Contributed Paper

Should We Protect the Strong or the Weak? Risk, Resilience, and the Selection of Marine Protected Areas

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Abstract: *It is thought that recovery of marine habitats from uncontrollable disturbance may be faster in marine reserves than in unprotected habitats. But which marine habitats should be protected, those areas at greatest risk or those at least risk? We first defined this problem mathematically for 2 alternate conservation objectives. We then analytically solved this problem for both objectives and determined under which conditions each of the different protection strategies was optimal. If the conservation objective was to maximize the chance of having at least 1 healthy site, then the best strategy was protection of the site at lowest risk. On the other hand, if the goal was to maximize the expected number of healthy sites, the optimal strategy was more complex. If protected sites were likely to spend a significant amount of time in a degraded state, then it was best to protect low-risk sites. Alternatively, if most areas were generally healthy then, counterintuitively, it was best to protect sites at higher risk. We applied these strategies to a situation of cyclone disturbance of coral reefs on Australia's Great Barrier Reef. With regard to the risk of cyclone disturbance, the optimal reef to protect differed dramatically, depending on the expected speed of reef recovery of both protected and unprotected reefs. An adequate consideration of risk is fundamental to all conservation actions and can indicate surprising routes to conservation success.*

Keywords: catastrophes, coral reefs, cyclones, habitat disturbance, marine reserves, reserve selection

¿Debemos Proteger al Fuerte o al Débil? Riesgo, Resiliencia y la Selección de Áreas Marinas Protegidas

Resumen: *Se piensa que la recuperación de hábitats marinos a partir de perturbaciones incontrolables puede ser más rápida en reservas marinas que en hábitats desprotegidos. Pero, ¿qué hábitats deberán ser protegidos?, ¿aquellas áreas con mayor riesgo o las de menor riesgo? Primero definimos este problema matemáticamente para dos objetivos de conservación alternativos. Posteriormente resolvimos este problema analíticamente para ambos objetivos y determinamos las condiciones bajo las cuales era óptima cada una de las diferentes estrategias de protección. Si el objetivo de conservación era optimizar la probabilidad de tener por lo menos un sitio sano, entonces la mejor estrategia fue la protección del sitio con menor riesgo. Por otra parte, si la meta era maximizar el número esperado de sitios sanos, la estrategia óptima fue más compleja. Si era probable que los sitios protegidos estuvieran en estado de degradación durante un período de tiempo significativo, entonces era mejor proteges sitios con riesgos bajos. Alternativamente, si la mayoría de las áreas estaban sanas en general entonces, contra intuitivamente, era mejor proteger sitios con riesgos mayores. Aplicamos estas estrategias a una situación de perturbación por ciclón en arrecifes de coral en la Gran Barrera Arrecifal de Australia. En relación con el riesgo de perturbación por ciclón, el óptimo arrecife*

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a proteger difirió dramáticamente, dependiendo de la velocidad de recuperación esperada en los arrecifes protegidos y desprotegidos. Una adecuada consideración de los riesgos es fundamental para todas las acciones de conservación y pueden indicar rutas sorpresivas hacia el éxito de la conservación.

Palabras Clave: arrecifes de coral, catástrofes, perturbación de hábitat, selección de reservas, reservas marinas

Introduction

Most researchers assessing the efficacy of marine reserves have focused on the ability of reserves to improve the recovery trajectory of commercially harvested stocks (see Russ 2002). It is also thought that recovery of marine habitats from uncontrollable disturbance may be faster in marine reserves than in unprotected habitats (Bellwood et al. 2004; Bevilacqua et al. 2006; Mumby 2006). The expectation of faster recovery times arises from the observation that exploitation of marine resources and the subsequent simplification of previously complex food chains have eroded the resilience of many marine ecosystems (Hughes et al. 2005). Although it is challenging to empirically demonstrate exploitation leading to a loss of resilience, globally there is increasing evidence in support of this assumption, for a number of important marine ecosystems including coral reefs (Hughes et al. 2003; Bellwood et al. 2004; Hughes et al. 2007), shallow temperate reefs (Tuya et al. 2005), deepwater benthic communities (Thrush & Dayton 2002), and kelp forests (Steneck et al. 2002).

Recognition of this property of marine reserves has instigated a new paradigm for marine stewardship: managing areas with the explicit goal of maintaining ecosystem resilience (Hughes et al. 2005). A resilience-oriented question about marine reserves asks, Where should marine reserves be placed to promote resilience? This question has been answered in 2 very different ways: (1) in areas most sensitive to anthropogenic pressures (Roberts et al. 2003) and (2) in areas likely to be inherently resilient either through lower rates of disturbance or increased functional redundancy (West & Salm 2003).

There is a growing awareness that large-scale threats, often beyond the control of management agencies, may play an increasingly important role in determining the success of marine reserve networks (Allison et al. 2003; Game et al. 2008). Perhaps the most striking example is the threat that catastrophic coral bleaching or cyclone events pose to protected coral reefs (Hughes et al. 2003; Gardner et al. 2005). Because the risk of such events is not spatially uniform, considering the risk of individual areas during the reserve-selection process can dramatically alter the persistence prognosis of reef habitat within the resulting reserve network (Game et al. 2008). The persistence of habitat (i.e., live coral cover) is particularly important on coral reefs because these reefs provide many ecosystem services that are intimately related to the condition of the habitat (Mumby 2006).

Even though the actual occurrence of large-scale disturbances such as cyclones or mass coral bleaching may not be mitigated by reef protection, evidence suggests that the resilience gained by complete protection makes the recovery trajectory in these areas better than that of reefs that remain heavily fished (Mumby 2006; Mumby et al. 2006; Hughes et al. 2007). Chronic exploitation of herbivorous fishes on coral reefs can lead to dramatic increases in macroalgae abundance, ultimately suppressing both the recruitment and survival of coral (Kuffner et al. 2006). In many instances reefs subject to such chronic anthropogenic stress have failed completely to recover from natural disturbances such as tropical storms (Connell et al. 1997). Local control of fishing effort on coral reefs is being advocated as a way to promote habitat resilience and to help mitigate the impact of disturbances that cannot be controlled (Hughes et al. 2007).

We focused exclusively on the disturbance and recovery of benthic habitats. There will almost certainly, however, be wider ecosystem effects as a result of large-scale disturbances, such as declines in reef-associated fish fauna (Jones et al. 2004; Graham et al. 2006). Although it is not well known how marine reserves influence these wider impacts of disturbance, the response of some ecosystem components appears to be closely linked to the condition of benthic habitats (Jones et al. 2004; Graham et al. 2006).

If the fate of those habitats currently targeted for protection were the only interest and the fate of all unreserved areas could be ignored, then a clear strategy exists. In the absence of fiscal considerations, conservation targets should be met by protecting the areas of lowest risk. Unprotected areas, however, are likely to make a substantial contribution to biodiversity and ecosystem-service conservation (Margules & Pressey 2000), and rarely is their fate of no concern. Given this reality, the ultimate goals of conservation—maintenance of biodiversity and functioning ecosystems—are perhaps best served by considering the health of the entire system, not just a network of protected areas.

If concern extends to all sites, protected and unprotected, the best protection strategy with regard to uncontrollable disturbances is less clear. Protection of areas at lowest risk from uncontrollable disturbance ensures that protected habitats have such a high probability of being in a healthy state that they are able to compensate for the poor state of unprotected areas. Alternatively, if the recovery of habitat following disturbance is substantially faster in protected areas, then an argument could be made that it is better to prioritize protection of high-risk areas because they stand to gain the most from the improved recovery trajectory that full protection offers. In essence, should the strong or the weak areas be protected?

We describe this problem and explore the conditions under which the 2 protection strategies are likely to be optimal. Because the optimality of a particular strategy can only be assessed relative to the objectives of the reserve network, we compared the utility of both strategies with regard to 2 different reserve objectives, maximizing the expected number of healthy sites and maximizing the probability that at least one site is in a healthy state. To illustrate the problem of making optimal conservation decisions under conditions of uncontrollable risk, we considered the case of physical damage to coral reef communities from cyclone-generated waves on Australia's Great Barrier Reef.

Methods

To systematically decide which areas to protect within a given region it is necessary to translate broad conservation goals, such as maintaining biodiversity, into specific objectives that can be quantified and defined mathematically. We considered 2 alternate objectives of the reserve-selection problem, both of which are consistent with the general goal of maintaining biodiversity and ecosystem functionality but are characterized by different levels of risk aversion. The first objective was to select reserve sites such that the expected number of healthy sites in the system at any point in time is maximized:

$$\max \sum_{i=1}^{n} p_i, \tag{1}$$

where p_i is the probability site i is in a healthy state at any point in time. *System* in this sense refers to the entire region of interest such that p_i is summed across all potential sites, protected and unprotected. The second objective, and the more pessimistic one, was to select sites with the aim of ensuring that at least one healthy site is present in the system at all times. This objective can be interpreted as maximizing the probability that at least one site is in a healthy state:

$$\max 1 - \prod_{i=1}^{n} (1 - p_i). \tag{2}$$

Although this may seem a relatively dire conservation objective, its utility is more obvious if one interprets the objective as seeking at least one healthy example of each conservation feature, for instance habitat types. In this case p_i is multiplied across all sites, protected and unprotected.

We assumed the probability of a site being in a healthy state is a function of the average time it takes to recover from a disturbance and the frequency with which it is disturbed. Importantly, the average recovery time is independent of disturbance frequency such that, on average, the time spent recovering from a disturbance event and therefore being in an unhealthy state is $1/r_i$, where r_i is the resilience of site i expressed as an annual recovery probability. Similarly, the time spent waiting until the next disturbance event is $1/d_i$ on average, where d_i is the annual probability of a catastrophic disturbance at site i. Assuming independent disturbance events, the probability a site is healthy at any point in time can therefore be expressed as

$$p_i = \frac{r_i}{d_i + r_i}. \tag{3}$$

The parameter p_i can also be interpreted as the proportion of time site i spends in a healthy state and thereby effectively contributes to the maintenance of ecosystem functioning and services.

To understand the impact of protected areas with both objectives in mind, we solved a very simple reserve-selection scenario with just 2 potential reserve sites, in this case coral reefs. We assumed both reefs contained only one habitat type and were of equivalent conservation value. The only difference between the 2 reefs (without loss of generality) was that reef 1 was exposed to a higher risk of catastrophic cyclone damage than reef 2 such that $d_1 > d_2$. In this case, we defined ***risk*** as a potential negative impact on the characteristics of each reef that is valued from a conservation point of view: the presence of a living coral framework. Here, we considered ***risk*** equivalent to disturbance probability. A reef was considered healthy only when it had fully recovered from disturbance. Recovery occurred when coral cover returned to some predisturbance level, and the process of recovery simply referred to the increase in live coral cover up this predisturbance extent. In the absence of protection, we assumed both reefs recovered from disturbance at the same rate. Nevertheless, if action were taken to protect a reef from fishing by placing it in a reserve, then this reef would benefit from an improved recovery rate such that $r_u > r_f$, where r_u is the annual recovery probability of an unfished, or protected, reef and r_f is the annual recovery probability of a fished, or unprotected, reef.

Because eliminating fishing pressure from a reef incurs a cost, in this case the same for both reefs, solutions to this 2-reef problem are subject to the budgetary constraint: $y_1 + y_2 = 1$, where y_i is a control variable that defines the action taken at each site such that $y_i = 1$ if a decision is made to protect reef i and $y_i = 0$ if the reef is not protected. Because this budgetary constraint allows for protection of only 1 of the 2 reefs, it is necessary to know under what combinations of recovery and disturbance rates it is optimal to invest in protecting the reef at higher risk ($y_1 = 1$), as opposed to protecting the reef at lower risk ($y_2 = 1$). Because the goal of both the problems described above is to optimize the conservation outcome within a fixed budget, they can both be considered maximum-coverage approaches (Camm et al. 1996).

Pairwise comparisons between different levels of risk provide a useful basis to begin exploring the problem of making conservation decisions under the specter of uncontrollable risk. In reality, it is more likely that decisions as to which areas should be protected will have to be made between a group of sites encompassing a spectrum of risk. In the 2 reef examples above, decisions on whether to protect reefs at higher or lower risk are constrained by polarity (i.e., protecting the site at either highest or lowest risk). It is not clear whether such polar protection strategies will lead to optimal conservation outcomes in situations in which sites under more than 2 levels of risk are available for reservation.

We extended the problem of maximizing the expected number of healthy reefs to a case in which there was a cluster of n reefs but only one reef could be protected from fishing. The protected reef recovered from disturbance with an annual probability of r_u, whereas all other reefs in the cluster recovered with probability r_f. If the first reef in the cluster was protected, from Eq. 1 the expected number of healthy reefs in our n reef system would be

$$p_1 + p_2 + \ldots\ldots p_n = \frac{r_u}{d_1 + r_u} + \frac{r_f}{d_2 + r_f} + \ldots\ldots \frac{r_f}{d_n + r_f}. \tag{4}$$

As an example, we considered the case in which each reef in the cluster had a unique annual disturbance probability with average return times ranging from 100 years ($d = 0.01$) to 2 years ($d = 0.5$). These values capture the spectrum of disturbance regimes that could be expected on coral reefs. On the basis of coral recovery rates commonly reported, we allowed fished or unprotected reefs to recover with an annual probability of $r_f = 0.05$, an expected recovery time of 20 years. Protected and therefore unfished reefs must recover faster than this.

Great Barrier Reef Case Study

We investigated the optimal reef to protect with regard to cyclone risk in 2 groups of 5 reefs on the Great Barrier Reef (GBR), Australia. One group was located in the Torres Strait in the far northern part of the GBR, an area at low risk of cyclonic disturbance (Puotinen 2007). The second group was in the middle section of the reef, an area of very high cyclone risk (Puotinen 2007). All the reefs within each group represent a single reef bioregion (Commonwealth of Australia 2005). Aiming to protect 1 reef of each bioregion would be a realistic conservation target for many nations with coral reefs. In 2004 the Great Barrier Reef Marine Park was rezoned with the goal of having at least 20% of the area of each reef bioregion within no-take marine reserves. By protecting 1 reef out of each group of 5, we used essentially the same target.

We based estimates of the risk of physical damage from cyclone-generated waves at each reef on modeled predictions of cyclone disturbance on the GBR from 1969 to 2003 (see Supporting Information for full details). Because most of the reefs on the GBR are protected from long-period oceanic swells by the outer barrier reefs, the intensity and duration of surface winds provide a reasonable estimate of the wave climate likely to arise from cyclones (Madin et al. 2006). In addition to wave-induced physical damage, cyclonic events can also have other disturbing effects on coral reefs, such as the presence of low-salinity water due to river outfall and heavy rain. We did not consider the impact of these additional factors.

We found the optimal reef to protect under a series of expected recovery probabilities on protected reefs and for 2 different recovery scenarios on unprotected reefs. First, an average of 10 years ($r_f = 0.1$), realistic for the GBR where there is no current or historical exploitation of herbivorous fishes (Connell et al. 1997), and second, an average of 50 years ($r_f = 0.02$), more likely for reefs exposed to heavy exploitation of grazing herbivores (Mumby 2006).

Results

Maximizing the Probability of at Least One Healthy Reef

Maximizing the probability that at least 1 of the 2 reefs was always in a healthy state was equivalent to minimizing the chance that both reefs would be in a bad state. On the basis of Eq. 3 and the budgetary constraint, we expressed the probability that at least one of our reefs was healthy as

$$1 - (1 - p_1)(1 - p_2) = 1 - \left(\frac{d_1}{d_1 + r_u y_1 + r_f(1 - y_1)}\right) \times \left(\frac{d_2}{d_2 + r_u(1 - y_1) + r_f y_1}\right). \tag{5}$$

We were interested in knowing under what conditions this value would be maximized by protecting the higher-risk reef (reef 1), strategy $y_1 = 1$. By maximizing Eq. 5 we found that when

$$\left(\frac{r_u}{r_f} - 1\right)\left(\frac{d_1}{d_2} - 1\right) < 0, \tag{6}$$

the higher-risk reef (choose $y_1 = 1$, $y_2 = 0$) should be protected. Because recovery on the protected reef r_u, was always faster than on the unprotected reef r_f , r_u/r_f must be >1. Similarly d_1 was constrained to have a higher disturbance probability than d_2, so d_1/d_2 must also be >1. These 2 conditions combined mean the inequality in Eq. 6 would never be true (see Supporting Information for proof of this with multiple reefs). Therefore when the conservation objective was to ensure that at least 1 of the 2 reefs was in a healthy state, the best strategy was always to protect the reef at lower risk of catastrophic disturbance, and we set $y_1 = 0$.

Maximizing the Expected Number of Healthy Reefs

From Eq. 1 we derived the expected number of healthy reefs in our 2-reef system with

$$p_1 + p_2 = \frac{r_u y_1 + r_f(1 - y_1)}{d_1 + r_u y_1 + r_f(1 - y_1)} + \frac{r_u(1 - y_1) + r_f y_1}{d_2 + r_u(1 - y_1) + r_f y_1}. \tag{7}$$

We were interested in knowing under what conditions this value would be maximized by protecting the higher-risk reef (reef 1) or in other words when would $y_1 = 1$ be the best strategy. On the basis of Eq. 7, when

$$\frac{r_u r_f}{d_1 d_2} > 1, \tag{8}$$

the higher-risk reef should be protected (Fig. 1). We simplified this result into 2 variables, the annual recovery probability for the low-risk reef when protected relative to its disturbance probability (r_u/d_2) and the annual probability of recovery for the higher-risk reef when unprotected relative to its disturbance probability (r_f/d_1) (Fig. 1). Because r_u was assumed to be greater than r_f and d_2 was constrained to be $<d_1$, it followed that r_u/d_2 must be larger than r_f/d_1, such that all possible scenarios were captured in the bottom right-hand half of Fig. 1. Within this decision space, 3 general rules arose. (1) If the lower-risk reef were expected to be in a degraded state more than half of the time, even when unfished ($r_u/d_2 < 1$, from Eq. 3), then protection would always be given to the lower-risk reef (section A of Fig. 1). (2) If on the other hand, the higher-risk reef were likely to be in a healthy state more than half the time, even when fished ($r_f/d_1 > 1$), then the expected number of healthy reefs in the system would always be maximized by offering protection to this higher-risk reef (section B of Fig. 1). (3) If neither of these conditions applied then the decision as to whether the higher- or lower-risk reef should be protected would depend on whether the specific scenario fell above or below the inequality described in Eq. 8 (section C of Fig. 1). This result contrasted with the previous case in which the lower-risk reef was always protected. The change in optimal protection strategy occurred because the return from investing in one reef or the other varied depending

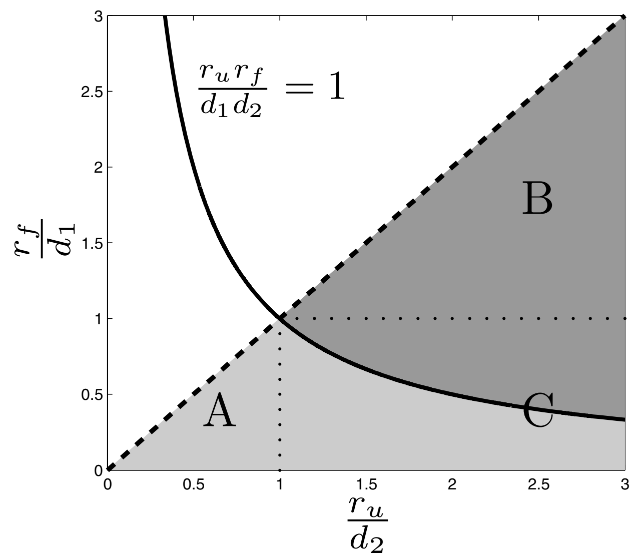

Figure 1. Illustrated decision space for maximization of the expected number of healthy reefs in a 2-reef system. The decision space is simplified into 2 variables: the recovery rate of the reef at low risk when protected, relative to its disturbance rate (x-axis), and the recovery rate of the reef at high risk when unprotected, relative to its disturbance rate (y-axis). In section A it is always preferable to protect the lower-risk reef. In section B it is always preferable to protect the higher-risk reef. In section C the best decision depends on which side of the solid black line the scenario falls. See text for definitions of variables.

on the system. When recovery rates were assumed to be slow, the biggest gain, in terms of the probability of a reef being in a healthy state, occurred with protection of the reef with low disturbance risk (Fig. 2). As the expected speed of recovery increased, the low-risk reef was likely to be in a healthy state regardless of protection status, whereas investing in the higher-disturbance-risk reef resulted in a big improvement in expected reef health and therefore a greater return on investment.

Maximizing the Expected Number of Multiple Reefs

When reefs encompassed a wide spectrum of disturbance risk, protection of neither low- nor high-risk reefs provided the optimal conservation outcome. At very low levels of disturbance risk ($<\sim 0.1$), the expected number of healthy reefs in the system increased rapidly with the reservation of progressively higher-risk reefs. At higher levels of disturbance risk ($>\sim 0.15$), the reservation of progressively higher-risk reefs resulted in a gradual decline in the expected number of healthy reefs. Increasing the expected recovery probability of protected reefs increased the level of risk at which conservation benefit was maximized, thus increasing the range of risk

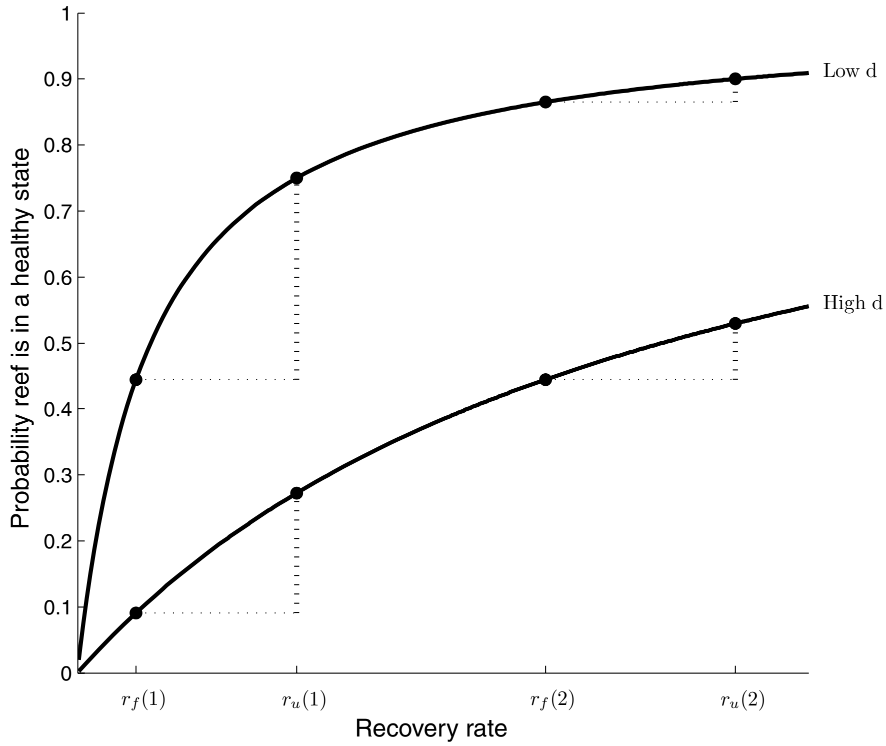

Figure 2. Conceptual diagram of how the expected benefit of reserving reefs with different disturbance rates (d), changes as a function of the expected recovery rate. When the expected recovery rate is low (scenario 1), the benefit of reservation (vertical dashed line) is maximized be protecting the low-disturbance reef. When the expected recovery rate is higher (scenario 2), the expected benefit of reservation is instead largest on the high-disturbance reef. In this context, a healthy reef is a reef with relatively high live coral cover and recovery rate is the speed at which coral cover increases following disturbance. See text for definitions of variables.

over which it was optimal to protect the more vulnerable reefs. The actual conservation benefit in terms of an improvement in the expected number of healthy reefs depended on how many reefs were included in the cluster.

For each curve in Fig. 3 it was possible to analytically derive the annual disturbance probability at which the benefit of reservation was maximized. This occurred for the value of *d* where the difference between the expected

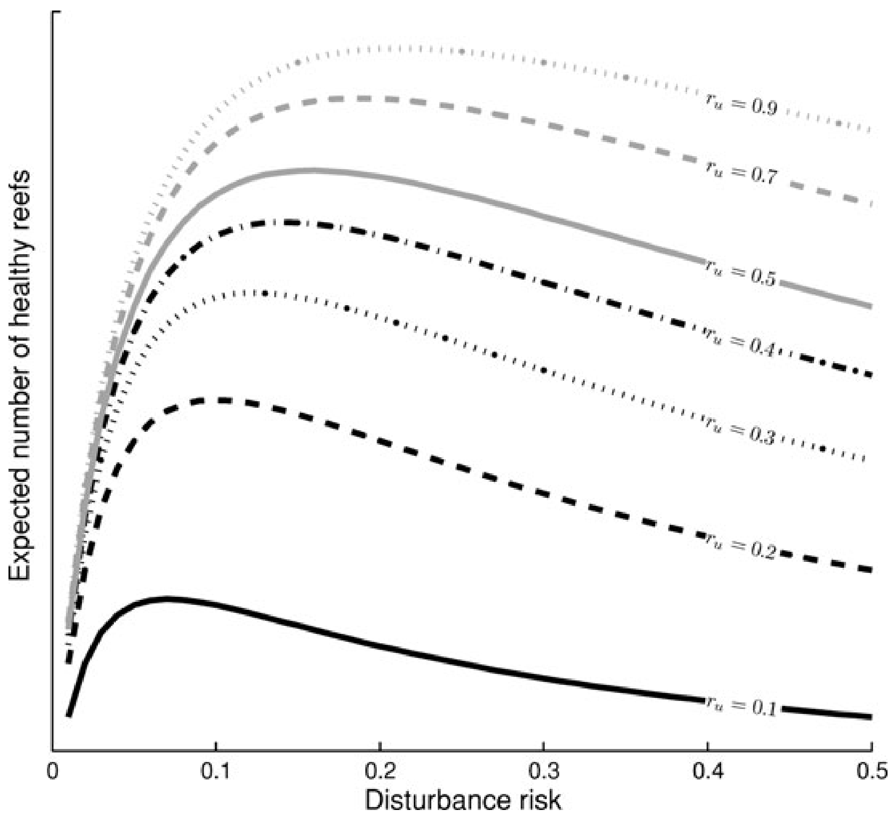

Figure 3. The relative number of healthy reefs expected as a result of reserving a single, successively higher-risk reef, out of a cluster of reefs. The y-axis is unitless because the actual number of healthy reefs expected depends on how many reefs are included in the cluster. Each line represents a different expected recovery rate on the protected reef (r_u). In all cases the recovery rate on unprotected reefs is set at $r_f = 0.05$, an average recovery time of 20 years.

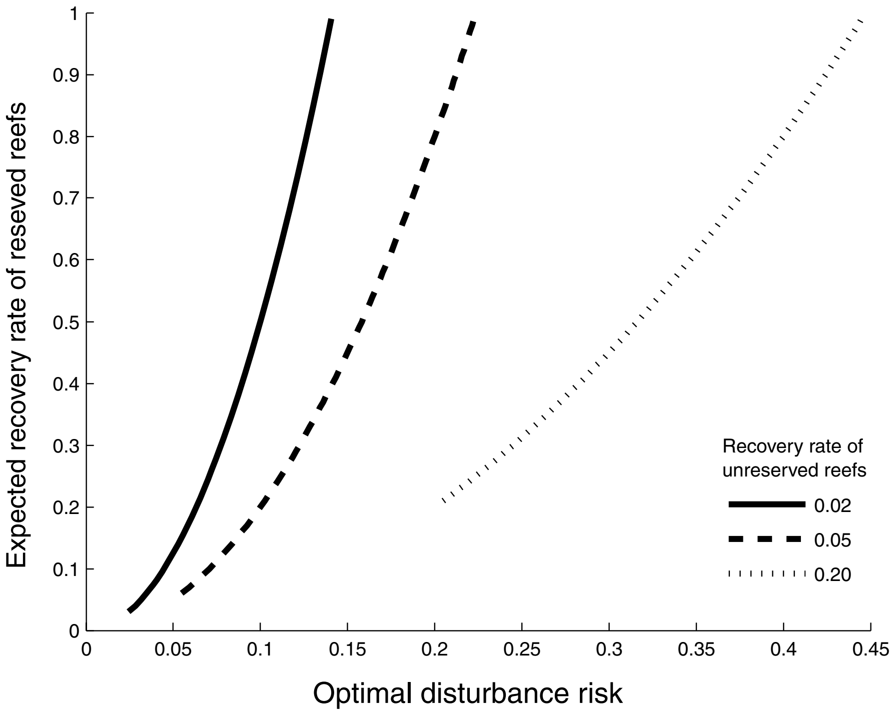

Figure 4. The level of disturbance risk in which the return on investment from reservation is the greatest. This value is plotted as a function of the expected recovery on protected reefs for 3 different expected rates of recovery on unprotected reefs.

health of a protected reef $r_u/(r_u + d)$ (from Eq. 3) and the expected health of a fished reef $r_f/\left(r_f + d\right)$ (from Eq. 3) were the largest. The annual disturbance probability, d^*, which gave the maximum benefit of reservation, was found by differentiating the benefit function, equating it to zero, and solving for d. The benefit of reservation was maximized when,

$$d^* = \left(r_u r_f\right)^{\frac{1}{2}}. \tag{9}$$

This provided an elegant solution to the problem of deciding the best reef to protect given a number of reefs with different disturbance probabilities. With regard to disturbance risk, the best reef to protect was the one with d closest to d^*, or in essence, the reef that delivered the highest rate of return (Fig. 2). The optimal value of d was the geometric mean of the 2 recovery probabilities, r_u and r_f. Increasing the expected recovery probability of unprotected reefs raised the optimal risk tolerance for all expected probabilities of recovery on protected reefs (Fig. 4). As was the case in the 2-reef example, when we expected the unprotected reefs to do well, the optimal conservation outcome was more likely to be achieved through the protection of higher-risk reefs. A single group of reefs might not encompass the pronounced variation in disturbance risk displayed on the *x*-axis of Fig. 3. If the actual range of risk fell on the right-hand side of the optimal line in Fig. 4, then the expected benefit would be maximized through protection of the lowest-risk reef in the group. If on the other hand all risk predictions fell on the left-hand side of the same line, then it would be advisable to direct protection to the highest-risk member of the group.

Great Barrier Reef Case Study

The annual risk of cyclone damage in the Torres Strait group ranged from $d = 0.08$ to $d = 0.12$. Risks in the midreef group ranged from $d = 0.32$ to $d = 0.45$. On the basis of these predictions of risk, the optimal reef to protect depended on the expectation of recovery on protected reefs and on the scenario of recovery on unprotected reefs.

Even within the same reef system (i.e., the GBR), the optimal conservation decision with regard to risk can change substantially across space. In general the expected number of healthy reefs in the low-risk group was maximized by protecting the higher-risk reefs within the group, whereas protecting the lower-risk reefs maximized the expected number of healthy reefs in the high-risk group (Fig. 5). The optimal reef to protect could also change depending on the expected performance of reserves in improving the postdisturbance recovery of protected reefs. Under the slow nonreserve recovery scenario ($r_f = 0.02$), increasing the expected annual recovery probability of the protected reef above $r_u = 0.1$ had the effect of switching the optimal strategy in the low-risk group from protecting Uluf Reef ($d = 0.08$), the lowest-risk reef, to protecting progressively higher-risk reefs (Fig. 5). For expected recovery probabilities inside the reserve of greater than $r_u = 0.3$, it was always optimal to protect Murabar Reef ($d = 0.12$), the

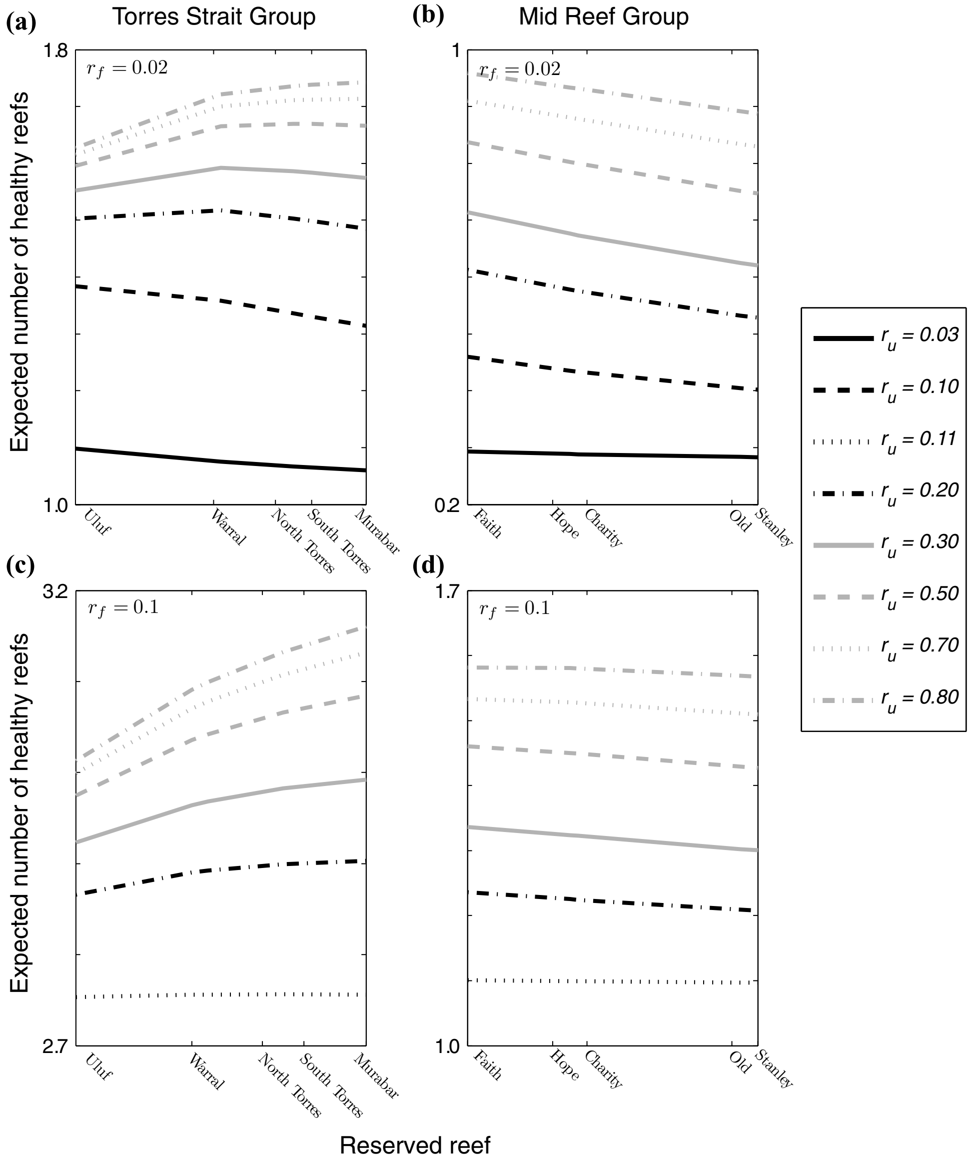

Figure 5. The overall number of healthy reefs that could be expected as a result of reserving each different member of 2-reef groups on the Great Barrier Reef. The results are presented for a series of expected recovery rates (r_u) inside reserves and for 2 different scenarios of recovery on unprotected reefs (an average of 50 years [$r_f = 0.02$, panels a and b] and an average of 10 years [$r_f = 0.1$, panels c and d]). Reefs increase in cyclone disturbance rate from left to right along the x-axes (see Supporting Information).

highest-risk reef in the group. If reefs outside the reserve were able to recover with the improved annual probability of $r_f = 0.1$, the expected number of healthy reefs in the low-risk group would always be optimized by protecting Murabar Reef, regardless of the expected recovery rate inside the reserve. In contrast, within the higher-risk group, it was always optimal to protect Faith Reef ($d = 0.32$), the lowest-risk reef, regardless of the expected recovery in either protected or unprotected areas (Fig. 5).

Discussion

The general goal of conservation action on coral reefs is to sustain the ability of reefs to provide the ecosystem goods and services on which so much human welfare depends (Bellwood et al. 2004). The specific conservation objectives used to achieve this goal embody different levels of risk aversion. Consequently, the optimal protection strategy with regard to the risk of uncontrollable disturbances can differ dramatically from one objective to another. Aiming to ensure that at least one healthy reef remains in an area is a particularly risk-averse objective, and with this objective there is no reward for having more than one healthy reef, so there is no point tolerating any risk to achieve it. As a result of this risk aversion, the optimal strategy is always to invest conservation efforts in the lowest-risk site, the place where the return on investment is most certain. In contrast, aiming to maximize the overall number of healthy reefs is a more risk-tolerant objective in which, under some circumstances, one is willing to accept additional conservation risk in the hope of a larger payoff. Although it is possible to mathematically determine the strategy that will best achieve the stated objective, the answer as to which conservation objective should be used, and therefore how much risk should be tolerated, is a social rather than an ecological question.

When applying a conservation objective that is tolerant of some risk, such as maximizing the expected number of healthy reefs, the extent to which one expects protection to improve the resilience of an area can profoundly change the optimal conservation strategy with regard to the risk of uncontrollable disturbance. In many instances, if reserves act as one hopes and improve the postdisturbance recovery of habitats within their bounds, then the greatest systemwide benefits may be gained by offering protection to sites at higher risk of being damaged by large-scale disturbances such as cyclones. The optimal protection strategy is, however, determined by the expected benefit of protection in concert with the actual level of disturbance risk and the resilience of those sites outside reserves. If disturbance probabilities are very high, then it is best to protect lower-risk sites regardless of the expected recovery inside reserves. We considered one type of disturbance in one region, so it is not clear which one of these strategies is likely to be more prevalent globally. Although cyclone risk is higher on the GBR than for other coral regions such as the Caribbean (Gardener et al. 2005), the high level of protection afforded to the GBR suggests that potential recovery rates are also greater than those that could be expected elsewhere. Despite this, the range of cyclone risks over much of the GBR (Puotinen 2007) suggest that even under very high recovery rates, the majority of the reef would be best served by protecting the lowest-risk sites. Given that the annual risk of other major disturbances, such as coral bleaching, can be equally high, if not greater (Hoegh-Guldberg 1999; Donner et al. 2005), it may be the case that for many regions of the world, protecting the weak will never be the optimal strategy.

Seeking to protect low-risk reefs should not, however, be considered a substitute for seeking representative protection of reef habitats. This would be detrimental for reef biodiversity, and because reefs are unlikely to be completely independent with regard to risk, protecting only lower-risk sites may have the unintended consequence of congregating protection in a limited area. Similarly, the assumption is made here that the mean health of reefs in a system is a good indication of reserve success. It may be the case that other motivations for creating marine reserves, such as fisheries spillover, are perhaps better served by having a small number of very healthy reefs rather than a large number of reasonably healthy reefs.

We acknowledge that fine-scale data on the kind of disturbance risk we considered is challenging to obtain. Events such as cyclones are inherently nonlinear and therefore hard to predict with certainty. Although we did not explicitly consider uncertainty in our disturbance predictions, the expected benefit of reservation declined more gently on the higher-risk side of optimal, which suggests that where there is some uncertainty as to the true spectrum of disturbance risk it is safest to protect slightly higher-risk sites. Substantial uncertainty is also likely to exist in the predicted resilience of unprotected areas. This uncertainty arises in part because of the wide spectrum of anthropogenic disturbances that unprotected areas are exposed to and in part because the scientific community has generally paid scant attention to the role unprotected areas should play in marine conservation. Here we have shown that even when the recovery of habitat at unreserved sites is almost negligible it can, under realistic rates of disturbance, still be optimal to protect high-risk sites. An important distinction exists between risk and uncertainty, with risk being an inherently more quantifiable property (Knight 1921). Our results provide a guide to making conservation decisions under conditions of risk. Although the results give some indication of the appropriate response to uncertainty in the parameters, a different set of approaches are needed to determine optimal decisions in cases of severe uncertainty, for example the “infogap” method described by Halpern et al. (2006).

We used a very simple example to illustrate how specific conservation objectives and the expected performance of marine reserves can influence conservation prioritization under uncontrollable risk. Our study had 4 main simplifications. First, we considered cyclonic disturbance a binary condition rather than an event that can cause a spectrum of damage to reef habitat. Second, we assumed recovery probabilities are independent of both disturbance frequency and the number of healthy reefs. Although there is often an expectation that cyclone damage will be more severe on reefs with longer historical return times between events (Gardner et al. 2005), in a long-term study on the Great Barrier Reef, Connell et al. (1997) concluded that disturbance history does not influence vulnerability. Similarly, recovery rates may be depressed when there are few healthy reefs in the system. Despite the plausibility of this scenario, there is little empirical evidence to suggest that reef recovery is limited by the number of available recruits.

Third, we have not accounted for the likely change in disturbance probability with time. We based our cyclone predictions on records from a relatively quiet period for cyclonic activity on the GBR (Puotinen et al. 1997). Considering longer periods of time may substantially change our assessment of disturbance regimes (Nott 2003). It is also likely that the frequency of severe tropical storms will increase under the influence of global climate change (IPCC 2001). Fourth, we ignored possible positive effects of cyclone disturbance on coral reefs. Given appropriate information, the first 3 of these simplifications could easily be addressed within a risk-benefit framework, such as the one described here. The potential benefits of disturbance, such as maintenance of coral diversity, are, however, extremely difficult to quantify, and it is far from clear how such benefits should be traded against the negative effects of a damaged reef environment. Considering the chronic stress that many of the world's reefs are under, the negative aspects of storm damage may substantially outweigh the benefits.

The presence of uncontrollable risk is a pervasive aspect of marine conservation. The proper treatment of risk has become a cornerstone of all forms of investment and insurance, fundamentally changing the nature of these industries and pulling successful outcomes away from shear luck and into the realms of predictability (Bernstein 1996). Conservation investment should be no different. Here we offer a guide to the optimal amount of risk to tolerate in marine conservation actions. Perhaps the best answer to the question, Should we protect the strong or the weak? is protect the weak of the strong and the strong of the weak. Much has been made of the link between protected areas and resilient marine habitats; surely, it is now appropriate to look beyond the obvious benefits of resilience and consider how this resilience can best be used to deliver on conservation objectives. We encourage marine conservation planners to be less passive in the face of uncontrollable risk because the optimal conservation decision will always be out of reach without an adequate treatment of risk and the consequences of reservation.

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Supporting Information

Details of cyclone-disturbance modeling methodology and predictions for the GBR (Appendix S1) and proof of inequality in Eq. 6 with multiple reefs (Appendix S2) are available as part of the on-line article. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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