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M. Karnauskas and C. B. Paris

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A Lagrangian biophysical modeling framework informs stock structure and spawning-recruitment of red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico

M. Karnauskas[1] and C. B. Paris[2]

[1]Southeast Fisheries Science Center
Sustainable Fisheries Division
75 Virginia Beach Drive
Miami, FL 33149-1099

[2]University of Miami
Rosenstiel School of Marine and Atmospheric Science
Department of Applied Marine Physics
4600 Rickenbacker Causeway
Miami, FL 33149

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Introduction

This research employs a biophysical modeling framework to provide insights into patterns of red snapper (*Lutjanus campechanus*) stock structure with respect to larval supply. We use the Connectivity Modeling System (CMS; Paris et al. 2013), an individual-based model which estimates the movement of particles in a 3-D velocity field. The framework has previously been used to estimate recruitment strength variability due to the effects of oceanographic current regimes. Here we use the CMS to simulate the entire process of recruitment, from spawning to settlement, and estimate the flow of larvae across different regions in the Gulf of Mexico. The results can inform where there are areas of limited larval exchange due to the presence of oceanographic breaks. The occurrence of population substructure due to these oceanographic breaks could potentially be accounted for in the stock assessment model by denoting subareas, within which some dynamics could be modeled separately.

Methods

Model setup

The Connectivity Modeling System (CMS) is a biophysical modeling system based on a Lagrangian framework, and was developed to study complex larval migrations such as those displayed by fish larvae (Paris et al. 2013). The CMS uses outputs from hydrodynamic models and tracks the three-dimensional movements of advected particles through time, given a specified set of release points and particle behaviors. Optional modules are provided to allow for complex behaviors and movements, simulating observed biological phenomena such as egg buoyancy, ontogenetic vertical migration, and tidal stream transport. The specific model set up used for this study was outlined in detail Karnauskas et al. (2017a; SEDAR 52); here we provide only a brief summary of the inputs.

The primary ocean velocity fields considered were the HYCOM + NCODA Gulf of Mexico 1/25° Analysis, a hybrid isopycnal coordinate ocean model (i.e., isopycnal in the stratified open ocean, fixed-depth in the unstratified surface layers, and terrain-following in shallow coastal waters), which allows for optimal simulation of both coastal and open-ocean features simultaneously (Chassignet et al. 2007). The model is data-assimilative, using real-time observations of the ocean's surface via satellite altimetry, as well as vertical profile information from CTDs, the ARGO observation program, and other sources; this allows for a three-dimensional depiction of ocean currents in real time at a relatively high resolution. We used experiment 32.5, which is available from 2014 to 2018. Because the selection of oceanographic model can sometimes have a significant impact on the results (Karnauskas, *unpublished*) we considered an alternate model for comparison, the 1/12° Mercator GLORYS version 12v1 reanalysis from the Copernicus Marine Environment Monitoring Service (CMEMS). The Mercator model is largely based on the CMEMS real-time forecast system and is also data assimilative; it is driven at the surface by ECMWF ERA-Interim and uses a reduced-order Kalman filter to assimilate sea level anomaly, sea surface temperature and sea ice concentration from satellite measurements, and *in situ* temperature and salinity vertical profiles from the CORA (Coriolis Ocean database ReAnalysis). Hydrodynamic fields for the Mercator model were available for the years 2013 to 2017.

The location of egg releases is based on a probabilistic model of red snapper biomass across space (Karnauskas et al. 2017b). The analysis included surveys of artificial structures (e.g., oil rigs and artificial reefs) and thus accounts for spawning from these locations. Because the model is age-structured, and the fecundity at age has been estimated, the distribution map is calculated in terms of expected number of eggs released over the spatial domain. This map then forms the basis of the locations of the simulated egg releases, with numbers of eggs scaled to the relative predicted density. To account for seasonal variation of average spawning fraction throughout the spawning season (Cowen et al. 2002), spawning releases are scaled by a reported statistical relationship relating the proportion of red snapper females bearing spawning markers with time of year (Porch et al. 2015). Particle releases are simulated every 6 days throughout the spawning period for all years. Spawning was 5 m above the ocean floor up to 45 m depth; eggs were released at 45 m for depths greater or equal to 50 m.

In CMS, vertical movements are defined via a probability matrix, which specifies the distribution of virtual larvae in the water column throughout time. Time steps for the probability matrix are most logically defined by using different larval stages (e.g., hatching, preflexion, postflexion), as lutjanids tend to shift in their vertical distributions with ontogeny. The same suite of sensitivity analyses were carried out as in Karnauskas et al. (2017a); these were based on comprehensive depth-stratified surveys from the region. The pelagic larval duration (PLD) is defined as 26 - 30 days; recruits must be transported to habitat within this time window to successfully settle. Settlement habitat is estimated to occur between 15 and 64 m depth and defined across 2,541grid cells of 10 km^2 resolution. This is the minimum feasible resolution corresponding to the scale of the spawning production map (Karnauskas et al. 2017b).

Analysis

We analyzed the resulting connectivity patterns at fine scales for the purposes of informing potential subpopulation boundaries, and also summarized results at the broader state level to understand patterns in larval connectivity with respect to state jurisdictions. The red snapper Stock Synthesis model has been historically configured as a two-area model with west and east subregions, with a boundary at approximately 89.1 degrees W. From the perspective of recruitment dynamics, the most appropriate longitudinal boundary would be that for which larval supply across regions is minimized, since recruitment is apportioned according to subregion and thus the dynamics within subregions regions would be accounted for separately within the assessment model. To understand the impact of the selection of any particular longitudinal boundary on the extent of larval transport across subregions, we considered a sliding window of possible longitudinal boundaries across the Gulf of Mexico from 96 to 83 degrees West, at a 1/10 degree resolution. We carried out an iterative process of splitting the Gulf into two regions -- essentially a “western” subregion and an “eastern” subregion on either side of the boundary -- and then calculated the total number of successful settlers that were spawned in one region but recruited to the opposite region. The total number of “non-resident” recruits are the sum of larvae spawned in the western sub-region and successfully settled in the eastern sub-region and the larvae spawned in the eastern sub-region and successfully settled in the western sub-region. We then plotted the series of longitudinal boundaries against the percentage of successfully settling larvae exchanged between regions for each given boundary, and looked for minimum values. Those minima represent longitudinal boundaries that maximize larval flow within sub-regions and minimize larval flow across sub-regions.

In Karnauskas et al. (2017a), a number of sensitivity analyses were carried out to evaluate the influence of model inputs and assumptions on results. We reran the analysis for each of these sensitivities and evaluated the final result to understand the impact of various model inputs on the final results.

Results

The overall results, in terms of longitudinal boundaries identified when simulations were averaged across all years analyzed, were very similar regardless of input assumptions or hydrodynamic model used. Most of the variability resulted from choice of hydrodynamic model or interannual fluctuations in currents; assumptions regarding ontogenetic vertical migration (OVM) had little impact on the final results. We therefore report a single base model using the HYCOM and Mercator oceanographic fields, respectively.

Spatial dynamics are easily viewed in the form of a connectivity matrix which shows the spatial patterns in source and sinks for larvae that have successfully settled (Fig. 1). In general, self-recruitment of larvae occurs where larvae settle at locations close to where they were spawned, (i.e. source node = receiving node, Fig. 1). Overall, larval transport occurs in a slightly eastward direction (i.e. spawners yield recruits that settle further east) along the Texas and Louisiana coasts. Successful recruitment is more spread out in Mississippi, Alabama, and the Florida Panhandle, and throughout the rest of the Florida Shelf settlement largely occurs in the areas in which spawning occurred.

With respect to larval transport rates at different longitudinal boundaries, two local minima were identified (Fig. 1 bottom panel). A primary barrier to dispersal occurs at 89.35 degrees West, in both HYCOM and Mercator models. Using HYCOM in CMS led to an estimated larval transfer rate across regions of 1.5%., while coupled with Mercator, CMS estimated a larval transfer rate of 1.8% (i.e, ~98% of successfully settling larvae were retained in the regions in which they were spawned). A secondary barrier to dispersal occurs at 85.45 degrees West using the HYCOM model and 85.55 degrees West with the Mercator model. At these breakpoints, larval transfer rates were estimated to be 2.2% and 2.7% for HYCOM and Mercator, respectively. There is high interannual variability in recruitment patterns, and the difference between coupling CMS with HYCOM versus Mercator models is more apparent at the annual scale (Fig. 2). However, regardless of the year or model considered, the analysis results in a primary barrier to dispersal near the Mississippi River, while a second local minima that occurs near the border of the Florida Panhandle and Big Bend region.

The connectivity matrix can be summarized according to political or regional levels in order to quantify the specific larval input within and among state boundaries (Fig. 3). Although there are some differences between coupling CMS with HYCOM versus Mercator models, the overall patterns and conclusions are similar for both models. Texas and Florida are highly self-recruiting – the vast majority of larvae settling within those state boundaries are estimated to have originated from those same states (Fig. 3). However, Louisiana is estimated to receive roughly half of its larvae from local waters and half of its larvae from Texas. Alabama retains a moderate proportion of its larvae, but is estimated to receive substantial subsidies from all states except for Texas. Mississippi is unique in that it retains very few of its locally produced larvae. Indeed, Alabama appears to be their primary supplier of larvae, followed by Louisiana.

Discussion

This analysis supports the potential designation of stock subpopulation structure with a boundary near the Mississippi River, as has been historically done in the red snapper stock assessment. The precise latitudinal barrier to dispersal identified by the analysis (i.e. minimizing larval exchange between regions) was 89.35° W, and this was corroborated by multiple sensitivity analyses of oceanographic models. Although 89.35 degree West was identified as the absolute minimum in both models, the curves are relatively flat in the longitudinal range of approximately 89.5° W and 89.0° W, and selection of any specific boundary within this range is likely to be functionally equivalent. For any stock subpopulation boundary near the Mississippi River, larval transport among regions is estimated to be less than 2% of the spawning production. A second local minima indicating a biophysical barrier to dispersal was also observed at the boundary of the Florida Panhandle and Big Bend regions. However, setting a subpopulation boundary near the Mississippi River minimizes nearly all of the cross-subregion larval transport, and designation of a second barrier has little additional benefit in terms of separating out functionally different regions with respect to spawning and recruitment dynamics.

The results obtained here are a function of large-scale oceanographic current patterns, larval OVM behavior, and the shelf bathymetry, which in turn drives the overall distribution of red snapper spawning biomass. Because larvae tend to settle close to where they were spawned, areas with less spawning biomass overall are more likely to act as effective barrier to dispersal. Due to a narrow shelf along the coast of Mississippi and slightly reduced relative biomass (Karnauskas et al. 2017b), only 1.3% of the total egg production is estimated to be sourced from within Mississippi waters. Low egg production combined with the findings that Mississippi acts as a source location rather than a receiving (i.e., dispersing many of its larvae and not attracting larvae from other locations, Fig. 2) confirms that the region effectively serves as a primary dispersal barrier for East and West spawning dynamics.

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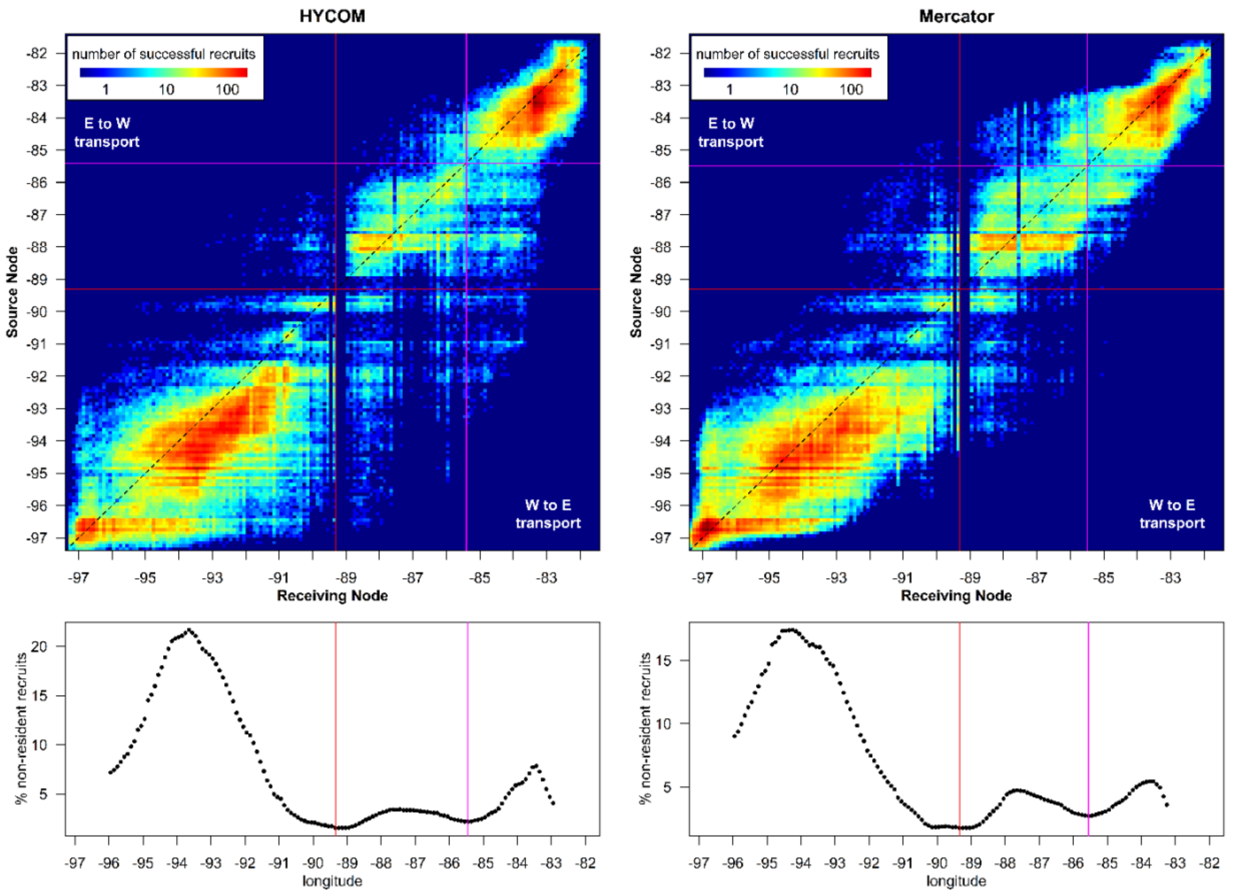


Figure 1. Top panels: Connectivity matrix for the base model run, averaged across all years, for the HYCOM model (left) and Mercator model (right). Rows are source nodes (particle release sites) and columns are receiving nodes (particle settlement sites); nodes are ordered according to longitude from Texas to Florida. Self-recruitment is indicated by the dashed diagonal line. Red line indicates primary break in population substructure as identified by the iterative analysis; pink line represents the secondary break. Bottom panels: Percentage of non-resident recruits as a function of respective boundary, set from 96 degrees W to 83 degrees W at intervals of 1/10 of a degree. For each respective cutoff, the percentages equate to the sum of values in the upper left and lower right boxes of the connectivity matrix, divided by the total number over the entire matrix. Red and pink lines again denote the primary and secondary breaks.

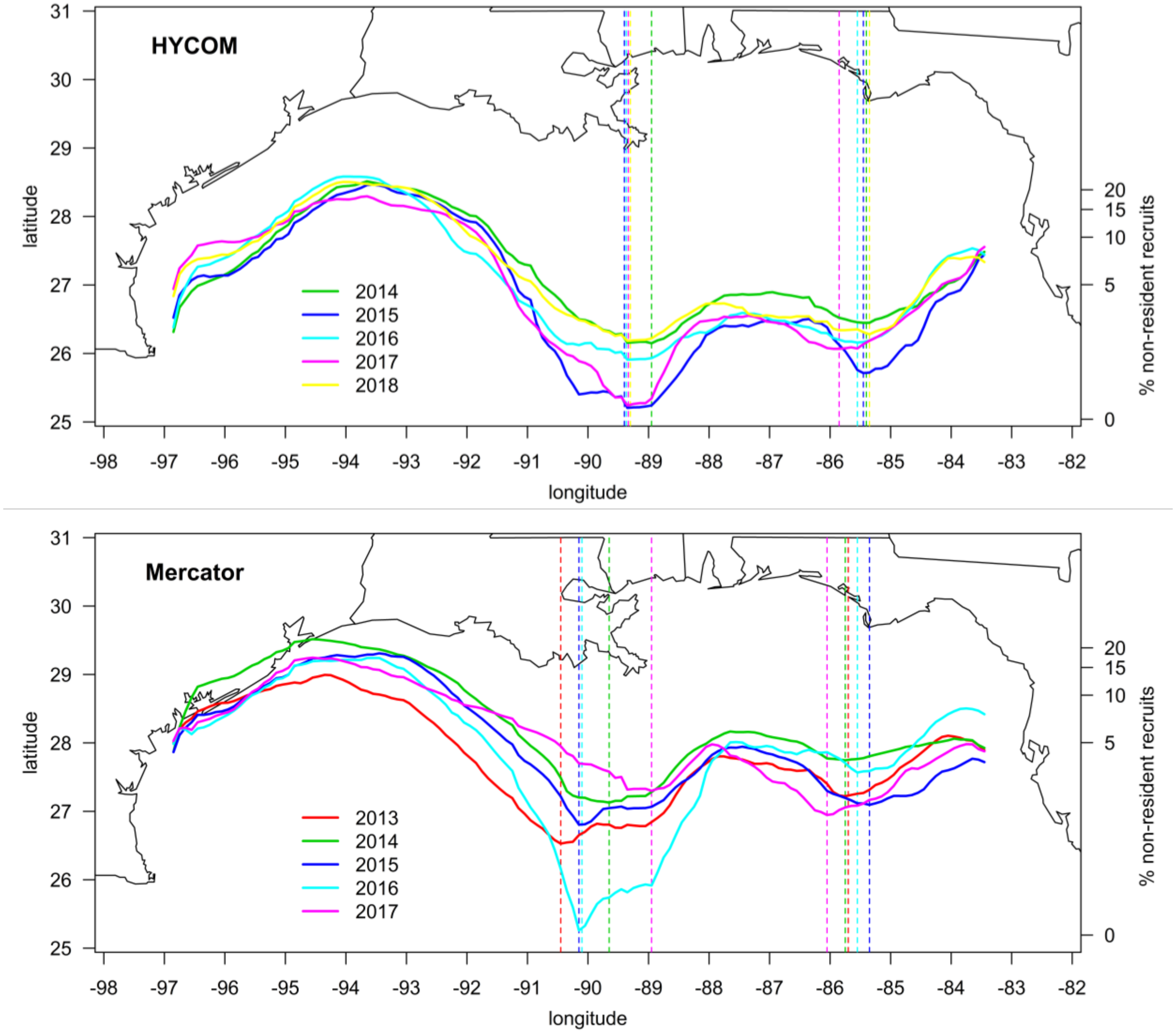
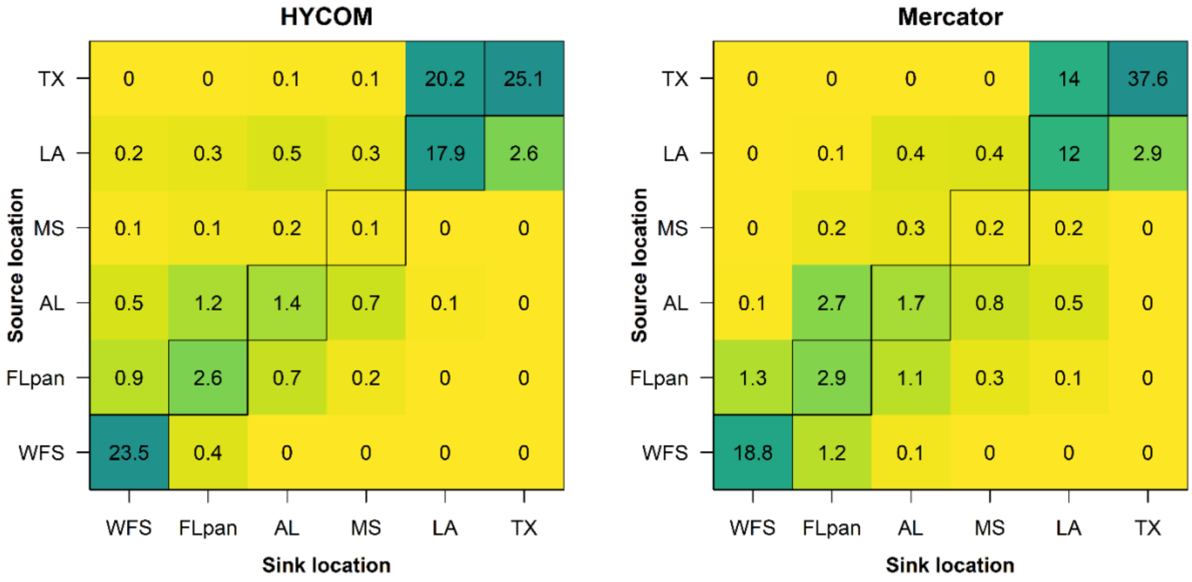


Figure 2. Same values as in Figure 1 bottom panel, but reported separately by year. Curves in different colors are the percentage of non-resident settlers for each respective latitudinal cutoffs from 97 degrees W to 83 degrees W, for each of five simulated years (note log scale; refer to right axis). Vertical dotted lines denote the two local minima identified for each individual year. Values are plotted on a map of the Gulf coastline with the same longitudinal axis for ease of interpretation.



HYCOM

Source location	WFS	FLpan	AL	MS	LA	TX
TX	0	0	0.1	0.1	20.2	25.1
LA	0.2	0.3	0.5	0.3	17.9	2.6
MS	0.1	0.1	0.2	0.1	0	0
AL	0.5	1.2	1.4	0.7	0.1	0
FLpan	0.9	2.6	0.7	0.2	0	0
WFS	23.5	0.4	0	0	0	0

Mercator

Source location	WFS	FLpan	AL	MS	LA	TX
TX	0	0	0	0	14	37.6
LA	0	0.1	0.4	0.4	12	2.9
MS	0	0.2	0.3	0.2	0.2	0
AL	0.1	2.7	1.7	0.8	0.5	0
FLpan	1.3	2.9	1.1	0.3	0.1	0
WFS	18.8	1.2	0.1	0	0	0

Figure 3. Connectivity matrices, summarized at the state boundary scale, for two different oceanographic models (HYCOM left; Mercator right). Source locations for each respective state appear as rows and settlement locations for each state appear as columns; the diagonal boxes outlined in black denote self-recruitment. For example, both models show that larval supply from TX to LA is much greater than supply from LA to TX. Greener shades indicate higher levels of relative recruitment; numbers in boxes are 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%).