

LETTER

Reserve design for uncertain responses of coral reefs to climate change

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Abstract

Rising sea temperatures cause mass coral bleaching and threaten reefs worldwide. We show how maps of variations in thermal stress can be used to help manage reefs for climate change. We map proxies of chronic and acute thermal stress and develop evidence-based hypotheses for the future response of corals to each stress regime. We then incorporate spatially realistic predictions of larval connectivity among reefs of the Bahamas and apply novel reserve design algorithms to create reserve networks for a changing climate. We show that scales of larval dispersal are large enough to connect reefs from desirable thermal stress regimes into a reserve network. Critically, we find that reserve designs differ according to the anticipated scope for phenotypic and genetic adaptation in corals, which remains uncertain. Attempts to provide a complete reserve design that hedged against different evolutionary outcomes achieved limited success, which emphasises the importance of considering the scope for adaptation explicitly. Nonetheless, 15% of reserve locations were selected under all evolutionary scenarios, making them a high priority for early designation. Our approach allows new insights into coral holobiont adaptation to be integrated directly into an adaptive approach to management.

Keywords

Acclimation, adaptation, algorithm, connectivity, conservation, coral, marine reserve.

Ecology Letters (2010)

INTRODUCTION

Periods of elevated sea temperature, which have already caused several catastrophic coral bleaching events (Wilkinson 2000), are set to become more frequent as the oceans continue to warm (Donner *et al.* 2005). Given the scale of ocean warming, we cannot mitigate the problem, but thermal stress does vary across the seascape (McClanahan *et al.* 2007). For example, the extent of wind-driven vertical mixing of the water column varies among reefs with better-mixed systems exhibiting lower levels of warming (Skirving

et al. 2006). Reef management may benefit by taking advantage of such hydrodynamics and stratifying the design of marine reserves by the level of physical stress (West & Salm 2003; McClanahan *et al.* 2007). Although reserves provide no refuge from physical stress, they can reduce some forms of biological stress, such as overfishing, that enhance coral's competition with macroalgae (Mumby & Harborne 2010). Thus, by targeting the placement of reserves towards areas of relatively low physical stress, corals inside reserves will experience the benefits of reduced biological stress whilst also experiencing relatively benign

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physical stress. This approach minimises overall stress upon the coral and may help maximise resilience.

Whilst the intention of stratifying conservation by physical environment is not novel (West & Salm 2003), a number of obstacles, most of which are generic in ecological and evolutionary science, have prevented its implementation. First, whilst many *ad hoc* observations of stress on corals have been made (Maina *et al.* 2008; Yee & Baron 2009), a generic classification of stress and the associated physiological response of corals has been lacking. Second, any conservation strategy for climate change must consider the scope for genetic adaptation and phenotypic acclimation to rising stress. Yet, the scope for genetic adaptation, and even phenotypic acclimation, in corals is uncertain (Baird *et al.* 2007; Baker *et al.* 2008). Thus, conservation strategies must ideally hedge against this uncertainty whilst providing the flexibility to allow modification as science provides answers. Third, conservation strategies for marine systems have to consider explicitly the larval connectivity among populations (Sale *et al.* 2005; Pelc *et al.* 2010). Not only do there remain great technical challenges in designing reserve networks from complex connectivity networks (Treml *et al.* 2008), but the problem is greatly complicated by the potential role of dispersal in shaping future genetic adaptation in populations (Palumbi 2003). A conservation approach is needed that considers the functioning of the reserve *network* under climate change. Moreover, although it might prove theoretically desirable to create networks of reserves that exhibit particular physical characteristics, such as benign thermal stress, this will only be possible if adequate larval dispersal exists at that scale. Put formally, to what extent does the scale of larval dispersal permit reserve design to be stratified by thermal stress?

Here, we ask how the design of marine reserve networks is influenced by the current uncertainty in the scope of corals to adapt or acclimate to climate change. In answering this question, we develop approaches to categorizing the response of corals to stress and for incorporating larval connectivity into the design of reserve networks. We test two hypotheses. The first investigates the feasibility of harnessing natural spatial variability in thermal stress to stratify reserve design. Then, assuming that larval connectivity does permit thermally stratified reserve design, the second hypothesis tests the sensitivity of decisions made today to our uncertainty about evolutionary responses of corals to climate change.

H₁: Marine reserve design can be stratified by thermal stress because adequate larval dispersal occurs among populations of corals in different thermal stress regimes.

H₂: Present uncertainty about the response of corals to rising sea temperatures has an important bearing on the design of marine reserve networks.

MATERIAL AND METHODS

Thermal stress regimes and hypothesised response of corals

To examine spatial patterns of thermal stress we began by separating chronic and acute forms of stress. Chronic stress represents the routine, ‘ambient’ summer temperature to which corals are acclimated (Ulstrup *et al.* 2006) and varies markedly at latitudinal scales of hundreds of kilometres. Acute stress occurs during bleaching events and may vary dramatically at local scales of kilometres because it is influenced by local hydrodynamics. A 20-year climatology of satellite-derived sea surface temperature (SST) was used to map chronic stress across reef habitats of the Bahamas. Chronic stress was measured as the maximum of monthly mean (MMM) temperatures for all years in the archive for which no acute stress occurred (i.e. for each pixel, the MMM is the single hottest month in the archive for which no bleaching occurred). Acute stress was measured as the number of degree heating weeks (DHW, °C week) experienced due to temperature anomalies between April and November during the 1998 bleaching event. The DHW is calculated from accumulating HotSpots of ≥ 1 °C that occur during a 12-week window, where a HotSpot is defined as the temperature above the MMM (Skirving *et al.* 2006). Chronic and acute stress measures were divided independently into terciles and pixels at the extremes of each stress measure (i.e. upper and lower tercile) were used to generate four contrasting thermal stress regimes (Fig. 1). Those sites falling in the middle tercile were left unclassified.

An evidence-based approach was taken to hypothesise the response of corals to climate change in each thermal regime. Predictions were based on two well-established

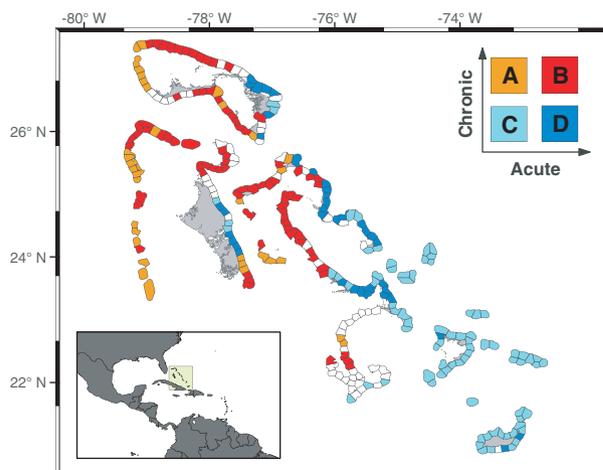


Figure 1 Categorization of coral reefs in the Bahamas by thermal stress regime. Empty (white) polygons are unclassified, falling between thermal regimes.

physiological principles. First, when confronted with a given stress event, organisms acclimated to higher chronic photosynthetic stress fare better than those acclimated to lower stress (Horton *et al.* 1996). This is because photoprotective processes and the recovery and maintenance costs of the photosynthetic apparatus are efficiently supported and routinely upregulated (e.g. Chow *et al.* 2009) under higher chronic stress. There is considerable empirical support for acclimation to stress in corals (Jokiel & Coles 1990; Brown *et al.* 2002) such that corals acclimated to cooler conditions fare worse than those acclimated to warmer conditions (Castillo & Helmuth 2005). Second, for a given level of acclimation (chronic stress), coral mortality will increase under higher acute stress. Again, laboratory studies support this assertion (Ulstrup *et al.* 2006; Berkelmans 2009). These two lines of evidence imply that corals in regime A (high chronic and low acute stress) are predicted to have the most resistant coral communities to current bleaching. Corals in regime C (low chronic and low acute stress) are also predicted to benefit from a lack of severe bleaching events but their acclimation to cooler conditions is likely to increase their vulnerability to even weak periods of rapid warming. In the Bahamas, reefs with low chronic stress are up to 2 °C cooler than those experiencing the highest stress. Corals have been shown to exhibit strikingly different responses to such differences in temperature (Jokiel & Coles 1990). Thus, we predict that corals in regime C will be moderately healthy but that mortality rates due to acute disturbance will be greater than those occurring in regime A. Corals in regime B may have some natural resistance to bleaching conditions by virtue of their acclimation to high chronic temperature, but their exposure to acute warming during bleaching events is likely to cause significant mortality. Finally, corals subjected to low chronic and high acute stress (regime D) are predicted to experience relatively severe mortality because of their lack of acclimation to severe thermal stress resulting in acute bleaching and possibly disease. Further details are given in the Appendix S1.

Field evidence for response of corals to thermal stress regimes

A definitive field test of the anticipated impact of thermal stress regimes on corals is lacking and extremely difficult to undertake given the plethora of influences acting on corals and the requirement for sampling over a wide geographic area. However, if we make the assumption that coral cover was not systematically biased by thermal stress regime before the first truly region-wide mass bleaching event of 1998, then a coarse field assessment is possible by comparing coral cover in the years following 1998. Thus, given that 1998 was a major source of coral mortality

(Kramer 2003) and that coral recovery is notoriously slow in the Caribbean (Connell 1997), then coral cover in the following years should decrease predictably from thermal regime A to C to B to D. We recognise that major disturbances after the 1998 bleaching event could undermine this relationship, particularly where field data were used from 2002 to 2004. Thus, a lack of field support for the hypothesised response of corals after the 1998 bleaching event does not necessarily imply that the hypothesis is incorrect; the patterns generated by thermal stress may have been obscured by other factors. All field data were collected at a depth of 7–10 m. A total of 58 Bahamian sites were extracted from 33 surveys between 2002 and 2004 and 25 sites from the Atlantic and Gulf Rapid Reef Assessment (AGRRA) database from surveys in 1999. Unfortunately, no data were available for reefs in thermal regime A, so we conducted an additional analysis for reefs of Belize for which enough data were available to encompass all regimes. Eighteen sites were surveyed using 15 half-metre randomly placed quadrats per site and four additional reefs were available from the AGRRA database in 1999.

Prioritization of stress regimes for reserve network design

In recognition of the uncertainty over genetic adaptation and scope for phenotypic acclimation in corals, multiple scenarios for adaptation/acclimation were considered and a compromise option provided that hedges against present uncertainty (Fig. 2). A list of assumptions and caveats are provided in the Appendix S1.

Scenario 1: Response of corals to thermal stress today persists into the future

This scenario posits that chronic stress does not become lethal in future and could arise for several reasons. First, if the coral holobiont undergoes sufficient genetic adaptation and/or phenotypic acclimation to rising *mean* temperatures that relative sensitivity patterns today persist and future bleaching responses follow the magnitude and duration of today's thermal anomalies. Second, local factors prevent sea temperature from following the increasing global trend, such as suggested by the Thermostat hypothesis for the Western Pacific Warm Pool (Kleypas *et al.* 2008). In either case, the long-term plan for siting reserves is based on the current response of corals to thermal stress (Fig. 2a).

In selecting sites for future marine reserves, it would be logical to give highest priority to protecting sites that are predicted to lie in the healthiest regimes (A) and to facilitate larval supply among such reefs and to reefs that can persist between bleaching events but may experience somewhat higher mortality during bleaching (i.e. connections from A to C; Fig. 2). However, we also speculate that the likelihood

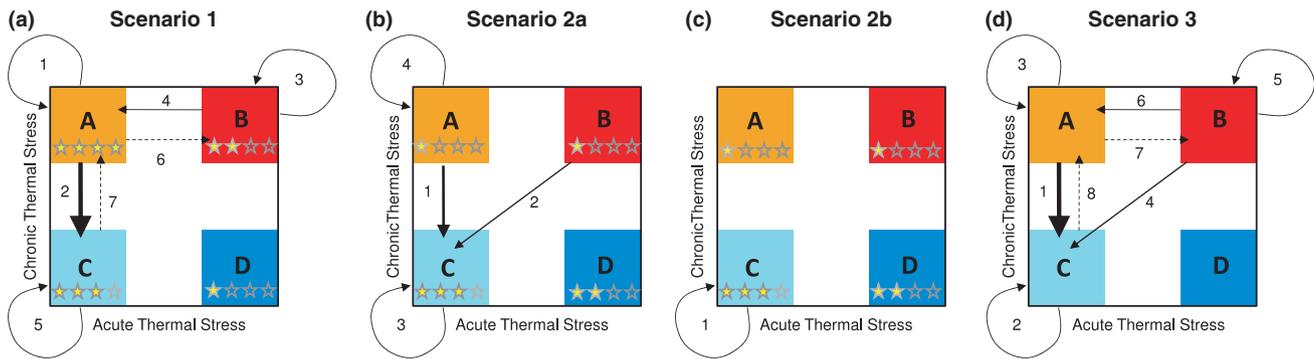


Figure 2 Hypothesised future reef health and ranking of larval connectivities among thermal stress regimes under different scenarios of the coral holobiont's response to climate change. Stars denote relative health of coral community. Lines denote larval connections and dashed lines indicate that only weak connections are required or desired. Numbers denote ranking of connections, where 1 is top priority. Scenario 1 (a) assumes adequate adaptation or acclimation to rising sea temperature and prioritises connections among healthy reefs (A) and to those reefs that survive well between bleaching events (C). If adequate adaptation is possible, then reefs in category B serve as an 'evolutionary pump' and should ideally have similar thermal regimes upstream and some downstream connectivity to reefs in benign environments. Scenario 2 (b, c) assumes that adaptation or acclimation are inadequate and recognises two cases. Scenario 2a (b) assumes that the present pattern of higher thermal tolerance in areas of high chronic stress has a genetic basis and prioritises the migration of thermally-resistant genotypes from A and B to cooler areas that encounter relatively benign stress during bleaching (C). Connections are maintained among the healthiest reefs in long-term (C) and among healthiest reefs in short-term (A) to maximise scope for migration before A and B and possibly D become lethally stressed. Scenario 2b (c) assumes that present acclimation patterns only have a phenotypic basis and prioritises connections among C because acclimation to warmer conditions may still occur in those corals that currently lie in cooler areas, far from their thermal maximum. Scenario 3 (d) is a bet-hedging strategy that recognises uncertainty among scenarios 1, 2a and 2b. Calculate (i) number of times, N, a connection was prioritised in scenarios 1, 2a, and 2b and (ii) the average ranking when each connection was prioritised, R (where ranking 1 denotes the most important connection). Overall bet-hedging ranking calculated from N/R such that larger values denote higher overall importance.

of more resistant coral genotypes emerging will be greatest in regime B, particularly where the local oceanography reduces contamination of the local gene pool from corals in other thermal regimes. Our reasoning is that random advantageous mutations are most likely to become fixed in relatively uncontaminated reefs of this thermal regime because the selection pressure is high (high acute stress), the coral abundance is predicted to be fair (relative to regime D) and the limited replenishment of genetic diversity will enhance the directionality of genetic drift. Those corals that survive in thermal regime B may become the best adapted to severe thermal stress, but genetic diversity is likely to be low. Whilst facilitating drift is contrary to the widely held principle of enhancing genetic diversity (Almany *et al.* 2009), it should be borne in mind that genetic diversity insures against unpredictable changes in the environment, whereas corals face a predictable and directional rise in thermal stress and are likely to benefit from adaptation, should any occur.

Scenario 2: Corals exhibit limited local acclimation or adaptation that is unable to keep up with rising sea temperatures

A rise in global sea temperatures of 1–2 °C (Hoegh-Guldberg *et al.* 2007), together with inadequate acclimation

and/or adaptation in the coral holobiont during the forthcoming decades is likely to push many corals past their upper thermal tolerance – around 31–33 °C (Ulstrup *et al.* 2006). Under this scenario, we predict that many corals identified in regimes A and B (high chronic stress) could become lethally stressed during bleaching events, reducing coral cover and diversity (Fig. 2b,c). Reefs that currently experience relatively low chronic thermal stress would, in future, behave like reefs that currently experience high chronic stress. Therefore, we speculate that reefs currently in regime C would likely fare best under a warming scenario without adaptation, and it would be appropriate to protect and prioritise larval connections among reefs in this regime. We sub-divide this scenario to distinguish whether the present-day patterns of thermal 'acclimation' to chronic stress have a genetic basis (Scenario 2a, Fig. 2b) or purely a phenotypic basis (Scenario 2b, Fig. 2c).

Scenario 3: Bet-hedging strategy

Overall, the conservation prioritization of reefs by thermal stress regime differs according to the assumptions made about present and future adaptation. However, a bet-hedging strategy was created that weights the importance of each type of larval connection from scenarios 1, 2a and 2b (Scenario 3, Fig. 2d).

Modelling larval connectivity

To investigate the feasibility of implementing the conservation networks postulated here, we used a spatially explicit 3D individual-based model of larval dispersal developed by Paris *et al.* (2002) and adapted for the wider Caribbean (Cowen *et al.* 2006). The model stratified the release of coral larvae of the dominant reef-building species, *Montastraea annularis*, by reef habitat throughout the Bahamas (Mumby *et al.* 2007). Following Baums *et al.* (2006), larvae advected passively during the 4 day pre-competent period then switched to active settlement behaviour during the competent period of days 5–72. Active settlement behaviour was simulated by allowing individual larvae to settle if they occupied a cell adjacent to or on reef habitat. Daily mortality rates increased from 0.001 for days 6–30 to 0.01 for days 31–72 to allow for a rapid increase in senescence over time (Graham *et al.* 2008). Current-driven advection and turbulence-driven dispersion of larvae were modelled using the high-resolution (5 km) Regional Ocean Modeling System that is driven by observed winds (QuikSCAT/SeaWinds scatterometer, <http://manati.orbit.nesdis.noaa.gov/datasets/QuikSCATData.php/>) and climatology fluxes from the Center for Ocean-Atmospheric Prediction Studies. Note that we did not consider the migration of larvae from outside the Bahamas because genetic studies (Galindo *et al.* 2006), and wider analyses of dispersal (Cowen *et al.* 2006) have found the region to be dominated by internal connections and relatively isolated.

Reserve design algorithms for connectivity and thermal stress

Recent advances in the theory of reserve design include the development of decision-support tools such as Marxan (Possingham *et al.* 2000; Game *et al.* 2008). These tools employ reserve-selection algorithms to minimise the cost of the reserve system whilst aiming to meet specified conservation objectives. At each time step, small changes to a reserve network are considered and the effect on a function for the cost of reserves determined. Reserve cost is often measured as a function of area (McDonnell *et al.* 2002; but see Costello *et al.* 2010), under the assumption that larger reserve areas will result in greater economic losses (Balmford *et al.* 2004). The cost function has the potential to integrate a wide range of information, thereby enabling reserve design to extend beyond the simple representation of species or habitats. Here, we demonstrate how information on the thermal regime of sites and larval dispersal among sites can be incorporated into the cost function with the use of a connectivity metric M .

The algorithm allows the practitioner to seek a near-optimal collection of reserve locations that conform to a

pre-conceived set of design objectives. We assume that the conservation planner has a priority ranking of connections among sites of different thermal regimes (e.g. A–A, A–C, etc.). Whilst we suggest rankings in this article (Fig. 2; Appendix S1), we do not specify them below to avoid confusion and leave the method as generic as possible. Each connection (e.g. A–C) can be weighted $w(A, C)$ based on its importance relative to the most desired connection.

Let N be the number of sites in the landscape and $x_i = 1$ if site i is in a reserve and 0 if site i is outside a reserve. The metric M , which we aim to maximise, can be written as

$$M = \sum_{i=1}^N \left[x_i \left(\sum_{j=1}^N [x_j w(T_i, T_j) L_{i \rightarrow j}] \right) \right],$$

where T_i is the thermal regime of site i , and $\sum_{j=1}^N x_j L_{i \rightarrow j}$ is the total number of larvae released from site i that arrive in reserve sites j .

Like much reserve theory (Hastings & Botsford 2003), the method makes the conservative assumption of a scorched earth in that larvae from non-reserve areas do not contribute to the analysis. This requirement will be relaxed in a follow-up study but would be reasonable if, for example, overfishing of herbivores combined with increasing environmental pressures led to limited recovery of coral populations outside reserves. The reserve-selection process aims to minimise the objective function

$$\sum_{i=1}^N x_i a_i - \lambda M, \quad (1)$$

subject to the constraint

$$\sum_{i=1}^N a_i x_i \geq t \sum_{i=1}^N a_i \quad (2)$$

$$x_i \in \{0, 1\} \quad \text{for all } i = 1, \dots, N,$$

where λ is an adjustable parameter that controls the importance of maximizing the connectivity metric M relative to the goal of minimizing the area of reserves. Equation 1 is the objective function, used to describe the cost of the reserve network. Equation 2 represents the constraint that has to be met by the algorithm. In this case, eqn 2 describes the representation target level (t), between zero and one, where a_i is the area of site i .

In the Bahamas case study, sites have approximately equal area and are assigned equal cost. Connection weights are determined from the ranking of priority larval connections defined for each scenario (Fig. 2). Connection types are ranked 1–7 and the weights $w(T_i, T_j)$ are set linearly to give the highest weight (7) to the top rank, and the lowest weight (1) to the bottom rank.

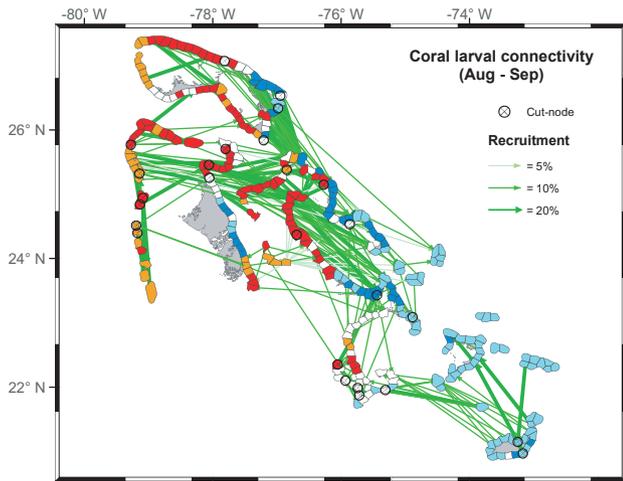


Figure 3 Graph-theoretical representation of coral larval connectivity among reefs in the Bahamas. Polygons represent reefs of habitats *Montastraea* and hardbottom and lines denote predicted flux of *Montastraea* larvae during a single spawning and recruitment event. Graph cut-nodes (crossed circles) are important locations for maintaining network cohesion and cause network fragmentation if such reefs are lost.

As aspirations for reef conservation often fall between 10 and 30% of available habitat, each simulation sets aside 20% of the available reef area into reserves. Within the total area to be set aside in reserves (20%), the algorithm was further constrained to represent a proportion of each thermal regime based on the frequency of its usage among priority connections. For example, in scenario 1, thermal regime A features a total of six times in the connectivity pairings (Fig. 2; A–A, A–C, B–A, A–B, C–A), whereas regimes B and C occur only four times each. Thus, the proportion of sites of regime A targeted within the reserve network was set at 0.43 (6/14). The optimization algorithm was repeated 1000 times using a combination of simulated annealing followed by a two-step iterative improvement (Ball *et al.* 2009). For each scenario, we report the optimal run which is the reserve network that met the desired targets whilst maximizing the strength of connection types that we prioritised.

RESULTS

Acute stress was quantified for the severe 1998 bleaching event and found to be highest in the central Bahamas and lowest in the south of the archipelago. Chronic stress was highest to the west near the Gulf Stream and lowest to the east bordering the cooler Atlantic Ocean (Fig. 1).

Modelled larval dispersal showed a general west–east pattern often crossing banks and passing through shallow creeks (Fig. 3). These patterns emerge because of two

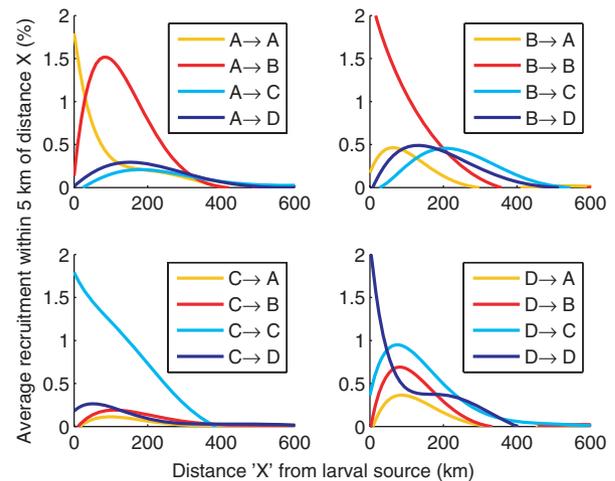


Figure 4 Larval connectivity regimes of the spawning coral, *Montastraea* spp., across the Bahamas Archipelago stratified by thermal stress regime.

forcing processes unique to the Bahamas. First is the intense evaporation of water on the shallow Bahamas banks during summer, which yield high salinity waters that create density currents, local eddies and high connectivity (Hickey *et al.* 2000). Second are tidal currents that create strong cross-shelf transport over the bank (Otis *et al.* 2004). When these two processes combine with wind forcing, a clockwise circulation is created around the Banks, thereby generating the observed west to east pattern of connectivity when corals spawn in summer.

Disaggregating larval connectivity by thermal stress regime reveals that most local recruitment (<50 km) tends to occur within a single stress regime (Fig. 4). However, fluxes across thermal stress regimes do occur and differ from one regime to another. For example, comparing the strength of connectivity between sites of category A and all other thermal regimes, the flux of recruits to other category A reefs was almost equal to category B reefs, and these were almost eight times that to reefs in categories C and D (Fig. 4). Reefs in category C had relatively weak connections to reefs in other thermal stress regimes, whereas reefs in category B and D were relatively well connected to other regimes (Fig. 4). We speculated that reefs of category B might exhibit faster and more directional adaptation providing that contamination of larvae arriving from other thermal regimes was low. Relatively uncontaminated reefs of category B do exist but only 20% have a predicted larval contamination (i.e. input of non-category B larvae) of <40% (Appendix S1). In short, whilst the most desirable connections among thermal regimes are readily available (e.g. A–A, C–C, B–B), others will be found less often (e.g. A–C).

Field testing the proposed response of corals to each thermal stress regime was wholly consistent with expecta-

tions for the more comprehensive dataset from Belize; stratification of cover after the 1998 bleaching event followed the expected order of significant declines from A > C > B > D (see Appendix S1). Sites predicted to be relatively healthy in the Bahamas (category C) had significantly higher cover than those in B and D, though cover between the latter categories was low and indistinguishable.

Including thermal stratification and connectivity into reserve design had a significant impact on network configuration and performance. If the reserve network ignored both thermal regime and connectivity so that it simply minimised the area needed to achieve 20% of reefs in reserves, it included thermal regime D which was not selected under any of the climate change scenarios and achieved less than half the larval flux among priority connections (Figure S6 in Appendix S1). Even when thermal stratification was included, optimizing reserve networks for connectivity achieved a much greater flux of larvae among desired thermal regimes than occurred without assigning a cost for connectivity (Table 1). The improvement in connectivity was particularly striking for those connections that were relatively scarce, such as A–C (Fig. 4), resulting in up to a sixfold improvement (Table 1).

The optimal design of reserve networks differed among scenarios for the response of corals to climate change

Table 1 Impact of using the larval connectivity algorithm to increase the flux of larvae among networked reserves falling in priority thermal stress regimes

Connection	Ratio of larval flux within reserve network			
	Scenario for coral acclimation and adaptation			
	1	2a	2b	3
A–A	4.13	4.01	–	3.79
A–C	4.90	6.30	–	5.20
B–B	1.58	–	–	1.01
B–A	1.40	–	–	0.25
C–C	1.03	2.14	6.54	1.09
A–B	1.05	–	–	2.68
C–A	2.54	–	–	2.78

Results are expressed as the ratio of flux generated using the algorithm to that achieved without optimizing for connectivity (i.e. a value of 1 implies no benefit).

(Fig. 5). Differences in reserve design outcomes were strongly associated with whether the present-day differences in coral response to stress have a genetic or merely phenotypic basis (i.e. scenario 2a vs. 2b). Thus, whilst scenarios 2a and 2b both assume that climate change will outpace the scope for coral adaptation or acclimation, the

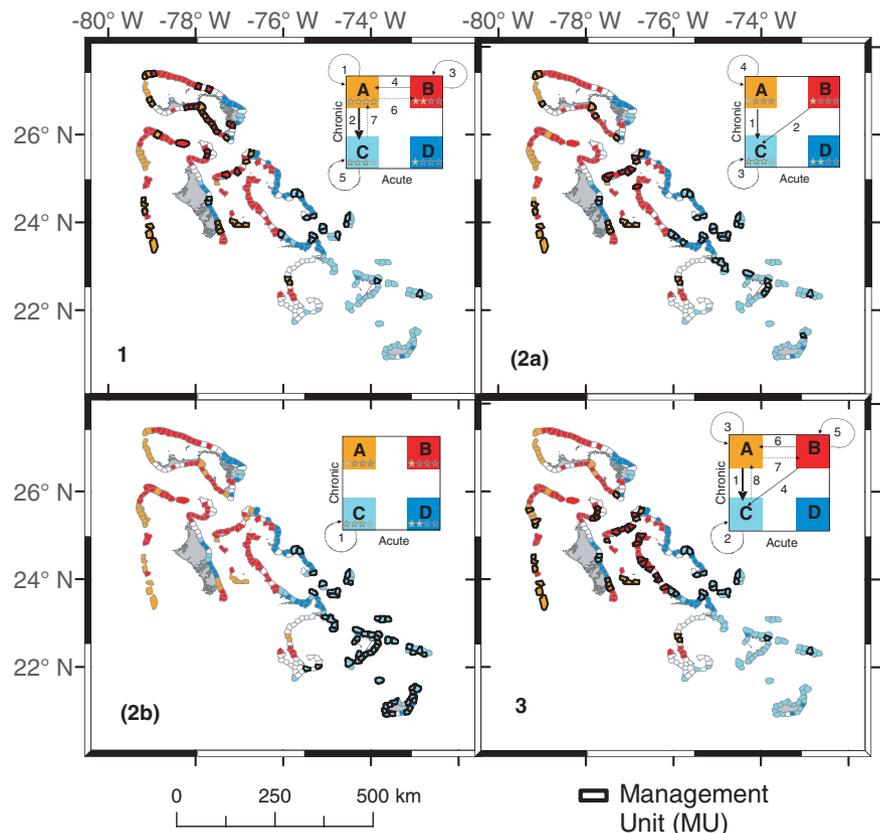


Figure 5 Optimal reserve networks for scenarios 1, 2a, 2b, and the bet-hedging strategy, 3. Figures show the location of individual reef planning units and those with bold edges are reserves. Inset diagrams reveal the prioritization of connections for each scenario.

reserve designs are quite different, with only 36% of reserve locations being common to both scenarios (Table S6 in Appendix S1). Making a fundamentally different assumption – that adequate adaptation or acclimation can occur so that the response of reefs today persists into the future (scenario 1) – led to a fairly similar reserve design to 2a (66% reserves in common). In other words, scenarios 1 and 2a were quite compatible whereas scenario 2b – assuming a phenotypic-only basis for present-day patterns of coral tolerance – was highly incompatible (e.g. 17% of reserves in common with scenario 1). Reconciling such differences was difficult. Only 15% of reserve locations were selected by all three scenarios 1, 2a and 2b. Comparing the similarities in reserve design between each pair of response scenarios (i.e. 1 vs. 2a, 1 vs. 2b and 2a vs. 2b), we find an average similarity of 40% of sites in common. Use of the bet-hedging strategy raised the average similarity to 50% of sites being in common between the bet-hedging outcome and that of the three individual response regimes (1, 2a and 2b).

DISCUSSION

We proposed two hypotheses concerning the design of marine reserve networks for an uncertain response of corals to climate change. Our first hypothesis, that the spatial scales of thermal stress and larval connectivity are sufficiently similar that functioning networks can be stratified by the response of corals to bleaching, was accepted. Satellite measurements of SST clearly reveal the existence of large-scale patterns of thermal stress. Whilst the majority of coral larval flux was found to occur within a single thermal stress regime, a considerable level of flux connected reefs from different regimes at scales exceeding 100 km. The existence of such fluxes allows reserves to be designed as functional networks (Baskett *et al.* 2007). In this case, we stratify the reserve design based on the underlying response of the ecosystem engineers – spawning corals – to physical radiative stress brought on by high temperature (Iglesias-Prieto 2006).

Once the priority connections for each scenario of coral response to climate change had been determined, it became clear that some connections would be more feasible than others. However, explicitly optimizing reserve design to seek such connectivity resulted in a sixfold increase in the level of flux achieved between appropriate parts of the network. In short, whilst the average larval supply among some thermal regimes is relatively low, there are enough opportunities to generate a reserve network if the problem is made mathematically explicit and optimal solutions are sought using algorithms.

Our second hypothesis, that uncertainty over the response of corals to climate change will impact reserve design, was borne out by the analysis. The most funda-

mental difference in response scenarios contrasted whether or not corals had some capacity to keep up with continued global warming (scenario 1 assumed yes and scenarios 2a and 2b assumed no). Surprisingly, however, this dichotomy was not the major driver of difference in reserve design. Rather, the difference between scenarios 2a and 2b led to contrasting reserve designs with the latter confining most reserves to the southeast region of the Bahamas Archipelago. Scenarios 2a and 2b both place great importance on the future health of reefs in stress regime C, which are currently located in relatively cool environments. The first scenario (2a) assumes that the observed difference in thermal tolerance with acclimation temperature (Castillo & Helmuth 2005; Ulstrup *et al.* 2006) has a genetic basis. If this were the case, then larval connectivity would be needed to permit the migration of more resistant genets in warm areas to those that are currently cooler but, through global warming, might reach the chronic temperatures currently found in warmer areas (i.e. prioritizing connections from A or B to C). The alternate scenario (2b) assumed that the observed differences in thermal resistance are merely the product of phenotypic acclimation to different temperatures. A reserve design based on this assumption does not require the migration of stress-tolerant genets and therefore the emergent network was confined to regions where reefs of stress regime C were heavily concentrated.

The incorporation of connectivity into reserve design is an active area of research (Almany *et al.* 2009; Beger *et al.* 2010) and presents a complex problem, partly because of the bewildering number of connections within the system. The scale and asymmetry of such connections are becoming increasingly clear with the advent of high-resolution spatially realistic models of larval dispersal (Cowan *et al.* 2006). To harness such complex information we optimised a popular reserve-selection algorithm, Marxan, to incorporate specific forms of connectivity into reserve design. The outcomes could not be predicted *a priori* because they result from the complex interactions among patterns of larval dispersal, patterns of thermal stress and the existence of multiple optimization criteria (the rankings for different forms of connectivity). Such complexity may preclude generalizations being made about the adequacy of bet-hedging strategies for uncertain responses of corals to climate change.

A robust record of physiological theory and experimental observation allowed us to predict the relative response of corals to each thermal stress regime (Horton *et al.* 1996; Brown *et al.* 2002; Castillo & Helmuth 2005). Seeking further field evidence to support this is challenging because of the diversity of other factors that can influence coral cover (e.g. hurricanes) and the requirement for large-scale sampling stratified by thermal regime. Whilst we do not

consider our tests from Belize and the Bahamas to be definitive, the complete agreement with expectations in Belize and partial agreement in the Bahamas was at least consistent with theory. We explicitly point out, however, that understanding of the response of corals to stress is incomplete (Baker *et al.* 2008) and our intention is to provide a framework that can be adapted as new results emerge.

Understanding the response of organisms to climate change is a fundamental scientific challenge (Millennium Ecosystem Assessment 2005). Here, we ask whether uncertainty over the response of corals to climate change affects the decisions we make today. By developing and implementing alternate scenarios, we find that it is difficult to create a compromise strategy that hedges effectively against all scenarios. However, we also found that a small proportion of sites (15%) were selected under all scenarios, making them exceptionally robust sites for inclusion into a reserve network. As the designation of reserves within a network is rarely undertaken simultaneously (Costello & Polasky 2004; Wilson *et al.* 2006), we suggest that such sites could be heavily prioritised for early designation. Then, as science progresses and refines the evidentiary basis of alternate adaptation/acclimation scenarios, future reserve sites would be chosen, in part, by running the algorithms for the 'most-likely' evolutionary scenario.

Our approach to reserve selection is envisaged to contribute to a wider analysis that includes socioeconomic constraints and the needs of particular target species (Pressey *et al.* 1993; Noss *et al.* 2002). An advantage of focusing on spawning corals is that they build the reef framework on which so much biodiversity depends. However, future studies will have to reconcile the dispersal needs of ecosystem engineers with those of other species in the community. The approach described here can be improved by exploring the efficacy of alternative measures of chronic stress (e.g. mean summer temperature), whether acute stress can be disaggregated further to differentiate the rate of change of temperature during bleaching (Glynn & D'Croz 1990), and the contribution of exceptional radiative stress (Iglesias-Prieto 2006; Yee & Baron 2009). It is also important to study the contribution of deep-water populations of corals to thermal/radiative stress and assess the degree to which such areas may act as natural refugia from stress. Our approach is based on available theory, laboratory and field evidence but we reiterate that it offers an explicit framework by which new science can inform the prioritization of larval connections and choice of scenario for organismal response to climate change. Thus, as our certainty about the response of corals to climate change improves, we are beginning to assemble the tools needed to translate science into marine spatial planning as part of an adaptive approach to reef management.

ACKNOWLEDGEMENTS

This project was funded by the GEF Coral Reef Targeted Research Project, Khaled bin Sultan Living Oceans Foundation, Natural Environment Research Council, European Space Agency and EU Seventh Framework Programme (P7/2007–2013) under grant agreement no. 244161. CBP and LMC are funded by NSF-OCE-0825625. The manuscript contents are solely the opinions of the authors and do not constitute a statement of policy, decision or position on behalf of NOAA or the US Government. We thank Carrie Kappel, Alastair Harborne, Jodene Williams and Michelle Rome for determining coral cover for sites in the Bahamas. Andrew Baker and Ove Hoegh-Guldberg engaged in useful discussions.

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Appendix S1 Additional methods, caveats, assumptions, field testing, and rationale.

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Editor, Howard Cornell

Manuscript received 15 August 2010

First decision made 24 September 2010

Manuscript accepted 22 October 2010