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## Evaluating the use of larval connectivity information in fisheries models and management in the Gulf of Mexico

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Evaluating the use of larval connectivity information in fisheries models and management in the  
Gulf of Mexico

by

Michael Drexler

A dissertation submitted in partial fulfillment  
of the requirements for the degree of  
Doctor of Philosophy in Marine Resource Assessment  
College of Marine Science  
University of South Florida

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## **Dedication**

To Ivy, my wife,  
...most giving person I know.  
...can give some time back.

To Cai, who grew  
as I wrote all these pages;  
now it's time for fun

To Ari, who's new  
But we couldn't be without  
Here's to the next page

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## **Abstract**

Connectivity is a major contributor to the overall dynamics of marine populations. However, it still remains challenging to describe connectivity on ecologically meaningful scales of time and space. This is a major impediment to evaluating the impacts of marine protected area with respect to fisheries management objectives.

This dissertation brings together a wide array of spatial and connectivity information in the Gulf of Mexico (GOM) with the goal of 1) understanding the spatial distribution of fish populations and source-sink dynamics and 2) evaluating whether this information can be integrated, through a modeling framework, to identify closed areas that could be beneficial to fisheries management in the Gulf of Mexico.

First, a generalized additive modelling (GAM) approach is used to describe the distribution of a large number of species groups (i.e. functional groups) across the Gulf of Mexico (GOM) using a large fisheries independent data set (SEAMAP) and climate scale (decades) oceanographic conditions. Next a numerical Lagrangian particle transport model was developed that incorporates two major connectivity processes; site specific larval production and oceanographic transport for an entire large marine ecosystem and over multiple years. The two components are then combined to develop larval dispersal patterns for the entire GOM and identify areas operating as larval sources and sinks. Last, this information is integrated into an end-to-end ecosystem model to evaluate effectiveness of closing source and sink areas for the management of reef fish fisheries.

Closed area management simulations for reef fish indicated closing reef fish source areas, as opposed to sinks, in the GOM is most efficient method of increasing total biomass and yield. However, the impacts across individual functional groups were site specific. Ultimately, these simulations demonstrate the inclusion of connectivity information could improve fishery management objectives in an ecosystem context.

## **Chapter 1: Introduction**

### **1.1 Introduction**

Marine protected areas (MPAs) have been embraced as a key tool in achieving conservation and biodiversity targets and increasing ecosystem resilience. (Lester et al. 2009, Pendelton 2017). Generally, MPAs can be defined as geographic areas in the ocean that limit fishing or other impactful activities by humans (Lorenznzo et al. 2016). Currently, an estimated 11,000 MPAs protect 3.6% of the world's oceans (Marine Conservation Institute, 2018.). Closing or limiting areas of the ocean to fishing has been shown to provide a wide range of potential benefits to habitat, biodiversity, ecosystem services, spawners, and export of larvae and fish (Lubchenco et al. 2003, Harrison et al. 2012).

In addition to conservation oriented MPAs, many MPAs have been established explicitly for the purpose of aiding fishery management (Murawski et al. 2000, Roberts et al 2001, Gell and Roberts 2003, Hilborn et al. 2004; Sale et al. 2005). In a regulatory capacity, MPAs can be used to reduce fishing effort and thus catch. As a biological tool MPAs can be used to increase the size, density, and production of fish inside of the MPA (Lester et al. 2009, Kerwath et al. 2013). In some cases research has shown the potential for a spillover effect, in which production from within the MPA supplements the surrounding fished areas (Gell and Roberts 2003, Kellner et al. 2007, Halpern et al. 2009). This export of fish can occur via two mechanisms: 1) active movement of juvenile and adult fish from inside the MPA or 2) through a recruitment subsidy

from additional reproduction occurring from inside the reserve (Almany et al. 2007, Gruss et al. 2011, Paris and Cowen 2004).

Understanding how MPA size and placement will affect ecosystem dynamics requires some understanding of species and habitat distribution over space, degree of connectivity, and fishing patterns (Sale et al. 2005, Kaplan et al. 2009, Agardy et al. 2011). Models are needed to understand the impacts of implementing an MPA *a priori* and whether MPAs *could* help achieve fishery management objectives (Stelzenmüller et al. 2013, Fulton et al. 2015).

In theory, an improved understanding of the spatial connectivity of populations could help achieve existing fishery management goals such as rebuilding stocks and increasing fisheries yield. This is especially relevant in the (GOM), where there are strong spatial gradients of fish (Fischer et al. 2004, Gruss et al. 2018) and fishermen (Ainsworth et al. 2015). It is incumbent on the community of modelers to develop tools that can utilize spatial and connectivity data in a meaningful way for fisheries management.

This dissertation brings together a wide array of spatial and connectivity information in the GOM with the goals of: 1) understanding the spatial distribution of fish populations and source-sink dynamics and 2) evaluating whether this information can be integrated through a modeling framework to identify closed areas that could be beneficial to fisheries management in the GOM. The results from this dissertation are a first step in using this information in management and determining whether information on connectivity *can* be better utilized for more efficient and effective fisheries management.

The first component of understanding species connectivity is to identify where species live and reproduce. Chapter 2 develops an approach to generate distribution maps of a large

number of species and groups of species (termed functional groups throughout this document) in the Gulf of Mexico. Currently, detailed species distribution maps do not exist for most species. This is especially true for the southern Gulf of Mexico. In this chapter, the possibility of using habitat maps to predict the spatial distribution of species is explored. A generalized additive modelling (GAM) approach was developed to describe the spatial distribution of 40 functional groups across the GOM using a large fisheries independent data set of fish abundance (SEAMAP trawl surveys) and environmental and oceanographic predictors. The modeling process for pink shrimp (*Farfantepenaeus duorarum*) is demonstrated in detail as an example. The results indicate that there is sufficient spatial and environmental information to develop highly resolved distribution maps. This general framework was then applied to other fish functional groups. The predicted distribution maps, although sometimes imprecise, were suitable for initializing ecosystem model simulations as they provide sufficient gradients of density over space.

A second component of connectivity is larval dispersal. Understanding where species live and reproduce allows one to link that information to where the larvae disperse to produce a measure of connectivity between populations. In chapter 3, regions of GOM that operate as larval sources or sinks are identified by simulating the long term dispersal patterns for numerous functional groups. This accomplished by incorporating information of where larvae are produced, from the results of chapter 2, and simulating where larvae drift and settle using current information from a hydrodynamic model (GOM HYCOM). To this end, a particle tracking model was developed that incorporates two major connectivity processes: site specific larval production and oceanographic transport for an entire large marine ecosystem over multiple years. Larval settlement patterns were then compared to site specific larval production to identify source and sink populations. A case study of white shrimp (*Litopenaeus setiferus*) indicates anomalous

years of local recruitment and source sink areas that could be considered in siting MPAs.

Source-sink index maps were then generated for every functional group

In chapter four larval connectivity of the functional groups, estimated in chapter three, was integrated into an end-to-end ecosystem model (Atlantis-GOM). Atlantis integrates the additional components of species connectivity including adult movement and predator prey interactions which are important to capture post settlement mortality. Previous studies using the Atlantis ecosystem model have relied on simplistic assumptions about spatial recruitment. Therefore as first step towards understanding the use of connectivity information in this context, the sensitivity of the Atlantis-GOM ecosystem model to connectivity information was evaluated. The influence of the local recruitment assumption in the GOM (Suprenand et al. 2015, de Mutsert et al. 2016) on the spatial distribution of productivity and the estimation of safe fishing rates was then evaluated. The full model (including connectivity information) was then used to evaluate a range of MPA scenarios for the GOM to assess their utility in management.

The results of these simulations are not intended for tactical management advice as there are a number of simplifying assumptions and caveats that would need to be addressed on a species by species basis. Rather, these simulations are meant to evaluate the sensitivity of the model and advice generated from it from shifting away from the pervasive assumption local recruitment in ecosystem models with the goals of developing a simulation tool able to capture a range of ecosystem dynamics useful for developing fishery management scenarios.

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## **Chapter 2: Generalized additive models used to predict species abundance in the Gulf of Mexico: an ecosystem modeling tool.**

### **Note to Reader**

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### **2.1 Abstract**

Spatially explicit ecosystem models of all types require an initial allocation of biomass, often in areas where fisheries independent abundance estimates do not exist. A generalized additive modelling (GAM) approach is used to describe the abundance of 40 species groups (i.e. functional groups) across the Gulf of Mexico (GOM) using a large fisheries independent data set (SEAMAP) and climate scale oceanographic conditions. Predictor variables included in the model are chlorophyll *a*, sediment type, dissolved oxygen, temperature, and depth. Despite the presence of a large number of zeros in the data, a single GAM using a negative binomial distribution was suitable to make predictions of abundance for multiple functional groups. We present an example case study using pink shrimp (*Farfantepenaeus duorarum*) and compare the results to known distributions. The model successfully predicts the known areas of high abundance in the GOM, including those areas where no data was inputted into the model fitting. Overall, the model reliably captures areas of high and low abundance for the large majority of functional groups observed in SEAMAP. The result of this method allows for the objective

setting of spatial distributions for numerous functional groups across a modeling domain, even where abundance data may not exist.

## **2.2 Introduction**

The need for ecosystem-based approaches to fisheries management has been widely recognized throughout the world (Pikitch et al. 2004). Marine ecosystem models (e.g., Ecospace, Atlantis, InVitro, OSMOSE, Gadget, IBEM, etc.) are becoming an important tool in achieving those goals as they incorporate predator-prey dynamics and environmental interactions in a spatially explicit context. Spatially explicit models allow managers to better understand certain ecosystem processes, but they require large amounts of data in comparison to models that assume homogeneous space. One example of these additional requirements is that these models require an initial spatial allocation of functional group biomass or abundance. It is not straightforward to develop biomass distribution grids due to the lack of comprehensive stock assessments outside a handful of commercially valued species and there is a particular lack of spatial distribution data from international waters. In most cases, this limits the development of ecosystem models to those areas that are rich in fisheries independent data. Efforts have been made to extrapolate data from limited spatial areas to larger scales using a variety of methods including interpolation over arbitrarily assigned regions (Brand et al. 2007) and similarity matrices (Ainsworth et al. 2011). Generalized additive modeling offers an objective way to predict abundance or biomass according to the known ecology of the animals over broad geographic areas. Generalized additive models (GAMs) are a semi-parametric approach to predicting non-linear responses to a suite of predictor variables (Hastie and Tibshirani 1986) In general, GAMs can be used to identify optimal conditions for a given species using environmental variables (e.g., depth and temperature) in order to predict the likelihood that a

given species would inhabit a particular environment, or their abundance (Stoner et al. 2001, Maravelias 1999, Yee and Mitchell 1991, Walsh and Kleiber 2001). The outputs of these models are often used to interpolate species distributions at high resolution within coarsely sampled areas (Katsanevakis and Maravelias 2009, Stoner et al. 2001, Yee and Mitchell 1991). Model testing and sensitivity analysis can also help identify influential environmental variables and their corresponding range of influence. In comparative studies, GAMs have often been shown to perform as well or better than other types of predictive models based on environmental conditions (Walsh and Kleiber 2001, Moisen and Frescino, Guisan et al. 2002). Despite their acknowledgment as a proven tool for ecological analyses, albeit with some caveats (Guisan et al. 2002), few studies, have applied the method to make predictions outside of a sampled area.

Fisheries independent sampling efforts typically result in many zero observations for any given species, particularly in surveys that cover a broad range of habitats or depths. To deal with this problem a number of approaches have been developed to fit these types of data including lognormal delta distributions (Aitchison and Brown 1957, Pennington 1983), delta method approximation of variance (Stefánsson), and zero inflated distributions Barry and Welsh 2002, Minami et al. 2007). All of these methods can be applied to either generalized linear models, or generalized additive models. The latter of the two allows for greater flexibility in the model fitting. Despite these advanced methods dealing with zero inflation, Warton (2005) found that in most cases a negative binomial was sufficient to model data with many zeros. In this paper we utilized a negative binomial GAM to predict the relative abundance of functional groups across shelf areas of the entire Gulf of Mexico (GOM) including Mexican and Cuban waters and areas where fisheries independent surveys do not exist, based on environmental and habitat predictors.

The purpose of this study was to find a single parsimonious framework to predict the distribution of multiple functional groups within an ecosystem. This framework can then be utilized in the objective distribution of relative abundance for a spatially explicit Atlantis ecosystem model of the GOM (Atlantis-GOM) in preparation for NOAA's Integrated Ecosystem Assessment and other applications (Fulton et al. 2004, Fulton et al 2005). In order to provide better spatial management of fisheries, a better understanding of the ecosystem-wide influences on that stock requires modeling of the entire ecosystem and not just those parts that are adequately sampled. We validate the model by predicting the distribution of pink shrimp (*Farfantepenaeus duorarum*) throughout the Gulf of Mexico and compare the model performance of both the aggregated results used in ecosystem models and the high-resolution gridded values taken directly from the GAM. While numerous species were considered in the model fitting, only the summer abundance of pink shrimp is illustrated here. Pink shrimp were chosen as an example species because they were well represented in the available observational data set used in model training and their distribution is strongly correlated with environmental and habitat predictor variables.

## **2.3 Methods**

### *2.3.1 Study Area*

The Gulf of Mexico (GOM) is one of the world's 64 Large Marine Ecosystems (Sherman et al. 2008). This ecosystem spans tropical and subtropical climates and is enveloped by the economic exclusive zones (EEZ) of the United States, Mexico, and Cuba. The EEZ of the United States alone supports 25 million recreational fishing trips (NOS 2008) and a commercial fisheries harvest in excess of one million tonnes per year (Vidal and Pauly 2004). Gulf shrimp remain one of the most important fisheries in the region with combined landings value of 368

million dollars (NOAA 2010). In this article, we estimate the abundance and spatial distribution of 40 functional groups (groups of species aggregated according to niche similarities). The single-species functional group of pink shrimp is illustrated here in detail as a case study. The range of pink shrimp extends through the entire GOM coastal waters (Mulholland 1984). Nearly 94% of the pink shrimp harvested in the GOM are landed on the west coast of Florida (NOAA 2010) where they are particularly abundant. Known “hot spots” for pink shrimp include the area surrounding the Dry Tortugas as well as the eastern coast of the Golfo de Campeche (Figure 2.1). The highest adult abundance is found between 9 and 44m of water (GMFMC 2006, Bielsa et al. 1983)..

### 2.3.2 *SEAMAP Groundfish survey*

The Southeast Area Monitoring and Assessment Program (SEAMAP) is a multiagency fisheries independent data collection program coordinated by the Gulf States Marine Fisheries Commission (GSMFC 2011). Groundfish surveys are conducted on an annual, and sometimes seasonal, basis using a 40-ft otter trawl throughout the northern GOM. The general area surveyed by SEAMAP includes most the continental shelf up to 200m depth, but only within the territorial waters of the United States in the northern Gulf of Mexico (Figure 2.1). Survey data was extracted from the public SEAMAP database (Rester 2011) and aggregated by functional groups. Sampling effort was estimated as the total area swept of each SEAMAP tow using the Euclidean distance between start and end points and an assumed 40-ft trawling width.

### 2.3.3. *Environmental Conditions*

Predictor variables included in the model were surface chlorophyll *a* (chl *a*), sediment type, bottom dissolved oxygen (DO), bottom temperature, and depth (Table 2.1). These

variables were chosen due to the wide spatial coverage throughout the Gulf of Mexico. Sediment type was divided into the following categories: mud, sand, gravel, and rock. A 0.1° gridded map of seasonal environmental parameters was made for each season (Winter: Jan-Mar, Spring: Apr-Jun, Summer: Jul-Aug, Fall: Sep-Dec) with data collected from the following sources. Measurements of bottom temperature and DO at the maximum depth recorded for each grid point were extracted for each season from the National Oceanographic Data Center (NODC) regional climatology database (Boyer et al. 2009). Surface chl *a* measurements were obtained by averaging the seasonal composites of MODIS–Terra satellite measurements and the NASA Ocean Biogeochemical Model from 2005-2010 accessed through the GIOVANNI portal (<http://disc.sci.gsfc.nasa.gov/Giovanni/overview/index.html>). A continuous raster of bathymetry was derived from the SRTM30\_PLUS global bathymetry grid Becker et al. 2009, which was accessed from the Gulf of Mexico Coastal Ocean Observing System ([gcoos.tamu.edu](http://gcoos.tamu.edu)). The best available data on bottom sediment type, dbSEABED2006 (Buczkowski 2006, Jenkins 2011) does not provide complete coverage for the entire Gulf of Mexico, although the area sampled by SEAMAP has substantial coverage. A nearest neighbor function was executed on a 0.1° grid using the natural neighbor function in GIS v10.0 (ESRI 2011) for those grid points lacking any sediment data. Incomplete and low resolution environmental data was subjected to a spline interpolation using the same grid and GIS software in order to provide a contiguous surface from which to make model predictions. The seasonal environmental conditions grid was then overlaid with the SEAMAP starting locations for a given season. These environmental grids were used both in the fitting of the model and in predicting abundance distributions for unsampled areas.

#### 2.3.4. Model description

A GAM approach was used to predict relative abundance of Atlantis-GOM functional groups in shelf areas across the entire Gulf of Mexico based on estimates of abundance and regional oceanographic conditions occurring at SEAMAP trawl locations. Due to the large number of zero observations and the need for a single parsimonious model to make predictions for a large number of functional groups, a GAM was developed using a negative binomial distribution with an offset for effort (Barry and Welsh 2002). Prior to the fitting of the final model, the data was randomly split into training and test sets: 2/3 of the data was for training and 1/3 for model validation. Once validated, the full set of pink shrimp summer abundance data was then used to fit the model and make the final predictions for the ‘summer’ season. All models were fit using the ‘mgcv’ package in the R version 2.14.0 environment (Wood 2006) following the equation:

$$g(\eta) \sim s(\text{depth}) + s(\text{chl a}) + s(\text{temp}) + s(\text{oxygen}) + \text{factor}(\text{sediment type}) + \text{offset}(g(\text{effort})) \quad (\text{Eq.1})$$

where  $\eta$  represents the expected abundance resulting from the generalization of the predictor terms according to the link function  $g$ . The abundance data was modeled using a negative binomial distribution with a log link function, including an offset, with equivalent link function, to allow for variations in effort. Function  $s$  is a thin plate regression spline fit to a given environmental parameter. The smoothness selection was fit using spline-based penalized likelihood estimation. Theta parameters and weighted penalties were determined by Un-Biased Risk Estimator (UBRE) which is similar to an AIC rescaled (Wood 2006). Estimation of the theta parameter was limited to a range of 1-10. An extra penalty was applied to each parameter as the smoothing parameter approached zero, allowing the complete removal of a term from the

model when the smoothing parameter is equal to zero. This extra penalty allows for partially automated model selection and is especially useful given the models broad application to numerous functional groups.

The initial training model fits were evaluated by analyzing the total deviance explained and UBRE score. Model performance was evaluated by predicting the abundance at each of the data points in the test data set, given the environmental conditions at that point. The predictions were then compared to the observed values at each respective point. Plots of the predicted vs. observed abundance were made for each group, and a least squares regression was used to evaluate any trends. Once the predictions of the training/test model were compared and deemed suitable for analysis, the entire data set was then used to predict abundance from the environmental conditions within each  $0.1^{\circ}$  grid cell for depths up to 200 m. To illustrate the usefulness of this method as a way of initializing spatially explicit ecological models, the results of the pink shrimp distributions were averaged according to the Atlantis-GOM spatial polygons and displayed with their associated 95% confidence intervals.

### **2.3 Results**

For pink shrimp, the model described 45.5% (UBRE=1.6) of the deviance. The models for the remaining functional groups described between 10% and 83% of the deviance with a median value of 33.6% (Appendix A). All of the functional groups observed in SEAMAP trawls also had a positive slope of the observed/predicted line indicating that we can reliably predict low and high density areas at least qualitatively. All of the continuous predictors were found to have a smoothing term significantly different from zero ( $p < 0.001$ ) and thus contributed to the model fit for pink shrimp. This was also true for most demersal invertebrate groups. However,

the significance of the predictors from other groups not commonly selected by a benthic trawl varied widely.

Individual parameter values were in general agreement with the habitat suitability index model derived by Mulholland (1984). Mulholland reports catches of shrimp over a wide range of temperatures (5°-38°C) with the highest density of catch from 20-38°C. The curve fit to the modeled distribution found the highest abundance to be in the range of 18-32°C (Figure 2.2). Values higher than 38°C likely reflect the error associated with the interpolation of environmental data. Temperatures lower than 15°C had a negative effect on the expected abundance.

Mulholland (1984) also predicts sandy-silt and silty-sand to be the sediment types with the highest suitability for pink shrimp, followed by hard bottom. The lowest suitability was in soft bottom. The modeled data predicted significantly greater densities of shrimp on sand and rock habitats ( $p < 0.05$ ; Figure 2.3). Depth only had a slight positive effect on the estimated abundance up to 30-40 m; any depth greater than this had a negative effect on the estimated abundance. Chlorophyll *a* concentrations were inversely correlated to pink shrimp abundance for values up to 15 mg/m<sup>3</sup> at which point the expected abundance dropped sharply. The influence of dissolved oxygen did not fluctuate greatly across the range of values between 2.0-4.5 mL/L. Dissolved oxygen values greater than 6 had a positive effect on the model, but were not common in the seasonal averages of the environmental conditions. Therefore, the fitted model reflects previous research pertaining to the habitat preference for pink shrimp with regard to temperature and sediment type and introduces some additional suitability parameters.

Using the test set of SEAMAP data, the ability of the model to predict the response was evaluated. In general, the model predicted a higher mean abundance for those stations where

high abundances were observed (Figure 2.4). Although less than ideal, ideal being equivalent 1:1 slope, the difference captures the general trend of the data. In every functional group assessed using this model, the slope of the least square line was greater than zero.

The model predictions were then aggregated by polygon and compared to the mean abundance occurring within those polygons with fisheries independent data. The aggregated predictions were in better agreement with the observed data with a normal distribution of residuals around the least square line. However, like the point estimates, the intercept was greater than zero, and may indicate an overestimation of abundances close to zero.

The spatial distribution of the gridded values, predict high abundance along the entire mid-depth portion of the West Florida Shelf, and some additional hotspots near the Dry Tortugas, Louisiana-Texas border, Texas-Mexico border, and on the north-western Campeche Bank (Figure 2.5). The highest abundance was found in the areas north of the Florida Keys/Dry Tortugas with abundances approaching 1.2 million shrimp per grid cell. Abundances near the Florida panhandle were two orders of magnitude less than those found near the Florida Keys. The hotspots around the Texas-Mexico border and Campeche Bank were a similar order of magnitude less than those near the Dry Tortugas although those distributions were patchy and smaller in area.

The Atlantis-GOM polygon spatial distributions reflect the general distribution of pink shrimp in the 0.1<sup>0</sup> gridded results (Figure 2.6). Highest abundance occurs at mid depth over the West Florida Shelf and Dry Tortugas, and the nearshore polygons along the western gulf. The comparison of the observed to predicted values of the aggregated polygons were in better agreement than the higher resolution gridded values (Figure 2.4). The observed mean of those polygons with SEAMAP data (3.52) was found to be significantly different from the predicted

mean (6.62) through a paired t-test ( $t=3.90$ ,  $p=0.0002$ ). The 95% confidence intervals were inversely related to the mean abundance, and ranged between 0 and 1.65 on a log scale for the majority of the cells. The few polygons with very few data points (estuarine and deep water polygons) had much higher confidence intervals approaching 12 orders of magnitude, and the estimates are not reliable.

## **2.4 Discussion**

The method described here provides a standardized way to generate abundance distributions for models that 1) require comprehensive spatial distributions for 2) a large number of species 3) but are limited in terms of fisheries independent data. Therefore it is an ideal supporting application for spatial ecosystem models. In this paper we extend the use of the GAM approach to make predictions of abundance based on the environmental conditions beyond the sampling domain of the data used to fit the model. I also show how the data derived in this model will be incorporated into the Gulf of Mexico Atlantis ecosystem model in Figure 2.6. The absolute predictions for individual functional groups may not be precise using the limited abundance data set from SEAMAP employed here. Also, the environmental data used in making predictions is averaged over time and space, missing environmental extremes that may have significant influence on species distributions. Future studies might test environmental data with a higher temporal resolution, given the data is available. Also, the presence of spatial autocorrelation on a regional basis may be addressed by splitting the training/test data into regional blocks and examining the residuals in the remaining sub-regions. In our case we considered this approach impractical due to data scarcity and the application of the modeled results to a coarse resolution ecosystem model.

The high degree of correlation between model results and the validation data set indicates that we can reliably predict qualitative differences between low- and high-biomass regions, especially in terms of relative abundance. Regardless of the degree of precision provided by this model, the results offer a vast improvement over the assumption of a homogenous distribution of a population commonly used in stock assessments. Further, when aggregated to the level used for spatially explicit ecosystem models, the model provides a better fit to the observed data points. Therefore, the information supplied by this modelling framework can be used to initialize the spatial distribution of species for dynamic ecosystem models whose spatial distributions will settle to a new, but related, equilibrium at run-time. This proof of concept application can be improved as additional CPUE and environmental data become available. Additional data could be incorporated from fisheries-dependent data such as spatially referenced commercial catch statistics and observer data. Coupling these models with spatially explicit estimations of pressures can ultimately determine the absolute contributions of these predictors on species abundance in lieu of pressure.

We demonstrated the utility of the model by predicting areas of high abundance of pink shrimp near the historical fishing areas where no observational abundance data was available. The model results were also in general agreement with previous research regarding the suitability of each parameter used. Thus the extension of this model to the entirety of the southern Gulf of Mexico should provide reasonable estimates of abundance. It should be noted that although pink shrimp occur throughout the Gulf of Mexico, one would expect the species composition of other groups of animals to vary with latitude. While the use of multispecies functional groups occupying similar niches does provide some added flexibility to the final predictions, the inclusion of a latitude parameter could explicitly differentiate these variations in species

abundance. Unfortunately, no data is available for latitudes south of Texas-Mexico border to the west, and south of Florida to the east. Thus, including this terms will limit the predictive capabilities to only those latitudes where data exist, undermining the purpose of the model.

While the magnitude of abundance from a benthic trawl may be expected to reflect the absolute abundance of pink shrimp, estimating the abundance of other functional groups, particularly non-demersal and non-benthic species using the same gear will be subject to a catchability bias. There was adequate data to predict the distributions of 40 of the 90 Atlantis-GOM functional groups. Those groups which are less vulnerable to benthic trawling gear, such as large sharks, greater amberjack, king mackerel, spanish mackerel, and squid, did not show a close relationship between observed and predicted abundance values (Appendix A). Abundance estimates for these functional groups may be unreliable until additional abundance data from other sampling gear types can be incorporated into the training data set. Abundance was better predicted for slower moving, smaller, mainly demersal species that would be selected by a benthic trawler, such as benthic grazers, bivalves, blue crab, flatfish, pink shrimp, and sessile filter feeders. It is worth re-iterating that predictions of these functional groups were limited by the depth range sampled by SEAMAP trawling. For this reason, the current application should only be used to set distributions on the continental shelf. However, the substitution of a general set of predictors suitable to the pelagic or Deepwater environments should yield plausible results.

Despite the positive relationship between the predicted and observed values, none of the least squares lines approached a slope of one. Therefore, the model tends to overestimate abundance where no catch was observed. However, the model did manage to consistently detect a lowered combined abundance at sites where no catch was observed. This bias is likely related to the fact that these simple environmental indices are not satisfactory to explain a portion of the

variability in the distribution of these functional groups. The model tends to fail at low population densities that may be heavily influenced by minute differences in oceanographic conditions, patchiness, or other unexplained variability. These differences will not be captured by the regional/seasonal environmental data used in this study. The environmental variables chosen for this study were done so for their wide spatial distribution spanning the entire modelling domain. Given this caveat, these high resolution errors become less important when used to initialize a course resolution model such as the Atlantis-GOM; where polygons are on the order of thousands of square kilometers (Figure 2.6). The final gridded spatial distributions for all 40 functional groups can be found in Appendix C.

Aggregating the results to a courser resolution, i.e. the Atlantis-GOM polygons, allows us to average out the variance, as the large polygons will tend to be closer to the global average. The general distribution of pink shrimp is adequately represented by the Atlantis-GOM polygons (Figures 2.5, 2.6). This aggregation provided a better fit to the observational data than the individual points (Figure 2.4). The significant differences detected between the overall polygon means suggests, as in the gridded model, that we may still be slightly overestimating the total abundance across the entire system. As stated before, this bias may be related to the fact the model was fitting our model to seasonal data. The same reasoning for the bias in the gridded values also applies here. GAMs require many degrees of freedom and introduce a tradeoff between including addition degrees of freedom by aggregating data across seasons or spatial scales, or more highly resolved data with low predictive power to which we chose the prior.

In conclusion, this paper notes the utility of GAMs beyond the common applications of identifying influential environmental variables and interpolating abundance and biomass within sampling regions. For applications like initializing biomass distributions in spatial ecosystem

models, where wide spatial and taxonomic coverage is desirable but the benefit of high precision estimates is lost at run-time, these statistical approaches hold unrealized potential.

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## 2.6 Tables

Table 2.1. Data sources for model. List of data sources used in the model, the resolution of that data, and any manipulations that were required to attain a contiguous surface with which to make model predictions.

<b>Environmental Parameter</b>	<b>Data Source</b>	<b>Resolution</b>	<b>Manipulations</b>
Abundance	Southeast Area Monitoring and Assessment Program (SEAMAP)	varies	Standardized to area swept centered around each starting point
Surface chlorophyll <i>a</i> (chl <i>a</i> )	MODIS-Terra 4km Satellite -NASA Giovanni Portal	4km	NA
Sediment	dbSEABED – GoM Data Atlas	low	Nearest neighbor interpolation
Bottom Temperature	NODC/GoM regional Climatology	0.1 <sup>0</sup>	Spline interpolation
Bottom Dissolved Oxygen (DO)	NODC/GoM regional Climatology	1.0 <sup>0</sup>	Spline interpolation
Depth	DOC/NOAA/NESDIS/NGDC – GoM Data Atlas	1.85 km	NA

List of data sources used in the model, the resolution of that data, and any manipulations that were required to attain a contiguous surface with which to make model predictions.

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## 2.7 Figures

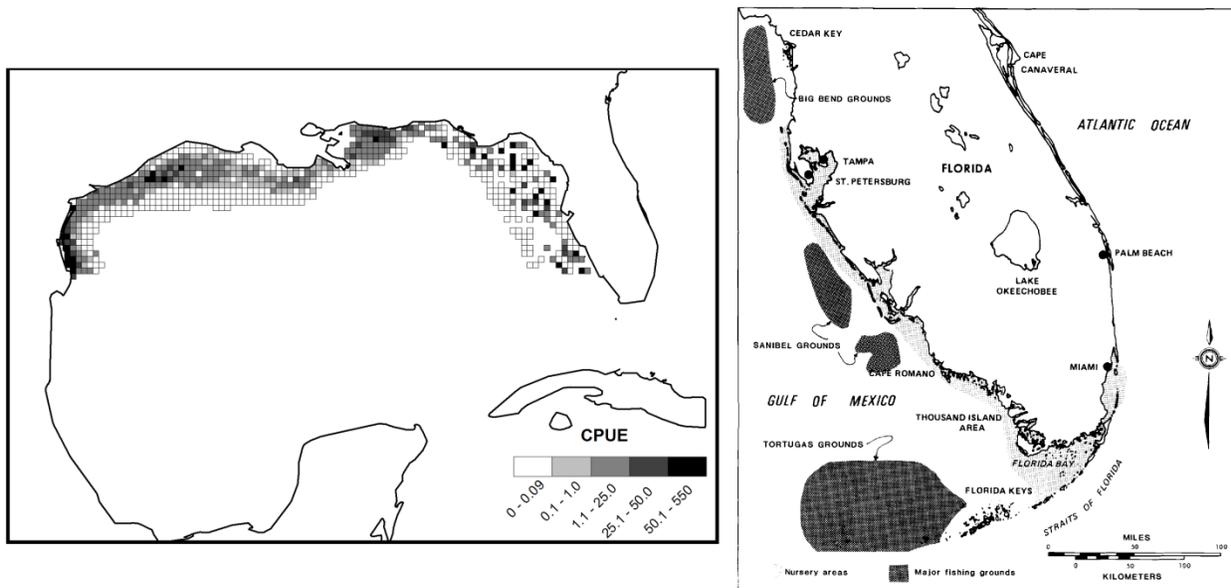


Figure 2.1. Pink shrimp abundance data. Historical fishing grounds of pink shrimp (*Farfantepenaeus duorarum*) off of the west coast of Florida in 1983 (right) and the observed abundance sampled from SEAMAP sampling locations from 1987 to 2009 in terms of individuals caught per one-hour tow of 40-ft shrimp trawl (left). Reproduced with permission from Bielsa et al. (1983).

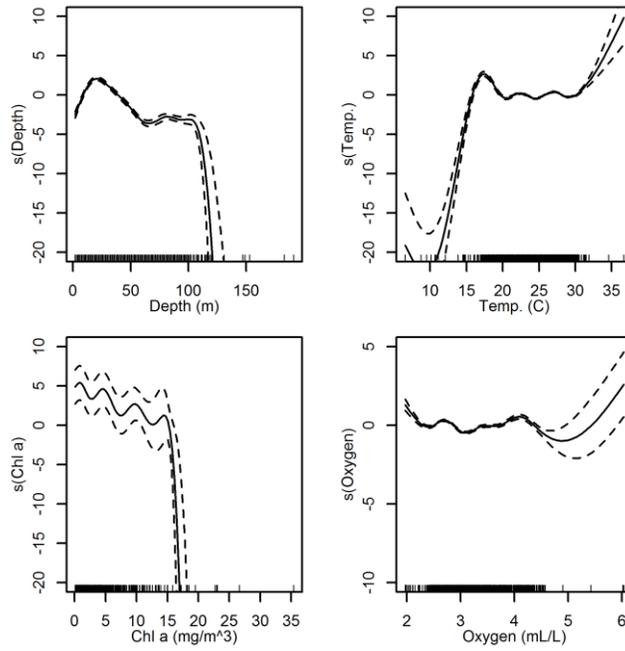


Figure 2.2. Model fits. Smoothed curve of the additive effect to the estimated abundance of pink shrimp for the individual environmental parameters in the GAM. Dotted lines represent 95% confidence intervals, marks along the lower axis represent a single observation. A straight line represents an additive effect of zero.

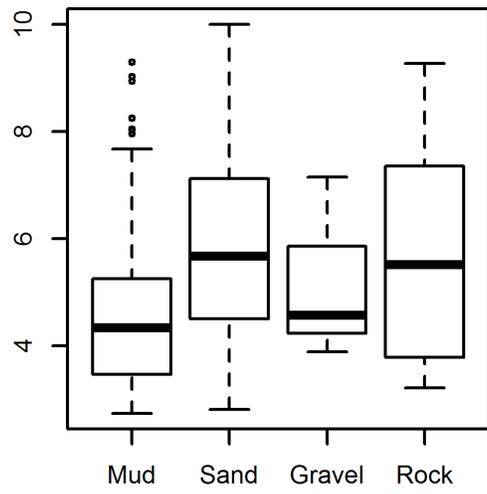


Figure 2.3. Sediment type vs. pink shrimp abundance. Natural log distribution of pink shrimp abundance for each sediment type. Since we are primarily interested in which category of sediment type is suitable for pink shrimp the zeros have been removed for display purposes

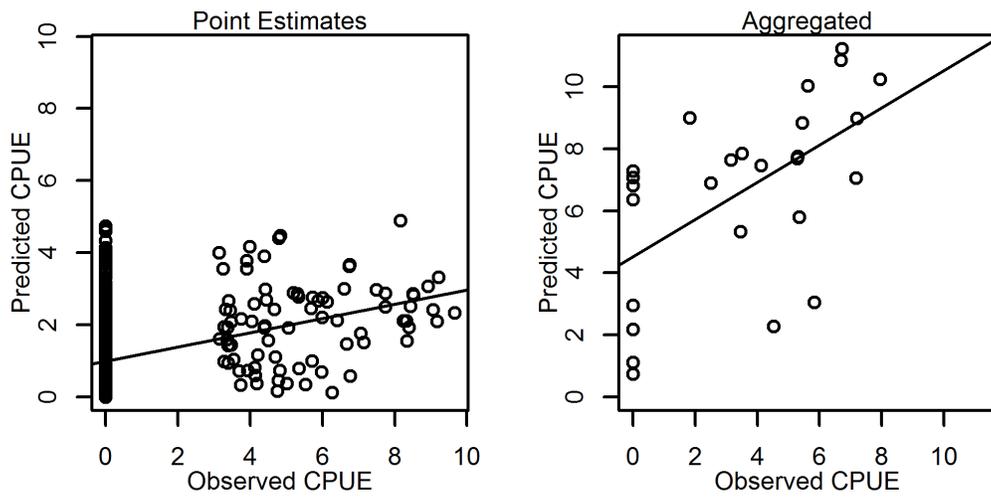


Figure 2.4. Model performance. Comparison of model predictions to observed  $\ln(\text{abundance})$  estimated from the environmental conditions of the test data set and compared to the observed values. The resulting scatterplots and least-squared line of fit is shown for both the grid estimates from the model and those estimates aggregated to the Atlantis-GOM polygon level.

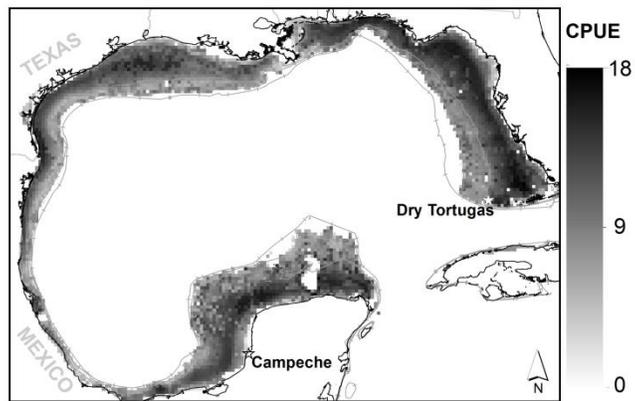


Figure 2.5. Modeled pink shrimp abundance for the entire GOM. Results of the pink shrimp GAM predicting estimate of abundance. Bathymetric contours of 50 m, 100 m, and 200 m also shown. CPUE expressed as  $\ln(\text{ind./km}^2)$ .

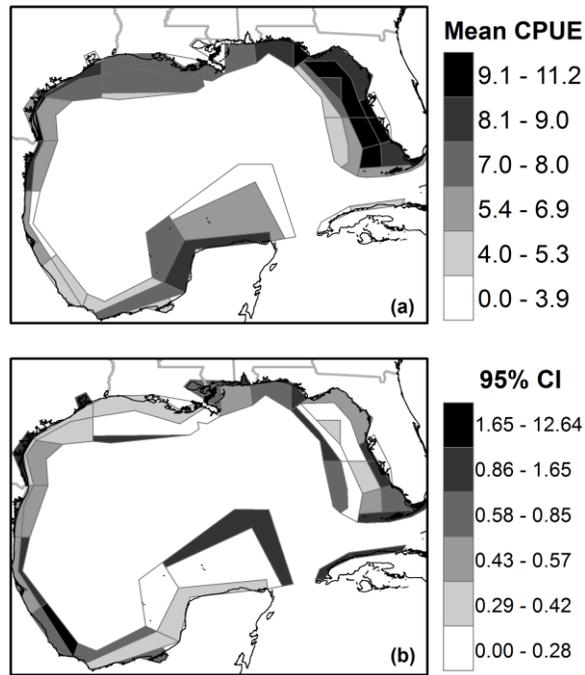


Figure 2.6. Aggregated model results. Example of the spatial aggregation that can be performed from the GAM predictions of pink shrimp  $\ln(\text{abundance})$ . Mean CPUE  $\ln(\text{ind./km}^2)$  derived from Figure 2.5 is calculated according to (a) the box geometry of the Gulf of Mexico Atlantis ecosystem model and (b) the associated 95% confidence intervals ( $\pm \ln(\text{CPUE})$ ) for each box. The few boxes with a confidence interval greater than 1.65 did not have high spatial coverage and the results should be thrown out.

## **Chapter 3: Larval source-sink dynamics can inform spatial management: a Gulf of Mexico case study**

### **3.1 Abstract**

Connectivity is a major contributor to the overall dynamics of marine populations. However, it still remains challenging to describe connectivity on ecologically meaningful scales of time and space. A numerical particle tracking model was developed that incorporates two major connectivity processes; site specific larval production and oceanographic transport for an entire large marine ecosystem and over multiple years. These first order simulations were able to identify localized settlement patterns of 45 individual and groups of species. Larval settlement patterns were then compared to site specific larval production to identify source and sink populations. Simulations of white shrimp (*Litopenaeus setiferus*) indicated anomalous years of local recruitment and source sink areas that could be utilized to improve management.

### **3.2 Introduction**

Population connectivity is defined by Cowen and Sponaugle (2009) as the exchange of individuals among geographically separated subpopulations that comprise a meta-population. Connectivity is a major contributor to the overall population dynamics of marine species (Botsford et al. 2001). Variability in local recruitment, the degree to which marine populations are open or closed, and the relationship between genetic and ecological demographic connectivity underpins many of the foundations of marine ecology and fisheries management.

Ultimately, to properly infer demographic connectivity from genetics, it must be linked to estimates of local reproductive success and dispersal (Lowe and Allendorf 2010). However, it remains challenging to describe these characteristics on ecologically meaningful scales of time and space. The ability to describe population connectivity at the large marine ecosystem scale will allow a better understanding of the spatial and temporal population dynamics driving those ecosystems and lead to adaptable management approaches.

The main processes mediating population connectivity include spawning, dispersal, behavior, and survival. Given our limited ability to observe these processes models are needed to simulate connectivity dynamics. Numerical connectivity models, as opposed to classic analytical model that derive a single solution such as those illustrated by Botsford et al. (2001), utilize Lagrangian transport to simulate individual larval movement. This manuscript describes a numerical model that simulates site specific larval production and particle movement to allow greater flexibility in simulating connectivity dynamics over varying scales of time and space and integrating subpopulation effects into meta-population estimates relevant for fisheries management. .

The distribution of spawning stock biomass is one important component of population connectivity. Numerous studies have indicated that accounting for subpopulations may accelerate the recovery of depleted metapopulations (Berkeley et al. 2004; Hastings and Botsford 2006; Petigas 2010). The spatial structure of stocks plays a critical role in determining spatial recruitment subsidies (Sale et al. 2005). However, the spatial structure is often not considered in the context of fisheries management and therefore is not routinely estimated. Results from a Chapter 2 provided an estimate of the spatial distribution of spawning biomass for numerous

species and aggregate groups throughout the Gulf of Mexico (GOM) to inform the connectivity model described herein.

In addition to spawning distributions, the physical dispersal of larvae from those spawning grounds also affects population connectivity (Roughgarden et al. 1988; Caley et al. 1996). Simulation of the modeled oceanographic processes is likely the best tool to address questions pertaining to large scale dispersal pathways.

The GOM is a semi enclosed basin situated between the countries of Mexico, the United States, and Cuba. Circulation within the GOM is driven primarily by the Loop Current which enters through the Yucatán Strait, heads towards the north-western center of the GOM and loops back towards Cuba to the east, exiting through the Florida Straits (Sturges and Evans 1983). Variability in the loop current position causes the spinoff of anti-cyclonic eddies which move large parcels of water westward (Maul and Vukovich 1993). These eddies are thought to play a major role in the transport of larvae and nutrients throughout the GOM (Müller-Karger et al. 1991; Lee et al. 1992; He and Weisberg 2003).

Dispersal modelling efforts in the GOM include Lugo-Fernández et al. (2001) who studied the dispersal patterns of corals from the Flower Garden banks Northern GOM, the Connectivity Modeling System developed by Paris et al. (2013), and a Lagrangian particle model estimating coral connectivity in the southern GOM (Sanvicente-Añorve et al. 2014). These studies observe five modes of particle transport including transportation via eddies and Mississippi river to the west, some consistent westward transportation, recirculation, and entrainment in the Loop current.

In the GOM, management units are typically described using genetic connectivity (SEDAR 2011, SEDAR 2013) and fall into three main categories: a single unit for the entire

gulf as in the case of greater amberjack (SEDAR 2011), an east and west stock with the division occurring roughly between the Mississippi River and Cape San Blas, Florida such as with red snapper (SEDAR 2013), or shared stocks outside the GOM such as highly migratory pelagic fish (Teo and Block 2010). There have been numerous studies indicating these units actually represent sub-populations and are likely to play a significant role in the overall structure and dynamics of the meta-populations (Patterson 2007; Karnauskas et al. 2013).

Given all of the uncertainties regarding the spatial structure of marine populations in the GOM and difficulty in defining connectivity, this study incorporates two major connectivity processes; site specific larval production and oceanographic transport to estimate connectivity. Larval sources and sinks are then identified by comparing larval dispersal patterns to the distribution of adult spawning biomass. While more complex models exist that allow for larval behavior and fine scale regional oceanography (Paris et al. 2013, Weisberg et al. 2014), this approach provides a first order approximation of connectivity for a large number of data-poor species. Further, simulations are performed over an entire large marine ecosystem and over multiple years to identify source/sink patterns relevant at large (and aggregated) spatial scales. Results will be used to inform the larval connectivity pathways in the Atlantis – GOM ecosystem model (Ainsworth et al. 2015) for species that do not have previous connectivity information available. Applications of the source sink dynamics identified in this study will be further explored through additional policy testing using the Atlantis-GOM modeling environment.

### *3.2.1 White Shrimp*

The methods described in this manuscript were used to provide larval dispersal patterns in Atlantis-GOM for 45 functional groups. An example using white shrimp (*Litopenaeus*

*setiferus*) is illustrated in detail. Results and supporting information for other species can be found in the supplementary materials and in Ainsworth et al. (2015).

White shrimp primarily occur in the northern GOM where, along with other shrimp species in the same region, they comprise the GOM's most valuable fishery. White shrimp spawners have been identified depths of 3 to 31 m starting in late spring with peak spawning occurring in June or July (Turner and Brody 1982). After spawning, white shrimp progress through a series of larval stages and after 15-20 days attempt to enter an estuary on an inbound tide at which point they settle to the benthos. Recruitment of larvae to estuaries occurs between June and September in Louisiana with some variation in other estuaries Muncy (1984). The northern GOM is a critical region for white shrimp due to the abundant marshes are known to be important habitat for the white shrimp Muncy (1984).

### **3.3 Methods**

The connectivity and spatial structure of numerous populations in the GOM was assessed by combining previous adult distribution models with a particle tracking model that estimates the long term mean dispersal patterns of species. The resulting dispersal patterns are described conceptually as 'recruitment' throughout the manuscript, although processes of pre- and post-settlement mortality are not explicitly included. Individual particles represent the relative number of larvae produced at each location, where each larval particle is weighted proportional to the spawning stock biomass in the source location. Trajectories are defined via daily mean velocities averaged over several years based on a specific spawning date and larval durations collected from the literature (Table 3.1).

### 3.3.1 Spawning biomass

A generalized additive model (GAM) approach was used to predict the relative biomass of single species and aggregated species groups, termed functional groups henceforth, from climate scale environmental predictors. These methods and data follow those of Drexler and Ainsworth (2013), but estimate total biomass instead of abundance. Due to the large number of zero observations and the need for a single parsimonious model to make predictions for a large number of functional groups, a used a negative binomial distribution with an offset for effort (Barry and Welsh 2002). All models were fit using the ‘mgcv’ package in the R version 2.14.0 environment (Wood 2006) following the equation:

$$g(\eta)=s(\text{depth})+s(\text{temp})+s(\text{oxygen})+\text{factor}(\text{sediment type})+\text{offset}(g(\text{effort})) \text{ (Eq. 3.1)}$$

where  $\eta$  represents the expected biomass resulting from the generalization of the predictor terms according to the link function  $g$ . The biomass data was modeled using a negative binomial distribution with a log link function, including an offset, with equivalent link function, to allow for variations in effort. Function  $s$  is a thin plate regression spline fit to a given environmental parameter. The smoothness selection was fit using spline-based penalized likelihood estimation. Theta parameters, for dispersions, and weighted variable penalties were determined by Un-Biased Risk Estimator (UBRE) which is similar to an AIC rescaled (Wood, 2006). Estimation of the theta parameter was limited to a range of 1–10. An extra penalty was applied to each parameter as the smoothing parameter approached zero, allowing the complete removal of a term from the model when the smoothing parameter is equal to zero. This extra penalty allows for

partially automated model selection and is especially useful given the models broad application to numerous functional groups.

The site specific adult biomass was used as an index for fecundity or larval production, which typically exhibits a linear relationship to spawning biomass (Armstrong and Witthames 2012), to define the spatial reproductive output. Adult distributions were generated for a summer-spring and winter-fall seasons. The seasonal distribution coinciding with peak spawning was then chosen to represent the site specific spawning biomass for each group (Table 3.1 and Figure 3.1). Each individual particle was weighted according to the relative percent of total spawning biomass in the GOM occurring within each cell and referred to henceforth as larvae; which is technically a measure of the proportion of the spawning biomass and conceptually the number of eggs/larvae released at each site. Due to a few unrealistically high predictions of outlying adult biomass from the GAM, the highest 5 percent of those biomass predictions were set equal to the value representing the 95th percentile.

### *3.3.2 Dispersal and Connectivity*

A Lagrangian particle tracking model was developed to track larval drift for 45 functional groups which represent key trophic guilds in the GOM ecosystem. The spawning schedule for each of the modeled groups is shown in Table 3.1 and Figure 3.1. Daily particle movement for each individual was estimated from the mean daily velocities from the GOM HYCOM + NCODA experiment 20.1 (Chassignet et al. 2007). The HYCOM + NCODA utilizes the Navy Coupled Ocean Data assimilation system (NCODA) to incorporate satellite altimetry data with in-situ observations such as those of ARGO floats and moored buoys into a single data framework. These observations are then incorporated into the Hybrid Coordinate Ocean Model (HYCOM) which utilizes a hybrid coordinate approach - isopycnal coordinates in the open

ocean, terrain following coordinates in shallow coastal regions, and z-level coordinates in the surface mixed layer.

Particle movement was tracked as follows: (1) the entire GOM was seeded with 25669 equally spaced particles (Figure 3.2); (2) each particle was assigned a site specific proportion of total spawning biomass which represented the number of larvae produced; (3) each particle was then released on the day of year corresponding with the peak in the spawning cycle (Figure 3.1; Table 3.1) and tracked over their entire larval duration; (4) daily movement of each particle was estimated by identifying the four nearest reference grid points in the GOM HYCOM model ( $1/25^0$  resolution), averaging both the u and v vectors as 0, 5, and 10m depths for each reference point, and then averaging the depth averaged velocity across all four reference points. The final particle locations and their respective weighting at the end of each spawning cycle were then recorded; (6) the sum of the weighted larval transported to each grid cell was then calculated for each year simulated from 2003-2009 for both the fine scale  $1/25^0$  resolution, as well as by the Atlantis-GOM polygons.

Connectivity, measured as long-term settlement of larvae, was then estimated by running larval dispersal simulation over seven years from 2003-2009 resulting in an a total number of larvae for each high resolution cell, or low resolution Atlantis polygon, after 7 spawning cycles. As a result, the final connectivity index combines long-term estimates of site specific larval production and drift indicating the relative strength of population connectivity between each region. The index also captures the mean relative displacement distance of larvae that is likely to occur given the annual oceanographic variability during those years which include two La Niña events and several large hurricanes including Katrina.

### 3.3.3 Source/Sink Dynamics

The source sink dynamics were estimated as the difference between the fractions of total larvae emitted ( $P_e$ ) and the fraction of total larvae absorbed from each grid cell within the model (Eq. 3.1).

$$\sum(Pe_i - Pa_i) \quad \text{Eq. 3.1}$$

### 3.3.4 White Shrimp

The results of model simulation pertaining to white shrimp are described in detail throughout this manuscript, specifically the dynamics occurring in the northern GOM where the population is centered. The distribution of white shrimp was estimated using the GAM model from SEAMAP observations (Rester 2011) occurring during the spring/summer season which corresponds with the peak spawning months. White shrimp were simulated by releasing the particles on June 1st of every year and tracked for their estimated 30 day larval duration. The resulting larval distribution maps and source sink indices are shown. In addition, the final displacement of each particle was also summarized to identify anomalous years of recruitment to the northern GOM.

### 3.3.5 Other GOM functional groups

A similar approach was applied to the remaining functional groups in Figure 3.1. Site specific biomass, spawning dates, and larval durations were applied separately to each group to initialize the simulation and the resulting settlement and source and sink patterns were summarized.

## 3.4 Results

### 3.4.1 Spawning Biomass

For white shrimp the GAM described 43.4% of the deviance between observed and predicted biomass (Chapter 2). GAMs fit to the additional functional groups found in the appendices explained between 10% and 83% of the total deviance with a median value of 33.6%. Detailed GAM modeling results for these groups can be found in Drexler and Ainsworth (2013). The parameters of depth, surface Chl a, bottom temperature and sediment factors of mud and sand were all found to have a significant effect on white shrimp biomass ( $p < 0.01$ ). Dissolved oxygen was not found to be significant. Sediment type was included as a categorical variable. Both mud and sand were found to be highly significant ( $P < 0.02$ ) predictors of white shrimp biomass while gravel and hard bottom were not.

Observations of white shrimp in the SEAMAP database occurred in depths ranging from 21 up to 191m (Figure 3.4). Biomass of white shrimp indicated a positive relationship with depth occurring between 10 and 40 m. Depths greater than 40m and shallower than 10 m exhibited decreased biomass of white shrimp. Depths beyond 70 m also exhibited a sharp drop in white shrimp biomass. Temperature data ranged between 6.6 and 36.6°C. Bottom temperatures were found to exhibit a positive relationship with predicted biomass up to 25°C. Locations with bottom temperatures greater than 25°C were not favorable for white shrimp, and exhibit a strong negative relationship. Surface chlorophyll exhibited a positive relationship to biomass at levels above 2 mg/m<sup>3</sup>. The contribution of chlorophyll to total biomass remains relatively flat for most values above this threshold, and starts to decrease at values above 30 mg/m<sup>3</sup>. Overall the GAM fits of adult biomass to environmental descriptors were in good agreement with Muncy 1984 and Turner and Brody 1983; spawning depths between 10-40 m,

optimal bottom temperature of 25°C, a positive relationship with primary productivity, and a preference for soft substrates.

The predicted distribution of white shrimp estimated large proportions of white shrimp occurring in the northern GOM centered on Louisiana. The predicted plot bears a strong resemblance to the distribution of white shrimp from Muncy (1984). The GAM model also predicted white shrimp to occur on the shallow portions of the West Florida Shelf and the southern Mexico. Compared to these other areas, white shrimp in the northern Gulf occur at higher densities and in deeper waters (88-95°W). Also, there are relatively few white shrimp occurring east of Mobile Bay (88°W) in the northern gulf.

#### *3.4.2 Dispersal and Connectivity*

The annual dispersal pathways of the five regions contributing the greatest proportion of the total larvae to the region representing the northern GOM are shown in Figure 3.4. Regions coincide with the spatial configuration of the Atlantis-GOM model. These regions also roughly coincide with the center of population biomass (Figures 3.4 and 3.5). In general most particles released inshore of the shelf remained on the shelf. Those particles that were swept off the shelf became entrained in a number of hydrodynamics features including the loop current and westward moving eddies. East and west movement appears to be highly dependent on the annual oceanographic conditions. Years 2003, 2005, 2006, and 2008 carried particles onto the western-GOM shelf as far as Brownsville, Texas, while other years experienced no recruitment in that same area. Eastward movement of particles from these regions was common, but very few particles that traveled east were able to move onto the West Florida Shelf. Some shoreward easterly movement of particles did occur around Mobile Bay and in some years the Florida

Panhandle. Year 2009 was a particularly strong year for recruitment to the Florida Panhandle as most other years did not receive many recruits.

The displacement distance of every particle for white shrimp larvae was summarized to identify potential anomalous recruitment years (Figure 3.5). Overall the average displacement of all of the larvae released was centered around 250km. The outlying displacement varied between years with some particles travelling as much as 1500km from their release point. The displacement distances of each particle recruiting to the northern GOM region (for all the boxes in the GOM and not just the sources identified in Figure 3.4) varied annually. Years 2006 and 2009 showed a higher average displacement distance than all other years (Figure 3.5).

Roughly 18% of total white shrimp recruitment in the GOM occurred in the northern GOM region. Over 83% of the total recruitment to the northern GOM regions was self-recruitment originating from the same region. The annual contribution of self-recruitment to the northern GOM box ranged from 61% to nearly 100%. The other four regions contributing to the recruitment in the northern gulf were the adjacent and inshore of the target northern-GOM region (Figure 3.6). Each of these regions contributed 6% or less of total recruitment on average.

### *3.4.3 Source/Sinks*

The source/sink index was estimated as the average larvae absorbed over all of the years simulated minus the larvae produces for each grid cell. Source and sink patterns for white shrimp did not appear to be a direct function of spawning biomass nor average recruitment; but an interaction of the two (Figure 3.7). Strong sink regions occur along the Texas coast and Yucatan Peninsula in addition to offshore habitat where white shrimp do not occur. Moderate sinks occur at mid-depth on the West Florida Shelf, south of Mobile Bay, and offshore of Texas. Relative source areas included some inshore habitat along Louisiana and Texas. Shallow to

moderate depths on the West Florida shelf also indicated a source habitat index. Despite the relatively high proportion of larval self-recruitment in the northern GOM this region was still identified as net source of larvae.

#### *3.4.4 Other GOM functional groups*

In general the settlement patterns generated across multiple groups had a few commonalities (Appendix D). First, there was little to no recruitment occurring near the Straits of Yucatan for any of the groups modeled. Second, most functional groups had fairly broad dispersal patterns with particles arriving to every area of the GOM. Last, while not consistent across every group, the highest density of settlement occurred on the shelf break and inshore areas on the WFS and the shelf break of the eastern Yucatan peninsula, depending on the group.

Source areas tended to occur offshore near the shelf break for the range of groups simulated (Appendix E). The region of those sources along the shelf varied by species. Similar to the area of high settlement, the WFS was identified as sink more often than any other region across all of the groups.

### **3.5 Discussion**

This study develops a framework that can be readily used to estimate population connectivity and spatial recruitment as a function of spatially explicit spawning biomass given limited direct observations of biomass. Since the HYCOM oceanography model is global in scale, this approach can be adapted to any large marine ecosystem. Given estimates of site specific adult biomass and recruitment, a comparison of the two allows for the investigation of spatial source/sink dynamics. These types of simulations are excellent for providing a first order approximation of connectivity to inform ecosystem based models and assessments. The results of this study, including the additional species simulated in Appendices A-C, will be used to

inform a full ecosystem model for the GOM (Atlantis-GOM; Ainsworth et al. 2015) and define connectivity between regions. As with any model, the model results discussed in this paper are bound by the implicit assumptions within the model. The major assumptions in this model include lack of larval behavior, homogenous predation mortality over time and space, and the inability to account for larvae entering from the Caribbean.

It is worth noting that biological movement including direct swimming and selective transport cannot be ignored on a local scale. Unfortunately, information pertaining to larval behavior is rare, especially for non-commercial species like those functional groups simulated in the appendices. Since the larval behavior of many species is not known, the inclusion of behavior may introduce unfounded assumptions. Nevertheless several studies have identified a dominance of physical transport over biological behavior as dictating larval movement (Kim et al. 2010). This is especially true for connectivity of populations on the scale of large marine ecosystem such as the GOM, and when considering larval movement between large Atlantis polygons. Further studies that incorporate animal behavior may be better suited to develop connectivity estimates, especially for local scale questions. Here I provide a first order approximation of larval connectivity which likely represents the high end of transport distances (Cowen and Sponaugle 2009). However, fine scale movement is not considered in Atlantis due to spatial aggregation.

The fine scale dynamics of larval predator interactions and density dependent survival are not practical to simulate on a broad scale but will undoubtedly act as a significant modifier to the source sink dynamics of the system. The source/sink dynamics are estimated as simple ratio of larvae produced and larvae received. The inclusion of site specific carrying capacity via Beverton-Holt stock recruitment dynamics may further improve simulation results.

Conveniently, The GOM is a semi enclosed basin with a uni-directional flow of surface water in through the Straits of Yucatan, and out the Straits of Florida. This model explicitly considers the proportion of particles exiting the GOM through the Florida straits, but not the contribution of larvae entering the system from the Caribbean. Thus, the source sink ratio may be skewed in some areas, particularly those areas in the southeastern GOM as well as those areas strongly affected by the loop current and larval contributions from the Caribbean.

Depth appears to be a strong driver of the predicted distribution of white shrimp. However, depth, surface Chl a, bottom temperature and sediment all contributed significantly to the overall fit. This is evidenced by the differences between the depths inhabited by white shrimp in the northern western GOM as compared to other areas, where white shrimp only occurred inshore. It appears that this strong influence of depth to overall model fit may have overestimated the levels of white shrimp along the coast of Florida. While present, white shrimp are not observed in great densities in this area. Further improvements to the adult distribution model fit may be achieved by adding additional species specific parameters, although the goal of this study is to develop a generalized framework for all the species.

Overall, the connectivity of white shrimp to the northern GOM, representing the center of the population distribution and the fishery, appears to be mainly driven by self-recruitment over this general area. Exchange of particles between the western and eastern GOM did occur, but on a relatively smaller scale. Many of the previously identified modes of physical transport in the GOM were also identified in this study and suggests general agreement with both observational and modeled dispersal studies.

In summary, the framework developed in this study proved useful for simulating populations on a larger marine ecosystem scale. Coupling dispersal studies with site specific

spawning biomass allows further comparison of spatial source and sink metapopulations that may be utilized to design effective closed area management that encourages spillover effects to increase fisheries yield.

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### 3.7 Tables

Table 3.1. Spawning data used to estimate the spawning schedule for each simulated species or group of species in the Gulf of Mexico

Group	Est. Spawning date	Source
Small demersal fish	January 22nd	Ainsworth et al. 2015
Sheepshead	Early Spring	Jennings (1985)
Blue marlin	Spawn in Caribbean	Ainsworth et al. 2015
Red grouper	April	Coleman et al. 1996
Pink shrimp	Peaks in August	Bielsa et al. 1983
Black drum	January	Nieland and Wilson 1993
Gag grouper	Mid-February	Coleman et al. 1996
White shrimp	March - Sept	Fishwatch.org
Other shrimp	April 31st	Ainsworth et al. 2015
Flatfish	November	Gilbert 1986
Brown shrimp	Feb.-Aug.	Hart 2012
Lutjanidae	July-Aug.	Domeier et al. 1996
Other demersal fish	July-Aug.	Ainsworth et al. 2015
Deep serranidae	Feb. to Nov.	SEDAR 22
Jacks	March to early Sep.	Richards 2006
White marlin	Spawn in Caribbean; April-June	Ainsworth et al. 2015
Small reef fish	June 12th	Ainsworth et al. 2015
Other tuna	June 29th	Ainsworth et al. 2015
Bluefin tuna	April to June	Teo et al. 2007
Greater amberjack	March, April and May	Harris 2004
Little tunny	April through Nov.	Ainsworth et al. 2015
Vermilion snapper	June to Aug.	Fishwatch 2015
Bioeroding fish	July 17th	Ainsworth et al. 2015
Large reef fish	July 17th	Ainsworth et al. 2015
Ladyfish	September 2nd	Zale and Merrifield 1989
Pompano	July 17th	Ainsworth et al. 2015
Other billfish	July 17th	Ainsworth et al. 2015
Deep water fish	July 17th	Ainsworth et al. 2015
Medium pelagic fish	July 17th	Ainsworth et al. 2015
Large pelagic fish	July 19th	Ainsworth et al. 2015
Swordfish	Year-round	Ainsworth et al. 2015
Spanish sardine	spring and summer	Houde et al. 1979
Mulletts	Fall-Winter (Nov.)	Ibáñez and Gutiérrez Benítez 2004
King mackerel	May-Sept	Ainsworth et al. 2015
Menhaden	Oct.-March	Ainsworth et al. 2015
Seatrout	June through August	McMichael and Peters 1989
Sciaenidae	November to February	Handes 1969
Spanish mackerel	May through September	ICCAT 2014
Red snapper	May through September	Collins et al. 1996
Yellowfin tuna	July-August	Lang et al 1994
Shallow serranidae	September 16th	Ainsworth et al. 2015
Small pelagic fish	September 16th	Ainsworth et al. 2015
Snook	May-Sept	Taylor et al. 1998
Red drum	Mid August - October	Wilson and Nieland 1994
Scamp	Late Feb-Early June	Coleman et al. 1996
Pinfish	November to March	Hansen 1969
Corals	September	Gittings et al. 1992

### 3.8 Figures

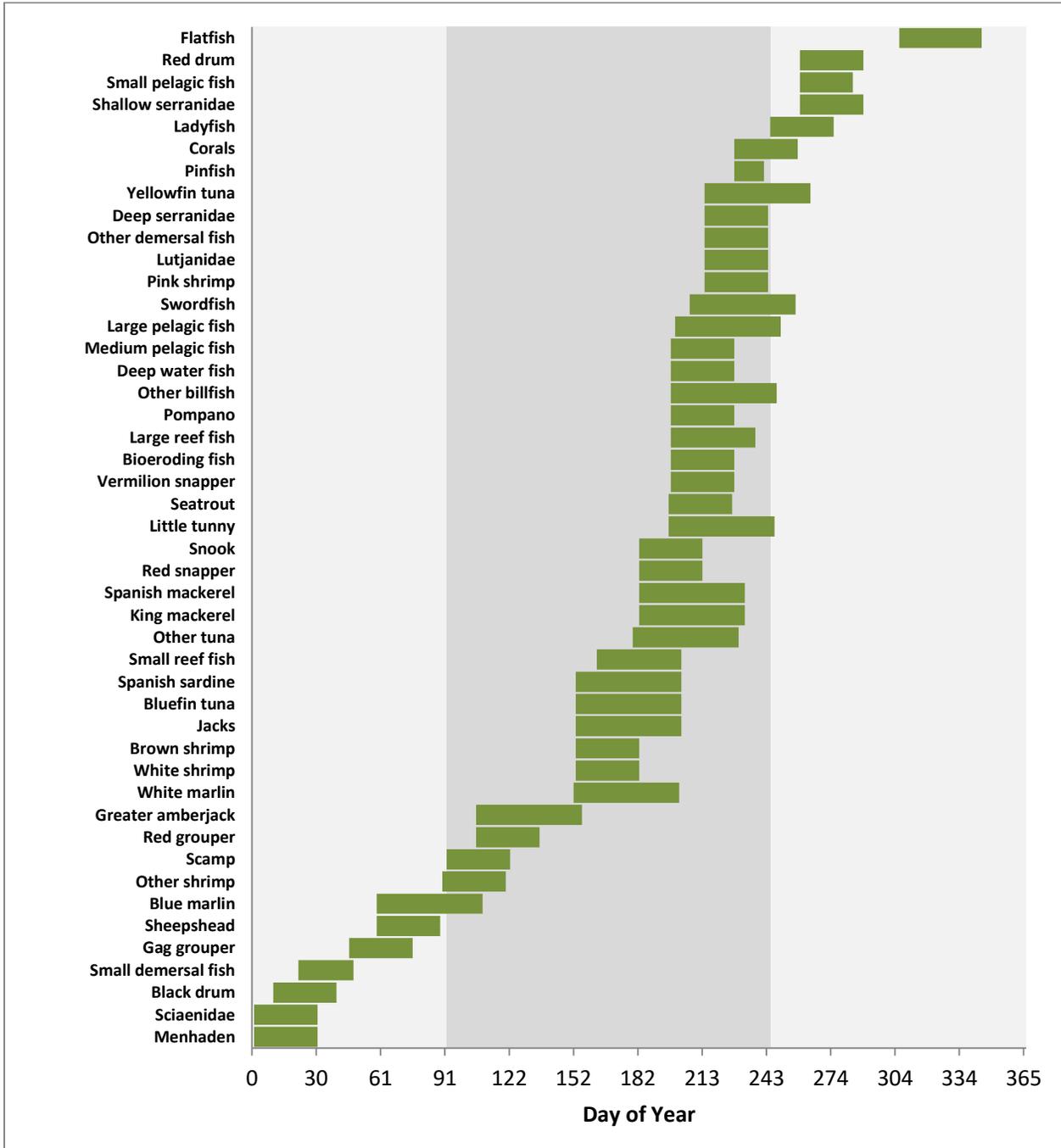


Figure 3.1. Spawning calendar for those species and species-groups modeled in this study. Grey bars represent the larval duration for each after the release date. Release dates coincide with peak spawning dates from the literature. Days 91 – 244 represent those groups with peak spawning biomass represent from the summer-spring distributions for the GAM model. Those groups with peak spawning outside those days were represented by the summer-spring distributions

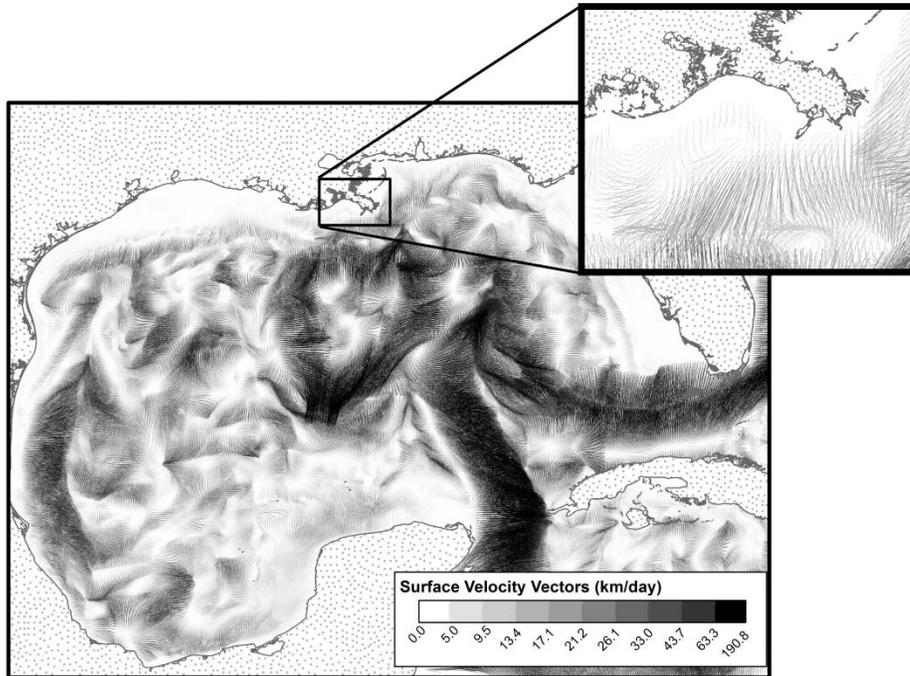


Figure 3.2. Example daily surface velocities for day 232 of year 2005 at each  $1/25^\circ$  observation from the HYCOM oceanographic model (Chassignet, 2007).

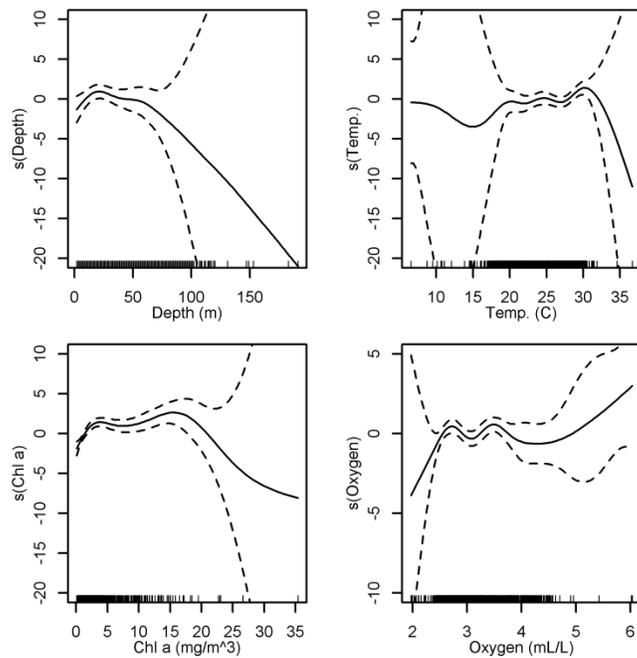


Figure 3.3. Smoothed curve of the additive effect to the predicted biomass of white shrimp for the individual environmental parameters in the GAM. Dotted lines represent 95% confidence intervals, marks along the lower axis represent a single observation. A straight line represents an additive effect of zero.

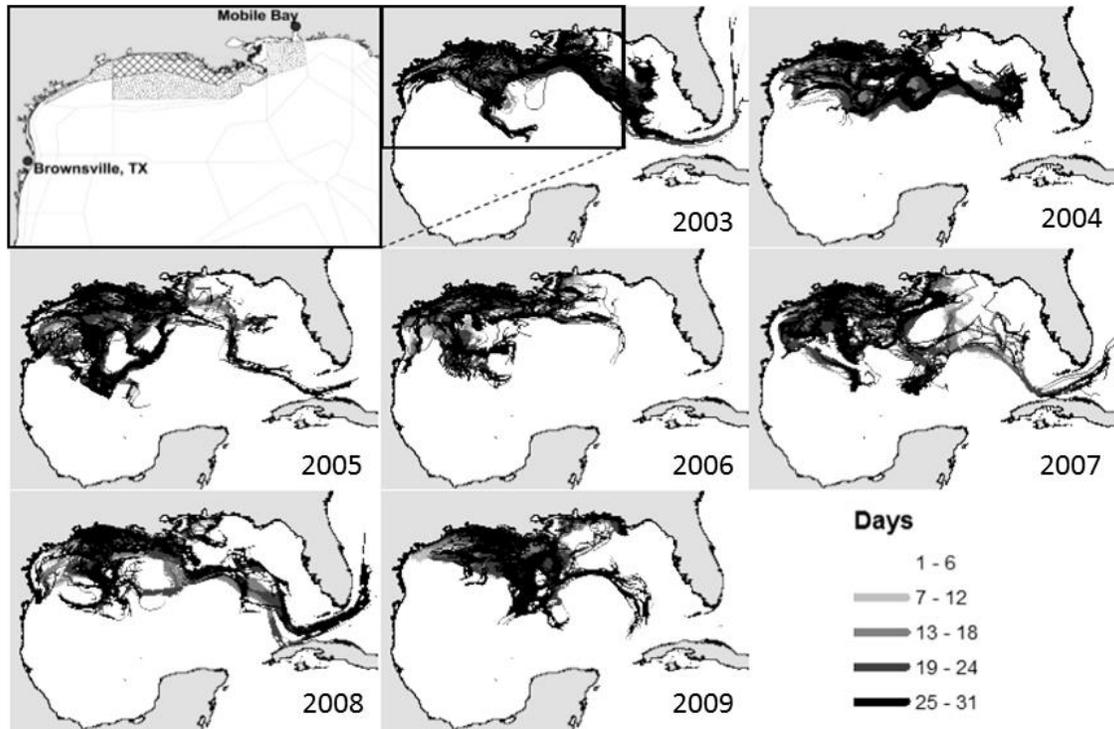


Figure 3.4. Annual particle trajectories from the top five polygons contributing larvae to the target box (upper left) in the northern GOM.

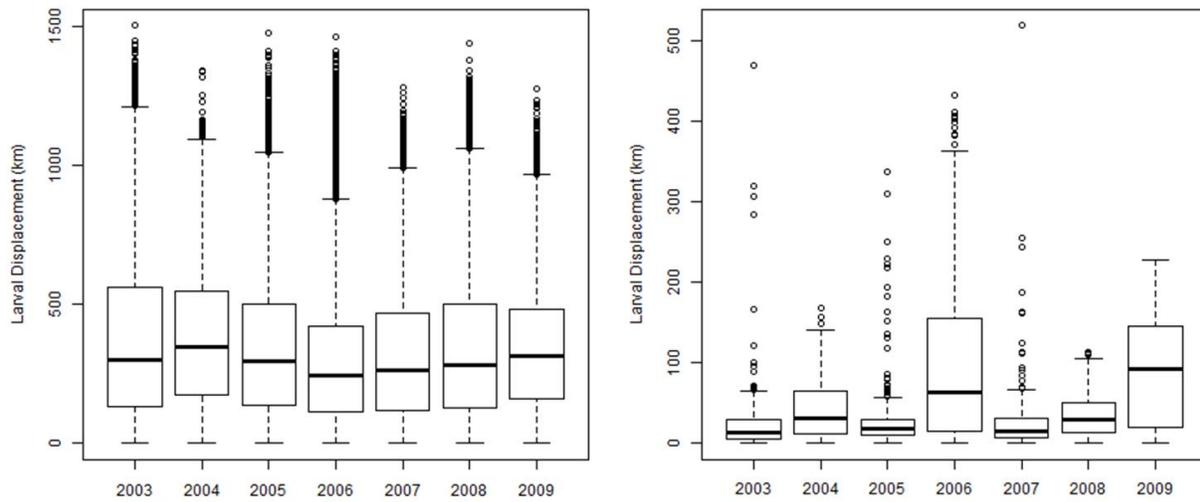


Figure 3.5. Annual displacement distances of white shrimp particles released throughout the entire GOM (left) and those particles recruiting specifically to the northern GOM target region.

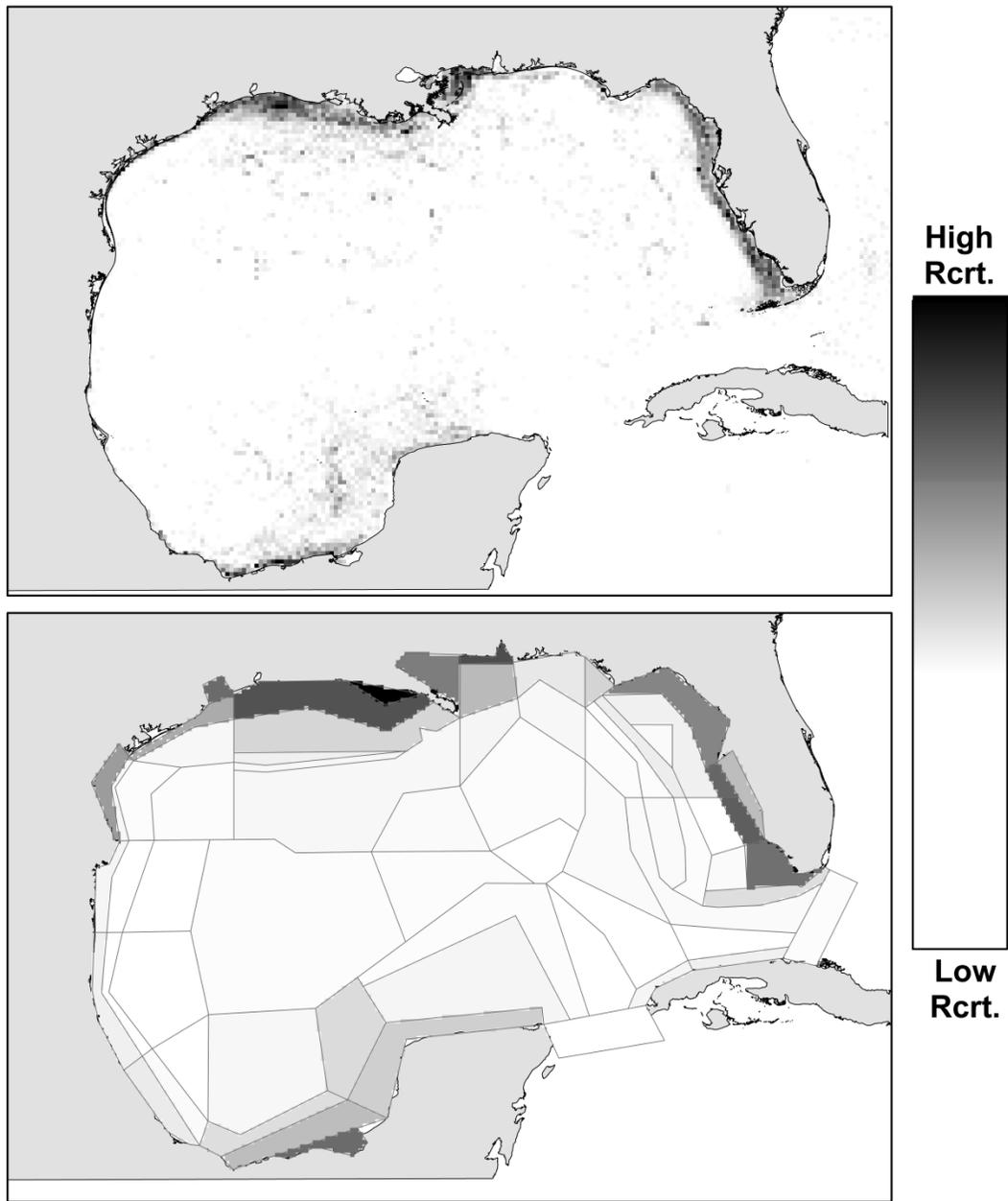


Figure 3.6. Relative larval settlement patterns for the simulated years 2003-2009 at both a high resolution (top) and summarized by Atlantis-GOM regions (bottom).

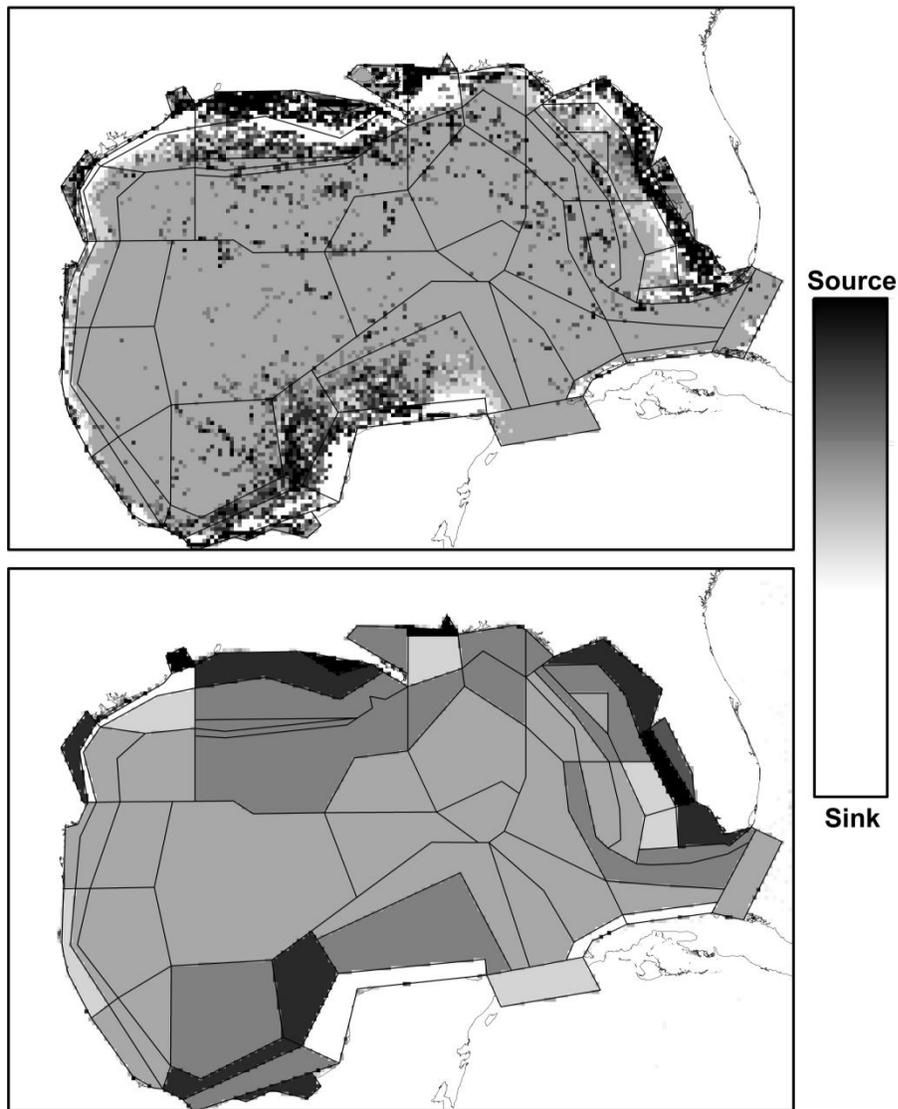


Figure 3.7. Source sink index representing the difference between larvae emitted and larvae absorbed in each grid cell across the simulated years (2003-2009). Light areas represent sinks, where larvae absorbed is greatest, or where larvae arrive to areas with no adult biomass. Dark colors represent areas receiving few larvae or those areas with very high adult biomass. Results are summarized at both a high resolution (top) and summarized by Atlantis-GOM regions (bottom).

## **Chapter 4: Investigating the use of Marine Protected Areas to achieve fisheries management targets using an end-to-end ecosystem model of the Gulf of Mexico**

### **4.1 Introduction**

From a management perspective, the connectivity of species is embodied by concept of a unit stock, or management unit, under national standard three of the Magnuson-Stevens Fishery Conservation and Management Act (2007). Management units are most often defined as a genetically linked population, thereby assuming a well-mixed population, able to recover across its entire range in the absence of fishing (Zatcoff et al. 2004). While this is a practical and often necessary basis to define a management unit, this definition of a population ignores spatial structure that may be important on shorter fishery management timescales, as opposed to evolutionary ones (Riess et al. 2009). Understanding connectivity within a management unit is important to designing effective management approaches, especially when designing MPAs or closed areas in order to ensure the resulting spillover effects outweigh fishing restrictions (Palumbi 2003).

In the Gulf of Mexico (GOM), most reef fish stocks do exhibit spatial structure, whereby localized depletions due to fishing patterns, geographical structure, and connectivity may lead to semi reproductively isolated subpopulations. For example, red snapper is known to exhibit at least two subpopulations (Gold and Saillant 2007, Karnauskas et al. 2017) and anecdotal information and expert opinion from fishers suggest these subpopulations can be divided into

east/west by the mouth of the Mississippi river, or by Cape San Blas in the panhandle of Florida (SEDAR 2018). By definition, the population dynamics of these semi isolated sub-populations can operate independently of one another over the short term yet are genetically linked to one another over evolutionary time scales. The scale of connectivity between these two units and international waters is an area of active research (Hollenbeck et al. 2015, Sluis et al. 2015) and a key component to estimating sustainable fishing rates for the combined stock.

The work from the previous chapters simulates larval dispersal patterns in the GOM. This chapter aims to integrate additional processes of population connectivity and productivity of subpopulations by incorporating connectivity information from previous chapters into an end-to-end ecosystem model. Previous studies using the Atlantis ecosystem model have relied on simplistic assumptions about recruitment over space whereby spawning and recruitment occurring in the same location (Brand et al. 2007, Fulton et al. 2007 Link et al. 2010, Ainsworth et al. 2011, Ainsworth et al. 2015). Therefore as a first step towards understanding how population connectivity can affect the productivity of subpopulations, the sensitivity of the Atlantis-GOM ecosystem model to larval dispersal patterns needs to be evaluated. The validity of the common assumption of local recruitment in the GOM (Suprenand et al. 2015, de Mutsert et al. 2016) and whether that assumption has a strong influence on the spatial distribution of productivity and safe fishing rates is also evaluated.

The full model, which includes connectivity information, is then used to evaluate a range of closed area fishery management scenarios for the GOM to assess their utility for management. The results of these analyses are not intended to provide tactical management advice as there are a number of simplifying assumptions applied to each functional group. These assumptions should be addressed on a species by species basis and include the vertical movement of larva,

refining the spatial distribution of younger age classes, simulating extended spawning seasons, and incorporating movement associated with spawning aggregations. However, the results of this study are meant to help us understand the importance of non-stationary recruits in the ecosystem functioning of the GOM and develop a framework to be expanded upon for implementation in a management context.

#### *4.1.1 Atlantis ecosystem model*

Atlantis is an ‘end-to-end’ model which represents trophic dynamics from apex predators to primary producers, fisheries, nutrient dynamics, microbial cycles, habitat, and physical oceanography in a three-dimensional, specially-explicit domain using a modular structure. In the GOM the Atlantis–GOM model has been used to evaluate the cumulative impacts of the Deepwater Horizon oil spill (Ainsworth et al. 2018) and develop ecological indicators for fisheries management (Masi et al. 2017). In addition to providing a spatial simulation tool to evaluate policy, Atlantis also incorporates several other components of connectivity not considered in previous chapters. For example, Atlantis simulates spatial primary production and detritus dynamics which can affect early life stage survivorship, diet connectivity of both predators and prey, and adult movement. All of these important dynamics affect connectivity, especially on temporal scales likely to be impacted by management decisions. Providing realistic spatial corridors of larvae transport from one region to the next in Atlantis provides a platform to integrate across all components of species connectivity and begin to understand how this may affect the management of reef fish.

The model extent is divided into 66 polygons, each containing up to 7 depth strata and spans the entire GOM including Mexican and Cuban waters. The Atlantis GOM model uses the Navy Coastal Ocean Model (NCOM) – American Seas model (AMSEAS) to force temperature

and salinity fluxes. Food web dynamics are simulated for 91 functional groups: including reef fish (11 groups), demersal fish (12), pelagic fish (15), forage fish (4), elasmobranchs (6), shrimp (4), seabirds (2), mammals (4), sea turtles (3), commercial benthos (3), structural species (4), macrobenthos (3), filter feeders (3), primary producers (8), pelagic invertebrates (4), and nutrient cyclers (4). The tuned model – without dispersal- recreates biomass, catch, and effort trends in the GOM from 1980 to 2010 based on historical catch and biomass data. The model also includes fisheries fleet dynamics representing the main fishing fleets in the US, Mexico, and Cuba.

#### *4.1.2 Connectivity*

Larval dispersal tends to be the most poorly understood component of population connectivity on a localized scale (Cowen and Sponaugle 2009). A number of sophisticated models of larval dispersal, specifically those that incorporate larval behavior, have been developed (James et al. 2004, Paris et al. 2007, Paris et al. 2013). However, most of these models rely on information that is not known for most species. For example, the vertical position of larvae in the in the water column and active swimming behaviors are thought to have important consequences for movement (Gerlach et al. 2007, Weisberg et al. 2014). In lieu of this information, a reasonable assumption could be to assume either surface or bottom transport of larvae as default; this chapter assumes surface transport. While the assumptions of surface transport may not be appropriate for some species the overall simulation can still inform the importance and feasibility of understanding connectivity in a management context. For example, even if the pattern of larval transport used in Atlantis does not represent reality, closing source and sink areas in Atlantis will still give us a representative picture of such a management decision. Furthermore, the combination of studies developed in this dissertation provide a

framework to incorporate connectivity information into ecosystem simulation models – useful for capturing the full range of mortality processes for management advice.

#### *4.1.3 Spatial Closures*

##### *4.1.3.1 Status Quo*

A large number of spatial closures have been implemented in the GOM, which aim to achieve the full range of goals typically associated with MPAs including conservation of biodiversity and habitat, fishery management, research and education, enhancement of recreation and tourism, maintenance of marine ecosystems, and protection of cultural heritage (Showalter and Schiavinato 2003). While very few MPAs, or closed areas, restrict fishing completely there are a number of restrictions in place, especially for bottom gears such as bottom longline, traps, and trawls (GMFMC 2018). For example, Marine sanctuaries such as the Flower Garden Banks protect important coral habitats by limiting contact by bottom fishing gear but allowing other forms of fishing (Figure 4.1). Coleman et al. 2004 estimate that there are 16 closed areas that affect reef fish or shrimp fishing in the GOM.

##### *4.1.3.2 Scenarios*

This chapter simulated the closures of source and sinks areas to fishing and evaluated their relative performance in terms of expected catch and biomass. All of the area closures simulated restrict all fishing in that area; i.e. they are no take closures. A source larval area is considered an area that produces more larvae than it absorbs, and a sink area absorbs more larvae than it produces. Benefits of source and sink area closures are also evaluated relative to the status quo scenario. Source and sink scenarios close the top 3 or 10 source or sink polygons for the reef fish complex. The status quo scenario is a representation of the real life gear-specific seasonal and annual fishing closures in the GOM, In addition, a ‘generic’ closure scenario is

evaluated that represents spatially homogeneous closures per unit area over the entire GOM which increase in size from 0-100%. This is equivalent to a randomized placement of MPAs. Larval trajectories were calculated outside of Atlantis using a Lagrangian particle tracking model driven by one-way coupled hydrodynamic data in Chapter 3. Each dispersal propagule (distributed over an equally spaced grid) was weighted by the total relative biomass of spawners at each location as a proxy to the number of larvae produced across a  $0.1^{\circ}$  latitude and longitude grid as determined in Chapter 2 and Drexler and Ainsworth (2013). From these trajectories, a connectivity matrix was developed representing how many weighted particles, or recruits, each polygon in the Atlantis map contributes to each other polygon.

## **4.2 Methods**

The Atlantis ecosystem model for the GOM was used as an operating model to simulate the impacts of various closed area scenarios to biomass and fishing. Spatial biomass (Chapter 2) and dispersal patterns (Chapter 3) were incorporated into the Atlantis model to define the spatial biomass and dispersal patterns of all of the functional groups in the model.

The full parameterization of the Atlantis model can be found in (Ainsworth et al. 2015). Key components relevant to simulating reef fish management are discussed here.

### *4.2.1. Biology*

Abundance and biomass, measured as (mg N, were tracked for each consumer group, including most fish species, for 10 age classes. Life history data for functional groups were collected and in the case of multispecies groups the average life history parameters (natural mortality, Von Bertalanffy growth rate  $k$ , length at infinity  $L_{\infty}$ , length-weight parameters  $a$  and  $b$ , and age at maturity) were used to develop growth rates and specify the proportional distributions of weight and numbers for each age group for a given functional group. Energy

transfer through the system is tracked as mg N and driven mainly by predation across all of the functional groups moderated by the assimilation efficiency and converted into predator biomass using the Redfield ratio. The maximum growth rates of primary producers are fixed however the realized growth rates are modulated by nutrient and light limitation.

Functional groups dynamics (growth, spawning, mortality, etc.) for groups that migrate or spawn outside of the Gulf of Mexico, such as highly migratory species and mammals, occur within the boundary boxes of the model but their dynamics are not connected to the GOM polygons until they explicitly migrate back into the model domain.

#### *4.2.2 Recruitment*

Most functional groups utilized a Beverton-Holt stock recruitment relationship to determine the number of offspring in a given year (Equation 4.1).

$$Rc = \frac{Sp \cdot BH\alpha}{Biom + BH\beta} \quad (\text{Equation 4.1})$$

Where BH $\alpha$  and BH $\beta$  are species-specific Beverton-Holt alpha and beta parameters, Sp is the actual spawn produced when accounting for individual fitness (mgN) and Biom is the species total biomass, independent of fitness. Large sharks, bird, and mammal groups reproduced as a fixed number of offspring per individual per year and do not account for density dependence to estimate production.

#### *4.2.3 Predator Prey interactions*

Trophic interactions were defined following the methods of Masi et al. (2014). Briefly, a probabilistic approach to analyzing existing stomach content data was used to generate a food web matrix for each functional group. Each diet interaction was based on the mode of a

statistical distribution representing the most probable contribution of prey to each predator's diet. Stomach content data was primarily collected from Florida Fish and Wildlife Research Institute and one supplemental study in Masi et al, (2014) and then expanded in Tarnecki et al. (2016) to include more data from the northern and western GOM. Note that a later contribution (Morzaria-Luna et al. in press) used the full statistical distribution of diet interactions in a sensitivity analysis of Atlantis behavior. Predation and consumption in Atlantis generally follows a Holling's type 2 functional response (Hollings 1959) which features density dependent rates of consumption based on the encounter rate of predator and prey. As implemented in Atlantis, this functional response requires two parameters, MUM, which is a measure of the maximum (asymptotic) production rate that a predator realizes when the encounter rate is at its maximum, and clearance (C), which represents the slope of the functional response near the origin where predator density is low.

#### *4.2.4 Dispersal*

Settlement patterns of 45 GOM functional groups were estimated according the larval dispersal model in Chapter 3. This model links site specific spawning biomass throughout the GOM to a Lagrangian transport model. Aggregated dispersal patterns were generated by tracking over 25,000 particles over several spawning cycles using daily time steps (Figure 4.2). The mean settlement patterns of all of the functional groups simulated were incorporated into the Atlantis model. This was done through a connectivity matrix which defines the relative contribution of the first age group from a given source polygon to each receiving polygon. Therefore recruitment was calculated as a function of the Beverton-Holt stock recruitment relationship (estimated from the entire mature population), allocated proportionally to the mature population in each box and then further distributed via the dispersal matrix.

#### *4.2.5 Model sensitivity*

An initial comparison of the Atlantis model to sensitivities in dispersal was first evaluated by comparing the differences in the base model (without dispersal) to the model with dispersal included with respect to spatial reef fish biomass.. Given the different model dynamics some additional tuning of the Beverton-Holt parameters (mainly BH alpha) was required. The sensitivity of the overall model to the inclusion of dispersal is then evaluated.

#### *4.2.6 Closed Areas Management Scenarios*

Several hypothetical closed area scenarios were developed for management strategy simulation. Closed areas tested include those areas identified as larval source and sinks in the previous chapter, areal closures of 0, 10, 25, 50, and 100% and the status quo - representing the current day configuration of closed areas (Table 4.1).

##### *4.2.6.1 Status quo*

The development of the status quo closed area scenario is outlined in Ainsworth et. al. (2015) and reproduced in this section. The GOM contains a large number of spatial closures and areas of protection (Figure 4.1). Several efforts have been made to synthesize a complete record of marine protected areas in the GOM although a comprehensive document spanning all three countries does not currently exist. These efforts include spatially referenced databases (e.g., United Nations 2018Frick 2011) and several manuscripts (Yáñez-Arancibia 1999, Beck and Odaya 2001, Coleman et. al 2004). In addition to these large closures, the MPA spatial databases listed hundreds of additional MPAs within the GOM. The size, scope, and restrictions of each individual MPA varied widely.

A merged GIS layer was created from the MPAs listed in each database from Cuba, Mexico, and the USA. From that layer the proportion of each Atlantis-GOM polygon affected

by each MPA listing was calculated. The year of implementation and any seasonality associated with these restrictions was also included as layer information. When data pertaining to fisheries restrictions were not included in the database, additional supplemental data were consulted from local, state, and national park websites, fisheries management agency websites, Google scholar searches by MPA name, as well as fishing and travel blogs. If no fishing restrictions were identified during the search the MPA was not included in the model. Only a small portion of those MPAs included in the previously mentioned databases had specific restrictions on fishing and tended to be federally managed areas. For example, areas such as national wildlife refuges and state and local parks did not have any specific restrictions beyond their respective state and national regulations. Those MPAs with site specific management plans, such as the waters within state parks, may restrict fishing in a few small localities but were not considered due to their size.

The resulting list of 24 spatial fisheries closures, the date enacted, seasonality, and the boxes affected are listed in Table 4.2. These MPAs were included in the historical reconstructions in the Atlantis-GOM simulations. For each polygon in which an MPA is located, fishing effort was reduced in proportion to the area of the MPA divided by the total area of the polygon. These closed area acted as a total reduction of effort rather than a redistribution of that effort. Their reductions were toggled on and off to reflect seasonal closure patterns specified by MPA regulations. The configurations of MPAs in 2010 are represented in the scenarios presented here. The starting date of the simulations is Jan 1, 2010.

#### *4.2.6.2 Generic closures*

Additional simulations were included to establish the sensitivity of the Atlantis model to an increasing proportion of closed area in the GOM: 0%, 10%, 25%, 50, and 100% of total area.

In these scenarios, an equal proportion of each polygon was closed to all fishing fleets and represents randomly placed MPAs.

#### 4.2.6.3 Source/Sink Closures

An aggregate reef fish complex source/sink index was created to identify those areas acting as reef fish sources and sinks in a multispecies context. This was accomplished by summing the individual functional group source and sink indexes developed in chapter 3 across all reef fish functional groups within each box (Equation 4.2).

$$\sum_f \sum (Pe_i - Pa_i)_f$$

Where  $(Pe_i - Pa_i)$  is the source sink index for a reef fish functional group, from chapter 3, summed across all reef fish functional groups ( $f$ ). Scenarios were then developed that closed the polygons to all fishing gear types representing the top 3 and 10 source and sinks polygons for the reef fish complex (Figure 4.3). Selecting the three and ten highest boxes of source and sinks resulted in less than 11% of the GOM being subjected to closures although the actual areas closed in each scenario were not equivalent. The 10 source and 10 sink closures closed 10.5 and 6% and the 3 source and 3 sink closures closed 2.3 and 1.1% percent of the GOM respectively.

#### 4.2.7 Performance Indicators

The closed area scenarios described above were all evaluated with respect to reef fish functional group biomass and landings. The results were synthesized with respect to four subgroups in an attempt to delineate target and non-target reef fish species. Those subgroups are 1) Large reef fish which contains the functional groups of large reef fish (LRF) and bioeroding fish (BIO); 2) Small reef fish, containing small reef fish (SRF), Shallow Serannidae (SSR), and

Lutjanidae (LUT); 3) Groupers containing Scamp (SCM), Red Grouper (RGR), and Gag (GAG), and Deep Serranidae (DSR); 4) Snappers, containing Vermillion snapper (VSN), Red Snapper (RSN),

## **4.3 Results**

### *4.3.1 Model sensitivity to dispersal*

Overall, the Atlantis model was highly sensitive to the addition of larval dispersal. Turning on larval dispersal in the model and eliminating the assumption of self-recruitment to each polygon resulted in a large increase in the survival of the age 1 groups across almost all species where dispersal was implemented. To account for this, the alpha parameter in the Beverton-Holt stock recruitment relationship was tuned to reflect the perceived increase in productivity. In general, the tuned model required a reduction of two orders of magnitude of the alpha parameter in the stock recruitment relationship as defined in Equation 1.

The distribution of biomass was significantly altered by dispersing the larvae according to the dispersal patterns developed in Chapter 3. Comparing the two scenarios after 10 years revealed a complex pattern of differences in biomass between the scenarios with and without larval dispersal (Figure 4.4). Notably some biomass of reef fish occurred in the deep water polygons of the GOM. The tuned model with dispersal on and the current configuration of closed areas was then considered the status quo model from which to compare model simulations.

### *4.3.2 Generic Closed Areas*

The generic closures provided an inverse tradeoff in total reef fish biomass and catch (Figure 4.5). None of the generic closure scenarios achieved similar biomass or catch to the status quo concurrently. Generic closures of roughly 35% provided equivalent total biomass of reef fish and higher catch relative to the status quo. Conversely generic closures of roughly 50%

of the GOM would achieve the same catch and results in additional biomass. Once the size of the closure exceeds 50% the biomass of reef fish approaches an asymptote and catch declines rapidly. Overall, generic closures between 30-60% provided results where both biomass and yield are higher than the status quo scenario.

Reef fish subgroup biomasses and catch responded similarly to an increasing closure size up to 50% of the GOM. The responses of catch and biomass were fairly consistent across subgroups for generic scenarios (Figures 4.6 and 4.7). There was a somewhat linear increase in biomass as the size of the closed area increased from 0-50% for every group. The 100% closure had mixed impacts: 100% closure resulted in a general increase in biomass for targeted groupers and snappers compared to the status quo but resulted in a decrease in biomass compared to the 50% closure, and the Small reef fish group resulted in roughly equivalent biomass levels to the 50% closure.

Catch for each reef fish subgroup was higher than the status quo. Generally increasing the size of the closure led to lower catch in a linear fashion. Large reef fish appear to be disproportionality impacted by the generic closures in terms of percent change in catch. Groupers were the most affected in terms of percent change with Small reef fish, Groupers, and Snapper exhibiting similar increases in catch across each subgroup. Groupers catch appears to be the most sensitive to the generic closures in terms of absolute changes in biomass and catch.

#### *4.3.3 Source/sink closures*

The initial slopes of catch and biomass of the source and sink closures Figure 4.5 are steeper than the generic closures and converge towards the status quo biomass and catch levels more rapidly. Increasing the number of sink polygons closed from three to ten resulted in a near doubling of biomass while causing a 45% reduction in catch. However, closing source polygon

closures did not have the same response. Increasing the source polygon closures from three to ten resulted in a similar increase in biomass (2.5 times) while only reducing catch by 20%.

Projecting those source and sink slopes forward, they would both intersect at the baseline at roughly 15%, suggesting that closing 15% of all sink areas would provide similar benefits to the status quo. Conversely increasing the area of source closures causes relatively minor decline in catch but large increases in biomass. These two curves intersect at roughly a 20% area closure. However the catch and biomass curves for the source closures intersect well above the baseline and results in greater biomass and catch than the status quo with an equivalent 20% closure of sources. Overall both the source and sink closures appear to provide similar or increased catch and biomass by closing a smaller total proportion of the GOM compared to the generic (random) closures.

The reef fish subgroup responses (Figure 4.7) were less consistent in their responses to the size of source and sink closures. The difference between the 3 source and 10 source scenarios varied across each subgroup. For example, the biomass of Groupers increased substantially between 3 and 10 sink scenarios (orange lines) whereas a similar response did not occur when source polygons were closed (purple lines). The alternate case was true for the other three subgroups where closing source boxes appears to have a disproportionate impact on the subgroup biomass level.

#### **4.4 Discussion**

This is the first Atlantis model where specific dispersal patterns were estimated for all functional groups across an entire large marine ecosystem. Previous dispersal studies have generally focused on a single species (Pedersen et al. 2003. Paris et al. 2005) and those studies typically results in some measure of connectedness and identify valuable areas for protection as

was done in Chapter 3. This chapter attempts to take the next step and integrate that information into a dynamic ecosystem model framework with the goals of assessing impacts and providing actionable advice.

It is worth noting the simulations discussed here are oversimplified in many ways and in some instances may not be highly realistic. This model represents a necessary step towards building a fully functional and realistic model of the GOM for fisheries management simulations. Information on species distributions and the implicit assumption of surface transport of larvae can be improved upon on a species by species basis.

#### *4.4.1 Model sensitivity to dispersal*

Overall, the Atlantis model was highly sensitive to the incorporation of dispersal patterns. The impacts of dispersal were identifiable and persistent across space. The inclusion of dispersal significantly altered the productivity of the system, likely due to the redistribution of the first age group into new areas. As indicated in Figure 4.4 this resulted in fish occurring in the deep GOM, Campeche Bank, and number of coastal polygons where they were absent in the non-dispersal models.

While the Atlantis-GOM model does include habitat preferences – used as a function of movement – it does not include habitat suitability in this parameterization. The diet matrix acts as the main moderator of survival and groups will only persist if there is food available in each polygon. Unfortunately the diets of juvenile fish are not well resolved and are highly generalized in the Atlantis model. Therefore new fish could potentially persist for some amount of time in the offshore environment as juveniles and could be contributing in part to the large increases in biomass. In addition to the offshore polygons, fish that are transported inshore may also be contributing to the increase in production through the same mechanisms. Inshore habitats are

more productive and have higher available phytoplankton, zooplankton, and other juvenile groups to consume. The inshore boxes appear to have slightly lower densities of new biomass compared to the offshore boxes, and this is likely due to increased predation.

The implicit assumption in recruitment applied to previous studies using Atlantis is that the adult habitat is the most suitable for recruitment. This assumption is often wrong, especially for demersal fish in the GOM, many of which exhibit ontogenetic migration and predominantly recruit to habitats that are not populated by adults. However introducing a dispersal matrix derived from Lagrangian models without imposing a penalty for habitat suitability introduces a new set of assumptions which require additional information. The main data source that is assumed to be 'known' in food web models is the diet matrix which mediates ecological interactions from which we can solve for a range of ecological outcomes. I assumed this would be the case for juveniles (age group 1). However it appears the resolution of the diet information for younger fish may be limited by our ability to account for 100% of the mortality to juvenile groups that should be occurring in offshore polygons. The inclusion of suitability layers for juveniles may also be possible for some species but presents yet another tradeoff of requiring the information to make an informed map of suitability for very small fish and invertebrates and ultimately limiting the emergent connections that are outcome of this exercise.

#### *4.4.2 Closed area Scenarios*

Overall it appears the status quo closed areas are providing a reasonable balance of catch and biomass of reef fish in the GOM. This should be the case as the as fisheries in the GOM are reasonably well managed with stocks that are at or approaching the biomass that supports maximum sustainable yield. Not surprisingly the random generic closures were the least efficient method. However they do provide a helpful baseline to ground truth the results as the absolute

values of biomass and catch will be sensitive to the tuning process which alters the Beverton Holt alpha parameter. In this simulation there appears to be a diminishing return on increasing biomass which asymptotes at around 8,000mt and can be achieved by closing a random 50% of the GOM.

Comparing the current day closed areas to the generic closures is not straightforward. In the real world (and model) closed areas are implemented seasonally and only for specific targeted fisheries. The generic closures evaluated here are year round and affect all fisheries. Regardless, the current configuration of closed areas do appear to be serving their intended purpose and providing many of the same benefits to the reef fish and fishery than a relatively large closed area would provide.

#### *4.4.3 Source/sink closures*

The source and sink scenarios are fundamentally different in two ways from the generic closures. First, they target specific polygons in prime reef fish habitat for closures. Second the limited number of polygons closed (3 or 10) means there are polygons that were previously restricted to fishing that are now fully exploitable. Generally, protecting source boxes in an overexploited system should allow fish biomass to increase within the closed area and export that production. This is not equivalent to one of those systems as restoring the age structure of an exploited stock is a key component of achieving spawning potential ratio targets of the GOM Fishery Management Council. Regardless, the targeting of source and sinks did provide some additional benefits generic closures and the status quo although those gains are relatively small in an absolute sense. These marginal improvements demonstrate the importance of well-planned closures and protecting some portion of the stock although the total gains to be made in either catch or biomass are likely much smaller than other heavily exploited systems.

The mixed effects of targeting source and sink closures on biomass and catch suggest targeting source and sink closures have distinct and complex impacts of fishing and ecological dynamics in the GOM. In both the source and sink closures, the increases in biomass were similar to one another, yet the change in catch was not. Increasing the area of the sink closures from 3 to 10 polygons resulted in 45% reduction of catch whereas the source closures resulted in only 12% catch. This suggests that closing source areas will provide similar increases in biomass while still allowing for higher catch levels by opening new areas to fishing while protecting some spawners.

In general the areas that were identified as reef fish sinks were inshore and concentrated on the West Florida Shelf (WFS) where fishing pressure is high. These areas contain abundant younger reef fish (Appendix C) and experience modest fishing effort. This explains the disproportionate increase in the biomass of Small reef fish and Groupers, especially red grouper which is predominantly found on the WFS, by closing additional sink areas. However, unlike Groupers, the catch of Small reef fish did not show an equivalent response and was hardly affected by the number of sink polygons closed to fishing or increases in biomass. In general the Small reef fish group is composed of non-fished species. So, even as the inshore areas are closed and biomass is allowed to accumulate those fish are still not caught and provide very little benefit to fisherman. Subsequent to closing the inshore polygons, offshore protected areas become open to fishing and the model predicts a large increase in target grouper catch but is still sensitive to the amount of closed areas.

The spatial configuration of source closures was more broadly distributed throughout GOM, unlike the sink closures which focused primarily on the WFS. This had strong implications on the reef fish group dynamics. Like the sink scenarios, Small reef fish were

extremely sensitive to the area of the source closures while increases in total biomass had little impact on catch. Unlike the sink scenarios, increases in the number of source polygons closed had relatively little impact on grouper biomass and catch, likely do to the fact that most of the WFS remained open to fishing while protecting the large spawners offshore. The lack of response in grouper biomass also suggests the two source boxes on the WFS that are closed in the Pulley Ridge area provide sufficient protections for groupers and that closing four boxes on the WFS as was done in the 10-source scenario may not be necessary.

#### *4.4.4 Summary*

The goal of this chapter was to better understand how source/sink dynamics could be used to achieve improved fisheries management. Therefore, improvements to management should be measured relative to the status quo. In this chapter I've attempted to measure improvements as a win-win scenario in terms of the two common objectives in any fishery system, biomass and catch. The operating hypothesis for this chapter was that protecting source areas would provide spillover effects for reef fish and provide that win-win scenario.

The initial results appeared to confirm the operating hypothesis that targeting source areas for closures provides a more effective strategy which could yield gains in catch and biomass for reef fish species as whole. However parsing the sub group effects suggests the impacts of closed areas are highly specific to each region of the GOM and those impacts can be variable across space and time. None of the scenarios identified here actually resulted in a net increase of the target snapper or groupers. In a political sense these scenarios are extremely unlikely to be implemented. However the overarching results – where sinks provide the greatest net benefit are in some ways a validation of the approach taken here and the parameterization of the Atlantis –GOM model.

These results indicate three major findings. First, from a practical standpoint this study shows that dispersal can be incorporated into the Atlantis model framework and the model is sensitive to those inputs. Second, dispersal did have effects on the overall productivity of reef fish stocks in the GOM. Third, the current configuration of closed areas perform well in terms of preserving reef fish biomass and catch. However, incorporating a better understanding of connectivity can improve upon existing management outcomes.

While these findings are important to consider for strategic fisheries management, there are important assumptions that require further investigation before these findings should be applied. A number of research projects are already underway and include projects to incorporate additional survey databases and methodologies into developing species distribution models (Grüss et al. 2018) and improving dispersal modeling methods and validation of those models (Grüss et al. 2014). One avenue for future research would be to validate the larval dispersal patterns against observations which would eventually allow for more accurate predictions of spatial production patterns and is an active area of research.

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## 4.6 Tables

Table 4.1 Model scenarios evaluated.

Name	Description	Details
<b>Calibration</b>		
Tech Memo	Model from Ainsworth et al. 2015 NOAA Tech Memo	Age-1 fish self-recruit to polygon they were generated in
Tech memo + dispersal	Non-tuned Model from Ainsworth 2015 NOAA Tech Memo with dispersal included but not retuned	Utilize dispersal matrices for all species where available
Status Quo	Tuned Model from Ainsworth 2015 NOAA Tech Memo with dispersal included	Closed areas represent the current day (2010) configuration
<b>Generic Closures</b>		
0%	No closures	
10%	10% closure Gulfwide	10% of each box is closed to all fishing
25%	25% closure Gulfwide	10% of each box is closed to all fishing
50%	50% closure Gulfwide	10% of each box is closed to all fishing
<b>Source/ Sink Closures</b>		
10-source	Aggregate Reef fish source closure top 10 source boxes	Close boxes: 12,64,43,25,1,35,17,40,20,41
3-source	Aggregate fish source closure top 3 source boxes	Close boxes: 12,64,43
10-sink	Reef fish sink closure top 10 sink boxes	Close boxes: 34,33,19,61,24,55,5,6,54,27
3-sink	Reef fish closure top 3 sink boxes	Close boxes: 34,33,19

Table 4.2. Major fishery closed area identified in the Gulf of Mexico represented in the Atlantis model. See Figure 4.2 for their spatial configuration.

Year enacted	Name	Boxes affected	Restrictions
2005	Madison and Swanson Sites	31	No fishing, Nov1 to April 30th
2000	Desoto Canyon Closed Area	1,8,9,12,33,23,25,26,29,38,39,42	No pelagic longline
1980	Dry Tortugas National Park	28	No lobsters, no spearfishing
2000	East Florida Coast Closed Area	28	No pelagic longline
2009	East Hump MPA	29	No commercial (bottom gear)
1990	Florida Keys National Marine Sanctuary -	27,28,29,32	No removal of coral or benthos
1990	Florida Keys National Marine Sanctuary	28	No Take
1984	Florida Middle Grounds Habitat Area of Particular Concern	42	No bottom longline, trawl, or dredge, pot, or trap
1992	Flower Garden Banks National Marine Sanctuary	20, 43	Only hook and line, no fishing of any other type allowed
1998	Isla Contoy	0	No fishing, no removing coral
1980	John Pennekamp Coral Reef State Park	27,28	No Spearfishing or collection of tropical fish
1989	John Pennekamp Coral Reef State Park, Harvest Prohibited or Restricted Area	27	No Lobsters, no spearfishing
1994	Laguna de Terminos	40	92.5% reduction in all fisheries
2006	McGrail Bank Habitat Area of Particular Concern	43	no bottom gear, buoy gear, traps etc.
2006	Pulley Ridge Habitat Area of Particular Concern	29, 64	no bottom gear, buoy gear, traps etc.
1990	Reef Fish Longline and Buoy Gear Restricted Area	1,5,6,17,20,21,22,23,24,25,27,28,31,32,33,34,39,42,43,51,53,60,61	no bottom gear, buoy gear

## 4.7 Figures

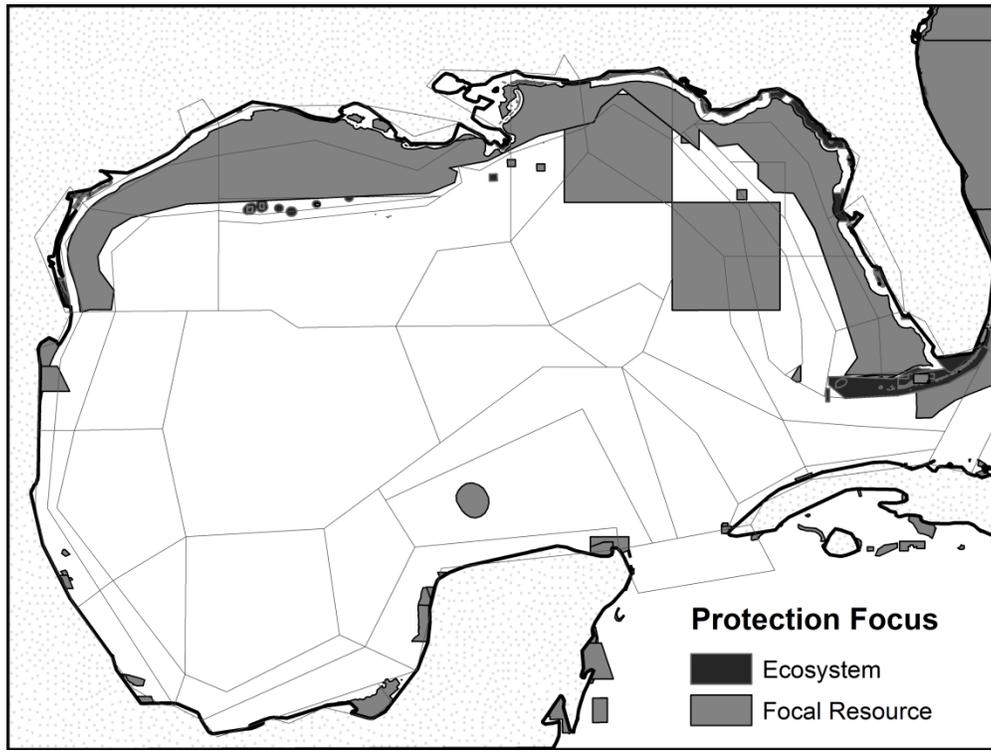


Figure 4.1. Spatial fishing closures in the Gulf of Mexico.

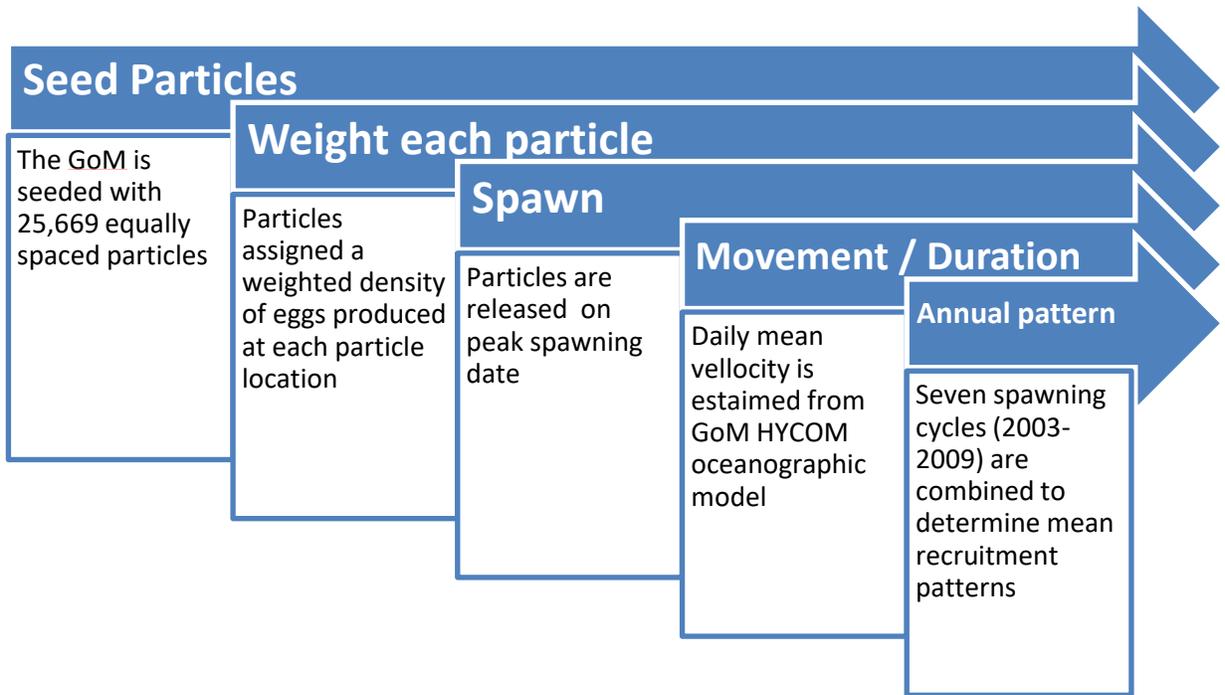


Figure 4.2 Stepwise process for estimating larval dispersal patterns for an individual functional group.

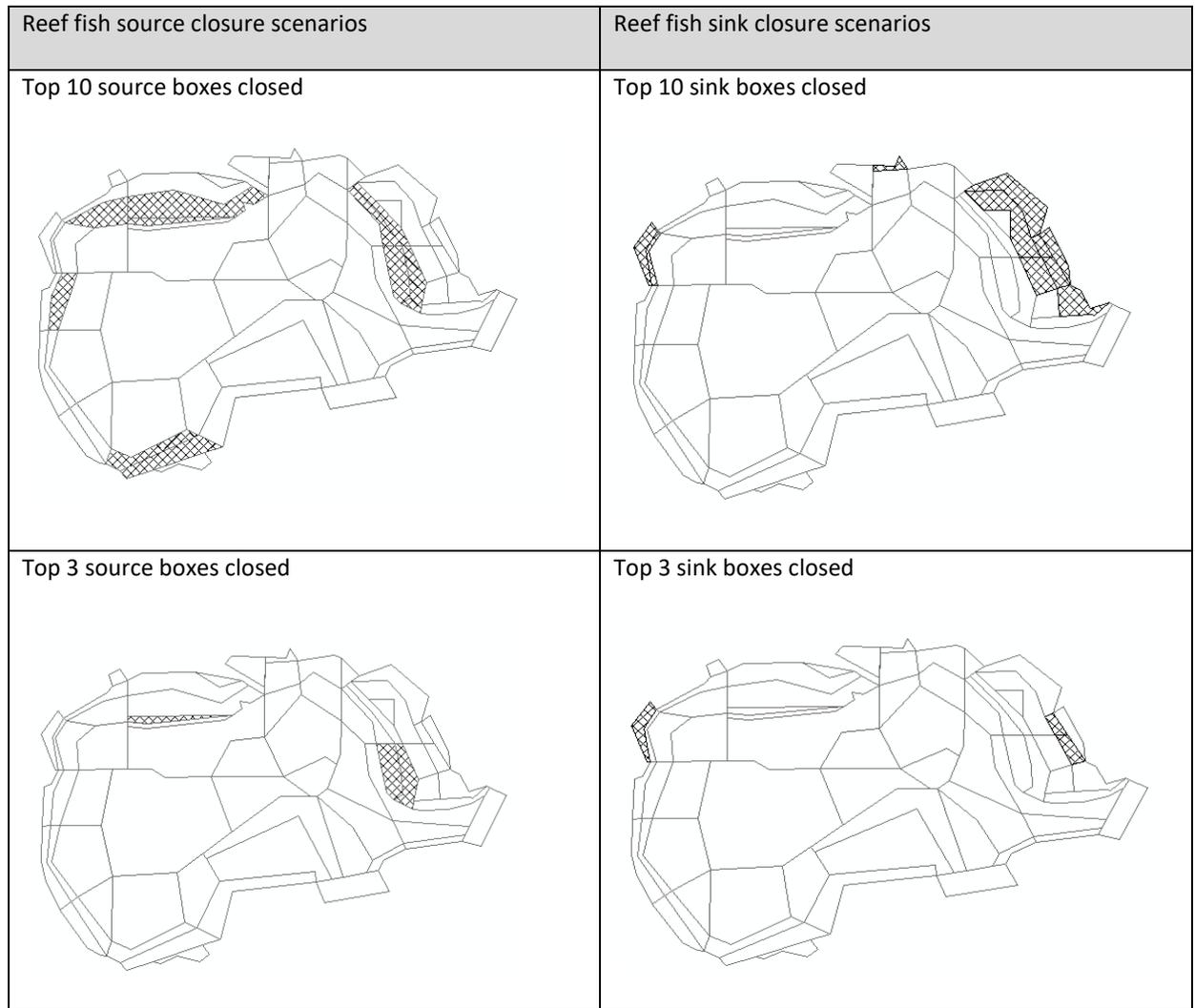


Figure 4.3. Aggregate reef fish source and sink closures simulated in Atlantis.

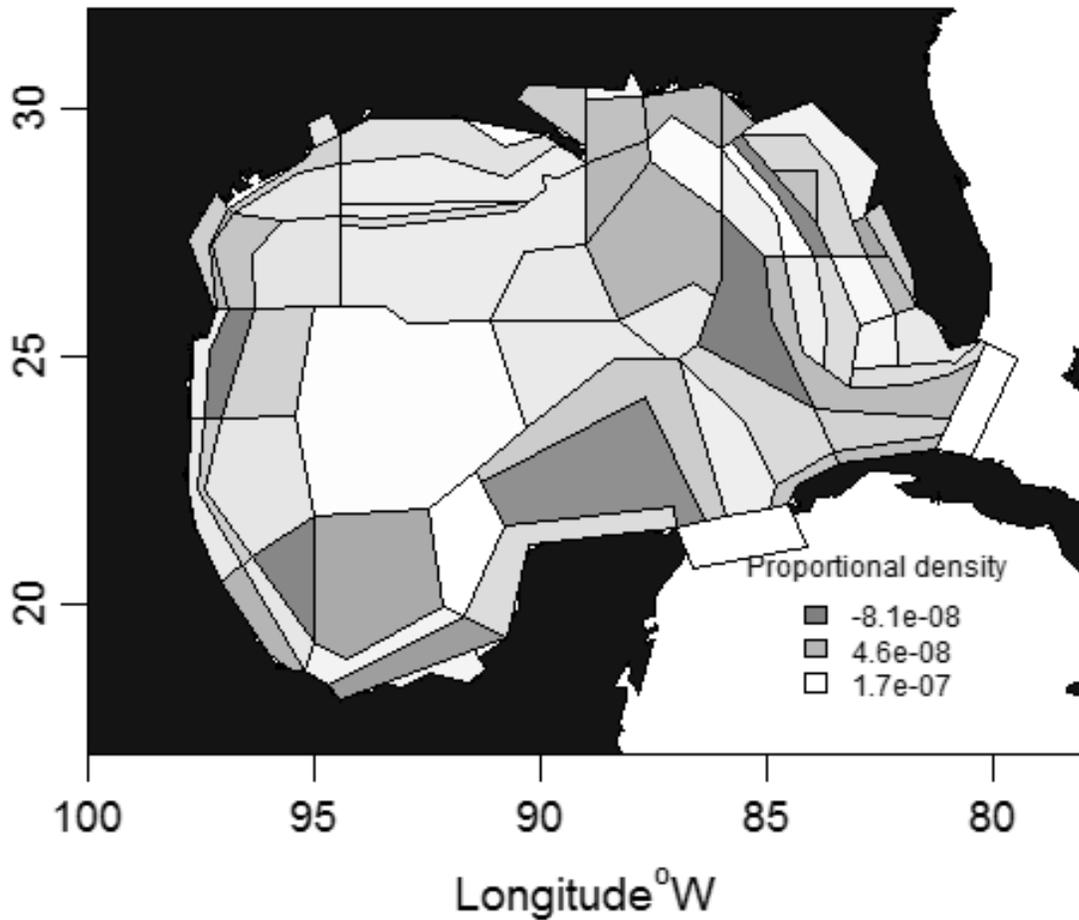


Figure 4.4. Comparison of the spatial distribution of relative biomass of the reef fish aggregate group between the dispersal and non-dispersal (untuned) scenarios after 10 years of simulation. Units are measured in proportional density (% of total biomass/area) of each polygon. The shading indicates the difference between two runs (dispersal- no dispersal) where negative values indicate a higher proportional density in the dispersal runs.

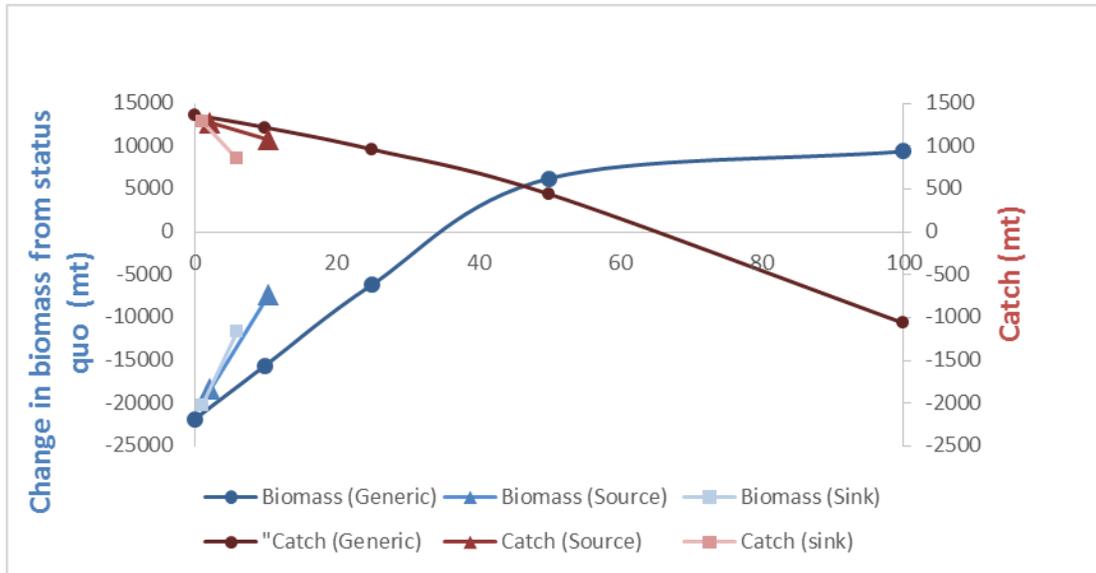


Figure 4.5. A comparison of catch (reds) and biomass (blues) across all of the closed area scenarios compared against the percent of area closed. All of the values are scaled relative to the status quo.

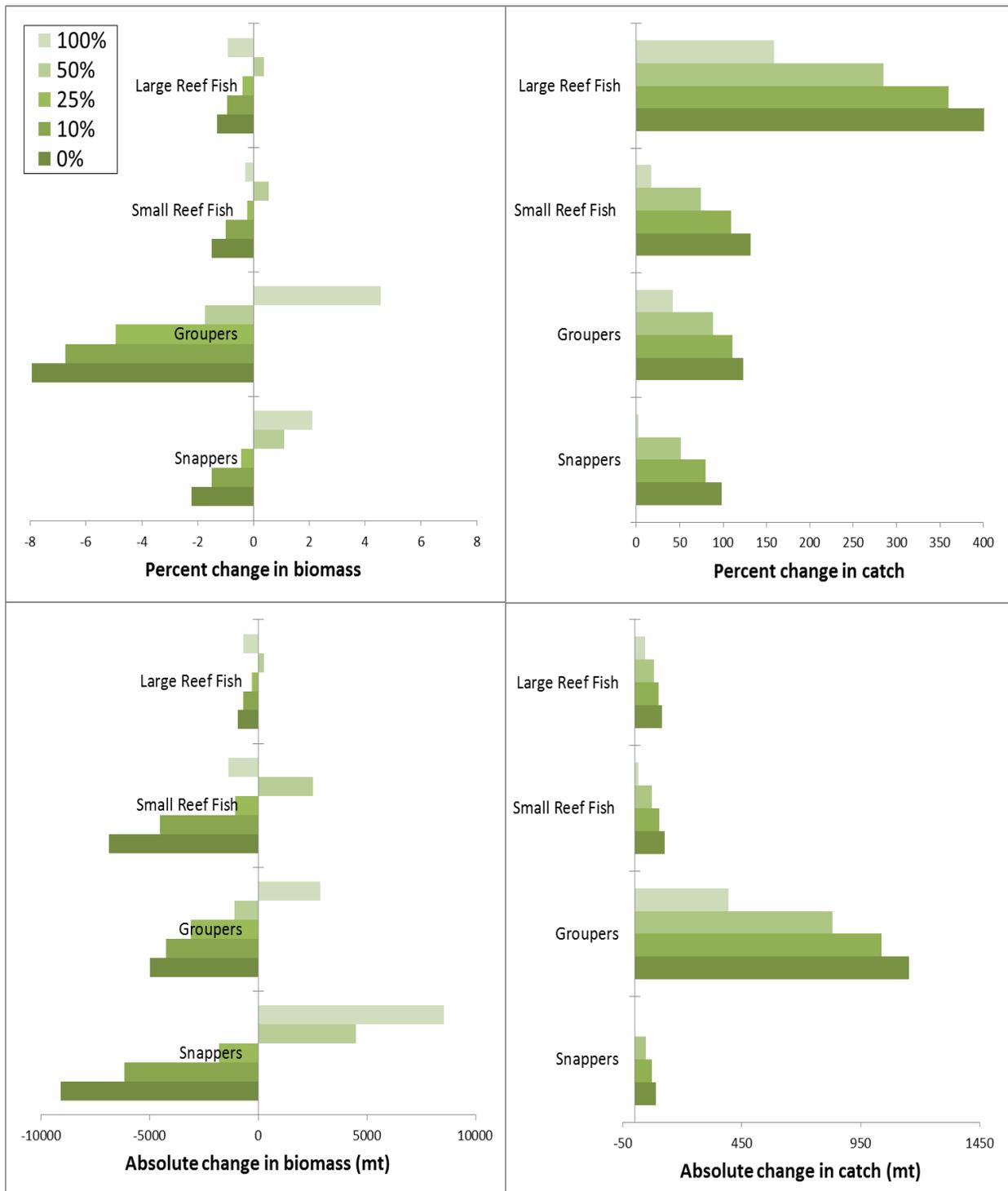


Figure 4.6. Comparison of biomass (left) and catch (right) for the reef fish subgroups for the generic closure scenarios where 0-100% of the GOM is closed to fishing. Catch for the 100% closure is not shown and is equal to zero.

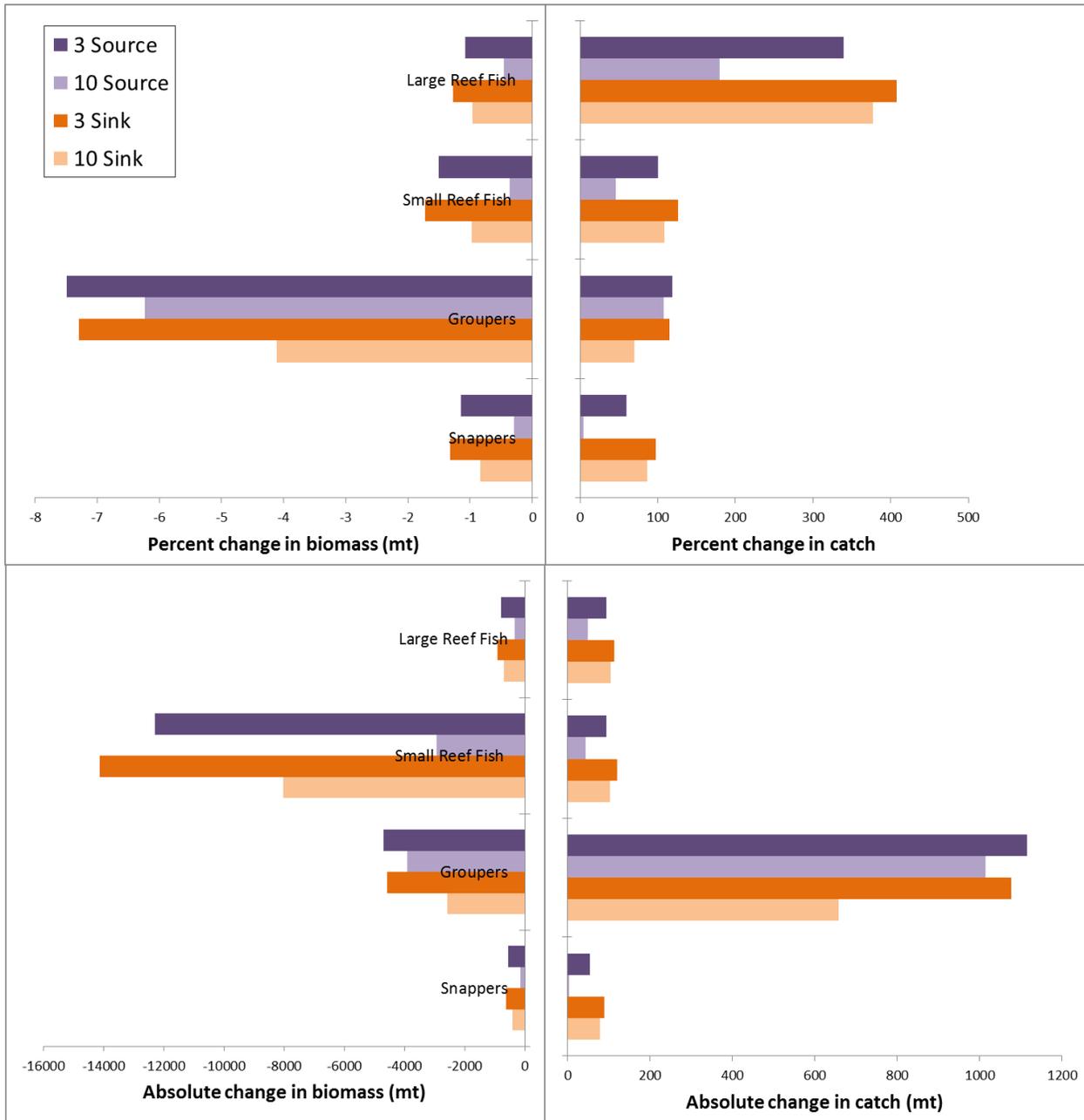


Figure 4.7. Comparison of biomass (left) and catch (right) for the reef fish subgroups for the source and sink scenarios where either three or ten polygons with the highest source/sink index were closed to fishing.

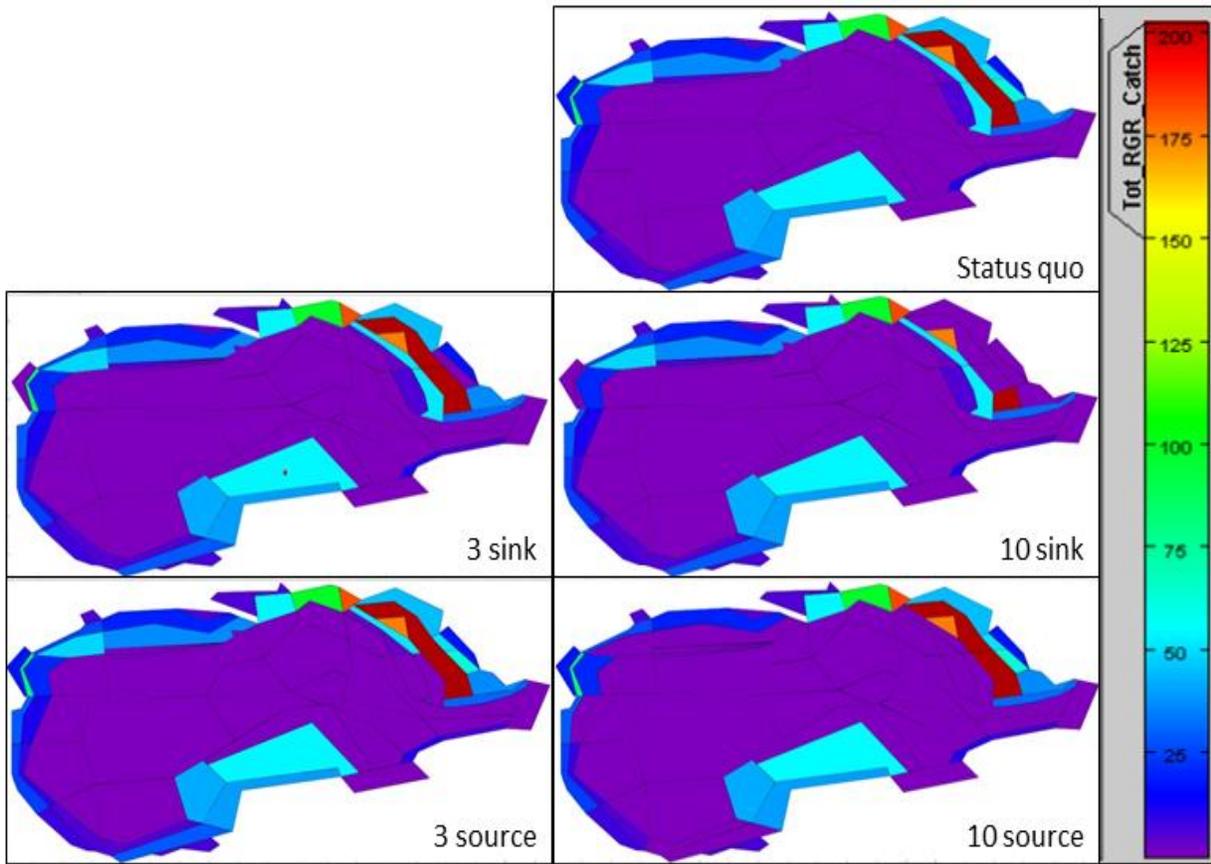


Figure 4.8. Comparison of RGR catch patterns for the status quo source, and sink closed area scenarios.

## **Chapter 5: Conclusions and recommendations**

Closed areas or MPAs remain a valuable tool for fisheries management, especially for multispecies fisheries. However, their effectiveness depends on a deep understanding of the ecosystem dynamics of the region, including humans. This dissertation is a first attempt to integrate the full range of components that affect connectivity- from developing spatial distribution maps of species to incorporating dispersal dynamics into management strategy simulations. There are a number of simplifying assumptions, data, and methodologies to be improved upon. As the old aphorism goes, all models are wrong, some are useful. These simulations provide the basis from which to understand the importance of each component of connectivity and the feasibility of this approach given the current available data and data requirements. In addition I was able to provide some measure of the importance of closed areas in the Gulf of Mexico (GOM) and the benefits they are providing, while identifying some suggested management alternatives.

The overarching conclusions of this research are:

- 1) Placement of fish and their larvae in models matter, especially in relation to closed area simulations;
- 2) Every component of ecosystem connectivity can be incorporated into ecosystem models and thus for use in management simulations;
- 3) Ecosystem models and management indicators are sensitive to connectivity information;

- 4) The current configuration of closed areas in the GOM appear to be performing well;
- 5) Improvements conservation and yield fisheries objectives is possible, but require a tradeoff between yield and biomass;
- 6) Protecting sink areas provides the greatest potential for increased biomass and yield.

In the remainder of this section I will provide some recommendations for future studies and note that many of these improvements are already underway.

**Recommendation 1: Future Atlantis simulations should incorporate the distribution maps and modeling approaches that incorporate a broad range of survey data.**

Chapter 2 developed an approach to generate distribution maps for a large number of functional groups in the GOM. Prior to this study detailed species distribution maps did not exist for most species, especially throughout the southern GOM where survey data does not exist. The results of this approach were appropriate to develop spatial distribution maps for the initialization of the Atlantis – GOM model, which averages over very large areas. For those ecosystem models that require highly resolved spatial maps, such as OSMOSE (Shin and Cury 2001, Shin and Cury 2004) where fish operate as agents, greater model skill may be required.

Since the publication of Chapter 2 (Drexler and Ainsworth 2013), which has been cited 52 times since its publication, I have been involved with a large project led by Arnaud Grüss to increase the resolution, skill, and utility of spatial distribution maps for marine species in the GOM (Grüss et al. 2014, Grüss et al. 2016, Grüss et al. 2018a, Grüss et al. 2018b). This body of work first compares the importance and need of spatial information in three types of ecosystem models, develops a comprehensive survey database of fish in the GOM consisting of 37

monitoring datasets, and develops the methodology to develop distribution maps from blending multiple survey types. Moving forward the maps developed by this project will provide a more comprehensive snapshot of species distributions as it incorporates data from a wide array of surveys and fuller range of age classes for fish species.

**Recommendation 2: Vertical distributions of larvae and their movement are poorly understood, larval surveys such as the SEAMAP ichthyoplankton and other surveys can improve the skill of dispersal models in the GOM.**

In Chapter 3, I developed two products. First, the larval connectivity matrices to inform the Atlantis model for simulations were developed by simulating multiple years of larval dispersal. Second, the dispersal dynamics were used to evaluate whether regions of GOM can be identified that operate as larval sources or sinks. This approach provided a first order approximation of connectivity across the GOM. The main assumption in these simulations is the lack of active swimming behavior and the vertical migrations of larvae. These two factors have been shown to be important factors regulating settlement (Paris et al. 2007). However, information on larval movement, especially for individuals transported large distances, does not exist for most species (McCook et al. 2009, Metaxas and Saunders 2009). In the GOM some progress is being made in utilizing larval survey information into similar agent based approaches (Karnauskas et al. 2017 Grüss et al. 2014) although information on the larval position of individual species larvae will remain a limiting factor in any similar effort - including commercially important species such as red snapper. Regardless, data limitation is a persistent issue in fisheries management and creative ways to extract information from existing data are needed. This methodology attempts to do just that. Going forward the skill in any of these

dispersal prediction efforts could be improved through a better understanding vertical distributions and movement of larvae. For example, the vertical profiles and location of observed larvae could be used to back calculate the origin of each particle in space. The SEAMAP ichthyoplankton surveys (GSMFC 2018) could be better utilized for this purpose (Lyczkowski-Shultz 2013) and is currently being investigated by Kelly Vasbinder at the USF College of Marine Science

**Recommendation 3: Additional data on the diets of juvenile fish or habitat suitability can greatly improve food web models such as Atlantis.**

Ecosystem models that incorporate food web dynamics such as Atlantis and Ecospace rely on ecological interactions to mediate the energetic flows through the system and compete for resources within a given habitat. Typically those interactions can be calibrated to replicate known trends in the system under a given set of assumptions. The Atlantis-GOM model was calibrated under the assumption of self-recruitment to each polygon and thus recruitment/production and consumption was tuned to match the known productivity of the system.

The inclusion of dispersal into the model through Lagrangian methods, as opposed to direct observations of recruitment, results in a large proportion of larvae being transported to new areas that may be unsuitable habitat. In this study reef fish larvae were transported offshore into the deep GOM where red grouper do not dwell. In the tuned model newly arriving recruits would be quickly consumed. However the inclusion of dispersal drastically changes the overlap patterns of predator and prey for the first age class. Presumably red grouper larvae are transported offshore to some degree where they die naturally due to a lack of suitable habitat or

predation. Additional data on the suitability and diets of juvenile fish and invertebrates could greatly improve the spatial realism of these simulations.

**Recommendation 4: Utilizing source and sink dynamics in management may provide some additional benefits to catch, biomass, or area closures in the GOM.**

In Chapter 4 I evaluated the potential to leverage the source/sink dynamics in the GOM to improve management using the Atlantis-GOM model. I was able to demonstrate that incorporating this type of information is possible on a large marine ecosystem scale for many species simultaneously. Furthermore, I was able to glean some insights in to the effectiveness of the current configuration of closed areas relative to the source/sink closures. Overall the targeting of source areas for closures could generate some additional catch and biomass for the system. However, the simulation demonstrated complex technical interactions between species that should be considered.

This finding clearly demonstrates the need for improved operating models to test and evaluate fisheries policy in the GOM. Incorporating the recommendations listed here may drastically improve the overall skill of these types of approaches and would be better positioned to provide management advice and evaluate those tradeoffs.

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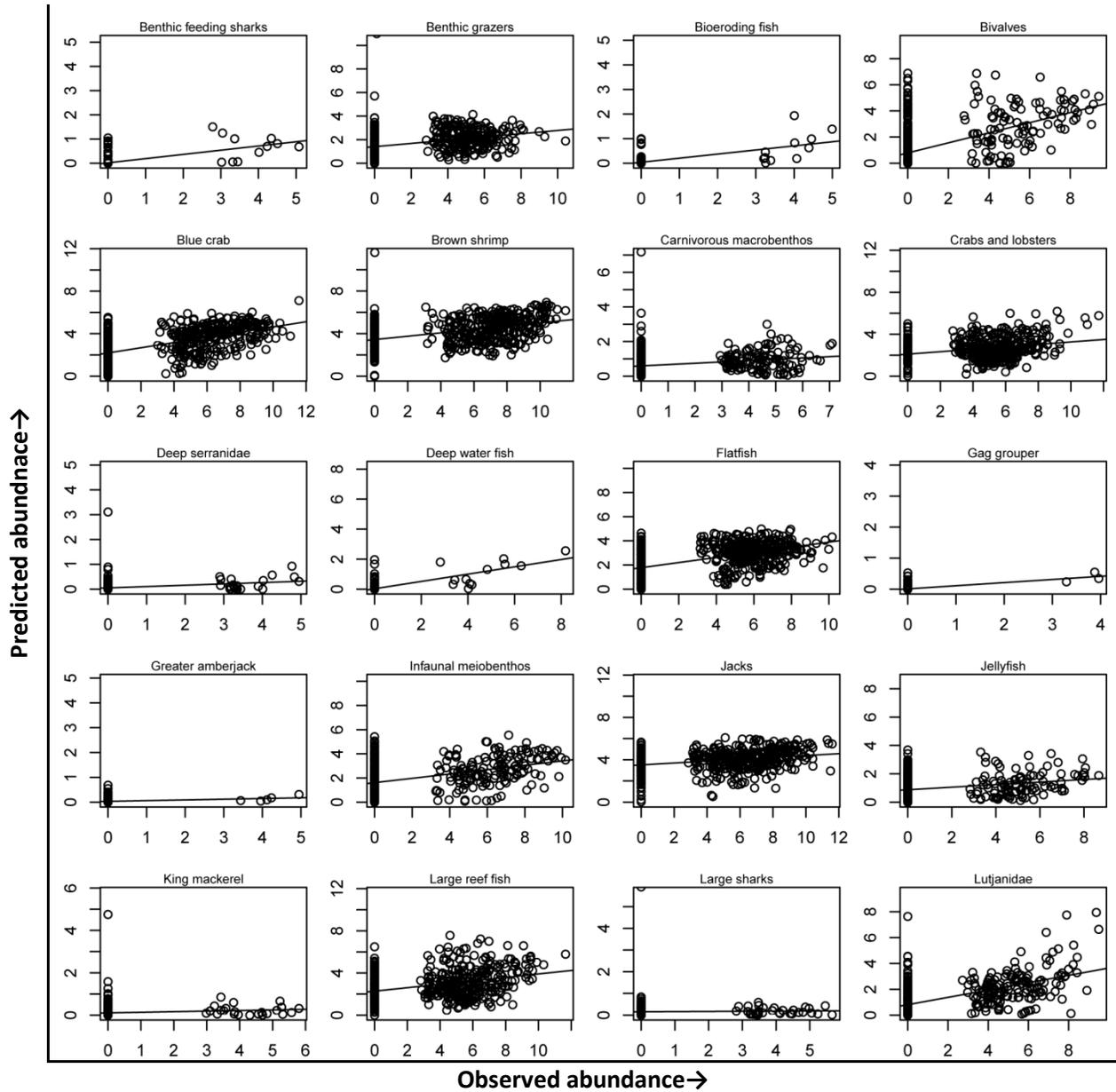
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## **Appendices**

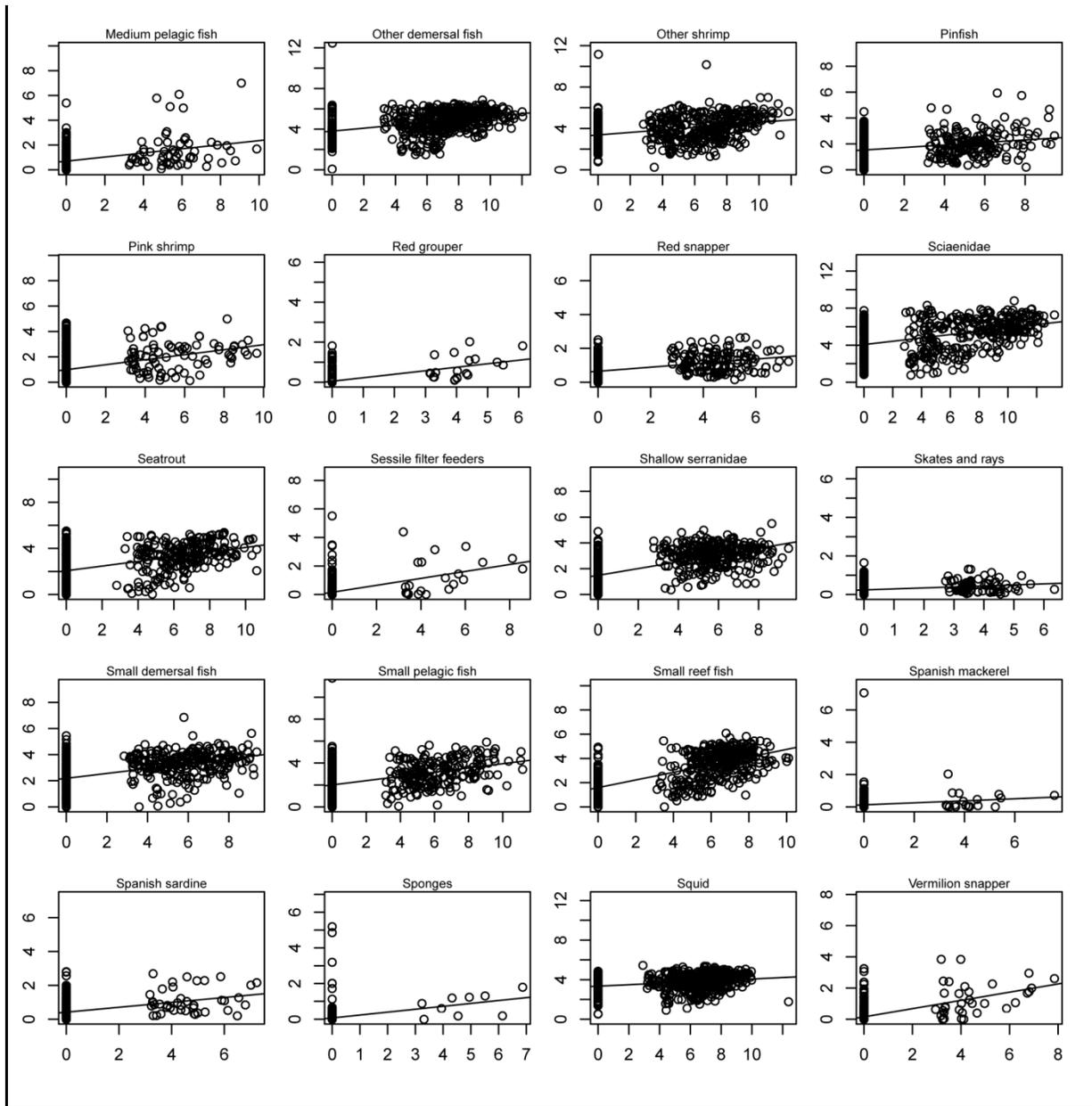
**Appendix A. Summary of individual model performance in terms of deviation explained for every Atlantis-GOM functional group observed during SEAMAP sampling from 2005-2010**

<b>Functional Group</b>	<b>Deviance exp.</b>	<b>Functional Group</b>	<b>Deviance exp.</b>
Benthic Feeding Sharks	82.7	Medium Pelagic Fish	41.7
Benthic grazers	21.4	Other demersal fish	13.9
Bioeroding fish	61.6	Other shrimp	19.3
Bivalves	73.3	Pinfish	31.1
Blue Crab	29.6	Pink shrimp	45.5
Brown Shrimp	18.0	Red grouper	70
Carn. macrobenthos	21.6	Red snapper	22.9
Crabs and Lobsters	26.1	Sciaenidae	26.7
Deep Serranidae	32.7	Seatrout	36.6
Deep Water Fish	82.1	Sessile filter feeders	62.8
Flatfish	26.2	Shallow serranidae	26.1
Gag grouper	72.9	Skates and rays	20.7
Greater Amberjack	36.3	Small demersal fish	23.7
Infaunal meiobenthos	43.4	Small pelagic fish	34.8
Jacks	16.4	Small reef fish	33.6
Jellyfish	40.1	Spanish mackerel	51.1
King mackerel	33.6	Spanish sardine	37.7
Large reef fish	43.8	Sponges	66.1
Large Sharks	16.3	Squid	10.1
Lutjanidae	45.5	Vermilion snapper	72.8

**Appendix B.** Combined model fits of the observed (x-axis) versus predicted (y-axis) values of data for 40 functional groups estimated from this model. The log-log line of least squares is plotted for visualization. Those functional groups with a slope less than or equal to zero ('deepwater fish' and 'large sharks') are not reliable and should be estimated with a separate set of parameters.



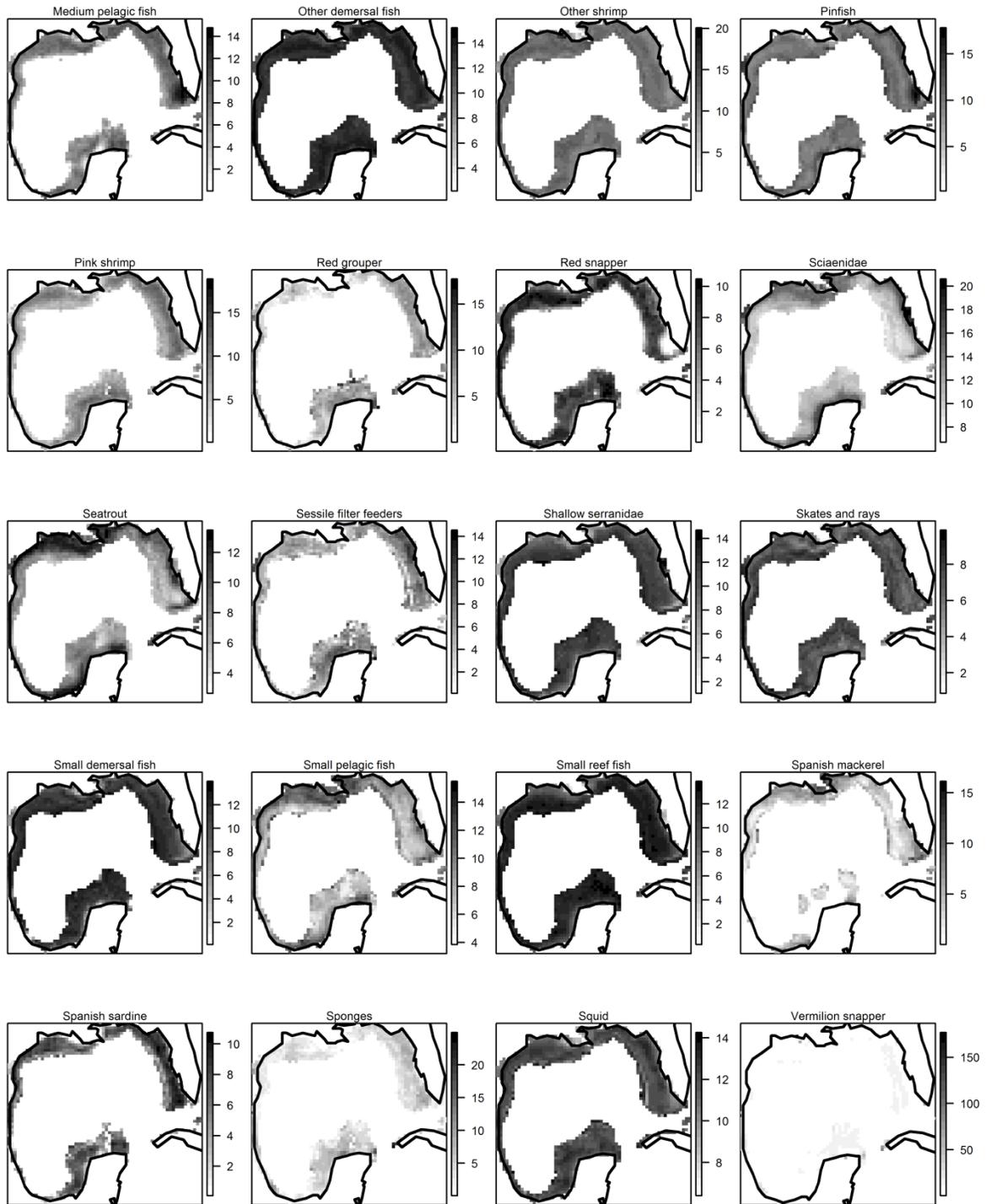
Predicted abundance →



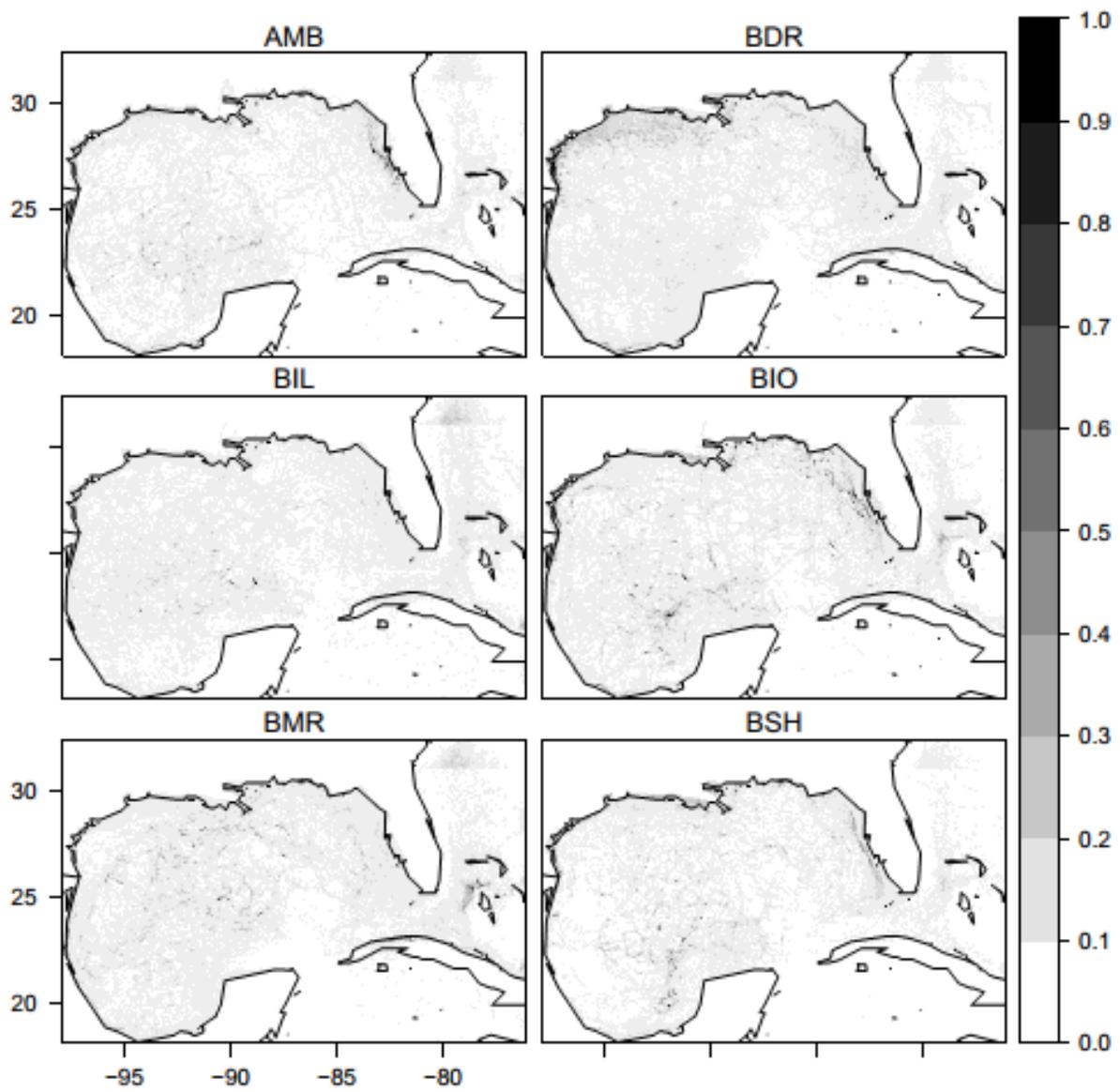
Observed abundance →

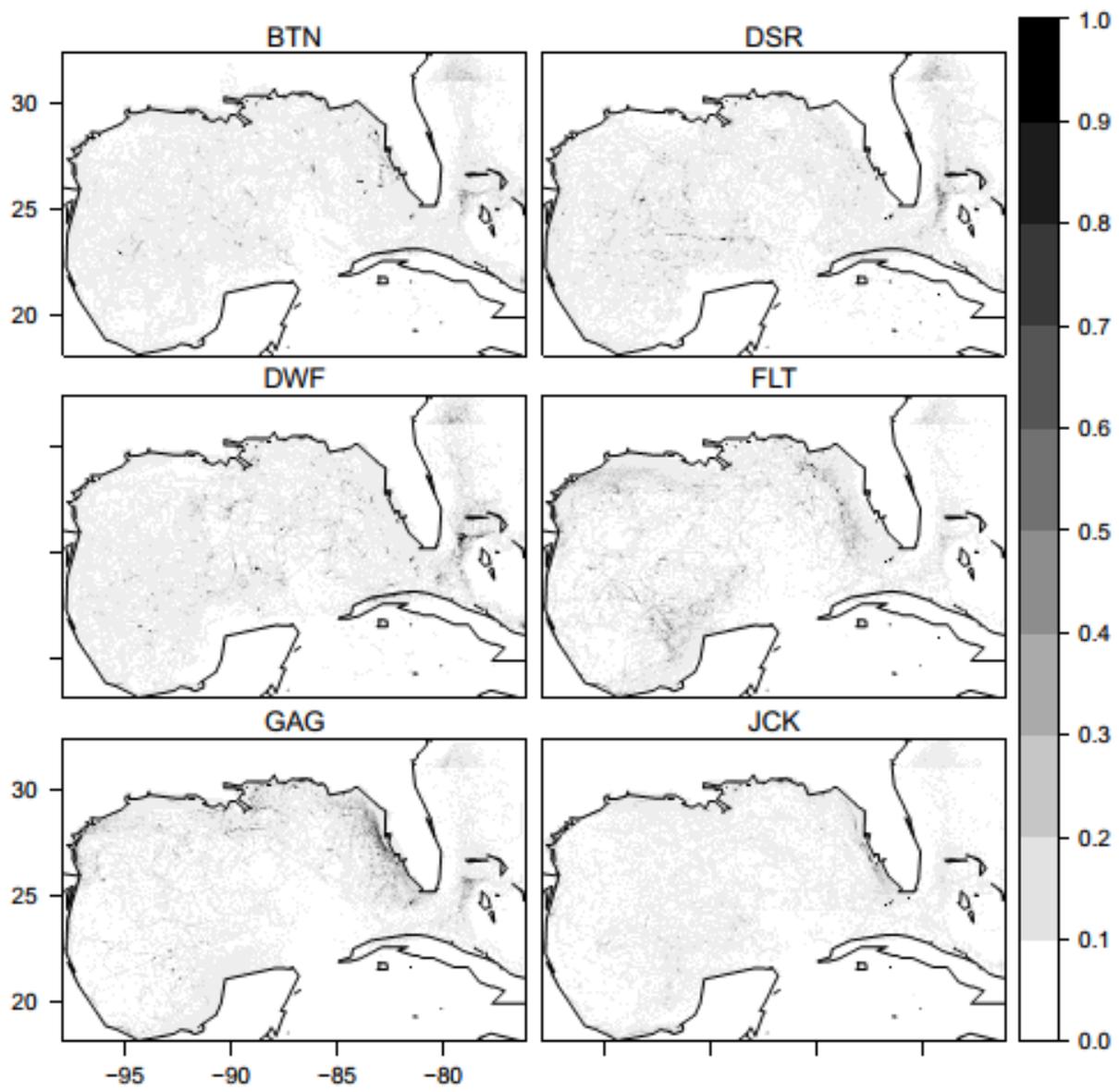
**Appendix C.** Spatial distribution maps predicted by the combined GAM model for 40 functional groups observed in the SEAMAP database. Grey scale represents the log transformed abundance per square kilometer of each functional group

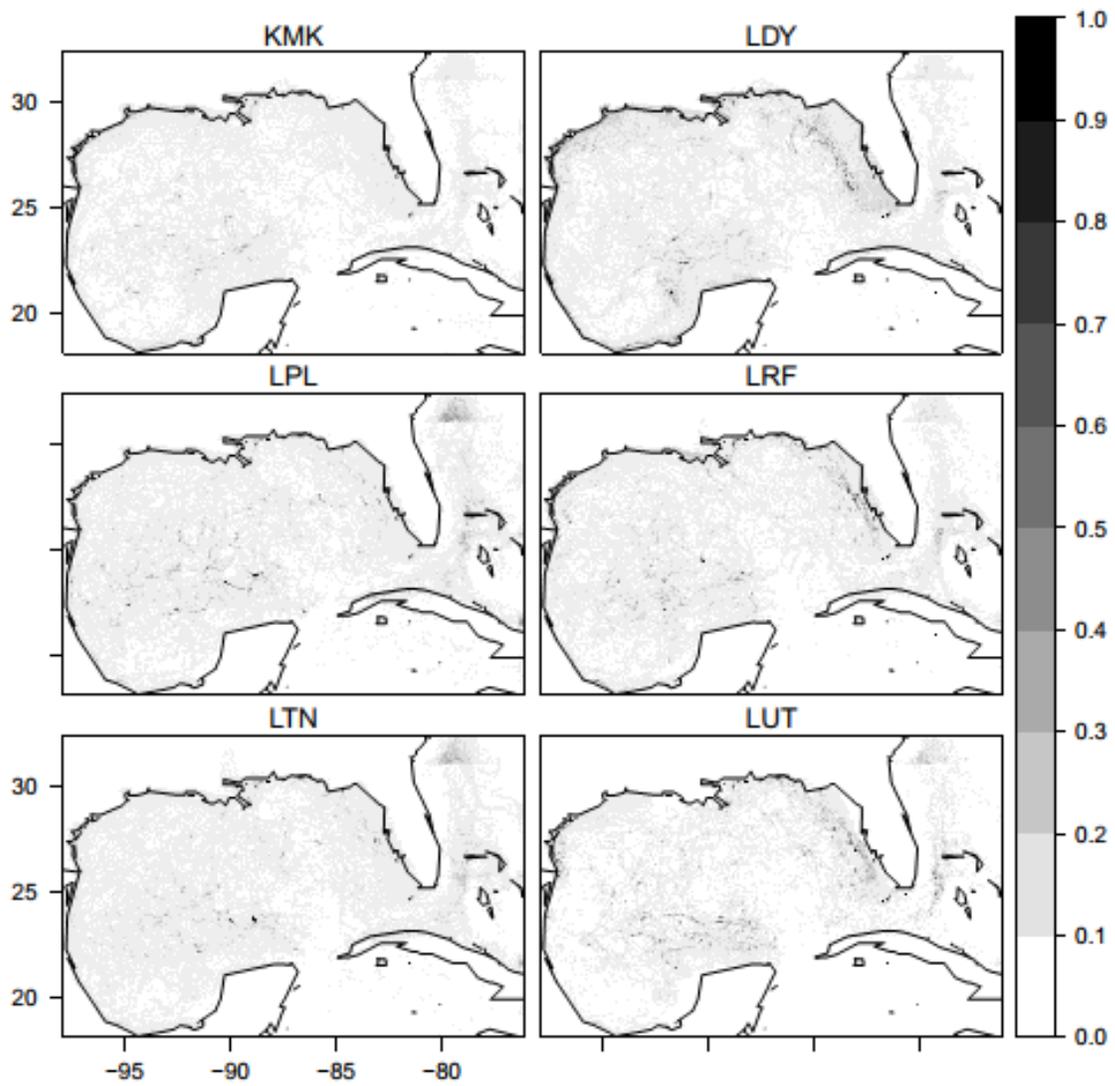


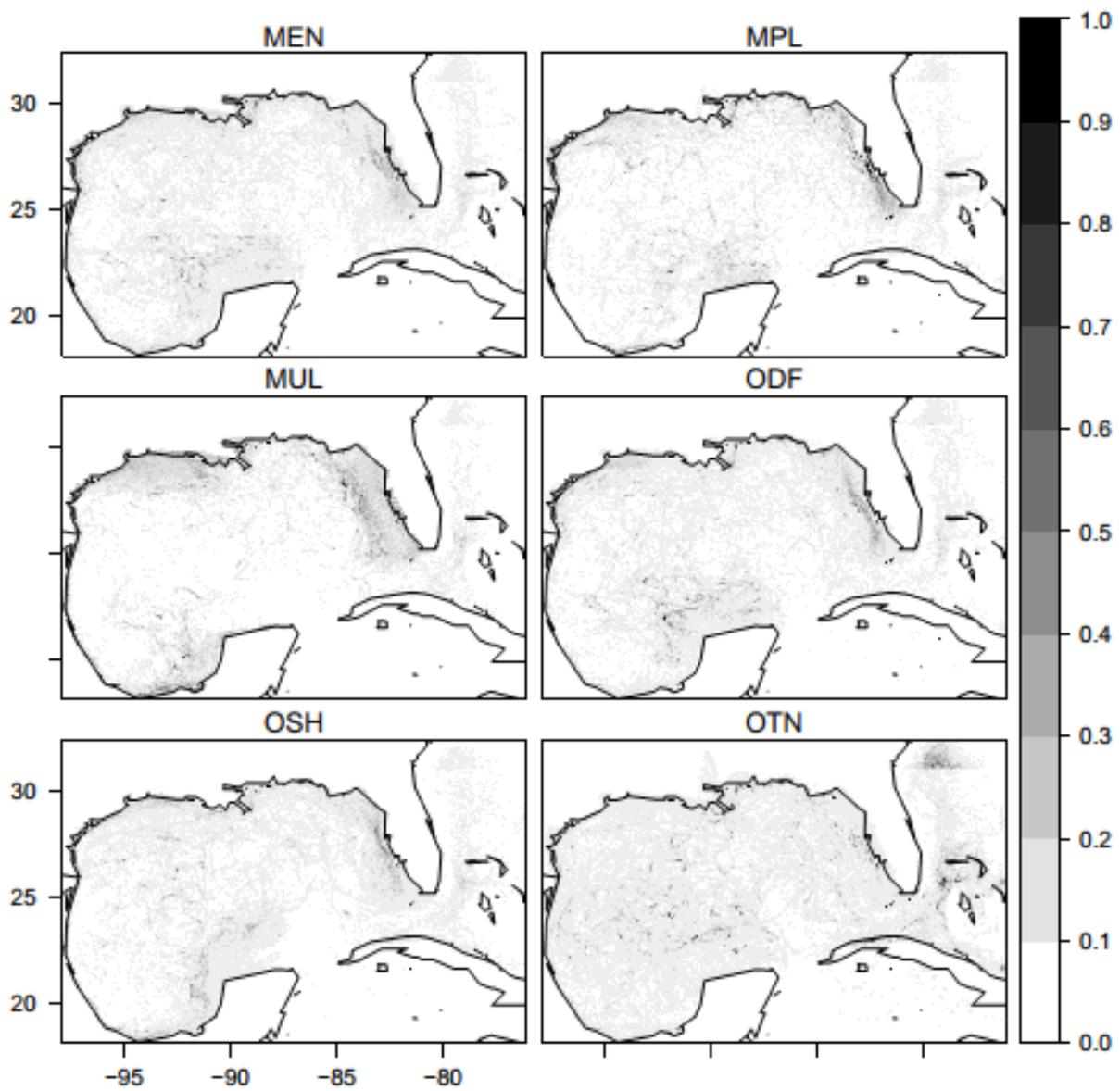


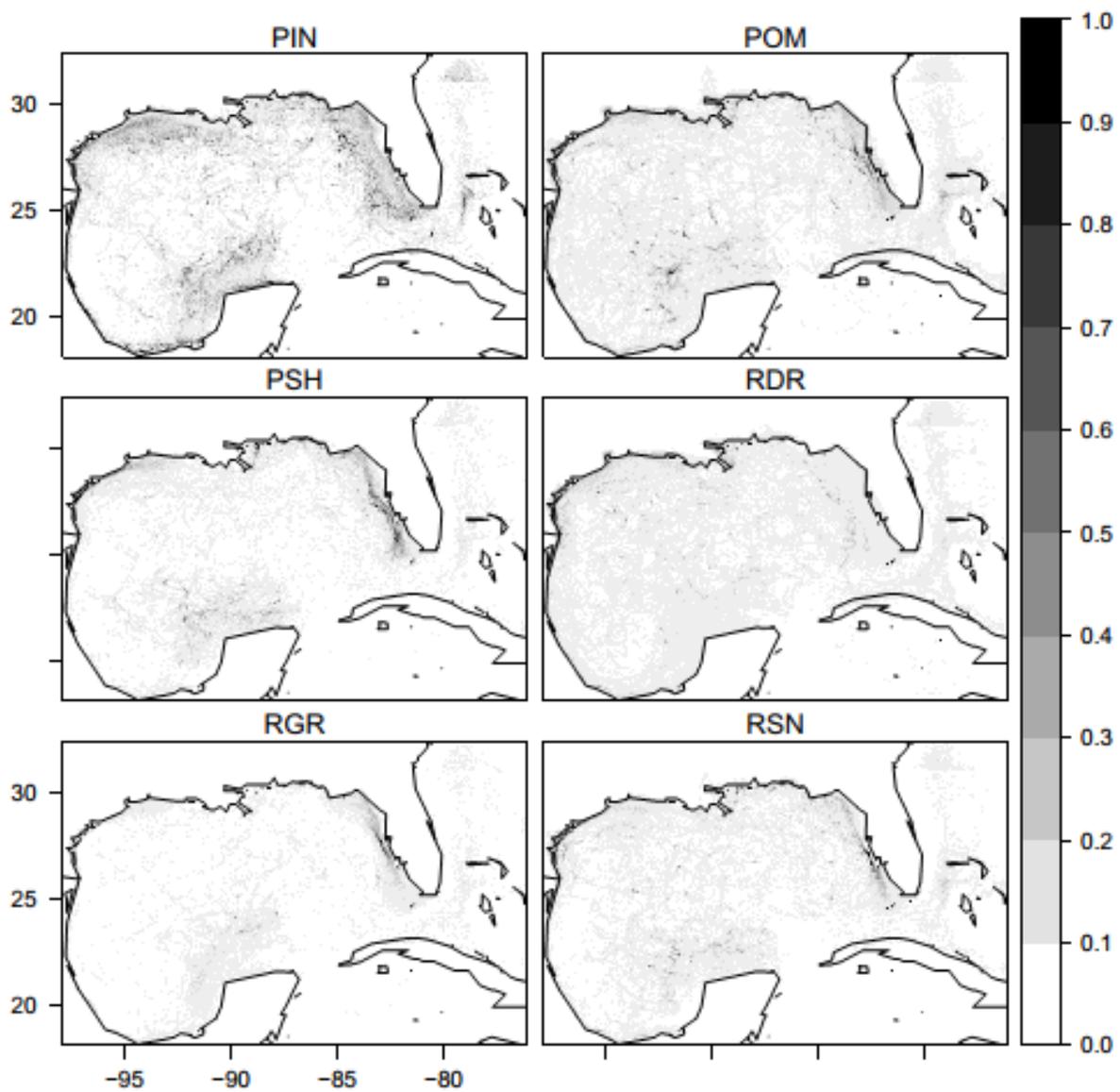
**Appendix D.** High resolution larval settlement patterns for the simulated years 2003-2009 for all modeled species normalized to 0 (low) and 1(high).

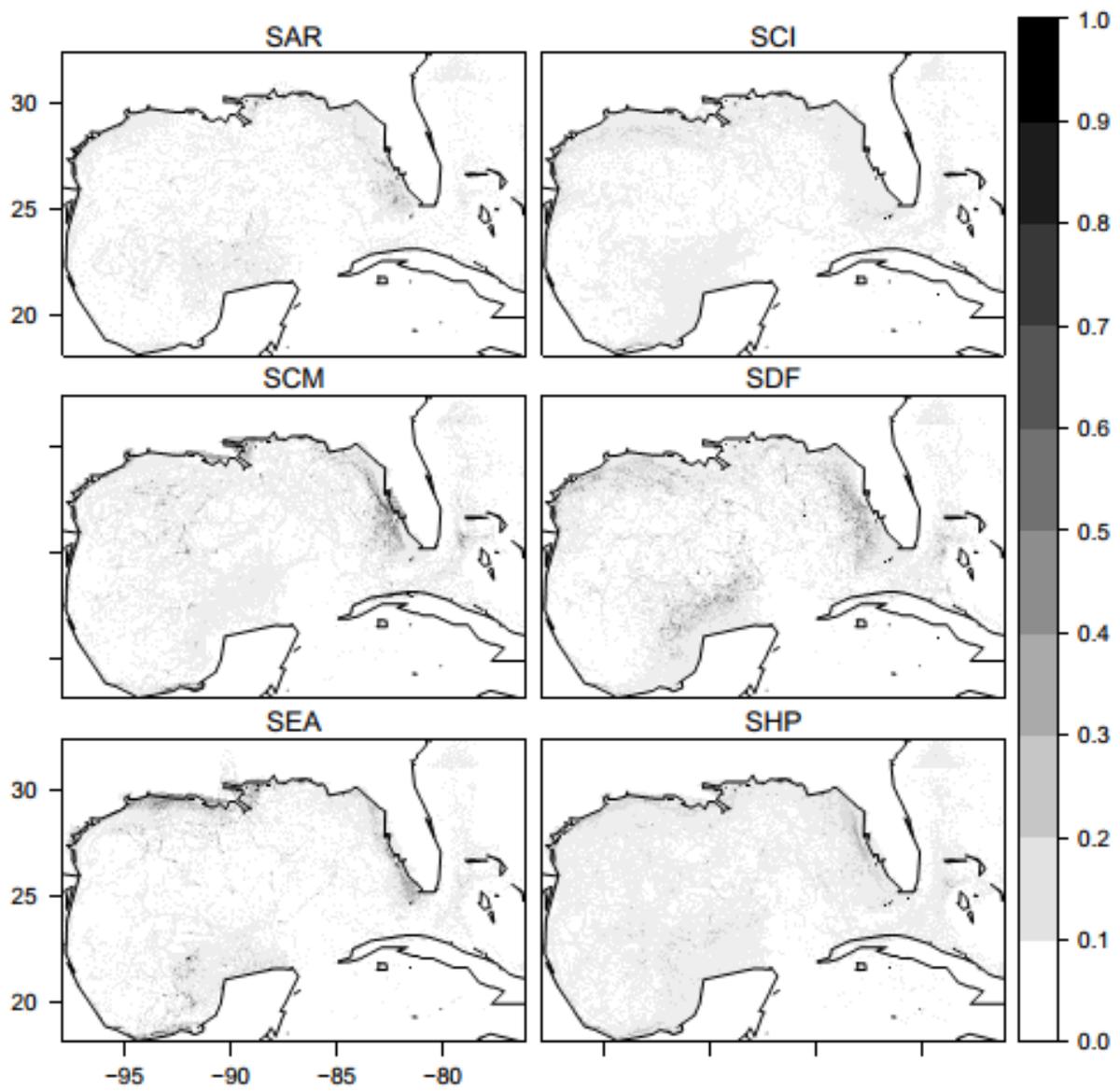


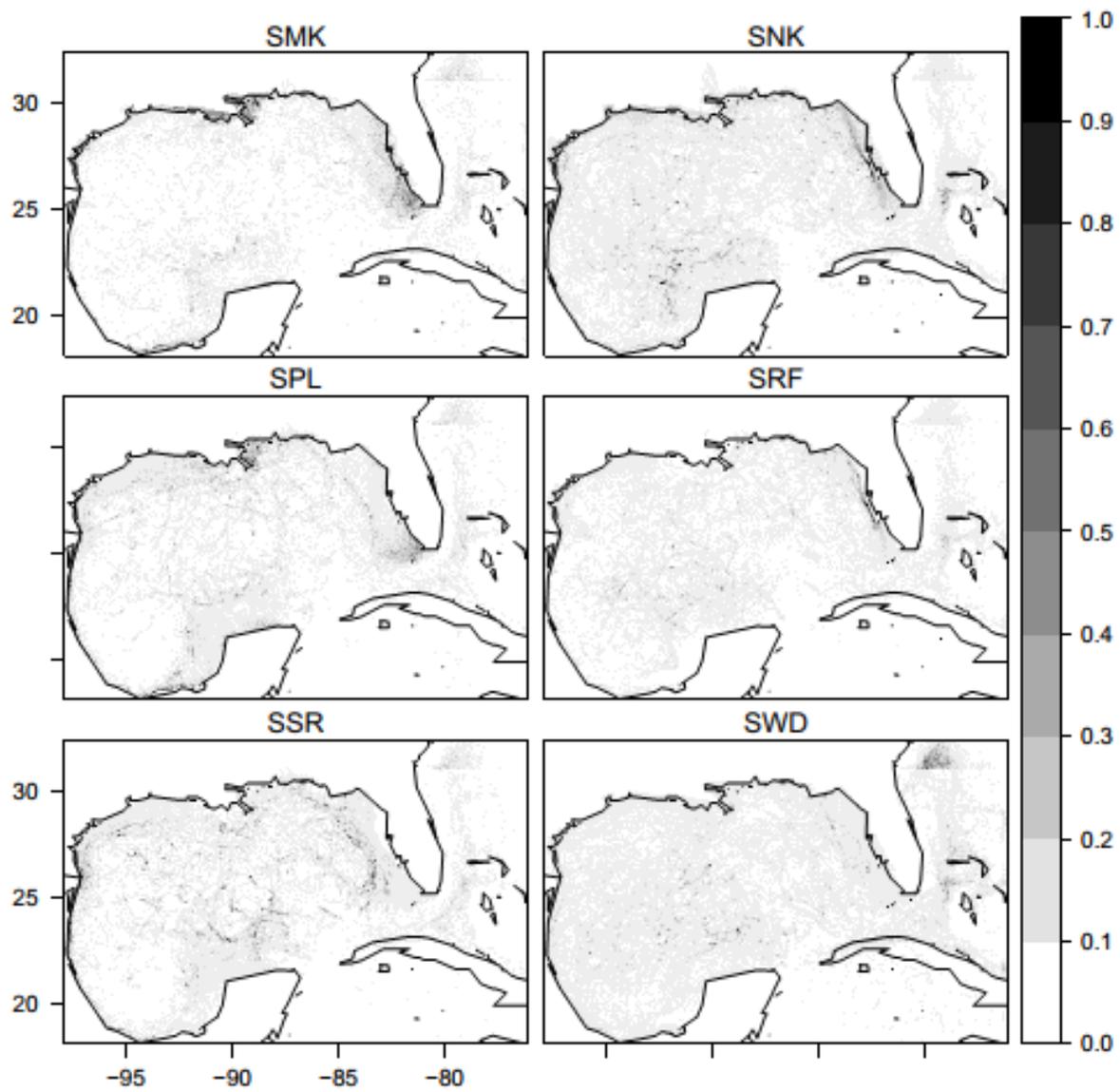


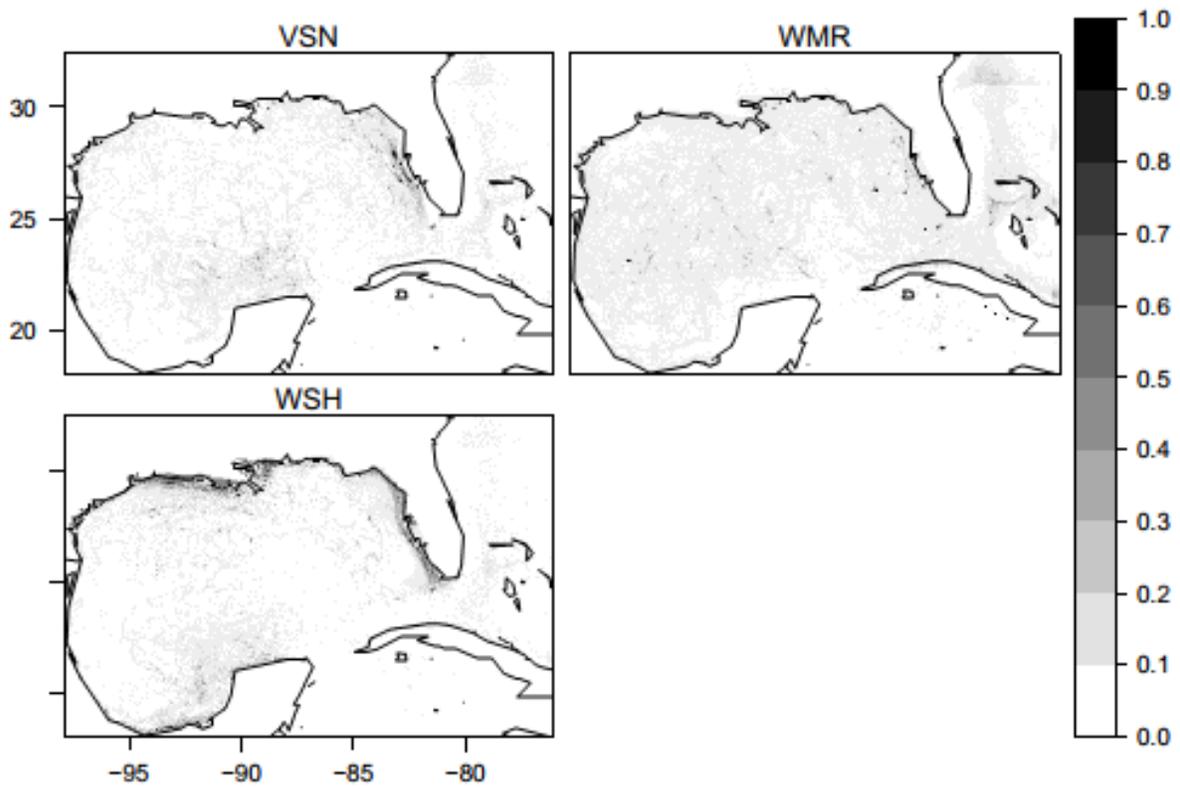




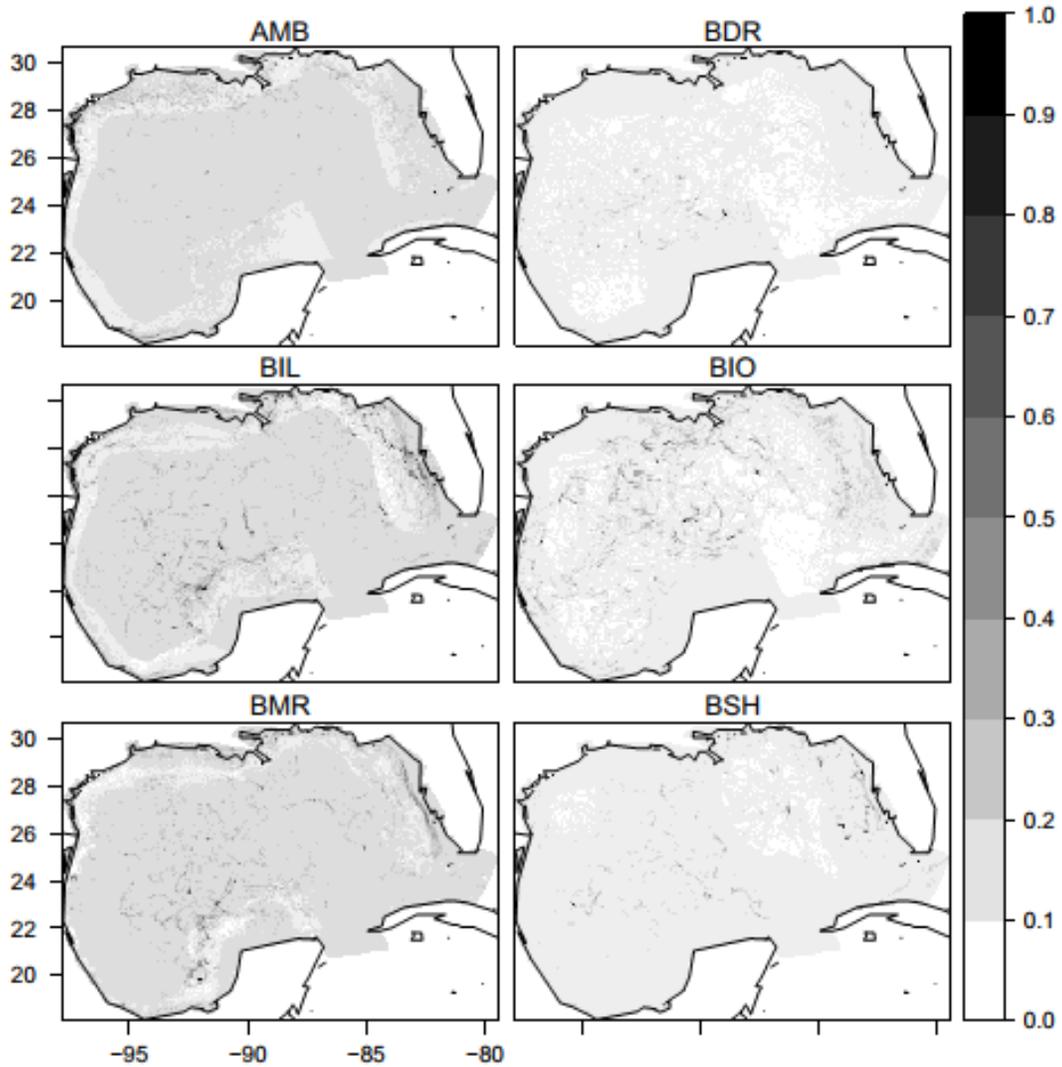


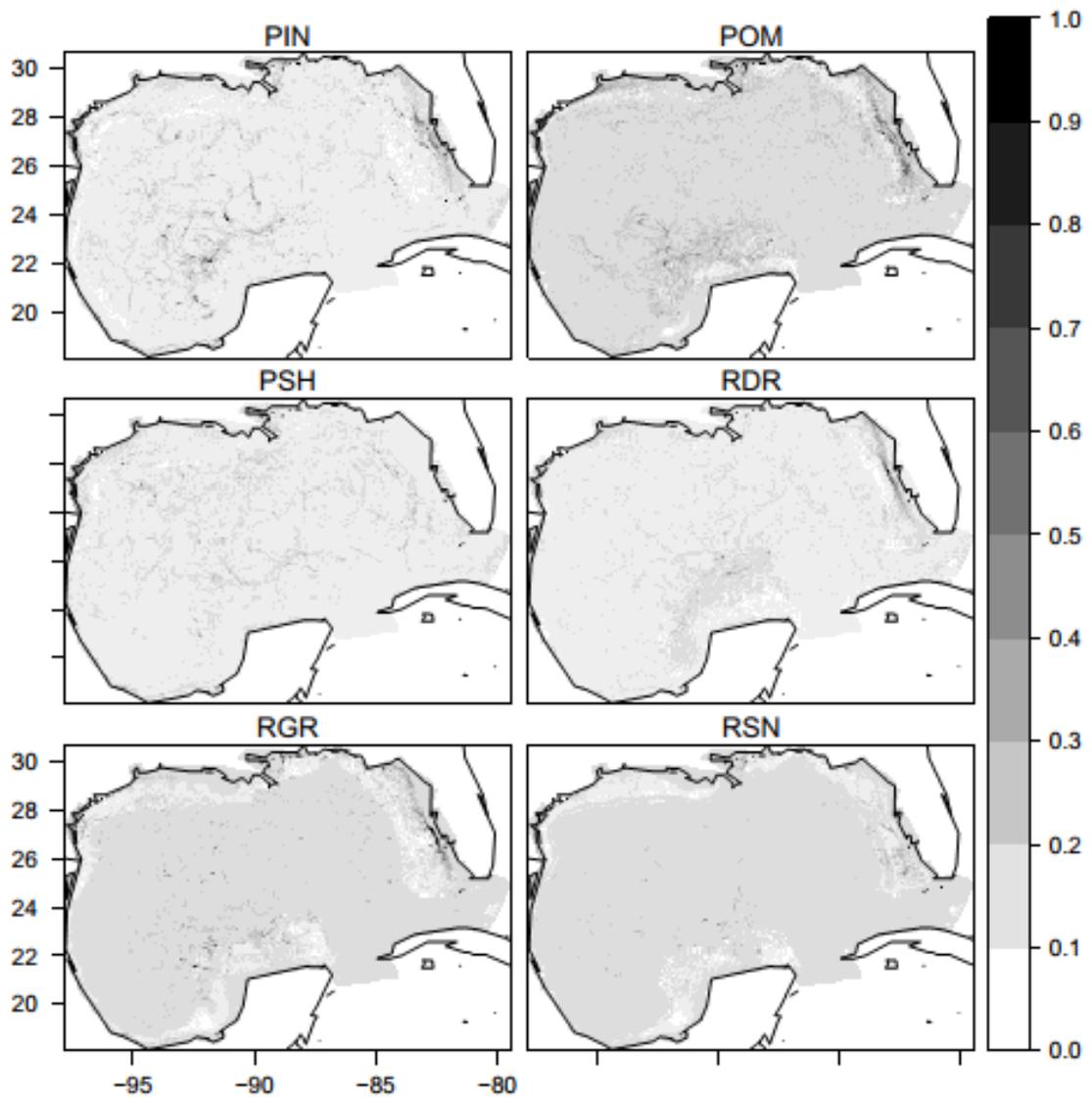


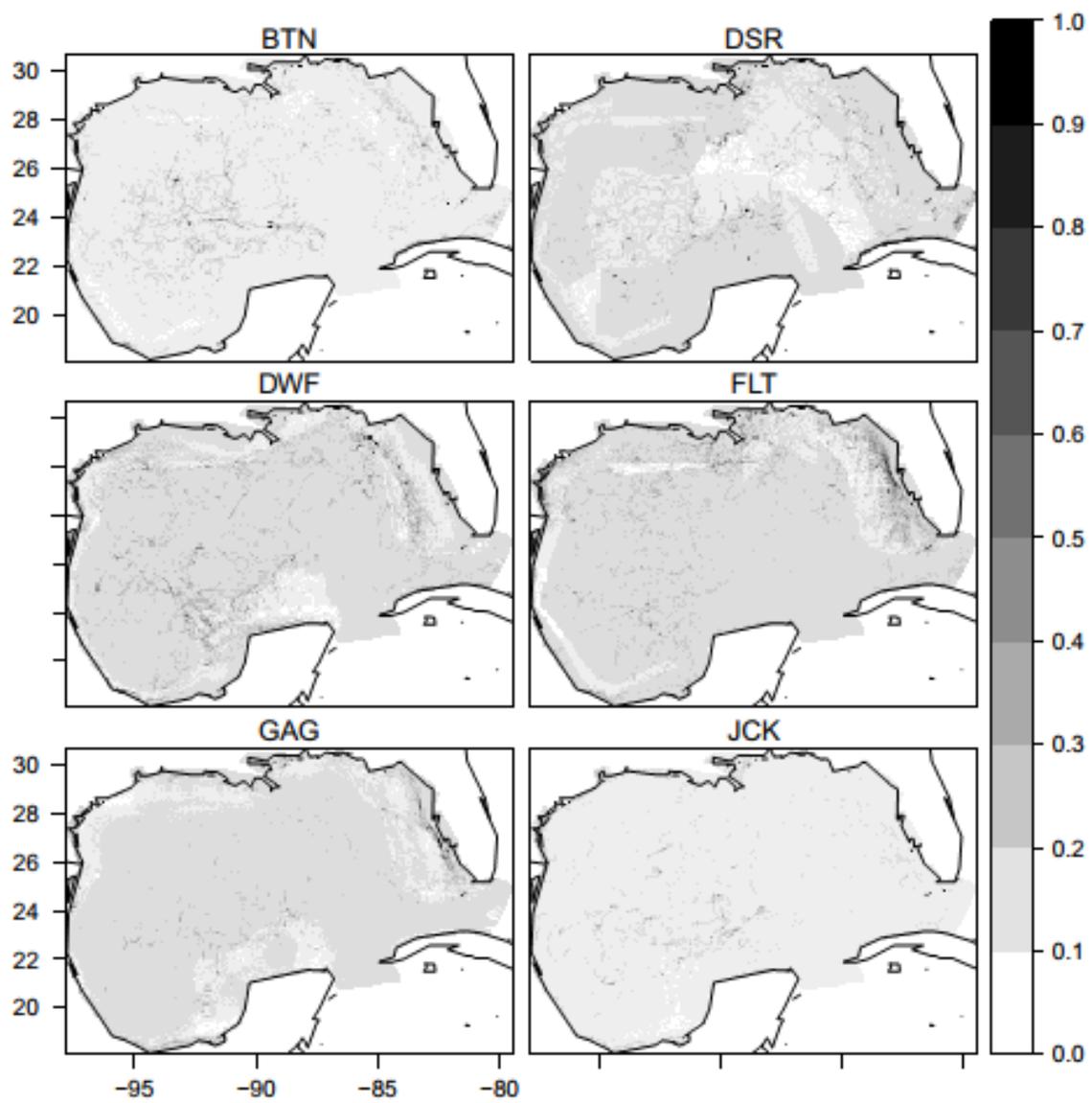


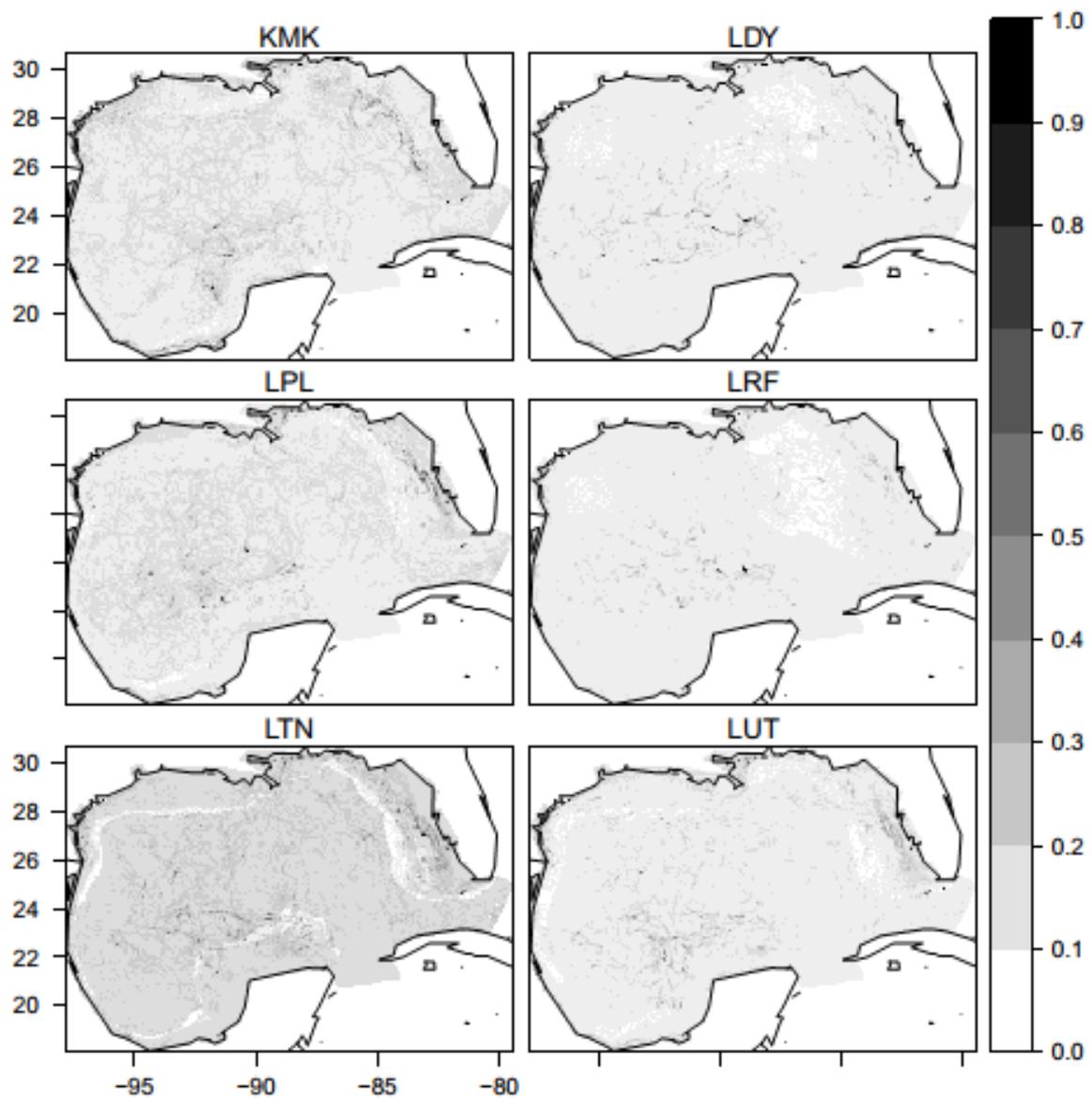


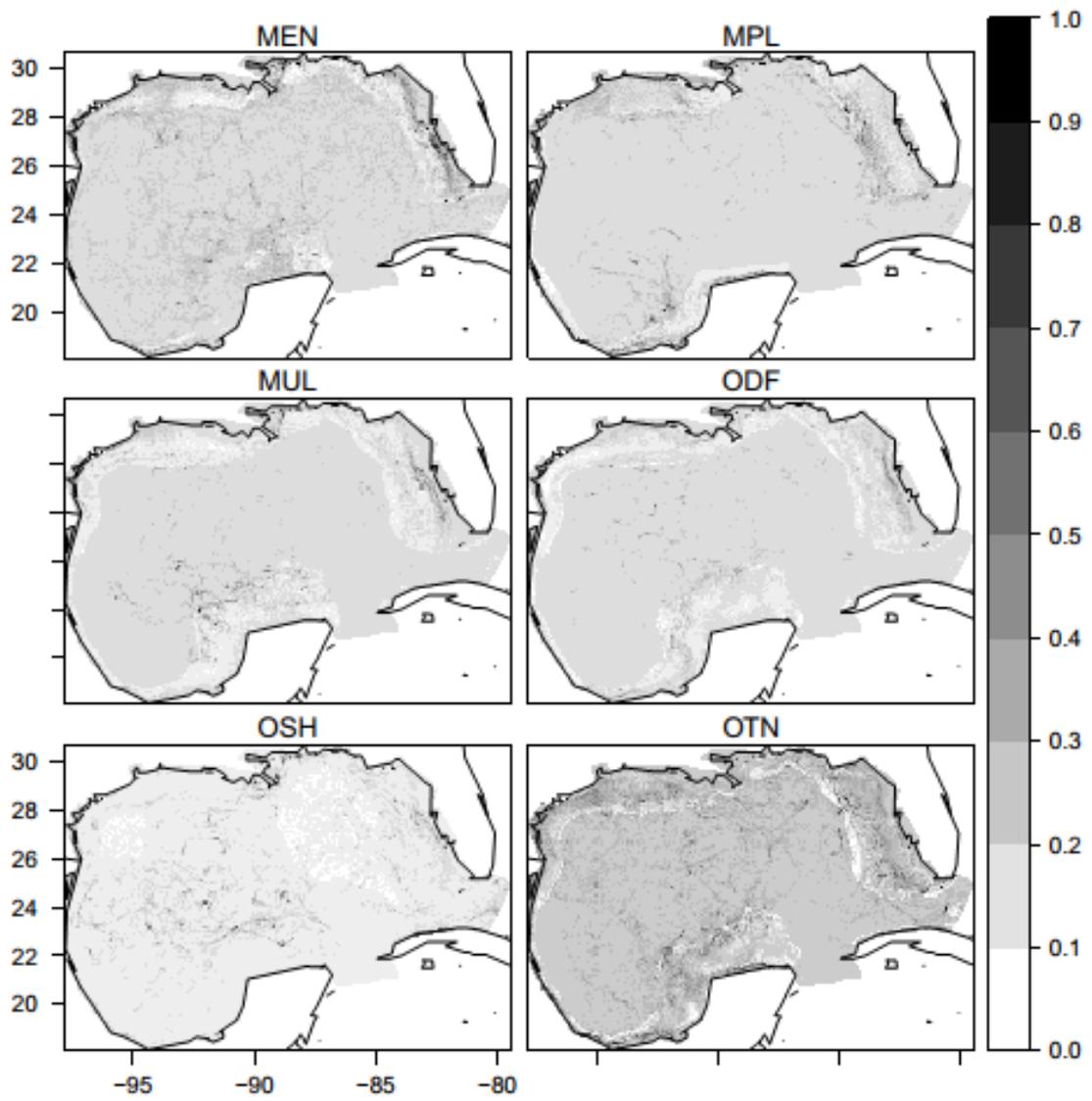
**Appendix E.** Source sink index representing the difference between larvae emitted and larvae absorbed in each grid cell across the simulated years (2003-2009). Dark areas represent sinks, where larvae absorbed is greatest, or where larvae arrive to areas with no adult biomass. Lights colors represent sources or areas receiving few larvae or those areas with very high adult biomass.

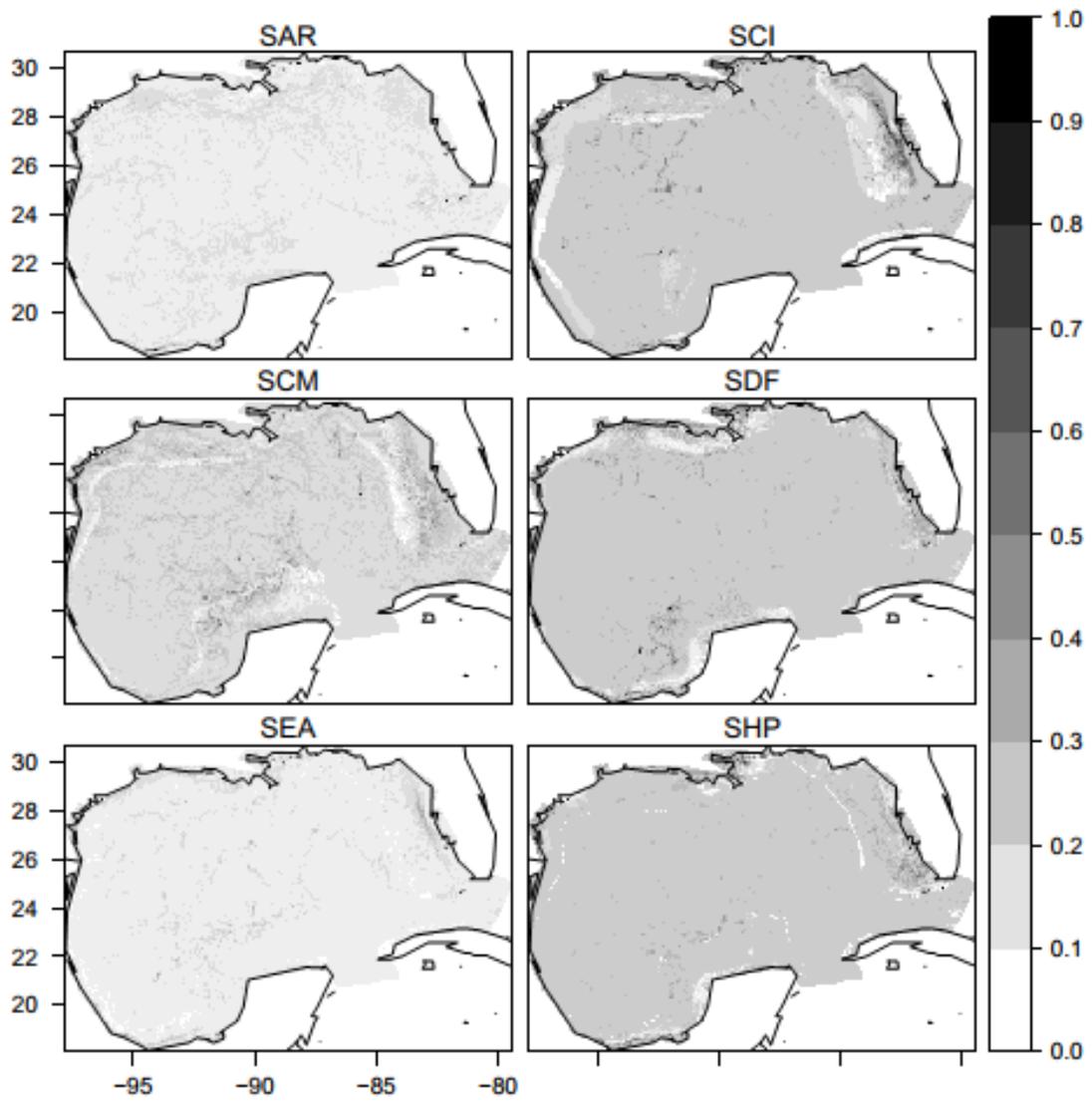


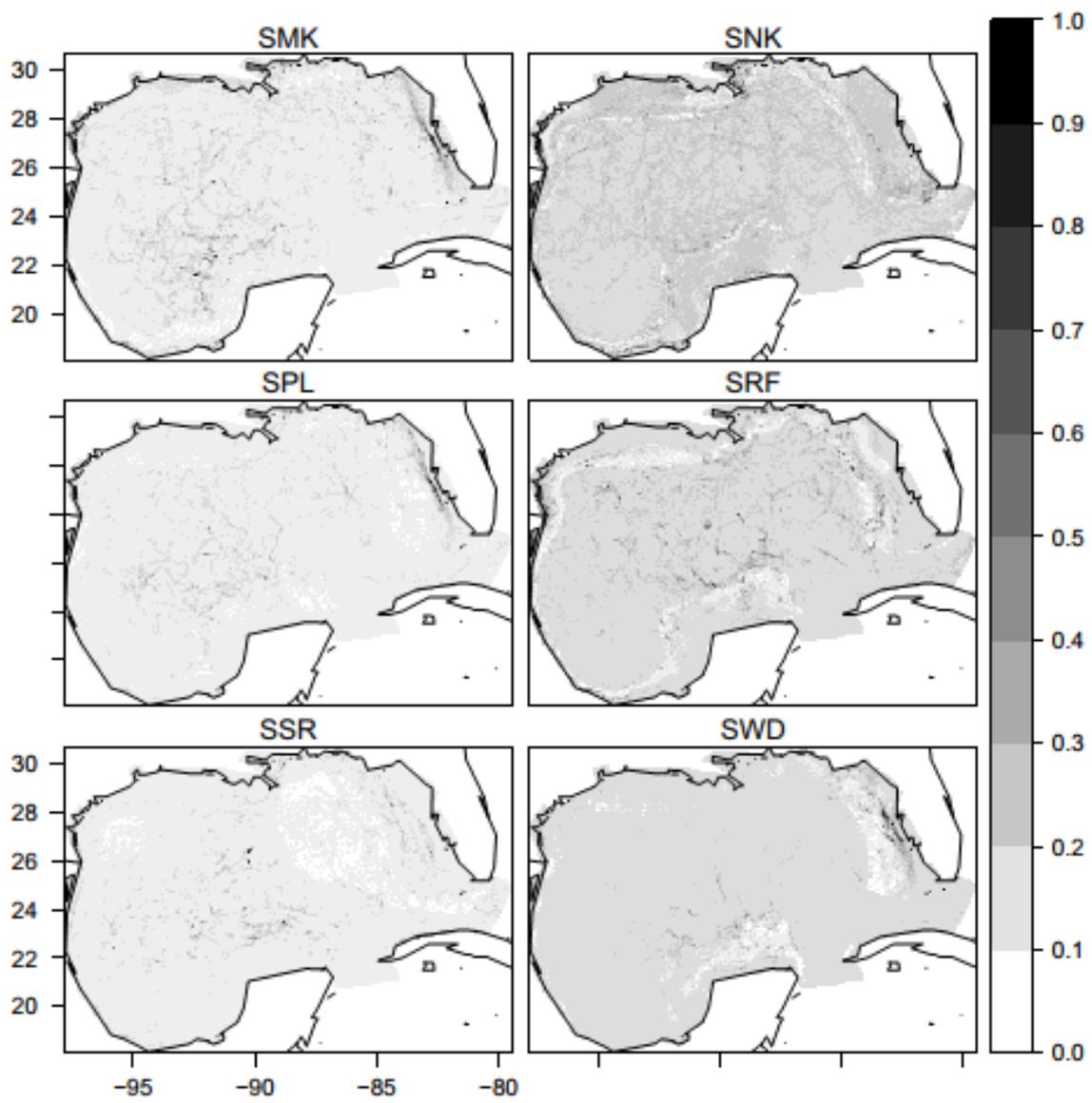


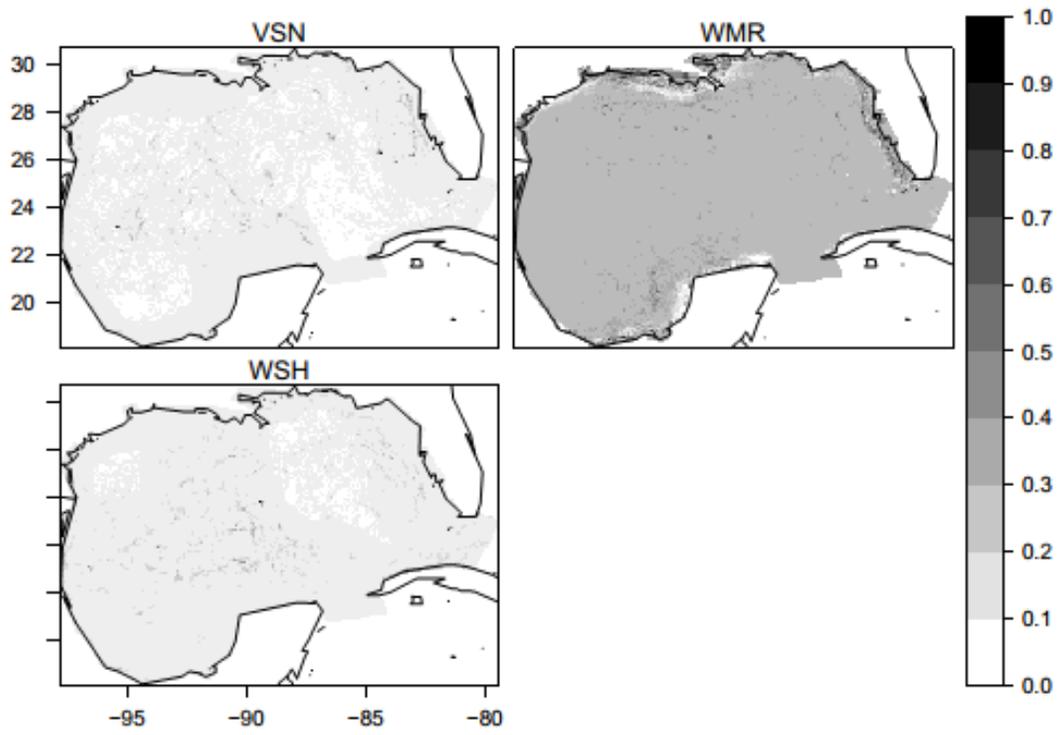












## **About the Author**

Michael earned his B.S. in Marine Biology from the University of Massachusetts Dartmouth and his M.S. in Biological Oceanography from the University Of South Florida College Of Marine Science. His Ph.D. research was focused on the application of ecosystem models to fisheries management. His research interests lie in pragmatic approaches to sustainable management of ocean resources. He continues to develop and implement a range of models and tools to achieve these goals in national and international fisheries management in his role of Fisheries Scientist for the Ocean Conservancy.