Coral Reefs (2009) 28:353–366
DOI 10.1007/s00338-008-0463-7

REVIEW

Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs

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Received: 16 September 2008 / Accepted: 10 December 2008 / Published online: 13 February 2009

Abstract The global decline in coral reefs demands urgent management strategies to protect resilience. Protecting ecological connectivity, within and among reefs, and between reefs and other ecosystems is critical to resilience. However, connectivity science is not yet able to clearly identify the specific measures for effective protection of connectivity. This article aims to provide a set of principles or practical guidelines that can be applied currently to protect connectivity. These 'rules of thumb' are based on current knowledge and expert opinion, and on the philosophy that, given the urgency, it is better to act with incomplete knowledge than to wait for detailed understanding that may come too late. The principles, many of which are not unique to connectivity, include: (1) allow margins of error in extent and nature of protection, as insurance against unforeseen or incompletely understood threats or critical processes; (2) spread risks among areas; (3) aim for networks of protected areas which are: (a) comprehensive and spread—protect all biotypes, habitats and processes, etc., to capture as many possible connections, known and unknown; (b) adequate—maximise extent of protection for each habitat type, and for the entire region; (c) representative—maximise likelihood of protecting the full range of processes and spatial requirements; (d) replicated—multiple examples of biotypes or processes enhances risk spreading; (4) protect entire biological units where possible (e.g. whole reefs), including buffers around core areas. Otherwise, choose bigger rather than smaller areas; (5) provide for connectivity at a wide range of dispersal distances (within and between patches), emphasising distances <20–30 km; and (6) use a portfolio of approaches, including but not limited to MPAs. Three case studies illustrating the application of these principles to coral reef management in the Bohol Sea (Philippines), the Great Barrier Reef (Australia) and Kimbe Bay (Papua New Guinea) are described.

Communicated by Ecology Editor Professor Peter Mumby

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Keywords Ecological connectivity · Reef management · Margin of error · Resilience · Risk spreading · Rules of thumb

Introduction

The catastrophic decline in the world's coral reefs (Pandolfi et al. 2003; Hoegh-Guldberg 2004; Wilkinson 2004) demands urgent management responses on two fronts: reduction of immediate direct threats such as climate change, over-fishing and water pollution, and actions to protect or enhance the resilience of reef ecosystems in the face of existing and unavoidable future threats (Allison et al. 1998; Hughes et al. 2003; Bellwood et al. 2004). Much has been written about the factors that contribute to ecosystem resilience (e.g. Scheffer et al. 2001; Elmqvist et al. 2003; McCook et al. 2007) and in some cases, the appropriate management responses are relatively straightforward and feasible (at least in theory; West and Salm 2003; McCook et al. 2007). For example, the need to maintain biodiversity or trophic structure can be addressed, in part, by preventing destructive or excessive fishing. However, the management actions required to protect other aspects of resilience are not as clear or feasible. In particular, there is ample evidence that resilient marine ecosystems require intact biological and ecological connectivity, to allow reseeding of populations after disturbances (Hughes et al. 2003; Jones et al. 2007; Birrell et al. 2008), and to maintain intact life cycles, trophic or biogeochemical connections (e.g. Nagelkerken et al. 2001; Dorenbosch et al. 2007; Jones et al. 2007; Almany et al. 2009; Botsford et al. 2009). While current scientific knowledge indicates a need to maintain and understand the natural patterns of connectivity, the existing knowledge is far from sufficient to provide clear strategies for how to directly, adequately and realistically provide that protection. This remains a critical gap in our knowledge of how to manage for resilience on coral reefs: how should reef managers protect ecological connectivity?

Ecological connectivity is critically important to the resilience of populations inhabiting coral reefs habitats and other ecosystems to which they are linked (Roberts 1997; Nyström and Folke 2001; McCook et al. 2007). The capacity of reefs to recover after disturbances or reorganise in the face of new stresses depends critically on the supply of larvae or propagules available to reseed populations of key organisms, such as fish and corals (Roberts 1997; Hughes and Tanner 2000; Birrell et al. 2008). Even if a particular reef is well protected and soundly managed, alterations in the surrounding seascape may erode resilience if the supply of recruits for ecologically important organisms, such as reef-building corals, is reduced (McClanahan et al. 2002). Maintenance of connectivity is not only important for the maintenance of biodiversity and ecological integrity, but also for fisheries and other goods and services provided by ecosystems.

This article aims to combine emerging scientific information with lessons learned from practical experience in managing coral reefs in order to provide a set of practical recommendations for how reef managers can best protect ecological connectivity. Lessons are drawn from case studies of the Bohol Sea in the Philippines, the Great Barrier Reef (GBR) in Australia, and Kimbe Bay in Papua New Guinea.

The scope of the article includes ecological connectivity in the broadest sense (e.g. review by Cappo and Kelly 2001), but does not include connections between human and ecological systems, despite their importance. Resilient ecosystems need to maintain connectivity within and between habitat patches of the same type (e.g. dispersal of fish and coral larvae between reefs, seed dispersal between seagrass beds) as well as connectivity between habitat types (e.g. between reefs and seagrass beds or mangroves) (Cappo and Kelly 2001; Mumby 2006; Mumby and Hastings 2008). Management options should not be limited to spatial management approaches, such as no-take areas, but should include any initiatives or actions that would enhance the protection of biological and ecological connectivity (e.g. temporal closures, management of runoff). In the context of networks of marine protected areas (MPAs), connections both between protected areas and between the protected areas and the rest of the ecosystem are sought (note that in this article, MPA is used in the broad sense to include a range of degrees of protection, including but not limited to no-take areas). For example, protection of a large proportion of the Great Barrier Reef in no-take zones was aimed not just at protecting biodiversity within the no-take zones, but also was aimed at benefiting the overall ecosystem, including areas outside the no-take zones (Fernandes et al. 2005). Finally, while the scope of this article is limited to protecting connectivity specifically, it is important to recognise that these goals must still be integrated with adequate protection of other elements of resilience (West and Salm 2003; McCook et al. 2007). Thus, for example, it is critical that larvae have suitable habitat to settle and grow once they reach a new reef or habitat (e.g. Birrell et al. 2008; Steneck et al. 2009).

From science to management practice: the challenge of 'How?'

The value of protecting ecological connections has long been recognised in both scientific recommendations (e.g. James et al. 1990; Day and Laffoley 2006) and in management objectives (see Case Studies). Management agencies are generally aware of the value of protecting connectivity; the major challenge is to identify specific actions or measures that will provide that protection. In few, if any, cases is current scientific information sufficient to know how to ensure maintenance of even limited aspects of connectivity. For example, population replenishment in marine systems is predominantly a function of the dispersal of planktonic larvae, and tracking these larvae to directly measure connectivity is either difficult and expensive or impossible (Levin 2006; Thorrold et al. 2006).

The science of population connectivity on reefs is advancing rapidly, and in doing so, it is overturning many previous assumptions and ideas (Cowen et al. 2007; Jones et al. 2009). For example, brooding corals, widely presumed not to disperse very far, do exhibit occasional long-distance dispersal (Underwood et al. 2007). On the other hand, a reef fish with a pelagic larval duration of over 35 days can produce many larvae that do not disperse away from their natal reefs (Almany et al. 2007). Dispersal of reef fish may be strongly influenced by larval behaviour (Gerlach et al. 2007; Paris et al. 2007), and cannot be considered as passive particles subject to simple hydrodynamic patterns (Werner et al. 2007). The emerging science suggests that there is a wide spread in dispersal distances, both within and among species, including both a greater level of localised recruitment and dispersal over extremely long distances (Jones et al. 2009). Connectivity patterns may also vary in different coral reef settings, depending on the size and degree of isolation of individual reefs. Inherent stochasticity in recruitment processes means that even where dispersal patterns have been documented at one point in time, this may provide an incomplete picture of temporal variability in connectivity (Siegel et al. 2008). Furthermore, global change may considerably alter many of the processes and drivers that underlie current patterns of connectivity (O'Connor et al. 2007; Munday et al. 2007, 2009).

It is important to distinguish between demographic (or ecological) and genetic (or evolutionary) connectivity (Cowen et al. 2007). In general, ecological connectivity requires the movement of significant numbers of individuals on ecological timescales; and hence, within a species, it occurs over shorter distances than genetic connectivity, which requires fewer individuals and involves longer time periods. Thus, estimates of connectivity based on genetic approaches (Hedgecock et al. 2007) are usually inappropriate for demographic questions (and vice-versa). In general, managers are concerned with ecological connectivity, such as population replenishment after losses due to mortality, such as bleaching or over-fishing. Maintenance of ecological connectivity will generally also ensure genetic connectivity.

Incorporating population connectivity into management of reefs and MPA networks requires explicit consideration of dispersal between network subunits (e.g. protected reefs). In order to maintain population connectivity for a broad range of species, MPA networks must cater for a variety of dispersal distances, and for distances that change on a temporal basis. As yet there has not been a complete description of the dispersal patterns for a single species and modelling approaches useful for incorporating connectivity information into MPA network designs cannot be applied yet (Botsford et al. 2009). Hence, there is limited prospect in the near future of obtaining sufficient information for the great variety of coral reef species.

Given the current extent and rate of coral reef degradation, waiting for science to provide all the answers before implementing management strategies is not an option. Instead, alternative strategies that anticipate the likely wide variation in connectivity patterns and provide adequate protection for them are needed, while also addressing other important objectives. These strategies should be based on principles, guidelines or 'rules of thumb' that collectively maximise the probability of successfully achieving a resilient, connected ecosystem with realistic amounts of scientific information. In the following sections, first broad principles are considered and then specific measures are aimed at achieving those principles. Then, three case studies are used to illustrate their implementation ('principles' are used here to mean guidelines or recommendations, rather than absolute rules). Many of the principles discussed are not unique or specific to protecting connectivity and most are widely accepted to be of value in reserve network design for a range of reasons (e.g. ANZECC 1998). However, as a package, these recommendations currently provide the most practical approaches for maximising connectivity, given the current state of scientific knowledge.

Broad principles for the protection of connectivity with limited scientific information

- Take a *system-wide approach* that considers patterns *and processes* of connectivity, within and among ecosystems, and integrates connectivity with aspects such as suitability of recruitment habitat, etc.
- Protect a *network of sites*, rather than individual sites, using appropriately spaced networks of protected areas, etc., which provide adequate proportional protection from likely threats (e.g. no-take for fishing pressures; areas protected from development for tourism, oil or mining development).
- Include in that network, sites that are most likely to serve as *refugia* from likely disturbances, providing sources of propagules to recolonise other sites after damage (e.g. reefs likely to be protected from coral bleaching, which may then provide a source of coral larvae).
- Ensure that management strategies, including network design, consider *processes of connectivity*, such as

– Corridors or 'stepping stones' which extend the connections between source and sink reefs or habitats. In contrast to terrestrial environments, marine connectivity often does not require contiguous corridors to support connections, provided stepping stone areas are spaced appropriately to provide ongoing ecological connections. Spacing of stepping stones or suitably protected habitat should include a wide range of distances, ideally providing an overall frequency distribution of dispersal distances (i.e. all the distances between all the components of an MPA network) that is either fairly uniform (Leis 2006) or similar to the natural spacing of habitat subunits (Almany et al. 2009);
– More isolated sites, for which stepping stones are not available (e.g. remote oceanic reefs), warrant higher levels of protection to balance the decreased connectivity (Almany et al. 2009). Such sites often 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).
– Nesting or spawning sites and times, perhaps requiring protection or closure of specific sites and specific times;
– Environmental quality of corridors, intermediate sites or habitats, e.g. adequate water quality and temperature, nursery sites, etc.;
– Physical connectivity, through water currents, etc. Note, however, that recent science has emphasised the extent to which larval dispersal is not simply a passive process, driven by water movement, but is often strongly influenced by larval behaviour, often with the effect of reducing dispersal distances;
– Migration patterns, including habitats for different life stages (e.g. fish such as the Red Emperor that migrates from coastal habitats to reefs, Fig. 1);

- Manage non-reserve areas, to ensure intact ecosystem processes, sustainable fisheries and environmental quality. This is required to ensure connectivity between reserve areas, between reserve areas and non-reserve areas, and to allow for limited subsidies of fisheries from protected areas. In particular, incorporating both maximum and minimum size restrictions for target fish species may dramatically enhance reproductive output and recruitment, with consequences for larval connectivity ('slot-limits', Steneck et al. 2009).
- Maximise acquisition and use of existing information to determine the best configuration, recognising the potential value of community and traditional knowledge (e.g. local fishers' knowledge of spawning aggregations).
- Consider small amounts of targeted new research to acquire key elements of information, but only where this will have maximal strategic value, and not at the cost of delaying implementation.
- Allow for uncertainty, by precautionary approaches such as *risk spreading and inclusion of margins of error*. Given insufficient science to accurately predict *which* reefs or habitat patches will be critical to connectivity in all future scenarios, we need to increase

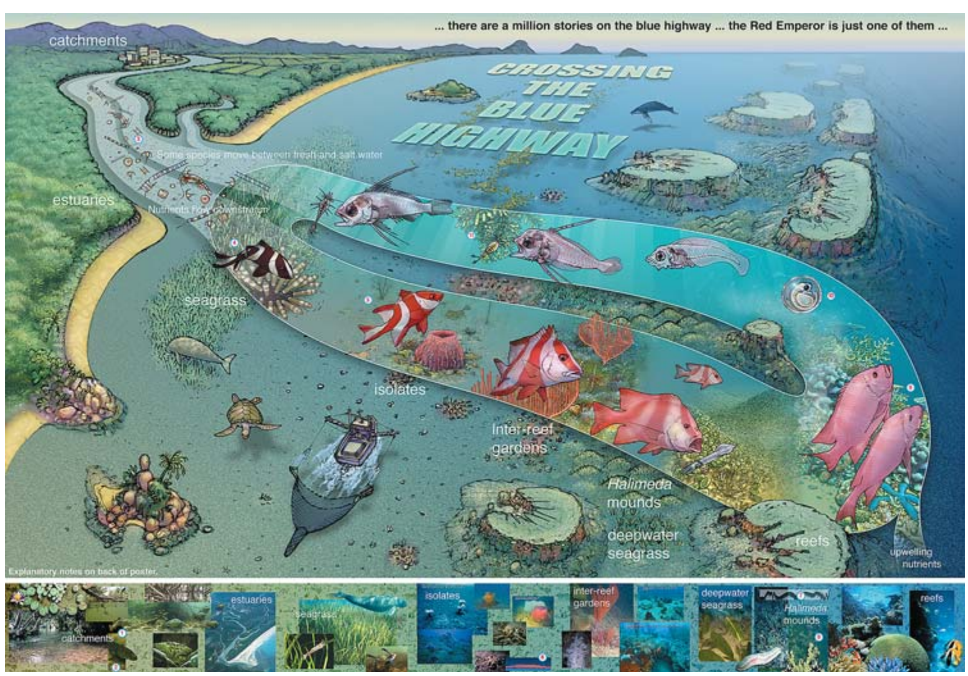

Fig. 1 The Blue Highway: a poster used to effectively communicate the concepts of connectivity on the Great Barrier Reef (www.byoguides.com/rk/Publications.html; reprinted with permission of the author, Russell Kelley, and the Australian Coral Reef Society). The poster illustrates the journey of the Red Emperor (*Lutjanus sebae*) as, at different stages of their growth and development, they utilise different habitats across the continental shelf. Any change in the natural habitat, such as pollution, can have dramatic effects elsewhere in this interconnected system (Cappo and Kelley 2001)

protection levels to increase the probability of successfully protecting the specific patches that will be critical under a range of possible scenarios. This requires inclusion of a range of *potential* source reefs, corridors, etc., not just the currently relevant ones, to provide a margin of insurance. This is perhaps the most important principle, and to some extent requires a reversal of the burden of proof: a particular site should be assumed important until proven unlikely to be so.

- Allow for review and flexible *adaptive management*, as new information and understanding of connectivity emerges, including the critical capacity to learn from current management outcomes. Coral reefs and other tropical marine environments are highly dynamic systems, increasingly so under global change (Munday et al. 2009), and connectivity science is a rapidly developing field, so that management responses to emerging information must also develop. In particular:
- Ensure readiness to *respond to events* by adaptively modifying and enhancing protection (e.g. responding to potential mass coral bleaching events by increasing protection in response to temperature stresses, etc.);
- *Communicate the importance of connectivity* to stakeholders and policy makers. Connectivity is more abstract and less immediately apparent than many aspects of resilience protection; yet, experience has shown that the concept is readily embraced if well communicated (e.g. Fig. 1).

Specific recommendations: what should management *actually do*?!

Given present limitations in even defining specific goals for protecting connectivity, and the need for risk-spreading strategies which maximise the likelihood of capturing as-yet-unknown connections, one of the most effective approaches is to aim for networks of protected areas which are comprehensively spread across the area of concern, adequate, representative (CAR, ANZECC TFMPA 1998) and replicated. As with most of the listed strategies, these principles are of wide relevance to conservation management, and not limited to protecting connectivity.

- *Comprehensive and spatially spread*: include protection for all major biological regions or habitat types, and processes, etc., spatially spread across geographic zones (encompassing gradients such as latitude, inshore–offshore location, depth and influences such as upwellings or river runoff). This is critical for connectivity between different habitat types and regions (e.g. protection of inshore nursery habitats as well as habitats for mature fish, Fig. 1). Protecting the full range of ecosystems or habitats maximises the likelihood of capturing the full range of connections between them, including especially connections which are not yet recognised or appreciated. Ideally, this criterion should be based on the prior identification of biological regions or 'bioregions' that incorporate all available data on physical and biodiversity patterns, and geographic gradients (latitude, cross-shelf positions, depth, etc.). The term 'bioregion', as used during rezoning of the GBR, referred to spatially contiguous regions of similar biological composition, but incorporates geographic location and gradients, and is thus more specific than simple habitat types. This specificity is important for enhancing comprehensive representation. However, even simple approaches, such as systematically protecting examples of inshore, mid-shelf and offshore areas, and of the full range of bathymetric and latitudinal gradients, increase the probability of capturing as many connections as possible.
- *Adequate:* Ensure a sufficient total proportion, configuration and level of protection for each bioregion or habitat type. Recent precedents have aimed for a *minimum* of 20% by area *of each bioregion* (Airamé et al. 2003; Fernandes et al. 2005). However, emerging information on the increased threats due to climate change, along with modelling work (Botsford et al. 2009) suggest that this level should be increased to 30–40% and Almany et al. (2009) also suggest greater protection for isolated reefs or habitats. In the context of connectivity, adequacy is important to increase the probability of sufficient connectivity (e.g. likelihood of capturing relevant sources of propagules, and providing sufficient, appropriate habitat for recruitment). Reef management should explicitly consider adequacy in this context. Further, adequacy is not simply a matter of proportional target areas, but must incorporate configuration and type/level of protection provided within protected areas. Importantly, adequacy requires consideration of the uncertainty and need for risk spreading: if we could accurately predict with certainty the key reef or patches which may be critical as future sources of propagules, we could protect them specifically. The margins of error in our knowledge of connectivity require that we avoid placing all our eggs in a few baskets, and provide margins of insurance in the adequacy of protection.
- *Representative*: Within bioregions or habitat types, it is important to ensure protection for areas which are representative of the full range of biological and physical characteristics and processes, again to maximise the

likelihood of capturing the full range of processes and spatial requirements.

- *Replication*: Ensuring multiple or replicated examples of each bioregion, habitat type or process is also critical to risk spreading, again providing a margin of error against the unpredictability of damage and disturbance to specific sites or patches.

Other strategies

- Where possible, protect entire biological units (e.g. whole reefs, seamounts, seagrass beds) within the same level of protection, avoiding splitting units into different zones, and including a buffer zone of intermediate protection around the core area of interest. The significance for connectivity here is to maintain local scale connections (e.g. within reefs).
- Where entire biological units cannot be included, choose bigger rather than smaller areas (this may be more appropriate where community livelihoods or benefits would be seriously compromised by protecting an entire reef).
- Networks should aim to include protected areas that provide for a wide range of dispersal distances between protected areas (including dispersal within the same reserve), but particularly ensuring protection for dispersal distances up to 10–20 km (at most 30 km), as the maximum distance between nearest stepping stones. Recent research suggests that distances less than this are very important for dispersal to several species of reef fish (Almany et al. 2007; also Shanks et al. 2003) and corals (Jones et al. 2009), and that dispersal over larger distances is more limited and may require 'stepping stones' to maintain connectivity. Shorter dispersal distances are often provided by dispersal within the borders of individual reserves. Within networks, dispersal distances greater than 10–20 km are generated automatically by multiples of this maximum spacing between neighbouring reserves. The longest distances between components within a network will likely depend on political boundaries, but should not be limited by present day biogeographic patterns, as these are likely to change in response to climate change.
- Review all available information, including non-scientific information, to manually check inclusion of key areas, sites, events or processes (e.g. spawning aggregations).
- Include review by experts and community stakeholders. Flexible application of a range of knowledge provides more flexibility and acceptance in handling the uncertainty than rigid implementation of narrowly specified rules.

Case studies

The following three case studies provide contrasting illustrations of how these principles have been applied in different geographic settings and socioeconomic circumstances in the West Pacific (Fig. 2).

Bohol Sea, southern Philippines

This case history draws on experiences in establishing a network of no-take reserves in the Bohol Sea, southern Philippines over a period of 35 years (see Alcala and Russ 2006), and the relatively recent steps taken to incorporate emerging information on larval connectivity information into the establishment process. The Philippines is a developing nation in the tropical Indo-West Pacific, close to the centre of marine biodiversity (Fig. 2). Despite the incredible productivity and richness of the natural resources of the Philippines, they are under substantial pressure from a rapidly growing human population (2.4% per annum) and widespread poverty (Alcala and Russ 2006).

Table 1 indicates that relatively few of the broad or specific principles for protecting connectivity were initially applied during establishment and development of the Bohol Sea Marine Reserve Network, but that in retrospect, the cumulative outcomes have been relatively successful. The first two no-take reserves in the southern Philippines (Sumilon, Apo) were established with the objectives of conserving coral reef habitats and enhancing the sustainability of reef fisheries. They were not originally considered, nor designed, as the first of a network of such reserves across the Bohol Sea. Their objectives had a strong local focus, to enhance the local fishing communities near the reserves.

Ironically, however, connectivity was a key aspect of the expectations of the reserves that proved vital in gaining initial community support for the no-take reserves. Angel Alcala, in the first meetings with local fishing communities in 1973 (Sumilon) and 1976 (Apo), stressed the possibility of improved fish catch near the reserve boundaries due to adult 'spillover' (Alcala and Russ 2006). Over time, the major economic and social benefit to the local communities has proven to be enhanced income from tourism generated by the reserves.

The establishment of the network of more than 60 no-take reserves in the Bohol Sea (see Fig. 5 in Alcala and Russ 2006) could be described in three steps:

1. *Identify the best way to establish individual reserves to ensure their long-term protection*: A 'community-based' management approach involved stakeholders in the process of reserve establishment from the very beginning. This process was vital in fostering a sense of ownership of the reserves, and in empowering the local

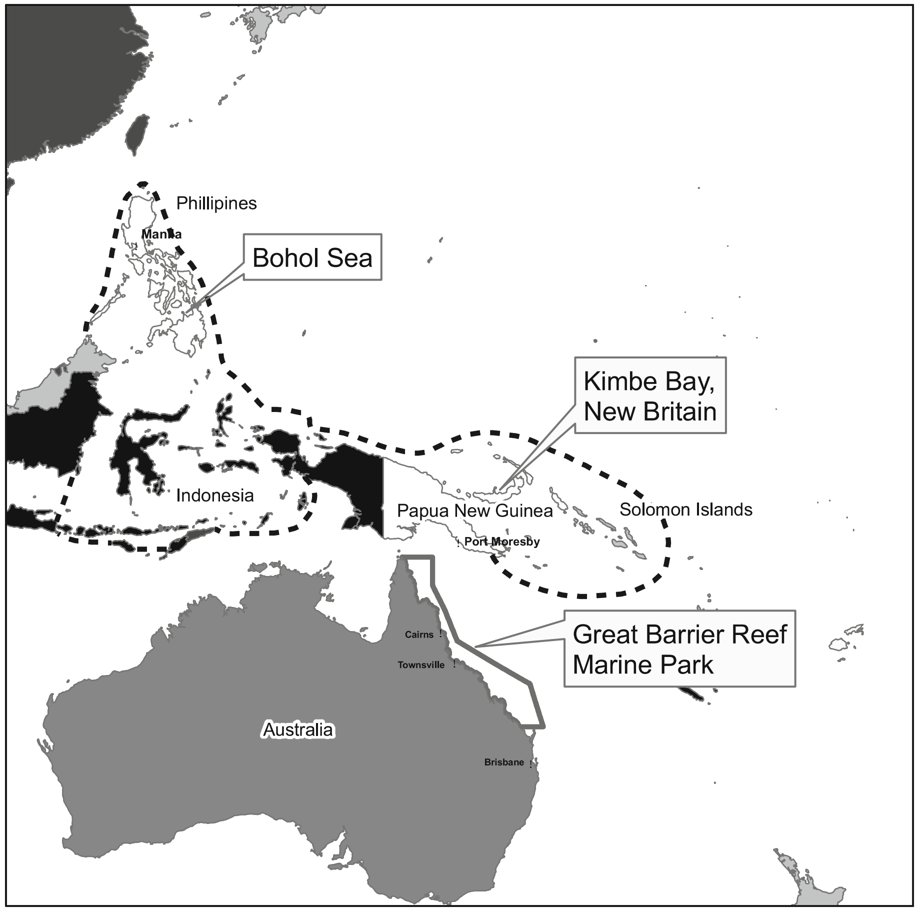

Fig. 2 Map of the West Pacific showing the locations of three case studies of marine management plans incorporating connectivity in coral reef ecosystems: the Bohol Sea, Philippines; Kimbe Bay, Papua New Guinea; and the Great Barrier Reef, Australia

fishing communities to take control of their own destinies, by encouraging formation of local marine management committees and establishing local government legislation to protect reserves (Alcala and Russ 2006). Current laws allow for co-management between local and national governments of marine resources up to 15 km off the coast, so this process of establishment of reserves also empowered coastal communities.

2. *Establish reserves spread over the entire area of interest* (*the Bohol Sea*). Once the mechanism of reserve establishment was determined, reserves were set up by as many local communities as possible, and efforts were spread across as wide an area as possible. This addresses geographic comprehensiveness and spread, and replication, but may not address comprehensiveness of habitats. In terms of adequacy, local protection in no-take reserves was generally on the order of 10–25% of the local fishing area, but over the wider expanse of the Bohol Sea, the amount of protection in no-take reserves is far less. The amount of area protected and the choice of sites (representation) are determined by what area the local communities are prepared to set aside as no-take area. Thus, the specific principles of Comprehensive and spread, Adequate, and Representative (CAR; see Table 1) were driven primarily by what local stakeholders were willing to commit (and thus support in the long-term). If emerging scientific information suggests that the current extent or representation of reserves is not adequate, this information can be put to stakeholders during further consultations. In the Bohol Sea network, the people are driving the CAR, rather than the CAR driving the people.
3. *Build connectivity information into the network design as that information emerges*. Although reserves were established with local objectives in mind, local communities were encouraged to set up reserves across as wide a spread of the Bohol Sea as possible, reflecting 'broad brush' ideas about potential larval connectivity based on large scale descriptions of the currents in the Bohol Sea (see Fig. 5 in Alcala and Russ 2006). Subsequent steps to incorporate connectivity information into the design of the Bohol Sea network included (in no particular order):

   - *Establish and map patterns of biogeographic biodiversity of reef fish and corals*. (e.g. Russ et al. 2005).
   - *Map patterns of reef usage*.

Table 1 Summary of case studies of principles for protecting connectivity in coral reef ecosystems

Guidelines	Bohol Sea, Philippines	Great Barrier Reef, Australia	Kimbe Bay, Papua New Guinea
Broad principles for protecting connectivity			
System-wide approach	Limited: coral reef focus	Yes: explicitly aimed to incorporate all habitat types and potential connections, through bioregionalisation, and zoning network	Yes: explicitly aimed to incorporate all habitat types and potential connections, through bioregionalisation, and zoning network
Network approach	Limited: strong local focus Emerging network emphasis	Strong and systematic emphasis, including location, size, shape and replication of zones, and integration of different zone types	Explicitly considered configuration of proposed protected areas as a network
Target refugia for protection	Inadequate information	Yes: specifically aimed to protect self-sustaining areas and special sites such as fish-spawning sites, nesting sites and key habitat for threatened species, generally in no-take zones	Yes: aimed to include sites considered resistant or resilient to global changes, fish aggregation sites, nesting habitats, cetacean habitats, vulnerable species (e.g. sharks)
Consideration of ecological processes	Yes, but not at network level	Yes	Yes, where information permitted
Manage non-reserve areas for ecosystem processes, sustainable fisheries and environmental quality	Limited: some community-based fisheries management; destructive fishing illegal	Yes: fisheries management plans, water quality improvement plans, temporal closures, etc.	Limited
Maximize use of existing information, including non-scientific sources and local knowledge	Yes: strong involvement by local communities	Yes: explicitly incorporated best available scientific and geographic information on physical, biological and ecological patterns and processes, along with information from 31,000 public submissions	Yes: used available environmental information, local knowledge and traditional management and conservation practices
Targeted research on key knowledge gaps	Yes (past 5 years)	No: emphasis instead on collation and integration of extensive existing information, along with statistical modelling to address gaps	Yes: field surveys of habitats; hydrodynamic modelling; surveys of socioeconomic and cultural information
Address uncertainty: risk spreading, margins of error	Not specifically	Yes: increased proportional protection, comprehensive representation and spatial replication	Yes: increased proportional protection; comprehensive representation; spatial replication
Review and adaptive management	Moderate: limited modification of existing management; widespread transfer and adaptation of successful MPAs	Yes: e.g. implementation of water quality protection plan and extensive revision of previous zoning in response to emerging information	Implementation of management currently in initial stages only
Specific principles or guidelines for protecting connectivity			
Comprehensive and spread	Reserves spread broadly	Yes: inclusions of examples of all 70 'bioregions' based on spatial distributions and biology; replication	Yes: inclusion of samples of each identified habitat type, spread across region
Adequate	Not necessarily—amount protected determined by local communities	Yes: *minimum* of 20% of each 'bioregion' included in no-take areas, and often much larger proportions protected by other zones	Yes: 20% target for each habitat type
Representative	Moderate: limited to coral reef habitats	Yes: examples of all bioregions and/or ecological processes chosen to be representative of type	Yes: representative examples of each habitat type
Replicated	Yes: ~60 separate reserves in Bohol Sea	Yes: aimed to protect 3–4 examples of each bioregion	Yes: aimed to include more than three examples of each habitat type
Include known spawning or nursery sites	Information unavailable, but awareness increasing	Yes: zoning aimed to protect likely fish nursery habitats, turtle nesting sites, etc.; additional temporal closures of fish spawning sites	Yes: protection of aggregations of key fisheries species and turtle nesting areas

Table 1 continued

Guidelines	Bohol Sea, Philippines	Great Barrier Reef, Australia	Kimbe Bay, Papua New Guinea
Corridors or stepping stones with dispersal distances of <15–30 km	Increasingly: reserves spaced generally by <15–30 km	Yes (Almany et al. 2009): Addressed through size, distribution and replication	Yes: maximum spacing distance of 15 km between protected areas
Water currents and movements	Now considered	Yes: currents and water circulation included in design of network	Yes: Bay was stratified into east and west sides on basis of water movement information
Water and environmental quality	Ad hoc consideration; increasing awareness	Yes: Reef Water Quality Protection Plan and Reef Rescue Plan specifically targeted at managing water quality; also addressed in zoning design	Yes; network design avoided areas of likely poor water quality
Migration patterns and life-cycles for key taxa	Not known	Yes: e.g. dugong protection areas, turtle nesting sites, whale protection area for humpback whale calving, bird rookeries, turtle and bycatch reduction devices in trawl fishery; also fish aggregation sites, etc.	Yes: protection of fish aggregations, cetacean habitats, turtle nesting sites, bird nesting and habitats
Entire biological units *where possible*	Usually not possible	Yes: zoning explicitly avoided fragmentation of habitats	Yes: design principles explicitly include entire biological units, and buffer areas where possible
Bigger area of MPAs	Limited: areas small, determined by amount local communities willing to set aside	Yes: zoning explicitly maximised size and recommended minimum size of no-take areas	Yes: design principles include bigger versus smaller areas (where entire biological units cannot be included)

Further explanation in text

- *Oceanographic modelling*. A combination of best-available information, with purpose-developed field and modelling studies, provided a framework to understand the physical oceanography of the Bohol Sea.
- *Larval dispersal modelling and testing*. Testing will use many of the tools described in other articles in this issue (Botsford et al. 2009; Jones et al. 2009).
- *Optimise placement*, *size*, *and spacing of reserves using computer-based reserve selection tools* (MARXAN/MARZONE; see Pressey et al. 2007) to develop a range of alternative potential network configurations as a basis for community assessment and adaptive management.

In summary, while many of the principles for protecting connectivity were not initially applied in the process of establishment and development of the Bohol Sea Marine Reserve Network (Table 1), many are now being incorporated as information becomes available, and as community awareness and acceptance increases.

Great Barrier Reef, Australia

The Great Barrier Reef Marine Park has many strong contrasts with the Bohol Sea network, including geographic extent, population, human development and population structure, and particularly in governance arrangements. Primary responsibility for policy development and management rests with a specific, national government agency, the Great Barrier Reef Marine Park Authority (GBRMPA), with State and local governments responsible for specific aspects of management (e.g. fisheries management). Amongst other consequences, this provides a mechanism for a strongly coordinated and integrated planning approach to management, in turn facilitating aspects such as large-scale network design and ecosystem-based management.

Although connectivity has been a consideration in planning for some time (e.g. James et al. 1990), as with the Bohol Sea network, explicit incorporation of connectivity information has featured much more strongly in recent management initiatives, especially the 2004 Zoning Plan (GBRMPA 2008a) and the Reef Water Quality Protection Plan (State of Queensland and Commonwealth of Australia 2003). This increasing emphasis reflects an adaptive management approach, with emerging information generating significant modifications of management policy.

Importantly, management of the Great Barrier Reef (GBR) aims to integrate a number of critical ecological dimensions, including but not limited to connectivity. This integration was most explicit in the 'Representative Areas Program' which underpinned the development of the 2004

Zoning Plan for the GBR (Day et al. 2004; Fernandes et al. 2005). Key aspects of that program included:

- A coordinated 'whole of eco-system' approach;
- Identification of 70 clearly defined and explained 'bioregions' to represent biophysically similar regions, based on habitat types, bathymetry, latitude and cross-shelf location, etc., based on the best available scientific information (GBRMPA 2008b);
- Development and implementation of 11 'Biophysical Operating Principles' (GBRMPA 2002a), along with four socio-economic principles to guide the overall planning (GBRMPA 2002b);
- Widespread community engagement and consultation, resulting in the incorporation of community knowledge and values, elicited from 31,000 public submissions;
- A network approach which includes seven marine zone types, including no-entry 'Preservation Zones', 'no-take' zones, 'limited fishing' zones (including 66% no-trawling areas), and 'General Use' zones. Zoning helps regulates a wide range of activities, such as tourism and recreation, as well as fishing, and is integrated with other spatial and non-spatial management strategies (Day 2002).

The effectiveness with which connectivity has been incorporated into management is summarised in Table 1, so only key aspects are discussed here. Importantly, connectivity benefits from a range of integrated management strategies, not just from spatial zoning (Day 2002). Thus, for example, the Reef Water Quality Protection plan addresses a key aspect of maintaining environmental quality of habitats and corridors or stepping stones, especially in the inshore nursery areas such as mangroves and seagrass beds. Other management initiatives include three temporal closures which prohibit reef fishing across the entire GBR, to protect key fish spawning aggregations.

A key feature for connectivity of the GBRMP Zoning Plan was the opportunity for a systematic, coordinated approach, using not just individual principles, but explicitly integrating all 11 'Biophysical Operating Principles' together as a package, especially those of comprehensive, adequacy, representation, and replication. These latter principles in turn were strongly enabled by the rigorous and comprehensive bioregionalisation process, ensuring that the full range of habitat types, biodiversity and geographic gradients could be systematically, comprehensively and adequately represented and replicated. Ecological and physical gradients and processes incorporated included community types, latitude, cross-shelf and bathymetric gradients, upwellings, exposure and hydrodynamics, and uses, including adjacent land-use; network design avoided areas of likely poor water quality. The consequence was a whole-of-ecosystem approach which provides significant margins of error for connectivity processes, such as inter-habitat connections or unrecognised connections.

Another significant aspect has been the enhanced community understanding and acceptance of the importance of connectivity, largely achieved through a single, strongly visual product, the poster diagram reproduced in Fig. 1. The combination of an effective visual presentation and a fish species of widespread interest to both commercial and recreational fishers generated popular interest in the concept of connectivity and, consequently, support for its protection.

In summary, protection of connectivity on the GBR appears to be as robust and systematic as feasible, given current information and political realities. Remaining challenges include adaptive responses to emerging information on interactions between fishing pressure and fish spawning and larval transport, and emerging information on the effects of climate change, especially on coral populations.

Kimbe Bay, Papua New Guinea: MPA network design

This case study contrasts with the previous two in that it refers only to the design of an MPA network, the implementation of which is well underway. Kimbe Bay is located on the north coast of the island of New Britain in the Bismarck Sea, Papua New Guinea (Fig. 2). Kimbe Bay is a large, well-defined bay (140 km × 70 km in area), which comprises a wide variety of shallow (coral reefs, mangroves, and seagrasses) and deepwater marine habitats (oceanic waters and seamounts) in close proximity. The bay is within the Coral Triangle (Allen 2007), the global centre for marine biodiversity, and is within the Bismarck Sea, a globally significant area for pelagic fishes (particularly tuna) and toothed whales.

In 2007, The Nature Conservancy and partners completed a scientific design of an MPA network for Kimbe Bay (Green et al. in press). The objectives were twofold: to conserve marine biodiversity and natural resources of the bay in perpetuity and to address local marine resource management needs. The outcome has been the identification of 14 Areas of Interest (proposed MPAs) that met specific conservation goals. The design process involved expert scientific advice, targeted research and monitoring, and an analytical design process (using the marine reserve software MARXAN). Scientific design principles were defined to incorporate biophysical and socioeconomic values and processes, based on those developed for the Great Barrier Reef Marine Park (Fernandes et al. 2005), but explicitly adapted for local conditions in Papua New Guinea and to specifically address the threat of climate change (West and Salm 2003; Green et al. in press).

Biophysical design principles included several of relevance to incorporating biological patterns of connectivity (Table 1). While some of these principles were applied successfully in Kimbe Bay, others will require refinement over time (Green et al. in press). They include:

- *System-wide approach that recognises patterns of connectivity within and among ecosystems*. This principle was applied with mixed success. Connectivity among shallow water habitats (coral reefs, mangroves and seagrass beds) was incorporated because the required information was easy to obtain (location of each habitat type) and the targets (habitat types) were automatically clustered as a function of the MARXAN analysis (Ball and Possingham 2000; Possingham et al. 2000). Connectivity among habitat types could not be incorporated at a fine scale because the detailed information required (e.g. biological patterns of connectivity among coral reefs) was not available. Connectivity among habitat types was therefore addressed at a broader scale, using three strategies: (i) risk spreading to address uncertainty (through representation, replication, and spread of each habitat type); (ii) stratification of the bay into east and west sections, reflecting differences in biological and physical characteristics (Green et al. in press; Steinberg et al. 2007); and (iii) using rules of thumb for minimum size for each MPA (10 km^2, 10–20 km in diameter) and maximum spacing distance between MPAs (15 km), based on the longest and shortest dispersal distances for conservation targets (Mora et al. 2006).
- *Include entire biological units and a buffer around the core area of interest; where entire biological units cannot be included, choose bigger versus smaller areas.* This principle was applied successfully. For example, offshore coral reefs are entirely included within proposed MPAs, whereas continuous coastal fringing reefs are included in as large areas as possible; both circumstances include buffer zones to increase the probability of protected relevant ecological connections.
- *Maximise acquisition and use of environmental information to determine the best configuration, recognising the importance of connectivity in network design*. High priority research was identified and implemented 2 years prior to completing the design. This included rapid ecological assessments of shallow water habitats (coral reefs, mangroves, and seagrass beds) and a hydrodynamic study of ocean currents (Steinberg et al. 2006). Research into biological patterns of connectivity among reefs is underway. Once completed, this information may be used to refine the MPA network design (if required).

The effectiveness of this design in protecting connectivity and ecosystem values will depend on implementation by local communities and governments at a range of scales. Local communities are the marine resource owners and decision makers in Kimbe Bay. The extent and nature of protection provided within MPAs therefore depends on those communities. This process is now well underway (Green et al. in press) and local communities have either signed or are in the process of developing management plans and agreements for eight Areas of Interest.

Discussion

This article aims to provide a set of general and specific recommendations or principles, which are relevant for a wide range of circumstances, including varying extent of scientific knowledge and background information. It is important to recognise that these recommendations remain inevitably a 'best-guess' or a set of 'rules of thumb' and will require careful consideration in each application. Further, although the scope of this article is limited to management aimed at connectivity, it is important to again stress that adequate protection of ecosystem resilience requires a number of elements: protecting connectivity is an important component but will not be sufficient unless well integrated with a range of other measures (e.g. McClanahan et al. 2002; McCook et al. 2007; Steneck et al. 2009).

As with any such approach, there are some associated risks, but overall, these risks are minor compared to those of delaying incorporation of connectivity into marine management until complete information is available. Risks associated with the recommendations in this article are principally those of taking a likelihood approach, that is, although this approach increases the chances of capturing the key processes of connectivity, it may still be insufficient for complete protection. The approach may also be vulnerable to 'pseudo-scientific' criticism from environmental sceptics suggesting that the principles here are not sufficiently rigorous. In assessing these risks, scientists and managers must also assess the risks associated with any currently feasible alternatives.

At present, the only alternative is to ignore connectivity, either permanently or as an interim measure, until better scientific information is available. In practice, these amount to the same thing, as adequate science for definitive protection of all aspects of connectivity is decades away. Certainly, the risks of inadequate management arising from ignoring connectivity are greater than those associated with the rules of thumb approach advocated here.

Improved scientific information still has significant prospects of contributing to improved management for connectivity, with two key aspects. First, managers require targeted information on connectivity in specific areas for which conservation strategies are being developed. Key information includes descriptions of oceanography and currents, bathymetry and habitat maps to aid in identification of 'bioregions' and in coupled biophysical models (Werner et al. 2007). Second, managers require improved understanding of key aspects of ecological connectivity. These include: (i) ecologically relevant dispersal distances or kernels for key organisms, especially habitat formers such as corals, seagrasses and mangroves, 'keystone' taxa, such as herbivorous fishes, and target species such as marketable fishes (at present, detailed information is only available for a relatively few species of fish and corals); (ii) mechanisms of dispersal and connectivity (e.g. passive, current-driven dispersal, or active movements; larval or adult dispersal); and (iii) perhaps most challenging, tools for reliably predicting probable source reefs or habitat patches. As our scientific understanding improves, it is critical to consider the application of that understanding to management strategies.

Effective implementation of connectivity science requires tools to communicate its importance to non-scientific audiences. Often, the most critical bottlenecks for implementation are not lack of detailed scientific information, but rather a lack of the community and political support for protection, which in turn require broad public acceptance of the importance of connectivity. As indicated above, during the rezoning of the Great Barrier Reef, an effective visual display (Fig. 1) was invaluable in generating understanding, acceptance, and support for the protection of ecological connectivity.

The three case studies demonstrate that the approaches outlined in this article, while not novel, have been successfully implemented under wide ranging circumstances. Compiling these principles is intended to enhance further implementation, especially as increasing international effort focuses on protection for coral reefs. Potential applications in the near future include the Coral Triangle Initiative (CTI Secretariat 2007), which aims to enhance protection of coral reefs and associated habitats throughout the Coral Triangle, an area of high biodiversity and complex connectivity. Management actions that protect the natural, ecological connectivity between coral reefs and other ecosystems should improve the overall resilience of those systems, with valuable consequences for the ecosystems, and the goods and services they provide.

Acknowledgements The ideas for this article emerged from a workshop entitled 'Connectivity and population resilience—sustaining coral reefs during the coming century' held 13–17 October 2007 in Townsville, Australia. We thank the participants in that workshop for valuable discussion, the *Australian Research Council Centre of Excellence for Coral Reef Studies* and the Connectivity Working Group of the global University of Queensland—World Bank—Global Environment Facility project, *Coral Reef Targeted Research and Capacity Building for Management* for support for the workshop, and the Pew Fellowship Program in Marine Conservation for support for L McCook. We are grateful to the Spatial Data Centre at the Great Barrier Reef Marine Park Authority and to Nate Peterson from TNC, for preparation of maps, to P Mumby and two anonymous reviewers for valuable comments, and to R Kelley for permission to reprint Fig. 1.

References

Airamé S, Dugan JE, Lafferty KD, Leslie H, McArdle DA, Warner RR (2003) Applying ecological criteria to marine reserve design: A case study from the California Channel Islands. Ecol Appl 13:S170–S184

Alcala AC, Russ GR (2006) No-take marine reserves and reef fisheries management in the Philippines: A new people power revolution. Ambio 35:245–254

Allen GR (2007) Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. Aquat Conserv 18:541–556

Allison GW, Lubchenco J, Carr MH (1998) Marine reserves are necessary but not sufficient for marine conservation. Ecol Appl 8:S79–S92

Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. Science 316:742–744

Almany GR, Connolly SR, Heath DD, Hogan JD, Jones GP, McCook LJ, Mills M, Pressey RL, Williamson DH (2009) Connectivity, biodiversity conservation, and the design of marine reserve networks for coral reefs. Coral Reefs (this issue)

ANZECC TFMPA (1998) Australian and New Zealand Environment and Conservation Council Taskforce on Marine Protected Areas Guidelines for Establishing the National Representative System of Marine Protected Areas, Commonwealth of Australia

Ball IR, Possingham HP (2000) MARXAN (V1.8.2): Marine reserve design using spatially explicit annealing, a manual. Available as a free download from http://www.uq.edu.au/marxan

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429:827–833

Birrell CL, McCook LJ, Willis B, Diaz-Pulido G (2008) Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceanogr Mar Biol Annu Rev 46:25–64

Botsford LW, White JW, Coffroth M-A, Paris CB, Planes S, Shearer TL, Thorrold SR, Jones GP (2009) Measuring connectivity and estimating resilience of coral reef metapopulations in MPAs: matching empirical efforts to modelling needs. Coral Reefs (this issue)

Cappo M, Kelley R (2001) Connectivity in the Great Barrier Reef World Heritage Area–An overview of pathways and processes. In: Wolanski E (ed) Oceanographic processes of coral reefs. CRC Press, Boca Raton, pp 161–187

CTI Secretariat (2007) The Coral Triangle Initiative: A proposal for a new multilateral partnership to help safeguard the marine and coastal resources for future generations. www.cti-secretariat.net

Cowen RK, Gawarkiewicz G, Pineda J, Thorrold SR, Werner FE (2007) Population connectivity in marine systems: An overview. Oceanography 20:14–21

Day JC (2002) Zoning–Lessons from the Great Barrier Reef Marine Park. Ocean & Coastal Management 45:139–156

Day JC, Laffoley Dd'A (2006) Self-assessment checklist for building networks of MPAs. World Commission on Protected Areas, IUCN. cms.iucn.org/about/union/commissions/wcpa/wcpa_work/wcpa_biomes/wcpa_marine/wcpa_mpachecklist/index.cfm

Day JC, Fernandes L, Lewis A, Innes J (2004) RAP – An Ecosystem Level Approach To Biodiversity Protection Planning Proceedings International Tropical Marine Ecosystem Management Symposium, Manila, Philippines, March 2003, Department of Environment and Natural Resources, Philippines, pp 251–265

Dorenbosch M, Verberk WCEP, Nagelkerken I, van der Velde G (2007) Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs. Mar Ecol Progr Ser 334:103–116

Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. Front Ecol Environ 1:488–494

Fernandes L, Day J, Lewis A, Slegers S, Kerrigan B, Breen D, Cameron D, Jago B, Hall J, Lowe D, Innes J, Tanzer J, Chadwick V, Thompson L, Gorman K, Simmons M, Barnett B, Sampson K, De'Ath G, Mapstone B, Marsh H, Possingham H, Ball I, Ward T, Dobbs K, Aumend J, Slater D, Stapleton K (2005) Establishing representative no-take areas in the Great Barrier Reef: Large-scale implementation of theory on marine protected areas. Conserv Biol 19:1733–1744

GBRMPA (2002a) Biophysical Operational Principles as recommended by the Scientific Steering Committee for the Representative Areas Program. Technical Information Sheet #6, Representative Areas Program background and history. GBRMPA, Townsville. www.gbrmpa.gov.au/corp_site/management/representative_areas_program/rap_publications/documents/tech_sheet_06.pdf

GBRMPA (2002b) Social, economic, cultural and management feasibility operational principles. GBRMPA, Townsville. www.gbrmpa.gov.au/corp_site/management/representative_areas_program/rap_publications/documents/tech_sheet_07.pdf

GBRMPA (2008a) Overview of the Representative Areas Program. www.gbrmpa.gov.au/corp_site/management/representative_areas_program

GBRMPA (2008b) Research and planning. www.gbrmpa.gov.au/corp_site/management/representative_areas_program/planning_and_researching

Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. Proc Natl Acad Sci 104:858–863

Green A, Smith SE, Lipsett-Moore G, Groves C, Peterson N, Sheppard S, Lokani P, Hamilton R, Almany J, Aitsi J, Baulia L (in press) Designing a resilient network of Marine Protected Areas for Kimbe Bay, Papua New Guinea. Oryx 'in press'

Hedgecock D, Barber PR, Edmands S (2007) Genetic approaches to mearuring connectivity. Oceanography 20:70–79

Hoegh-Guldberg O (2004) Coral reefs in a century of rapid environmental change. Symbiosis 37:1–31

Hughes TP, Tanner JT (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933

James MK, Dight IJ, Day J (1990) Application of larval dispersal models to zoning of the Great Barrier Reef Marine Park, 4th Pacific Congress on Marine Science and Technology, Tokyo, Japan. Great Barrier Reef Marine Park Staff Papers, Townsville, 6 pp

Jones GP, Srinivasan M, Almany GR (2007) Population connectivity and conservation of marine biodiversity. Oceanography 20:42–53

Jones GP, Almany GR, Russ GD, Sale PF, Steneck RR, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs (this issue)

Leis JM (2006) A practical rule of thumb for spacing in MPA networks. MPA News 8:5

Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. Integr Comp Biol 46:282–297

McClanahan T, Polunin N, Done T (2002) Ecological states and the resilience of coral reefs. Conserv Ecol 6:18

McCook LJ, Folke C, Hughes TP, Nyström M, Obura D, Salm R (2007) Ecological resilience, climate change and the Great Barrier Reef: An introduction. In: Marshall P, Johnson J (eds) Climate change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Australia, Townsville, pp 75–96

Mora C, Andrèfouet S, Costello MJ, Kranenburg C, Rollo A, Veron J, Gaston KJ, Myers RA (2006) Coral reefs and the global network of Marine Protected Areas. Science 312:1750–1751

Mumby PJ (2006) Connectivity of reef fish between mangroves and coral reefs: Algorithms for the design of marine reserves at seascape scales. Biol Conserv 128:215–222

Mumby PJ, Hastings A (2008) The impact of ecosystem connectivity on coral reef resilience. J Appl Ecol 45:854–862

Munday PL, Jones GP, Sheaves M, Williams AJ, Goby G (2007) Vulnerability of fishes of the Great Barrier Reef to climate change. In: Johnson J, Marshall P (eds) Climate change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Australia, pp 357–391

Munday PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009) Climate change and coral reef connectivity. Coral Reefs (this issue)

Nagelkerken I, Kleijnen S, Klop T, van den Brand RACJ, Cocheret de la Moriniére E, van der Velde G (2001) Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Mar Ecol Progr Ser 214:225–235

Nyström M, Folke C (2001) Spatial resilience of coral reefs. Ecosystems 4:406–417

O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc Natl Acad Sci 104:1266–1271

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958

Paris CB, Chérubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. Mar Ecol Progr Ser 347:285–300

Perez-Ruzafa A, Gonzelez-Wangemert M, Lenfant P, Marcos C, Garcia-Charton JA (2006) Effects of fishing protection on the genetic structure of fish populations. Biological Conservation 129:244–255

Possingham HP, Ball IR, Andelman S (2000) Mathematical methods for identifying representative reserve networks. In: Ferson S, Burgman M (eds) Quantitative methods for conservation biology. Springer-Verlag, New York, pp 291–305

Pressey RL, Cabeza M, Watts ME, Cowling RM, Wilson KA (2007) Conservation planning in a changing world. Trends Ecol Evol 22:583–592

Roberts CM (1997) Connectivity and management of Caribbean coral reefs. Science 248:1454–1457

Russ GR, Stockwell B, Alcala AC (2005) Inferring versus measuring rates of recovery in no-take marine reserves. Mar Ecol Progr Ser 292:1–12

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecol Appl 13:S159–S169

Siegel DA, Mitarai S, Costello CJ, Gaines SD, Kendall BE, Warner RR, Winters KB (2008) The stochastic nature of larval connectivity among nearshore marine populations. Proc Natl Acad Sci 105:8974–8979

State of Queensland and Commonwealth of Australia 2003 Reef Water Quality Protection Plan: for catchments adjacent to the Great Barrier Reef World Heritage Area October 2003 Queensland Department of Premier and Cabinet, Brisbane. www.gbrmpa.gov.au/__data/assets/pdf_file/0017/7514/rwqpp.pdf

Steinberg CR, Choukroun SM, Slivkoff MM, Mahoney MV, Brinkman RM (2007) Currents in the Bismarck Sea and Kimbe Bay, Papua New Guinea, Australian Institute of Marine Science and The Nature Conservancy, TNC Pacific Island Countries, Report No. 6/06, p 38

Steneck RS, Paris CB, Arnold SN, Butler MJ, Ablan-Lagman MC, Alcala AC, McCook LJ, Russ GR, Sale PF (2009) Thinking and managing outside the box: coalescing connectivity networks to build region-wide resilience in coral reef ecosystems. Coral Reefs (this issue)

Thorrold SR, Jones GP, Planes S, Hare JA (2006) Transgenerational marking of embryonic otoliths in marine fishes using barium stable isotopes. Can J Fish Aquat Sci 63:1193–1197

Underwood JN, Smith LD, Van Oppen MJH, Gilmour JP (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Mol Ecol 16:771–784

Werner FE, Cowen RK, Paris CB (2007) Coupled biological and physical models: Present capabilities and necessary developments for future studies of population connectivity. Oceanography 20:54–69

West JM, Salm RV (2003) Resistance and resilience to coral bleaching: Implications for coral reef conservation and management. Cons Biol 17:956–967

Wilkinson C (2004) Status of coral reefs of the world: 2004. Australian Institute of Marine Science, Townsville, p 572