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PLANNING FOR PERSISTENCE IN MARINE RESERVES: A QUESTION OF CATASTROPHIC IMPORTANCE

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Abstract. Large-scale catastrophic events, although rare, lie generally beyond the control of local management and can prevent marine reserves from achieving biodiversity outcomes. We formulate a new conservation planning problem that aims to minimize the probability of missing conservation targets as a result of catastrophic events. To illustrate this approach we formulate and solve the problem of minimizing the impact of large-scale coral bleaching events on a reserve system for the Great Barrier Reef, Australia. We show that by considering the threat of catastrophic events as part of the reserve design problem it is possible to substantially improve the likely persistence of conservation features within reserve networks for a negligible increase in cost. In the case of the Great Barrier Reef, a 2% increase in overall reserve cost was enough to improve the long-run performance of our reserve network by >60%. Our results also demonstrate that simply aiming to protect the reefs at lowest risk of catastrophic bleaching does not necessarily lead to the best conservation outcomes, and enormous gains in overall persistence can be made by removing the requirement to represent all bioregions in the reserve network. We provide an explicit and well-defined method that allows the probability of catastrophic disturbances to be included in the site selection problem without creating additional conservation targets or imposing arbitrary presence/absence thresholds on existing data. This research has implications for reserve design in a changing climate.

Key words: catastrophes; coral bleaching; Great Barrier Reef; marine reserves; MARXAN; probability of persistence; reserve selection.

INTRODUCTION

Marine reserves, spatial designations that restrict extractive or destructive practices within their boundaries, are becoming a common strategy for conservation and resource management in the marine environment. Goals for marine reserves include replenishing stocks of commercial species, protecting habitat and biodiversity, and maintaining areas for education, science, and tourism (Lubchenco et al. 2003). To achieve these desired goals, marine reserves must be successful in maintaining the structure and functioning of the ecosystems they encompass. The true effectiveness of any reserve system should be judged not by what is present now but what will persist there in the future (Williams and Araujo 2000, Cabeza and Moilanen 2001, Sarkar et al. 2004, van Teeffelen et al. 2006).

In recent years a substantial body of conservation literature has focused on the optimal design of reserve systems to efficiently meet targets for a range of conservation features (e.g., Airame et al. 2003, Leslie et al. 2003, Fernandes et al. 2005). Most of these studies

implicitly assume that the areas selected for protection will retain their biodiversity and ecological processes in perpetuity. However, reserve systems, essentially local in their effects, can provide no assurances that the features they contain will not continue to degrade due to factors beyond the control of local management. Large-scale catastrophic events, although rare, can potentially negate the contribution an entire marine reserve makes to the region's biodiversity or productivity. As a result the network of which this reserve is part may fail to reach (our) conservation objectives. For example, mass coral bleaching events and associated mortality can effectively degrade large amounts of reef habitat in protected areas (Goreau et al. 2000, Done et al. 2003). We know from experience, however, that not all areas are equally susceptible to catastrophic damage (West and Salm 2003). If we are designing a reserve system to protect a comprehensive and representative sample of biodiversity it would seem prudent to consider the threat of disturbances that we are unable to stop or mitigate.

In an attempt to allow for catastrophic disturbances compromising marine reserves, Allison et al. (2003) assume that all parts of a system are equally affected by catastrophes and propose protecting a greater proportion of each feature to accommodate the expected fraction of the system likely to be in a disturbed state, a

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form of generic insurance. Not only may setting higher targets for feature representation in reserves be politically infeasible, but this methodology ignores the inherent heterogeneity of risk arising from differences in the resilience or resistance of a site to catastrophic disturbances. A more pragmatic way to frame the problem is to ask, "Where, given our existing targets (such as conserving 20% of each feature), is it best to place reserves such that the risk of missing those targets through catastrophic disturbances is minimized?"

The conservation planning literature contains a number of solutions to an analogous problem, maximizing the likely persistence of biodiversity. The task of accommodating future threats to the persistence of biodiversity has generally been accomplished in one of three ways: solving a fully dynamic site selection problem (Costello and Polasky 2004, Meir et al. 2004); combining a series of indices with weightings (Cowling et al. 1999); or using information that may reflect the probability of persistence (Araujo and Williams 2000, Williams and Araujo 2000, 2002, Araujo et al. 2002, Cabeza 2003, Nicholson and Possingham 2006). Because persistence generally has a strong stochastic component, probability is its logical unit (Sarkar et al. 2004). The use of probability of persistence as a factor to be considered in site selection has been advocated as a rational way of combining the various social and biological factors that determine the survival of biodiversity (Williams and Araujo 2002).

Despite the potential usefulness of persistence probabilities in the area selection problem, we believe that there has been a failure to formulate the problem in a way that allows the correct trade-offs to be made. If we wish to minimize the risk of failing to achieve our conservation targets, the central question is "How much emphasis should be placed on securing sites with better persistence prognoses if it comes at the expense of both biodiversity coverage and reserve cost?" For instance, the heuristic method proposed by Williams and Araujo (2000) is set up explicitly to avoid areas with low persistence likelihoods. This is correct if all sites have equal costs, but constructing the problem in this way is to some extent preempting the result, as the optimal reserve system may actually be found through acquiring a large number of cheap sites with moderate or low persistence prognoses.

Here we formulate a reserve selection problem that explicitly considers information on the risk of catastrophic disturbances as well as the spatial extent of conservation features and the cost of conserving different sites. Following Allison et al. (2003) we define a catastrophe as an event causing widespread habitat loss through mortality of the dominant benthic community, leading ultimately to impairment of ecosystem functioning. The problem is to minimize the risk of missing our conservation targets as a result of such disturbances, within economic constraints. Although the term "risk" is used in numerous contexts within the field

of conservation, the notion of risk as the probability the return on our investment will be below some acceptable amount is perhaps most closely related to an intuitive conception of what risk is (Grinold and Kahn 2000). We solved this new "minimize-risk" problem by modifying an existing reserve selection algorithm, MARXAN (Ball and Possingham 2000). To illustrate the approach, we apply this method to a reserve selection problem on the Great Barrier Reef (GBR), Australia, where coral bleaching threatens biodiversity on coral reefs. The GBR is the world's largest reef system, stretching ~2500 km off the northeast coast of Australia. It represents a relatively contiguous habitat comprised of >3000 individual reefs. All of the reefs are managed as part of the 344 400-km² Great Barrier Reef Marine Park, an area larger than the United Kingdom and Ireland combined (Fernandes et al. 2005).

Coral reefs are one of the most productive and biodiverse ecosystems on earth (Reaser et al. 2000), but unfortunately they are also one of the most threatened (Bellwood et al. 2004). The mass coral bleaching events of 1998 and 2002, which impacted coral reefs in all regions of the world, served to highlight the threat climate change presents to reef environments already under considerable local stress from overharvesting and pollution (Goreau et al. 2000). Approximately 18% of the reefs on the GBR were severely bleached during the 2002 event (Berkelmans et al. 2004). In recent years many coral reefs have failed to recover from such severe natural disturbances, instead undergoing shifts to alternate and undesirable states dominated by fleshy algae, the reversibility of which is poorly understood (Bellwood et al. 2004). In Australia and elsewhere, marine reserves are the frontline strategy in coral reef conservation; if climate-change-induced mortality and the risk of other catastrophic disturbances are not explicitly addressed in their design, much of the investments made in managing site-specific threats may be in vain.

MATERIAL AND METHODS

In this section we first outline the ecological, economic, and catastrophic risk data used in the Great Barrier Reef case study. We then formally describe the new "minimize-risk" reserve selection problem and investigate its ability to find a reserve network that optimizes the persistence of coral reefs on the GBR.

Conservation targets and costs

Within the Great Barrier Reef, 30 distinct reef "bioregions" have been identified (Commonwealth of Australia 2005). These bioregions are defined based on a combination of biophysical data, species distribution data, and expert opinion. Given that the spatial distribution of such data is rarely uniform, the use of bioregionalization helps prevent bias in reserve selection due to sampling intensity (Pressey 2004). It is intended that each bioregion represent an area where the known

animal and plant assemblages and the physical features are sufficiently distinct from the surroundings and the rest of the Great Barrier Reef (Commonwealth of Australia 2005). In 2004 the Great Barrier Reef Marine Park (GBRMP) was rezoned with the goal of encompassing at least 20% of the area of each bioregion within no-take marine reserves (Fernandes et al. 2005). We use the same targets here. The cost of including each individual reef in the reserve network is calculated according to the equation given in Stewart and Possingham (2005):

$$c_i = (1 - \alpha)a_i + \alpha(a_i r_i). \quad (1)$$

Here the cost (c) of each reef (i), is a weighted function of the area (a) of each reef, assumed to reflect the cost to the general society of protecting that resource, and an estimate of the loss of commercial fishing revenue (r) that could be expected if that reef was included in the reserve network. Lost fishing revenue is calculated for each reef as a value (in kilograms per square kilometer) based on mean annual catch data collected by the reef line fishery from 1993 to 2004. The line fishery is the principal (and in many areas the only) commercial fishery targeting the reefs of the GBR. α is a weighting variable that allows a planner to prescribe the importance of fishing cost relative to area. In this example, we give equal weight to these two costs, $\alpha = 0.5$. Existing reserves are not assumed to be "locked in," and we consider all reefs available for selection. That said, those reefs already in no-take areas prior to 2004 will be slightly cheaper to acquire due to the absence of commercial fishing interests.

Bleaching risk assessment

The problem of choosing a reserve system that minimizes the negative influence of catastrophes forces us to consider a planning time frame. We will assume that our planning time frame is ~ 100 years, and hence the local risk of interest is the likely condition of each reef in the year 2100 in the context of catastrophic coral bleaching events. To simplify our calculations we consider "condition" to be a binary variable where a reef can be either healthy or degraded. Although a variety of conditions, such as reduced salinity, can induce coral bleaching, mass bleaching events are primarily triggered by unusually elevated water temperatures (Hoegh-Guldberg 1999). Because of the relationship of bleaching to water temperature, most attempts to predict its risk have generally focused on forecasting the future thermal environment of coral reefs (Hoegh-Guldberg 1999, Donner et al. 2005). As a proxy for the probability a reef is in a degraded state due to coral bleaching, we use the mean probability of sea surface temperature (SST) exceeding 2°C above the bleaching threshold in at least one year before 2100. The bleaching threshold is the highest temperature at which no bleaching is predicted to occur irrespective of exposure time.

The thresholds used here are taken from Berkelmans (2002) and are based on high-resolution in situ temperature records and historical observations of coral bleaching on the GBR. As the thermal tolerance of corals varies between locations, species, and growth forms, Berkelmans' (2002) thresholds are calculated based on the dominant coral communities present at 13 different reefs spread out across the GBR. These thresholds have subsequently been regionalized for the entire GBR (see Wooldridge and Done 2004). The bleaching thresholds for specific reefs were simply averaged for the particular thermal regions in which they were located, based on the results of Wooldridge and Done (2004). A major simplification of our case study is that, although these thresholds vary spatially, they are assumed to remain temporally constant. In reality there is the potential for these thresholds to increase through adaptation or fall through loss of resilience.

In using the probability of a 2°C threshold exceedance we are being quite conservative in our definition of a catastrophic bleaching event. A rise in SST of even 1°C above the threshold is enough to trigger widespread bleaching (Berkelmans and Willis 1999) but may not necessarily lead to coral mortality. Tank tests on tabulate and corymbose *Acropora* species, the dominant structural component of GBR reefs, indicate that temperatures 2°C above the threshold are likely to result in large-scale coral mortality, regardless of exposure time (R. Berkelmans, *personal communication*), a catastrophic event for any reef.

To predict the frequency with which future SSTs are likely to exceed the bleaching thresholds, we used the mean monthly output from eight global circulation models (GCMs) that reported changes in ocean temperature from as early as 1860 to 2100 (details of models and emission scenarios are given in the Appendix). As coral reefs are generally only present in shallow water, only the change in temperature of the topmost ocean layer (0–20 m in most models) was considered. Although averaging across all models assumes that they are all equally likely, we decided this was favorable to selecting a single model considering the significant uncertainty attached to each. A key limitation of using the output from GCMs is that the grid resolution of these models is only fine enough to capture major currents, eddies, and basic bathymetry. In reality, reef scale (< 1 km) bathymetry and hydrodynamics can have a significant bearing on bleaching risk (West and Salm 2003). A number of alternate methods of downscaling were investigated in an attempt to capture the local heterogeneity of the GBR but none produced noticeable improvements. Consequently, all data was linearly downscaled to a grid size of 10 km. In any given year the future SST for each grid cell is assumed to be drawn from a normal distribution with a mean determined by the average GCM output and a standard deviation determined by the long-run variation in SST observed at

fixed data loggers located at 13 points on the GBR. The standard deviation in SST was averaged across regions at the same scale as the bleaching thresholds (see Wooldridge and Done 2004). For each grid cell, the mean SST increases over time but the coefficient of variation around this value is assumed to be temporally uniform. Given that the standard deviation is based only on a small number of logger locations, we are simplifying spatial variation in this parameter. The probability of catastrophic bleaching occurring in future years is determined by the proportion of the normal distribution of reef temperatures being $>2^{\circ}\text{C}$ above the threshold temperature for that cell.

In order to combine future bleaching predictions into a single risk value we calculated the catastrophic bleaching risk in each cell at roughly 20-year intervals between now and 2100 and then calculated the geometric mean of these values. Risk values were then assigned to each of the 3600 GBR reefs based on their intersection with the 10-km grid cells. In cases in which a reef lay across the boundary between grid cells, the risk value assigned was the mean of all the grid cells containing that reef, weighted by the proportion of the reef present in each cell. This was calculated using the following formula:

$$\text{risk}_i = b_1 p_1 + b_2 p_2 + \dots + b_n p_n \quad (2)$$

where b_1 is the bleaching risk in one of the grid cells containing reef i and p_1 is the proportion of the reef contained within that grid cell.

The area selection problem

The goal of minimizing the expected number of reef bioregions that fail to meet their target at the end of our planning horizon for a fixed budget can be formulated as a mathematical programming problem: minimize expected number of bioregions that fail to meet their target, i.e.,

$$\text{Min} \sum_{j=1}^N \text{Pr}(A_j < t_j) \quad (3)$$

subject to the constraints we meet our targets for all bioregions in the absence of catastrophes and the whole reserve system does not exceed a preset budget, which mathematically is subject to

$$\sum_{i=1}^M a_{ij} y_i \geq t_j \quad \text{for } j = 1 \dots N \quad (4)$$

$$\sum_{i=1}^M c_i y_i \leq B \quad \text{for } i = 1 \dots M \quad (5)$$

where A_j is the area of bioregion j still in the reserve network at the end of the planning period and t_j is the conservation target for that bioregion. The area of bioregion j present on each reef i is a_{ij} and c_i is the cost of including reef i in the reserve network. The variable y_i is

a control variable that defines the reserve system such that $y_i = 1$ if reef i is included in the reserve system and $y_i = 0$ if otherwise. The parameter N is the number of conservation features, in this case the 30 reef bioregions; M is the number of possible planning units, in this case the 3600 reefs of the GBR; and B is a fixed budget that cannot be exceeded.

The objective function, Eq. 3, is the expected number of bioregions that do not meet their target at the end of the planning period. By summing across all bioregions the function avoids any assumptions regarding the independence of catastrophe risk across features (Sarkar et al. 2004) and treats all conservation features equally (Nicholson and Possingham 2006). Eqs. 4 and 5 are constraints that ensure the combination of reefs selected initially capture our target amount of each bioregion and that the total cost is socially acceptable. Because this problem involves acquiring the best set of reefs whose total cost remains below a specified threshold, it is most similar to the ‘‘maximum coverage’’ area selection problem (Camm et al. 1996).

Calculating the precise probability of having less than the target amount of each bioregion remaining in the reserve system at the end of the planning horizon, defined in Eq. 3, does not present a mathematical problem. To be of realistic use in a reserve selection application, however, this probability must be calculated extremely quickly. For instance, to efficiently find a solution to the GBR reserve problem using simulated annealing, it is necessary to compare this probability between different potential reserve networks in the order of 10 000 times a second. If each bioregion is composed of four or more reefs, this calculation becomes far too slow. It is possible, however, to closely approximate the chance each bioregion will fail to meet its target, $\text{Pr}(A_j < t_j)$, using the standard normal distribution. Here the probabilities of having successfully conserved different amounts of each bioregion are assumed to be normally distributed, with a mean based on the expected area of each bioregion conserved for a particular reserve system given by

$$E(A_j) = \sum_{i=1}^M a_{ij} y_i p_i \quad (6)$$

and the variance in this expected area given by

$$\text{Var} \left(\sum_{i=1}^M a_{ij} y_i p_i \right) = \sum_{i=1}^M a_{ij}^2 y_i p_i (1 - p_i) \quad (7)$$

where p_i is the probability that habitat representative of the bioregion of interest at reef i is still extant at the end of the planning period. In the GBR example, p_i is determined by the risk of catastrophic bleaching occurring at reef i . The probability of failing to conserve the target area of each bioregion is given by the proportion of the normal curve that is below the set target. These probabilities are subsequently summed

across all 30 bioregions according to Eq. 3 and minimized. Attached to the use of this method is the assumption that there is no covariance between values of p_i . Should information be available regarding the nature of any covariation that exists between p_i 's, then Eq. 7 should be replaced by a formula that considers this covariation when calculating the variance around the expected conserved area of each feature (Grimmett and Stirzaker 1982).

To solve this new area selection problem we modified the widely used reserve design software MARXAN (Ball and Possingham 2000). MARXAN uses an optimization method known as simulated annealing, which, unlike many heuristic algorithms, allows some "bad" moves to be made, thereby avoiding convergence on a local minimum early in the procedure and increasing the probability of finding a near-optimal solution (McDonnell et al. 2002). In its existing form, MARXAN solves a classic "minimum set" problem, the aim of which is to determine the cheapest reserve network that will satisfy our conservation criteria. Here MARXAN has been modified, allowing it to find a near-optimal reserve network beneath a specified cost threshold. In order to optimize the objective function given in Eq. 3, at each iteration the modified version of MARXAN uses the normal approximation described above to calculate the probability of missing the stated target for all conservation features, in our case reef bioregions, $\Pr(A_j < t_j)$. In this way, the new version of the MARXAN algorithm described here is able to maximize the chance of persistence (the long-run probability of meeting our conservation targets) in the face of catastrophic events, while trading this benefit off against overall reserve cost and the representation of biodiversity.

To determine the minimum cost at which our bioregion targets could reasonably be met we first solved the problem using the original MARXAN algorithm (see Stewart et al. [2003] for algorithm details). As MARXAN is set up to solve the "minimum set" problem, it represents a powerful method for the determination of the cheapest way to meet feature representation targets and is commonly employed by planning agencies for this purpose. As there will be some variation in reserve cost between runs we took the average minimum cost over 1000 runs. For the purposes of the results, this "minimize-cost" method is referred to as scenario I. We then optimized for persistence using this mean minimum cost as the budget constraint. This method aims to "minimize risk" and is referred to as scenario II. The results of these runs were compared with respect to conservation priority and the risk of missing conservation targets in the future. The effect of increasing the cost threshold on the number of bioregions successfully represented and their likely persistence within the reserve network was also explored. Because the probability of persistence will increase as a result of including more reefs in the reserve network, the results at each cost increment were

compared to both minimum cost and randomly selected reserve networks containing the same number of representative reefs for each bioregion. Finally, the consequence of relaxing the requirement for bioregional targets to be met in the initial reserve system, Eq. 3, while attempting to minimize risk, was investigated. This allows for the possibility that some high-risk and/or high-cost bioregions may be lost through triage in order to improve the survival prognosis of other bioregions. This is referred to as scenario III. For all scenarios, the results reported reflect the mean value over 1000 runs of the reserve selection algorithm. Each run was comprised of 1 000 000 reserve iterations.

RESULTS

Across the entire GBR the mean annual probability of a catastrophic bleaching event before 2100 ranged from 0.03 to 0.25 (Fig. 1). Consideration of this spectrum of risk during conservation planning had a substantial influence on the conservation priority of reefs on the GBR (Fig. 1). The prediction that catastrophic bleaching events may occur as frequently as every four years on the GBR is consistent with other modeled estimates previously reported by both Hoegh-Guldberg (1999) and Donner et al. (2005).

Using the minimize-cost approach to select reefs for reservation (scenario I) routinely resulted in failure to meet most of our bioregional conservation targets once the risk of catastrophic bleaching was considered. We would expect 24.1 ± 0.4 (mean \pm SD) of the 30 reef bioregions to fail to meet their target in 2100 (Fig. 2). In contrast, when the risk of catastrophic bleaching was considered during the reserve selection process by solving the problem defined in Eqs. 3–5 (scenario II), the expected number of bioregions that miss their conservation targets was reduced by over a third to 14.1 ± 0.5 bioregions, for an equivalent cost (Fig. 2). The effect of increasing reserve investment above this minimum threshold is shown in Fig. 2. Increasing the overall reserve cost by just 2% allowed the number of bioregions expected to meet their target to be improved by >60% to 4.8 ± 0.6 bioregions. Greater investment in the reserve network, up to 20%, further reduced the probability of missing our conservation targets, but only marginally.

Initial increases in reserve investment resulted in the acquisition of many cheap reefs, greatly increasing the total number of reefs in the reserve system (Fig. 2). An increased investment of >5%, however, resulted in a reduction in the number of reserved reefs (Fig. 2), suggesting that some low-risk but high-cost reefs were too expensive to be included in cheaper reserve systems but are important if we have more resources. This result was also supported by the fact that when the same numbers of reefs were randomly selected without regard to cost, the probability of missing conservation targets was initially lower than under the new minimize-risk method. However, even when forced to include the same

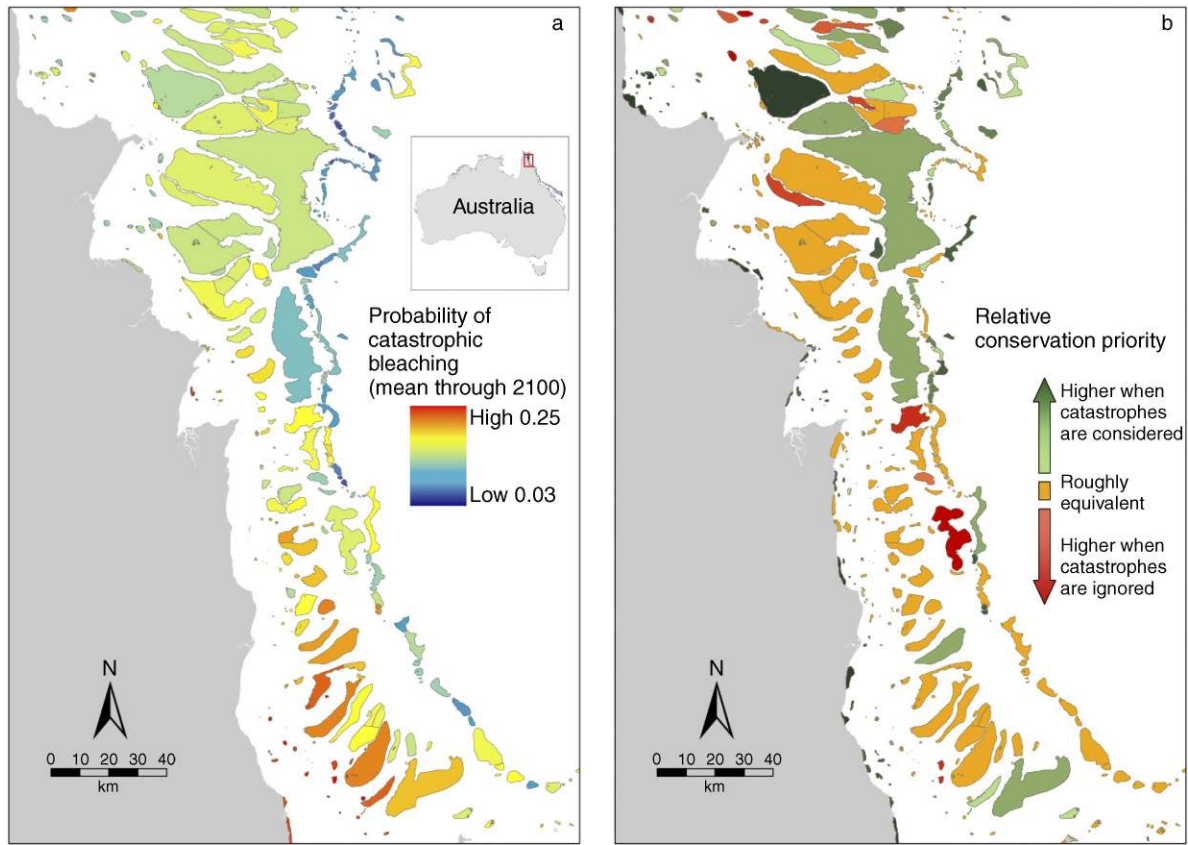


FIG. 1. (a) Mean annual probability (present through to 2100) of catastrophic bleaching events occurring on coral reefs in the northern section of the Great Barrier Reef (GBR). (b) Change in conservation priority for coral reefs on the northern GBR when the risk of catastrophic bleaching is considered during conservation planning.

number of reserved reefs, the minimize-cost method always performed more poorly than the minimize-risk method with respect to persistence likelihood (Fig. 3).

The frequency with which sites are selected as part of a reserve network is an indication of their importance to achieving an efficient reserve network and can be used as a measure of conservation priority (Possingham et al. 2000). When solving the minimize-cost problem, only a small number of reefs were consistently selected as part of the reserve network (Fig. 4). Although the largest number of reefs was selected less than one time in 10, many reefs were selected between 20% and 60% of the time (Fig. 4). This suggests that our bioregional conservation targets could be met in a large number of ways and that conservation priority is far from clear. The minimize-risk problem was more decisive, with the majority of reefs being selected with frequencies either >70% or <20% (Fig. 4).

By relaxing the requirement that the initial reserve system include 20% of each bioregion (scenario III), it became possible to reduce the expected number of bioregions that miss their conservation targets to 4.4 ± 0.5 , even when the budget was fixed at the mean minimum-cost value (Fig. 2). Removing this constraint

effectively allowed the exclusion through triage of four of the most common and therefore higher target bioregions, the extra funds being used to greatly improve the persistence probabilities of the remaining bioregions and the GBR as a whole.

DISCUSSION

Given the high likelihood of future catastrophic bleaching events on the GBR (Done et al. 2003, Wooldridge et al. 2005), designing a reserve network ignorant of this risk will almost certainly result in the failure of that reserve network to meet our conservation targets. In addition to coral bleaching, catastrophes that may beset marine populations include cyclones, disease epidemics, algal blooms, and hypoxia events (see Allison et al. 2003 and references therein). As the threat of such events is rarely considered in the design of marine reserves, the same inadequacy is likely to be true for most reserve networks. Here we show that by considering the threat of catastrophic events as part of the reserve design problem it is possible to substantially improve the likely persistence of conservation features within reserve networks for a negligible increase in cost. We provide an explicit, efficient, and well-defined

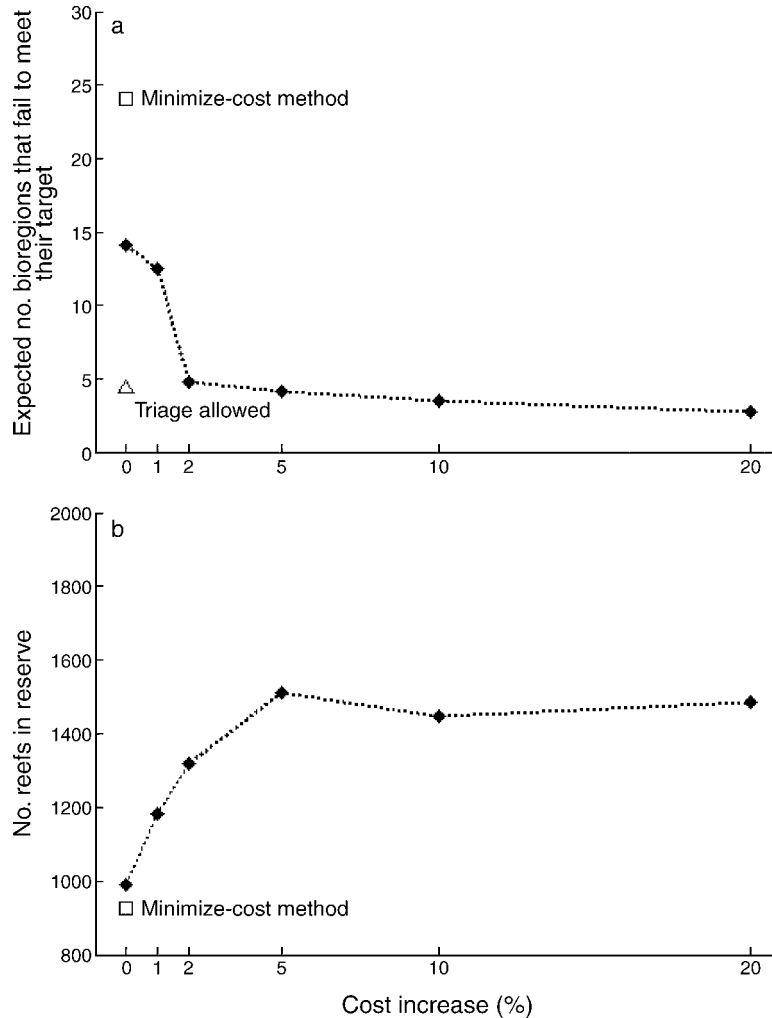


FIG. 2. The effects of increasing the available budget on the expected adequacy and composition of a reserve network on the Great Barrier Reef selected using the new minimize-risk method: (a) change in the expected number of bioregions that fail to meet their targets; (b) change in the number of reefs included in the reserve network. The 95% CI range is too small to be visible on the plot. Results for the minimum-cost (open squares) and triage-allowed (open triangle) problems are also shown.

method that allows the probability of catastrophic disturbances to be included in the site selection problem without the need to set additional conservation targets or impose arbitrary presence/absence thresholds on existing data.

Finding an optimal solution to the area selection problem including catastrophes requires formulating the problem in a way that allows the necessary trade-offs to be correctly evaluated. In this GBR example a large number of different reef combinations were able to efficiently meet our conservation targets. Because of this abundant choice, persistence probabilities could be improved without compromising either reserve cost or biodiversity coverage. This will not always be the case. In many instances trade-offs will need to be made in order to improve persistence. The key question then becomes "How much are we willing to pay to have a more secure portfolio of reserves in the face of

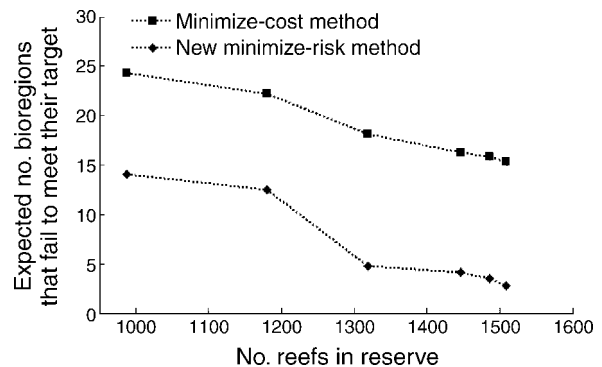


FIG. 3. The expected number of bioregions that fail to meet their target as a function of the number of reefs included in the reserve network. Results are given for both the minimize-cost and the new minimize-risk area selection problems. The 95% CI range is too small to be visible on the plot.

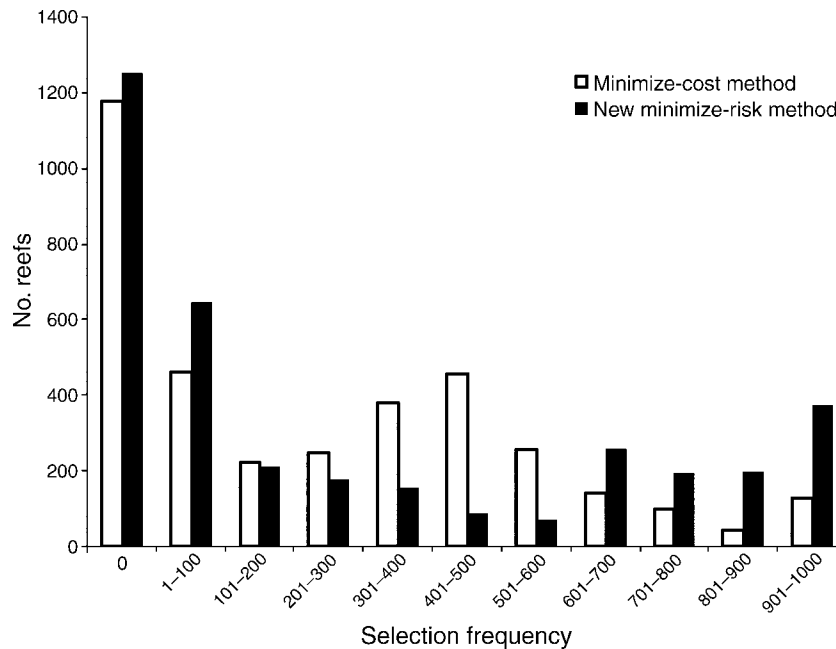


FIG. 4. The number of reefs selected with different frequencies as part of the near-optimal reserve networks. The frequency with which reefs are selected is an indicator of conservation priority. Open bars are the selection frequency using the minimize-cost problem; solid bars are the selection frequency under the minimize-risk method.

catastrophic and uncontrollable disturbances?" In the example here, some low-risk reefs were clearly too expensive to include in highly cost-constrained reserve networks. As greater funds were made available, however, these low-risk/high-cost reefs became viable targets for selection such that the probability of persistence increased even though the overall number of reefs in the reserve network decreased. This result suggests that simply aiming to avoid high-risk sites may actually lead to the suboptimal placement of protected areas. Because the conservation value of a site changes depending on available budget, it will be difficult for reserve selection methods based on iterative heuristic rule sets to find good solutions.

As cost is the principal constraint on conservation action (Naidoo et al. 2006), area selection methods often aim to minimize cost. The use of absolute minimum cost, however, precludes the possibility of finding an ecologically far-superior reserve system that could be achieved with only a marginal increase in expenditure, as was the case here. Society may very well be willing to pay this cost, especially given the public's disproportional desire to militate against catastrophic events (Zeckhauser 1996). In focusing so singularly on cost during conservation planning, there is a danger of putting political expediency over ecological relevancy. Although we only compared our new problem formulation with a minimum cost scenario, it is interesting to note that as the available budget increases, and more importantly a higher proportion of the system is reserved, the difference between the minimize-cost and

minimize-risk methods will decrease. Alternatively, if the budget is smaller or the conservation representation targets <20%, then the differences between the two methods will be even more pronounced than presented here.

Our quest for equity between conservation features also comes at a substantial cost in terms of persistence likelihood. By allowing for the exclusion through triage of four of the 30 coral reef bioregions in this example it was possible to improve the probability of meeting our conservation targets across all features by nearly 80%. Interestingly, the four bioregions excluded from the reserve network were not those in high-risk or high-cost areas but those that were most abundant and therefore arguably those most likely to persist regardless of protection.

In this paper, we considered only the influence of a single threat, coral bleaching. In reality, many conservation features will be threatened by multiple, potentially catastrophic events. There is no reason why multiple threats cannot be considered using the method described in this paper; however, each planning unit in our formulation is constrained to have just a single probability. The big challenge then is determining how to combine the probabilities of different threats. If the probabilities are all fairly small we advocate a simple additive strategy, such as that the insurance industry uses when determining risk from multiple threats (Dong et al. 1996). This can, however, hide the fact that there may be some synergistic effects of multiple events that increase risk above this level.

The aim of this paper was not to propose a new reserve system for the GBR but to provide a method that allows the threat of catastrophes to be rationally evaluated in the context of a reserve design problem. Consequently, we have made a number of assumptions that would need to be assessed more thoroughly during the development of an actual reserve network if and when areas such as the GBR are rezoned. These include (1) the assumption that a series of smaller reefs are of equal ecological value to a single large reef of equivalent area. While many marine ecosystems, and especially coral reefs, are naturally patchy (Sale et al. 2006) and therefore able to function effectively even when quite isolated, it is valuable to consider the natural tension that might exist between our desire to spread risk across many features and the negative effects of fragmenting an ecosystem (McCarthy et al. 2005). Similarly, we have put no additional value on reserving contiguous groups of reefs, something that may be desirable from a management point of view. (2) Coral reefs are unlikely to be completely independent with regard to catastrophe risk as assumed here. Selecting reefs with high covariance of risk between them would have the effect of increasing the variance around the expected value, thereby decreasing the probability of a reserve meeting our conservation targets. If known, it would be appropriate to include this information as mentioned in *Material and methods*; however, much of the evidence from past bleaching episodes points to reef scale hydrodynamics significantly influencing the severity of coral bleaching and the extent of associated mortality (West and Salm 2003). Similar evidence exists for cyclone damage to coral reefs (Puotinen 2004), suggesting that an assumption of independence may not be unreasonable in many cases. Third, we have assumed that the effects of catastrophic bleaching events are only negative with regard to the aims of our marine reserve. In reality some components of the reef biota are likely to profit from such disturbances. It is far from clear how such benefits should be traded against the negative effects of a damaged reef environment but considering the chronic stress that many of the world's reefs are under, the negative aspects of catastrophic damage are likely to substantially outweigh the positives. Finally, probability of persistence is intimately linked to the time frame of consideration. We have presented results for a single management time frame (~100 years) but would emphasize the importance of investigating the sensitivity of results to different periods of management. For instance, although an identical trend was evident when our analyses were run using a 50-year time frame, the number of bioregions expected to miss their targets was reduced by roughly a quarter across all scenarios.

This paper and the methodologies within it are constructed on the premise that, all things being equal, it is preferable to protect those reefs at lowest risk of catastrophic bleaching. Certainly if we are only interested in the persistence of reefs inside our reserves this is

the right foundation, but we would encourage those charged with the conservation of reefs to ask whether we want persistent reserves or persistent reef systems augmented by reserves. The optimal protection strategy may be quite different depending on the answer and may, counterintuitively, involve protecting those reefs at greatest risk from uncontrollable catastrophic disturbances (E. T. Game, E. McDonald-Madden, M. L. Puotinen, and H. P. Possingham, *unpublished manuscript*).

The minimize-risk reserve selection method presented here has its genesis in the issue of catastrophic disturbance on coral reefs but its applicability stretches far beyond this. The same framework could comfortably be used to investigate any reserve selection problems in which the occurrence of conservation features at sites is uncertain, either in the present or the future. As examples, conservation planners may be interested in optimally capturing temporally patchy pelagic resources or rapidly changing vegetation types in a reserve system. Alternatively they may be uncertain about the presence of particular species at a location, perhaps because occurrence is predicted based on modeled distribution data with varying degrees of confidence. From a rather more pragmatic point of view, this framework is also suitable for spatial data on the likelihood of conservation success, perhaps as a result of a landholders' willingness to participate in conservation initiatives or the ability to successfully enforce regulations.

Catastrophes may well be the most important factor in determining the long-term persistence of many marine populations (Mangel and Tier 1994). Given the contemporary influence of climate change, the occurrence of such events only appears likely to increase (IPCC 2001). Considering the risk of catastrophic events when designing marine reserves will dramatically improve the chances of protected areas meeting conservation targets but it must be done in the context of a clearly formulated problem that explicitly considers potential trade-offs in both biodiversity and cost.

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APPENDIX

Details of global circulation models used to predict future sea surface temperature patterns (*Ecological Archives* A018-021-A1).