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Introduction

The main purpose of the present study is to inform SEDAR 42 as to how oceanographic factors affect the annual recruitment success of the red grouper (*Epinephelus morio*) population of the U.S. waters of the Gulf of Mexico. We use the Connectivity Modeling System (CMS; Paris *et al.*, 2007, 2013) to estimate the larval dispersal, settlement patterns and annual recruitment anomalies due to oceanographic factors of red grouper on the West Florida Shelf over the period 2003-2013. The CMS is an individual-based model which estimates the movement of particles in a three-dimensional velocity field, and has the capacity to simulate complex behaviors such as those displayed by fish larvae (Paris *et al.*, 2007, 2013; Helgers *et al.*, 2013). Simulated red grouper larvae are tracked from their release (spawning) sites on the West Florida Shelf to suitable settlement habitat, given the specified biological parameters. In the U.S. waters of the Gulf of Mexico, almost all red groupers are found on the West Florida Shelf (Coleman *et al.*, 1996, 2011; Lombardi-Carlson *et al.*, 2008; Sagarese *et al.*, 2014). Therefore, the restriction of the modeled area to the West Florida Shelf is assumed appropriate to inform SEDAR 42. The modeling efforts presented here produce an index of annual recruitment deviations expected from oceanographic factors for the years 2003-2013, which can be directly input as an environmental covariate into the Stock Synthesis assessment model used for SEDAR 42.

Methods

Connectivity Modeling System

The Connectivity Modeling System (CMS) is a biophysical modeling system based on a Lagrangian framework, and was developed to study complex larval migrations (Paris *et al.*, 2007, 2013; Helgers *et al.*, 2013). The CMS uses outputs from hydrodynamic models and tracks the three-dimensional movements of advected particles through time, given a specified set of release points and particle behaviors. Optional modules are provided to allow for complex behaviors and movements, simulating observed biological phenomena such as egg buoyancy, ontogenetic vertical migration, and tidal stream transport (Helgers *et al.*, 2013). The specific model set up used for this study is outlined in detail below.

Ocean velocity fields

The hydrodynamic model we used was the HYbrid Coordinate Ocean Model (HYCOM) + NCODA Gulf of Mexico 1/25° Analysis, a freely available ocean model with daily velocity fields available from 2003 – present (http://www.hycom.org). HYCOM is a hybrid isopycnal coordinate ocean model (i.e., isopycnal in the stratified open ocean, fixed-depth in the unstratified surface layers, and terrain-following in shallow coastal waters), which allows for optimal simulation of both coastal and open-ocean features simultaneously (Chassignet *et al.*, 2007). The model is data assimilative, using real-time observations of the ocean's surface via satellite altimetry, as well as vertical profile information from CTDs, the ARGO observation program, and other sources. This allows for a three-dimensional depiction of ocean currents in real time at a relatively high resolution.

Initial conditions of the biological model

The biological traits specified for simulated red grouper larvae are outlined in the table below. The methods by which these traits are incorporated into the CMS are described following.

Biological trait	**Description of information used in model parameterization**	**Source**
Spawning time	Spawning occurs from late fall to late spring, with a peak from March to May; frequency of approximately every five days.	Moe (1969); Johnson *et al.* (1998); Collins *et al.* (2002); Fitzhugh *et al.* (2006)
Spawning location	Red groupers do not form spawning aggregations and spawn on their home sites. Adult red groupers are typically found at depths ranging from 65 to 100 m.	Coleman *et al.* (1996, 2010, 2011); Coleman and Koenig (2010)
Spawning depth	65-100 m depth.	Coleman and Koenig (2010)
Egg diameter	Red grouper eggs are approximately 0.95 mm in size.	Colin *et al.* (1996)
Egg buoyancy	Fertilized eggs (+4 hours) of red grouper are neutrally buoyant in 28-30 ppt seawater at 22°C. Fertilized eggs (+20 hours) are neutrally buoyant at 32 ppt.	Colin *et al.* (1996)
Pelagic larval duration (PLD)	40-60 days.	Coleman and Koenig (2010)
Settlement habitat	Juvenile red groupers are found in inshore hard bottom areas and offshore reefs, on grass beds and in estuaries, but evidence suggests that red grouper does not require specific settlement and nursery habitats contrary to gag grouper (*Mycteroperca microlepis*). The dominant habitat for juveniles of red grouper cannot be determined accurately because of the cryptic nature of the	Moe (1969); Koenig and Coleman (1998); Lindeman *et al.* (2000); Coleman *et al.* (2010); C. Koenig, pers. comm.

	species. The hydrodynamic model does not resolve circulation in shallow areas, nor does it account for swimming behavior of competent larvae, so we assume larvae reaching the shelf (<30 m) during the competency period have the ability to successfully settle.	
Timing of hatching and flexion	Hatching occurs 30 to 38 hours after fertilization. Red grouper reaches flexion ~16 day post hatching (i.e., ~17.5 days post fertilization) and at ~6.5 mm length.	Colin *et al.* (1996)
Vertical migration	See Table 1, Figure 1, and Appendix 1 in Karnauskas *et al.* (2013).	Karnauskas *et al.* (2013); C. Paris (unpubl. data); G. Zapfe (unpubl. data).

Red groupers do not form spawning aggregations and spawn on their home sites (Coleman *et al.*, 1996, 2010, 2011; Coleman and Koenig, 2010). Therefore, in the larval transport simulation, particles representing eggs were released from locations of the West Florida Shelf where adult red groupers (i.e., red groupers whose length is greater than 34.1 cm TL; SEDAR, 2009) are estimated to be present, during the period of peak spawning activity at the observed frequency.

To determine the locations of the West Florida Shelf where adult red groupers are present, which we used as a proxy for spawning activity, we employed a binomial generalized linear model (GLM) to predict the mean probability of presence of adult red grouper on the West Florida Shelf over the period 2003-2013 (Sagarese *et al.*, 2014). Research survey datasets used to fit the GLM include both fisheries-independent datasets (the SEAMAP trawl, NMFS bottom longline, Expanded Annual Stock Assessment vertical line, and Expanded Annual Stock Assessment longline datasets) and fisheries-dependent datasets (the Shark bottom longline observer program, Observer longline and Observer vertical line datasets).

Predictor variables included in the GLM are depth, sediment type, longitude, latitude, gear, year, month and hour. Small-scale residual variation in the probability of presence of adult red grouper was interpolated across the West Florida Shelf through the use of kriging (see Sagarese *et al.* (2014) for details on the GLM and kriging procedures). Kriged residual probabilities of presence were added to the mean probabilities of presence predicted by the binomial GLM to obtain 'final probabilities of presence'. We calculated a Receiver Operating Characteristic (ROC) curve, which expresses the true positive rate (sensitivity) as a function of the false positive rate (100-specificity) for each final probability of presence (R 'pROC' library; Robin *et al.*, 2011). An optimum probability threshold can be estimated where the sum of the sensitivity and the sum of specificity are at their maximum (Manel *et al.*, 2001; Hattab *et al.*, 2013). This allowed us to convert the final probabilities to either presence (above or equal to the threshold) or absence (below the threshold), and thus to define where red grouper spawning is not likely to occur (Figure 2).

The bottom depth of each spawning site was estimated from the global 30 arc-second bathymetry data grid available from GEBCO (General Bathymetric Chart of the Oceans; http://www.gebco.net). Spawning depth at each spawning site was either the average spawning depth for red grouper (82.5 m; Coleman and Koenig, 2010) or local bottom depth if shallower. Particles were initially released every five days during the period of peak spawning activity over the period 2003-2013 from the spawning depth at spawning sites, and their movements were then tracked in horizontal and vertical space. The number of particles released from each spawning site was proportional to the probability of presence of adult red grouper at that site (Figure 2). The number of particles released from a spawning site with an average probability of presence of adult red grouper was set to 50; this number was selected for being high enough to provide robust simulated patterns while allowing for reasonable computation time. The number of particles released from each spawning site was kept constant across months and across years, as our main goal is to understand differences in recruitment from year to year unrelated to the level of spawning stock biomass.

Because the simulated depth distributions of particles in the first few days can have significant effects on the ultimate dispersion patterns (Mullon *et al.*, 2002), the CMS includes a number of modules to more realistically parameterize vertical movements of eggs during this early period (Helgers *et al.*, 2013). For red grouper, we used CMS's buoyancy module, which simulates the sinking or floating of particles based on their physical properties. Vertical particle movements are defined according to Stoke's Law, which relates vertical velocity to the diameter and density of the particle, along with the density and viscosity of the water. The latter two variables are extracted directly from the oceanographic data for the location of the particle. The diameter and density of the particles are defined based on values from the literature. The CMS also allows for some variation in the specification of the size and density parameters by incorporating these values as a distribution rather than a fixed value (Table 2).

After one day and a half, at which point red grouper eggs hatch into larvae (Colin *et al.*, 1996), simulated particles are subject to a probabilistic vertical migration matrix based on empirical data (Table 1). Vertical distributions for preflexion larvae were calculated from winter SEAMAP surveys using the MOCNESS sampling (G. Zapfe, unpubl. data; see Appendix 1 in Karnauskas *et al.* (2013) for sampling description). Because grouper larvae are rare in the samples, and cannot easily be identified to species level, we used all Epinephelidae larvae in our calculations. Only eight postflexion stage Epinephelidae larvae were available for two SEAMAP winter surveys, so we combined these observations with MOCNESS samples from Barbados (C.B. Paris, unpubl. data) to come up with a hypothesized vertical distribution for this stage. As new MOCNESS samples become available, we will increase our sample size of postflexion larvae and adjust vertical migration specifications according to new data.

Because data to inform the vertical migrations of red grouper larvae are scarce, and because these parameters can have a large influence on the predictions of the CMS, sensitivity analyses were used to estimate variability and uncertainty envelopes around the calculated recruitment anomaly index. Sensitivity analyses are carried out by slightly modifying the specified vertical migration matrix, rerunning the simulation, and recalculating the recruitment anomaly index. For red grouper, we modified the vertical distributions by using kernel regression smoothers of differing bandwidths fit to the data (i.e., the observed percentage of larvae in each depth category). A larger bandwidth has the effect of flattening the distribution, whereas the smallest bandwidth used gave a distribution similar to the observed values. We further tested sensitivities by shifting the distribution means shallower and deeper by 2m and 4m. The different vertical distributions used in the sensitivity analyses are plotted in Figure 1.

Once the competency period is reached (i.e., 40 days post fertilization; Coleman and Koenig, 2010), simulated particles are allowed to settle, only when they reach appropriate settlement habitat as defined by the CMS (i.e., all the areas of the West Florida Shelf whose depth is less than 30 m). Throughout the remainder of the competency period, particles are allowed to successfully settle or continue to move if they have not yet reached suitable habitat. Following Ingram *et al.* (2013), we distinguished between 10 settlement regions in the West Florida Shelf, (1) Northwestern Florida; (2) the Saint Andrew Bay Region; (3) the Saint Joe Bay Region; (4) the Turkey Point Region; (5) the Mid Big Bend; (6) the Cedar Key Region; (7) the Tampa Bay Region; (8) the Sarasota Bay Region; (9) the Charlotte Harbor Region; and (10) Southeastern Florida. To define settlement polygons in the CMS, we extracted contours at the 0 and 30 m isobaths for the West Florida Shelf from the global 30 arc-second bathymetry data grid available from GEBCO and used the polygon shapefiles constructed for Ingram *et al.* (2013)'s study (Figure 2).

Other CMS specifications

We used the built-in turbulence module of the CMS, which adds a random component to the motion of the particles to represent turbulent diffusion (Helgers *et al.*, 2013). This component represents sub-grid turbulent processes not resolved by the resolution of the hydrodynamic model. Based on Okubo, (1971), we used a value of 10 $m^2.s^{-1}$ for horizontal diffusivity and 0.001 $m^2.s^{-1}$ for vertical diffusivity. We also used the ‘avoid coast’ algorithm built in the CMS, which helps to prevent particles from getting stranded on the land mass (Helgers *et al.*, 2013). Because fish larvae are not passive drifters, they can likely swim away from the coast to avoid being stranded. This module thus provides a more realistic estimate of the movements of fish larvae near coasts.

Results

The simulations we conducted indicate that recruitment anomalies of red grouper due to oceanographic factors varied significantly across years over the period 2003-2013 (Figures 3 and 4 and Table 3). While general trends in red grouper recruitment anomalies were similar across vertical distribution scenarios, the magnitude of recruitment anomalies varied considerably depending on the vertical larval distribution patterns assumed (Figure 3 and Table 3). Simulations estimate recruitment anomalies to be highest in 2012 (Figures 3 and 4 and Table 3). Other strong years of recruitment are estimated to be 2005 and 2006 (Figures 3 and 4 and Table 3). Recruitment deviations are predicted to be lowest in 2007 and 2009.

Mean spatial patterns of settlement of red grouper over the period 2003-2013 were similar for the base vertical distribution scenario and when all vertical distribution scenarios are combined (Figures 5 and 6). The bulk of red grouper settlement over the period 2003-2013 occurred in the Charlotte Harbor Region and Southeastern Florida (Figure 5). Red grouper settlement was also high in the Mid Big Bend and the Tampa Bay Region. Settlement did not occur in Northwestern Florida, the Saint Andrew Bay Region and the Saint Joe Bay Region (Figure 5), where adult red grouper was also predicted to be absent (Sagarese *et al.*, 2014; Figure 2). A large fraction of red grouper larvae were predicted to settle in the region where they were spawned, i.e., to be self-recruiting (Figure 6). However, the majority of red grouper larvae settling in the Charlotte Harbor Region, Sarasota Bay Region and Cedar Key Region originated from neighboring regions.

The Mid Big Bend and Turkey Point Region were predicted to be the spawning regions with the highest larval transport success over the period 2003-2013 (11.54% and 10.41%, respectively, under the base vertical distribution scenario; Table 4). The spawning regions with the lowest larval transport success were the Sarasota Bay Region, Southeastern Florida and the Charlotte Harbor Region (3%, 3.73% and 4.18%, respectively, under the base vertical distribution scenario).

Discussion

In the present paper, we conducted simulations with the CMS for West Florida Shelf red grouper over the period 2003-2013, where the number of particles released at each spawning site was kept constant across months and across years. This allowed us to estimate an index of annual recruitment deviations due to ocean current patterns, and independent of spawning stock biomass. Our recruitment anomaly index can be directly input as an environmental covariate into the Stock Synthesis assessment model used for SEDAR 42.

The exact vertical distribution of red grouper larvae is the major source of uncertainty in the CMS due to the few empirical observations of Epinephelidae vertical distributions available. To account for this, we carried out sensitivity analyses where we slightly altered the vertical distribution profiles of red grouper larvae. Sensitivity runs showed that the magnitude of recruitment anomalies of red grouper is significantly affected by changes in the vertical distribution patterns of larvae. The variance estimates that we constructed for annual recruitment anomalies (Table 3) help to account for this uncertainty; they should be taken into consideration when our recruitment anomaly index is input into the Stock Synthesis assessment model.

It is our hope that the recruitment anomaly index produced in the present study will explain a significant amount of the variation in the stock-recruitment deviates from the Stock Synthesis assessment model used for SEDAR 42. The consideration of our estimates of annual recruitment deviations in the Stock Synthesis assessment model will also inform the recent years of red grouper assessment where cohort strength is poorly estimated.

The index of annual recruitment anomaly due to oceanographic factors presented in this paper is based on the best available data and knowledge that have been compiled to date on the reproductive patterns and larval behavior of red grouper. Further model refinements, to be included as new data become available, are likely to alter the trends seen in the index. One of these refinements is the consideration of red grouper spawning sites on Campeche Bank (Mexico) in the CMS, because it has been hypothesized that a fraction of grouper larvae settling on the West Florida coast originates from the Campeche Bank (Fitzhugh *et al.*, 2005). We can note, however, that Johnson *et al.* (2013)'s and Karnauskas (unpubl. data)'s biophysical modeling studies found evidence of little connectivity between Campeche Bank and the northern Gulf of Mexico for red snapper (*Lutjanus campechanus*) and gag grouper (*Mycteroperca microlepis*), respectively.

We did not evaluate annual patterns of larval dispersal and settlement for red grouper in the present paper. Instead, we focused on the mean transport success and mean spatial patterns of settlement of red grouper over the period 2003-2013. We found that larval transport success from southern regions of the West Florida Shelf (Charlotte Harbor Region and Southeastern Florida) is low, while the bulk of red grouper settlement occurred in these regions. The Mid Big Bend and Turkey Point Region were predicted to be the spawning regions of the West Florida Shelf with the highest larval transport success. We will soon analyze the trajectories and settlement patterns of red grouper larvae for the different years of the period 2003-2013 in relation to ocean processes. This will allow us to determine whether the larval transport success from the different regions of the West Florida Shelf is relatively stable over time, and to thoroughly understand the mechanisms by which annual recruitment anomalies of red grouper are noticeably high (in 2012) or low (in 2007 and 2009).

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Tables

Table 1. Vertical migration base case parameters applied to simulated red grouper larvae in the Connectivity Modeling System. Columns are percentages of larvae to be distributed in each of the 20-m depth bins during the specified time periods.

	2-18 days	19-61 days
0-20 m	34	31
20-40 m	29	25
40-60 m	20	17
60-80 m	11	14
80-100 m	6	13

Table 2. Specifications of variability in the density and size of simulated particles in the Connectivity Modeling System.

Percentage of particles in each category	**25%**	**50%**	**25%**
Minimum density (kg.m^{-3})	1018.7	1019.7	1020.7
Maximum density (kg.m^{-3})	1019.7	1020.7	1021.7
Minimum particle size (mm)	0.900	0.925	0.950
Maximum particle size (mm)	0.950	0.975	1.000

Table 3. Annual recruitment anomaly indices estimated by the Connectivity Modeling System for the period 2003-2013 and associated coefficient of variations (CVs).

Year	Recruitment anomaly	CV of recruitment anomaly
2003	-0.31	1.55
2004	-0.31	0.35
2005	0.94	0.10
2006	0.73	0.50
2007	-0.89	0.53
2008	0.12	2.37
2009	-0.93	0.66
2010	-0.46	0.65
2011	-0.46	0.42
2012	2.19	0.05
2013	-0.63	0.49

Table 4. Larval transport success (in %) from the different spawning regions of the West Florida Shelf over the period 2003-2013 predicted by the Connectivity Modeling System, and associated coefficient of variation (CV).

Spawning region	**Larval transport success (%)**	**CV of larval transport success**
Turkey Point Region (TPR)	10.41	0.24
Mid Big Bend (MBB)	11.54	0.16
Cedar Key Region (CKR)	7.56	0.26
Tampa Bay Region (TBR)	6.47	0.24
Sarasota Bay Region (SBR)	3.00	0.29
Charlotte Harbor Region (CHR)	4.18	0.30
Southeastern Florida (SEF)	3.73	0.32

Figures

Figure 1. Vertical migration distributions used for sensitivity analyses. Bandwidth 60: base vertical migration distribution – **Bandwidth 40:** use of a kernel smoother of smaller bandwidth to fit to the data (i.e., the observed percentage of larvae in each depth category) distribution – **Bandwidth 70:** use of a kernel smoother of larger bandwidth to fit to the data distribution – **+2m:** vertical migration distribution means shifted shallower by 2 m – **+4m:** vertical migration distribution means shifted shallower by 4 m – **-2m:** vertical migration distribution means shifted deeper by 2 m – **-4m:** vertical migration distribution means shifted deeper by 4 m.

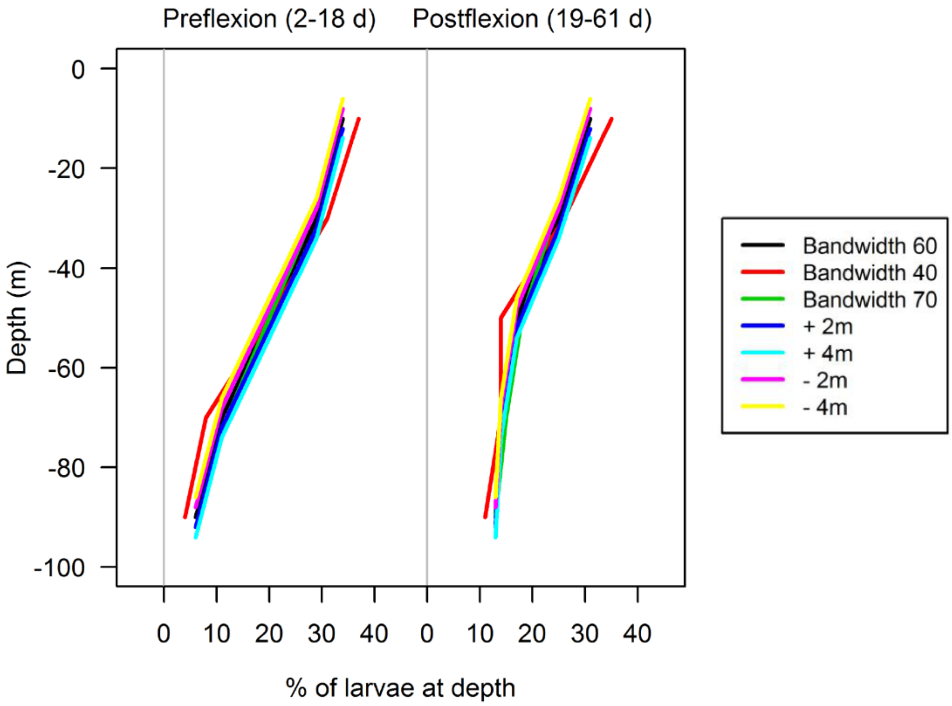


Figure 2. Map of the West Florida Shelf in the Gulf of Mexico showing the release (spawning) sites (colored dots) and settlement areas (black polygons) of red grouper (*Epinephelus morio*) considered in the Connectivity Modeling System. The number of red grouper eggs released from each spawning site is proportional to the probability of presence of adult red grouper at that site, which is predicted from Sagarese *et al.* (2014).

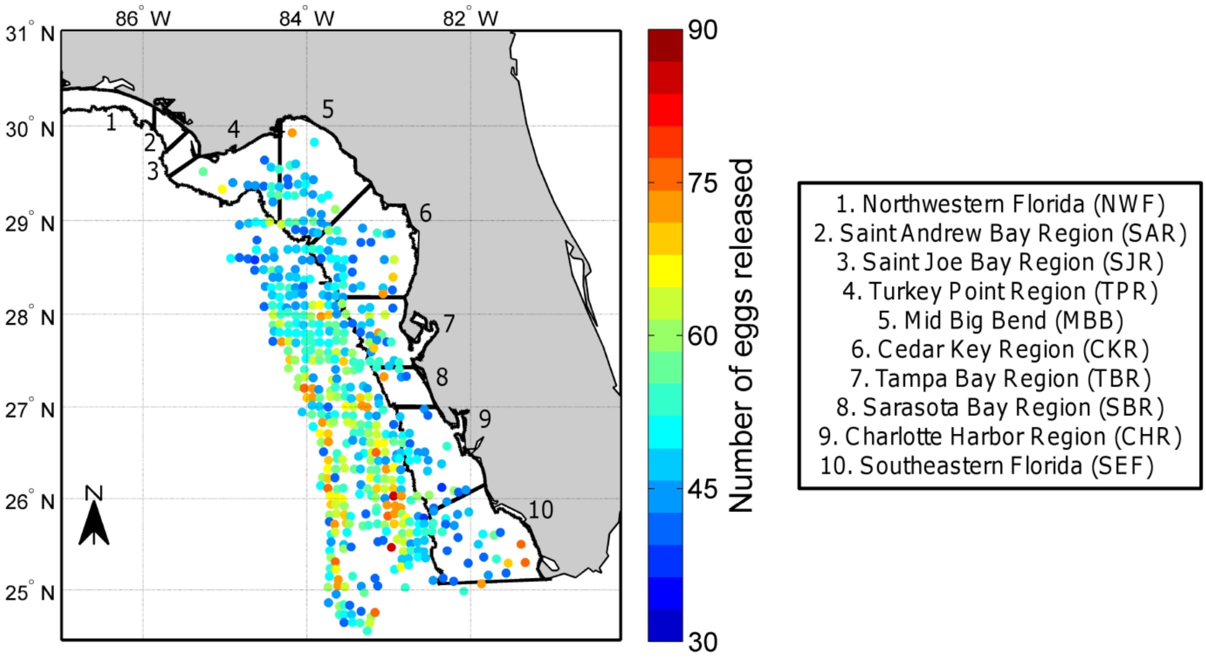


Figure 3. Annual recruitment success of red grouper (*Epinephelus morio*) on the West Florida Shelf over the period 2003-2013 estimated by the Connectivity Modeling System, for different sensitivity analysis simulations. Bandwidth 60: base vertical migration distribution – **Bandwidth 40:** use of a kernel smoother of smaller bandwidth to fit to the data (i.e., the observed percentage of larvae in each depth category) distribution – **Bandwidth 70:** use of a kernel smoother of larger bandwidth to fit to the data distribution – **+2m:** vertical migration distribution means shifted shallower by 2 m – **+4m:** vertical migration distribution means shifted shallower by 4 m – **-2m:** vertical migration distribution means shifted deeper by 2 m – **-4m:** vertical migration distribution means shifted deeper by 4 m.

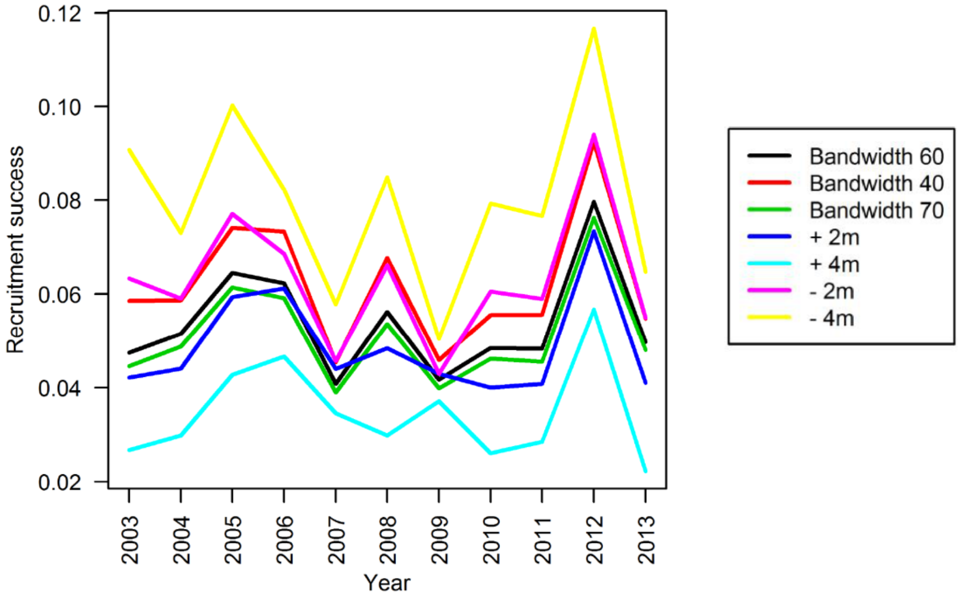


Figure 4. Annual recruitment anomalies for red grouper (*Epinephelus morio*) on the West Florida Shelf over the period 2003-2013 estimated by the Connectivity Modeling System. Simulated recruitment anomalies are shown for the mean (black dotted line) and range (shaded area) of simulations across all vertical distribution scenarios considered.

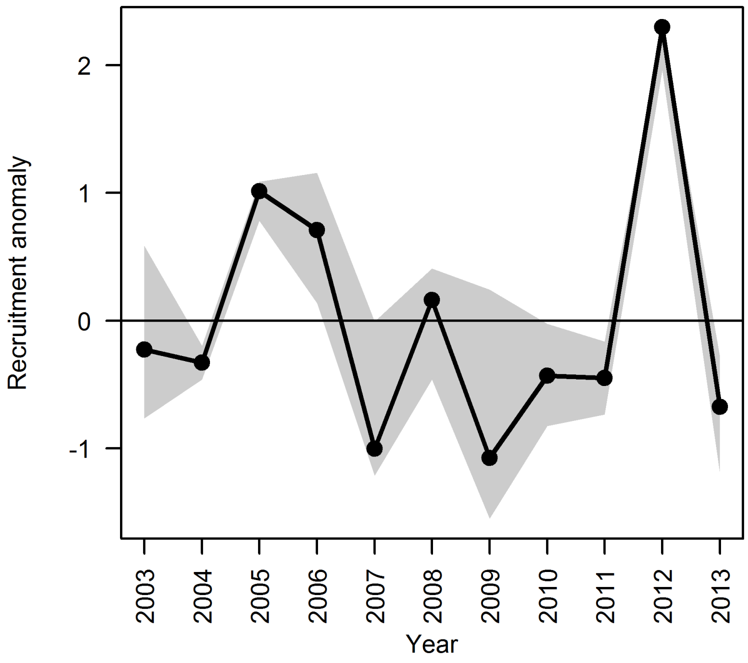
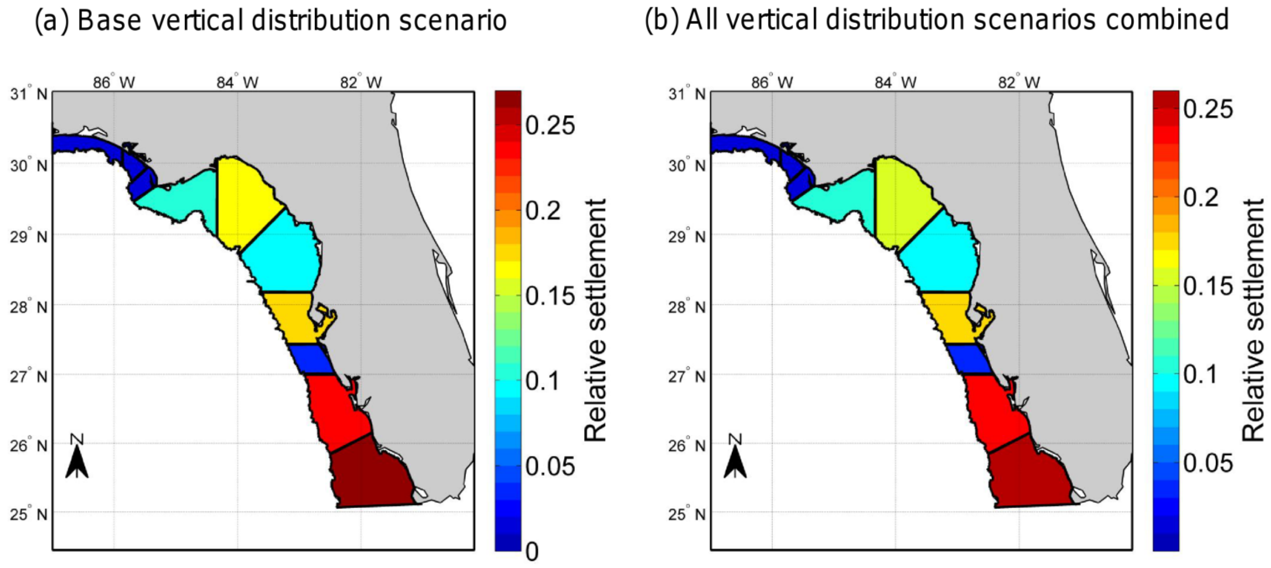
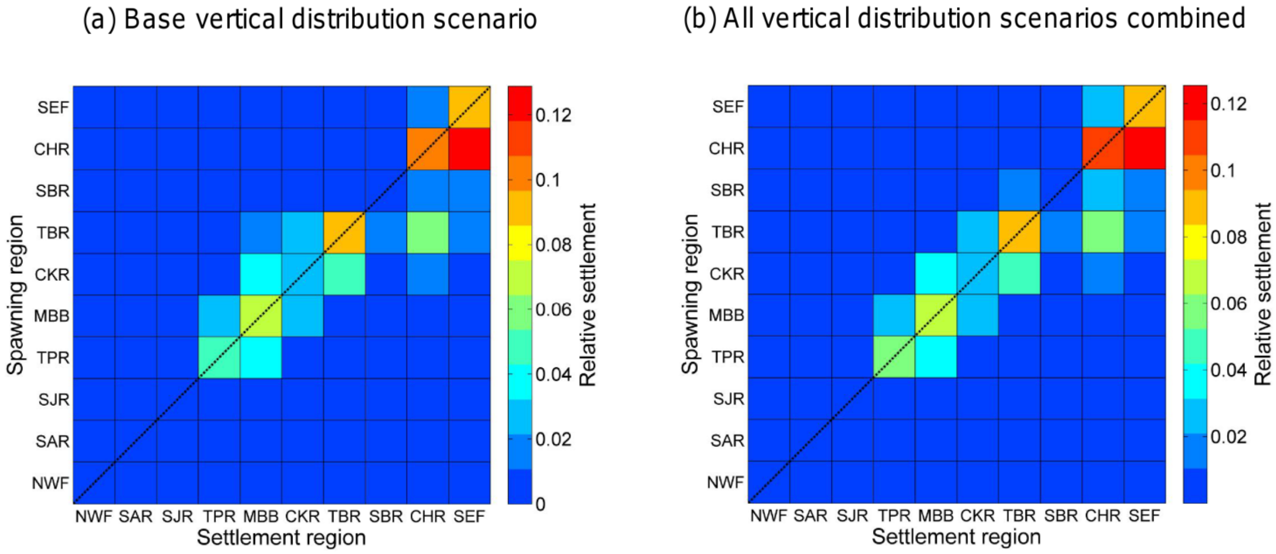


Figure 5. Mean annual spatial patterns of settlement of red grouper (*Epinephelus morio*) on the West Florida Shelf over the period 2003-2013 (a) for the base vertical distribution scenario ('Bandwidth 60'); and (b) when all vertical distribution scenarios are combined.


(a) Base vertical distribution scenario

(b) All vertical distribution scenarios combined

Figure 6. Mean annual connectivity matrices of red grouper (*Epinephelus morio*) in the West Florida Shelf over the period 2003-2013 for (a) the base vertical distribution scenario ('Bandwidth 60'); and (b) all vertical distribution scenarios combined. Rows of connectivity matrices are source nodes (spawning regions) and their columns are receiving nodes (settlement regions). Self-recruitment is indicated by the diagonal line. NWF: Northwestern Florida – SAR: Saint Andrew Bay Region – SJR: Saint Joe Bay Region – TPR: Turkey Point Region – MBB: Mid Big Bend – CKR: Cedar Key Region – TBR: Tampa Bay Region – SBR: Sarasota Bay Region – CHR: Charlotte Harbor Region – SEF: Southeastern Florida.


(a) Base vertical distribution scenario

(b) All vertical distribution scenarios combined