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Oyster Reef Connectivity: Ecological Benefits and Associated Vulnerabilities

by Safra Altman, R. Daniel Harris, S. Kyle McKay, Michael E. Kjelland, and Todd M. Swannack

OVERVIEW: Global oyster abundance has declined ~85 % over the past 200 years, primarily because of overharvesting (Beck, Brumbaugh, and Airoldi 2011; Kirby 2004). Healthy oyster reef systems benefit the environment in many ways, including water-quality improvement, shoreline protection, increased biological and habitat diversity, and carbon sequestration. To maintain these environmental benefits, reef-restoration efforts that produce healthy, sustainable oyster reefs are essential. To this end, the US Army Corps of Engineers (USACE) has been involved in reef-restoration projects in many locations, including extensive efforts in the Chesapeake Bay (Virginia, Maryland), coastal regions of New York and New Jersey, and the Gulf of Mexico.

There are many benefits to creating and maintaining oyster reef systems that are well connected, for both oysters and other organisms within the reef and surrounding habitats. This technical note presents the current knowledge of benefits and costs to restore oyster-reef connectivity along the East and Gulf Coasts of North America. Connectivity of oyster reefs can refer to the physical location of reefs with respect to one another as well as to the dynamics of the genetic links within a metapopulation or to the extent to which larval transport and recruitment unite reef communities. For the purposes of this technical note, connectivity is defined as the spatial aggregation of reefs, though we address impacts of genetic and larval flow as well. Reef connectivity positively affects many ecosystem services and dynamics but can also have unintended consequences (that is, negative externalities). This technical note reviews the benefits and costs of increasing connectivity and presents a brief example of how trade-offs may occur between these potentially opposing ecological objectives. Here, we focus on the eastern oyster, Crassostrea virginica, which inhabits the East and Gulf Coasts of North America, though many of the concepts and principles discussed may apply to other oyster species as well.

DISTRIBUTION AND LIFE HISTORY: The eastern oyster is a reef-forming bivalve that is both ecologically and economically important. C. virginica is distributed from the Gulf of St. Lawrence, Canada, to Key Biscayne, Florida, on the East Coast, and throughout the Gulf of Mexico and potentially Brazil (Bahr 1981). The expansive geographic distribution of C. virginica is attributed to its high tolerance for a large range of temperatures (Stenzel 1971).

The eastern oyster (oyster here on out) is a sequential hermaphrodite (that is, protandrous) and is typically sexually mature after two to three months of growth, when the shell is at least 1 cm in height. At this point, the young-of-the-year oysters are typically male. After one to two years, once the oysters have developed enough energy reserves to produce eggs, they change into females. Oyster spawning events are temperature driven, and usually occur when temperatures reach

~20°C–22°C between April and October. Populations have one to two peak spawning events per year. Following location-dependent temperature cues, broadcast spawning is initiated when male oysters release sperm. This, in turn, cues female oysters to release unfertilized eggs. Eggs are fertilized in the water column and over the course of about two weeks develop through five larval stages: blastula, gastrula, trochophore, veliger, and pediveligar. Pediveligar oysters develop eyes and, on the basis of biological and physical cues, move towards suitable substrate through a combination of drift and active swimming. Physical cues that affect settlement include the acoustic habitat signals (Lillis, Eggleston, and Bohnenstiehl 2013), surface texture, and near-bottom and local hydrodynamics and turbulence (Turner et al. 1993; Wheeler et al. 2015). Pediveligers are also attracted to enzymes on oyster shells (Bahr 1981). Adult oysters can tolerate a large range of temperatures and salinities. Galtsoff (1964) found that oysters could withstand water temperatures between −2°C and 36°C. He also reported an upper limit of 49°C for short low-tide periods; this upper limit is supported by additional studies (Ingle and Dawson 1952). Oysters can tolerate salinity ranges between 5 and 40 ppt and can survive up to a month at 2 ppt and for several days in fresh water (Gunter 1950).

Oysters are found intertidally and subtidally, although a clear description of distribution patterns is lacking. Intertidal oysters typically grow in densely packed reefs, where oysters need to grow vertically to avoid crowding and mud deposition (Bahr 1981). Intertidal oyster reefs are not good habitat for parasitic boring sponges, and as a result, intertidal oysters can afford to have thinner shells and focus resources towards growing vertically (Dunn, Eggleston, and Lindquist 2014). Subtidal oysters do not grow as densely as intertidal oysters and do not have the same crowding issues. Subtidal oysters are more susceptible to sponge damage and often grow thick, cupped shells in response (Dunn, Eggleston, and Lindquist 2014). There are currently no reported subtidal oysters in the Georgia Bight. Chesapeake subtidal oyster reefs have been classified into fringe, string, and patch reefs (M. G. McCormick-Ray 1998; J. McCormick-Ray 2005). Fringe reefs are parallel and close to shore. String reefs are perpendicular to the shore and traverse to shore edge, whereas patch reefs are in deeper water offshore and are irregular in shape. Habitat and reef variation are likely due to a number of biotic and abiotic factors (for example, flow, slope, predatory influence) that have not yet been described in great detail.

BENEFITS OF OYSTER REEF CONNECTIVITY: Marine populations that are connected through spatially complex linkages are recognized to be highly diverse and productive (see Coen, Luckenback, and Breitburg 1999, for example, for a review of relevant research). There are a number of ecological benefits of oyster reef connectivity—both for the oyster population itself as well as the surrounding community and habitat. These reef connectivity benefits are reviewed in association with benefits to oyster population dynamics, reef communities, and the surrounding off-reef communities.

Oyster population dynamics. The ability for reefs to grow as a result of new oyster settlement is linked to the relationship between spawning-stock biomass and subsequent recruitment as well as larval transport. How effective a given brood-stock reserve is at subsidizing or enhancing recruitment within a network "depends on spatiotemporal variation in . . . reproductive potential and subsequent larval connectivity" (Mroch, Eggleston, and Puckett 2012, 1091). Larger oysters have higher fecundity per capita, and reproductive potential increases with oyster density within a reef itself. Other stressors, such as parasitism and disease, can negatively affect reproductive output and growth, and these stressors can themselves be influenced by environmental conditions such as temperature and salinity. Larval transport is regulated by behavioral components as well as physical components like current and flow (Kjelland et al. 2015).

A system of well-connected reefs can result in a resilient reef metapopulation. Spatially linked reefs will be better able to withstand disturbances, whether because of mortality due to disease outbreak, freshet influence, and coastal storm events or because of natural variation in productivity. While individual reefs may be damaged by the disturbance event, others within the metapopulation can contribute larvae to ailing reefs. In unconnected reef systems, disturbance events may cause enough mortality that an individual reef cannot sustain itself over time. A network of healthy reefs able to withstand local disturbance will also be more resilient to population reduction due to commercial and subsistence harvesting, provided that harvest levels mimic natural population sinks.

Although many marine invertebrates, such as oysters, have populations with high levels of connectivity and low levels of restricted gene flow (that is, population differentiation), genetic variation that is adaptive in relation to environmental conditions (that is, ecological relevant) has been found (Sanford and Kelly 2011; Smee et al. 2013). Recent work suggests that intraspecific oyster variation actually increases oyster recruitment (Smee et al. 2013). It follows that greater connectivity between oyster reefs within and between estuaries facilitates increased intraspecific variation as a result of recruitment. Alternatively, Smee et al. (2013) suggest that a loss in intraspecific genetic diversity in oysters may have a cascading effect, where recruitment potential decreases and combines with other negative impacts such as habitat degradation and loss of associated ecosystem services. As stresses such as those associated with global climate change increase, the impact of intraspecific variation on population success will likely play a more important role (Smee et al. 2013).

Oyster larvae spend two to three weeks in the water column and could potentially travel hundreds of kilometers prior to settlement. Despite the oysters' potential for long-distance larval dispersal, there are cases in which populations appear to be genetically distinct over short distances as a result of hydrodynamics or larval behavior, or both. In the Chesapeake Bay, microsatellite markers show a pattern of isolation by distance, indicating that recruitment remains local within tributaries and subestuaries (Rose, Paynter, and Hare 2006). Given the hydrodynamic properties of the sites involved, the authors conclude that the pattern is most likely due to larval behavior and physical retention (Rose, Paynter, and Hare 2006). Productive reefs within systems with a high potential for self-recruitment could result in expansion of the range of the reef system. Continued self-recruitment and range expansion might extend to currently unexploited (or novel) environments and successful population growth in new habitats or areas with more extreme environmental conditions.

Reef communities. In many places (for example, Gulf Coast, much of the East Coast) oyster reefs primarily provide the only hard substrate. Oyster reefs serve as habitat and shelter for many benthic invertebrate species, such as mussels, oyster drills, polychaetes, and crustaceans, as well as essential fish habitat and nursery grounds for many commercial and recreational fish (Bahr 1981; Lenihan et al. 2001; Kennedy, Newell, and Eble 1996, 734; Beck, Brumbaugh, and Airoldi 2011; Coen, Luckenack, and Breitburg 1999, Tolley and Volety 2005). Peterson, Grabowski, and Powers (2003) calculated that a 10 m2 section of restored reef in the southeast region of the United States (that is, Maryland to Texas) is expected to yield 2.6 kg of fish and large mobile crustacean production per year. Reef systems serve as a food source for pelagic fauna from outside the footprint of the reef, cascading to higher-order predators like red drum (Sciaenops ocellatus) and tarpon (Megalops atlanticus), including apex predators such as sharks and dolphins (Peterson and Lipcius 2003; Byers et al. 2015). In addition, oyster reefs are an important food source for animals such as raccoons and oystercatchers, which transfer nutrients between the intertidal and coastal terrestrial environments (Bahr 1981).

Reef connectivity facilitates movement and use of refuge habitat for these reef-dwelling organisms. A connected reef system supports a larger population of reef inhabitants and affects the metapopulation dynamics of these organisms in addition to the oysters themselves. The cascading effect on the metapopulations of other species results in more resilient populations and more stable food webs across the reef and in surrounding areas.

Not only do oysters support a diverse community, they are also able to survive through a wide range of salinity levels and form reefs or reef aggregates that span salinity gradients (Gunter 1950). Many estuarine species like blue crabs migrate through salinity gradients, and connected oyster reef habitat that spans these gradients provides hydrologic corridors of food and shelter for these transient species (McCormick-Ray 2005).

OFF-REEF COMMUNITIES:

Water quality. Oysters and associated organisms (such as barnacles and mussels) filter suspended sediments, phytoplankton, and nutrients out of the water (Bahr 1981); oysters bind suspended particulates as feces and pseudofeces, which are less likely to be resuspended, improving water clarity and also providing a food source for benthic organisms. This process transforms pelagic-based nutrition into a usable benthic-based food bank (McCormick-Ray 2005). An adult oyster can filter up to 2.5 gal (9.46 L)* of water per hour (Messer and Reece 1937). This filtration capacity, when considered from the perspective of a water body containing extensive oyster reefs, can be considerable. Historically, oyster filtration capacity is thought to have been large enough to filter entire bays within water-residence times in both the Gulf and East Coasts. Today, the only water body that still has this filtration capability is Apalachicola Bay, Florida (Zu Ermgassen et al. 2013).

While improved water quality benefits life on oyster reefs, the enhancements extend to nearby habitats as well. As denitrifers, oysters help reduce anthropogenically sourced nitrogen and may improve the health of local submerged aquatic vegetation (SAV) by removing excess nitrogen in the system (Grabowski and Peterson 2007). With ever-increasing levels of eutrophication, this filtration is more important than ever (Zu Ermgassen et al. 2013). By reducing suspended solids in the water column, oysters may also benefit local SAV by increasing light availability for photosynthesis (Newell and Koch 2004; Zu Ermgassen et al. 2013).

The efficacy of oyster habitat in improving water quality has been reduced dramatically in the last 150 years as anthropogenic disturbance has reduced reef area and density and increased nutrient loading to estuaries (Zu Ermgassen et al. 2012). Greater than 80% loss in oyster-reef-filtration

* For a full list of the unit conversions used in this document, please refer to *US Government Publishing Office Style Manual*, 31st ed. (Washington, DC: US Government Publishing Office, 2016), 345–7, https://www.govinfo.gov/content/pkg/GPO-STYLEMANUAL-2016/pdf/GPO-STYLEMANUAL-2016.pdf.

ability over the last 100 years has led to a loss in ecosystem services (Dame et al. 2002; Newell and Koch 2004; Zu Ermgassen et al. 2013). Because connected reef systems are more resilient than isolated reefs, they also have a greater capacity to improve water quality over large spatial and temporal scales. This filtration capacity may be particularly important during disturbance events (for example, inland storms), when nutrient delivery is high.

Shoreline stabilization. Intertidal oysters grow in densely crowded reefs (Bahr 1981). Because of high shell and reef roughness, intertidal oyster reefs absorb wave, current, and boat-wake energy. This reduction in energy benefits both intertidal and submerged vegetation (Henderson and O'Neil 2003). For example, in Georgia, salt marsh vegetation extends to intertidal oyster reefs and is eroded where a protecting oyster reef is not present (R. D. Harris, pers. obs.). In the Gulf of Mexico, restored reefs are slowing down adjacent marsh loss, and increased levels of invertebrate and fish biodiversity have been found in the area between restored reefs and marsh (Piazza, Banks, and La Peyre 2005; Scyphers et al. 2011). A large, connected reef system can reinforce sizeable sections of coastline, physically armoring the shoreline.

Subtidal oysters typically form raised reef beds and, like intertidal oysters, absorb energy. Raised reef structures slow currents and reduce wave oscillations and as a result can reduce shoreline erosion. These beds are particularly important in mitigating storm surge damage (Scyphers et al. 2011; Meyer, Townsend, and Thayer 1997). Healthy shellfish reefs, seagrass beds, and salt marshes are key natural elements in shoreline defense (Beck et al. 2009), particularly in areas susceptible to storms and hurricanes (Karl et al. 2009; Emrich and Cutter 2011).

Carbon sequestration. As an oyster grows, it secretes calcium carbonate shells. Because of the high biomass of oyster reefs and short individual life span (intertidal oysters typically live two to four years), oyster reefs serve as carbon sinks (Peterson and Lipcius 2003; Beck, Brumbaugh, and Airoldi 2011). As a result, reefs have been conceptually explored as a mechanism for sustainable sequestration to generate carbon offsets (Peterson and Lipcius 2003). There does not appear to be active, current research on using reefs for carbon offsets (Grabowski et al. 2012). However, there are a number of groups investigating the biomimetic process of carbon sequestration using oysters as a model system (for example, Ma and Teng 2010; Lee et al. 2011). In addition, although biosequestration is beneficial, its efficacy has likely been reduced because of the phenomenon of ocean acidification. Ocean acidification is caused by reduced ocean pH due to rising atmospheric CO2. Ocean waters with reduced pH (that is, more acidic waters) affect oysters and other shell-forming organisms by reducing calcification rates (Doney et al. 2009; Waldbusser, Steenson, and Green 2011). Bivalve larvae are particularly vulnerable to ocean acidification during initial shell formation (Waldbusser et al. 2015). This impact on larvae could lead to reduced population recruitment.

COSTS OF OYSTER REEF CONNECTIVITY: In addition to the many benefits of oyster connectivity, some potential costs or vulnerabilities associated with oyster reef connectivity are described below.

Disease spread. While there are a number of diseases that affect oysters, Dermo and MSX (Multinucleated Sphere Unknown) are the most virulent. Both are caused by protozoans and are reported to cause high mortality (Kennedy, Newell, and Eble 1996). Dermo is caused by Perkinsus marinus, with a range across the Gulf and as far north as Massachusetts on the East

Coast. It prefers temperatures between 25°C–30°C and salinities greater than 15 ppt (parts per thousand) but has been reported to survive in both lower salinity and temperature conditions (Kennedy, Newell, and Eble 1996). The pathogen is transmitted from one oyster to another, primarily through surrounding water. The density of infective protozoan cells decreases rapidly because of dilution in the water, making transmission successful only over short distances (<3 m; Andrews 1979; White et al. 1989). This transmission method results in a patchy distribution of infected oysters within an individual reef. The snail Boonea impressa, an ectoparasite of the eastern oyster, has also been shown to spread Perkinsus from host to host (White et al. 1987). Because disease transmission is limited to short distances, proximity of reefs is a factor in transmission of these disease vectors, and reefs that are in close proximity can serve as a disease corridor.

The oyster disease MSX is caused by the protozoan Haplosporidium nelsoni and is found in the central portion of the East Coast but is reported as far north as Maine and as far south as Florida. The protozoan prefers waters that are above 10°C and 10 ppt salinity (Kennedy, Newell, and Eble 1996). It is unknown how the disease is transmitted. In contrast to Dermo transmission, attempts to transfer MSX infection from infected to uninfected oysters have not been successful (Sunila and LaBlanca 2003; Ford 2010). There does not appear to be a relationship between the presence, density, or infection of infected oysters and the prevalence of infection in surrounding areas (Ewart and Ford 1993). In addition, under favorable salinity conditions, the disease spreads easily over large distances (Ewart and Ford 1993). As such, it appears that oyster reef connectivity and the spread of MSX across reef systems are not strongly correlated.

Pests and predators. Some species that dwell in oyster-reef habitat can negatively affect the oysters themselves. For example, parasitism on oysters by the snail Boonea impressa reduces oyster growth and net productivity and can also transfer disease (White, Powell, and Kitting 1984; White et al 1987; White et al. 1988).

Another example of a reef dweller that can negatively affect connected reefs is boring sponges. These sponges weaken oyster defense by burrowing into oyster shell for habitat. This process, when repeated by multiple individuals, compromises the defensive ability of the shell and leaves oysters more vulnerable to predation. Boring sponges are more prevalent in the subtidal zone and have a larger impact on subtidal reef communities (Dunn, Eggleston, and Lindquist 2014). There are several species of boring sponge along the Gulf and East Coasts of the United States.

Recent research conducted in North Carolina's Pamlico Sound shows that some oyster-restoration methods actually aid the colonization of boring sponge to the detriment of the oyster reefs (Dunn, Eggleston, and Lindquist 2014). Dunn, Eggleston, and Lindquist (2014) have been studying subtidal marl mounds created in consecutive phases in close proximity to one another, for oyster habitat. Consecutive years of restoration efforts have seen a marked decrease in oyster recruitment and survival rates. Dunn, Eggleston, and Lindquist (2014) suggest that, with time, boring sponge recruits onto the marl and oyster mounds and tends to colonize most of the mound. As consecutive phases of marl-mound oyster habitat are added each year, pre-existing adjacent mounds have increasingly larger boring sponge colonies and as a result facilitate faster sponge colonization of the new mounds. On the basis of their research, future local restoration efforts will use alternative materials, such as concrete, that are less susceptible to sponge recruitment. Dunn, Eggleston, and

Lindquist (2014) indicated that salinity is likely a key factor in predicting boring sponge problem areas.

Invasive species. Among the diverse species that reef systems support are a number of nonindigenous species (NIS). Various NIS including algae, crabs, barnacles, tube-building worms, tunicates, bryozoans, and fish have been associated with oyster reef communities. NIS can have important impacts on food-web dynamics, even in cases in which NIS occupy roles within the community similar to those of native species. In California, oyster reefs dominated by the Olympia oyster (Ostreola conchaphila), non-native crabs and whelks had significantly different predator-prey interactions than their native counterparts, resulting in food-web shifts and oyster mortality (Kimbro et al. 2009). A number of non-native crabs are found in Eastern oyster reefs throughout the United States, including the European green crab (Carcinus maenus), the Asian shore crab (Hemigrapsus sanguineus), and the green porcelain crab (Petrolisthes armatus). These crabs can alter food-web dynamics, prey on oysters themselves and, in the case of the filter-feeding green porcelain crab, directly compete with the oyster for food or prey upon larvae prior to settlement (Hadley et al. 2010; Miron et al. 2005; Lohrer and Whitlatch 2002). While each NIS may have a specific impact on a reef, a connected network of reefs can serve as a corridor for NIS, contributing to a greater impact on the reef system and NIS range expansion (Sheehy and Vik 2010; Bulleri and Airoldi 2005). This expansion corridor is especially important when the NIS in question have short dispersal distances (for example, tunicates).

Recent reports indicate the presence of the invasive lionfish (Pterois volitans / P. miles) within the Loxohatchee River watershed, Florida (Jud et al. 2011). This sighting was the first report of the species being found in an estuarine habitat, as it is usually associated with coral-reef systems. Sampling revealed that the fish were found near constructed hard-substrate habitats (docks, seawalls) and that some individuals were as far as 5.5 km from the ocean (Jud et al. 2011). Surveys in 2003 and 2008 identified 10 ac to more than 15 ac of oyster habitat within the Loxohatchee (Bachman, Ridler, and Dent 2004; Howard and Arrington 2008). Although lionfish were not found in oyster-reef habitat, there was a gap of only ~500 m between the outermost reefs and the fish farthest upstream, indicating that the fish habitat might eventually overlap with a reef system. The impacts are currently unknown, but preliminary data show an impact of lionfish feeding on lutjanid (snapper) species within the Loxahatchee (Jud et al. 2011). As some species of snapper use oyster reefs as nursery habitat, cascading effects of lionfish predation may negatively affect reef diversity and function as nursery grounds. Proximity of nearby reefs could change how these predators affect a reef system as well as how their range spreads within the estuary.

Recreational navigation hazard. A possible negative impact of reef connectivity on recreational use and navigation also exists. Low-lying intertidal and subtidal reef corridors could create safety hazards for recreational kayakers, kitesurfers, and swimmers and could push users into waters farther offshore and closer to navigation channels (an additional hazard). However, reef restoration efforts are much more likely to improve recreation habitat use because of the positive impacts on water quality, recreational oyster harvesting, and sport fisheries (Beck, Brumbaugh, and Airoldi 2011; Grabowski and Peterson 2007). Proximity to tourism should be considered when designing restoration programs.

DISCUSSION: The network of costs and benefits associated with reef connectivity are summarized below as a conceptual model (Figure 1). Many positive links physically connect distinct habitats (for example, benthos, reef, upland) and provide food-web links (for example, plankton, reef dwellers, apex predators). Alternatively, negative links such as the spread of certain diseases and non-native species can be enhanced by increased connectivity. The strength of each link, whether positive or negative, is influenced by local conditions within each reef system. The impact of the combined benefits and costs associated with a particular reef system should be determined on a case-by-case basis.

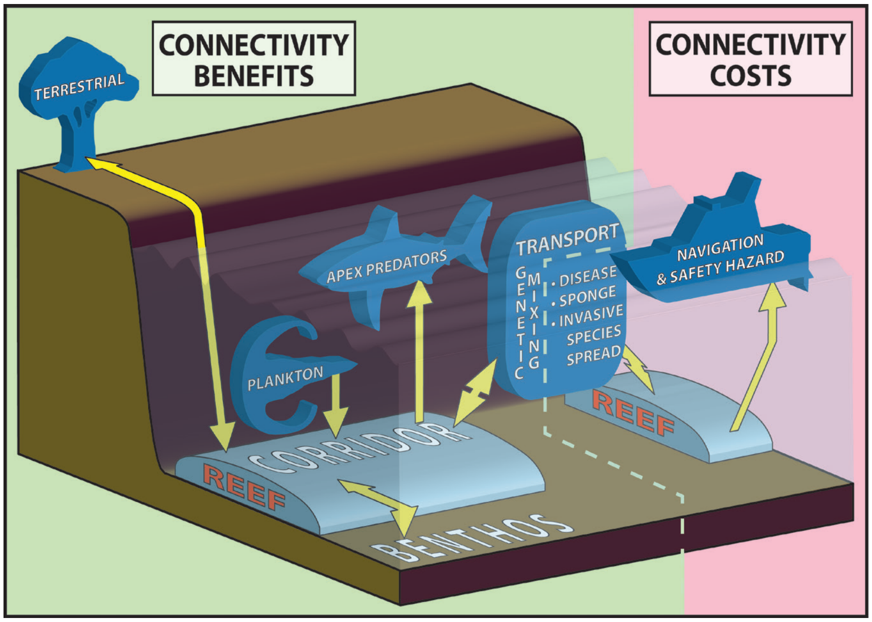

Figure 1. Conceptual model of benefits and costs associated with oyster reef connectivity.

Connectivity could influence the reef-system response to climate change in a number of ways. As described in dynamic models of coral dispersal (Figueiredo et al. 2014), increased water temperatures could shorten larval development times and potential dispersal distance. These combined effects could increase larval retention within a reef system. A well-connected reef system with higher larval retention may be able to retain higher genetic diversity, leading to a reef system that is more stable in the face of periodic disturbance. However, climate change affects a number of complex variables (for example, change in current direction and speed, patchiness of plankton distribution, larval mortality), making the overall effect on connectivity uncertain (Munday et al. 2008). Reef systems must also respond to climate-induced sea-level rise (SLR). Model simulations often posit reef-accretion rates that are lower than SLR, but these rates have not been verified with direct measures of growth and are estimated using bathymetry and radiocarbon dating. A recent study using direct measurements from intertidal reef cores and lidar-derived digital-elevation models concluded that vertical growth is fastest in underwater portions of the reef and slower at the reef crest (Rodriguez et al. 2014). Vertical growth of the whole reef is an order of magnitude faster than previously reported and can keep pace with predicted rates of SLR (Rodriguez et al. 2014). Although the vertical growth rate of intertidal reefs is faster than subtidal reefs (Bishop and Peterson 2006), the effect of spatial aggregation of reef systems is unclear.

Connectivity and management have a joint effect on the oyster fishery. In the Chesapeake Bay, reef systems are well connected within the southern, Virginia, portions and have minimal connectivity in the northern, Maryland, regions. Both states and the federal government manage the fishery. The well-connected reefs are managed through the creation of permanent sanctuaries with no harvest and sites with rotational harvest, where reefs are harvested at a planned frequency (USACE 2012). The goal is to maximize environmental services, maintain connectivity between sanctuaries and harvested areas, and maintain the fishery. The minimally connected reef systems in Maryland are managed through the Maryland Oyster Restoration and Aquaculture Development Plan (adopted 2010, Maryland Department of Natural Resources 2010), expanded sanctuaries, and restoration initiatives that increased the protected reef area to 25% of the Maryland portion of the bay's oyster habitat and closed these areas to oystering. The Maryland initiative includes enhanced law enforcement in closed areas, fishing restrictions in open areas, and a focus on aquaculture, hatchery production and rehabilitation (Maryland Department of Natural Resources 2010).

Restoration programs should be designed with reef connectivity in mind, so that source-sink dynamics with nearby reefs benefit the system as a whole. Spatial siting of constructed reefs based on maximizing positive and minimizing negative connectivity requires information on local hydrodynamics, larval transport, and population dynamics. Recent work by Kjelland et al. (2015) describes a multimodel approach that uses these three components to evaluate different management strategies with the Great Wicomico River, Chesapeake Bay, Virginia. North et al. (2010) developed an oyster-restoration optimization model to quantify benefits due to interactions between the physical characteristics, biological processes, and socioeconomic objectives within the Chesapeake Bay system. These approaches serve as tools to support restoration and management efforts to increase the benefits of connectivity.

It is important to note that oyster-reef systems, as well as the estuaries in which they reside, are integrally connected to water flow from upstream. The quantity, timing, and quality of freshwater input can impact salinity, turbidity, and the amount of dissolved and particulate material present downstream (Alber 2002). A severe drought in the southeastern United States during 2007–2008 resulted in decreased freshwater input into Apalachicola Bay, Florida. This decreased input caused high-salinity drought conditions within the bay, leading to significant disease-related oyster mortality due to Dermo infection (Petes, Brown, and Knight 2012). Because Dermo is transmitted from oyster to oyster, its spread is correlated to oyster proximity. This example highlights the impact of habitat connectivity on the effect of reef connectivity: reduced freshwater input from upstream amplified a negative cost of reef connectivity downstream. Changes in salinity regime within the estuary also change larval transport and distribution of fish and crustaceans associated with reef habitat (Tolley et al. 2006). Thus, management approaches should consider connectivity within the reef system as well as connectivity within the watershed.

SUMMARY: This technical note presents the current knowledge of benefits and costs or vulnerabilities associated with oyster-reef connectivity in the East and Gulf coasts of North America. We briefly describe the life history and distribution of Crassostrea virginica, the eastern oyster and then describe the identified connectivity benefits and present a conceptual model. Finally, we discuss impacts due to climate change and the importance of connectivity relative to management of recreational fisheries, restoration design, and water management. Plans for the creation, maintenance, and management of oyster reefs should consider whether the benefits of connectivity for a particular location—including increased metapopulation resiliency, robust reef

communities, improved water quality, shoreline stabilization, and carbon sequestration—will outweigh the vulnerabilities that also result from connected reef systems, such as increased spread of disease and invasive species, susceptibility to predators and pests, and impacts to recreational navigation.

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POINTS OF CONTACT: For additional information, contact the author, Dr. Safra Altman (601-634-3435, Safra.Altman@usace.army.mil), or the manager of the Ecosystem Management and Restoration Research Program, Dr. Brook Herman (601-634-3248, Brook.D.Herman@usace.army.mil), or the authors as listed below:

University of Georgia, Athens, Georgia, Phone: 706-580-4482, rdharris@uga.edu

ERDC-EL, New York, New York, Phone: 601-415-7160, Kyle.McKay@usace.army.mil

Mayville State University, Mayville, North Dakota, Phone: 701-788-4733, michael.kjelland@mayvillestate.edu

ERDC-EL, Vicksburg, Mississippi, Phone: 601-415-3509, Todd.M.Swannack@usace.army.mil

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