

FEATURE ARTICLE

Red Snapper connectivity in the Gulf of Mexico

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Abstract

Objective: Red Snapper *Lutjanus campechanus* is a valued, heavily exploited fish species in the Gulf of Mexico. The species is distributed over a wide variety of habitats through its life history, and current evidence suggests moderate to high site fidelity, with particularly small home ranges and high residency times when fish are associated with reef structures. Given these life history traits, it is not surprising that within the gulf, there is evidence that the overall population is composed of multiple subpopulations. Thus, dispersal of early life stages plays an important role in the Red Snapper gulf population structure and dynamics, as embryo and larvae can be transported for longer distances, driving stock mixing and supplying recruits to sustain and replenish local subpopulations. Here, we assess the connectivity patterns of Red Snapper driven by larval dispersal in the Gulf of Mexico by simulating dispersal and recruitment.

Methods: This study employs a modeling approach to examine the probabilistic connectivity patterns of Red Snapper influenced by larval dispersal in the Gulf of Mexico. It investigates the impact of local oceanography, species behavior, and demographics on Red Snapper population structure. We estimate the spatial characteristics of Red Snapper dispersal, quantifying connectivity and larval supply fluxes between management jurisdictions, including state boundaries and the three-area boundaries recently selected during the stock identification portion of the Gulf of Mexico Red Snapper Research Track Assessment. We use the modeled probability of settlement as a proxy for recruitment.

Result: Our results indicate that Red Snapper recruitment occurs mostly close to their spawning sites (median distance 80 km). Simulated dispersal revealed exchange of Red Snapper larvae across state boundaries, with Alabama, Mississippi, and Louisiana receiving a considerable supply of recruits from other states. Finally, estimation of subpopulations based on larval exchange support the areal divisions used within the research track stock assessment.

Conclusion: Our results suggest that interstate cooperation in heavily connected regions could benefit management of the species by optimizing sustainable exploitation across the Gulf of Mexico.

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KEYWORDS

connectivity, Gulf of Mexico, larval transport, Red Snapper

INTRODUCTION

Fisheries management boundaries often align with geopolitical boundaries and, thus, might not represent population structure and dynamics, particularly considering heterogeneous patterns of species distributions, reproductive output, and recruitment (Pinhorn and Halliday 1990; Kerr et al. 2017; Song et al. 2017; Berger et al. 2020; Palacios-Abrantes et al. 2020). Assuming spatial structures for management that are inconsistent with stock structure can have detrimental consequences, even resulting in overharvesting and local depletion (Stephenson 1999; Ciannelli et al. 2013; Goethel and Berger 2017; Kerr et al. 2017; Bosley et al. 2019; Palacios-Abrantes et al. 2020; Liu and Molina 2021). Fish behavior, including movements through ontogeny, from dispersal of embryos and larvae to migration of adults, is one of multiple factors underlying stock spatial structure (Stephenson 1999; Kerr et al. 2017; Lowerre-Barbieri et al. 2017; Goethel et al. 2021). Fish movement also shapes source-and-sink dynamics between subpopulations, playing a fundamental role in overall population persistence and recovery (Karnauskas et al. 2022; Vaz et al. 2022).

The Red Snapper *Lutjanus campechanus* (family Lutjanidae) is a valued fish species distributed along the eastern coasts from northern South America to the southeastern United States. In the U.S. Gulf of Mexico exclusive economic zone (hereafter, "gulf"; Figure 1), Red Snapper has been harvested by recreational and commercial fisheries for nearly two centuries and currently supports a multibillion-dollar fishery sector (Carpenter 1965; Hood et al. 2007; Porch et al. 2007; Rindone et al. 2015). The population in federal waters (farther than 3 nautical miles from the coasts of Louisiana, Mississippi, and Alabama and 9 nautical miles for Texas and Florida) is managed by the Gulf of Mexico Fishery Management Council (hereafter, "Gulf Council") as one population (or stock; see Table 1 for a glossary of terms) defined by geopolitical limits—the Texas border in the west and the Florida Keys in the east. In the gulf, the species is distributed over a wide variety of habitats through its life history (Patterson et al. 2005; Dance and Rooker 2019), and while the degree of adult Red Snapper migration within the gulf is still unresolved, evidence from telemetry and traditional mark-recapture studies suggest moderate to high site fidelity, with particularly small home ranges and high residency times when fish are associated with natural or artificial reef structures (Patterson et al. 2001; Patterson and Cowan 2003; Strelcheck

Impact statement

Our study reveals substantial exchange of Red Snapper larvae between states. In particular, Alabama, Mississippi, Louisiana and the Florida Panhandle receive a substantial fraction of their recruits from neighboring states. The state of Mississippi is unique in that it receives a greater percentage of recruits from outside state boundaries than within. Collaboration among highly connected states could enhance management.

et al. 2007; Topping and Szedlmayer 2011; Piraino and Szedlmayer 2014; Addis et al. 2016; Williams-Grove and Szedlmayer 2016; Froehlich et al. 2019; Everett et al. 2020; Friess et al. 2021; SEDAR 2021; Stunz et al. 2021). Given these life history traits, it is not surprising that within the gulf, genetic evidence suggests that the overall population is composed of multiple subpopulations, although their boundaries and spatial scales could not yet be resolved (Pruett et al. 2005; Gold and Saillant 2007; Saillant et al. 2010; Hollenbeck et al. 2015; Portnoy et al. 2022). Thus, dispersal of early life stages potentially plays an important role in the Red Snapper population structure and dynamics, as embryo and larvae can be transported for longer distances than the range of adult movement, driving mixing and supplying recruits to sustain and replenish subpopulations (Johnson et al. 2009; Karnauskas et al. 2022).

The Red Snapper in the gulf were fished to low abundance levels, and since the late 1980s, a complex series of management regulations have been created to stop overfishing and support rebuilding the Red Snapper stock under pertinent legislation (Hood et al. 2007; Porch et al. 2007; Cowan et al. 2011). In 2018, the stock was considered no longer overfished but remains in a rebuilding plan to reach target biomass levels (SEDAR 2018). While the gulf Red Snapper is managed as one stock by the Gulf Council, the stock assessment model of Red Snapper attempts to replicate the species spatial structure within U.S. gulf waters, which is driven by demographic, biological, and harvesting patterns. Until 2018, the gulf Red Snapper assessment was conducted using a two-area model with a western and an eastern gulf area (divided at 89.1°W, around the Mississippi River mouth; SEDAR 2018). In 2021, the two-area model assumption was reviewed considering

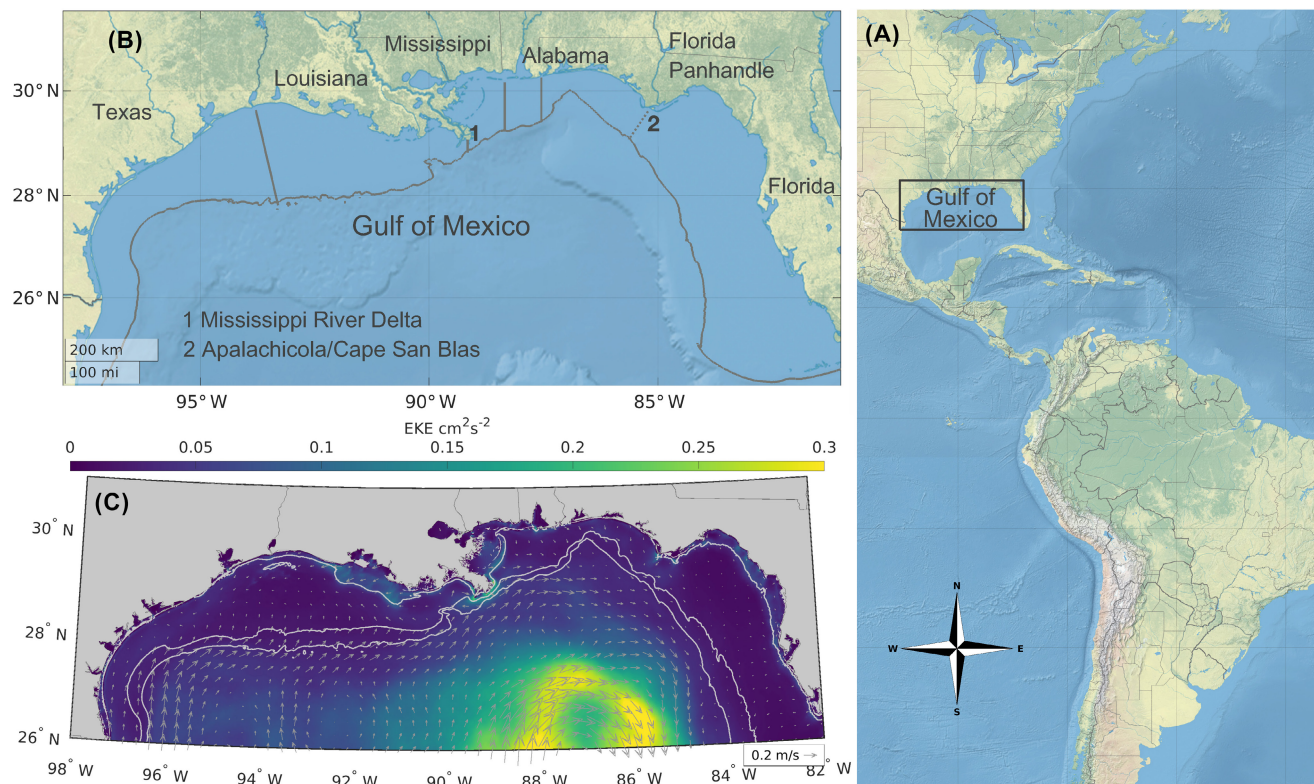


FIGURE 1 Maps of the study area, showing (A) the Gulf of Mexico location; (B) the boundaries between states (gray solid lines), Red Snapper habitat, and geographic references; and (C) the average surface velocities and eddy kinetic energy (EKE; m^2/s^2) for our study period (2011–2017). Bathymetric lines reflect the boundaries of the Red Snapper habitat and show 10, 64, and 140 m. Spawning occurs between 10 and 140 m and settlement between 10 and 64 m. State boundaries follow Amendment 50A, State Management Program for Recreational Red Snapper (Fisheries of the Caribbean, Gulf of Mexico, and South Atlantic 2020) and, to facilitate visualization, only extend to 140 m (limit of Red Snapper habitat in our simulations). The dashed line at the Apalachicola peninsula represents the division considered here between the Florida Panhandle and Florida. The EKE is a measure of the variability of the flow.

the species life history, movement, genetics, and fishery patterns (see details on SEDAR 2021), and a three-area model—eastern, central, and western gulf—was proposed for use in the 2023 Red Snapper research track stock assessment (Figure S3 in the Supplement available separately online; SEDAR 2021). Thus, a refined understanding of the larval dispersal dynamics in relation to the three-area assessment is needed, both to further support the current division and to estimate the exchange of recruitment between the model areas.

Red Snapper management in the gulf is further complicated by the participation of multiple fishery components that are regulated on different space and time scales by both state and federal agencies. In 2015, answering to requests of states to have increased flexibility to implement management that better met their individual needs, sector separation was adopted for the recreational sector at the federal level. This allowed for separate management to be implemented for the for-hire sector and private recreational sector, and the states were given control over the private sector in both state and federal waters (Fisheries of the Caribbean, Gulf of Mexico, and South Atlantic 2015).

The federally permitted for-hire recreational component and the commercial components are managed by the Gulf Council, with each component receiving a fixed percentage of the total annual catch limit (20.73% and 51%, respectively). Since 2018, the private-angler component of the recreational annual catch limit (28.27% of the total) has been individually managed by the five states in both state and federal waters, resulting in state-specific seasonal closures and allocations (Figure S2; Fisheries of the Caribbean, Gulf of Mexico, and South Atlantic 2020). Each state is granted a fixed proportion of the private recreational quota (Alabama: 26.3%, Florida: 44.8%, Louisiana: 19.1%, Mississippi: 3.6%, and Texas: 6.2%) and can establish individual management measures for private anglers reporting landings to that state (Fisheries of the Caribbean, Gulf of Mexico, and South Atlantic 2020).

Considering the current state-specific management approach for the private-angler component of the recreational fishery, Red Snapper in the gulf is equivalent to a transboundary resource (Song et al. 2017; Palacios-Abrantes et al. 2020), with migration between management jurisdictions largely constrained to its early life

TABLE 1 Glossary of terms used in this study.

Term	Definition
Population or stock	Population is usually defined by biological criteria (as in Wells and Richmond 1995). In our study context, however, we refer to population and stock interchangeably, defined as the portion of the species population within a predefined geopolitical management division, the U.S. Gulf of Mexico.
Subpopulations	In our study, these are (1) the results of analyses to identify subpopulations in the gulf where self-recruitment is maximized and larval subsidies exchange between subpopulation is minimized and (2) defined by geopolitical management boundaries at the state level. Consistent with Wells and Richmond (1995) definition: “arbitrary spatially delimited subset of individuals from within a population.”
Local populations	Here, local populations are the combination of individuals located within habitat grid cells (sensu Wells and Richmond 1995).
Ecological connectivity	Ecological connectivity refers to the probabilistic connectivity obtained from larval dispersal simulations, considering unique larval dispersal events (Vaz et al. 2022).
Recruitment	Settlement is used as a proxy for recruitment (as in Karnauskas et al. 2022) since we do not explicitly consider postsettlement processes.
Self-recruitment	Self-recruitment is defined as the fraction of recruitment in a subpopulation that is spawned locally (sensu Paris and Cowen 2004; Botsford et al. 2009; Burgess et al. 2014; Drury et al. 2018).
Export	Export here refers to settlers from a subpopulation that did not settle locally (Pelc et al. 2010; Kough et al. 2013).
Barriers (to larval dispersal)	As there is no evidence of complete isolation of the Red Snapper local populations in the U.S. Gulf of Mexico, barriers here are defined as locations where the least exchange of larval flow are likely to occur, analogous to leaky barriers.

history. Consequently, it is useful to consider its connectivity across management boundaries, which provides an understanding of the rate at which one area seeds another (Kough et al. 2013; Dubois et al. 2016; Andreollo et al. 2017; Karnauskas et al. 2022). For example, it was recently estimated that the South Atlantic Red Snapper population receives up to one-third of its larvae from the Gulf of Mexico stock; therefore, rebuilding rates and exploitation potential in the Atlantic Ocean are partially a function of the levels of spawning biomass in the gulf (Karnauskas et al. 2022). Thus, reducing the risk of local depletion and collaboratively working to rebuild the stock in the gulf also helps to rebuild and sustain the stock in the Atlantic Ocean. Similarly, if the spawning stock contained in one state's waters serves largely as a source of recruits for another state's waters, then the amount of exploitation that the larval recipient state can withstand will be a function of how the exploitation in the source state is managed. Understanding how larval source and sink areas occur across management boundaries can thus help identify where cooperation among states would help to optimize management by considering regional recruitment dynamics and thus maximizing potential exploitation across the overall population range.

Here, we use a modeling approach to assess the probabilistic connectivity patterns of Red Snapper driven by larval dispersal in the gulf, exploring how larval dispersal

driven by the local oceanography, species behavior, and demographics can shape Red Snapper population structure and dynamics. We expand upon previous studies of Red Snapper larval dispersal (Johnson et al. 2009, 2013; Karnauskas et al. 2013, 2017a, 2017b; Karnauskas and Paris 2021; Vaz and Karnauskas 2022), updating the model configurations. Specifically, we estimate the spatial characteristics of Red Snapper dispersal, quantifying connectivity and larval supply fluxes between management jurisdictions, including state boundaries and the three-area model currently in use for the stock assessment of the species. Finally, we explore how our results can inform management of Red Snapper in the gulf by considering the spatial characteristics of spawner–recruitment dynamics. We particularly highlight how interstate cooperation in heavily connected regions could benefit management of the species by optimizing potential exploitation across space.

METHODS

Connectivity Modeling System

The Connectivity Modeling System (CMS) is a probabilistic, modular open-source biophysical model (Paris et al. 2013) developed initially to simulate dispersive

and connectivity processes in the oceans. The model can use the velocity fields of any hydrodynamic model to advect virtual larvae. Velocity fields are integrated in space with a fourth-order Runge–Kutta scheme. To represent the unresolved, subgrid-scale processes, virtual larvae move randomly with a random-walk model scaled by the turbulent diffusion. Virtual larvae are released from predetermined locations (spawning sites) at specific frequencies and advected by the maximum time determined by their pelagic larval duration. Larvae older than their competency period that are within the limits of a settlement site (given by polygons) are considered recruited and removed from the simulations. It is important to highlight that here we use settlement as a proxy for recruitment; however, we do not explicitly simulate postsettlement processes, which can shape recruitment through time and space.

Hydrodynamic models

Velocity fields used are from a state-of-the-art, high-resolution implementation of the Hybrid Coordinate Ocean Model (HYCOM), with $1/50^\circ$ horizontal resolution (~ 2 km) and 32 vertical layers (Le Hénaff and Kourafalou 2016). Daily outputs are available from 2011 to 2017. This GoM-HYCOM $1/50$ model experiment has been validated by comparisons with observations by multiple studies (Le Hénaff and Kourafalou 2016; Androulidakis et al. 2019; Le Hénaff et al. 2019), and this is the first use for estimating connectivity in the gulf.

This hindcast, data-assimilative simulation is forced with daily river discharges, implemented at 22 major river discharge points into the gulf. Minor river discharge points are represented by climatological values. Data assimilated includes altimetry and SST data from satellite observations, along with salinity and temperature profiles from Argo floats and expendable bathythermographs. The operational global HYCOM simulation (hycom.org) provides forcing at the open boundaries, while the surface is forced by the European Centre for Medium-Range Weather Forecasts atmospheric circulation ($1/8^\circ$ horizontal resolution, ~ 14 km).

Larval dispersal modeling

Spawning

For our larval dispersal simulations, we used the same domain as described in Karnauskas et al. (2013) and Karnauskas and Paris (2021). Spawning habitat is

distributed between depths of 7 and 140 m, which corresponds to the isobaths where adult Red Snapper were observed during surveys, as the species does not migrate large distances to spawn (Karnauskas et al. 2017b). Depth contours for the habitat definition are given from the General Bathymetric Chart of the Oceans (www.gebco.net), with a 15 arc-second resolution. The spawning and settlement habitat are represented by a grid of 10- by 10-km discrete polygons, or habitat cells.

Spawning follows Red Snapper seasonality for the gulf, with spawning occurring from May to October (Collins et al. 2001; Rooker et al. 2004). A frequency of spawning of 3 days is observed for the species in the gulf, but due to computational limitations, we use a frequency of spawning of 6 days, which still captures the smaller scales temporal variability (Kough and Paris 2015). The fecundity, defined as the number of embryos per spawning event, is scaled by the relationship of the proportion of females bearing spawning markers per time of year from Porch et al. (2015).

We consider reproductive output based on two different scenarios to account for the effects of biomass distributions on the probabilistic connectivity. The first is a “naïve” scenario, where we assume the same abundance and age composition on each habitat cell; thus, fecundity is constant and not scaled by biomass distribution. This naïve uniform scenario allows the assessment of the probabilistic connectivity between different Red Snapper habitats in the gulf without the uncertainty of biomass distributions. As estimates of the spawning biomass distribution across space can be uncertain, changing quite dramatically over time, our intent here was to consider how connectivity and recruitment patterns would change under this most extreme assumption of homogeneous distributions. The second scenario considers fecundity following biomass distributions based on the relative egg production model of Karnauskas et al. (2017a), which considered spatially explicit relative abundance and biomass distributions on natural and artificial structures in the gulf at a 10-km scale resolution. The model generates relative abundance and biomass at each habitat grid cell for four explicit age-classes (ages 1–2, 3, 4, 5+) by multiplying localized biomass by the fecundity-at-age relationship from Porch et al. (2015). As Red Snapper do not migrate for spawning and present a protracted spawning season over large part of its cycle, we assume the distribution of biomass to be a good approximation of egg production, and it has been used in previous Red Snapper larval transport studies (Karnauskas et al. 2013, 2017b; Vaz and Karnauskas 2022). Please refer to the [Appendix](#) for information about specific model parameters.

We acknowledge that the Karnauskas et al. (2017a) estimates are now outdated by over a decade and that more

recent information is available (e.g., Stunz et al. 2021); however, more recent data sets provide abundance estimates across a much lower spatial resolution and do not provide spawning biomass and fecundity considering age-classes.

Settlement habitat

A comprehensive literature review on the settlement habitat of Red Snapper in the gulf updated previous habitat definitions (Karnauskas et al. 2013), which were derived from the Johnson et al. (2013) review of Red Snapper juvenile habitat. In our literature review, we identified 15 studies (Gallaway et al. 1999; Szedlmayer and Conti 1999; Rooker et al. 2004; Szedlmayer and Lee 2004; Patterson et al. 2005; Geary et al. 2007; Wells et al. 2008; Johnson et al. 2013; Monk et al. 2015; Rindone et al. 2015; Switzer et al. 2015; Grüss et al. 2018; Powers et al. 2018; Dance and Rooker 2019; Erisman et al. 2020) that focused on elucidating habitat for age-0 juvenile Red Snapper. These studies vary in their spatial and temporal coverage. Some studies were localized (e.g., Szedlmayer and Conti 1999; Rooker et al. 2004; Szedlmayer and Lee 2004; Geary et al. 2007; Wells et al. 2008; Powers et al. 2018), while others covered the entire gulf or most of it by extension (Gallaway et al. 1999; Patterson et al. 2005; Johnson et al. 2013; Monk et al. 2015; Rindone et al. 2015; Switzer et al. 2015; Grüss et al. 2018; Dance and Rooker 2019; Erisman et al. 2020). Methods were diverse, but data from the Southeast Area Monitoring and Assessment Program (SEAMAP) Fall Plankton surveys were considered in most studies: seven directly analyzed the survey data, while an additional three indirectly considered the results through literature review.

Our resulting literature review is thus robust, incorporating all studies and large data sets available for juvenile Red Snapper distribution in the gulf. The results of preferred settlement habitat presented by Gallaway et al. (1999) are largely supported by most recent studies; however, age-0 juveniles appear to occur in shallower depths (~10 m) than previously considered (17 m), with individuals collected at depths as shallow as 4 m.

Considering these results, we conducted a sensitivity analysis to verify how much settlement is lost by not considering depths shallower than 17 m as viable habitat settlement regions. Using our current model simulations from 2011 to 2017, we selected all larvae inside the model domain and alive during their competency period (26–30 days). Competent larvae that were found inside polygons in depths shallower than 17 m were counted as settled and removed from the simulation. Our estimations have shown that yearly settlement at shallower settlement

sites vary between 5% and 12% of all larvae spawned. Shallow settlement represents 5–20% of total settlement. Since settlement in shallower habitat is significant, a second set of simulations was completed considering settlement habitat from 10 to 64 m. These are the simulation outputs we use here.

Larval traits

Following the results of detailed sensitivity analyses by Karnauskas et al. (2017b), hatching here was assumed to occur 1 day postspawning, with flexion occurring at day 12 and postflexion at day 16. We considered a pelagic larval duration from 26 to 30 days (Szedlmayer and Conti 1999; Drass et al. 2000; Rooker et al. 2004). Larvae that reach 26 days are considered competent, and thus, if found within the settlement habitat will be considered recruited and removed from the simulation. In CMS, the ontogenetic vertical migration (OVM; sensu Paris and Cowen 2004) is represented by a matrix of vertical distributions, which contains the probability of larval distributions by depth and time. Here, time is given by larval development (hatch, flexion, and postflexion) stages (see details on sensitivity analyses in Karnauskas et al. 2017b). We conducted a literature review and reviewed information available from several studies in the Gulf of Mexico, including data from the SEAMAP Fall Plankton surveys. The only data set with large coverage of Red Snapper larvae vertical distributions was conducted over shallow depths (<20 m; Frank Hernandez, National Marine Fisheries Service, personal communication), and thus, these results cannot be extrapolated over our entire area. Thus, we followed the approach from previous studies (Karnauskas et al. 2013, 2022), and we use the information of three congeners: Mutton Snapper *L. analis* (OVM 1), Lane Snapper *L. synagris* (OVM 2), and Gray Snapper *L. griseus* (OVM 3).

Postprocessing analysis

Dispersal kernels

We calculated dispersal kernels to estimate the probability of dispersal distances from spawning to recruitment sites for all recruits (Nathan and Muller-Landau 2000). Dispersal kernels are calculated by binning the distances from spawning to settlement site pairs for each recruit. We binned the distances by 10 km, which corresponds to the size of a habitat cell. We calculated dispersal kernels for individual simulation years, as well as an aggregate dispersal kernel considering all recruits from 2011 to 2017.

Connectivity

The CMS saves individual larval positions and attributes through time, together with connectivity files with the spawning and settlement sites of successful settlers. The connectivity output is used to generate transition matrices of connectivity (i, j), where the rows (i) represent the spawning sites and the columns (j) represent the settlement or recruitment sites (Bodmer and Cavalli-Sforza 1968; Paris et al. 2007). By normalizing the connectivity matrix by columns (i.e., by the total settlement from each spawning site i), we obtain the probability of settlers from a spawning site i to reach a settlement site j (P_{ij}), and the matrix main diagonal ($P_{ij}, j=i$) represents the probability that larvae settle within the same jurisdictional boundaries in which they were spawned (Paris-Limouzy 2011).

When the transition matrix is normalized by rows or by the total recruitment at each recruitment site (j), we obtain the relative contribution of each spawning area for each recruitment site (P_{ji}). In this case, the main diagonal of the matrix ($P_{ji}, i=j$) represents self-recruitment or the fraction of recruitment spawned locally over all recruitment in a site (or jurisdiction) (sensu Paris and Cowen 2004; Botsford et al. 2009; Burgess et al. 2014; Drury et al. 2018). This measure indicates if a jurisdiction is reliant on larvae from other jurisdictions.

Stratification

The connectivity is assessed by four different stratifications for subpopulations: assessment model areas, states, depth, and assessment model areas and depth.

States

States' jurisdictions are based on geographical state boundaries and encompass both state and federal waters, as defined in Amendment 50A (Fisheries of the Caribbean, Gulf of Mexico, and South Atlantic 2020). However, Florida is further divided into Florida and the Florida Panhandle, at Cape San Blas, to account for different demographic and exploitation characteristics (Figure S3; SEDAR 2021). Thus, our result for the state evaluation encompasses six jurisdictions: Texas, Louisiana, Alabama, Mississippi, Florida Panhandle, and Florida. The jurisdictional boundary of the Gulf Council is located at approximately 25.6° (the latitude of U.S. Highway 1), while the boundary in our simulation extends up to 24.9°N, which is a reasonable approximation of the Gulf Council jurisdiction.

Assessment model areas

The Red Snapper assessment model areas are based on the stock structure recommendations made by the SEDAR

Stock ID working group, which was comprised of genetic, life history, and spatial distribution experts and was tasked with determining the spatial structure for the Red Snapper assessment model. The working group recommended dividing the gulf Red Snapper population into three areas: west, central, and east gulf (Figure S3; SEDAR 2021). The western gulf includes the continental shelves of Texas and Louisiana, whereas the central gulf includes the shelves of Mississippi, Alabama, and the Florida Panhandle (limit of 85°W and 29°N). The eastern area is thus composed of the remainder of the Florida Shelf.

Depth

Depth for each spawning and settlement habitat centroid is interpolated from the General Bathymetric Chart of the Oceans data set (15 arc-second). Shallow habitat is defined as depths under 40 m, middepth from 40 to 100 m, and deep over 100 m (Figure S5).

Assessment and depth

Assessment model areas and depth (Figure S6) are based on the combination of the former divisions.

Analyses of subpopulations

In this study, we aim to characterize the larval transport between state jurisdictional boundaries. One important measure is to understand how larval transport between stock assessment model areas changes based on the longitudinal boundary selected. We conducted two distinct analyses to identify subpopulations in the gulf where self-recruitment is maximized and larval subsidies exchange between subpopulations is minimized. First we provide varying longitudinal boundaries along the gulf (Karnauskas and Paris 2021) for the quantification of larval exchange and then apply a second method based on Jacobi et al. (2012), where boundaries are selected by a minimization algorithm and independent of any management jurisdiction or geographic bound.

In our first method, based on Karnauskas and Paris (2021), we considered a sliding window of possible longitudinal boundaries across the gulf from 96°W to 83°W, at a 1/10° resolution. We carried out an iterative process of splitting the gulf into two subpopulations on either side of the boundary: a western and an eastern subpopulation. We then calculated the total number of successful settlers that were spawned in one subpopulation but recruited to the other subpopulation.

The total number of nonresident recruits is given by the sum of the larvae spawned in the western subpopulation and recruiting to the eastern, with the total of recruits from the eastern subpopulation recruiting into the western. The

percentage of recruits is calculated by dividing the number of nonresident recruits by the total number of recruits in the entire gulf. The percentage of nonresident recruits was recorded for each possible boundary, allowing plots of the longitudinal series of nonresident recruits and to find the minimum values, representing barriers of larval flux.

To identify self-recruiting subpopulations independently of management or geographic boundaries, we applied a graph theory method from Jacobi et al. (2012). The method seeks solutions that minimize connection between subpopulations while maximizing connections within subpopulations (Jacobi et al. 2012; Garavelli et al. 2014; Vaz et al. 2022). We used the Jacobi et al. (2012) implementation from the ConnMatTools open-source R package (Kaplan et al. 2017). Here we did 180 interactions of the method, using different penalty parameters. This parameter is designed to avoid aggregating sites into only one population. From these interactions, we selected the solutions with the smallest quality values, where quality is given by one-relative local retention (connectivity between clusters normalized by the self-recruitment).

RESULTS

Dispersal kernels

The dispersal kernels show that Red Snapper larvae that successfully settle are likely to settle close to their source location (Figure 2), and this is observed for both spawning scenarios: naïve uniform scenario (Figure 2A) and realistically scaled by the observed biomass distributions (Figure 2B). The median dispersal in the naïve uniform scenario is 60 km, while for the modeled fecundity based on Karnauskas et al. (2017a), median dispersal is 80 km. The highest probability of settlement occurs at 50 km for both scenarios—considering our habitat configuration (10-km by 10-km grid), this is the equivalent of five grid points. However, the magnitude of the dispersal kernel, which represents the larval survivorship (Botsford et al. 2009; Steneck et al. 2009), was 10% lower in the spatially explicit fecundity scheme than in the naïve uniform. While some interannual variability is observed for the curves, the main patterns observed (i.e., median distance of dispersal for settlement and higher likelihood of settlement) remain stable among years for both scenarios.

Lastly, the curve expected if dispersal patterns were to occur solely due to distance between habitat patches, given by the potential connectivity, greatly differs from the dispersal kernels obtained from the simulated larval dispersal. The potential connectivity does not show peak settlement close to spawning site, and the likelihood of settlement reaches a maximum at around 100 km.

Subpopulation connectivity under different fecundity assumptions

The connectivity matrices reveal the most likely settlement habitat for a successful settler spawned at a particular location. The connectivity matrices for the entire simulation period, and for all individual spawning and settlement habitat, corroborates the likelihood of self-settlement, which is represented by higher values along the diagonal of the matrix (Figure 3). The higher likelihood of recruitment to the local population is evident both at the naïve uniform and spatially variable fecundity scenarios. Some places present particularly high probabilities of local settlement, such as Florida and the Florida Panhandle.

In these matrices, probabilities above the diagonal represent westward transport (downstream) and probabilities below the diagonal represent transport eastward (upstream). Transport across state boundaries is limited. States located in the western gulf (Texas and Louisiana) contribute larval subsidies to states in the central area (Alabama, Mississippi, Florida Panhandle). Larvae from states in the central area can be exported to either the western or eastern gulf. Most of the Florida larvae recruit locally, but exported subsidies can recruit to the Florida Panhandle, Alabama, and Mississippi.

In the scenario with realistically scaled fecundity (Figure 3B), some spawning sites (represented along the x -axis) do not hold reproductively mature settlers and therefore spawning does not occur. In sites where spawning does not occur, the connectivity probabilities are sparser than in the naïve uniform scenario, as expected. However, the connectivity patterns are very similar for both fecundity scenarios, as already described, indicating that connectivity patterns are mostly impacted by the dominant currents combined with the shape of the shelf, rather than the specific distribution of spawning biomass across the shelf. Thus, for the next analyses we focus on results from the spawning scenario where spawning is realistically scaled by fecundity.

Connectivity stratified

States

It is important to highlight that here we present results considering each area as both sources and sinks of larvae. By analyzing the connectivity matrices, we evaluate the probability of a particular location providing recruits to other areas. And by identifying the relative contribution of distinct spawning sites for the recruitment in a determined area, we assess what areas are supplying recruits. The connectivity matrix stratified by

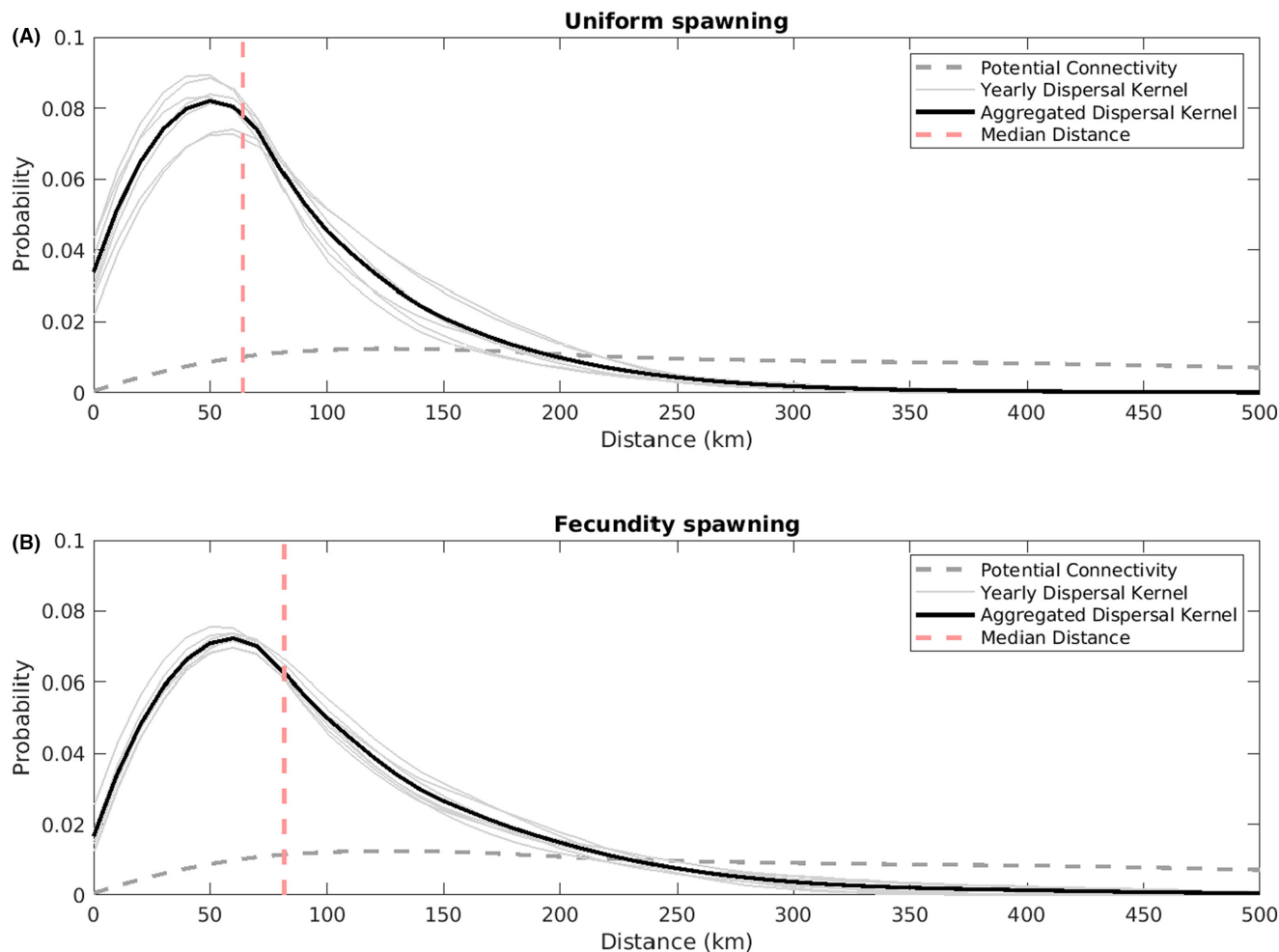


FIGURE 2 Dispersal kernels of settlers in the Gulf of Mexico for Red Snapper larvae (A) spawned uniformly at all habitat cells (naïve uniform) and (B) in a spatially variable fecundity scenario, following the fecundity modeled by Karnauskas et al. (2017a) based on abundance and biomass of Red Snapper in the Gulf of Mexico. Pairs of distance from spawning to settlement site for each larva are binned every 10 km (the size of a habitat grid cell). Aggregate dispersal kernel and median are based on larval dispersal simulations from 2011 to 2017. Potential connectivity is based on the distances between all spawning and settlement sites.

states (Figure 4A) shows the high likelihood of recruitment within the same area of spawning. As expected, the states exporting the most larval subsidies are the states located in the middle of the gulf, Mississippi, and Alabama (43% and 30%, respectively), while the highest probabilities of local recruitment are observed for the states on the boundary of the gulf—Florida and Texas (probabilities of about 96% and 79%, respectively). Notably, larvae spawned in Alabama can settle from the Florida Panhandle to Louisiana, with a particularly high likelihood of export to the Florida Panhandle (46%). Larvae from Mississippi can also be exported upstream to Louisiana or downstream to the Florida Panhandle (18% and 25%).

By considering stratification of subpopulations by state, we can observe a similar picture emerging (Figure 5B; Table S2 in the Supplement available separately online), with higher self-recruitment in the

boundary states (Texas and Florida) in the gulf, with higher exchange for the centrally located states. The highest self-recruitment estimate is consistently for southwest Florida, with an average of $98.5 \pm 1.2\%$ (mean \pm SD) across different years and ontogenetic vertical distributions. Similarly, the second highest self-recruitment is for Texas ($89.3 \pm 3.8\%$). On the other hand, the lowest self-recruitment was estimated for Mississippi, where only $17.6 \pm 5.3\%$ of recruits are spawned locally. Almost half ($50.6 \pm 11.7\%$) of recruits in Mississippi come from Alabama, with an additional $23.24 \pm 12.3\%$ transported from Louisiana. While Alabama's recruits tend to be locally spawned ($61.4 \pm 10.4\%$), the state can receive substantial contributions to recruitment from other states (average 19.3% from the Florida Panhandle, 6.5% from Mississippi, and 10.7% from Louisiana). Similarly, about half of the recruits in the Florida Panhandle are spawned locally ($51.2 \pm 7.9\%$). The region receives sizable larval

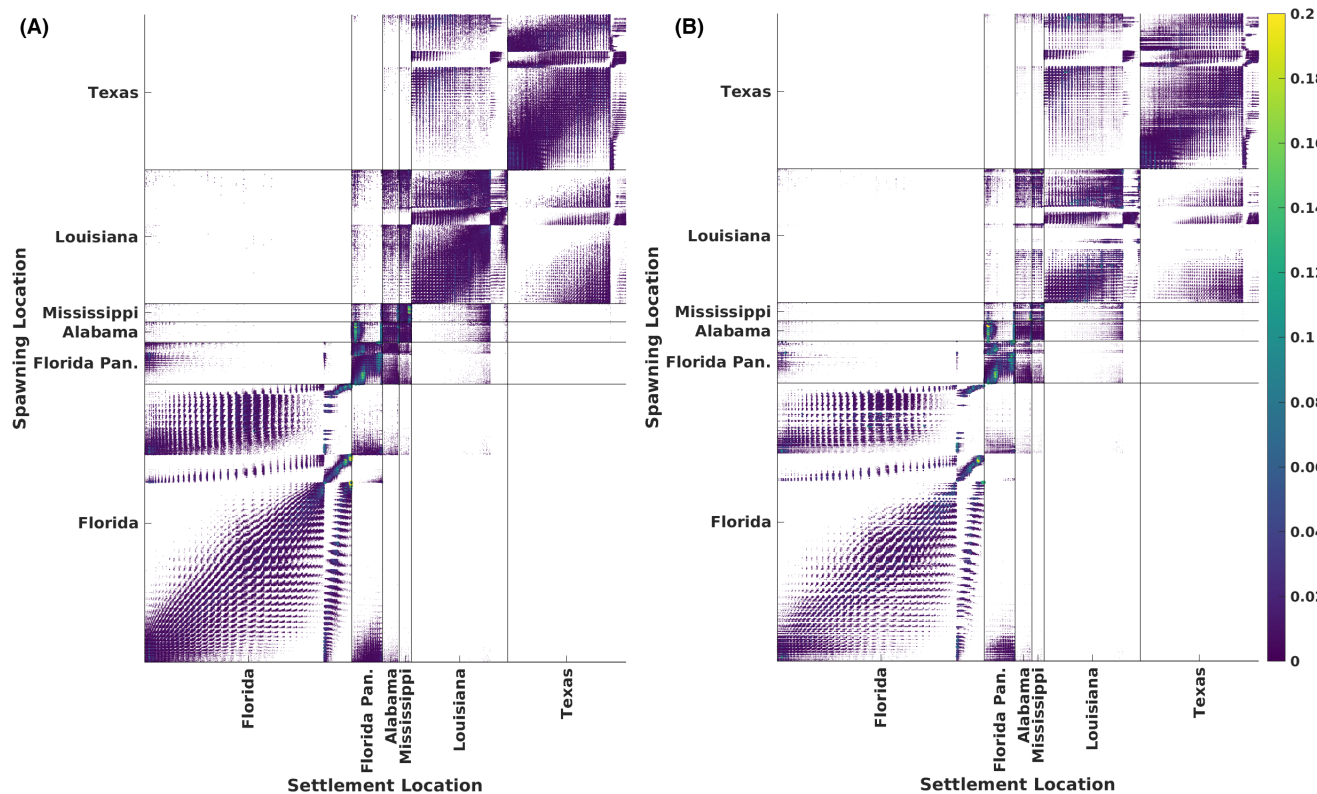


FIGURE 3 Connectivity matrices for Red Snapper larvae (A) spawned uniformly at all habitat cells (naïve uniform) and (B) in a spatially variable fecundity scenario, following the fecundity modeled by Karnauskas et al. (2017a) based on abundance and biomass of Red Snapper in the Gulf of Mexico. Matrices are based on 7 years of dispersal simulations (2011–2017), with spawning occurring every 6 days from May to September.

subsidies from Alabama ($38.2 \pm 6.1\%$). Louisiana is the only state to receive a large proportion of recruits from Texas ($41.3 \pm 9.5\%$), while over half of recruits are spawned locally ($54.9 \pm 7.6\%$).

Stock assessment model areas

When observing connectivity by stock assessment model areas (Figure 4B), the three stock areas are mostly self-sustained, with high probabilities of larvae recruiting locally: 92%, 93%, and 97% for the eastern, central, and western gulf, respectively. The highest probabilities of export are from larvae spawned in the eastern gulf and recruited in the central gulf (about 7%). When considering the spawning area of the recruits in each assessment model area (Figure 5A; Table S1), recruits are mostly locally spawned. This is particularly evident for the western and eastern gulf, where local recruits on average account for 98.8% and 97.1% of the total recruitment, respectively. While most recruits in the central gulf are the product of local spawning ($86.2 \pm 6.4\%$), the area receives the highest external contributions to recruitment, on average $13.7 \pm 7.1\%$.

Depth

When connectivity is calculated by depth of spawning and settlement sites (Figure 4C), there is a lack of settlement in deep areas because settlement habitat extends up to the 64 m isobath. Our simulations show that settlers from shallow areas are likely to self-recruit (about 81% probability), with likelihood of transport to mid-depths up to 18%. Larvae from middepths are 72% likely to recruit locally. Larvae from deep, offshore areas are most likely to recruit at middepths (about 78%), with about 21% probability of transport to shallower recruitment sites.

When exploring connectivity stratified by both assessment model areas and depth, the results for the depth connectivity for the entire gulf are corroborated, with some differences evident between assessment areas (Figure 4D). In the central gulf, we observe that near-shore, shallow depths are the most likely to receive larval supply while also exhibiting the highest probability of local settlement. Recruits from the western and eastern gulf from middepth and deep areas are mostly likely to settle at middepth.

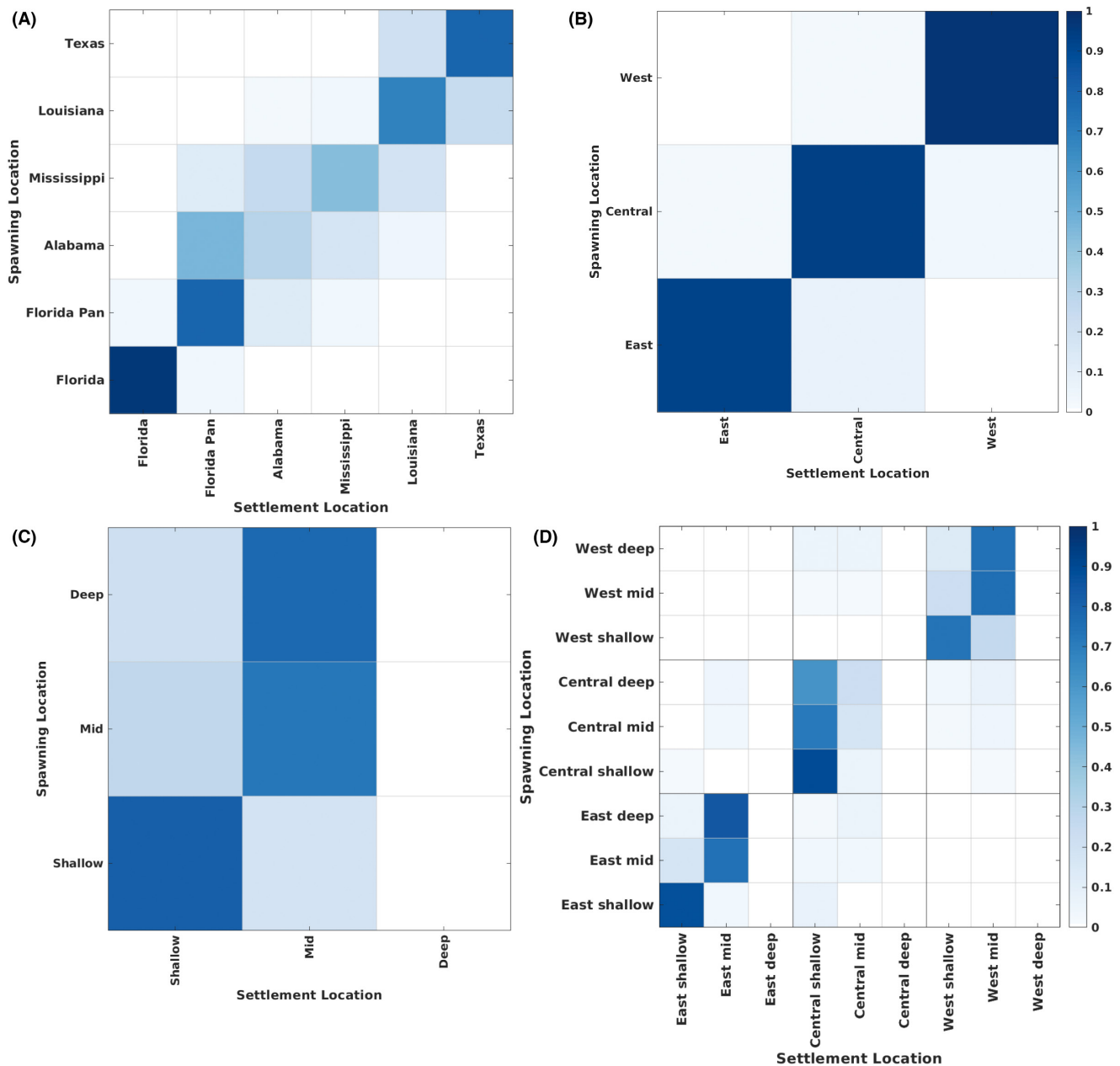


FIGURE 4 Connectivity probabilities of Red Snapper larvae by the various subpopulation stratifications: (A) states, (B) assessment model areas, (C) depth, and (D) assessment model areas and depth. Strata spatial configuration is presented in [Figures S2–S5](#). Connectivity, determined through larval dispersal simulations from 2011 to 2017, is expressed as a probability and thus is independent of the total number of sourced larvae.

Subpopulations

The longitudinal boundaries for larval transport identified by the iterative analysis ([Figure 6](#)) were robust across years and assumptions of larval distributions in the water (column OVM; see [Figure S1](#)); thus, in [Figure 6](#) we present the barriers obtained with the aggregation of all simulations. The primary barrier occurs around the longitude of Cape San Blas (-85.65°W), with the secondary barrier at the Mississippi River (-89.45°W). The first barrier results in a transfer of 1.1% of recruits

and the second 1.9%. Thus, for each barrier, the self-recruitment in both the eastern and western gulf is over 98%. Despite the variability of the flow, these barriers are consistent between years, with the first barrier presenting very low interannual variability in the recruit transfer rates (from 0% to 1.6%; see [Figure S7](#) for the interannual variability of the barriers). The secondary barrier at the Mississippi River mouth presents slightly higher variability (0.6–3.6%).

If we consider a three-area scenario, where the two boundaries correspond to minimum larval exchange, the

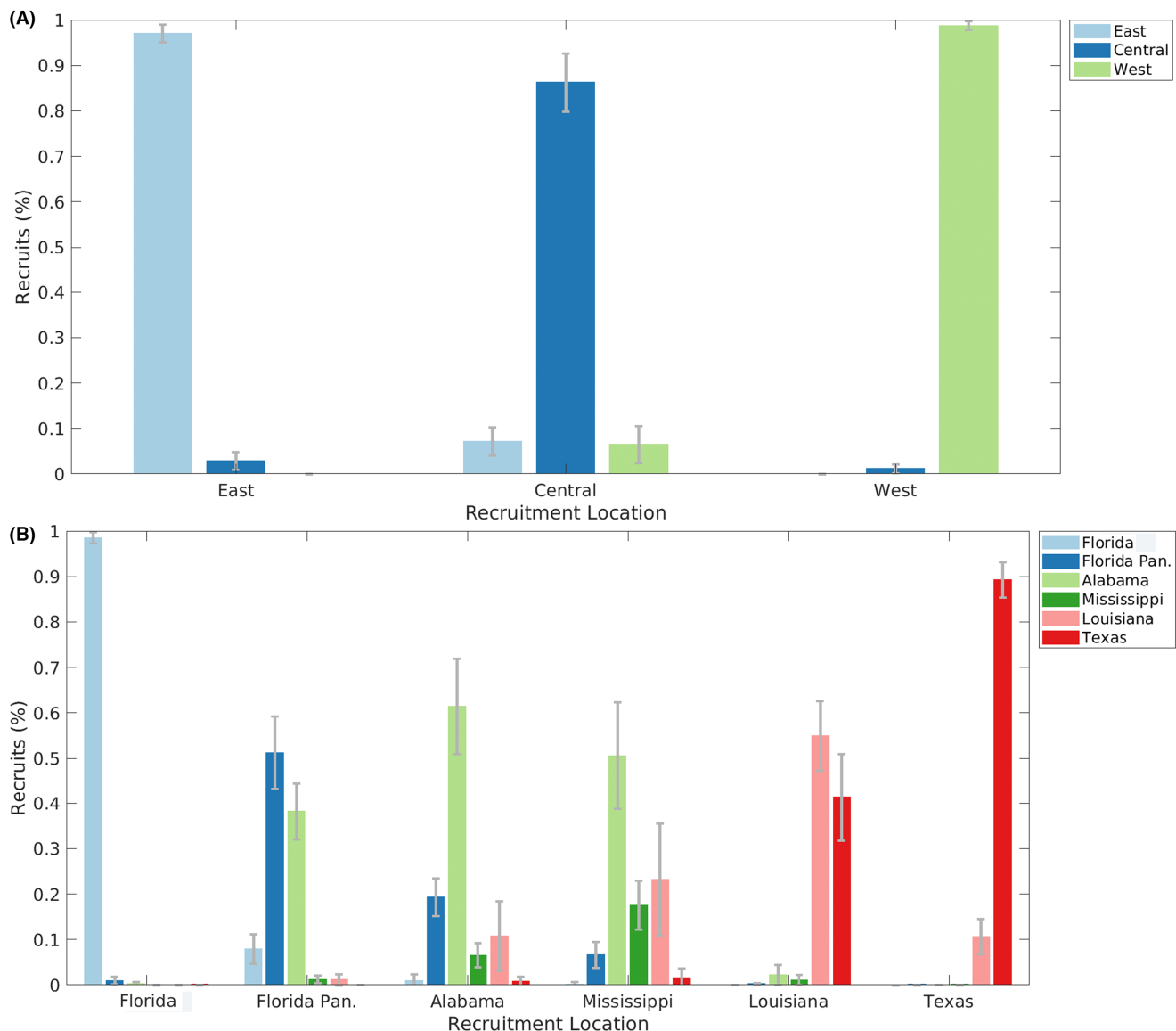


FIGURE 5 Larval connectivity estimates summed by (A) stock assessment model areas (i.e., subpopulations) and (B) state jurisdictions. Bar plots denote the proportion of larvae successfully settling in each area (or state) that originated from each of the respective areas (or states). Error bars show standard error and pertain to uncertainty surrounding different sensitivity runs (three ontogenetic vertical distributions and 7 years of spawning events).

recruit transfer between areas is 3.47% of all recruits in the gulf.

The results of the minimization algorithm from Jacobi et al. (2012) (Figure 7) largely agree with our iterative analysis (Figure 6). The solution yielding the smaller exchange between areas is a solution presenting two areas, with a boundary approximately around Cape San Blas. This solution yielded a percentage of nonresident recruits of 0.96%. The next best solution, with two divisions present, included one barrier about Cape San Blas and another barrier west from the mouth of the Mississippi River. The percentage of nonresident recruits for this configuration of subpopulations is 3.11%. It is important to highlight that here the solution is not bounded by any geographic

or management boundary; thus, self-sustaining areas can present any configuration.

DISCUSSION

Self-recruitment patterns

Our simulations of Red Snapper larval dispersal revealed strong self-recruitment patterns throughout the gulf, considering a range of plausible modeling configurations and interannual variability over 7 years (Figures 2–4). Self-recruitment is a useful connectivity value for ecologists and conservationists alike since it reveals the degree that a local

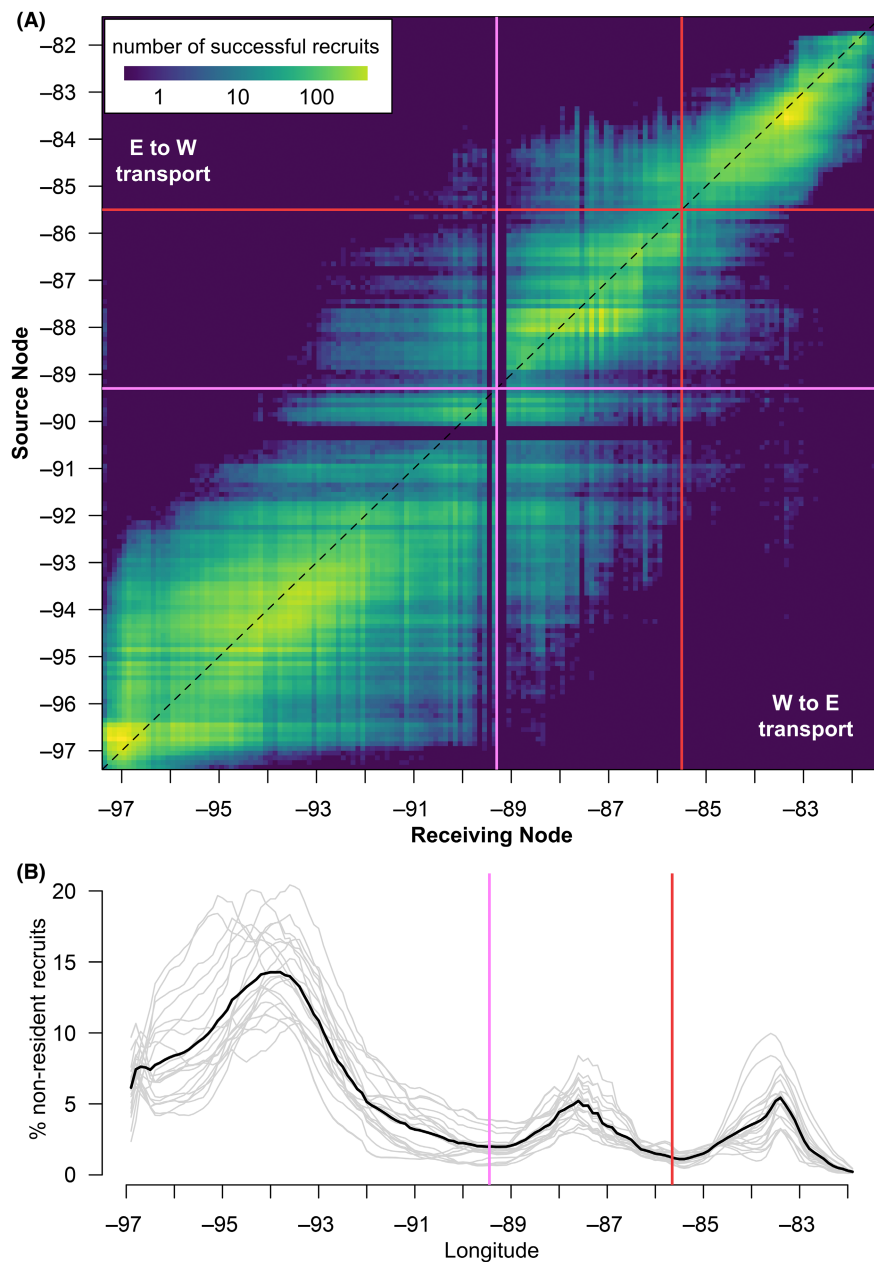


FIGURE 6 Connectivity matrix for all simulations combined (top panel; three ontogenetic vertical migration distributions and 7 years of spawning, 2011–2017). Rows represent spawning sites (sources) and columns are recruitment sites (receiving node), with recruitment sites (habitat cells of 10- by 10-km grid) ordered by longitude from Texas to Florida. Self-recruitment is indicated by the dashed diagonal line. Red and pink lines indicate the primary and secondary (leaky) barriers as identified by the two minimum values of nonresident recruits. The bottom panel shows the percentage of nonresident recruits as a function of longitudinal boundaries in the Gulf of Mexico (from 96°W to 83°W at intervals of 0.1°). For each cutoff, the percentages of nonresidents recruits are equal to the total of recruits exchanged between the eastern and western gulf, divided by the total number of recruits in the gulf. Light-gray lines represent the percentage of nonresident recruits by longitudinal boundaries for each of the 21 individual simulations (yearly spawning for three ontogenetic vertical distributions). The dark line represents the values obtained from the aggregated connectivity matrix for all simulations (as shown in the top panel).

population may be isolated (Botsford et al. 2009; Almany et al. 2013). It might also have implications to the level of long-term persistence of local populations, particularly to disturbances (Berumen et al. 2012). Our simulations estimated that half of recruitment occurs within an 80-km radius from spawning. Thus, self-recruitment was mostly

evident when considering spatial scales of connectivity larger than 80 km, as for example in the connectivity scaled by the three-area assessment model. In contrast, when connectivity was scaled by state boundaries, the states with the narrowest continental shelves (e.g., Alabama) presented the highest larval exchange with neighbors.

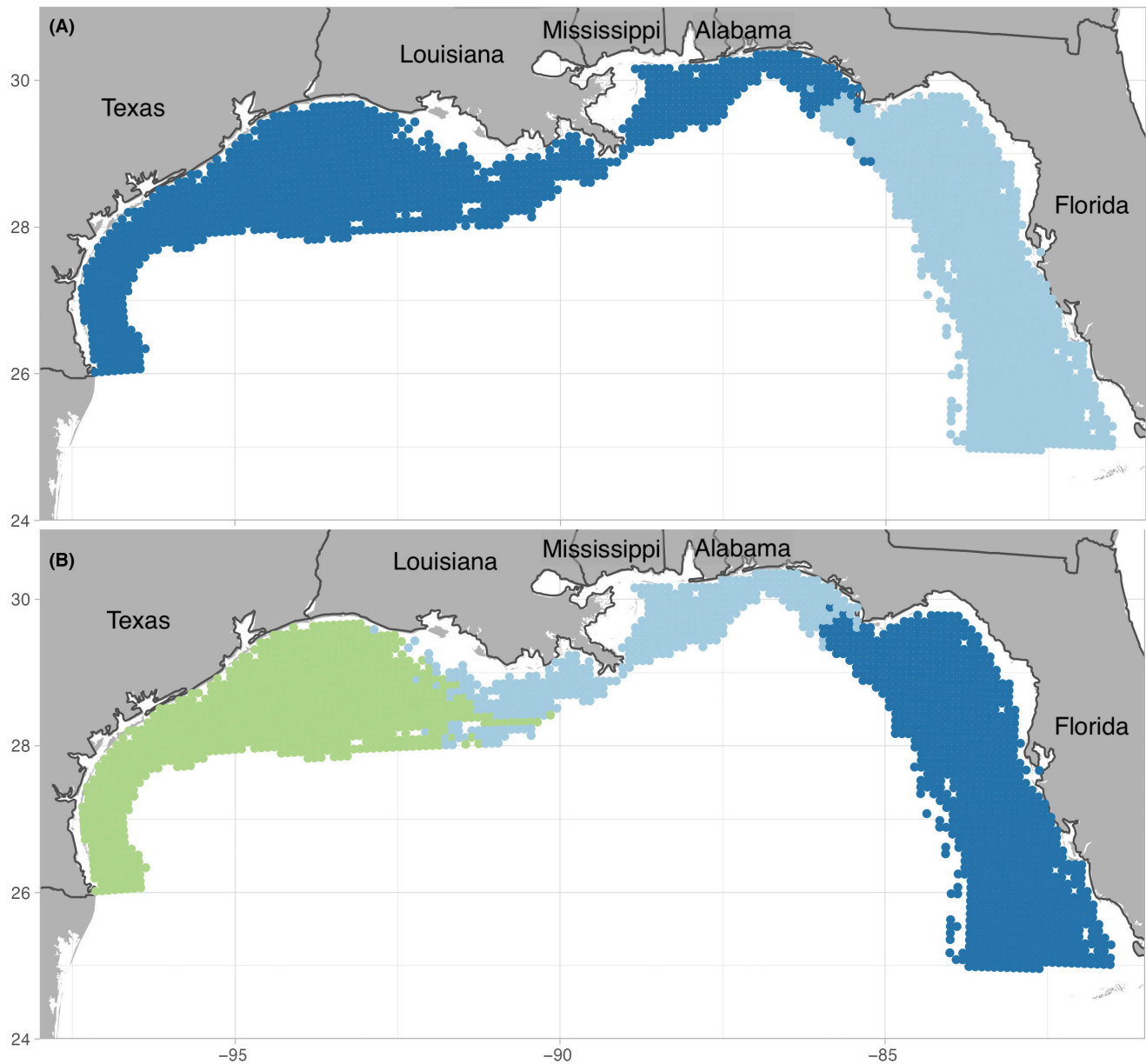


FIGURE 7 Subpopulations, mostly self-sustained, identified with a minimization algorithm based on the connectivity matrix encompassing three ontogenetic vertical migration distributions for 7 years (2011–2017) of simulations. Panels represent the two combinations yielding the smallest larval export to other jurisdictions: (A) 0.96% and (B) 3.11%.

Indeed, our analyses suggest a large range of self-recruitment levels of Red Snapper among states in the gulf. Central states are more likely to receive recruits from other states, while Florida and Texas present the highest levels of self-recruitment, where most of their recruits are locally spawned. In this study, the relative importance of self-recruitment for each state is influenced by the geographical extent of our simulation, which was guided (by necessity due to data limitations) by geopolitical boundaries. As our focus is to understand Red Snapper dynamics within the U.S. exclusive economic zone, we have not accounted for settlers incoming from other jurisdictions in the gulf (i.e., Mexico and Cuba), particularly because

we have no compatible abundance data available for other countries. Thus, it is expected that Texas and Florida—as de facto endpoints of our simulated network—will present higher self-recruitment. In reality, Red Snapper is distributed over the Intra-Americas Sea, but transboundary contributions to the U.S. Gulf of Mexico is not fully resolved. A previous modeling study indicated a likelihood of cross-jurisdictional recruitment to Texas and Louisiana, with larval influx from Campeche Bay (Paris et al. 2020), whereas transport from Campeche Bay was corroborated by genetic analyses of Red Snapper through the gulf (Portnoy et al. 2022). However, dispersal models of Red Snapper and other congeners suggest that western Florida

Shelf is unlikely to receive subsidies from the northern Yucatan Peninsula (Paris et al. 2020), Cuba (Paris et al. 2005; Kough et al. 2016), and the southeast United States (Karnauskas et al. 2022), while Portnoy et al. (2022) genetic analyses suggest that western Florida might differ from the rest of the gulf. Considering these results, the high self-recruitment for Florida would unlikely change if transboundary larval subsidies were explicitly incorporated in our model. Nevertheless, elucidating further downstream sources to the U.S. gulf is beyond the scope of our current work.

Links to genetics

Our results suggested a lack of impenetrable barriers to larval dispersal and, consequently, to gene flow. Despite the lack of impenetrable barriers to transport, the estimated ecological connectivity suggested that at some spatial scales, Red Snapper stock in the gulf might operate as various subpopulations. The Apalachicola peninsula emerged as the most significant barrier for larval transport, albeit leaky, with a secondary barrier around the Mississippi River outflow. This finding matches several lines of evidence that point to these regions as significant boundaries for the gulf Red Snapper subpopulations, as we will briefly review.

The direct comparison of ecological connectivity estimations obtained by larval dispersal with genetic estimations poses many challenges, primarily since each reflects largely different spatial–temporal scales. Our estimated ecological connectivity reflects unique events of dispersal of early life stages between spawning and recruitment sites (Vaz et al. 2022), while genetic connectivity typically reveals exchanges occurring during multiple generations or evolutionary timescales, exchanges that might occur at different ontogenetic stages and, thus, are not directly related to spawning–recruitment patterns (Bryan-Brown et al. 2017). However, there are some insights to be gained by a broad comparison of our simulated connectivity and patterns revealed by multiple genetic studies focused on Red Snapper in the gulf (Pruett et al. 2005; Gold and Saillant 2007; Saillant et al. 2010; Hollenbeck et al. 2015; Puritz et al. 2016; Portnoy et al. 2022). Firstly, while previous studies were unable to reject panmixia of the stock, nonetheless they indicated the existence of a population structure, with subpopulations exchanging periodic gene flows strong enough for genetic homogenization (Pruett et al. 2005; Gold and Saillant 2007; Saillant et al. 2010; Hollenbeck et al. 2015; Portnoy et al. 2022). However, attempts to localize genetic barriers were inconclusive (Portnoy et al. 2022). Additionally, Puritz et al. (2016) observed small-scale (~5 km) genetic heterogeneity among

young-of-year Red Snapper in the northern gulf, which might indicate that contributions from spawning varies spatially and temporally.

Taken together, our results agree with the large picture emerging from genetic analyses. The estimated connectivity shows that both the Apalachicola peninsula and the Mississippi River can serve as barriers to larval dispersal. While the barrier at the Apalachicola peninsula was stable, we noted large interannual variability in the larval supply crossing the Mississippi River. Our simulations also indicated that larvae settling within individual habitat grids in the northern gulf might spawn in different locations, as similarly observed by Puritz et al. (2016) in a fine-scale survey of single nucleotide polymorphisms of young-of-year Red Snapper on the northern gulf shelf.

Links to life history

Additional lines of evidence also support that the larval dispersal leaky barriers identified here can influence the demography of the species. There is extensive indication that these barriers are stable through the ontogeny of the species. For instance, adult Red Snapper exhibit high site fidelity, with limited long range movement, and there is no indication of adults crossing the boundaries represented by the Mississippi River and the Apalachicola peninsula (Patterson et al. 2001; Patterson and Cowan 2003; Strelcheck et al. 2007; Topping and Szedlmayer 2011; Piraino and Szedlmayer 2014; Addis et al. 2016; Williams-Grove and Szedlmayer 2016; Froehlich et al. 2019; Everett et al. 2020; Friess et al. 2021; SEDAR 2021; Stunz et al. 2021). Analyses of otolith chemical signatures identified movement of postsettlement juveniles within the western gulf but not with the eastern gulf (Sluis et al. 2012, 2015).

Finally, the most comprehensive study of Red Snapper larval distributions in our study area, Hanisko et al. (2007), analyzed a 16-year time series of larval abundance from the SEAMAP Fall Plankton surveys, where abundance is given by the number of larvae under 10 m² of sea surface. The authors found that Red Snapper larval abundances in the Texas–Louisiana Shelf were almost three times greater than in Mississippi–Alabama, and abundances in Mississippi–Alabama were in turn four times greater than in Florida (Hanisko et al. 2007). Aside from reflecting differences in the spawning state subpopulations, these results also suggest the presence of mechanisms favoring local retention of larvae and, indeed, that a small fraction of Red Snapper larvae are transported eastward crossing the Apalachicola peninsula or the Mississippi River outflow, which corroborates the barriers identified by our simulations.

Previous larval transport studies, using different model configurations and hydrodynamic forcing, drew similar conclusions (Johnson et al. 2009; Karnauskas and Paris 2021). Johnson et al. (2009) used an array of multidecadal observations over the northern gulf to compute a near-surface climatological current field. Our simulations driven by a three-dimensional high-resolution model generally agree with the transport patterns noted by Johnson et al. (2009), particularly that the Apalachicola peninsula worked as the major barrier for larval flow. However, our model allowed the resolution of higher variability in the local oceanography (daily temporal resolution), as well as three-dimensional transport of larvae following their ontogenetic development and differential behavior, while Johnson et al. (2009) was restricted to two-dimensional near-surface climatological fields (i.e., mean monthly velocity fields). It is beyond the scope of this study to detail transport pathways and oceanographic features underlying transport, as well as reveal why patterns obtained here differ from Johnson et al. (2009), particularly regarding offshore transport. Here we observed that transport by offshore currents and mesoscale eddies, along with shelf flows, drives recruitment patterns and larval exchange in the gulf. These results imply that the three-dimensional spatial and temporal resolution of the hydrodynamic field can influence recruitment and connectivity patterns in the gulf, and this relationship should be further investigated.

Model uncertainties

Model inputs are a source of uncertainty about connectivity and recruitment estimations (Karnauskas et al. 2022; Vaz et al. 2022), and our model configuration relies on assumptions regarding the local hydrography and Red Snapper life history. This is the first larval dispersal study in the gulf using this particular high-resolution (~2 km horizontal resolution) hydrodynamic fields model (Le Hénaff and Kourafalou 2016), which has been validated with observations by multiple studies in the gulf (Le Hénaff and Kourafalou 2016; Androulidakis et al. 2019; Le Hénaff et al. 2019). This model's reliability to resolve the buoyant flow driven by the Mississippi River output was essential to unveil the connectivity patterns between the western and central gulf.

Another important input for our simulations is the spatial distribution of Red Snapper fecundity in the gulf. Our reproductive output is based on the most comprehensive model of Red Snapper fecundity conducted to date in the gulf, Karnauskas et al. (2017a). The authors calculated fecundity per grid cell habitat (10 by 10 km) considering

distinct age-class abundances and the fecundity-at-age relationship from Porch et al. (2015). Given the potential effect of the spatial reproductive output for larval transport and fate, we quantified how changes in spatial fecundity altered the connectivity patterns. By including a spatially explicit fecundity, the magnitude of the dispersal kernel (i.e., recruitment) was slightly reduced, the median displacement increased (from 50 to 80 km), and the width of the dispersal kernel curve, representing the stochastic dispersal around the mean, modestly increased. Together, these results suggest that while spatial fecundity patterns can influence larval dispersal characteristics, changes estimated between our naïve assumption of uniform reproduction throughout the gulf and the modeled fecundity from surveyed abundances from Karnauskas et al. (2017a) were minimal.

When contrasting the connectivity patterns for all habitat grid cells, for both the naïve uniform spawning and the spatially explicit fecundity model of Karnauskas et al. (2017a), the broad connectivity in the gulf is not generally sensitive to changes in the fecundity. As expected, the connectivity matrix following the Karnauskas et al. (2017a) fecundity model is sparser, given the heterogeneous distribution of adults and the lack of spawning at discrete habitat grid cells. Nonetheless, similar patterns of connectivity are apparent between the two scenarios. Importantly, these similarities are still apparent when connectivity is stratified by management jurisdictions and depth of habitat cells. These results indicate that the spatial distribution of fecundity is not the dominant factor shaping connectivity for Red Snapper in the gulf. In other words, connectivity patterns in the gulf are largely influenced by the shape of the shelf (particularly with respect to the areal extent between Red Snapper depth limits) and its interaction with the dominant current regimes as opposed to the configuration of spawning biomass distributions across the shelf. Thus, while the distributions of Red Snapper have changed significantly over time due to changing fishing pressure (SEDAR 2018, 2021; Stunz et al. 2021), we would not expect connectivity patterns to be significantly altered by these dynamics. However, more research is needed to investigate the importance of the spatial and temporal variability of maternal effects driving fecundity and egg quality.

Finally, we also considered assumptions regarding the vertical distributions of larvae through ontogeny by drawing distributions from congener snapper species given the lack of species-specific information for Red Snapper. Our results reflected that interannual variability was a bigger source of uncertainty around recruitment and connectivity patterns than the vertical migration patterns considered, which is corroborated by the Karnauskas et al. (2022) sensitivity analyses around

vertical distributions and different hydrodynamic models. Additionally, vertical migration patterns are consistent within families (D'Alessandro et al. 2010; Huebert et al. 2010; Irisson et al. 2010). Yet further studies of Red Snapper OVM could increase the accuracy of modeled connectivity and recruitment, also allowing a better understanding of the environmental drivers of such complex behaviors (Hernández et al. 2023). Indeed, under a future climate change scenario, connectivity and recruitment patterns can also be altered. Changes in the gulf temperature, salinity, and oxygen are forecast to occur over the next century (Dee et al. 2019; Lawman et al. 2022), which can alter growth and size (Lema et al. 2019; Avaria-Llautureo et al. 2021) and ultimately fecundity, while changes in the ocean circulation of the gulf are also expected (Liu et al. 2015). Thus, putative changes can bring unforeseen consequences for spawner–recruitment dynamics in the gulf, potentially altering population structure, and these changes might be necessary to be considered in future studies (Munday et al. 2009; Pinsky et al. 2018; Goethel et al. 2022; Goethel et al. 2021).

Management implications

Our results and conclusions have several implications for management of Red Snapper in the gulf. Primarily, the connectivity estimated by modeling larval dispersal confirmed that there is significant exchange of the gulf Red Snapper larvae across the boundaries of individual states. In particular, the states of Alabama, Mississippi, and Louisiana receive significant supplies of recruits from outside their state boundaries, and the Florida Panhandle is also dependent on larval supply from outside state boundaries (primarily Alabama). The state of Mississippi is unique in that it receives a greater percentage of larval supply from outside state boundaries than within.

Our results suggest that states highly connected by larval transport could cooperate for a more effective management strategy, which considers the spatial complexity of source–sink recruitment dynamics. The high proportion of external larval subsidies from states such as Mississippi highlights that potential changes in exploitation patterns in one state (e.g., Alabama) can lead to recruitment changes in neighboring states. Ultimately, these changes can influence the persistence of the entire Red Snapper population in the gulf as highlighted by a large body of research considering spatial dynamics of stocks, management scales, and depletion patterns (Stephenson 1999; Goethel and Berger 2017; Kerr et al. 2017; Bosley et al. 2019).

The primary barrier at Cape San Blas and the secondary barrier at the Mississippi River are relevant barriers to the exchange of larval supply fluxes. Importantly, our results not only corroborate the two-area model used in the previous Red Snapper stock assessment (SEDAR 2018), but also provide some support for an additional area that is currently in use for the 2023 research-track assessment of Red Snapper. It is important to highlight that these areas are used in the stock assessment to consider a combination of differences in life history and fleet behavior and do not signify complete biological population boundaries. Moreover, these areas are not completely lined up with our leaky barriers for larval dispersal, as other factors, such as life history, genetics, landings and effort data, and the spatial resolution of available fishery-dependent data, support the proposed boundaries of the three assessment areas (SEDAR 2021). It must be noted that increasing the complexity of the assessment boundaries may increase the realism of the spatial dynamics in the assessment model by allowing it to match the gulf Red Snapper population dynamics, but it also comes with additional challenges. To estimate population parameters according to these barriers, adequate and standardized data must be collected across the gulf. For such a complex model to work, data received from fishery-independent and dependent surveys must be comparable within and among these boundaries, meaning common units of measure are needed. With the current management boundaries and the differences in state-specific management, common units of measure become difficult to obtain. Thus, implementing a stock assessment model using the optimal boundaries presented here is a difficult task.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT


The data underlying this article will be shared upon reasonable request to the corresponding author.

ETHICS STATEMENT

All ethical guidelines were followed and no animals were handled in the development of this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

APPENDIX: SENSITIVITY ANALYSES

Previous modeling work of Red Snapper evaluated the effect of considering different biological characteristics of Red Snapper, including distinct ontogenetic vertical migration schemes (Karnauskas et al. 2017b). Here we considered the maximum number of eggs to be released.

Maximum number of eggs released

We conducted sensitivity analyses to evaluate how the maximum number of larvae spawned per spawning site or event (10, 40, or 100 larvae) affected settlement strength and connectivity patterns. We evaluated the sensitivity of the results regarding the number of embryos released considering (1) the probability of connectivity between populations, (2) the proportion of settlement per scenario, (3) the proportion of local settlers, and (4) the likelihood of local settlement.

We found that there are no differences in the proportion or likelihood of settlement or local settlement between different scenarios of the number of eggs released. The difference of connectivity between the scenarios due to different number of larvae spawned per event is very small (order of 10^{-3}), and differences are stochastic—there is no clear pattern of different number of larvae modifying settlement in the main diagonal line (representing self-settlement) or for a particular region. Thus, we considered the release of a maximum of 10 embryos per release per site to optimize the computational resources.

Diffusivity coefficient

We tested different diffusivity coefficients used in the estimation of the stochastic displacement in the Connectivity Modeling System. Three different coefficients were tested (10, 20, and $30\text{ m}^2/\text{s}$), along with different time steps for integration of the velocity field. Sensitivity was based on a 1-year release (2014). Results presented no significant differences between the diffusivities tested, considering the proportion of (1) settlement per diffusivity case, (2) settlement per state, and (3) proportion of local settlers per state. The anomaly of the connectivity matrices also showed very small (10^{-3}) differences between the scenarios.