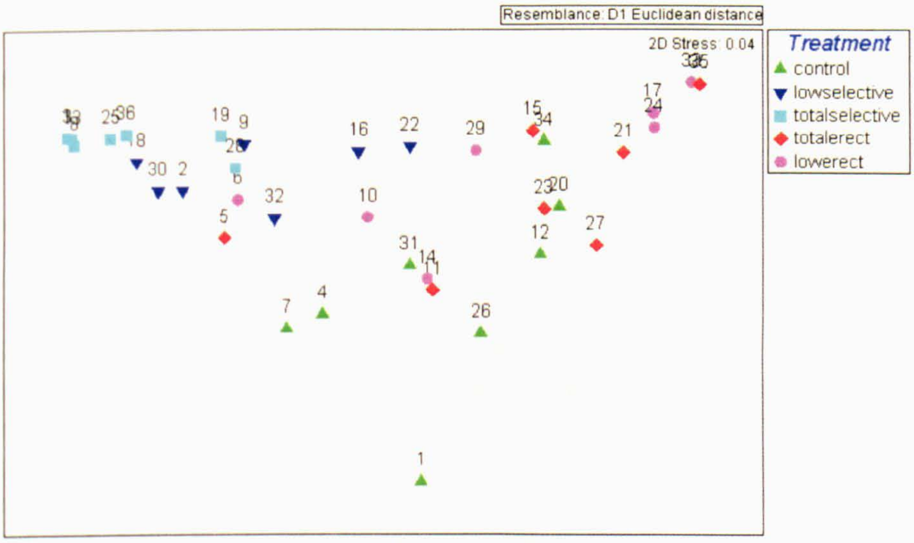

Figure 5.16. Multi-dimensional scaling, using Euclidean distances, for the net change in communities prior to and 6 months after a disturbance regume, minus the direct effects of the disturbances (**c**). Low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Sample size n=7 except for control (n=8).

Perturbations

The values of the parts (species) of the net change measure **c** varied among treatments (Figures 5.17-5.21: note that the vertical scales of these figures differ). Net change for *Ciona intestinalis* was highest for the total selective treatment (Fig. 5.17).

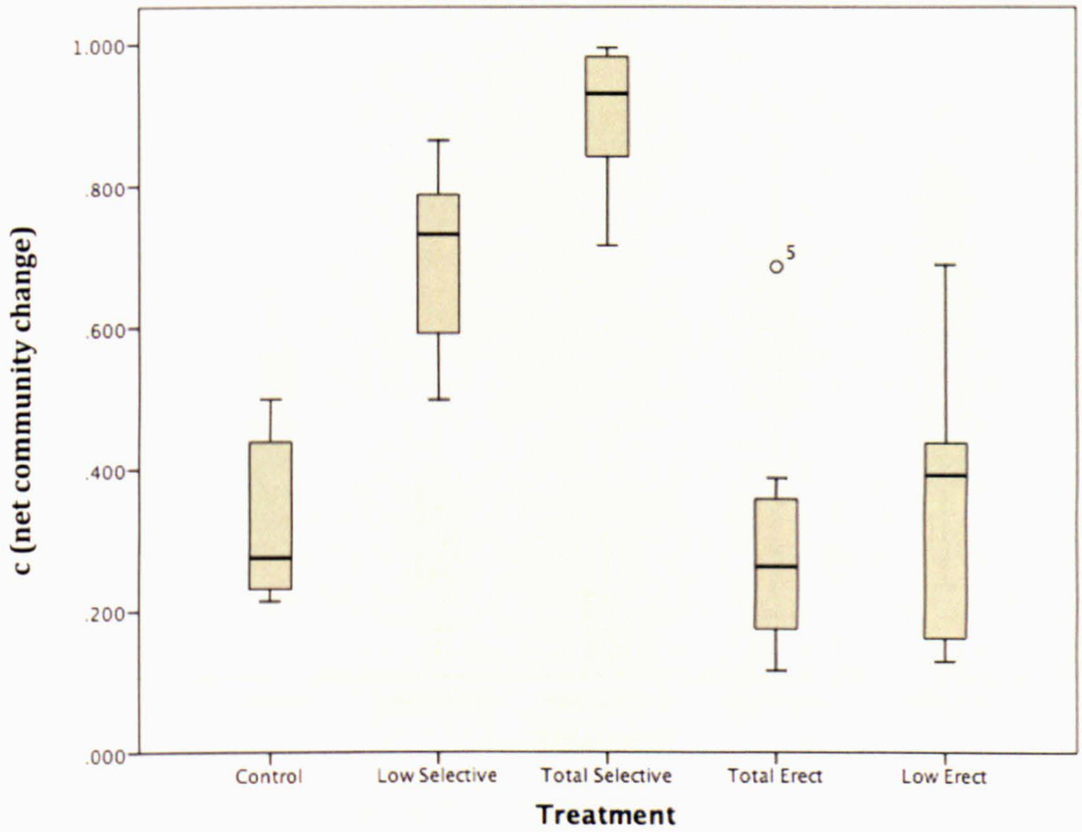

Figure 5.17. Net change **c** for *Ciona intestinalis*, where **c** is our approximation of change over a one year period which included a six month disturbance regime and a six month recovery period. Disturbance treatments were carried out on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Sample size n=7 except for control (n=8).

For *Styela clava*, net change was highest for the total selective treatment (Fig. 5.18). For *Botryllus schlosseri*, net change was highest in the control treatment (Fig. 5.19), while for *Mytilus edulis* (Fig. 5.20) and *Dendrodoa grossularia* (Fig. 5.21), there was relatively little variation among treatments.

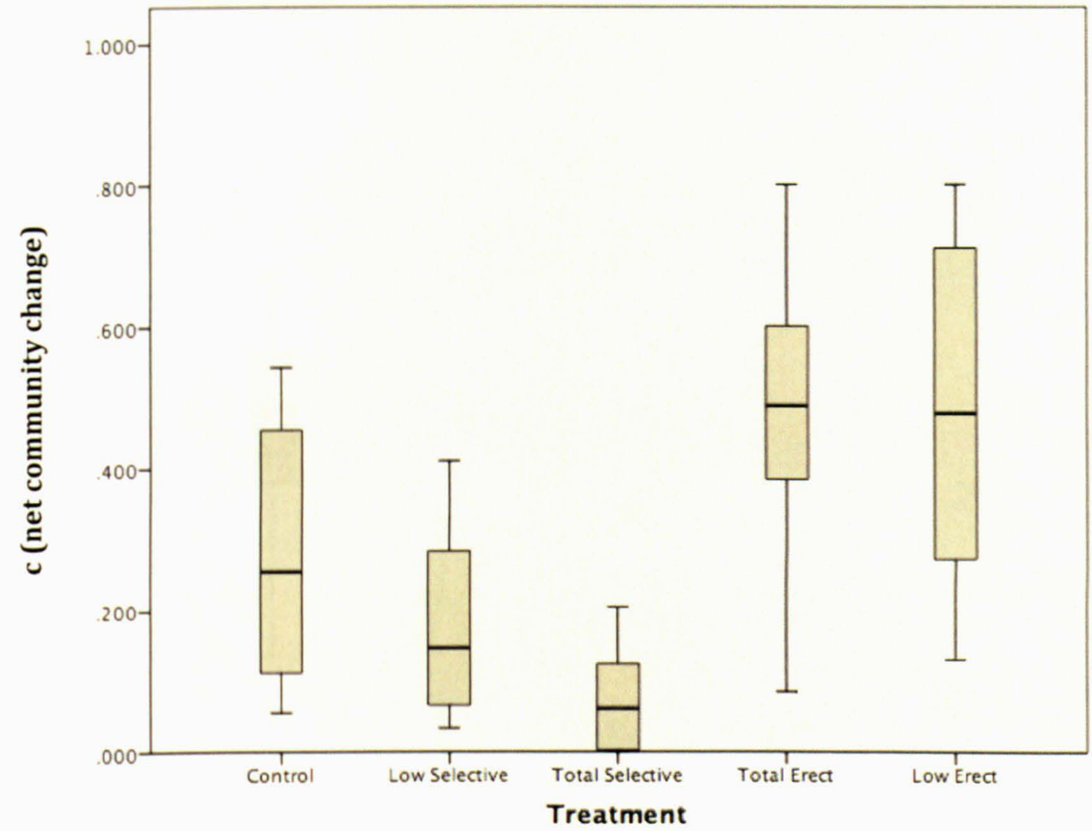

Figure 5.18. Net change **c** for *Styela clava*, where **c** is our approximation of growth over a one year period which included a six month disturbance regime and a six month recovery period. Disturbance treatments were carried out on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Sample size n=7 except for control (n=8).

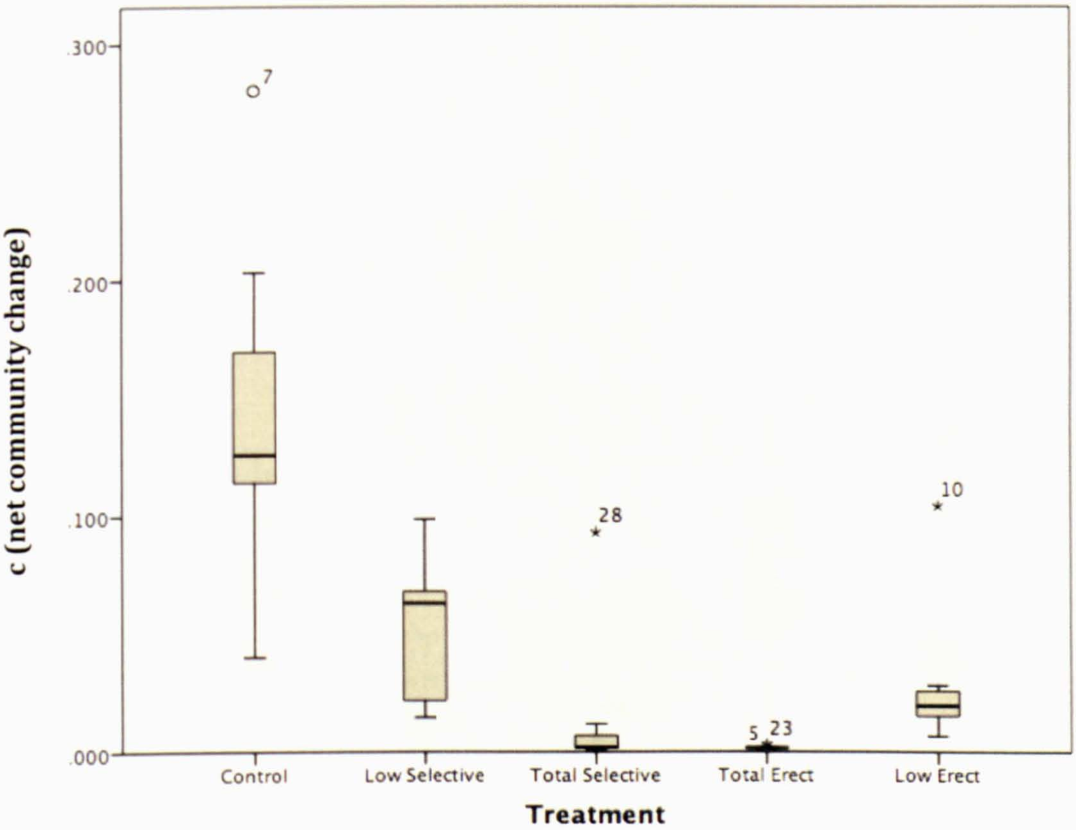

Figure 5.19. Net change **c** for *Botryllus schlosseri*, where **c** is our approximation of growth over a one year period which included a six month disturbance regime and a six month recovery period. Disturbance treatments were carried out on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Sample size n=7 except for control (n=8).

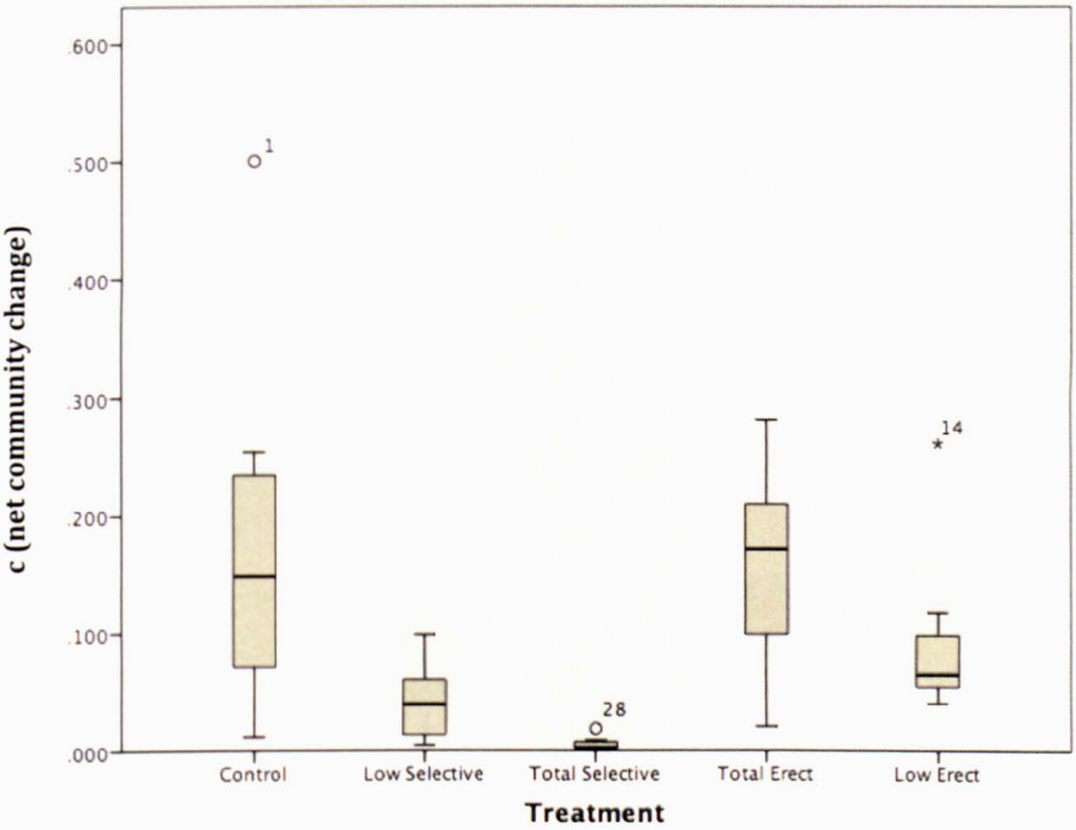

Figure 5.20. Net change **c** for *Mytilus edulis*, where **c** is our approximation of growth over a one year period which included a six month disturbance regime and a six month recovery period. Disturbance treatments were carried out on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Sample size n=7 except for control (n=8).

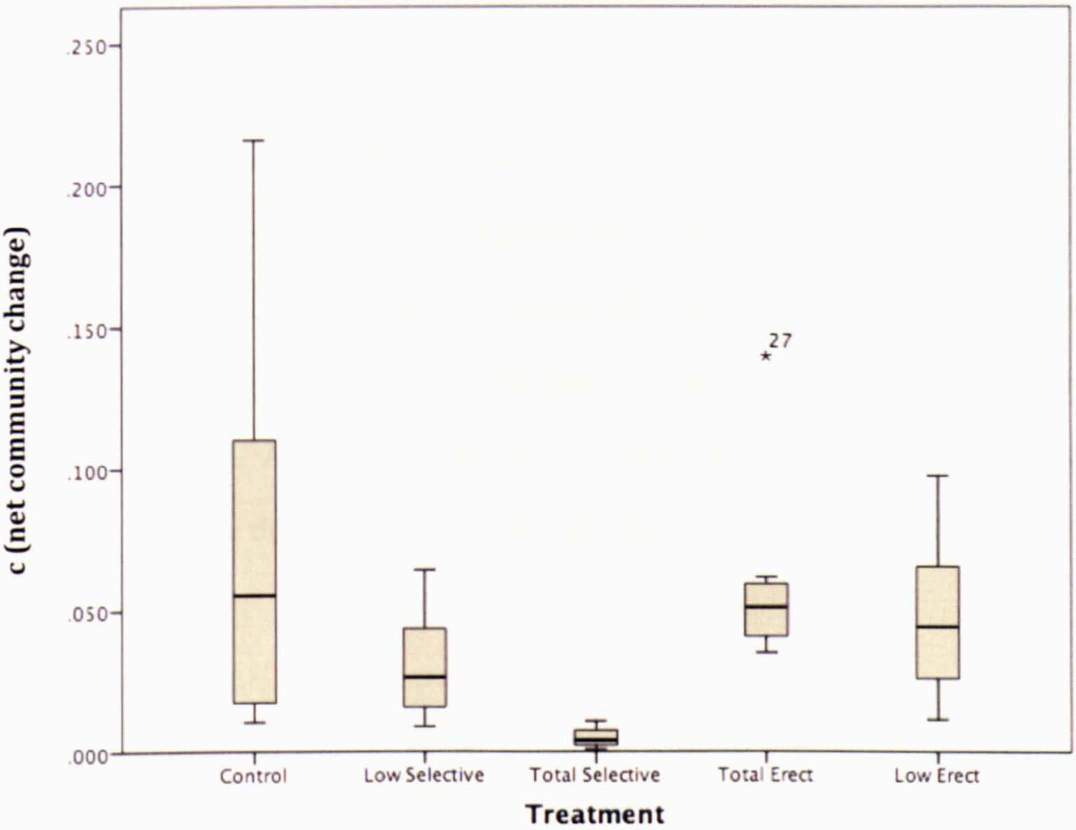

Figure 5.21. Net change **c** for *Dendrodoa grossularia*, where **c** is our approximation of growth over a one year period which included a six month disturbance regime and a six month recovery period. Disturbance treatments were carried out on panels in Salthouse Dock, Liverpool where low is 50% removal, total is 100% removal, selective is removal of dominant species (*Ciona intestinalis*), and erect is removal of erect organisms. Sample size n=7 except for control (n=8).

Transition probabilities

There was little evidence for differences in transition probabilities among the different treatments (p>0.9999, lambda =144.9737, l_0 =-2.9851e+03, l_a =-2.9126e+03, df =224).

Discussion

There was no significant difference in wet or dry weight between treatments, which shows that biomass recovered to pre-disturbance levels within the six month recovery period. Species richness and Shannon-Weiner diversity decreased in all treatments over the time interval, and the decreases were not significantly different from one another. Abundance and Berger-Parker dominance increased in all treatments over the time interval, and the increases were not significantly different from one another.

The multi-dimensional scaling (MDS) showed no patterns with respect to treatment in either the pre or post-disturbance communities. MDS of both the pre and post communities showed clustering of each with transitions moving in the same direction of dissimilarity. MDS of **p**, total change, showed no patterns. There was some clustering, especially in the low selective and total selective treatments, in the MDS of **c**, net community change. There was no significant difference in the transition probabilities between treatments.

Taken together, these results suggest that the fouling community on our experimental panels was able to recover from realistic levels of disturbance, and did not show any evidence for disturbance-induced phase shifts. A simple, abstract mathematical model for communities of this type may help to explain why this happened. We define $x_i(t)$ as the proportional cover of species i at time t. If we have D species in total, $x_{D+1}(t)$ denotes the amount of free space at time t. For each species $i=1,2,\ldots,D$, its cover at time t+1 consists of two contributions: the proportion s_i of cover at time t that survives to time t+1, and the proportion r_i of free space at time t that is colonised by species i at time t+1. We assume that this proportion does not depend on the amount of space already occupied by species *i*; this assumption is plausible as the panels form an open system, in which most increases in the cover of a species are likely to be the result of colonisation by larvae originating elsewhere in the docks. Then

$$\begin{aligned} x_1(t+1) &= s_1 x_1(t) + r_1(x_{D+1}(t)) \\ x_2(t+1) &= s_2 x_2(t) + r_2(x_{D+1}(t)) \\ &\vdots \\ x_D(t+1) &= s_D x_D(t) + r_D(x_{D+1}(t)) \end{aligned} \tag{5.3}$$

where $0 \le r_i \le 1$, $\sum_{i=1}^{D} r_i \le 1$, and $0 \le s_i \le 1$. The amount of free space at time t+1 is then the proportions of free space at time t that was not colonised by any species, plus the sum of the proportions of each species at time t that did not survive.

$$x_{D+1}(t+1) = (1 - \sum_{i=1}^{D} r_i) x_{D+1}(t) + \sum_{i=1}^{D} (1 - s_i) x_i(t) \tag{5.4}$$

Equations 5.3 and 5.4 can be written in matrix form:

$$\begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ \vdots \\ x_D(t+1) \\ x_{D+1}(t+1) \end{bmatrix} = \begin{bmatrix} s_1 & 0 & \cdots & 0 & r_1 \\ 0 & s_2 & \cdots & 0 & r_2 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_D & r_D \\ 1-s_1 & 1-s_2 & \cdots & 1-s_D & 1-\sum_{i=1} r_i \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_D(t) \\ x_{D+1}(t) \end{bmatrix} \tag{5.5}$$

This is a discrete-time Markov model, because the matrix on the right hand side of 5.5 is non-negative, and all of its columns sum to 1. It is therefore a transition probability matrix. The well-known Roughgarden *et al.* (1985) model for an open size-structured population is also a discrete-time Markov model, although the way they wrote it doesn't make that obvious. The possible transitions between states are shown in Figure 5.21. The transition probability matrix for this model is irreducible, because there is a path in Figure 5.21 from any state to any other state (Caswell 2001, p79). There are loops of lengths one and two in Figure 5.21 that do not pass through any state more than once. The greatest common divisor of the loop lengths is one, so the transition probability matrix is primitive (Caswell 2001, p81). By the Perron-Frobenius theorem (Caswell 2001, p79) this model therefore has a unique stationary distribution.

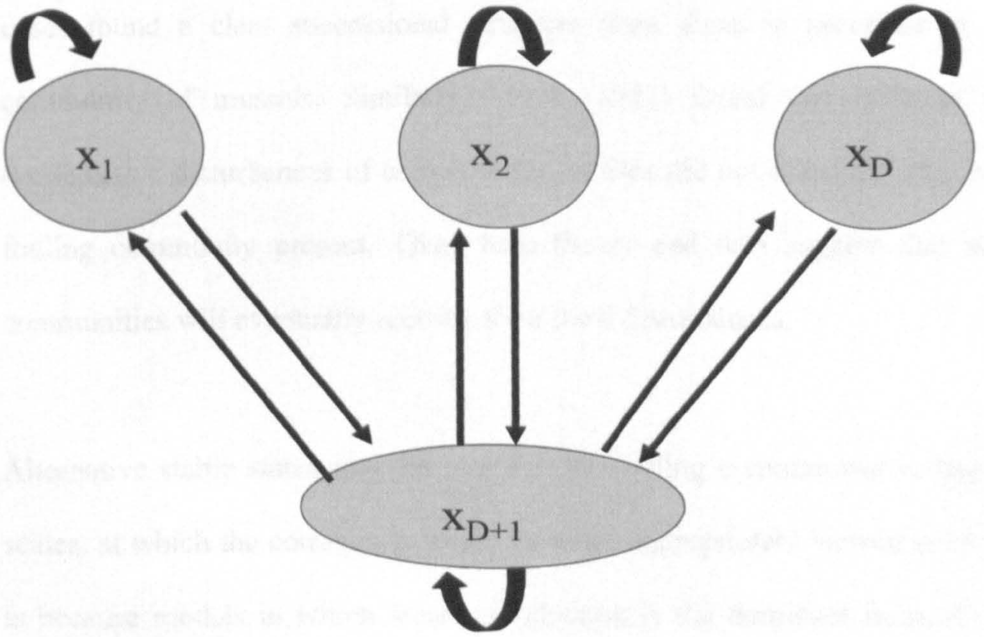

Figure 5.21 Diagram of transitions between states, where D is the number of states, and x_{D+1} is empty space.

The consequence of this is that whatever disturbance we apply, the modelled system will eventually recover. We cannot say in general how long this recovery will take, but it was rapid in our experiment. A possible exception to this result is priority effects. If several species cause permanent (or at least very long-term) habitat alterations of different kinds, which then determine the set of other species that can occupy the habitat, there may not be a unique stationary distribution (e.g. reef-building organisms such as *Sabellaria* spp.). The addition of overgrowth (one species directly replacing another) does not alter the result, provided that at least one state has a non-zero probability of persisting for more than one time step (so that there is at least one loop of length one).

Other empirical data support the idea that open fouling communities do not have alternative stable states at the local scale. For example, Scheer (1945) examined the changes in composition over time of communities on submerged objects and in all cases found a clear successional structure from algae to ascidians to a climax community of mussels. Similarly, Mook (1981) found that different levels of nonselective disturbances of communities on tiles did not affect the structure of the fouling community present. Thus, both theory and data suggest that most open communities will eventually recover from local disturbances.

Alternative stable states may be possible for fouling communities at larger spatial scales, at which the community might be more appropriately viewed as closed. This is because models in which local reproduction is the dominant form of change in abundance tend to be nonlinear (e.g. the continuous-time model in Chapter 2), and often have multiple equilibria (May 1977). For example, the dock system as a whole was in a quasi-stable state before the Tall Ships of 1984 (Jones 2004, p34) with dense phytoplankton populations and without mussels (Hawkins *et al.* 1999). The closed system became an open population with the opening of the dock gates. A large natural settlement of mussels occurred in the South Docks in 1988, which may have been due to the movement of vessels during the Tall Ships race (Hawkins *et al.* 1999). The dense mussel settlement created a secondary substrate for a rich associated fauna (Hawkins *et al.* 1999). This allowed colonisation by mussels, which grew to dominate the system (Hawkins *et al.* 1999). The mussel populations are now thought to be self-supporting, so that the current state of the system is also stable. Genetic analysis could be undertaken to determine whether the populations of mussels within the docks are currently genetically isolated from the mussel populations in the Mersey Estuary (so that the docks as a whole represent a closed system), or whether there is still substantial exchange with the outside world.

In conclusion, our experimental finding was that the fouling community that we studied recovered quickly from small scale disturbances. This can be explained by a simple mathematical model that may apply generally to other similar communities. Nevertheless, at larger spatial scales, such as the entire dock system, alternative stable states may be possible.

Chapter Six: Conclusions

There has been a trend in ecological modelling to produce complicated, mechanistic models that can be applied to different ecological systems. Levins (1966) stated models must sacrifice generality, precision, or realism in order to achieve the other two attributes. More complicated models introduce more model uncertainty with each additional parameter, and are therefore precise, or able to be used to make accurate predictions.

The models produced in this study were simple statistical models, which were designed to be used to be able to make predictions about future ecological states. Previous models of this system have not explained the variability in the data; environmental data was added in the model to make the model better 'fit' the data.
We were also concerned about changes in future environmental conditions due to climate change, and the impact of these changes on ecological communities.

Models are assessed using different validation techniques; Rykiel (1996) identified 13 different methods of model validation that are commonly used. Quantitative model validation is ideal, but many models do not have sufficient or relevant data against which they can be tested. Qualitative methods of model validation are highly subjective; different visualisation techniques can appear to demonstrate different results (Tufte, 1993).

This study aimed to advance our ability to predict the dynamics of marine communities using statistical models. This involved adding environmental data to models, investigating the impact of climate change on disturbances, evaluating predictions using new data, and investigating the methodology used in making these predictions.

Chapter 2 showed that coral mortality due to cyclones is not very large, and recovery is quite fast. The addition of cyclones improved the fit of the model, with cyclones causing some coral mortality. The continuous-time Lotka-Volterra model, which had a large increase in coral mortality associated with cyclones, also fitted better than a discrete-time Markov model with cyclone effects. The continuous-time model is nonlinear, and its transition rates depend on local abundances. Therefore, recruitment is likely to be less important than the growth and mortality of existing corals. We are uncertain about what happens to algae in the model, as the model resolution cannot detect the fast algal dynamics.

Chapter 3 used the model from Chapter 2 as a baseline against which we can assess alternative past scenarios. Coral cover over the period we modelled would have been different had the cyclone regime been different. Under current or slightly increased cyclone frequency, the timings of cyclones caused one of two things to happen. When the corals had a long period where they were not disturbed by cyclones, they increased their cover to a level that was able to withstand subsequent losses due to cyclones. When cyclones hit early on in the model, the coral was unable to recover between subsequent disturbances, and cover dropped to low levels. With increasing cyclone frequency, there was a transition from the outcome being contingent on chance events to being almost certain about the outcome.

In Chapter 4, I showed that the continuous-time model predicted significantly less coral than was observed in 2008. Conversely, the discrete-time model predicted significantly more coral than was observed. Overall, the predictions made by the continuous-time model are closer to the observed proportions of coral, algae, and free space. There appear to be changes over time in the system that are not accounted for in the model.

In Chapter 5, recovery from experimental disturbances to the fouling community in Salthouse Dock, Liverpool, was rapid, with biomass returning to pre-disturbance levels. There were no differences in diversity measures between the treatments. The selective treatments, where the dominant organism *Ciona intestinalis* was targeted, had much higher net growth of *C. intestinalis* over the period, so that they remained dominant despite being selectively removed. A simple mathematical model suggests that recovery is almost inevitable in systems of this kind, especially for species with planktonic larval stages.

Our continuous-time model for coral community dynamics is different to many ecological models as it is relatively simple and is based on a relatively large data set. Many ecological models are much more complicated and use fewer data (e.g. McClanahan 1995, Wolanski *et al.* 2004). Developing models without fitting them to data tells us what could happen. Fitting models to data is closer to telling us about what actually does happen. It could be argued that the history of ecology is characterised by excessive focus on the former question at the expense of the latter. Much of theoretical ecology consists of adding refinements to existing models, with no attempt to confront them with data. For example, one of the classic explorations of what could happen in a predator-prey system is Rosenzweig and MacArthur (1963). ISI Web of Knowledge reports 528 citations for this paper, of which 18 were in 2011 (up to 24/9/11). Of these 18, only one (Shelton and Mangel 2011) uses models as descriptions of real data, rather than as objects of study in their own right or as metaphors. Directing a higher proportion of effort towards the challenge of building models for data might help to advance both applied ecology (by giving us better answers to questions of real-world importance) and theoretical ecology (by suggesting genuinely new directions for model development).

The Heron Island model has no external inputs, whereas the Docks model is entirely driven by external inputs. Heron Island is in reality an open system, whereas the Docks study site is neither strictly an open nor a closed system. Both of our study sites recovered from disturbances quickly, and in the case of Heron Island, more quickly than we expected. This may be due to the underlying resilience of these systems. Supply-side dynamics are thought to be important for open populations (Roughgarden *et al.* 1985). But although Heron Island is apparently open, a closed model fitted the data much better; this may be because the growth of existing coral colonies makes a greater contribution than the settlement of recruits from outside.

In both the Heron Island dataset and the Docks experiment, the communities recovered faster than we expected. Therefore, they are resilient to the current levels of disturbance. Heron Island had a rapid recovery because of recruitment from surrounding areas. In the Docks experiment, removal of the dominant species created empty space, which was re-colonised by the dominant species. This demonstrates that recruitment of the dominant species, *Ciona intestinalis*, is high and that recruitment is not dependent on current abundance. *C. intestinalis* dominates the study site, and therefore when empty space becomes available through its removal, it also dominates the colonisation of the new empty space. Further work at the Docks study site could include a genetic comparison of the sessile populations in the Mersey Estuary and within the dock system, to determine if these populations are isolated. This would tell us how open or closed the system is and would inform our knowledge of the system. On coral reefs, it has been shown that the state of the surrounding area has enhanced the resilience of coral-dominated systems (Elmhirst *et al.* 2009). In their model, Elmhirst *et al.* (2009) showed that, for both coral and algal dominated systems, recruitment was only an important part of resilience when grazing was optimal (low or high, depending on the dominant species). There may be other factors affecting how these species re-colonise an area after a disturbance. In coral reefs, a framework of dead coral, and coral rubble provide a substratum for the settlement of larvae (Nystrom and Folke 2001). This change in habitat complexity may increase coral recruitment, and assist a faster recovery from a disturbance.

In the Heron Island dataset the species are grouped into coral, algae, and free space. Although coral cover was recovering after disturbance by cyclones, the relative abundance of coral species within that group may be changing. It may be the case that coral species that are more resilient are replacing those that are more vulnerable to the effects of disturbance. The most recent data from the Heron Island site, collected in 2008, show that Acroporid corals dominate the study site. Acroporid corals are characterized by rapid growth and competitive dominance and have been shown to dominate coral assemblages on the Great Barrier Reef that are recovering from disturbances (Halford *et al.* 2004).

We could improve on our coral model by adding in a recruitment parameter. If there are patches of disturbance, then recovery will be faster as other patches that have not been disturbed will provide recruits. This would indirectly put ecological resilience into the model, and make our predictions more accurate. Adding dispersal and recruitment dynamics into models of these systems would improve both our understanding of the system and the model predictions.

In both systems, we did not apparently need many species categories to understand the fundamental dynamics of the system. This may be because neither system had a very large number of species, and most of the species that we found were not abundant. Generally, most species are rare in most communities (May 1975). This suggests that we might only need to model a few, numerically dominant species if we want to make accurate predictions of dynamics in most situations. On the other hand, it has been suggested that large numbers of species may make important contributions to ecosystem function (Loreau 2010, xi). For example, out of 147 grassland plant species studied in a set of 17 experiments, 84% made positive contributions to ecosystem functions such as biomass production and nutrient uptake on at least one occasion (Isbell *et al.* 2011). One possible explanation for this apparent contradiction is that there are many ways to define importance. In Isbell *et al.* (2011), a species was defined as making an important contribution to an ecosystem function if it was included in a multiple regression model chosen by backward elimination, using AIC as the model selection criterion. This "statistical importance" does not necessarily imply that the contribution was large enough to be biologically significant. In a highly replicated experiment, even relatively small effects might be detectable. AIC is also well known to select over-complicated models when the true model has finite dimension (e.g. Bozdogan 1987), which is the case for experimental studies. In consequence, some of the species in the experiments analysed by Isbell et al (2011) might not even be genuinely important in a statistical sense.

Both sites were dominated by one species or a group of species having at least a moderate level of functional similarity. One obvious approach to reducing model complexity is to group functionally similar species (as we did for the Heron Island models). Another possibility is to retain all species, but ignore the differences between them. Hubbell's (2001, pp320-321) unified neutral theory of biodiversity makes the obviously false assumption that all species are identical. There may be situations in which this assumption is a reasonable approximation. For example, trees within a forest in Panama all have the same life history trade-off between shade tolerance and growth rate (Hubbell 2001, pp322-323). Every species in the community must obey this constraint to survive, therefore the community can be described using many fewer parameters than treating every species individually (Hubbell 2001, p323). However, Wootton (2005) demonstrated that, for a rocky intertidal community, Hubbell's theory performed poorly at predicting experimental results. Therefore, there are situations where we can treat species identically, which will enable us to use much simpler models of community dynamics. But, this is not always the case, and we should not assume that species can always be grouped, or treated as if they were identical.

Returning to Levins's (1966) model trade-offs between generality, precision, and realism, I believe that if we are to create models that will generate accurate predictions then we have to discard the 'one size fits all' approach and sacrifice generality to produce models that are realistic and precise. Creating models based on a long-term dataset still generated model uncertainty and limited our ability to make predictions into the future. These tools are however still useful from a management perspective; they can be used to choose between management decisions to obtain relative rather than absolute outcomes. In order to advance the understanding of ecological dynamics, I believe that we must be able to quantitatively validate ecological models. This requires the funding and maintenance of long-term ecological datasets.

In this thesis, I have shown that simple statistical models can be used to understand the behaviour of complicated ecosystems. Simple models have been used for a long time in ecology (e.g. Leslie 1945, May 1974, Skellam 1951, Volterra 1926) but they were never meant to describe actual data. In my thesis, the models are intended as descriptions of real dynamics: admittedly imperfect, but nevertheless representing much closer linkage between data and theory than the situation that May described in the 1970s: "Unfortunately, the complications inherent in multi-species systems almost invariably preclude any quantitative confrontation between theory and data. For multi-species communities, the empirical observations remain largely anecdotal, and the theory remains largely metaphorical" (May 1977). In my thesis, empirical observations, rather than being anecdotal, were systematically collected and subjected to detailed study on the basis of models. This synergy between data and theory is becoming a major theme in modern ecology.

Appendix I.

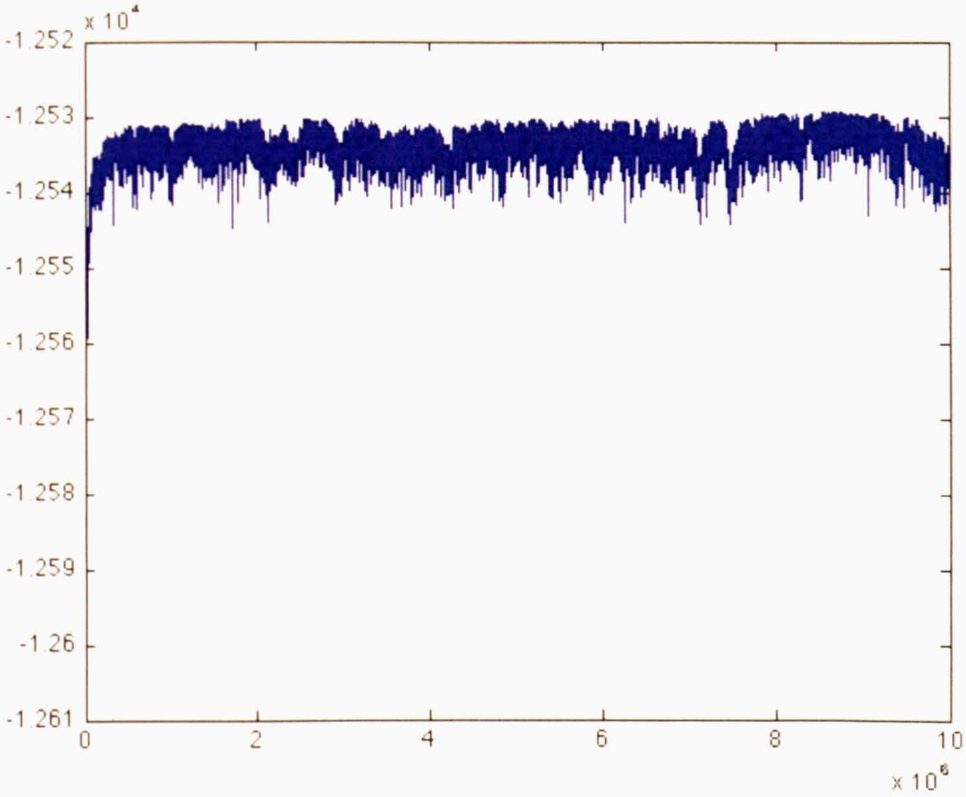

Figure A1.1 Log likelihood for the first run of the continuous-time model with cyclones, where the y-axis is log likelihoods and the x-axis is iterations of the model.

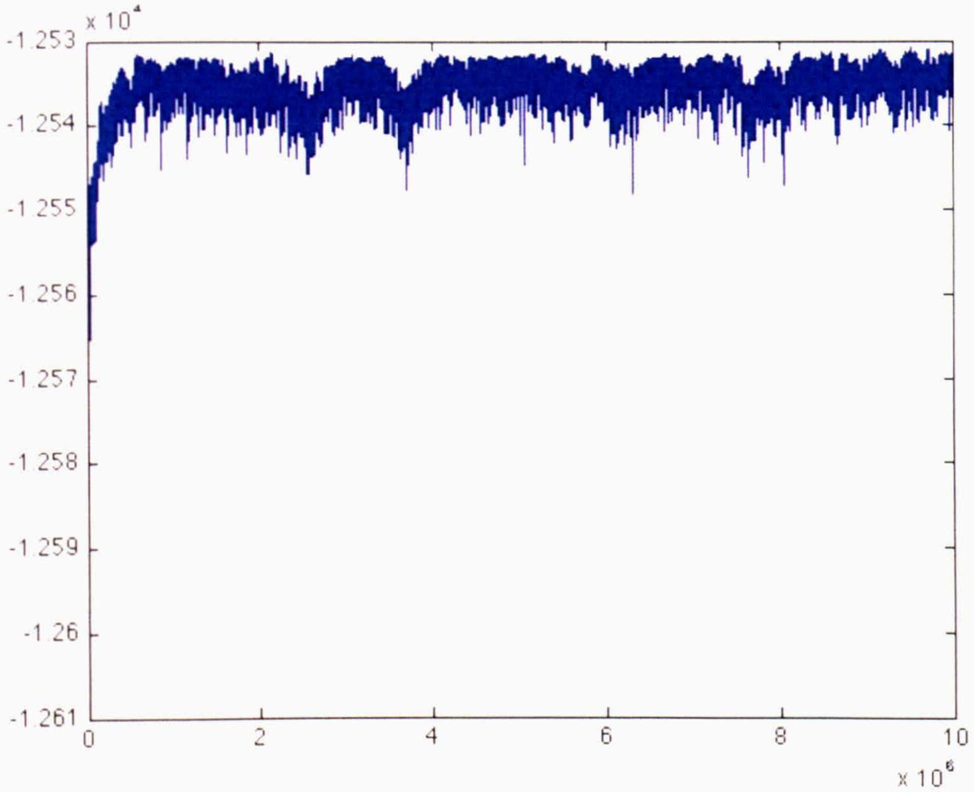

Figure A1.2 Log likelihood for the second run of the continuous-time model with cyclones, where the y-axis is log likelihoods and the x-axis is iterations of the model.

References

Adjeroud, M., Y. Chancerelle, M. Schrimm, T. Perez, D. Lecchini, R. Galzin, and B. Salvat. 2005. Detecting the effects of natural disturbances on coral assemblages in French Polynesia: A decade survey at multiple scales. Aquat. Living Resour. **18**:111-123.

Agren, G. I., R. E. McMurtrie, W. J. Parton, J. Pastor, and H. H. Shugart. 1991. State-of-the-art of models of production-decomposition linkages in conifer and grassland ecosystems. Ecological Applications **1**:118-138.

Aitchison, J. 1986. The statistical analysis of compositional data. The Blackburn Press, New Jersey, USA.

Aitchison, J. 2003. The statistical analysis of compositional data (postscript). The Blackburn Press, New Jersey, USA.

Allen, J. R. 1992. Hydrography, ecology, and water quality management of the South Docks, Liverpool. University of Liverpool, Liverpool, UK.

Artzy-Randrup, Y., R. Olinky, and L. Stone. 2007. Size-structured demographic models of coral populations. Journal of Theoretical Biology **245**:482-497.

Australian Bureau of Meteorology 2011a. Tropical cyclone definitions. http://www.bom.gov.au/cyclones/faq/index.shtml#definitions. Date accessed 26/09/2011. Australian Bureau of Meteorology.

Australian Bureau of Meteorology 2011b. Previous tropical cyclones. http://www.bom.gov.au/cyclone/history/index.shtml. Date accessed 26/09/2011. Australian Bureau of Meteorology.

Babcock, R. 1991. Comparative demography of three species of scleractinian corals using age-and size-dependent classifications. Ecological Monographs **61**:225-244.

Bacelar, F. S., S. Dueri, E. Hernandez-Garcia, and J. Zaldivar. 2009. Joint effects of nutrients and contaminants on the dynamics of a food chain in marine ecosystems. Mathematical Biosciences **218**:24-32.

Bak, R. and B. Luckhurst. 1980. Constancy and change in coral reef habitats along depth gradients at Curacao. Oecologia **47**:145-155.

Beissinger, S. and M. Westphal. 1998. On the use of demographic models of population viability in endangered species management. The Journal of Wildlife Management **62**:821-841.

Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nystrom. 2004. Confronting the coral reef crisis. Nature **429**:827-833.

Blackwood, J., A. Hastings, and P. Mumby. 2010. The effect of fishing on hysteresis in Caribbean coral reefs. Theoretical Ecology:1-10.

Bozdogan, H. 1987. Model selection and Akaike's information criterion (AIC): The general theory and its analytical extensions. Psychometrika **52**:345-370.

Brook, B., J. O'Grady, A. Chapman, M. Burgman, H. Akcakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature **404**:385-387.

Bruno, J., H. Sweatman, W. Precht, E. Selig, and V. Schutte. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology **90**:1478-1484.

Bruno, J. F. and E. R. Selig. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. PLoS One **2**:e711.

Burgman, M. A., S. Ferson, and A. H.R. 1993. Risk assessment in conservation biology. Chapman & Hall, London, UK.

Caswell, H. 1988. Theory and models in ecology: A different perspective. Ecological Modelling **43**:33-44.

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

Clancy, D., J. E. Tanner, S. McWilliam, and M. Spencer. 2010. Quantifying parameter uncertainty in a coral reef model using Metropolis-Coupled Markov Chain Monte Carlo. Ecological Modelling **221**:1337-1347.

Connell, J. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302.

Connell, J. 1997. Disturbance and recovery of coral assemblages. Coral Reefs **16**:101-113.

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

Connell, J., T. Hughes, C. Wallace, J. Tanner, K. Harms, and A. Kerr. 2004. A long-term study of competition and diversity of corals. Ecological Monographs **74**:179-210.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. pp.460-490 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, London, UK.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist **111**:1119-1144.

Connell, J. H. and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. The American Naturalist **121**:789-824.

Daskalov, G. M., A. N. Grishin, S. Rodionov, and V. Mihneva. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the National Academy of Science of the United States of America **104**:10518-10523.

Demott, R., A. Balaraman, and M. Sorensen. 2005. The future direction of ecological risk assessment in the United States: Reflecting on the U.S. Environmental Protection Agency's examination of risk assessment practices and principles. Integrated Environmental Assessment and Management **1**:77.

Diaz-Pulido, G., L. McCook, S. Dove, R. Berkelmans, G. Roff, D. Kline, S. Weeks, R. Evans, D. Williamson, and O. Hoegh-Guldberg. 2009. Doom and boom on a resilient reef: Climate change, algal overgrowth and coral recovery. PLoS One **4**:e5239.

Dobson, M. and C. Frid. 1998. Ecology of aquatic systems. Prentice Hall, Harlow, UK.

Dudgeon, S., R. Aronson, J. Bruno, and W. Precht. 2010. Phase shifts and stable states on coral reefs. Marine Ecology Progress Series **413**:201-216.

Elmhirst, T., S. Connolly, and T. Hughes. 2009. Connectivity, regime shifts and the resilience of coral reefs. Coral Reefs **28**:949-957.

Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature **436**:686-688.

Emslie, M. J., A. J. Cheal, H. Sweatman, and S. Delean. 2008. Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. Marine Ecology Progress Series **371**:177-190.

Evans, M., N. Hastings, and B. Peacock. 2000. Statistical distributions. 3rd edition. Wiley Interscience, Chichester, UK.

Fielding, N. J. 1997. Fish and benthos communities in regenerated dock systems on Merseyside. University of Liverpool, Liverpool, UK.

Frank, K. T., B. Petrie, J. A. D. Fisher, and W. C. Leggett. 2011. Transient dynamics of an altered large marine ecosystem. Nature **477**:86-89.

Fulton, E., A. Smith, and C. Johnson. 2004. Biogeochemical marine ecosystem models I: IGBEM--a model of marine bay ecosystems. Ecological Modelling **174**:267-307.

Fulton, E. A., A. D. M. Smith, and C. R. Johnson. 2003. Effect of complexity on marine ecosystem models. Marine Ecology Progress Series **253**:1-16.

Gardner, T. A., I. M. Cote, J. A. Gill, A. Grant, and A. R. Watkinson. 2005. Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. Ecology **86**:174-184.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. 2nd edition. Chapman & Hall, London, UK.

George, E. I. and R. E. McCulloch. 1996. Stochastic search variable selection. Pages 203-214 *in* W. R. Gilks, S. Richardson, and D. J. Spiegelhalter, editors. Markov Chain Monte Carlo in practice. Chapman & Hall, London, UK.

Ginzburg, L. R., L. B. Slobodkin, K. Johnson, and A. G. Bindman. 1982. Quasiextinction probabilities as a measure of impact on population growth. Risk Analysis **2**:171-181.

Glasser, J. W. 1982. On the causes of temporal change in communities: Modification of the biotic environment. The American Naturalist **119**:375-390.

Graham, N. A. J., T. R. McClanahan, M. A. MacNeil, S. K. Wilson, N. V. C. Polunin, S. Jennings, P. Chabanet, S. Clark, M. D. Spalding, Y. Letourneur, L. Bigot, R. Galzin, M. C. Ohman, K. C. Garpe, A. J. Edwards, and C. R. C. Sheppard. 2008. Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. PLoS One **3**:e3039.

Guillemot, N., P. Chabanet, and O. Le Pape. 2010. Cyclone effects on coral reef habitats in New Caledonia (South Pacific). Coral Reefs **29**:445-453.

Halford, A., A. Cheal, D. Ryan, and D. Williams. 2004. Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. Ecology **85**:1892-1905.

Hanson, N. and J. D. Stark. 2011. A comparison of simple and complex population models to reduce uncertainty in ecological risk assessments of chemicals: example with three species of Daphnia. Ecotoxicology **20**:1268-1276.

Harriott, V. 1985. Mortality rates of scleractinian corals before and during a mass bleaching event. Marine ecology progress series. Oldendorf **21**:81-88.

Harris, J., R. Hobbs, E. Higgs, and J. Aronson. 2006. Ecological restoration and global climate change. Restoration Ecology **14**:170-176.

Hawkins, S. J., J. R. Allen, and S. Bray. 1999. Restoration of temperate marine and coastal ecosystems: nudging nature. Aquatic Conservation: Marine and Freshwater Ecosystems **9**:23-46.

Hennessy, K., B. Fitzharris, B. C. Bates, N. Harvey, S. M. Howden, L. Hughes, J. Salinger, and R. Warrick. 2007. Australia and New Zealand. Pages 507-540 *in* M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E.

Hanson, editors. Climate change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Hilborn, R. and M. Mangel. 1997. The ecological detective. Princeton University Press, Princeton, New Jersey, USA.

Hill, M., J. Witman, and H. Caswell. 2004. Markov chain analysis of succession in a rocky subtidal community. The American Naturalist **164**:E46-E61.

Hiscock, H. 2008. *Botryllus schlosseri*. Star ascidian. Marine Biological Association of the United Kingdom, Plymouth, UK.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and freshwater research **50**:839-866.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Oxford, UK.

Hughes, T. 2003. Climate change, human impacts, and the resilience of coral reefs. Science **301**:929-933.

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

Hughes, T. P., N. A. Graham, J. B. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. Trends in Ecology & Evolution:1-10.

Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschaniwskyj, M. S. Pratchett, R. S. Steneck, and B. Willis. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology **17**:360-365.

Hyndman, R. 1996. Computing and graphing highest density regions. American Statistician **50**:120-126.

Isbell, F., V. Calcagno, A. Hector, J. Connolly, W. S. Harpole, P. B. Reich, M. Scherer-Lorenzen, B. Schmid, D. Tilman, J. van Ruijven, A. Weigelt, B. J. Wilsey, E. S. Zavaleta, and M. Loreau. 2011. High plant diversity is needed to maintain ecosystem services. Nature **477**:199-202.

Jeffries, C. 1976. Stability of predation ecosystem models. Ecology **57**:1321-1325.

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

Jones, R. 2004. The Albert Dock Liverpool. Ron Jones Associates Limited, UK.

Keith, D. 2009. Red listing: deciding which species are at risk. Significance **6**.

Kirkpatrick, J. B. and M. Fowler. 1998. Locating likely glacial forest refugia in Tasmania using palynological and ecological information to test alternative climatic models. Biological Conservation **85**:171-182.

Kruskal, J. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika **29**:1-27.

Lavine, M. 2010. Living dangerously with big fancy models. Ecology **91**:3487-3487.

Lees, K., S. Pitois, C. Scott, C. Frid, and S. Mackinson. 2006. Characterizing regime shifts in the marine environment. Fish and Fisheries **7**:104-127.

Leslie, L. M., D. J. Karoly, M. Leplastrier, and B. W. Buckley. 2007. Variability of tropical cyclones over the southwest Pacific Ocean using a high-resolution climate model. Meteorology & Atmospheric Physics **97**:171-180.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika **33**:183-212.

Levins, R. 1966. The strategy of model building in population biology. American Scientist **54**:421-431.

Lindenmayer, D. B. and H. P. Possingham. 1996. Modelling the inter-relationships between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum, in south-eastern Australia. Landscape Ecology **11**:79-105.

Liu, J., J. B. Dunning, and H. R. Pulliam. 1995. Potential effects of a forest management plan on Bachman's sparrow (*Aimophila aestivalis*): linking a spatially explicit model with GIS. Conservation Biology **9**:62-75.

Loo, S. E., R. Mac Nally, and P. S. Lake. 2007. Forecasting New Zealand mudsnail invasion range: Model comparisons using native and invaded ranges. Ecological applications **17**:181-189.

Loreau, M. 2010. From populations to ecosystems. Princeton University Press, Oxford, UK.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Science Ltd., London, UK.

Manning, C. D. and H. Schutze. 2002. Foundations of statistical natural language processing. The MIT Press, London, UK.

Massel, S. R. and T. J. Done. 1993. Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: meteorology, hydrodynamics and demography. Coral Reefs **12**:153-166.

MATLAB. 2009. R2009a. The Mathworks Inc., Natick, Massachusetts, USA.

May, R. M. 1974. Biological populations with non-overlapping generations: stable points, stable cyclones, and chaos. Science **186**:645-647.

May, R. M. 1975. Patterns of species abundance and diversity. Pages 81-120 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, London, UK.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature **269**:471-477.

McClanahan, T. R. 1995. A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. Ecological Modelling **80**:1-19.

McClanahan, T. R. 2002. The near future of coral reefs. Environmental Conservation **29**:460-483.

Mieszkowska, N., M. Kendall, S. Hawkins, R. Leaper, P. Williamson, N. Hardman-Mountford, and A. Southward. 2006. Changes in the range of some common rocky shore species In Britain, a response to climate change? Marine Biodiversity **183**:241-251.

Montgomery, D. C. and E. A. Peck. 1982. Introduction to linear regression analysis. Wiley, New York, USA.

Mook, D. 1981. Effects of disturbance and initial settlement on fouling community structure. Ecology **62**:522-526.

Mumby, P. 1999. Bleaching and hurricane disturbances to populations of coral recruits in Belize. Marine Ecology Progress Series **190**:27-35.

Mumby, P., N. Foster, and E. Fahy. 2005. Patch dynamics of coral reef macroalgae under chronic and acute disturbance. Coral Reefs **24**:681-692.

Mumby, P. J., J. D. Hedley, K. Zychaluk, A. R. Harborne, and P. G. Blackwell. 2006. 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.

Newton, M. A. and A. E. Raftery. 1994. Approximate Bayesian inference with the weighted likelihood bootstrap. Journal of the Royal Statistical Society. Series B (Methodological) **56**:3-48.

Nystrom, M. and C. Folke. 2001. Spatial resilience of coral reefs. Ecosystems **4**:406-417.

Osborne, K., A. M. Dolman, S. C. Burgess, and K. A. Johns. 2011. Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995-2009). PLoS One **6**:e17516.

Petraitis, P. S. and S. R. Dudgeon. 2004. Detection of alternative stable states in marine communities. Journal of Experimental Marine Biology and Ecology **300**:343-371.

Power, M. 1993. The predictive validation of ecological and environmental models. Ecological Modelling **68**:33-50.

Raftery, A. E. 1996. Hypothesis testing and model selection. Pages 163-187 *in* W. R. Gilks, S. Richardson, and D. J. Spiegelhalter, editors. Markov Chain Monte Carlo in Practice. Chapman & Hall, London, UK.

Raup, D. M. 1991. A kill curve for Phanerozoic marine species. Paleobiology **17**:37-48.

Regan, H., M. Colyvan, and M. Burgman. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. Ecological applications **12**:618-628.

Renshaw, E. 1995. Modelling biological populations in space and time. Cambridge University Press, Cambridge, UK.

Rosenzweig, M. L. and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. The American Naturalist **97**:209-223.

Roughgarden, J., Y. Iwasa, and C. Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology **66**:54-67.

Rykiel, E. 1996. Testing ecological models: the meaning of validation. Ecological Modelling **90**:229-244.

Sæther, B.-E., S. Engen, R. Lande, C. Both, and M. E. Visser. 2002. Density dependence and stochastic variation in a newly established population of a small songbird. Oikos **99**:331-337.

Scheer, B. 1945. The development of marine fouling communities. Biological Bulletin **89**:103-121.

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

Shelton, A. O. and M. Mangel. 2011. Fluctuations of fish populations and the magnifying effects of fishing. Proceedings of the National Academy of Science of the United States of America. **108**: 7075-7080.

Skellam, J. G. 1951. Random dispersal in theoretical populations. Biometrika **38**:196-218.

Soong, K. and T. Chen. 2003. Coral transplantation: Regeneration and growth of *Acropora* fragments in a nursery. Restoration Ecology **11**:62-71.

Spencer, M. 2006. Sensitivity analysis of Markov models for communities of competing sessile organisms. Journal of Animal Ecology **75**:1024-1033.

Spencer, M., S. N. R. Birchenough, N. Mieszkowska, L. A. Robinson, S. D. Simpson, M. T. Burrows, E. Capasso, P. Cleall-Harding, J. Crummy, C. Duck, D. Eloire, M. Frost, A. J. Hall, S. J. Hawkins, D. G. Johns, D. W.

Sims, T. J. Smyth, and C. L. J. Frid. 2011. Temporal change in UK marine communities: trends or regime shifts? Marine Ecology **32**:10-24.

Spencer, M. and E. Susko. 2005. Continuous-time Markov models for species interactions. Ecology **86**:3272-3278.

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

Sweatman, H., S. Delean, and C. Syms. 2011. Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. Coral Reefs **30**:521-531.

Tanner, J. 1997. Interspecific competition reduces fitness in scleractinian corals. Journal of Experimental Marine Biology and Ecology **214**:19-34.

Tanner, J., T. Hughes, and J. Connell. 1994. Species coexistence, keystone species, and succession: a sensitivity analysis. Ecology **75**:2204-2219.

Tanner, J., T. Hughes, and J. Connell. 1996. The role of history in community dynamics: a modelling approach. Ecology **77**:108-117.

Thackeray, S. J., T. H. Sparks, M. Frederiksen, S. Burthe, P. J. Bacon, J. R. Bell, M. S. Botham, T. M. Brereton, P. W. Bright, L. Carvalho, T. I. M. Clutton-Brock, A. Dawson, M. Edwards, J. M. Elliott, R. Harrington, D. Johns, I. D. Jones, J. T. Jones, D. I. Leech, D. B. Roy, W. A. Scott, M. Smith, R. J. Smithers, I. J. Winfield, and S. Wanless. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology **16**:3304-3313.

Travis, J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society of London. Series B: Biological Sciences **270**:467.

Tufte, E. R. 1993. The visual display of quantitative information. Graphics Press, Cheshire, Connecticut, USA.

Venables, W. N. and B. D. Ripley. 2002. Modern applied statistics with S. 4th edition. Springer, New York, USA.

Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. Nature **118**:558-560.

Wallace, C. C. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. Marine Biology **88**:217-233.

Walsh, K. J. E., K. C. Nguyen, and J. L. McGregor. 2004. Fine-resolution regional climate model simulations of the impact of climate change on tropical cyclones near Australia. Climate Dynamics **22**:47-56.

Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. Beebee, J. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Warwick, R. and K. Clarke. 1993. Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. Marine ecology progress series. Oldendorf **92**:221-231.

Webster, P. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. Science **309**:1844-1846.

White, P. S. and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: An introduction.*in* S. T. A. Picket and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press Inc., Florida, USA.

Wolanski, E., R. Richmond, and L. McCook. 2004. A model of the effects of land-based, human activities on the health of coral reefs in the Great Barrier Reef and in Fouha Bay, Guam, Micronesia. Journal of Marine Systems **46**:133-144.

Wootton, J. T. 2005. Field parameterization and experimental test of the neutral theory of biodiversity. Nature **433**:309-312.

Wootton, J. T. 2004. Markov chain models predict the consequences of experimental extinctions. Ecology Letters **7**:653-660.

Yodzis, P. 2000. Diffuse effects in food webs. Ecology **81**:261-266.