The Central Importance of Ecological Spatial Connectivity to Effective Marine Protected Areas and to Meeting the Challenges of Climate Change in the Marine Environment: A Scientific Synthesis

Marine Protected Areas Federal Advisory Committee

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Scientific Synthesis: Table of Contents

PART 1: Introduction

BACKGROUND AND CONTEXT

The Marine Protected Areas Federal Advisory Committee (MPA FAC) is a 20-member committee of outside experts that advises the United States Secretaries of Commerce and Interior on matters concerning marine protected areas (MPAs) in the United States. The Secretaries charge the MPA FAC, biannually, with questions of import to MPAs in the United States, and the Committee uses its members' expertise and experience to answer the questions and to respond with specific recommendations for the Secretaries. The MPA FAC was created by Executive Order 13158 (May 26, 2000) and has been operational since 2003. Additional information about the MPA FAC is available online, as is each of its products and sets of recommendations to the Secretaries, which date from 2005 to the present.[1]

In April 2015, the Secretaries charged the MPA FAC to advise them on incorporating knowledge about ecological spatial connectivity and climate change into the design, use, and management of MPAs and MPA networks. Incorporating knowledge about ecological spatial connectivity (hereafter "ecological spatial connectivity" or "connectivity") into MPAs and MPA networks (hereafter "MPAs" unless otherwise indicated) is essential for achieving goals of conserving marine populations and ecosystems. In addition, incorporating knowledge about connectivity best equips MPAs to achieve conservation goals as the marine environment undergoes significant changes due to climate change.[2]

The MPA FAC produced two products in response to the Secretaries' connectivity charge. The first product is this scientific synthesis. This synthesis defines ecological spatial connectivity, summarizes current knowledge about connectivity in the marine environment, and offers specific principles for incorporating knowledge about connectivity into the design, use, and management of MPAs. It shows that incorporating knowledge about connectivity is essential for effective MPAs. It also shows that incorporating knowledge about connectivity into MPAs best enables MPAs to achieve their goals in a marine environment undergoing significant changes due to climate change.[3] This scientific synthesis was drafted by the Connectivity Subcommittee of the MPA FAC, and was reviewed and approved by the full MPA FAC on November 10, 2016.[4]

The second product of the MPA FAC in response to the connectivity charge is an Action Agenda for the Secretaries of Commerce and Interior, entitled Connectivity-Informed MPAs and MPA Networks for Effective Marine Conservation and for Meeting the Challenges of Climate Change in the Marine Environment. The Action Agenda recommends six actions to the Secretaries. These include moving quickly to incorporate ecological spatial connectivity into the federal MPAs and MPA networks under their own jurisdictions, aiding other federal MPA programs and state, local, tribal, and territorial programs to incorporate connectivity into their respective MPAs and MPA networks, and leading efforts

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[1] See MPA FAC Products, http://marineprotectedareas.noaa.gov/fac/products/.

[2] For a Glossary of key terms used herein, see Appendix 1.

[3] This paper builds in part on an earlier product of the MPA FAC on climate change in the ocean and MPAs; see "Climate Change in the Ocean: Implications and Recommendations for the National System of Marine Protected Areas" (MPA FAC 2010), available at http://marineprotectedareas.noaa.gov/fac/products/ (2010 products). See also MPA FAC Scientific and Technical Subcommittee (2010), a background document, available at http://marineprotectedareas.noaa.gov/fac/products/fac-climate-background-042010.pdf (2010 background paper).

[4] For composition of the MPA FAC and of the MPA FAC Connectivity Subcommittee, see Appendix 2.

to develop key tools and methods for facilitating ongoing incorporation of connectivity. In addition, the Action Agenda includes a set of guidelines, for use by any MPA program, on how to incorporate connectivity into MPAs and MPA networks. Like the scientific synthesis, the Action Agenda was drafted by the Connectivity Subcommittee of the MPA FAC, and reviewed and approved by the full MPA FAC on November 10, 2016.

This scientific synthesis was written as a resource for the MPA FAC and for the Secretaries of Commerce and Interior. The MPA FAC used the information in this scientific synthesis, along with members' additional expertise and experience concerning MPAs, to create the recommendations and guidelines in the MPA FAC's Action Agenda. The MPA FAC hopes that this scientific synthesis will be a useful resource for MPA program managers at all levels of government throughout the nation, and for any persons interested in the design, use, and management of effective MPAs and MPA networks.

STRUCTURE AND OVERVIEW OF THE PAPER

The paper is divided into five parts.

Part 1 is this Introduction.

Part 2 - entitled What Is Ecological Spatial Connectivity and Why Does It Matter for Effective Marine Protected Areas? - defines ecological spatial connectivity, describes four types or scales of connectivity, and shows the critical importance of taking connectivity into account in designing, using, and managing MPAs (where design includes location, size, and shape of MPAs). At its core, connectivity refers to biological and physical processes that connect spatially discrete areas in the marine environment to one another in ways that are crucial to the lives of organisms, populations, ecological communities, and ecosystems. The central points of Part 2 are that the realities of ecological spatial connectivity pose both challenges and opportunities to place-based conservation tools in the marine environment (i.e., MPAs), and that these challenges and opportunities can be met and exploited if knowledge about connectivity is built into how we design, use, and manage these place-based tools.

Part 3 - entitled Design, Use, and Management Principles for Enhancing Ecological Spatial Connectivity Processes Within, Around, and Among MPAs and MPA Networks - expands upon Part 2. It offers specific principles for taking connectivity into account in the design, use, and management of ecological MPAs, MPAs aimed at restoring or maintaining ecological phenomena in the marine environment, i.e., populations, communities, ecosystems, and processes. As shown in Part 3, the principles to use in a given instance depend on the ecological focus of the MPA (whether the MPA is species-focused or community- or ecosystem-focused) and on the characteristics of the species, ecological communities, or ecosystems of interest. As also shown, the design, use, and management principles address a variety of parameters, including: (1) the location of an MPA; (2) the size of an MPA; and (3) whether the MPA is an individual, stand-alone MPA or part of a set of inter-dependent MPAs, i.e., a network of MPAs. They also include: (4) whether management of an MPA aims at intended effects within MPA boundaries or outside MPA boundaries (or both); (5) attentiveness to management regimes within an MPA and to management regimes in areas outside the MPA; and (6) attentiveness to the relationships between the management regimes inside an MPA and those outside an MPA.

Part 4 of the paper pivots to address the effects of climate change in the marine environment, with a focus on changes in marine species' distributions, abundances, and productivities, and the cascading effects these species-level changes produce in ecological communities and ecosystems. Entitled Climate

Change in the Marine Environment: Another Compelling Reason for Connectivity-Informed MPAs and MPA Networks, Part 4 demonstrates that MPAs built, used, and managed to foster ecological spatial connectivity processes - connectivity-informed MPAs and MPA networks - are best suited to address the shifts in species distributions and related changes in ecological communities and ecosystems associated with climate change in the marine environment. Part 4 also shows that connectivity-informed MPAs must be monitored, evaluated, and adaptively managed, so that their design, use, and management can respond to and possibly further anticipate changes in species' distributions, abundances, and productivities. While Parts 2 and 3 of this paper show that incorporating connectivity in (ecological) MPAs is essential for MPAs to meet conservation goals at any point in time, Part 4 shows that fostering connectivity processes in (ecological) MPAs is *also* critically important for MPAs to meet conservation goals in a time of significant, ongoing changes in the marine environment.

Finally, Part 5 is a brief conclusion.

PART 2: What Is Ecological Spatial Connectivity and Why Does It Matter for Effective Marine Protected Areas?

OVERVIEW

Part 2 defines ecological spatial connectivity and summarizes current knowledge about ecological spatial connectivity in the marine environment.[5] It shows the critical importance of taking ecological spatial connectivity into account in designing, using, and managing MPAs (where design includes location, size, and shape of MPAs). The central points of Part 2 are that the realities of ecological spatial connectivity pose both challenges and opportunities to place-based conservation tools in the marine environment (i.e., MPAs), and that these challenges and opportunities can be met and exploited if knowledge about connectivity realities is built into how we design, use, and manage these place-based tools.

ECOLOGICAL SPATIAL CONNECTIVITY AND MARINE PROTECTED AREAS

Ecological Spatial Connectivity

Entities in nature, such as populations, species, communities or ecosystems, regularly influence one another and inter-connect. ***Connectivity*** refers to processes that determine connections among entities. In conservation science the term connectivity is used to describe the levels and directions of movement and sharing of organisms, materials, energy or information among entities.[6] ***Spatial connectivity*** refers to movement among spatially distinct entities, and also includes connections in physical processes at varying spatial scales, from the interactions between local water masses to teleconnections that link atmospheric and oceanographic anomalies over vast distances. ***Ecological spatial connectivity*** refers to processes by which genes, organisms, populations, species, nutrients and/or energy move among spatially distinct habitats, populations, communities or ecosystems.

In the marine environment, ecological spatial connectivity can have profound influences on ecosystems; connectivity affects the species within an ecosystem as well as an ecosystem's productivity, dynamics, resilience, and capacity to generate services for humans. As shown below, there are four types or scales of ecological spatial connectivity (population connectivity, genetic connectivity, community connectivity, and ecosystem connectivity), each of which acts at multiple spatial scales (within MPAs, among MPAs, and, importantly, between MPAs and areas outside MPAs). Ecological spatial connectivity is also the primary process by which distinct ecosystems interact with and influence one another. Finally, connectivity is the process by which pollutants and other materials and effects of human activity move among spatially distinct habitats, populations, communities or ecosystems.

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[5] We use the term "marine environment" broadly, following the definition in the President's Executive Order on Marine Protected Areas: ''Marine environment'' means those areas of coastal and ocean waters, the Great Lakes and their connecting waters, and submerged lands thereunder, over which the United States exercises jurisdiction, consistent with international law" (Exec. Order 13158:2000). In addition, we follow NOAA's National Marine Protected Areas Center in including within coastal waters and associated submerged lands "intertidal areas, bays or estuaries" (MPA Center 2015:10).

[6] The term connectivity is also used in conservation contexts to refer to a variety of ways that people and organizations connect (i.e. communicate and interact) around common conservation or management concerns. We do not use the term in that sense here; our focus is ecological spatial connectivity, as described in the text.

Marine Protected Areas (MPAs)

Marine protected areas (MPAs) are place-based conservation tools used in the marine environment. More specifically, an MPA is a regime of rules restricting some or all human activities in a delineated area of the marine environment, designed to protect that area (or some or all ecological phenomena within that area) from the restricted human activities and, thereby, to achieve specified conservation or management objectives.[7] In the United States, MPAs are created under federal, state, tribal, territorial, and local authorities (collectively, these MPAs are termed "US MPAs"). Consistent with their specific objectives, MPAs vary in the types and levels of human activities they restrict: as examples, some MPAs prohibit the use of certain gears, some prohibit take of specified species, and some prohibit take of all species (i.e. "no-take" marine reserves). As of 2016, there were over 1200 US MPAs, and collectively these US MPAs covered 26% of US marine waters; however, only 3% of US marine waters were covered by no-take MPAs.[8]

NOAA's National MPA Center has analyzed the wide variety of US MPAs and determined that the objectives for which US MPAs are established are classifiable into three basic goals: conservation of natural heritage (biodiversity, populations, communities, habitats, and ecosystems), sustainable production (for sustainable fisheries and sustainable extraction of other renewable resources), and conservation of cultural heritage (tangible and intangible resources that support cultural identity and history). See Table 2.1. Some US MPAs have objectives that fall into two or three of these goal areas. MPAs with objectives in pursuit of natural heritage or sustainable production goals are *ecological MPAs*, in that they seek to restore or maintain ecological phenomena in the marine environment, namely, populations, species, ecological communities, or ecosystems. Depending on their particulars, cultural heritage MPAs may also be ecological MPAs. We use the term ecological MPA here not to detract from the multitude of human and cultural values served by MPAs but rather to highlight that this multitude of values is tied to our capacities to restore or maintain ecological phenomena in the marine environment.

The realities of ecological spatial connectivity pose challenges to, and opportunities for, ecological MPAs. Ecological phenomena within the delineated area of MPAs are affected by - and themselves affect - ecological phenomena outside the delineated areas of MPAs. However, knowledge about connectivity can be harnessed and used in designing, managing, and using MPAs, and can aid MPA designers and managers in maximizing the effectiveness of ecological MPAs. This is so whether these ecological MPAs are natural heritage MPAs, sustainable production MPAs, or cultural heritage MPAs.

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[7] Executive Order 13158 defines an MPA is: "any area of the marine environment that has been reserved by Federal, State, territorial, tribal, or local laws or regulations to provide lasting protection for part or all of the natural and cultural resources therein" (Exec. Order 13158: 2000). See also National MPA Center 2015:8-11.

[8] See Status of US MPAs at http://marineprotectedareas.noaa.gov/aboutmpas/status-of-usa-mpas-2016.html. "US marine waters" refers to all waters associated with the "marine environment" as defined in note 5 above.

Table 2.1: Goals and Objectives of US MPAs

Natural Heritage Goal: Advance comprehensive conservation and management of the nation's biological communities, habitats, ecosystems and processes and the ecological services, uses and values they provide to present and future generations through ecosystem-based MPA approaches.
Natural Heritage Objectives: Conserve and Manage: Reproduction areas and nursery grounds Biogenic habitats Areas of high species and/or habitat diversity Ecologically important geological features and enduring/recurring oceanographic features Critical habitat of threatened and endangered species Unique or rare species, habitats, and associated communities Areas for migratory species Linked areas important to life histories Areas that provide compatible opportunities for education and research
Cultural Heritage Goal: Advance comprehensive conservation and management of cultural resources that reflect the nation's maritime history and traditional cultural connections to the sea, as well as the uses and values they provide to present and future generations through a cultural landscape approach.
Cultural Heritage Objectives: Conserve and Manage: Cultural and historic resources listed on the National Register of Historic Places (NRHP) Cultural and historic resources determined eligible for the NRHP or listed on a State Register Cultural sites that are important to a culture's identity and/or survival Cultural and historic sites that may be threatened Cultural and historic sites that can be utilized for heritage tourism Cultural and historic sites that are under represented
Sustainable Production Goal: Advance comprehensive conservation and management of the nation's renewable living resources and their habitats and the social, cultural and economic values and services they provide to present and future generations through ecosystem-based MPA approaches.
Sustainable Production Objectives: Conserve and Manage: Reproduction areas, including larval sources and nursery grounds Areas that sustain or restore high-priority fishing grounds Areas for maintaining natural age/sex structure of important harvestable species Foraging grounds Areas that mitigate the impacts of bycatch Areas that provide compatible opportunities for education and research

(Table 2.1 is a reproduction of Table 2 in the National MPA Center's Framework for the National System of Marine Protected Areas, p. 13, March 2015; see http://marineprotectedareas.noaa.gov/nationalsystem/framework/ .)

Ecological Spatial Connectivity and MPAs

An understanding of ecological spatial connectivity is essential for the successful design and operation of ecological MPAs. It is also essential for the successful design and operation of effective *networks* of ecological MPAs. Below, we describe four types of ecological spatial connectivity and attendant ecological implications that bear on conservation outcomes and decisions about protected area management. Many of the points and examples presented pertain equally to MPAs designed to protect a subset of species, habitats or ecosystems within an area and to “no-take,” "no impact," and/or "no-access" marine reserves designed to protect everything within their boundaries.

Generally, ecological spatial connectivity is more important and also more achievable in the design and effectiveness of *marine* protected areas than it is in the design and effectiveness of *terrestrial* protected areas, for two reasons. First, there is greater movement of organisms and material in the ocean than on land because of the ocean's surrounding dynamic aqueous medium. Buoyant organisms or their propagules (spores, gametes, larvae or asexual fragments) and other materials can be carried vast distances rapidly by ocean currents with little effort or energy expenditure by the organisms. Second, the majority of marine invertebrates and fishes, including those attached to the seafloor as adults, produce larvae that are adapted to exist in the dynamic pelagic environment. These adaptations of early life stages are morphological (e.g., small, clear, buoyant) and behavioral (e.g., attracted to the ocean surface), and as a consequence these propagules can be carried great distances by ocean currents. These combined effects of the dynamic environment and species’ inherent mobility mean that routine movement across and among habitats – or ecological spatial connectivity -- is a fundamental characteristic of marine ecosystems.

As discussed above, MPAs are place-based conservation tools used in the marine environment. But, the existence of ecological spatial connectivity in the marine environment means that places in the marine environment are connected to one another in critical ways, and these connections must be taken into account in the design and use of place-specific tools to achieve conservation objectives. For example, in many instances the young produced by populations living inside an MPA leave the MPA and replenish populations outside the MPA. Conversely, populations within MPAs often rely on the delivery into the MPA of young produced by populations outside of the MPA. In a very different example, physical materials (e.g., sediments) and chemicals (e.g., nutrients or pollutants) can be readily transported from areas outside MPAs into MPAs, and these influxes into MPAs make the communities and processes within MPAs vulnerable to human activities conducted outside of MPAs (e.g., agricultural runoff, sewage discharges or coastal erosion). One additional example concerns critical spawning habitat MPAs and the seasonal movement of adults of a species into spawning habitat MPAs: the value of these spawning habitat MPAs depends critically on the availability of (i.e., the management of) adults and, also, indirectly, on protection of adult habitat beyond the boundaries of the spawning habitat MPAs.

FOUR TYPES AND SCALES OF ECOLOGICAL SPATIAL CONNECTIVITY

Ecological spatial connectivity refers to processes by which genes, organisms, populations, species, nutrients and/or energy move among spatially distinct habitats, populations, communities or ecosystems. There are four types or scales of ecological spatial connectivity - population connectivity, genetic connectivity, community connectivity, and ecosystem connectivity - each of which acts

Population connectivity results from the movement of individuals of a single species among patchily distributed “local” or "sub-" populations.
Genetic connectivity (also called “gene flow”) is the movement of genes among distinct populations of a single species and results from the movement of organisms - whether spores of marine algae or the larvae, juveniles or adults of marine animals - among these populations.
Community connectivity results from the movement of multiple different species among distinct ecological communities.
Ecosystem connectivity results from the movement of multiple species among distinct ecological communities, along with the movement of chemicals (e.g., nutrients and pollutants), energy (in the form of organisms), and materials (e.g., sediments and debris).

at multiple spatial scales (within MPAs, among MPAs, and between MPAs and areas outside MPAs).

Population Connectivity

Population connectivity, sometimes referred to as *demographic* connectivity, is the linkage among patchily distributed "local" or subpopulations of a single species that results from the movement of individuals among these populations (Figure 2.1A). Because habitats that species inhabit are often discontinuous in space, separated by gaps of uninhabitable habitat (e.g. coral or rocky reefs separated by expanses of sand), species populations often comprise several patchily distributed local populations. The movement of individuals among neighboring local populations influences the size of local populations (i.e. number of individuals) and also, importantly, the structure of local populations (i.e. the sizes, ages and sexes of individuals that constitute each local population). These characteristics of a local population in turn influence critical demographic rates (e.g., births, deaths, immigration and emigration), and these rates determine the dynamics of that population, including its vulnerability to extinction.

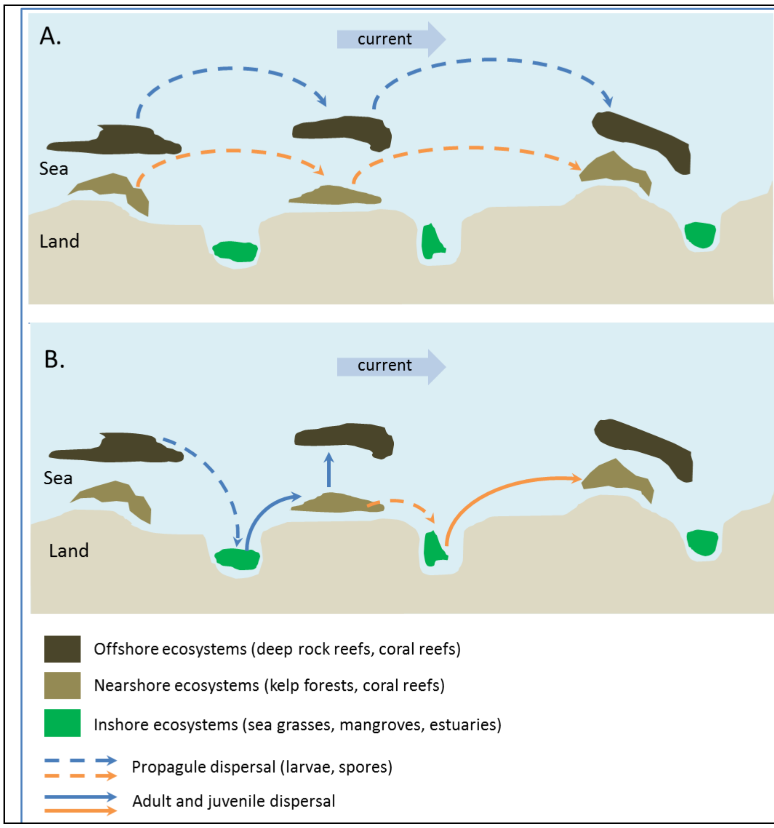

Figure 2.1: Population connectivity: the movement of individuals (spores, larvae, juveniles or adults) from one population to another. (A) Blue and orange dashed arrows represent the direction of larval dispersal of different species between similar ecosystems (see legend). Because populations are associated with suitable habitat separated by unsuitable habitat, much of the connectivity of among populations is achieved by larval transport. (B) Dispersal of larvae (dashed arrows) from nearshore and offshore adult populations to inshore nursery habitats (see legend) and subsequent offshore migration of juveniles to adult populations.

The adults of many coastal and benthic (i.e. bottom-dwelling) marine species exhibit very limited movement. Marine algae and many marine invertebrates are sessile, permanently attached to the seafloor as adults. Even mobile marine invertebrates and fishes, especially those associated with temperate rocky reefs, tropical coral reefs, or estuaries have very limited (< 1 km) home ranges (e.g., see reviews in and by Kritzer and Sale 2010, Freiwald 2012). However, most marine invertebrates and fishes produce young (eggs, larvae) that are typically dispersed by ocean currents over great distances (10's to 100's of kilometers). Thus much of the population connectivity achieved by marine species is by the transport of their young from one population to another in spatially separated similar habitats (Figure 2.1a).

In addition, mobile species (e.g., fishes, lobster) often inhabit different habitats or ecosystems over their lifetime, temporarily using “nursery habitats” as juveniles (Beck et al 2001). Larvae disperse from adult populations to inshore nursery habitats, and eventually migrate as juveniles to offshore adult populations (Figure 2.1B).

A collection of local populations connected by the movement of individuals (i.e. by connectivity), is referred to as a “metapopulation.” The existence and structure of a metapopulation greatly influences the likelihood of local populations going extinct, local populations' resilience (ability to recover from a perturbation), as well as the persistence of the metapopulation itself. Particularly persistent and productive local populations can act as “sources”, exporting individuals to replenish less persistent and productive “sink” populations. This export of individuals from one local population to another, which may be protected in one or more MPAs, influences both the role of MPAs for conservation and management and the design (e.g., size and spacing) of MPAs. These elements of population connectivity are critically important to ecological MPAs and ecological MPA networks.

Genetic Connectivity

Genetic connectivity, the transfer of genes among populations of a species (also called “gene flow”), results from the movement of organisms -- whether spores of marine algae or the larvae, juveniles or adults of marine animals -- among local populations. Genetic connectivity has profound consequences for the spatial patterns of the genetic composition and the genetic diversity of populations; it is critical to the ability of species to adapt to changing environmental conditions. Generally, populations of species whose individuals move greater distances tend to have fewer genetic differences (i.e., variation) across the species’ range because of the high mixing of genes among populations. In contrast, species whose individuals move little over their lifetime tend to vary more widely in their genetic composition across their geographic range (Palumbi 2003). In fact, the degree to which populations differ genetically with increasing distance from one another is one method used to estimate how far individuals, especially larvae, travel (referred to as “isolation by distance” Palumbi 2003, Kinlan and Gaines 2003). Another more powerful tool for detecting both population and genetic connectivity is “parentage analysis” in which parents and their young are matched by their genetic similarity. Young collected in one population can be traced back to their parents in “source” populations (e.g., Christie et al 2010; Figure 2.2.) The important exception to this relationship between movement distance and genetic structure is certain migratory species (e.g., salmon), which travel long distances, but return to breed within the same population.

There is growing recognition of the effects of fishing on the rapid evolution of key life history traits of species, including on their growth rates, age and size at maturity (Dunlop et al 2009). Evidence has been accumulating for some time suggesting that MPAs might provide fished species with a refuge from these anthropogenic selective effects by establishing populations not subjected to fishing selection (e.g., Davis 1975, Palumbi 2003, Baskett et al 2005, Dunlop et al 2009, Baskett and Barnett 2015). Indeed, connectivity can have a great effect on the ability of MPAs to counter changes in genetic structure and the diminishing genetic diversity among populations both inside and outside of MPAs. However, the effectiveness of MPAs in providing this protection depends very much on the extent of larval dispersal (i.e., connectivity and gene flow) into and out of MPAs and the relative sizes of the populations inside and outside of MPAs.

In light of species' differences in gene flow across habitats, MPAs and MPA networks may have very different impacts on species' genetic diversity and ability to cope with changing environmental conditions. If the genetic composition of a species differs across its geographic range, a single MPA might only protect a portion of a species' genetic diversity, whereas a network of MPAs can protect the genetic diversity of species across its entire range. As such, MPA networks can be more effective tools than individual MPAs for achieving objectives that require protection of the genetic diversity of species.

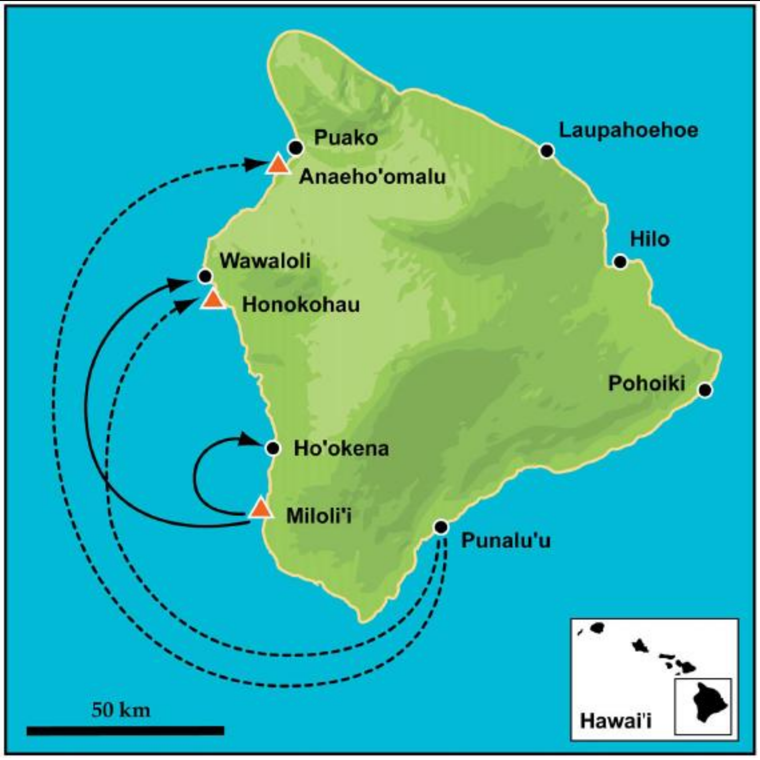

Figure 2.2. Example of population and genetic connectivity of a coral reef fish, the yellow tang, off the island of Hawai'i (from Christie et al 2010). Patterns of connectivity (larval transport) were detected by the genetic match of parents and their young. Sampled reefs are indicated by **circles (non-MPAs)** and **triangles (MPAs)**. Arrows indicate the direction of movement from parent populations to where young were collected. The identified parents were sampled at Miloli'i and Punalu'u. Arrows point to the settlement site of the offspring. Solid lines indicate the first unequivocal evidence of an MPA seeding unprotected sites. http://dx.doi.org/10.1371/journal.pone.0015715.g002

Community Connectivity

Community connectivity is the linkage of spatially separated ecological communities resulting from the independent movements of multiple species among these communities. Community connectivity influences the structure and functions of these ecological communities (Figure 2.3). An ecological community is the collection of species that co-occur and interact with one another in a particular habitat (e.g., a coral reef, kelp forest or seagrass bed). The structure of an ecological community (i.e., the identity, relative abundance and diversity of species and species groups) has important consequences for functional processes in a community, including a community's productivity and resilience to natural and anthropogenic perturbations. Like metapopulations, "metacommunities" are collections of distinct communities that, through connectivity processes, routinely exchange species; connectivity influences not only the structure, dynamics and persistence of individual communities, but also those of the metacommunity comprised of distinct, connected communities. For example, the fish assemblages that inhabit kelp forest communities in southern California comprise a unique combination of warm and cold water species from kelp forest communities in Mexico and central California, respectively (Holbrook et al 1997, Hamilton et al 2010, Carr and Reed 2015).

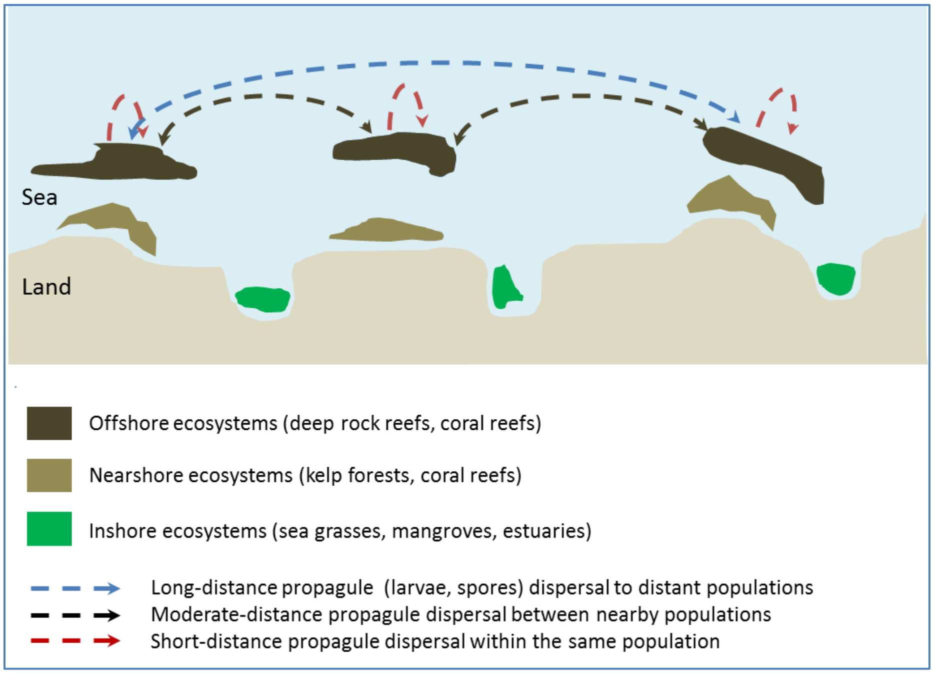

Figure 2.3. Community connectivity: the collective movement of species from one community to another. Different colored arrows represent propagule (spores, larvae) dispersal of different species between similar ecosystems (see legend) within each species' dispersal range. Because species are associated with suitable ecosystems separated by unsuitable habitat, much of the connectivity of among communities is achieved by propagule transport.

The design and management of MPAs affects connectivity among communities (Figure 2.3). Because species differ in the distance that individuals move (e.g., spores of algae and larvae of corals move much shorter distances than larvae of fishes), the size and spacing of MPAs needs to accommodate these differences to protect the communities they are intended to protect (Kinlan and Gaines 2003, Shanks et al 2003). These differences will also influence how well any one MPA or MPA network contributes to either natural heritage objectives (e.g., role of an MPA for protecting biogenic habitat that acts as nursery grounds) or sustainable production objectives (e.g., how effectively protected nursery grounds replenish fished populations).

Ecosystem Connectivity

Ecosystem connectivity is the most complex type of ecological spatial connectivity. It considers not only the movement of species, but also the movement of chemicals (e.g., nutrients and pollutants), energy (in the form of organisms), and materials (e.g., sediments and debris). Some of this matter and movement is a function of natural (non-human) processes, and some is a function of human activities. Ecosystem connectivity can have strong positive effects to "recipient" ecosystems, when the influx of nutrients or species enhances the productivity or resilience of the recipient ecosystem. Conversely, ecosystem connectivity can have strong negative effects to recipient ecosystems, when the influx of nutrients, species or materials reduces productivity or resilience of the recipient ecosystem (Stoms et al 2005).

Examples of positive ecosystem connectivity include the influx of phytoplankton or zooplankton from offshore to nearshore ecosystems, which sustains the many invertebrates and fishes that consume those plankton and which, in turn, are consumed by other species, fueling a plankton-based food web.

Similarly, the competing influx of freshwater and nutrients (e.g., nitrogen, carbon) from rivers, and saltwater and nutrients from the open ocean, influences the species that inhabit estuaries, such as seagrasses, their productivity, and the many species that depend on seagrasses for food or shelter. Algae produced in kelp forests and seagrasses produced in estuaries are exported as detritus or "drift" onshore to sandy beach ecosystems and offshore to deep rocky reef, sand bottom, and marine canyon ecosystems (Figure 2.4a). That influx of algae and seagrasses fuels critical detritus-based food webs in these recipient ecosystems that otherwise lack these sources of plant production. The movement of young of species that depend on nearshore "nursery" ecosystems (e.g. kelp forests, mangroves, seagrass beds) to offshore ecosystems inhabited by adults (e.g., coral reefs, deep rocky reefs, deep sandy habitats) is another key form of connectivity between these ecosystems (Heck et al 2003, Mumby et al 2004, Mumby 2006, Igulu et al 2014). The relative abundance of fishes that inhabit coral reefs depends on the proximity of those reefs to mangrove and seagrass ecosystems (Figure 2.4b; e.g., Neglekerken et al 2002, Olds et al. 2012b).

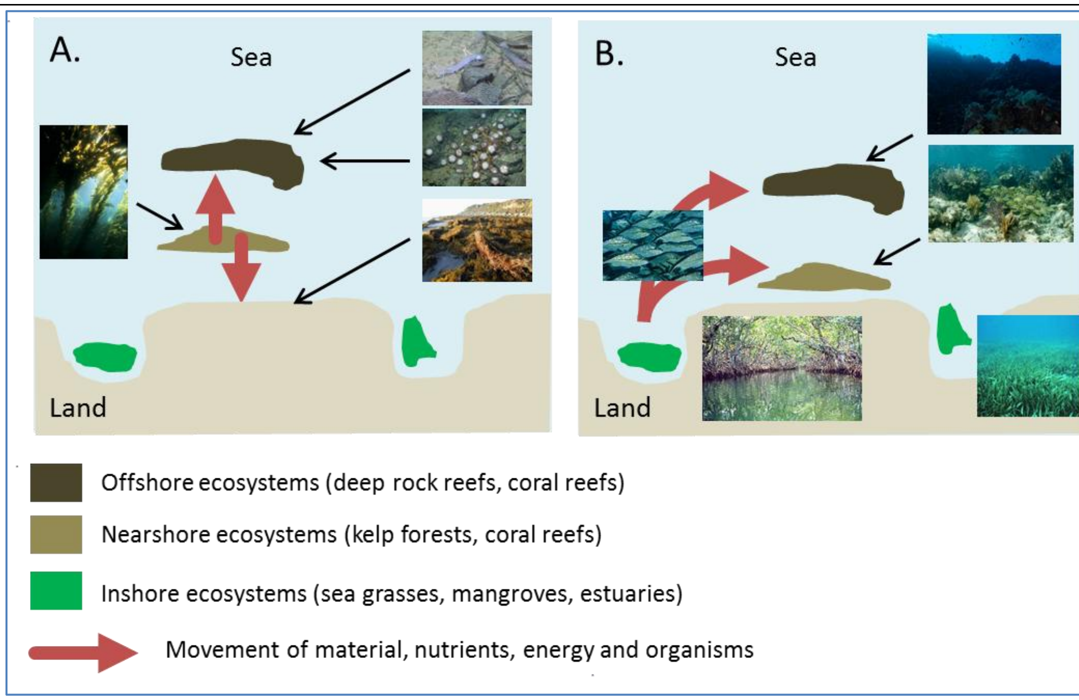

Figure 2.4. Ecosystem connectivity: movement of organisms, energy, and nutrients between "source" and "recipient" ecosystems. As examples: (A) red arrows depict transport of kelp that is removed from shallow reefs by waves and deposited inshore to sandy beaches, rocky intertidal, and offshore to shallow and deep rocky and soft-bottom ecosystems. Kelp provides habitat and fuels detritus-based food webs in recipient ecosystems. (B) Red arrows depict movement of young fishes from inshore ecosystems (see legend) to offshore shallow and deeper coral reef ecosystems. Image credits: (A) kelp forest (Ron McPeak Digital Library, UC Santa Barbara), drift kelp in soft-bottom ecosystem at 1100m depth (James Barry - Monterey Bay Aquarium Research Institute), kelp on beach in Santa Barbara, California (Shane Anderson). (B) mangroves and seagrasses (Heather Dine, Florida Keys National Marine Sanctuary), (NOAA digital library), fishes (G.P. Schmahl, Flower Garden Banks National Marine Sanctuary), shallow coral reef (Kara Wall), deep coral reef (Michael Hoban).

The importance of this influx of species, nutrients and materials to the structure, function and productivity of recipient ecosystems has long been recognized and referred to as “ecosystem subsidies” (Polis et al 1997). Even bi-directional migrations of species from one ecosystem to another and back, such as the annual migrations of lobster or horseshoe crabs from inshore to offshore ecosystems and anadromous/catadromous species (e.g., salmon, eels) in and out of watersheds create opportunities for species to influence multiple ecosystems by their movement among ecosystems.

But, as noted, ecosystem connectivity can also be detrimental to both recipient and donor ecosystems. The influx of land-based nutrients from agricultural activities can cause eutrophication, by which phytoplankton blooms draw down oxygen levels when they respire at night. The ensuing hypoxia (low oxygen) or anoxia (absence of oxygen) can be lethal to other algae, invertebrates and fishes. Similarly, sediment runoff from coastal erosion or other land-based activities (e.g., agriculture, forestry or urban development) can increase turbidity, smother benthic organisms or alter spawning habitat for fishes, altering the structure and functions and diminishing the productivity of recipient ecosystems (Stoms et al 2005; Figure 2.5).

Likewise, impacts to donor ecosystems that create intolerable conditions can drive populations from those ecosystems, altering their structure and functions and diminishing their productivity. These impacts can be transmitted from one ecosystem to another by altering ecosystem functions; hypoxia caused by terrestrial runoff can be lethal to organisms such as the juveniles of offshore fishes whose young use estuarine ecosystems as nursery habitat. The negative effects of ecosystem connectivity can translate into lost ecosystem services, such as fishery yields, when the replenishment of offshore populations declines with lost nursery habitat (Hughes et al 2015).

Thus the extent to which ecological MPAs can achieve their objectives - e.g., supporting healthy fish populations for sustainable fisheries - can be either enhanced or impaired through processes of connectivity among oceanic ecosystems, coastal marine ecosystems, and terrestrial ecosystems.

Figure 2.5. Turbid sediment plumes along the California coast following storms of February 1998. (Katherine L. Farnsworth and Jonathan A. Warrick (USGS) photo by Mark Defeo: http://pubs.usgs.gov/sir/2007/5254/)

ECOLOGICAL SPATIAL CONNECTIVITY, MPAS AND MPA NETWORKS: TWO LESSONS

The effectiveness of ecological MPAs is affected by the four types of ecological spatial connectivity described above: population connectivity, genetic connectivity, community connectivity, and ecosystem connectivity. Thus, an MPA's effectiveness can be contingent on the transport of both beneficial and detrimental materials from adjacent ecosystems and the influx of young that will replenish populations within the MPAs. Also, importantly, the existence of these four types of connectivity in the marine environment means that MPAs - unlike most terrestrial protected areas - are likely to have beneficial effects outside, as well as within, their boundaries. For example, fished populations may benefit from the export of materials and organisms generated within boundaries to populations and ecosystems outside boundaries (Table 2.2). In addition, assessments of MPAs and MPA networks with varying levels of connectivity can be used as tools to inform both conservation and fisheries management decisions depending on the nature of linkages between populations, communities and ecosystems inside and outside MPAs. Ways in which ecological spatial connectivity creates and influences these potential contributions of MPAs are summarized below in Table 2.2.

Table 2.2:

Benefits of incorporating ecological spatial connectivity for ecological MPAs with objectives in natural heritage and sustainable production goal areas: Intended effects, either inside or outside an MPA, pertain to species, habitats and ecosystem processes degraded by human activities. *The extent to which MPAs support these natural heritage and sustainable production goals depends, in large part, on the strengths of genetic, population, community and ecosystem connectivity inside and outside of MPAs. Other critical determinants are the extent to which impacts from human activities (e.g., fishing, pollution and habitat destruction) are controlled both within and outside the MPAs*.

MPA Goal	Benefits of Accounting for Connectivity - Inside the MPA	Benefits of Accounting for Connectivity - Outside the MPA
Natural Heritage Goal: : "Advance comprehensive conservation and management of the nation's biological communities, habitats, ecosystems and processes and the ecological services, uses and values they provide to present and future generations through ecosystem-based MPA approaches." (MPA Center 2015:13).	▪ protect critical habitats for reproduction, foraging and nurseries ▪ increase size, age structure and stability of populations ▪ increase functional effects of habitat and species in ecosystem ▪ increase species diversity by increasing size of protected populations ▪ protect integrity of habitat and beneficial effects on species and communities ▪ increase stability or resilience of populations, communities and ecosystems ▪ increase productivity of ecosystems	o enhance health and biodiversity of ecological communities in surrounding waters or in other connected MPAs by exporting individuals (young and adults) produced in MPAs o export beneficial materials (e.g., detritus) to ecosystems outside MPA

MPA Goal	Benefits of Accounting for Connectivity - Inside the MPA	Benefits of Accounting for Connectivity - Outside the MPA
Sustainable Production Goal: "Advance comprehensive conservation and management of the nation's renewable living resources and their habitats and the social, cultural and economic values and services they provide to present and future generations through ecosystem-based MPA approaches." (MPA Center 2015:13)	▪ increase size, age structure and stability of populations ▪ protect portion of populations and habitats within MPAs to support and replenish robust, resilient populations outside MPAs ▪ maintain genetic diversity by reducing harvest- induced genetic selection	o supplement fisheries harvest outside MPAs with exports of target species from MPAs into adjacent areas ("spillover" effect) o enhance fisheries by supplementing the habitat and ecosystems they depend on o protect against bycatch of overfished or protected species w/in the MPAs in order to avoid limits on fishing outside its borders. o Support resilience of coral communities that may succumb to and subsequently recover from episodic stressors. o Ensure adequate breeding/grazing areas for marine mammal and other migratory species to support population recovery and/or continued viability.

One Lesson of Connectivity: Protect Multiple Inter-Related Spatially Distinct Ecosystems within a Single MPA or within a Network of MPAs

The extensive connectivity of marine populations and ecosystems indicates a need to protect or enable ecologically important functional relationships among ecosystems in the design, use, and management of ecological MPAs and networks of ecological MPAs. This can mean protecting within a single MPA or a network of MPAs those ecosystems that function as nurseries for a given species or set of species *and* those ecosystems to which adult members of that species or set of species migrate, including spawning habitats (Figure 2.6). Mangrove forests, kelp forests and seagrass beds, all act as critical nursery habitat for juveniles of species whose adults inhabit offshore ecosystems. As such, protecting these nearshore ecosystems contributes to the structure, functions (including productivity), and services (e.g., fisheries) of the other ecosystems inhabited by adults.

These relationships can also influence the resilience of ecosystems. Coral reefs in French Polynesia and Australia that have experienced increases in cover of macroalgae due to sea urchin disease or hurricane damage can rebound when supported by adjacent seagrass and mangrove ecosystems. These ecosystems are nurseries for herbivorous fishes that continue to replenish populations on coral reefs, where they reduce algae and facilitate the recovery of corals (e.g., Adam et al 2011, Olds et al 2012a).

Similarly, adults of some marine fishes and some marine mammals migrate to different ecosystems to reproduce. For example, adult female lingcod, *Ophiodon elongatus*, a recreationally and commercially fished species along the West Coast of North America, migrate from deep rocky reefs to spawn with males on shallow rocky reefs each year. Male and female Nassau grouper, *Epinephelus striatus*, in the Caribbean annually migrate to and aggregate at specific sites on coral reefs to reproduce. Protecting spawning habitats by including both shallow and deep rocky reef ecosystems or spawning and nearby non-spawning sites on coral reefs within the same MPA facilitates these spawning migrations and the role of MPAs for conserving such species and the ecosystem services they provide (Figure 2.6A).

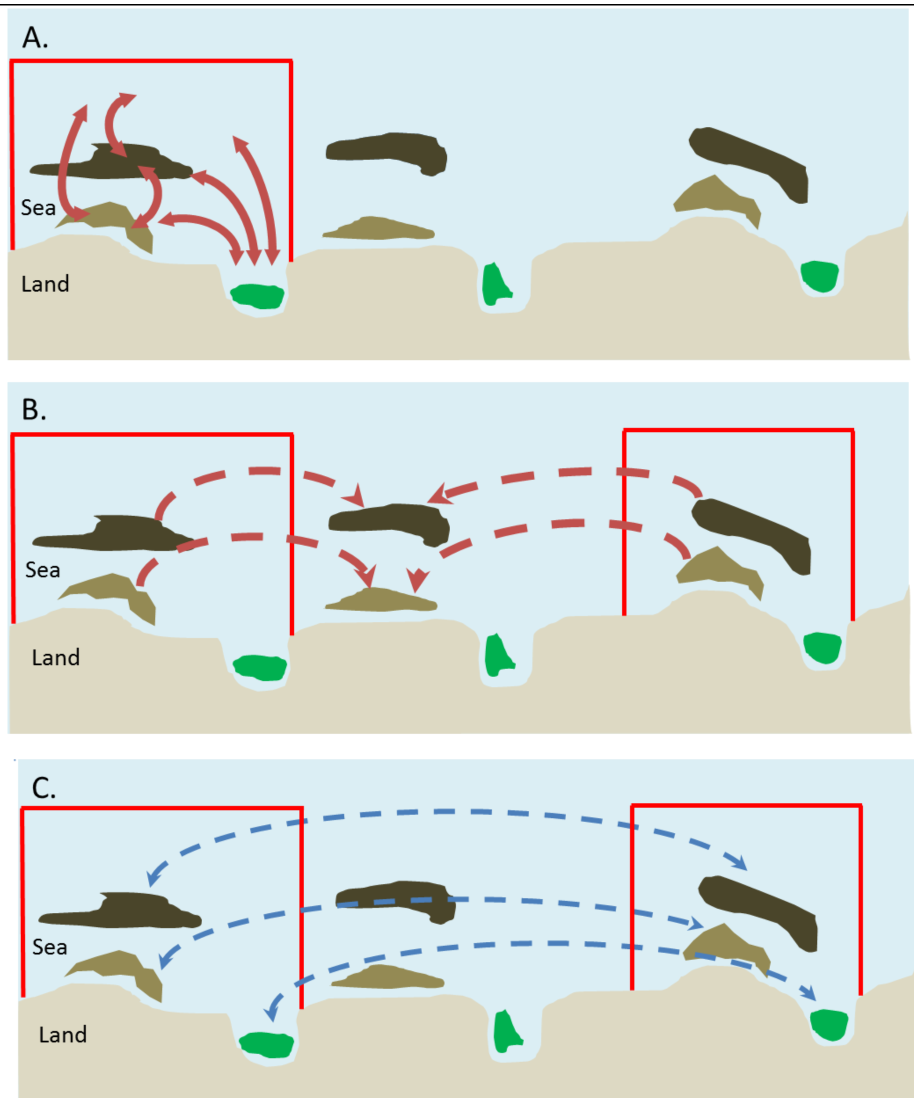

Figure 2.6. Patterns of ecological spatial connectivity relative to the placement of MPAs. Red lines depict MPA boundaries. (A) Solid red arrows depict ecosystem connectivity (movement of organisms, energy and nutrients between ecosystems) within an MPA. (B) Dashed red arrows depict export of individuals (larvae, spores) from inside to outside an MPA. (C) Dashed blue arrows depict dispersal of larvae from one MPA to another or to similar ecosystems in between adjacent MPAs (i.e. networked MPAs).

Another example involves nutrient and energy subsidies generated by one ecosystem for another. For example, large amounts of plant and algal detritus generated by seagrass beds in coastal embayments and kelp forests on shallow rocky reefs, respectively, are exported to, and are major sources of nutrient and energy for, adjacent intertidal and offshore ecosystems (e.g., deep rocky reefs, submarine canyons; Figure 2.4A). Similarly, the many anadromous species of salmon that are born in watersheds, migrate to sea as juveniles, and return to watersheds as adults to reproduce and die can create substantial influxes of energy and nutrients into watersheds where they are consumed by terrestrial predators (e.g., bears, eagles). Protecting these ecosystems that subsidize other ecosystems within an MPA help ensure those that functional relationships will be realized. All of these examples suggest that MPAs that encompass multiple adjacent ecosystems can enhance connectivity among ecosystems (Figure 2.6A)**.**

Another Lesson of Connectivity: MPAs Can Benefit Ecological Processes Inside *and* Outside MPA Boundaries

The functional relationships sustained by connectivity between linked ecosystems mean that MPAs can benefit ecosystems both inside and outside MPAs. These effects are dependent upon the degree to which the sites, and ideally networks of sites, are located, configured and managed to facilitate ecological linkages such as the movement of species and materials from ecosystems within MPAs to ecosystems outside MPAs (Figure 2.6B). Adult populations protected within MPAs can generate young that contribute to the replenishment of connected populations that are harvested (or have otherwise been diminished). As such, networks of MPAs that contribute to replenishment of populations across a mosaic of MPAs and populations contribute to both ecosystem and fishery conservation (Gaines et al 2010). Separately, as the number of adults builds within MPAs, juveniles and adults will move outside MPAs in search of resources (e.g., food). This "spillover" of adults can enhance local fisheries yield, especially of individuals larger than what is typically caught in the fishery. Because the number of older animals moving outside of MPAs is far fewer than the number of larvae, and because movement of older animals is over shorter distances, especially when they are fished close to the MPA, this influence on populations outside MPAs is generally much more limited in magnitude and distance. Tangible evidence of this phenomenon is the common practice of "fishing the line," in which fishing boats anchor immediately outside MPA boundaries in order to maximize their chances of catching fish moving outside the boundary.

For the many species whose young (algal spores, animal larvae and other propagules) are carried away from adult populations within MPAs, replenishment of those protected populations can be enhanced by locating them such that young generated in one MPA replenish populations in nearby MPAs (Figure 2.6C). These networks of MPAs enhance the replenishment of populations within MPAs across the network while also contributing to replenishment of populations between those MPAs.

CONCLUSIONS

In the ocean, living things often swim, drift, fly or walk from place to place throughout their lifetimes. This natural movement within and among habitats and ecosystems, here termed ***ecological spatial connectivity***, profoundly influences the structure and composition of local populations, communities and ecosystems. Each of the four types of ecological spatial connectivity outlined here (genetic, population, community and ecosystem) bears on ecological MPAs or networks of ecological MPAs, and so each must be taken into account in the use, design, and management of individual and networks of MPAs. How well MPAs succeed as tools for meeting natural heritage, sustainable production, and (some) cultural heritage objectives depends on how well these various forms of connectivity have been incorporated in MPAs' design and how well they are sustained by management of MPAs.

PART 3: Design, Use, and Management Principles for Enhancing Ecological Spatial Connectivity Processes Within, Around, and Among MPAs and MPA Networks

OVERVIEW

Part 3 expands upon Part 2. Part 3 offers specific principles for taking connectivity into account in the design, use, and management of ecological MPAs. As shown here, design, use, and management principles depend, first, on the ecological focus of the MPA, and, second, on the particular biological and ecological characteristics of the species, communities, or ecosystems of concern in an MPA. Principles are offered here for design, use, and management of two sorts of MPAs: (1) those that aim to restore, maintain, or enhance specific populations of one or more marine species, and (2) those that aim at enabling marine communities and ecosystems to flourish.

ECOLOGICAL MPAS AND PRINCIPLES FOR INCORPORATING CONNECTIVITY

As discussed in Part 2, many US MPAs are ecological MPAs, aimed at restoring or maintaining ecological phenomena in the marine environment. One major subset of ecological MPAs is species-focused, i.e., MPAs established to enhance, maintain or restore specific populations of one or more species, either for sustainable production (e.g., sustainable fisheries), for natural heritage conservation (e.g., protection of rare or endangered species from human use or negative influence), or, in some cases, for cultural heritage conservation. Another major subset of ecological MPAs is community- or ecosystem-focused, i.e., MPAs established to enable the non-human component of ecological communities and ecosystems to flourish, for natural heritage conservation (e.g., protection of biodiversity or ecosystem structure and function), for sustainable production (e.g., protection of the habitats of economically important species), or for cultural heritage conservation. See Table 3.1.

Table 3.1: Ecological MPAs, by Ecological Focus and by MPA Goal Area

		Ecological Focus	
		species	community or ecosystem
MPA Goal	natural heritage	x	x
	sustainable production	x	x
	cultural heritage (some)	x	x

As Part 2 showed, the realities of ecological spatial connectivity pose challenges and provide opportunities for ecological MPAs. To address these challenges and opportunities, scientists and policy-makers have used knowledge about connectivity to generate design, use, and management principles for taking ecological spatial connectivity into account in ecological MPAs and MPA networks. Use of these principles incorporates connectivity processes into ecological MPAs and MPA networks and so maximizes the effectiveness of these MPAs and MPA networks in meeting their specific objectives.[9]

Design, use and management principles for taking connectivity into account depend, in given instances, on the ecological focus of the MPA or network of MPAs. The discussion below first discusses design, use and management principles for species-focused MPAs, and then discusses design, use, and management principles for community- or ecosystem-focused MPAs.

Principles for taking connectivity into account also depend, in given instances, on the specific biological and ecological characteristics of the species, communities, and ecosystems of concern in the MPA or the network of MPAs. Thus, design, use, and management principles are tailored *both* to the ecological focus of an MPA or network of MPAs *and* to the specific biological and ecological characteristics of the species, communities, and ecosystems of concern in the MPA or network of MPAs.

The design, use and management principles address numerous parameters. These include: (1) the location of an MPA; (2) the size and shape of an MPA; and (3) whether the MPA is an individual, stand-alone MPA or is part of a set of inter-dependent MPAs, i.e., a network of MPAs. They also include: (4) whether management of an MPA aims at intended effects within MPA boundaries or outside MPA boundaries (or both); (5) attentiveness to management regimes within an MPA and to management regimes in areas outside the MPA; and (6) attentiveness to specific relationships between the management regimes inside an MPA and those outside an MPA.

WHEN THE ECOLOGICAL FOCUS IS RESTORING OR MAINTAINING SPECIES POPULATIONS

Many MPAs are created to restore, maintain, or enhance populations of one or more specific species. ***Population connectivity*** (the movement of individuals between spatially distinct subpopulations) creates both profound opportunity and challenges for such MPAs. Different species have different population connectivity characteristics, and these specific population connectivity characteristics must be taken into account. Most marine species produce young (spores, eggs, larvae) that can be carried 10's to 100's of kilometers by ocean currents, while some species produce young that typically disperse much shorter distances. Generally, the greater the distance that young typically disperse from adult populations, the greater the degree of connectivity among spatially distinct populations.

Species with short distance dispersal (the rarer case)

For species with short-distance dispersing young, the larger the MPA and higher the habitat quality, the more likely populations within the MPA will be self-sustaining within that individual MPA (Figure 3.1).

[9] The many implications of spatial ecological connectivity for the design, use and management of MPAs summarized here are drawn from the literature (see recent review by Botsford et al 2014).

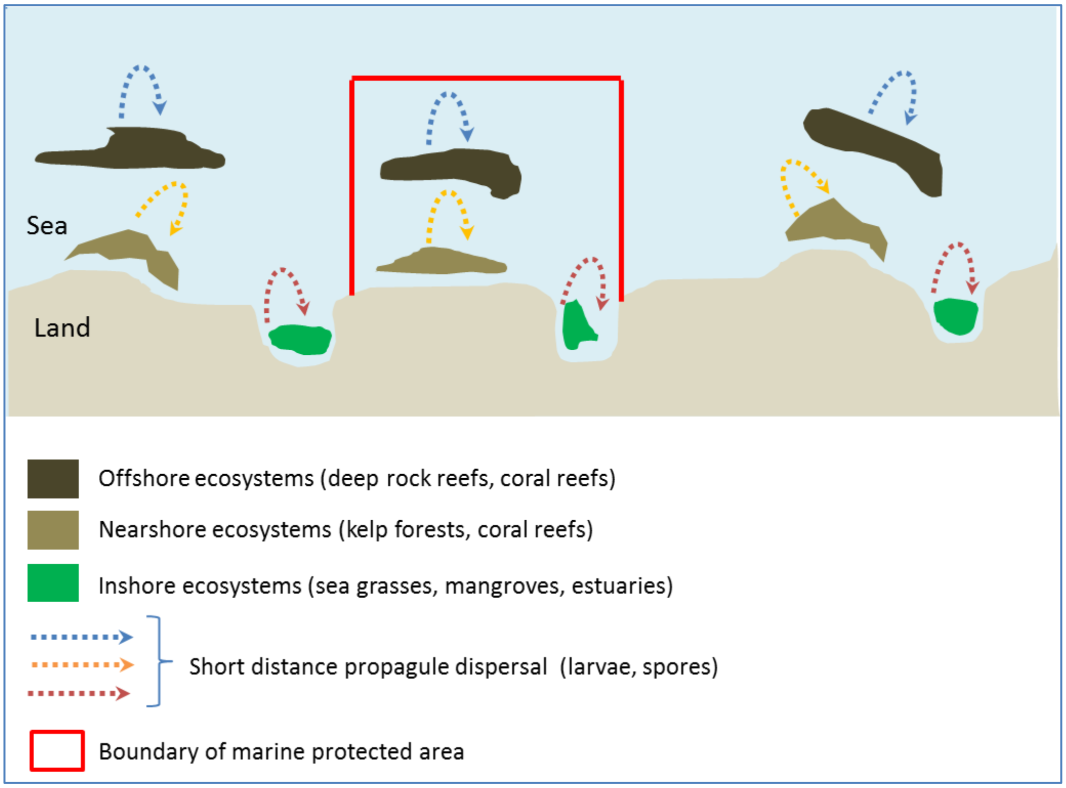

Figure 3.1. Production of short distance dispersing young (larvae and juveniles of some fishes and invertebrates, or spores of many algae) within MPAs is retained within MPAs. Such populations are self-replenishing, but contribute little to the replenishment of populations beyond their immediate boundaries (other MPAs or populations outside MPAs).

Species with long distance dispersal (the more common case)

For species with long distance dispersal, the young produced by adults within an MPA are as, if not more, likely to replenish populations *outside* that MPA than inside (i.e. high population connectivity; Figure 3.2). For these long distance dispersal species, MPAs can be used to help replenish (i.e. sustain or restore) populations outside of MPAs. However, this same high population connectivity poses a challenge to the goal of protecting populations of these same species *within* MPAs because maintenance of an adult population within the MPAs can be reliant on the delivery of young produced elsewhere (i.e., outside the MPAs) to sustain or restore the adult populations within MPAs.

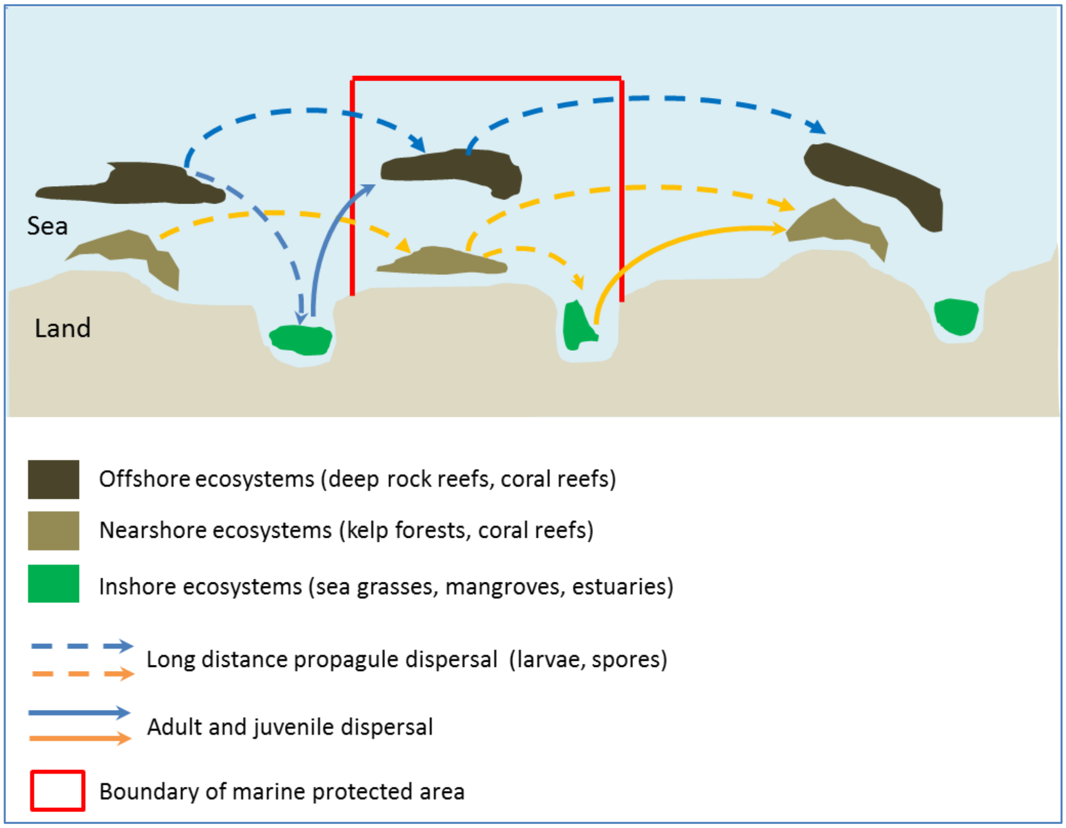

Figure 3.2: Production of long distance dispersing young (larvae of fishes and invertebrates, or spores of some algae) within MPAs are transported to populations outside MPAs, leaving the replenishment of populations of these species within MPAs reliant on delivery of young produced elsewhere (other MPAs or populations outside MPAs).

Long distance dispersal species: Enabling populations *within* the boundaries of an MPA

For species whose young disperse long distances, the replenishment of populations *inside* MPAs is complex as a population inside an MPA depends heavily on the import of young from outside the MPA's borders. The replenishment of populations inside MPAs in this circumstance can be greatly influenced by the condition (i.e. number, size, reproductive condition of adults) of the populations outside the MPA, and hence often depends on use and management of the populations outside the MPA.

There are two key management approaches that can enhance the condition and ability of populations outside an MPA to contribute to replenishment of populations inside the MPA. The first is to adopt programs to actively *manage the condition of the populations outside the MPAs (e.g., to manage fisheries, water quality, habitat quality outside the MPA).* The second is to *create networks of individual MPAs such that young produced in one MPA migrate and recruit into another MPA* (Figure 3.3). The successes of these two approaches to sustaining populations inside MPAs depend, for the first approach, on how well the populations and habitats outside the MPAs are managed (the better that populations and habitats outside MPAs are managed, the more they will enhance the condition of populations within MPAs) and, for the second approach, on a number of MPA design criteria, including the overall area set aside in a network of MPAs and the size and spacing of the individual MPAs in a network (reviewed in Botsford et al 2014).

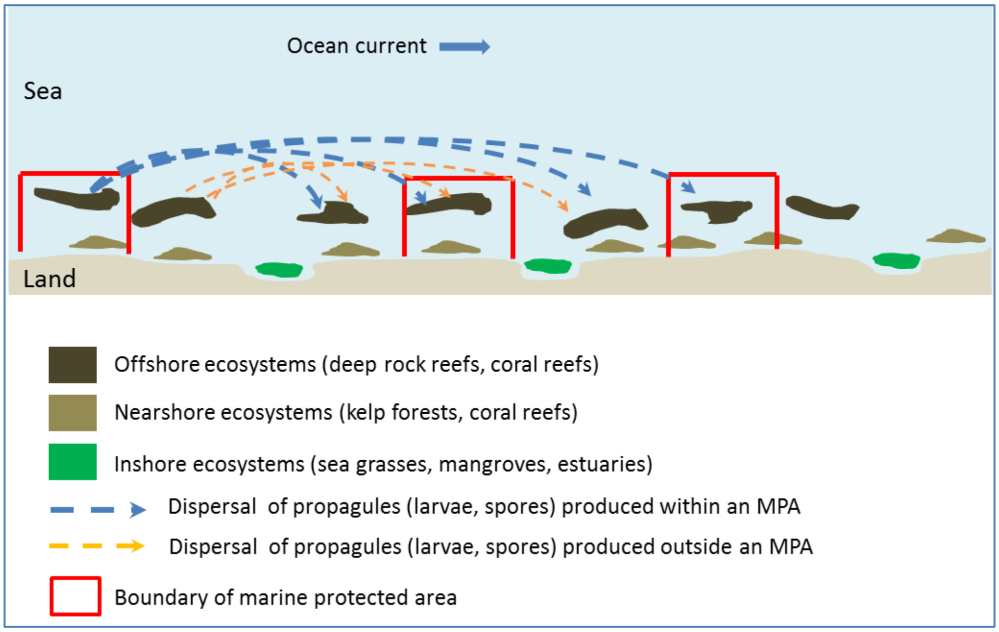

Figure 3.3: Depiction of a MPA network in which long distance dispersing propagules (animal larvae, algal spores) produced by adults inside and outside MPAs are transported by ocean currents to other MPAs and the populations between them. Blue and orange arrows distinguish propagules produced inside and outside MPAs, respectively. Line thickness reflects the number of larvae dispersing from a population. The thicker blue line represents the greater number of larvae dispersing from populations of adults protected within MPAs.

For either of these methods (fisheries management and other environmental management in areas outside MPAs or MPA networks) to contribute to the sustainability of populations both inside *and* outside of MPAs, the quality of *habitat* that species depend on must be protected. (See point 5 below.)

Long distance dispersal species: Contributing to populations *outside* the boundaries of an MPA

MPAs can contribute to the sustainability of exploited populations outside of MPAs and the fisheries they support in three key ways: through larval production, through adult "spill-over," and through juvenile habitat protection:

(1) <u>Sources of larval production</u>*:* First and most importantly, MPAs can function as sources of larval production, which is exported to replenish populations outside MPAs. For MPAs to contribute, through larval production, to the replenishment of populations outside of MPAs, *many smaller MPAs may be more effective than single large MPAs of the same area (or proportion of a regional population)* (Figure 3.4).

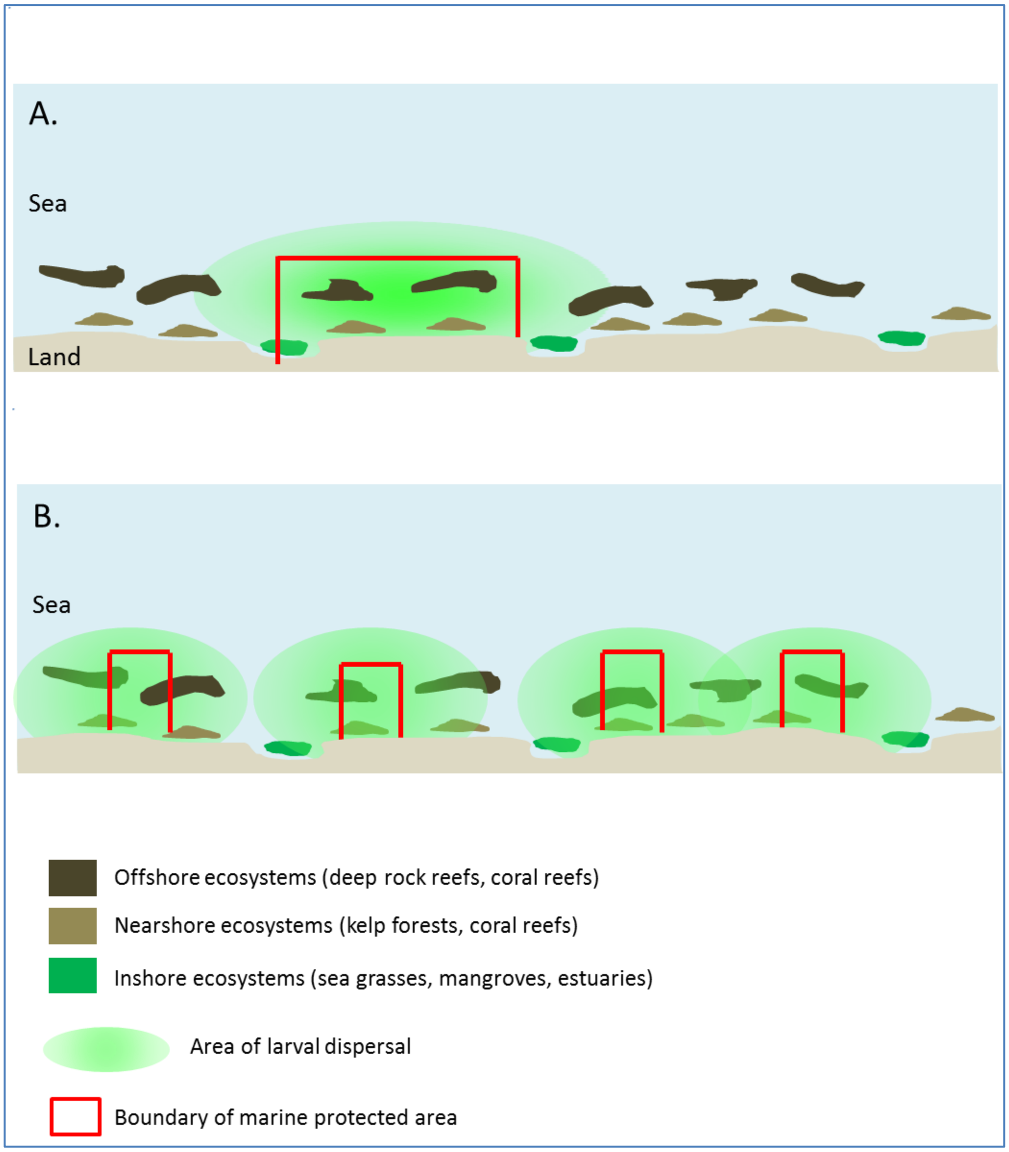

Figure 3.4: Comparison of area of coastline replenished by larvae (green oval) produced in (A) a single large MPA versus (B) several smaller MPAs. Because larval dispersal distances are similar for a species in large and small MPAs, the area of coast replenished by several small MPAs is greater than the area of coast replenished by a single large MPA of a size equal to the combined areas of the several small MPAs.

The proportion of young exported from a population within an MPA increases as MPA size decreases. Only a portion of the young produced in a single large MPA will disperse to populations outside the MPA and the area over which they replenish populations is limited to the distance that young disperse from that MPA. By distributing the same amount of total area across multiple MPAs separated by the distance that young disperse, more of the region will be replenished by larvae produced in MPAs (Figure 3.4). Also, importantly, smaller MPAs can often be more easily accommodated by fishing communities along the coast, and a greater number of fishing communities can benefit from larval production in multiple smaller MPAs than could benefit from larval production in one single large MPA, even where the total area within the MPAs (the one large MPA or the multiple smaller MPAs) is the same.

As already noted, for MPAs to be productive sources of larvae, *MPAs should include high quality, productive adult habitat and species need to be well protected*.

Finally, the distance and direction that larvae travel from an MPA depend on ocean currents, and therefore *the location of an MPA in a pattern of ocean circulation will determine whether and to which populations the larvae are delivered.*

(2) Spill-over effects (adults)*:* A second means by which MPAs can enhance populations outside of MPAs is the "spill-over" of adults that migrate out of MPAs in response to crowding caused by high densities of protected individuals. The *smaller the MPA relative to the home range of the adults or the greater the ratio of the length of the MPA border to the MPA area - and the better the continuity of habitat and movement corridors - the greater the movement of individuals out of MPAs into adjacent areas*. This said, however, *a minimum MPA size is required to ensure sufficient population protection and size to sustain a spill-over effect* (Figure 3.5).

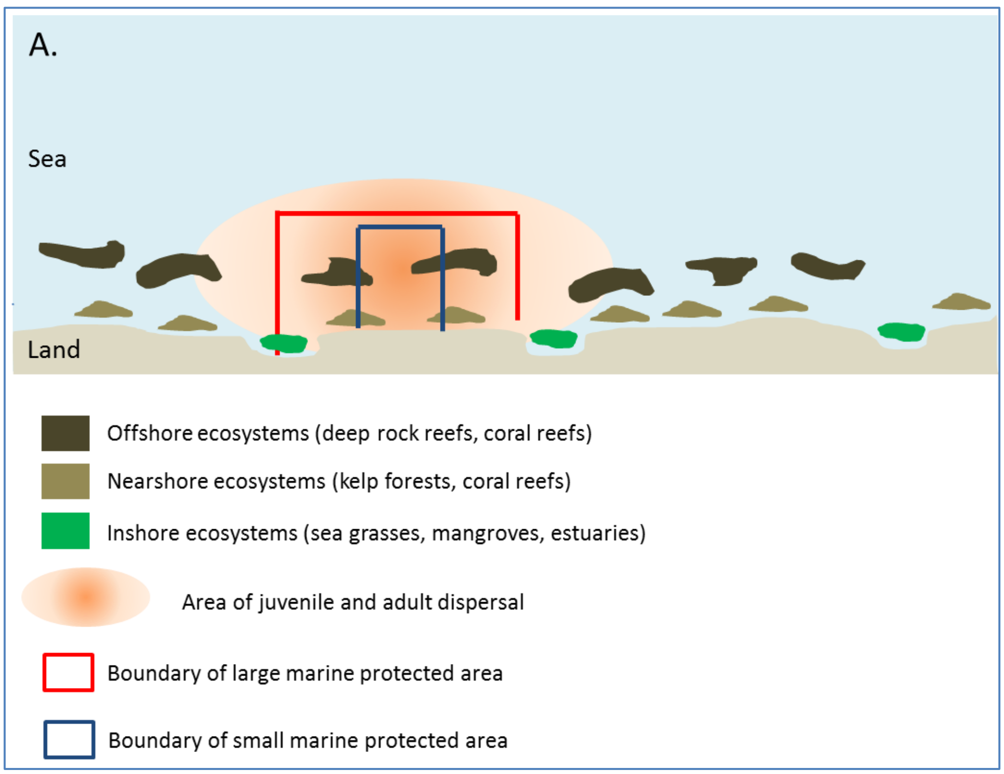

Figure 3.5: The distance that juveniles and adults disperse (orange oval) is independent of the size of an MPA. Therefore, the smaller the MPA, the greater the number and proportion of individuals in a population will emigrate from the MPA.

(3) Nursery habitat protection (juveniles): The third way that MPAs enhance populations outside their boundaries is to act as productive nursery habitat. When this is the objective, there are three key design and management factors. First, the *MPAs should be located on productive nursery grounds.* Second, *the MPAs should be located in close proximity to adult populations outside their boundaries*. Third, MPA management needs to *protect the quality of nursery habitat by protecting the biotic (e.g., seagrasses, mangroves) and abiotic (e.g., water quality, seafloor features) conditions required for the growth and survival of juveniles*. This protection of important nursery grounds is a key means by which MPAs can enhance the sustainability of populations in a region, including fished populations.

The critical importance of ensuring multiple high quality habitats for conservation target species

As noted throughout, a key management and design goal of MPAs that aim to restore, maintain or enhance populations of one or more particular species is to *include and protect high quality habitat for those species within the boundaries of the MPAs*. MPAs can help sustain populations *inside or outside* their boundaries by *protecting habitat essential for either reproduction or that acts as nursery grounds* regardless of whether young remain within the MPA or migrate to adult habitat outside of MPAs. For populations within MPAs to be replenished by young that use particular nursery habitat, *nursery habitats should be protected within the same MPA inhabited by adults* or *MPAs should be located in close proximity to nursery habitats to ensure that young will migrate to and replenish populations within the MPAs*. Including nursery habitat and adult habitat within the same MPA increases the likelihood that young will replenish populations within the MPA and that the nursery habitat will be protected. Examples include the inclusion of ecosystems known to be important nursery habitats for fishes and invertebrates (e.g., mangrove forests, seagrass beds, estuaries, kelp forests) (Figure 3.6).

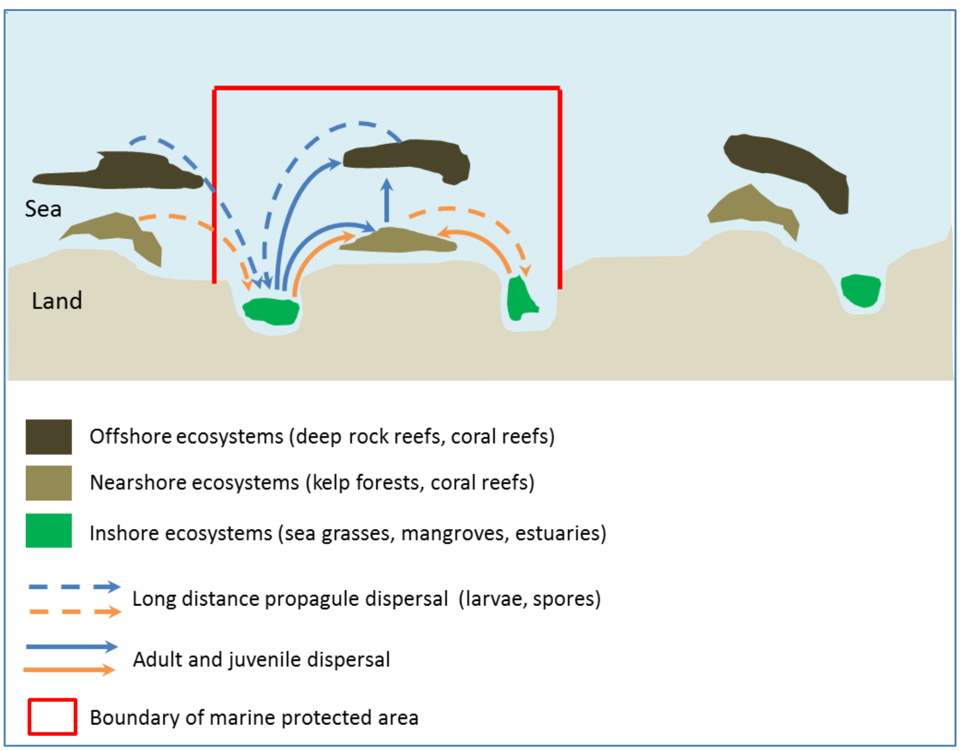

Figure 3.6: Inclusion of multiple habitats (ecosystems) used by individuals over their lifetime (larvae, juveniles and adults) ensures that adult populations within an MPA will be replenished.

individuals among populations) is essential for maintaining genetic diversity across a species' range. Fishing and other human activities can reduce the genetic diversity of fish, invertebrate and algal populations. *MPAs distributed across a species' range in order to contribute to gene flow throughout the species' range are more likely to protect the breadth of a species' genetic diversity* and not simply the genetic composition unique to some portion of a species range.

WHEN THE ECOLOGICAL FOCUS IS PROTECTING THE STRUCTURES AND FUNCTIONS OF ECOLOGICAL COMMUNITIES AND ECOSYSTEMS

The structure of an ***ecological community*** comprises the particular species that inhabit an ecosystem, their relative abundance and species diversity. The structure of an ***ecosystem*** includes the ecological community and also the physical and chemical characteristics of the geologic (e.g., seafloor types and features) and oceanographic (water masses, quality and features) elements of the environment. The functions of an ecological community include the ways nutrients and energy are incorporated into the community (e.g., through primary producers, planktivores, detritivores), the community's biological productivity, and its other ecological functions (e.g., nursery habitat). Ecosystem function includes the function of abiotic elements such as buffering physical and chemical stressors and the export of nutrients and energy to other ecosystems. Just as with populations, communities are associated with specific habitats (e.g., substratum type, water depth), and ***community connectivity*** and ***ecosystem connectivity*** occurs between communities and ecosystems of similar habitat features.

Connectivity between protected communities and ecosystems requires that MPAs near one another include similar habitats and ecosystems. To address community connectivity, *MPAs should be spaced within the dispersal distances of the species that constitute the communities* to ensure that those species replenish and sustain the communities (Figure 3.7; this is analogous to the principles for addressing population connectivity, discussed above). Because different species have different dispersal distances, *MPA size and spacing are inter-related. MPAs need to be spaced close enough for long and intermediate dispersing species to disperse between MPAs with similar ecosystems. For the short dispersing species that can't disperse between adjacent MPAs, MPAs need to be large enough for short dispersing species to be self-replenishing*. *Larger, more self-replenishing MPAs can be spaced further apart, whereas smaller MPAs should be spaced closer together to enhance connectivity.* MPAs that are linked through larval dispersal, as depicted in Figure 3.7, constitute a *network* of MPAs.

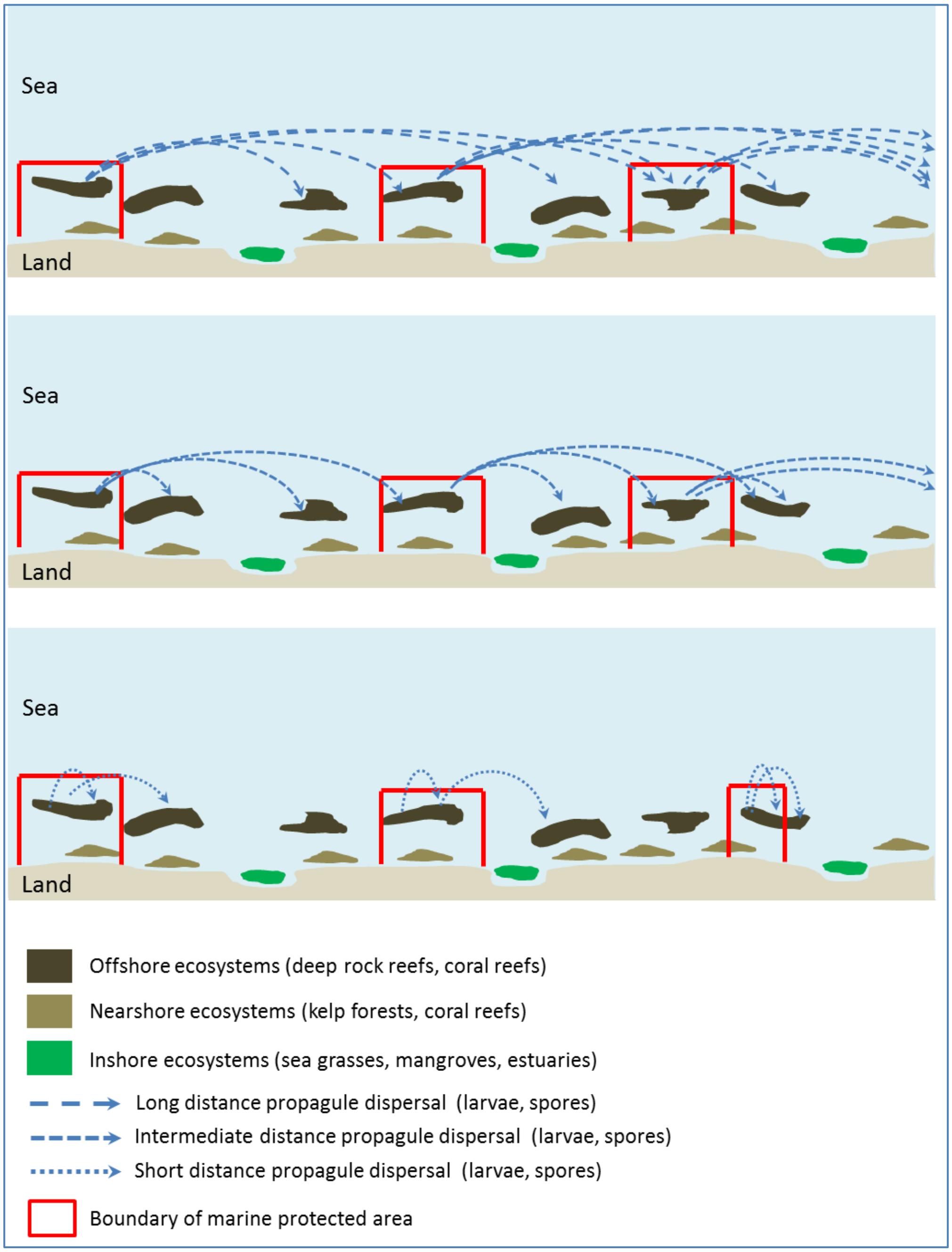

Figure 3.7: MPA size and spacing are inter-related. MPAs should be spaced based on dispersal distances of species that constitute the communities they are created to protect. Here, dispersal of long-distance and intermediate-distance dispersing species contribute to replenishing communities in adjacent MPAs, as well as to communities between the MPAs (top and middle panel, respectively). However MPA spacing here is too distant for connectivity of short-distance dispersing species (bottom panel). To also protect the short-dispersing species in a community, the individual MPAs need to be large enough to encompass dispersal of short-distance dispersers such that those populations are self-replenishing. Note that there may also be dispersal from communities in habitats *between* the MPAs depicted here (see Figures 3.2 and 3.3 and accompanying discussion); the extent of dispersal from communities outside the MPAs depends on the condition of those communities. And the condition of those communities depends in large part on the success of management regimes for areas outside the MPAs.

Communities and ecosystems interact with one another (e.g., there is movement of nutrients, energy, species between communities and ecosystems) and these interactions allow "donor" ecosystems that export material to have strong influences on adjacent "recipient" ecosystems. These influences include strong effects on the productivity and diversity of the recipient ecosystems. *MPAs that include multiple habitat types and associated communities and ecosystems are more likely to protect the natural structure and function of each of those communities and ecosystems by ensuring connectivity*. Two of the strong determinants of community and ecosystem structure are water depth and substratum type. Therefore, *MPAs that extend across a range of water depths and include multiple substratum types are likely to include a diversity of communities and ecosystems and facilitate interaction among those communities and ecosystems* (Figure 3.8).

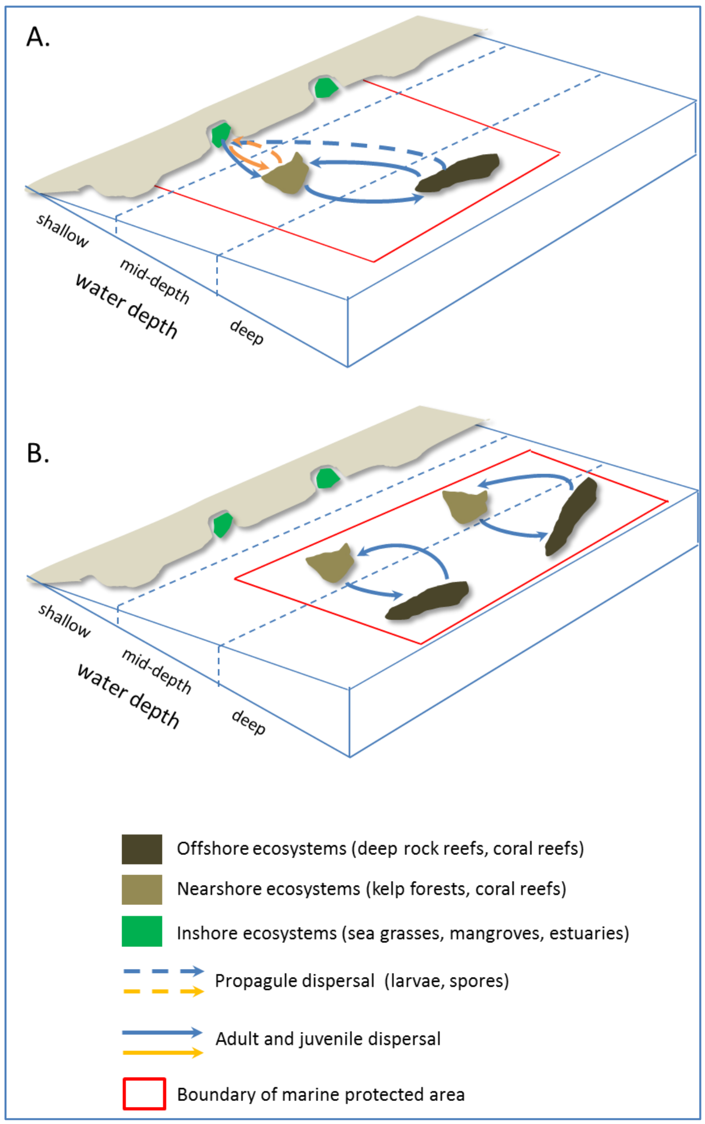

Figure 3.8: MPAs that extend across depth zones protect species that migrate among ecosystems at different depths over their lifetime. (A) MPAs that extend from offshore to inshore enhance connectivity between inshore and offshore ecosystems, including the use of inshore nursery habitat (e.g., seagrasses, mangroves) by adult populations offshore (coral and rocky reefs). (B) Offshore MPAs that extend across depths enhance connectivity between ecosystems at different depths, including adults that migrate between deep and shallow reefs to spawning habitats.

Specific ecosystem and community types, though characterized by certain commonalities, vary by geographical location in important particulars. As examples, kelp forest ecosystems and coral reef ecosystems are each characterized by certain characteristics, but their particular species compositions and aspects of their structure and function vary with geographical location. Kelp forests distributed along the coast of California differ markedly in their species compositions as do coral reefs distributed along the Florida Keys. This geographic variation within a single ecosystem or community type can include differences in the economically important species or services the ecosystem or community supports (e.g., fisheries, ecotourism). Therefore, *protecting the diversity of species, structures and functions of a specific community or ecosystem type and the resources and services it supports requires that MPAs protect that ecosystem or community type across a broad geographic gradient*.

Ecosystem connectivity can be a cause of concern when adjacent ecosystems have deleterious effects on one another. This is especially the case at the land-sea interface when coastal run-off or riverine discharges expose coastal marine ecosystems to eutrophication or contaminants. Therefore, *adjacent ecosystems, including those on land, need to be managed such that deleterious impacts to ecosystems within an MPA are prevented.* In places where the coastal environment is well managed - where agricultural run-off, industrial pollution, and the like are well-managed – an MPA that designed to improve ecological connectivity and conditions is more likely to succeed.

CONCLUSIONS

Taken together, genetic, population, community and ecosystem connectivity are all extremely important ecological processes that greatly influence many of the attributes that ecological MPAs are meant to protect and enhance (e.g., biodiversity, productivity, ecosystem services). Knowledge of the various forms of ecological spatial connectivity can be applied to both the design and management of single MPAs or networks of MPAs to better achieve their intended conservation and management goals.

PART 4: Climate Change in the Marine Environment: Another Compelling Reason for Connectivity-Informed MPAs and MPA Networks

OVERVIEW

Part 4 links the importance of taking connectivity into account in the design, use, and management of MPAs to meeting the challenges of climate change in the marine environment.[10] Physical and chemical changes in the marine environment are producing changes in species' distributions, abundances, and productivities. These ongoing and future changes in species' distributions, abundances, and productivities can greatly complicate the use of place-based conservation tools in the marine environment, i.e., MPAs and MPA networks. However, MPAs and MPA networks that are built, used, and managed to foster connectivity processes - connectivity-informed MPAs and MPA networks - can best address the ecological changes brought about by climate change. For example, MPAs and networks of MPAs designed, used, and managed around knowledge of organisms' movements through space and their population structures across space can help facilitate changes over time in these movements and structures. These connectivity-informed MPAs and MPA networks must be monitored, evaluated, and adaptively managed, however, so that they can respond to and possibly further anticipate changes in species' distributions, abundances, and productivities.

GLOBAL CLIMATE CHANGE AND THE MARINE ENVIRONMENT

Physical and Chemical Changes in the Marine Environment

Global climate change manifests in many ways in the marine environment (Figure 4.1, Table 4.1, Harley et al 2006, Hoegh-Guldberg and Bruno 2010, Hoegh-Guldberg et al 2014, Doney et al 2012, 2014, Poloczanska et al 2013, Bruno et al 2014). Some of these manifestations or changes are occurring more rapidly in the marine environment than they are on land (Burrows et al 2011).[11] The changes are both physical and chemical, and they have myriad ramifications for organisms, populations, and ecosystems as well as for the services that these organisms, populations, and ecosystems provide society (e.g., fisheries, coastal protection, recreation, carbon sequestration). Few of the changes are or will be in the same direction (i.e., increase or decrease) everywhere. For example, salinity will increase in areas of the ocean where evaporation exceeds precipitation and decrease where precipitation and coastal runoff exceeds evaporation. This geographic mosaic of varying changes in environmental conditions is most complex along the coast, where complex interactions across the land-sea interface and coastal currents (including coastal upwelling) interact with the heterogeneous coastlines (e.g., headlands, embayments). Thus, most environmental responses will vary depending on local and regional conditions.

Changes in one environmental variable can lead to changes in others. For example, changes in sea surface temperature, heated by increasing air temperature, can lead to changes in salinity, dissolved oxygen levels, pH, nutrient levels, and the direction and velocity of ocean currents. Similarly, changes in coastal winds and surface currents cause changes in the location, frequency, seasonal timing, and intensity of coastal upwelling (a process whereby surface waters move offshore and are replaced by

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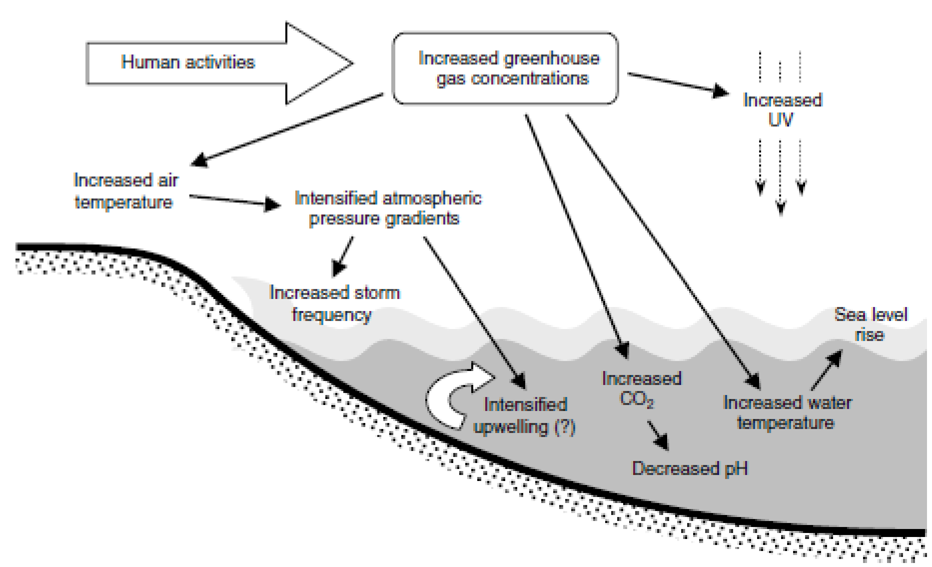
[10] As noted, this paper builds in part on an earlier set of MPA FAC recommendations; see "Climate Change in the Ocean: Implications and Recommendations for the National System of Marine Protected Areas" (MPA FAC 2010), available at http://marineprotectedareas.noaa.gov/fac/products/ (2010 products). See also MPA FAC Scientific and Technical Subcommittee (2010).

[11] As noted (see n. 5 above), the marine environment includes intertidal areas, bays, and estuaries, and many of the physical and chemical changes described here are particularly pronounced in these areas.

colder, nutrient rich waters from depth and which greatly enhances ocean productivity; Bakun and Nelson 1991). Predicted changes in the location, frequency, and intensity of upwelling (Bakun 1990, Bakun and Weeks 2004, Snyder et al. 2003, Diffenbaugh et al. 2004) appear to be occurring, including along the West Coast of North America (Sydeman et al 2014). The intensity and frequency of episodic climatic events such as El Niño and La Niña are predicted to increase (Trenberth and Hoar 1997, Gergis and Fowler 2009) or at least change (Collins et al 2010). Often, strong storms and waves are associated with El Niño events (Barnard et al 2015). The impact of these storms could be exacerbated by predicted rising sea levels (e.g., Church and White 2006, Harley et al 2006). Otherwise, changes in wave height and frequency are unclear, though the angle of swell and waves is also predicted to change (Erikson et al 2015). Localized changes in physical conditions along the coast include changes in turbidity and river plumes associated with changes in storms, precipitation and freshwater discharge into coastal waters. Chemical changes include hypoxia (low oxygen) events (Rabalais et al. 2009, Doney et al 2012), reduced salinity associated with freshwater influx, and ocean acidification (Orr et al., 2005, Doney et al 2009, 2012, Feely et al., 2009) directly related to increasing atmospheric carbon, a driver of climate change.

Figure 4.1: Many of the physical and chemical changes in the marine environment associated with climate change (from Harley et al 2006).



Ecological Changes in the Marine Environment

All of the physical and chemical changes in the marine environment can directly influence growth, survival, and reproduction of individual marine organisms, which in turn influence the size, distribution, seasonal timing, and dynamics of marine populations, the species composition of their ecological communities, and the structure and functions (including productivity) of the ecosystems where they occur (Bruno et al 2014). See Table 4.1 for an overview. Following this tabular overview, three types of highly significant ecological changes - shifts in species distributions, changes in ecological communities, and changes to ecosystems - are reviewed more fully.

Table 4.1: Examples of physical and chemical environmental variables in marine and coastal waters that will change with changing global climate, and their ecological consequences (see additional citations in main text)		
Environmental variable	***Predicted / observed change***	***Ecological consequences***
Ocean temperature	Increase in some locations, decrease in others	Change in individual growth rate, survival, larval durations; species abundance, phenology and distributions; structure and productivity of communities and ecosystems (e.g., Edwards and Richardson 2004, Richardson 2008)
Ultraviolet radiation (UVB)	Increase	Direct mortality to a wide variety of taxa (e.g., references in Harley et al 2006, Llabres et al 2013)
Sea level	Increase	Increase or decrease in estuarine and intertidal habitat
Ocean salinity	Increase in some locations, decrease in others	Reduced growth rate, survival, larval durations, change in species abundance and distributions
Dissolved oxygen	Decrease	Reduced growth rate, survival, larval durations, change in species abundance and distributions
Ocean acidity (pH)	Increase in ocean acidity as pH decreases.	Reduced growth rate, survival, change in species abundance and distributions (Kroeker et al 2010, 2013)
Storms, waves	Increases in the intensity and frequency of wave energy, alters intertidal habitat (e.g., sandy beaches), increases coastal erosion, etc.	Causes mobile species to move, dislodges sessile organisms, including foundation species (seagrasses, mangroves, corals, algae), changes the species composition and functions of coastal ecosystems.
Winds, coastal upwelling	Increase in some locations, decrease in others	Changes the distribution and magnitude of coastal ocean productivity. Influences local ocean chemistry (hypoxia, temperature, etc.) and local manifestation of ocean acidification.
Ocean currents	Change	Changes in the direction and distance that spores and larvae are transported; changes in the distribution of tolerable and intolerable environmental conditions and habitat quality for all life stages; changes in coastal upwelling.
Sea ice	Decrease	Shifts in species distributions (Mueter and Litzow 2008).

Table 4.1: Examples of physical and chemical environmental variables in marine and coastal waters that will change with changing global climate, and their ecological consequences (see additional citations in main text)		
Environmental variable	***Predicted / observed change***	***Ecological consequences***
Precipitation, runoff (changes in estuarine salinity, nutrients)	Increase in some locations, decrease in others	Most pronounced in coastal embayments and estuaries where changes in salinity, pH and nutrients influence the physiological performance of individuals and the distribution, abundance and productivity of populations and ecosystems.
ENSO (El Niño, La Niña)	Change in frequency, intensity	Altered frequency and intensity of changing water temperature and productivity influences the distribution and productivity of populations, and storms impact nearshore ecosystems (see above).

<u>Shifts in species distributions</u>:

Among the most obvious and pronounced ecological responses to physical and chemical changes in the marine environment are shifts in species distributions. These shifts can occur in various ways. Because the distributions of pelagic species in the open ocean correspond with highly productive ocean fronts that form between major currents and other features, predicted changes in the distribution of currents and fronts suggest changes in the distribution of pelagic species from phytoplankton to cetaceans. In both pelagic and coastal waters, shifts in the latitudinal distributions of species corresponding with changing water temperatures have been predicted (e.g., Cheung et al 2009, Burrows et al 2014), and observed in paleoclimatic and paleobiogeographic records (e.g., Roy et al 2001, Precht and Aronson 2004, Aronson et al 2009), and contemporary distributional records of many species (Perry et al 2005, Parmesan 2006, Helmuth et al 2006, Harley and Paine 2009, Lejeusne et al 2009, Ling et al 2009, Sumalia et al 2011, Yamano et al 2011, Pinsky and Fogarty 2012, Pinsky et al 2013). For example, fisheries records in the North Sea indicate a gradual shift of species northward and to deeper waters as average annual temperatures in the North Sea have risen (Perry et al 2005, Dulvy et al 2008).

Such changes in species ranges reflect shifts in patterns of dispersal of algal spores and invertebrate and fish larvae and/or the movement of adults in response to changing environmental conditions. Both mechanisms of range shift (larvae and adults) are likely to occur for pelagic species, whereas spore and larval dispersal are likely to play a greater role for bottom-dwelling algae, invertebrates, and fishes, especially sessile species (algae and many invertebrates), relatively sedentary invertebrates, and fishes with small home ranges. Patterns of larval dispersal are affected by a number of factors including timing and location of spawning, current direction and velocity (advection, diffusion), prey availability, habitat suitability, and the behavior, duration, and survival of larvae (e.g., Pineda *et al*. 2007). All of these environmental variables and larval traits are known to be influenced by conditions associated with climate change. For example, the duration of the larval stage decreases with increasing water temperature, and this decrease shortens the time and distance that larvae are transported. Thermal stratification and lower productivity in surface waters reduce prey production and availability, reducing the survival and number of larvae transported between populations.

Alternatively, or in addition, some species shift their depth distributions, moving to deeper cooler water as the temperature of surface waters increase (e.g., Harley et al 2006, Dulvy et al 2008). In contrast, inshore encroachment of deep hypoxic waters forces species to move into shallower waters, such as Dungeness crabs along the coast of Oregon (Keller et al 2010). Without wholesale shifts in species ranges, those portions of a species' populations that inhabit refugia from intolerable conditions become very important to the persistence and re-establishment of a species across its range. For example, coral species off Panama whose depth ranges extended to deeper cooler waters effectively retracted to this thermal refuge via differential survivorship during an El Niño event that greatly increased shallower water temperatures. These species were able to persist at depth and recolonize shallower waters from this deep water refuge when conditions in shallow waters became tolerable again. Other species whose range did not extend or did not shift via larval dispersal to deeper waters were driven locally extinct (Smith et al 2014).

Separate from the processes that determine where larvae are transported and where adults move is the condition of the habitats in which they relocate. Larval settlement of many species is facilitated by chemical and physical cues (e.g., sea urchins, abalone and corals settle to coralline algae), including biogenic structure (e.g., sea grasses, mangroves, corals, algae) that provide refuge from predators. To ensure that species distributions can shift across latitudes and depths, appropriate habitat that is not degraded by climate change (e.g., temperature, hypoxia) or other anthropogenic impacts (e.g., pollution, habitat destruction, coastal development) must be intact and available.

Shifts in species distributions lead to changes in ecological communities

Changes in species ranges lead to changes in the species composition of ecological communities, creating new competitor and predator-prey interactions. For example, the extension of the geographic range of the tropical sea urchin, *Centrostephanus rodgersii*, south along the east coast of Tasmania allowed this species to overgraze and remove sections of kelp forests. However, urchin numbers were kept in check - and kelp was maintained - in marine reserves that helped to maintain numbers of large native lobster, the urchins' predator (Ling and Johnson 2012). Results such as these demonstrate how MPAs can enhance the resistance and resilience of ecosystems to species invasions and their detrimental effects caused by climate change. Changing environmental conditions can also increase or decrease the strength of important existing species interactions in a community. Examples include the changes in abundance and interaction strengths of foundational species, including algae, seagrasses and corals (e.g., Harley et al. 2012), ecosystem engineers (e.g., sea urchins), and keystone species (e.g., Sanford 1999).

Changes to ecosystems

Climate change can alter ecosystem functions and services. In particular, the critical functions of estuaries and embayments as either nursery grounds or spawning habitat can be diminished by changing water temperature, oxygen levels, pH, salinity, and other environmental variables. Impacts of climate change on terrestrial and freshwater ecosystems (e.g., changing hydrological cycles) can translate to marked changes in coastal marine ecosystems (Stoms et al 2005). Similarly, the outputs of more productive ecosystems that export nutrients and energy to less productive ecosystems (donor and recipient ecosystems, respectively) can be diminished, reducing the magnitude of these ecosystem subsidies, which can be critical to species and communities in the recipient ecosystems. For example, macroalgae produced on subtidal and intertidal rocky reefs are transported by storms to sandy beaches, where they are important sources of nutrient and energy to the recipient sandy beach ecosystems (Polis and Hurd 1996). Declines in macroalgal production caused by increased water temperature or reduced coastal upwelling will in turn reduce productivity of sandy beaches and the shorebird populations they support. Understanding how these relationships between ecosystems might change, depending on the vulnerabilities of each ecosystem, is critical to predicting species and ecosystem responses to a changing climate.

CONNECTIVITY-INFORMED MPAS AND MPA NETWORKS AND CLIMATE CHANGE IN THE MARINE ENVIRONMENT

Connectivity-informed MPAs and MPA networks are best suited to address shifts in species distributions and related changes in ecological communities and ecosystems associated with climate change in the marine environment (Salm et al 2001, 2006, McLeod et al 2008, Carr et al 2010). A connectivity-informed MPA or MPA network is one that is designed, used, and managed with consideration of species' movements through space, their use of habitats (different types of habitats through the life history of organisms and multiples of each habitat type used), their population structures, and their species ranges. When populations shift in response to physical and chemical changes in the ocean, they shift within existing species ranges before they shift - if they can - beyond these existing species ranges. Hence, connectivity-informed MPAs and MPA networks, which are designed, used and managed to accommodate species' range of movement, can best enable the initial population shifts that occur in response to the physical and chemical effects of climate change.

Species not only shift their distributions in response to physical, chemical and attendant ecological changes in the ocean, they may also adapt and evolve, given enough time. Connectivity-informed MPAs and MPA networks that are designed, used, and managed to foster genetic connectivity within a species, i.e., to maintain a species' full genetic diversity, help enable this adaptation and evolution: The more genetic diversity within a species, the more able a species is to adapt and evolve as its environment changes. Thus, connectivity-informed MPAs and MPA networks - those designed, used, and managed to foster the full genetic diversity of a species - best enable species to respond to adapt and evolve in response to physical, chemical, and ecological changes in the ocean brought about by climate change.

Connectivity-informed MPAs and MPA networks can be an effective and necessary tool to achieve marine conservation objectives - whether species-focused or ecosystem-focused - in a complexly changing marine environment. However, these connectivity-informed MPAs and MPA networks must be adaptively managed on an ongoing basis. Without ongoing adaptive management, the edge or advantage that connectivity-informed MPAs and MPA networks give to the species, communities, or ecosystems on which they are focused will quickly fade. (See discussion below regarding adaptive management.)

Thus, the design, use, and management principles for connectivity-informed MPAs and MPA networks, outlined in Part 3 of this paper, should be followed for two inter-related reasons. One, their use enables connectivity in MPAs and MPA networks (and thereby best enables ecological MPAs and MPA networks to achieve their objectives). Two, in enabling connectivity in MPAs and MPA networks, these principles produce ecological MPAs and MPA networks best able to achieve their objectives in the face of a fast and complexly changing marine environment. But, as just noted, this latter point comes with a serious caveat: these connectivity-informed MPAs and MPA networks must be adaptively managed on an ongoing basis - on the basis of ongoing monitoring and evaluation - to keep pace in this fast and complexly changing marine environment.

The design, use, and management principles discussed in Part 3 concerned both species-focused MPAs and MPA networks and community- or ecosystem-focused MPAs and MPA networks. Below we outline some of the ways in which these design, use, and management principles help enable achievement of ecological conservation goals in the face of climate change in the marine environment. We first address individual, stand-alone MPAs, and then MPA networks.

Individual, Stand-Alone MPAs

Individual MPAs can be used to enhance the resistance (i.e. ability to resist change in the face of perturbation) or resilience (i.e. ability to return to a pre-perturbed state or condition) of ecosystems to the effects of climate change.

(1) If the ability of or rate at which populations rebound from environmental perturbations (e.g., storms, episodes of hypoxia) is influenced by population size, then larger populations protected in MPAs may be more resistant or resilient to climate variation than smaller populations outside MPAs. Here, MPAs act as refugia to enhance recovery of populations inside MPAs; in some cases they can also aid population recovery outside MPAs (e.g., through larval dispersal or through spill-over of adults). For example, Micheli et al (2012) observed that populations of abalone in marine reserves rebounded faster from an episode of hypoxia than populations outside. They attributed this to the greater number of survivors within the reserve. Similarly, as noted above, large lobsters protected within reserves prevented overgrazing of kelp forests by invasive sea urchins that were transported southward along the coast of Tasmania by warm water currents associate with climate change (Ling and Johnson 2012). One important design implication of these results is that larger MPAs and/or MPAs located in habitats that support large species populations may provide added conservation value for protecting species and ecosystems from effects of climate change.

(2) MPAs may also provide protection to species in the face of climate change if they encompass a range of depths of each ecosystem targeted for protection. Individual MPAs that extend from shallow to deep will provide protection to species by protecting habitats and accommodating shifts in the depth distribution of that species within an ecosystem (e.g., spawning migrations, movement to deeper water with age). This role of MPAs also applies to MPA networks if different MPAs include different depth ranges of each ecosystem that are within larval dispersal distances of one another. For example, young produced in a vulnerable shallower coral reef within one MPA can recruit to deeper coral reefs in another MPA. As such, networks can accommodate potentially rapid shifts in depth that involve larvae dispersing from shallower to deeper portions of an ecosystem.

(3) Another important design consideration is to locate MPAs in areas where species are less vulnerable to the effects of climate change (Salm et al 2001, 2006, McLeod et al 2008). For example, corals appear to be more resistant (i.e., exhibit less bleaching) or resilient to effects of increasing temperature in certain environmental conditions (e.g., coastal upwelling, strong currents, well shaded, higher turbidity, and emergent corals). Locating MPAs at sites with these conditions may protect critical natural refugia for these species. MPAs located at these refugia can also mitigate impacts to an ecosystem elsewhere if they are located such that young produced in that MPA disperse to and replenish more vulnerable populations (McLeod and Salm 2006).

(4) Individual MPAs that include multiple ecosystems facilitate ecosystem connectivity that enhances the resilience of those individual ecosystems to climate effects. For example, MPAs designed to protect coral reefs should, if possible, also include within their borders nearby mangroves and/or seagrasses. The young of herbivorous fishes migrate from these inshore ecosystems (mangroves and seagrasses) to coral reefs and replenish fish populations there; these fish populations graze algae around the reefs and thereby facilitate recruitment and survival of the corals (Mumby 2006, Olds 2012a,b).

MPA Networks

In the face of a changing climate and its effects in the marine environment, there are strong reasons to use MPA networks to achieve ecological conservation objectives. With the large geographic shifts predicted for some species in response to climate change, individual MPAs are unlikely to contain these shifts, leaving species to move from the protection afforded them by that one MPA. In contrast, networks of MPAs composed of multiple MPAs with similar habitats and ecosystems - and spaced so as to accommodate movement of larvae from one MPA to another - could provide protection to species by accommodating latitudinal shifts in the dispersal of adults and larvae. Such networks might actually facilitate large-scale distributional shifts by protecting the habitats to which individuals of the species disperse. MPAs in the marine environment may be more effective conservation tools than reserve systems on land. The latter require protected corridors to facilitate movement of individuals or populations from one reserve to another as species' ranges shift. In the ocean, by contrast, species range shifts largely reflect shifts in larval dispersal, and ocean currents constitute effective "corridors," irrespective of the state of the intervening benthic habitats.

MPA networks also buffer impacts of climate change that exhibit spatial variation. For example, if hypoxic water masses occur patchily along a coast, multiple MPAs *protecting like ecosystems* increase the likelihood that some of the protected ecosystems will not be exposed to this stressor. This is in sharp contrast to a single MPA in which case the entire conservation value is lost with the loss of a single MPA (Allison et al 2003).

ADAPTIVE MANAGEMENT

To best enable place-based marine conservation tools - ecological MPAs and MPA networks - to reach their objectives, knowledge about connectivity realities must be built into these tools' design, use, and management. This is because the ecological foci of these tools - species, ecological communities, and ecosystems - exist in a world structured and sustained by ecological spatial connectivity. It is also because, due to climate change, these conservation foci - the species, ecological communities and ecosystems - exist *in a fast changing marine environment*, one in which they themselves, and the ecological processes in which they are enmeshed, are changing.

This is, to be sure, a challenging environment for marine conservation. But the use of connectivity-informed MPAs and MPA networks offers significant opportunities for achieving marine conservation objectives, both species-focused and community and ecosystem-focused. That said, it is essential that these connectivity-informed MPAs and MPA networks be monitored and evaluated on an ongoing basis (Pomeroy 2004; MPA FAC 2008, 2010; Carr 2011), and adaptively managed based on the results of this monitoring and evaluation, so that they can continually meet their objectives in a changing marine environment. This in turn requires that the agencies and managers responsible for MPAs and MPA networks possess institutional capacity and resources to carry out monitoring, evaluation, and adaptive management.

The challenge of place-based conservation in the marine environment requires ongoing feedback about the effects of that conservation under any circumstances. But under the emerging circumstances of a fast and complexly changing marine environment, this need is redoubled many times over. Without monitoring, evaluation, and adaptive management, the advantages that connectivity-informed MPAs and MPA networks afford to their conservation targets - species, ecological communities, and ecosystems - will likely be outrun by changes in the marine environment. But with monitoring, evaluation, and adaptive management, connectivity-informed MPAs and MPA networks can be powerful, dynamic, flexible tools for marine conservation in the face of climate change. Central to the success of adaptive management of connectivity-informed MPAs and networks, however, is a set of realistic conservation objectives and associated metrics of effectiveness, coupled with enhanced capacity to understand, and respond appropriately to, the nature, time scales and persistence of these environmental changes.

The actual practice of adaptive management of MPAs and MPA networks is nascent, and considerable work needs to be done to determine how best to implement adaptive management principles. Adaptive management in MPAs and MPA networks consists of monitoring and evaluation, and, as needed, changes in management measures in an existing MPA, including regulatory and boundary changes, and the addition or removal of MPAs in a network. Adaptive management depends, of course, on clear articulation of the specific conservation objectives of the MPA or MPA network, so that protocols for monitoring can be properly designed and so that effectiveness of the MPA or MPA network can be measured against specific, articulated aims. Given the importance of adaptive management to ensuring connectivity processes in MPAs and MPA networks, it is imperative that resources - staff, funds, partnerships - be devoted to developing best practices for adaptive management. These best practices should address all aspects of adaptive management, scientific, legal, policy, and others.

NO-TAKE, NO-IMPACT, AND/OR NO-ACCESS MPAS TO EVALUATE THE EFFECTS OF FISHING IN THE CONTEXT OF CLIMATE CHANGE

Much concern about the effects of climate change on species and ecosystems focuses on the synergistic effects of climate change in the ocean and other human stresses on marine species and ecosystems. When no-take, no-impact, or no-access MPAs have been created for conservation purposes, they can also be used as a tool for evaluating these synergistic effects and for teasing out the relative contributions of climate change and other human stresses on marine species and ecosystems. The classic instance involves untangling the relative contributions of fishing and climate change to changes in marine species and ecosystems. Thus, the condition over time of marine species in no-take MPAs (MPAs that prohibit human take of marine species) can be compared with the condition over time of those same marine species in adjacent waters in which human take of those species is not prohibited. If the species of interest do not flourish in the absence of fishing (i.e., in the no-take MPA), then it becomes likely that fishing (human take) of the species is not the cause of the decline in the species. In such cases, the suggestion is that the effects of climate change (or other indirect human stresses) may be responsible for the species' failure to flourish. If, however, the species of interest *do* flourish inside no-take MPAs (but not outside the MPAs), the implication is that fishing (human take) of the species - and not climate change-induced effects or other indirect human effects - is responsible for the failure of the species to flourish outside the no-take MPA. Monitoring environmental conditions and ecosystems inside and outside no-take, no-impact, and no-access MPAs over time is a critical means for better understanding the ecological consequences of climate change and/or other remote human stressors (Carr et al 2011).

CONCLUSIONS

Climate change will alter environmental conditions and processes that underpin the ecological spatial connectivity of populations, ecological communities, and ecosystems. These changes create challenges to the effectiveness of MPAs as conservation tools. However, *connectivity-informed* MPAs and networks of MPAs provide valuable tools for protecting species, ecological communities, and the ecosystems they constitute in the face of a changing climate. MPAs also provide managers and scientists with critical tools for better understanding the ecological consequences of climate change and how stresses caused by other human activities interact with the effects of climate change. Individual connectivity-informed MPAs can help to achieve conservation goals in the face of a changing climate, but connectivity-informed *networks* of MPAs provide additional and more robust protection from the impacts of a changing global climate. By understanding how both individual MPAs and networks of MPAs can be designed, used, and managed to enhance the resistance and resilience of species, ecological communities, and ecosystems to the effects of climate change, managers can better apply MPAs as conservation tools to reduce, mitigate, and adapt to our changing global climate.

PART 5: Conclusions

In the marine environment, living things often swim, drift, fly or walk from place to place throughout their lifetimes. This natural movement within and among habitats and ecosystems, here termed ***ecological spatial connectivity***, profoundly influences the structure and composition of local populations, communities and ecosystems in the marine environment.

While US MPAs have a wide range of objectives, a great many US MPAs are ecological MPAs, i.e., intended to restore or maintain ecological phenomena in the marine environment. Ecological MPAs consist of MPAs that focus on restoring or maintaining particular species or populations and MPAs that focus on restoring or maintaining whole ecological communities and/or whole ecosystems. The specific objectives of ecological MPAs -- whether species-focused or community- or ecosystem-focused -- vary widely, and may be classified into one or more of three goal categories, namely, natural heritage conservation, sustainable production, and, in some cases, cultural heritage conservation.

All ecological MPAs - no matter their ecological focus, no matter their specific objectives - depend for their success on incorporation of knowledge about ecological spatial connectivity into their design, use, and management. Connectivity processes are fundamental in the marine environment, and must be taken into account in the use of place-based conservation tools to achieve *any* conservation or management objective that involves ecological phenomena in the marine environment. The good news is that much is known about connectivity processes and this knowledge has been (and is being) distilled into principles for design, use, and management of ecological MPAs. Use of these principles enables MPA managers to use knowledge about connections among places to achieve the management and conservation objectives associated with particular places in the marine environment.

Climate change is altering and will alter environmental conditions and processes that underpin the ecological spatial connectivity of populations, ecological communities, and ecosystems in the marine environment. These changes create challenges to the effectiveness of MPAs as conservation tools. Connectivity-informed MPAs and networks of MPAs can help maintain or restore populations and species as well as whole communities and ecosystems in the face of a changing climate. MPAs can also provide managers and scientists with critical tools for better understanding the ecological consequences of climate change and how stresses caused by other human activities interact with the effects of climate change. Individual MPAs can help to achieve these conservation goals, but networks of MPAs provide additional and more robust protection to the impacts of a changing global climate. By understanding how both individual MPAs and networks of MPAs can be designed, used, and managed to enhance the resistance and resilience of species, ecological communities, and ecosystems to the effects of climate change, managers can better apply MPAs as conservation tools to reduce, mitigate, and adapt to our changing global climate.

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APPENDIX 1: Glossary

adaptive management – a structured, iterative process of monitoring, evaluation, and management decisions in the face of uncertainty. Adaptive management in MPAs and MPA networks consists of monitoring and evaluation, and, as needed, changes in management measures in an existing MPA, including regulatory and boundary changes, and the addition or removal of MPAs in a network. Adaptive management depends on clear articulation of the specific conservation purposes of the MPA or MPA network, so that protocols for monitoring can be properly designed and so that effectiveness of the MPA or MPA network can be measured against specific, articulated aims.

connectivity-informed MPA or MPA network – an MPA or network of MPAs designed, used, and managed to foster the ecological spatial connectivity processes important to the populations, species, communities, and/or ecosystems of concern in the MPA or network of MPAs.

community connectivity – the transfer of species between ecological communities resulting from the movement of one or more species among spatially separated ecological communities.

ecological community – the collection of species that co-occur and interact with one another in a particular habitat (e.g., a coral reef, kelp forest or seagrass bed).

ecological MPA - an MPA that focuses on restoring or maintaining ecological phenomena in the marine environment, i.e., populations, species, ecological communities, ecosystems or processes.

ecological spatial connectivity – the transfer of genes, organisms, species, materials (e.g., sediment), chemicals (e.g., nutrients), or energy (ecosystem connectivity) resulting from their movement among spatially separated populations, communities or ecosystems.

ecosystem – the biotic (i.e. organisms) and abiotic (i.e. physical and chemical) components of an environment that interact with one another, including species, geological features and oceanographic features (e.g., water currents, chemistry).

ecosystem connectivity – the transfer of species, chemicals (e.g., nutrients and pollutants), energy (in the form of organisms), and materials (e.g., sediments and debris) between ecosystems, resulting from their movement between spatially separated ecosystems.

genetic connectivity – the transfer of genes among populations of a species (also called "gene flow"), resulting from the movement of organisms between spatially separated local populations, whether spores of marine algae or the larvae, juveniles or adults of marine animals.

habitat – biotic and abiotic elements of the environment used by an organism.

marine environment - "'Marine environment' means those areas of coastal and ocean waters, the Great Lakes and their connecting waters, and submerged lands thereunder, over which the

United States exercises jurisdiction, consistent with international law" (Exec. Order 13158: 2000). "Marine environment" includes "intertidal areas, bays or estuaries" (MPA Center 2015:10).

metacommunity – A collection of spatially separated communities that are connected to each other by the movement of species (i.e. by community connectivity).

metapopulation – A collection of spatially separated local or sub-populations of a species that are connected to each other by the movement of individuals of that species (i.e. by population connectivity).

population – A collection of individuals of the same species that co-occur in space and time and interact with one another.

population connectivity – The transfer of individuals among populations of a species resulting from the movement of individuals (spores, larvae, juveniles or adults) of a single species among spatially separated local or sub-populations.

resilience – The internal capacity of a system (e.g., organism, population, ecological community, human community, ecosystem, institution) to return to its original state or condition subsequent to a perturbation.

resistance – The internal capacity of a system (e.g., organism, population, ecological community, human community, ecosystem, institution) to resist change in the face of perturbation.

sink population – A local or subpopulation within a metapopulation that receives more individuals (spores, larvae, juveniles or adults) than it contributes to other subpopulations in the metapopulation.

source population – A local or subpopulation within a metapopulation that contributes more individuals (spores, larvae, juveniles or adults to other subpopulations) than it receives from other subpopulations in the metapopulation.

US MPAs - MPAs created and maintained by federal, state, tribal, territorial, or local authorities in the United States. US MPAs include federal MPAs but are not limited to federal MPAs.

APPENDIX 2: Membership of MPA Federal Advisory Committee and the MPA FAC Connectivity Subcommittee

MPA FAC:

George J. Geiger, Chair (2009-2016)
Della Scott-Ireton, Ph.D., Vice-Chair (2009-2016)
Brian Baird (2014-2018)
Rick Bellavance (2014-2018)
Mark Carr, Ph.D. (2014-2018)
Gary Davis (2009-2016)
Martha Honey, Ph.D. (2014-2018)
John Jensen, Ph.D. (2011-2016)
Stephen Kroll (2011-2016)
Stephanie Madsen (2014-2018)
Samantha Murray, J.D. (2014-2018)
Ryan Orgera, Ph.D. (2014-2018)
Jason Patlis, J.D. (2011-2016)
Catherine Reheis-Boyd (2011-2016)
Sarah Robinson, J.D., S.J.D. (2009-2016)
Ervin Joe Schumacker (2009-2016)
Peter Stauffer (2014-2018)
Trisha Kehaulani Watson, J.D., Ph.D. (2014-2018)
Stephen Welch (2011-2016)
Margaret Williams (2014-2018)

See http://marineprotectedareas.noaa.gov/fac/membership/ for more information.

MPA FAC Connectivity Subcommittee (2015-2016):

Mark Carr, Ph.D., Co-Chair
Sarah Robinson, J.D., S.J.D., Co-Chair
Gary Davis
Stephen Kroll
Samantha Murray, J.D.
Ervin Joe Schumacker
Margaret Williams

Charles Wahle, Ph.D., National MPA Center staff liaison to Connectivity Subcommittee