

REVIEW

Connectivity corridor conservation: A conceptual model for the restoration of a changing Gulf of Mexico ecosystem

Charles H. Peterson¹, Kelly P. Franklin², and Erik E. Cordes²

The ability of the ocean to continue to sustain human society depends on adequate protections of its ecosystem function and services. Despite the establishment of marine protected areas, formal protection of critical connectivity corridors to link habitats and thereby maintain necessary demographic transitions in marine species under threat is now rare. Such protections are critical to future resilience of food webs as climate and ocean change continues. Here, we focus on the Gulf of Mexico to support an integrative, holistic approach to marine and coastal habitat restoration, rehabilitation, and conservation in an ecosystem context following the extensive environmental and living resource injuries from the *Deepwater Horizon* oil well blowout. Critically important physical, chemical, and biological connectivity processes drive nutrient transport from the nearshore, mid-waters, and even deep ocean into coastal terrestrial habitats, enhancing primary production and terrestrial species populations. The emerging scientific understanding of the nature, habitat specificity, locations, and directions of transport in connectivity processes can help build natural ecosystem capital through protecting flows from land to sea and from the sea to multiple coastal habitats. We expose a dire need for a new conservation imperative, recognizing that oceanic and coastal protected areas established around the reliance of individual species on critical habitats are insufficient without also conserving relevant connectivity corridors that service ontogenetic migration pathways and ecosystem-support processes. Such connectivity must be explicitly understood, protected, and often actively enhanced through restoration intervention to ensure the success of various site-specific conservation actions and be continually modified in anticipation of and in response to multiple impacts of changing climate.

Keywords: *Deepwater Horizon*, Ecosystem-based management, Fisheries, Climate change, Ontogenetic migration

1. Introduction

Human society relies on the ocean for a wide range of services from food provision to climate regulation. The ability of the ocean to provide all of these ecosystem services requires adequate protection of its key habitats and processes (Worm et al., 2006). For example, global fisheries productivity is dependent on levels of primary productivity as well as the ability of commercially significant fish species to complete their entire life cycle. The primary tool available to ensure that these processes proceed without interruption is the establishment of marine protected areas (MPAs; Halpern, 2003).

Designing MPAs involves many different considerations. Proper design requires the determination of the

distribution of the focal species, the relevant pressures, and the desired outcomes (Mangel, 1998). For fisheries species, the inclusion of “essential fish habitat” (EFH) has been recognized as a critical component of any management plan (Rosenberg et al., 2000). The determination of EFH, however, may be focused on one life stage, when one type of EFH rarely encompasses the full range of ontogenetic migrations that spatially structured populations of fisheries species will undertake, making management of these populations challenging (Burgess et al., 2014; Levin and Stunz, 2005).

The Gulf of Mexico (GoM) is the ninth largest body of water in the world, and its large marine ecosystem consists of numerous individual components that are all inextricably linked (Yáñez-Arancibia and Day, 2004). The components include the watersheds of rivers (covering 60% of the United States and 40% of Mexico) that feed into bays and estuarine systems, the salt marshes and mangrove habitats that punctuate the extensive sandy beaches lining the Gulf coast, the nearshore islands and banks where the marine system makes its approach to land, the subtidal oyster reef habitats, the mesophotic coral banks, the

¹ Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina, USA

² Department of Biology, Temple University, Philadelphia, Pennsylvania, USA

* Corresponding author:
Email: ecordes@temple.edu

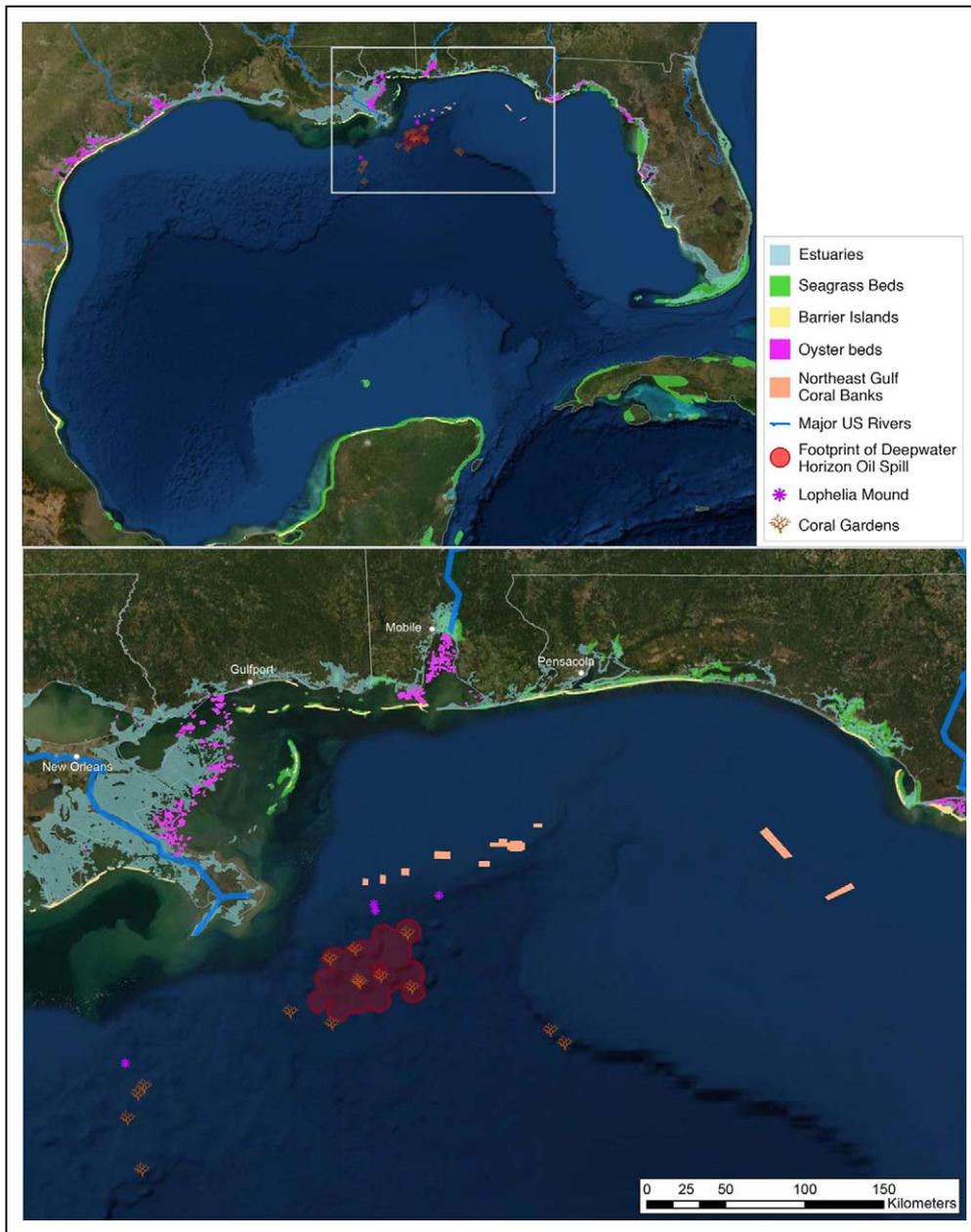


Figure 1. Map of the northern Gulf of Mexico. Inset is the region in the vicinity of the *Deepwater Horizon* drilling rig. The close proximity of the different habitats, including riverine, estuary, oyster beds, barrier islands, coral banks, coral mounds, and coral gardens within 30 to 40 nautical miles, is apparent in their distribution in this region. The area of the deep-sea spill impacts is also shown, although impacts were also observed in the mesophotic coral banks and exposure was evident at the *Lophelia* coral mound sites. DOI: <https://doi.org/10.1525/elementa.016.f1>

pelagic ecosystem overlying the continental shelf and deeper waters, the soft-bottom benthos, and the deepwater coral banks, mounds, and gardens (**Figure 1**).

Here, we present an integrated approach to ecological restoration of habitats from watersheds to the deep sea. First, we survey the linkages among these habitats and their role in providing the connectivity that is an essential component of ecosystem function. We then identify the most vulnerable linkages as a component of an overall integrated ecosystem assessment. We then propose the use of “Connectivity Corridor Conservation” as a key concept in the design and implementation of MPAs to ensure the preservation of habitats along the typical ontogenetic

migrations of key species. We further focus on the GoM as a case study because of the use of MPAs in the restoration activities following the 2010 *Deepwater Horizon* oil spill. This approach follows the relevant principles as set out by the Society for Ecological Restoration (Gann et al., 2019) in that it draws on many types of knowledge, supports ecosystem recovery processes at the highest level, gains cumulative value at large scales, and would be implemented as part of a larger restoration program.

2. GoM as a changing ocean basin

The GoM is fed by water flows from the Caribbean coming through the deep Yucatan Channel and drained by flows

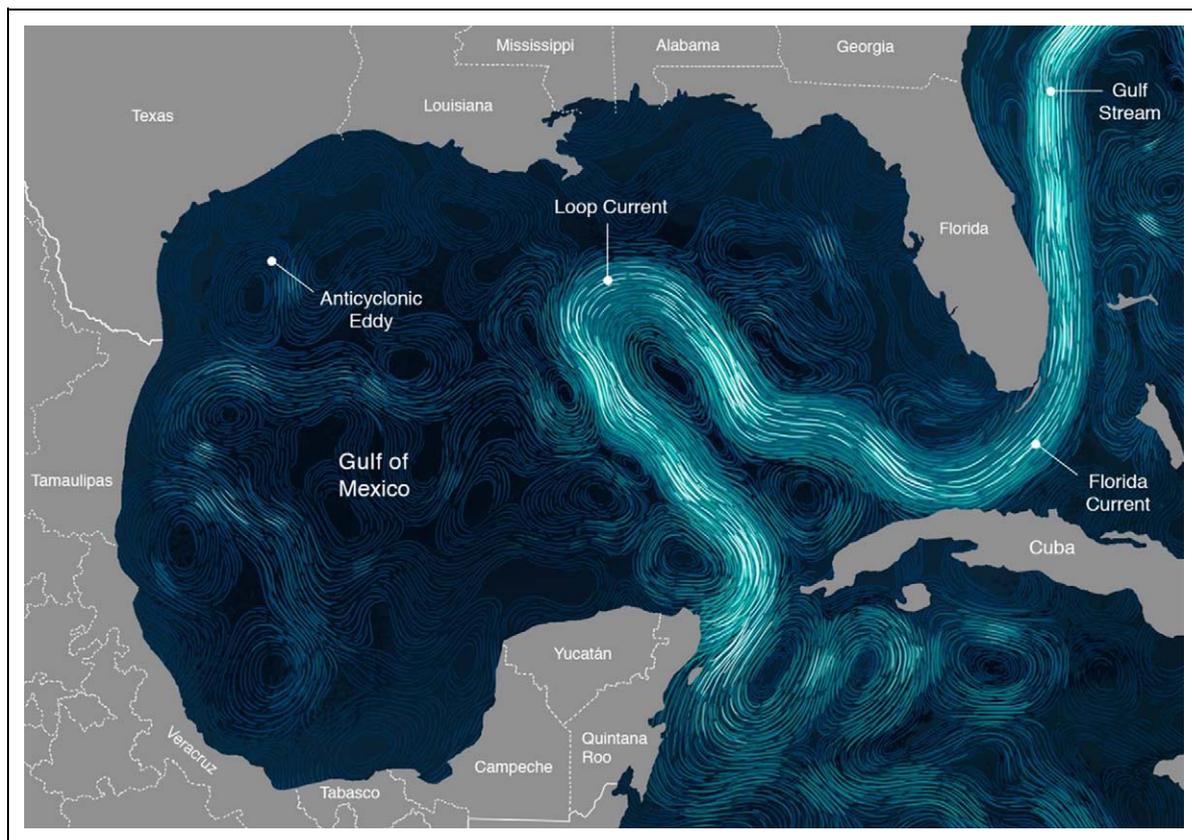


Figure 2. Surface currents of the Gulf of Mexico. This snapshot reflects the situation where the loop current extends into the northern Gulf and the vicinity of the Deepwater Horizon and the habitats discussed here. Also depicted is the formation of anticyclonic eddies and their persistence in the Western Gulf. DOI: <https://doi.org/10.1525/elementa.016.f2>

out the Straits of Florida, which together comprise the Loop Current that dominates basin-wide, large-scale current flows in the GoM (**Figure 2**). The Loop Current ultimately feeds the Gulf Stream that forms the boundary current on the western margin of the North Atlantic Basin first running northward up the east coast of Florida. Basin-wide downstream flow effects of the Yucatan Channel flows, the Loop Current, and the current along the Straits of Florida to the Gulf Stream include the Atlantic Meridional Overturning Circulation (AMOC) and the Atlantic Multi-decadal Oscillation (AMO).

The AMOC flow transports heat energy from the surface tropics to the far north in the Atlantic basin and brings deep cold Atlantic waters back to the surface in the tropics of the South Atlantic, driving the conveyor belt circulation of and heat exchange in the North Atlantic Ocean. The AMO is a measure of basin-wide variation in sea surface temperature and switches from warm to cold phases. These phases of the AMO play important roles in global climate regulation and hence control how multiple aspects of climate change affect the entire Atlantic Basin, including the GoM. For example, Karnauskas et al. (2015) showed that the shift in the AMO to the warm phase in the mid-1990s coincided with an important ecosystem reorganization gulf-wide. The AMOC is expected to weaken during the next century and be associated with

slower Yucatan Current transport, thereby inducing cooling of surface waters of the GoM (Rahmstorf et al., 2015).

Changing ocean temperatures as climate responds to global warming have been clearly associated with many examples of behavior modifications of key species reflecting, for example, the emergence of new preferred habitats for several fishes of importance. Movements toward the poles and toward deeper waters have been predicted and demonstrated (Fulton, 2011; Pinsky et al., 2013; Sydeman et al., 2015). The continuous landmass of the Gulf states that forms the northern border of the GoM prohibits GoM fishes and marine mammals from responding to climate warming as globally predicted—with distributions shifting poleward—because the landmasses block that behavioral response.

Consequently, latitudinal shifting is probably being replaced by distributional shifts in depth to deeper, cooler waters. Pinsky et al. (2013) demonstrated a southwest shift in the distribution of groundfishes in the northern GoM from 1987 to 2001, contrary to northward range shifts in other Northern Hemisphere oceanic regions. Fodrie et al. (2010) sampled fishes occupying northern GoM seagrass beds and compared their set of samples to analogous sampling results from the 1970s, revealing evidence of invasion and establishment of several fishes with subtropical or tropical biogeographic affinity. These included

many families, genera, and species of commercial and recreational value, such as various snappers and groupers. The additions of reef fishes from warm-water regimes imply the emergence of novel interspecific interactions and dependencies among species not accustomed to co-occurring in the same community and thus there is a high potential for a substantial, unpredictable reorganization of the valuable reef fish communities of the northern GoM. This reorganization will, in turn, affect the interactions between land and sea along the northern Gulf coast.

Another consequence of climate change is increasing wind-driven circulation in the oceans, inducing eddy formation and upwelling (England et al., 2014). The convective energy created by wind interactions with the sea surface can also create greater frequencies of passive encounters between phytoplankton and zooplankton and between zooplankton and small zooplanktivorous fishes (Bakun, 2017). Increased frequency of encounter can enhance or depress the production of zooplankton at the herbivorous trophic level and of small zooplanktivorous fishes at the primary predator level, including several fish larvae, yet alternatively can interfere with feeding strategies of the consumers (Mackenzie and Kiorbe, 2000; Visser and Stips, 2002). These physical mixing processes at the sea surface arising from injection of convective energy can thus influence primary productivity and inhibit or enhance the ability of zooplankton to avoid consumption by larval fishes. These basin-wide changes and physical dynamics operate on scales that can and do influence important biological processes and populations in the GoM, such as fishes and marine mammals, indicating that global climate change will probably induce biological transformations of importance to the Gulf ecosystem and to people with economic dependencies on living resources within that ecosystem.

3. Connecting land and sea

The fundamental process in first considering functionally important linkages between the ocean and land is the transport of material that occurs from land to sea through riverine flows during and after major rainfall events over the collecting basins of major rivers. Rivers play a major role throughout the Gulf, except perhaps in the extreme southern tip of Texas, in the transport of nutrients, sediments, chemicals, organic particles, microbes, detritus of various size classes, and living organisms away from land to the coastal ocean, and even further into the deep sea. Montagna (2011), for example, demonstrated how the pattern of declining rainfall along the Gulf Coast of Texas from north to south plays a major role in dictating the extent of estuarine contributions to the oceanic ecosystem. Coastal barrier habitats themselves (islands and spits) are created from sands transported to the coast by riverine flows.

Nutrient loading from the drainage of Midwestern agricultural lands into the Mississippi River is sufficiently high as to cause excessive primary production, oxygen depletion, and a large benthic dead zone of hypoxia reappearing every summer off the coast of Louisiana on an annual basis (Rabalais et al., 2007). Although the Loop Current

drives a clockwise circular flow of Gulf waters, cold-core rings spin off frequently enough to induce flows to the northwest (**Figure 2**), which introduce additional nutrients into nearshore habitats and generate enhanced primary production fueling pelagic food webs (Spies et al., 2017). While the delivery of nutrients via cold-core rings generally enhances food web production throughout the Gulf, too much nitrogen loading in runoff from land depresses the food web production in a large area off the Louisiana coast.

Predatory vertebrates of several types provide the vehicle to transfer large amounts of ocean production back to the land through their feeding on fishes at varying distances out to sea and their return to land-based or freshwater-based nesting sites, breeding, or feeding grounds (**Figure 3**). Largely piscivorous seabirds, such as brown pelicans, laughing gulls, other gulls, and multiple species of terns, establish breeding colonies on land along the GoM coast, from which they forage at sea and transport fishes back to their developing chicks at the nest. Transport of fish to birds at the nest is often diverted to the stomachs of terrestrial scavengers, such as raccoons, feral hogs, opossums, coyotes, and feral cats, each benefiting from feeding on fishes pirated from nestling seabirds.

Transport even further into the terrestrial habitats on coastal lands is achieved by anadromous fishes returning to natal streams, rivers, and lakes for egg deposition and fertilization before they die. Salmonids on the Pacific coast, shad on the mid-Atlantic (McPhee, 2002), and other fishes engaging in such migrations back to natal streams and lakes generate dense food subsidies for terrestrial and riverine scavengers and promote riparian vegetation growth through transport and land-based deposition of nutrient-rich fish carcasses. Catadromous fishes, such as sturgeons, occupy freshwater habitats of lakes, streams, and rivers as adults, then make large-scale migrations into the ocean, even into the Sargasso Sea for American eels, where they reproduce, releasing larvae that endure the perilous migration back into freshwater habitats adjacent to land. Connectivity corridors for catadromous fishes can be exceptionally long, making their protection especially critical but also increasingly more challenging.

4. Estuarine fluxes and connectivity

The dependence of seaward estuarine and coastal ocean habitats on the import of nutrients and detritus from up-river and up-estuary represents the widespread paradigm of high-estuarine food web production fueled by the import of nutrients and detritus, as advanced by Eugene Odum (2000). The seaward transport of waters running off slightly elevated landmasses toward the coastal marshes and then into the ocean provides a mechanism for enhanced nutrient loading in coastal marsh habitats. These processes fuel even higher productivity of marsh plants like *Spartina alterniflora*, *Juncus roemerianus*, and *Phragmites communis*, as well as benthic microalgae.

Detritus derived from the enhanced marsh plant production is itself then carried by downstream riverine flows to support the development of largely detritivorous food chains in coastal marshes and benthic soft-bottom

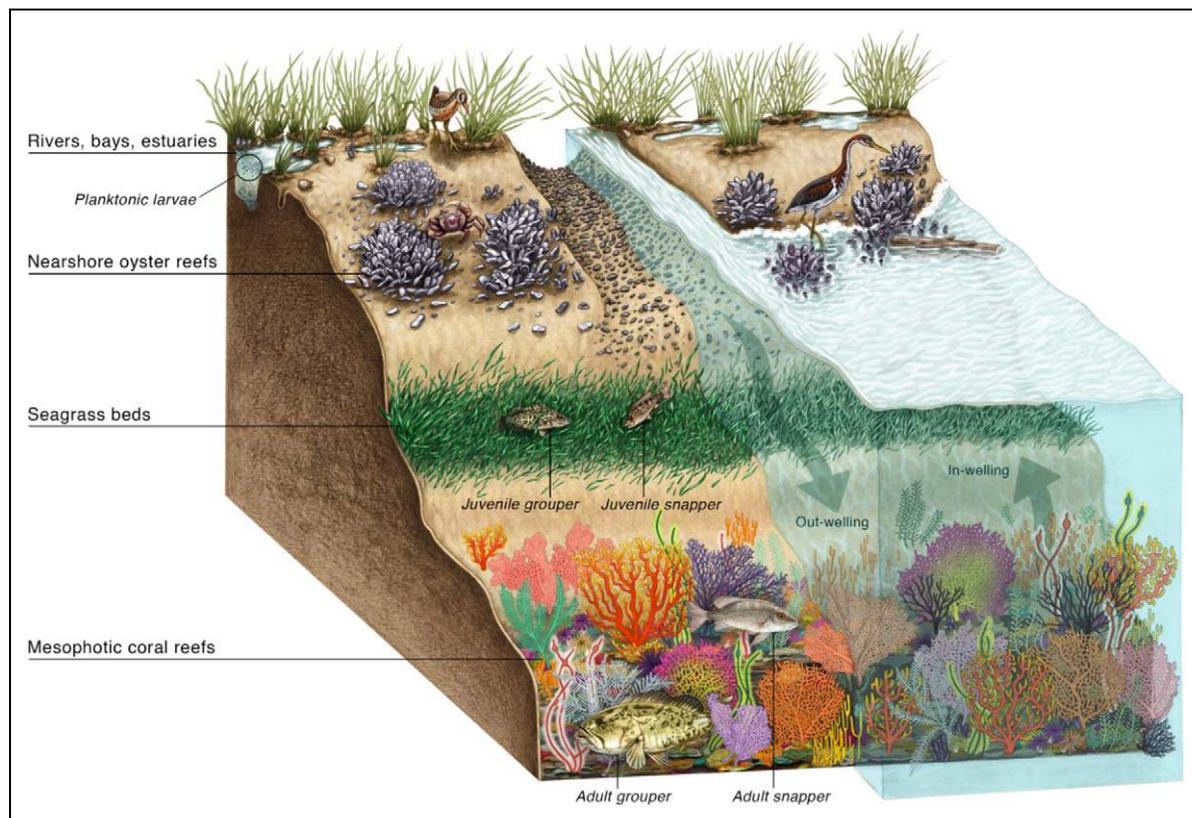


Figure 3. Illustration of Gulf of Mexico habitats along ontogenetic pathways. Included are the key habitats utilized by fishes of the snapper–grouper complex during their ontogeny. Fish larvae link to estuarine settings including salt marshes, juvenile fishes to subtidal seagrass beds and oyster reefs, and adults to deeper coral garden and reef habitats. DOI: <https://doi.org/10.1525/elementa.016.f3>

habitats of the estuary, the coastal ocean, and even the deep sea (**Figure 3**). This process became characterized as “out-welling”—the transport of biological production out of the estuary and into the sea. Odum (2000) likewise confirmed high levels of production of fishes and crustaceans in coastal marshes, which benefit from elevated marsh productivity and the increase in structurally emergent marsh habitat that protects fish and crustaceans from potential predators. After feeding and developing in the coastal marsh habitat, these stone and blue crabs, penaeid shrimps, spiny lobsters, and demersal fishes proceed to move out into the estuary and then typically into the coastal ocean and beyond.

The premise that pulsed out-welling of organic matter generally characterizes estuarine transport processes was challenged by Nixon (1980), who demonstrated net “in-welling” of nutrients and biologically produced materials in New England estuaries, indicating that net out-welling of organic materials and living nektonic organisms is not universal among estuaries. Similarly, Haines and Montague (1979) used stable carbon isotopes to show that much of the production of oysters, clams, and other suspension-feeding marsh invertebrates is based upon consuming phytoplankton and suspended benthic microalgae from the water column. Valiela et al. (2000) demonstrated that denitrification induced by salt marsh sediments protects seagrass meadows in deeper estuarine waters from the negative influence of nitrate overloading.

In-welling is a very important connectivity vector from locally productive marine ecosystems to islands and terrestrial coastal lands, which are generally arid and relatively unproductive. Subsidies of nutrients and food energy at low trophic levels play a quantitatively significant role in stimulating the growth of terrestrial consumer populations and food webs on small islands in temperate, tropical, and subpolar systems worldwide (Polis and Wine-miller, 1996). Export of ocean-produced primary production in the form of macroalgae and kelps supports populations of soil invertebrates, terrestrial arthropods, birds, and carnivores on low-productivity islands: specifically, coyotes, kit foxes, and ring-tailed cats in Baja and the Gulf of California; jackals and lions along the Skeleton Coast of Namibia; arctic and red foxes on boreal North American shores; and feral cats on islands in general. The externally subsidized production of these predators on tropical and warm-temperate island shores carries with it a possible threat to sea turtles, whose hatchlings emerge from eggs buried on many of the ocean beaches of these islands (Peterson et al., 2013).

Connectivity from marshes and shore habitats to the offshore realm of the Gulf are clearly evidenced by the life-history transitions of the Gulf menhaden, perhaps the primary forage fish in the Gulf that supports wide-reaching pelagic and terrestrial food webs (Geers et al., 2014; Short et al., 2017). Larval and early juvenile menhaden utilize salt marsh habitat when the fish are small and

benefit from marsh structure as protection from predators while the Gulf menhaden are consuming phytoplankton and marsh plant detritus. By the end of summer, the now juvenile menhaden utilize passive offshore transport to rejoin schools of adults in the nearshore ocean, where they become zooplanktivorous.

The offshore transport phase of the Gulf menhaden life history depends on the large volumes of riverine outflow of rainfall runoff to achieve successful offshore transport of the small fish into the coastal ocean waters to grow on their zooplankton diet, thereby increasing their size and gaining in swimming ability. Earlier in their life history, these same menhaden had relied on passive transport in the opposite direction to bring the newly released Gulf menhaden larvae from the offshore oceanic location of the spawning adults into the coastal juvenile rearing habitat of the salt marsh (Short et al., 2017). Hence, all of these forms of physical transport interconnectivity that link estuarine to coastal and offshore habitats play a major role in preserving the integrity of ecosystem-wide habitat functions.

5. The shoreline and barrier islands

The GoM shoreline is characterized by extensive sandy beaches, coastal marsh, and increasingly black mangrove habitats that serve as nurseries for many marine fishes and crustaceans, as foraging habitats for wading seabirds like herons, egrets, ibises, and rails, and as nesting and chick feeding habitats for shorebirds, pelicans, terns, and gulls. While nesting and raising hatchlings, adult pelicans, terns, gulls, and other piscivorous seabirds forage widely for fishes from nearshore waters outward onto the continental shelf, inducing quantitatively significant fluxes of organic matter and nutrients from the pelagic oceanic environments to the seabird nesting grounds on coastal lands and to nearby coastal waters (Polis et al., 1997). Coastal barrier landmasses also serve important roles in the marine environment as nesting grounds for sea turtles, foraging habitats for surf fishes like pompano, flounders, and redfish, and suitable open beach habitats for nesting and feeding by numerous migratory shorebirds, including threatened and endangered species, such as the piping plover and red knot (Peterson et al., 2006).

The beaches of the coast and barrier islands may represent the habitat most seriously challenged by global climate change. They are impacted directly, as rising sea level and the increasing frequency of violent storms expose the ocean shoreline of sandy beaches to greater erosion, higher waves, and more sediment transport (Dugan et al., 2010), and indirectly as human responses to climate change involve ecological impacts. These include dredge-and-fill disturbances called “beach nourishment” and hardening of beaches with engineered groins, seawalls, jetties, and other structures that induce sand erosion from the beaches and consequent habitat loss (Trembanis et al., 1998). Such losses of beach habitat lead almost inevitably to subsequent dredge-and-fill projects to replace the lost sandy sediments—not for the sake of wildlife, with obligate ties to beaches for nesting, foraging, and/or breeding but because of the economic

value of recreation, tourism, retirement, and residential properties along intact beaches. Hence, the loss of sediments during storms is a perturbation that directly affects valuable and sensitive coastal and barrier beach habitats, particularly ocean beaches and sand dunes, and resident species during and after the storm.

The subsequent, indirect effects of the predictably harmful beach nourishment responses to beach erosion add another layer of perturbation affecting wildlife like sea turtles, surf fishes, shorebirds, and piscivorous seabirds like gulls, terns, gannets, and pelicans (Peterson and Bishop, 2005). These negative impacts of beach nourishment persist for at least 3 to 4 years for shorebirds, and some species of benthic invertebrate prey for shorebirds, like haustoriid amphipods, show no evidence of population recovery 3 to 4 years after nourishment (Peterson et al., 2006, 2014). Therefore, even transient events on beaches can impact the ecosystem functions and connectivity of land and offshore habitats for years.

Beach deposition of macroalgal detritus, such as algal fronds, seagrass blades, and salt marsh macrophytes, is a result of storm-driven transport by persistently strong south winds and by cold-core ring dynamics. Shoreward transport is critical in bringing live floating *Sargassum* close to and even onto the ocean beaches, where its deposition in the wrack line supports high production of wrack-associated crustaceans and insects. In turn, these serve as prey for several shorebirds, including the endangered snowy plover in California (Dugan et al., 2003), analogous to the piping plover on Atlantic and Gulf coast beaches.

The presence of floating live *Sargassum* close to ocean beaches facilitates higher survival of hatchling and juvenile sea turtles and juvenile-to-adult fishes, such as mahi mahi, billfishes, bluefin tuna, and cobia, which can ride this biogenic habitat along the Loop Current of the GoM and make connections with the eastward-flowing Florida Current and then to the Gulf Stream (**Figure 2**). Strong south winds generated by winter storms and transport of cold-core rings shed off the Loop Current move water masses with their *Sargassum* and associated organisms clockwise, northward then southward in the Atlantic Ocean, and ultimately back to ocean beaches of the windward Caribbean islands and eventually into the estuaries of the northern GoM.

The connectivity between sea turtle nesting beaches and the circum-basin boundary currents of the North Atlantic Ocean plays an important part in fulfilling the life history of sea turtles. *Sargassum*, a floating biogenic structural habitat, can be transported along with its associated invertebrates and fishes away from the coastal ocean and into ocean-basin boundary currents like the Loop Current and the Gulf Stream. Loggerhead and green sea turtles depend on the use of *Sargassum* habitat for food provision and protection from predators as they transit the North Atlantic Ocean Basin back home to natal beaches of the Caribbean and GoM shores where they nest and reproduce. This transport of living *Sargassum* also helps support the base of the detrital food chains of oceanic habitats at numerous distances from shore and at

water depths as deep as 3,600 m (Rowe and Staresinic, 1979).

6. Connectivity between coastal and offshore habitats

The connections from the shoreline to the offshore surface waters also extend to the seafloor on the continental shelf and slope. Migration of larval and juvenile reef fishes in the Southeast United States commonly serves to transport many new recruits to nearshore benthic nursery habitats, often biologically structured habitats like oyster reefs, mangroves, and seagrass beds (**Figure 1**). While some oyster reefs remain along the Gulf coast, core sampling of continental shelf sediments and paleontological evaluations of the shallow, nearshore continental shelf have indicated evidence of a greater historical abundance of oyster reef habitats on the northern GoM shelf.

These biogenic structures rose meters above the seafloor and provided multiple ecosystem services when populated by living oysters. First, the elevation of this reef would allow it to serve as a breakwater, reducing wave energy striking the shoreline and thereby protecting structured shoreline habitats and shoreline development from the worst of wave damage. Second, these reefs represented a likely sustainable source of oysters for harvest, which were probably depleted after mechanical dredges were permitted and proliferated, leading to degradation of the reefs and damage to their oyster crop (Lenihan and Peterson, 1998).

For many fishes of fringing reefs, the use of reef-retention current flows provides the necessary connectivity corridor to assure their survival. This process has been demonstrated best in the demersal coral reef damselfish and clownfish (Jones et al., 1999; Planes et al., 2009; Swearer et al., 1999) but also applies to numerous Gulf species of economic significance that are commonly associated with the mesophotic reef habitat. Juvenile fishes could remain and develop in the physically structured coral reef habitat, but the physical structure harbors several other fishes that pose serious predation risk to juvenile reef fish. Consequently, these early-stage larvae take advantage of outflowing currents to escape the fringing reef vicinity and achieve passive transport beyond the coral reef in locations where structural hiding places for larger predators are limited.

The deeper water system beyond the fringing reef itself can serve as a refuge from most predation risk for juvenile reef fish. Nevertheless, these fishes are motivated to live in the structurally complex coral reef habitat as they grow and mature. This system can elevate the survival chances of reef fish recruits by promoting both their escape from the reef as small, vulnerable juveniles and their return to the reef after outgrowing their high risk of being consumed by predators residing on the reef. Consequently, fringing reefs possess not only an outflowing current to use as the passive carrier off the reef for small juvenile reef fishes but also a returning flow back to the reef structure. This passive transport off these nearshore, fringing reefs and back again provides larvae with a mechanism to maximize early life history survival and thus fitness.

This generic life history cycle typically involves the use of a series of biologically structured, high-relief shelf habitats, acting as a network of stepping-stones in the pathways of migration toward the deeper ocean areas where the reefs can be larger and more structurally complex. Such stepping-stones allow travel to deeper water reefs on the inner, mid, and outer portions of the continental shelf that serve as foraging and/or spawning habitat for reef fishes (**Figure 1**).

Deepwater, hard-bottom features include seep-related authigenic carbonates and the steep walls of canyons like DeSoto and Mississippi Canyons (Gardner et al., 2002). Although the nutritional input of seep productivity is exported over a relatively short distance (MacAvoy et al., 2002), seep-related carbonates are the most prevalent hard-bottom structures in large parts of the central and western GoM (Cordes et al., 2009). Authigenic carbonates form as a result of the anaerobic oxidation of methane in seafloor sediments and can persist for tens of thousands of years, long after the methane and other seep-related chemicals have disappeared (Aharon et al., 1997; Aharon and Fu, 2000). Once the rate of fluid flux has declined, the hard substrates can be colonized by deep-sea corals (Cordes et al., 2009), thus serving as the type of high-quality habitat that provides the all-important connectivity among habitats.

Offshore canyons provide clear pathways for the export of coastal organic materials to the deep sea (Puig et al., 2014). The Mississippi and De Soto Canyons extend from relatively shallow shelf regions toward deep waters off the continental shelf. In addition to serving as conduits for the rapid transport of sediments and detritus (Bianchi et al., 2006), they induce upwelling of nutrients leading to plankton blooms (Gilbes et al., 1996). The habitat heterogeneity and productivity of the canyons provide key habitat for sperm whales (O'Hern and Biggs, 2009), giant squid (Roper et al., 2015), and other valuable biological resources. The canyons act as another link in the series of stepping-stones that lead juvenile reef fishes further offshore to the mesophotic and deepwater coral-reef habitats and enhance the foraging and breeding grounds for adult snapper–grouper species of such high value and conservation concern.

7. Function of offshore reefs within the GoM ecosystem

The northern GoM is characterized as having functionally significant populations of corals of several different types in different locations and conditions (**Figure 1**). At mesophotic depths, coral-based systems arise on the shoreward edge of the continental shelf–slope break on high-relief carbonates in the form of remnants of pinnacles and drowned reefs, such as the flat plates of scleractinians at 60-m depth along the Pulley Ridge or on salt domes in the northern GoM like those at Flower Garden Banks (Rezak et al., 1990). In deeper waters, corals are found primarily on the authigenic carbonates, formed as a by-product of natural hydrocarbon seepage, and along the Florida Escarpment, an outcropping of Jurassic age igneous rock from the Florida platform. In the deeper waters of the

continental slope, large reefs are formed primarily by the scleractinian coral *Lophelia pertusa* between depths of 300 m and 600 m (Cordes et al., 2008), and coral gardens are formed by octocorals and black corals at depths down to the abyssal plain (Quattrini et al., 2014).

Deep-water coral reefs, similar to shallow-water reefs, are responsible for active nutrient recycling and enhanced secondary productivity. The elevated biomass of the reefs (Mortensen et al., 1995; Henry and Roberts, 2007; Cordes et al., 2008) and the distinct communities in the surrounding sediments (Demopoulos et al., 2014) efficiently process the dissolved and particulate organic material raining down from the surface (van Oevelen et al., 2009). The corals produce copious amounts of mucous that then fuels a coral-sponge loop resulting in augmented remineralization of surface-derived carbon and nutrients (Cathalot et al., 2015; Rix et al., 2016). Further driving these processes, coral mounds and reefs may enhance down-welling of surface productivity and effectively sequester anthropogenic carbon from surface waters (Soetaert et al., 2016). Transport of nutrients from the deep reefs back to the oligotrophic waters of the offshore Gulf can be accomplished by interactions with diel vertical migrators as well as by periodic upwelling over the reefs (Mienis et al., 2007; Davies et al., 2009, 2010). These processes provide clear, bidirectional links between surface production and the deep sea.

These offshore, hard-bottom habitats support greater production of prey and can be colonized by valuable and depleted reef fishes such as snappers, groupers, and other exploited reef fishes. The patterns of sequential stepwise movements offshore allow juvenile reef fishes to take advantage of feeding in highly productive estuarine habitats, then successfully transition to the continental shelf to use deeper and more structurally diverse reefs with age, leading ultimately to the use of hard-bottom, rocky, and coral reefs in deeper waters of the continental shelf and slope (Peterson et al., 2012). Reef fishes known to share this life history include the gag grouper and mangrove (gray) snapper, but other snappers and groupers are also suspected of employing a stepping-stone migration from estuarine shoreline nurseries toward deeper water offshore reefs as they grow and mature (Peterson et al., 2012). Populations of these fishes are commonly found on mesophotic reefs that line the shelf break along the northern GoM at depths between 60 m and 120 m and also on reefs structured by *Lophelia pertusa* stony corals, as well as the long-lived black coral species, *Leiopathes glaberrima*, and a diversity of octocorals at depths between 250 m and 600 m. The ontogenetic shifts of these species and their large depth ranges provide further links from shallow to deep and back again.

Shallow-water corals have exhibited great sensitivity to exposure to warming water, responding with coral bleaching and mortality (e.g., Coles and Riegl, 2012). Increasing ocean acidification with escalating global climate change is forecast to produce declining carbonate saturation in the oceans, affecting the aragonite saturation depth, critical to the sustained growth of scleractinian coral skeletons (Guinotte et al., 2006; Georgian et al., 2016). Corals in

the GoM also have been shown to suffer losses from disease (Harvell et al., 1999) and recently from transient and undetermined causes. The cold-water corals may prove to be even more sensitive to ocean changes such as warming, acidification, and deoxygenation (Lunden et al., 2014). Removal of these foundation species and the biogenic habitats they create, first by increased mortality of live corals and then by the dissolution of standing dead skeletons, will result in significant loss of habitat heterogeneity, which will then lead to reductions in diversity and biomass (Cordes et al., 2010), including many fishes of value (Koslow et al., 2001; Ross and Quattrini, 2007).

Octocoral-dominated habitats suffered oiling by the *Deepwater Horizon* blowout, resulting in partial mortality of the coral colonies and changes in the associated fish assemblages at mesophotic depths around 100 m (Silva et al., 2016), as well as the corals and the communities they support at depths below 1,000 m (White et al., 2012; Fisher et al., 2013; Demopoulos et al., 2016; Girard et al., 2016). These octocoral gardens and the *Lophelia pertusa* reefs at upper slope depths create a highly heterogeneous habitat that supports elevated diversity and biomass of occupying species (Cordes et al., 2008; Lessard-Pilon et al., 2010; Demopoulos et al., 2014). All of these epibiotic communities, even including ones without corals, provide EFH for many reef fishes, including the depleted snapper–grouper complex (Ross et al., 2010). Analogous deepwater *Solenosmilia variabilis* corals on seamounts south of Tasmania have been shown to offer valuable habitat to several fishes, including some targeted by fisheries (Koslow et al., 2001; Clark and Koslow, 2007), but the degree of fishing impacts on the cold-water scleractinian corals of the deep GoM remains understudied. These dependencies are being documented increasingly and recognized globally in management through the establishment of MPAs and fishing prohibitions or restrictions (Cordes et al., 2016a).

8. Migration pathways as restoration targets

As outlined above, the successful restoration of the GoM large marine ecosystem and, in particular, the fishes of commercial significance on which numerous Gulf coast communities (both human and ecological) rely is predicated on ensuring that sufficient habitats are available to these species to carry out their entire life cycle. The use of various structured habitats as stepping-stones presumably enhances survival, growth, reproduction, and fitness of the juvenile reef fishes, defining the migration corridors from juvenile habitats in the estuary (oyster reef, seagrass bed, mangrove forest, coastal marsh, and perhaps others) to the rocky and coral reef habitats occupied by larger juvenile and adult fish. Their mobility allows juvenile reef fishes to take advantage of highly productive estuarine habitats, yet successfully pass across the continental shelf to adult feeding grounds and habitats associated with deeper hard-bottom reefs. Structured bottom habitats all act as feeding and refuge grounds during migration toward deeper ocean areas, where the reef habitats are larger, may support more prey, and can be populated themselves by valuable reef fishes, like adult snappers and groupers.

Ecosystem-based protection and restoration of migration corridors from the productive habitat in estuaries out to the heads of canyons and deep offshore reefs should constitute an overarching adaptive management strategy. This type of novel protected area, a Connectivity Corridor Area, would provide high-quality habitat to support the ontogenetic migrations of fishes and also offer several marine mammals safer connectivity among critical feeding grounds, overwintering sites, and calving areas. An example of such an area would begin at the Apalachicola River and Bay with its associated barrier islands and extend to the shallow-water oyster reefs, the offshore mesophotic coral habitats of the Coral Trees and Madison-Swanson sites (easternmost mesophotic sites on **Figure 1**), along the DeSoto Canyon, and to the deepwater coral sites within the canyon, on the Florida Escarpment walls, and around the salt domes in the vicinity of the *Deepwater Horizon* site.

This effort would begin in the freshwater tributaries that feed the Gulf. Numerous, high-quality wetlands and forests on land and healthy rivers with oyster reef habitat, such as the Apalachicola in particular, provide the aquatic medium through which the migrating juvenile fish swim and feed sufficiently to reach the next stepping-stone in their ontogenetic migration offshore (Peterson et al., 2012). Protecting the riparian habitats of maximal benefit to preserving estuarine and riverine water quality along waterways used by out-migrating juvenile reef fishes could facilitate the establishment of connectivity conservation corridors of critical importance to early life histories of reef fishes destined for adulthood on the continental shelf, slope, and deep canyons.

The next step in the restoration of the connectivity corridor would be in the estuaries and nearshore salt-marsh and mangrove habitats that line the Gulf coast. Over decades of experience, restoration ecologists have devised methods to convert intertidal flats without macrophytic vegetation into intertidal coastal marshes of *Spartina alterniflora* and/or other marsh vegetation. This vegetation serves as a foundation species enhancing abundances and production of marsh-associated crustaceans and small-to-large fishes, as well as retaining sediments and providing a buffer against storm surge and rising sea levels. This capacity to create productive coastal marsh habitat, with its known high value as a fish and crustacean nursery as well as a producer of marsh macrodetritus, on unvegetated flats or on disused farmlands has spread widely and is typically the first restoration option considered for compensatory restoration after an oil spill or on Superfund sites of persistent toxicity.

Especially along the shores of the Mississippi River delta, subsidence, marsh channelization for boat access, and storm-driven erosion have led to a huge reduction in areal extent of coastal marsh habitat and in the ecosystem services associated with that habitat. In recent years, the expansion of mangrove habitats has also resulted in the loss of salt marsh habitat (Armitage et al., 2015; Osland et al., 2018), although the mangroves themselves provide habitat for other species. This history and the continuation of marsh habitat loss in southern Louisiana and elsewhere on the northern GoM shores underscore the urgency of

marsh restoration efforts in the northern Gulf, particularly on the Mississippi River Delta in Louisiana. The implementation of this wider-scale restoration is justified by the large number of candidate smaller rivers flowing through estuaries into the GoM that together, as a group, hold promise for successful coastal marsh restoration, rebuilding of oyster and coral reef breakwaters on the shelf, and conservation on the scale required for a connectivity corridor to make a meaningful difference in the production of valuable estuarine-dependent oceanic fishes in the GoM (Peterson et al., 2012).

However, the restoration and enhancement of estuarine and coastal habitats must be considered within the broader connectivity corridor conceptual framework. Efforts to enhance primary production (and subsequently available marsh-plant detritus) in many places at essentially the same point in time may lead to the development of a trophically unbalanced nearshore food web if not coupled with the restoration of the higher trophic levels that can take advantage of this productivity. To avoid such a trophic imbalance, the GoM restoration programs should include stock enhancement of marine fishes, choosing species harmed by the oil spill and/or spill responses, with known track records of success in stocking efforts. The success of stock enhancement projects has been demonstrated recently in a series of rigorous studies using individual-level fish tagging and multiple samplings over time to quantify the augmentation in numbers of fishes successfully added to the recipient ecosystem (Blankenship and Leber, 1995; Brennan et al., 2008; Lorenzen et al., 2010; Leber, 2012). The focal species for stock enhancement should be those that could be predicted confidently to feed at sufficiently low trophic levels to take advantage directly or indirectly of the injection of so much marsh macrophyte detritus. Strong coordination of restoration projects linking primary macrophyte productivity with foraging by animals higher in the food web would help prevent excessive amounts of detritus from decaying and contributing to hypoxia.

The restoration of the complete connectivity corridor continues to the oyster reefs and other emergent structures fringing the shoreline, then further offshore to the coral habitats of the mesophotic banks, *Lophelia* reefs, and deeper coral habitats of the slope where the oil spill originated. Networks of hard-bottom reefs (including, in a restoration context, wrecks and intentionally scuttled artificial-reef structures) at varying distances and depths offshore can serve as stepping-stones to enhance connectivity between juvenile reef-fish nursery habitats in fringing reefs and estuaries and adult feeding and spawning reefs in deeper ocean waters. Less is known about the patterns of connectivity in these habitats or even the locations, historical and present-day, of these biogenic habitats.

The demarcation of significant connectivity corridors first requires knowledge of the habitat use of the targeted species, which requires scientific survey validation using multiple methods (e.g., Worboys et al., 2015). Use of acoustic fish tags to track adequately large samples of reef fishes from estuaries to adult reef habitat could reveal important

new information on migration routes used by reef fish species or groups. Results of tracking studies could guide restoration planning for the enhancement of commercially important reef fish stocks at a species level. Following up the mapping of migration corridors with side-scan sonar and/or multibeam acoustic bathymetry, along with visual surveys by divers or submersible vehicles (autonomous underwater or remotely operated vehicles, or manned submersibles), could characterize bottom habitat along the entire migration corridor from nursery to deeper adult habitat. These surveys may reveal some poorly documented but potentially critical functional uses of reefs along the stepping-stone paths, shedding light on habitat use as well as locating the potentially limiting types of bottom habitats along the corridor.

The remaining extensive reef habitats are threatened significantly by the continued expansion of offshore oil drilling in the northern GoM. Most of the direct effects of oil and gas development are limited by the rules of the U.S. Bureau of Ocean Energy Management to suppress exploration and development on emergent hardgrounds that support deepwater coral reefs and chemosynthetic communities. However, more extensive habitat mapping and exploration is required as smaller reef structures may be missed and thus stand unprotected, leading to direct physical impacts or exposure to drilling discharges affecting the health (i.e., growth and reproduction) of mesophotic and deepwater corals (Cordes et al., 2016b). An important and potentially highly effective conservation and restoration action is the expansion of deep-reef habitat protections to ensure the integrity of a continuous corridor of habitat across the full range of water depths. This strategy would protect the successive life stages of fish from this class of human impacts.

Considering connectivity even more broadly, the strength of the Gulf-Atlantic-Caribbean circum-basin flow, essential to transport *Sargassum* and complete the life cycle of sea turtles and other organisms, is affected negatively by global climate change, which has been shown to slow the speed of the Gulf Stream (Ezer et al., 2013). This broader connectivity can only be protected by focusing on the preservation and restoration of the relevant connectivity corridors. Perhaps the only feasible management response to counter this slowing can be found among the suggestions for reducing greenhouse gas emissions (i.e., CO₂ and methane) or counteracting emissions by equal or higher C sequestration, which might be achievable in the coastal GoM by restoring coastal marsh, submerged aquatic vegetation, mangroves, oyster reef, and coral habitats in amounts that are large enough to compensate for a meaningful fraction of the ongoing emissions of global change gases in the region.

9. A way forward

In summary, our strong recommendation is for comprehensive and integrated ecosystem-based restoration projects that recognize the corridors that link important habitats used by numerous species during different life stages. We note the value of connections between coastal nearshore habitats and offshore habitats, including those

in the deep sea, that can be maintained by protecting existing connectivity corridors and restoring damaged corridors. We note that many patterns of movement between habitats, especially during ontogenetic offshore migrations, are facilitated by using stepping-stones of supportive habitat along connectivity corridors, which should be considered as high priorities for conservation protection.

The most valuable ecosystem service provided by many of the living organisms of the northern GoM may well be their provision of habitat and their role as the foundation of food webs that support fish, edible crustaceans, and other exploited species in fisheries of many sorts. Sustaining these fisheries may require a new conservation thrust that identifies and classifies connectivity corridors as a type of EFH that is factored into fisheries management and conservation actions.

We also maintain that the maintenance of ecosystem-level processes, especially giving due attention to sustaining balanced food webs while habitat restorations are contemplated, designed, and implemented, is critical to successful and sustainable ecosystem dynamics. Trophic-level balance may be required for sustainable functioning of restored habitats: Restoration is rarely conducted at the level of entire food webs, yet that may be necessary to achieve resilience of critical habitats after implementing traditional coastal habitat restoration projects.

Synthesis of such knowledge about connectivity between and among critical habitats in the ocean and on land can form the basis of a new type of protected area, a Connectivity Corridor Area. We suggest that this approach to the restoration of migratory and trophic connectivity pathways, in conjunction with restoration actions targeted at individual habitat types, can provide the most robust and holistic plan for the recovery of the entire Gulf ecosystem and the human communities that it supports.

Data Accessibility Statement

There are no original data sets included in this article and all data presented are publicly available elsewhere.

Dedication

This manuscript is dedicated to the memory of Dr. Charles “Pete” Peterson, the lead author who left us for greener marshes. He was a towering figure in Ecology and his leadership, dedication, and stewardship will be sorely missed.

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- Contributed to analysis and interpretation of reviewed data: CHP, KPF, EEC.
- Drafted and revised the article: CHP, KPF, EEC.
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