

LETTER

Dynamic marine protected areas can improve the resilience of coral reef systems

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Abstract

Marine Protected Areas are usually static, permanently closed areas. There are, however, both social and ecological reasons to adopt dynamic closures, where reserves move through time. Using a general theoretical framework, we investigate whether dynamic closures can improve the mean biomass of herbivorous fishes on reef systems, thereby enhancing resilience to undesirable phase-shifts. At current levels of reservation (10–30%), moving protection between all reefs in a system is unlikely to improve herbivore biomass, but can lead to a more even distribution of biomass. However, if protected areas are rotated among an appropriate subset of the entire reef system (e.g. rotating 10 protected areas between only 20 reefs in a 100 reef system), dynamic closures always lead to increased mean herbivore biomass. The management strategy that will achieve the highest mean herbivore biomass depends on both the trajectories and rates of population recovery and decline. Given the current large-scale threats to coral reefs, the ability of dynamic marine protected areas to achieve conservation goals deserves more attention.

Keywords

Coral reefs, dynamic management, marine reserves, periodic closures, resilience.

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INTRODUCTION

Marine protected areas (MPAs) are a popular and well-established tool for the management and protection of biodiversity in marine environments (Russ 2002; Wood 2007). Although MPAs are generally established as permanent closures, discussions in the recent conservation literature have argued that a shift to more dynamic and adaptive management of marine resources is demanded by the current challenges facing marine environments (Agardy *et al.* 2003; Tompkins & Adger 2004; Gerber *et al.* 2007; Hughes *et al.* 2007a). Moveable MPAs are attractive for a host of reasons: managers can adaptively learn from present actions, and respond to new information (Grafton & Kompas 2005; Hughes *et al.* 2007a); they can help ensure that MPAs adequately capture spatially dynamic resources (Hobday & Hartmann 2006); they address the social reluctance of subsistence fishermen to permanently close important resources (McClanahan *et al.* 2006); re-opening of closed areas to extraction allows material access to the benefits accrued in protected areas (Cinner *et al.* 2005).

Importantly, dynamic reserves allow managers to avoid the diminishing returns naturally associated with MPAs. Reservation yields are temporally dynamic and depend heavily on a reef's current condition and its likely trajectories of recovery (Game *et al.* 2008). These gains are clearly subject to diminishing returns because MPAs cannot continue to improve reef condition indefinitely. Once habitats or populations inside a protected area have fully recovered, further protection of the same area will maintain a high level of condition, but will yield negligible improvement. If this protection were offered to a degraded site instead, the expected improvement each year will be comparatively large in the short term, and could potentially outweigh the loss of condition on the newly unprotected reef. Tuck & Possingham (2000) also point out that establishing fixed protected areas removes management options and hence, in theory, cannot be superior to strategies that allow adjustment in the placement of MPAs.

Of all marine environments, coral reefs are probably the most commonly managed through the creation of MPAs (Wood 2007). A suite of anthropogenic impacts have left

many of the world's coral reefs degraded and at risk of shifting into alternate and undesirable states from which it is difficult to return (Hughes *et al.* 2003; Bellwood *et al.* 2004; Mumby *et al.* 2007). In many cases, these phase-shifts are triggered by natural disturbances such as hurricanes, to which coral reefs had been previously resilient (Gardner *et al.* 2005). The ability of coral reefs to resist such phase shifts primarily depends on the presence of grazing herbivores (typically teleost fish), that help prevent fast-growing algae from outcompeting corals for space (Bellwood *et al.* 2004; McManus & Polsenberg 2004; Newman *et al.* 2006; Hughes *et al.* 2007b; Mumby *et al.* 2007). In many countries, populations of herbivorous fish on coral reefs have been substantially depleted as a result of fishing pressure (Aswani & Hamilton 2004; Bellwood *et al.* 2004). Herbivore populations can be protected from fishing through the creation of no-take MPAs, and these have been strongly advocated as a way to promote the resilience of reef systems (Mumby *et al.* 2007). This includes the threat of large-scale catastrophes such as coral bleaching, which are beyond the control of managers (Hughes *et al.* 2007b). From both social and ecological perspectives, a high herbivore biomass is a good measure of effective conservation as it increases the fish available for consumption, helps maintain important ecosystem processes and promotes the resilience of the system to perturbations (Hughes *et al.* 2003).

By periodically moving protection to reefs that stand to gain the most (those with low herbivore biomass) a dynamic MPA strategy may be able to maintain adequate herbivore populations on a larger number of reefs than a static MPA strategy, thereby ensuring greater average resilience across the system. In addition, there are further reasons to believe that a dynamic MPA strategy would improve the resilience of coral reef systems. Because of the high level of exploitation commonly experienced by unprotected coral reefs (Aswani & Hamilton 2004; Hawkins & Roberts 2004), the static application of fully protected areas risks the creation of a small number of healthy reefs and a large number of reefs where herbivores are functionally absent. Letting unprotected reefs decline to near zero resilience is likely to negatively impact both the ecological and social systems associated with coral reefs (Adger *et al.* 2005; Hughes *et al.* 2005).

There is a long and well-documented history of traditional spatial management of coral reef resources being dynamic, especially in the Asia-Pacific region (Johannes 1982; Colding & Folke 2001; Cinner 2007). This management usually takes the form of periodic prohibition of harvest on particular reefs, akin to a dynamic strategy of rotational closures (Cinner 2007). A number of studies have investigated whether the dynamic application of a single protected area can improve the social and conservation yields of subsistence fisheries, and how this approach affects

the successful implementation of coral reef MPAs (Cinner *et al.* 2005, 2006; McClanahan *et al.* 2006; Cinner 2007). However, investigations into whether explicitly dynamic protected area strategies can improve the resilience of entire reef systems, either empirical or theoretical, have been largely absent.

Dynamic MPA management can be implemented either with or without knowledge of the reefs' current condition (Table 1). Protected areas could simply be moved in a rotational fashion, assuming that the herbivore populations always decline on unprotected reefs and therefore previously unprotected reefs will benefit most from protection. Alternatively, an adaptive management strategy would monitor reefs to determine which locations are likely to experience the maximum benefit from protection. Although an adaptive approach to protected areas should be able to deliver better outcomes in terms of system resilience, acquiring the knowledge needed to successfully implement it may be prohibitively expensive. As the funds spent acquiring the information necessary to adaptively move protected areas may be spent on other conservation actions, a reef manager must be confident that the benefits gained justify the expense (Hauser *et al.* 2006). In this study we focus solely on the utility of rotational protection as, relative to full adaptive management, there are fewer financial, knowledge, and institutional barriers to implementing this strategy.

Explicitly aiming to promote and maintain ecosystem resilience has been embraced as a new paradigm for the management of coral reef systems (Hughes *et al.* 2005). With the objective of maximizing the average resilience of coral reef systems (measured as mean herbivore biomass achieved in the reef system), we investigate whether it is ever beneficial to periodically move the location of no-take protected areas.

METHODS

To compare the relative performance of rotational and static MPA strategies, we consider a system of N reefs, R of which are reserved and protected from fishing at any one time. The total herbivore biomass on each reef, b , ranges between 0 and b_{\max} . In the absence of protection, the population of herbivores on a reef is subject to fishing and will always decrease with time according to a decline model $f(b)$. If a reef is protected, the population of herbivores is freed from fishing pressure and the biomass is assumed to increase according to a density-dependent recovery model $g(b)$. Both decline and recovery functions are assumed to be independent of the amount of protection. This assumption implies that fishing effort is the same on any fished reef, and that external recruitment from larval spill-over does not significantly affect the rate of herbivore recovery.

Table 1 Three conceptual strategies for MPA implementation

1. *The static strategy.* *R* reefs are designated as static MPAs. The remaining reefs are never protected and therefore herbivore populations on them decline to near zero ('very low levels', or 'functionally extinct/absent').
2. *The rotational strategy.* *R* reefs are protected initially, and this protection is moved subsequently. With a set frequency, protection is removed from the reefs that have been protected for the longest, and is placed onto the reefs that have remained unprotected the longest.
3. *The adaptive strategy.* The *R* reefs chosen for protection are moved at each time step to the reefs that are predicted to experience the greatest increase in condition if protected, based on the expected recovery trajectory. However, the predicted increase in reef condition depends on the current condition of the reefs, a quantity not always known. Managers are able to learn about this quantity by monitoring the condition of reefs.

Strategies 2 and 3 are dynamic.

Despite herbivores being important targets of artisanal fisheries in most coral reef regions (Aswani & Hamilton 2004; Bellwood *et al.* 2004; Hawkins & Roberts 2004; McClanahan *et al.* 2007), very few data exist on the decline in herbivores on coral reefs as a result of fishing pressure. This is because few previously closed reefs have been studied for any significant length of time after protection was removed, and where it has, research has generally been focused on larger, more commercially important species (e.g. Russ & Alcala 1996; Mapstone *et al.* 2004), which are rarely herbivorous. Additionally, short observation periods and stochasticity have made it difficult to determine the entire decline trajectory. Intuitively, catch rates are likely to be slow at very low levels of herbivore biomass, although by this point resilience is likely to be functionally zero. Given that insufficient information currently exists for a complicated parameterization of the decline function, in each of the following analyses, we model the decline in fished herbivore biomass as asymptotic:

$$\frac{db}{dt} = f(b) = -\lambda \left[\frac{b}{b_{\max}} \right]. \quad (1)$$

The trajectory that a recovering herbivore population will take following protection is similarly uncertain (Micheli *et al.* 2004; Newman *et al.* 2006). Although information on recovery rates is crucial for determining optimal protected area strategies, good descriptions of recovery trajectories have been limited 'by an inability to study well enforced closed areas over sufficiently long and undisturbed periods' (McClanahan *et al.* 2007). Three plausible, and theoretically intuitive models of the recovery trajectories taken by herbivorous fishes on coral reefs are: linear, asymptotic, and logistic (McClanahan *et al.* 2007). These models can be mathematically described as follows.

The linear recovery model

The biomass of herbivores increases by a constant amount each year, until the maximum herbivore biomass is reached (Fig. 1a):

$$\frac{db}{dt} = g(b) = \begin{cases} r_1 & \text{for } 0 \leq b < b_{\max} \\ 0 & \text{for } b = b_{\max} \\ -r_1 & \text{for } b > b_{\max} \end{cases}. \quad (2)$$

The asymptotic recovery model

The biomass of herbivores increases by an amount each year that declines linearly as biomass approaches its maximum. The protection of reefs with low biomass therefore results in a rapid increase in total biomass; at higher levels of biomass, density dependence reduces the rate of increase (Fig. 1b):

$$\frac{db}{dt} = g(b) = r_a \left(1 - \frac{b}{b_{\max}} \right). \quad (3)$$

The logistic recovery model

Herbivore biomass on protected reefs increases at a rate that responds quadratically (nonlinearly) to the current level of biomass. At very low levels, biomass increases slowly, however as the population grows, the rate of biomass accumulation increases before slowing again under the influence of density dependence. Therefore, the protection of reefs with an intermediate level of herbivore biomass results in the greatest absolute biomass increase (Fig. 1c):

$$\frac{db}{dt} = g(b) = r_g b \left(1 - \frac{b}{b_{\max}} \right). \quad (4)$$

For all three recovery models, we compare the mean herbivore biomass across our reef system as a result of (1) static MPAs and (2) dynamic rotational MPAs. The adaptive movement of protected areas is not considered here. There are therefore six different scenarios that can be treated analytically – a combination of linear, asymptotic or logistic recovery, protected by either rotational or static schemes (Table 2). To compare the relative benefits of static and rotational closures, we model the reef system deterministically, using continuous-time differential equations. For the rotational strategy, this method assumes that the frequency

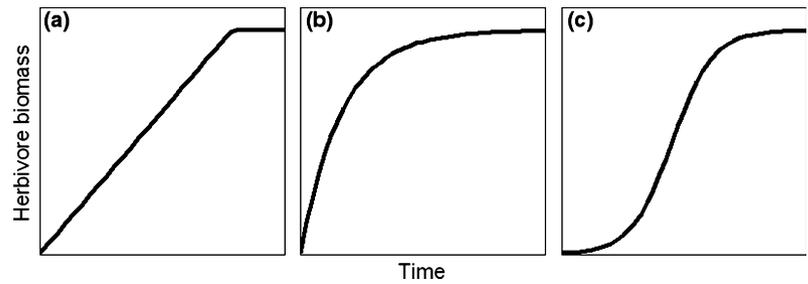


Figure 1 Three possible models for the recovery of herbivore biomass within marine protected areas: (a) Linear recovery; (b) Asymptotic recovery; (c) Logistic recovery.

of protected area rotation is much faster than the rates of reef recovery and decline. Deterministic analyses give an analytic (and thus more easily interpretable) solution to the effect of the management outcomes.

Deterministic dynamics

The dynamics of the three static protection scenarios (scenarios 2, 4 & 6) can be expressed very simply. The herbivore biomass on the protected reefs reaches its maximum, b_{max} , while the unprotected reefs decline until herbivores are functionally absent ($b = 0$). The resilience of the average reef in the system (measured using the mean herbivore biomass) is therefore defined entirely by the proportion of reefs protected, regardless of the herbivore recovery model,

$$b^* = b_{max} \frac{R}{N}, \tag{5}$$

where, b^* , is the equilibrium time-averaged mean herbivore biomass across the reef system.

Under a rotational protection strategy, the resilience of the average reef is slightly more complicated. On average, each reef experiences protection, and therefore herbivore recovery, R out of every N years. In the other $(N-R)$ years, the reef will be fished, and herbivore biomass will decline. The expected change in the mean herbivore biomass can therefore be approximated by the general equation:

$$\frac{db}{dt} = g(b) \frac{R}{N} + f(b) \frac{(N-R)}{N}. \tag{6}$$

Table 2 Six different protected area scenarios resulting from the intersection of herbivore population recovery models and protected area strategies

Scenario	Recovery model	Decline model	Protection strategy
1	Linear	Asymptotic	Rotational
2	Linear	Asymptotic	Static
3	Asymptotic	Asymptotic	Rotational
4	Asymptotic	Asymptotic	Static
5	Logistic	Asymptotic	Rotational
6	Logistic	Asymptotic	Static

This continuous-time approach does not consider the temporal variability introduced by the discrete nature of temporary closure. However, the analytic equilibrium results closely approximate stochastic simulations that includes this factor (see Data S1). Using the asymptotic decline model (eqn 1) and the three alternative recovery models (eqns 2–4), the equilibrium herbivore biomass on the average reef, b^* , under the three recovery models can be calculated by solving eqn 6 for b when $\frac{db}{dt} = 0$: For linear recovery (scenario 1);

$$b^* = \frac{r_1 b_{max} R}{\lambda(N-R)}. \tag{7}$$

For asymptotic recovery (scenario 3);

$$b^* = \frac{r_a b_{max} R}{r_a R + \lambda(N-R)}. \tag{8}$$

While for logistic recovery (scenario 5);

$$b^* = b_{max} - \frac{\lambda(N-R)}{r_g R}. \tag{9}$$

RESULTS

Using eqns 7–9 we can determine when rotational protection results in greater mean herbivore biomass than static protection. These conditions depend on both the herbivore biomass recovery model and the proportion of reefs in a system that are reserved at any given time.

When recovery is linear, rotational protection is better than static protection when the proportion of a system in protected areas is greater than:

$$\frac{R}{N} > 1 - \frac{r_1}{\lambda}. \tag{10}$$

Rotational protection is therefore preferred when large proportions of the reef system can be protected. If the linear growth rate η is greater than the intrinsic rate of decline λ , then a rotational MPA strategy is always superior to a static strategy.

When recovery is asymptotic, rotational protection is better than static protection when the proportion of a system protected is greater than:

$$r_a > \lambda. \quad (11)$$

Equation 11 reveals that when herbivore recovery and decline both follow an asymptotic trajectory, a rotational MPA strategy will always perform either better or worse than a static strategy, regardless of the proportion of the system protected. Which strategy is best depends entirely on the relative rates of population recovery and decline.

For logistic recovery, rotational protection is better than static protection when the proportion of a system protected is greater than:

$$\frac{R}{N} > \frac{\lambda}{r_g b_{\max}}. \quad (12)$$

As with linear recovery, the rotational MPA strategy is superior when large proportions of the reef system can be protected.

Case study

Based on data published by (McClanahan *et al.* 2007), we parameterized the three models of herbivore biomass recovery for rates measured in fully protected areas in the Western Indian Ocean. These gave the following values: linear recover, $r_l = 8.27 \text{ kg ha}^{-1} \text{ year}^{-1}$; asymptotic recovery, $r_a = 30.14 \text{ kg ha}^{-1} \text{ year}^{-1}$; logistic recovery, $r_g = 0.36 \text{ kg ha}^{-1} \text{ year}^{-1}$. For all three recovery models, $b_{\max} = 250 \text{ kg ha}^{-1}$. Similarly, we assumed that on reefs subject to constant fishing pressure, herbivore biomass declines at a rate of $\lambda = 34.65 \text{ kg ha}^{-1} \text{ year}^{-1}$, roughly equivalent to 10% of the original biomass each year, for the first 5 years. This represents a decline rate similar to, but slightly high than, those previously reported for herbivorous reef fish fisheries (Jennings & Polunin 1996). As such, this decline model represents an estimate of heavy, unrestricted fishing pressure, and therefore, a conservative test of the utility of a rotational MPA strategy.

Given these parameter estimates and eqns 10–12, static MPAs always result in the highest mean herbivore biomass if less than 38.5% of system is reserved (Fig. 2). Under a rotational MPA strategy, each reef receives the benefit of protection too infrequently to arrest the decline in herbivore biomass that occurs during the frequent unprotected periods.

Logistic recovery model

If recovering herbivore populations follow a logistic trajectory, then rotating MPAs between reefs becomes the best strategy once 38.5% or more of the system is protected (Fig. 2; red line). With enough protection, a rotational strategy can lead to substantial gains in mean biomass compared with a static strategy. For example, at 60% reservation, the expected mean biomass resulting from a

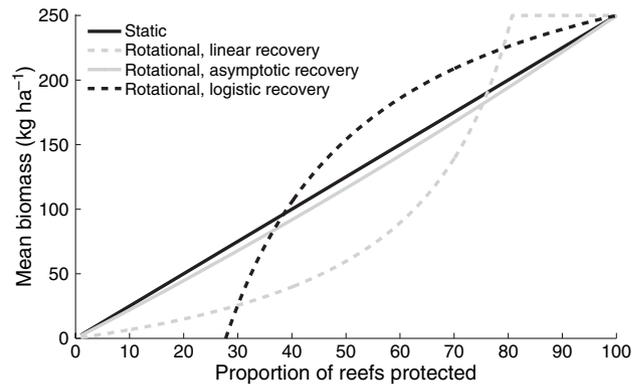


Figure 2 Comparison of the equilibrium mean herbivore biomass on the average reef under both static and rotational MPAs, with increasing levels of system protection. The black line represents static protection under all recovery models and the remaining lines represent rotational protection under different possible herbivore recovery models; logistic (red), asymptotic (blue) and linear (green) growth.

rotational strategy is 25% greater than under a static strategy. However, in the ecosystem modelled here, if less than 28% of the system is protected, a rotational strategy cannot ensure the persistence of any herbivore populations.

Asymptotic recovery model

If the herbivore populations follow an asymptotic recovery model, a rotational strategy never outperforms static protection, with the expected mean biomass remaining marginally lower than the static strategy across all levels of reservation (Fig. 2; blue line). This result is apparent from eqn 11, as the intrinsic biomass decline rate on fished reefs (λ) is faster than the intrinsic recovery rate on protected reefs (r_a).

Linear recovery model

When herbivore populations recover linearly (arguably the least realistic of the three recovery trajectories) then 76.1% of the system needs to be protected before the mean biomass is greater than with static protection (Fig. 2; green line).

These results indicate the conditions under which rotating protection across *all* reefs in the system is the best strategy, for the parameters of this case study. However, it is also possible to rotate protection among a subset of the total reefs (e.g. in a system of 100 reefs, rotating 10 MPAs between only 20 reefs, leaving the remaining 80 reefs unprotected). Using this ‘subset’ strategy, it may be possible to protect each reef in this subset frequently enough to maintain a higher mean herbivore biomass than static protection of the same number of reefs. This would mean that a dynamic rotational strategy could in fact be better

than the static strategy when only a small proportion of the system can be protected. For a given herbivore recovery model, we can determine the optimal number of reefs, S^* , to include in a dynamic rotational protected area system. An alternate interpretation of S^* is the maximum number of reefs that can be sustained with a rotational protected area strategy. First, we replace the total number of reefs, N , in eqn 6 with the subset size, S :

$$\frac{db}{dt} = g(b) \frac{R}{S} - f(b) \frac{(S - R)}{S}. \tag{13}$$

We then solve eqn 13 for b when $\frac{db}{dt} = 0$, to determine the mean herbivore biomass within the subset of protected reefs, b_S^* . The mean biomass within the entire system of N reefs is therefore:

$$b^* = b_S^* \frac{S}{N}, \tag{14}$$

given that the biomass on the reefs outside the subset will decline to zero. To determine the optimal subset size, S^* , we solve eqn 14 for S when $\frac{db^*}{dS} = 0$. Under the assumption of linear recovery this number is given by:

$$S^* = \min \left\{ R \left(1 + \frac{\eta}{\lambda} \right), N \right\}. \tag{15}$$

This function shows that the optimal subset size is always greater than the number of protected reefs, R , by a factor equal to the relative rates of recovery and decline, $\frac{\eta}{\lambda}$. The optimal subset size is restricted by the total number of reefs, N . Under the assumption of asymptotic recovery the optimal subset size is:

$$S^* = \begin{cases} N & \text{if } r_a \geq \lambda \\ R & \text{if } r_a < \lambda \end{cases}. \tag{16}$$

Equation 16 reveals that if the intrinsic rate of biomass recovery on protected reefs is equal to or faster than the intrinsic rate of decline on fished reefs, then the MPAs should be rotated among the entire set of reefs in the system. On the other, if recovery is slower than decline, the optimal subset is the number of reefs available for protection, R , in effect a static MPA strategy. If herbivore biomass recovers logistically, the optimal subset number is:

$$S^* = \max \left\{ \min \left\{ \frac{R}{2} \left(1 + b_{\max} \frac{r_g}{\lambda} \right), N \right\}, R \right\}. \tag{17}$$

Where again, the subset size cannot be larger than N , the total number of reefs in the system. With a logistic recovery function, however, we must constrain the subset size to be smaller than the number of protected reefs, R (the static MPA strategy), as it is not possible to rotate R MPAs among fewer than R reefs.

The subset strategy extends the range of conditions over which a dynamic rotational MPA strategy is superior to a

static strategy. Given the same parameters as those in Fig. 2, for a system of $N = 100$ reefs, rotating the available protection between the optimal subset of reefs always delivers a mean herbivore biomass equal to or higher than the static strategy, regardless of the amount of protection available, or the functional form of biomass recovery (Figs 3–5). This is in contrast to the full rotational strategy which, for linear recovery required that more than 70% of the reefs be protected, to outperform static protection (Fig. 3). For the asymptotic recovery model, rotation among the full set of reefs never outperformed the static MPA strategy, but the subset rotation strategy yielded equal

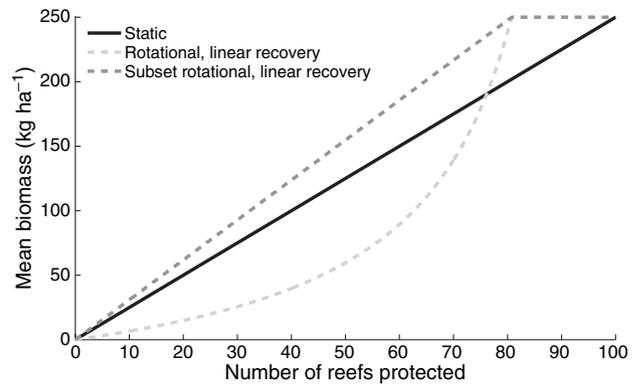


Figure 3 Comparison of expected mean herbivore biomass across a system of 100 reefs, under three different protected area strategies: static MPAs (black line), MPAs rotated amongst all 100 reefs (green line) and MPAs rotated amongst the optimal subset number (dashed grey line). All herbivore populations are assumed to recover linearly. The x-axis indicates the number of reefs able to be reserved.

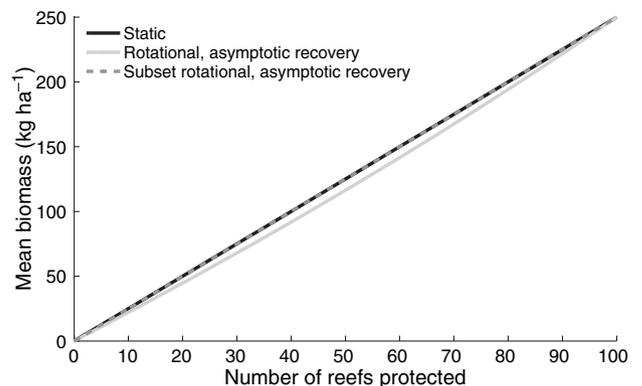


Figure 4 Comparison of expected mean herbivore biomass across a system of 100 reefs, under three different protected area strategies: static MPAs (black line), MPAs rotated amongst all 100 reefs (blue line) and MPAs rotated amongst the optimal subset number (dashed grey line). All herbivore populations are assumed to recover asymptotically. The x-axis indicates the number of reefs able to be reserved.

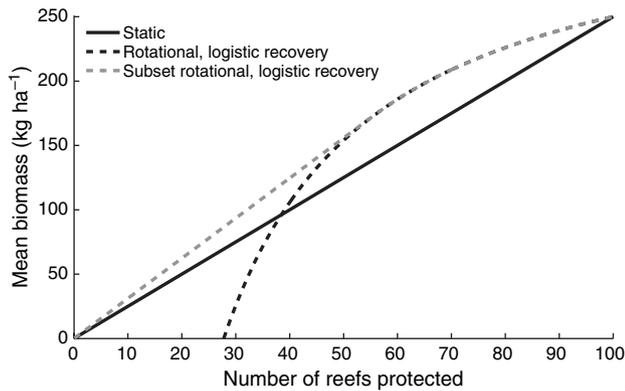


Figure 5 Comparison of expected mean herbivore biomass across a system of 100 reefs, under three different protected area strategies: static MPAs (black line), MPAs rotated amongst all 100 reefs (red line) and MPAs rotated amongst the optimal subset number (dashed grey line). All herbivore populations are assumed to recover logistically. The x -axis indicates the number of reefs able to be reserved.

herbivore biomass (Fig. 4). Finally, for the logistic recovery model, full rotation only outperformed the static MPA strategy when more than 39% of reefs were protected (Fig. 5), but the subset rotational strategy consistently outperformed the static MPA strategy. The superiority of the subset solution is ensured by the fact that the static MPA strategy is a limiting case, when the optimal subset size is equal to the number of protected areas ($S^* = R$; e.g. rotating 50 MPAs between 50 reefs, in a system of 100 reefs).

With the exception of asymptotic recovery, at higher levels of system protection (> 80% of reefs for linear recovery, and > 55% of reefs for logistic recovery), the full rotational and optimal subset strategies deliver the same result (Figs 3 and 5). This happens because at high levels of protection, the optimal subset size is greater than the total number of reefs available, therefore the full and subset rotation strategies converge.

DISCUSSION

Political factors have historically constrained the protection of coral reefs to between 10 and 30% of total area. At this level of protection, a dynamic closure strategy appears unlikely to improve the mean biomass of herbivorous fishes on coral reef systems, if MPAs are rotated among all reefs. However, moving MPAs among a subset of the reefs can lead to improvements in the mean herbivore biomass relative to static protection. This improvement can be considerable, even at low levels of protection. In pursuit of greater herbivore biomass and the improved resilience this confers, it was our explicit intention to compare different MPA management strategies. This does not, however,

preclude the possibility that the most efficient and equitable solution to this problem might lie in the effective implementation of non-spatial fisheries management methods, such as catch or gear restrictions, rather than in protected areas.

Opposing the benefits of a dynamic protection strategy will be the considerable transaction costs incurred by moving MPAs. In most cases, there will be substantial expenses associated with the politics of re-designating the protection status of reefs, and in communicating these changes to stakeholders. For these reasons, strategies that involve movement of protection are perhaps most feasible on smaller reef systems, with fewer and more localized stakeholders, (e.g. within reef systems subject to customary management arrangements, Aswani & Hamilton 2004; Cinner 2007). However, the severity of current threats to coral reef systems (Bellwood *et al.* 2004) and the importance of the ecosystem services they provide (Moberg & Folke 1999), mean that effective management strategies with high transaction costs cannot automatically be discounted.

Our comparison between different MPA strategies was based on the expected mean herbivore biomass across all reefs in the system. This averaged performance measure obscures the variance in condition across reefs. For example, under static protection, the observed mean biomass results from a bimodal distribution of well-protected reefs at carrying capacity, and unprotected reefs which suffer a total loss of resilience. This variability in reef condition is less marked under dynamic protection strategies (even across a subset of the total reef system). In the case of a fully rotational strategy, herbivore biomass will be roughly equal across all reefs, and variance will therefore be zero. The potential to maintain adequate herbivore grazing (and therefore resilience) across all reefs in a system represents a considerable potential benefit of dynamic protection strategies. Although the resilience of coral reefs has been well explored (Nyström & Folke 2001; West & Salm 2003; Halford *et al.* 2004), it is difficult to empirically demonstrate or quantify the benefits to resilience of a more uniform distribution of grazing herbivores. It can be reasonably argued, however, that a reliance on fewer reefs, even ones with large herbivore biomass, constitutes reduced resilience, given that catastrophic events will have a greater effect (Bascompte *et al.* 2002). Similarly, the apparent difficulty in reversing coral-algal phase shifts when they do occur (McManus & Polsenberg 2004; Bellwood *et al.* 2006; Mumby *et al.* 2007), strongly encourages us to avoid this outcome on as many reefs as possible.

In pursuit of overall system resilience, it might be better to tolerate some reduction in mean herbivore biomass, if such a decision also encourages lower variance between reefs. A clear example of this is under the assumption of asymptotic recovery (Fig. 4). Here, the full rotational

strategy yields a slightly lower mean biomass across the system compared with the static strategy, but ensures that every reef has the same biomass. In contrast, the static MPA strategy slightly improves the mean biomass by increasing the biomass on some reefs, but completely eliminating biomass on unprotected reefs. A trade-off also exists between the number of reefs that receive protection, at least periodically, and the mean biomass that can be maintained on those reefs. The static MPA strategy clearly maintains the highest biomass on the protected reefs, but does so on only a small number of reefs. In contrast, the full rotational strategy attempts to protect every reef in the system, but in doing so can potentially fail to maintain significant biomass on any of them. The subset rotational strategy generally results in an inter-reef variability that falls somewhere between static and full rotation (the exception being under asymptotic recovery). While this strategy does lead to a lower herbivore biomass on protected reefs compared with the static strategy, it is able to protect a greater number of resilient reefs. This result reinforces the argument that the application of triage principles will lead to the most efficient conservation solutions (Bottrill *et al.* 2008).

In the context of no-take MPAs, concerns over the dichotomous fate of protected and unprotected areas have generally been rebutted by appealing to potential spill-over from healthy protected populations into unprotected areas. There is, however, limited evidence that current levels of protection on coral reefs (generally < 30% of reefs protected) are sufficient to maintain healthy fish populations on the large proportion of unprotected reefs (Russ 2002; Robbins *et al.* 2006). Although we did not explicitly consider the influence of spill-over on the best strategy, the high rate of herbivore exploitation commonly observed on unprotected reefs (Aswani & Hamilton 2004; Hawkins & Roberts 2004), suggests that spill-over alone is unlikely to maintain herbivore populations on these reefs when the total level of system protection is low. Both static and dynamic strategies could conceivably encourage spill-over benefits to unprotected reefs, but the high herbivore biomass and preponderance of large fish associated with the static MPA strategy is likely to generate higher spill-over rates than rotational closures. As such, incorporating spill-over effects in the recovery functions used here is likely to improve the performance of the static strategy. On the other hand, although rotationally protected reefs will have neither the total biomass nor the individual fish sizes of static MPAs, they will be much more numerous, and more evenly distributed throughout the reef system. These properties might allow spill-over to effectively influence a larger number of reefs, while avoiding debate over the placement and spacing of protected areas to promote spill-over (Kaplan & Botsford 2005).

Uncertainty regarding the functional response of herbivore populations to exploitation and protection is likely to be systemic across all coral reef ecosystems. There were surprisingly large differences in the performance of the fully rotational strategy under the three different recovery models explored here. Additionally, while the subset rotational strategy was consistently the best strategy, the optimal subset size varied with the population recovery trajectory. Our analyses assume that herbivore populations are not subject to Allee or threshold effects at very low biomass. Such effects have been documented in other fish populations subject to exploitation (Myers *et al.* 1995) and if present, dynamic protection strategies might fare poorly if the frequency of protection is not enough to maintain herbivore biomass above the threshold level. Although the sensitivity of our results to uncertainty in the herbivore decline trajectory was not explored, we also tested the three different MPA strategies under the assumption of linear herbivore decline (see Data S2). While the major results proved reasonably robust to the choice of decline function, it did influence the performance of the different strategies. Most notably, when the decline and recovery trajectories are symmetric (e.g. linear recovery and linear decline), the performance of the full rotational strategy is governed strictly by the relative rates of population decline and recovery, rather than the proportion of system protection. These results suggest that an understanding of the trends in herbivore populations under protection and exploitation is critical for effective management decision-making.

We present a simplistic model of coral reef resilience, quantifying this poorly defined property by the total herbivore biomass on the average reef. Although there is no doubt that grazing herbivores play a key role in the resilience of coral reefs (Mumby *et al.* 2006; Hughes *et al.* 2007b; Green & Bellwood 2009), it is unlikely that herbivore biomass equates directly and linearly with a reef's capacity to resist phase-shifts to an algal dominated state. Depending on their functional group and individual size, herbivorous reef fish contribute differently to the removal of competitive algae (Bellwood *et al.* 2003; Green & Bellwood 2009). In addition to total biomass, the assemblage structure (number of functional groups represented) and size distribution (biomass of large fishes) of herbivorous fishes are also important indicators of coral reef resilience (Green & Bellwood 2009). Further factors, such as nutrient levels, also play an important role in mediating the coral-algae balance (McClanahan *et al.* 2003; McManus & Polsenberg 2004).

It is clear that the functional resilience of a reef can decline very rapidly under fishing pressure (Mumby 2006), especially as, amongst herbivores, the important functional group of large excavating and bioeroding herbivores will typically be removed first (Aswani & Hamilton 2004; Green & Bellwood 2009). In our example, the loss of resilience due

to fishing pressure on unprotected reefs is severe, declining rapidly, albeit asymptotically, to near zero. As such, restrictions on fishing catch or effort have the potential to slow the decline in resilience on unprotected reefs (McClanahan & Cinner 2008), thereby improving the performance of dynamic MPA strategies. In comparing dynamic vs. static MPA strategies we assumed that fishing pressure on unprotected reefs remained roughly constant, regardless of the proportion of the system protected. This assumption depends on fishing effort being controlled such that MPA designation does not displace fishing effort onto the reefs that remain open. Were fishing effort to increase on unprotected reefs in response to increasing reservation, unprotected reefs would suffer more rapid declines in herbivore biomass, even if only unprotected for short periods. The likely consequence of this redistribution of effort is a reduced performance of rotational closures at high levels of reservation. The use of a range of fishing gears as well as the varying proximity of reefs to human populations also mean that the decline in resilience is unlikely to be uniform across all unprotected reefs. Greater stochasticity in the biomass and assemblage structure of herbivores on reefs would provide greater incentive for adaptive management strategies, because changes in the resilience will be more difficult to predict, and must be ascertained through monitoring. Finally, we only consider the resilience lost through declines in grazing herbivores. Fishing gears that also damage the coral framework on unprotected reefs are likely to lead to further losses in resilience (McManus *et al.* 1997). Such damage might engender longer recovery times, undermining the relative performance of dynamic strategies.

Ultimately, the decision to implement a dynamic MPA strategy will not be made solely on the basis of expected herbivore biomass. While dynamic MPA strategies are likely to have a number of social benefits over static strategies (Cinner *et al.* 2005; McClanahan *et al.* 2006), our assumption of uniform exploitation on unprotected reefs also raises practical concerns about fishers' access to reefs under dynamic strategies. The purported social benefits of rotating MPAs is predicated on the assumption that fishers will maintain access to the same number of reefs during any given rotation. For this to be the case, either the system must be small and open enough for fishers to have access to all reefs in the system, or protected areas must be stratified such that the number of closed and open reefs in each part of a larger system remains roughly constant. From a scientific point of view, by making it more difficult to study the same closed area over a long period of time, the widespread application of dynamic MPAs would also serve to propagate uncertainty regarding the rate or functional form of herbivore population recovery and decline. Although this uncertainty will constrain future decision-

making, it can be partly offset by the acquisition of good empirical data on the performance of dynamic closures under different conditions.

At current levels of reservation, the periodic rotation of MPAs among all reefs in a system appears unlikely to improve the herbivore biomass across coral reef systems. However, for the reasons outlined in the introduction, it is also probable that societies are willing to tolerate far higher levels of total protection if implemented as periodic closures rather than permanent exclusions. Given the strong performance of rotating protection area amongst a subset of reefs, and the trade-offs that exist between mean herbivore biomass and the variability in biomass between reefs, understanding how the distribution of herbivores across reefs influences both social and ecological resilience of coral reef systems should be considered a research priority.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1 Comparison of analytic and simulation results for mean herbivore biomass under rotating protection.

Data S2 Comparison of static, rotational and subset MPA strategies under the assumption that herbivore biomass declines linearly on fished reefs.

Figure S1 Comparison of the equilibrium mean herbivore biomass of a rotational MPA system, calculated by; (a) a deterministic analytic solution (black line), and (b) stochastic simulation (coloured bars). Simulations were conducted for three different periods of rotation; monthly (red), annually (blue), and every 2 years (green). Dots indicate mean biomass across all reefs. Bars show the range of biomass values across all reefs. In all cases, herbivore populations on protected reefs are assumed to recover linearly.

Figure S2 Comparison of the equilibrium mean herbivore biomass of a rotational MPA system, calculated by; (a) a deterministic analytic solution (black line), and (b) stochastic simulation (coloured bars). Simulations were conducted for three different periods of rotation; monthly (red), annually (blue), and every 2 years (green). Dots indicate mean biomass across all reefs. Bars show the range of biomass values across all reefs. In all cases, herbivore populations on protected reefs are assumed to recover asymptotically.

Figure S3 Comparison of the equilibrium mean herbivore biomass of a rotational MPA system, calculated by; (a) a deterministic analytic solution (black line), and (b) stochastic simulation (coloured bars). Simulations were conducted for three different periods of rotation; monthly (red), annually (blue), and every 2 years (green). Dots indicate mean biomass

across all reefs. Bars show the range of biomass values across all reefs. In all cases, herbivore populations on protected reefs are assumed to recover logistically.

Figure S4 Comparison of the equilibrium mean herbivore biomass on the average reef under both static and rotational MPAs, with increasing levels of system protection. The black line represents static protection under all recovery models and the remaining lines represent rotational protection under different possible herbivore recovery models; logistic (red), asymptotic (blue) and linear (green) growth. The dotted red line indicates the hysteretic mean biomass under logistic recovery if the mean system biomass either begins or is allowed to decline too low.

Figure S5 Comparison of expected mean herbivore biomass across a system of 100 reefs, under three different protected area strategies: static MPAs (black line), MPAs rotated amongst all 100 reefs (blue line) and MPAs rotated amongst the optimal subset number (dashed grey line). All herbivore populations are assumed to recover asymptotically and decline linearly. The x-axis indicates the number of reefs able to be reserved.

Figure S6 Comparison of expected mean herbivore biomass across a system of 100 reefs, under three different protected area strategies: static MPAs (black line), MPAs rotated amongst all 100 reefs (red line) and MPAs rotated amongst the optimal subset number (dashed grey line). All herbivore populations are assumed to recover logistically and decline linearly. The x-axis indicates the number of reefs able to be reserved.

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