

# A Literature Review of Current Knowledge on the Biophysical Aspects of Marine Protected Area Network Design and Implementation

Jennifer Skilbred, Colleen Corrigan, Jeanine Almany, Elizabeth McLeod, Al Lombana, and Helen Fox  
Marine Learning Partnership, Global Conservation Program  
October 2006

## ABSTRACT

The available literature related to designing and implementing networks of marine protected areas is increasing as more governments and institutions are scaling up their marine conservation efforts. Overall, the main elements that are critical to designing ecologically-functional and socially-sustainable MPA networks include: representation and replication of all biogeographic areas and habitats; permanent, long-term full protection so species can replenish and ecologically functional roles are maintained; connectivity that addresses essential life stages of all critical species in the system; size, shape and spacing of MPAs within the network that consider the 10 to 200 km range of larval dispersal distances; and critical areas that protect the source and sink of fishery and biodiversity target species. While some debates exist, including designing networks for habitats versus species and dispersal distances of some species, there is agreement that MPA networks should not wait for further research and can be developed using existing scientific data and tools. Finally, MPA networks are most effective when planned in concert with socioeconomic considerations and other tools outside the scope of protected areas, including traditional fisheries management techniques, such as limiting total allowable catch, restricting gear types, and limiting entry into the fishery.

## INDEX

<b>Introduction.....</b>	<b>2</b>
<b>Methods.....</b>	<b>2</b>
<b>Executive Summary.....</b>	<b>3</b>
<b>Results and Discussion.....</b>	<b>4</b>
<b>Review of Literature:</b>	
<b>Purpose of Network Approach .....</b>	<b>6</b>
<b>Ecological Criteria:</b>	
<b>Representation and Replication .....</b>	<b>7</b>
<b>Connectivity .....</b>	<b>11</b>
<b>Permanence .....</b>	<b>13</b>
<b>Size, Shape and Spacing.....</b>	<b>15</b>
<b>Critical Areas.....</b>	<b>17</b>
<b>Gaps in Knowledge and Future Direction of Research .....</b>	<b>19</b>
<b>Appendices</b>	
<b>1. Definitions.....</b>	<b>23</b>
<b>2. Case Studies.....</b>	<b>24</b>
<b>3. Annotated Bibliography of most relevant publications.....</b>	<b>27</b>
<b>4. Key Management Recommendations.....</b>	<b>36</b>
<b>5. Biophysical Questionnaire.....</b>	<b>39</b>
<b>6. References.....</b>	<b>41</b>
<b>7. List of Biophysical Tools.....</b>	<b>48</b>

## **INTRODUCTION**

The Marine Protected Area Networks Learning Partnership, a collaboration between The Nature Conservancy, World Wildlife Fund, Conservation International, and Wildlife Conservation Society, seeks to increase the use of networks of Marine Protected Areas (MPAs) as a tool for marine conservation across the globe. To better understand how various organizations use this tool at project sites, it is critical to explore current scientific literature and other documentation, such as regional publications and institutional literature sources, to determine the latest knowledge regarding principles of MPA network design. Where possible, we also include review of other publications and literature that is applicable to management. Specifically, this report synthesizes current sources of information that can inform our efforts to implement MPA networks to meet global and institutional mandates and political agreements.

MPA network design is a complex and broad topic, with many different facets contributing to how we make decisions. We have organized our literature review process around key ecological criteria that span the breadth of topics related to biophysical MPA network design. Several sources have already identified these basic criteria (CBD 13; WCPA/IUCN 2005; Roberts 2003a). We used our institutional knowledge and lessons learned from these documents to organize the outline for our review.

This literature review will help our field staff, partners, and the marine conservation community design MPA networks that are resilient to anthropogenic and environmental threats. We anticipate that this document will be updated as new information becomes available.

Finally, while understanding biophysical aspects is a key step in MPA network design and the focus of this document, it is equally important to consider and analyze social, economic, political, and other factors that can impact the final design and implementation of fully-functional networks. As a result, a second literature review assessing the concept of social resilience complements this review.

## **METHODS**

Literature searches were completed using a variety of databases including: WWF Conservation Science Program Marine references, CI Marine portal, internal documents, Web of Knowledge and Web of Science databases, as well as using Google Scholar search engine. Information was gathered on marine reserves and MPAs, as well as MPA networks, and other relevant protected areas. There was considerably more research available on single MPAs than on MPA networks; however, the review is focused on the network scale while including particularly relevant non-network MPA information.

Several publications agree on basic ecological criteria required for selecting and designing MPA sites and networks, though there is some slight divergence in nomenclature. We have chosen to focus on the following criteria because they are most relevant for decision-making by marine managers and practitioners: (1) Representation and Replication, (2) Connectivity, (3) Permanence, (4) Size, Shape, and Spacing, and (5) Critical Areas. These five principles are based on insights from the following documents:

- Reef Resilience Working Group, The Nature Conservancy, “MPA Selection Criteria”
- Convention on Biological Diversity Ad Hoc Technical Experts Group on Marine and Coastal Protected Areas, Technical Series No. 13, *Technical Advice on the Establishment*

*and Management of a National System of Marine and Coastal Protected Areas.*

[<http://www.biodiv.org/doc/meetings/mar/imcam-01/other/imcam-01-cbd-ts-13-en.pdf>]

- IUCN/WCPA, “Guide for establishing Marine Protected Area Networks” (in draft)
- Roberts, et al *Applications of Ecological Criteria in Selecting Marine Reserves and Developing Reserve Networks*. Ecological Applications, 13(1), Supplement, 2003. pp. S215-S228.

## **EXECUTIVE SUMMARY**

While uncertainty is one of the greatest obstacles in conservation planning (Nicholson in press, Reagan et al 2002, and other articles), we know enough to move forward in most cases of MPA network design. Improving the knowledge base of MPA networks may increase protection for specific species or regions, but a well designed habitat-based reserve can be created using a subset of desired data (Ariame 2003). Modeling techniques and adaptive management practices are continually being developed to improve design and implementation in the face of uncertainty (Halpern et al 2006).

While gaps and uncertainties are highlighted in many articles, the general consensus seems to be that networks can be set up, filling gaps along the way, especially if monitoring and adaptive management techniques are being used to continually reassess the network. Even without data on many important criteria, it is possible to identify effective potential reserve networks using models and available data (Ariame 2003).

Marine protected area networks have the potential to provide more benefits to both conservation and fisheries goals than single MPAs alone can provide. These benefits increase when traditional fishery management techniques are integrated with network implementation, and clear goals are set early in the design process. Five ecological criteria have been identified to consider when designing or implementing a network. They include: representation and replication, connectivity, permanence, size shape and spacing, and critical areas. Current knowledge in each area was reviewed and the major gaps in knowledge are highlighted.

The current consensus is that the most effective network should be representative of all biogeographic units and habitats in the region, particularly any rare or essential habitats, with 20 % or more of each biogeographic unit or habitat type protected. There is a need to protect replicates of each representative unit as well, which spreads risk from accident or catastrophe. The number of replicates of each represented site is limited by social concerns such as monitoring and enforcement costs. Designing MPA networks to match the spatial scale of larval dispersal is one step toward ensuring connectivity. The idea of permanent closure of a protected area is often considered the most effective for achieving network objectives, yet beneficial impacts have been seen from seasonal closures as well, and in cases when permanent closure is not an option this may be an effective alternative. Optimal MPA size, shape, and spacing are closely related to other characteristics such as connectivity and representation. There are no steadfast guidelines for these criteria since MPA network objectives and practical limitations will vary according to the political, social, biological, and economic contexts of the area. A variety of sizes and spacings of reserves within networks should be considered, with a focus on intermediate sizes as the most frequently recommended option. Critical areas that protect habitats associated with certain life stages of a range of species, such as spawning, socializing, or feeding, should also be considered closely when designing networks to ensure replenishment and viability. Population sources and natural refuges should be included while sinks should be avoided. These suggestions and others are elaborated in the report below.

While this report focuses on incorporation of the biophysical factors, key social, political, and economic factors are equally crucial to effective network design. If either biophysical or socioeconomic criteria are ignored, the implemented network will fail to achieve objectives. The social resilience literature review covers these factors of MPA network design in depth.

## **RESULTS and DISCUSSION**

The overall findings and key management recommendations from this research are summarized here and discussed in detail in the Ecological Criteria section below. In general, MPA networks have more potential to achieve conservation and fishery objectives than single MPAs (Roberts 1997) and the most effective MPA networks are a product of clear goals determined at the outset of the design process (Roberts et al 2003b and others).

The incorporation of replicated representatives of every biogeographic area and habitat type in the region should be one of the first goals of network design (Roberts 2001). It is recommended that networks of fully protected reserves cover 20 % or more of all biogeographic regions and habitats (Roberts and Hawkins 2000; National Research Council [NRC] 2000; Roberts et al 2003a), although the biological basis for this number has not been empirically tested in relation to specific habitats (Sale et al 2005).

It is important to include reserves in both transition zones (between biogeographic areas) and core zones within each biogeographic unit (Roberts et al 2003b). MPA network design can be based on habitats or species, though the latter is implemented less frequently, likely due to the relative scarcity of comprehensive species data available (Airame 2003). Sites should generally be selected such that they will not be affected by catastrophes in the same way (Airame 2003) and areas with frequent catastrophic occurrences should not be selected as they rely on recruitment from other areas (Allison 2003). It is important to incorporate areas of high resistance and resilience to climate change (West and Salm 2003) and spawning aggregation sites in MPA network design (Sadovy 2006). Protecting ecosystem processes is often just as important as protecting all habitats (Roberts et al 2003b).

Biophysical connectivity of MPAs within a network is critical to ensure the network is functional (Roberts et al 2003a) and viably sustainable (Crowder et al 2000, Stewart et al 2003). This connectivity is based in part on the spatial scale of larval dispersal (Palumbi 2004). MPAs in a network must be able to receive larvae from “upflow” MPAs and supply it to “downflow” MPAs, as well as supply individuals to fisheries outside reserve boundaries (Halpern et al 2006). Some habitats are functionally linked due to species life cycle patterns, such as coral reefs, seagrass, and mangroves, and thus these connections should be incorporated into network design (Ogden and Gladfelter 1983; Roberts 1996; Nagelkerken et al 2000). Networks should be designed to fit many possible connections and not just a few probable ones (Roberts 2001). While ocean currents do not always sufficiently represent dispersal distances or directions (Barber et al 2000), MPAs should be located in a wide variety of locations in relation to the prevailing currents (Roberts 2001). Self-seeding occurs only if a reserve is as large as the mean dispersal distance of the target species (at least 4 to 6 km in diameter; Shanks 2003). Palumbi suggested that sites in a network be 10 to 20 km apart and Shanks (2003) suggests 20 km as a minimum spacing distance (Palumbi 2003). Connectivity is more local than previously thought, and regionally it is more variable (Cowen et al 2006). Short-lived species may require more regular recruitment from connected sites (Steneck 2006). Due in part to the amount of data needed and differences for different target species, one approach to network design is to establish the size of reserves based on adult neighborhood sizes of highly fished species, and space the reserves based on larval neighborhood scales (Palumbi 2004). Highly migratory species do not fit the general rules of dispersal distances, spacing, or connectivity (Palumbi 2004), and so need extra consideration (Roberts 2003a). Developing dynamic MPAs and MPA networks for highly migratory species where certain oceanographic areas related to key behaviours (feeding, breeding, and socializing) are protected both spatially and temporally will provide an additional

approach to protection (Hyrenbach et al 2000). Using varied reserve sizes is recommended in order to meet both fishery and conservation goals (Palumbi 2003).

Fully protected permanent marine areas are considered critical for a functional network of MPAs (CBD 2004). Long-term management and monitoring plans are seen as increasingly important (Babcock et al 1999). Whether the goal of the MPA site or network is fisheries management or biodiversity conservation, there is agreement among scientists that having long-term, permanent closures, such as a marine reserves, provides the greatest level of protection and benefits to the species populations (Willis 2003 and others). It is important to protect large, old, long-lived fish, which have a high likelihood of reproductive success (Birkeland and Dayton 2005), throughout their geographic range (Berkeley et al 2004). While fully protected areas are most effective, rotational or seasonal closures are more accepted, have less immediate social impacts, and are easier to monitor and enforce (Cinner et al 2005). Networks should be able to sustain populations and ecosystem processes through natural cycles of variation (Wells 2006). They should be independent of outside processes, and the overall networks should be considered permanent, even if all sites are not (Wells 2006).

The optimal size of MPAs within a network has been discussed in the literature more than the shape and spacing; however, all are critical in meeting various network goals (Gaines et al 2003). Larger reserves may be ideal for conserving biodiversity, but smaller reserves might serve fishery goals better as spillover is more likely (Allison et al 1998). Therefore, variation in MPA size within a network is considered ideal (Roberts 2001) for achieving both types of goals. There are no upper limits on MPA size due to biological constraints, but socioeconomic and practical guidelines often limit maximum MPA size (Roberts et al 2003a). MPAs that are larger offshore and smaller nearshore allow for less negative impacts to the local community and can provide the same conservation and fishery benefits in some areas (Roberts 2001). When designing shape, it is important to consider minimizing edge habitat while maximizing interior protected area (Carr et al 2003). A shape that allows for clear marking of boundaries for both resource users and enforcement personnel benefits may increase effectiveness (California Dept. of Fish and Game 2005). Varying distances between MPAs within a network has been suggested to promote effective connectivity for a variety of species (Roberts 2001, and others). Not all refugia provide optimum conditions for survival during all settlement seasons; therefore, spatial dispersion of MPAs may be beneficial (Larson 1999). A good starting point may be reserves 10 to 20km in size and spaced 15 km apart; then stakeholder and target species information should be incorporated to adjust the size and spacing assumptions (Mora et al 2006). Dispersal distances for marine organisms may range from 10 to 200 km, and these should be considered when developing guidelines for spacing (Palumbi 2004). Suggestions for varying spacing range from a 10 to 20 km minimum to 100 km maximum distance apart (Shanks et al 2003, Sala et al 2002).

MPA network design should include consideration of any 'critical areas' in the region. This includes: source and sink populations, important refuges for target species, and viability of sites. Where possible, MPAs should be located at source populations rather than sink populations (Pulliam and Danielson 1991, Roberts 1998, Stewart et al 2003). Significant larval settlement must remain in the local area; one way to design for this is to create reserves which are larger than the mean larval dispersal distance for the target species (Botsford et al 2001). Marine reserves have the potential to act as fish refuges from many anthropogenic impacts (Airame 2003). Understanding the different needs of a target species in different life stages, as well as the risk of mortality in each stage, can help to determine which areas best act as refuges for the species and therefore should be selected as reserve sites (Allison et al 1998). Critical areas to consider include: feeding grounds, spawning grounds, nursery grounds, areas of high species diversity, socializing areas, etc. (Allison et al 1998). Vulnerable marine habitats often provide critical ecosystem processes and should be included in MPA network design (Airame 2003). Gaps in current knowledge as well as suggestions for future study are also noted in the following report.

## Using a Network Approach

### *Why Networks?*

There is general consensus that MPA networks are more desirable than individual MPAs (i.e. Ballantine 1997; Salm et al 2000; Allison et al 2003; Roberts et al 2003b). For example, a single reserve is unlikely to reduce overall mortality for a species because of migration during different life stages (Gerber and Heppell 2004). Planned networks can provide important spatial links to maintain ecosystem processes and connectivity, as well as improving resilience in the case of a localized catastrophe, such as an oil spill (Stewart et al 2003). Due to these factors networks can help to ensure long-term sustainability of populations better than single sites are able to (NRC 2001). Using networks of MPAs can provide an ecosystem based approach to meeting the multiple goals of coastal and ocean management, as well as an opportunity to provide for more inclusive representation of stakeholders (NRC 2001).

There are some questions regarding what to do with already established individual MPAs when creating a network (Stewart et al 2003) since networks are rarely considered from the start of MPA designation in a region. Networks can be designed in an evolving way as each new reserve is added, according to what is left unprotected (Roberts 2001). Stewart et al 2003, examine this possibility in the South Australian marine reserve network, using MARXAN to determine the efficiency of reaching goals by retaining previously designated reserves. They found that locking in currently designated reserves presented significant opportunity costs. When possible a systematic selection of reserve networks should be applied instead of opportunistic selection because it increases the chance of effectively reaching diverse network goals, such as fisheries management and biodiversity conservation (Roberts et al 2003b).

Though MPA networks may be designed to achieve specific and varying results, such as conserving an endangered species or managing for economically-viable reef fish, they may also have unintended impacts on ecological systems. While MPA networks cannot protect against bleaching events, they can reduce overfishing and other human impacts by providing refuge for populations to rebound, thereby making the reef more resilient to things such as bleaching (West and Salm 2003), as well as spreading risk so that unaffected MPAs can act as larval sources to affected areas (Hughes et al 2003).

While MPA networks are currently one of the best management tools for conserving coral reefs because of the protected habitat they provide, especially when integrated with other management techniques, they should not be the only conservation tool used (Hughes et al 2003). Network effectiveness relies in part on what occurs outside the protected areas; for example, unsustainable fishing effort can undermine a species population by removing individuals before they have adequate time to survive to reproductive age. Also, uncontrolled anthropogenic pollution outside the protected areas clearly will have a negative effect (Kaiser 2005). Other forms of fisheries management are needed as well (Beger 2003, Allison 1998). Traditional management tools such as catch limits and gear restrictions to control fishing effort should continue to be used in areas where fishing occurs, as well as incorporating new management techniques as they emerge (Kaiser 2005).

### *Setting Clear Goals*

MPA networks are usually established to improve fish catch, to conserve biodiversity, or for a combination of these two reasons. Being clear about the goals of an MPA network is critical and leads to increased effectiveness. There is certainly a common goal of target population persistence in both fishery oriented and biodiversity conservation oriented reserve management (Botsford 2003). However, while these goals may overlap considerably,

management responsibilities are often fragmented among agencies, resulting in uncoordinated efforts and more problems than solutions (Roberts et al 2003b).

When objectives are initially undetermined or less explicitly agreed upon it can become more difficult to evaluate effectiveness of the network (Leslie 2005). There are often different factors to review when assessing reserve effectiveness depending on reserve goals (i.e. changes in fish biomass outside of reserves for fishery goals), and monitoring might be focused on different target species depending on goals (Botsford et al 2003). In the literature, fishery goals are covered much more in depth than biodiversity conservation goals in regards to MPA effectiveness, whereas MPA network design is usually concerned with both goals (Botsford et al 2003).

In certain cases, different goals may lead to somewhat different management choices or design decisions (Allison et al 1998). For example, according to Allison et al, biodiversity goals may benefit more from large reserves whereas fishery goals may benefit more from smaller reserves (1998). It is very important to determine the goals of an MPA network as early as possible in the design process, and to keep them in mind when evaluating network performance (Roberts et al 2003b; Leslie et al 2003; Leslie 2005; Botsford et al 2003; Halpern 2003).

It is also important to note that while most current literature discusses reserves, there are a wide variety of MPA regulations and not all are no-take reserves. The type of MPA regulations implemented must be decided upon with both ecological and socioeconomic factors in mind.

## **Ecological Criteria**

### ***1. Representation and Replication***

This section helps to answer one of the most fundamental questions of MPA network design: which areas should be selected for protection? In general, designing for representation aims to enhance protection of a region's biodiversity through development of reserves which represent the range of habitats and communities within the region (Day et al 2002). This criterion was recently considered by the Representative Areas Program in the Great Barrier Reef Marine Park, and they found a need to improve representation in the park (Day et al 2002). Replication is the repetition of these biogeographic units throughout the network, where multiple sites of each unit are protected. Incorporating both components will ensure that networks of MPAs are more resilient to catastrophes, induced by nature or human (Roberts 2001).

#### ***a. Factors to consider (composition, structure, function, quality, replications)***

The available literature overwhelmingly states the importance of replicated representatives of all biogeographic areas as well as the myriad habitat types within them (Roberts et al 2003a; Wells et al 2006; Roberts 2001; Hockey and Branch 1994; Ballantine 1997; Day and Roff 2000; Friedlander et al 2003). It is important that expert judgment be used in regards to the specific situation of each region (human threats and natural catastrophes) as to the precise percentage of area of representative habitats protected (Airame 2003).

There is no single set of guidelines that can be applied across the board when assessing representation and replication for MPA network design: however, there are several factors to consider. MPA network planning should consider biodiversity composition, biogeographic structure and ecosystem function (i.e. ecological processes) (Noss 1990, Stewart et al 2003). In general, there is an increase in species diversity as you increase habitat diversity for both terrestrial and marine systems (Carr et al 2003); therefore, the greater the variety of protected habitats, the greater the biodiversity conservation. Representation should be considered at all biological scales, from genes to ecosystems (Wells et al 2006). The network should aim to include all species, particularly species of special interest for both conservation and fisheries, areas in which unique ecosystem services occur, vulnerable habitats (i.e. deep sea mounts), and localities that are important for vulnerable life stages of species (Gerber and Heppel 2004, Wells

et al 2006, Roberts et al 2003a). The quality of the representative habitats selected should also be considered. Higher quality habitat may prove more beneficial for quick results, but certain lower quality sites may really benefit from added protection. DeVantier et al, state that to protect all rare coral reef species, habitats normally considered marginal or poorer quality would need to be protected (1998).

It is important to select representative areas in the most efficient configuration so as to maximize ecological goals in design as well as respect socioeconomic limits. For example, selecting a variety of optimal configurations of representative habitats for protection and presenting options to stakeholders is helpful (simulated annealing) (Leslie et al 2003). This simulated annealing technique also includes spatial information, so the biophysical aspects of connectivity and clustering can be incorporated into design (Leslie et al 2003). The options provided using these tools (or similar ones) can be evaluated with stakeholder input to select configurations that satisfy representation as well as community goals (Day 2002).

#### *b. Percent representation*

It is estimated that in order to meet all fishery and conservation goals networks of fully protected reserves should cover 20 % or more of all biogeographic regions and habitats (Roberts and Hawkins 2000; National Research Council [NRC] 2000; Roberts et al 2003a). The World Parks Congress calls for strictly protected marine reserves covering 20 to 30 % of all habitats by 2012 (WPC/IUCN 2003). It was recently estimated that approximately 10 to 50 % of the ocean should be placed in reserves in order to sustain fisheries outside these reserves; the exact amount varies depending on the objectives considered (Kaiser 2005; Gell and Roberts 2003). Some precaution should be taken when using representation and fixed percentage targets to achieve conservation goals to ensure that the best sites are selected based on biophysical characteristics and not to avoid controversy (Reeves 2000).

The first step in planning for adequate representation is to assess the range of habitats in the area.. One way to do this is to subdivide the area of interest into biogeographic regions based on physical and biological factors, such as sea surface temperature, or bathymetry (Airame 2003). To identify representative and unique habitats to address conservation goals, a simple multidimensional classification of habitat, including but not limited to depth, exposure, substrate, and dominant flora and fauna can be essential in design planning (Airame 2003). It is suggested that effective design decisions can be made before completion of this time intensive data gathering as long as monitoring and evaluation efforts continue (Roberts 2003a).

#### *c. Habitat vs. Species Approach*

A habitat-based approach is often applied as more data are commonly available on habitats than on specific species (Airame 2003). Roberts et al 2001, suggest that habitat representation in networks should be roughly proportional to coverage, incorporating significant fractions of each habitat, and should be larger offshore than nearshore. It is important to include reserves in both transition zones (between biogeographic areas) and core zones within each biogeographic unit (Roberts et al 2003b). Networks should include variations in habitat which occur at different depths as well as different geographical areas (Roberts et al 2003b).

There is some debate over whether to rely on single species designs (thinking that species protection can ensure habitat protection), or to focus on protecting critical or rare ecosystems, or a combination of the two. Single species approaches can help determine during which life stage a particular species would benefit most from protection, and then use this information to determine optimum reserve size and location for conservation of the species of concern (Gerber and Heppell 2004). The distribution of some charismatic species is well documented and therefore could be used in network design, resulting in an umbrella of protection for other marine life (Wells et al 2006). However, managing for all species within an area leads to multiple layers of complexity in MPA design (Kaiser 2005). Current descriptions of species do not always include



the variations in behaviors of individuals and populations (Airame 2003). If species-specific tools are used for planning, choosing a study species to focus on can be controversial, particularly because decisions are based on what information is available (Nicholson 2006). Planning for specific species is often difficult due to the limited amount of available data (Gerber and Heppell 2004).

Large scale ecosystem processes can be important regardless of the network goal and can be overlooked by species-specific siting processes, such as single species fisheries management (Roberts et al 2003b). Despite this, there are significant limitations of design based solely on habitat, due to lack of data in general, as well as long-term data since habitats can change significantly over seasons, environmental variation and climate regime shifts (Airame 2003). A combination of a habitat-based approach with some species-specific components to ensure inclusion of target or rare species (Beger 2003) can be a good way to ensure representation.

While increasing fish size and biomass is evidence of the benefit of permanent protection for coral reefs, there has been far less documentation of designing MPA networks with consideration to marine megafauna whose survival requires access to large-scale oceanic features, particularly pelagic areas. Effective conservation of ocean basins and pelagic areas requires that migration routes of far-ranging marine species are protected (Hyrenbach et al 2000). Thus, design of MPA networks that protect highly migratory species, such as marine mammals, turtles, and tuna, should take into consideration permanent protection of the spaces in the pelagic zone related to some key life history patterns, including breeding, feeding, and migratory routes. Because some of these elements fluctuate, including currents and some upwellings, MPA networks can be designed in dynamic ways that include a mixture of permanent closures with more temporal and spatial closures that fluctuate with fisheries (Hyrenbach et al 2000). King and Beazley are using the geographic range and life history patterns of far-ranging focal species, such as the Northern Atlantic right whale, as a biological consideration for designing MPA networks (2005). They expect that smaller species with a narrower range and area requirement will also be protected when networks are designed to protect the feeding, breeding, and socializing grounds of large marine mammals. Developing dynamic temporal and spatial MPAs and MPA networks for highly migratory species, including certain oceanographic areas related to key behaviours, will provide an additional approach for ocean basin protection (Hyrenbach et al 2000). Refuges can be created for highly migratory species by incorporating sites that constitute migration bottlenecks or critical life stages, such as breeding, feeding, nursing, into networks, even if only for temporary or seasonal closures (Roberts 2001). Despite this effort to regard highly mobile species in MPA network design, the resulting effectiveness is a topic of concern. According to Horwood (2000), excluding up to 25 % of the North Sea from fishing would still only have a negligible effect on improving numbers of wide-ranging species such as Atlantic Cod (Kaiser 2005, Horwood 2000).

#### *d. Site Selection*

Replication, or designation of multiple sites of each representative biogeographic region and habitat, is an important component of site selection. Designating several representatives of every habitat type in different reserves allows for less vulnerability to smaller scale perturbations, such as one site being negatively affected while another is not, and may be able to act as a population source, or at least another refuge, for damaged sites and species (Carr et al 2003). This approach spreads risk since habitat types are buffered against destruction or species extinction from a localized disturbance, such as an oil spill. Roberts et al suggest that habitats should be protected in proportion to the prevailing frequency and severity of natural or human disasters (2001). For example, a strong El Nino occurs in the Galapagos approximately every decade, wreaking havoc on marine systems. In this case, having more replications of protected habitats leaves a higher potential for life to spring back when more favorable conditions return (Roberts et al 2001). The impacts of additional educational and recreational use in a reserve should be sufficiently

considered when planning and evaluating replications of each habitat within each biogeographic unit (Roberts et al 2003a).

Areas with high potential for natural or human disasters should be avoided as reserve sites, because they will need to rely on outside populations for re-colonization if a catastrophic event were to occur (Roberts et al 2003b; Allison 2003). Sites should be situated in a network such that they will not all be affected by catastrophes in the same way. Airame states that increased network and reserve sizes can reduce the negative impacts of potential disasters (2003). A larger reserve or network provides more of a buffer against losses from natural catastrophes by protecting more individuals to re-establish any affected populations.

Resilience and resistance are critical aspects of MPA network design, especially in the face of global climate change (West and Salm 2003). Resilience refers to the ability of a community to return to its previous state through growth and reproduction of surviving organisms following a disturbance; and resistance refers to the ability of an ecosystem or species to maintain diversity, integrity and ecological processes during or following a disturbance (i.e. corals that resist bleaching or survive after bleaching events) (West and Salm 2003). They are critical characteristics to take into account when selecting a site because of uncertainty with natural environmental fluctuations and human induced incidents (Allison et al 2003). If a reserve (or reserve network) is resilient and resistant, it can bounce back from or withstand environmental fluctuations or unexpected catastrophes and support populations which can potentially replenish other damaged populations (West and Salm 2003). According to West and Salm, there are four main categories of factors that correlate with coral resistance from bleaching events. The first three are physical factors that reduce temperature stress, reduce light stress, and increase water movement. The fourth includes any factors that favor the physical tolerance of corals to bleaching events (2003). Strong resilience can include both intrinsic factors, such as biological or ecological characteristics of a community (i.e. potential for recruitment success) and extrinsic factors, such as physical features (i.e. current patterns that may favor larval dispersal or effective management regime) (West and Salm 2003). Sites displaying these traits should be given higher priority in the selection process.

If using species-specific approaches for planning it is important to consider that planning focused solely on sites with the greatest number of species often leads to clustering of MPAs in the one biogeographic region of greatest species richness (Roberts et al 2003a). To avoid this, a complementarity analysis can be used so that biogeographic representation is weighted, giving the area with the greatest number of species in the region the highest rank, then the second highest weight goes to the area that contains the greatest number of species not found in the first site, and so on down the list, to ensure a wide variety of habitats and species are protected in the region (Roberts et al 2003a).

To maintain ecosystem processes, protecting species-poor communities may be just as important as protecting species-rich systems. As the number of species within each functional role is reduced, the system is affected more quickly when declines in essential processes occur (Roberts et al 2003a).

Another way to address the goal of biodiversity conservation is through the use of objective functions of extinction risk for multiple species, which is a form of population viability analysis (Nicholson 2006). Assessment of extinction risk for a single species is fairly common, but does not meet overall biodiversity conservation goals. Using multiple species extinction risk assessments may prove helpful in achieving this objective (see Nicholson 2006 for details).

Sites with low potential for reaching objectives, or low probability of populations rebounding, should not be targeted for selection. Fish populations may not always recover when fishing pressure is released as a result of changes in the trophic system or habitat (Birkeland 2004). For example, sites where intense fishing has altered the structure of habitat to a possible point of no return, such as the removal of all grazers or top predators, probably should not be considered optimum for selection (Roberts et al 2003b).

The number of replications of each habitat type must be a balance between ensuring representation and ensuring effective monitoring and enforcement (Airame 2003). One to four reserves have been recommended for designation within each biogeographic region in the California Channel Islands National Marine Sanctuary (Airame 2003, Roberts et al 2003a). However, this maximum of four in relies in part on specific characteristics of the region, such as the impacts of closing fishing grounds on the resource users, the degree of clustering of certain habitat types, or the available monitoring and enforcement resources. Ecologically speaking, increasing the effectiveness of replications for each representative habitat increases the likelihood of protecting that habitat.

## **2. *Ecological Connectivity***

While a major benefit of incorporating marine reserves in MPA network planning is the dispersal of individuals to non-protected habitats, there is little hard data that can be used to estimate the exchange of larvae among local populations. However, it is beneficial to understand how larvae disperse and are transported to effectively design marine protected areas. The spatial scale of MPAs needs to match the spatial scale of larval dispersal to ensure that the MPA is large enough to sustain marine populations (Palumbi 2004). Scaling up to an effective MPA or no-take zone network requires careful consideration of ecological connectivity issues (Steneck 2006).

Connectivity among reserve sites can provide for transfer of larvae and material among biological populations and ecosystems (Roberts et al 2003b). This can help to ensure sustainability of populations for both conservation (supplying populations inside reserves) and fisheries enhancement (supplying populations outside the reserves) (Halpern et al 2006). It is thought that for reserves to interact effectively in maintaining biodiversity, they need to be located close enough together that they can obtain larvae from upstream reserves and deliver them to downstream reserves (Roberts 1997). However, marine reserves may be ineffective in providing benefits if local fish populations depend on unprotected larvae from outside the reserve (Roberts 1997).

Many species undergo different phases of their life cycles in different habitats, moving between them as they develop (Appeldoorn et al 1997). Links among mangrove and seagrass nursery areas and coral reefs are well known (Ogden and Gladfelter 1983; Roberts 1996; Nagelkerken et al 2000). Thus, connectivity is important for the exchange of offspring, for movement of adults and juveniles, and for functionally linked habitats such as coral reefs, seagrasses, and mangroves.

Reserve networks should not be built on the dispersal knowledge of just one species (Roberts 2001). Reserves should be located in a wide variety of places in relation to currents to compensate for constantly changing ocean conditions (Roberts 2001). To increase resilience, networks should be designed to ensure many potential connections are available between them, not designed to fit one probable connection (Roberts 2001). For example, deliberate spacing of coral reef MPAs within a network can provide “stepping stones” for associated species (i.e., the reefs fall within the dispersal ranges of adjacent reefs) (Steneck 2006).

Networks should be as large as the mean larval dispersal distance of that species for self-seeding of a species in a reserve to occur (Botsford et al 2003) and they should be between 10 to 20 km apart (Palumbi 2003). Shanks et al suggest that reserves should be at least 4 to 6 km in diameter and spaced 20 km apart, which should be close enough to allow even the lower end of long-range dispersers to settle into adjacent reserves (2003). They found a mean larval dispersal distance of 25 to 150 km for fish and invertebrates with pelagic larvae (Shanks et al 2003). These estimates are based on propagule dispersal estimates and do not explicitly account for adult movement (Shanks et al 2003). Reserve networks that are sufficiently dense to exchange offspring, especially of vulnerable species, may prove more beneficial than single larger reserves (Roberts 2001).

### *a. Larval dispersal distances*

Cowen et al (2006) demonstrated through the use of hydrodynamic models that typical larval dispersal distances of ecologically-relevant magnitudes are on the scale of only 10 to 100 kilometers. Through these studies it was determined that connectivity is more local among reef fish and more variable regionally than previously thought (Cowen et al 2006).

It is important to understand life scales of target species when designing for connectivity, especially with non-permanent regulations. This is because short-lived species may require more regular recruitment to sustain populations while longer lived species may be sustained by periodic pulses (Steneck 2006). Failure of stocks to rebound even within reserves is often linked to lack of reproductive stocks outside reserves (Roberts 2001).

Fishing pressure reduces both the population density and body size of harvested species, which can reduce larval abundance and thus shrink the dispersal distance and the effective connectivity distance (Steneck 2006). Thus, it is important to consider increases in fishing pressure due to area closures from a biological standpoint as well as a socioeconomic one.

The term “ocean neighborhood” is used to describe an area centered on a set of parents that is large enough to retain most of its offspring (Palumbi 2004). When adults move widely, neighborhoods are larger and more spread out; when adults are sedentary and larval dispersal is low, they tend to be small; finally, when adults are sessile and long-distance larval dispersal is high, neighborhoods tend to be larger (Palumbi 2004). One approach to network design is to establish the size of reserves based on adult neighborhood sizes of highly fished species, and space the reserves based on larval neighborhood scales (Palumbi 2004). Marine reserves that cover populations over scales of 10 km to 100 km are likely to cover the adult neighborhood of most commercially important fish species and ecosystem dynamics, but this standard will not be enough for highly migratory species (Palumbi 2004). In the end, accommodating species with the highest adult dispersal capacity should protect lower adult dispersal distances as well. For example, reserve sizes designed to ensure self-seeding for 100 km adult dispersal species should be sufficient for self-seeding of 10 km adult dispersal species as well (Palumbi 2004).

### *b. Relation to spillover*

If there is low dispersal between a reserve and surrounding areas, then the reserve will likely not enhance the overall productivity of the fishery because the larvae, eggs, and adults will not disperse beyond the reserve (Palumbi 2003). However, small reserves which will have more spillover of fish into the unprotected area may not be able to provide protection for adults with large ranges (Palumbi 2003). Therefore a variety of reserve sizes is recommended to meet both conservation and fisheries goals.

### *c. Currents and dispersal*

For populations with sedentary adults and dispersing larvae, Roberts proposed that ocean currents are convenient stand-ins for the connections among different reserves (1997). He suggests that currents and other oceanographic phenomena can greatly influence the transport and dispersal of many marine organisms, especially the early planktonic larval stages (Roberts 1997). Recent evidence suggests that patterns of ocean movement are not well represented by average current speed and direction because ocean currents vary over small temporal and spatial scales (Palumbi 2003). In addition, indirect measurements of marine dispersal do not always correspond to predictions based on simple current models (Barber et al 2000). Although ocean current patterns are one proxy of the connectivity among and between reserves and their regional ecosystems, physical patterns do not always perfectly predict biological connectivity (Barber et al 2002). Gaines et al suggests that advection (directional transport by currents) is important in developing effective marine reserves in areas with strong currents; however, it is not currently included in most models, which focus on non-directional transport (2003).

#### *d. Magnitude of dispersal distances*

Although Roberts (1997) suggested that many marine populations were dependent on substantial larval inputs from distant upstream populations, Cowen et al (2006), using more sophisticated modeling, have demonstrated that larval transport via passive diffusion cannot sustain reef fish at current levels unless there is substantial self-recruitment.

Previous studies suggest long distance dispersal is common, but current emerging information suggests that larval dispersal may be limited (Jones et al 1999, Swearer et al 1999, Thorrold et al 2001, Palumbi 2003, Paris and Cowen 2004, Jones et al 2005). Analyses of larval dispersal patterns indicate that local retention of larvae is surprisingly high, larval dispersal ranges are much smaller than previously suspected, and long distance dispersal may be unusual (Palumbi 2004).

### **3. Permanence**

In 2004, the Convention on Biological Diversity's ad hoc technical expert group on marine and coastal areas recognized that permanence is an important aspect of individual highly protected marine and coastal areas (CBD 2004). More recently, the World Commission on Protected Areas, in conjunction with the World Conservation Union, considers fully protected, permanent marine areas critical for networks of MPAs (WCPA/IUCN 2005). It can take several seasons or decades for benefits to be evident in an MPA network because of variations such as target species life history, habitat conditions at implementation of protection, and management effectiveness outside the network (WCPA/IUCN 2005). There is general consensus among the scientific community that the protection of target fisheries and biodiversity conservation, two of the main goals of MPA networks, rely on large-scale protection efforts that include areas of full, permanent protection.

Even though aquatic environments are fluid and pose less restriction on population movement compared to terrestrial habitats, there is evidence in temperate regions that the mobility of fish species does not reduce the positive effects of site-based protection for maintaining viable populations (Willis 2003). The scientific community has seen mounting evidence for the benefits of long-term management schemes that prohibit the take of marine resources (Babcock et al 1999). As data collection increases and more marine management programs see the utility in monitoring the effectiveness of their conservation efforts, there are growing numbers of case studies around the world that exhibit increasing trends in species biomass over the long term, such as the Philippines (Russ 1996), Hawaii (Williams et al 2006), and New Zealand, where it took over 20 years for two highly protected marine reserves to yield recovery in fish populations (Willis 2003). For MPAs where fisheries management is the main objective, predatory fish densities increased substantially over 11 years of protection in the Apo reserve in Philippines (Russ and Alcala 1996). Whether the goal of the MPA site or network is fisheries management or biodiversity conservation, there is agreement among scientists that having long-term, permanent closures, such as a marine reserves, provides the greatest level of protection and benefits to the species populations.

In general, the biological characteristics of individual reef fish, such as size and age, are critical to the health of the overall marine system and an important factor in the design of MPA networks. Long-living, large fish have high metabolic stores and confer more energy to their offspring than smaller fish (Birkeland and Dayton 2005). As a result, these fish produce the most viable larvae, ultimately supplying the next generation of fish to the reef, supporting sustainable fisheries, and contributing to the biodiversity of the system. According to Birkeland and Dayton (2005), protection of larger and older long-living fish species, rather than regulating total fish harvests, is critical for sustaining the populations of target species. Because recruitment of larvae can be affected by oceanographic features, it's important for populations of

spawning fish to be protected across their entire geographic range. Thus, establishing networks of marine reserves is the only option for preserving long-lived fish species (Berkeley et al 2004).

Maintaining populations of large fish contributes to maintenance of coral reef ecosystem function (Friedlander and DeMartini 2002). For example, small parrotfish have significantly less impact on a reef when compared to large parrotfish, which more extensively graze algae and erode reef frames while feeding (Bruggemann et al 1996). Recovery of ecological function and structure of the biotic community, which relies heavily on large predatory fish in tropical marine environments, often takes a least 10 or more years once fishing has been removed from the system (Russ and Alcala 2004, McClanahan and Graham 2005).

While establishing permanent closures is critical to the success of large-scale marine conservation measures (Cinner et al 2005), it is often not the most viable management tool. Providing effective enforcement and compliance of areas that are permanently closed can be overwhelming to some regions and institutions that have low finances or capacity to conduct regular surveillance. Permanent closures often displace fishers who have traditionally or historically fished in an area that is now off limits. This can result in increased conflict over natural resources, where biological successes can be disrupted with social failures (Christie 2004). Thus, another approach to marine conservation is the strategy of rotating closures, where a managed area is occasionally opened to fishing. Rotational or seasonal closures provide an alternative to permanent closures. For MPAs that have a goal of fisheries management, seasonal closures are typically introduced for the purpose of providing a surplus of natural resources for harvesting (Cinner et al 2005). They are often more acceptable to fishers because they are part of traditional management. Local experience in Hawaii indicates that fishers perceive rotational closure as an acceptable option when compared to permanent closures because it does not forever prohibit access to the resource (Williams et al 2006).

The effectiveness of closures is often directly related to social and economic factors within an area. Evidence in small communities in Indonesia and Papua New Guinea showed that adaptive periodic closures can increase coral reef fish biomass and size inside managed areas relative to open access sites (Cinner et al 2005). The socioeconomic conditions in these two communities, including exclusive tenure over marine resources, traditional ecological knowledge that allows rapid assessment of ecological conditions, relatively small human populations, and low dependence on fisheries, may contribute to the positive trends in fish growth and abundance because fishing pressure in recently opened managed areas is likely equal to those that are always open to fishing. The local community also has social customs, such as fishing in groups and managing closed areas that are clearly visible from the community, that increase compliance with the managed areas. While periodic closures will unlikely conserve the same amount of resources and biological processes as large marine reserves and thus cannot replace these strategies, they are a potentially useful tool for managing marine resources, particularly when large marine reserves fail or are unrealistic. Overall, the use of periodic closures as an effective adaptive management practice would be best applied in communities with these similar traits. While temporary, rotational, or seasonal closures are not as effective as large reserves, they provide a suitable and useful tool for conservation and fisheries goals when certain community conditions apply.

Regional and cultural contexts can dramatically affect closure success, whether permanent or seasonal. Where fishing pressure is simply transferred from the closed area to an adjacent area in communities that are heavily reliant on marine resources, periodic closures may not be effective (Cinner et al 2005). In many cases, fishing effort may actually increase when fishing activities must be transferred to a less productive area. (Hyrenbach 2000). Over 20 years of data collection in Oahu, Hawaii, has indicated that rotational closures are not as effective as permanently-closed areas in conserving fish stocks (Williams et al 2006). Williams and colleagues found that while fish biomass increases when the managed areas are temporarily closed, there are immediate reductions in biomass once the areas are opened to fishing. In

contrast, fully-protected reserves have had no decline in the maximum fish size of target species over two decades. Overall, target fish biomass has been double that in areas that are closed on rotation (Williams et al 2006).

Like the important, seasonal protection of pelagic breeding grounds, some reef fish may require closures associated with life history traits on a seasonal basis. Sadovy (2006) recommends that planning for MPAs includes protecting spawning aggregation sites through the establishment of seasonal closures. In some cases, these aggregations may be spatially fixed, but some species' aggregating locations shift yearly. Incorporating seasonal protection of SPAG sites in an MPA network design would ensure that critical reproductive behaviours are conserved. MPAs with extraction may prove limited in effectiveness at protecting coral reefs, because of the myriad factors they rely on (including large herbivorous and predatory fish) (Mora et al 2006). Even a non-constant fishery can reduce the size and amount of these fish, thereby reducing the effectiveness of the reserve and the functioning of the coral reef. It seems that a combination of some reserves as well as other protected areas may be the best compromise between conservation and fisheries.

Reserves often displace fishing efforts and increase fishing pressure in adjacent areas, making it difficult to quantify immediately whether or not reserves enhance fisheries. The designated sites must supply more larvae than the increased amount removed in the surrounding area. This happens through spillover of fish within the reserve or through larval dispersal to the surrounding area (Halpern et al 2004).

There can be a substantial time lag before recruit success is seen or before signs of population recovery are seen (Russ and Alcala 1996; Gerber 2003). These time lags can differ for different species and depend in part on the current population status in the region at time of implementation. For example, many species (which are commonly fisheries targets) are long-lived and slow growing, and fishery exploitation can and has drastically reduced their numbers, as well as the size and age structure of surviving populations; changes such as these may take several years or more to recover from (Russ and Alcala 1996).

There is evidence, as seen in Hawaii (Williams et al 2006), that rotational closures are not effective at conserving reef fish stocks. However, insights from studies in the Indo-Pacific region suggest that seasonal closures, when used as part of adaptive management, can increase fish biomass and average size (Cinner et al 2005). Socio-economic conditions and cultural variations among these two areas seem to have an effect on the success rate of non-permanent closures. More research in this area is needed to better understand the effectiveness of non-permanent closures.

#### ***4. Size, Shape, and Spacing***

Gaines et al claim that most literature on marine reserve network design focuses on the question of optimal reserve size (2003). Few published insights are given on reserve location and numbers. This section discusses the optimal sizes of MPAs in designs used to meet various network goals, as well as concerns and thoughts correlated with optimal shape and spacing of MPAs.

##### ***a. Size***

The objective of MPA network implementation is essential to consider before designing the size of the MPAs. Several small reserves will be best to meet fishery goals and reduce the impact of closing off areas from fishing (Allison et al 1998). In contrast, larger reserves are better for meeting conservation goals. According to Roberts et al, there is no biological upper limit to reserve size, but there is often an upper limit due to practical considerations (Roberts et al 2003a). A single large reserve might best isolate biological hotspots from threats (Allison et al

1998). Yet most MPA networks are designed to meet a combination of fishery and conservation goals.

#### *b. Combination of goals (fishery and conservation)*

Two major suggestions have been made on MPA size regarding both conservation and fisheries goals: intermediate sizes work best (Roberts 2001) and a variety of sizes in connected networks work best (Halpern 2003, PISCO 2002).

Yield benefits from fisheries may peak at an intermediate reserve size where it's large enough to provide refuge and self-recruitment but small enough to ensure export (Roberts 2001). Intermediate size reserves may also be seen as a compromise between conservation goals and practical needs, such as not closing off too much of the current fishing grounds (Allison et al 1998), or avoiding too many small reserves which requires greater monitoring and enforcement efforts (Roberts 2001). Multiple smaller reserves are tougher to monitor and enforce than a reserve of equal total size (Roberts 2001). Local stakeholders may be less likely to support a MPA network which does not try to minimize closed areas within current fishing grounds.

Small reserves alone may not function very well, so there is a need for a variety of reserve sizes (Halpern 2003). As is true with terrestrial reserves, the importance of top predators in the ecological system has implications for reserve size since these species often have wider ranges (Carr et al 2003), resulting in larger MPAs. It is noted that a variety of reserve sizes can be beneficial to both conservation (of many species) and fisheries, and if selected with stakeholder participation they could minimize negative impacts on the community (Halpern 2003). It has also been suggested that reserves be larger offshore than nearshore to allow for conservation with less impact on local communities (Roberts 2001).

There are few current models that consider larval dispersal explicitly (Gaines et al 2003). This is due in part to the currently limited understanding of dispersal distances (Gaines et al 2003). Gaines notes that dispersal may be directional, which is important to understand when assessing connectivity; however this is often overlooked by previous dispersal models (Gaines et al 2003). A new model was developed which incorporates a simplified two-dimensional advection-diffusion equation, parameters related to sessile adults, and the flux of larvae into and out of the plankton (Gaines et al 2003). They show the importance of considering reserve size, reserve configuration, and regional flow conditions in relation to dispersal distances for effective network design (Gaines et al 2003).

#### *c. Shape*

There currently is not much literature available on the optimal shapes of MPAs within a network. However, the terrestrial protected area concept of minimizing edge habitat versus interior protected area habitat issue may apply to MPAs (Carr et al 2003). It is important to consider the ratio of edge habitat versus core interior habitat, as the edges of MPAs are often extensively fished, and therefore do not offer the same refuge to fish species as core interior protected areas do (Willis et al 2003).

To ensure protection of the varied species in a region it is important to include a variety of depths and transition zones while planning for representation of all habitat types within a network (Roberts 2001). It is also important to consider obvious reference points for ease of monitoring and enforcement as well as building awareness of boundaries with resource users (California Dept. of Fish and Game 2005). Therefore a shape which allows for clear marking of boundaries while incorporating biological considerations may be optimal.

#### *d. Spacing*

In general, size and spacing rules of marine reserves are guided by estimates of how far larvae disperse (connectivity between reserves) and the patterns of adult movement (spillover out of reserves) (Gerber et al 2003). This is discussed in detail in the connectivity section above and



summarized here. Current guidelines for reserve spacing rules are based on estimates of average dispersal distances for marine organisms ranging from 10 to 20 km (Shanks et al 2003) to 10–100 km for invertebrates and 50–200 km for fish (Palumbi 2004). Using uncertainty modeling, Halpern et al (2006) finds similar dispersal distance and suggests similar spacing rules – roughly 20–200 km. Shanks et al (2003) suggests that reserves spaced ~10-20 km apart are close enough to allow for recruitment between each other. Sala et al (2002), recommend that adjacent reserves are not farther than 100 km away from one another. They also used an average spacing of 40 km between sites to ensure connectivity for most species of concern. Because species' dispersal characteristics vary widely, the ideal distribution and sizing of reserves for one species may be very different from that for another (Roberts 1998; Grantham et al 2003). Concepts on larval, juvenile, and adult dispersal are discussed in greater detail in the connectivity section above. It may also be important to consider socioeconomic factors when defining spacing, as a somewhat spatially condensed network may reduce enforcement and management costs (Roberts 2003b).

Currently many authors suggest a variety of distances between different sized MPAs within a network (Roberts 2001). Larson argues for the spatial dispersion of refugia because studies have shown that conditions of larval settlement may have a strong effect on adult reproduction (Larson 1999). This may be so strong in fact that larvae may not survive in regions with imperfect conditions, to the extent that genetic changes can be seen between year classes, because such a small percentage of larvae survive to reproductive age (known as the “sweepstakes-chance matching” theory) (Larson 1999). Therefore, not all refugia will be ideal every season, and dispersing these reserves increases the chances that larvae will not only settle in a region with necessary survival conditions, but also that this region will be protected, thus increasing the chances for survival.

## **5. Critical Areas**

Critical areas, such as spawning aggregations sites, are biologically and ecologically significant areas that play a crucial role in ecosystem function and thus require extra consideration when beginning the design and implementation process of a network. Some key factors of critical areas to consider include the likelihood that the site is a population source or sink, the importance of the site as refugia for species of concern, and the viability of the site as well as the sites' contribution to species viability.

### *a. Source and sink*

MPAs strategically located at source populations retain sufficient recruits, or larvae, to sustain local populations, and will export surplus larvae to other areas. In contrast, MPAs located at sink populations often depend upon replenishment from outside areas, thereby diminishing prospects for long-term viability as well as fishery benefits if the source is removed or depleted (Pulliam and Danielson 1991; Roberts 1998; Stewart et al 2003). Maintaining sustainable populations of reef fish and other marine species requires that the fraction of natural larval settlement remaining in a local area must be significant (Botsford et al 2001). Thus, either a large portion of the coastline must be protected in reserves (>35 %) or the reserves must be larger than the mean larval dispersal distance of the target species to ensure that the MPA is a population source (Botsford et al 2001).

Position of MPAs along a shoreline may be critical for the outcome of a network regardless of the population source and sink status of its sites (Gaines et al 2003). There may be directional bias of larvae migration related to the local ocean currents, which means that the position of a site may determine whether or not it is successful for both fishery and conservation goals (Gaines et al 2003). A network of marine reserves can solve for this problem when multiple reserves (i.e. 1 upstream, 1 downstream, and 1 centered) are located such that they can support a thriving population even in challenging physical conditions (Gaines et al 2003). This is

most likely where there is a somewhat rapid flow and appropriate spacing to ensure connectedness of reserves (Gaines et al 2003).

Allison et al determine four patterns of species dispersal to consider when designing marine reserves: short dispersal/single source populations, limited distance dispersers, longer dispersal fewer source populations pattern, and the species where dispersal is essentially random, such as when larvae is supplied to a large pool and stays in the water column for a while (1998). If the pattern of species dispersal is known for a target species, source populations can be selected for protection when possible. Along these lines it is important to consider direction of water flow and transport, as well as water quality (or activities that might affect water quality) “up flow” of the reserve (Allison et al 1998).

### *b. Refugia*

The term refugia refers to locations which are protected from fishing and other potentially damaging human impacts and provide characteristics of ideal habitat for certain marine organisms. Several natural refuges were available to fish populations in the past, but at depths that fishers couldn't reach, in remote areas, or in areas that were too rough for fishing (Roberts 2001). The populations in these natural refuges then supplied recruits to fished areas, such as the large Cape Cod lobsters of the past (Roberts 2001). However, due to advances in fishing methods, few of these refuges are left untouched (Roberts 2001). Marine reserves have the potential to act as refuges for many species as well. Limiting the fishing impacts on a specific area may give even a fairly barren site a chance to rebound to a healthy level, thereby creating more refuge for marine organisms (i.e. lobsters, sea urchins, and kelp forest) (Airame et al 2003).

A single reserve is not likely to reduce mortality for a species at all life stages, further complicating MPA design for a target species (Gerber and Heppell 2004) by requiring a complex array of MPAs. However, different species face significant threats at a variety of life stages. Gerber and Heppell describe use of population growth models to determine which species are most likely to benefit from a reserve that reduces mortality in a particular life stage (2004). This type of information can be helpful in deciding which areas can act as a refuge for a particular species at its most threatened life stage.

Reserves also have the potential to provide relatively natural refuge to organisms and thereby provide a form of a baseline to understand fishing effects more clearly (Airame 2003). A baseline of this type may be essential in ensuring true adaptive management techniques, based on science and not guesses (Agardy 2000).

Reserves are essential tools for protecting critical areas, and thus should be sure to include nursery grounds, spawning grounds, focus areas of high species diversity, and other such critical sites (Allison et al 1998; Sale et al 2005). They function, possibly most importantly, as a refuge from fishing for individuals of certain species, thus allowing population structure to be determined more according to natural mortality, often leading to an increase in the number of larger, older individuals who carry a more important role for reproduction in the community (Allison et al 1998). While it's difficult to demonstrate in practice, these reserves, if properly placed, can potentially act as sources of propagules for other areas (Allison 1998).

In general, habitat complexity increases with species richness (Friedlander et al 2003). Ideally, areas of high complexity and thus more essential fish habitat should be protected from fishing effort; however, Friedlander et al notes the overall importance of protecting some fish habitat from human impacts while demonstrating the importance of habitat quality on the effectiveness of reserve designation (2003).

### *c. Viability*

Certain marine habitats are particularly vulnerable to human threats and natural catastrophes (i.e. coral reefs, seagrasses, mangroves). These ecosystems often provide essential processes that many target species rely on, such as acting as nurseries or other key habitats at

certain life stages for specific species. Therefore special attention should be given to vulnerable systems when designing a MPA network (Airame 2003). Oftentimes areas that serve these critical ecological functions are concentrated in near shore zones, which can easily be identified by physical parameters (i.e. estuaries, reef formations, shelf breaks) (Agardy 2000).

Long term viability and persistence relies on degree of connectivity through factors of meta-population dynamics such as patch size/quality, recruitment, mortality, and dispersal (Crowder et al 2000, Stewart et al 2003). Networks should be configured with these local oceanographic characteristics in mind, so that each site in a network interacts positively with others (Stewart et al 2003). The South Australian reserve system was planned using this approach.

MPA networks should also be self-sustaining to be considered viable, where ecosystem processes are maintained through natural cycles of variation (Wells 2006). Viability is improved if the MPA network is as independent as possible of the activities in the surrounding area outside the network, where regulations do not apply (Wells 2006). For example, ensuring connectivity between MPAs within a network will alleviate the need for any MPAs to rely on inputs of recruits from unregulated non-network areas. Permanence of the MPA network itself regardless of changes in regulations of specific units is also considered crucial for long-term viability of the network (Wells 2006).

## **GAPS IN KNOWLEDGE and FUTURE RESEARCH**

### *Representation*

There is no simple formula for identifying whether a network is representative or will be most effective (CBD 13). Designers of MPAs often lack knowledge on the distribution of marine biodiversity (CBD 13) and ecological processes (e.g., larval dispersal, migration, spawning and reproduction, and trophic cascades) that would be conservation targets or constraints (Leslie 2005). Comprehensive descriptions of marine biodiversity would be helpful in prioritizing conservation sites, as has been the case with terrestrial protected areas. These classifications are scarce in the marine realm (Carr et al 2003). Sale et al recommend using existing science in adaptive management to fill in the missing biological information on target species, such as incorporating information from current and previous deliberate adaptive management approaches in network design (Sale et al 2005).

### *Ecosystem function*

Although ecosystem linkages are clearly important in marine reserve functioning, they have yet to be fully explored and should be considered more carefully in the design process (Roberts et al 2003a). The effects of altered biodiversity on ecosystem function are not well understood, though it is clear that they are subject to serious disruption and may be irreplaceable (Roberts et al 2003b). Better understanding of the linkages between environmental shifts and life-history characteristics, such as population growth and larval dispersal, is needed to incorporate the dynamic nature of biological and physical systems into reserve design (Airame 2003). There is a need for more knowledge of fishing impacts on ecosystems and to understand things such as trophic cascades and the impacts of placing reserves in certain areas (Sale et al 2005).

### *Connectivity and Dispersal*

There is much to learn about variations in larval behavior and vertical flow structure (Gaines et al 2003, Gerber 2003, Palumbi 2003, Sale et al 2005). Gaps remain in current understanding of sources, fates, and impacts of contaminants in the sea, and understanding of currents eddies, and local areas of mixing (Allison et al 1998). We know relatively little about the extent of connectivity, particularly at ecological scales, among local populations of target

species (Sale et al 2005). To complicate matters, ocean currents greatly affect larval dispersal necessitating additional understanding of hydrodynamics of an area (Warner et al 2000, Sale et al 2005).

Evidence from hydrodynamic models and genetic structure data indicates that the average scale of dispersal can vary widely even within a given species, at different locations in space and time (e.g. Cowen et al, 2003; Sotka et al, 2004; Levin et al 1993). Dispersal distances range from meters to thousands of kilometers, and the time species spend in the planktonic form ranges from minutes to months to years and are largely unknown (Steneck 2006; Halpern et al 2006). The more time propagules spend in the water column, the farther they tend to be dispersed (Shanks et al 2003). Propagule dispersal can be difficult to measure empirically. There is a future need for more than just assumptions about larval dispersal; further investigation into uncertainty and environmental viability would be beneficial (Gerber 2003). Palumbi indicated a need to understand larval transport inside and outside of reserves to design MPA networks more effectively (2003). Sale et al recommend specifying larval dispersal of target species and its relation to population connectivity, which is an area that currently needs more study (2005).

### *Temporal and physical scales of management and science*

Design criteria should focus on relationships between spatial and temporal scales of biophysical processes as well as the characteristics of species, populations, communities, and ecosystems (Carr et al 2003). Genetic dissection of population structure could allow for incorporation of unusual but important life history traits in MPA design processes (Hughes et al 2003). Genetic studies that discover ‘genetic breaks’ may help to identify connectivity boundaries where marine reserve networks are not likely to function well (Palumbi 2003). However, genetic studies are normally used on a different time scale (evolutionary) than most management plans are developed (Palumbi 2003).

It is essential that the dynamic nature of marine systems is not overlooked or undervalued, and that MPA networks are seen as flexible management measures and simply not static units (Agardy 2000). Management units are often on the scale of a state or entire island, but resource monitoring, such as fish assemblages, is not often managed at the same large scale. The results may be more effective if the scales of management and scales of evaluation were better correlated (Friedlander et al 2003). We also currently need more rigorously studied reviews of reserves (i.e. empirically monitored continuously in order to improve available knowledge on impacts of network implementation) (Sale et al 2005).

Improved understanding of levels of viable population size could better ensure that enough individuals of a rare species are within an MPA to protect the population (Beger 2003). Coral reef research is often short term; longer term research is necessary, particularly in relation to climate change (Hughes et al 2003). There is also a need to pay more attention to temporal regional or global patterns of species abundance, and genetic responses to temperature change, to promote resilience (Hughes et al 2003).

### *Modeling*

Modeling is a good way to fill gaps for the short term to take action in the present. Network design would benefit from some simplifying assumptions to develop MPAs as there much is still unknown about ecological and physical processes (Guichard 2004). Design will benefit from incorporation of the complexity and dynamics of ecological communities, as well as ‘macroscopic patterns from microscopic processes’ and the feed back loops influencing both (Guichard 2004). However, it is important to remember not all marine species have large dispersal distances, nor are all ‘open systems’ (Guichard 2004).

### *Empirical research needed*

Sale et al call for more rigorous empirical studies of reserves, including empirical tests of whether reserve spillover displaces the loss in fishing when areas are closed, which can be very hard to study (Sale et al 2005). They do not advocate delay of implementation, but do propose steps are taken to improve current MPA knowledge (Sale et al 2005).

### *Management Effectiveness*

Sale et al recommend empirically testing the effectiveness of reserves, using new experimental design tools (2005). One such approach currently being promoted is before-after, control-impact pairs, BACI or BACIP (Halpern 2004, Sale et al 2005). BACI is a sampling design that enables unambiguous testing of the effects a particular impact, such as MPA network implementation, has on the surrounding ecological system (Sale et al 2005). These types of studies can show the differences between control and reserve sites prior to protection and after MPA network implementation (Halpern 2004). This allows for study of possible spillover effects if differences are seen in control sites after reserve implementation, these effects are a current topic requiring future study (Halpern 2004).

### *Closures*

Further studies should be conducted to measure the impacts of various closure regimes to determine what element of MPA network design works best for a given tropical region and the local community structure. As we increase efforts to scale up marine conservation and design MPA networks so they are ecologically functional and socially sustainable, it will be important to develop further studies that can show the extent of benefits to fishing communities from both permanent and periodic closures, as well as the social factors that can contribute to success of these managed areas. Though increasing numbers of studies indicate that permanently protected areas can improve marine resource availability and ecosystem health as compared to open access areas, more evidence for what impact closed areas have on marine systems is necessary, particularly where large no-take areas may not be enforceable or generally dangerous because of illegal activities of intense pressure from fishing communities.

## APPENDICES

### Appendix 1: Key Definitions

**MPA (Marine Protected Area)** - These units are defined as areas of the ocean which are specifically designated to enhance conservation of marine resources (Lubchenco et al 2003).

**Marine reserve** – a specific type of MPA which is considered more protected than others, often used synonymously with the term “no-take” zone (Lubchenco et al 2003).

**MPA systems** – a group of protected areas that have an element of governance and management as well as biological rationale for design and structure (Wells 2006). System thus has a functional sense it describes geographical and physical relationships as well as consistent institutional and managerial relationships and coordinated planning (Wells 2006).

**MPA networks** –Thought of in a geographical and physical sense, as a group of protected areas that have connectivity between components, and often a physical connection (Wells 2006). Also considered “a group of protected areas designed to meet objectives that single areas cannot achieve on their own, networks of reserves are linked by dispersal of marine organisms and by ocean currents” (Roberts and Hawkins 2000; NRC 2001). The term is also used to describe organized groups of people and institutions working on protected area management/implementation - ‘human’ network (Wells 2006).

**Advection** – directional transport by currents (Gaines et al 2003).

**Source and sink** – source areas are ones in which larvae of local species are dispersed out into surrounding areas, and sink areas are ones in which individuals move in and do not spill out.

**Source Populations** – usually refers to the location of populations that supply offspring outside reserve boundaries.

**Sink Populations** - usually refers to locations where there is a higher influx of individuals than export.

**Viability** – Viability refers to both persistence of target species, and persistence of functional habitat, especially in the face of human impacts.

**Refugia** – Can be defined as areas of the ocean that fish can go to get away from fishing pressure or other human impacts (Allison et al 1998). Can also be used to describe critical areas such as spawning grounds, in which species find refuge.

**Permanence** – In regards to MPAs, permanence refers to the amount of time an area is closed or is subject to certain restrictions, or whether or not the restrictions are permanently in place.

**Larval dispersal** - the intergenerational spread of larvae away from a source to the destination or settlement site (Palumbi 2004).

**Larval transport** - the horizontal movement of larvae between two point often in cross and along-shore directions for coastal environments (Palumbi 2004).

**Connectivity** - the extent to which populations in different parts of a species' range are linked by the exchange of larvae recruits, juveniles, or adults (Palumbi 2003). More simply, connectivity is the exchange of individuals among sites (Gaines et al 2003).

**Bathymetry** - landform features beneath the water surface (usgs.gov).

**Resistance** - refers to the ability of an ecosystem or species to maintain diversity, integrity and ecological processes following/during a disturbance (i.e. corals that resist bleaching or survive after bleaching events) (West and Salm 2003).

**Resilience** –refers to the ability of a community to return to its previous state through growth and reproduction of surviving organisms following a disturbance (West and Salm 2003).

**Replication** –refers to protecting multiple sites of each biogeographic unit or habitat throughout the network.

**Critical Area** – refers to biologically and ecologically significant areas that play a crucial role in ecosystem function and thus require extra consideration when beginning the design/implementation process of a network. (i.e. key spawning grounds).

**Pelagic** – refers to marine organisms that live in the water column of the open ocean.

**Ocean neighborhood** – describes an area centered on a set of parents that is large enough to retain most of the offspring of those parents (Palumbi 2004). It changes size depending on the motility of the parents and larvae.

**Lag time** – refers to the time between implementation and first results or impact can be seen.

**Spillover** - increases in fish inside the reserve supplying the surrounding area with fish.

**Recruits** – refers to the new age group of the population entering the exploited component of the stock for the first time or young fish growing into or otherwise entering that exploitable component (fao.org).

**BACI (before-after, control-impact)** - sampling design that enables unambiguous testing of the effects a particular impact, such as MPA network implementation, has on the surrounding ecological system (Sale et al 2005).

## Appendix 2: MPA Network Biophysical Case Studies

Reference	Location	Description	Usefulness	Siting/design approaches
Airame 2003	Channel Islands National Marine Sanctuary	MPA reserve network, habitat based approach can work to protect a target species when biological data is unavailable	Very useful paper, describing network design steps, and key factors to consider.	Describes overall network design.
Appeldorn et al 2003	Old Providence – Santa Catalina, Colombia network	Looks at distribution, connectivity, and habitat representation.		Discusses designing and development of MPA systems.
Ardron 2002	British Columbia	Examined possible networks based on ecological characteristics using computer modeling to assist in siting process.		Uses MARXAN and other GIS approaches to classification based on physical and biological characteristics.
Beck 2001	Northern Gulf of Mexico	Identifying priority conservation sites that represent the habitats and biology of the nearshore area.	Discusses identification of conservation targets, goals, and site selection as well as collection of data.	Discusses site selection etc.
Beger et al 2003	Kimbe Bay	Using terrestrial site selection methods in coral reefs		
Chiappone 2000	Exuma Cays Land and Sea Park, Bahamas	One of the largest and oldest no-take zones in the Western Atlantic. Little to no historical data available. Calls for network.	Describes benefits of no-take reserves, greater spawning-stock biomass, but little data on export to fished areas. Explains why it will not fulfill goals on its own, and calls for a network.	Not discussed, but discusses siting/location recommendations, network/single reserve approaches, implications for reserve design, and impacts of closure to fishing.
Claudet et al 2006	Northwestern Mediterranean Marine Reserve	Assessment of performance of MPAs in regards to management objectives.	Conservation benefits seen for some commonly fished species, highly variable responses to protection by different fish species.	Offers options of metrics for community level changes after MPA implementation. Uses BACI (before-after, control-impact) study design.
Dahl-Tacconni 2005	Indonesia	Identifying the information needs of managers and other stakeholders at different sites in Indonesia.	Looks at information needed to design an evaluation of management effectiveness of MPAs.	
Day 2002	Great Barrier Reef Marine Park	Describes the Representative Areas Program which was used to design the GBRMP in order to protect biodiversity.		Uses MARXAN and TRADER among others.
Edgar et al 2004	Galapagos Marine Reserve	Discusses biases in the locations of fully protected zones – fishers push for no-take zones in	Results from density surveys within and outside protected areas highlight	Discusses some sociopolitical aspects of site-selection.



		resource poor areas, and tourism operators push for no-take zones in areas with atypical resources.	possible biases in the socio-political processes of reserve selection.	
Elliot et al 2001	Wakatobi National Park, Sulawesi, Indonesia	A coral reef park with marine resource dependent indigenous people. Discusses current research using participatory appraisal methods to understand the relationship between locals and the park and the potential for more local management.	The setup of this park did not include the local needs and desires, and therefore it is not a good model for MPA design.	Discusses participatory management, goal setting, and design.
Friedlander et al 2003	Hawaiian archipelago	Comparisons of depth, wave exposure, and other habitat characteristics, as well as MPA status on the relative abundance of coral reef fish on a scale consistent with mgmnt. (larger)		Species richness, level of biomass, and abundance as indicators; explained when indicators showed what... Might be helpful in selecting (most important) indicators to use
Kamukuru 2004	Mafia Island Marine Park, Tanzania	Researched impacts of an MPA on local needs in a developing nation.	Through the use of visual surveys and examination of the local fish catch, results showed that the area in the MPA had higher fish numbers and larger fish.	
Leslie 2003	A review of 27 marine conservation planning case studies.			
Leslie et al 2003	Florida Keys	Habitat based network site design, created multiple alternative networks for use in decision making process.		Simulated annealing (SPEXAN, MARXAN)
McClanahan 1999	Coral reefs of Northern Tanzania	Discusses differences in fish densities between protected and fished sites, including some trophic interaction changes.	Uses a coral reef ecosystem-fisheries model to explore impacts of fishing and catch selection. Also discusses potential for protecting currently unprotected areas.	
McClanahan 2005	Kenya (coral reef assemblages)	Looks at time to full recovery of coral reef fish after closure of no-take zones.	Results indicate time to full recovery may be longer than originally thought (over 20yrs), and may fluctuate through time due to outside variables.	Promotes no-take zones as an integral part of marine management.
Meyer 2003	Waikiki Marine Life	Looks at a small no-take	Discusses reserve	

	Conservation District, Hawaii, US	reserve, discusses size of reserve, size and abundance of fish within and outside the reserve, and distribution/impact of fishing in the area.	success, and possibility of factors other than fishing impacting reserve success.	
Mumby 1999	Caribbean coral reefs	Systematic classification of marine habitats, as opposed to ad hoc approaches which confound interpretation of maps.	Illustrate this approach using extensive field data from Turks and Caicos, and Belize.	
Murray 2005	Mexico	Discusses importance of considering biological/ecological effect as well as political/social/economic effects of an MPA when evaluating impacts.		Discusses socioeconomic aspects of MPA design.
Russ and Alcala 1996	Philippines (Sumilon, Apo)	Empirical data on rates and patterns of increase in density and biomass of target species after reserve implementation		
Sala et al 2002	Gulf of California – temperate rocky reef	Study uses optimization algorithms, ecological processes information and socioeconomic factors to design a network of reserves.	Uses larval dispersal to determine spacing, discusses uncertainty issues, details on network design.	Reserve network design
Shears 2003	Cape Rodney to Okari point Marine Reserve (Leigh Reserve), New Zealand	Differences in reserve and non-reserve sites such as trophic interactions, and resiliency.	Results indicate lower resiliency of non-reserve sites, as well as the presence of trophic cascades not seen in reserve sites.	
Stewart 2003	South Australian marine reserve system	Uses MARXAN, to explore benefits from current marine reserves and new marine reserve system, which may or may not include the same sites, in order to decide how best to move forward with MPA network design in the region.	Discusses the inefficiency of ad hoc marine reserve systems, and the possible merits of starting the network over using all new sites.	Discusses design of networks in regions which already include a number of marine reserves.

### **Appendix 3: Annotated Bibliography of Key References**

Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* 8:S79-S92.

This article describes principal considerations for evaluating biological effectiveness of reserves, which involve goals, restrictions, and enforcement. They explain the importance of reserves as refugia, and that critical areas should be selected as reserves. They discuss dispersal patterns in detail, as well as the importance of reserve placement (in regards to “up flow” activities etc.). The authors state, that the effectiveness of reserves depends to some degree on what occurs outside the reserve, and therefore they cannot be relied on alone. Gaps in current knowledge are discussed as well.

Airame, S., J. E. Dugan, K. D. Lafferty, H. Leslie, D. A. McArdle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: A case study from the California Channel Islands. *Ecological Applications* 13:S170-S184.

This is an interesting case study on the design of a marine reserve network in the Channel Islands. It discusses objectives, size, representation, resilience, and spacing. They take a habitat based approach as not much information was available in the area in regards to species population dynamics, and use simulated annealing to identify potential scenarios. The authors state that maximal benefit of fully protected marine reserves for fisheries occurs when the reserve is large enough to export sufficient larvae and adults, and small enough to minimize the initial negative financial impact to fisheries. It was recommended that between one and four sites are designated within each ecological region, in order to fulfill representation/replication goals as well as to limit the amount of monitoring/enforcement necessary. For the Channel Islands, it was determined that 30-50% of the representative habitats in each biogeographic region needed to be put in reserves to meet both conservation and fisheries goals. To take into account human threats and natural catastrophes, you can multiply the total area of reserve by an insurance factor that takes into account the frequency of disturbance in the area. For the Channel Islands they used a 1.2-1.8x insurance factor and ended up with a reserve size of 36-54% of the original area. Ideally, the size of a single reserve depends on characteristics of the target species (i.e. potential dispersal distance, population growth rate, and fishing pressure). Individual reserves may be smaller if they are part of a network connected through dispersal of adults and larvae. One way to ensure connectivity is to distribute the network through the planning region and to vary the size and spacing of reserves.

Babcock, R.C, S. Kelly, N.T. Shears, J.W. Walker, and T.J. Willis. 1999. Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series*. 189: 135-134.

Fisheries inside two marine reserves indicate that the most common predatory fish is five and eight times higher in abundance inside the reserve than outside. Lobsters measured within the reserve boundaries had carapace length several mm larger than those outside.

Ballantine, B. 1997. Design Principles for Systems of No-Take Marine Reserves. Presented at a workshop on: The design and monitoring of marine reserves, Fisheries Center, University of British Columbia, Vancouver, February 1997.

According to Ballantine et al, the most effective size and spacing of reserves is inversely proportional to the ecological diversity at the scale of consideration. Where there is high coastal indentation and/or rugged bottom topography, the habitat diversity will also be high. In this case the size and spacing of reserves should be smaller in order to maintain representation and connectivity.

Berkeley, S.A, M.A. Hixon, R.J. Larson, and M.S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29, 23-32.

Evidence from northern cod shows genetic shifts in growth rates and size, where fish reach maturity earlier and at a smaller size, which results when heavy fishing pressure continuously removes older and larger fish from the population. Evolutionary shifts such as these, that may be irreversible, need to be addressed in adapted management for sustainable fishing and recovery of target and critical species. The authors suggest that the minimum management response should be the establishment of reserves where all fishing of target species is prohibited, so that some portion of the fish population is continuously protected. In addition, marine reserves should that some portion of the population. Since larvae and individual recruitment may fluctuate in time and space according to oceanographic features, it's recommended that minimum spawning stock sizes should be protected over the entire geographic range of the stock. The authors suggest that marine reserves strategically located in areas representing different habitats within biogeographic and oceanographic regions is critical for providing benefit to fish stocks. No other method of management can preserve the potential for longevity as well as marine reserves and allow the unique contributions of older fish to accrue to the population. Marine reserves, in combination with other approaches, is essential for replenishing and sustaining groundfish stocks.

Birkeland, C and PK Dayton, 2005. The importance in fishery management of leaving the big ones. Trends in Ecology and Evolution 20: 356-358.

Birkeland and Dayton build on past research and findings that indicate larger and older individuals of some fish species produce larvae that survive better than those from younger fish (due to higher metabolic stores in large fish and thus greater energy transferred to offspring). As a result, it's critical to implement and enforce management measures that aim to protect larger and older fish. Some fishers believe they are favoring population growth of species by leaving the young fish, but this can result in fewer numbers of slow-growing fish and distort the dynamics of the overall community. Some large fish species, such as grouper, learn routes to spawning migration sites from older individuals. Reducing the number of older, larger fish could disrupt reproductive behaviours of the entire population. The authors suggest that we should be protecting older, larger fish individuals rather than regulating total fish harvests. Finally, the preservation of long-lived fish is best achieved by establishing networks of marine reserves. Simple observation is one method of analysing the presence of large fish on the reef.

Botsford, L. W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. Ecological Applications 13:S25-S31.

This is a model based study which discusses dispersal in relation to reserve design, as well as size and placement. It also compares reserves and traditional management techniques to some extent. Larger fractions of coastline on reserves are required for species with longer larval dispersal. Sustaining a species by reserves alone would nominally require 35% or more of a coastline. If not possible then 1) effort would need to be controlled so that shortfall in larval production could be made up in fished areas or 2) larger reserves could be employed with a lower fraction of coastline in reserves. Reserves are more sensitive to uncertainty in dispersal while conventional fisheries management is more sensitive to uncertainty in harvest rate. Recommendation is that a combination of reserves plus conventional management is used.

California Department of Fish and Game, Draft Master Plan Framework (August 2005).

This is based on rocky reefs in California. They recommend an MPA shape that covers an increasing area as distance offshore increase (i.e. wedge shape). This accommodates species with offshore planktonic life stages and species with deeper movement ranges. They recommend that the size of an MPA should be large enough to facilitate enforcement and to limit the deleterious

effects caused by fishing adjacent to the MPA, and that shape be ultimately decided case by case. Based on data from around the world, it is shown that larval movement of 50-100km appears common in marine invertebrates, and 100-200km for fish (based on genetic data). Therefore it is recommended that MPAs be no more than 50-100km apart, in order for groundfish and invertebrate species to benefit from connections. Yet they may need to be more closely spaced where retention is substantial, and dispersal distances are shorter.

Cinner, J., M.J. Marnane, T.R. McClanahan, and G.R. Almany, 2005. Periodic closures as adaptive coral reef management in the Indo-Pacific. *Ecology and Society* 11 (1): 31.

This study explores the social, economic, and ecological context within which communities in Papua New Guinea and Indonesia use adaptive coral reef management. This is a useful reference for work that integrates both biophysical and social sciences in the context of socio-ecological systems. The authors tested the effect of periodic closures on marine resources and found that reef fish biomass and average size were greater in closed areas when compared to continuous open access areas. Both long-lived and short-lived fish species benefit from closed areas, a surprising phenomena that may be linked to socioeconomic characteristics of the two tested communities where fishing pressure typically does not reduce the larger, slow-growing fish population. These socioeconomic conditions, such as exclusive tenure over marine resources, traditional ecological knowledge that allows rapid assessment of ecological conditions, relatively small human populations, and low dependence on fisheries, may contribute to equal fishing pressure in managed areas that are recently opened to fishing and those that are always open to fishing. The local community also has social customs, such as fishing in groups and closing areas that are clearly visible from the community, that increase compliance with the managed areas. While periodic closures will unlikely conserve the same amount of resources and biological processes as large marine reserves and thus cannot replace these strategies, they are a potentially useful tool for managing marine resources, particularly when large marine reserves fail or are unrealistic. Overall, the use of periodic closures as an effective adaptive management practice would be best applied in communities that have similar traits as those tested in this study.

Friedlander, A., Nowlis, J. Sladek, Sanchez, J.A.; Appeldoorn, R., Usseglio, P.; McCormick, C., Bejarano, S., Mitchell-Chui, A.. 2003. Designing effective marine protected areas in seaflower biosphere reserve, Colombia, based on biological and sociological information. *Conservation Biology*. 17(6): 1769-1784.

This is a case study designing MPAs in the Seaflower Biosphere Reserve, Colombia. For the Seaflower reserve, a minimum reserve size was set at 10km<sup>2</sup> to contain viable populations of a wide range of species. The authors suggest that enforcement and compliance may be aided if reserve borders are straight lines running north and south, east and west or utilizing other obvious navigational reference points, in order to make borders clear to everyone. They also state that size and shape should be in large part decided by stakeholder input.

Gaines, S. D., B. Gaylord, and J. L. Largier. 2003. Avoiding current oversights in marine reserve design. *Ecological Applications* 13:S32-S46

There are gaps in assessing effectiveness in terms of biodiversity conservation. Most models do not consider larval dispersal explicitly, because the data is not available. They discuss previous model errors and describe a model for benthic populations with dispersing larvae. They also examine the effects of reserve size and configurations in a variety of flow conditions on connectivity. Flow should not be considered only as non-directional diffusion, but must be looked at in terms of directional transport by currents as well. Multiple reserves are more effective in areas with strong currents than single reserves are, and when strong currents are present reserve networks also outperform traditional fishery management methods alone. They

discuss the importance of integrating reserves with other management techniques in order to ensure effectiveness.

Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R. et al. (2003). Population models for marine reserve design: a retrospective and prospective synthesis. *Ecol. Appl.*, 13, S47–S64.

The authors review models of marine reserves in order to synthesize what is known and what is missing. They state that most current models focus on fisheries goals and that very few consider larval dispersal. They call for more review of spatial configurations of reserves in relation to species dispersal distances. Other issues that were found to be overlooked in the modeling literature include: certain forms of density dependence, multi-species interactions, fisher behavior, and impacts of concentrated fishing on habitat.

Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13:S117-S137.

This study reviews empirical and theoretical work to assess the impacts of marine reserves on a variety of biological measures. He focuses on density, biomass, size of organisms, and diversity in relation to reserve size. It is important to note that Halpern lists a variety of inherent problems and caveats to consider while reviewing this study. His results show that the relative impact of reserves, such as proportional differences in density or biomass, may be independent of reserve size, suggesting that the effects of marine reserves increase directly rather than proportionally with the size of a reserve. However, this usually translates into greater absolute differences for larger reserves, and so larger reserves may be necessary to meet reserve objectives. Reserves regardless of their size (with some exceptions) seem to lead to increases in density, biomass, individual size and diversity in all functional groups. While some small reserves do show positive effects, relying solely on small reserves to provide solutions to our conservation and fisheries issues is not recommended.

Halpern, B. S., H. M. Regan, H. P. Possingham, and M. A. McCarthy. 2006. Accounting for uncertainty in marine reserve design. *Ecology Letters* 9:2-11.

The authors review several modeling frameworks that acknowledge and incorporate uncertainty; they then use these methods to evaluate reserve spacing in network design. They recommend a rule of approximately 20-200 km apart for reserves which is similar to other findings. They then discuss the advantages of using uncertainty modeling techniques, including evaluating risks, quantifying costs and benefits of reducing uncertainty, and communicating challenges to stakeholders.

Hyrenbach, K. D., K. A. Forney and P. K. Dayton 2000. Marine protected areas and ocean basin management. *Aquatic Conservation-Marine and Freshwater Ecosystems* 10(6): 437-458.

Findings from this paper indicate that all reserve designs must be guided by an understanding of natural history and habitat variability. Pelagic marine systems, though highly dynamic, contain some habitats that are used predictably by far-ranging species for breeding and foraging. MPAs can be designed to encompass these areas. It's important to understand the physical aspects, including static, persistent, and ephemeral conditions, of these deep sea environments before implementing pelagic areas. The design will ultimately require dynamic boundaries and large buffer components similar to biosphere reserves if pelagic reserves are to effectively protect highly migratory species, such as marine mammals, turtles, and large fish. Dynamic boundaries would be defined by large-scale oceanographic features. Also critical to these MPAs would be enforcement, research, and monitoring programs. Innovative tools, such as judicious use and selection of MPAs, are an important aspect of designing and managing marine areas across the ocean basin.

Kaplan, D.M. and L.W. Botsford. 2005. Effects of Variability in Spacing of Coastal Marine Reserves on Fisheries Yield and Sustainability. Canadian Journal of Fisheries and Aquatic Science, 62: 905-912.

This study looks at varying the space between reserves and its effects on fisheries goals, specifically a coastal species with a planktonic larval phase and sedentary adults in a temperate system. It has been suggested that non-evenly spaced reserves could better protect fish populations. They suggest that reserves work best in previously overfished areas. Results of this study suggest that varying the spacing of reserves along a coastline could have a benefit for those species that are most threatened by overfishing. Results indicate that if the purpose of placing only a small fraction of the coast in reserves were to demonstrate the benefits of marine reserves, then that fraction should be concentrated in an area on the order of the dispersal distance of the species to be protected rather than being evenly distributed along the coast. However spacing should be reviewed with resource users as well and the study did not review all possible influences.

King, M.C. and K.F. Beazley, 2005. Selecting focal species for marine protected area network planning in the Scotia-Fundy region of Atlantic Canada. Aquatic Conservation: Marine and Freshwater Ecosystems 15: 367-385.

The authors argue that placing consideration on focal species, because they are often vulnerable to threats and serve as indicator species, can be a very important complement to other approaches for designing MPA networks, such as consideration of habitat representation. This approach would include defining critical habitat requirements for viable populations of focal species. The Scotia-Fundy region of Canada is considering the North Atlantic right whale as a focal species where seasonally-important feeding, nursery, and socializing grounds would be protected within an MPA network. In turn, these areas would protect other species that have smaller ranges and area requirements.

Mora, C., S. Andrefouet, M. J. Costello, C. Kranenburg, A. Rollo, J. Veron, K. J. Gaston, and R. A. Myers. 2006. Coral reefs and the global network of marine protected areas. Science 312:1750-1751.

This report provides a global assessment of the extent and effectiveness of coral reef MPAs. Mora et al state that of the world's roughly 527,072km<sup>2</sup> of coral reefs, 5.3% lie inside extractive MPAs, 12% inside multipurpose MPAs and 1.4% inside no take MPAs. Unfortunately most MPAs do not have strong continuous monitoring and enforcement, which means that numbers and coverage can be misleading indicators of effective conservation.

Scales of dispersal and species movement are critical to designing effective MPAs. Data on species home ranges is improving, particularly for coral reef fishes, and it is showing that most species ranges are small but some can cover large areas. These large range species are usually most sought after by fisher's and are seen as very important to the functioning and resilience of coral reef systems. Since most MPAs are in the 1-2 km<sup>2</sup> range, many are not protecting the species whose ranges are broader than the boundaries established by the MPA.

Propagule dispersal in coral reef organisms may be on scales on the order of a few tens of kilometers (Palumbi 2004, Shanks et al 2003 and Mora and Sale 2002). Thus it has been recommended that MPAs should be 10 to 20km in diameter and in distance apart from each other to ensure exchange of propagules (Shanks et al 2003). Currently most reserves are too broadly spaced to be considered a functional network. Roughly 5% of the coral reefs of the world (distributed over a sparser network) need protection to meet this goal of functional networks.

National Marine Protected Area Center Report. 2004. An inventory of GIS-based decision support tools. NOAA Coastal Services Center.

This report looked at GIS-based MPA related, publicly available, and participatory or interactive decision-support tools. They list nine tools and summarize what it does, what data you need to run it, who developed it, how it is relevant to MPAs, and any geographical specificities. They then give a detailed explanation of two more tools and case studies of their use in actual MPA design and monitoring activities (MARXAN – Great Barrier Reef Marine Park Authority, and OceanMap – incorporating local fisher’s knowledge in California).

Nature Serve Report. 2004. Tools for coastal and marine ecosystem-based management. For the David and Lucille Packard Foundation.

This report is an evaluative survey of available software tools that have potential uses in coastal and marine ecosystem based management (CMEBM). The tools are evaluated based on a stated framework of criteria and then categorized to describe potential contributions. Most of the tools were actually developed for terrestrial use. Yet the paper includes detailed information on the tools that fared the best with potential for CMEBM use. They also note gaps in current software tools, and tested their results with an expert workshop.

Palumbi, S. R. 2004. Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. Annual Review of Environment and Resources 29:31-68.

The author discusses movement of individuals and defines their spatial neighborhoods, relating to the area centered on a set of parents that is large enough to retain most of the offspring of those parents. He discusses the necessary size of reserves in relation to species neighborhoods, and suggests that reserve size be based on adult neighborhood sizes of highly fished species. He then suggests that spacing of reserves be based on larval neighborhoods or dispersal distances. However, he notes that networks with multiple species of concern must take into account the different life histories of each species, as well as the local human communities’ use of marine resources.

Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO). 2002. The Science of Marine Reserves. <http://www.piscoweb.org>. 22 pages.

The authors state that small reserves can have benefits, but when the reserve is small the overall benefits are also small since few species are protected. They also discuss that while a large reserve may benefit conservation it may lead to fisheries crowded in small places and be less effective and enhancing fish take. They claim that reserve areas of moderate size can protect and restore important habitats, plants, and animals while leaving substantial areas of the ocean open to fishing. They also promote developing a network of reserves of several different sizes, strategically located in critical habitats, to benefit both conservation and fishery objectives.

Roberts, C., B. Halpern, S. R. Palumbi, and R. R. Warner. 2001. Designing Marine Reserve Networks: Why small, isolated protected areas are not enough. Pages 10-17. Conservation Biology in Practice.

This paper discusses the effectiveness of marine reserves and the need for connected reserve networks, as well as network design. They recommend that a variety of reserve sizes be used within a network (a few kilometers to tens of kilometers across), separated by varying distances (a few kilometers to tens of kilometers), representation and replication of every habitat type (roughly proportional to actual coverage in the region, 20-50% of total habitat), larger offshore reserves than nearshore, and be physically/ecologically connected (taking into account dispersal distances). They also discuss edge effects in regards to the shape of reserves, and the potential to create effective reserve networks from the few reserves already in place.



Roberts, C. M., G. Branch, R. H. Bustamante, J. C. Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, M. Ruckelshaus, and R. R. Warner. 2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecological Applications* 13:S215-S228.

This paper focuses on permanently closed reserves, and the design of numerous alternative biophysically connected networks of these reserves. There is a discussion of important criteria to consider such as: representation, replication, connectivity, population demographics, size, and catastrophes as well as others. They discuss ensuring the provision of ecosystem services, as well as meeting both fishery and conservation goals. The paper defines steps to creating a network, focusing first on ecological elements with stakeholder involvement then secondly on socioeconomic concerns. Roberts et al state that reserves must be large enough to be viable and to fulfill network objectives. The probability of fish leaving a given reserve will decrease as the area of the reserve grows. They state that defining ‘too large’ an area is likely to be based on practical considerations, cost, or user conflict not on biological considerations. Smaller reserves spread over a management area will thus be better than fewer larger reserves, but only up to a point where reserves are still large enough to provide effective protection of species. The safest option would be to have a range of reserve sizes in the network, which is a natural outcome of selecting and combining areas to cover all habitats representatively.

In discussing connectivity they note that larger reserves will maximize the probability of self-recruitment within reserves for short distance dispersers, while for long-distance dispersers, smaller reserves spaced at broader intervals may have greater connectivity. There is no absolute figure as to how close reserves should be. In spacing reserves, locations that lie midway between existing reserves might be favored because they reduce inter-reserve distance and provide a stepping stone for recruitment. In places where currents are strongly directional, reserves sited in upstream locations will be more likely to support recruits to the rest of a management area than to help meet fishery goals. Where currents are complex or reversing, a more even spread of reserve locations may be best. There are too many variables for precise limits to be set for what constitutes ‘too close’ or ‘too far’ and it will be safest to have a range of distances among reserves.

Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J. C., Dayton, P. K. 2002. A General Model for Designing Networks of Marine Reserves. *Science* 298, 1991-1993.

This study used optimization algorithms and multiple levels of information on biodiversity, ecological processes (spawning, recruitment and larval connectivity) and socioeconomic factors in the Gulf of California, in order to make recommendations on network design. It is a temperate rocky-reef example. They state that distances between reserves should be based on dispersal, although not much is known on dispersal distances. Based on this they determined that the distance between adjacent reserves in the Gulf of California should not exceed 100km, which has been shown to be the mean dispersal distance for marine fish. The network created includes individual reserves that are sufficiently large (50km) to ensure more than 90% local retention of algal propagules and more than 45% local retention of fish and invertebrate larvae. They do not explicitly address connectivity for macroalgae and some invertebrates, which can disperse at distances shorter than 5km or certainly at distances shorter than 100km. They chose 40km as the average distance between reserves, ensuring connectivity for most fishes and invertebrates. They also discuss the minimum fraction of the coastline to protect, and in this case the smallest network protects 40% of the habitat.

Salm, R.V. Clark, K. and Siirila, E. 2000. Marine and Coastal Protected Areas: a guide for planners and managers. IUCN: Washington DC (USA), 371 pages.

This study states that species should be evaluated and not just enumerated when monitoring or analyzing the system. They also discuss that many coastal and marine habitats

normally behave as clusters of areas. They are not continuous, but comprise numerous spatially discrete components that may be divided by headlands, creeks, and river mouths (like mangroves), or surge channels, deep passes, bays and sandy patches (like coral reefs). These components function as small “islands of habitats” and could provide survival opportunities to different members of a set of competitive species in the context of a larger MPA.

Secretariat of the Convention on Biological Diversity (2004). Technical advice on the establishment and management of a national system of marine and coastal protected areas, SCBD, 40 pages (CBD Technical Series no. 13).

This publication is the report from the *Ad Hoc* Technical Expert Group on Marine and Coastal Protected Areas which determined that marine and coastal protected areas (MCPAs) are an essential element in the conservation and sustainable use of biodiversity. If they are well-managed, they can assist recovery of fisheries and diverse habitats while promoting alternative livelihoods, such as tourism, and increased catch from spill-over effects outside of managed areas. The World Summit on Sustainable Development’s Plan of Implementation agrees to establish a global network of MPAs by 2012, an ambitious goal given that less than .5 percent of the marine environment is currently protected. Therefore, increasing the number, coverage, representativeness and effectiveness MCPAs is essential for achieving sustainable use of marine resources, and for meeting the target of significantly reducing the current rate of biodiversity loss by 2010. The focus of this document is developing MPAs at the national level, but some insights can be extrapolated for larger, regional marine areas. The objective of this document is to provide technical advice on the establishment and management of MCPAs and networks of MCPAs. Summary of current scientific understanding and best practice approaches. This document has relevance to other areas of this literature review, including the design principles of MPAs and MPA networks that relate to representation and key ecological criteria.

Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13:S159-S169.

Shanks et al compiled available information on the dispersal distance of the propagules of benthic marine organisms and used this information in the development of criteria for the design of marine reserves. Their data comes from a combination of lab and experimental sources, using temperate examples. The study suggests that propagules are not distributed passively by currents. The authors then recommend that reserves be designed large enough to contain the short-distance dispersing propagules and be spaced far enough apart that long-distance propagules be released from one reserve can settle in adjacent reserves. They state that a reserve 4-6 km in diameter should be large enough to contain the larvae of short-distance dispersers and reserves spaced 10-20km apart should be close enough to capture propagules released from adjacent reserves. They also recommend that reserves be set-up along the coast so that larvae from one reserve can disperse and settle into adjacent reserves. These recommendations are based solely on an analysis of the dispersal distance of coastal benthic propagules.

Steneck, R.S. 2006. Staying Connected in a Turbulent World. Science 311: 480-481.

The author discusses that dispersal kernels are often greater where eggs are hatched and decline with increasing distance from this location. They find that larval subsidies are very limited in some regions which suggests that managers must directly manage their reefs on a local scale and not depend on substantial larval subsidies from distant upstream sources. They also state that short lived species may require more regular recruitment than longer lived species.

Wells, S. 2006. Establishing national and regional systems of MPAs – a review of progress with lessons learned. Second Draft. UNEP World Conservation Monitoring Centre, UNEP Regional Seas Programme, ICRAN, IUCN/WCPA – Marine.

This report helps to identify indicators and mechanisms for measuring progress in developing national and regional systems of MPAs. It provides a review of certain UNEP regional Seas MPA case studies and discusses key criteria for ensuring effective MPA systems are being implemented. It provides an overview of principles, concepts, and issues to consider in MPA system development. It looks at ecological criteria, socio-economic factors, and governance to some degree.

West, J. M., and R. V. Salm. 2003. Resistance and Resilience to Coral Bleaching: Implications for Coral Reef Conservation and Management. Conservation Biology 17:956-967.

This study discusses strategies to deal with climate change impacts on coral reefs. They suggest that areas which are naturally more resistant to bleaching (conditions result in little to no temperature related mortality) and areas that are naturally more resilient (conditions result in extensive recovery of reef communities after bleaching mortality events), should be target areas for inclusion in the design of MPA networks. Factors to look for reduce temperature stress, enhance water movement, decrease light stress, increase physiological tolerance, or enhance recovery potential.

Williams, I.D, W.J. Walsh, A. Miyasaka, and A.M. Friedlander, 2006. Effects of rotational closure on coral reef fishes in Waikiki-Diamond Head Fishery Management Area, Oahu, Hawaii. Marine Ecological Progress Series 310: 139-149.

This study looks at the effects of rotational closures in Hawaii by comparing data collected from a long-term no-take marine reserve with data from managed areas that have been opened and closed in one- and two-year intervals. While no-take marine reserves can be effective biodiversity conservation and fisheries management tools, the authors found little indication in the literature or elsewhere that would suggest the benefit of rotational management to coral reef fish stocks. The results of rotational management at one site, Waikiki-Diamond Head Fishery Management Area (FMA) on Oahu, indicate that the increase in fish biomass gained during the closed periods could not compensate for declines that occurred during open periods. Overall, from 1972-2002, this resulted in a long-term reduction of reef fish biomass by two-thirds. In addition, large fish were recorded less and less during this period. In comparison, part of this area was converted to a permanently closed reserve in 1988, the Waikiki Marine Life Conservation District (MLCD). Data collected from this site indicates that fish biomass has doubled as compared to the rotational closure. Maximum fish size has remained stable. Overall, rotational management, as implemented at the Waikiki FMA, has not been an effective means of conserving fish stocks or revitalizing public fishing grounds.

#### **Appendix 4: Key Management Recommendations**

1. General Network Recommendations:

- a. A habitat based design approach is often used over a species based approach because there is more data available (Airame 2003). However both are considered to some degree in the report.
  - b. In order to protect large spawning fish populations throughout their geographic range (due to uncertainty of dispersal) networks of reserves are crucial (Berkeley et al 2004).
  - c. Networks are more effective at meeting both fishery and biodiversity conservation goals than single MPAs alone.
  - d. Clear goal setting with stakeholder involvement must be completed at the beginning of the design process.
2. Incorporate replicated representatives of every biogeographic area and the habitat types within them (Roberts 2001 and others).
    - a. Networks of fully protected reserves should cover 20% or more of all biogeographic regions and habitats (Roberts and Hawkins 2000; National Research Council [NRC] 2000; Roberts et al 2003a).
    - b. It is important to include reserves in both transition zones (between biogeographic areas) and core zones within each biogeographic unit (Roberts et al 2003a).
    - c. Sites should be selected such that they will not be affected by catastrophes in the same way (Airame 2003).
    - d. Areas with frequent catastrophic occurrences should not be selected as they rely on recruitment from outside areas (Allison 2003).
    - e. Areas of high natural resistance/resilience should be incorporated where possible (West & Salm 2003).
    - f. Protecting ecosystem processes is often just as important as protecting all habitats (Roberts 2003a).
    - g. One to four reserves per biogeographic region has been recommended as a good tradeoff between replication (for resilience) and efficient monitoring and enforcement (Airame 2003). (although other numbers have been suggested, the idea is that their must be a balance between beneficial replication and practicality)
  3. Biophysical connectivity of MPAs within a network is critical in order to ensure the network is functional (Roberts et al. 2003).
    - a. The spatial scale of MPAs should match the spatial scale of larval dispersal, to ensure that populations are connected, and thus more resilient (Palumbi 2004).
    - b. MPAs in a network must be able to receive larvae from “upflow” MPAs and supply it to “downflow” MPAs, as well as supply individuals to fisheries outside reserve boundaries (Halpern et al 2006).
    - c. Some habitats are functionally linked due to species life cycle patterns, such as coral reefs, seagrass, and mangroves, and thus these connections should be incorporated into network design (Ogden and Gladfelter 1983; Roberts 1996; Nagelkerken et al. 2000).
    - d. Networks should be designed to fit many possible connections not just a few probable ones (Roberts 2001).
    - e. MPAs should be located in a wide variety of locations in relation to the prevailing currents (Roberts 2001).
    - f. Connectivity is more local than previously thought, and regionally it is more variable (Cowen et al 2006).
    - g. Short-lived species may require more regular recruitment from connected sites (Steneck 2006).

- h. Although tough to accomplish one approach to network design is to establish the size of reserves based on adult neighborhood sizes of highly fished species, and space the reserves based on larval neighborhood scales (Palumbi 2004).
  - i. Highly migratory species do not fit the general rules of dispersal distances, spacing, or connectivity (Palumbi 2004).
  - j. Ocean currents do not always sufficiently represent dispersal distances or directions (Barber et al 2000).
4. Fully protected permanent marine areas are considered critical for a functional network of MPAs (CBD 2004).
- a. Long-term management and monitoring plans are seen as increasingly important (Babcock et al 1999).
  - b. Whether the goal of a site or network is fisheries management or biodiversity conservation, there is agreement among scientists that having long-term, permanent closures, provides the greatest level of protection and benefits to the species populations (Willis 2003 and others).
  - c. Important to maintain larger, older, longer-living fish, for recruitment and ecosystem impact (Birkeland & Dayton 2005).
  - d. Rotational or seasonal full closures are more accepted, have less immediate social impacts, and are easier to monitor/enforce (Cinner et al 2005).
    - i. Rotational closures have shown some success, and can work to some degree in areas where permanent closures are not acceptable, however they will not be as effective (Cinner et al 2005).
    - ii. They are most effective in communities with the following traits: exclusive tenure over marine resources, traditional ecological knowledge that allows rapid assessment of ecological conditions, relatively small human populations, and low dependence on fisheries (Cinner et al 2005).
  - e. In order to develop dynamic MPAs and MPA networks for highly migratory species, “bottlenecks,” or areas with certain oceanographic features related to key behaviours (feeding, breeding, and socializing) should be protected both spatially and temporally (depending on season of focal species use) (Hyrenbach et al 2000).
5. The optimal size of MPAs within a network has been discussed in the literature more than the shape and spacing; however all are critical in meeting various network goals (Gaines et al 2003).
- a. Varying reserve sizes is recommended in order to meet both fishery and conservation goals (Palumbi 2003).
  - b. To some extent, larger reserves may be better for biodiversity conservation goals, but smaller reserves may be better for fishery goals (Allison et al 1998).
  - c. There are no upper limits on MPA size due to biological constraints, but socioeconomic and practical guidelines often limit maximum MPA size (Roberts 2003a).
  - d. Intermediate sizes of MPAs, and a variation of sizes within a network is considered ideal (Roberts 2001).
  - e. If design is focused on target species, optimal sizing may differ depending on the particular species characteristics (Carr et al 2003).
  - f. To ensure self-seeding of a reserve it must be as large as the mean larval dispersal distance of the target species (at least 4-6 km in diameter) (Shanks 2003, Botsford 2001).

- g. A good starting point may be reserves 10 to 20km in size and spaced 15 km apart; then stakeholder and target species information should be incorporated to adjust the size and spacing assumptions (Mora et al 2006).
  - h. MPAs that are larger offshore and smaller nearshore allow for less negative impacts to the local community, and can provide the same conservation and fishery benefits in certain areas (Roberts 2001).
  - i. Varying distances between MPAs within a network has been suggested to promote effective connectivity for a variety of species (Roberts 2001 CB, and others).
  - j. Not all refugia provides optimum conditions for survival during all settlement seasons, therefore spatial dispersion of MPAs may be beneficial (Larson 1999).
  - k. The position of a site along the shoreline may determine the direction of dispersal, placing at least one site “upflow,” one “downflow,” and one centered is one way to plan for this uncertainty (Gaines et al 2003).
  - l. Dispersal distances for marine organisms may range from 10 to 200 km, and these should be considered when developing guidelines for spacing (Palumbi 2004).
  - m. Palumbi (2003) suggests that sites in a network are at the minimum 10 to 20 km apart, and Shanks (2003) suggests 20 km as a minimum spacing distance, while Sala et al (2002) suggests a maximum spacing distance of 100 km.
  - n. When designing shape for biodiversity conservation it is important to consider minimizing edge habitat while maximizing interior protected area (Carr et al 2003).
  - o. A shape that allows for clear marking of boundaries for both resource users and enforcement personnel awareness may increase effectiveness (California Dept. of Fish and Game 2005).
6. MPA network design should include consideration of any ‘critical areas’ in the region. This includes: source and sink populations, important refuges for target species, and ensuring viability of selected sites and their populations.
- a. MPAs should be located at source populations, and sink populations should be avoided when designing networks (Pulliam & Danielson 1991, Roberts 1998, Stewart et al 2003).
  - b. Incorporating spawning aggregation sites in MPA networks may be beneficial as well (Sadovy 2006).
  - c. Marine reserves have the potential to act as fish refuges from many anthropogenic impacts (Airame 2003).
  - d. Understanding the different needs of a target species in different life stages, as well as the risk of mortality in each stage, can help to determine which areas best act as refuges for these species and therefore should be selected as reserve sites (Allison et al 1998).
  - e. Critical areas to consider include: feeding grounds, spawning grounds, nursery grounds, areas of high species diversity, socializing areas, etc. (Allison et al 1998).
  - f. Vulnerable marine habitats often provide critical ecosystem processes and should be included in MPA network design (Airame 2003).
  - g. Long term reserve network viability relies in large part on degree of connectivity (Crowder et al 2000, Stewart et al 2003).
  - h. Networks should be able to sustain populations and ecosystem processes through natural cycles of variation (Wells 2006).
  - i. The network should be independent of outside processes, and the overall networks should be considered permanent, even if all sites are not (Wells 2006).

## **Appendix 5: Biophysical Questionnaire**

### **Biophysical Datasheet, Marine Learning Partnership, May/June 2006**

Name of MPA \_\_\_\_\_

Name of MPA Network (if applicable) \_\_\_\_\_

Country \_\_\_\_\_

#### **Design and Management:**

When was the MPA established?

Is it part of a planned MPA network (one that is designed to function as a collective entity)?

Are you planning new MPAs in the MPA network?

What was the reason for the MPA/network establishment? Mark all that apply.

\_\_\_ Conservation

\_\_\_ Fisheries Management

\_\_\_ Other (please specify)

What are the regulations (no-take, gear restrictions, etc)?

Are there other costs and constraints (socio-economic, cultural, etc) that influenced MPA establishment in the past or that would affect future MPA design and creation?

What monitoring has been done of which species, and where (this can be both within and outside of the MPAs and the MPA network)?

Are historical records or oral histories of traditional good fishing grounds available?

#### **Critical Areas**

What are the target species for conservation?

What are the target species for fisheries?

Where are the key spawning, feeding, and nursery grounds, if known?

#### **Representation**

What are the habitat types within the area of concern (this means the jurisdiction and can be country, ecoregion, etc)?

Are they mapped?

Are any major habitat types not represented in any MPA?

#### **Resilience**

How many instances of each habitat type are present in your MPA network?

Are there replicate MPAs (that serve similar function) within the MPA network or in the area of concern?

**Connectivity**

What do you know about target species' behavior such as motility and dispersal distances (larvae, juveniles, or adults)?

What data regarding oceanography, currents, and hydrodynamics are available?

What tools/methods have you used to study the degree of connection between MPAs in your network?

**Size, Shape, and Spacing (see Excel spreadsheet for your country)**

What is the total area of the area of concern?

What is the size and location of each MPA in the Network?

Are spatial data available in GIS or other electronic form? If not, may we have use of paper maps?

**Appendix 6: Full References**



- Agardy, T. 2000. Effects of fisheries on marine ecosystems: a conservationist's perspective. *Ices Journal of Marine Science* 57:761-765.
- Airame, S., J. E. Dugan, K. D. Lafferty, H. Leslie, D. A. McArdle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: A case study from the California Channel Islands. *Ecological Applications* 13:S170-S184.
- Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* 8:S79-S92.
- Allison, G. W., S. D. Gaines, J. Lubchenco, and H. P. Possingham. 2003. Ensuring persistence of marine reserves: catastrophes require adopting an insurance factor. *Ecological Applications* 13:S8-S24.
- Appeldoorn, R.S., A. Friedlander, J. Sladek Nowlis, P. Usseglio, A. Mitchell-Chui. 2003. Habitat connectivity in reef fish communities and marine reserve design in Old Providence- Santa Catalina, Colombia. *Gulf and Caribbean Research* 14(2):1-15.
- Appeldoorn, R. S., C. W. Recksiek, R. L. Hill, F. E. Pagan, and G. D. Dennis. 1997. Marine protected areas and reef fish movements: the role of habitat in controlling ontogenetic migration. Pages 1917–1922 in H. Lessios and I. G. Macintyre, editors. *Proceedings of the Eighth International Coral Reef Symposium. Volume 2.* Smithsonian Tropical Research Institute, Balboa, Republic of Panama.
- Babcock, R.C, S. Kelly, N.T. Shears, J.W. Walker, and T.J. Willis. 1999. Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series*. 189: 135-134.
- Ballantine, B. 1997. Design Principles for Systems of No-Take Marine Reserves. Presented at a workshop on: The design and monitoring of marine reserves, Fisheries Center, University of British Columbia, Vancouver, February 1997.
- Barber, P. H., S. R. Palumbi, M. V. Erdmann, and M. K. Moosa. 2000. A marine Wallace's line? *Nature* V406:692-693.
- Barber, P. H., S. R. Palumbi, M. V. Erdmann, and M. K. Moosa. 2002. Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences. *Molecular Ecology [Mol. Ecol.]*. 11:659-674.
- Beck, M. W., and M. Odaya. 2001. Ecoregional planning in marine environments: identifying priority sites for conservation in the northern Gulf of Mexico. *Aquatic Conservation: Marine and Freshwater Ecosystems* 11:235-242.
- Beger, M., G. P. Jones, and P. L. Munday. 2003. Conservation of coral reef biodiversity: a comparison of reserve selection procedures for corals and fishes. *Biological Conservation* 111:53-62.
- Berkeley, S.A, M.A. Hixon, R.J. Larson, and M.S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29, 23-32.
- Birkeland, C. 2004. Ratcheting Down the Coral Reefs. *Bioscience* 54:1021-1027
- Birkeland, C and PK Dayton, 2005. The importance in fishery management of leaving the big ones. *Trends in Ecology and Evolution* 20: 356-358.
- Black, K. P. 1993. The relative importance of local retention and inter-reef dispersal of neutrally buoyant material on coral reefs. *Coral Reefs* 12:43–53.
- Bohonak AJ. 1999. Dispersal, gene flow, and population structure. *Q. Rev. Biol.* 74: 21–45.
- Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* 4:144-150.
- Botsford, L. W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. *Ecological Applications* 13:S25-S31.
- Bruggemann, J.H, A.M. van Kessel, J.M. van Rooij, and A.M. Breeman. 1996. Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*:

- implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series* 134: 59-71.
- California Department of Fish and Game, Draft Master Plan Framework (August 2005).
- Carr, M. H., J. E. Neigel, J. A. Estes, S. Andelman, R. R. Warner, and J. L. Largier. 2003. Comparing marine and terrestrial ecosystems: Implications for the design of coastal marine reserves. *Ecological Applications* 13:S90-S107.
- CBD 13 - Secretariat of the Convention on Biological Diversity (2004). Technical advice on the establishment and management of a national system of marine and coastal protected areas, SCBD, 40 pages (CBD Technical Series no. 13).
- Chiappone, M., and K. M. S. Sealey. 2000. Marine reserve design criteria and measures of success: Lessons learned from the Exuma Cays Land and Sea Park, Bahamas. *Bulletin of Marine Science* 66:691-705.
- Christie, P. 2004. MPAs as biological successes and social failures in Southeast Asia. Pages 155-164 in J. B. Shipley, editor. *Aquatic protected areas as fisheries management tools: design, use, and evaluation of these fully protected areas*. American Fisheries Society, Bethesda, Maryland, USA.
- Cinner, J., M.J. Marnane, T.R. McClanahan, and G.R. Almany, 2005. Periodic closures as adaptive coral reef management in the Indo-Pacific. *Ecology and Society* 11 (1): 31.
- Claudet, J., D. Pelletier, J. Y. Jouvenel, F. Bachet, and R. Galzin. 2006. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. *Biological Conservation* 130:349-369.
- Cowen, R.K., Paris, C.B., Olson, D.B. & Fortuna, J.L. 2003. The role of long distance dispersal versus local retention in replenishing marine populations. *Gulf and Caribbean Research Suppl.*, 14, 129–137.
- Cowen, R.W., C.B. Paris, and A. Srinivasan. 2006. Scaling of Connectivity in Marine Populations. *Science* 311: 522-527.
- Crowder, L.B., S.J. Lyman, W.F. Figuera, et al. 2000. Source sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* 66 (3): 799-820.
- Dahl-Tacconi, N. 2005. Investigating information requirements for evaluating effectiveness of marine protected areas - Indonesian case studies. *Coastal Management* 33:225-246.
- Day, J., L. Fernandes, A. Lewis, G. De'ath, S. Slegers, B. Barnett, B. Kerrigan, D. Breen, J. Innes, J. Oliver, T. Ward, D. Lowe. 2002. The representative areas program for protecting biodiversity in the Great Barrier Reef World Heritage Area. Proceedings of the Ninth International coral Reef Symposium, Bali, Indonesia, 2000.
- DeMartini, E. E. 1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin* 91:414–427.
- De Vantier, L. M., G. De'ath, T. J. Done, and E. Turak. 1998. Ecological assessment of a complex natural system: A case study from the Great Barrier Reef. *Ecological Applications* 8:480-496.
- Edgar, G. J., R. H. Bustamante, J. M. Farina, M. Calvopina, C. Martinez, and M. V. Toral-Granda. 2004. Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. *Environmental Conservation* 31:212-218.
- Elliott, G., B. Wiltshire, I. A. Manan, and S. Wismer. 2001. Community participation in marine protected area management: Wakatobi National Park, Sulawesi, Indonesia. *Coastal Management* 29:295-316.
- Friedlander, A.M. and E. E. De Martini, 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Marine Ecology Progress Series* 230: 253-264.

- Friedlander, A., Nowlis, J. Sladek, Sanchez, J.A.; Appeldoorn, R., Usseglio, P.; McCormick, C. , Bejarano, S., Mitchell-Chui, A.. 2003. Designing effective marine protected areas in seaflower biosphere reserve, Colombia, based on biological and sociological information. *Conservation Biology*. 17(6): 1769-1784.
- Friedlander, A., E.K. Brown, P.L. Jokiel, W.R. Smith, K. S. Rodgers. 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22: 291-305.
- Gaines, S. D., B. Gaylord, and J. L. Largier. 2003. Avoiding current oversights in marine reserve design. *Ecological Applications* 13:S32-S46
- Gell, F. R., and C. M. Roberts. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution* 18:448-455.
- Gerber, L. R., L. W. Botsford, A. Hastings, H. P. Possingham, S. D. Gaines, S. R. Palumbi, and S. Andelman. 2003. Population models for marine reserve design: A retrospective and prospective synthesis. *Ecological Applications* 13:S47-S64.
- Gerber, L. R., and S. S. Heppell. 2004. The use of demographic sensitivity analysis in marine species conservation planning. *Biological Conservation* 120:121-128.
- Grantham, B. A., G. L. Eckert, and A. L. Shanks. 2003. Dispersal potential of marine invertebrates in diverse habitats. *Ecological Applications* 13:S108–S116.
- Guichard, F., S. A. Levin, A. Hastings, and D. Siegel. 2004. Toward a dynamic metacommunity approach to marine reserve theory. *Bioscience* 54:1003-1011.
- Halpern, B. S., and R. R. Warner. 2003. Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270:1871-1878.
- Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13:S117-S137.
- Halpern, B.S., S.D. Gaines, R.R. Warner. 2004. Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecological Applications*. 14(4): 1248-1256.
- Halpern, B. S., H. M. Regan, H. P. Possingham, and M. A. McCarthy. 2006. Accounting for uncertainty in marine reserve design. *Ecology Letters* 9:2-11.
- Harriott, V. J. and S. A. Banks. 1995. Recruitment of scleractinian corals in the Solitary Islands Marine Reserve, a high latitude coral-dominated community in Eastern Australia. *Mar. Ecol. Progr. Ser.* 123:155-161.
- Hockey, P.A.R, G.M. Branch. 1994. Conserving marine biodiversity on the African coast – Implications of a terrestrial perspective. *Aquatic Conservation – Marine and Freshwater Ecosystems* 4 (4):345-362.
- Horwood J.W. 2000. No-take zones: a management context. The effects of fishing on non-target species and habitats: biological, social, and economic issues. Blackwell Science, Oxford.
- Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nystrom, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929-933.
- Hyrenbach, K. D., K. A. Forney and P. K. Dayton 2000. Marine protected areas and ocean basin management. *Aquatic Conservation-Marine and Freshwater Ecosystems* 10(6): 437-458.
- Jones, G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. *Nature (London)* 402:802-804.
- Jones, G.P., S. Planes, and S.R. Thorrold. 2005. Coral reef fish larvae settle close to home. *Curr. Biol.* 15, 1314.
- Kaiser, M. J. 2005. Are marine protected areas a red herring or fisheries panacea? *Canadian J. Fish. Aquat. Sci.* 62:1194-1199.

- Kamukuru, A. T., Y. D. Mgaya, and M. C. Ohman. 2004. Evaluating a marine protected area in a developing country: Mafia Island Marine Park, Tanzania. *Ocean & Coastal Management* 47:321-337.
- Kaplan, D.M. and L.W. Botsford. 2005. Effects of Variability in Spacing of Coastal Marine Reserves on Fisheries Yield and Sustainability. *Canadian Journal of Fisheries and Aquatic Science*, 62: 905-912.
- King, M.C. and K.F. Beazley, 2005. Selecting focal species for marine protected area network planning in the Scotia-Fundy region of Atlantic Canada. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15: 367-385.
- Kinlan B, Gaines S. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–20.
- Kinlan, B. P., S. D. Gaines, and S. E. Lester. 2005. Propagule dispersal and the scales of marine community process. *Diversity & Distributions* 11:139-148.
- Larson, R. J., and R. M. Julian. 1999. Spatial and temporal genetic patchiness in marine populations and their implications for fisheries management. *California Cooperative Oceanic Fisheries Investigations Reports* 40:94-99.
- Leslie, H., M. Ruckelshaus, I. R. Ball, S. Andelman, and H. P. Possingham. 2003. Using siting algorithms in the design of marine reserve networks. *Ecological Applications* 13:S185-S198.
- Leslie, H.M. 2005. A synthesis of marine conservation planning approaches. *Conservation Biology* 19 (6): 1701-1713.
- Levin, L.A. (1990) A review of methods for labeling and tracking marine invertebrate larvae. *Ophelia*, 32, 115–144.
- Levin, L. A., D. Huggett, P. Myers, T. Bridges, and J. Weaver. 1993. Rare-earth tagging methods for the study of larval dispersal by marine-invertebrates. *Limnology and Oceanography* 38:246–360
- Levin, P. S. 1996. Recruitment in a temperate demersal fish: Does larval supply matter? *Limnology and Oceanography* 41:672-679.
- Lubchenco, J., S.R. Palumbi, S.D. Gaines, S. Andelman. 2003. Plugging a hole in the ocean: The emerging science of marine reserves. *Ecological applications* 13(1): S3-S7.
- McClanahan, T. R., N. A. Muthiga, A. T. Kamukuru, H. Machano, and R. W. Kiambo. 1999. The effects of marine parks and fishing on coral reefs of northern Tanzania. *Biological Conservation* 89:161-182.
- McClanahan, T.R. and N.A.J. Graham, 2005. Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. *Marine Ecological Progress Series* 294: 241-248.
- McMillan, W. O., R. A. Raff, and S. R. Palumbi. 1992. Population genetic consequences of developmental evolution in sea urchins (Genus *Heliocidaris*). *Evolution* 46:1299-1312.
- McShane, P. E., K. P. Black, and M. G. Smith. 1988. Recruitment processes in *Haliotis rubra* (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae. *Journal of Experimental Marine Biology and Ecology* 124:175-204.
- Meyer, G. C. 2003. An Empirical Evaluation of the Design and Function of a small Marine Reserve (Waikiki Marine Life Conservation District). Page 143. *Zoology (Marine Biology)*. University of Hawaii.
- Mora, C., S. Andrefouet, M. J. Costello, C. Kranenburg, A. Rollo, J. Veron, K. J. Gaston, and R. A. Myers. 2006. Coral reefs and the global network of marine protected areas. *Science* 312:1750-1751.
- Mumby, P. J., and A. R. Harborne. 1999. Development of a systematic classification scheme of marine habitats to facilitate regional management and mapping of Caribbean coral reefs. *Biological Conservation* 88:155-163.

- Murawski, S. A., R. Brown, H.-L. Lai, P. J. Rago, and L. Hendrickson. 2000. Large scale closed areas as a fishery management tool in temperate marine systems: the Georges Bank experience. *Bulletin of Marine Science* 66:775–798.
- Murray, G. D. 2005. Multifaceted measures of success in two Mexican marine protected areas. *Society & Natural Resources* 18:889-905.
- Nagelkerken, I., M. Dorenbosch, W. C. E. P. Verberk, E. C. de la Moriniere, and G. Van der Velde. 2000. Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Marine Ecology Progress Series* 202:175–192.
- National Marine Protected Area Center Report. 2004. An inventory of GIS-based decision support tools. NOAA Coastal Services Center.
- Nature Serve Report. 2004. Tools for coastal and marine ecosystem-based management. For the David and Lucille Packard Foundation.
- Nicholson, E., and H. P. Possingham. 2006. Objective for multiple-species conservation planning. *Conservation Biology*, 20 (3): 871-881.
- NRC National Research Council. 2000. Marine Protected Areas: tools for sustaining ocean ecosystems. National Academy Press, Washington, D.C., USA.
- Ogden, J. C., and E. H. Gladfelter. 1983. Coral reefs, seagrass beds, and mangroves: their interaction in the coastal zones of the Caribbean. *UNESCO Reports in Marine Science* 23: 1–133.
- Palumbi, S. R., G. Grabowsky, T. Duda, N. Tachino, and L. Geyer. 1997. Speciation and the evolution of population structure in tropical Pacific sea urchins. *Evolution* 51:1506-1517.
- Palumbi, S. R. 2001. The ecology of marine protected areas. Pages 509–530 *in* M. Bertness, S. D. Gaines, and M. E. Hay, editors. *Marine ecology: the new synthesis*. Sinauer, Sunderland, Massachusetts, USA.
- Palumbi, S. R., S. D. Gaines, H. Leslie, and R. R. Warner. 2003. New wave: high-tech tools to help marine reserve research. *Frontiers in Ecology and the Environment* 1:73-79.
- Palumbi, S.R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* 13(1): S146-S158.
- Palumbi, S. R. 2004. Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. *Annual Review of Environment and Resources* 29:31-68.
- Paris, C.B. and R.K. Cowen. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnol. Oceanogr.* 49, 1964.
- Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO). 2002. *The Science of Marine Reserves*. <http://www.piscoweb.org>. 22 pages.
- Pelletier, D., and S. Mahevas. 2005. Spatially explicit fisheries simulation models for policy evaluation. *Fish and Fisheries* 6:307-349.
- Polacheck, T. 1990. Year round closed areas as a management tool. *Natural Resource Modeling* 4:327-354.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks and habitat selection: A landscape perspective on population dynamics. *American Naturalist* 137:S50-S66.
- Reeves, R. 2000. *The Value of Sanctuaries, Parks, and Reserves (Protected Areas) as Tools for Conserving Marine Mammals*. Final Report to the Marine Mammal Commission, contract number T74465385. Marine Mammal Commission, Bethesda, MD. 1-50.
- Roberts, C. M. 1996. Settlement and beyond: Population regulation and community structure of reef fishes. Pages 85-112 *in* N. V. C. Polunin, and M. R. C, editors. *Fish and Fisheries Series, 20. Reef fisheries*. Chapman and Hall Ltd., London, England, UK; New York, New York, USA.
- Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. *Science* (Washington D C) 278:1454-1457.

- Roberts, C. 1997. Ecological advice, for the global fisheries crisis. *Tree* 12:35-40.
- Roberts, C. M. 1998. Sources, sinks, and the design of marine reserve networks. *Fisheries* 23:16-19.
- Roberts, C. M., and J. P. Hawkins. 2000. Fully-Protected Marine Reserves: A Guide. Page 131. World Wildlife Fund.
- Roberts, C., B. Halpern, S. R. Palumbi, and R. R. Warner. 2001. Designing Marine Reserve Networks: Why small, isolated protected areas are not enough. Pages 10-17. *Conservation Biology In Practice*.
- Roberts, C. M., G. Branch, R. H. Bustamante, J. C. Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, M. Ruckelshaus, and R. R. Warner. 2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecological Applications* 13:S215-S228.
- Roberts, C. M., S. Andelman, G. Branch, R. H. Bustamante, J. C. Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, H. P. Possingham, M. Ruckelshaus, and R. R. Warner. 2003. Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* 13:S199-S214.
- Russ, G. R., and A. C. Alcala. 1996. Marine reserves: Rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* 6:947-961.
- Russ, G.R. and A.C. Alcala, 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138:622-627.
- Sadovy, Y, 2006. Protecting the spawning and nursery habitats of fish: the use of MPAs to safeguard critical life-history stages for marine life. In *MPA News, International News and Analysis on Marine Protected Areas*, 8 (2):1-3.
- Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J. C., Dayton, P. K. 2002. A General Model for Designing Networks of Marine Reserves. *Science* 298, 1991-1993.
- Sale, A., R. K. Cowen, B. S. Danilowicz, and e. al. 2005. Critical science gaps impede the use of no-take fisheries reserves. *Trends in Ecology & Evolution* 20:74-78.
- Salm, R.V. Clark, K. and Siirila, E. 2000. *Marine and Coastal Protected Areas: a guide for planners and managers*. IUCN: Washington DC (USA), 371 pages.
- Sammarco, P.W. and J.C. Andrews. 1989. The HELIX experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals. *Limnol. Oceanogr.* 34, 896.
- Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13:S159-S169.
- Shears, N. T., and R. C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology-Progress Series* 246:1-16.
- Shulman, M. J., and E. Bermingham. 1995. Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution* 49:897-910.
- Sotka, E.E., Wares, J.P., Barth, J.A., Grosberg, R.K. & Palumbi, S.R. (2004) Strong genetic clines and geographical variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. *Molecular Ecology*, 13, 2143–2156.
- Steneck, R.S. 2006. Staying Connected in a Turbulent World. *Science* 311: 480-481.
- Stewart, R. R., T. Noyce, and H. P. Possingham. 2003. Opportunity cost of ad hoc marine reserve design decisions: an example from South Australia. *Marine Ecology Progress Series* 253:25-38.
- Swearer, S. E., J. E. Caselle, D. W. Lea, and R. R. Warner. 1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature (London)* 402:799-802.
- Swearer, S. E., J. S. Shima, M. E. Hellberg, S. R. Thorrold, G. P. Jones, D. R. Robertson, S. G. Morgan, K. A. Selkoe, G. M. Ruiz, and R. R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science* 70: 251-271.

- Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal Homing in a Marine Fish Metapopulation. *Science* 291:297-299.
- Tremblay, P. C., J. W. Loder, F. E. Werner, C. E. Naimie, F. H. Page, and M. M. Sinclair. 1994. Drift of sea scallop larvae, *Placopecten magellanicus* on Georges Bank: a model study of the roles of mean advection, larval behavior, and larval drift. *Deep-Sea Research* 41:7-49.
- Warner, R. R., S. E. Swearer, and J. E. Caselle. 2000. Larval accumulation and retention: Implications for the design of marine reserves and essential fish habitat. *Bulletin of Marine Science* 66:821-830.
- WCPA/IUCN, 2005. Establishing networks of marine protected areas: a guide for developing capacity for building MPA networks.
- Wells, S. 2006. Establishing national and regional systems of MPAs – a review of progress with lessons learned. Second Draft. UNEP World Conservation Monitoring Centre, UNEP Regional Seas Programme, ICRAN, IUCN/WCPA – Marine.
- West, J. M., and R. V. Salm. 2003. Resistance and Resilience to Coral Bleaching: Implications for Coral Reef Conservation and Management. *Conservation Biology* 17:956-967.
- Williams, I.D, W.J. Walsh, A. Miyasaka, and A.M. Friedlander, 2006. Effects of rotational closure on coral reef fishes in Waikiki-Diamond Head Fishery Management Area, Oahu, Hawaii. *Marine Ecological Progress Series* 310: 139-149.
- Willis, T.J, R.B. Millar, and R.C. Babcock, 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology*, 40: 214-227.
- Wolanski, E., R.H. Richmond, G. Davis, E. Deleersnijder, R.R. Leben. 2003. Eddies around Guam, an island in the Mariana Islands group. *Continental Shelf Research*, 23: 991-1003.

**Appendix 7: List of Biophysical Tools**

<b>Name of Tool</b>	<b>Reference</b>	<b>Description</b>	<b>Helpful for</b>	<b>Location used</b>	<b>Usefulness/Limitations/Assumptions</b>
Simulated annealing	Leslie 2003	Targets habitats with siting algorithms (used SPEXAN) habitat based site design (previously applied in terrestrial systems) by applying simulated annealing.	Generates multiple network scenarios that include specified amounts of all habitat types, while minimizing reserve system area and system perimeter	Florida Keys data set	Data compilation very time consuming.
SITES – simulated annealing	Airame 2003	Marine network application of siting algorithm, (“greedy” or simulated annealing)	Identify potential networks that minimize set costs and meet specified goals, such as representation.	Channel islands marine reserve network	Does not explicitly consider spatial relationships among sites, but does allow control of degree of clustering
FISHeries simulation (ISIS – Fish)  And review of models used to explore consequences of possible policies on fisheries resources.	Pelletier/Mahevas 2005	Spatially explicit fishery simulation models for policy evaluation.	Used to investigate the effects of combined management strategies, on multiple species of target fish	Simplified example described.	Different assumptions/limitations for the different models reviewed.
Demographic sensitivity analysis	Gerber/Heppel 2004	Different species will benefit more from protection in different life stages, demographic sensitivity analysis can show which stages are most beneficial for protection for different species.	Used for comparing conservation goals and MPA designs with species of varying life histories	<i>Littorina</i> (intertidal snail) example	
ECOPATH	Gerber/Botsford 2003	Multispecies focused, spatially explicit reserve	Estimates changes in biomass after reserve	Not available in this reference	



		design model	establishment based on trophic interactions		
List of different types of models/different model attributes and their effects on reserve design	Gerber/Botsford 2003	No specific models (tools) identified and discussed	good reference if deciding between tools because of certain characteristics	Not available in this reference	
Siting algorithms (general summary)	Roberts et al 2003 (#2)	Mathematical means of finding network solutions, can also provide guidance on “irreplaceability” of a site, goal is to minimize cost (user sets cost and goals)	Require technical expertise (except some of the programs that use algorithms, which are easier to use) requires extensive data sets	n/a	
Protective multiplier (“insurance factor”)	Allison et al 2003	Mechanism for calculating ‘insurance factor’ to facilitate consideration of possible catastrophes	Used to ensure that enough area is being protected in the best places to buffer against the effects of catastrophes.	Example: oil spills on the US West Coast	Complexities in every case that must be considered separately; ignores areas outside the reserve. Assumptions - Can choose varying equations with more/less assumptions that are less/more complicated.
Mathematical objective extinction risk functions	Nicholson/Possingham in press	Maximizing probability of species persistence; combining multiple species persistence plans; can be used in an optimization problem	Consider ways in which the information on extinction risk of multiple species can best be used to develop effective protected areas	n/a	Choosing different equations will lead to different outcomes, must consider goals closely before selecting an equation. Assumptions - Different for different equations listed.
Compensation factor formula	Halpern et al 2004	Promotes BACI (before-after, control-impact) design; equation incorporating, settlement rate of larvae per unit habitat, reserve size, and	Used for understanding increase in mortality outside the reserve (due to fisher displacement) and its offset of increased fish (due to	n/a	Assumptions - 1. general larval pool of all larvae, that settles everywhere equally 2. larval mortality is density independent

		increased fishing pressure outside of the reserve	export of production within the reserves.)		3. adult fish are evenly distributed throughout their range
Genetic/ dispersal simulation models	Palumbi 2003	Using genetics to understand larval dispersal, connectivity, and reserve locations.	Looks at genetic structure and isolation by distance, can be used to suggest the spatial scales of larval dispersal for target species	n/a	Assumes species are distributed evenly and larvae are distributed equally throughout the range
WORLD MAP	Beger et al 2003	Site selection based on complementarity (rarity), complementarity (richness), and hotspots (rarity)	progressive rarity algorithm, ranks sites based on user defined criteria	Kimbe Bay, New Britain, Papua New Guinea	
Metacommunity model	Guichard et al 2004	Model based on dynamics of communities, dispersal distances, uses both habitat criteria and population connectivity for site selection.	Includes local interactions between species within each site, and local interactions among sites through larval dispersal kernels	Wave-disturbed intertidal musselbed community	(excludes highly migratory species)
Hydrodynamic models	Cowen et al 2006	Models for estimating the spatial probability of dispersal (dispersal kernels) for multiple species from a variety of potential spawning sites.	Define the scale of connectivity by helping to understand genetics, population structure and biogeography of many species	Caribbean region	10 – 100 km for many important species
Visual counts (surveys) during timed swims	Beger et al 2003	Presence-absence species counts from timed swims (60-80 minutes, beginning at 25 m, swimming back and forth while slowly moving shallower.)	Used to survey hard corals and fish species at different sites used in the reserve selection process.	Kimbe Bay, New Britain, Papua New Guinea	Assumes that since each survey covered a similar area in a set time, the area of each site was roughly the same, but information on selection criteria for reefs was not available.
Expert; workshops; interviews of scientists and managers; SITES	Beck 2001	Identify sites that would fully represent biological diversity of the nearshore region	SITES used to provide preliminary sets of locations that were then used at workshops and	Northern Gulf of Mexico	Overall SITES results matched fairly well with expert opinion.

			in interviews to gather data from experts.		
Ecopath with ecoism (EwE)	<a href="http://www.ecopath.org">www.ecopath.org</a>  (National MPA Center report 2004))	Address ecological questions; Evaluate ecosystem effects of fishing; Explore management policy options; Evaluate impact and placement of marine protected areas; Evaluate effect of environmental changes.	GIS-based		
OCEAN – Ocean communities 3E Analysis Network	<a href="http://www.ecotrust.org">www.ecotrust.org</a>  (National MPA Center report 2004)	Economic patterns of spatial behavior and marine management decisions	Participatory approach; effect of fisheries management on coastal communities	Pay consulting fee to use (covers US West Coast)	
Oceanographic Analyst Extension	<a href="http://www.absc.usgs.gov/glba/gistools/index.htm">www.absc.usgs.gov/glba/gistools/index.htm</a>  (National MPA Center report 2004)	Can use oceanographic base data to make siting and monitoring decisions for MPAs; specifically set to use CTD info	Works through ArcView 3x GIS		
Sites	<a href="http://www.biogeog.ucsb.edu/projects/tnc/overview.html">www.biogeog.ucsb.edu/projects/tnc/overview.html</a>  (National MPA Center report 2004)  Leslie (2003) example of use in Florida keys	A reserve siting tool that incorporates spatial design criteria (units, elements of units, and goals) into site-selection.	Graphical interface uses ArcView 3x		
MARXAN	(National MPA Center report 2004)  Great Barrier Reef Marine Park’s Representative Areas Program	Develop a network that adequately represents all habitats and communities within the park, also used expert opinion, stakeholder involvement, and	Uses an objective function to apply operational principles, and simulated annealing to then identify the optimal networks.	Participatory elements	

	(Nature Serve report 2004)	analytical approaches.			
OceanMap	(National MPA Center report 2004)  California Department of Fish and Game  SCOOP (Pacific Marine Conservation Council)	Use GIS-based tool to elicit and incorporate fisher's knowledge into MPA planning process, and tests spatial methods for incorporating socioeconomic assessments quickly into the planning process.	Runs within ArcView,	Participatory, uses scientific and socioeconomic info, runs a variety of analyses (simple overlap – complex suitability)	Simple processes most GIS analysts could perform without program – good for people with less GIS experience
COSMO	(Nature Serve report 2004)	Demonstrates steps in design analysis and evaluation of CZM plans. Iterative, allows exploration of impacts of development and protection.			
SimCoast	(Nature Serve report 2004)	Incorporates impacts of dominant processes and issues as well as expert knowledge from diverse research fields, looks at effects of activity on itself and within transect, as well as the effect of activities occurring outside the designated area. Weighting of impacts in terms of targets,			
RamCo	(Nature Serve report 2004)	Aimed at policy-makers, model that represents physical, environmental, economic, and social processes in the coastal zone.			
CommunityViz Scenario	(Nature Serve report	View, analyze and	GIS-based		

360	2004)	understand land-use alternatives and impacts, includes economic, social, environmental, and visual aspects			
Scoring/ranking systems	Roberts et al (2003 2)	Allocate a score to sites based on predetermined criteria, can be weighted, however mixing biological and social factors here can lead to undue weight being placed on a particular aspect.	Require little technical expertise		
Current meter, satellite altimetry and numerical oceanic current model	Wolanski, 2003	Used to predict currents and eddies.	Helpful in understanding connectivity for network design and analysis.	Guam, Mariana Islands	Relies on the quality of data used.
TRADER	Day 2002			Great Barrier Reef Marine Park, Australia	
Mark-recapture studies	Wells 2006	Used to track highly migratory species.	Helpful in understanding patterns of movement and in designated sites that are the appropriate size, shape, and spacing for focal species.		
Four algorithms for conservation planning in reef and mangrove habitat	Mumby 2006	Used to take into account mangrove habitats as a nursery, habitat for reef fish, reef connectivity with mangroves, and priority mangrove restoration sites.			
C-Plan	Margules and Pressey 2000	Similar to MARXAN, but uses a statistical method to generate irreplaceability instead of simulated annealing. C-Plan cannot minimize cost or improve spatial			

		reserve design, but does have a graphical interface, and powerful database building system.			
PORTFOLIO	Urban 2002	This is a reserve siting program, that is designed to be maximally flexible rather than to maximize constraints or optimize decisions.	Only appropriate for small sets of candidate sites.		