

Precursors for resilience in coral communities in a warming climate: a belief network approach

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Marine Ecology Progress Series 295:157–169 (2005)

Appendix 1. Network linking functions

BLEACHING EVENT GENERATION

We modelled the arrival of future bleaching events as an intrinsic environmental feature whose dynamics depend on the future rate of warming in (sea surface temperature, SST). For our study area, we applied the modelling package 'ReefClim' (R. Jones et al. unpubl.) to determine the local change in SST degree⁻¹ (°C) of global warming, where global warming estimates were based on IPCC predictions for a range of greenhouse gas emissions and climate sensitivities (IPCC 2001). Through application of the LARS-WG weather generator (Semenov et al. 1998), we generated an artificial sample (n = 100) of year long daily SST sequences for each decade (to 2050) that was consistent with this local pattern of warming. The statistics used to generate the systematic daily variability (around background warming) were based on measures of sea temperatures recorded at Australian Institute of Marine Science weather stations and underwater temperature loggers at the study site from 1990 to 2000; i.e. we assume this variability remains the same until 2050.

By filtering the generated sequences of daily SST (100 decade⁻¹) through the cumulative 'bleaching onset' thresholds (see Fig. 4c) we determined the likelihood of exceedance for each decade between 1990 and 2050. Division of the threshold exceedance data into 6 intensity levels (Table A1) allowed for development of characteristic

Table A1. Assigned bleaching intensity levels based on number of bleaching days yr⁻¹

Bleaching level	Bleaching days (n)
1. Base level	0–20
2. Very low	20–40
3. Low	40–60
4. Medium	60–80
5. High	80–100
6. Catastrophic	>100

frequency distributions for the annual encounter probability of a bleaching event of given intensity (Fig. A1).

By assuming that the onset of a bleaching event was governed by a Poisson process (in which probability of onset within a small interval of time depends only on the size of the interval and not on any history of onset prior to that time), we simulated randomised streams of bleaching sequences that were consistent with the encounter probability statistics. For events governed by a Poisson process, the time between successive events (i.e. recurrence interval) is described by the exponential distribution

$$F(t) = \lambda e^{-\lambda t} \quad (\text{A1})$$

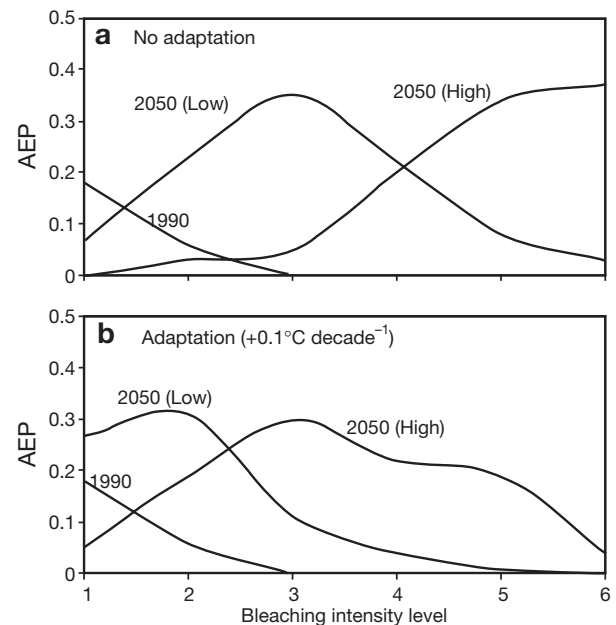


Fig. A1. (a) Comparison of projected annual encounter probability (AEP) for each bleaching intensity level in 1990 (baseline) and 2050 (low and high warming) (intermediate decades not shown); (b) comparison as in (a), but with inclusion of +0.1°C decade⁻¹ increase in thermal bleaching threshold

where λ is the average number of events per unit time (i.e. arrival rate), and t is the event-window timeframe. λ , is explicitly related to the rate of SST warming, so we used and acceptance-rejection algorithm to alter a rate function, $\lambda(t) > 0$, so as to account for decadal increases in the frequency of arrival of events.

MORTALITY BELIEF NETWORK

We used survival analysis (Hosmer & Lemeshow 1999) to help characterise the conditional distributions relating bleaching intensity (Table A1) to the level of mortality in our indicator corals (no macroalgae mortality was associated with any level of bleaching). Survival analysis uses time-to-death data to characterise the probability of death as it relates to the level of a stressor and exposure time.

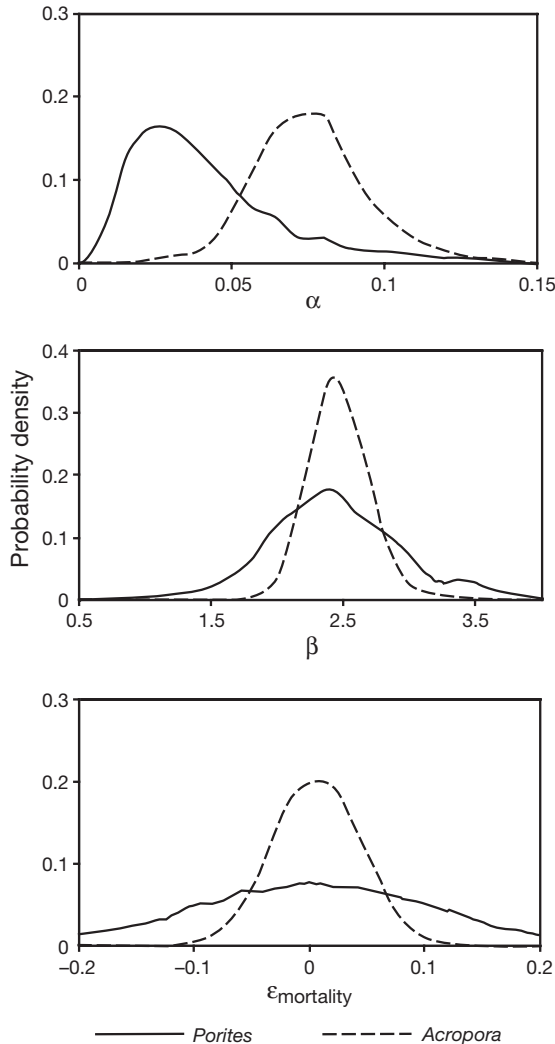


Fig. A2. *Acropora*-like and *Porites*-like corals. Bayesian posterior density functions for the mortality (α , β , $\epsilon_{\text{mortality}}$) parameters in 'ReefState' model. $\epsilon_{\text{mortality}}$ represents standard deviation of the model lack-of-fit terms

By using a combination of field data and elicited expert opinion (for as yet unrealised event intensities) we found that a survival model based on a 2-parameter Weibull distribution most adequately represented the bleaching mortality response. The distribution is described by

$$P = 1 - \exp(\alpha I^\beta) + \epsilon_{\text{mortality}} \quad (\text{A2})$$

where P is mortality (%), I is bleaching intensity level, α and β are fitted constants, and $\epsilon_{\text{mortality}}$ represents a lack-of-fit error term.

To aid the expert elicitation of mortality information (for as yet unrealised high values of I), we developed a series of questions aimed at establishing points on the cumulative distribution function of times-to-death for multiple event intensities. A typical question was, 'Given a population of 100 individuals, how many would one expect to die at X days above the bleaching threshold'. We relied upon the expert judgment of 3 coral ecologists (T. Done, R. Berkelmans and P. Marshall) to provide their best estimates, along with an estimated confidence interval.

In an effort to make formal the uncertainty in the experts judgments, and also to facilitate the automatic propagation of that uncertainty into causal projections, we regarded that that uncertainty into causal projections, we regarded the α , β , and $\epsilon_{\text{mortality}}$ parameters of the mortality function (Eq. A2) as random variables in the mortality belief network (Fig. 3b) to which probability distributions were assigned (Fig. A2). Characterisation of the probability distributions for both the heat-tolerant (*Porites* spp.) and heat-sensitive (*Acropora* spp.) indicator species was achieved using Bayesian inference with non-informative

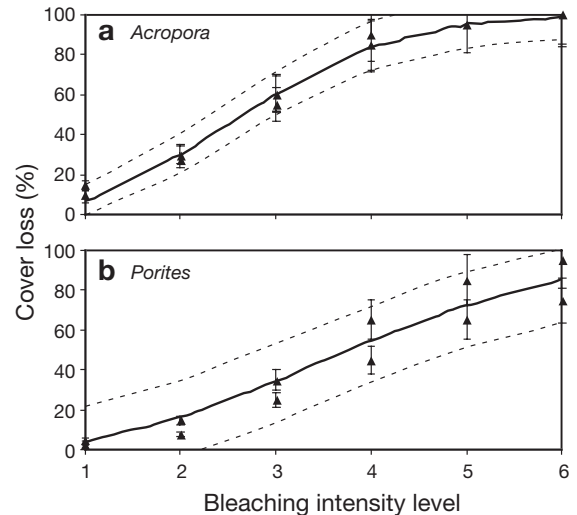


Fig. A3. *Acropora*-like and *Porites*-like corals. Cumulative distribution plots for *Acropora*-like (thermally sensitive) and *Porites*-like (thermally tolerant) corals, showing survival model fit to assessed expert data (\blacktriangle) for each of the 6 bleaching intensity levels. Continuous curves: median values of predictive distributions resulting from survival models; dashed lines: 5th and 95th predictive percentiles; vertical error bars: assessed expert uncertainty of 15% in either direction

priors (Kuczera 1997). The lack-of-fit error term $\epsilon_{\text{mortality}}$ corresponds to the distribution of regression residuals, assumed to be normal with a standard deviation estimated by the root mean squared error of the regression. To ensure we fully captured the tails of the distribution for each parameter, we used Markov chain sampling in the form of the Metropolis algorithm (Kuczera & Parent 1998) to sample the posterior distribution for each parameter. For the current application, 5 parallel sequences were generated, each with 2500 samples. The first 500 samples in the sequence were discarded, leaving a total of 10 000 samples. An acceptable R -statistic (Gelman et al. 1997) indicated approximate convergence.

By sampling over the entire posterior probability distribution of each parameter, we were able to characterise the joint probability distribution described by the mortality belief network. Fig. A3 shows the most likely (50th percentile) mortality response for the indicator *Acropora* and *Porites* coral types for each of the bleaching intensities shown in Table A1. The experts' assessments (including confidence intervals) for each coral type fell within the 90% prediction limits, suggesting that there was insufficient evidence to reject the Weibull survival model.

RECOVERY BELIEF NETWORK

We introduced 2 simplifying assumptions for the recovery modelling process, consistent with a neutral theory construct (Hubbell 1997, van Woesik 2002). First, recruitment of new corals and algae to damaged reefs is not limiting. While they can be so limited, evidence suggests that many coral reefs on the Great Barrier Reef are often saturated with recruits (Hughes et al. 1999, van Woesik et al. 1999). Instead, we assume that the balance between lateral extension and post-settlement mortality (partial and whole colony) is what determines the trajectory of coral cover. Second, we do not differentiate between increases in coral cover resulting from net growth of new colonies on the one hand and that of established colonies (including remnant patches) on the other. Rather, coral recovery is modelled as a lumped process (implicitly incorporating species specific recruitment, survivorship, growth and repair) using a simple logistic growth function

$$c_{(i,t+1)} = c_{(i,t)} + c_{(i,t)} \gamma_i \left(c_{\text{max}} \sum_{i=1}^n c_{(i,t)} \right) + \epsilon_{\text{growth}_i} \quad (\text{A3})$$

where $i = \textit{Porites}$ spp., *Acropora* spp. or algae, γ_i is their specific growth rate parameter, c_{max} is the maximum permissible cover of all benthic categories combined, and ϵ_{growth} represent their individual lack-of-fit error terms. In summary, the growth function describes a sigmoidal growth curve that approaches the maximum cover ($c_{\text{max}} = 1$) at a reducing rate, as the combined cover (i.e. $c_{\text{combined_cover}} = c_{\text{porites}} + c_{\text{acropora}} + c_{\text{algae}}$) approaches c_{max} . The

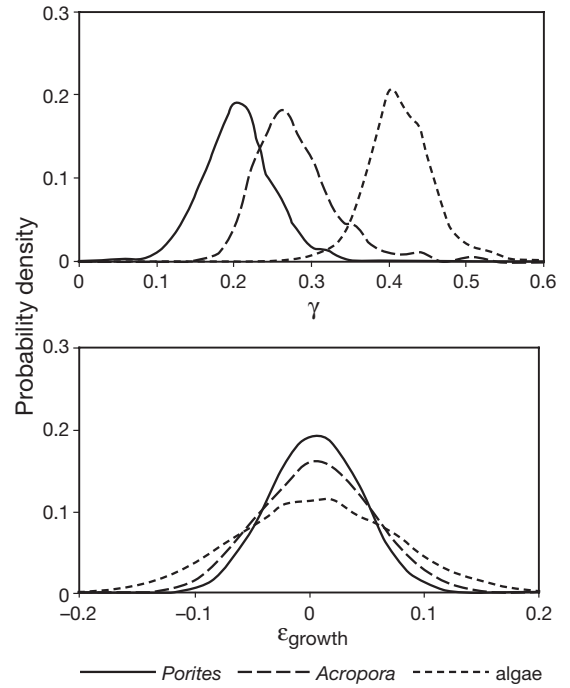


Fig. A4. *Acropora*-like and *Porites*-like corals and algae. Bayesian posterior density functions for recovery (γ , ϵ_{growth}) parameters in the ReefState model. ϵ_{growth} represents standard deviation of the model lack-of-fit terms

'realised' rate of growth for each community element thus declines as a proportion of its 'potential' rate γ_i , as space available for unobstructed growth (i.e. $c_{\text{max}} - c_{\text{combined_cover}}$) declines. The recovery function also includes specification of competitive growth preference rules, which rank corals as superior competitors to algae (after McCook 2001, Diaz-Pulido & McCook 2002, 2004), but giving no competitive advantage (other than growth rate per se) between *Porites* spp. and *Acropora* spp. Wins and losses were determined at random on an event basis. These preference rules explicitly determine that a simulated algal dominated reef state is not the result of algal overgrowth of established corals, but rather the result of algal pre-emption of spaces created by disturbance. The 'realised' rate of algal expansion into vacated spaces, and hence the area at large, is less than the 'potential' rate, due to manageable 'constraints' such as nutrient limitation and herbivory (Diaz-Pulido & McCook 2003, McClanahan et al. 2003). We define 'medium' and 'high' constraints as those constraints that result in contractions of 50 and 100% respectively, of the expansion of algal area cover that could have occurred in the absence of constraints (e.g. 100% constraint represents the situation in which the accumulation of algal biomass during a recovery period is equal to the total losses).

In order to calibrate the 'potential' rates of return for the *Porites* and *Acropora* indicator species, we chose to use recovery data for an ephemeral mid-shelf coral community (Rib Reef: 146° 52' E, 18° 28' S) located in an opti-

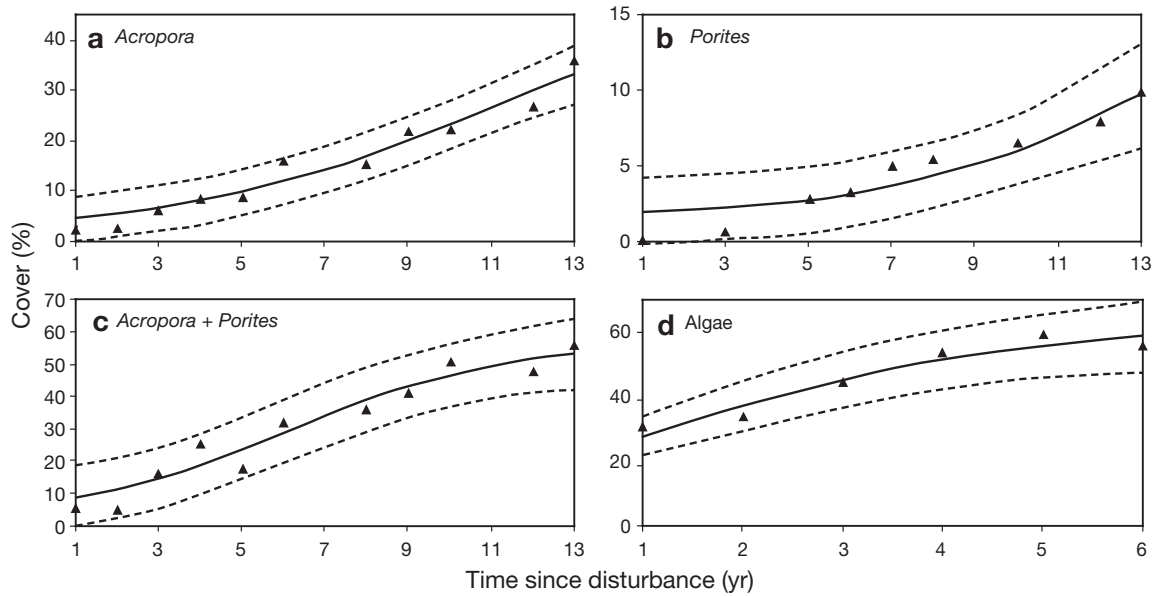


Fig. A5. (a) *Acropora*-like, (b) *Porites*-like and (c) combined corals; (d) algae. Calibration data utilised to characterise 'potential' recovery characteristics. Continuous curves: median predicted model value; dashed lines: bounds of 5th and 95th predictive envelope

mal setting, i.e. strong recruitment and growth of corals (Ninio et al. 2000). The data set describes 13 yr of post-disturbance recovery following almost total mortality caused by the starfish *Acanthaster planci*. For calibrating the coral recovery responses, this data set was ideal as the site was essentially devoid of a standing crop of macroalgae over the entire recovery period, thereby avoiding confounding effects. In order to capture the 'potential' rate of return of algae we used an alternate data set, which recorded the 6 year expansion of algae at Pandora Reef (146° 26' E, 18° 49' S) following the 1998 mass bleaching event. Previous studies at the reef (Scott & Russ 1987, Klumpp & McKinnon 1992) have documented the prevalence of high nutrient and sediment conditions, with only low levels of herbivory. We were therefore confident that the rate of expansion of algae

would be at near potential rates for the region, given the adequate free space made available by recent bleaching induced coral mortality (Diaz-Pulido & McCook 2002).

To identify the species-specific recovery rate parameters from the 2 data sets, we used the same sampling strategy as outlined for the mortality parameter identification. Fig. A4 displays the identified Bayesian posterior density functions for the γ and ϵ_{growth} parameters for the *Porites*, *Acropora* and algae indicator species. Fig. A5 displays the most likely (50th percentile) recovery response for the *Acropora*, *Porites*, combined *Acropora* and *Porites* (i.e. resulting from the randomised preferential growth scheme), and (d) algae response data. For each species type, the recovery response data fell within the 90% prediction limits, suggesting that there was insufficient evidence to reject the recovery model.