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Source–sink recruitment of red snapper: Connectivity between the Gulf of Mexico and Atlantic Ocean

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Abstract

Geopolitical fishery management boundaries are often misaligned with the ecological population structure of marine species, which presents challenges for assessment and management of these species. Red snapper, *Lutjanus campechanus*, is an iconic and heavily exploited species in both the US Gulf of Mexico and off the southeastern US Atlantic coast and is managed separately in the two jurisdictions. It is hypothesized that the Atlantic red snapper stock is sustained partially by larval subsidies from the Gulf of Mexico. Here we use a biophysical modeling approach to simulate recruitment of red snapper across the entire Southeastern US region, and quantify rates of larval exchange across management jurisdictions. The biophysical framework simulates realistic red snapper behaviors and traits with respect to spatial distribution and timing of spawning, larval vertical migration and pelagic larval duration, and settlement habitat. Our results suggest that areas of the West Florida Shelf south of Tampa Bay are important sources of larvae for the Atlantic population, supplying as much as one third of the recruitment during some years. Yet, contributions of Gulf-spawned red snapper to the Atlantic stock are highly dynamic given large variability in spatial and temporal patterns of red snapper recovery in each region. As such, effective management of the Gulf of Mexico red snapper stock, particularly the spawning population in southwest Florida, may have important consequences for the sustainable harvest of red snapper off the Atlantic coast.

KEYWORDS

biophysical modeling, fisheries management, larval connectivity, Loop Current, recruitment processes, West Florida Shelf

1 | INTRODUCTION

Fisheries science has long recognized that important marine population dynamics occur on fine spatial scales, yet reproductive potential is typically measured as mature female biomass or total egg production at the spatial scale of the management unit. Management jurisdictions are often defined by geographical or political boundaries and may not align with the actual spatial structure of populations, potentially leading to misinformed management (Berger et al., 2021). Furthermore, there are a variety of processes at the adult and larval stages that are relevant to reproductive resilience, population structure and source–sink dynamics (Lowerre-Barbieri et al., 2019), and these can be explicitly modeled to understand how locally or regionally depleted areas may be repopulated by areas where higher spawning biomass occurs. Recent advances in computing power have allowed for increasing complexity in stock assessment models, along with growing interest in incorporating fine-scale spatial dynamics (Berger et al., 2016; Cadrin, 2020; Cadrin et al., 2019). Additionally, advances in ocean modeling, ocean observation systems, and data assimilation techniques have allowed for precise representation of hydrodynamic fields (e.g., Fringer et al., 2019). Ocean models can be coupled with biophysical modeling frameworks to simulate realistic complex movements of marine organisms (Paris et al., 2013). Such biophysical modeling frameworks are now being used to estimate source–sink dynamics of economically important marine species to inform the appropriate spatial scales of management (Criales et al., 2019; Le Corre et al., 2020; Zeng et al., 2019).

Red snapper, *Lutjanus campechanus*, is a highly valued reef fish found throughout the Gulf of Mexico (Gulf) and southeastern US Atlantic (Atlantic) contributing to multibillion dollar commercial and recreational fisheries (Rindone et al., 2015). This species is managed as two separate stocks, by the Gulf of Mexico Fishery Management Council (Gulf Council) from Texas to the Florida Keys and by the South Atlantic Fishery Management Council (SA Council) from the Florida Keys to North Carolina within the federal waters of the US Exclusive Economic Zone (Figure 1). In 2005, the Gulf Council established a new rebuilding plan for red snapper, which included dramatically reduced catch limits, a recreational bag limit, a commercial individual fishing quota program, and controls on shrimp trawl fishing effort to reduce red snapper bycatch. Since the implementation of these additional management measures, red snapper fishing mortality has been reduced to levels below the limit set by managers, the stock size has increased, and the average size in the catch has doubled (Farmer et al., 2020). As of 2018, the stock had not yet recovered to its optimal population size but was considered no longer overfished or undergoing overfishing, and red snapper had repopulated much of the West Florida Shelf where it had previously been heavily overexploited (SEDAR, 2018).

In the Atlantic, where the red snapper fishery has historically been one of the most important in terms of recreational appeal and commercial value, the stock has been considered overfished and undergoing overfishing since 2009 (SEDAR, 2021). In 2010, the SA Council established a rebuilding plan for red snapper within the Atlantic. Initially, landings were prohibited, but starting in 2013, some landings were permitted with annual catch limits enacted for the recreational and commercial sectors. The recreational sector has primarily been managed through the use of short mini-seasons allowing one fish per person per day, and the commercial sector has been managed through trip limits and also seasonal closures when the annual catch limit is reached. Still, the rate of removals has remained higher than the Atlantic Council's threshold, due almost entirely to mortality from recreational discards (SEDAR, 2021). This occurs because red snapper is part of a mixed stock fishery and thus continues to be caught even when landings are prohibited.

For both stocks of red snapper, assessments have found no clear relationship between spawning biomass, measured as population fecundity, and subsequent recruitment to the population (SEDAR, 2018; SEDAR, 2021). This lack of evidence for a spawner–recruit relationship is not uncommon (Lowerre-Barbieri et al., 2017; Szuwalski et al., 2015; Vert-Pre et al., 2013) and even when such a relationship exists, it can be difficult to estimate (Conn et al., 2010; Miller & Brooks, 2021). Unexplained variability in recruitment stems from demographic, environmental, and ecological factors, the effects of which can override any variance explained by size of the parent stock. For marine fishes with pelagic larvae, biophysical processes are critical to the dispersal and success of larvae (Hidalgo et al., 2019; Lowerre-Barbieri et al., 2017). Uncertainties in recruitment make it challenging to understand stock productivity and can impact estimates of management benchmarks such as maximum sustainable yield, complicating efforts to gauge whether current fishing effort levels are too high. These uncertainties also affect near-term stock projections of population abundance levels and, consequently, annual catch limits—underscoring the need for estimates of connectivity between management jurisdictions.

Genetic research indicates homogeneity between the Gulf and Atlantic populations (Garber et al., 2004; Gold et al., 2001). However, genetic studies do not allow quantification of the percentage of Gulf larvae contributing to the Atlantic stock nor of the small-scale source–

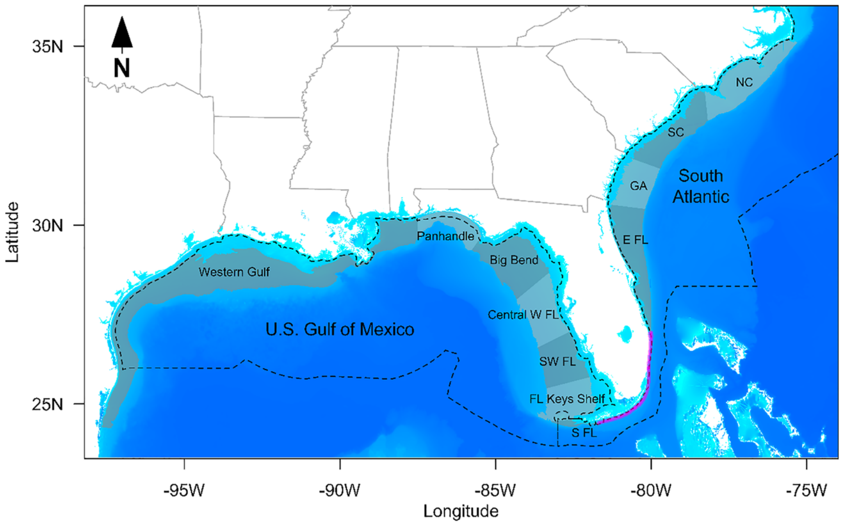

FIGURE 1 Map of the region of study, showing jurisdictional and subregional boundaries referenced in the study. Shaded areas represent defined settlement habitat. Pink polygons in southeast Florida indicate the areas removed for the settlement habitat sensitivity analysis.

sink dynamics. The apparent lack of a spawner–recruit relationship (SEDAR, 2018; SEDAR, 2021) has led to speculation about what drives recruitment of red snapper. In the Atlantic, one hypothesis is that recruitment is subsidized by the Gulf stock, such that recruitment in the Atlantic is driven more by spawners in the Gulf than by those in the Atlantic. In such a system, recruitment of the sink population (or stock) is subsidized by larvae from the source population. From the perspectives of stock assessment and management, the critical consideration is how many recruits come from outside the system relative to the number of recruits being produced from inside the system.

The purpose of this study is to estimate the extent of red snapper larval connectivity across management jurisdictions in the Southeastern US. We use hydrodynamic ocean and biophysical modeling approaches to simulate recruitment events of red snapper in the US Gulf of Mexico and US South Atlantic regions. We combine an individual-based larval transport model, the Connectivity Modeling System (CMS; Paris et al., 2013) with several oceanographic hindcast models to understand sources and sinks of recruits in the regions. We find evidence of significant connectivity between jurisdictions, which has important implications for the assessment and management of one the region's most iconic species.

2 | METHODS

2.1 | CMS

To simulate the process of spawning and recruitment, we used the CMS, a biophysical modeling system based on a Lagrangian framework that was developed to study complex larval migrations (Paris et al., 2013). The CMS is an individual-based model that estimates the movement of particles in a three-dimensional velocity field, as forced by an oceanographic model. The framework has been used in a wide variety of modeling studies, including simulation of fish and invertebrate recruitment and oil spill modeling, and optional modules are provided that allow for complex behaviors and movements (Berenshtein et al., 2020; Drury et al., 2018; Faillettaz et al., 2018; Kough et al., 2016; Vaz et al., 2021). The specific CMS parameterization for red snapper has been outlined in detail within publicly available stock assessment literature (Karnauskas, Walter, & Paris, 2017), and we briefly summarize the details here.

2.2 | Ocean velocity fields

Because the underlying oceanographic flows can be a major source of uncertainty in CMS, we considered several oceanographic models, as well as an ensemble approach using multimodel inference. The velocity fields used on our simulations are from three different hydrodynamic products: (1) the Mercator GLORYS12V1 reanalysis (hereafter Mercator), (2) the HYCOM + NCODA Gulf of Mexico 1/25° Analysis nested within the Global HYCOM + NCODA Global Ocean Forecasting System (GOFS, hereafter HYCOM), and (3) the South Atlantic Bight and Gulf of Mexico (SABGOM) model (Table 1 and Figure 2). Mercator is the reanalysis from the Copernicus Marine Environment Monitoring Service (CMEMS), largely based on the CMEMS real-time forecast system. It presents global coverage at 1/12° (approximately 8 km) horizontal resolution and 50 vertical levels, and it is available at daily intervals for our study period; we used years 2013–2017. The HYCOM + NCODA Gulf of Mexico 1/25° Analysis has 27 coordinate surfaces in the vertical and a 1/25° (approximately 3.5 km) horizontal resolution; it covers the entire Gulf of Mexico and most of the South Atlantic Bight. Because the region north of 32°N is not covered by the Gulf of Mexico HYCOM, we nested the fields within the Global HYCOM, which has 41 vertical layers and a 1/12° (approximately 8 km) and covers the missing domain in the northern portion of the Atlantic region. The specific HYCOM experiments used were the GOMl0.04/expt_32.5 analysis and the GOFS Analysis (experiments 56.3, 57.2, 92.8, 57.7, 92.9, and 93.0) for years 2014–2018; these were downloaded at daily intervals. The SABGOM model implementation (Hyun & He, 2010; Xue et al., 2015) is based on the Regional Ocean Modeling System (ROMS); spatial resolution of the model is 5 km, with 36 vertical layers that are weighted to better resolve surface and bottom boundary layers. For open boundary conditions, the model is nested inside the 1/12° global data assimilative HYCOM and superimposed by tidal harmonics from the ADCIRC western Atlantic tidal database. Surface forcing conditions are obtained from the NCEP North American Regional Reanalysis. Major rivers in the region are also implemented in the model using USGS daily stream flow data from USGS river gauges. Daily SABGOM fields for the years 2006–2010 were used in the analysis. The years available for different hydrodynamic models do not overlap in all cases; however, we note that the purpose of this analysis was not to conduct a year-by-year comparison of connectivity. Rather, we are interested in determining average connectivity over time, and 5 years of simulation data was deemed sufficient to capture interannual variability (subsampling three of the 5 years and recalculating outputs yielded similar results as the 5-year average).

2.3 | Spawning locations

For red snapper and other reef-associated species in this region, adults tend to demonstrate relatively high site fidelity, and dispersal is

TABLE 1 Characteristics of the three hydrodynamic models considered

	Mercator	HYCOM	SABGOM
Horizontal resolution	1/12°	1/25°	1/25°
Vertical resolution (in upper 100 m)	22 layers	20 layers	20 layers
Years of simulation	2013–2017	2014–2018	2006–2010
Type of product	Reanalysis	Hindcast	Hindcast

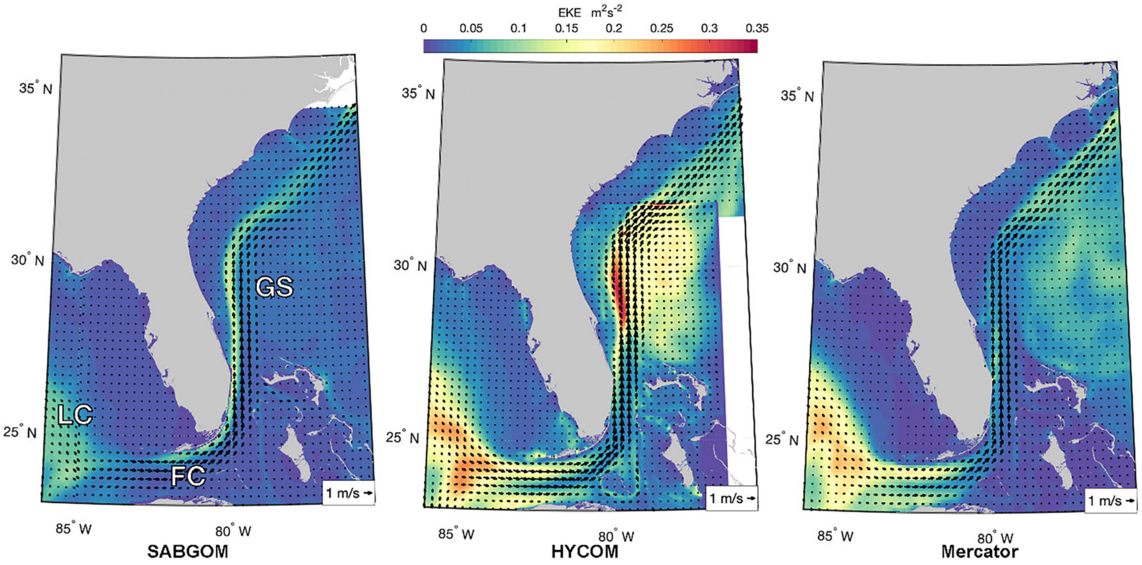

FIGURE 2 Average eddy kinetic energy and current velocity over the time series, for each oceanographic model used in the simulation. Densities of arrows reflect the model resolution. Labels on the left panel identify the major currents in the region (LC = Loop Current, FC = Florida Current, GS = Gulf Stream).

believed to occur predominantly during the larval stage of the life history (Friess et al., 2021). In the Atlantic, red snapper spawns on protruding hardbottom locations (Lowerre-Barbieri et al., 2015) from May to October (Sedberry et al., 2006), with peak spawning predicted in 24.7–29.0°C water prior to the new moon in the 24–30 m depth range off northeast Florida during June and July (Farmer et al., 2017). In the Gulf, red snapper forms schools of hundreds to a few thousand fish and spawns in 15–75 m depths over a widely distributed array of coastal and offshore habitats (natural rocky ridges and relatively steep delta terrace drop-off, artificial reefs, and oil platforms) from May to September, with a peak from June to August (Biggs et al., 2018; Coleman et al., 2011).

Because red snapper has protracted spawning over a large part of the annual cycle and does not migrate large distances to spawn, we assumed a species distribution map of spawning biomass to be a good proxy for the locations from which we can expect eggs to be released. We used two existing species distribution models, which were previously used to estimate spatially explicit relative spawning biomass in the Gulf and Atlantic, respectively. In the Gulf, we based the location of egg releases on the distribution model from Karnauskas, Walter, Campbell, et al. (2017), which reported spatially explicit estimates of relative abundance, biomass, and egg production at a 10 km^2 resolution. The analysis included biomass on artificial structures (e.g., oil rigs and artificial reefs) and thus accounts for spawning from these locations. We used the index of relative egg production from Karnauskas, Walter, Campbell, et al. (2017); this map forms the basis of the locations of the simulated egg releases, with numbers of eggs scaled to the relative predicted density. For the present study, we extended the prediction map from Karnauskas, Walter, Campbell, et al. (2017) slightly south to cover the region around the Dry Tortugas; this was done by calculating the predictions over this area based on the model covariates. This area was not covered in the previous study as it was beyond the boundaries of the sampling; although it is generally undesirable to create statistical inferences beyond the extent of data, the area contains similar habitat types and red snapper is observed near the Dry Tortugas during fishery surveys conducted for stock assessments, and we presumed this area to be critical in the question of connectivity between jurisdictions. The Karnauskas, Walter, Campbell, et al. (2017) study was based on a survey that collected information on abundance and age composition; however, data on spawning condition were not available. To account for variable spawning during the annual cycle, we used the relationship between time of year and spawning activity as reported by Porch et al. (2015). Particle releases were scaled according to this relationship to simulate realistic spawning activity, in both time and space, for the Gulf of Mexico.

For the Atlantic, we updated the framework published by Farmer et al. (2017) which modeled, for a suite of species including red snapper, the probability of detecting a female in spawning condition as a function of various factors: gear, habitat, latitude, year, month, lunar phase, depth, temperature, and bathymetric features. We updated the model with additional years of data (which increased the sample size from 158 to 515 fish) and slightly altered the model structure; the goal of the previous effort was to identify potential spawning locations, whereas for the present study, we needed to estimate an expected distribution of spawning biomass across space in units of total egg production (as in the Gulf). To update the modeling framework, we first calculated the total red snapper egg production per site using the reported relationship between total length of the observed individuals and expected batch fecundity (Klibansky, 2015). We then used delta-lognormal modeling methods (Lo et al., 1992) to model relative egg production across the study domain, as a product of the probability of observing a red snapper female in spawning condition and the egg production when spawning condition females are present.

Presence or absence of spawning females was modeled using a logit link function, and egg production was log transformed. We used the same model factors considered in Farmer et al. (2017) except for bathymetric variables which were excluded as they were not available across the entire prediction domain and described relatively little variance; year was included as a random effect. Model selection was carried out as in Farmer et al. (2017) based on AIC and the amount of deviance explained and then candidate models were subject to k-fold cross-validation. Final presence–absence models were selected by building a receiver operating characteristic curve and calculating the overall predictive performance (true positive rate and false positive rate) and calculation of area under the curve (AUC). For the present study, we considered a generalized linear modeling framework and a generalized additive model (GAM) framework. GAMs were fitted with the *mgcv* package in R (version 3.6.3), using thin plate regression splines; model residuals were inspected to ensure reasonable fit, and basis dimensions were checked to ensure oversmoothing did not occur. Predictions from the best fitting model (Figure S1) were made on all combinations of lunar phase and temperature and years, for the particular latitude, depth, and day of year and then averaged to create a distribution model specific to the annual spawning cycle. The result was then a set of particle releases (at a 10 km^2 resolution) that were used to simulate realistic spawning patterns in both space and time, as in the Gulf; the Gulf and Atlantic maps were then scaled to each other on a per-unit area basis (Figure 3; see *Calculation of the magnitude of larval contribution* for specifics). We note that the predictive maps do not cover the Florida Keys and southeastern Florida region (Figure S2), and this is consistent with the documented range of the species; a visual survey of reef fish species in this region that has been conducted since 1978 has not documented any occurrences of red snapper (https://grunt.sefsc.noaa.gov/rvc_analysis20/). However, a recently initiated cooperative survey conducted in deeper waters, as well as social media photos from charter businesses in the area, suggests that abundance of red snapper exists at some level along the Florida Keys in depths >30 m; presumably, there could be some spawning activity occurring within the narrow sliver of suitable depth ranges in that region. Lacking a comparable data source, we were unable to estimate relative egg production in this small area; however, the estimated production just north of that area is extremely low and we expect that any low levels of spawning may be negligible.

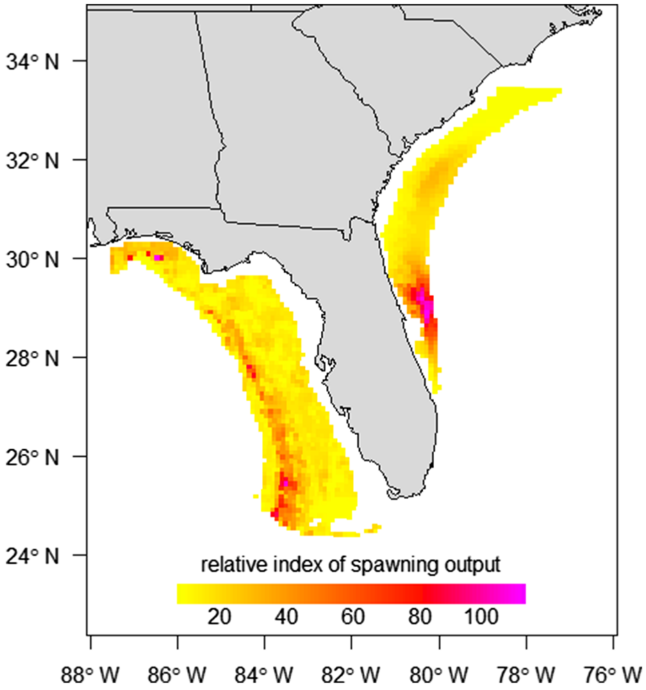

FIGURE 3 Underlying distribution map of spawning output used in the simulation. The total number of particles in the Gulf (West Florida) and Atlantic (East Florida to South Carolina) jurisdictions are scaled such that there are an equal number of particles per the total area (i.e., West Florida has 2.0 times the area of the Atlantic and 2.0 times the spawning output).

Spawning depth was set at 10 m above the ocean floor, as anecdotal observations from fishermen indicate that red snapper is observed to spawn near the bottom of the water column. Because we were interested in considering the uncertainty in choice of ocean model, we wanted to use exactly the same release file set up for all simulations. Therefore, the "ocean floor" was defined as the minimum depth, for a given location, among all ocean models, and the release depth was 10 m shallower than that minimum. In a small number of cases (<1%), releasing particles at this defined depth caused them to become trapped in complex bathymetry (e.g., around Dry Tortugas region). In those cases, we decreased the depth gradually until there were zero instances of larvae being stuck.

2.4 | Egg buoyancy and vertical migration

In the CMS, vertical movements are defined via a depth × time matrix, which specifies the probability distribution of virtual larvae in the water column throughout time. Time steps for the probability matrix are most logically defined by using different stages of larval metamorphosis (e.g., hatching, preflexion, and postflexion), as larvae tend to shift in their vertical distributions with these changes. We used the setup as described in Karnauskas, Walter and Paris (2017), which assumed hatching occurs at day 1 post hatch, flexion at day 12, and postflexion at day 16, with vertical migration behaviors specified separately for each of these stages (Figure S3). Karnauskas, Walter and Paris (2017) carried out a series of sensitivity analyses regarding vertical migration behavior, and it was determined that the choice in assumptions regarding the fate of eggs during the first 24 h had little influence on the results. However, results were sensitive to assumptions regarding the vertical migration behavior during the preflexion and postflexion stages. Thus, for the present study, we used a single assumption for the egg stage (a simple uniform distribution, which was approximated by the available data) but carried out sensitivity analyses with respect to different assumptions regarding ontogenetic vertical migration (OVM) of the hatched larvae. Given a lack of relevant data on red snapper, we used the observed depth distribution patterns of three congeners: lane snapper *Lutjanus synagris* (OVM

1), mutton snapper *Lutjanus analis* (OVM 2), and gray snapper *Lutjanus griseus* (OVM 3), to parametrize vertical distributions over time for our model (Karnauskas, Walter & Paris, 2017).

2.5 | Mortality and settlement

Red snapper begins settling out of the pelagic stage no earlier than 26 days, with most settling by 28 days of age, and maximum settlement age is estimated to be about 30 days (Drass et al., 2000; Rooker et al., 2004; Szedlmayer & Conti, 1999). We acknowledge that temperature influences larval growth and that environmental conditions could have an impact on their pelagic duration; however, we lack data on the relationship between temperature and larval duration for red snapper. Furthermore, based on the available literature, the competency period and development patterns do not appear to be highly variable; Drass et al. (2000) showed that similar development patterns were observed in lab-reared and wild-caught larvae. We therefore specified the settlement competency period as lasting for 5 days (26–30 days).

Because of the short window in which larvae are allowed to settle, and due to the fact that the majority of larvae settle within the first day of the competency period in our simulation, we did not specify any larval mortality in our simulations. Simulating realistic levels of larval mortality would be computationally expensive (i.e., simulating many more larvae only to remove the majority prior to settlement due to death) and would not alter the results, because mortality is a function of time and all of the settlement is occurring within a short time frame. For species with a much longer settlement window (e.g., grouper), specification of mortality could have some effect on the results, but this is not the case for our study.

Based on limited information that exists on settlement and recruitment habitat, high-value settlement habitat was estimated to occur between 15 and 64 m depths (Gallaway et al., 2009; Johnson et al., 2009; Rindone et al., 2015; Szedlmayer & Conti, 1999). Using the global 30 arc-second bathymetry data grid available from GEBCO (General Bathymetric Chart of the Oceans; www.gebco.net), we extracted contours at the 15 and 64 m isobaths for the northern Gulf and the Atlantic (Figure 1). Suitable settlement habitat was defined by the area between these isobaths, with all areas within this area defined as having equal probability of settlement. Successful settlement is defined by those particles that reach the suitable settlement habitat during the competency window, given the suite of previously described parameterized behaviors and attributes. While the maximum depth of settlement is somewhat poorly informed, we note that in the simulations, the vast majority (98.5%) of particles settle at depths <45 m; therefore, the selection of a more restrictive boundary (e.g., a cutoff at 45 m) would have had minimal impact on the simulation results.

Due to a paucity of information on red snapper recruitment in the South Atlantic, particularly with respect to the Florida Keys region, we carried out a sensitivity analysis with respect to settlement habitat. Relatively little is known about juvenile settlement habitat in the Atlantic, and most of the available survey data do not cover the Florida Keys region (Rindone et al., 2015). A long-standing visual survey conducted by divers has been carried out since 1978 (https://grunt.sefsc.noaa.gov/rvc_analysis20/), and red snapper has not been documented in this data set, although due to diving limitations the sites are generally limited to 30 m depth. Misidentification of juvenile red snapper in this visual survey is unlikely (J. Grove, personal communication) and the fact that red snapper juveniles <150 mm total length are common in the Gulf of Mexico at this depth range (Rindone et al., 2015) suggests that red snapper is generally not settling in this area. Based on available data, we could not determine whether the Florida Keys represent suitable habitat for red snapper, and thus, we recalculated the results excluding the settlement polygons extending from just east of the Dry Tortugas (81.7°W) extending to 27°N along eastern Florida (Figure 1).

2.6 | Scope of the simulations

A series of preliminary runs with SABGOM, HYCOM, and Mercator models determined that there was zero larval transport to the Atlantic for larvae released to the west of the Florida/Alabama border. A domain bounded by state boundaries facilitates the use of statistical comparisons, because many data sources and surveys are available at a state level. Thus, for the purposes of our reported simulations, we used that border as a boundary and ran simulations for Florida waters to the full extent of the South Atlantic up to North Carolina. On the Atlantic side, the species distribution model identified two prominent hotspots that were separated by an area of very low estimated egg production. The northern hotspot was near Cape Hatteras, an area with dynamic currents that is only covered by the low-resolution HYCOM model and that the SABGOM model domain does not fully cover. Therefore, prior to running the larger Gulf–Atlantic simulations, we investigated transport mechanisms from this hotspot independently, using the lower resolution (1/12°) Mercator and Global HYCOM velocities we had available and also using a higher-resolution regional ocean circulation model (ROMS) specific to the region with a similar setup to the SABGOM model (Gong et al., 2015). The southern hotspot was off the east coast of Florida, covered by the higher-resolution (1/25°) grids of the SABGOM and HYCOM.

Once the spatial scope of the domain was determined, we carried out the full suite of sensitivity analyses; this process was initiated by evaluating the appropriate number of particles to be used in the simulation. Simulating realistic egg production (i.e., trillions of particles) is not computationally feasible, so we applied a constant scaling factor to the egg production map (Figure 3) that resulted in a relatively large number of particles (a total of 224,604 particles released per year). We ran all years of a simulation for each oceanographic model under one vertical migration assumption and summarized the results. We then reduced the number of particles approximately fivefold (43,404 per year) to evaluate the influence of the choice of number of particles released on the final results. Comparing both probabilistic connectivity matrices as well as the results in terms of percent larval transfer between the Gulf and Atlantic, there were no noticeable differences in the results from using reduced numbers of particles. We therefore carried out the full suite of sensitivity analyses (i.e., running the biophysical simulation for all combinations of hydrodynamic models and assumptions regarding vertical migration) using the reduced particle numbers, and the reported results are based on these analyses.

2.7 | Calculation of the magnitude of larval contribution

A key quantity of interest in this study is the extent to which Gulf-spawned larvae recruit to the Atlantic; to estimate this quantity requires knowledge of both the larval transfer rates between and within management jurisdictions, as well as the comparative egg production (the relative number of larvae released from each basin). Calculation of the transfer rates is done directly from the connectivity model by tracking source and settlement locations. However, calculating the relative egg production from each jurisdiction is problematic for two reasons. Recall that the definition of spawning locations is based on two different distribution maps which estimate the relative egg production across space; these egg production estimates are relative within each region, but as the maps are based on two separate models, the estimates are not relative across regions. Unfortunately, there are no comprehensive surveys carried out in both basins that would allow definition of relative catch rates; fishery-dependent data are also limited because of the moratorium or strictly regulated landings in the Atlantic since 2010. Secondly, the Gulf:Atlantic ratio of egg production is a moving target, because management measures, exploitation patterns, and recovery trajectories are highly variable in space and time. Therefore, rather than trying to pinpoint a "present-day" scenario, we report the results in terms of a baseline scenario where the egg production of each jurisdiction is equal on a per-unit area basis—the equivalent to the assumption that habitats in West Florida and Atlantic support the same densities of red snapper (Figure 3). While this is not necessarily realistic (e.g., because there are likely differences in the percentage of high-quality red snapper habitat in each region which could lead to more egg production per area), it facilitates understanding of the results under a simplistic baseline scenario, as well as the statistical extrapolation of alternative scenarios. We report the results and figures using this baseline scenario and then subsample the simulation data to account for different Gulf:Atlantic ratios of biomass and generate results based on these different assumptions. The probability of an Atlantic red snapper being spawned from the Gulf is given as follows:

$$R_{G\to A}/(R_{G\to A}+R_{A\to A})$$

where R is the total number of successfully recruiting larvae, $G\to A$ represents larvae spawned in the Gulf and recruiting in the Atlantic, and $A\to A$ represents larvae spawned in the Atlantic and recruiting in the Atlantic. We note that there can also be transport from the Atlantic to the Gulf, particularly where the jurisdiction boundaries meet along the Florida Keys, and Florida Current frontal eddies cause some recirculation; however, this relative magnitude of this transfer was expected to be extremely limited.

3 | RESULTS

3.1 | Distribution of spawning in the Atlantic

GAMs were used to develop predictions of egg production across the Atlantic jurisdiction. It was found that GAMs outperformed generalized linear models; the highest performing GAM in the suite of presence/absence models had a combined false positive and false negative rate of 44%, whereas the highest performing GLM had a combined rate of 52%. Within the suite of GAMs considered for each of the two models (the presence/absence model, and egg production when present model), a single model had the lowest AIC, the highest deviance explained, and the best performance in cross-validation tests (AUC $=0.86$ indicating a good fit). This best-performing model had the same set of factors in both presence/absence and egg production when present (depth, latitude, day of year, lunar phase, temperature, and year as a random effect) but no interactive effects (Figure S1). The deviance explained by the presence/absence model was 20.92% and the deviance explained by the egg production when present model was 29.45%.

Model predictions across the domain estimated that a pronounced area of high red snapper egg production occurs off the east coast of northern Florida (Figure S2). Another area of slightly elevated egg production occurs offshore of the Georgia/South Carolina border. North of this area, red snapper egg production is estimated to be low, except for a pronounced and very localized hotspot just south of Cape Hatteras. Relatively high egg production is observed in the raw data at the northernmost limit of the statistical domain, and the GAM accurately captures this peak. While related data are limited, it is unlikely that this hotspot extends northward beyond Cape Hatteras due to the general lack of appropriate (natural reef) spawning habitat north of Cape Hatteras.

3.2 | North Carolina hotspot

We first report the results of the simulations of the region surrounding the dynamic Cape Hatteras region which were carried out separately from the full model due to limitations with hydrodynamic model coverage; we used a separate suite of models that better resolve this portion of North Carolina. Simulations of this region estimate that the red snapper egg production hotspot off North Carolina produced larvae that settled directly back in this region but did not contribute to areas farther south. The Mercator model estimated that of the particles spawned from this region, 2.3% successfully settled, whereas SABGOM estimated 9.1% and HYCOM estimated that 14.1% of the particles successfully settled. Few larvae were transported further south, and no larvae were observed settling in other elevated areas of red snapper biomass (e.g., the area offshore of the Georgia/South Carolina border). The vast majority (>99%) of successfully settling larvae settled offshore of North Carolina, that is, north of 34°N latitude. This pattern was consistent among hydrodynamic models (Figure 4), although the SABGOM and Mercator models showed higher likelihood of settlement nearshore, whereas successful settlers in the HYCOM model were uniformly distributed across all depths. Of all simulations using SABGOM, Mercator, and HYCOM, the southernmost location of successful settlement was at 33.97°N, 33.58°N, and 33.33°N, respectively. In other words, there was no evidence that larvae spawned off North Carolina waters are contributing to centers of red snapper biomass located off South Carolina, Georgia, or Florida. Based on these results, and given the fact that a separate set of ocean models were available for the area surrounding Cape Hatteras, we excluded red snapper biomass in North Carolina waters from the broader set of simulations by cutting off the egg production map at the local minima estimated by the GAM at 33.4°N (according to the GAM, the area removed accounts for 16% of the total egg production in the region). However, in order to quantify the extent of input from other regions to the North Carolina red snapper center of biomass, we allowed for settlement to occur in this region.

3.3 | Overall connectivity patterns

Overall, the simulations indicated that the majority of larvae are self-recruiting to the same regions in which they were spawned (Table 2 and Figure 5, diagonal cells). The three models were in close agreement regarding the percentage of particles spawned in the Gulf that recruited back to the Gulf (53.7% for SABGOM, 56.9% for HYCOM, and 57.9% for Mercator). However, there was higher variability among the oceanographic models regarding the percentage of particles in the Atlantic recruiting back to the Atlantic (76.8% for SABGOM, 49.0% for HYCOM, and 56.9% for Mercator). All three models agreed that self-recruitment was particularly strong in Eastern Florida, although the HYCOM model suggested that nearly half of the larvae spawned from that region settle in Georgia waters (Figure 5). SABGOM suggested that self-recruitment was stronger within Georgia and South Carolina, whereas HYCOM and Mercator suggested a greater tendency for each state to export many of its larvae to states further downstream (i.e., north). On the West Florida Shelf and Florida panhandle region, SABGOM suggested lower levels of self-recruitment, with most larvae being transported downstream (settling to the south of where they were spawned). HYCOM and Mercator models both suggested stronger self-recruitment along the West Florida Shelf, although there were a number of larvae settling in areas either north or south of where they were spawned.

Gulf spawners contributing to Atlantic recruits were generally limited to those occurring offshore of the Tampa Bay region, and south to the Dry Tortugas, with a few contributions from the Big Bend (Figure 6). This result was generally robust, regardless of

TABLE 2 Total number of successfully settled particles for each oceanographic model simulation (combined results for all years and vertical larval behavior assumptions), by management jurisdiction of spawning source and settlement location

		Settlement	
SABGOM		**Atlantic**	**Gulf**
Source	Atlantic	166,739	0
	Gulf	8,050	232,790
		Settlement	
HYCOM		**Atlantic**	**Gulf**
Source	Atlantic	106,452	620
	Gulf	20,616	247,027
		Settlement	
Mercator		**Atlantic**	**Gulf**
Source	Atlantic	123,526	857
	Gulf	29,744	251,247

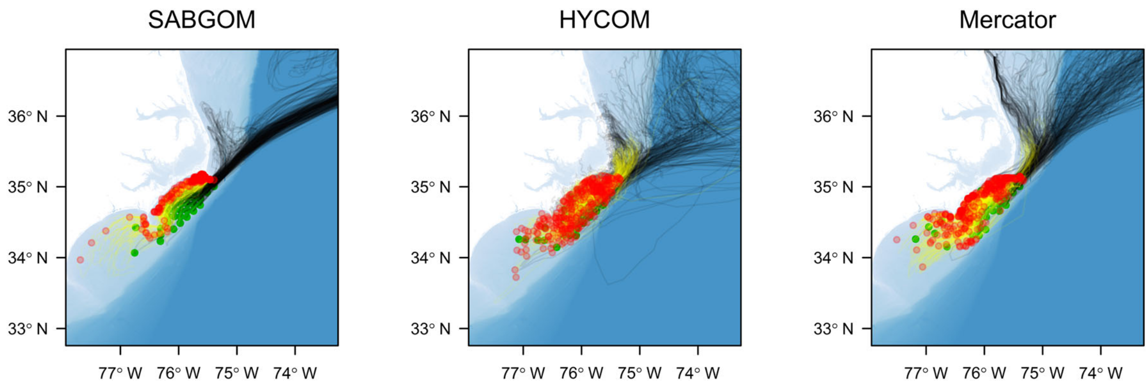

FIGURE 4 Random subset of larval trajectories for the simulation of red snapper spawners off North Carolina. Spawning locations are represented by green points, and settlement locations are represented by red points; yellow lines are the trajectories for successfully settling larvae, and black lines are trajectories for larvae that did not successfully settle. Points are transparent such that darker colors represent greater numbers of larvae spawning or settling in those areas.

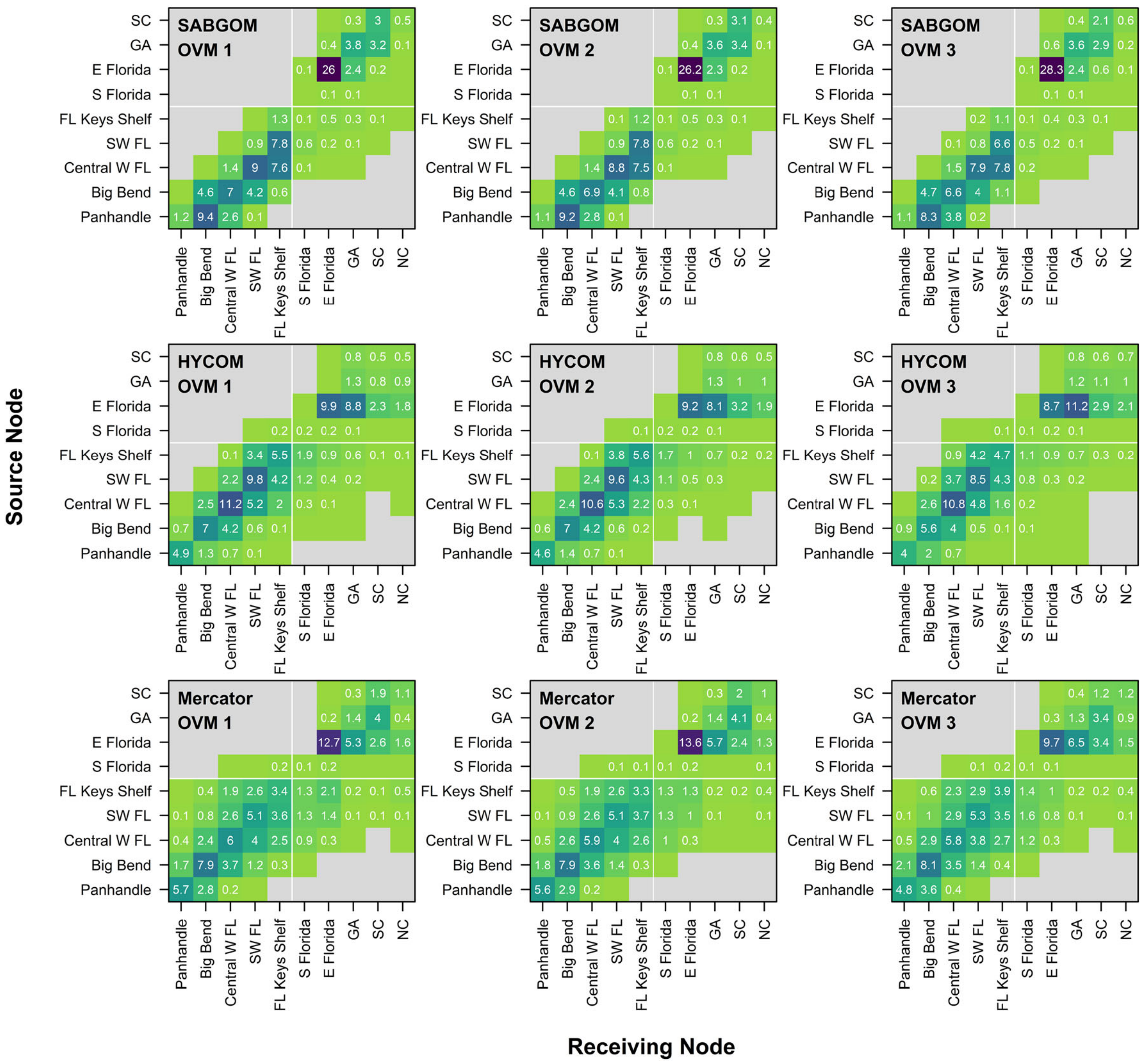

FIGURE 5 Connectivity matrices, summarized at the subregional scale, for different assumptions regarding oceanographic forcing (in panel rows) and ontogenetic vertical migration (OVM; in panel columns). Source locations appear as rows, and settlement locations appear as columns; the diagonal denotes self-recruitment. Numbers represent the percentage of successful recruits in each box out of the total number of successful recruits (i.e., the sum of all numbers in each respective subplot is 100). Blank boxes indicate numbers <0.1%, and gray boxes indicate no larval transfer.

oceanographic forcing or OVM pattern considered. SABGOM was the most conservative in that it suggested that only spawners south of approximately 27°N could contribute to the Atlantic; it also differed in that it showed more connectivity with spawners located closer to shore. HYCOM suggested that spawners up to approximately 27°N were largely responsible for contributing to the Atlantic but suggested that some spawners in the Big Bend area could also contribute. The Mercator model suggested that spawners up to 28°N could contribute to the Atlantic (offshore Tampa Bay area and extending slightly into the Big Bend). SABGOM suggested that there were very limited connections between the Gulf and the northern extent of the Atlantic domain (North Carolina waters), whereas HYCOM suggested that spawners in the southernmost part of the Gulf could contribute to the hotspot off Cape Hatteras. The Mercator model suggested that a substantially broader area of the West Florida Shelf could contribute to the population near Cape Hatteras, and, in some years (e.g., 2013) it estimated that Gulf contributions to the North Carolina hotspot were nearly as important as contributions from the Eastern Florida Atlantic population (Figure S4).

3.4 | Gulf–Atlantic connectivity

Under an assumption that red snapper egg production in West Florida and the Atlantic (East Florida to South Carolina) is equal on a per-unit area basis, the estimated probability that an Atlantic recruit has originated from the Gulf is 11.0% (2.8%–34.8%; median and 95% confidence intervals). The uncertainty represents variation due to alternative hydrodynamic fields, assumptions regarding OVM, and interannual variability. For the sensitivity analysis where recruitment

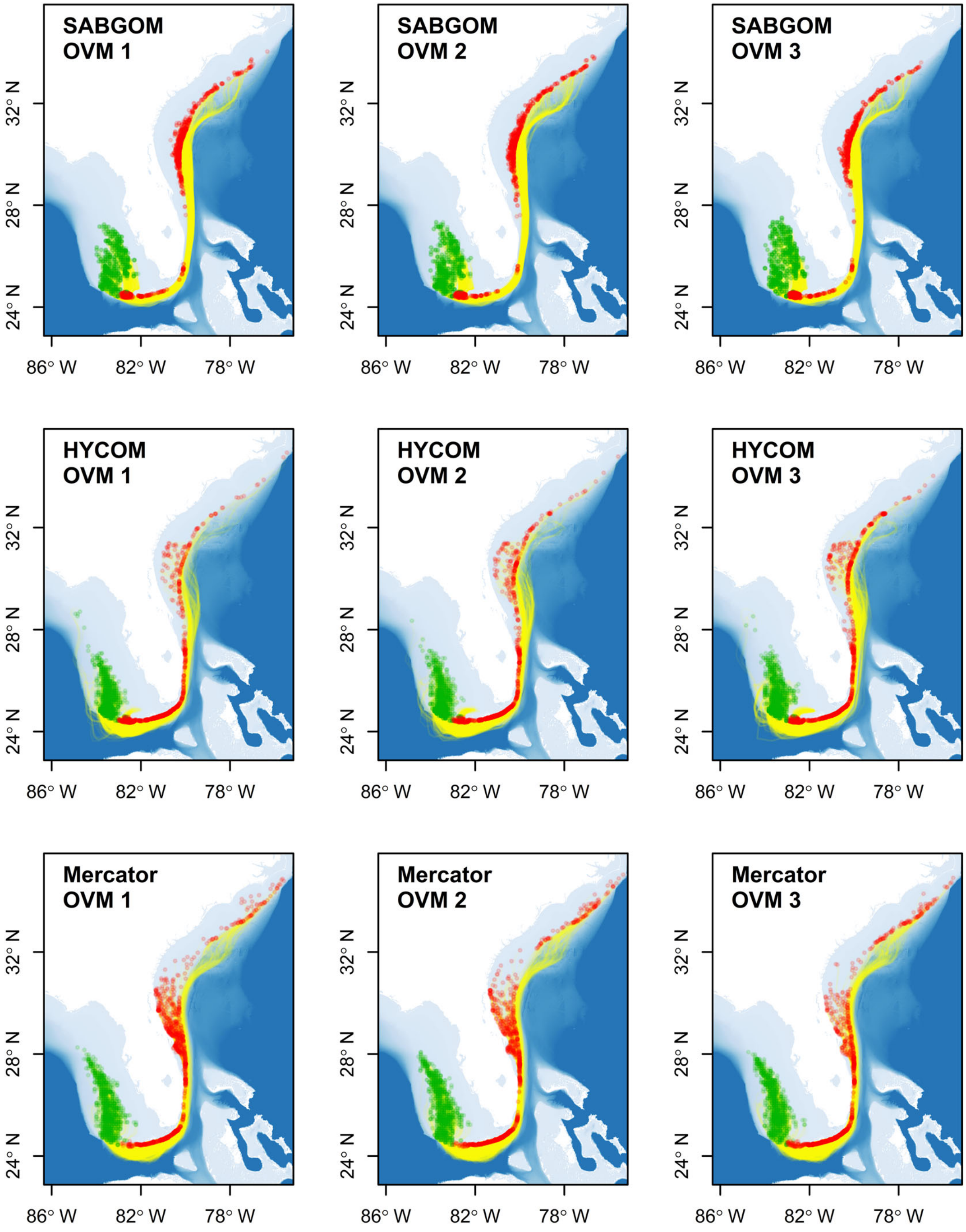

FIGURE 6 Trajectories of larvae spawned in the Gulf that successfully recruited to the Atlantic, for different assumptions regarding oceanographic forcing (in panel rows) and ontogenetic vertical migration (OVM; in panel columns). Spawning locations are represented by green points, and settlement locations are represented by red points; yellow lines are the larval trajectories. Points are transparent such that darker colors represent greater numbers of larvae spawning or settling in those areas.

to the Florida Keys was excluded, the probability that an Atlantic recruit has originated from the Gulf is reduced to 7.3% (1.9%–24.2%). These probabilities are most highly dependent on assumptions regarding the hydrodynamic fields driving larval transport patterns; the relative contribution of Gulf spawners to the Atlantic population is predicted to be lower based on the SABGOM model, whereas the HYCOM and the Mercator models are in agreement that the Gulf contribution is more significant (Figure 7 and Table 3). The SABGOM model was somewhat of an outlier in comparison with results from the HYCOM and Mercator models; this result is driven by the much higher settlement rate of Atlantic-spawned recruits and lower Gulf-to-Atlantic transport (Table 2), both of which contribute to the reduced probability that a settler in the Atlantic was sourced from the Gulf. The estimated connectivity is a function of both the percentage

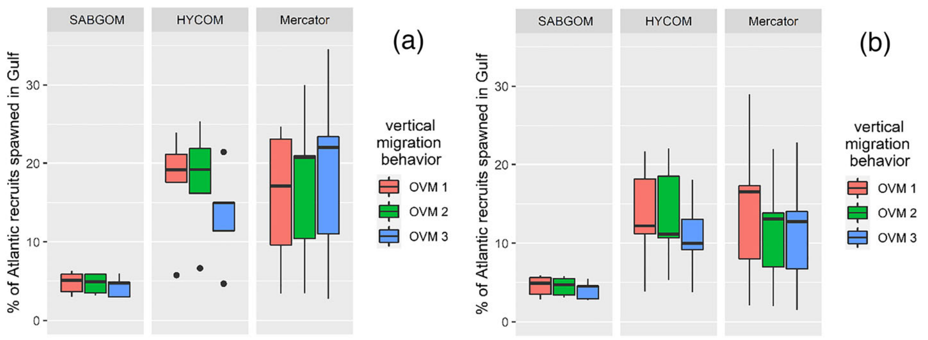

FIGURE 7 Boxplots of the estimated percentage of Atlantic recruits originating from the Gulf, for different assumptions regarding oceanographic forcing and ontogenetic vertical migration (OVM) behavior. Box plots capture the interannual variations in the estimates for each model and OVM combination. Panel a: baseline simulation; panel b: sensitivity analysis where settlement was not allowed to occur in the Florida Keys.

TABLE 3 Median probability that a recruit in the Atlantic originates from the Gulf of Mexico as a function of the relative ratio of egg production of the Gulf (West Florida) versus Atlantic (27 N to 33.4 N) stock for each oceanographic model

Gulf:Atlantic ratio	SABGOM	HYCOM	Mercator	Overall	Overall—no Florida Keys recruitment
1:1	4.8 (2.8–6.5)	17.4 (4.6–25.5)	21.1 (2.8–36.2)	11.0 (2.8–34.8)	7.3 (1.9–24.2)
2:1	9.2 (5.6–12.0)	30.0 (8.9–40.6)	34.7 (5.4–53.2)	18.6 (5.6–51.2)	13.3 (4–38.9)
3:1	13.3 (8.2–17.0)	39.0 (12.9–50.6)	44.3 (7.8–63.1)	27.2 (8.1–61.3)	18.1 (5.1–55.7)
4:1	16.9 (10.7–21.4)	46.2 (16.3–57.7)	51.7 (10.2–69.5)	34.5 (10.6–68.0)	23.4 (6.4–55.9)
5:1	20.4 (12.9–25.4)	51.8 (19.7–63)	56.9 (12.4–73.9)	38.6 (13.0–72.4)	27.8 (8.9–67.8)
6:1	23.3 (15.2–28.9)	56.4 (22.7–67.1)	61.4 (14.6–77.3)	41.7 (15.1–76.0)	32.0 (11.2–65.5)
7:1	26.3 (17.3–32.3)	59.6 (25.5–70.4)	64.9 (16.7–79.9)	46.2 (17.3–79.8)	35.2 (13–68.8)
8:1	29.0 (19.3–35.3)	63.3 (28.2–73.2)	68.0 (18.6–82.0)	49.8 (19.4–81.0)	41.7 (14.4–71.6)
9:1	31.4 (21.3–38.0)	65.7 (30.7–75.4)	70.4 (20.4–83.6)	52.8 (21.1–82.6)	40.9 (16.1–79.3)
10:1	33.8 (23.2–40.4)	68.3 (33.0–77.3)	72.7 (22.2–85.0)	56.6 (22.9–84.1)	47.2 (17.7–76)

Note: Reported numbers denote the median percentage of successful Atlantic recruits originating from gulf spawners, with 95% confidence intervals encompassing the interannual variability and varying assumptions regarding vertical migration. Note that the ratios are on a per unit area basis, and according to the spatial domain defined for red snapper in this study, the Gulf has two times the area of the Atlantic.

of recruits from a given location and the relative spawning biomass from that location; thus, the estimated probability of an Atlantic recruit originating from the Gulf is heavily dependent on assumptions surrounding relative biomasses, and this uncertainty was incorporated in our results (Table 3). For example, if the relative egg production per-unit area is four times higher on the Florida West coast as compared with the Atlantic, then the probability that an Atlantic recruit has originated from the Gulf is 34.5% (10.6%–68.0%) or 23.4% (6.4%–55.9%) for the no Florida Keys recruitment scenario (Table 3).

4 | DISCUSSION

Our simulation results suggest that the Eastern Gulf red snapper population, primarily the portion of the population distributed offshore of southwest Florida, contributes significantly to the Atlantic red snapper population. These results were robust across different sensitivity analyses carried out with respect to uncertainties regarding oceanographic currents, interannual variability, and assumptions about larval vertical migration behavior and settlement habitat. Connectivity between these regions is corroborated with multiple lines of evidence. A genetics study based on mitochondrial DNA indicated that the Eastern Gulf and Atlantic were essentially a single population with some genetic differences between regions (Hollenbeck et al., 2015) although these results are derived from connections at evolutionary scales and do not necessarily represent processes unique to recent decades. Estimated stock abundance trajectories from stock assessments in both regions show a sudden uptick in recruitment in the years following recovery in the Eastern Gulf (SEDAR, 2018; SEDAR, 2021), also suggesting that increasing numbers of Gulf spawners may have contributed significantly to the subsequent recovery seen in the Atlantic (beyond that expected from increases in Atlantic spawning stock biomass).

The specific estimated contribution of Gulf-spawned larvae to the Atlantic red snapper population is a function of both the rate of larval transport as well as the ratio of relative biomasses in each region. While the former is well characterized by the present study, estimates of the relative biomasses of red snapper between the two regions are highly uncertain due to a lack of comprehensive fishery-independent data sources that are consistent across both management jurisdictions. Historical landings may serve as a crude indicator of the relative carrying capacity of red snapper in each region. From 1950 to 1960, the earliest years for which the landings data are considered reliable; estimates indicate that landings in the Eastern Gulf (average of 1138.5 metric tons per year, SEDAR, 2018) were approximately four times the landings in the Atlantic (303.9 metric tons, SEDAR 2021);

however, a commercial fishery for red snapper in the Gulf was operating as early as the 1870s, and some areas were depleted by the 1900s (Porch et al., 2004). A more contemporary comparison can be made using catch data for the recreational headboat fleet, which is collected in a standardized manner in both management jurisdictions (see Appendix 1). Comparison of headboat catch-per-unit-effort (CPUE) between regions (1988–2009; only considered prior to 2010 because of the implementation of the Atlantic harvest moratorium) suggests that abundances in the West coast of Florida were 4.4 times higher than the Atlantic. However, this interpretation of the catch rates assumes that catchability does not differ across regions and that there is no hyperstability in catch rates (i.e., fishermen maintain stable catch rates even as the population decreases); these assumptions are difficult to validate. Finally, two fishery-independent data sources are available from the Fish and Wildlife Research Institute: a video survey which was carried out in a standardized manner on both coasts of Florida in 2016 and a hooked-gear survey carried out from 2016 to 2018. Both surveys indicate that relative abundance in the South Atlantic is less than that in the Panhandle or Big Bend but much higher than that off Tampa and Southwest Florida. However, these surveys are based on abundance only, and habitat quality and quantity are not taken into account.

Taken together, the available data sources suggest that the ratio of biomass in West Florida versus the Atlantic within the past several decades has been somewhere in the range of 1:1 to 4:1. We note that this estimate is not only uncertain but also a dynamic ratio due to variance over space and time in fishing pressure and other influences on abundance. The most recent Gulf stock assessment estimates that red snapper abundance in the Eastern Gulf has remained relatively stable from 2010 to 2016 (the terminal year of the assessment); meanwhile, it is estimated that since 2010, abundance of red snapper in the Atlantic has increased approximately fourfold. Furthermore, the trajectories indicate that based solely on the changes in relative biomass due to fishing pressure, the contribution of Gulf spawners to the Atlantic population would be highly variable over time. We note that several absolute abundance estimates of red snapper are forthcoming and should provide a more precise answer regarding the relative biomasses across management jurisdiction. Recently, the "Great Red Snapper Count" estimated a total of 70 million red snapper in Florida Gulf waters (https://www.harte.org/snappercount). A similar initiative is currently underway for the Atlantic; once an estimate is available, the appropriate ratio can be referenced (Table 3) to get a more precise annual estimate of larval contribution from the Gulf to the Atlantic.

The numbers reported here represent the expected connectivity based on total spawning biomass in the Gulf versus Atlantic, but our results also show that connectivity would be affected by subregional variations in fishing pressure, which may vary substantially over time. Gardner et al. (2022) estimated red snapper exploitation rates at fine spatial scales and showed that patterns of depletion are likely to be highly heterogeneous. Most of the contribution from the Gulf to Atlantic is in the biomass located well offshore of southwest Florida; this area was estimated to be undergoing light commercial exploitation by Gardner et al. (2022); however, comparisons across years indicate that the fishery was moving southward in more recent years, probably in response to rebuilding of red snapper and increasing densities in these regions. Increasing densities of red snapper on the West Florida Shelf would be expected to contribute substantially to Atlantic according to the present study. Indeed, we see a significant increase in red snapper age-1 numbers in the Atlantic in 2014 that was preceded by significant stock recovery in the eastern Gulf (Figure 8). Recruitment in the Atlantic has been recovering more quickly than had been expected when the rebuilding plan was first implemented, and the last several years have had the highest abundances over the entire assessment period (1950–2019) with the recovery dominated by high numbers of age-1 fish in 2014–2019 (SEDAR, 2021). We suggest that the recovery of Eastern Gulf red snapper and sourcing of Gulf-spawned larvae to the Atlantic in years following have contributed to the expedited recovery pattern observed in the Atlantic.

Recovery of red snapper in the Eastern Gulf may also have some relation to the isolated area of relatively high red snapper abundance off the coast of North Carolina. Our simulations suggest that red snapper in this area is largely self-sustaining; that is, most of the recruits in this area would have been sourced from local spawners, although there is some sporadic input from the high red snapper density area off Eastern Florida and even some contribution from southwest Florida according to some models. A more comprehensive understanding of the dynamics in this region was complicated by several factors. Firstly, the surveys used to develop the species distribution estimates cut off just at the point where very high densities were observed, and comparable surveys do not exist farther north; thus, we lack information on the areal extent of both adult biomass and suitable larval recruitment habitat. Therefore, we could not statistically resolve the northern extent of this area of high abundance, which would impact the estimates of local self-recruitment. Secondly, the ocean dynamics in this region are difficult to model because of the complex bathymetry and the intersection of the strong Gulf Stream with the convergent shelf currents from the South Atlantic Bight and Mid-Atlantic Bight (e.g., Savidge & Bane, 2001), and two of the large-

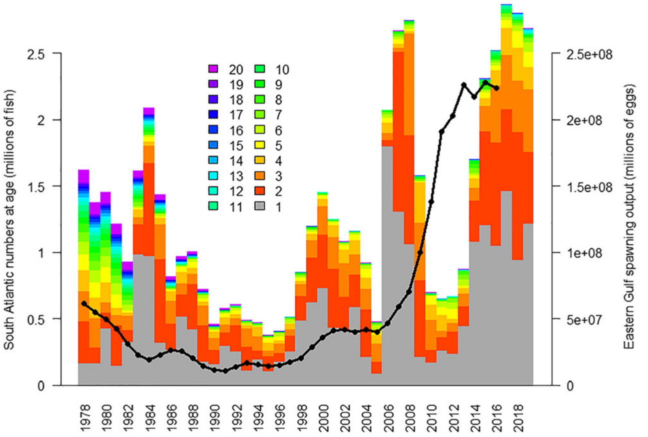

FIGURE 8 Estimated numbers at age for the Atlantic (colored bars) plotted against Eastern Gulf spawning output (black line), as estimated by stock assessments in each region (SEDAR, 2018, SEDAR 2021)

domain ocean models used for our regional study have boundaries at or near this region, so the area could not be well-resolved in our broader regional summary results. What we are able to conclude from our simulations is that the North Carolina subpopulation is unlikely to be contributing many larvae, if any, to the eastern Florida subpopulation. Understanding to what extent the persistence of this North Carolina subpopulation relies on its own larvae would require expanded survey data and hydrodynamic models to the north to better resolve both the fishery and ocean dynamics in this region.

We found that our conclusions are generally robust; however, our sensitivity analyses allowed us to quantify the uncertainty stemming from various sources. The choice of ocean model can substantially affect the conclusions drawn; HYCOM and Mercator models estimated a much higher probability of Atlantic recruits being sourced from the Gulf than did SABGOM. This result is driven by several patterns in the transport estimates; SABGOM predicts somewhat higher self-recruitment rates in the Atlantic, and substantially lower rates of successful recruitment from Gulf to Atlantic, compared with both HYCOM and Mercator (Table 2). Taken together, the probability of a recruit in the Atlantic being spawned in the Atlantic is much higher based on the SABGOM model.

HYCOM and Mercator appear to present more variability (higher eddy kinetic energy) around the major currents (e.g., Loop Current, Florida Current, Gulf Stream) than the SABGOM model (Figure 2), and lower variability can result in fewer stochastic events (e.g., eddies, shifts in current) that can contribute to mixing of populations (Cetina-Heredia et al., 2019; Goldstein et al., 2020). Indeed, the rate of export from the Gulf to the Atlantic is more variable for Mercator and HYCOM experiments, both between years and between vertical distributions of larvae, corroborating that lower variability in the currents in SABGOM might lead to the patterns observed. Because the years simulated are not overlapping across the hydrodynamic models, it is difficult to pinpoint the specific reasons behind interannual variability; this could be due to either particularly anomalous years being selected, or because the model in general produces more variable velocity fields. Lower variability could also lead to the higher local retention patterns we see for SABGOM in the Atlantic. There are also some notable differences in the settlement patterns over the entire Eastern Florida shelf, for both Global Hycom and Mercator when compared with SABGOM, for which settlers seem to concentrate around the shelf break/western limit of the Gulf Stream. This again could be a reflection of less variability of the currents on the shelf, such that the Gulf Stream dominates the transport (and larvae “access” fewer settlement sites).

Interannual variability was the second most influential source of uncertainty, which could be expected given that the dynamics of the region are driven by large-scale currents (Loop Current, Florida Current) which have no significant seasonal trends. Running the simulation for a series of 5 years for each hydrodynamic model captured much of the interannual variability. We also considered multiple vertical migration assumptions; although we lacked vertical distribution information specific to red snapper, there is generally high consistency in patterns of vertical migration within families (D'Alessandro et al., 2010; Huebert et al., 2010). Our sensitivity analyses showed that variations in distribution patterns within the upper 30 m did not have a major influence on the results (Figures 5–7). Misspecified settlement habitat could potentially introduce large bias in the results; however, red snapper is known to settle to a wide variety of substrates and depths, and we accounted for uncertainty in settlement habitat in the Florida Keys region through our sensitivity analysis.

Finally, there are uncertainties in the underlying spawning production maps that were not accounted for in this analysis. For the areas covered by fishery surveys, the underlying distributions are highly informed; the distribution maps are based on thousands of data points and statistical analysis to remove sampling artifacts. The precision of these distributional maps is likely to be high, particularly considering the resolution of the maps compared with the larger spatial scales of interest. However, we were unable to estimate egg production in areas beyond the statistical survey domain on the Atlantic side; specifically, deeper waters along the Florida Keys and at the northern limit of the survey south of Cape Hatteras. At the northern extent, we lack information to determine how much further the egg production and suitable recruitment habitat extends; limitations in the spatial domain of available oceanographic models also precluded direct inclusion of this region in our final results. Given that the rate of settlement is much lower (<15% of particles from near Cape Hatteras successfully settle, as compared with >50% for particles spawned off the east coast of Florida), inclusion of this area would likely result in an overall reduced rate of Atlantic-to-Atlantic recruitment and thus increase the probability that Atlantic recruits are sourced from the Gulf. On the other hand, our simulations may have underestimated egg production along the Florida Keys region; if substantial spawning is occurring in this region, it would likely increase the probability of local recruitment in the Atlantic. Our results must be interpreted in light of the specific areas of study that we could reasonably quantify and can be updated when further information is available regarding the relative red snapper egg production and the suitability of recruitment habitat along the fringes of the South Atlantic's jurisdiction.

4.1 | Implications for stock assessment and management

The results of our study have implications for monitoring, assessment, and management of red snapper in the United States. Our simulation results characterize the primary source and sink locations of red snapper recruits in the Eastern Gulf and Atlantic and can guide future monitoring of key areas of spawning stock biomass as well as likely areas of settlement to develop recruitment indices. In the Atlantic, there is essentially no published information documenting the occurrence, distribution, and habitat preferences of red snapper juveniles (Rindone et al., 2015). Identifying red snapper probable settlement locations, as done here, is a critical first step toward developing surveys to generate recruitment indices, which could subsequently be incorporated into stock assessments. Probable source populations to the Gulf have only recently been studied (Johnson et al., 2009), and source–sink dynamics in the Atlantic were previously unstudied. From a stock assessment perspective, substantial input of recruits from an external population would complicate detection of any spawner–recruit relationship. The current approach to assessment in the Atlantic region—an approach supported by our findings—is to estimate recruitment as variability around a mean value. This approach makes no assumptions about the source of recruitment, whether local or external.

Our results also have implications for red snapper management, both among jurisdictions and within. Given that productivity of the Atlantic stock appears to be significantly impacted by dynamics of recovery and exploitation in the southern extent of the West Florida Shelf, more insights into these patterns could improve management advice. Recent research initiatives with improved monitoring in these areas (e.g., https://restoreactscienceprogram.noaa.gov/projects/reef-fish-survey) may lead to additional insights into patterns of abundance and may improve predictions of recruitment subsidies in the region. In the Atlantic, the center of biomass off the coast of Florida may be relatively robust to localized depletion, so long as it is subsidized by recruits from Southwest Florida. The compact area of high red snapper biomass off the coast of North Carolina may be even less susceptible to localized depletion as it appears to be only a sink location; it receives substantial input from both East and West Florida centers of red snapper abundance.

Future research to improve management should focus on understanding the physical dynamics behind interannual fluctuations in recruitment. A key need for these studies is a validated oceanographic hindcast; ideally at least a decade of hydrodynamic fields would be needed to understand the conditions leading to strong and weak recruitment years (e.g., Karnauskas, Walter & Paris, 2017). A study of the Pulley Ridge area in southern Florida found that Pulley Ridge-sourced settlement peaks to the Florida Keys were related to the position of the Florida Current entering the Florida Straits; years where the Florida Current was closer to the straights were correlated with higher local retention rates in the West Florida Shelf (Vaz et al., 2016). Closer evaluation of the current dynamics in each year could lead to similar generalizations regarding the expected input of larvae from the Gulf to the Atlantic in any given year, given the prevailing current regimes at the time of spawning. It is also important to recognize that the present simulations represent a “static” connectivity scenario based on the best available near-present-day information, but future spatial exploitation patterns and environmental conditions may differ substantially from present conditions. Changing conditions could have implications for spawning timing and location, behavior and duration of larvae in their pelagic phase, the current patterns driving their dispersal, and settlement habitat. The biophysical framework used in the present study can be easily modified to explore questions relating to future scenarios and could also be extended to understand connectivity patterns in other managed species in the region.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

All authors contributed to the conception and design of the study. CP, KS, NF, TS, SL-B, RH, and AV contributed to acquisition of data, models, and/or methods for the work. KS, CP, NF, TS, and AV assisted with statistical analysis, and MK ran the simulations. All authors contributed to the interpretation of results. MK, KS, and NF drafted the manuscript with assistance from all other authors. All authors contributed to literature review, manuscript review, and read and approved the submitted version.

AUTHOR DISCLAIMER

The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of NOAA or the Department of Commerce.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. These data are simulation outputs with large storage requirements and are therefore not publicly posted. Codes and data used to develop the model inputs and process model outputs are available online (https://github.com/mandykarnauskas/GoM-Atl-red-snapper-connectivity indicating the units of coordinates).

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