The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment

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ABSTRACT

1 The several forms of spatial ecological connectivity – population, genetic, community, ecosystem - are among the most important ecological processes in determining the distribution, persistence and productivity of coastal marine populations and ecosystems.

2 Ecological MPAs focus on restoring or maintaining marine populations, communities, or ecosystems. All ecological MPAs - no matter their specific focus or objectives - depend for their success on incorporating ecological spatial connectivity into their design, use (i.e. application), and management.

3 Though important, a synthesis of the implications of spatial ecological connectivity for the design, use, and management of MPAs, especially in the face of a changing global climate, does not exist. We synthesize this information and distill it into practical principles for design, use, and management of MPAs and networks of MPAs.

4 High population connectivity among distant coastal ecosystems underscore the critical value of MPA networks for MPAs and the populations and ecosystems between them.

5 High ecosystem connectivity among coastal ecosystems underscore the importance of protecting multiple connected ecosystems within an MPA, that MPAs should be located to maximize ecosystem connectivity across their boundaries, and that ecosystems outside MPAs need to be managed to minimize influxes of detrimental organisms and materials.

6 Connectivity-informed MPAs and MPA networks – designed and managed to foster the ecological spatial connectivity processes important to local populations, species, communities, and ecosystems - can best address ecological changes induced by climate change. Also, the protections afforded by MPAs from direct, local human impacts may ameliorate climate change impacts in coastal ecosystems inside MPAs and, indirectly, in ecosystems outside MPAs.

KEY WORDS: ocean, coastal, fish, benthos, dispersal, marine reserve, climate change, fishing

INTRODUCTION

Ecological spatial connectivity is a critical process in the ecology and evolution of marine species, profoundly influencing their population and genetic structure, and the structure, functions and dynamics of the communities and ecosystems they constitute. Connectivity is also of central importance to the use (i.e. application), design, and management of effective ecological marine protected areas (MPAs) and networks of MPAs.[1] Nonetheless, the significance and implications of ecological spatial connectivity for MPA effectiveness - and for MPA effectiveness in light of global climate change -have not been synthesized in a form useful for MPA practitioners, stakeholders and policy-makers.

This paper draws on the extensive literature on ecological spatial connectivity in the marine environment to describe the profound consequences of ecological spatial connectivity for the design, use, and management of effective MPAs, and the implications of ecological spatial connectivity for the roles of MPAs in a changing global climate. The paper focuses on MPAs and MPA networks in coastal marine environments, including intertidal, embayments and estuarine ecosystems, and on important interactions between ecosystems across the land-sea interface. However, ecological spatial connectivity is also important in open ocean ecosystems (pelagic, epipelagic, etc.), and is crucial to the more dynamic nature of MPAs there (e.g. Ban et al., 2014; Game et al., 2009; Maxwell et al., 2015).

The paper has three sections. The first section - 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 ecological spatial connectivity, and 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). At its core, ecological spatial 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 conclusions of the first section are that ecological spatial connectivity poses both challenges and opportunities for MPAs, and that connectivity must be incorporated explicitly into the design, use, and management of MPAs.

The second section - Design, Use, and Management Principles for Enhancing Ecological Spatial Connectivity Processes Within, Around, and Among MPAs and MPA Networks - offers specific principles for taking ecological spatial connectivity into account in the design, use, and management of ecological MPAs in coastal marine environments. The principles to use in a given instance depend on whether the MPA is species-, community-, or ecosystem-focused and on the environmental and ecological characteristics of the target species, communities, or ecosystems.

[1] The terms "ecological MPAs and networks of MPAs" mean MPAs and MPA networks intended to restore or maintain populations, communities, ecosystems, and ecological processes. Hereafter, the terms MPA and MPA network are used to refer to ecological MPAs and ecological MPA networks, unless otherwise noted.

The third section - Climate Change in the Marine Environment: Another Compelling Reason for Connectivity-Informed MPAs and MPA Networks – addresses the effects of climate change on the marine environment, focusing on changes in marine species' distributions, abundances, and productivities, and the cascading effects these species-level changes produce in ecological communities and ecosystems. This section shows that MPAs designed, used, and managed to foster ecological spatial connectivity processes 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. This section also shows that ecological spatial 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 the first two sections of this paper show that incorporating ecological spatial connectivity into MPAs is always essential for MPAs to meet their conservation goals, this section shows that fostering connectivity processes in MPAs is particularly important for MPAs to meet conservation goals in a time of significant, ongoing changes in the marine environment.

This paper is based on a synthesis produced for and adopted by the United States Marine Protected Areas Federal Advisory Committee (MPA FAC), a committee of outside experts that advises the United States Secretaries of Commerce and the Interior.[2] The MPA FAC used the synthesis, along with its members' various expertise and experience concerning MPAs, to produce an action agenda for the two Secretaries: Connectivity-Informed MPAs and MPA Networks for Effective Marine Conservation and to Meet the Challenges of Climate Change in the Marine Environment.[3] While the MPA FAC used the synthesis in the United States, the principles for design, use and management of MPAs and MPA networks contained in the synthesis apply to MPAs worldwide. It is hoped that this synthesis will be a useful resource for MPA programme managers globally, and for any persons interested in the design, use, and management of effective MPAs and MPA networks.

WHAT IS ECOLOGICAL SPATIAL CONNECTIVITY AND WHY DOES IT MATTER FOR EFFECTIVE MARINE PROTECTED AREAS?

Ecological Spatial Connectivity

Biologically-based entities in nature, such as populations, species, communities or ecosystems, regularly influence one another and inter-connect. *Connectivity* refers to processes that determine those connections and their strength, timing, directionality and consequences. In conservation science the term connectivity is used to describe the levels and directions of movement and

[2] http://marineprotectedareas.noaa.gov/fac/. The authors constitute the MPA FAC subcommittee that produced the Scientific Synthesis for the MPA FAC (with Carr and Robinson as co-chairs) and the NOAA MPA Center staff liaison to the subcommittee (Wahle).

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

sharing of organisms, materials, energy or information among entities.[4] *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. As detailed 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 nested spatial scales (within MPAs, among MPAs, and, importantly, between MPAs and areas outside MPAs).

- **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") results from 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).

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. Ecological spatial connectivity is also the primary process by which an ecosystem interacts with and influences 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.

Population Connectivity

Population connectivity, sometimes referred to as demographic connectivity, is the linkage among discontinuous "local" or subpopulations of a single species that results from the movement of individuals from one group to another (Figure 1(A)). Because habitats are often discontinuous in space, separated by gaps of uninhabitable habitat (e.g. coral or rocky reefs separated by expanses of sand), a species' population often comprises several patchily distributed local subpopulations.

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[4] 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. The term can also be used to refer to connections among MPAs, as in linkages among MPAs in an MPA network. The term is used in neither of these two senses here; rather, the focus is *ecological* spatial connectivity, as described in the text.

The movement of individuals among these neighbouring local populations influences the size (i.e. number of individuals) and structure (i.e. sizes, ages and sexes of individuals) of each local population. These characteristics of local populations can, in turn, influence critical demographic rates (e.g. births, deaths, immigration and emigration) and vulnerability of the overall population to impacts and extinction.

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 sea floor 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 Freiwald, 2012; Kritzer & Sale, 2010). However, most marine invertebrates and fishes produce young (eggs, larvae) that are typically dispersed by ocean currents over great distances (10s to 100s of kilometres). 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 1(A)).

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; Cabral et al., 2016). Larvae disperse from adult populations to inshore nursery habitats, and eventually migrate as juveniles to offshore adult populations (Figure 1(B)).

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 by 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 MPAs and 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 spatially distinct local populations. Genetic connectivity has profound consequences for the spatial patterns of the genetic diversity within populations and 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 (referred to as genetic structure) 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 from one another with increasing distance is one method used to estimate how far individuals, especially larvae, travel (referred to as "isolation by distance", Kinlan & Gaines, 2003; Palumbi, 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 distant "source" populations (e.g. Christie et al., 2010; Figure 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 changes in growth rates, age and size at maturity (Dunlop, Enberg, Jørgensen, & Heino, 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 mortality and selection (e.g. Baskett & Barnett, 2015; Baskett, Levin, Gaines, & Dushoff, 2005; Davis, 1975; Dunlop, Baskett, Heino, & Dieckmann, 2009; Palumbi, 2003). Indeed, connectivity can greatly influence 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 on the relative sizes and compositions of the populations inside and outside of MPAs.

In light of the routine transfer of genes 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 a wider spectrum of genetic diversity of a 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.

Community Connectivity

Community connectivity is the linkage of spatially separated ecological communities resulting from the movements of multiple species among these areas in ways that affect their species composition and ecological structure and processes (Figure 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 but similar communities that, through connectivity processes, frequently exchange individual organisms and species; connectivity influences not only the structure, dynamics and persistence of individual communities, but also those of the metacommunity comprising 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 (Carr & Reed, 2015; Hamilton, Caselle, Malone, & Carr, 2010; Holbrook, Schmitt, & Stephens Jr., 1997). These distinct communities are connected by the dispersal of larvae of the species that constitute them, which profoundly influences the structure of a local community in a kelp forest along the West Coast.

The design and management of MPAs affects connectivity among communities within the protected areas and adjacent to them (Figure 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 – especially those intended to conserve entire ecosystems - needs to accommodate these differences to protect the communities they are intended to protect (Kinlan & Gaines, 2003; Shanks, Grantham, & Carr, 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 encompasses 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 processes independent of human activities, and others are a direct result of human activities. Ecosystem connectivity can have strong positive effects on “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 on recipient ecosystems’ productivity or resilience when that influx impairs organisms’ health or ecological interactions. (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, fuelling a plankton-based food web. Similarly, the relative 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 4(A)). That influx of nutrients fuels critical detritus-based food webs in these recipient ecosystems that otherwise lack these sources of plant production.

Another vector of ecosystem connectivity that can benefit species and ecosystems is the movement of organisms from one ecosystem to another. For species that use different ecosystems during different life stages, migration of young from nursery habitats (e.g. seagrass beds, kelp forests, mangrove forests) to offshore adult habitats (e.g. coral reefs, deep rocky reefs, deep sandy habitats) is another key form of connectivity between these ecosystems (Heck, Hays, & Orth, 2003; Igulu et al., 2014; Mumby, 2006; Mumby et al., 2004). As a result of ecosystem connectivity, proximity to nursery ecosystems can greatly influence the diversity and abundance of fish species in adult habitats (Figure 4(B); e.g. Naglekerken et al., 2002; Olds, Pitt, Maxwell, & Connolly, 2012). Consequently, protecting these nearshore ecosystems in a network of MPAs 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 faced with climate change impacts. 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 that are nurseries for herbivorous fishes that reduce algae and facilitate the recovery of corals (e.g. Adam et al., 2011; Olds, Connolly, Pitt, & Maxwell, 2012). 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).

Similarly, adults of some marine fishes and 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 or network facilitates these spawning migrations and the role of MPAs for conserving such species and the ecosystem services they provide (Figure 5(A)).

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, Anderson, & Holt 1997). Even bi-directional migrations of species from one ecosystem to another and back, such as the annual migrations of lobster or horseshoe crabs between 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.

In contrast, some forms of 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). Likewise, impacts to donor ecosystems that create inhospitable 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 cumulative and distributed 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 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, coastal, and terrestrial ecosystems.

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 aspects of that area) from the restricted human activities and, thereby, to achieve specified conservation or management objectives. Depending upon their specific objectives, MPAs vary in the types and levels of human activities they restrict: as examples, some MPAs prohibit the use of certain fishing gears; some prohibit take of particular species; and some prohibit take of all species (i.e. "no-take" marine reserves).[5]

In the United States, MPA objectives fall into one or more of three basic categories: conservation of natural heritage (biodiversity, populations, communities, 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

[5] In the United States, the official definition of 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). The IUCN definition of a protected area, which applies to MPAs (Day et al., 2012), is: "A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature with associated ecosystem services and cultural values" (Dudley, ed., 2008).

and history).[6] MPAs with natural heritage and sustainable production objectives seek to restore or maintain ecological phenomena in the marine environment, namely, populations, species, ecological communities, or ecosystems; depending on their particulars, MPAs with cultural heritage objectives may also seek to restore or maintain ecological phenomena in the marine environment. Globally, the range of objectives for MPAs is very broad (Agardy, Claudet, & Day, 2016; Álvarez-Fernández, Fernández, Sánchez-Carnero, & Friere, 2017). Within and across this wide diversity of objectives, a great many MPAs around the globe seek to restore or maintain ecological phenomena in the marine environment. This may be inferred from the much-used IUCN definition of protected area, which provides, in part, that a protected area (including an MPA) is an area managed "to achieve the long term conservation of nature with associated ecosystem services and cultural values" (Day et al., 2012; Dudley, ed., 2008).

Ecological Spatial Connectivity and MPAs

The existence in the marine environment of the four types of ecological spatial connectivity creates both challenges and opportunities for the design, use and management of MPAs. For example, in many instances, the young produced by populations living inside an MPA leave the MPA and replenish populations outside the MPA (e.g. Christie et al., 2010; Figure 2). Conversely, populations within MPAs often rely on the delivery into the MPA of young produced by populations outside of the MPA (e.g. Christie et al., 2010; Figure 2). 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. These influxes into MPAs can make the communities and processes within MPAs vulnerable to human activities conducted outside of MPAs (e.g. agricultural runoff, sewage discharges or coastal erosion). Examples of such land-based, connectivity-driven impacts to coastal MPAs include the Great Barrier Reef (Brodie et al., 2012; Brodie & Waterhouse, 2012), Kenya (McClanahan & Obura, 1997), Solomon Islands (Halpern et al., 2013), and Philippines (Quiros, Croll, Tershy, Fortes, & Raimondi, 2017). An additional example concerns seasonal movement of adults of a species into critical spawning habitat located in MPAs. The value of these MPAs depends critically on the availability of (i.e. the management of) spawning adults from outside the MPAs and, also, indirectly, on protection of adult habitat beyond the boundaries of the spawning habitat within MPAs (Gruss, Robinson, Heppell, Heppell, & Semmens, 2014).

Generally, it is more important to recognize and incorporate ecological spatial connectivity in the design, use, and management of *marine* protected areas than it is to consider and incorporate in *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 dynamic aqueous medium. Buoyant organisms or their propagules (spores, gametes, larvae or asexual fragments) and other materials can be carried vast distances rapidly by constantly-moving ocean currents with little effort or

[6] National MPA Center, 2015.

energy expenditure by the organisms. Second, the majority of marine invertebrates and fishes, including those attached to the sea floor 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 the inherent mobility of most species propagules and young mean that routine movement across and among habitats – or ecological spatial connectivity – will have even greater influences on the effectiveness of protected areas in meeting their conservation and management goals in the sea than on land (Carr et al., 2003).

Two key lessons about ecological spatial connectivity and MPAs and MPA Networks

Lesson One: 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 MPAs and networks of 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. Protecting ecosystems that subsidize other ecosystems within an MPA helps ensure that those functional relationships will be realized. MPAs or MPA networks that encompass multiple adjacent ecosystems can enhance connectivity among ecosystems (Figure 5)**.**

Lesson Two: 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 (Table 1). These effects are dependent upon the degree to which the sites, and ideally networks of sites, are located, configured and managed to facilitate important ecological linkages such as the movement of species and materials from ecosystems within MPAs to ecosystems outside MPAs (Figure 5(B)). Adults in populations protected within MPAs can generate young that contribute to the replenishment of connected populations that have been harvested (or have otherwise been diminished). As such, MPAs that contribute to replenishment of populations across a network of MPAs can contribute to both ecosystem and fishery conservation (Gaines, White, Carr, & Palumbi, 2010). Separately, as the number of adults builds within MPAs, juveniles and adults of mobile species 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 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 effective 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) do not recruit locally but instead are carried away from adult populations within their MPAs, replenishment of those protected populations will depend heavily on, and can be enhanced by, capturing multiple source-sink populations in a network of MPAs designed for that purpose. (Figure 5(C)). These networks of MPAs enhance the replenishment of populations within MPAs across the network while also contributing to replenishment of populations between those MPAs.

DESIGN, USE, AND MANAGEMENT PRINCIPLES FOR ENHANCING ECOLOGICAL SPATIAL CONNECTIVITY WITHIN, AROUND, AND AMONG MPAS AND MPA NETWORKS

There are practical principles for enhancing ecological spatial connectivity within, around, and among MPAs and networks of MPAs. Use of these principles produces connectivity-informed MPAs and MPA networks, and so aids MPA practitioners to maximize the effectiveness of MPAs and MPA networks. The principles address several factors, including: the location of an MPA; the size and shape of an MPA; whether the MPA is an individual, stand-alone site or is part of a set of inter-dependent MPAs, i.e. a network of MPAs; whether the species, communities, and/or ecosystems of concern are located inside or outside of MPA boundaries; and the operative management regimes in the areas around an MPA.

Below, two sets of principles are presented, the first for MPAs and MPA networks that seek to restore or maintain species, and the second for MPAs and MPA networks that seek to restore or maintain ecological communities and ecosystems. The actual principles are *italicized.* (In addition, these principles are summarized in Tables S1 and S2 in Supporting Information.)

When the Aim is to Restore or Maintain Species Populations

Population connectivity creates both profound opportunities and challenges for MPAs that seek to restore or maintain species populations. Different species have different population connectivity characteristics and potentials, and these differences must be taken into account. Most marine species produce young (spores, eggs, larvae) that can be carried 10s to 100s of kilometres 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.

MPAs for short distance dispersal species: Enabling populations within the boundaries

For species with short-distance dispersing young, populations are less reliant on delivery of young from outside MPAs and, like many terrestrial species, are more reliant on the persistence and successful reproduction of, and local recruitment from, populations within MPAs. As such, their persistence is heavily dependent on how well that MPA is designed and managed locally. *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 6). *MPA size should be scaled to match the home range of adults (the area an adult individual inhabits over its lifetime) to ensure that adults remain and are protected within that MPA.* For this reason, coastal MPAs are more effective at protecting species with smaller adult home ranges and stronger habitat affinity, and less effective for more mobile migratory species (e.g. salmon, sharks, tuna). Population persistence increases with size of an adult population, which is, in turn, related to the area of the habitat required to support that population and the amount and quality (e.g. productivity) of resources in that habitat. *For species whose adults migrate among adjacent ecosystems (e.g. across depth gradients), siting and sizing MPAs to include multiple ecosystems increases the protection and access to those ecosystems.*

MPAs for long distance dispersal species: Enabling populations within the boundaries

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 7). 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 and net export of larvae and young poses a challenge to the goal of protecting populations of these same species within their home MPAs. In this case, maintenance of an adult population within the MPA can be reliant on the delivery of young produced elsewhere (i.e. outside the MPAs). Because of the prevalence of marine species with long distance dispersing young, this common situation makes it vitally important to ensure the existence of robust adult populations that can contribute larvae to the MPA. There are two means of doing so. One is to *create and manage MPA networks that facilitate recruitment within and among the MPAs so that adults from MPAs in the network contribute larvae to other MPAs in the network* (Figure 8). The other is to *manage fisheries in the areas outside the MPA to ensure that the adult fish populations outside the MPA are sufficiently robust to contribute larvae to the MPA*. In either case, attention must also be paid, as necessary, to water quality management and habitat protection.

MPAs that contribute to populations outside their boundaries

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 protection of juvenile habitat:

(1) <u>Sources of larval production</u>*:* First and most importantly, MPAs, and the populations they protect, can function as sources of larval production, which are exported to and replenish populations outside MPAs. In larger MPAs, the relative proportion of young that recruit and remain in the immediate area is greater than those that disperse and are exported beyond the MPA's boundaries (Figure 9(A)). Conversely, smaller MPAs export proportionally more of their

young to adjacent areas, including to other MPAs (Figure 9(B)). This means that by distributing the same amount of total protected area across multiple MPAs separated by the distance that young disperse, more of the region will be replenished by larvae produced in MPAs (Figure 9). *For MPAs to contribute to target populations outside their boundaries, many smaller MPAs may be more effective than single large MPAs of the same area (or proportion of a regional population).* However, while reducing the size of an MPA increases the proportion of larvae that replenish populations outside the MPA, MPAs need to be of sufficient size to support a persistent and productive adult population (e.g. Cabral et al., 2016; López-Duarte et al. 2012). To that end, *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, larvae are delivered.*

Maximizing the contribution of populations within MPAs to replenishing populations outside MPAs requires a balance of the relative benefits of smaller vs. larger MPAs. 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.

(2) <u>Spill-over effects (adults)</u>*:* A second means by which MPAs can enhance populations outside of MPAs is the "spill-over" of adults that migrate beyond the boundaries in response to crowding within protected populations, or due to other ecological or biological phenomena (e.g. travelling to mating grounds, seeking seasonal food sources, etc.). 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 higher the rate of 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 10).

(3) <u>Nursery habitat protection (juveniles)</u>: The third way that MPAs enhance populations outside their boundaries is to act as productive nursery habitat. When this is the objective, three key design and management factors must be considered. First, the *MPAs should be located on productive nursery grounds.* Second, MPA management needs to *protect the quality of that natural 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*. Third, the *MPAs should be located in close proximity to adult populations outside their boundaries*. 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

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 11).

Protecting genetic diversity and the capacity of species to adapt

The genetic diversity of populations is essential to the capacity of populations to resist and adapt to changes in their environment. Genetic connectivity is, therefore, critical for maintaining genetic diversity across a species' range. Fishing and other human activities can reduce the genetic diversity of fish, invertebrate and algae 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 aim is to Restore or Maintain Ecological Communities and Ecosystems

Many MPAs were established to conserve the full range of ecological features, processes and services contained within their boundaries. Their effectiveness depends on the incorporation of ecological spatial connectivity into their design, use, and management.

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 key species that constitute and shape the communities* to ensure that those species replenish and sustain the communities (Figure 12; 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 example, in the design of California's state-wide network of MPAs, no greater than 50-100 km was recommended for spacing between MPAs with similar habitats based on a general larval dispersal for fishes and invertebrates (Saarman et al., 2013). *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*. In the California network example, MPA size was based on adult fish movement distances (i.e. home range) and considered sufficient for short-distance dispersing larvae: minimum alongshore span of 5-10 km (preferably 10-20 km) and extending offshore to the boundary of state jurisdiction (ca. 5 km) for a minimum size range of 23-47 km^2 (Saarman et al., 2013). *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 Figure 12, constitute a network of 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 13).

Although ecosystems are defined by key environmental (e.g. seafloor type, water depth) and biological (e.g. seagrass beds, kelp forests, corals, mangroves) attributes, their actual species composition and community structure can vary over geographic gradients. As examples, kelp forest ecosystems and coral reef ecosystems are each characterized by these structure-forming taxa, but their particular species compositions and aspects of their structure and function vary with geographical location. Kelp forests distributed along the west coast of North America differ markedly in their species compositions as do coral reefs distributed along the Florida Keys. This geographic variation *within a single ecosystem or community typ*e 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 MPA networks 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 designed to improve ecological connectivity and conditions is more likely to succeed.

CLIMATE CHANGE IN THE MARINE ENVIRONMENT: ANOTHER COMPELLING REASON FOR CONNECTIVITY-INFORMED MPAS AND MPA NETWORKS

Physical and Chemical Changes in the Marine Environment

Global climate change manifests in many ways in the marine environment (Figure 14, Table 2; Bruno, Harley, & Burrows, 2013; Doney et al., 2012, 2014; Harley et al., 2006; Hoegh-Guldberg and Bruno 2010; Poloczanska et al., 2013, 2016). Some of these changes are occurring more rapidly in the marine environment than they are on land (Burrows et al., 2011) and are particularly acute (or obvious) in shallower coastal marine environments such as intertidal zones, coral reefs, bays, and estuaries, than deeper offshore marine environments. These impacts are both physical and chemical, and they have myriad ramifications for organisms, populations, and ecosystems as well as for the services they provide society (e.g. fisheries, coastal protection, recreation, carbon sequestration).

Few of these changes are, or will be, in the same direction (i.e. increase or decrease) everywhere. For example, salinity will increase in certain areas of the ocean where evaporation exceeds precipitation and decrease where precipitation and coastal runoff exceeds evaporation. The resulting 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.

Additionally, 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 colder, nutrient-rich waters from depth and which greatly enhances ocean productivity; Bakun & Nelson, 1991). Predicted changes in the location, frequency, and intensity of upwelling (Bakun, 1990; Bakun & Weeks, 2004; Diffenbaugh, Snyder, & Sloan, 2004; Snyder, Sloan, Diffenbaugh, & Bell, 2003) 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 (Gergis & Fowler, 2009; Trenberth & Hoar, 1997) 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 & 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, Hegermiller, Barnard, van Ormondt, & Ruggiers, 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 (Doney et al., 2012; Rabalais, Turner, Diàz, & Justić, 2009), reduced salinity associated with freshwater influx, and ocean acidification (Doney, Fabry, Feely, & Kleypas, 2009; Doney et al., 2012; Feely, Doney, & Cooley, 2009; Orr et al., 2005) directly related to increasing atmospheric carbon, a driver of climate change.

Ecological Changes in the Marine Environment

All of these physical and chemical changes in the marine environment – alone or in combination - can directly influence growth, survival, and reproduction of individual marine organisms. This in turn can change 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., 2013). Among the many environmental changes and their ecological consequences (Table 2), three ecological responses warrant particular emphasis with respect to their implications for MPAs: shifts in species distributions, changes in ecological communities, and changes to ecosystems.

Shifts in species distributions

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. Burrows et al., 2014; Cheung et al., 2009), and observed in paleoclimatic and paleobiogeographic records (e.g. Aronson et al., 2007; Precht & Aronson, 2004; Roy, Jablonski, & Valentine, 2001), and contemporary distributional records of many species (Harley & Paine, 2009; Helmuth, Mieszkowska, Moore, & Hawkins, 2006; Lejeusne, Chevaldonne, Pergent-Martini, Boudouresque, & Perez, 2010; Ling, Johnson, Frusher, & Ridgway, 2009; Parmesan, 2006; Perry, Low, Ellis, & Reynold, 2005; Pinsky & Fogarty, 2012; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Sumalia, Cheung, Lam, Pauly, & Herrick, 2011; Yamano, Sugihara, & Nomura, 2011). 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 (Dulvy et al., 2008; Perry et al., 2005).

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 behaviour, duration, and survival of larvae (e.g. Cowen & Sponaugle, 2009; Fox, Henry, Corne, & Roberts, 2016; Pineda, Hare, & Sponaugle, 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. Dulvy et al., 2008; Harley et al., 2006). 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, Glynn, Maté, Toth, & Gyory, 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' main predator (Ling & Johnson, 2012; Ling et al., 2009). 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 nutrients and energy to the recipient sandy beach ecosystems (Polis & 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 (Saunders et al., 2014).

Connectivity-Informed MPAs and MPA Networks in a Changing Marine Environment

MPAs and networks of MPAs can be used to enhance the resistance (ability to resist change in the face of perturbation), resilience (ability to return to a pre-perturbed state or condition) or transformation (ability to reorganize) of species, communities, and ecosystems in the face of climate change in the marine environment. First and foremost, MPAs and MPA networks must be connectivity-informed, i.e. designed, used, and managed according to the principles described in the preceding section and to evolving principles for incorporating ecological spatial connectivity.

Connectivity-informed MPAs and MPA networks can help address the shifts in species distributions and related changes in ecological communities and ecosystems associated with climate change in the marine environment (Carr, Saarman, & Caldwell, 2010; McLeod, Salm, Green, & Almany, 2008; Mumby et al., 2011; Salm, Done, & Mcleod, 2006; Salm, Smith, & Llewellyn, 2001). A connectivity-informed MPA or MPA network accounts for species' movements through space, their use of habitats throughout their life histories, their population structures, and their geographic and depth ranges. When populations move in response to physical and chemical changes in the ocean, they shift within existing species ranges before they shift - if they can - beyond them to entirely new areas. Connectivity-informed MPAs and MPA networks, designed, used and managed to accommodate a species' predicted range of movement can best enable population shifts that occur in response to the physical and chemical effects of climate change.

In addition, connectivity-informed MPAs and MPA networks can best enable species to adapt and evolve in response to climate change. Species not only shift their distributions in response to the physical, chemical and attendant ecological changes brought about by climate change, they may also adapt and evolve, given enough time. The more genetic diversity within a species, the more able a species is to adapt and evolve as its environment changes. Connectivity-informed MPAs and MPA networks that protect the genetic diversity of a species thus best enable a species to adapt and evolve in response to changes in their environment.

The following two subsections identify insights for the use of MPAs and MPA networks to enhance species', communities', and ecosystems' capacities for resistance, resilience, and transformation in response to the changes in their environment brought about by climate change. The first centres on insights for individual, stand-alone MPAs, the second on insights for networks of MPAs.

Insights for Individual, Stand-Alone MPAs in a Changing Environment

(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 (Grafton & Kompas, 2005). 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 associated with climate change (Ling & Johnson, 2012; Ling et al., 2009;). 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* (McLeod et al., 2008; Salm et al., 2006; Salm et al., 2001). 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 that experience more extreme environmental conditions (e.g. higher temperatures) or greater variation in 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 & 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 recovery of the corals (Mumby, 2006; Olds, Connolly et al., 2012; Olds, Pitt et al., 2012).

Insights for MPA Networks in a Changing Environment

(1) In the face of a changing climate and its effects in the marine environment, there are strong reasons to use MPA networks to achieve conservation objectives. With the large geographic shifts predicted for some species in response to climate change, existing individual MPAs are unlikely to contain these shifts, leaving species to move beyond the protection afforded them by that one MPA. In contrast, *networks of MPAs composed of multiple MPAs with similar habitats and ecosystems - and spaced to accommodate movement of larvae from one MPA to another - could provide protection to species by accommodating likely latitudinal shifts in the dispersal and recruitment of adults and larvae*. Such networks might actually facilitate large-scale distributional shifts by protecting the habitats to which individuals of the species disperse. MPA networks may be more effective conservation tools in a changing environment 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” – from one MPA to another in a network - irrespective of the state of the intervening benthic habitats.

(2) As ocean currents shift in response to changing atmospheric conditions, changes in patterns of larval dispersal will alter patterns of connectivity and jeopardize the functional integrity of previously connected MPA networks (Fox et al., 2016). Networks that take into account predicted or observed shifts in population connectivity in their design and adaptive management will enhance the overall integrity of the network. For example, Fox et al. (2016) demonstrated how particular MPAs were critical to maintaining network connectivity with climate variation. Reflecting basic metapopulation theory, broadly distributing MPAs in space is more likely to maintain connectivity across a network with uncertain changes in climate-driven ocean circulation patterns.

(3) *MPA networks distributed across species ranges are more likely to include and protect the full genetic diversity of species whose genetic composition varies across its range*. This capacity to adapt to changing environmental conditions or inclusion of local populations resistant to such changes enhances resistance and resilience of species to climate change (e.g. Mumby et al., 2011).

(4) MPA networks also buffer localized impacts of climate change. 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 or impacted by this stressor*. This is in sharp contrast to a single MPA in which case the entire conservation value of the area's ecosystems are lost with the loss of a stand-alone MPA (Allison, Gaines, Lubchenco, & Possingham, 2003; Blowes and Connolly 2012).

(5) To the extent that MPA networks better protect (i.e. enhance or restore) populations and communities than stand-alone MPAs, networks will foster greater resistance and resilience to climate change. The greater ability to protect key species (e.g. foundation species, ecosystem engineers, keystone species) that especially influence the resilience of communities and ecosystems throughout a network can increase the geographic area over which those species and MPAs enhance broad ecosystem resilience.

Using MPAs to Evaluate the Separate and Combined Effects of Anthropogenic Stressors and Climate Change

Much concern about the effects of climate change on species and ecosystems focuses on the synergistic effects of climate change and other human stressors 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 stressors on marine species and ecosystems. The classic instance involves untangling the relative contributions of fishing and climate change to changes in species and ecosystems. Thus, if trends in a species or ecosystem over time are compared inside and outside of no-take MPAs (e.g. Babcock et al., 2010) and no difference in the trends is detected, then it is likely that some stressor, including climate effects, rather than fishing, is the cause of the observed trend. If, however, differences in trends in species or ecosystems inside versus outside no-take MPAs are detected, the implication is that fishing, either independently or interacting with climate change or some other human stressor, is responsible for the differences. One nice example of this potential application of MPAs is an evaluation of activities associated with recreational fishing on the prevalence of coral disease. Lamb, Williamson, Russ & Willis (2015) found that corals outside of no-take MPAs subjected to abrasion associated with recreational fishing experienced four-fold greater prevalence of disease than corals not subjected to these activities within no-take reserves. Because increasing temperatures associated with climate change are also known to induce disease in corals (Bruno et al., 2007), corals subjected to activities that cause coral abrasion may be much more susceptible to the affects of climate change than those not subjected to abrasion. Comparing the rates of increase in disease prevalence at these sites with changing water temperatures can identify the combined effects of climate change and recreational fishing. More generally, environmental and ecological monitoring inside and outside MPAs over time can be a critical means for better understanding the ecological consequences of climate change and/or other human stressors (Carr et al., 2011).

Adaptive Management

Successful implementation of either single MPAs or MPA networks – with success defined as meeting specific and clear objectives -- requires that these discrete areas be managed adaptively (sensu Folke, Hahn, Olsson, & Norberg, 2005; Parma et al., 1998; Rist, Campbell, & Frost, 2013; Walters, 1986). This is the case under any circumstances, but it is especially critical for connectivity-informed MPAs and networks of MPAs in a fast-changing marine environment. Without adaptive management, and the monitoring and evaluation on which it depends, the advantage or edge that connectivity-informed MPAs and networks of MPAs afford species, communities, and ecosystems could be outrun by changes in the marine environment. Adaptive management requires well-designed and ongoing monitoring and evaluation of how well individual MPAs and networks of MPAs are performing with respect to clearly articulated metrics of effectiveness (Carr et al., 2011; MPA FAC, 2008, 2010; Pomeroy, Parks, & Watson, 2004; White, Baskett, Barnett, Barr, & Hastings, 2011). These evaluations need to consider both appropriate spatial patterns and temporal rates of ecological responses to regulatory measures in the MPA (Moffitt, White, & Botsford, 2013; White et al., 2013). Adaptive management also requires that agencies and managers possess institutional capacity and resources to carry out monitoring, evaluation, and to respond to these evaluations with appropriate changes in design (e.g. boundary changes, the addition or removal of MPAs in a network) or management (e.g. regulations) of MPAs (Grafton & Kompas, 2005; Hockings, 2003), and/or change of management (regulations) outside the MPA or MPA network.

For connectivity-informed MPAs, adaptive management requires understanding how connectivity influences the MPAs and surrounding areas (Burgess et al., 2014). Measures of population connectivity include proximate metrics of connectivity (e.g. larval production and delivery as proxies of export and influx of organisms from and into an MPA) and ultimate metrics including regional population models that incorporate population demographics (e.g. size structure and density-dependence), circulation models of larval dispersal, and spatial and temporal patterns of fishing mortality (Grorud-Colvert et al., 2011, 2014; Jacobi & Jonsson, 2011; White et al., 2011; White, Schroeger, Drake, & Edwards 2014). Such models can be applied to evaluate the relative contribution of each MPA to network connectivity and regional population performance by altering design criteria (e.g. size, shape, location of MPAs) and management measures (e.g. levels of protection). For evaluation of ecosystem connectivity, metrics of production and export of organisms and materials in donor ecosystems (e.g. juveniles in nursery habitats, macrophytes and detritus), import of these products to recipient ecosystems, and metrics of exchange (e.g. tracking and modeling movement trajectories from one ecosystem to another).

CONCLUSIONS

The several forms of spatial ecological connectivity – population, genetic, community, ecosystem - are among the most important ecological processes in determining the distribution, persistence and productivity of marine populations and ecosystems. Not surprisingly, most MPAs focus on restoring or maintaining those very features. Consequently, the principles provided here for incorporating spatial ecological connectivity into the design, use and management of MPAs are essential to ensuring these areas meet their specified ecological objectives. Moreover, much about connectivity processes is already known and can be readily incorporated into the design and adaptive management of MPAs and networks. Our summary and distillation of this knowledge provides guiding principles that can be applied by planners, managers and stakeholders now to enhance the design, use, and management of existing or proposed MPAs and networks of MPAs.

For most marine organisms, population connectivity is achieved through the dispersal of young (larvae, algal spores) by ocean currents. Ocean currents also transport materials (e.g. nutrients, sediments) between distant ecosystems. High spatial connectivity among distant ecosystems means that populations and ecosystems within MPAs can help replenish populations in, and provide material subsidies (e.g. nutrients) to, ecosystems outside MPAs. Knowledge of the spatial scales, patterns and rates of connectivity enable managers to design and apply MPAs to the benefit of populations and ecosystems beyond their borders. This same connectivity also increases the reliance of populations and ecosystems within a given MPA on delivery of young and subsidies from populations and ecosystems outside that MPA. It also increases MPAs' vulnerability to influxes of detrimental organisms and materials from outside their boundaries. Recognizing and incorporating this understanding into the design of MPAs and networks is central to their success. Thus management practices inside and outside of MPAs will influence the success of one another, requiring managers to integrate management regionally to both increase the success of MPAs in meeting their goals and for MPAs to best benefit management goals (e.g. sustainable fisheries and ecosystems) outside MPAs.

MPAs that both include multiple ecosystems (e.g. inshore, nearshore and offshore) and are linked (i.e. networked) to one another by larval connectivity provide the most effective design for integrating regional management goals inside and outside of MPAs. Spacing of MPAs scaled to intermediate distances of larval dispersal contribute both to the replenishment of populations in adjacent MPAs as well as the populations and ecosystems in between them. Because the species composition and structure of communities that constitute an ecosystem vary across environmental gradients ("bioregions") in any given biogeographic region, distributing MPAs in networks across that area can incorporate the breadth of species ranges and biodiversity that constitute those ecosystems. Multiple biogeographic regions include even greater variation in the species composition and structure of communities that constitute ecosystems. Networks in multiple biogeographic regions extend protection to that greater breadth of ecosystem diversity and the biodiversity they support.

Climate change is altering environmental conditions and processes that underpin the ecological spatial connectivity of populations, communities, and ecosystems in the marine environment. These changes create challenges to the effectiveness of MPAs as conservation tools, but also provide managers with means to mitigate those impacts. One of the most profound consequences of climate change is shifts in species ranges across depths or latitudes. For the vast majority of marine species, these shifts reflect changes in patterns of larval dispersal and the survival of organisms in newly colonized tolerable environments. The proposed design of MPAs -- each including multiple ecosystems (inshore, nearshore, offshore) and linked to adjacent MPAs by larval dispersal -- protects accessible habitats to which adults move (e.g. across depth gradients) and larvae disperse (e.g. across latitudes). Because of the difficulty in predicting spatial patterns of environmental changes, including shifts in ocean current patterns and the dispersal of larvae, MPA networks distributed across a biogeographic region increase the likelihood of protecting ecosystems to which larvae may be redirected to. Indeed, the potential for larvae to colonize more favourable environments has long been hypothesized to explain the evolution of a dispersive larval stage. By providing protection to species, communities and ecosystems as they redistribute spatially, networks of MPAs can facilitate the persistence of healthy and productive oceans, important places and valued species in the face of a changing climate.

MPAs can also provide managers and scientists with tools for better understanding the ecological consequences of climate change and how those impacts interact with effects of other human activities to either ameliorate or exacerbate their effects. Networks of MPAs, each with multiple ecosystems, distributed across biogeographic regions allow managers to apply this tool to all ecosystems. Well-designed evaluations of the changing state or condition of species and ecosystems simultaneously inform managers how well MPAs are meeting their objectives and goals. Comparisons of the relative performance of MPAs allow managers to evaluate design criteria and management practices and identify those that perform best. Adjusting the design or management accordingly to optimize MPA performance is the central tenet of adaptive management and will foster the adaptive evolution of MPAs in a changing world.

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[7] http://marineprotectedareas.noaa.gov/fac/; The authors constitute the MPA FAC subcommittee that produced the Scientific Synthesis for the MPA FAC (with Carr and Robinson as co-chairs) and the NOAA MPA Center staff liaison to the subcommittee (Wahle).

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Table 1. 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).	▪ enhance connectivity among distant MPAs ▪ 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
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	▪ 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

MPA Goal	Benefits of Accounting for Connectivity - Inside the MPA	Benefits of Accounting for Connectivity - Outside the MPA
provide to present and future generations through ecosystem-based MPA approaches." (MPA Center 2015:13)		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.

Table 2. 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 & 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 (.e.g. dissolution of corals), change in species abundance and distributions (Kroeker et al., 2013; Kroeker, Kordes, Gim, & Singh, 2010). Impact on reproduction, larval survival, settlement and recruitment.
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 & Litzow, 2008).
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).

List of Figures

Figure 1. Population connectivity: the movement of individuals (spores, larvae, juvenile s 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.

Figure 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

Figure 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.

Figure 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).

Figure 5. 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).

Figure 6. 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).

Figure 7. 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).

Figure 8. 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.

Figure 9. 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.

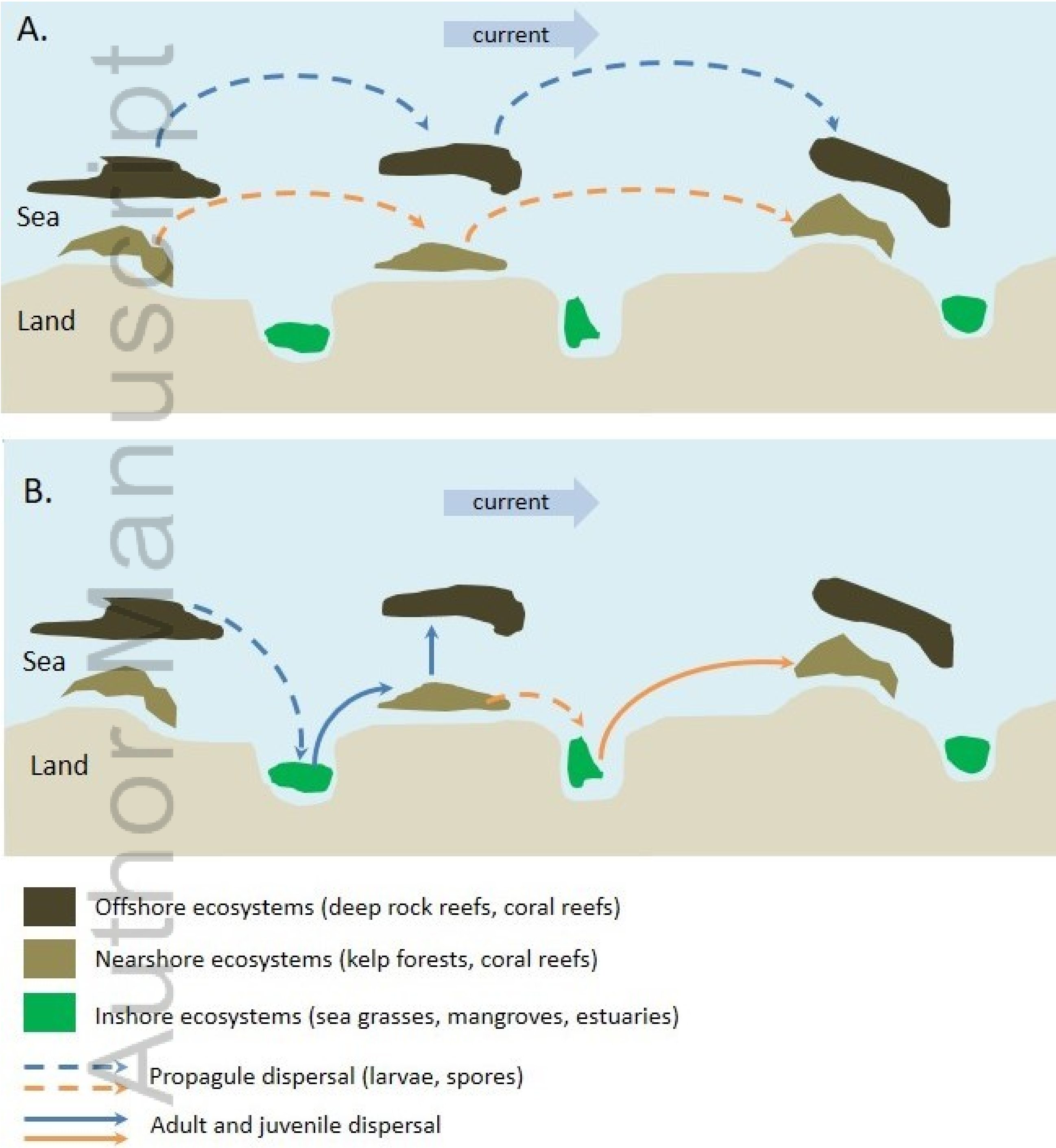
Figure 10. The distance that juveniles and adults disperse (orange oval) is independent of the size of an MPA. Therefore, the smaller the MPA, the greater the number and proportion of individuals in a population will emigrate from the MPA.

Figure 11. 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.

Figure 12. 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 82 and 9 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.

Figure 13. 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.

Figure 14. Many of the physical and chemical changes in the marine environment associated with climate change (from Harley et al., 2006).



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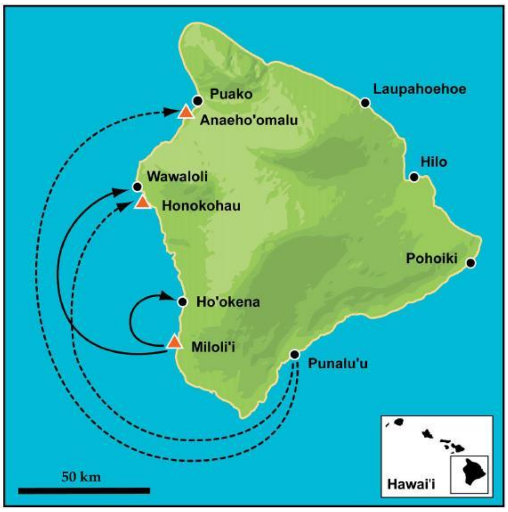

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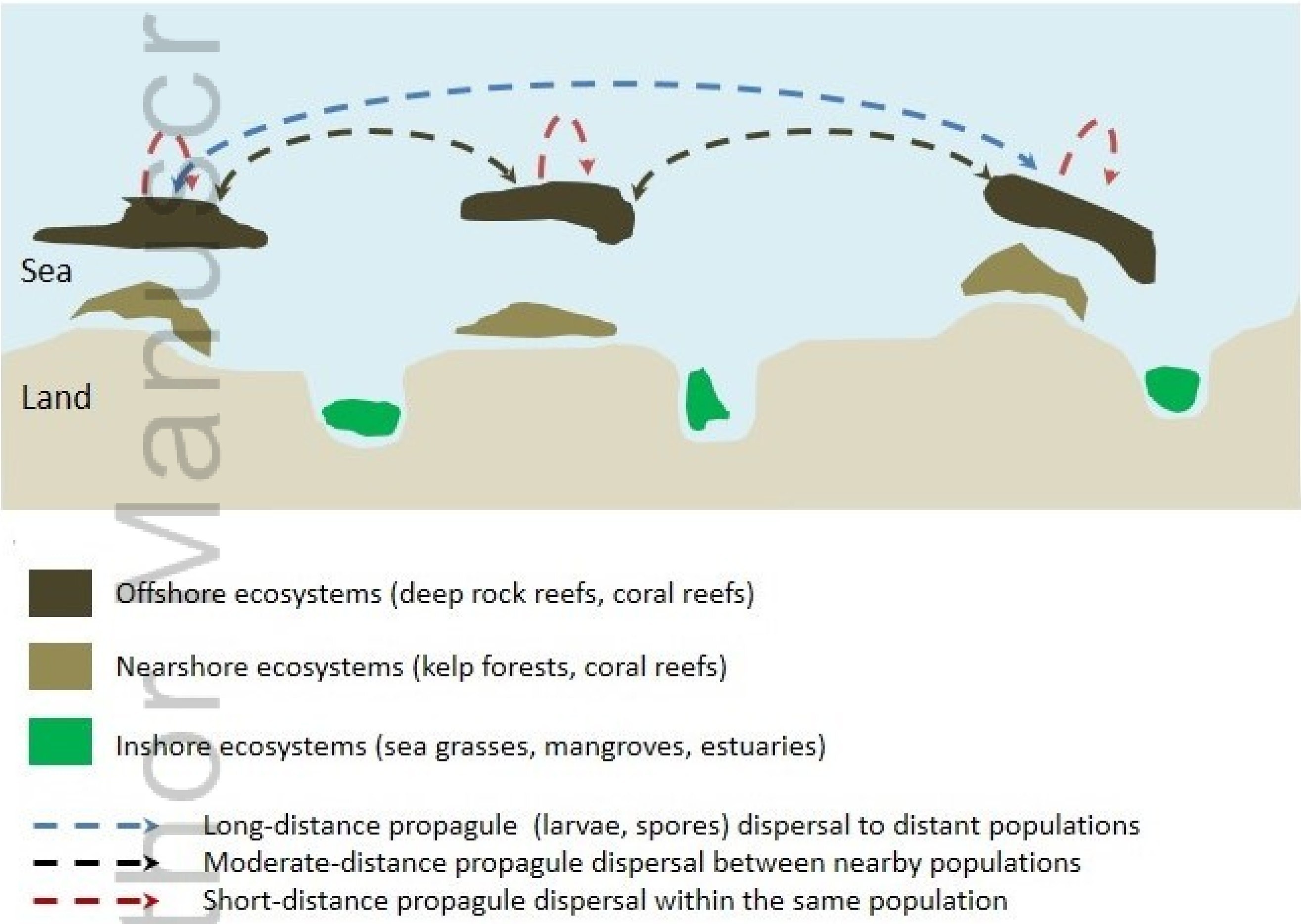

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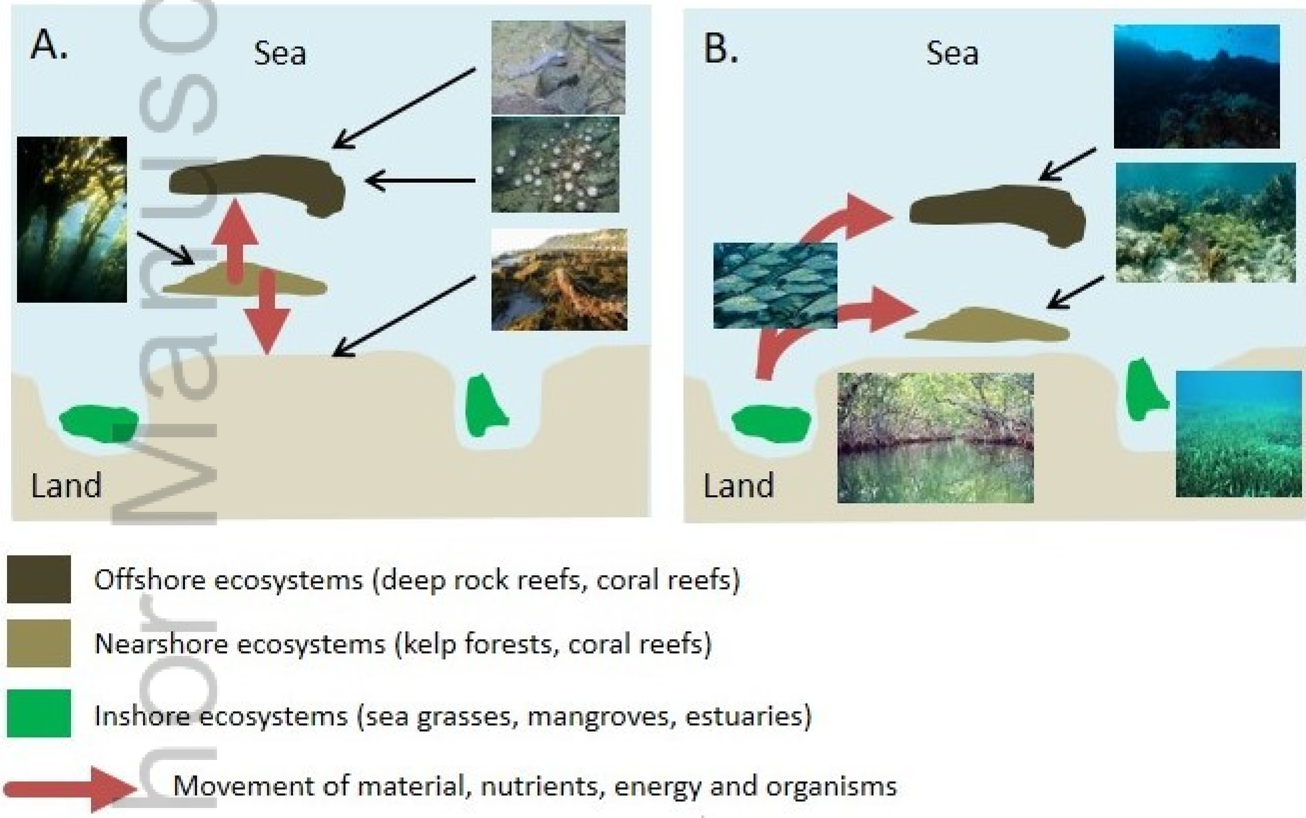

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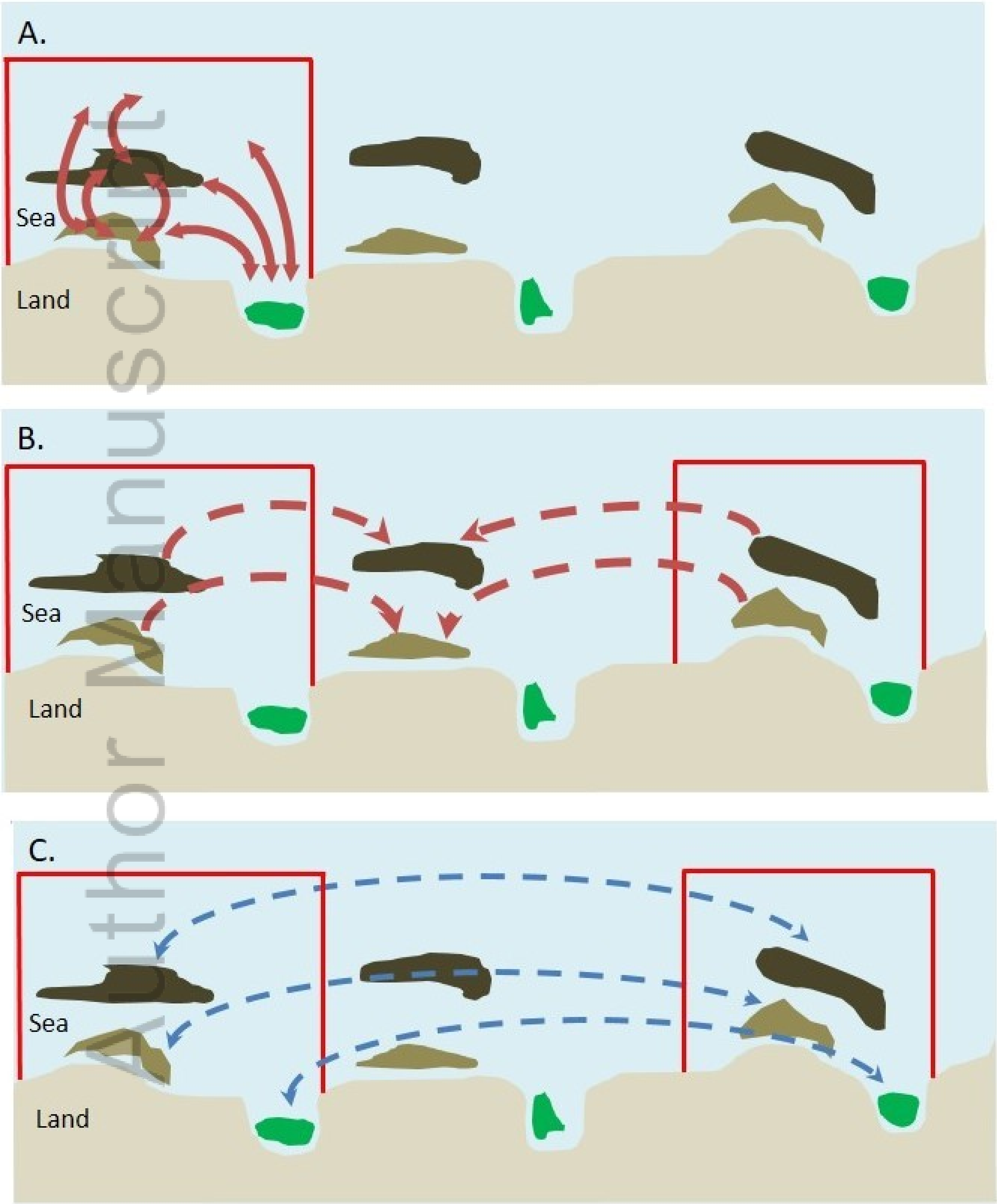

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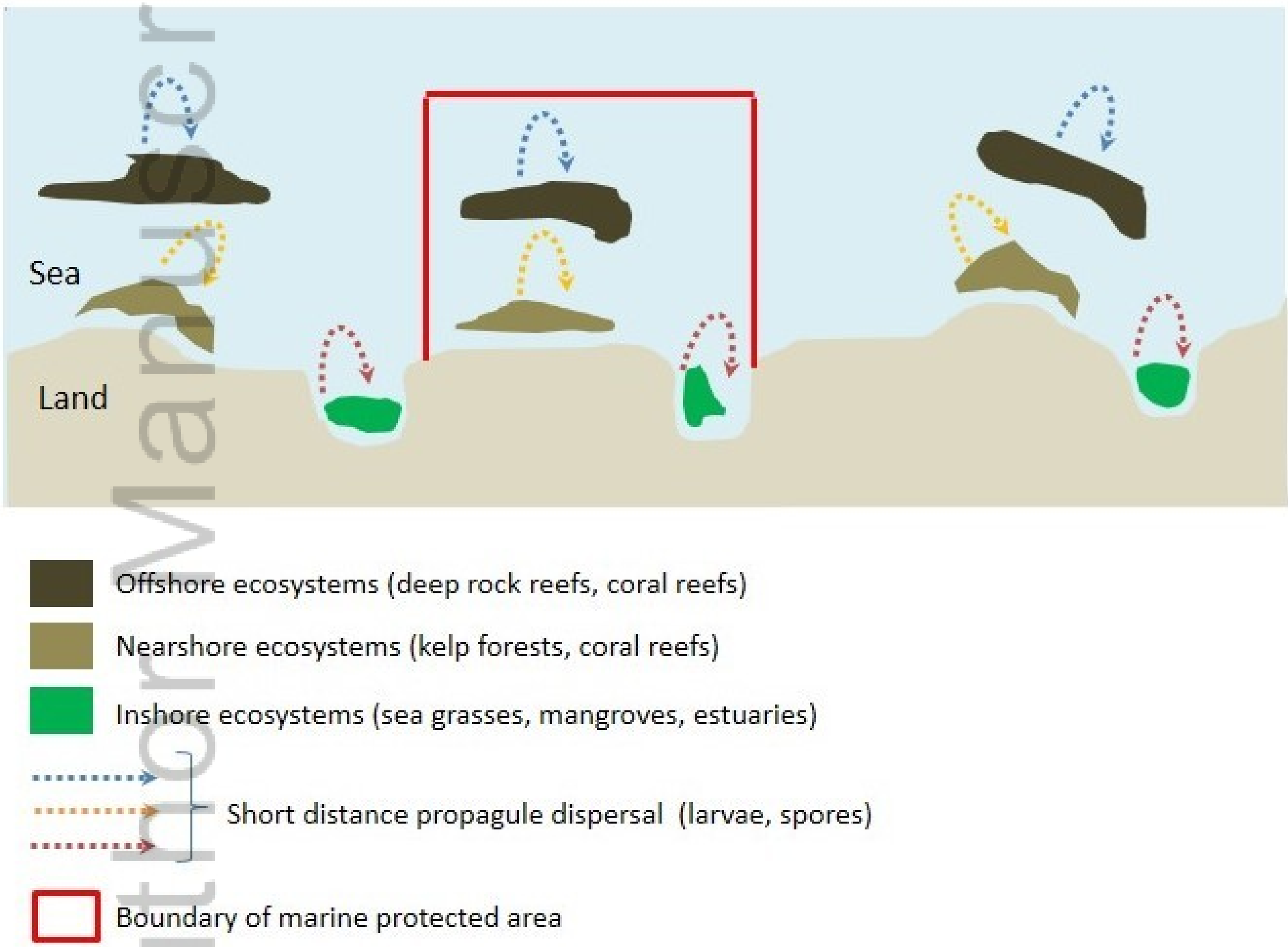

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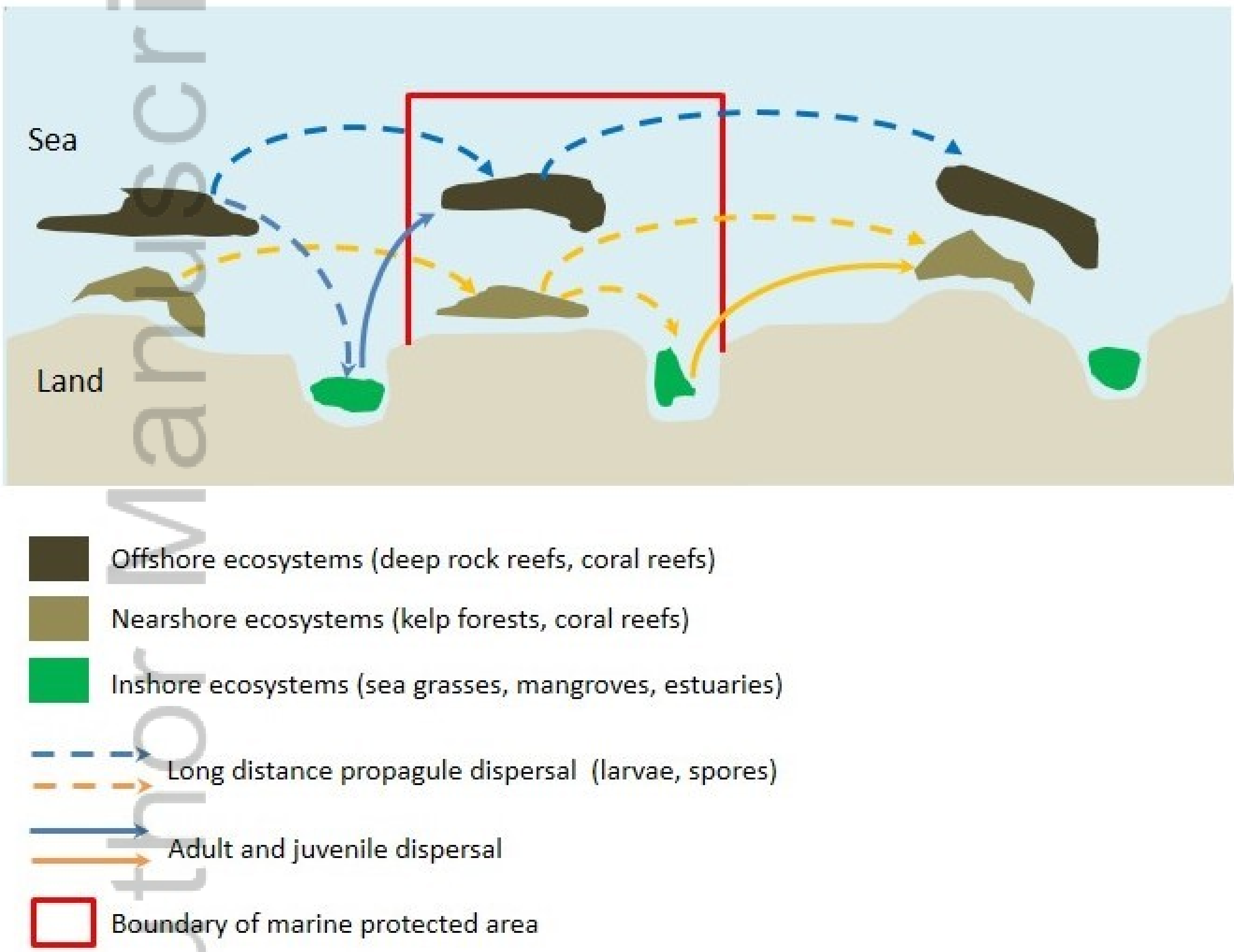

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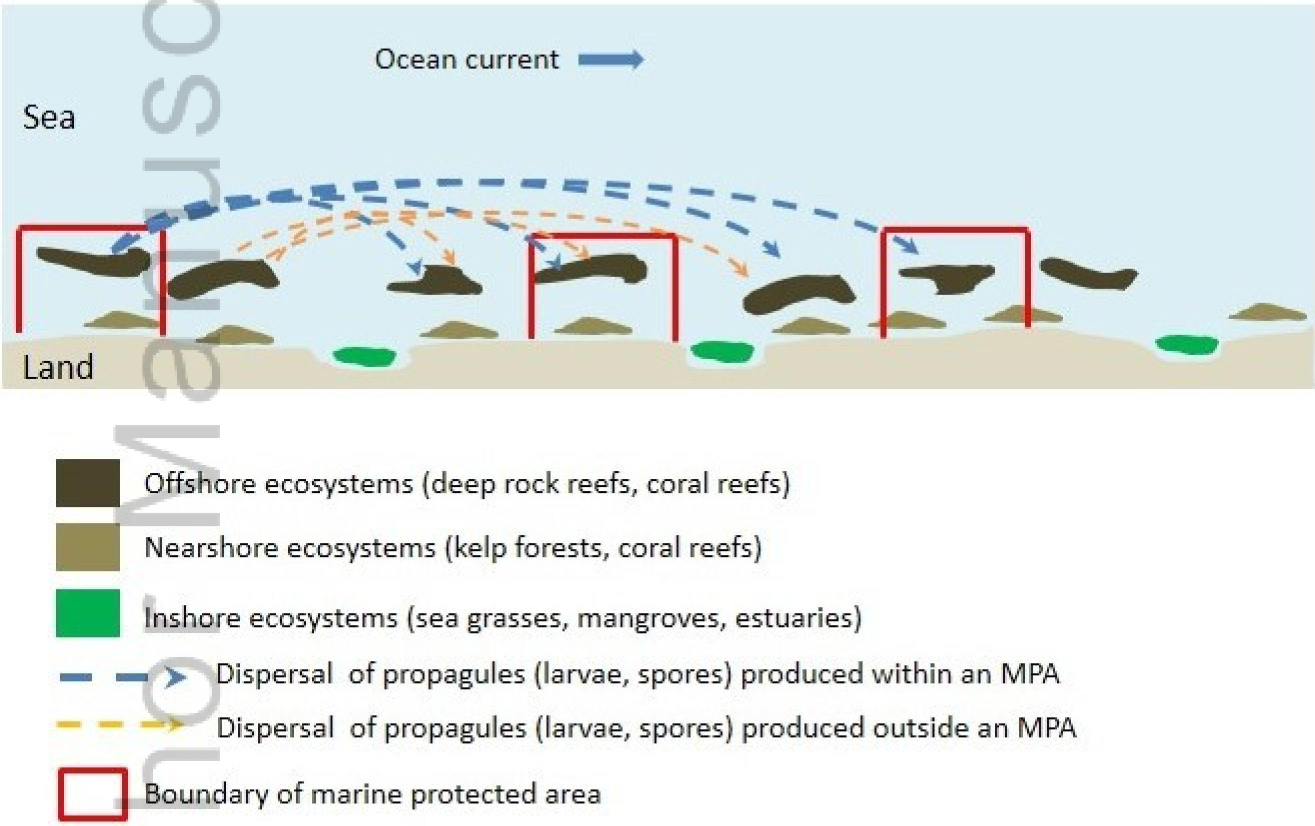

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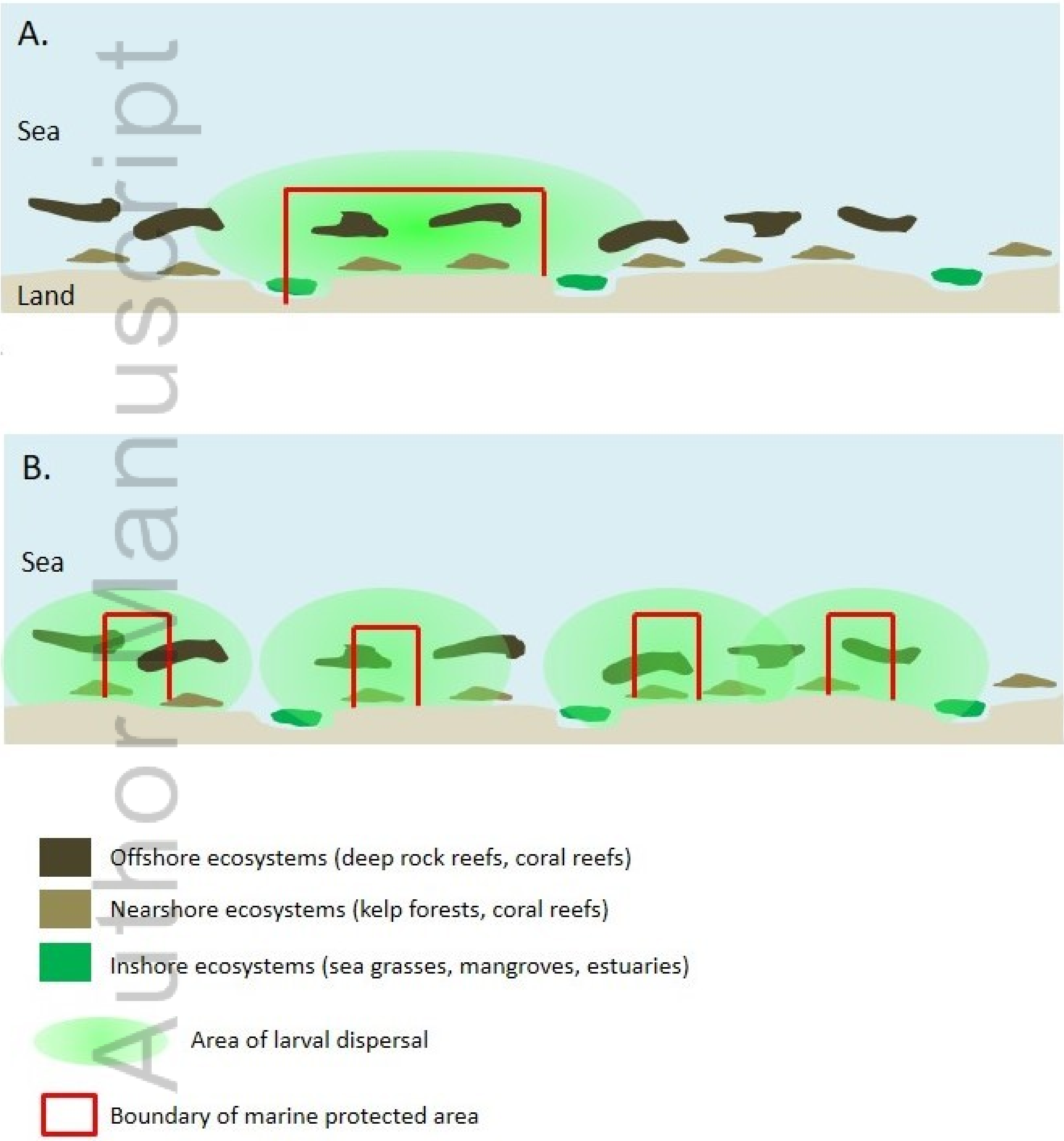

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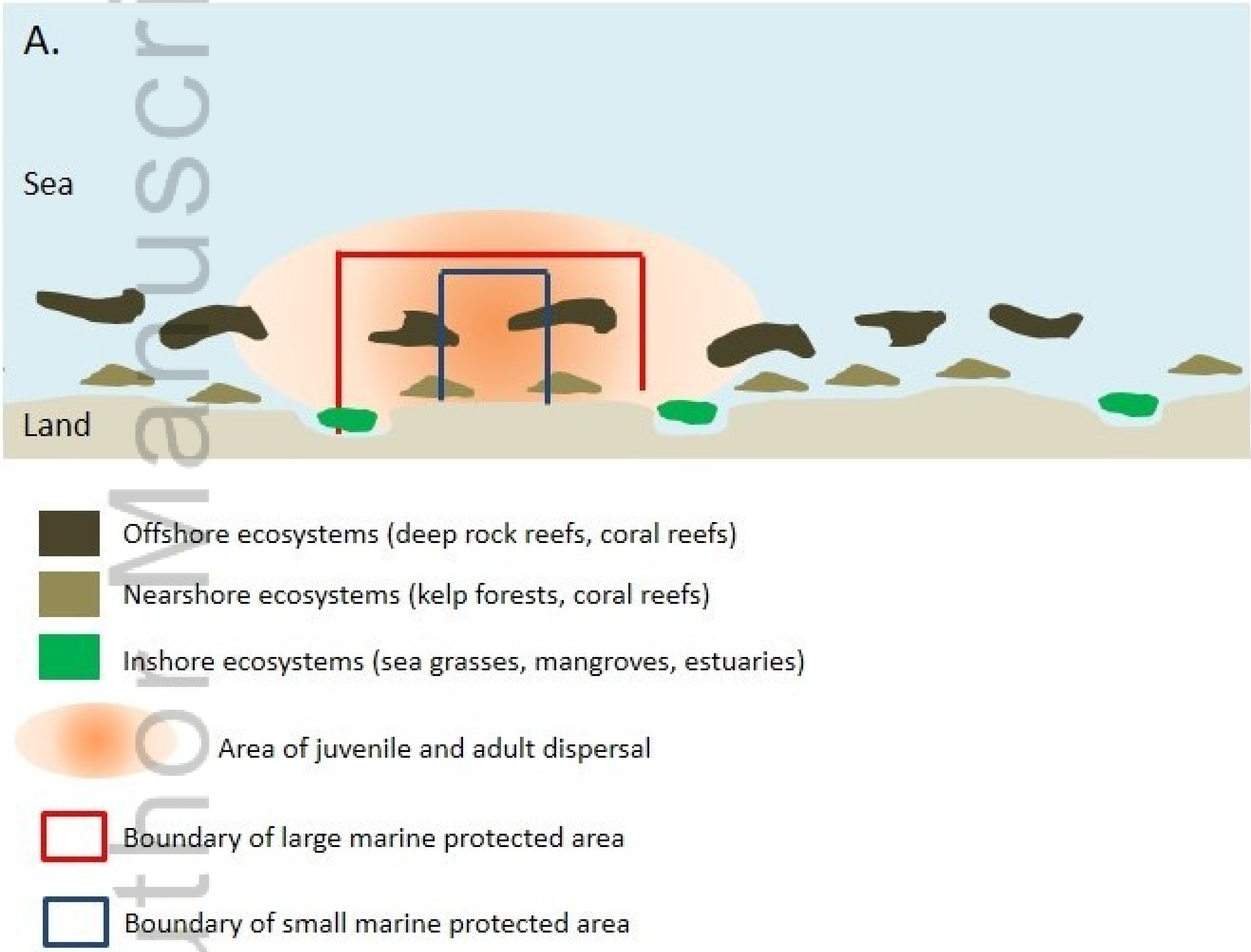

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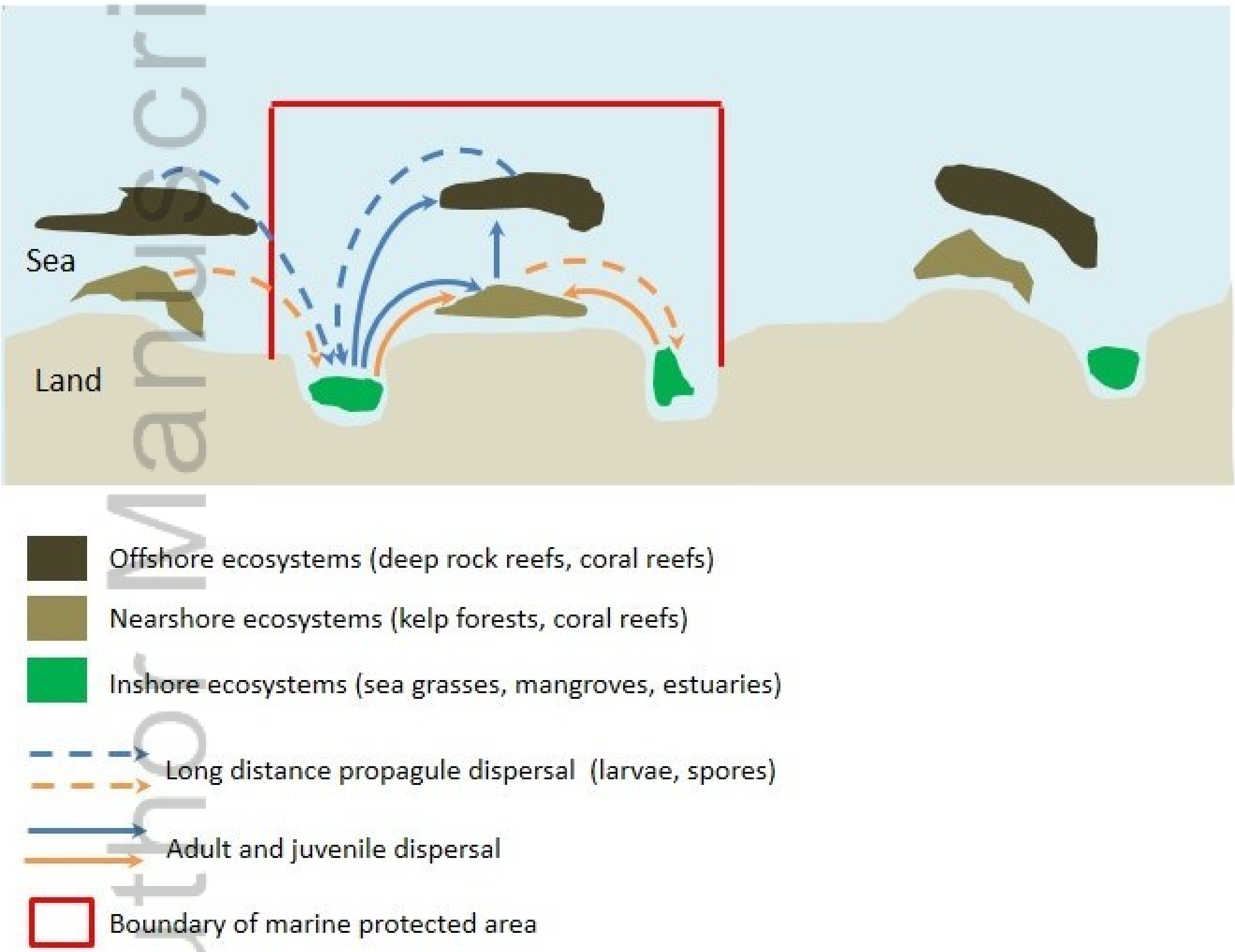

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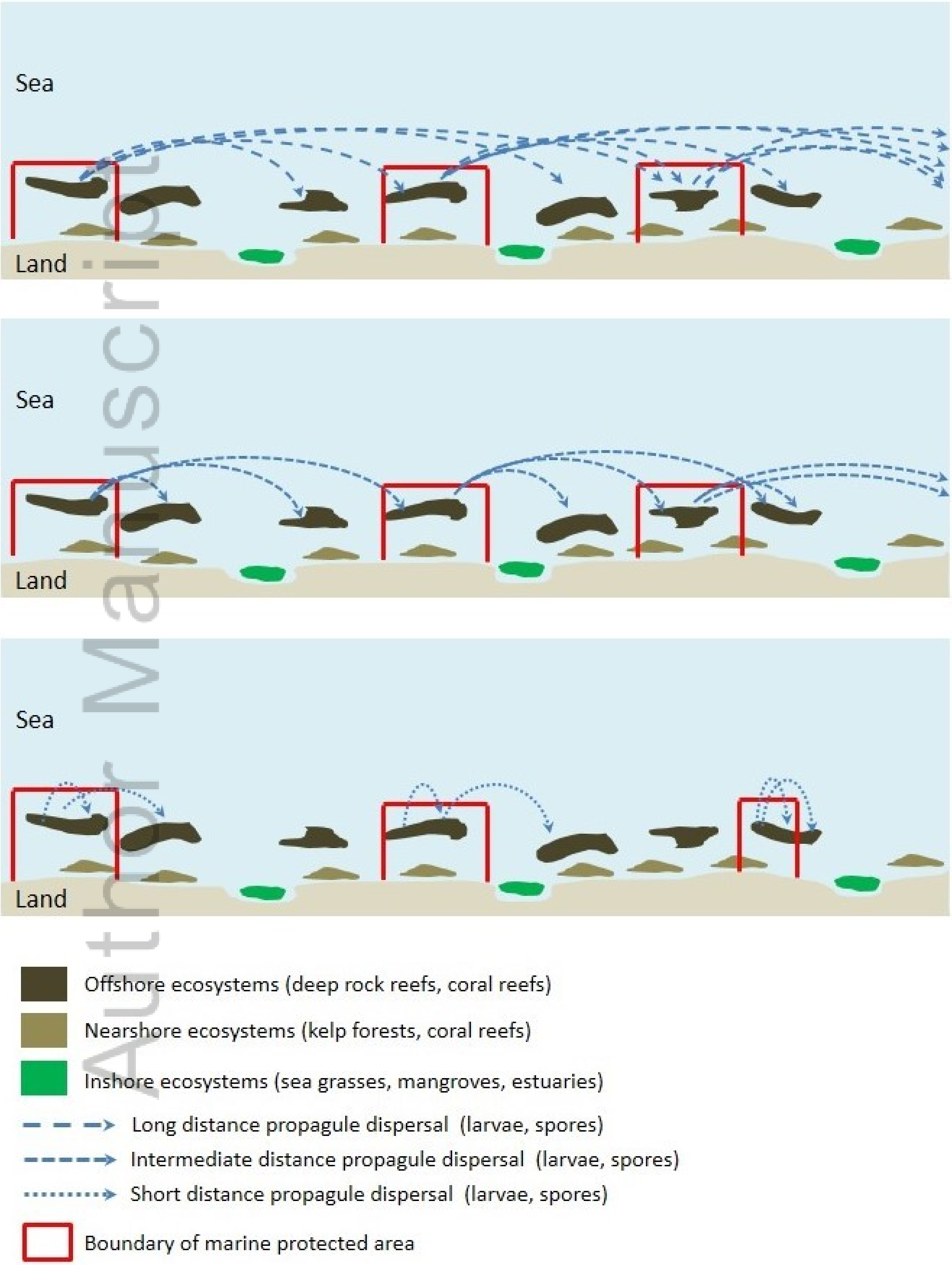

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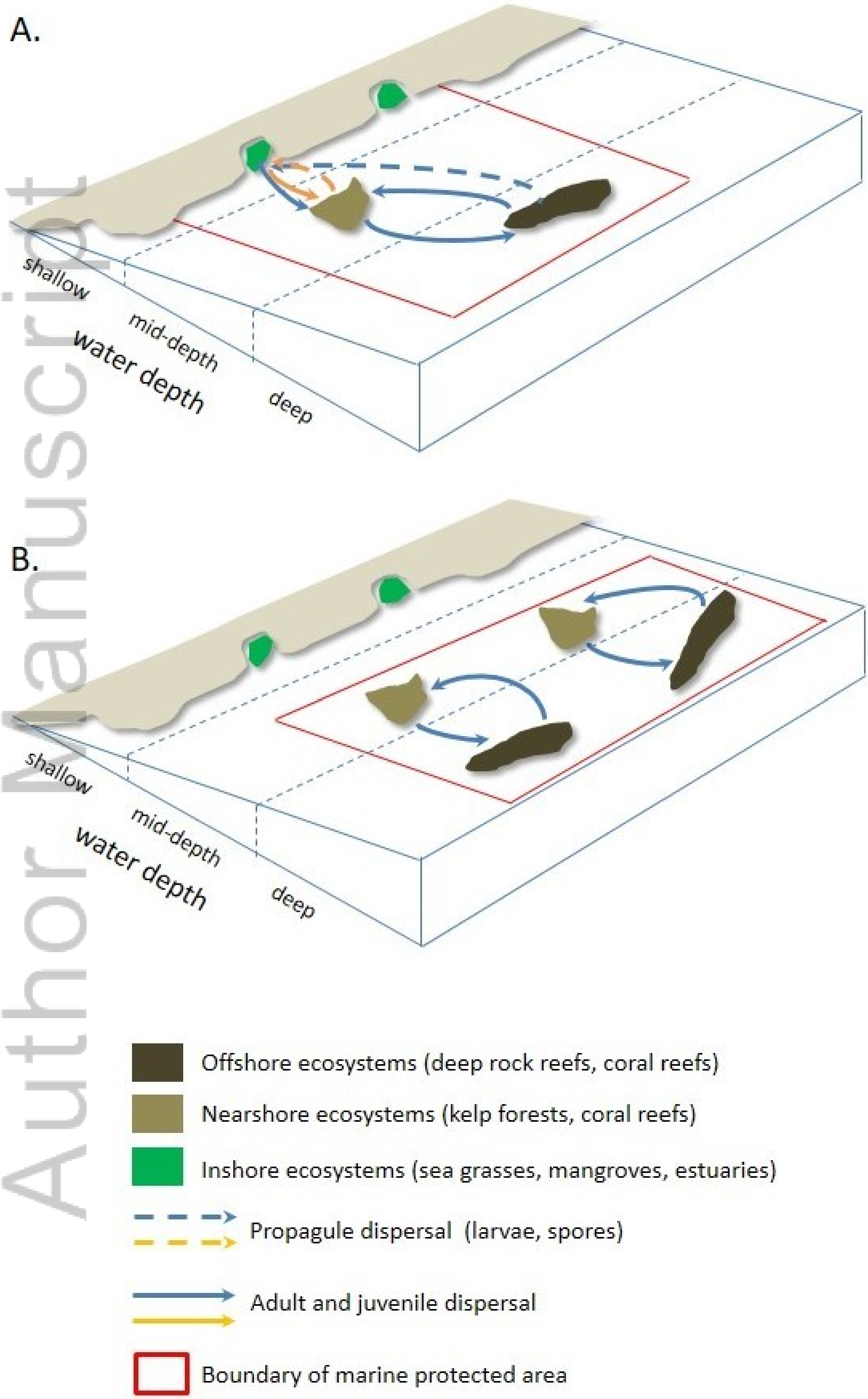

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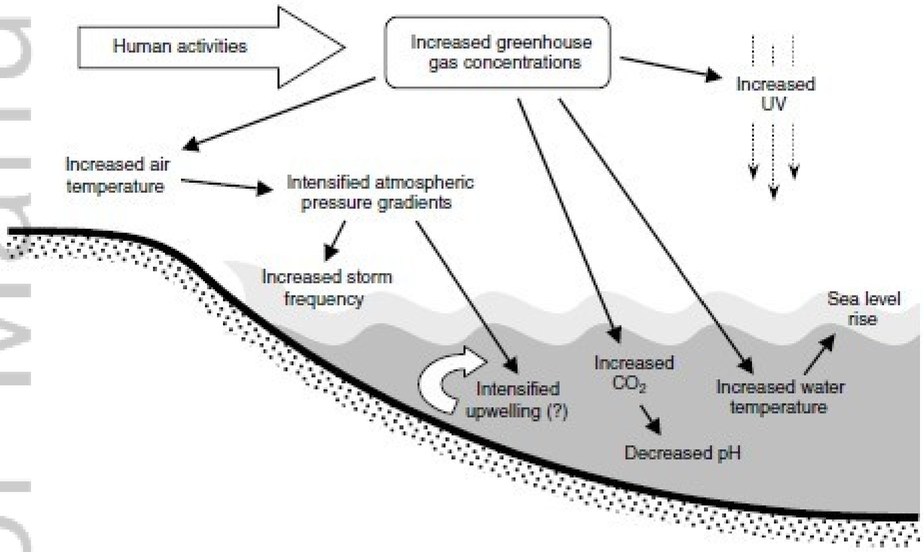

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