A GREATER GRAY:

A LARVAL CONNECTIVITY ASSESSMENT OF GRAY'S REEF NATIONAL MARINE SANCTUARY

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The Group Project is required of all students in the Master of Environmental Science and Management (MESM) Program. The project is a year-long activity in which small groups of students conduct focused, interdisciplinary research on the scientific, management, and policy dimensions of a specific environmental issue. This Group Project Final Report is authored by MESM students and has been reviewed and approved by:

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ABSTRACT

Grays Reef National Marine Sanctuary (GRNMS), under the direction of the National Oceanic and Atmospheric Association (NOAA), is situated off the coast of Savannah, Georgia, and is home to a thriving and diverse marine community. With commercial and recreational fishing pressure on fish species in the region, NOAA hopes to identify areas in the region that, if protected, would build on the benefits of GRNMS to these economically important species. We identified potential new conservation areas to complement GRNMS by modeling ecological connectivity of larval dispersal to GRNMS using Marine Geospatial Ecology Tools (MGET). Four species were modeled to represent the diversity of species in the region — red snapper, black sea bass, gag grouper, and scamp grouper. Model outputs map the expected regional sources of fish larvae throughout the Carolinian Ecoregion that ultimately supply recruits to GRNMS. Over 400 model runs were performed to explore variability in connections to other sites across the peak spawning months from 2009-2015. Model runs over multiple years were aggregated to identify sites that contribute the most new fish recruits to GRNMS. The results suggest that the most efficient way to increase regional protection is to expand the size of the current sanctuary and create a connected protected area to the south. This study provides a framework for connecting protected sites in the region, and provides a model for use in other settings within the National Marine Sanctuary system where the current level of protection is inadequate.

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LIST OF ABBREVIATIONS

EEZ	Exclusive Economic Zone
GMFMC	Gulf of Mexico Fisheries Management Council
GRNMS	Gray's Reef National Marine Sanctuary
NMFS	National Marine Fisheries Service
NMSA	National Marine Sanctuaries Act
NOAA	National Oceanic and Atmospheric Administration
MGET	Marine Geospatial Ecological Tools
MPA	Marine Protected Area
PLD	Pelagic Larval Duration
SAFMC	South Atlantic Fisheries Management Council
SMZ	Special Management Zone

EXECUTIVE SUMMARY

Grays Reef National Marine Sanctuary (GRNMS), under the direction of the National Oceanic and Atmospheric Association (NOAA), is situated off the coast of Savannah, Georgia within the Carolinian Ecoregion, and is home to a diverse marine community. Many current stressors, including excessive fishing pressure and degradation of nearshore nursery grounds, are currently compromising the ability of the GRNMS to provide sufficient protection. Most notably, species in the Snapper-Grouper complex, a group of 59 diverse fish species, are experiencing heavy fishing pressure in the region. As one of the smallest national marine sanctuaries in the country, GRNMS is currently unable to provide adequate management benefits. This project was developed by NOAA, GRNMS, and Master's students at the Bren School of Environmental Science & Management to identify areas in the region that, if protected, would offer the greatest benefits to this complex of Snapper-Grouper species. Important conservation areas were identified by modeling the ecological connectivity of larval movements to Gray's Reef.

Spatial management measures including the creation or expansion of Marine Protected Areas (MPAs) can serve multiple purposes for conservation. MPAs can directly protect species from fishing pressures and can boost abundance, size, and diversity of species. They also harbor healthy marine communities that can build resiliency to other ecosystem stressors such as pollution, habitat degradation, or climate change. Designing MPAs to benefit one another by creating connected MPA networks can bring additional conservation and fisheries benefits while still leaving large areas unprotected. MPA networks can protect species across their geographic ranges, and can serve as an insurance policy if one protected area within the network is heavily impacted by a catastrophic event.

To determine size and potential locations for areas that could be part of an MPA network with GRNMS, this project modeled larval movements to uncover ecological connectivity between fish spawning habitats and Gray's Reef. Understanding ecological connectivity specifically in the larval phase can identify spawning habitats that will seed fish populations at GRNMS. Additionally, since larvae are not subject to fishing pressures when they leave the protection of an MPA, larval movement can connect widely separated sites in ways that adult movement cannot.

Four species were modeled to represent the diverse species within the Snapper Grouper complex: red snapper, black sea bass, gag grouper, and scamp grouper. Multiple scenarios of larval dispersal were performed using Marine Geospatial Ecology Tools (MGET). The main inputs into this model for a given species were oceanographic currents data, known spawning locations, suitable habitat locations, the pelagic larval duration (PLD – duration of larval development before they are ready to settle), and peak spawning dates. Model outputs map the expected contribution of different sites in the region to the larvae that ultimately arrive at

Gray's Reef. Over 400 model runs were performed using data on currents for peak spawning months between 2009-2015. Model runs over multiple years were aggregated to visualize average annual larval contribution to Gray's Reef. Sensitivity analyses were performed to test model assumptions with the greatest scientific uncertainty.

Connectivity varied between species and years. However, connectivity was sufficiently consistent to identify sites that could have broad benefits over time and across species. A large area directly to the south of GRNMS showed the highest consistent larval contribution for the species and years tested.

The trends seen in our results suggest that the most efficient way to protect a group of connected sites is to expand the size of the sanctuary to the south, incorporating the high connectivity seen in this area. The optimal size of the expanded protected area depends both on the objectives of the sanctuary, and the expected success of management outside the Sanctuary boundaries. Sanctuary managers will need to decide how serious threats to target species are likely to be outside of the sanctuary, and how much larval recruitment to GRNMS is needed to ensure vibrant populations given the uncontrolled threats. We created contour maps to help managers visualize how to make decisions based on the fraction of fish recruitment warranting protection.

Our modeling provides an initial framework for future planning decisions. There are a number of important next steps. Most importantly, our results only factor in the expected biological benefits of different patterns of protection. They do not currently incorporate the potential costs of different management choices. However, our framework could readily be coupled to spatial analyses of spatial patterns of economic, social or political costs to identify the most cost effective ways of achieving given levels of protection. In addition, our studies do not explore the negative consequences of adult movement. When fish move beyond the boundaries of the MPA, they are suddenly vulnerable to higher levels of fishing mortality. Fortunately, our larval connectivity results suggest the greatest benefits from expanding the size of the current Sanctuary as opposed to creating multiple small additional sanctuaries. Such an expansion in size would have the added benefit of expanding the range of species that would likely benefit from the adult protection.

We hope that the robust modeling of our four target species provides a model framework for understanding larval connectivity for any National Marine Sanctuary. This report highlights major trends of connectivity and outlines how this modeling approach can be improved upon at Gray's Reef or in other regions. With increasing human pressures and a constantly changing ocean, a deeper understanding of connectivity will lay the foundation for more impactful spatial management, which will benefit our treasured marine ecosystems and the people who rely on them.

CLIENT INTRODUCTION

The National Oceanic and Atmospheric Administration's (NOAA) Office of National Marine Sanctuaries works to protect areas in United States' waters that demonstrate unique ecological and cultural significance. Under the National Marine Protection, Research, and Sanctuaries Act (NMSA) of 1972, 14 areas throughout the country have been designated as National Marine Sanctuaries. The NMSA authorizes the Secretary of Commerce to "designate and protect areas of the marine environment with special national significance" (NOAA NMSA, 1972). These federally managed areas promote conservation while simultaneously allowing for certain recreational and commercial uses. Sanctuary offices also provide education, research, and monitoring programs in conjunction with conservation efforts.

Gray's Reef National Marine Sanctuary (GRNMS) is a NOAA-designated National Marine Sanctuary located 27 km off the coast of Savannah, Georgia, encompassing approximately 56 square km of ocean. Oceanographic surveys of the Georgia coast in the early 1960s introduced the area as an important live-bottom reef ecosystem, rare to the Carolinian Ecoregion. Sanctuary designation was granted in 1981 to protect the unique features of this reef, which contributes to the biodiversity of the South Atlantic coast.

Gray's Reef Superintendent, Sarah Fangman, and NOAA Office of Sanctuaries Program Specialist, Helene Scalliet, proposed this connectivity assessment project in partnership with the Bren School to better understand the ecological connectivity of marine species under pressure at Gray's Reef and in the surrounding region. Data gathered from this project will be used to inform the GRNMS management plan update, slated for 2018.

PROJECT SIGNIFICANCE

A variety of anthropogenic pressures present in the marine environment create the need for informed management. Increases in fishing and coastal development in many regions have led ocean managers to search for effective strategies to support fish stocks and protect ecosystems. One such way is through the creation of Marine Protected Areas (MPAs), delineated areas that limit human pressures within their borders. However, dependent on the specific conservation goal to be achieved from an MPA, difficulty arises in deciding exactly how much area to protect, and where.

To maximize the protection provided by individual MPAs, their design can incorporate connectivity with other MPAs in the region. Protecting areas that are connected in some way allows for synergistic conservation benefits between these areas, beyond the benefits expected from similar protection of unconnected areas. This "connection" refers to the concept of *ecological connectivity*—the relatedness of two or more areas to each other through population dynamics. This is more commonly thought of in terrestrial spaces as the physical connection of areas that allow organisms within populations to more move freely between important habitat. Land managers and conservation parks have successfully used this idea to create wildlife corridors; areas cleared and protected to preserve or increase the ecological connectivity of similar habitats (Haas, 1995; Laurance & Laurance, 1999; Lees & Peres, 2008).

In the marine environment, largely free from the physical barriers that bound terrestrial landscapes, ecological connectivity must be thought of differently. As most areas of the ocean are already physically connected, their ecological connection cannot just be based on a physical connection, and necessitates a greater understanding of both population dynamics and hydrodynamics. With a limited understanding of where fish, are and how they move throughout ecosystems, establishing ecological connectivity in the ocean is difficult, and remains an evolving science. Larvae, the microscopic juvenile stage of many marine organisms, are dispersed by ocean currents. Therefore, by combining knowledge of spawning and settlement habitats with oceanographic modeling of currents, we can develop models that provide estimates of larval connectivity throughout essential habitats in a region.

As larvae are extremely small, they do not face the same pressures as those that survive into their adult stage. Although potentially more susceptible to pressures of pollution and predation, larval movement between two potential protected areas is largely safe from human fishing pressures, unlike the movement of adults between areas of protection. Therefore, modeling ecological connectivity specifically with larval movement can be an asset to maximizing protection for species in high fishing areas. Modeling larval connectivity is also helpful with species that do not have large adult home ranges. If certain species remain within a small area in their adult stage, the main method of new recruitment to a habitat comes not from adult migration, but rather from larval movements. Therefore, a greater understanding of the connection between the sources of larval recruitment to a given protected area can illuminate areas that provide important population replenishment.

Gray's Reef National Marine Sanctuary (GRNMS) serves to protect the unique ecology of the Carolinian Ecoregion, along the U.S. South Atlantic coast, while simultaneously providing for a variety of human uses, including recreational fishing, boating, and SCUBA diving. Managing for both biological and human needs requires management tools based on a scientific understanding of the ecosystem to address the complex and dynamic nature of the broader ecosystem of GRNMS.

As one of the smallest national marine sanctuaries, at only 56 square km (for comparison, the Channel Islands National Marine Sanctuary in Santa Barbara, California, spans 3,807 square km), it is likely that GRNMS cannot fully protect important fish species with larger home ranges. Several commercially and recreationally important fish populations in the region are experiencing overfishing (NOAA, 2016), affecting both the ecosystem and the surrounding fishing industry. One path to increasing the ability of GRNMS to help address overfishing is to view it as an anchor for a network of protected areas that cumulatively have much greater benefits than the contributions of any single protected area. Modeling the impact of limited fishing in a network of protected spaces connected with GRNMS can illuminate the potential cumulative impact on conservation in the Carolinian Ecoregion.

This project investigates the potential for increasing the impact of GRNMS to buffer fish populations from regional fishing pressures by exploring the pattern of connections between reefs in the region for a diverse array of important fish species. While directly addressing fishing pressure in the region, this project's exploration of extending protection for populations at GRNMS can also address resiliency of these populations to other pressures, such as pollution or the destruction of nursery habitats. We use a larval connectivity model to increase ecological understanding of the Carolinian Ecoregion, and to determine the potential benefit to GRNMS fish populations of protecting spawning areas of connected habitat. With an upcoming update to the GRNMS management plan in 2018, knowledge gained of ecological patterns or important areas for protection can be of direct use to inform management decisions.

Beyond Gray's Reef, this larval modeling protocol can be applied to different species throughout the NOAA sanctuary system to establish connection between sanctuaries and areas important for further protection. In the face of imperfect or limited data in many fisheries throughout the country, this type of larval connectivity modeling can provide management with insights into how and where to prioritize protection for a substantial portion of a target species' recruitment. The inclusion of a research prioritization to improve this model for future use at Gray's Reef, and recommendations for managers to use this tool beyond the Carolinian

Ecoregion context make this project relevant outside this one connectivity assessment.

PROJECT OBJECTIVES

This project hopes to aid GRNMS in using larval connectivity modeling to improve management decisions. To achieve this outcome, the project design had the following objectives:

1. Model larval ecological connectivity of the Carolinian Ecoregion to GRNMS for a range of recreationally and commercially important fish

2. Create recommendations to improve the use of this modeling protocol at GRNMS and beyond

INTRODUCTION

Spatial Management

Marine Protected Areas have been shown to boost the abundance, size and diversity of species within their borders (Halpern, 2003; Gaines, 2010). Not only can MPAs protect species from fishing pressures, but they can also increase the ecological resiliency of these areas to other stressors that affect the ecosystem, such as habitat destruction or pollution (Barnett, 2015). As climate change continues to alter marine environments with rising sea temperatures, ocean acidification, and more frequent and extreme weather events, MPAs can be designed to help buffer these impacts (McLeod et. al, 2009).

There are multiple ways that managers can attempt to increase the protections provided by a given MPA. One such method is an expansion in size, which has already been successfully implemented in many MPAs including some NOAA sanctuaries (Cordell Banks and Gulf of the Farallones). Expansion of a protected area can be particularly beneficial for species with large home ranges whose adult migratory patterns are not fully encompassed by the original MPA. An expanded area would also potentially benefit species if the expansion will cover their important spawning areas outside of the original MPA. Research suggests that larger MPAs are often more successful because dispersal, certain trophic interactions (i.e. prey depletion), and concentration of fishing along MPA boundaries are all likely to reduce the effectiveness of small MPAs (Walters, 2000).

Although increasing protection for species within its borders, large-scale MPA expansion can be both potentially costly and politically contentious. A similar effect can be achieved through the creation of MPA networks. These networks of smaller, ecologically connected protected areas provide many of the same benefits as larger protected areas, but may also offer unique advantages. MPA networks can serve to protect species that have large ranges that cannot be contained by one protected space, or ranges that may shift dramatically with climate change (Gaines et al., 2010). In the face of catastrophic events (e.g., oil spills) or climate change induced weather events (e.g., hurricanes), a network of properly placed MPAs can also serve as an insurance policy (Lubchenco et. al, 2003). If one protected area within the network is heavily impacted by a catastrophic event, the other areas can continue to provide protection for vulnerable species.

Human uses are limited by MPAs, and therefore it is important to consider the spacing and size of MPAs in order to limit the negative impact on fisheries. Beyond greater protection of certain species, well-designed MPA networks can serve to simultaneously enhance biological conservation and fishery yields (Gaines et al., 2010). Additionally, the spillover effect, where protection of species within an MPA increases the biomass directly outside the confines of the area to the benefit of fishing interests, can sometimes result from the creation of MPAs (Goni, 2008). MPAs have also been shown to successfully seed other, unprotected sites with larvae (Christie et al., 2010).

A network of MPAs can work together to create greater protection for species under pressure. Successful MPA networks are connected to each other through larval dispersal or adult movement (Gaines et al., 2010, Anadón. 2013). A study conducted by Oregon State University found the fish species *Amphiprion percula* was connected within several areas in Kimbe Bay, Papua New Guinea. OSU then proposed a network of marine reserves within the Kimbe Bay to sustain the fish populations through reserve-to-reserve larval dispersal and the self-replenishment of each reserve (Planes et al., 2009). This study not only provided the basis for where and how large reserves should be, but gave reason to create an entire network of many MPAs to adequately protect the given species.

Large networks of MPAs have already been implemented in some parts of the U.S. For example, with the passage of the 1999 Marine Life Protection Act, California created a statewide network of protected areas. This network includes multiple types of MPAs, including the federally managed Channel Islands National Marine Sanctuary, state managed no-take reserves, and other limited use protected areas. This network of multi-use MPAs can be replicated with other NOAA Sanctuaries to increase the benefits that the sanctuaries can provide to their resident species.

Larval Connectivity as a Tool for Management

The Carolinian Ecoregion possesses considerable suitable habitat for the fish species we elected to model. In addition to the seagrass estuaries and salt marshes that line much of the South Atlantic coast with ideal nursery grounds for many juvenile species, live, hard-bottom reefs add essential spawning and fish habitat throughout the region.

There are many important "islands" of this live, hard bottom habitat along the continental shelf where Gray's Reef is located, ranging from rocky areas with little vertical relief that support patchy communities of sponges and corals, to areas of outcroppings with abundant invertebrate growth. These live-bottom habitats support growth and reproduction of hundreds of species of plants, invertebrates and fish species within the region (DeBlieu, J et al., 2005). Patches of this suitable fish habitat weave hard bottom reefs throughout the Carolinian Ecoregion together in a web of ecological connectivity. This project will reveal where, and how strong, these connections are using larval transport throughout the region.

Understanding ecological connectivity specifically in the larval phase allows for greater protection of organisms in an MPA network, as larval movement between protected areas can avoid fishing pressures in popular fishing regions that adult fish cannot. Additionally, using a model-based approach based on known currents data can estimate connectivity in the absence of reliable data establishing adult fish movements.

After fish larvae are released in a spawning event, they are borne upon prevailing ocean currents and remain planktonic, suspended in the water column and largely subject to the dominant currents, until they are mature enough to settle on suitable habitat. The distance larvae can travel, and their likelihood of survival and eventual settlement, are a function of the currents in the region, availability of suitable habitat, the pelagic larval duration (PLD), and the behavior of the larvae.

Larval behavior can influence where larvae settle if their vertical swimming or changes in buoyancy interact with spatial variability in currents to alter their movement (Cowen et al., 2009). Relying solely on currents to determine larval transport may overestimate the scales of larval movement (Cowen et al., 2000). In addition, significant variability is imposed by geographic settings and the time of larval release. These central factors represent crucial research priorities for advancing the understanding of the connectivity process and metapopulation outcomes (Treml et al., 2015).

Although variability in life history and larval behavior introduces uncertainty into larval modeling, trends seen in model results can be used to inform possible conservation areas. A recent study analyzed larval dispersal across coral reefs in the Caribbean and Gulf of Mexico to identity important reef connections on a regional scale (Schill, 2015). The resulting connectivity matrix enabled researchers and managers to cooperate in an effort to strategically expand marine protected areas to preserve key ecological connections.

Larval connectivity between habitats in the Carolinian Ecoregion is important because reef seascapes in the region are characteristically patchy, and the resilience of a species to anthropological impacts will rely largely on the species' larval dispersal abilities (Almany et al., 2009, and Magris, 2015). When an area is protected, larval connectivity plays an imperative role in determining rates and mechanisms of recruitment on both nearby and distant habitat patches (Kininmonth et al., 2011, and Magris, 2015). Quantifying these spatial patterns of connectivity improves the understanding of the current structure of biological and ecological communities, and could help identify subpopulations that might face high risk of extinction and thus require further protection (Treml et al., 2008, and Magris, 2015). Larval connectivity from protected areas is also important in rebuilding populations in connected areas after major environmental or human disturbances (Gaines et al., 2010).

Our study utilizes observed spawning locations, daily oceanographic currents data, and computer modeling software to demonstrate the potential migration of fish larvae for our four species of interest. In this project, we will identify spawning areas within the Carolinian Ecoregion that demonstrate larval ecological connectivity to Gray's Reef, and use this connectivity to determine where further conservation would most benefit species at Gray's Reef.

Study Area

The Carolinian Ecoregion

The Carolinian Ecoregion is a designated area in the coastal waters off the Southeastern United States. This area was chosen as our study site because, as an ecoregion designated by the World Wildlife Fund, this bounded area exhibits "a geographically distinct assemblage of species, natural communities, and environmental conditions" (WWF, 2017). The Carolinian Ecoregion encompasses the bays, estuaries, coastal marshes, waters, and deep reefs of the continental shelf for North Carolina, South Carolina, Georgia, and east Florida. Its seaward boundary is the shelf edge at the 200-meter isobath (DeBlieu et al., 2005).

The offshore region is characterized by sandy bottom (70%) and hard bottom reef (30%) along the continental shelf (Hopkinson, 1991). The hard-bottom sites of the Carolinian Ecoregion support hundreds of species of plants, invertebrates, and reef fishes such as groupers, grunts, snappers, and sea bass (SEAMAP-SA 2001). Coastal estuaries, wetlands, and seagrass beds characterize inshore areas. The shoreline and inshore areas of the U.S. South Atlantic coast have experienced environmental degradation, with an estimated loss of 37% of coastal wetlands between the 1780s and 1980s (Dahl, 1990). Therefore, freshwater runoff from coastal rivers has a significant effect on water quality off the coast. The impacts of declining water quality can be seen further offshore, with major losses in overall productivity and substantial decreases in the size and abundance of top predators (Myers and Worm, 2003). The coastal marshlands that still remain are of great importance. Marshes from Beaufort, South Carolina, to Brunswick, Georgia provide food, structure and refuge from predators for more than 90 percent of the commercially and recreationally sought after fish in the region (DeBlieu et al., 2005).

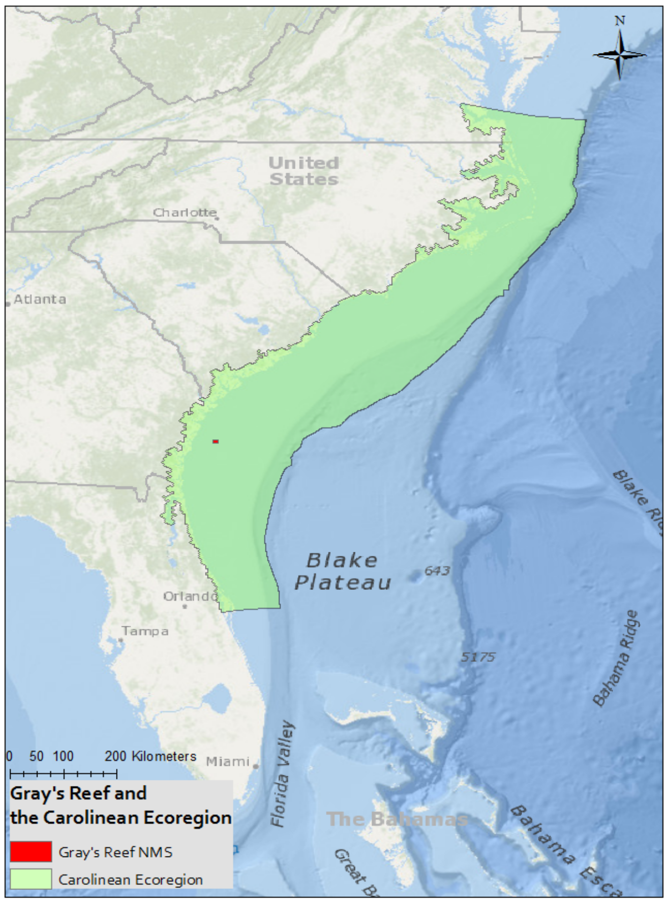

Figure 0. ***Gray's Reef in the context of the Carolinian Ecoregion.***

The waters of the Carolinian Ecoregion are fed partially by the Gulf Stream, which carries warm, tropical water northward as it follows the edge of the continental shelf. The Gulf Stream creates eddies and upwelling across the shelf as it moves north. A geographic anomaly to the region, the Charleston Bump is a topographically complex bottom feature located southeast of Charleston, South Carolina, and is responsible for the offshore deflection of the Gulf Stream. This deflection of the Gulf Stream also creates the Charleston Gyre, an eddy of warm Gulf Stream water that splits the stream at the bump, and moves it inshore (Sedberry et al., 2001). The Charleston Gyre brings up deep, nutrient-rich waters that contribute significantly to primary and secondary production within the region (SAFMC, 1998). This mixing of temperate and tropical waters produces variability in habitat types. Reef communities show high variability in fish species composition from reef to reef in this area (Parker, 1994).

Gray's Reef

Gray's Reef is a natural live-bottom reef (rocky seafloor capable of supporting high numbers of invertebrates) located 27 km off the coast of Savannah, Georgia. Gray's Reef is the only protected natural reef on the continental shelf off the Georgia coast. Lying 18-22 m deep, in the transition zone between temperate and tropical waters, Gray's Reef is home to a thriving and diverse marine community. The sanctuary encompasses approximately 56 square km in area, and consists of four main bottom habitat types (listed with their respective regional percent cover): flat sand regions (8%), rippled sand bare regions (67%), sparsely populated hard bottom regions (25%), and densely populated hard bottoms (<1%)(Kracker, 2008). Hard bottom reefs are distributed along the sandy shelf floor in an unpredictable pattern from the nearshore zone to the shelf edge. The high levels of production, respiration and nutrient recycling in the Gray's Reef water column are a contrast to the low levels of production found in the mostly sandy mid-shelf region. This high level of production in the waters of Gray's Reef suggests the influence of a strong connection with the nearshore waters of the Georgia coast (Hopkinson, 1991).

GRNMS supports a wealth of species, including the endangered North Atlantic Right Whale, the threatened loggerhead turtle, and multiple overfished species of the Southeast Atlantic region (NMFS, 2016). The limestone ledges and protrusions of Gray's Reef offer a diverse and productive habitat for around 300 marine invertebrates, 65 species of macroalgae, and over 180 fish species (Kendall et al., 2008). Densely populated live bottom areas and rocky ledges of the reef offer the greatest diversity of niche habitat to support fish (Kendall, 2007). The understanding of fish range and behavior must also be evaluated temporally at Gray's Reef — as the assemblage of fish species varies significantly between seasons, with the highest number of species and densities occurring in the summer (Parker, 1994).

As a rocky offshore reef, Gray's Reef provides essential fish habitat (EFH) for snapper and grouper species in the region, because it provides rocky outcroppings and ledge-like bottom formations that form the basis of productive benthic communities. Many species of snapper and grouper spawn at offshore rocky reefs, and produce larvae that can travel hundreds of miles, which allows productive reef habitats to influence not just a specific region, but an entire fishery (Coleman et al., 2000).

The unique benthic features and diverse habitats of Gray's Reef contribute to its importance for fishing interests in the region. These benthic features increase primary production at the reef, and allow a high fish biomass when compared with surrounding bottom topographies (Hopkinson, 1991). Recreational fishing in the area targets both reef fish and highly migratory, open water fish. The three major identified species being targeted in the area are black sea bass (*Centropristis striata*), gag grouper (*Mycteroperca microlepis*), and scamp grouper (*Mycteroperca phenax*), though many other species are targeted by fishing interests.

Species of Interest

Ocean managers in the U.S. South Atlantic have highlighted a designated group of fish species as important to fisheries yet difficult to manage (SAFMC, 2017). This group of 59 diverse fish species, managed together, is known as the Snapper-Grouper complex. With limited time and resources, not all 59 species within the Snapper-Grouper complex could be modeled. To explore the wider use of this larval modeling tool, four fish from this management complex, representing a range of life history characteristics and spatial patterns, were chosen as species of interest.

These four fish species with differing life histories were selected to highlight vulnerable or recreationally important species in the region: black sea bass (*Centropristis striata*), gag grouper (*Mycteroperca microlepsis*), scamp grouper (*Mycteroperca phenax*), and red snapper (*Lutjanus campechanus)*. NOAA resource managers as well as scientists in the region provided additional guidance in the identification of these four fish species.

For a profile on each species, including specific management regulations, please refer to Appendix 1.

Socioeconomic Considerations

Although not explicitly included in this connectivity assessment, it is important to understand the socioeconomics of this area to provide context for the use of our results in making management decisions. Socioeconomic data are limited, but a general understanding of ocean users in this area can be drawn. Fishing is the biggest activity that occurs within the boundaries of GRNMS. Survey data from 2002 indicates that fishing is the primary activity at Gray's Reef, with around 95% of users participating, compared to a relatively low 27% of users participating in non-consumptive forms of recreation such as whale watching, sailing, or SCUBA (no-take) (Leeworthy, 2002). Commercial fishing is not seen at Gray's Reef due to specific gear restrictions.

Outside Gray's Reef, in the larger Carolinian Ecoregion, socioeconomic and fishing location data are relatively sparse. Ocean based recreational fishing is marginal compared to freshwater fishing in Georgia. A study done in 1996 estimated Georgia recreational saltwater fishermen make up only 5.1% of Georgia fishermen as most fishing in the state is done on lakes and rivers (American Sportfishing Association, 1996.) Commercially, fishing is of larger economic importance in South Carolina and Florida than in Georgia (Leeworthy, 2002). The biggest fishery in Georgia is the nearshore shrimp fishery, making up about 80 percent of the value of the total catch. Outside of the shrimp fishery, the majority of catch in the Georgia finfish fishery is offshore in federal waters. In 1999, the Snapper-Grouper complex fish species provided the highest value of finfish landings in Georgia (66 %)(Leeworthy, 2002).

Although fishing appears less intensive in Georgia waters than in the surrounding region, it may be because there are fewer reefs present than in other areas. Artificial reefs have been put in place both inshore and offshore to attract species of recreational and commercial fishing importance. Fewer reefs present in these waters could result in more pressure put on each of these reefs by local fishing interests. With no data describing the effort or location of fishing in this area, especially for recreational fishing, it is difficult to make any inferences regarding which areas are under the most pressure. For socioeconomics and income figures in greater depth, please refer to Appendix 2.

Regulatory Landscape

Gray's Reef Management

Under the National Marine Sanctuaries Act of 1972, NOAA can designate ocean areas to be protected as sanctuaries, but no specific regulations are mandated; each sanctuary can be regulated differently based on its particular needs. GRNMS has strict fishing gear restrictions within its confines, outlawing all gear types except for hook and line. Since most commercial fishermen in the area use wire traps or bottom-trawling rather than hook and line, GRNMS is used solely by recreational fishermen. As of 2011, the southern third of the area has been closed to all recreational activities and anchoring for the purpose of scientific study. Sanctuary studies show fish abundance and size of multiple fish species is larger in the areas of low fishing pressure than that in areas of high fishing pressure (Kendall, 2008). This would suggest that the recreational fishing pressure in the rest of the Sanctuary is significant and has an effect on the population dynamics of resident species.

The South Atlantic Fisheries Management Council

Gray's Reef lies within the management purview of the South Atlantic Fisheries Management Council (SAFMC). Much of the South Atlantic waters are located within the boundary of the federally managed Exclusive Economic Zone (EEZ) that runs from 3 to 200 nautical miles offshore from the Atlantic coast, and grants exclusive and sovereign rights to the resources therein to the United States. The SAFMC manages fisheries and marine environments in this EEZ for the states of North

Carolina, South Carolina, Georgia, and east Florida to Key West. Any mobile species that moves beyond 200 miles offshore will be considered in international jurisdiction, and any species that moves within 3 miles of shore will be under the jurisdiction of state waters. As fish often move freely beyond regulatory borders, species-specific management across these jurisdictional borders can be challenging.

The SAFMC manages eight fisheries in the region, though it identifies only one fishery complex that contains species considered to be overfished - the Snapper-Grouper complex. The four species chosen to model in this project are all managed under the Snapper-Grouper complex. Though both commercial and recreational fisheries are strictly regulated by the SAFMC, certain qualities of the Snapper-Grouper complex make it difficult to manage effectively.

The Snapper-Grouper Complex

The Snapper-Grouper complex fishery management plan was first implemented in 1983 for the U.S. South Atlantic region (SEDAR, 2016). The plan now includes 59 listed species, seven of which are officially designated as overfished or experiencing overfishing. The large variety of species and available data in the complex makes overarching management policies challenging to effectively design or implement.

The specific biology of the Snapper-Grouper complex provides yet another challenge to successful management. Snappers and groupers are generally slow-growing, long-lived reef fish that mature later in life (SAFMC, 2016). Due to this slow growth and late maturity, high site fidelity and seasonal spawning migrations, complex social structure, and even sex reversal, conventional management measures may not work well for snapper and grouper management. The combination of these ecological and behavioral characteristics make the Snapper-Grouper complex difficult to manage effectively, which is corroborated by the overfished status of species within the complex (Coleman, 2000). As such, stock recovery and area recruitment is a long-term process and highly subject to fishing and environmental pressures that can benefit from increases in protected area.

As this management complex provides specific challenges from issues discussed above, certain management strategies are favored. A combination of reducing Total Allowable Catch (TAC) and implementing spatially restrictive MPAs are thought to be the best management strategy for species within this complex (Coleman, 2000). Additionally, individual transferable quotas (ITQs) should be considered in reef fish management plans to limit an increase in fishing effort that might result to offset the effect of MPA restrictions (Coleman, 2000).

Spawning Special Management Zones (SMZs)

SAFMC is currently in the process of reviewing a new System Management Plan (SMP) to further protect hard-bottom, live-bottom, and artificial reefs that are considered important spawning habitat for the Snapper-Grouper complex through a network of protected areas SMZs.

These proposed SMZs are designated specifically as *spawning* SMZs, designed to protect areas where spawning has been observed, or where it is likely to occur in the region (SAFMC Amendment 36, 2016). Once the plan is finalized, it will then be sent to the National Marine Fisheries Service (NMFS), who will then approve or deny the Amendment and begin implementation.

Within these Special Management Zones, commercial and recreational take of species in the Snapper-Grouper complex would be prohibited year-round. The SMZ's are proposed in waters off the coasts of North Carolina, South Carolina, and Florida. There are currently no proposed spawning SMZs off the coast of Georgia. Whether or not these proposed SMZs off of neighboring states show connectivity and a resulting benefit to fish populations at GRNMS specifically remains to be seen.

Modeling Goals

With the complex nature of the regional ecology and regulatory landscape described above, effective spatial management to buffer Snapper-Grouper species from fishing pressure in the Carolinian Ecoregion is needed. Beyond fishing pressures, properly designed spatial management can help increase the resiliency of these species to pollution, loss of important coastal nursery habitats, and the impending threats of climate change. Modeling connectivity to GRNMS from spawning habitats in the region will identify areas best suited for sanctuary expansion or for the creation of an MPA network.

METHODS

Approach Overview

To identify the size and potential locations for conservation areas, this project first performed an in-depth literature review to understand the species under pressure, the ecology of the Carolinian Ecoregion study area, and the potential for using larval connectivity as a lens for conservation modeling. Based on this review and consultation of relevant experts, the species chosen to model were red snapper, black sea bass, gag grouper, and scamp grouper; these four fish display different life histories and are somewhat representative of the diverse species within the Snapper-Grouper complex.

From this review, we chose to model multiple scenarios of larval dispersal using Marine Geospatial Ecology Tools (MGET), a toolset housed in ArcGIS. MGET can model the transport of larvae from observed spawning locations in the study area to Gray's Reef. The main inputs into this model for a given species were: ocean currents data, known spawning locations, suitable habitat cover within the study area, the pelagic larval duration (PLD, or the duration larvae exist in the water column before being competent to settle), and peak spawning dates. The output of the model is a spatial map of the expected contribution of larvae that arrive at Gray's Reef from each 8x8 km cell of ocean where females are known to spawn within the Carolinian Ecoregion.

To account for changes in currents throughout the lunar cycle, seasons, and years, we generated model forecasts on different moon cycles for each peak spawning month, for a given species, from 2009-2015. Results from the multiple model runs were aggregated and analyzed to find average larval dispersal patterns per year, per species. Results are displayed in both maps and figures. Maps show where larval connectivity was found between our target (GRNMS) and surrounding areas measured as the percent contribution of total larvae released in each model simulation. The figures created show an area curve expressing how much space must be protected to hit a particular value of larval contribution.

As this model does not account for certain biological parameters thought to be important to larval transport, model results should be used to demonstrate trends, and not as absolute certainties of larval movement. For this reason, we performed a series of sensitivity analyses to see if, and how, the areas of highest larval contribution to Gray's Reef changed across years or other model parameters such as larval mortality, diffusivity, competency and number of iterations.

Lastly, an analysis of model results was used to inform management recommendations for GRNMS. We provide a list of these recommendations to prioritize future research needs in an attempt increase the accuracy of model projections, and to provide a generalizable approach for other marine protected areas.

Larval Connectivity Model

The Connectivity Analysis tools were developed as part of MGET out of Duke University's Marine Geospatial Ecology Laboratory to provide marine ecologists and conservationists spatially-explicit ecological modeling techniques. MGET is a collection of open-source geoprocessing tools accessed from ArcGIS that integrates Python, R, MATLAB, and C++. The Connectivity Analysis tools were created to analyze marine ecosystem connectivity (Roberts et al., 2010). These tools simulate the dispersal of larvae from suitable areas by ocean currents using the multidimensional positive definite advection transport algorithm (MPDATA) (Smolarkiewicz 1983; Smolarkiewicz and Margolin 1998; Smolarkiewicz 2006).

The model utilized in our project uses four tools from the Connectivity Analysis toolbox, as described below:

1. The first tool creates the larval dispersal simulation. Inputs into the model are in the form of ArcGIS rasters. These rasters include a **water mask** which informs the model which cells are land and which are water, a **patch ID raster** which specifies the location of each cell where larvae can be released from and settle on, as well as gives each cell a unique habitat ID, and a **patch cover raster** which specifies the proportion of each cell's area occupied by suitable settlement area.

2. The second tool loads the currents data, HYCOM GLBa0.08, into the larval dispersal simulation. The currents data used are HYCOM GLBa0.08 as they fit the spatial extent for the region of interest. These currents data sets are available from September 2008 to present and have a time step of one day. The HYCOM GLBa0.08 currents data have a depth range of 0 – 5500m.

3. The third tool runs the larval dispersal simulation based on specified parameters for each species we modeled and MPDATA.

4. The last tool converts the results produced from the third tool into a line feature class visualization.

For a list of the assumptions and limitations of the MGET model, refer to Appendix 3.

Species Specific Parameters

The MGET tools used in this analysis allow for three species-specific parameters that can be changed to model different life histories.

1. The first parameter specifies what areas are to be considered as suitable habitat for the species in question. As each species may have different known spawning behaviors or spatial patterns, different patch ID and cover rasters were created for each species. Patch ID and Patch Cover rasters for each species in our model were modified from raster data provided from Farmer et al., In Press. These raster data represent the probability of finding a spawning condition female in a given patch. The primary source of data for Farmer et al. came from the Southeast Reef Fish Survey (SERFS) database (Farmer et al., In Press). For scamp grouper, red snapper, and black sea bass, input spatial layers for the model were created based on their known spawning locations as larvae "donors" while Gray's Reef was designated as the specified "acceptor" of larvae (data from Farmer et al., see Appendix 4). Because Gray's Reef overlaps four of our 8x8 km cells, we chose those four cells to represent the target area of Gray's Reef. As these three species are thought to first settle on reef habitats before potentially moving to inshore nursery grounds, we assumed that these larvae could settle directly onto Gray's Reef. With only one known spawning location for gag grouper, the input spatial layer for this species used this location as well as known spawning locations of scamp, as studies have suggested these species overlap in their spawning locations (Gilmore and Jones, 1992). Gag grouper are thought to be estuary dependent and settle in these areas first (Keener et al., 1988). For this reason, coastal seagrass estuaries along the coast of Georgia, adjacent to Gray's Reef, were considered the larvae "acceptors" from known spawning reefs with the assumption that these seagrass nurseries can potentially seed Gray's Reef with adult gag grouper.

2. The second parameter specifies the pelagic larval duration (PLD), which identifies the amount of time larvae spend in the water column before they are competent to settle out. Since PLDs are a characteristic of fish species that are difficult to measure and as such are not known with certainty, we chose PLDs based on estimates found in the literature during our literature review (Table 1). Larvae take some time to become competent before they are physically able to settle out. The third tool used in the model uses a gamma cumulative distribution function to represent the onset of larval settlement competency. Over a PLD of 50 days, we set the larvae to be competent to settle at 20 days (Figure 2). For a more in-depth explanation of this competency calculation, see Appendix 3.

3. The third species parameter is the start time of the simulation (which represents the peak spawning date). Peak spawning of our species of interest

was also collected during the literature review. The parameters for each of the species are specified in (Table 1) and were found during our literature review. Model runs for each modeled species were started on different days corresponding with the phases of the moon cycle (new moon, first quarter, third quarter, full moon) in each month of peak spawning for years 2009-2015.

Table 1: *Species of interest and their specific parameters included in the MGET tools*

Species	**Pelagic Larval Duration (PLD) *assumed for model**	**Peak Spawning Months**	**References:**
Black Sea Bass (*Centropristis striata*)	30	February - May	PLD: (Edwards et al., 2008) Spawning: (Sedberry et al., 2006)
Red Snapper (*Lutjanus campechanus*)	30	June – September	PLD: (Johnson et al., 2013) Spawning: (Sedberry et al., 2006)
Gag (*Mycteroperca microlepis*)	43	February-April	PLD: (Keener et al., 1988) Spawning: Estuarine Dependent (Keener et al., 1988), Dates (Farmer et al., In Press)
Scamp (*Mycteroperca phenax*)	40	March-July	PLD: 30-50 days (Lindeman et al., 2000) Spawning: (Sedberry et al., 2006)

Data Analysis

For every run (or iteration), the MGET model outputs a raster file containing the percent contribution of larvae each cell contributes to Gray's Reef, in the form of an attribute table. An R script was then used to extract all the attribute tables, for all the runs of different species through 2009 to 2015, as CSV files. Maps showing the percent contribution of those cells to Gray's Reef for each species, and all the species across the seven years were also generated. Readers can refer to these maps to see the locations of the highest contributing cells (reef areas), and the exact percent contribution values they possess. Contour maps showing the cumulative percent contribution of those cells to Gray's Reef were also made, which show the reef areas corresponding to a certain larvae conservation goal. For example, if the manager would like to protect forty percent of the larvae that settle at Gray's Reef from these contributing reefs, they could just reference areas on the contour maps that correspond with a forty percent conservation goal. However, these contour maps highlight the most efficient way to reach these target larval percentages, and are often noncontiguous. If management was instead interested in contiguous space to reach a target larval percentage, a larger area than what is provided on the contour map would be needed. Cumulative area graphs were also created to assign numerical values to the area highlighted on the contour maps.

Sensitivity Analysis

The MGET model involves several biological parameters that are important factors influencing larval transport and could potentially change model results. These parameters are larval mortality, diffusivity, and competency. A series of sensitivity analyses were performed to see how the reef percent contributions were affected by changes in these three parameters. We also performed a sensitivity analysis to test the model's sensitivity to an increased number of iterations.

Larval mortality

In the MGET model, mortality is expressed as the amount of larvae that will be removed from the simulation at each time step (12 hours) as a result of larval death. Because of the uncertainty surrounding larval mortality, we chose to run our models with a mortality of zero to get an understanding of the full range of connectivity in the region. Moving forward, a more realistic mortality rate will need to be incorporated. To test the sensitivity of a zero mortality rate to a more realistic larval mortality rate, we chose February 2, 2009, and ran the MGET model three times for black sea bass with a larval mortality rate of 0, 0.1 and 0.2. Because the time step was every 12 hours, these rates translated into 0%, 20%, and 40% mortality each day (24 hours). Percent contribution maps for these three larval mortality rates were made to demonstrate the changes in the contributing reef areas, and their percent contribution values.

Diffusivity

Diffusivity refers to the rate at which larvae can spread throughout the water column. Diffusivity is measured in square meters per second. The default diffusivity in MGET is 50 m2/s. Higher diffusivity allows more larvae to spread by diffusion. We picked the dates of February 2, 2009, for black sea bass, and June 29, 2009 for red snapper, as the moon cycle for these two dates are both in the full quarter. We then ran the model twice for black sea bass and red snapper respectively, with the diffusivities of 75 m2/s and 100 m2/s. Percent contribution maps were made to demonstrate the changes in contributing reef areas, and their percent contribution values. See Figures 23 and 24 in Appendix 5 for black sea bass and red snapper results in map form.

Competency

Competency represents the amount of time larvae stay suspended in the water column before they became capable to settle out onto suitable habitat. Our model assumes larvae are immediately capable to settle after a 20-day competency period. To test the sensitivity of this parameter, we chose to model black sea bass, and altered the competency rate so that larvae become competent gradually, and not immediately, after 20 days.

Number of iterations

The start dates we chose for each species are the moon cycles for each peak spawning season. To test the results' sensitivity to the number of iterations that were performed, we picked black sea bass, and added the days that are one day before or after the moon cycles as start dates for running the model. This increases model runs to 51 during peak spawning instead of 12 during peak spawning, as modeled originally. Percent contribution maps were made to see the changes in the contributing reef areas and their percent contribution values.

RESULTS

For each species, the model was set to run one iteration per moon cycle for every month in a species-given peak spawning season. These iterations were then repeated for the years 2009 – 2015. This resulted in over 400 model runs. The result of each iteration was a feature line class that connects “source” cells to either Gray's Reef, in the case of black sea bass, red snapper, and scamp grouper, or seagrass estuaries in the case of gag grouper. Each feature line class, and its associated quantity of larvae, represent each cell's strength of connectivity to their target area (Gray's Reef or the seagrass estuaries). Our results were reclassified so that each 8x8 km cell in the original raster now represents the quantity of larvae delivered. The mean of each cell's contribution was calculated over all iterations over the seven years 2009 - 2015. The yearly average of each cell's contribution was calculated over all months in a given year. Each yearly average was then aggregated over the seven years modeled (2009-2015) to create the mean average of larval contribution over seven years. Percent contribution was calculated by dividing the mean quantity by the sum of the mean quantity and multiplying by 100.

Black Sea Bass

Black sea bass has an estimated PLD of 30 days, and observed peak spawning months of February through May. The percent contribution map for black sea bass shows that areas surrounding GRNMS and areas close to the coast of Georgia and the top of Florida have the highest connectivity to GRNMS, and deposit the highest percent of larvae there. Areas off the coast of North and South Carolina are the least connected (Fig. 1).

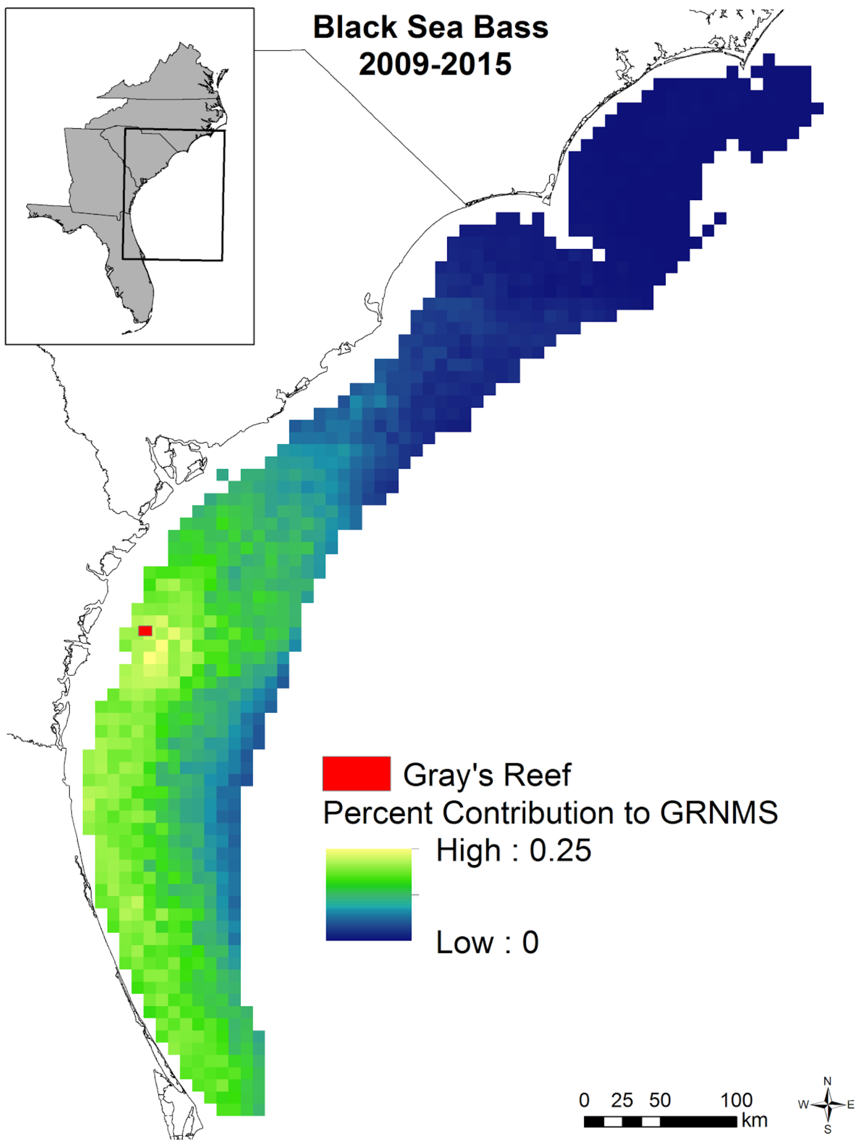

Figure 1. ***Black Sea Bass Percent Contribution Map.*** *Mean quantity of black sea bass larvae for all iterations over the peak spawning season of February – May from 2009 – 2015 delivered to GRNMS. The lightest yellow cells represent the strongest connectivity and highest percent contribution to GRNMS. The darkest blue cells represent the weakest connectivity and lowest percent contribution to GRNMS.*

Red Snapper

Red snapper has an estimated PLD of 30 days and peak spawning months of June through September. Results show that areas of strongest connectivity and highest percent contribution of larvae delivered to GRNMS are the areas slightly north east of Gray's reef, off the northern coast of Georgia and southern coast of South Carolina. Additional hotspots of connectivity can be seen off the Florida coast, as well as in the upper corner of our study region off the coast of North Carolina as well as slightly below it, off the upper coast of South Carolina. (Fig 2.)

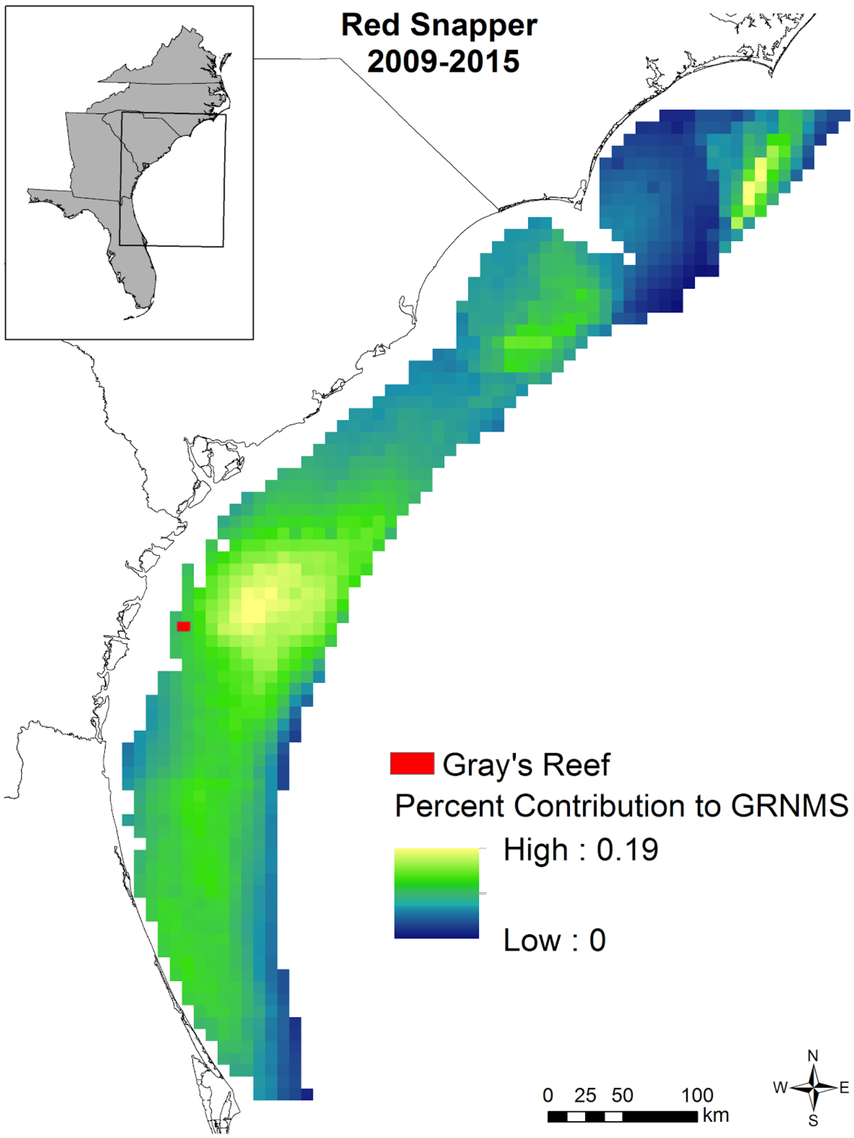

*Figure 2. **Red Snapper Percent Contribution Map.** Mean quantity of red snapper larvae for all iterations over the peak spawning season of June - September from 2009 – 2015 delivered to GRNMS. The lightest yellow cells represent the strongest connectivity and highest percent contribution to GRNMS. The darkest blue cells represent the weakest connectivity and lowest percent contribution to GRNMS.*

Scamp Grouper

Scamp has an estimated PLD of 40 days and peak spawning months of March through May. The percent contribution map for scamp show that the areas of strongest connectivity and highest percent contribution to GRNMS are south of the Sanctuary, off the upper coast of Florida. Although not as strongly connected as the lower region, the areas off the coast of Georgia and the lower half of South Carolina show connectivity to GRNMS (Fig 3).

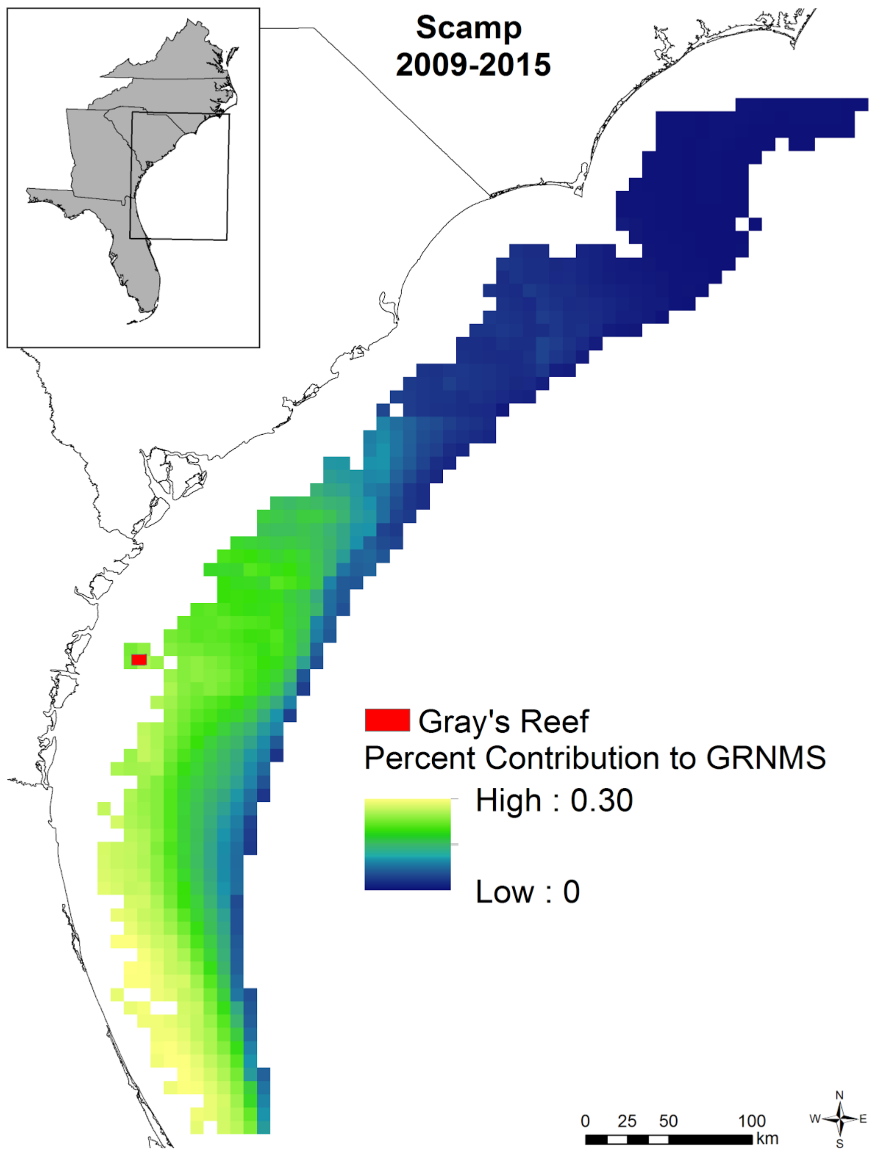

*Figure 3. **Scamp Percent Contribution Map.** Mean quantity of scamp larvae for all iterations over the peak spawning season of March - May from 2009 – 2015 delivered to GRNMS. The lightest yellow cells represent the strongest connectivity and highest percent contribution to GRNMS. The darkest blue cells represent the weakest connectivity and lowest percent contribution to GRNMS.*

Gag Grouper

Gag has an estimated PLD of 43 days and peak spawning months of February through April. In the case of gag, connectivity is represented by each cell's percent contribution of gag larvae to seagrass estuaries off the Georgia coast. The percent contribution map for gag show that the areas of strongest connectivity and highest percent contribution of larvae come from areas closest to the coast of Georgia and top of Florida. The highest contributing areas are those directly surrounding GRNMS (Fig. 4).

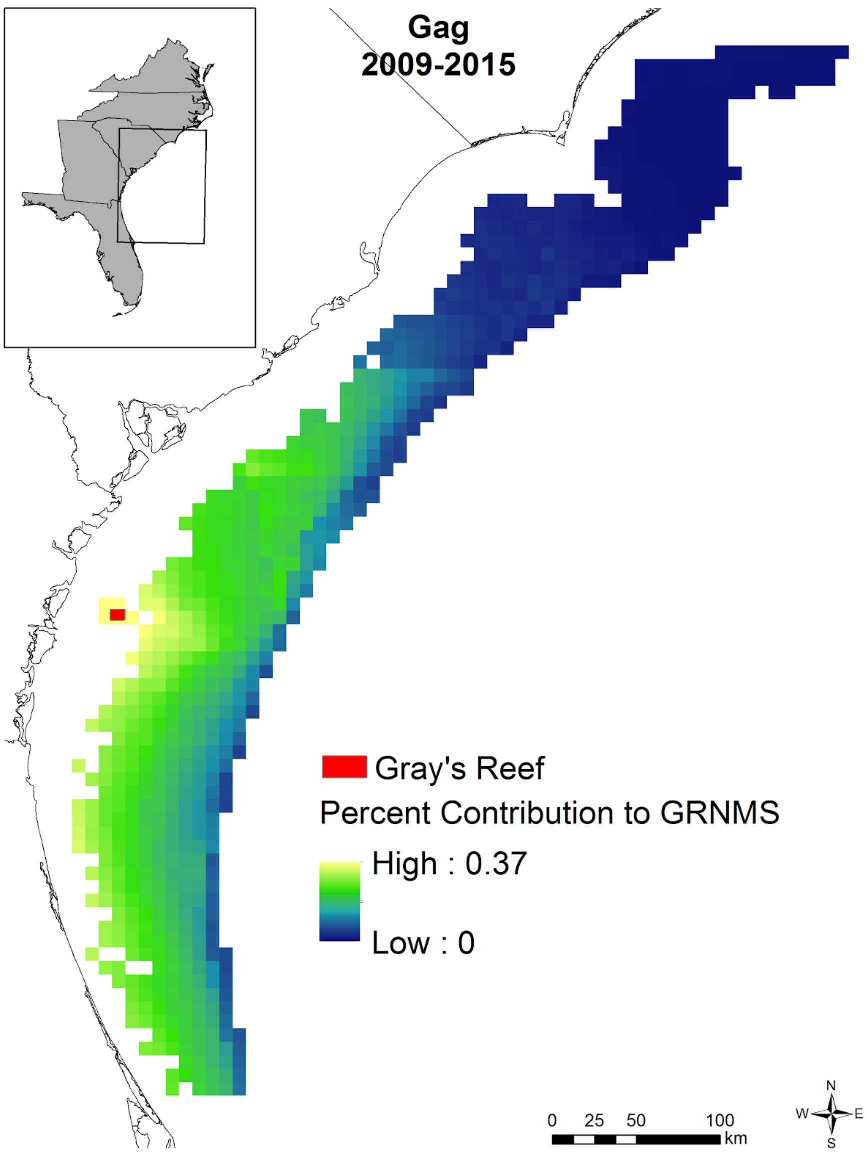

*Figure 4. **Gag Percent Contribution Map.** Mean quantity of gag larvae for all iterations over the peak spawning season of March - May from 2009 – 2015 delivered to seagrass beds off the Georgia coast. The lightest yellow cells represent the strongest connectivity and highest percent contribution to those seagrass estuaries. The darkest blue cells represent the weakest connectivity and lowest percent contribution.*

All Species Aggregated

When comparing each species' percent contribution map, it is evident that species specific parameters influence model results (Fig 5). We see similar trends for black sea bass, scamp, and gag, which might be explained by the overlap in their peak spawning seasons. All four species show areas of strong connectivity in those cells surrounding Gray's Reef, and those areas south of it, which allows for a clear opportunity to select sites that would benefit all four species. Red snapper differs slightly, with one of its highest contributing areas being to the north of GRNMS, whereas the other species' highest contributing areas are mostly surrounding or south of GRNMS. As each of these four species were identified as important to the region, we also aggregated all iterations for all species over the seven years to better understand the trends that would inform management of all four species at once (Fig. 6). Again, we see the strongest connectivity in surrounding areas closest to GRNMS and off the coast of Georgia, the upper coast of Florida, and lower coast of South Carolina.

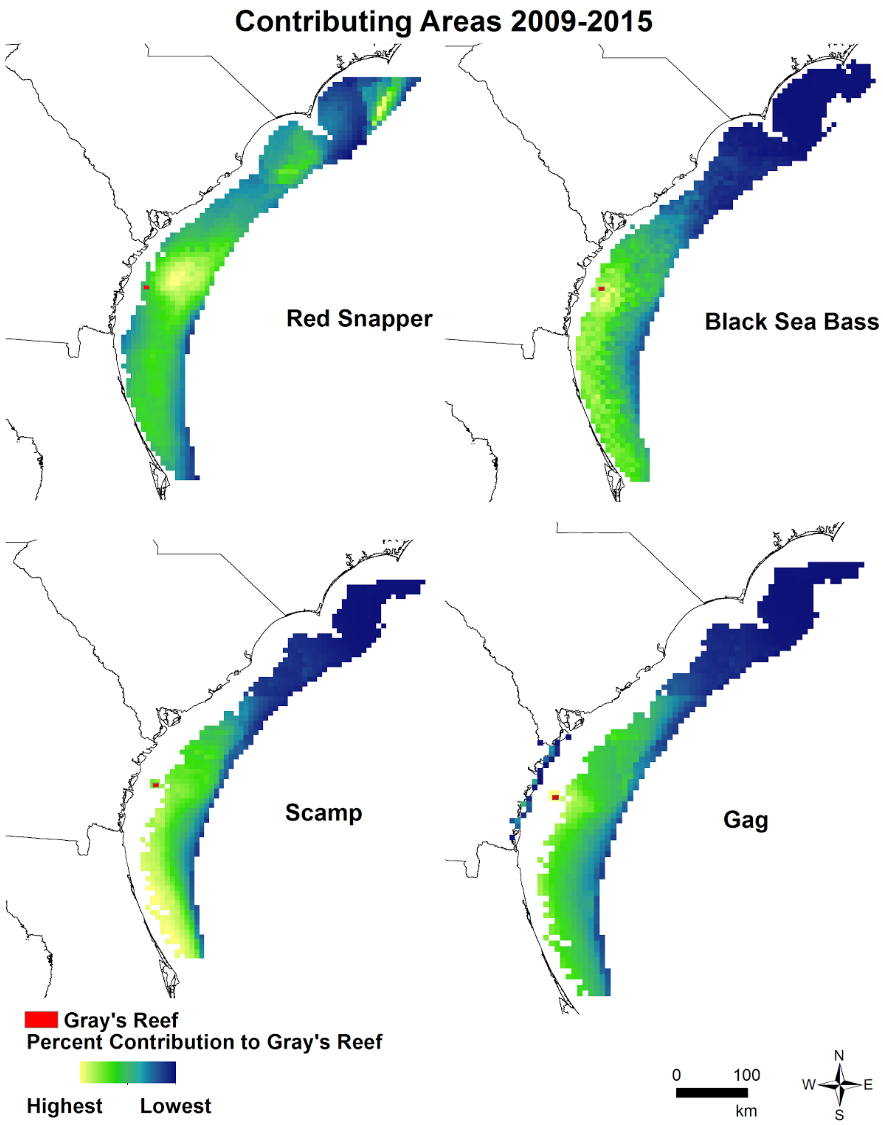

Figure 5. ***Comparison of Red Snapper, Black Sea Bass, Scamp, and Gag Percent Contribution****. Variation among species as a result of species specific parameters used in each MGET model. The lightest yellow cells represent the strongest connectivity and highest percent contribution to GRNMS. The darkest blue cells represent the weakest connectivity and lowest percent contribution to GRNMS.*

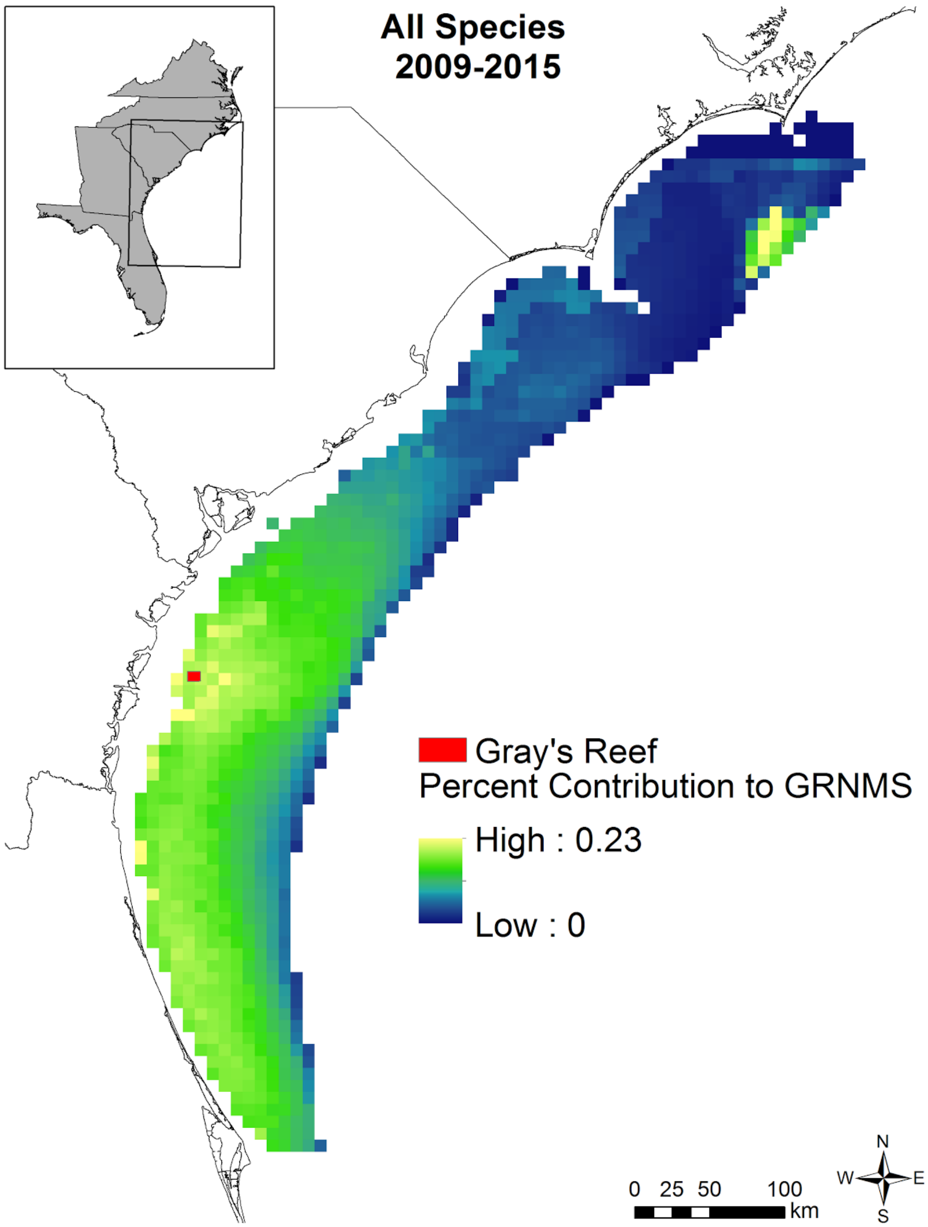

Figure 6. ***Aggregated Species Percent Contribution Map.*** *Aggregated mean quantity of larvae for black sea bass, red snapper, scamp, and gag for each of their iterations over their peak spawning season from 2009 – 2015.*

Contour maps were made for each species individually and for the four species aggregated to illustrate protecting different increments of larvae that are delivered to GRNMS (and seagrass estuaries adjacent to GRNMS in the case of gag grouper) (Fig. 12-16, see appendix). Contour maps were created for the purpose of visualizing our results to inform management decisions. These figures aid in the visualization of how much area should be protected to achieve a target percentage of larval contribution, in the most efficient way. To better understand exactly how much area needs be protected for a given percentage of larvae, we also created area curve graphs (Fig. 17 – 21, see appendix). Looking at the first three quantiles of our contour maps, 20%, 40%, and 60% cumulative larvae contribution, we can evaluate the implication of how much area of protection is required to most efficiently reach a target larval contribution (Table 2). The amount of area reserved for protection will depend on the management target.

Table 2. Amount of area (km^2) to most efficiently gain 20%, 40%, or 60% larval contribution

Cumulative Area (km^2)					
	Black Sea Bass	**Red Snapper**	**Scamp**	**Gag**	**Aggregated Species**
20% larval contribution	760	1176	568	600	1000
40% larval contribution	1616	2600	1200	1320	2128
60% larval contribution	2608	4176	1944	2152	3400

Sensitivity

The full range of connectivity in the region is sensitive to mortality; however, the general trends of the most connected areas do not change. As the rate of mortality increases from .1 (10% every twelve hours, 20% every 24 hours), to .2 (20% every twelve hours, 40% every 24 hours) the number of cells that show connectivity decrease. As mortality increases the probability of cells further away from the target delivering larvae decrease, however the areas of highest connectivity remain the same across the mortality rates tested (Fig. 22, Appendix 5).

Diffusivity is also not a sensitive parameter, though it still displays a small degree of variability to areas with lower connectivity. Visually, the comparison of the diffusivities 50 m^2/s, 75 m^2/s, and 100 m^2/s for black sea bass show little variation between rates (Fig. 23, Appendix 5). The percent contribution of the highest contributing cell decreases slightly, from 1.78% to 1.58%, as diffusivity increases. However, when comparing the same rates of diffusivity for red snapper, there is a slight visual difference between the diffusivity of 50 m^2/s, and that of 100 m^2/s. The percent contribution also changes when considering the diffusivity sensitivity of red snapper. As diffusivity increases, the percent contribution of the highest contributing cell decreases from 7.18% to 5.06%.

When twelve iterations for black sea bass in the year 2009 were compared to 51 iterations in the same peak spawning months and year, the results were visually very similar (Fig. 24). The percent contribution change of the highest contributing cell from 0.28% to 0.29% is minimal, lending to the conclusion that twelve iterations per year were sufficient for our model. The model was not sensitive to the change in iterations from 12 to 51.

DISCUSSION

Results from the model simulations show a high variability in the highest contributing cells of larvae to Gray's Reef. Maps aggregating model simulations over a seven-year period (Figs. 1 - 6) show, for every species, that no cell averages a larval donation of more than 1% of all larvae ending up at Gray's Reef. This has both positive and negative implications for management. High variability over model runs signifies that there may not be one or two specific "hotspots" that must be protected to increase larval donation to GRNMS, but rather there may be many possible combinations of area that are important to protect spawning locations that seed Gray's Reef. This allows for a greater flexibility in management. If there are multiple areas that can be protected to accomplish the same goal of larval donation, managers can have multiple options of where to increase protections or limit fishing. Conversely, although this creates flexibility in decision making, it also equates to more area needing to be protected in order to meet a given conservation goal.

With the aforementioned flexibility in choosing areas for conservation in mind, we have created multiple visual tools to help managers at Gray's Reef make decisions. These visual figures characterize the connectivity, and its corresponding variability over seasonal and yearly model iterations, found in the Carolinian Ecoregion with respect to GRNMS.

The ***percent contribution maps*** (Figs. 1 - 6) show the areas that have the highest average contributing percentage of larvae over a seven-year period. As these percentages of contribution are relatively low per cell (<1%), these maps should not be used to point out a few specific cells that need to be protected, but rather to show trends of where, within the ecoregion, areas of highest contributing cells are located. As an example, for black sea bass (Figure 1) we see that most of the highest contributing cells are immediately surrounding and south of Gray's Reef. The specific cells are less important, due to their low percentage of average connectivity, than the trend that areas near Gray's Reef may be more beneficial for black sea bass larval connectivity.

The ***coefficient of variance maps*** (Figs. 7- 11) show the large amount of variability in connectivity results from simulations aggregated over the seven years modeled. This shows that the low percentages (<1%) shown in the percent contribution maps are a result of high variation of percentages through the years.

The ***area curve figures*** (Figs. 17- 21) give a continuum of how much area must be protected to reach goals of percent larval contribution to Gray's Reef as stated in the cumulative percent contour maps. As each species shows a unique curve, this will help managers compare what would be needed spatially to protect larval connection for any conservation goals set for individual species or all four species together.

The ***cumulative percent contour maps*** (Figs. 12 - 16) complement these area curves and give managers yet another way of understanding our model results. These maps show where protection should occur based on the most efficient way to reach a target percent larval contribution. As management goals change, these maps can show where conservation should take place, with contribution targets to Gray's Reef broken into in 20% increments. Trends from these maps can highlight regions of interest for conservation.

Lastly the ***sensitivity analysis maps*** show how specific parameters of the model affect the output maps. These maps highlight the parameters that lack concrete data for the species we modeled. From these maps (Figs. 22 -25), one can see that model results do not change very much for all of these parameters. Results are the most sensitive to the rate of larval mortality. When looking at the change in connectivity with increased larval mortality (Fig. 22), we see that the spatial extent has shrunk considerably, though the strongest connected areas remain the same, or very close to the original results. Without a good estimate of larval mortality, model results may be skewed. Understanding this sensitivity, results from our model simulations most likely overestimate the outer bounds of connectivity of all species. Although we chose to model with a larval mortality rate of 0 in order to show the full range of possible larval connection, managers should weight areas of connectivity that appear towards the edges of the study area as less important. These areas are less likely to show connection with a higher larval mortality rate.

Limitations of the model

The results presented give a good indication of larval connectivity trends in the region, however, there are limitations to the conclusions that can be drawn. With limited data available, and the inherent uncertainty that accompanies environmental modeling, understanding the assumptions made can help assess the limits of the model.

Spatially, we chose to limit our study to the Carolinian Ecoregion. In most cases, across species, most cells of highest connectivity do not appear along the furthest edges of the northern, southern, and eastern border of the study area, signifying that this likely was an appropriate spatial extent for our modeling for most species. In addition, our sensitivity analysis of larval mortality rates suggests that the true connectivity is most likely closer to GRNMS than our model outputs, as we assumed a mortality of 0. There remains the possibility that, if modeled with a larger spatial extent, new and different connectivity could be seen. In the case of scamp grouper, high connectivity cells are seen at the southern border of the Carolinian Ecoregion. This would suggest that for this species in particular, future modeling should include more area to the south.

On the western border of the map, a small gap between our modeled area and the coast can be seen. This is because the data (Farmer et al., In Press) (see Appendix 4) that was used to select spawning areas did not cover this small area of shallow coastal waters. As some of the cells showing highest connectivity are seen along this western border of the study area, there may be important cells in the nearshore environment that were not modeled due to this spatial limitation. If and when data for this area becomes available, more modeling would be of value to find if these nearshore cells have high connectivity.

Within the model itself, we have iterated parameters to incorporate the life histories specific to the species in question. Although model runs for different species have differing PLDs, spawning seasons, and identified suitable habitats and spawning sites, there are still some aspects of larval behavior the model does not account for. Movement of larvae in this model is controlled mostly by hydrodynamic currents data, and does not factor in the vertical movement patterns that we know are present in most larvae. With very little understanding of the extent of this movement and how much it affects larval displacement, there was no clear way to add this to our model outputs. However, this should be taken into consideration while making management choices, as some in the science community assert that it can change the spatial range of connectivity (Cowen et al., 2000). In this case, a decrease in the extent of connectivity due to vertical larval movement, along with a similar result from increased larval mortality could reduce the amount of overall cells that show connectivity, and therefore change connectivity patterns. The model also assumes that larvae remain at or near the surface during the entire length of the simulation. Because the spatial extent of available currents data will shrink as depth increases, we ran our models with larvae remaining at the surface (Roberts et al., 2010). Additional runs are planned to test the sensitivity of running the model at different depths using each species' unique spawning depths. As currents can change in strength and direction as one moves vertically through the water column, it is unsure how much this assumption is ultimately affecting the model results.

Beyond differences in larval behavior, larger assumptions about how to use these results to inform management decisions must be understood. GRNMS management highlighted the Snapper-Grouper complex as the top priority when assessing larval connectivity, but, due to constraints in time, our project only focused on a select group of these species. Though the four species chosen represent different life histories, they do not encapsulate the full diversity of life histories and behaviors within the entire Snapper-Grouper complex. For this reason, looking at our species aggregated percent contribution map should not be taken to fully represent the entire complex as a whole, but rather to show connectivity trends for the complex. This complex is notoriously difficult to manage as there is a significant amount of variability in both the species biology and life history. To make a more informed assessment for managing this group as a whole, we suggest more species should be modeled to add to the results produced for the four species in the report.

Within the species we did model, gag grouper was modeled differently because their larvae first settle in coastal estuaries and migrate to offshore reefs later in life. With little spatial understanding of which estuaries gag grouper leave for their adult stages at Gray's Reef, it is possible that we did not include estuarine habitat in our model that shows high connectivity with Gray's Reef. An adult fish tagging survey could be a useful study to track migration patterns of gag grouper from coastal estuarine habitat to reef habitats off the coast. Fish tagging surveys are routinely done in Gray's Reef for the four species that are modeled in this project, however they focus on fish movements within the confines of the Sanctuary. A larger scale fish tagging survey including a greater area of the Carolinian Ecoregion would inform future model simulations of gag grouper's larval movements.

Research Priorities

With the limitations present in our modeling study, it is clear that more research to inform larval inputs would be of great value to using model outputs for effective management. In this section we highlight the most important research needs, in no particular order, to increase the accuracy of the model as well as needed research to apply these results to management decisions.

1. Specifics of Larval Behavior

While populating the model with relevant life history parameters, we found a scarcity of larval data for the fish species in the Carolinian Ecoregion. Literature review and interviews of expert scientists revealed the difficulty of gathering data about the larval stage, including the PLD, the larval mortality rate, the diffusivity of larvae, and the competency period. As our results have shown that different species can show noticeably different connectivity patterns, organisms of interest need more specific data. We suggest a research project focused on identifying larval parameters for species important to management priorities. The PLD and larval mortality rate seem to have the greatest effect on model results, and therefore should be prioritized in data gathering.

Understanding the larval vertical migration of species modeled, and their average depth during the larval stage, is also an important research gap. Although not explicitly used in the model, as described in the limitations section, this movement can have an effect on the overall displacement of larvae. Prioritizing study of vertical placement of larvae in the water column can validate or refuse assumptions made in the models.

Another option is to look to technological solutions to fill this research gap. Emerging technologies that tag larvae with geochemical markers could be explored as a potential complement to modeling efforts (Thorrold et al., 2007) to add to the robustness of results. These new methodologies are both expensive and time-consuming (Thorrold et al., 2007) and therefore should not be used widely to understand multiple species. However, performing a one-time study with a species of importance could potentially inform continued modeling, a cheaper and faster method of determining connectivity, with updated larval parameters that mirror real-life results. Beyond showing certain larval movement parameters, this type of study could also serve to cross-check model results. Finding where actual larvae end up could help to identify further the strengths and weaknesses of a modeling approach to larval connectivity in the Carolinian Ecoregion.

2. Informed Model Simulations

Time limited the analyses we were able to perform. With more time, we would have continued to run model simulations to get an even clearer picture of larval connectivity. Results from our sensitivity analysis have led us to prioritize re-running models over the seven years of available currents data, with a higher larval mortality rate. Although a more precise number for the larval mortality of each species would be an ideal input into future larval modeling, running simulations with a few different mortality rates can give a better understanding to managers of the average connectivity. We know that larval mortality is not zero, so any further modeling would create more realistic accurate results for GRNMS. Also, re-running models with a theoretical expanded sanctuary may change connectivity as described in the previous section. We feel that GRNMS should invest in these two particular modeling studies.

3. Reef to Estuary Movements

Research shows that many organisms in the Carolinian Ecoregion use the seagrass estuaries along the coast as habitat at some point in the juvenile phase of their life history. Understanding how different species at GRNMS move from reef to estuary, and from estuary to reef, is also important in understanding connectivity in the region.

This connectivity might demonstrate which seagrass nurseries have connection with GRNMS. If we know which areas of seagrass estuary habitat seed Gray's Reef with adult fish, we can prioritize coastal areas for conservation that will directly benefit adult populations at GRNMS. Our model for gag grouper could be improved by changing the cells of estuary to reflect research-identified areas, instead of areas of estuary habitat that are simply adjacent to GRNMS, as was assumed in the model.

We were unable to find research to explain if fish migrating from reef habitats to estuary habitats return back to these same reefs. If fish do not return to reef areas they originated from but rather show a more random migration, this would have implications for our model results. If certain species settle at Gray's Reef but quickly migrate to estuarine habitat and never return, protecting their larval connection to GRNMS may be of less interest to managers. Continuing fish tagging studies for any species of concern or interest is a research priority.

4. Spawning locations

Data used for the model inputs of spawning locations, supplied by Farmer et al., In Press, clearly identified known locations where spawning females were collected, for the fish species we modeled. Of course this data is based on sampling and therefore does not capture all actual spawning areas. Any additional research to add to known spawning locations would be beneficial to future monitoring and management decision-making. The research priority in this category is understanding where gag grouper are spawning. The data we received for this species only identified one spawning location. If more data can be found to identity actual areas where spawning has been witnessed, or spawning females have been caught, this would increase the accuracy of our gag grouper model.

5. Socioeconomics and Fishing Data

As a goal of the sanctuary system to balance the needs of the ecosystem with the needs of human user groups, our results must be used in tandem with an in-depth socioeconomic study of the region. With up to date social and economic data lacking in the region, a clear understanding of the impacts of conserving these areas are unknown. A measure of how many people are involved with fishing species of interest and how much money is made in the fishing industry in this area is important to grasp. Understanding the economic value of fishing each specific species will help prioritize which fish need more protection and what larval connectivity models are of greatest importance to management.

To accompany socioeconomic research, a spatial understanding of fishing behavior is also important. Research into where fishing pressure occurs in the Carolinian Ecoregion, and how much pressure occurs in each area, would be highly beneficial to cross-reference against these larval connectivity results. This comparison would allow the identification of potential conservation areas that may be politically feasible to protect, and areas that must be protected because they are receiving too much fishing pressure. For further studies, if location-based fishing data does become available, it is possible to use a conservation modeling tool to weight economic and ecological costs. Conservation modeling tools, such as MARXAN, can help managers pick areas to protect with higher larval connectivity to GRNMS that minimize economic costs. However, this type of spatial fishing data is of course difficult to collect, as fishers are unlikely to want to give out fishing location data. Emerging technology, such as the Global Fishing Watch software, tracks movements of fishing boats using AIS technology. This only works for vessels with an AIS device on board, which is only mandatory for U.S. vessels 65 feet or longer. Although this will not encapsulate many of the recreational fishermen that frequent Gray's Reef and the surrounding areas, it could help to better understand the commercial pressures on species throughout the Carolinian Ecoregion.

6. Climate Change Impact

Climate change could have a wide range of effects on the life history and important habitats of many marine species. The number of tidal wetlands, estuaries, mangroves and other shallow-water habitats may gradually decrease if climate change continues at current rates (Liu, 2000). Climate change can also affect changes in water temperature, dissolved oxygen content, and salinity, which all have been shown to decrease the foraging, growth, and fecundity of fish species, as well as potentially altering their migratory behavior (Moyle and Cech, 2004). Changes of this kind could affect the biological and ecological characteristics that we have used to model larval movements, such as PLD and peak spawning seasons, and would create the need for future modeling as ocean ecosystems continue to change.

Climate change may also have an impact on the physical movements of larvae. Studies show that changes to the climate system may cause alterations to the thermohaline circulation of ocean water, ultimately causing the weakening or even the possible breakdown of ocean currents. This might adversely affect the reproduction of fish species (Vellinga and Wood, 2002).

Further study into these six research priorities will contribute to a more robust connectivity assessment, which in turn will provide a deeper understanding of the management opportunities and challenges at GRNMS and in the Carolinian Ecoregion moving forward.

RECOMMENDATIONS AND CONCLUSIONS

Larval modeling allows us to learn more about the population dynamics of marine species on a large, regional scale. The larval connectivity assessment performed for Gray's Reef can be used to gain a deeper understanding of larval movements of selected species within the Carolinian Ecoregion in relation to the Sanctuary. This can directly protect fish species from the threat of overfishing in the region and can indirectly support resiliency from habitat degradation and climate change by supporting healthy fish populations.

Although model results showed some variability between species, they also showed considerable overlap. Areas directly surrounding GRNMS, and areas to the South, showed the highest larval contribution for a range of species and therefore suggest that there are areas which, if protected, would benefit multiple species at once. If one species is of much greater importance to protect in the eyes of local managers, this species' connectivity may need to be looked at separately so as to maximize benefits for this species in particular. With such a variable group of species within the Snapper-Grouper complex, our model may not fully represent the needs of all 59 species present in this group. However, our modeling can highlight general connectivity trends, as our four species were chosen to encompass the diverse life histories present in the Snapper-Grouper complex.

The variability in connectivity shown throughout seven years of modeling for each species allows for flexibility in management. Without a specific area identified as the "silver bullet" for conserving larval contribution to GRNMS, there are many options for protected area selection that could benefit from the creation of an MPA network with GRNMS. As some cells in close proximity to GRNMS, and a large group of cells to the south more consistently contribute a higher average percentage of larvae to Gray's Reef (shown in yellow in supporting figures), these cells should be the highest priority for conservation for the species modeled. This result suggests that both an expansion of GRNMS, and the creation of a connected MPA to the south would together provide the most efficient way to realize greater larval contribution. Given that our model showed substantial sensitivity to the parameter of larval mortality, conservation efforts near Gray's Reef may be more important than those further away and should be prioritized as such.

Continued modeling is suggested to determine the benefits of protecting distinct combinations of priority areas shown in model results. With the relatively small size of GRNMS, the sanctuary has less area for larvae to settle on than would a larger area. For this reason, an expansion of the sanctuary would most likely result in a greater quantity of larvae deposited at GRNMS, and potentially a greater strength of larval connectivity with surrounding areas than was seen in our model. Also, if managers wish to design a contiguous expansion of the sanctuary or a contiguous new MPA to serve in a network with GRNMS, these areas would have to be larger than shown in model results to account for protecting some areas that do not show the highest larval contribution. The change in area and location of model results to incorporate contiguous areas are unknown at this time but can be easily modeled once GRNMS spatial conservation goals are decided upon.

Though spawning Special Management Zones (SMZs) are proposed throughout the region for the Snapper-Grouper complex species, SAFMC does not advocate for adoption of SMZs in Georgia waters (SAFMC Amendment 36, 2016) as it does for other states such as Florida and South Carolina. Given that most cells of highest contribution come from areas in close proximity to Gray's Reef, we feel that exploring the establishment of an additional spawning SMZ in the immediate vicinity of GRNMS as part of the SMZ network could help these species of interest in the region and at GRNMS. If year-round closures are not a feasible option at these sites, peak spawning seasonal closures that prevent take during spawning months would likely help species at Gray's Reef.

Looking at these results, we can see that protecting all of the area the model indicates to reach meaningful larval contribution targets would require a sizeable increase in protected area. Although results show these areas to be large in relation to the size of GRNMS, when compared to other national marine sanctuaries, they seem less extreme. For example, for a 40% increase in average larval contribution of all four species, our model suggests a 2,128 km^2 of protected space. In comparison, the Channel Islands National Marine Sanctuary is 3,807 km^2, while the Monterey Bay National Marine Sanctuary is 15,783 km^2. If little spatial protection can be realized due to burdensome costs or political pushback, other protections such as fishing regulations at the state or national scale may be more impactful to Gray's Reef. For species such as the red snapper, for which fishing is already prohibited, this may do very little, while for other species, stricter regulations regarding size limits may serve to protect the species that seed Gray's Reef more than any one small marine reserve, even if ecologically connected.

The MGET larval model that we utilize in this project is a comprehensive first step in understanding the larval connectivity between Gray's Reef and the Carolinian Ecoregion as a whole. As management or species priorities change, future iterations of this model will provide a more holistic view of these dynamics. Similarly, as more specific larval behavior and life history data becomes available for the four species that we studied, the robustness of MGET outputs will undoubtedly increase.

As the model is tailored to the specific life history of a species and temporal oceanographic data, it does not incorporate any of the crucial elements of human impact in the region. Further research into the socioeconomic factors that influence the designation of protected areas in a region must be conducted as outlined in the research prioritization.

As this assessment has proved successful in increasing the knowledge of larval connectivity to and around GRNMS, we see an exciting opportunity to expand the use of this type of assessment to aid other National Marine Sanctuaries. Modeling as performed in this project could help other sanctuaries to map connectivity in their region to identify areas that "seed" their sanctuaries with larvae, and therefore may benefit from conservation. This can also inform the creation of MPA networks that incorporate or benefit marine sanctuaries.

Modeling tools such as MGET are incredibly powerful and cost-effective ways to aid management, yet are rather complicated to use for the non-expert. With outside consultation, MGET can be used to understand species habitat connectivity across a large area, or in a difficult study environment with limited data. To help Sanctuary managers understand the uses of larval connectivity modeling tools like MGET as part of a larger connectivity assessment, we have created recommendations for exploring the potential of using these tools for their management needs.

It is our hope that the robust modeling of our four species of interest in Gray's Reef opens the door for understanding larval connectivity of GRNMS within the Carolinian Ecoregion. This report highlights major trends of connectivity and outlines how this modeling approach can be improved upon at Gray's Reef, within the National Marine Sanctuary system, and beyond. With increasing human pressures and a constantly changing ocean, an increased understanding of connectivity will lay the foundation for informed spatial management to benefit our valued marine ecosystems and the humans who rely on them.

REFERENCES

Allen, G. R. (1985). FAO species catalogue. 6. Snappers of the world. An annotated and illustrated catalogue of *Lutjanid* species known to date. FAO Fisheries Synopsis, 125 (6). 208 pp

Allman, R. J., Lombardi-Carlson, L. A., Fitzhugh, G. R., & Fable, W. A. (2002). Age and growth of red snapper, *Lutjanus campechanus*, in the northwestern Gulf of Mexico by fishing mode and region.

Almany, G. R., Connolly, S. R., Heath, D. D., Hogan, J. D., Jones, G. P., McCook, L. J., ... & Williamson, D. H. (2009). Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs, 28(2), 339-351.

Anadón, J. D., del Mar Mancha-Cisneros, M., Best, B. D., & Gerber, L. R. (2013). Habitat-specific larval dispersal and marine connectivity: implications for spatial conservation planning. Ecosphere, 4(7), 1-15.

Barnett, L. A., & Baskett, M. L. (2015). Marine reserves can enhance ecological resilience. *Ecology letters*, *18*(12), 1301-1310.

Christie, M. R., Tissot, B. N., Albins, M. A., Beets, J. P., Jia, Y., Ortiz, D. M., ... & Hixon, M. A. (2010). Larval connectivity in an effective network of marine protected areas. PloS one, 5(12), e15715.

Coleman, F. C., Koenig, C. C., Huntsman, G. R., Musick, J. A., Eklund, A. M., McGovern, J. C., ... & Grimes, C. B. (2000). Long-lived reef fishes: the grouper-snapper complex. *Fisheries*, *25*(3), 14-21.

Cowen, R. K., & Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual review of marine science*, *1*, 443-466.

Cowen, R. K., Lwiza, K. M., Sponaugle, S., Paris, C. B., & Olson, D. B. (2000). Connectivity of marine populations: open or closed?. *Science*, *287*(5454), 857-859.

Dahl, T. E. (1990). Wetlands losses in the United States 1780s to 1980s. Jamestown, ND: U.S. Department of the Interior, Fish and Wildlife Service/Northern Prairie Wildlife Research.

DeBlieu J., Beck M., Dorfman D., Ertel P. (2005). Conservation in the Carolinian Ecoregion: An Ecoregional Assessment. Arlington, VA, USA: The Nature Conservancy.

Edwards, K. P., Hare, J. A., & Werner, F. E. (2008). Dispersal of black sea bass (*Centropristis striata*) larvae on the southeast US continental shelf: results of a coupled vertical larval behavior–3D circulation model. *Fisheries Oceanography*, *17*(4), 299-315.

Ehler, R., & Leeworthy, V. R. (2002). A socioeconomic overview of Georgia's marine related industries and activities. *National Oceanic and Atmospheric Administration, National Ocean Service, Silver Spring, Maryland*.

Farmer NA, Heyman WD, Karnauskas M, Kobara S, Smart T, Ballenger J, Reichert M, Wyanski D, Tishler MS, Lindeman KC, Lowerre-Barbieri S, Switzer T, Solomon J, McCain K, Marhefka M, Sedberry GR. (2017). Timing and location of reef fish spawning activity in the Atlantic Ocean off the southeastern United States. PLOS ONE (*In Press*).

Gaines, S. D., White, C., Carr, M. H., & Palumbi, S. R. (2010). Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences, 107(43), 18286-18293.

Gilmore, G. R., & Jones, R. S. (1992). Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax.* Jordan and Swain. *Bulletin of Marine Science*, *51*(1), 83-103.

Goñi, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, A., Reñones, O., Criquet, G., ... & Bonhomme, P. (2008). Spillover from six western Mediterranean marine protected areas: evidence from artisanal fisheries. *Marine Ecology Progress Series*, *366*, 159-174.

Haas, C. A. (1995). Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation biology*, *9*(4), 845-854.

Halpern, B. S. (2003). The impact of marine reserves: do reserves work and does reserve size matter?. *Ecological applications*, S117-S137.

Harris, P. J., Wyanski, D. M., White, D. B., & Moore, J. L. (2002). Age, growth, and reproduction of scamp, *Mycteroperca phenax*, in the southwestern North Atlantic, 1979–1997. *Bulletin of Marine Science*, *70*(1), 113-132.

Heemstra, P.C. and J.E. Randall (1993). FAO Species Catalogue. Vol. 16. Groupers of the world (family Serranidae, subfamily Epinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date. Rome: FAO. FAO Fish. Synop. 125(16):382 p.

Hopkinson, C.S., Jr, R.D. Fallon, B.-O. Jansson, and J.P Schubauer (1991). Community Metabolism and Nutrient Cycling at Gray's Reef, a Hard Bottom Habitat in the Georgia Bight. Marine Ecology Progress Series. 73:105-120.

Kendall, M.S., L.J. Bauer and C.F.G. Jeffrey (2007). Characterization of the Benthos, Marine Debris and Bottom Fish at Gray's Reef National Marine Sanctuary. Prepared by National Centers for Coastal Ocean Science (NCCOS) Biogeography Team in cooperation with the National Marine Sanctuary Program. Silver Spring, MD. NOAA Technical Memorandum NOS NCCOS 50. 82 pp.

Keener, P., Johnson, D. G., Stender, B. W., Brothers, E. B., & Beatty, H. R. (1988). Ingress of postlarval gag, *Mycteroperca microlepis* (Pisces: Serranidae), through a South Carolina barrier island inlet. *Bulletin of Marine Science*, *42*(3), 376-396.

Kendall, A.W., Jr. (1972). Description of black sea bass, *Centropristis striata*, (Linnaeus), larvae and their occurrence north of Cape Lookout, North Carolina. Fish. Bull. (U.S.) 70: 1243-1259.

Kendall MS, Bauer LJ, Jeffrey CJG (2008) Influence of benthic features and fishing pressure on size and distribution of three exploited reef fishes from the southeastern United States. Transactions of the American Fisheries Society 137: 1134–1146.

Kininmonth, S., Beger, M., Bode, M., Peterson, E., Adams, V. M., Dorfman, D., ... & Possingham, H. P. (2011). Dispersal connectivity and reserve selection for marine conservation. *Ecological Modelling*, *222*(7), 1272-1282.

Kracker, L., M. Kendall, and G. McFall (2008). Benthic Features as a Determinant for Fish Biomass in Gray's Reef National Marine Sanctuary. Marine Geodesy. 31: 267-280.

Laurance, S. G., & Laurance, W. F. (1999). Tropical wildlife corridors: use of linear rainforest remnants by arboreal mammals. *Biological Conservation*, *91*(2), 231-239.

Lees, A. C., & Peres, C. A. (2008). Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conservation biology*, *22*(2), 439-449.

Leeworthy, V.R. (2012). Knowledge, Attitudes and Perceptions of Management Strategies and Regulations of the Gray's Reef National Marine Sanctuaries by Users and Non Users of the Sanctuary. Marine Sanctuaries Conservation Series NMSP-12-01. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, MD. 48 pp.

Liu, S. (2000) Effects of climate change and sea level on coastal systems. In: Sheppard, C., Global Issues and Processes, III. Pergamon, Amsterdam, Netherlands, 187-196.

Lubchenco, J., Palumbi, S. R., Gaines, S. D., & Andelman, S. (2003). Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological applications*, *13*(1), S3-S7.

Magris, R. A., Treml, E. A., Pressey, R. L., & Weeks, R. (2015). Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. Ecography.

Mahood, R (2010). Snapper-Grouper Amendment 17B. South Atlantic Fisheries Management Council.

Moyle, P. B., and Cech, Jr., J.J. (2004) Fishes: An Introduction to Ichthyology, 5th Ed. Prentice
Hall, Upper Saddle River, NJ, 726 pages.

NOAA (2015) Marine Protected Areas. (2015, November 25). Retrieved from http://oceanservice.noaa.gov/ecosystems/mpa/

McGovern, J. C., Collins, M. R., Pashuk, O., & Meister, H. S. (2002). Temporal and spatial differences in life history parameters of black sea bass in the southeastern United States. *North American Journal of Fisheries Management*, *22*(4), 1151-1163.

McLeod, E., Salm, R., Green, A., & Almany, J. (2009). Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment*, *7*(7), 362-370.

Myers, R. and Worm, B.A. (2003). Rapid worldwide depletion of predatory fish communities. Nature 423:280-283.

NOAA Fisheries (2015) *Status of Stocks 2015: Annual Report to Congress on the Status of US Fisheries*. Rep. April 2016. Print.

Parker Jr., R. O., A. J. Chester and R. S. Nelson (1994). A Video Transect Method for Estimating Reef Fish Abundance, Composition, and Habitat Utilization at Gray's Reef National Marine Sanctuary, Georgia. Fishery Bulletin. 92: 787-799.

Planes, S., Jones, G. P., & Thorrold, S. R. (2009). Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences*, *106*(14), 5693-5697.

Potts, J. C., & Brennan, K. (2001). Trends in catch data and estimated static SPR values for fifteen species of reef fish landed along the southeastern United States. *Methods*, *2*(4).

Roberts JJ, Best BD, Dunn DC, Treml EA, Halpin PN (2010) Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. *Environmental Modelling & Software 25(10): 1197-1207*. doi: 10.1016/j.envsoft.2010.03.029

Robins, C.R., and Ray G.C. (1986). *A Field Guide to Atlantic Coast Fishes of North America.* Houghton Mifflin Co., Boston, 354 pp.

South Atlantic Fisheries Management Council (SAFMC), "Snapper Grouper" Web 17 Mar. 2017.
http://safmc.net/useful-info/snapper-grouper/

SEDAR. (2011) SEDAR 25 – South Atlantic Black Sea Bass Assessment Report. SEDAR, North Charleston SC. 480 pp.

SEDAR. (2016) SEDAR 41 – South Atlantic Red Snapper Assessment Report. SEDAR, North Charleston SC. 660 pp.

Sedberry, G. R., Pashuk, O., Wyanski, D. M., Stephen, J. A., & Weinbach, P. (2006). Spawning locations for Atlantic reef fishes off the southeastern US.

Sedberry, G. R., McGovern J.C, and Barans C.A. (1998). A Comparison of Fish Populations in Gray's Reef National Marine Sanctuary to Similar Habitats off the Southeastern U.S.: Implications for Reef Fish and Sanctuary Management. Proceedings of the 50th Gulf and Caribbean Fisheries Institute. 452-481.

Smith, C.L., (1997). National Audubon Society field guide to tropical marine fishes of the Caribbean, the Gulf of Mexico, Florida, the Bahamas, and Bermuda. Alfred A. Knopf, Inc., New York. 720 p.

Smolarkiewicz, P. K. (1983). A simple positive definite advection scheme with small implicit diffusion. *Monthly weather review*, *111*(3), 479-486.

Smolarkiewicz, P. K., & Margolin, L. G. (1998). MPDATA: A finite-difference solver for geophysical flows. *Journal of Computational Physics*, *140*(2), 459-480.

Smolarkiewicz, P. K. (2006). Multidimensional positive definite advection transport algorithm (MPDATA): an overview. *International Journal of Numerical Methods in Fluids*, *50*, 1123-1144.

South Atlantic Fishery Management Council (SAFMC) (2016). Amendment 36, Actions to Implement Special Management Zones in the South Atlantic.

Steimle, F. W. (1999). *Essential fish habitat source document. Black sea bass, Centropristis striata, life history and habitat characteristics*. DIANE Publishing.

Thorrold, S. R., Zacherl, D. C., & Levin, L. A. (2007). Population connectivity and larval dispersal: using geochemical signatures in calcified structures.

Treml, E. A., Ford, J. R., Black, K. P., & Swearer, S. E. (2015). Identifying the key biophysical drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the sea. Movement ecology, 3(1), 1-16.

Treml, E. A., Halpin, P. N., Urban, D. L., & Pratson, L. F. (2008). Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. Landscape Ecology, 23(1), 19-36.

Vaughan, D. S., Collins, M. R., & Schmidt, D. J. (1995). Population characteristics of the black sea bass *Centropristis striata* from the southeastern US. *Bulletin of Marine Science*, *56*(1), 250-267.

Vellinga, M., and Wood, R.A. (2002). Global climatic impacts of a collapse of the Atlantic thermohaline circulation. Clim. Chang. 54, 251-267.

Walters, C. (2000). Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be?. *Bulletin of marine science*, *66*(3), 745-757.

Wenner, C. A., Roumillat, W. A., & Waltz, C. W. (1986). Contributions to the life history of black sea bass, *Centropristis striata*, off the southeastern United States. *South Carolina State Documents Depository*.

WWF, "Ecoregions," World Wildlife Fund. Web 17 Mar. 2017.
https://www.worldwildlife.org/biomes

APPENDICES

Appendix 1. Full Species Profiles for Modeled Fish

Black Sea Bass

Centropristis striata

Range and Life History

Black sea bass have a range along the Atlantic coast from Canada to Cape Canaveral, Florida, and throughout the Gulf of Mexico (SAFMC). Genetic testing has shown that this entire range is a single genetic stock (McGovern, 2002). Although there are no genetic differences, there are behavioral and ecological differences of the stocks north and south of Cape Hatteras, North Carolina (Wenner, 1986). The black sea bass of the southern population are year-round residents of the continental shelf, but they may move seasonally to deeper waters during cold winter months (Steimle, 1999).

Black sea bass are usually found in rocky bottom or rock jetty habitats in shallow water (Robins and Ray 1986) at depths 2-120 m (Vaughan, 1995). Gray's Reef is an ideal habitat for these fish with studies showing black sea bass occurring at 98% of the surveyed ledges (Kendall, 2007).

Black sea bass spawn on the continental shelf and along shelf-edge reefs from March-May (Wenner et al., 1986). Juvenile settlement first happens in coastal waters, then these juveniles find their way to estuarine nurseries (Kendall, 1972). Estuarine nursery habitats used by black sea bass tend to be shallow, hard bottom areas with structures. These include shellfish, sponges, seagrass, wrecks, artificial reefs, crabs, and cobble grounds, etc. (Steimle, 1999). Although vertical migration plays a part in spawning dispersal, study results show that spawning time and location of adults may be more important than vertical migration in determining dispersal along the shelf (Edwards, 2008).

Black sea bass eggs have been collected mostly in shallow (<50 m) water due to their buoyant nature. However, some eggs have been found much deeper and further offshore (>240 m) in May and October, reflecting not only a large spawning period but also the potential differences in the Gulf Stream throughout the year (Steimle, 1999). This implies that spawning at certain times of year may give black sea bass more or less of an opportunity to settle inshore and subsequently find their way to an estuary.

Status and Current Management

The South Atlantic black sea bass stock is not considered overfished or experiencing overfishing (SEDAR, 2011), however it has experienced overfishing in the past and continues to be a highly valued species in the recreational fishery. The southern Atlantic black sea bass stock is a limited entry fishery managed within the Snapper-Grouper complex under the South Atlantic Fisheries Management Council jurisdiction. Amendments to the Snapper-Grouper Fishery Management Plan for black sea bass prohibit trawls, fish traps, entanglement nets, and longline gear. They also delineate special managed areas for *Oculina*, a known coral habitat of these fish.

Gag Grouper

Mycteroperca microlepsis

Range and Life History

Gag grouper inhabit waters in the Western Atlantic ranging from North Carolina to the Yucatan Peninsula, and also exist throughout the Gulf of Mexico. Gag abundance in the United States is greatest along the northern and eastern Gulf of Mexico, and from Fort Pierce, Florida, north to North Carolina (SAFMC).

There are three primary habitat types that are considered critical for gag to flourish: shallow, near-shore and estuarine nursery sites, preferably with seagrass; broad, continental shelf ecosystems with rocky structure; and shelf-edge rock or coral habitat (SAFMC).

Gag form spawning aggregations on shelf-edge reefs at 70-100 meters of depth, usually near food-rich frontal zones. Gag are most likely estuarine-dependent, and larvae generally enter estuaries after 29-59 days, with a mean pelagic larval duration of 43 days (Keener et al., 1988). Off the coast of the southeastern United States, gag spawn from December through May, with a peak in March and April (McGovern et al., 1998). In the Carolinas specifically, spawning takes place in February. The spawning season has been predicted to last 114 days (SAFMC).

Status and Current Management

As of the latest SAFMC stock assessment, gag is considered to be experiencing "overfishing", but is not considered "over-fished". Gag are vulnerable to overfishing, because they are long-lived, late to mature, change sex, and aggregate to spawn (Coleman et al., 2000). Current management under the SAFMC is governed under the Snapper-Grouper complex and has an Annual Catch Limit (ACL) for both commercial and recreational fisheries (SAFMC). This species is part of the shallow water grouper spawning seasonal closure, which prohibits all commercial and recreational take from January 1 through April 1.

Scamp Grouper

Mycteroperca phenax

Range and Life History

Scamp grouper are found in the Western Atlantic with a range from North Carolina to Key West. They are also found in the Gulf of Mexico, and in parts of the Caribbean (NOAA, 2005). Scamp grouper can sometimes be found on high-relief rocky bottoms, but are most often found on low-profile, live bottom areas in water 75-300 feet deep (SAFMC). Also, scamp is abundant in patches of *Oculina* coral formations from 70 to 100m off the East coast of Florida (Heemstra & Randall, 1993). This species often will move inshore when bottom temperatures fall. Juveniles can be found in shallow and estuarine waters (Heemstra & Randall, 1993).

In the South Atlantic Bight, spawning of scamp occurs February-July with a peak in March to mid-May (Harris et al., 2002). They are thought to spawn in the late afternoon and evening. Scamp aggregate to spawn at specific reef edge sites, 50-100m in depth (Sedberry, 2006). Both spawning locations and time of spawning events overlap with gag grouper (Gilmore and Jones, 1992).

Status and Current Management

The scamp grouper is no longer considered overfished (SAFMC). It is currently managed within the Snapper-Grouper complex under the South Atlantic Fisheries Management Council jurisdiction. There is an Annual Shallow-water Grouper Spawning Season Closure January 1 through April 30. The population is managed under a limited entry fishery with ACL (SAFMC).

Northern Red Snapper

Lutjanus campechanus

Range and Life History

Along the eastern coast of the United States, red snapper are found from the Gulf of Mexico northward to Massachusetts, though they are rare north of the Carolinas (Smith, C.L., 1997). Adults of the species are found in rocky bottom habitats at depths between 10 and 190 meters, but most commonly between 30 and 130 meters. Juveniles inhabit shallower waters, often over sandy or muddy bottoms. (Allen, G.R., 1985).

Females are open water or substratum egg scatterers (also known as batch spawners). In the Gulf of Mexico, the fish primarily spawn away from reefs, at depths of 18-37 meters, over firm, sandy bottoms. Spawning season occurs in August and September off the southwestern coast of Florida, extending into late October off of South Carolina (Allen, G.R., 1985). Spawning season for female red snapper off the southeastern United States extends from May to October, peaking in July through September (White and Palmer, 2004).

Status and Current Management

The last fishing (recreational and commercial) for red snapper in the SAFMC region was in 2014. Due to a serious decline in red snapper catches, the season was completely closed in 2015 and remains so in 2016 (Southeast Fisheries Science Center, 2015).

Appendix 2. Socioeconomic Considerations

Recreational

Outside of Gray's Reef, the U.S. Fish and Wildlife Service, Survey of Fishing, Hunting and Wildlife Associated Activity (USFWS-SFHW) estimated that, in 1996, a total of $51.8 million was spent on saltwater fishing in Georgia, with an average of $349 spent per angler. This total included food and lodging, transportation, equipment, and other trip costs. A study done by American Sportfishing Association in 1996 estimated Georgia saltwater anglers to make up only 5.1% of Georgia fishermen with expenditures at $57.1 million and 1,576 related jobs accounting for wages and salaries of $32.0 million (Leeworthy, 2002). Charter boat fishing also contributes to the regional economy — the total market value of Georgia charter operations was estimated at $857,500 in 2002 (Leeworthy, 2002).

Commercial

Commercial fishing is not seen at Gray's Reef due to certain gear restrictions, however it is present throughout the Carolinian Ecoregion. Commercial fishing shows a larger importance in South Carolina and Florida than off the coast of Georgia where Gray's Reef lies. Commercial boats typically work north and south along the shelf break offshore of Gray's Reef and normally land most of their catches in Florida and South Carolina. The biggest fishery in Georgia is the mostly nearshore (0-3 miles) shrimp fishery, making up about 80 percent of the value of the total catch. The majority of catch in the finfish fishery is found in the 3 – 200 miles offshore in federal waters. In 1999, the Snapper-Grouper complex fishery has provided the highest value of fin-fish landings in Georgia (66 %). At this time, Grouper species landings were valued at $298,000 and Snapper species landings valued at $237,000. The National Marine Fisheries Service (NMFS) ranked Darien-Bellville, GA, 64th in terms of value ($9.2 million) in comparison to other major U.S. ports showing this area to be a much smaller fishery in comparison with other US coastal regions (Leeworthy, 2002).

Commercial fishing in this area saw large increases during the 1970s, with a slow-down in the 1980s and even greater drops in the 1990s. Preliminary total ex-vessel value of landings in the state of Georgia was $21.13 million in 1999. NMFS estimated that 350 commercial fishing vessels operated out of Georgia ports in 1998, while the South Carolina estimate was 569 and Florida was 2,384. It can be assumed that the majority of vessels operating out of South Carolina and Florida do not primarily fish off the coast of Georgia (Leeworthy, 2002).

NMFS also reported that in 1998, 8 processing plants and 66 wholesalers operated in Georgia employing 1,259 and 586 people respectively. This shows a relatively small fishing industry when compared to Florida, which had 108 processing plants employing 3,142 people and 374 wholesalers employing 2,984 people. It should be noted that the Georgia figures for processing facilities include two very large processors (e.g., King & Prince Seafood, Rich-SeaPak). These processors rely heavily on imports from elsewhere and not on the local fishery (Ehler and Leeworthy, 2002).

Appendix 3. Model Assumptions

General model Assumptions and Limitations

MGET makes many assumptions while running simulations, specifically with respect to larval behavior and suitable habitat usage. General model assumptions are as follows: All rasters were re-projected into the "NAD_1983_StatePlane_Georgia_East_FIPS_1001" coordinate system. We chose to represent connectivity by the percent contribution of larvae transmitted from each contributing reef to Gray's Reef (estuaries for gag grouper), rather than probability. Within each model tool multiple assumptions are made. Although this model makes many assumptions, it is the best available tool to illustrate ecological connectivity through larval dispersal. The connectivity network of larvae supplying reefs is important to understanding how increasing protection of connected areas can affect the overall fish stock in the region.

Below are the specific assumptions made in each model tool:

1. Create Larval Dispersal Simulation from ArcGIS Rasters:

It is required that each of the three input rasters have the same cell size, spatial extent, and number of rows and columns. The cell size chosen was an 8 km cell size due its close match to the resolution of the currents data used and because a higher resolution would drastically increase the run time of the model. The water mask and patch cover rasters must have the same coordinate system, dimensions, and cell size as the patch ID raster. Large rasters can cause the model to fail or greatly increase run time. Ideally dimensions should be less than 500x500 cells. The water mask raster serves as a boundary; larvae that are moved in the direction of land are "blocked" and stay in the adjacent water cell. Larvae that are moved beyond the extent of the raster from water cells on the edge are lost from the simulation. The patch ID raster has a unique integer ID value that specifies the location of suitable habitat patches from which larvae will be released from and settle on. In this analysis suitable habitat is defined as spawning habitat. Data included in the patch cover raster are responsible for the assumption that reef cells are allocated quantities of larvae they can both release, and accept from, based on the amount of suitable habitat in each cell. For example, a cell with a suitable spawning condition cover of one would be able to release and/or receive one unit of larvae. The simulation assumes that both suitable habitat and larvae are distributed uniformly across each cell at all times. The cell size of 8 km was chosen for this analysis because the authors of the tools recommend the simulation be conducted at a coarser resolution similar to the ocean currents data, and because although the tools provided to load currents into the simulation will automatically interpolate the currents data to the resolution of the habitat patches via bilinear or cubic spline interpolation, there is no assurance that this interpolation is realistic. Conducting the analysis at a significantly finer resolution than the ocean currents data will introduce an unknown degree of uncertainty into the results. Another limitation of this tool is that when a cell is used for both spawning and settlement, the same proportion of it is used for both roles.

2. Load HYCOM GLBa0.08 Currents into Larval Dispersal Simulation:

The currents data chosen for this analysis is the HYCOME GLBa0.08 currents data because they fit the spatial extent for the region of interest. This data has a time step of one day and depth range of 0 – 5500m. When the ocean currents data are loaded, they will automatically be projected and clipped as needed into the same coordinate system, extent, and cell size as the patch ID raster. The hydrodynamic algorithm performs calculations using Cartesian coordinates with meters as the unit. When MGET loads ocean currents data into the simulation, the original data come as vector components-pairs of u and v images giving current speed in the north/south and E/W directions. When MGET projects them, it does not know how to adjust the results to account for the fact that north/south/east/west may no longer be up/down/right/left on portions of our map. The resampling algorithm selected is a cubic convolution resampling technique or also known as bicubic interpolation. This method was chosen because, although slower, it produces more accurate values. The method chosen for estimating missing currents values is Del2a. This method is used to guess ocean current values for cells marked as water by the water mask but for which no estimate is available in the currents data. Del2a uses laplacin interpolation and linear extrapolation to estimate missing currents values. This assumption is important because if cells are left as NO Data, then larvae cannot leave the cells by advection, only by diffusion. Lastly, this tool includes a depth parameter that assumes that larvae remain at the same depth for the entire simulation and does not allow for vertical migration or other larval behaviors.

3. Run Larval Dispersal Simulation (2012 Algorithm):

The third tool includes parameters that specify the start date of the simulation which represents peak spawning time of species, the Pelagic Larvae Duration (PLD) which represents the amount of time larvae spend in the water column before they are competent to settle out, and which patches of suitable area are allowed to release and accept larvae. The time step parameter defines the period at which larvae density is recalculated using a numerical advection-diffusion model. Smaller time steps increase the stability and accuracy of the model but increase the runtime and memory requirements. Our model set the time step to 0.5 so that the density is recalculated once every twelve hours or twice every twenty-four hours. The simulation summarization period parameter determines the temporal frequency of summary visualizations, such as a time series of raster that show the density of larvae as the simulation progresses. Our analysis uses a simulation summarization period of 24 hours. The settlement parameter is set by using a competency gamma *a*b* competent to settle after 20 days and drift for 30 more days to settle out. The competency curve is configured by the competency gamma (*a*) and competency gamma (*b*) parameters. The settlement parameter specifies the rate at which competent larvae will settle when suspended over a patch and is expressed as the proportion of larvae that will settle per day. The settle parameter for our analysis was kept at the default value of 0.8, which indicates 80% of the larvae suspended over a patch of suitable habitat for a day will settle. The habitat patches set to disperse larvae are all patches in our patch id and patch cover rasters. The patches set to accept larvae are those we are calling GRNMS (four patches). The value of 50 was used as the horizontal diffusivity coefficient, in meters squared per second, based on what was used in other studies from our literature review (Schill, 2015). When larvae drift over a patch, they immediately settle there and are removed from the simulation, making them unavailable to downstream patches.

4. Visualize Larval Dispersal Simulation Results (2012 Algorithm):

Since the mortality rates for our species of interest are not well known, we ran the simulation assuming a mortality rate of zero. We also conducted a sensitivity analysis to test the model's sensitivity to the mortality rate by using mortality rates other than 0. Incompetent larvae are excluded from Density Rasters. The connection line feature class is created if a patch experienced sufficient recruitment. The minimum dispersal threshold was set to 0.00001 for recruitment. Larvae released by a patch and settled on the same patch form a circular line instead of the straight line that forms when larvae are recruited from other patches.

When determining the species-specific parameters, the competency of larvae was calculated for each species using a gamma cumulative distribution function. The Gamma competency "*a*" and "*b*" parameters control the shape of the cumulative distribution function. The units for this computed function is in days. At *a*b* days, approximately half the larvae will be competent. The Gamma competency "b" parameter is the scale parameter of the gamma cumulative distribution function which controls the rate at which the larvae become competent, centered on this *a*b* value, with smaller values of *b* producing a faster rate. Gamma competency “a” is the shape parameter of the gamma cumulative distribution function used to represent the onset of larval settlement competency. Competency in our analysis was derived with the *a* parameter = 2000 and *b* parameter = 0.01. A small *b* parameter speeds up the rate at which all larvae become competent. We also did a sensitivity analysis regarding competency by using a relatively smaller b, so that the rate at which the larvae become competent is slower.

Appendix 4. Data Used

Marine Geospatial Ecology Tools (MGET)	Roberts JJ, Best BD, Dunn DC, Treml EA, Halpin PN (2010) Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. Environmental Modelling & Software 25: 1197-1207. doi: 10.1016/j.envsoft.2010.03.029
Black Sea Bass, Red Snapper, Scamp, and Gag, "probability of female in spawning condition" Rasters	Farmer NA, Heyman WD, Karnauskas M, Kobara S, Smart T, Ballenger J, Reichert M, Wyanski D, Tishler MS, Lindeman KC, Lowerre-Barbieri S, Switzer T, Solomon J, McCain K, Marhefka M, Sedberry GR. 2017. Timing and location of reef fish spawning activity in the Atlantic Ocean off the southeastern United States. PLOS ONE (In Press).
States shapefile	DeBlieu, J., M. Beck, D. Dorfman, and P. Ertel. (2005) Conservation in the Carolinian Ecoregion: An Ecoregional Assessment. The Nature Conservancy, Arlington, VA
Marine Ecoregions of The World (MEOW)	World Wildlife Fund: Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas Credits: Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J (2007) Marine Ecoregions of the World: a bioregionalization of coast and shelf areas. BioScience 57: 573-583.
Bathymetry	Jarvis A., H.I. Reuter, A. Nelson, E. Guevara, 2008, Hole-filled seamless SRTM data V4, International Centre for Tropical Agriculture (CIAT), available from http://srtm.csi.cgiar.org.
Grays Reef National Marine Sanctuary Boundary	*Originator*: NOAA / National Marine Sanctuaries Program *Publication Date*: 200412 *Title:* Grays Reef National Marine Sanctuary Boundary (polygon) Edition: 200412 *Geospatial Data_Presentation Form:* vector digital data *Publication Information:* *Publication Place:* Silver Spring, MD *Publisher:* NOAA / National Marine Sanctuary Program

Appendix 5. Maps and Results

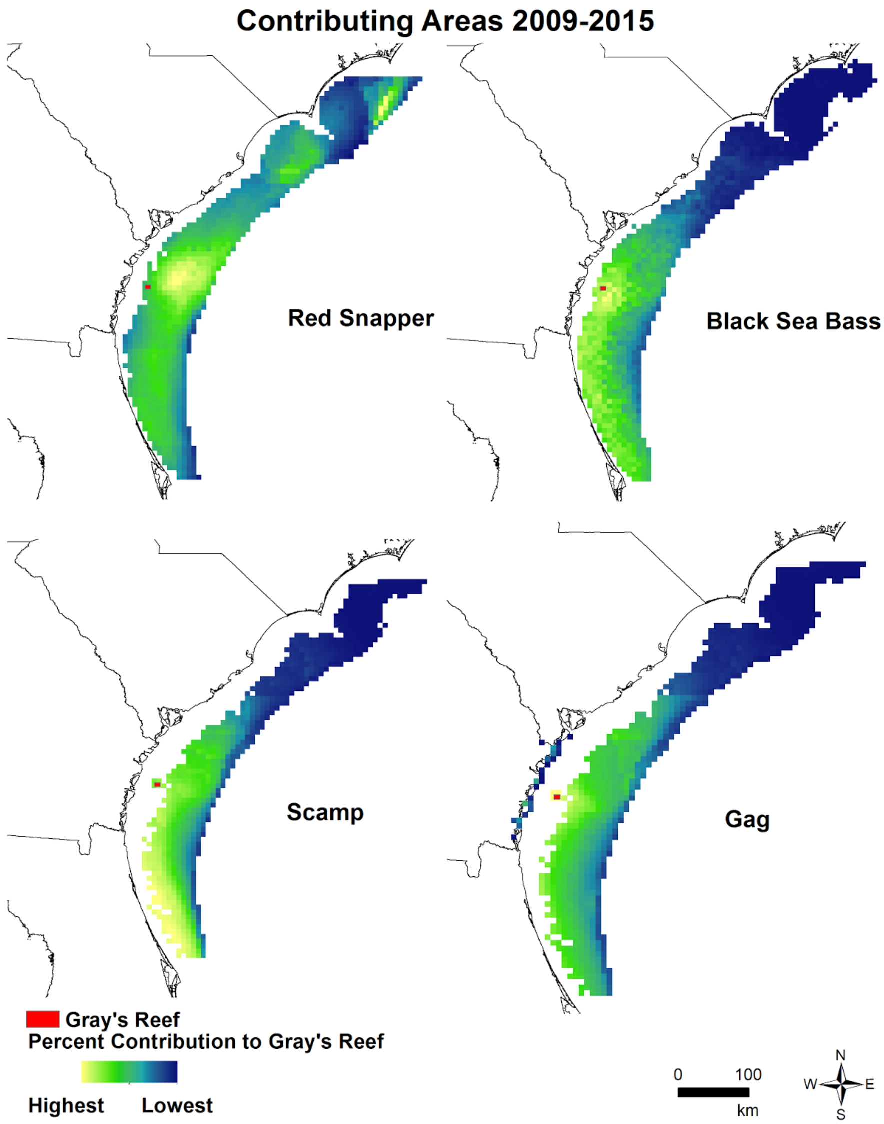

*Figure 7. **Comparison of Red Snapper, Black Sea Bass, Scamp, and Gag Percent Contribution**. Variation among species as a result of species specific parameters used in each MGET model. The lightest yellow cells represent the strongest connectivity and highest percent contribution to GRNMS. The darkest blue cells represent the weakest connectivity and lowest percent contribution to GRNMS.*

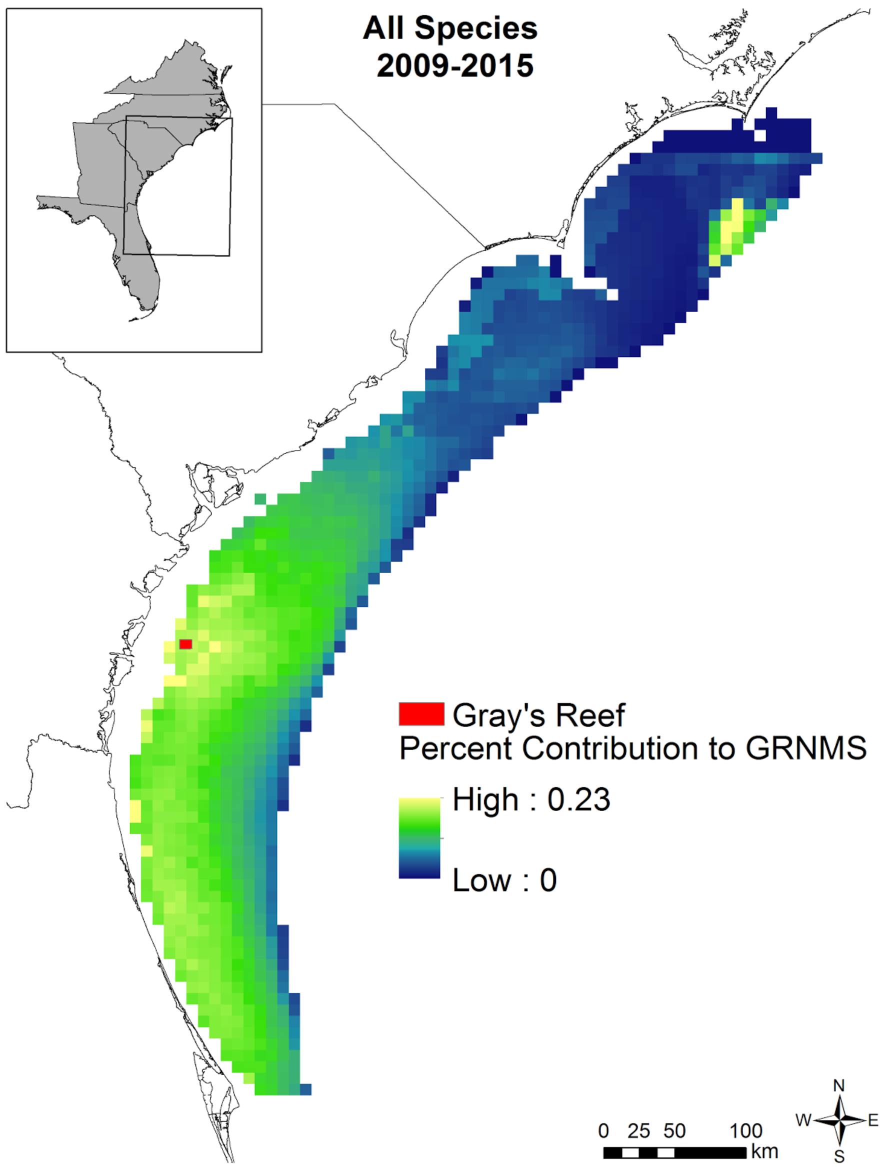

Figure 8. ***Aggregated Species Percent Contribution Map.*** *Aggregated mean quantity of larvae for black sea bass, red snapper, scamp, and gag for each of their iterations over their peak spawning season from 2009 – 2015.*

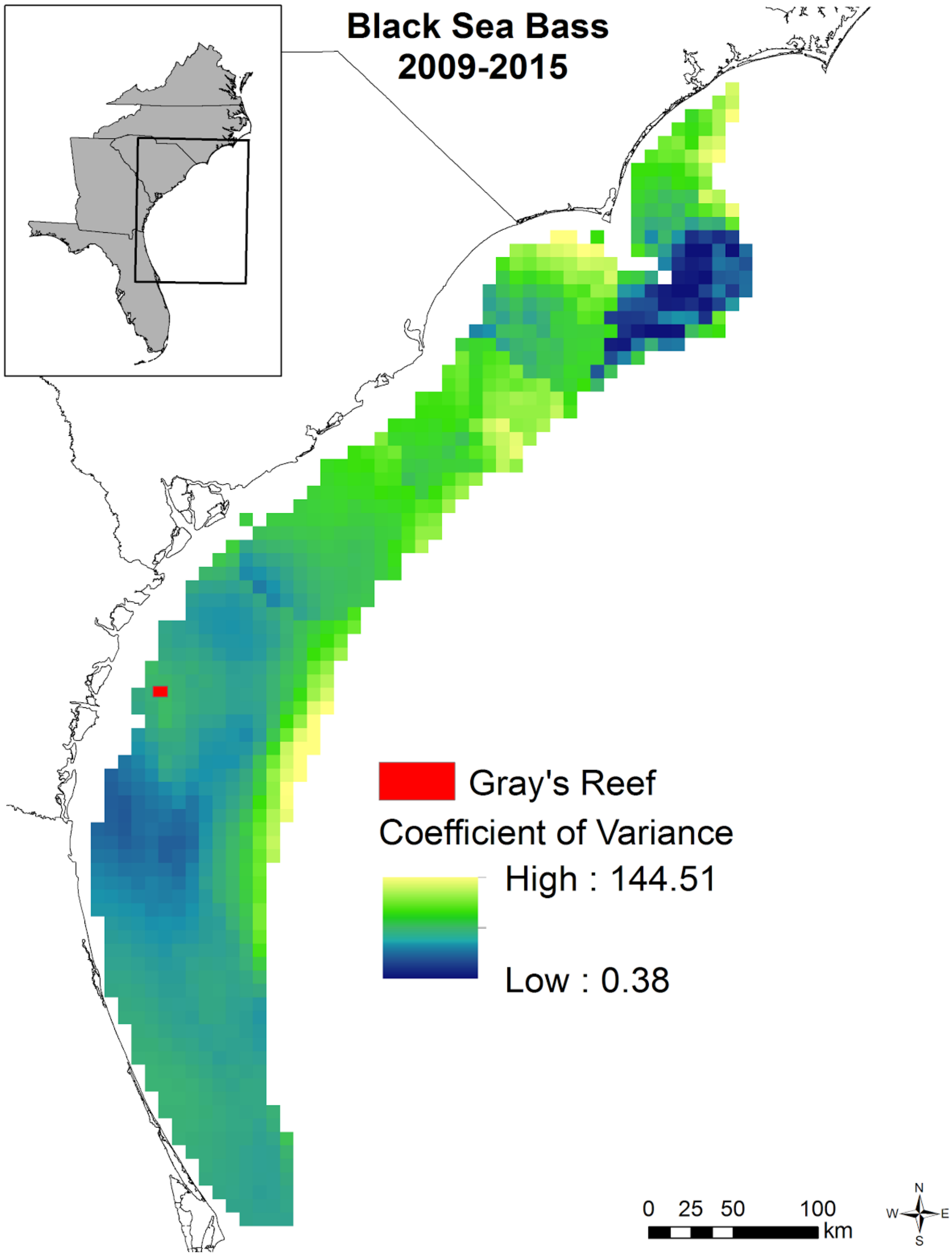

Figure 9. ***Black Sea Bass Coefficient of Variance.*** *Variance in black sea bass percent contribution for peak spawning in 2009 – 2015. Yellow cells represent areas of high variance in percent contribution and dark blue cells represent areas of low variance in percent contribution among black sea bass iterations.*

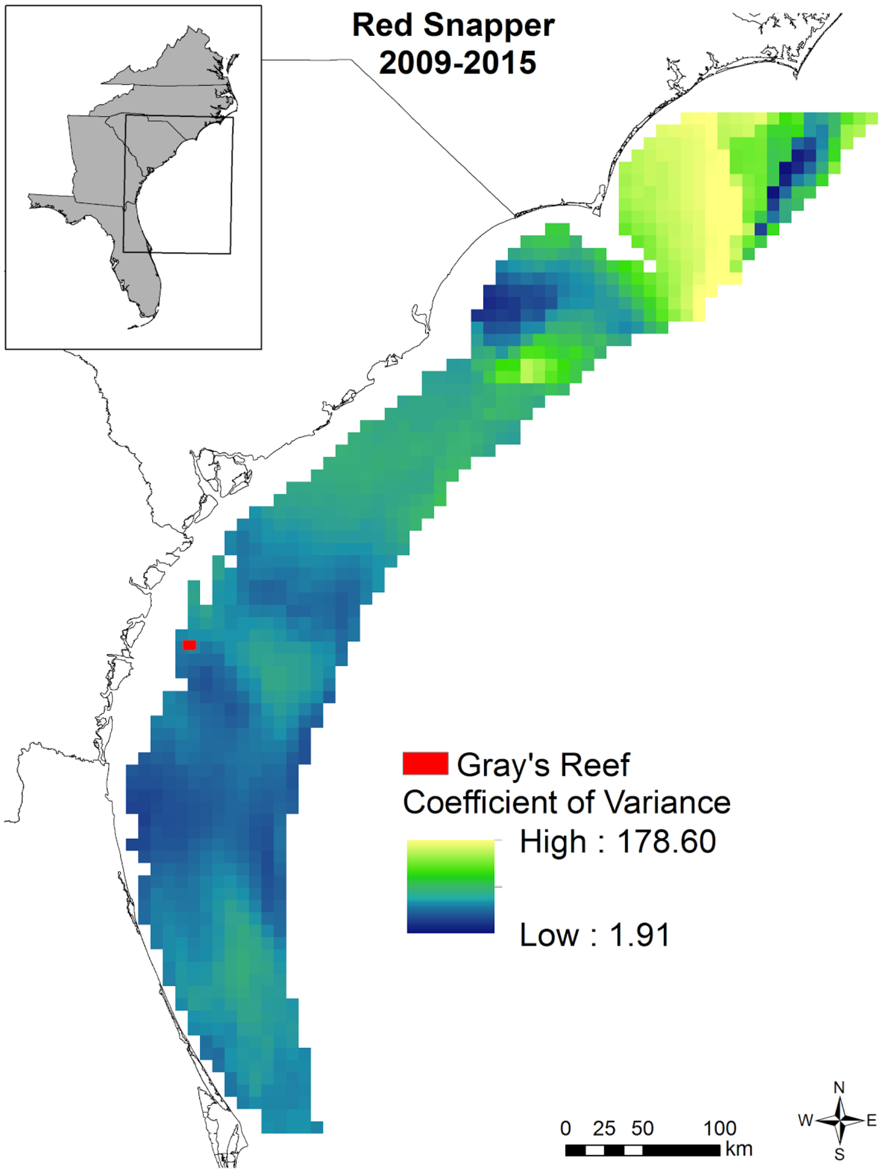

Figure 10. ***Red Snapper Coefficient of Variance.*** *Variance in red snapper percent contribution for peak spawning in 2009 – 2015. Yellow cells represent areas of high variance in percent contribution and dark blue cells represent areas of low variance in percent contribution among black sea bass iterations.*

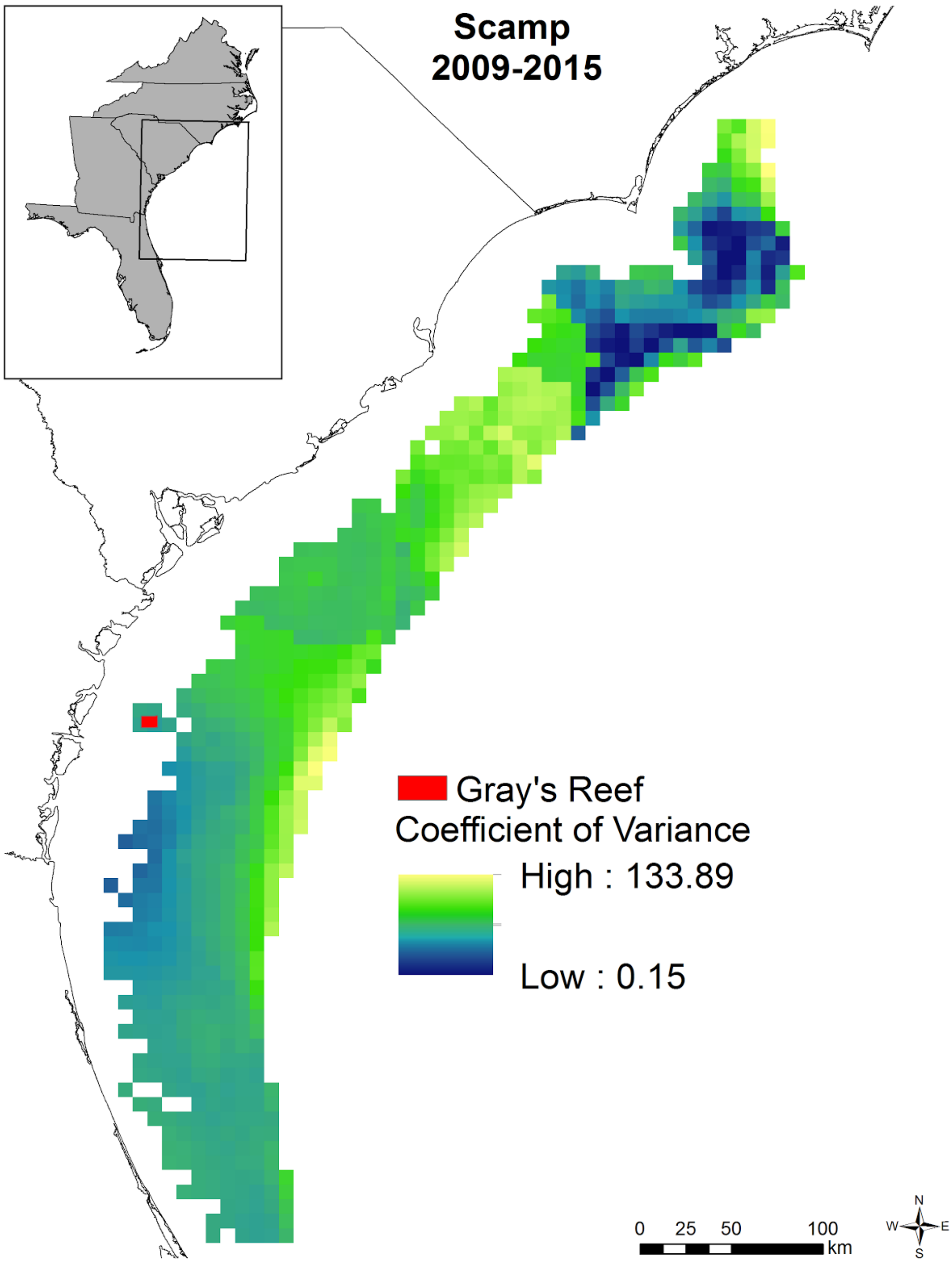

Figure 11. ***Scamp Coefficient of Variance.*** *Variance in scamp percent contribution for peak spawning in 2009 – 2015. Yellow cells represent areas of high variance in percent contribution and dark blue cells represent areas of low variance in percent contribution among black sea bass iterations.*

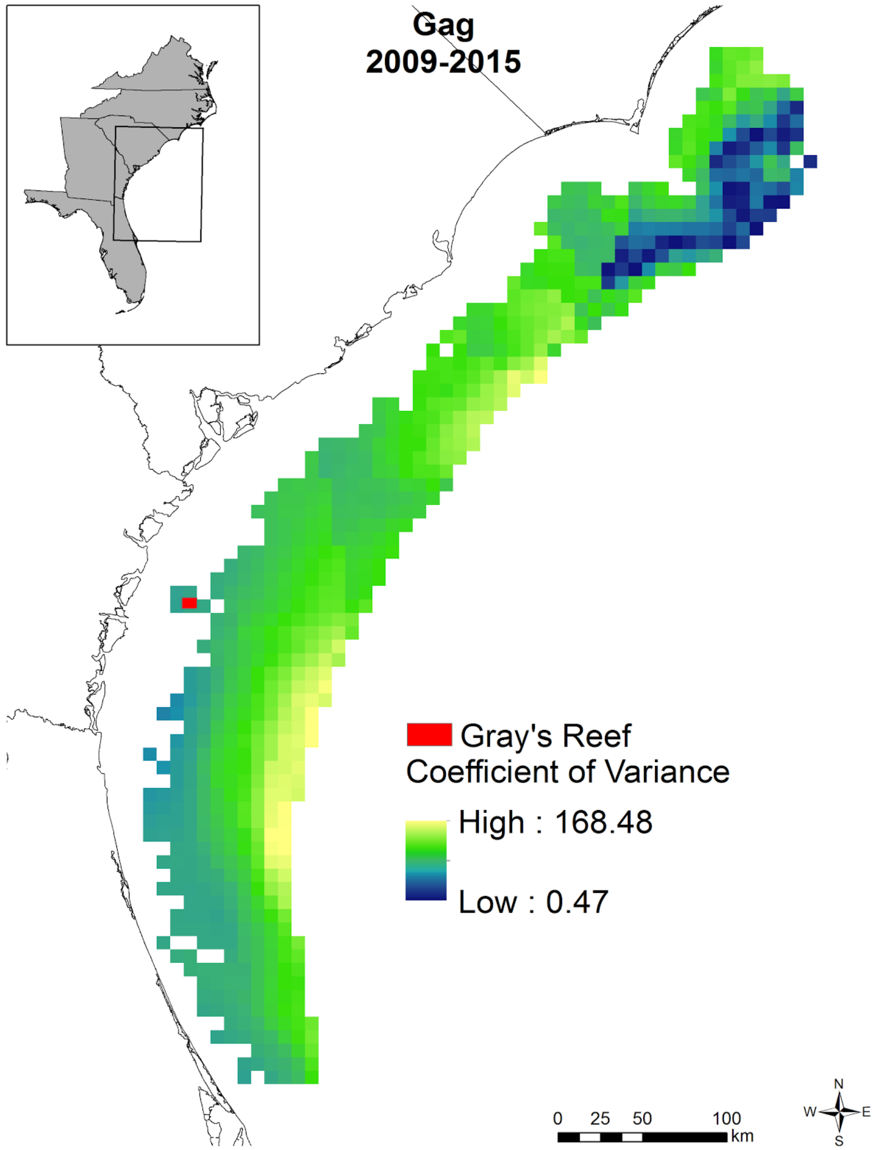

Figure 12. ***Gag Coefficient of Variance.*** *Variance in gag percent contribution for peak spawning in 2009 – 2015. Yellow cells represent areas of high variance in percent contribution and dark blue cells represent areas of low variance in percent contribution among black sea bass iterations.*

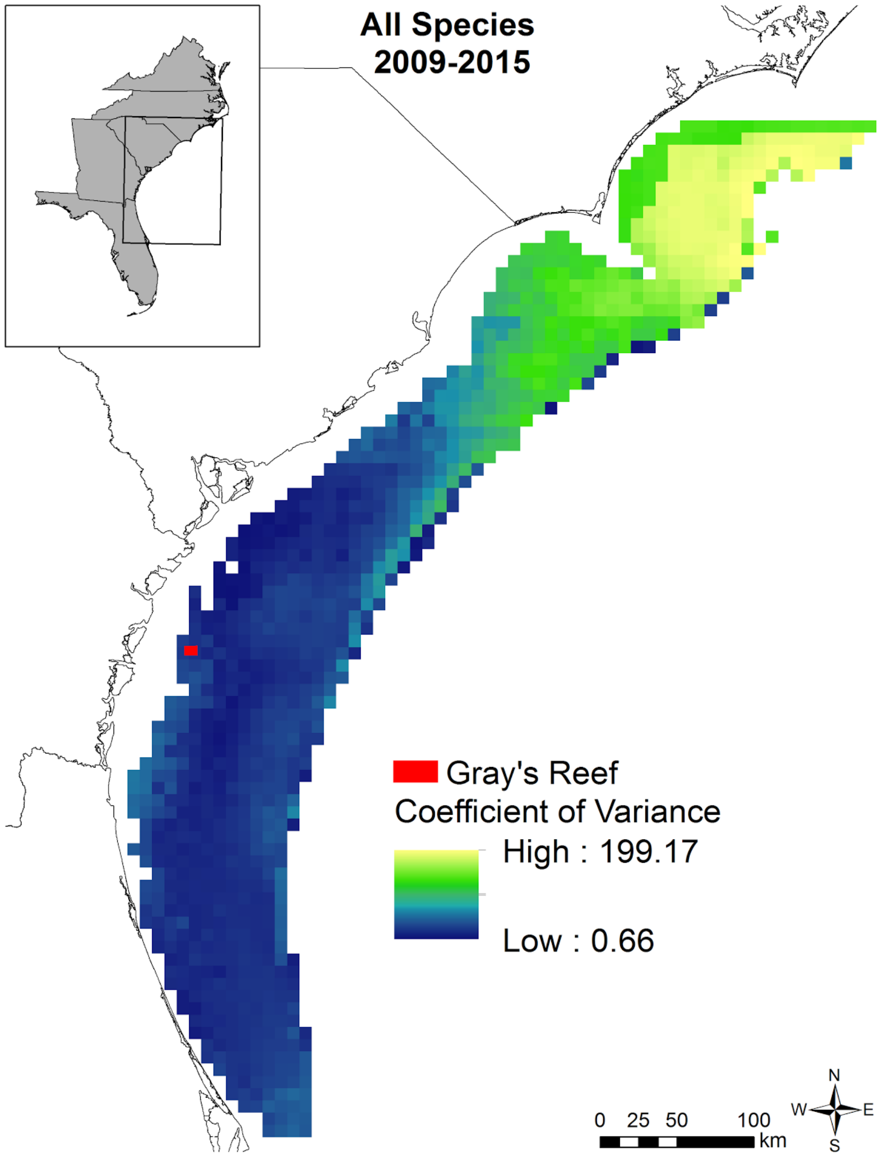

Figure 13. ***Species Aggregated Coefficient of Variance.*** *Variance in species aggregated percent contribution for peak spawning in 2009 – 2015. Yellow cells represent areas of high variance in percent contribution and dark blue cells represent areas of low variance in percent contribution among black sea bass iterations.*

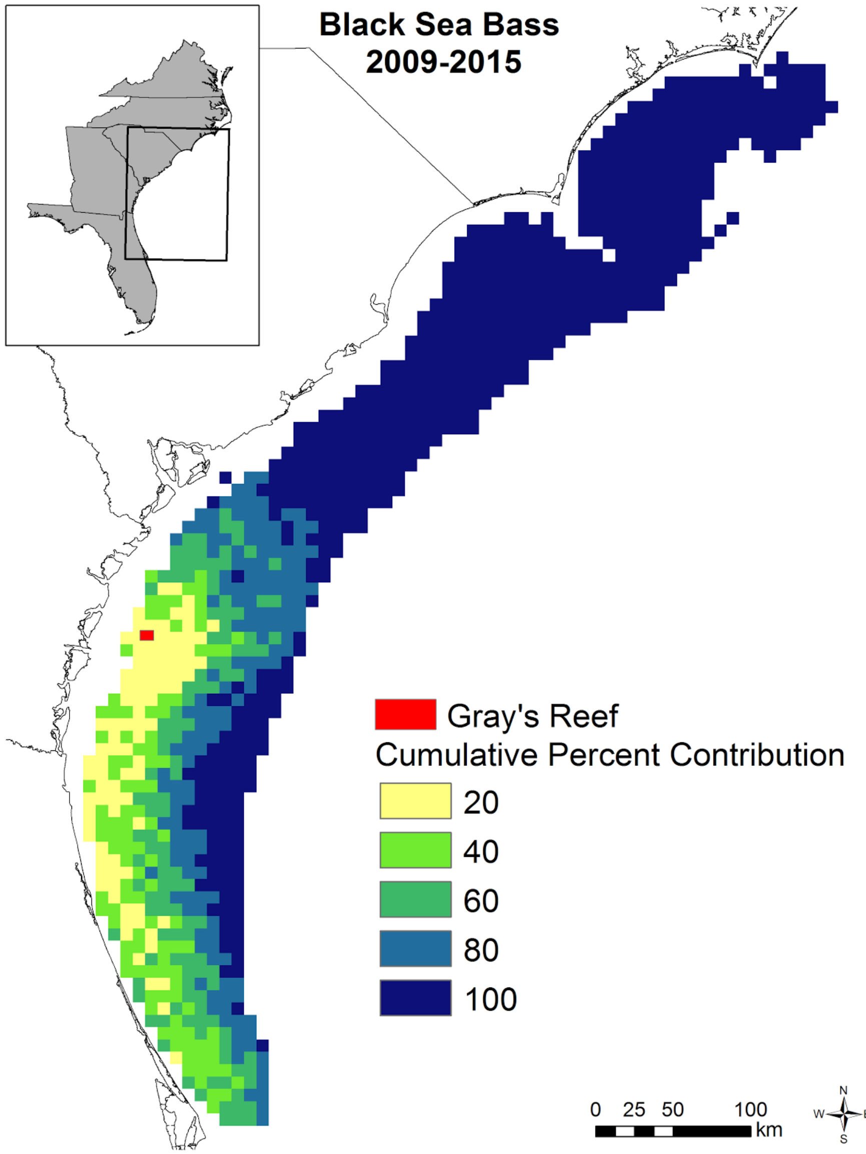

Figure 14. ***Black Sea Bass Contour Map.*** *Cumulative percent contribution of larvae summed in 20 percent quantiles.*

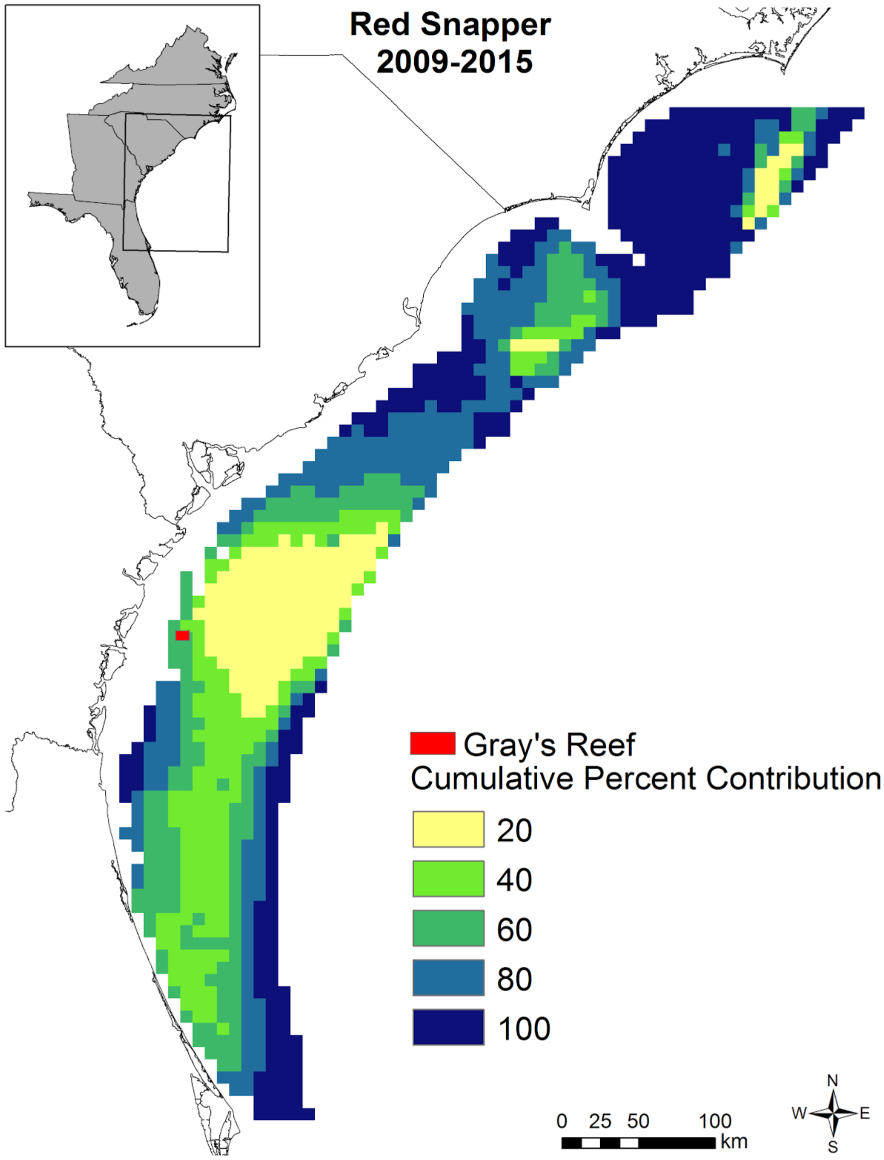

Figure 15. ***Red Snapper Contour Map.*** *Cumulative percent contribution of larvae summed in 20 percent quantiles.*

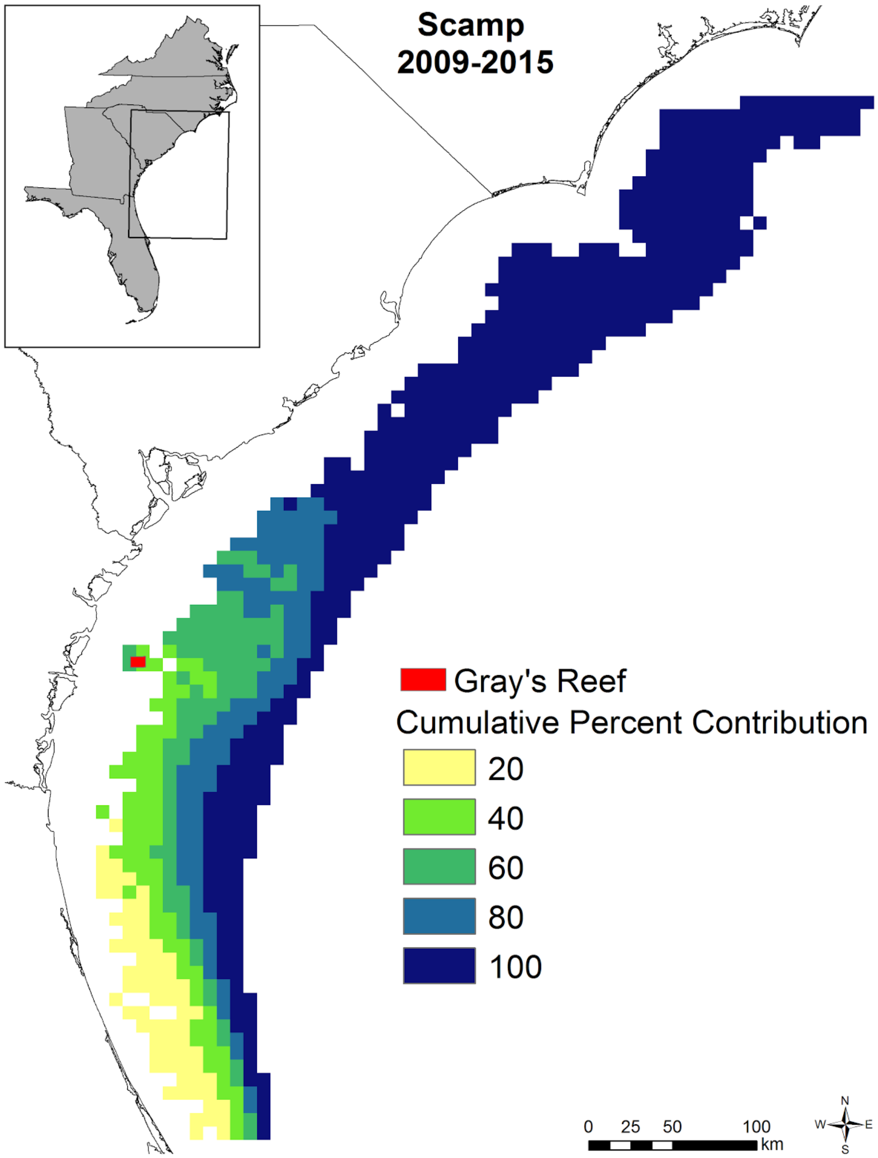

*Figure 16. **Scamp Contour Map**. Cumulative percent contribution of larvae summed in 20 percent quantiles.*

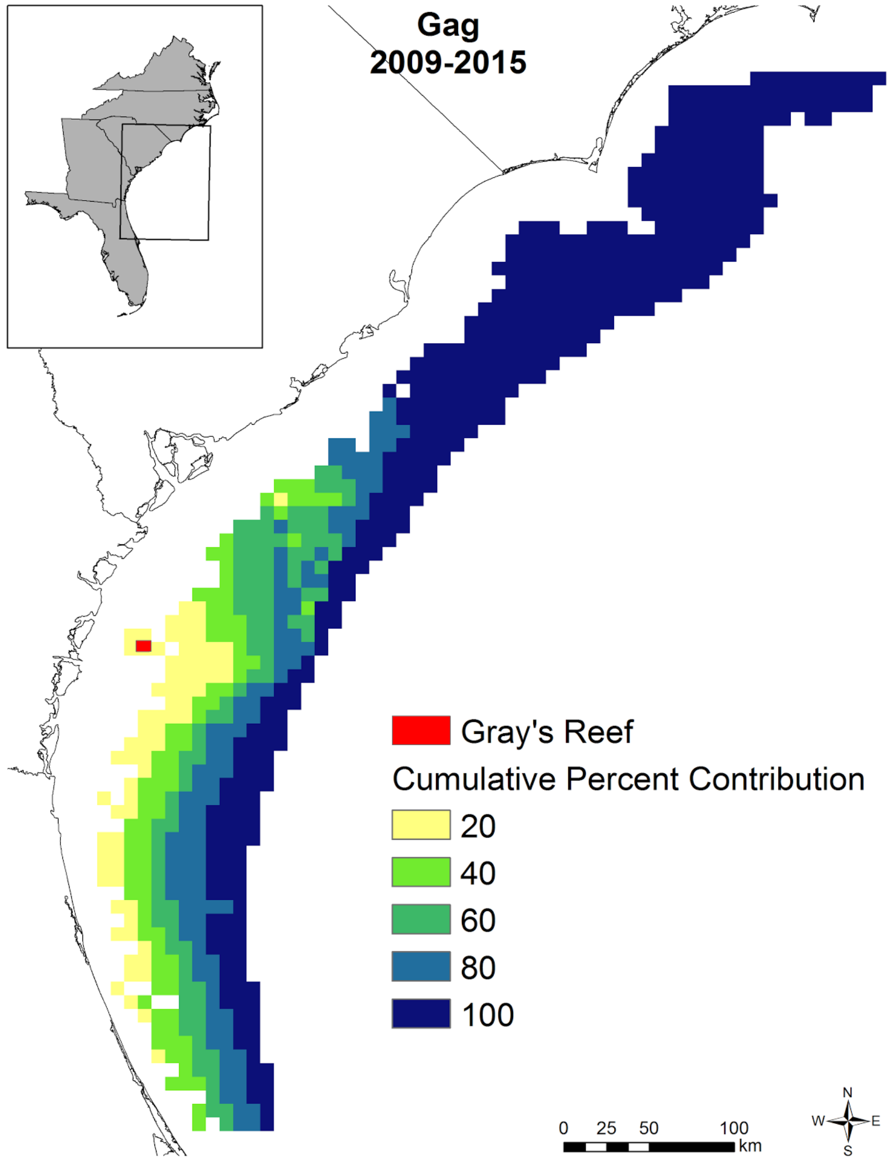

Figure 17. ***Gag Contour Map.*** *Cumulative percent contribution of larvae summed in 20 percent quantiles.*

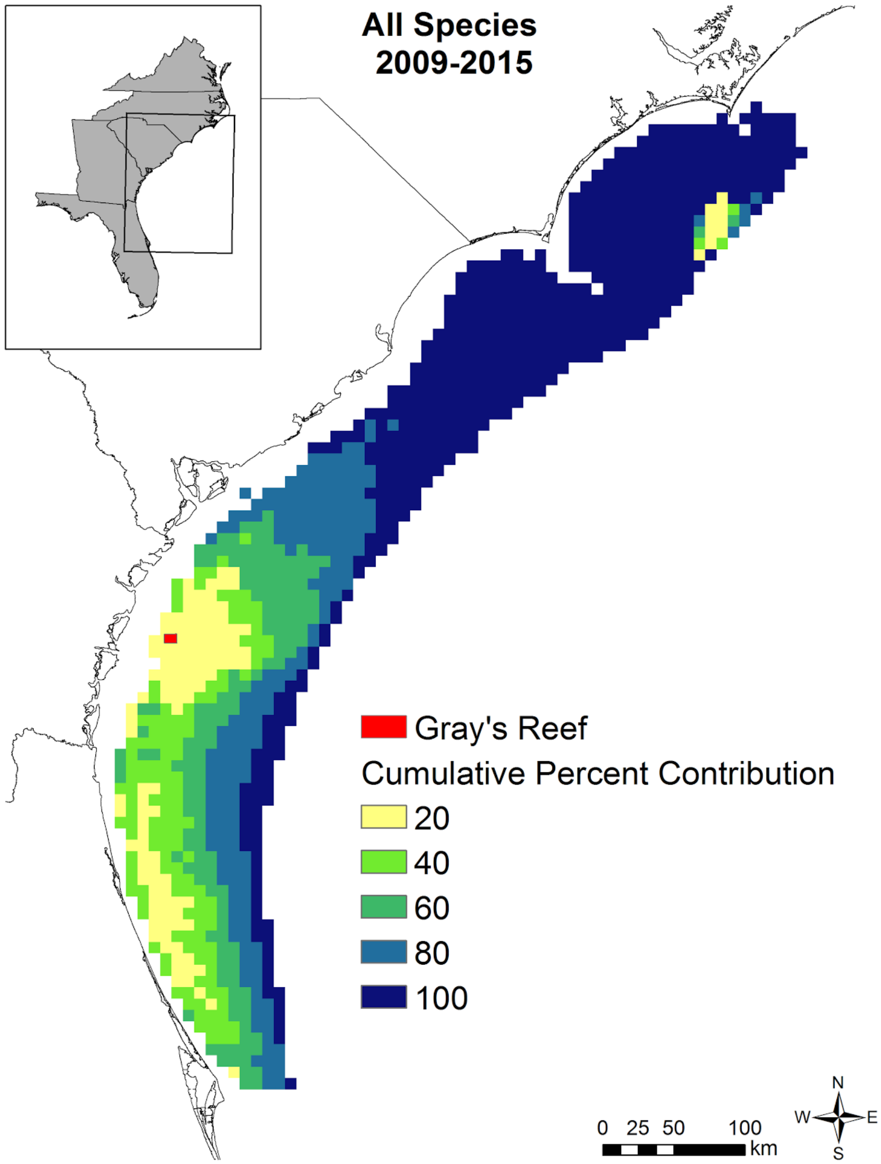

Figure 18. ***Species Aggregated Contour Map.*** *Cumulative percent contribution of larvae summed in 20 percent quantiles.*

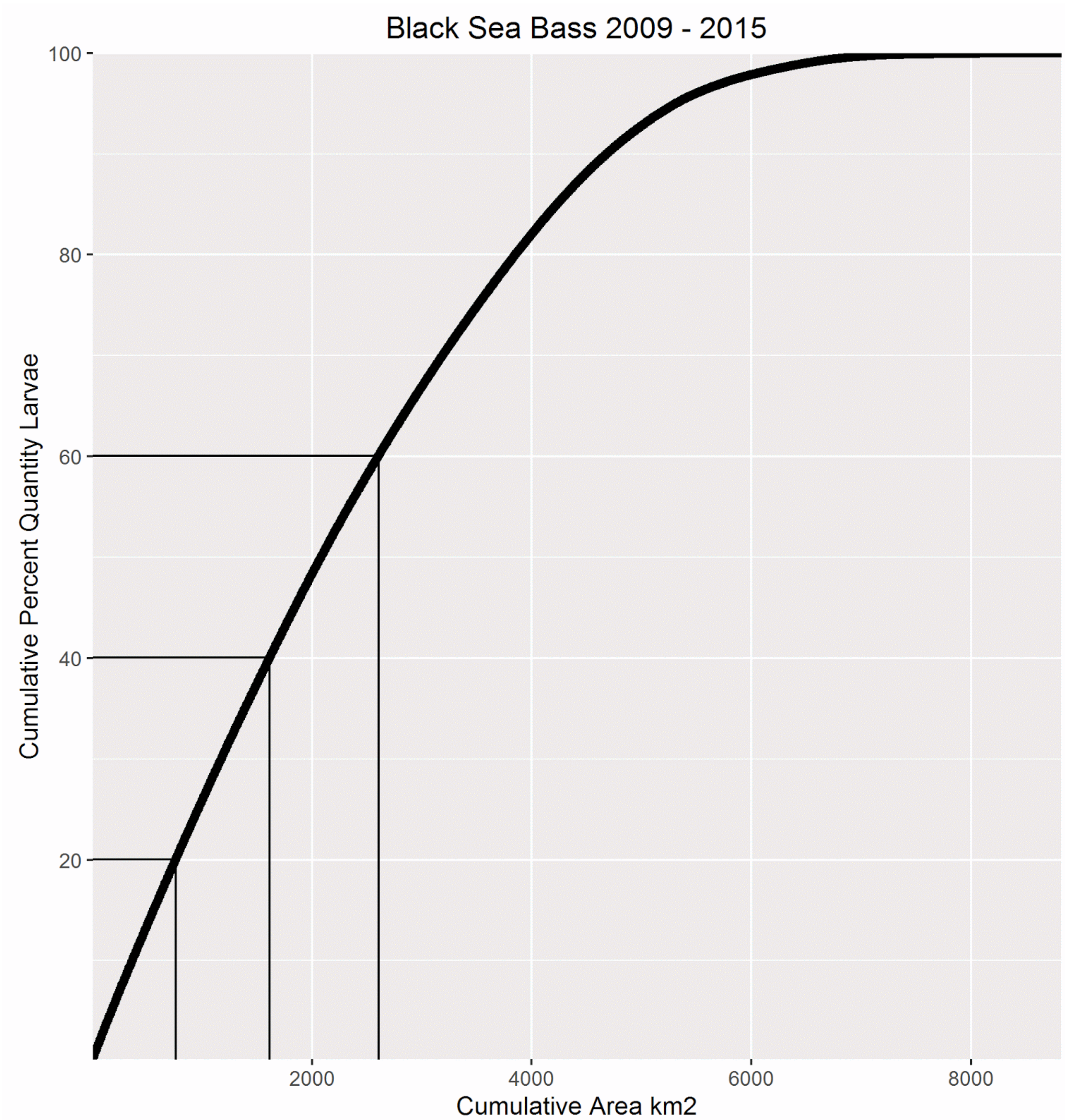

Figure 19. ***Black Sea Bass Area Graph****. Cumulative area required to most efficiently attain a target cumulative percent quantity of larvae. In the case of black sea bass, 20% larval contribution requires 760 km2, 40% larval contribution requires 1616 km2, and 60% larval contribution requires 2608 km2.*

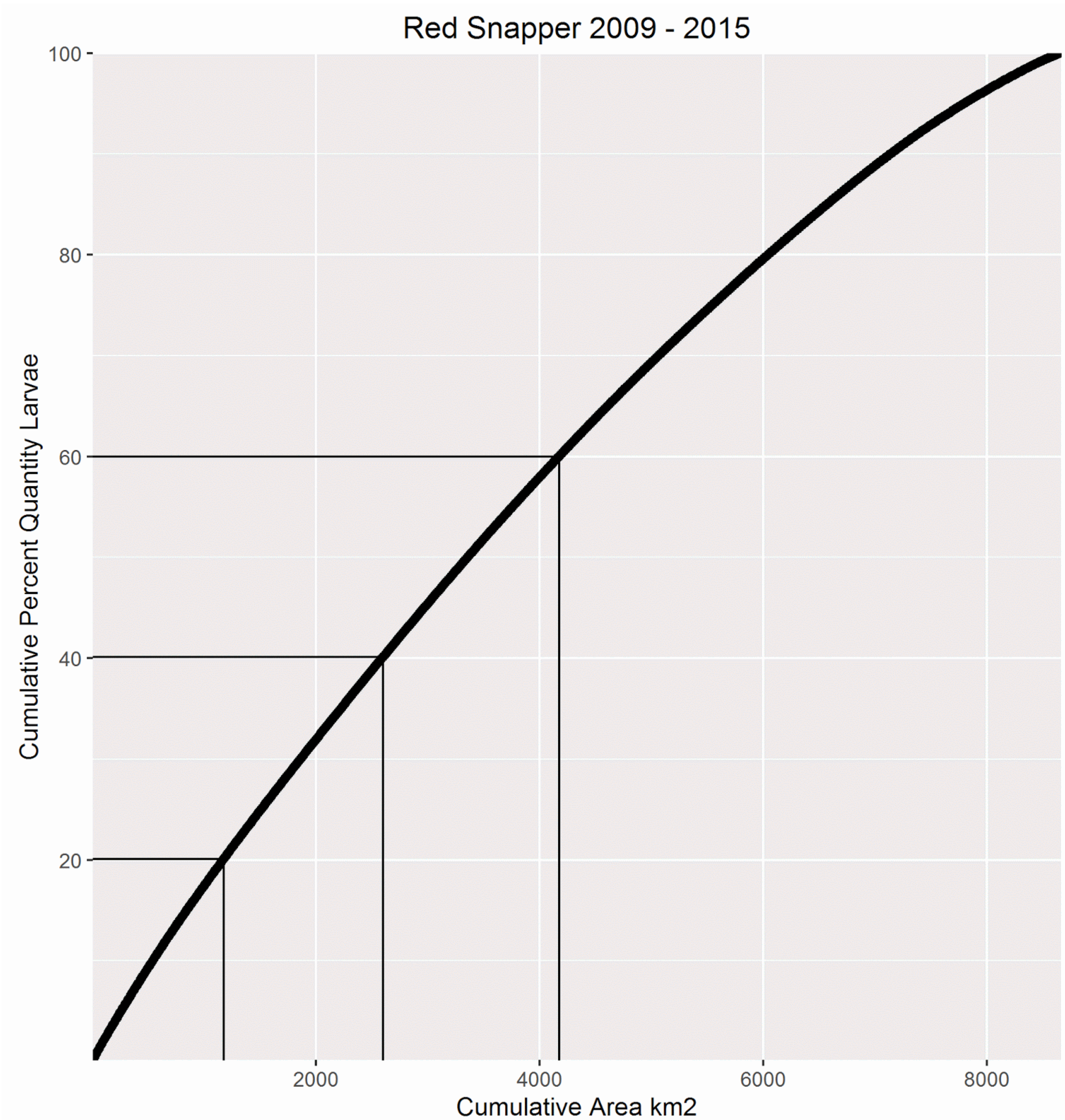

Figure 20. ***Red Snapper Area Graph****. Cumulative area required to most efficiently attain a target cumulative percent quantity of larvae. In the case of red snapper, 20% larval contribution requires 1176 km2, 40% larval contribution requires 2600 km2, and 60% larval contribution requires 4176 km2.*

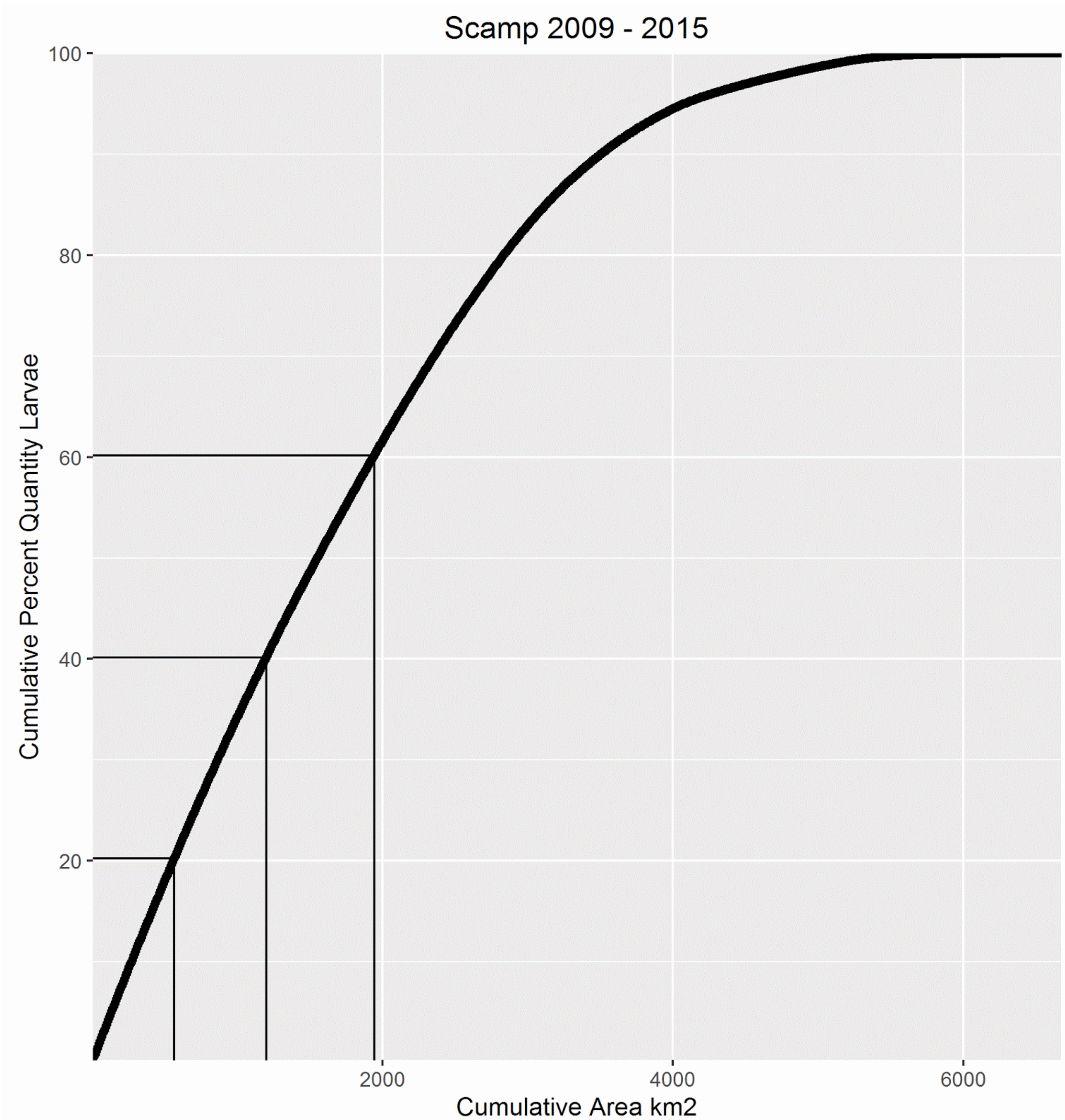

Figure 21. ***Scamp Area Graph****. Cumulative area required to most efficiently attain a target cumulative percent quantity of larvae. In the case of scamp, 20% larval contribution requires 568 km2, 40% larval contribution requires 1200 km2, and 60% larval contribution requires 1944 km2.*

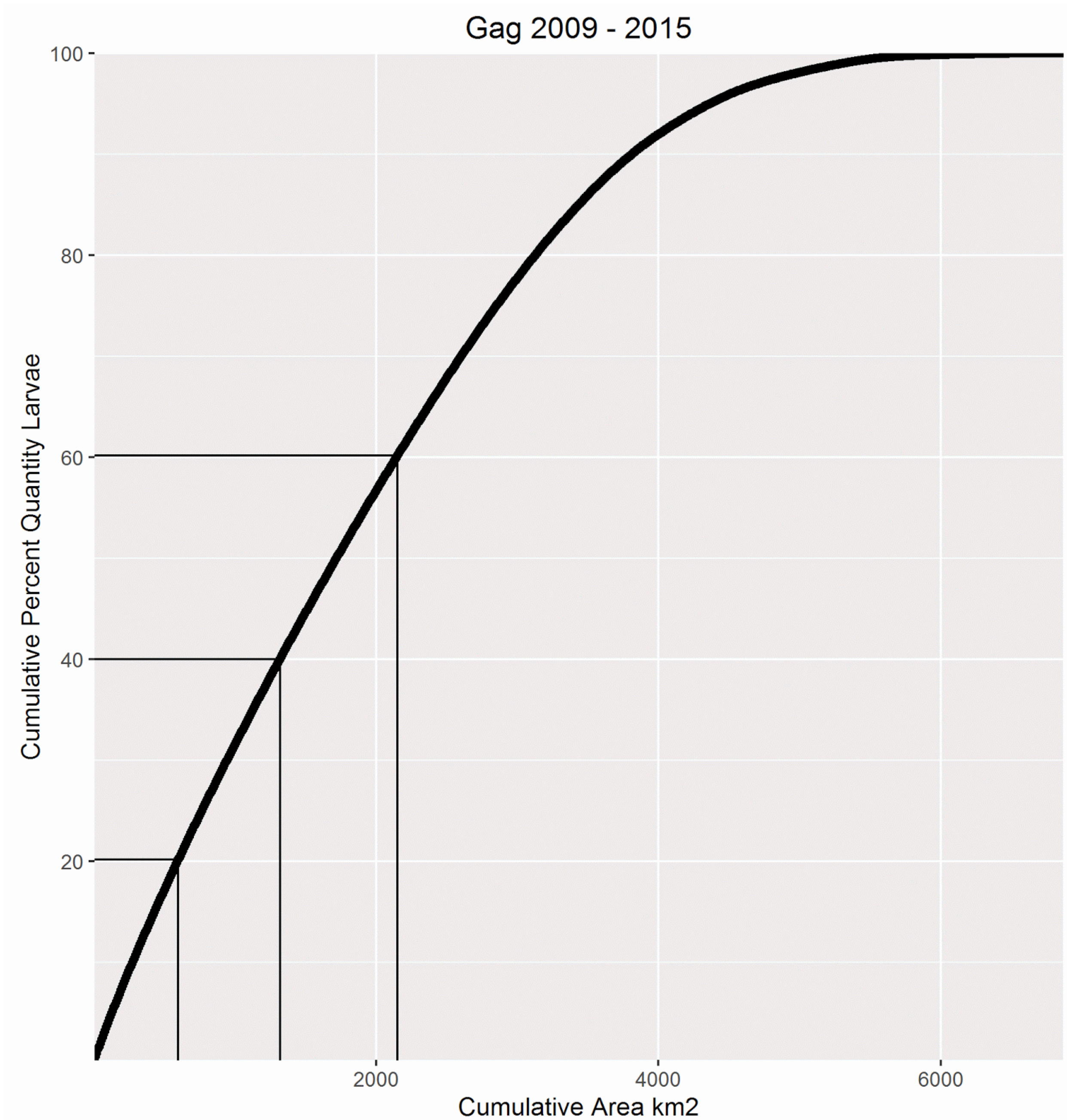

Figure 22. ***Gag Area Graph***. *Cumulative area required to most efficiently attain a target cumulative percent quantity of larvae. In the case of gag, 20% larval contribution requires 600 km2, 40% larval contribution requires 1320 km2, and 60% larval contribution requires 2151 km2.*

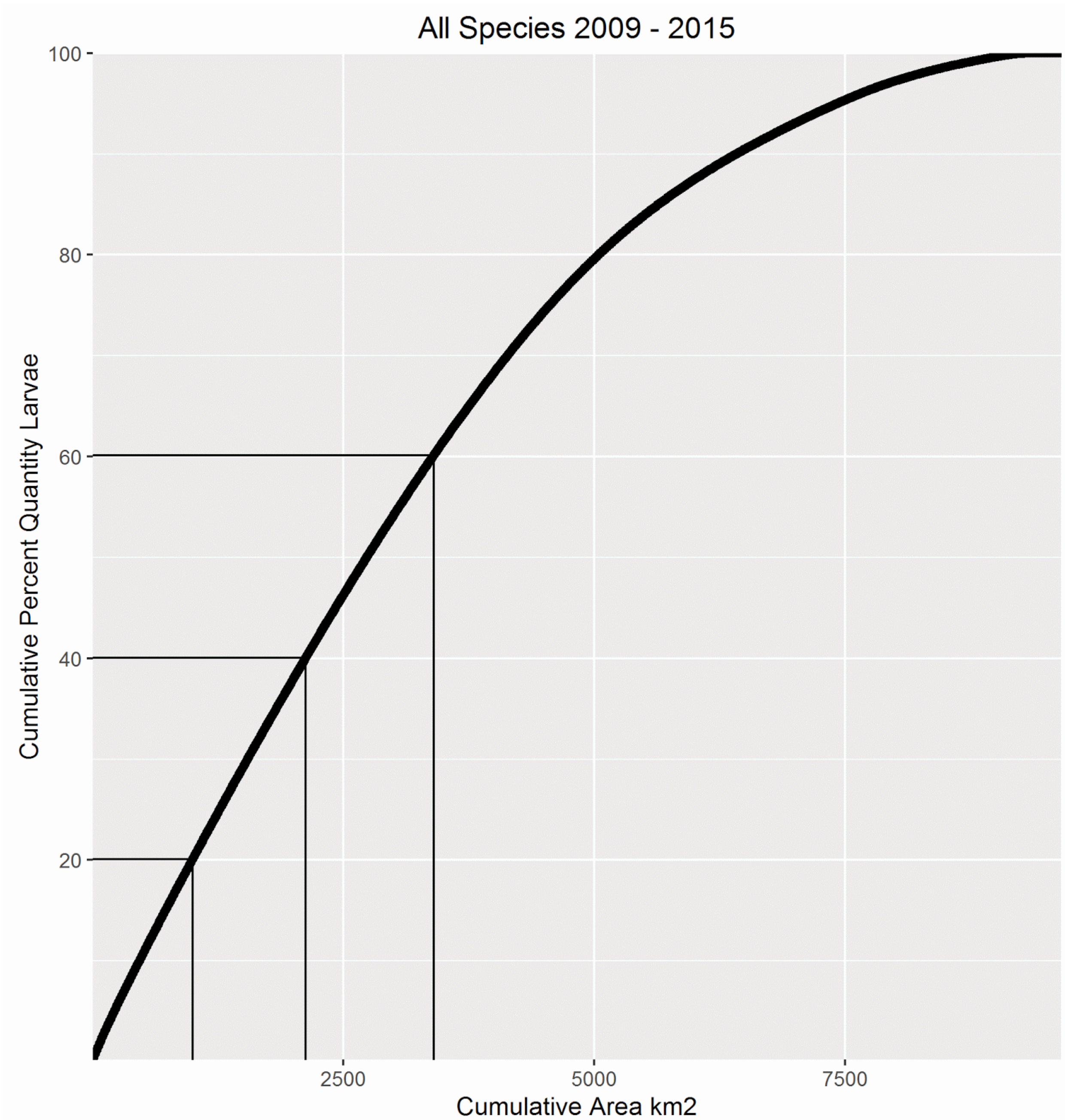

*Figure 23. **Species Aggregated Area Graph**. Cumulative area required to most efficiently attain a target cumulative percent quantity of larvae. In the case of aggregating over all species, 20% larval contribution requires 1000 km2, 40% larval contribution requires 2128 km2, and 60% larval contribution requires 3400 km2.*

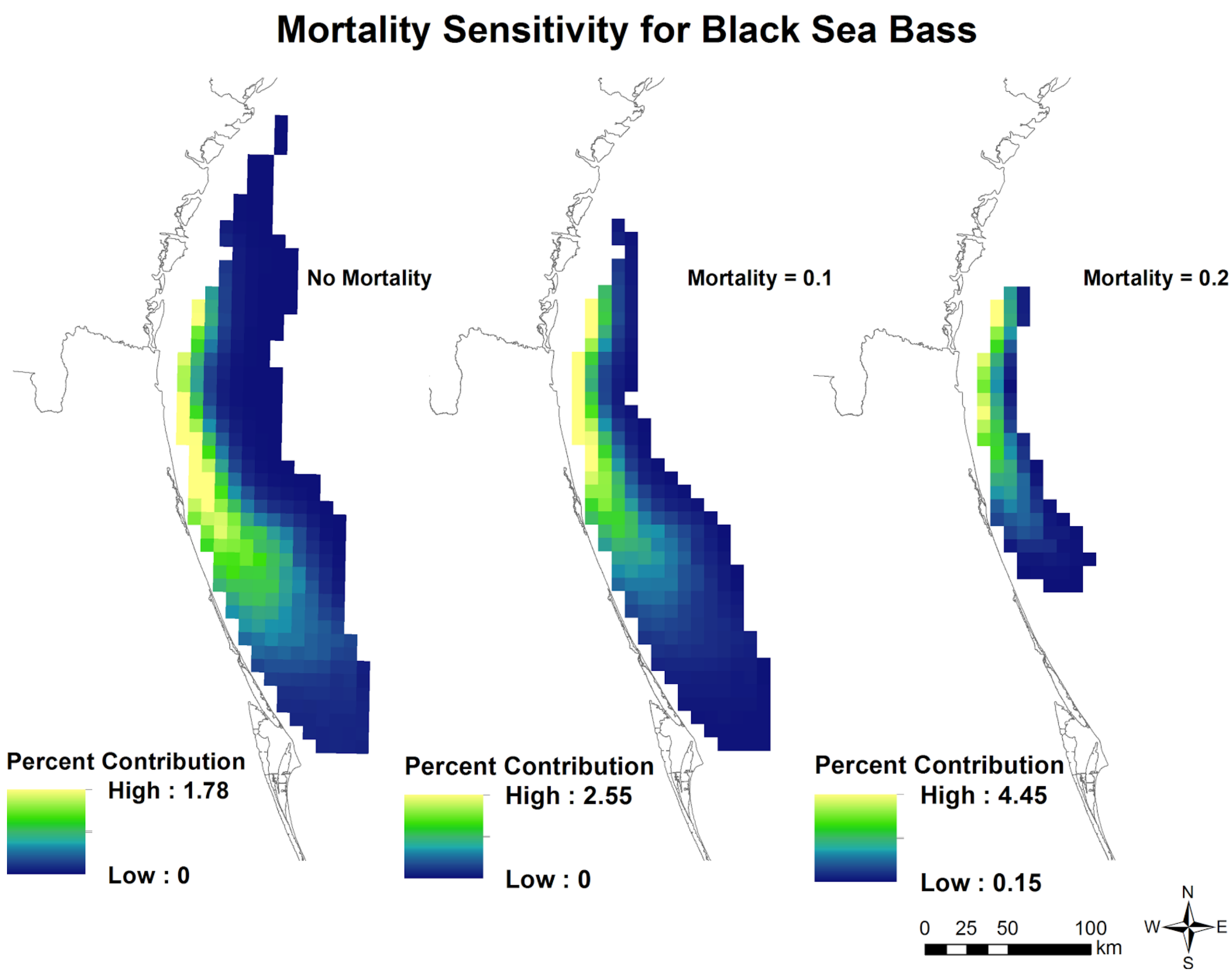

Figure 24. ***Black Sea Bass Mortality Sensitivity.*** *As the rate of mortality increases for black sea bass, the number of cells that show connectivity further away from Gray's Reef decrease. The general trends in areas of highest connectivity remain similar.*

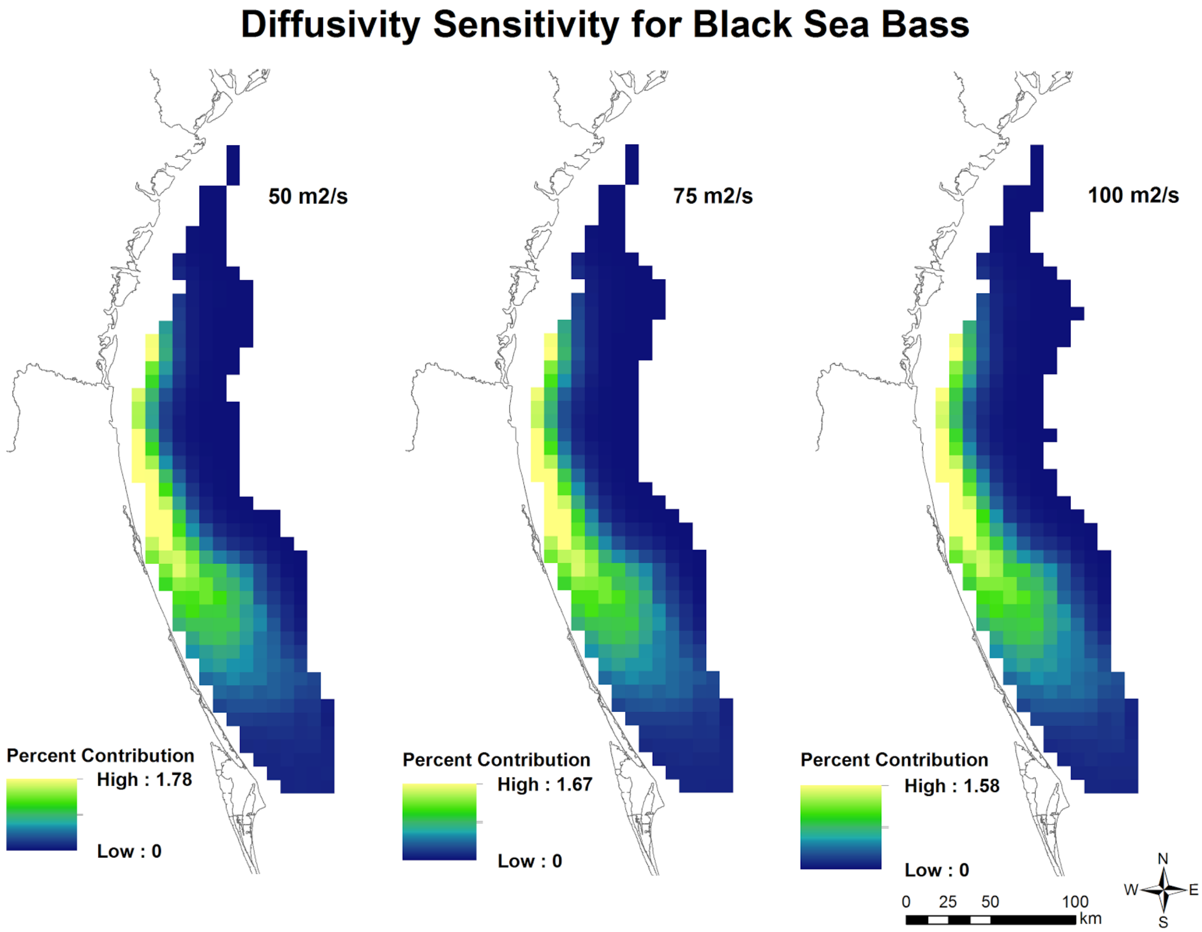

*Figure 23. **Black Sea Bass Diffusivity Sensitivity**. Visually there is little change to model results as the diffusivity rate is changed from 50 m2/s to 75 m2/s and 100 m2/s. Areas of strongest connectivity stay consistent across rates.*

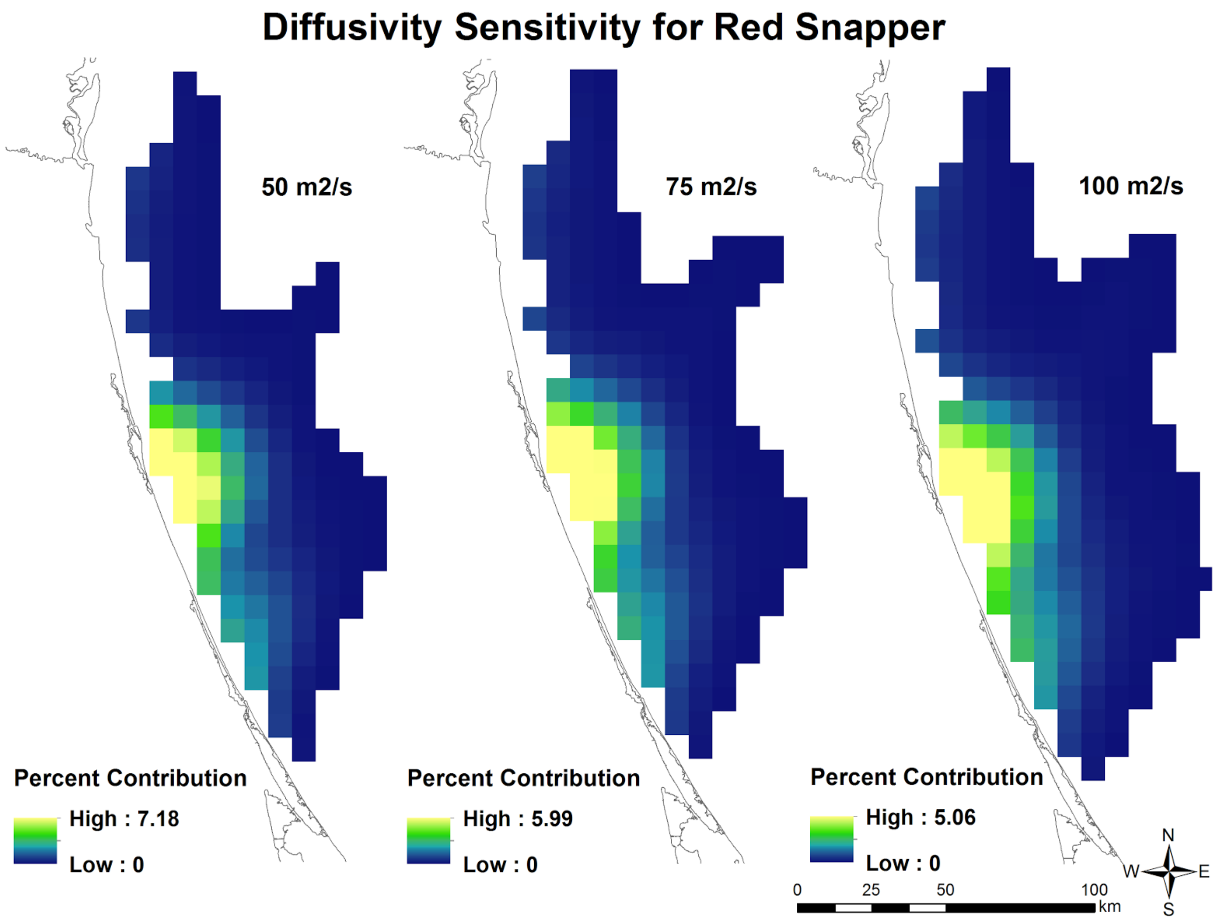

Figure 25. ***Red Snapper Diffusivity Sensitivity****. Visually there is a slight change to model results as the diffusivity rate is changed from 50 m2/s to 75 m2/s and 100 m2/s. Areas of strongest connectivity stay consistent across rates.*

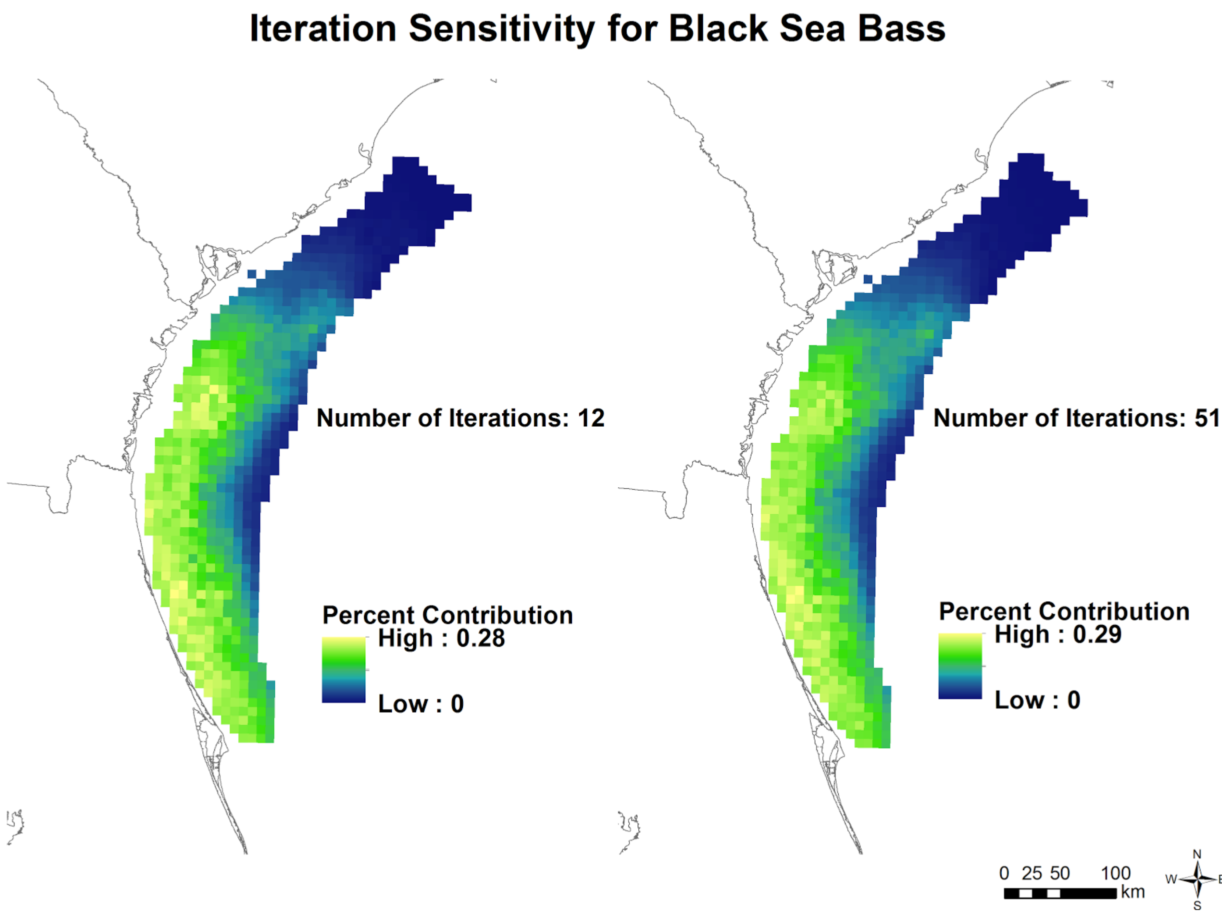

*Figure 26. **Black Sea Bass Sensitivity to Number of Iterations**. For the year of 2009, aggregate of 12 iterations was compared to the aggregate of 51 iterations. Very little difference is evident between the different number of iterations, areas of strongest connectivity stay consistent.*