

Lengthening reef recovery times from crown-of-thorns outbreaks signal systemic degradation of the Great Barrier Reef

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ABSTRACT: Repeated outbreaks of crown-of-thorns starfish *Acanthaster planci* have been observed on the Great Barrier Reef (GBR) since the mid 1960s. Several authors have conjectured that long-term degradation of reef community structure is a possible consequence of such repeated outbreaks. In this paper we use the data from the Australian Institute of Marine Science's (AIMS) annual synoptic surveys (1985 to 1996) of the whole GBR as a statistical database with which to investigate this question. We use a simple mathematical model of transition between 3 reefs states—AO (active outbreak in progress), RE (recovering from recent outbreak), and NO (no evidence of a recent outbreak)—which we show is adequate to track the large-scale data over time. A more refined analysis, using Bayesian statistical methods, is then employed to generate a (posterior) probability distribution for a key model parameter, β , which represents the potential for non-stationary, temporal variation in the rate of recovery of reefs from outbreaks. If $\beta = 0$, the rate of recovery is constant, if $\beta < 0$, the rate of recovery increases with time, and if $\beta > 0$, the rate of recovery decreases with time. We conclude from this distribution that there is a clear signal showing that the average reef recovery time is lengthening over the period for which data is available, i.e. $\beta > 0$. We interpret this signal as evidence that it is harder for reefs to recover from outbreaks in later years than in earlier years, other things being equal, indicating that key features of reef community structure have been damaged over time.

KEY WORDS: Crown-of-thorns · Active outbreaks · Reef recovery · Community structure · Reef degradation · Mathematical model · State transition probabilities · Bayesian statistics

INTRODUCTION

In a new study of the crown-of-thorns starfish controversy, Jan Sapp builds a strong argument for its significance as a key event in the recent history of science (Sapp in press). He argues that the outbreaks of this starfish were central to the genesis and evolution of the interaction between the science of ecology and the politics of environmentalism. He goes further and suggests that the emergence of environmental awareness during the 1960s and 1970s can be seen clearly in the struggles between and among scientists, conservationists and politicians as they attempted to ignore, accept,

define and, finally, begin to understand this new phenomenon.

Now that a new series of outbreaks is being reported in the 1990s (Engelhardt & Lassig 1996, Engelhardt 1997), a recurrence predicted by some (Reichelt et al. 1990, Seymour & Bradbury 1992), the need to deepen our understanding of the phenomenon takes on a new significance. The issue has shifted from causes to consequences (Bradbury 1991). The key issue today (Bradbury & Seymour 1997) is not whether the outbreaks are real (as it was in the 1960s), nor whether they are novel (a key issue of the 1970s), nor even whether they are anthropogenic (an issue resolved in the affirmative, we believe [Antonelli et al. 1990], in the 1980s). It is instead: What are the consequences of repeated episodes of outbreaks on the integrity—the 'complex-

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ity'—of reef ecosystems (Cameron & Endean 1985, Bradbury et al. 1996, Hatcher 1997)? Regardless of the cause, the contingent fact of repetition forces us to consider the consequences.

This issue is particularly critical on Australia's Great Barrier Reef (GBR). As a predator of hermatypic or reef-building corals, the crown-of-thorns starfish *Acanthaster planci* Linnaeus 1758 is a widely distributed, though often rare, member of Indo-Pacific coral reef communities, including the GBR. While outbreaks of the starfish, together with serious destruction of the living coral cover on infested reefs, have been reported throughout the region since the early 1960s, the GBR has been particularly affected (Moran 1986). It has suffered 3 widespread outbreak episodes since the mid-1960s (Seymour & Bradbury 1992), and a fourth episode, which our models successfully predicted, is now under way (Bradbury & Seymour 1997).

Our earlier work on the outbreaks of the crown-of-thorns starfish on the GBR (Seymour & Bradbury 1992, 1994) clearly shows the dynamics to have 2 interesting properties: each successive outbreak episode is involving a smaller proportion of reefs than before, and the outbreaks are more or less synchronous throughout the system. Each of these properties suggests that the GBR is undergoing some sort of degradative change. That the first, the declining proportion of infested reefs, is a signal of degradation may seem counterintuitive until it is appreciated that it represents a declining ability of reefs to host an outbreak. This is surely a measure of degradation. The second, synchronicity, has been strongly associated in modelling studies with chronic infestations and degradation (Bradbury et al. 1990, van der Laan & Bradbury 1990, van der Laan & Hogeweg 1992). Together they paint a picture of systemic decline as a response to repeated outbreak episodes.

The question of whether this conclusion—systemic degradation as the key consequence of repeated starfish outbreaks—is sustainable under further analysis is confounded by the problem of the outbreak data. Any analysis of the nature of outbreaks themselves needs to derive from a subtle understanding of the nature of the data upon which the analyses depend.

Starfish outbreaks are difficult to observe. They are intensely local phenomena, yet widely scattered over spatial scales of hundreds to thousands of kilometres and time scales of years to decades. While it is relatively straightforward to gather information about the dynamics of outbreaks within any one reef (with spatial scales of tens to hundreds of metres and time scales of weeks to months), gaining synoptic data of the dynamics of outbreaks at the scale of the whole GBR has proved to be logistically difficult.

As a result of these difficulties, there have only been organised synoptic surveys of the GBR since 1985,

when the Australian Institute of Marine Science (AIMS) initiated a major program of systematic annual synoptic surveys of the whole GBR, typically involving more than 100 reefs per year. However before 1985, the surveys were neither systematic nor synoptic, but rather sparse, opportunistic and responsive. Nonetheless, these imperfect early observations comprise all our historical empirical knowledge of the outbreak dynamics since they cover all of the first 2 episodes and much of the third. Indeed, in a strong sense, these data are the phenomenon, since we have no other way but through such historical documents to understand the past (Collingwood 1961).

Essentially, these synoptic data are 'million dollar' data points. Not only do they deserve to be carefully accumulated and critically assessed using modern principles of 'data mining' (Fayyad et al. 1996), but they also deserve to be thoughtfully analysed. A summary of the present benchmark historical dataset (1966 to 1989) was published as an appendix in Reichelt et al. (1990), and it has served as the basis of a series of analyses by ourselves and others to 'squeeze' as much understanding as possible from these important observations (Antonelli et al. 1989, Bradbury & Mundy 1989, Reichelt et al. 1990, Moran et al. 1992).

We are presently reassessing all the historical data using modern 'data mining' principles, and plan to create a new benchmark historical dataset and to make it freely available through the World Wide Web.

In this paper, we forgo analysis of the full dataset in favour of an analysis of the synoptic post-1985 data. We wish to explore the nature of the degradation of the GBR, and for this we need the richer data from the AIMS surveys, which include the most reliable information on recovering as well as outbreaking and normal reefs. While recognising that there are many factors at work in structuring reef communities, we are particularly interested to examine if the data contain a signal at the scale of the whole GBR of the responses (either predicted or empirically measured) at the scale of individual reefs to repeated starfish outbreaks. These within-reef studies have suggested that the community structure is affected by repeated outbreaks, through a loss of long-lived (major) coral species that build the reef framework or architecture (i.e. architectural species), resulting in progressively longer recovery periods for reefs (Done et al. 1988, Endean et al. 1988). If this were so, it would provide a proximate cause for the growing inability of individual reefs to 'host' outbreaks. We would also expect this individual-reef effect to be reflected at the synoptic scale in lengthening recovery times for the GBR as a whole, and our analysis, based on a simple model of transitions between reef states, is designed to reveal this phenomenon, if present.

THE MODEL

The available survey data, collected by the Australian Institute of Marine Science (AIMS) over many years, comes in the form of annual estimates of the states of a sample of reefs from the whole of the GBR (Oliver et al. 1995). The most reliable data, collected over the last decade or so, and which we shall use in conjunction with our model, designates each reef sampled as being in 1 of 3 mutually exclusive states: AO, *active outbreak*, indicating that the reef is currently undergoing an outbreak of crown-of-thorns starfish; RE, *recovering*, indicating that the reef has recently experienced an outbreak from which it is currently recovering; NO, *no outbreak*, indicating that the reef has either never experienced an outbreak, or, as far as can be ascertained, has completely recovered from any previous outbreaks. This classification of reef status has been used in many previous analyses (Moran & De'ath 1992, Seymour & Bradbury 1992, 1994, Bradbury & Seymour 1997).

For a given year, let a , x and y denote the *proportions* of all reefs in the GBR which are AOs, REs and NOs, respectively. Clearly, $y = 1 - a - x$, so that only the AO and RE proportion variables, a and x , are independent. These proportions will change (slowly) from year to year, and we write a_t and x_t to denote the proportions of AOs and REs in year t . Here, and in the following, t denotes time, measured in years, and is always taken to be a whole number. The model we shall investigate describes how the proportion of REs in year $t + 1$ depends on the state of the system in year t , and has the form

$$x_{t+1} = q a_t + (1 - p_t)x_t \quad (1)$$

Here, q is the probability of a reef transition from AO to RE in 1 yr, and p_t is the probability of a transition from RE to NO between years t and $t + 1$. Implicit in Eq. (1) is the assumption that reefs have to be in the NO state to be susceptible to outbreaks; that is, there are no (significant) transitions from RE to AO. This apparently strong assumption simply asserts that recovering reefs do not have enough food on them to host a significant starfish population, an assumption that appears to be justified for the GBR (Bradbury et al. 1985, Moore 1990).

We assume further that q is constant (independent of t) because of its dependence on properties of starfish populations. In fact, outbreaks appear to form and disperse over relatively short time periods, lasting a few years at most, and are usually found to consist of a single age and size cohort, which matures in unison, consumes a large proportion of coral on a reef and then (presumably) dies (Moran 1986, also cf. Seymour & Bradbury 1992). We therefore take it that q depends on relatively constant features of starfish life history.

The more significant, and possibly time-dependent, transition probability, p_t , represents the rate of recov-

ery of reefs after an outbreak. If p_t decreases as t increases, then reefs which have suffered outbreaks more recently are taking longer (on average) to recover (i.e. revert to the pristine NO state) than reefs which experienced outbreaks further in the past. The reverse is true if p_t is increasing with t , and there is no effect either way if p_t is constant. To capture these ideas in a simple and tractable way, we assume that p_t has the 2-parameter form

$$p_t = \frac{\alpha}{1 + e^{\beta t}} \quad (2)$$

with $0 \leq \alpha \leq 1$, and β any real number. Here, α represents the overall scale of the recovery rate, and β its potential for change over time. The restriction of α to the range between 0 and 1 is necessary to constrain the probability p_t to lie in this range for all positive times t and all possible values of β . Graphs of p_t for $\alpha = 1$ and various values of β are shown in Fig. 1. Thus, when β is positive, p_t is decreasing as t increases, and when β is negative, p_t is increasing. Note that the graphs are symmetrical between β and $-\beta$. This feature is the main reason for choosing the form of Eq. (2), because p_t has no intrinsic bias between positive and negative values of β .

In addition to the variables a and x , the model defined by Eqs. (1) & (2) contains 3 exogenous parameters, q , α and β . Our aim is to use the available data to estimate these parameters, and in particular to determine whether or not β is positive. If so, then reefs are not recovering as fast as they used to from the effects of starfish outbreaks.

Of course, the model defined above is very simple, certainly oversimple. In particular, 'recovery' is an extended process over time, taking many years, yet the class of recovering reefs is treated in the model as homogeneous in any one year, irrespective of the distribution of recovery histories within this class. How-

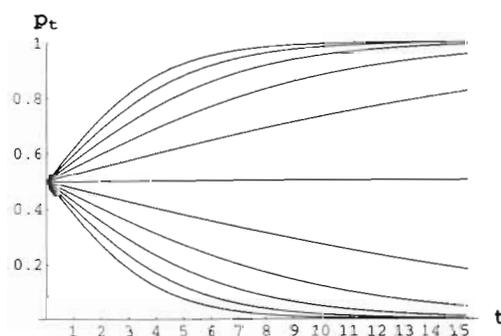


Fig. 1. The curve p_t defined by Eq. (2) for $\alpha = 1$ and various values of β , in the range $0 \leq t \leq 15$. The upper (concave) curves are $\beta = -0.05, -0.1, -0.15, -0.2$, and -0.25 (bottom to top), and the lower (convex) curves are $\beta = 0.05, 0.1, 0.15, 0.2$ and 0.25 (top to bottom). The horizontal line is $\beta = 0$

ever, we are obliged to make this simplification due not only to the lack of relevant, specific, detailed information on recovery histories, but also to the shortness of the available data time series, which makes it imperative to keep the number of undetermined model parameters as low as possible. The time-dependence of p_t is one of the prices we pay for this simplification. Nevertheless, since the model variables, and the data we use, are 'averaged out' by taking proportions over the whole GBR, there will always be some (idealised) year-on-year transition probabilities between reef states, whatever the real time scale over which recovery occurs. Local effects will certainly be episodic and variable, but the model we have defined is suitable only for analysing smoothed-out effects at the scale of the whole GBR. Our first priority therefore will be to show that our simple model is indeed adequate to represent the data at this scale.

ANALYTICAL STRATEGY

The AIMS data come in the form of a sequence of triples, (A_t, R_t, Σ_t) , with Σ_t the number of reefs sampled over the whole GBR in year t , A_t the number of these in

state AO, and R_t the number in state RE (and $\Sigma_t - A_t - R_t$ the number in state NO). Such data exist for the 11 yr from 1985 to 1996, with sample sizes ranging from 85 reefs (in 1992) to 264 reefs (in 1985) and an average sample size of 137 reefs. We set $t = 0$ in 1985, so that data exist for $0 \leq t \leq 10$. We therefore have sequences of data-derived (as opposed to model-derived) proportions, $\hat{a}_t = A_t/\Sigma_t$, and $\hat{x}_t = R_t/\Sigma_t$, corresponding to the model variables a_t and x_t in Eq. (1). The raw data sequences \hat{a}_t and \hat{x}_t are shown in Fig. 2.

Our aim is to use this data to estimate the parameters q , α and β in the model defined by Eqs. (1) & (2). However, as it stands, the model specifies an updating rule for x_t , but does not specify such a rule for the a_t variable. Though it would be easy in principle to write down such a rule, this would involve further assumptions about time dependence in transition probabilities, and the introduction of yet more unspecified parameters. Furthermore, realistic assumptions are likely to be complicated (see Seymour & Bradbury 1992 for a model using just the AO variable and data). Since the length of our chosen data set is limited, we refrain from the introduction of yet more parameters.

Instead, we adopt a 2-part strategy. First a preliminary, but naive, exploration of the fit of the model to the data. This analysis is naive in the sense that it accepts the data at face value, that is, as a true representation of 'reality', give or take some unspecified, presumably normally distributed, random errors. The main conclusion we draw from this analysis is that our simple model is, *prima facie*, adequate to track the data very closely. Without this conclusion, our model could be rejected without further analysis.

However, this naive analysis is, on its own, insufficient to provide clear answers to the questions we wish to address. The ranges of values of the model parameters which fit the data very well are simply too great to yield unambiguous conclusions. Further, we know from other work that a more serious analysis must confront the nature of the uncertainty inherent in the data, rather than consign it to unanalysed random error terms, in the hope that the usual parametric assumptions about such errors are reasonable. Thus, in the second part of our strategy we develop a more sophisticated Bayesian analysis, which explicitly models the effects of possible uncertainties in the data (Howson & Urbach 1991, Seymour & Bradbury 1994). Of course, the price to be paid for Bayesianism is the abandonment of the pretence that the probability distributions underlying our statistical analysis are objective features of Nature and, instead, the recognition, through the explicit use of prior probabilities, that we are really analysing our own (collectively subjective) uncertainty about the state of the world, both before and after data are brought to bear. Our prior assumption (before tak-

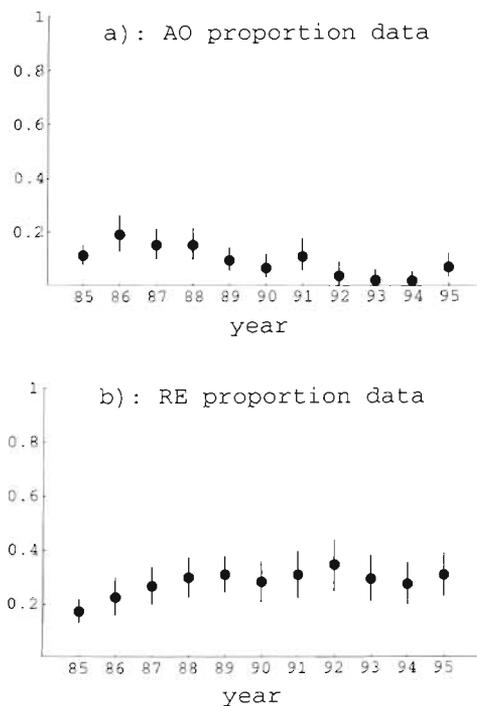


Fig. 2. (a) AO proportion data, $\hat{a}_t = A_t/\Sigma_t$, in each of the years 1985 to 1995. (b) RE proportion data, $\hat{x}_t = R_t/\Sigma_t$, in each of the years 1985 to 1995. The marked intervals are the minimal Bayesian 95% confidence intervals, based on the data, in which the true proportions lie with probability 0.95. See Appendix 1 for explanation and derivation

ing account of the data) is that we have no basis on which to distinguish between models of the form we consider. In particular, *a priori* we are neutral between positive and negative values of the key parameter β . A positive value implies that the probability with which an individual reef makes the transition between the RE state (recovering) and the NO state (recovered) is decreasing with time, and hence that the set of reefs comprising the systems of the GBR is taking longer on average to recover. Similarly, a negative value implies that this probability is increasing and that, on average, reefs in the GBR are recovering more quickly. Our aim then is to generate a clear (posterior) signal from the data as to the likely sign (positive, negative or zero) of β .

PRELIMINARY EXPLORATION

We begin with the simplest possible approach, and take the AO data at face value by setting $a_t = \hat{a}_t$. That is, the true value of the model variable a_t is assumed to be given by its data-derived analogue, \hat{a}_t . If we now specify the quadruple $M = (x_0, q, \alpha, \beta)$, then the model defined by Eqs. (1) & (2) generates a sequence of values $x_t, t \geq 0$, which can be compared with the data-derived analogues \hat{x}_t . We refer to the quadruple M as a *model specification*.

It is important to note that we do *not* take the initial point x_0 from the data, but regard it as a model parameter to be determined from the data by a best-fit algorithm. Taking x_0 from the data would have assigned a special significance to this data point, and thereby to a particular (arbitrary) point in time. Leaving x_0 open to be determined by the data means that equal weight can be given to all points along the time series.

To simplify the situation still further, we fix the value of q (necessarily between 0 and 1, since it is a probability), and then obtain the remaining parameters, x_0, α and β , by a least-squares fit of the model to the RE data. We repeat this procedure for various different values of q , sampling the whole allowable range. The results are shown in Fig. 3, and a typical fit of the model to the RE data is shown in Fig. 4.

Although the model apparently fits the data well, as shown in Fig. 4, this is true for most values of q in the range 0 to 1. Further, the statistics of these fits, as represented by the percentage variance accounted for by the model, R^2 (Fig. 3c), is high for all values of q greater than about 0.2, and is rather insensitive to variation in q above this level. However, the best-fitting model, as indicated by R^2 , occurs when $q \approx 0.25$, which is in the region of the large discontinuity in the value of the decay rate, β (Fig. 3b), which jumps from positive to negative around this value. Since our aim is to use the

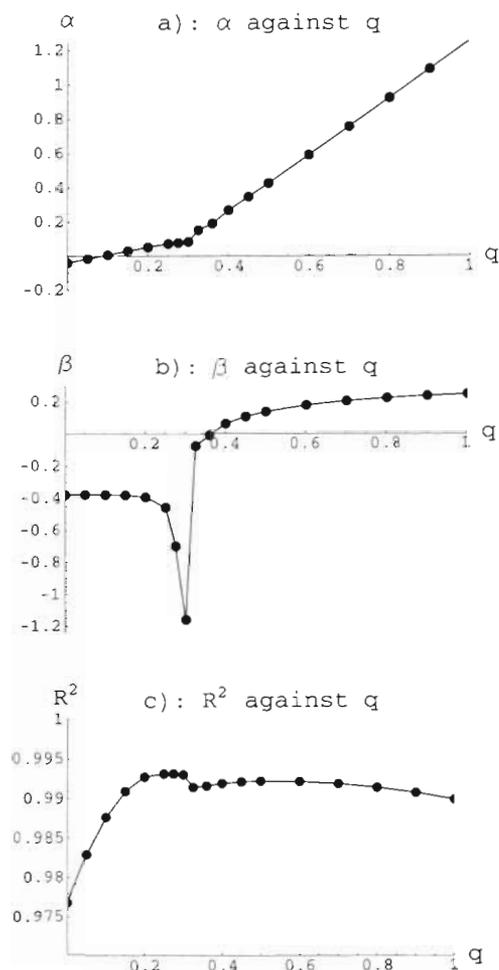


Fig. 3. (a) Amplitude α in Eq. (2) for various values of the AO \rightarrow RE transition probability q in Eq. (1) between 0 and 1 (b) 'Decay rate' β in Eq. (2), plotted against the same values of q . (c) Proportion of variance accounted for by the model, R^2 , plotted against the same values of q

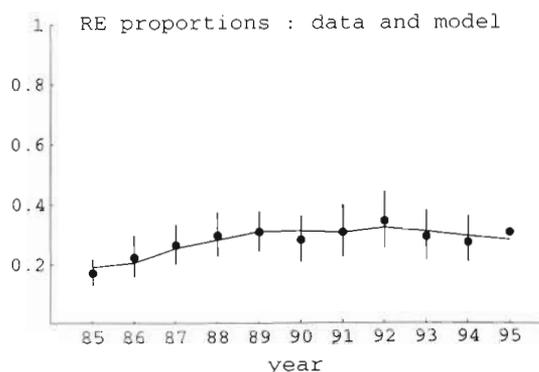


Fig. 4. Typical least-squares fit of the model defined by Eqs. (1) & (2) (solid curve) to the RE proportion data (●). This fit has $q = 0.3$. The 95% confidence limits are the minimal Bayesian limits for the RE data (see Appendix 1)

data to decide whether the decay rate is positive or negative, we have to concede that the naive analysis presented above is inconclusive. Nonetheless, it has shown that the underlying model form given by Eqs. (1) & (2) offers an adequate representation of the data. However, for the model to yield significant insights, we need to adopt a more sophisticated approach to matching the model and dataset.

BAYESIAN ANALYSIS

We shall adopt instead a more sophisticated approach, based on Bayesian statistics as developed in Seymour & Bradbury (1994), which we now describe.

As before, we suppose a fixed sequence of AO values, which could, but need not necessarily, be provided by the data. As above, we consider models $M = (x_0, q, \alpha, \beta)$, defined by sample values for each parameter. Thus, by definition, each of x_0 , q and α must lie between 0 and 1, and we choose a set of 21 equally spaced values in this range, namely

$$A = \{0, 0.05, 0.1, 0.15, \dots, 0.95, 1\} \quad (3)$$

to act as representative sample values for each of these parameters. In contrast, β can, in principle, take any real value. However, we can only reasonably expect a *small* tendency in p_t to increase or decrease with t , and therefore we anticipate a correspondingly small value of β . This expectation is largely borne out by the preliminary analysis summarised in Fig. 3, in spite of the jump to large negative values of β at $q \approx 0.3$. In fact, for large values of β , p_t essentially attains a constant value very fast, so that, for example, $p_t = c$ (a constant) can be realised either by taking $(\alpha, \beta) = (2c, 0)$ in Eq. (2), i.e. with small β , or by taking $(\alpha, \beta) = (c, -\infty)$, i.e. with large β . The expectation is also borne out in the broader biological context. Field teams have never reported large year-to-year changes in the rate of reef recovery, not even anecdotally. Thus, since very rapid change, followed by near constancy, seems biologically implausible—particularly in view of the fact that our ‘year zero’ is arbitrarily chosen by the availability of data, rather than because it has any particular biological significance—we shall constrain β to lie in a fairly tight range around $\beta = 0$, and take as sample values the set of 21 possibilities

$$B = \{0, \pm 0.05, \pm 0.1, \pm 0.15, \dots, \pm 0.5\} \quad (4)$$

These values are chosen so that p_t does not reach more than 90% of its asymptotic value until t is at least 5 (halfway along the data set), thereby ruling out very rapid initial change.

Our chosen sample values from the sets A and B allow each of the model parameters to vary in multi-

ples of 0.05. Thus, the points $M = (x_0, q, \alpha, \beta)$ in the set $\mathbf{M} = A \times A \times A \times B$ define a set of $21^4 = 194481$ model specifications. This is the model ‘universe’ we shall investigate, under the assumption that reality is reasonably well described within it. In order to remain neutral with respect to any possible outcome of a particular survey, we assume as a *prior hypothesis* that each of these models carries equal probability. These assumptions about our prior knowledge of system behaviour—that reality is embedded somewhere in the model universe, and that we have no prior knowledge as to where in this universe reality is to be found—now set the scene for our Bayesian analysis.

Thus, if $P(M)$ is the prior probability for the model M , then $P(M) = 1/21^4$. It follows that the prior probability that $\beta > 0$, which is equal to the prior probability that $\beta < 0$, is $\frac{1}{2}(1 - P_0)$, where P_0 is the prior probability that $\beta = 0$, i.e. $P_0 = 21^3 \times 1/21^4 = 1/21 = 0.047619$ (there are 21^3 models with $\beta = 0$ in M , each of which carries prior probability $1/21^4$). Thus,

$$P(\beta > 0|\emptyset) = P(\beta < 0|\emptyset) = \frac{1}{2}\left(1 - \frac{1}{21}\right) = 0.476191 \quad (5)$$

where the notation $P(H|\emptyset)$ denotes the probability of the hypothesis H conditional on no evidence (i.e. the prior probability).

The evidence, on the basis of which the posterior probabilities are calculated, is in the form of a sequence of survey data, $\mathbf{E} = (E_0, E_1, \dots, E_{10})$, covering the 11 years from 1985 to 1996, with $E_t = (A_t, R_t, \Sigma_t)$ the data for year t . The posterior probability for the model M is denoted by $P(M|\mathbf{E})$, and is calculated in Appendix 1 [see Eqs. (A1), (A2) and (A3)]. Thus, if \mathbf{m} is the subset of \mathbf{M} consisting of those models for which $\beta > 0$, the posterior probability for the hypothesis $\beta > 0$ is

$$P(\beta > 0|\mathbf{E}) = \sum_{M \in \mathbf{m}} P(M|\mathbf{E}) \quad (6)$$

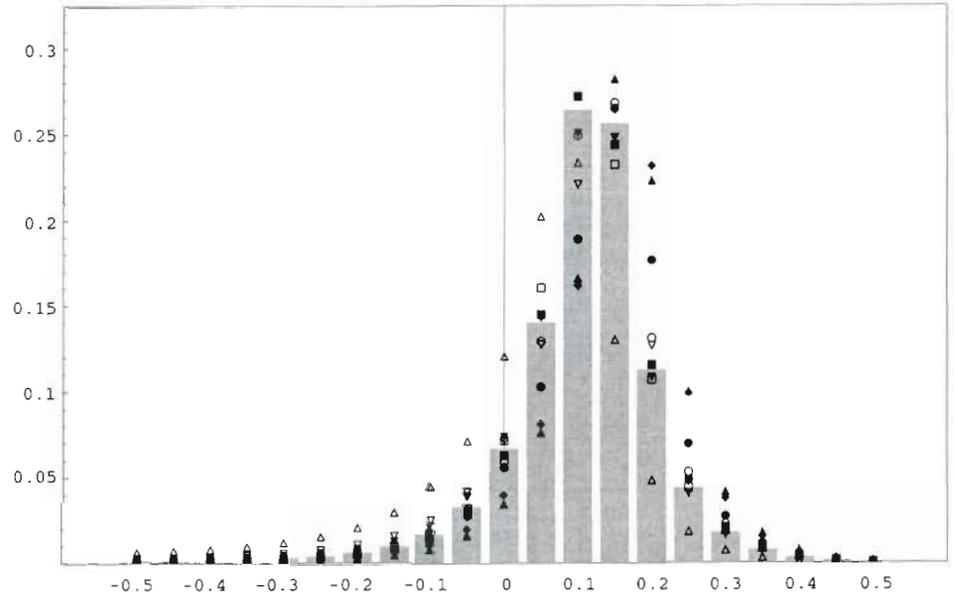
with similar formulae for the posterior probabilities, a $P(\beta < 0|\mathbf{E})$ and $P(\beta = 0|\mathbf{E})$. That is, to obtain the aggregate posterior probability, we merely sum the posterior probabilities for models in the relevant part of the universe. From Eqs. (5) & (6) we then obtain the *proportional increase in certainty* for the hypothesis $\beta > 0$, provided by the evidence

$$\begin{aligned} PU(\beta > 0|\mathbf{E}) &= \frac{P(\beta > 0|\mathbf{E}) - P(\beta > 0|\emptyset)}{P(\beta > 0|\emptyset)} \\ &= 2.1 \times P(\beta > 0|\mathbf{E}) - 1 \end{aligned} \quad (7)$$

If this quantity is positive, then the evidence has increased our confidence in the hypothesis; if negative, it has decreased our confidence. Note that, since $P(\beta > 0|\mathbf{E})$ lies between 0 and 1, $PU(\beta > 0|\mathbf{E})$ lies between -1 and 1.1 .

So far, we have assumed a fixed sequence of AO values, $\mathbf{a} = (a_0, a_1, \dots, a_{10})$; for example, the values obtained

Fig. 5. Marginal posterior probability distribution, $P(\beta|\mathbf{E})$, defined in Eq. (6). The vertical bars give this distribution for the modal universe, $\mathbf{M}(\hat{\mathbf{a}})$, and the various symbols give the distributions for the other 10 universes, $\mathbf{M}(\mathbf{a})$, with randomly chosen \mathbf{a} (see text for explanation)



from the survey data, $\hat{a}_t = A_t/\sum_t$. However, our basic philosophy, which motivates the Bayesian approach, is that we should not take the survey data too literally as a reflection of the underlying reality, but take account of the possibility that the *actual* values of the a_t may differ from the observed values \hat{a}_t . We do this by constructing, for each t , a (marginal) posterior Bayesian probability distribution (with mode \hat{a}_t), for the possible values of a_t , and using this distribution to obtain an optimal 95% confidence limit for these values [see Appendix 1, Eqs. (A6) & (A7)]. These limits provide reasonable restrictions within which we may look for alternative values for the a_t . Nevertheless, although these limits are obtained using the survey evidence (with a uniform distribution of values for each a_t assumed as prior), and are in that sense posterior, we actually want our chosen values of each a_t to be prior (they are an integral feature of the underlying model universe). For this reason we take random values from a *uniform* distribution over each such confidence interval. The only reason for bothering with the confidence limits at all (we could, and in principle should, have chosen the a_t from a uniform distribution over the *whole* interval between 0 and 1) is to cut down on the amount of unproductive computation involving very unlikely values of the AO proportion variables, far from the modal

values \hat{a}_t . In this way, we allow for the uncertainty in the AO data (by sampling over some interval), but acknowledge that this uncertainty is in practice constrained (by restricting the size of the interval).

The upshot of the above discussion is that we can now introduce a degree of flexibility in our choice of the (fixed) AO sequence \mathbf{a} on which our model universe \mathbf{M} is built. In fact, we have a model universe, $\mathbf{M}(\mathbf{a})$, corresponding to any given choice of \mathbf{a} , and we can obtain posterior probabilities, and proportional increases in certainty, Eqs. (6) & (7), within each such universe. In particular, we can use the *modal* universe, $\mathbf{M}(\hat{\mathbf{a}})$. To check the robustness of conclusions obtained from this modal universe, we construct several other universes, $\mathbf{M}_k = \mathbf{M}(\mathbf{a}_k)$, $1 \leq k \leq K$, with \mathbf{a}_k obtained by randomly sampling the 95% confidence limits in each year, as described above. If we obtain consistency in our conclusions over such a set of universes, then we can be more confident that these conclusions are correct. We take $K = 10$ in the following.

The result of our analysis is summarised in Fig. 5, which shows the marginal posterior probability distributions, $P(\beta > 0|\mathbf{E})$, for various universes, $\mathbf{M}(\mathbf{a}_k)$, for $0 \leq k \leq 10$, with $\mathbf{M}(\mathbf{a}_0) = \mathbf{M}(\hat{\mathbf{a}})$, the modal universe. The values of $P(\beta > 0|\mathbf{E})$, and the corresponding $PU(\beta > 0|\mathbf{E})$ —see Eqs. (6) & (7)—are listed in Table 1.

Table 1. Values of $P = P(\beta > 0|\mathbf{E})$ and $PU = PU(\beta > 0|\mathbf{E})$ for the various model universes, $0 \leq k \leq 10$, illustrated in Fig. 5, listed in decreasing order, with $k = 0$ the modal universe, which also has the highest values of P and PU

	$k:$	0	1	2	3	4	5	6	7	8	9	10
P		0.88	0.82	0.82	0.79	0.76	0.74	0.73	0.69	0.66	0.66	0.56
PU		0.84	0.72	0.72	0.65	0.60	0.56	0.53	0.45	0.38	0.38	0.18

Note that all the *PU* values in Table 1 are positive, showing that, essentially independently (within limits) of what the AO sequence actually is, the evidence increases our certainty that $\beta > 0$, and quite considerably in most model universes, in particular in the modal universe. This is strong evidence that, if our models capture the relevant features of reality, then indeed there is good reason to believe that the recovery time for reefs has increased over the past decade or so.

DISCUSSION

It was recognised by some authorities from the beginning of scientific attention to the phenomenon of crown-of-thorns starfish outbreaks on the GBR that these outbreaks had the potential to cause serious damage to the reef structure (Endean 1969). However, it remained the considered view of many (perhaps most) experts that any threat was likely to be short term only. Thus, the Crown of Thorns Advisory Committee reflected a widespread view among scientists when it concluded that 'The destruction of hard coral by aggregations of *A. planci* poses a serious threat to the organisation and functional relationships within some reef communities within the Great Barrier Reef, at least in the short term.' (Back 1985, p 1). However, Done et al. (1988) and Endean et al. (1988) provided field data to support the hypothesis that long-lived, slow-growing massive corals may not recover their earlier abundances in the relatively short intervals between outbreak episodes, and that this may lead to long-term changes in reef community structure.

It is this hypothesis—that long-term degradation of reef community structure is occurring—which we have investigated in this paper using a simple mathematical model of transition between reef states (see 'The model') together with AIMS survey data over an **11 yr period from the mid 1980s**. Our Bayesian statistical approach has been specifically designed to take account of the impressionistic and uncertain nature of these data, but nevertheless is based on the assumption that the AIMS surveys, in any one year, are random trials over the whole GBR (cf. Seymour & Bradbury 1992, 1994).

The results show that our model is adequate to track this data sequence, at least in a qualitative sense (see 'Preliminary exploration'), and hence that it is reasonable to assume that the class of models of the sort we consider contains an accurate reflection of reality. Our Bayesian analysis generates a posterior probability distribution for values of the parameter β over the class of models we consider (Fig. 5), derived from the survey evidence. This distribution shows a clear bias in favour of positive β , which is, crucially, insensitive to variations

in the other components of the model. The existence and robustness of this positive bias therefore provide strong evidence that reefs are recovering with lower frequency in later years than in earlier years.

This is counterintuitive for 2 reasons. First, it might be expected that there would be more reefs in the later stages of recovery in recent years than there were in earlier years, because the wave of outbreaks under consideration seems to have begun around 1980. This should mean that fewer RE \rightarrow NO transitions were occurring in earlier years than in later years. Second, one of the key findings of our earlier work (Seymour & Bradbury 1992, 1994) was that the extent of crown-of-thorns outbreaks has generally decreased since the mid 1980s—i.e. the proportion of reefs in the AO (active outbreak) state has declined—a period which contains the data sequence considered in this paper. Thus, we would expect that reefs which were making the transition RE \rightarrow NO early in the sequence had suffered their outbreaks at a time of higher overall outbreak activity, and hence had been exposed to a higher probability of multiple attacks from nearby foci. Such multiple attacks would cause greater damage to reefs, and should make the RE \rightarrow NO transition more difficult (less probable). In contrast, a reef making the transition RE \rightarrow NO in later years should have had less likelihood of suffering multiple attacks, thereby making the RE \rightarrow NO transition easier. Nevertheless, it is always possible that the bout of faster recoveries early in the data sequence was merely episodic, perhaps stemming from a cohort of more or less synchronously recovering reefs from an earlier peak of outbreak activity.

However, these intuitive considerations depend on the recovery phase being comparatively short, and we have little knowledge of this process. The thrust of most studies at the individual reef level is that reefs recover in terms of living coral cover and density of colonies in 10 to 15 yr (Pearson 1981, Moran 1986). Consistent with this, but based on synoptic survey data for the entire central sector of the GBR, Seymour & Bradbury (1992) estimate a period of approximately 12 yr for short-term recovery. This time scale is thought to depend on *Acanthaster planci*'s preference for faster-growing coral species such as *Acropora* spp. and *Pocillopora* spp. (Moran 1986, De'ath & Moran 1998). In any case, this short-term recovery time is longer than our data sequence. However, the consensus concerning recovery of species richness is more equivocal, mainly because the data are lacking. Such characteristics as colony size structure, rates of reproduction and growth, species composition and diversity are all imperfectly known (Connell 1997). Done et al. (1988) point out that, while the recovery of coral cover (mainly through the rapid growth of *Acropora* spp.) can be accommodated within a 10 to 15 yr time frame, the re-

covery of slower-growing massive corals (such as *Porites* spp.) could take centuries, in worst case scenarios of total kills, to 'one to several decades' when remnant colonies remain. Thus, our 'counterintuitive' result is consistent with the action of a longer-term process, in which the role of slow-growing, longer-lived taxa is probably crucial, progressively undermining the capacity of reefs to recover from starfish outbreaks. Such a process might involve changes in the species

composition (Cameron & Endean 1985, Done et al. 1988, Endean et al. 1988) or changes in other ecosystem level components (Bradbury et al. 1996, Hatcher 1997) of reefs suffering repeated outbreaks.

We conclude that, in spite of the relative shortness of the time-series we consider, our analysis, taken in conjunction with other studies, provides further evidence for long-term degradation of reef community structure at the scale of the whole Great Barrier Reef.

Appendix 1

Suppose given a model specification, $M = (x_0, q, \alpha, \beta)$, in the sense given in the sections 'Preliminary exploration' and 'Bayesian analysis', and also the actual AO proportion values for a sequence of years, $\mathbf{a} = (a_0, a_1, \dots, a_{T-1})$. The model defined by Eqs. (1) & (2) then generates a sequence of model values for the RE proportion variable, $\mathbf{x} = (x_0, x_1, \dots, x_{T-1})$. Let $E_t = (A_t, R_t, \Sigma_t)$ be the survey evidence for year t , where Σ_t is the number of reefs sampled, A_t the number of these in state AO, and R_t the number in state RE. Assuming that \mathbf{a} and \mathbf{x} represent the true situation, the probability of obtaining the survey evidence E_t in year t is given by the multinomial distribution

$$P(E_t|M) = \binom{\Sigma_t}{A_t, R_t} a_t^{A_t} x_t^{R_t} (1 - a_t - x_t)^{\Sigma_t - A_t - R_t} \quad (A1)$$

where $\binom{\Sigma}{A, R} = \Sigma! / A! (\Sigma - A - R)!$ is the usual multinomial coefficient. If $\mathbf{E} = (E_0, E_1, \dots, E_{T-1})$ is the sequence of survey evidence for the T years, we have therefore

$$P(\mathbf{E}|M) = \prod_{t=0}^{T-1} P(E_t|M) \quad (A2)$$

Suppose \mathbf{M} is the (finite) 'universe' of models under consideration (see 'Bayesian analysis'), then we may apply Bayes' Theorem (Howson & Urbach 1991) to obtain

$$P(M|\mathbf{E}) = \frac{P(\mathbf{E}|M)P(M)}{\sum_{L \in \mathbf{M}} P(\mathbf{E}|L)P(L)} = \frac{P(\mathbf{E}|M)}{\sum_{L \in \mathbf{M}} P(\mathbf{E}|L)} \quad (A3)$$

where $P(M|\mathbf{E})$ is the posterior probability that the model M is the correct one, conditional on the evidence \mathbf{E} , and $P(M)$ is the prior probability for M , which is the same for each M and equal to $1/21^4$ (see 'Bayesian analysis').

We now consider confidence limits (cf Seymour & Bradbury 1992, appendix therein). Consider the hypothesis, $H_{\xi, \eta}$, that the AO proportion variable a (in a given year) lies in the

interval $[\xi, \xi + d\xi]$, and the RE proportion variable x (in the same year) lies in the interval $[\eta, \eta + d\eta]$. For survey evidence $\mathbf{E} = (A, R, \Sigma)$, we have

$$P(\mathbf{E}|H_{\xi, \eta}) = \binom{\Sigma}{A, R} \xi^A \eta^R (1 - \xi - \eta)^{\Sigma - A - R} + O(d\xi + d\eta)$$

Taking a uniform prior probability density, $p(H_{\xi, \eta}) = d\xi d\eta$, for the hypothesis $H_{\xi, \eta}$, we obtain, from Bayes' Theorem, the posterior probability density

$$p(H_{\xi, \eta}|\mathbf{E}) = P(\mathbf{E}|H_{\xi, \eta}) / \int_0^1 \int_0^1 P(\mathbf{E}|H_{u, v}) du dv = (\Sigma + 1)(\Sigma + 2) \binom{\Sigma}{A, R} \xi^A \eta^R (1 - \xi - \eta)^{\Sigma - A - R} + O(d\xi + d\eta) \quad (A4)$$

The marginal posterior probability density for the AO proportion variable can now be obtained from (A4),

$$p(H_{\xi, \cdot}|\mathbf{E}) = \int_0^{1-\xi} p(H_{\xi, \eta}|\mathbf{E}) d\eta = (\Sigma + 2) \binom{\Sigma + 1}{A} \xi^A (1 - \xi)^{\Sigma + 1 - A} \quad (A5)$$

It is the density (A5) which we use to compute 95% confidence limits for the AO proportion data, with $\mathbf{E} = E_t$ in year t . The optimal confidence interval, (ξ_0, ξ_1) —optimal in the sense that, amongst all possible such confidence intervals, it is the one which has minimum length—is obtained by solving the equations,

$$\int_{\xi_0}^{\xi_1} p(H_{\xi, \cdot}|\mathbf{E}) d\xi = 0.95 \quad (A6)$$

$$\xi_0^A (1 - \xi_0)^{\Sigma + 1 - A} = \xi_1^A (1 - \xi_1)^{\Sigma + 1 - A} \quad (A7)$$

(cf Seymour & Bradbury 1992, appendix therein). It is these confidence intervals which are used in the construction of the random AO sequences, \mathbf{a}_k , $1 \leq k \leq K$, discussed in 'Bayesian analysis'. Similar confidence intervals may be obtained from the marginal posterior distributions for the RE proportion data. These intervals are shown in Figs. 2 & 4.

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