Advancing marine conservation through ecological connectivity:
Building better connections for better protection

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ABSTRACT
The incorporation of ecological connectivity, the unimpeded movement of species and the flow of natural processes that sustain life on Earth, into protected area design and management is critical to achieving conservation outcomes. However, the understanding and implementation of ecological connectivity in marine protected areas (MPAs) lags behind that of their terrestrial counterparts. Here, we highlight the important role of ecological connectivity in the design and management of MPA networks through an introduction to marine connectivity and the challenges and benefits of incorporating it into management. The paper also provides guidance for policy and practice, including “rules of thumb”

Through NAMPAN (the North American Marine Protected Areas Network), Canada, Mexico, and the United States work together to protect shared resources such as highly-migratory whales.  ED LYMAN / NOAA PERMIT #14682
for incorporating connectivity into MPA design and management, and case studies. MPA managers have the potential to increase the effectiveness, adaptability, and resilience of the resources under their stewardship through the purposeful incorporation of ecological connectivity into MPA design and management.

INTRODUCTION
The global conservation community is on the verge of a formal commitment to protect 30% of our lands and waters by 2030. Scientists have been clear that there is a need for increased management, conservation, and restoration of natural systems to sustain global biodiversity, regulate our climate, and provide a host of other benefits. Yet marine and terrestrial protected areas must be effectively connected in order to reach beyond the numeric target of protection to achieve desired conservation outcomes (Hilty et al. 2020). Ecological networks are essential tools for incorporating ecological connectivity into the design and management of protected areas. Such networks include core habitats (protected areas), other effective conservation measures, and other intact natural or semi-natural areas connected by ecological corridors, which have been established, restored, and maintained to conserve biodiversity in often fragmented systems (Hilty et al. 2020).

Ecological connectivity is the unimpeded movement of species, and the flow of natural processes, that sustain life on Earth (Hilty et al. 2020). This includes the movement of populations, and that of individuals, genes, gametes, and propagules between populations, communities, and ecosystems, as well as that of non-living material from one location to another (Hilty et al. 2020). Historically, protected areas on land and in the ocean have been established and managed as “conservation islands” to protect particular resources of biological, historical, or cultural significance and enhance biodiversity. Scientists and managers increasingly recognize that these areas cannot be managed in isolation if they are to achieve their goals in the face of the dual crises of biodiversity loss and climate change. The successful design of ecological networks depends on identifying, maintaining, and enhancing connectivity among distinct sites within the network. Further, in the ocean the management of ecological networks requires coordination among and between marine protected areas (MPAs) and the multiple jurisdictions and authorities they represent. Enhancing ecological connectivity through ecological networks improves conservation outcomes by promoting biodiversity, population persistence, and resilience while increasing the capacity of species and ecosystems to adapt to both natural and anthropogenic environmental change (Olds et al. 2016; Balbar and Metaxas 2019). Through effective design and management, ecological networks can potentially reduce the footprint of individual protected areas, while increasing their effectiveness, thus decreasing potential conflicts with other uses.

CONNECTIVITY CONSERVATION IN THE OCEAN
Much of our understanding of the importance of ecological connectivity to conservation outcomes is derived from the study of terrestrial protected areas and processes. While the same basic principles apply (e.g., structural and functional connectivity, stepping stones), the processes that govern connectivity in the ocean are substantially different than on land. Successfully achieving the goal of protecting 30% of the ocean by 2030 through well connected MPAs requires an understanding of the unique nature of connectivity in the ocean.

Passive (oceanographic) connectivity is the incidental movement of organisms, nutrients, and materials through physical processes such as currents, sinking, or upwelling. An example of passive connectivity would be fish, shellfish, or coral larvae dispersing via ocean currents, or nutrients being moved to the surface by upwelled water. In contrast, active (migratory) connectivity is the purposeful, self-directed movement of organisms from place to place. Migrations of large animals such as whales and turtles are the most obvious example of active connectivity, but this category also includes other movements such as the daily vertical migrations of mesophotic species between the surface and deeper waters. Another difference between terrestrial and marine environments is that habitat connectivity, the linkage between habitat patches of the same type, applies to both, while seascape connectivity, the linkage between habitats of differing types, such as a fish moving from mangroves to seagrasses, is exclusive to the ocean (Figure 1).

While connectivity between habitat types is also important in terrestrial systems, the fluid nature of the ocean, its high environmental variability, and the prevalence of currents, eddies, and other physical
processes make movement and dispersal over large distances and between habitats more dynamic, and complex, thus warranting the term “seascape connectivity.” This results in an increased importance of both passive and seascape connectivity compared with their counterparts on land. This higher capacity for connectivity can present challenges to the management of MPAs. High mobility and connectivity can allow for greater dispersal of pollutants and increase the potential spread of disease and invasive species (analogous to dispersal by wind in terrestrial systems). Further, the three-dimensionality of marine connectivity can result in activities that occur at one depth (such as dredging) impacting another (such as the impacts of sediment moving through the water column).

As on land, marine life and processes do not recognize political or management boundaries. Connections to locations outside of protected areas can challenge management, particularly when those areas are outside of the jurisdiction of managers or managed by a different authority. Natural connectivity of marine ecosystems and species occurs between national waters, neighboring state/provincial waters, and the high seas, and is influenced by environmental factors, human uses, and climate change impacts that cross those political boundaries. It is not uncommon for marine organisms to spend part of their lives in the exclusive economic zones (EEZs) of multiple countries and part in Areas Beyond National Jurisdictions (ABNJs, the “high seas”), while also moving in and out of protected areas and other jurisdictions. This presents inherent challenges to management and requires increased collaboration between agencies both within and between countries. Marine life is also directly affected by land-based impacts, such as sedimentation or other land-based pollution, that can originate hundreds of miles inland and directly affect MPA resources through river outflows and coastal run-off.

While the high connectivity of the ocean presents management challenges, it also offers a wealth of opportunities for conservation. Better connected biological populations have higher genetic diversity, increasing their resilience to disease and other stressors, and can recover more quickly from disturbances as individuals or propagules arrive from connected, unaffected areas. Management strategies focused on maintaining and restoring connectivity, particularly the establishment of MPA networks, increase resilience to stressors such as disturbance, fishing, and climate change.

**CLIMATE CHANGE AND CONNECTIVITY IN THE OCEAN**

As complex as ocean connectivity can be, it is made even more so by the changing climate. Climate change is altering ocean temperature, hydrodynamics, water chemistry (e.g., acidification), the physiological and life history processes of organisms, and even the viability of habitats. These impacts have direct
effects on connectivity, altering the timing and pathways of migrations, larval dispersal, and other behaviors and life cycle processes. The high mobility of marine species and connectivity of the ocean are facilitating the poleward shift in the ranges of many marine species, which are shifting six times faster on average than terrestrial species (Lenoir et al. 2020). Moreover, the Gulf Stream—one of Earth’s major climate-regulating ocean currents—is moving slower than it has in a thousand years and human-induced climate change is largely to blame (Caesar et al. 2021). This unprecedented slowdown could impact weather patterns, sea levels, habitats, and species connectivity patterns on both sides of the Atlantic.

Together, these changes are altering the ecological communities found in MPAs and other conservation zones, leading to unexpected changes that can threaten conservation objectives. Poleward-expanding tropical herbivorous fishes have overgrazed macroalgae and seagrasses along coasts from Japan and Australia to the Mediterranean and United States (Vergés et al. 2014). Further, warming-driven changes in the timing and intensity of plankton blooms in MPAs on the West Coast of North America have led to mass mortalities and decreased production of the seabirds, marine mammals, and fish that travel hundreds to thousands of miles to feed. These and future changes to marine connectivity will require the management of MPA networks to be adaptive and flexible to achieve conservation goals. In some cases, managers may need to make difficult decisions, such as revisiting conservation objectives if, for example, a key species moving out of the protected area results in the MPA being unable to meet its conservation goals.

Despite these challenges, MPA networks remain a key tool in addressing the climate crisis. Perhaps most directly, MPAs and MPA networks can protect climate refugia, areas that exhibit persistent conditions that reduce the vulnerability of a species to climate change (Kapsenberg and Cyronak 2019). Refugia can either be areas where changes are occurring more slowly (“spatial refugia”), giving species time to adapt or evolve to changing conditions, or areas where conditions are already similar to projected future conditions (“adaptive refugia”) which contain populations that are pre-adapted to change (Kapsenberg and Cyronak 2019). Within an MPA network, species can move into spatial refugia to gain protection from suboptimal changing conditions while pre-adapted individuals, larvae, and genotypes move out of adaptive refugia to other connected areas of the marine ecological network, increasing the genetic diversity and adaptive capacity of the larger metapopulation or species (Kapsenberg and Cyronak 2019). By incorporating refugia into ecological networks, MPAs can leverage the high connectivity of ocean habitats to help species and ecosystems adapt to climate change.

MPA networks can also provide “safe landing places” for species undergoing range shifts. As species change their ranges in response to warming and other environmental changes, they may leave the protection provided by MPAs. Ecological networks of MPAs can provide safe landing places and protected routes for shifting species. Designing ecological networks with range shifts in mind will be particularly important for species that may shift across jurisdictions and those with limited dispersal capabilities that may need targeted protection as their ranges change. Even if networks are not designed with the shifts of particular species in mind, simply by enhancing and conserving connectivity ecological networks of MPAs can provide species undergoing range shifts with some level of protection.

INCLUDING CONNECTIVITY IN MARINE PROTECTED AREA NETWORKS: GUIDANCE FOR POLICY AND PRACTICE

While the concept of connectivity between terrestrial protected areas is well established, most efforts to incorporate it into MPA management are still in their early stages. Some governments, such as Australia and the state of California (Figure 2), have established MPA networks that explicitly consider ecological connectivity by using design tools such as Marxan (Balbar and Mataxas, 2019). Many other countries and management agencies are now considering how to incorporate protection and restoration of ecological connectivity into existing MPAs and systems. Leveraging ocean science and technology that advances our understanding of marine and coastal ecological connectivity is a critical first step.

Just as connectivity science and management in marine systems is much less advanced than for terrestrial systems, the same is true for policy and law supporting marine connectivity (Lausche et al. 2013). Marine connectivity operates across all dimensions of marine space, from the air to the ocean surface, within and across the water column, to the
ocean floor and below (e.g. seabed) and over the broad reaches of the ocean, including in the land-sea interface and between national waters and ABNJs. In these spaces, marine ecosystems and species interact and function in MPA networks and across marine environments.

Scientists have long recognized the critical role marine connectivity plays in sustaining marine habitats and biodiversity. More than a decade ago, the World Commission on Protected Areas (WCPA) of the International Union for Conservation of Nature (IUCN) published guidelines for establishing resilient MPA networks. Guideline 4, “ensure ecological linkages,” stressed that MPA network design should seek to maximize and enhance the linkages among individual MPAs and groups of MPAs within a given network. These linkages may include:

- **Connections between adjacent or continuous habitats**, such as coral reefs and seagrass beds, or among mangrove and seagrass nursery areas and coral reefs.
- **Connections through regular larval dispersal** in the water column between and within MPA sites.
- **Regular settlement of larvae** from one MPA to another that promotes population sustainability.
- **Movements of mature marine life** in animal home ranges from one site to another or because of regular or random spillover effects from MPAs (IUCN 2008).

In 2020, IUCN published new *Guidelines for Conserving Connectivity through Ecological Networks and Corridors* (Hilty et al. 2020). This global effort, covering both terrestrial and marine environments, was more than two decades in the making. The guidelines consolidate what we know about connectivity conservation, provide guidance for conserving ecological corridors, and recommend that conserved ecological corridors be tracked by the World Database on Protected Areas. Further, the guidelines define “ecological connectivity” (see above) and explore the scientific basis for connectivity, planning and implementing ecological corridors, law and policy needs, monitoring, and basic documentation for reporting. The report also includes two marine case studies highlighting the incorporation of ecological connectivity in MPA management (Hilty et al. 2020).

A second new publication, *Ecological Connectivity for Marine Protected Areas*, led by the National MPA Center of the National Oceanic and Atmospheric Administration (NOAA), focuses on the important role of ecological connectivity in the design and management of MPA networks. This well-illustrated document discusses why ecological connectivity is important for MPAs and highlights four crucial steps for moving forward: (1) strengthen legal authorities for ecological connectivity in MPA design; (2) communicate the benefits of connectivity; (3) design more ecologically connected networks; and (4) understand how marine connectivity works in different places (NOAA 2020).

Finally, with respect to ABNJs, the Deep-Ocean Stewardship Initiative in 2020 endorsed the need for
ecological connectivity as part of ocean governance (DOSI 2020).

RULES OF THUMB FOR DESIGNING CONNECTIVITY INTO MPA NETWORKS

The relative lack of tangible examples of applying marine ecological connectivity to MPA networks may be, in part, a result of the lack of clear guidance for MPA managers and decision-makers. To meet this need, IUCN-WCPA, under the umbrella of its Connectivity Conservation Specialist Group, established a Marine Connectivity Working Group (MCWG) in 2019 with the goal of developing “rules of thumb” for building connectivity conservation into MPA network design. While the full list is under review by MCWG members, the points below represent some of the main rules of thumb being considered.

• **Identify the role each MPA plays in supporting connectivity** when designing an MPA network. Some MPAs may have self-replenishing populations supporting connectivity, whereas others may serve as sources, sinks, stepping stones, or corridors.

• **Take into account the effects of ocean processes** on connectivity of target species when designing and managing MPAs and MPA networks.

• **Incorporate climate change adaptation measures** in the design and management of MPAs and MPA networks that take into account ecological connectivity.

• **Use habitat modeling** to develop scenarios that can provide information on habitat linkages.

• **Recognize relationships between different types of area-based management**, e.g., between MPA management and management of fisheries outside MPAs.

ADVANCING SCIENCE AND TECHNOLOGY FOR UNDERSTANDING MARINE CONNECTIVITY

Advances in science and technology are rapidly improving our understanding of the ocean’s interconnected physical, biological, and chemical properties; unique biodiversity; and life-support functions. In large part, this has been due to

California’s statewide MPA network includes all marine and estuarine habitats in state waters, including vibrant kelp forests. ROB SCHWEMMER / NOAA
significant advances in ocean technology. Progress has been especially impressive with respect to the development of genetic technology (omics and eDNA); the research and exploration of the deep-sea environment, hydrothermal vents, seeps, and seamounts; the role of microorganisms; and the interconnected nature of marine processes throughout the water column from deep to shallow waters as well as between national waters and ANBJs.

Many tools and techniques have been developed and/or leveraged to make these advances. Some tools are deployed as autonomous devices, while other instruments accompany scientists and research teams collecting data and making real-time observations. Some tools and strategies used by scientists and managers to understand and measure connectivity include:

- **eDNA.** DNA that is released by an organism into the environment. By analyzing eDNA, scientists and managers can track the presence of species without direct observation or disturbance.
- **Telemetry.** The use of sensors or tags attached to animals to track their movement and/or behavior. These sensors can report data to satellites, land or ship-borne receivers, or log data themselves and be retrieved after a timed release from the animal.
- **Acoustic monitoring.** The technique of tracking or identifying animals by the sounds they make. These data are often gathered by hydrophones placed on ships, shore-based stations, or buoys. Sensors can also track human-caused noise that may affect animal behavior.
- **Submersibles and autonomous underwater vehicles (AUVs).** Submersibles, both piloted and autonomous, allow for the collection of data in locations in which it may otherwise be too dangerous or expensive. By carrying equipment such as audio-video recorders, water samplers, and eDNA samplers, these vehicles can collect data valuable to determining and tracking ecological connectivity.
- **Data management and access.** Making connectivity data accessible to managers is key to advancing the incorporation of ecological connectivity into the design and management of MPAs. Partnerships like the Animal Telemetry Network make connectivity-relevant data accessible to managers in an understandable and easy-to-use format.

The digitization of ocean research data is another major technological breakthrough, allowing the viewing and processing of spatial and species information from a computer anywhere in the world. Ocean laws and policies should give marine planners and practitioners authority to actively engage in and rely on the use of such digitized forms of data, build skills and equipment capacity, and tap into such information networks as a key aspect of their responsibilities.

**MANAGEMENT APPLICATIONS: CASE STUDIES OF MARINE CONNECTIVITY CONSERVATION IN ACTION**

**Flower Garden Banks: Expanding an MPA in the Gulf of Mexico**

In 1992, NOAA established Flower Garden Banks National Marine Sanctuary to protect three shallow banks in the Gulf of Mexico about 80 miles offshore from the Louisiana/Texas border. The banks are small mountains of hard bottom patches created by underlying salt domes—vertical migrations from a thick layer of salt deposited by evaporating seawater over 190 million years ago—and are home to thriving communities of coral reefs and sponges, as well as manta rays and threatened or endangered sea turtles, and are habitat for recreationally and commercially important species. The banks protected by the sanctuary are among dozens scattered throughout the northern Gulf of Mexico. These ecological hotspots have been studied for decades to understand their habitat value, connectivity, and vulnerability to oil and gas development, fishing, climate impacts and other activities in the region.

Over the past two decades, sanctuary and partner scientists have studied the physical and ecological connectivity of the banks of the northwestern Gulf of Mexico. New technology has allowed the creation of high-resolution bathymetric maps that show geological features between the more prominent banks. These rocky outcroppings act as stepping stone-like connectivity corridors, providing habitat and food for species transiting between banks. Scientists are also studying the role of ecological connectivity among these banks in sustaining coral and fish communities throughout the Gulf of Mexico, including larval dispersal and movement of adults.

Recognizing the importance of ecological connectivity in sustaining marine ecosystems, as well as its influence on impacts and recovery following incidents such as oil spills, the sanctuary’s stakeholder advisory
council recommended expanding the sanctuary boundaries in 2007, with ecological connectivity as a criterion for its recommendations. Options for expansion ranged from adding 11 to 57 new banks, to be managed as a network of marine protected areas. In January 2021, the sanctuary was expanded to add 14 additional banks, increasing its area from 56 mi² to 160 mi² (Figure 3).

Connectivity among Gulf of Mexico MPAs is also being explored at the basin scale. Areas across the Gulf and Caribbean are connected by the Gulf Loop Current, which enters the Gulf of Mexico as a river of warm water through the Yucatan Channel between Cuba and Mexico, and flows northward before turning clockwise along the Florida shelf to the Florida straits. The United States, Mexico, and Cuba have formed a Gulf of Mexico MPA Network (RedGulfo) to work together to protect similar habitats and the species that move among the three countries.

Connecting at the continental scale: North American MPA Network
Canada, Mexico, and the United States have worked together for years to conserve shared marine habitats and species. Recently, marine protected area programs in the three countries have established a formal partnership, coordinated by the UN Environment Programme, to connect MPA managers through the North American MPA Network (NAMPAN). Following a series of in-person and virtual meetings across the three countries in 2020 to understand the needs and priorities of MPA managers, NAMPAN hosted a virtual “deep dive” on the topic of ecological connectivity in April 2021. The event featured discussions among managers in the three countries on opportunities to collaborate, such as establishing “sister sanctuaries”; working through MPA networks at the regional scale,
FIGURE 3. Map of Flower Garden Banks National Marine Sanctuary before (top) and after (bottom) expansion in 2021. NOAA
such as the Great Lakes; and developing and sharing best practices to protect shared species. NAMPAN work builds on over 20 years of cooperation on marine conservation through the Commission for Environmental Cooperation (CEC), the organization formed to support environmental protection as part of the trilateral trade agreement between the United States, Canada, and Mexico. In recent years, CEC has focused on tools and capacity building for MPA managers to address climate impacts, including how they may impact connectivity across the continent’s waters. In 2018, CEC hosted “sister site” workshops for MPAs to identify opportunities to share management strategies for migratory species such as gray whales and white sharks.

**Assessing a decade of network protection:**

**California’s statewide MPA network**

California’s development of an ecologically connected, representative MPA network, which was completed in 2012 after an extensive public engagement process, has established the state as a global leader in marine conservation. The science-based network was authorized by a state law, the Marine Life Protection Act, and resulted in a statewide network of 124 MPAs covering almost 17% of state waters, including 9.5% in no-take protection (Figure 2). California’s MPA network includes all marine and estuarine habitat types in state waters (from zero to three nautical miles offshore), from sandy beaches and intertidal areas to deep-water canyons and islands.

The Marine Life Protection Act says that California’s MPAs should be “designed and managed, to the extent possible, as a network.” The MPA planning process included the development of guidelines for the size and spacing of MPAs, based on best available knowledge of home ranges and dispersal distances for larvae of certain nearshore species. These guidelines aimed to ensure the conservation of species with different patterns of movement through the network. In 2022, the statewide network will conduct a management review to evaluate its performance.

**MOVING MARINE CONNECTIVITY CONSERVATION FORWARD**

Connectivity tools are needed to support the conservation outcomes of MPAs and MPA networks at all spatial scales. These tools include improvements in scientific knowledge about the marine environment, consistent monitoring and assessment tools to evaluate effectiveness, major advances in ocean-observing technology, ecosystem-based marine management, integrated marine and coastal zone management, marine spatial planning, ocean zoning, and basic rules of thumb to help guide the incorporation of connectivity needs into the design and management of marine conservation areas.

Most coastal and island nations have legislation covering aspects of marine conservation, management, and sustainable use that have some regulatory controls, standards, and requirements for coastal and marine space and resources. These laws may include protected areas legislation covering marine areas, site-specific laws for particular MPAs, specific marine species protection laws (for example, sea turtles, whales), and coastal development laws.

A better understanding of ecological connectivity can greatly enhance the effective implementation of existing laws, but there is also a need to strengthen or develop new legislation to support more effective and adaptive management. Important elements to consider when strengthening or developing legislation include a focus on ecologically based MPA networks, rather than individual sites; providing scientific and ecological criteria for selecting sites within such networks; requiring an ecosystem-based approach to overall marine spatial planning, management, and conservation, including for connectivity; and authorizing the formal and evidentiary use of ocean-observing technology and the data it generates to better understand and sustainably manage the ocean and its connectivity.

MPA managers find themselves in a challenging position: simultaneously faced with biodiversity and climate crises while restricted by policy and law not well designed to respond to either. The current rapid rate of change requires managers to be flexible and adaptive, responding quickly and decisively to gradual changes like species range shifts as well as sudden shifts due to tipping points, while at the same time confronting growing threats from non-climate stressors. Better understanding and incorporating ecological connectivity into the design and management of MPA networks is key to achieving conservation outcomes, including enhancing the resilience of species and ecosystems in the face of global change and other stressors.
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