

# Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs

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**Abstract** Networks of no-take reserves are important for protecting coral reef biodiversity from climate change and other human impacts. Ensuring that reserve populations are connected to each other and non-reserve populations by larval dispersal allows for recovery from disturbance and is a key aspect of resilience. In general, connectivity between reserves should increase as the distance between them decreases. However, enhancing connectivity may often tradeoff against a network's ability to representatively sample the system's natural variability. This "representation" objective is typically measured in terms of species richness or diversity of habitats, but has other important elements (e.g., minimizing the risk that multiple reserves will be impacted by catastrophic events). Such representation objectives tend to be better achieved as reserves become more widely spaced. Thus, optimizing the location, size and spacing of reserves requires both an understanding of larval dispersal and explicit consideration of how well the network represents the broader system; indeed the lack

of an integrated theory for optimizing tradeoffs between connectivity and representation objectives has inhibited the incorporation of connectivity into reserve selection algorithms. This article addresses these issues by (1) updating general recommendations for the location, size and spacing of reserves based on emerging data on larval dispersal in corals and reef fishes, and on considerations for maintaining genetic diversity; (2) using a spatial analysis of the Great Barrier Reef Marine Park to examine potential tradeoffs between connectivity and representation of biodiversity and (3) describing a framework for incorporating environmental fluctuations into the conceptualization of the tradeoff between connectivity and representation, and that expresses both in a common, demographically meaningful currency, thus making optimization possible.

**Keywords** Conservation planning · Great Barrier Reef · Larval dispersal · Marine protected area · Resilience · Risk-spreading

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## Introduction

Coral reefs are renowned for their stunning biodiversity, which includes both seen (e.g., habitat, species) and unseen (e.g., genetic) diversity (Soulé 1991). Reef biodiversity is severely threatened by an oft recited litany of human-caused disturbances (Knowlton 2001; Hoegh-Guldberg 2004), and increasing consensus identifies networks of reserves (no-take areas) as a key conservation strategy (Roberts et al. 2006; Jones et al. 2007). Coral reef reserves have proliferated, and most have been established to protect biodiversity (Mora et al. 2006; Jones et al. 2007; Wood et al. 2008). An implicit assumption in this approach is that no-take status contributes to population persistence inside reserves (i.e.,

offspring from reserve populations contribute to the persistence of their own and/or other reserve populations).

Connectivity refers to the exchange of individuals between populations, a process that in the sea occurs primarily through dispersal of planktonic larvae or propagules (hereafter “larvae”). Coral reef seascapes are inherently patchy and fragmented, consisting of spatially distinct subpopulations connected to an unknown degree and distance by larval dispersal (Kritzer and Sale 2004; Jones et al. 2007). In general, connectivity between subpopulations should increase as the distance between them decreases. Connectivity is increasingly recognized as a key conservation objective because of its importance to population persistence and recovery from disturbance (Roberts et al. 2006; Salm et al. 2006). Designing reserve networks (e.g., reserve location, size and spacing) that adequately protect connectivity requires an understanding of larval dispersal. However, existing networks have not incorporated empirical estimates of larval dispersal in their design, and may therefore fail to protect connectivity, ensure population persistence or protect biodiversity. In addition, protecting connectivity is only one of several key objectives that should be considered in reserve network designs, and these objectives may tradeoff against each other.

Systematic conservation planning (SCP) provides a framework for designing reserve networks using explicit, usually quantitative, objectives (Margules and Pressey 2000; Leslie 2005). Typically, decision support algorithms are used to integrate spatially explicit data to assist in selecting the location, size and spacing of reserves to meet conservation objectives (Sarkar et al. 2006). Some common objectives, such as maximizing the total number of species or habitat types inside reserves (“representation”) (Day et al. 2003; Pressey 2004) and minimizing the probability that multiple reserves are affected by a single event (“risk-spreading”) (Salm et al. 2006; McLeod et al. 2009) are best achieved by increasing the spacing between reserves. For example, widely spaced reserves are more likely to capture the full range of species and habitats in a coral reef ecosystem than clumped reserves, and fewer reserves will be affected by environmental fluctuations or discrete events (e.g., cyclone, oil spill) if they are widely spaced. As a result, achieving such objectives likely trades off against the goal of maintaining adequate connectivity between reserves. Understanding, formulating and incorporating such tradeoffs in the design of reserve networks is a major goal because doing so can enhance network resilience.

Historically, there have been few estimates of larval dispersal distance to utilize in reserve network designs, and this has impeded the formulation and validation of specific design criteria to protect connectivity (McCook et al. 2009). Recent studies have employed a variety of new technologies to measure larval dispersal, and much of this work has been

conducted on coral reefs (review by Jones et al. 2009). While an understanding of larval dispersal is far from complete (Botsford et al. 2009), these data provide opportunities to refine reserve network design principles and evaluate whether existing networks protect connectivity. Consequently, this article has three general aims. (1) Review and update recommendations for the location, size and spacing of reserves in a network designed for biodiversity protection. Previous work has largely focused on species diversity or population replenishment; to stimulate further discussion, an examination of how network design influences genetic diversity is included. (2) Use a new spatial analysis of the Great Barrier Reef Marine Park to examine the potential tradeoff between connectivity and representation objectives. (3) Present a framework for expanding the conceptualization of “representation” to incorporate risk-spreading, an important aspect of population growth in the presence of environmental fluctuations. The tradeoff between risk-spreading and connectivity is formalized by expressing both in a common, demographically meaningful currency, thus making optimization possible.

### Connectivity and the location, size and spacing of reserves

Most previous studies have addressed how larval dispersal influences the design of reserve networks for fisheries management, not biodiversity conservation, but these clearly illustrate how optimal reserve location, size and spacing are dependent on larval dispersal (e.g., Botsford et al. 2001; Lockwood et al. 2002; but see Hastings and Botsford 2003). Of primary consideration is whether the goal is to maximize benefits within or beyond reserves, or to achieve a balance between the two. Recent studies on coral reefs document high variance in larval dispersal distance in a few species, with some larvae returning to (or staying within) their small natal population, while others successfully disperse 10–100s of km (Jones et al. 2009). If such high variance is a general property of coral reef species, achieving benefits both within and beyond reserves should be feasible because populations inside reserves can be both self-replenishing and provide recruitment subsidies to other populations.

#### Location of reserves

Three main issues influence reserve location with respect to larval dispersal and connectivity: (1) source/sink populations, (2) isolated or island populations and (3) spawning aggregations (Jones et al. 2007).

Resilient source populations can provide larvae to “rescue” other depleted populations (Roberts et al. 2006;

Salm et al. 2006). In general, sites that function strictly as sources must be substantially self-replenishing to persist and provide above-average recruitment subsidies to areas outside reserves (Jones et al. 2007). In contrast, some have argued that sinks—populations relying largely on larvae from elsewhere for their persistence—are low conservation priorities. However, while sinks are less able to rescue or replenish other populations, they may be important repositories of genetic diversity, especially where they receive inputs from multiple sources and are partially self-replenishing. Furthermore, if sinks respond to environmental fluctuations differently than sources, their inclusion in reserve networks can enhance reserve-wide population persistence (see Integrating Connectivity and Representation below). Identifying sources and sinks is typically accomplished using oceanographic models (e.g., Roberts 1997; Bode et al. 2006), although recent models incorporating larval mortality rates and behaviour suggest that the spatial scale over which sources can provide significant recruitment subsidies may be limited (Cowen et al. 2006; Paris et al. 2007). Studies integrating biophysical models with predicted effects of climate change (e.g., changes to ocean currents, temperature, salinity and productivity) should prove useful in determining whether source/sink locations are resilient to climate change (e.g., Vikebø et al. 2007; Munday et al. 2009).

Isolated populations and islands that are largely self-replenished have high conservation value, especially where they harbour endemic species and/or unique assemblages (Jones et al. 2002; Perez-Ruzafa et al. 2006; Roberts et al. 2006). Low connectivity makes them less resilient to disturbance, so protecting a large fraction of these systems may be required to ensure population persistence and maintain genetic diversity, particularly for small populations (Frankham 1996). Genetic drift (random changes in allele frequencies in a population) can lead to fixation of deleterious alleles, and drift is compounded in small populations (Freedland 2005). A similar effect results from inbreeding, which is more likely in small populations (Crnokrak and Roff 1999). Furthermore, island populations may have inherently lower genetic diversity than coastal populations (Perez-Ruzafa et al. 2006). Thus, small, isolated populations are at greater risk of extinction due to genetic drift, inbreeding and the loss of adaptive heterozygote conditions (Reed 2005). Therefore, all else equal, more individuals are required to maintain genetic diversity in isolated populations relative to more connected populations.

Some coral reef species form spawning aggregations at predictable times and sites (Claydon 2004). For example, some heavily exploited groupers (Serranidae) travel several 10s of km to reach an aggregation site, which can draw adults from several 100 km<sup>2</sup> (Nemeth et al. 2007; Rhodes

and Tupper 2008). Aggregations are larval point sources for regional population replenishment and connectivity, and their predictability makes them especially vulnerable to overexploitation (Sadovy and Domeier 2005). Where and how far larvae disperse from aggregations remains unknown, although recent modelling suggested a high regional (several 1,000 km<sup>2</sup>) self-replenishment around snapper (Lutjanidae) aggregations in Cuba (Paris et al. 2005). On coral reefs, many aggregations have been fished to extinction (Sala et al. 2001; Sadovy and Domeier 2005; Aguilar-Perera 2007). Protecting aggregation sites, either permanently or through temporal closures, is a high priority (Roberts et al. 2006). However, additional management strategies will be required to sustain most aggregating species (Hilborn et al. 2006).

#### Size of reserves

Given that there are often practical limits to the amount of habitat inside reserves (e.g., 30–50%), and that a reserve network is preferable to a single large reserve of the same total area (see Integrating Connectivity and Representation below), should there be fewer large reserves or many small reserves (Diamond 1975; Simberloff 1988)? The answer depends somewhat on the tradeoff between reserve size/number and reserve spacing to maintain connectivity. If, as argued below, connectivity can be maintained over a wide range of inter-reserve distances, fewer large reserves may be preferable to many small reserves (Fernandes et al. 2005).

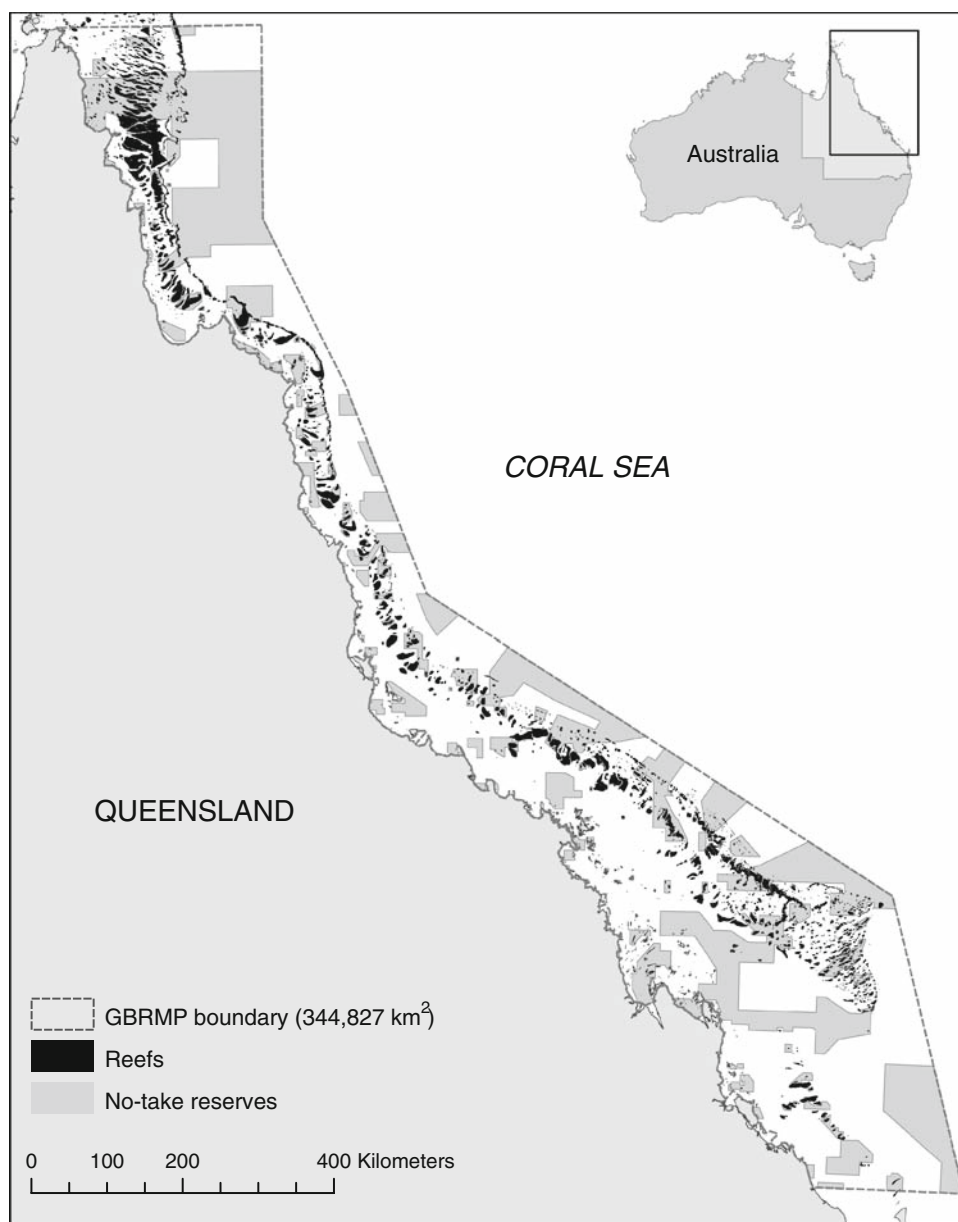
Considering individual reserves, large reserves protect biodiversity better than small reserves because (1) they protect a greater proportion of critical habitats and ecological processes necessary to sustain populations of multiple species and (2) they can support larger populations, which enhances the maintenance of genetic diversity. Loss of genetic diversity can decrease population viability (through genetic drift and inbreeding) and decrease the ability to adapt to a changing environment (Frankham 2005). Genetic drift is quantified by estimating effective population size ( $N_e$ ), which can be conceptualized as the number of individuals actually contributing to the next generation.  $N_e$  is sensitive to historic genetic drift, inbreeding and unequal reproductive success (Frankham 1995). Estimates of  $N_e$  are typically much lower than actual population size ( $N$ ), and the ratio  $N_e/N$  is typically  $10^{-2}$ – $10^{-5}$  (Hauser et al. 2002; Turner et al. 2002; Hutchinson et al. 2003; Hoarau et al. 2005; Ovenden et al. 2007). Note that if  $N_e/N = 10^{-5}$ , only one in 100,000 individuals contributes to the next generation. Low  $N_e/N$  is likely common in coral reef species (Stoddart 1984; Planes and Lecaillon 1998; Ovenden et al. 2007). However, because estimating  $N_e$  is logistically difficult, a conservative

estimate of  $N_e/N = 10^{-4}$  might be advisable for most reef species. Frankham (1995) suggested that  $N_e \geq 500$  should minimize effects of genetic drift and inbreeding; this suggests protecting  $\sim 5,000,000$  individuals. While this is achievable for the many small-bodied coral reef species, for other larger-bodied species it is prohibitively large. However, large reserves protect large-bodied species better than small reserves because they are more likely to contain the home ranges of such species (Palumbi 2004). For many wide-ranging vulnerable species (e.g., sea turtles, some sharks), reserve networks must always be augmented by ecosystem-level management strategies.

With respect to connectivity, there have been few reserve size recommendations. Based on larval dispersal

estimates in 32 coastal benthic taxa (algae, a seagrass, invertebrates and fishes), Shanks et al. (2003) suggest a reserve diameter of 4–6 km to retain many larvae of short-distance dispersers and enhance reserve population persistence. In general, as larvae disperse farther, reserve size must increase to retain a sufficient proportion of recruitment to enhance reserve population persistence (Jones et al. 2007). With significant self-recruitment, as appears to be common (Jones et al. 2009), within-reserve benefits should increase dramatically with reserve size. Furthermore, larval export from reserves increases as reserve perimeter length increases, so bigger reserves export more larvae. However, increasing reserve size beyond that required to ensure reserve population persistence may be unnecessary, and

**Fig. 1** Location of 3,788 individual reefs and 164 no-take reserves (143 that contain coral reefs) within the Great Barrier Reef Marine Park (GBRMP), Queensland, Australia



Lockwood et al. (2002) suggest that for isolated reserves entirely dependent on self-replenishment, this condition is met when reserve diameter is twice mean dispersal distance. Finally, small reserves provide minimal recruitment benefits because they protect small populations that produce few larvae (Palumbi 2004; Jones et al. 2007).

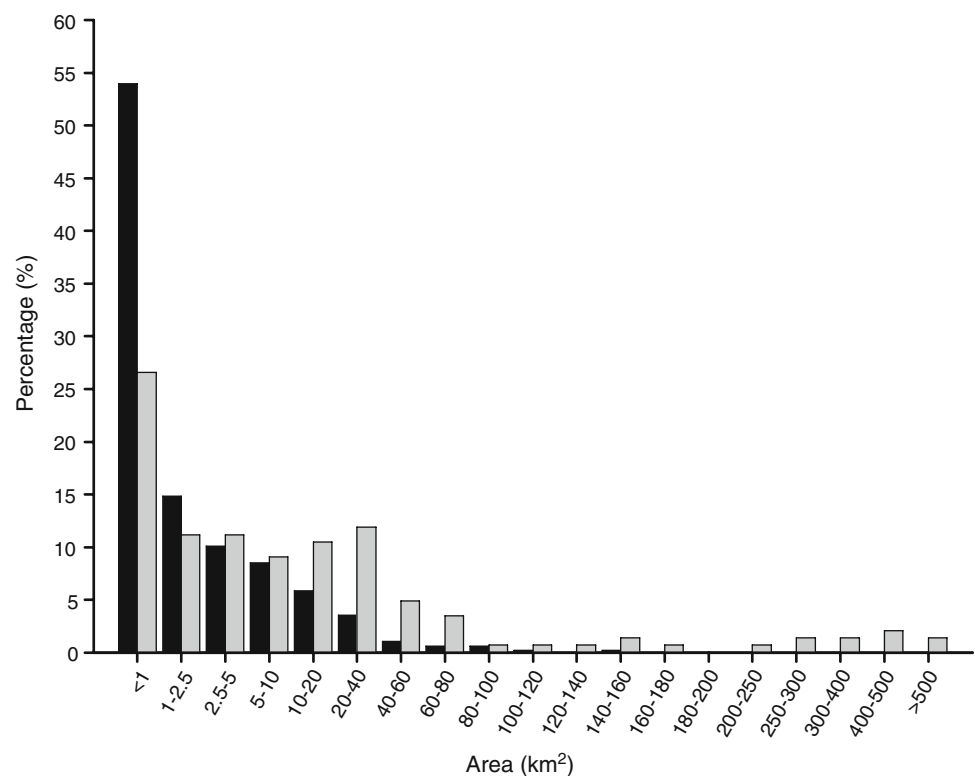
How does reserve size and spacing in existing networks relate to estimates of larval dispersal on coral reefs? Recently, a new reserve network was designed for the Great Barrier Reef Marine Park (Fernandes et al. 2005) before many of the recent studies of larval dispersal in corals and fishes were available. The network, implemented in 2004, consists of 143 reserves containing coral reefs (164 reserves in total) spread over 344,827 km<sup>2</sup> (Fig. 1). A new spatial analysis of the park identified 3,788 reefs with a total area of 24,896 km<sup>2</sup>. Median reef area is 0.80 km<sup>2</sup>, more than 50% of all reefs are <1 km<sup>2</sup> and few reefs (~7%) are larger than 20 km<sup>2</sup> (Fig. 2). Jones et al. (2009) demonstrate that coral and fish populations are often partially self-replenishing, even on reefs <1 km<sup>2</sup>, but also linked to other populations 10–100s of km away by larval dispersal. The 143 reserves protect 1,144 reefs (or parts of reefs) with a total area of 7,722 km<sup>2</sup>. Reef area protected inside reserves encompasses the natural range of individual reef areas, but has a longer tail because many reserves contain multiple reefs (Fig. 2). Thirty-eight reserves (27%) protect <1 km<sup>2</sup> of reef. While these small reserves will produce fewer larvae due to their smaller populations, they

are likely to contribute to overall network connectivity and population persistence if they collectively represent a significant proportion of reef habitat and are connected to other reserves (see below). Some reserves protect large reef areas; 45 protect  $\geq 20$  km<sup>2</sup> of reef, and 12 of these protect >150 km<sup>2</sup>. These large reserves are likely substantially self-replenishing, provide large recruitment subsidies beyond their boundaries, and will better protect large-bodied, wide-ranging species (Palumbi 2004).

#### Spacing of reserves

Reserve spacing should consider variation in dispersal distance both within and among coral reef taxa (Palumbi 2004). Intuitively, connectivity decreases as reserve spacing increases, and this decrease will be particularly rapid for short-distance dispersers (Jones et al. 2007). With respect to reserve population persistence, if reserves are large enough to be substantially self-replenishing the distance between them may have little impact (Botsford et al. 2001; Jones et al. 2007). Furthermore, modelling studies suggest population persistence is not sensitive to reserve spacing or dispersal distance if a network protects a minimum fraction of habitat (Botsford et al. 2001; Kaplan and Botsford 2005). Populations may persist marginally better if reserves are closer together due to greater recruitment subsidies from other reserves (Roberts et al. 2006). Reserve spacing is more important for recruitment subsidies beyond

**Fig. 2** Area of individual reefs (black bars;  $N = 3,788$ ) and reef area inside reserves (grey bars;  $N = 143$ ) within the Great Barrier Reef Marine Park. Geographic Information System (GIS) data delineated (1) reefs and (2) reserves (scale = 1:25,000). Reefs delineated based on a visual assessment of satellite imagery. Area measured using ArcMap 9.2 (ESRI 2006). Where adjacent reef polygons shared a boundary, they were merged





reserve boundaries; in general, as variability in dispersal distance increases (i.e., more larvae disperse farther), spacing between reserves that achieves recruitment subsidies beyond boundaries or inter-reserve connectivity can increase (Jones et al. 2007).

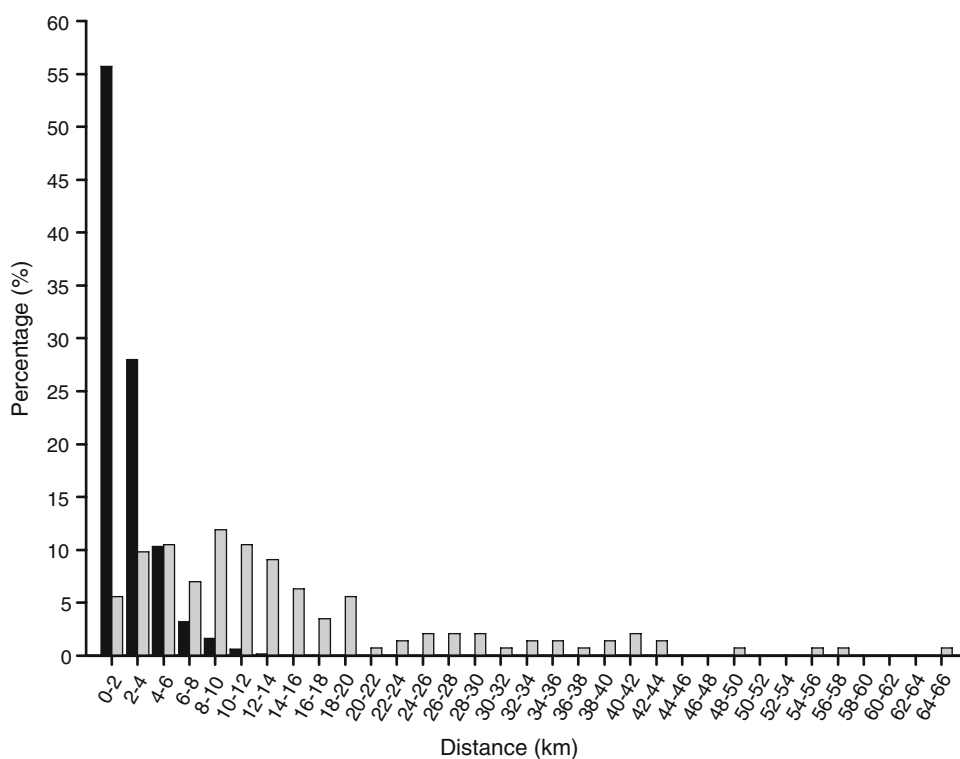
Reserve spacing required to maintain genetic diversity is generally greater than required for demographic connectivity. This is true because exchange of relatively few individuals (i.e., the tail of the dispersal curve) maintains genetic connectivity (Palumbi 2004; Cowen et al. 2006). Genetic diversity within a population is related to the number of other populations from which it receives genes (individuals). Decreased connectivity threatens genetic diversity, especially where population size is low (Frankham 1995). In general, spacing reserves to ensure demographic connectivity should maintain genetic diversity.

There are few recommendations for reserve spacing based on reviews of dispersal distances. Based on Kinlan and Gaines' (2003) review of dispersal estimates from genetic data, Sala et al. (2002) argue that gaps between reserves should be  $\leq 100$  km to maintain inter-reserve connectivity and provide recruitment subsidies to fished areas. Shanks et al. (2003) suggest a spacing of  $\leq \sim 20$  km to promote connectivity among reserves for many species with pelagic larvae, whereas Palumbi (2004) argues for greater variation in spacing (10–200 km) to reflect dispersal variation among taxa. However, Kaplan and Botsford (2005) used a spatially explicit, size- and age-structured model for species with

relatively sedentary adults to demonstrate that there was little value in variable spacing. Recent evidence from corals and reef fishes demonstrates that, for many species, larvae successfully disperse from meters to many 10s of km (Jones et al. 2009); this suggests that reserves will be connected over a broad range of distances (e.g., 1–50 km).

In the Great Barrier Reef reserve network, distance separating neighbouring reefs ranges from 4 m to 52 km (median = 1.8 km) and more than 99% of reefs have a neighbouring reef within 14 km (Fig. 3). Based on current evidence, coral and fish populations on most reefs are connected to populations on several, possibly many, other reefs (Jones et al. 2009). With respect to distance between reefs in adjacent reserves, 64% of reserves have a neighbour within 14 km, whereas a minority of reserves are more isolated; 14% by 20–40 km and 2% by  $>50$  km (Fig. 3). Coral and fish populations in even the most isolated reserves are likely connected to populations in other reserves (Jones et al. 2009), but reserves isolated by  $>50$  km likely receive decreased recruitment subsidies from other reserves. Finally, the distribution of between-reserve distances has greater variance and a longer tail than the distribution of between-reef distances (Fig. 3). Although on the Great Barrier Reef this pattern likely occurs because many close reefs are included within a single reserve, the pattern does illustrate the potential for a tradeoff between achieving adequate representation of species/habitats inside reserves and maintaining connectivity between reserves.

**Fig. 3** Distance between neighbouring reefs (black bars;  $N = 3,788$ ) and neighbouring reefs in adjacent reserves (grey bars;  $N = 143$ ) within the Great Barrier Reef Marine Park. Distances were measured from the centroid of one reef to the closest edge of its neighbour. Centroid estimated using ArcMap 9.2 (ESRI 2006) function 'shapes to centroids' function. Distance measured using ArcView 3.3 (ESRI 2002) and Nearest Feature (Jenness 2004)



## Integrating connectivity into the design of reserve networks

As reviewed above, most recommendations for reserve spacing are based on dispersal distances alone, and assume (at least implicitly) a single, homogeneous habitat. However, as noted earlier, systematic conservation planning often focuses on “representation”: capturing a large proportion of species or habitat types across a seascape. Representation has been addressed in two ways. Most commonly, the objective is to identify a set of complementary areas that together achieve target levels for each feature (e.g., habitat, species) at minimum cost (e.g., area, forgone opportunities for extractive uses). Less commonly, the objective is to maximize representation of features subject to an upper limit on total management cost (Camm et al. 1996). Usually, cost of full representation is minimized, and the extent of partial representation within cost limits is maximized, when reserves are small and widely scattered (Kiestler et al. 1996; Pressey and Logan 1998). Conversely, connectivity-based approaches typically emphasize the importance of keeping reserves close enough to ensure sufficient connectivity between them. Designing reserve networks for connectivity usually requires representation to be achieved at larger cost (Rothley 2006). Given that conservation management is generally severely constrained by costs, planners and managers must manage a tradeoff between connectivity (i.e., inter-reserve spacing) and representation.

One major practical problem is that connectivity and representation are measured in different and not directly comparable units, and thus, it is unclear what quantity to optimize. Moreover, “representation” has typically been viewed either as a species accumulation problem (get as many species into a reserve as efficiently as possible), or a habitat representation problem (ensure a minimum level of representation of each habitat type in an overall network). Such approaches tend, like most connectivity studies, to adopt a static view of representation. However, because environments fluctuate in space and time, the conditions that prevail at any given location (and potentially the species that are found there) will also change. Thus, a robust framework for trading off connectivity and representation will ultimately need to incorporate this stochastic aspect of ecological dynamics. Here, a first step towards such a framework is presented, beginning with a single-species framework that considers a single metapopulation in isolation, followed by a description of how this tradeoff holds when extended to a multi-species context. For simplicity, reproductive success outside of reserves is assumed to be negligible. This assumption is common in terrestrial reserve design problems where non-reserve areas are likely to be converted to unsuitable habitat, but may be relevant

to some marine contexts (e.g., very intense harvesting outside reserves). Nevertheless, the framework can be extended to incorporate reproductive contributions from non-reserve areas. The framework builds on the population-dynamic approach commonly used in connectivity studies, but incorporates fluctuations in the contributions that each reserve makes to population growth. This allows for explicit consideration of how a reserve network’s incorporation of variation present in the system influences population viability and, ultimately, the maintenance of biodiversity. It also does so in a way that expresses representation and connectivity in a common currency, an essential component of any attempt to optimize, or even quantify meaningfully, tradeoffs between these two conservation objectives.

### Single-species framework

The goal here is maximizing long-run density-independent population growth rate: in other words, to maximize the population’s capacity to recover from depletion. High connectivity contributes to population growth because a greater proportion of offspring leaving the natal reserve arrive at other reserves, thereby conferring greater reproductive success. Often, as reserves become farther apart connectivity declines.

However, in fluctuating environments, reserve spacing has another, countervailing, effect on long-run population growth. Temporal fluctuations in birth and death rates in one reserve will covary to some degree with fluctuations in other reserves. In general, this covariance will be greater for nearby reserves because some environmental factors responsible for fluctuations are more likely to impact nearby sites. For instance, many episodic disturbances (e.g., oil spills, cyclones, disease outbreaks) are more likely to impact multiple reserves when reserves are close to one another. This tendency for distance-decay in the covariance of fluctuations in demographic rates is important because long-run population growth rates increase as this covariance decreases. This is the essence of risk-spreading.

To illustrate risk-spreading, consider a simple, idealized example (following Roughgarden 1998): a population of semelparous organisms is distributed between two reserves, A and B: offspring are distributed equally between the reserves: and the environment fluctuates between good and bad years. Density-independent growth of the metapopulation follows:

$$N_{t+1} = f_{A,t} \frac{N_t}{2} + f_{B,t} \frac{N_t}{2} = \left( \frac{f_{A,t} + f_{B,t}}{2} \right) N_t \quad (1)$$

Where  $N_t$  is metapopulation size at time  $t$ , and  $f_{i,t}$  is individual fecundity in reserve  $i$  ( $i = A$  or  $B$ ) at time  $t$ . The value in parentheses is the metapopulation’s annual growth

rate: the fraction by which it grows (or shrinks) in year  $t$ . Over time, growth compounds as:

$$N_{t+1} = \left(\frac{f_{A,t} + f_{B,t}}{2}\right) N_t = \left(\frac{f_{A,t-1} + f_{B,t-1}}{2}\right) N_{t-1} \dots \left(\frac{f_{A,1} + f_{B,1}}{2}\right) N_1 \tag{2}$$

If fecundities vary randomly among years, then long-run metapopulation growth rate depends on how strongly fluctuations covary between the two reserves. At one extreme, a good year in A is always a good year in B (i.e., if  $f_{A,t} = f_{\text{good}}$ , then  $f_{B,t} = f_{\text{good}}$ ), and likewise for bad years. In this case, annual metapopulation growth rate is either  $f_{\text{good}}$  or  $f_{\text{bad}}$ . If good and bad years are equally likely, then:

$$N_{t+1} = \begin{cases} \left(\frac{f_{\text{good}} + f_{\text{good}}}{2}\right) N_t = f_{\text{good}} N_t & \text{in good years} \\ \left(\frac{f_{\text{bad}} + f_{\text{bad}}}{2}\right) N_t = f_{\text{bad}} N_t & \text{in bad years} \end{cases} \tag{3}$$

and, in the long run, good years about half the time, and similarly for bad years:

$$N_{t+1} = \left(f_{\text{good}}^{1/2} f_{\text{bad}}^{1/2}\right) N_t = \left(f_{\text{good}}^{1/2} f_{\text{bad}}^{1/2}\right)^t N_1 \tag{4}$$

The quantity in parentheses represents long-run annual metapopulation growth rate, and is the *geometric* mean of the individual annual growth rates. This is generally true: long-run population growth rate in a randomly varying environment is the geometric mean of the year-by-year population growth rates. Importantly, as variability of a set of numbers increases, geometric mean decreases, even if arithmetic mean remains the same. Thus, year-to-year variability in metapopulation growth rate will decrease if fluctuations in fecundity are weakly correlated among reserves (i.e., extremes in growth rates occur only when all reserves experience extreme conditions in the same year). For instance, if reserves A and B experience environmental fluctuations independently, then overall metapopulation growth rate is  $f_{\text{bad}}$  only 25% of the time (when  $f_{A,t} = f_{B,t} = f_{\text{bad}}$ ) and  $f_{\text{good}}$  only 25% of the time (when  $f_{A,t} = f_{B,t} = f_{\text{good}}$ ), whereas 50% of the time it is the average of  $f_{\text{good}}$  and  $f_{\text{bad}}$  ( $f_{A,t} = f_{\text{bad}}$  and  $f_{B,t} = f_{\text{good}}$ , or  $f_{A,t} = f_{\text{good}}$  and  $f_{B,t} = f_{\text{bad}}$ ). Thus, overall, year-to-year variation decreases and long-run population growth rate increases.

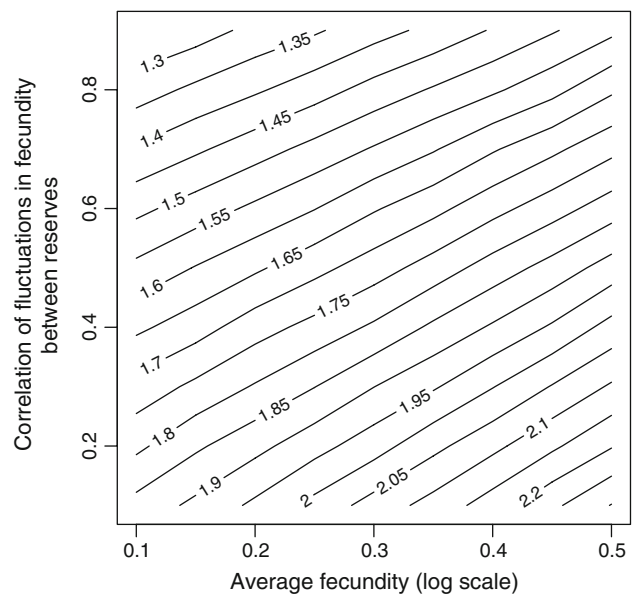
The risk-spreading principle is extremely general; it is true regardless of population subdivision and in scenarios of year-to-year environmental fluctuations more complex

than the simple good year/bad year dichotomy described above. Risk-spreading provides the greatest benefit when spatial covariance in environmental fluctuations is low and dispersal between reserves is maximized (i.e., individuals are re-allocated among reserves every year). Nevertheless, as long as fluctuations are not perfectly correlated among reserves, and there is dispersal between reserves, some risk-spreading will occur. Furthermore, risk-spreading occurs when reserves contribute unequally to metapopulation growth rate. For example, adding a low-quality patch to a reserve network can make a greater contribution to long-run metapopulation growth rate than adding a high-quality patch, if environmental fluctuations in the former are less correlated with fluctuations in existing reserves (e.g., compare upper right and bottom left of Fig. 4).

The tradeoff between risk-spreading and local productivity means that adding a distant second reserve can increase long-run metapopulation growth rate more than if that reserve were nearby and thus, more environmentally correlated with the first, even if connectivity between reserves declines. To illustrate, the previous model can be extended by stipulating that the two reserves are separated by some distance,  $x$ :

$$\begin{aligned} n_{A,t+1} &= (1 - m) f_{A,t} n_{B,t} + m D(x) f_{B,t} n_{B,t} \\ n_{B,t+1} &= (1 - m) f_{B,t} n_{B,t} + m D(x) f_{A,t} n_{A,t} \end{aligned} \tag{5}$$

$m$  is the fraction of offspring not recruiting back to their natal reserve, and  $D(x)$  is a function describing the fraction



**Fig. 4** Contours of long-run metapopulation growth rate resulting from adding a second reserve to an existing reserve, from the model in Eq. 2, as a function of the second reserve’s productivity (horizontal axis) and its covariation with the first reserve (vertical axis). Fecundity is lognormally distributed over time;  $\ln(f)$  has a variance of 3.0 in both reserves and a mean of 0.2 in the first reserve

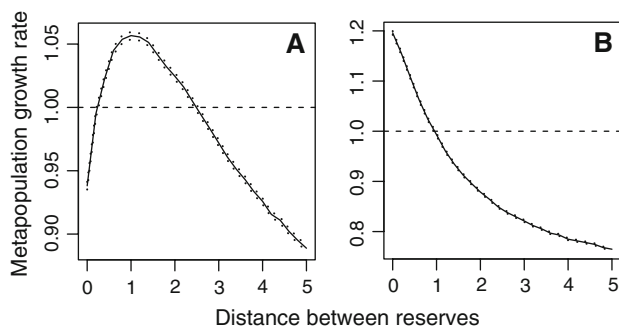


of these offspring that successfully disperse to a reserve  $x$  distance away. In general, this tends to decrease as  $x$  increases, leading to reduced metapopulation growth rate as reserves get farther apart. For instance, dispersal distances are often assumed to be exponentially distributed, in which case:

$$D(x) = e^{-\lambda x} - e^{-\lambda(x+r)} \quad (6)$$

where  $\lambda$  is the rate at which dispersal declines with distance, and  $r$  is reserve size. Simultaneously, covariance of  $f_{A,t}$  and  $f_{B,t}$  tends to decrease with distance, leading to reduced inter-annual variability in metapopulation growth rates (and thus higher long-run metapopulation growth rates) as reserves get farther apart. Optimal spacing occurs where this tradeoff maximizes long-run metapopulation growth rate, and that spacing is zero only when dispersal success decreases very rapidly relative to covariance of fecundity (Fig. 5). Similarly, if dispersal success peaks at intermediate distances, then distance-decay in the covariance of birth or death rates should maximize long-run metapopulation growth rates at reserve spacing somewhat greater than mean dispersal distance.

Research on this distance-mediated tradeoff between environmental covariance and successful dispersal has been limited to two studies that considered similar special cases of this general phenomenon; both used patch-occupancy models



**Fig. 5** Long-run metapopulation growth rate for two reserves as a function of between-reserve distance (from Eq. 5). **a** For nearby reserves, dispersal success is high but environmental fluctuations affect both reserves similarly and there is little risk-spreading. Consequently, the metapopulation declines over time (i.e., growth rate  $<1$ ). Conversely, for distant reserves, environmental fluctuations are less correlated but dispersal success is too low to sustain the metapopulation. Long-run metapopulation growth rate is maximized at intermediate dispersal distances due to the tradeoff between connectivity and risk-spreading. For this graph,  $m = 0.5$ ,  $\ln(f_A)$  and  $\ln(f_B)$  are normally distributed over time with a mean of 0.3 and variance of 2.0, the covariance of  $\ln(f_A)$  and  $\ln(f_B)$  decays exponentially with distance at rate 1, and  $D(x)$  follows Eq. 6 with  $\lambda = 0.5$ . Distance measured in units of reserve size (i.e., each reserve has size 1). **b** Identical scenario to panel (A), but connectivity decreases more strongly with distance ( $\lambda = 1.5$ ). Here, benefits of increased connectivity from moving reserves closer together outweighs reduction in risk-spreading, so long-run metapopulation growth rate is highest when reserves are adjacent

of two reserves subject to local extinction by environmental catastrophe (McCarthy et al. 2005; Wagner et al. 2007). The likelihood of a single catastrophe being large enough to cause extinction in both reserves (and thus extinction of the metapopulation) decreased as reserve spacing increased, an example of distance-decay in environmental covariance. Conversely, probability of re-colonization of an extinct reserve decreased as reserve spacing increased, a special case of distance-decay in dispersal success. Optimal reserve spacing was intermediate, where this tradeoff maximized metapopulation persistence time.

Insights from existing work notwithstanding, several questions, both theoretical and empirical, remain. (1) Degree of self-replenishment and extent of successful between-reserve dispersal likely vary randomly among years; whether or to what extent does distance-decay in covariances of such fluctuations enhance persistence? (2) Does variability in reserve spacing or reserve size in a network influence persistence when fluctuations in connectivity occur (e.g., Kaplan 2006)? (3) Advection can increase connectivity initially as inter-reserve distance increases in the direction of transport; how strongly does this asymmetry influence optimal reserve spacing in the presence of environmental fluctuations? (4) How do contributions to population growth from non-reserve patches influence the effect of reserve spacing on long-run metapopulation growth rates? (5) Conservation objectives could include maintenance of threshold population size, or local recovery rates, in non-reserve areas; how well do these correlate with whole-metapopulation conservation objectives?

Empirically, data from regional-scale population monitoring undoubtedly contains information about how strongly fluctuations in recruitment, survival, and overall rates of population change correlate over space; such questions are usually addressed with approaches such as variance partitioning (e.g., Hughes et al. 2000). Those data could be used to quantify distance-decay in spatial covariances of demographic rates. Indeed, how demographic changes during particular events (e.g., mass-bleaching) covary spatially could reveal how effects are spatially structured. For example, contour maps of degree-heating weeks are often highly patchy, and effects of some disturbances (e.g., cyclones) vary with distance from a centre. However, compared to the growing body of literature on dispersal distances in marine organisms, there has been little work on the spatial structure of environmental fluctuations and little recognition of its potential influence on marine reserve network design.

#### Multi-species framework

The above framework treats single species in isolation and would be well suited to management driven by one species

of high conservation or fisheries value. However, marine reserve networks typically focus on protecting many species. If these species interact weakly, the issue becomes one of combining model predictions (as in Fig. 5) for many individual species. For example, one could find the reserve spacing that maximizes the number of species able to persist in the long run (i.e., metapopulation growth rates  $>1$ ).

Often, however, long-term stability or persistence of ecosystem-level properties (e.g., coral cover) is influenced by interactions between species. For example, as space occupied by one coral species increases, space available to other species decreases. Insights from competition theory suggest that if competitors respond differently to environmental variability, then that variability promotes species coexistence. Specifically, if environmental conditions affect per-capita population growth rates more when competition is weaker, then population growth rates of rare species tend to increase relative to common species in the presence of spatial variation in environmental conditions (Chesson 2000). These conditions are likely common because population growth rate tends toward zero as competition intensity increases, regardless of the impact of environmental conditions. Conversely, when competition is weak, population growth rates may differ dramatically between favourable and unfavourable years. For example, if live coral cover is high, space available for recruitment or colony growth is limited, regardless of whether conditions are favourable. However, if most space is unoccupied, then colonization via recruitment and colony growth is

possible, especially when energy for reproduction and growth is high due to favourable environmental conditions (Fig. 6; see Chesson 2000 for further development).

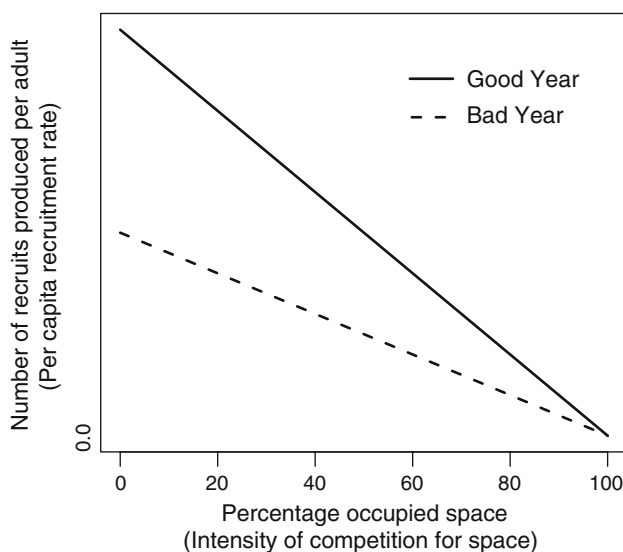
How relationships illustrated in Fig. 6 promote population growth of rare species has been demonstrated by rather technical analysis of competition models, but is not amenable to intuitive explanation (Chesson 2000). Nevertheless, this result is based on competition theory that is quite general, and it has some experimental support (Sears and Chesson 2007). This tends to argue against conservation approaches that focus exclusively on habitats sharing particular features (e.g., bleaching resistance), and instead for approaches that tradeoff the higher average growth rates of bleaching-resistant locations against the coexistence-promoting benefits of locations that increase the spatial environmental variability captured within a reserve network.

## Conclusions

Although reserve networks alone are insufficient for protecting coral reefs (Allison et al. 1998; Jones et al. 2004; Steneck et al. 2009), they are a key part of biodiversity conservation strategies. Reserve network and metapopulation persistence is to some degree dependent on whether and how much reserves/populations are connected, a process largely driven by larval dispersal. Recent studies on corals and fishes reveal a general pattern: within species there is typically wide variation in dispersal distance that appears unrelated to life history characteristics (Jones et al. 2009). Self-replenishment, even at spatial scales  $<1 \text{ km}^2$ , appears to be common, as is larval exchange over 10–100s of km. High variability in dispersal distance is good news because it implies that reserves can provide benefits both within and beyond their boundaries over a broad range of reserve size and spacing. Because choosing the location, size and spacing of reserves is an important practical problem for planners and managers, the following principles are proposed to guide the design of reserve networks (see also McCook et al. 2009). These are based on maintaining demographic connectivity between reserves and genetic diversity for coral and fish populations (Jones et al. 2009):

### Reserve location

- Resilient source populations can “rescue” other populations;
- Some sink populations may contribute greatly to genetic diversity when they receive inputs from multiple populations;
- Adding populations that respond differently to environmental fluctuations than other reserve populations enhances metapopulation persistence;



**Fig. 6** Per-capita recruitment (recruits per adult) as a function of percent space occupancy in good and bad years. Illustrates how effect of environmental fluctuations in recruitment might vary as a function of competition. If all space is occupied, recruitment must be zero (little difference between good and bad years). When competition is weak (i.e., free space plentiful; left side of graph), per-capita recruitment differs between good and bad years

- (d) Islands/populations isolated by >100 km are less resilient due to low connectivity, often harbour unique assemblages/endemic species and may have inherently low genetic diversity: a large proportion of the island/population must be protected to ensure persistence;
- (e) Spawning aggregations supply most (if not all) larvae for regional population replenishment of aggregating species and are extremely vulnerable to overexploitation.

#### Reserve size

- (a) Bigger is better: large reserves protect biodiversity better because they contain (1) a larger proportion of critical habitats and ecological processes needed to sustain multiple species and (2) a larger population, thereby minimizing negative effects of genetic drift and inbreeding, producing more larvae and increasing recruitment subsidies beyond reserve boundaries;
- (b) In general, a reserve network should protect a range of reef sizes that reflects natural variation in reef area.

#### Reserve spacing

- (a) Given high variability in dispersal distance, connectivity should be maintained over a broad range of between-reserve distances;
- (b) Conservatively, between-reserve distances of  $\leq 50$  km should ensure sufficient demographic connectivity for most species;
- (c) In general, variation in between-reserve distances in a network should reflect natural variation in between-reef distances.

While an understanding of dispersal and connectivity is growing quickly, it has historically been rather limited. Many existing reserve networks were designed using simple “rules of thumb” for protecting connectivity (see McCook et al. 2009 for update) and focused principally on “representation” objectives, as conventionally understood (e.g., adequately representing species and habitat diversity inside reserves). Representation objectives are often best achieved by increasing the spacing between reserves, and thus, may tradeoff against the goal of maintaining connectivity. The framework presented here for conceptualizing representation more broadly, and for quantifying and optimizing representation-connectivity tradeoffs, could be further developed and incorporated into systematic conservation planning approaches to improve reserve network designs. Typically, protecting multiple habitat types or habitats with differing species composition, consistent with the conventional understanding of representation (e.g., Day et al. 2003;

Fernandes et al. 2005; Marshall and Schuttenberg 2006), will also tend to promote risk-spreading because species perform differently across habitats, and habitats experience environmental fluctuations differently. However, the simple models presented here illustrate how this concept also applies to similar habitats subjected to spatially variable environmental fluctuations, such as disturbance events (e.g., storms, disease outbreaks, sediment plumes) (see Figs. 4 and 5).

In general, the risk-spreading principle suggests that reserve spacing based solely on maximizing connectivity likely underestimates optimal reserve spacing. The level of underestimation depends on how rapidly connectivity changes with distance relative to distance-decay in the covariance of environmental fluctuations. Thus, attempts to quantify dispersal should be complemented by efforts to quantify temporal fluctuations in birth and death rates over regional scales. This amounts to a generalization of representation to include consequences of capturing environmental variation within habitat types and over time, and is an example of planning to enhance representation of biodiversity processes (Pressey et al. 2007). Further theoretical work focused on contributions of non-reserve areas, directionality in dispersal, and effects of spatio-temporal environmental fluctuations on non-competitive interactions (e.g., predator–prey dynamics) may lead to additional rules of thumb and identify productive avenues for further empirical work.

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