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Decadal analysis of larval connectivity from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling

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ABSTRACT: Variability in environmental conditions and ocean currents can influence population connectivity and the exchange of larvae among locations. This is especially true for species that spawn in aggregations during a limited temporal window, such as many of the commercially and ecologically valuable species of snapper (Lutjanidae) in Cuba. Biophysical modeling has been used for over a decade to describe the pelagic pathways, sources, and sinks of lutjanid larvae. Here, we build on earlier studies by incorporating more advanced modeling techniques, higher resolution oceanography, and an expanded temporal scope using circulation from 2004 to 2013. Our goal was to revisit the relative linkages of Cuban snapper larvae among regions of the Cuban shelf and neighboring countries by investigating their interannual variability and spatial patterns. Biophysical simulations suggest the majority of larvae produced from snapper spawning aggregations are retained on-island, often within the region where they were spawned, with the exception of an aggregation in northwest Cuba. We used multinomial logistic regression to identify consistency in patterns of simulated biophysical larval transport, and to determine the number of years of simulation required to approximate connectivity. The best fit model correctly identified major connections from each spawning location to greater Caribbean destinations for each species. However, connections at smaller spatial scales were less predictable, and variance increased if fewer years of larval transport were considered. While the magnitude of settlement varies annually, the spatial arrangement of connectivity is relatively consistent such that modeled pathways from spawning aggregations can effectively inform connectivity planning, such as the placement of spawning reserves.

KEY WORDS: Lutjanidae · Snapper · Larval dispersal · Connectivity · Cuba · Biophysical modeling · Spawning aggregation

INTRODUCTION

The species of Lutjanidae (snappers) comprise one of the most globally important reef-associated fishery resources in tropical and subtropical areas (Allen 1985). Snappers are the largest reef fishery resource in Cuba (Claro et al. 2009) on the largest insular shelf system in the Caribbean. Commercial catches of all snapper species in the 1970s reached over 7500 metric tons (mt) annually. Many species of western Atlantic snappers can migrate during their life-history stages across the shelf from seagrass and mangrove to reef habitats of the Greater Caribbean (Stark 1971, Aiken 1993, Nagelkerken 2009) and can also move

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across the shelf as adults during shorter-term spawning migrations (Stark 1971, Sadovy & Colin 2012). Many factors have negatively affected snapper populations in Cuba, such as the fishing harvest of migrating pre-spawners and spawners at aggregation sites (Claro & Lindeman 2003).

A noticeable decline in snapper populations began in the mid-1970s with overfishing of lane snapper *Lutjanus synagris*, and later mutton snapper *L. analis*, gray snapper *L. griseus*, and yellowtail snapper *Ocyurus chrysurus* (Claro et al. 2001). As a result, fishing efforts decreased by the 1990s. Over the last 30 yr, commercial snapper catches in Cuba have fluctuated between 3500 and 4500 mt annually, decreasing to between 2370 and 2700 mt during 2010, 2011, and 2012 (the last years with reported data). Even factoring in recreational and subsistence catches of more than 2000 mt yr^{-1} (Claro & Lindeman 2008), the Cuban snapper fishery is at a fraction of its 1960 and 1970 levels, due in large part to overfishing of spawning aggregations of major fishery species, such as mutton and lane snapper (Claro et al. 2009).

Most marine fish, including snappers, have a complex life cycle that includes dispersion during a distinct larval phase that can facilitate long- or short-distance dispersal and population connectivity. Variability in environmental conditions and ocean currents may limit or increase potential population connectivity (Snyder et al. 2014). This especially applies to species such as many lutjanids that spawn in aggregations over a limited temporal window (Sadovy & Colin 2012, Kobara et al. 2013). Much progress has been made in empirically tracking connectivity using methods such as chemical tagging and parentage analysis (e.g. Jones et al. 2009); however, such logistically expensive techniques cannot yet explore year-to-year larval exchanges over large temporal and spatial scales.

Biophysical modeling is a tool that is useful for describing the pelagic pathways, sources, and sinks of larvae of many dispersing marine organisms. Lagrangian stochastic models of larval transport probabilistically predict connectivity, and provide ecological insight (Werner et al. 2007) and valuable data for marine protected area (MPA) design and fishery management (Botsford et al. 2009, Pelc et al. 2010). However, early life history dispersal and recruitment patterns are subject to high variability (Werner et al. 2007, Sponaugle et al. 2012). The resulting changes and year class variations at an ecosystem level remain an enduring focus in fisheries science (Hjort 1914). Oceanographic features such as eddies (Paris et al. 2007), along with environmental factors like temperature (Feng et al. 2011), and ecological elements such as interspecific competition and predation (Bakun 1996) all combine to variably affect larval dispersal and settlement. These factors may lead to seemingly stochastic pulses of settling larvae through time in idealized simulations (Siegel et al. 2003, Harrison et al. 2013), which may be important for the dynamics of relatively long-lived species such as snapper and grouper. For example, the storage effect (Warner & Chesson 1985) for these species may result in particularly successful year-classes dominating a fishery, and allow for enhanced coexistence in coastal environments with limited habitat.

One modeling framework, the Connectivity Modeling System (CMS), published as an open-source code by Paris et al. (2013), has been used for over a decade to probabilistically describe larval connectivity (Paris et al. 2005, Cowen et al. 2006). The realistic performance of CMS, coupled with ocean circulation models of varying resolutions, has been verified to accurately forecast subsea oil plume transport and its surface expression (Le Hénaff et al. 2012, Paris et al. 2012), to project time series of larval settlement (Sponaugle et al. 2012, Kough et al. 2013), and to improve the projections of recruitment indices in fisheries (Karnauskas et al. 2013). The computing power and publicly accessible resources available to the scientific community have grown, as have the number of studies that use similar coupled biophysical modeling techniques (Miller 2007, Peck & Hufnagl 2012). Reproducibility is the gold standard of peer-reviewed literature, yet the continuous improvement of modeling tools has hindered repetition as the models and questions change from year to year.

In this study, we revisited and expanded on a decade-old study of larval transport from Cuban snapper aggregations (Paris et al. 2005), using greater temporal scope, an evolved biophysical modeling framework that includes ontogenetic vertical migration in 3D currents, and near real-time access of regional and global ocean prediction systems. We expanded the probabilistic connections from Cuban snapper spawning aggregations, from a single year in Paris et al. (2005) to a decade in this study. We followed the prior protocol for spawning locations, magnitudes, and lunar periodicity with higher-resolution and data-assimilated circulation models over a greater time span. Our major ecological goals were to describe (1) the relative linkages among and between Cuban regions and neighboring countries for the nation's most important fish family, and (2) the annual variability and consistency of these linkages. In answering these questions, we also evaluated how many years would be required to assess connectivity and describe the scales of retention for Cuban snapper — fundamental information required for conservation planning in Cuba and its neighboring countries.

MATERIALS AND METHODS

Physical parameterization

We used a coupled biophysical Lagrangian stochastic model of larval transport (CMS open-source v.1.69; Paris et al. 2013) to simulate snapper spawning from aggregations around Cuba along with the modeled transport of eggs and larvae. CMS is a probabilistic, individual-based model that uses a tricubic interpolation of the physical fields and a fourth-order Runge-Kutta temporal and spatial integration scheme to advect particles offline with high fidelity, using an array of nested general ocean circulation models (Paris et al. 2013). Specific parameters for the simulation are provided in Table 1. Horizontal and vertical diffusivity were included to account for subgrid scale turbulent diffusion (Okubo 1971, Polzin et al. 1997). We used the navy coupled ocean data assimilation (NCODA) assimilated Gulf of Mexico (GoM) Hybrid Coordinate Ocean Model (HYCOM) with a horizontal grid of 1/25° (ca. 4 km) and interpolated 40 *z*-layers in the vertical. These layers included 5 m layers to 30 m, and 10 m layers from 30 to 100 m, the maximum vertical distribution of snapper larvae (D'Alessandro et al. 2010). GoM–HYCOM was nested offline within the NCODA data assimilated global HYCOM with a 1/12° grid (ca. 7 km), a CMS feature that allows seamless tracking of larvae moving across the boundaries of models with different grid sizes (Paris et al. 2013). These ocean circulation models (Bleck 2002, Chassignet et al. 2007) are publicly available (https://hycom.org/dataserver/) and have been widely used in biophysical studies of larval dispersal. We used hydrographic data from 1 January 2004 through 31 December 2013; thus, the current study spans a decade.

Biological parameterization

The CMS couples the hydrodynamic model to a stochastic Lagrangian framework where individual variability is introduced by drawing particles' attributes at random from species-specific distributions of traits (Paris et al. 2013). We examined dispersal for 5 snapper species in Cuba: *Lutjanus synagris* (lane), *L. analis* (mutton), *L. jocu*, *L. griseus*, and *L. cyanopterus* (dog-gray-cubera complex). The dog-gray-cubera complex was grouped because they often share spawning aggregation sites and times (Paris et al. 2005). These species form major spawning aggregations around Cuba, spawn at different times of the year, and can spawn during different phases of the lunar cycle (Claro & Lindeman 2003). In our CMS simulation, each spawning event released 6000 particles over an 8 d period in accordance with the lunar

Table 1. Connectivity Modeling System (CMS) parameterization. HYCOM: hybrid coordinate ocean model; NCODA: navy coupled ocean data assimilation

Module	Parameter	Input
Physical	Ocean circulation, nest 1	HYCOM Global + NCODA assimilated
Physical	Ocean circulation, nest 2	HYCOM Gulf of Mexico expt 30.1
Physical	Horizontal diffusivity, nest 1	15 $m^2 s^{-1}$
Physical	Horizontal diffusivity, nest 2	8 $m^2 s^{-1}$
Physical	Vertical diffusivity, nests 1, 2	0.05 $m^2 s^{-1}$
Physical	Time step	45 min
Physical	Tracking time	40 d
Physical	Time span	2004 through 2013
Biological	Competence	25 d
Biological	Habitat site size	8 × 8 km
Biological	Habitat site numbers	3202 reef polygons
Biological	Ontogenetic vertical migration	Enabled, species specific (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m550p175_supp/)
Biological	Release pattern	8 d decaying after each spawning peak
Biological	Release magnitude	6000 distributed over each spawning event

schedule for each species specified in Paris et al. (2005), and following information on the reproductive physiology of Cuban snapper populations in García-Cagide et al. (2001). The amount of virtual larvae that were released decreased from a peak as per the previous study (Day 1: 1800; Day 2: 1200; Day 3: 1080; Day 4: 840; Day 5: 540; Day 6: 300; Day 7: 180; Day 8: 60).

In this model, each species also exhibited an ontogenetic vertical migration (OVM) scheme following available ichthyoplankton information (D'Alessandro et al. 2010) (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m550p175_supp/). In the previous work, coastal retention was simulated over a range of temporal periods based on observed larval retention patterns (Paris & Cowen 2004), yet specific vertical migration schemes could not be incorporated because the model that was used (Miami Isopycnic Coordinate Ocean Model) did not have multiple depth levels within the mixed layer (Paris et al. 2005, Cowen et al. 2006). The higher vertical resolution HYCOM models allow the addition of OVM, which is a clear improvement and a step towards more realistic modeling of larval transport. In this study, snapper larvae were competent to settle at 25 d of age and could be transported for up to a maximum pelagic larval duration (PLD) of 40 d (e.g. reviews in Denit & Sponaugle 2004, Lindeman et al. 2006).

Snapper utilize multiple marine habitats during their life cycle. Most of the species we included in the present study are known to settle in seagrass or shallow reef habitats. In the previous work by Paris et al. (2005), settlement habitat was modeled as a 9 km buffer around Caribbean coral reefs and segmented into 4 Cuban regions and 8 other Caribbean nations, resulting in a total of 12 habitat polygons. Despite this coarse resolution of settlement habitat, it was the first inclusion of larval movement behavior in response to modeled habitat cues in any biophysical model. Here, we increased the habitat resolution with 8 × 8 km habitat polygons located over coral reef habitat throughout the Caribbean (as per Holstein et al. 2014), which is a coarse enough resolution to also encompass adjacent seagrass beds where snapper larvae settle. The 4 Cuban regions — northwest (NW), north central (NC), southwest (SW), and southeast (SE) (Fig. 1) — were comprised of the following number of polygons: NW (n = 85), NC (n = 104), SW (n = 148), and SE (n = 253), which were pooled to quantify regional settlement. Similarly, polygons outside Cuba were pooled by nation and region. Despite these differences, the settlement habitat modeled by both the previous work and this study are conceptually similar and include coral reef and seagrass habitats. Modeled larvae from Cuban spawning aggregations did not disperse beyond the subset of the locations shown (Fig. 1). This assumption was fostered by the habitat data available, and we recognize that snappers may settle further inshore. However, this assumption did not affect the identification of regions at the scale of generic settlement. The region in which the larva settle will not be affected whether settlement occurs on the outer reefs of the coast or further inshore. In addition, planktonic snapper larvae have not been found in samples collected from inshore of Cuban reefs (Dejnik et al. 1966, Guitart 1978, Gutiérrez & Salabarría 1982, Orozco 1983).

Statistical testing

The use of frequentist statistics to assess significance in simulation modeling studies poses a quandary for researchers, as highlighted by White et

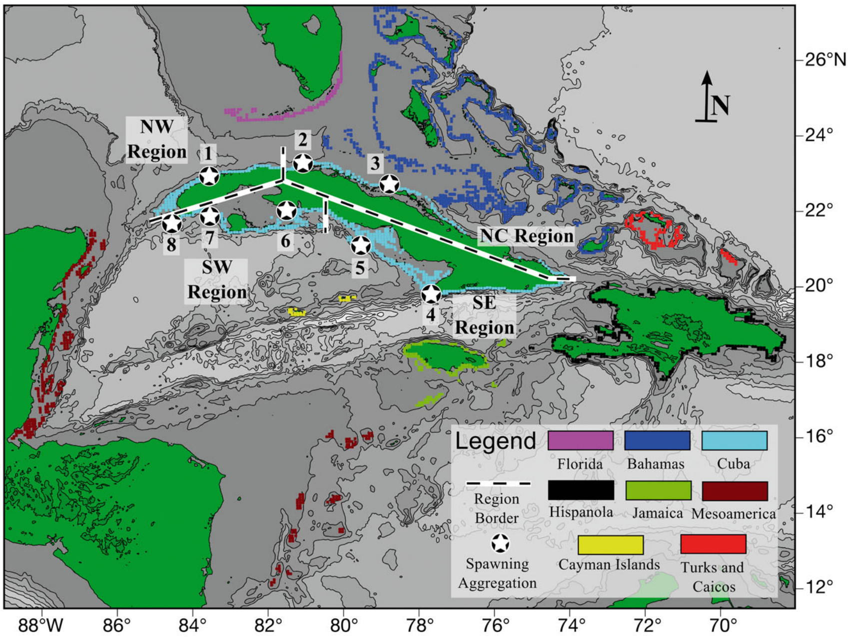

Fig. 1. Snapper *Lutjanus* spp. spawning aggregation sites and larval settlement habitat. Dashed lines delineate four primary Cuban shelf regions: northwest (NW), north central (NC), southeast (SE), and southwest (SW); stars: positions of spawning aggregations (Claro & Lindeman 2003)

al. (2014). In short, we have *a priori* knowledge that our results will be different between spawning locations, species, and years because we parameterized the simulations differently in each case. Furthermore, the ensemble simulation of 3D trajectories (i.e. generated from a large number of individual particles and their attributes) results in high degrees of freedom and small significance thresholds. Therefore, instead of using frequentist-based tests, we used statistical models to describe the relative effect size of different parameters within our simulation and to show predictability (White et al. 2014).

Variability in larval pathways through space and time was examined by modeling their effects on connections. A connection is defined as any probabilistic linkage between source location and a destination (sensu Cowen et al. 2006), whether it is between spawning aggregations or between spawning ecoregions (i.e. location factors on different spatial scales). We used multinomial logistic regression (MNR) to investigate how connections between Cuban ecoregions and throughout the Caribbean were influenced by year, species, and location. Each factor was treated as a nominal category and the output levels were the different destination locations. The categorization of the destination set the spatial scale of the analysis. We used 2 different spatial scales: a Caribbean-wide analysis, which used output levels of Florida, The Bahamas, The Turks and Caicos, Cuba, Hispañola, Jamaica, the Cayman Islands and Mesoamerica (Mexico, Belize, and the Colombian Archipelago combined to increase sample sizes and reach a predictable quantity), and a Cuban analysis, which used output levels of Cuban ecoregions (NW, NC, SE, SW; see Fig. 1). In both cases, the response variable was the amount of larval settlement modeled by the CMS that arrived at each destination.

To identify the best fit, we systematically tested a suite of MNRs built with different combinations of factors. Performance of the MNR was assessed by the residual between 'observed' (CMS) and predicted (MNR) values of settlement to each destination. Each combination of factors was used and ranked based on the calculated residuals. Interactions between different nominal factors would have increased the complexity of the analysis by orders of magnitude and would have rendered a less interpretable result, thus they were not included. The 2 location factors (spawning ecoregion and spawning aggregation) were mutually exclusive in the suite of MNRs, and were not simultaneously included as there was only a single aggregation in NW Cuba, resulting in complete separation of factors.

Predictions change with temporal replication

We used MNR to investigate how the number of years used in a simulation changed the predictions, describing consistency in CMS larval transport through time and the resilience of the probabilistic connections. Our approach was to systematically rebuild the MNR using different combinations of annual settlement. For example, we built the MNR using every possible combination of any 2 years (2004 + 2005; 2004 + 2006; 2004 + 2007 … 2012 + 2013), then every possible combination of 3 years (2004 + 2005 + 2006; 2004 + 2005 + 2007; 2004 + 2005 + 2008 … 2011 + 2012 + 2013), and so forth. Each resulting MNR was then used to predict the settlement destinations of 12 000 larvae (the annual quantity released at each aggregation site), and the variation and means within each year group (i.e. 2 yr, 3 yr, …, *n* yr) were calculated. All statistical analyses were done using MATLAB (MathWorks).

RESULTS

Cuban aggregations: Caribbean connectivity

The biophysical model (see Supplementary animations at www.int-res.com/articles/suppl/m550p175_supp/) shows the relative linkages among and between neighboring countries (Fig. 2), 4 Cuban regions (Fig. 3), and the annual variability of these linkages. Although some snapper originating from Cuban aggregations settled out of the country, most of the modeled settlement was within the Cuban regions. Connections to Mesoamerica (Belize, Mexico), and the Colombian Archipelago were not common, nor were connections to Florida, although each species had at least one spawning location and year in which such connections were possible, if not probable. Settlement to the Bahamas was the second most probable destination from northern Cuban regions (NW and NC), Jamaica was the second most probable destination from the SE, and the Cayman Islands were the second most probable from the SW. Settlement as a percentage of the total larvae released (including advective mortality), rather than the proportion of the total successfully settling larvae to each destination (already shown in Fig. 2), was as follows: from NW Cuba, mean Cuban settlement was 29 % (ranging from 6 to 68 % over years and species), and mean Bahamian settlement was 18 % (4 to 48 %); for NC Cuba, mean Cuban settlement was 50 % (22 to 97 %) and mean Bahamian settlement was 21 %

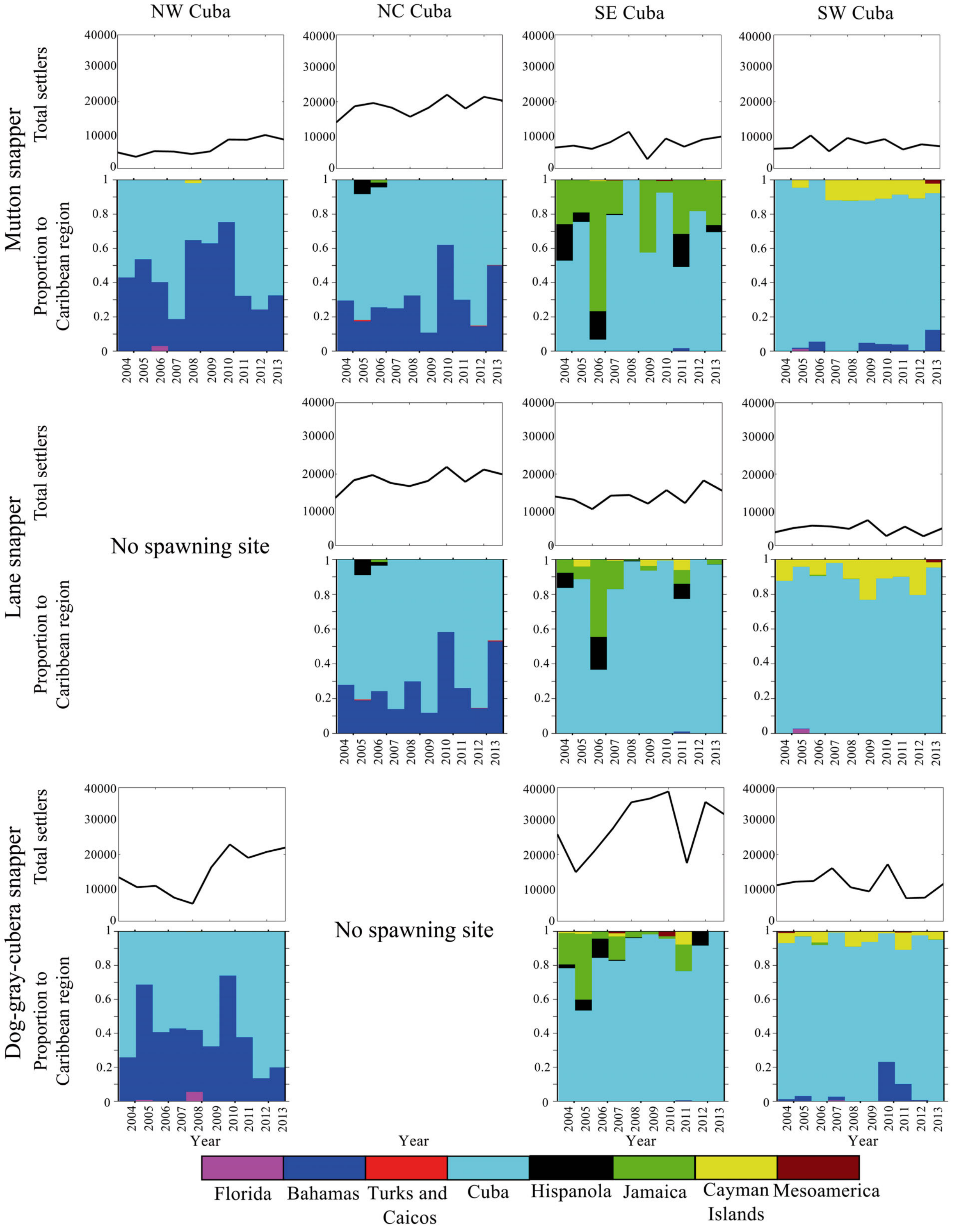

Fig. 2. Snapper larval settlement in Cuba and export from each region of Cuba (NW, NC, SE, and SW; see Fig. 1) to other countries. Line plots show predicted total annual larval settlement for snapper species (mutton, lane, and dog-gray-cubera complex) and spawning aggregations; bar plots show settlement outside Cuba for each country as a proportion of yearly total settlement

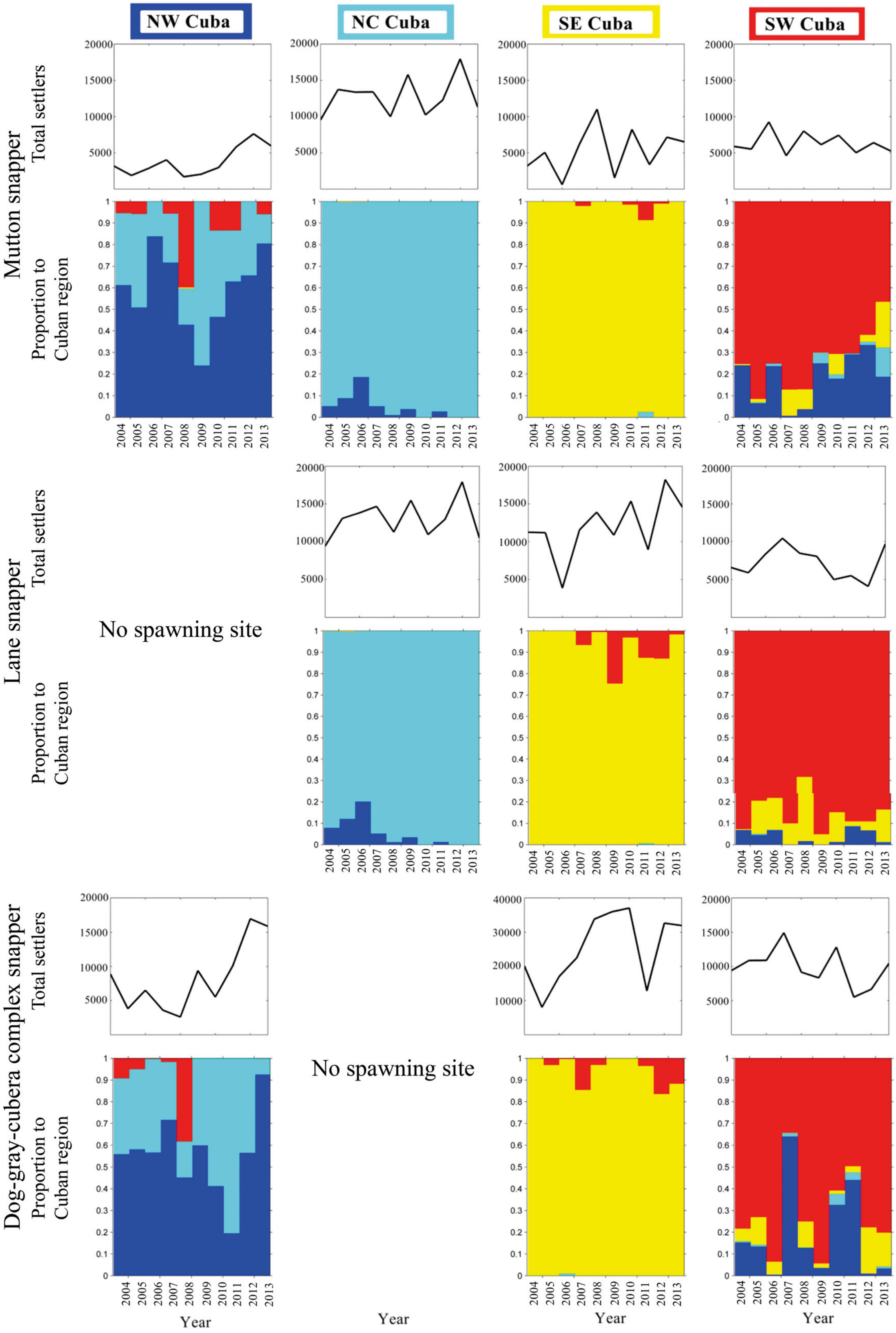

Fig. 3. Modeled snapper *Lutjanus* spp. larval settlement within the 4 Cuban regions (NW, NC, SE, and SW; see Fig. 1). Line plots show total annual settlement for snapper species (mutton, lane, and dog-gray-cubera complex) and group of spawning aggregations. Bar plots show settlement within each Cuban region as a proportion of yearly total settlement

(2 to 60%); for SE Cuba, mean Cuban settlement was 52% (2 to 99%) and mean Jamaican settlement was 6% (0 to 51%); and for SW Cuba, mean Cuban settlement was 35% (6 to 87%) and mean Cayman Island settlement was 3% (0 to 19%).

Cuban aggregations: inter-shelf connectivity

The biophysical model indicated that the primary destination for aggregations within each Cuban ecoregion was habitat within the ecoregion itself. Thus, local retention is important in each of the shelf regions. The region with the lowest amount of local retention was NW Cuba, in which mean local retention was 18% (ranging from 3 to 60% over years and species). For NC Cuba, mean local retention was 48% (18 to 97%); for SE Cuba, mean local retention was 50% (2 to 99%); and for SW Cuba, mean local retention was 28% (4 to 83%).

Multinomial logistic regression: Caribbean

The best fit MNR included the factors spawning ecoregion, species, and year (Table 2). Of the 2 different factors we used for location, spawning ecoregion yielded better results than spawning aggregation. Location was the single most important factor to include in the MNR, as it was featured in the 8 highest-ranked models. Further, the coefficients for location in the best fit MNR were the furthest from zero among all the factors for each destination, again suggesting that location plays the greatest role (Table S1 in the Supplement). The MNR performed best when predicting settlement at destinations with consistently higher amounts of settlement, such as Cuba and The Bahamas (Fig. 4). However, the MNR did not capture changes in year-to-year connectivity in areas that were sporadic destinations. In these cases, the MNR was several orders of magnitude different than the larval transport model, with a trend towards over-prediction of settlement by the MNR (see Fig. 4A). Indeed, the proportions of settlement predicted by the MNR to Florida, the Turks and Caicos, and to Mesoamerica were so small compared to the major connections that these destinations only faintly appear in visualizations (Fig. 5).

The average predictions from the Caribbean MNR indicated that Cuba was the most probable destination for snapper larvae spawning within Cuban aggregations, independent of species or spawning region (Fig. 5). The Bahamas was the second most important recipient of snapper larvae from the northern side of the Cuban archipelago, while other islands (Jamaica, Hispanola, and the Caymans) were more prominent destinations for spawning aggregations on the southern side of Cuba (Fig. 5). The agreement between the biophysical model and the MNR suggests that these are consistent patterns.

Multinomial logistic regression: Cuban connections

The best-ranked MNR included the nominal factors spawning aggregation and year (Table 3). Location (spawning aggregation) was the factor with the largest effect in the MNR (Table S2 in the Supplement). However, the residuals were much greater at

Table 2. Ranking candidate multinomial logistic regression (MNR) models of Caribbean larval snapper *Lutjanus* spp. exchange. Parameterizations of the MNR included combinations of the nominal factors species (3 levels), spawning region (4 levels), spawning aggregation (8 levels), and year (10 levels). Models were ranked to minimize the residuals between the MNR and Connectivity Modeling System (CMS)

Model rank	Species	Spawning region	Spawning aggregation	Year	Sum of residuals	Difference
1	Yes	Yes	No	Yes	368154	–
2	No	Yes	No	Yes	369305	1151
3	Yes	Yes	No	No	380697	12543
4	No	Yes	No	No	382743	14589
5	Yes	No	Yes	Yes	414766	46612
6	No	No	Yes	Yes	418423	50269
7	Yes	No	Yes	No	420503	52349
8	No	No	Yes	No	424064	55910
9	Yes	No	No	Yes	428013	59859
10	Yes	No	No	No	488545	120391
11	No	No	No	Yes	490710	122557

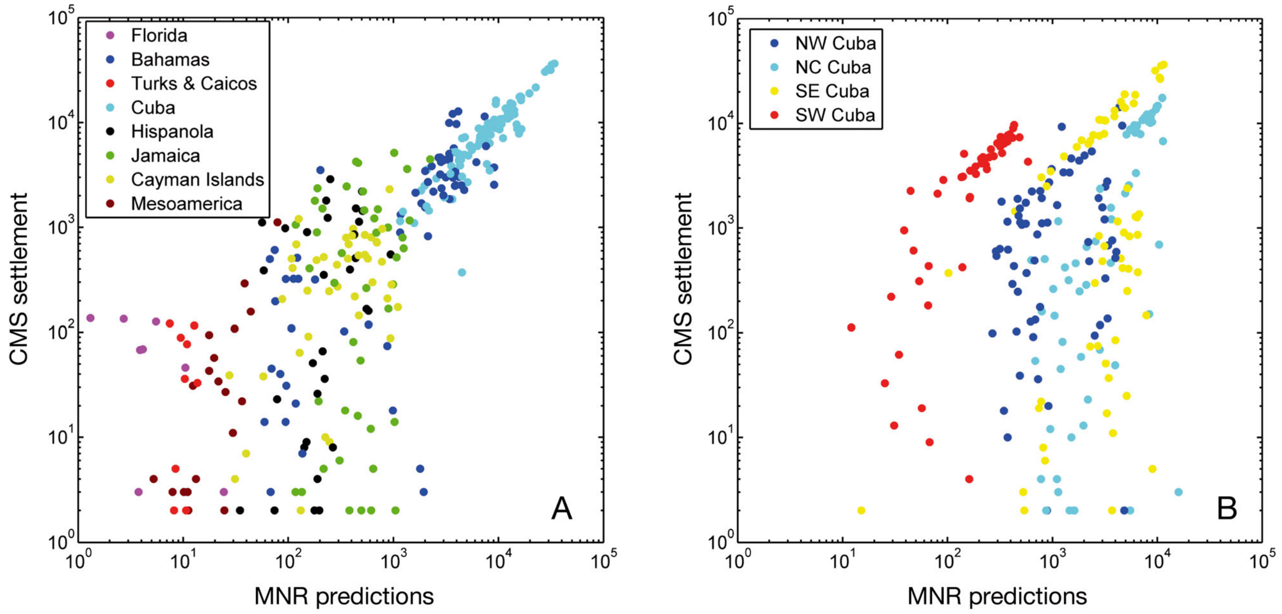

Fig. 4. Predictability of simulated snapper *Lutjanus* spp. settlement originating from Cuban spawning aggregations. Our highest-ranking multinomial logistic regression (MNR) models of larval exchange, within (A) the Caribbean and (B) Cuban regions were built using, and compared to, successful larval settlement from a biophysical transport model (the Connectivity Modeling System; CMS). Colors on the plot represent the destination where settlement occurred

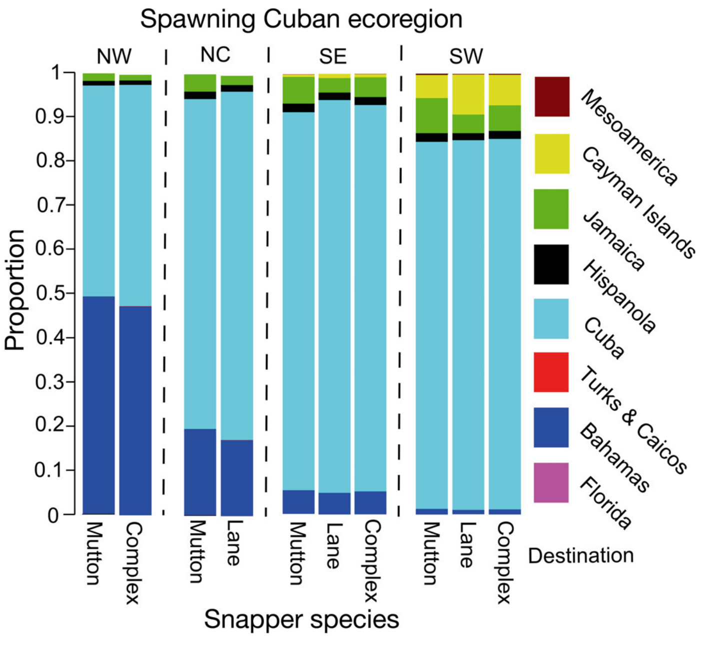

Fig. 5. Mean export of snapper *Lutjanus* spp. to Caribbean countries predicted by a multinomial logistic regression (MNR) model. Proportion of settlement to each Caribbean destination was predicted by the best-ranked MNR, averaged over the 10 yr simulation. MNR included nominal factors species (3 levels), Cuban ecoregion (4 levels), and year (10 levels), and modeled settlement to Caribbean ecoregions (8 levels). Bar plots are grouped to show similarity within Cuban ecoregion (separated by dotted lines, labels at top) and between species (labels at bottom)

the Cuban scale than at the Caribbean scale (Fig. 4). The variable connections that CMS portrayed between the 4 Cuban shelf regions (Fig. 3) were not as apparent or predictable in the MNR. Indeed, the mean proportions of dispersal from each spawning aggregation to each Cuban ecoregion do not appear to visually match those expected based on CMS (Fig. 3) and the residuals in the best-ranked MNR were higher (Table 3). Of particular concern, the connections to NW Cuba were greatly diminished and/or lacking from regions where they were expected (NW and SW Cuba). Further, the probability of connection as predicted by the MNR to both SE and NC Cuba was too high. Indeed, CMS did not show the strong connections predicted by the MNR from NC to SE or vice versa (Fig. 3).

Predictions change with temporal replication

Including more years of simulation resulted in lower prediction variance for all Caribbean destinations except Jamaica (Fig. 6) in a suite of MNRs. In addition, when MNR was parameterized with fewer years of simulation, a year with rare or improbable connections could cause higher variance and an inaccurately high mean (Fig. 6A,C,E,G,H). The converse occurred as well, with a lower probability of dispersal to Cuba and the Bahamas and an increase

Table 3. Ranking candidate multinomial logistic regression (MNR) models of larval snapper *Lutjanus* spp. exchange between Cuban ecoregions. Parameterizations of the MNR included combinations of the nominal factors species (3 levels), spawning region (4 levels), spawning aggregation (8 levels), and year (10 levels). Models were ranked to minimize residuals between the MNR and Connectivity Modeling System (CMS)

Model rank	Species	Spawning region	Spawning aggregation	Year	Sum of residuals	Difference
1	No	No	Yes	Yes	348699	–
2	No	No	Yes	No	349103	404
3	Yes	No	Yes	Yes	356646	7947
4	Yes	No	Yes	No	357198	8499
5	Yes	Yes	No	Yes	499494	150795
6	No	Yes	No	Yes	500327	151628
7	Yes	Yes	No	No	501118	152419
8	No	Yes	No	No	501852	153153
9	Yes	No	No	No	598908	250209
10	Yes	No	No	Yes	600344	251645
11	No	No	No	Yes	608186	259487

in variance when using only a few years of simulation (Fig. 6B,D). An asymptote mean occurred in most cases after only 3 to 4 yr of simulation, suggesting a threshold that would reduce the risk of rare connections artificially increasing predicted probabilities. Further, the mean probabilities of the major connections stabilized after 5 to 6 yr of simulation.

Model comparison

Modeled snapper settled within 9 different countries over the course of a decade, a biologically and oceanographically useful temporal scale. One of our goals was to revisit the biophysical study for the same aggregations as Paris et al. (2005), which was carried out using a single year of the best ocean circulation model available for the region at that date. Here, we address how the new decadal simulations, including more realistic larval behavior, compare to that previous study. The northern spawning sites were primarily connected with Cuba and the Bahamas (Fig. 2), as shown previously. The southern sites contributed snapper larvae to Cuba, but also to the islands in the central Caribbean and some into the Yucatan (Fig. 2). Connections with Nicaragua, Honduras, and Mesoamerica were less common than suggested by Paris et al. (2005), and only came from aggregations on the southern coast of Cuba (Fig. 2). These trends are consistent and appear in the mean connectivity as predicted by the MNR (Fig. 5).

The relative contributions of spawning sites did not correspond with Paris et al. (2005) for mutton or lane snapper. The simulation presented here projected that the mutton snapper aggregations that generate the largest volume of settlement in Cuba per unit spawned would be found in the NC region, not in the SW (Fig. 2). Similarly for lane snapper, the northern aggregations had relatively more successful settlement (Fig. 2). Note that these were data on the proportion of modeled successful settlement, and are not indicative of total possible settlement as they do not take into account the sizes of the spawning aggregations (e.g. the southern aggregations are larger and would generate more eggs, more larvae, and likely more settlement). For the early season spawning dog-gray-cubera complex, the results from the initial model by Paris et al. (2005) are supported here, with the SE aggregations generating the most Cuban settlement relative to spawning production (i.e. number of particles released).

DISCUSSION

The pathways of larval transport between Cuba and its neighboring countries (Fig. 2), and among Cuban regions (Fig. 3) can be predicted with improved consistency (Figs. 5 & 7) using the latest Lagrangian stochastic modeling techniques, such as the CMS (Paris et al. 2013). A decade of simulation using ocean circulation from 2004 through 2013 suggests that the majority of larvae produced from Cuban spawning aggregations are retained on-island, often within the same region where they were spawned. Cuba was the primary destination of settling larvae and the spawning region was the primary destination within Cuba, with the exception of the spawning aggregation in NW Cuba. At this location, Corona de San Carlos, snapper larvae were as likely to settle in the Bahamas

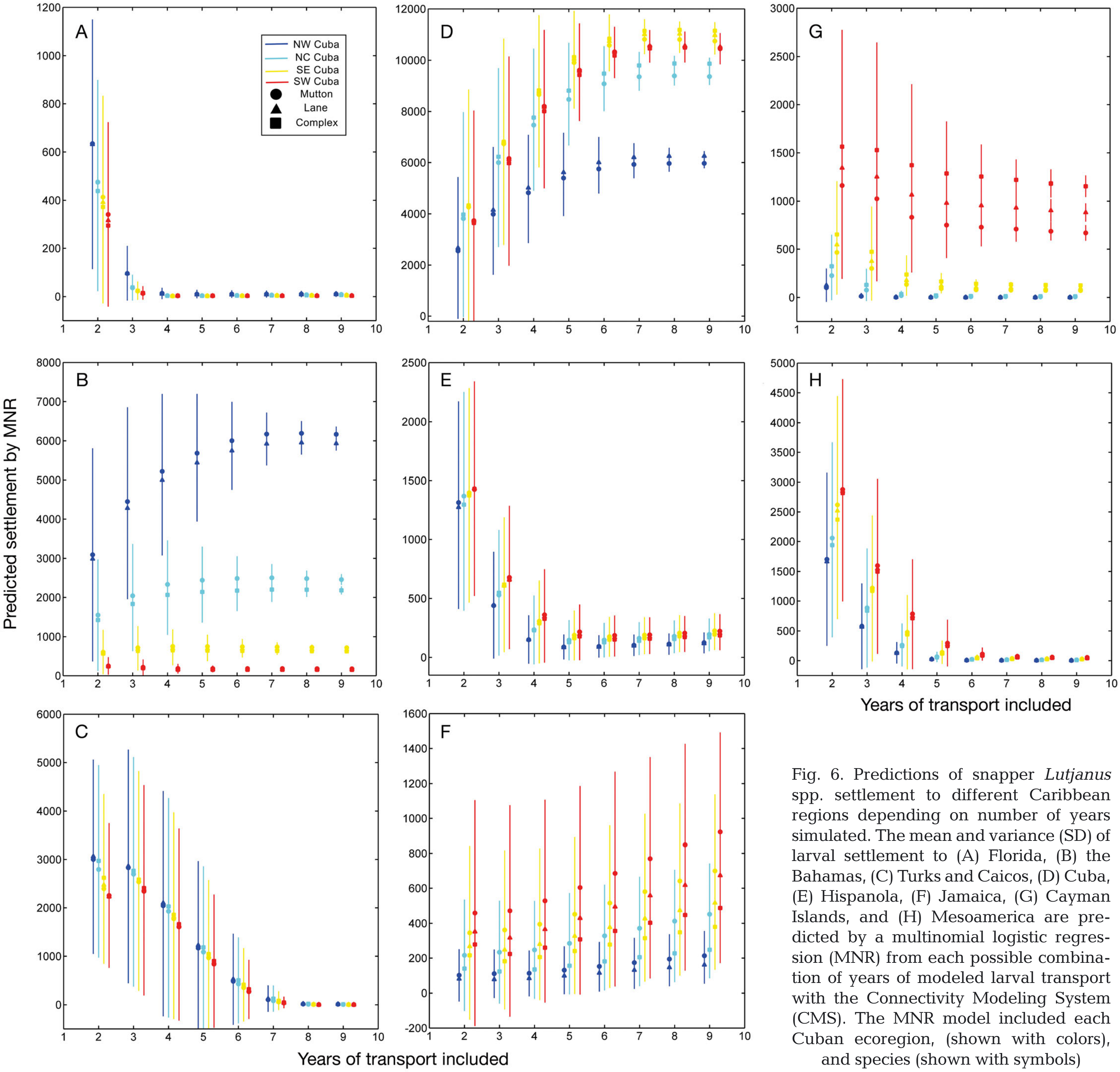

Fig. 6. Predictions of snapper *Lutjanus* spp. settlement to different Caribbean regions depending on number of years simulated. The mean and variance (SD) of larval settlement to (A) Florida, (B) the Bahamas, (C) Turks and Caicos, (D) Cuba, (E) Hispanola, (F) Jamaica, (G) Cayman Islands, and (H) Mesoamerica are predicted by a multinomial logistic regression (MNR) from each possible combination of years of modeled larval transport with the Connectivity Modeling System (CMS). The MNR model included each Cuban ecoregion, (shown with colors), and species (shown with symbols)

as in Cuba. Larval transport modeling suggests that connection with settlement areas in the United States and Mesoamerica from Cuban spawning aggregations is possible, but not likely. Overall, the patterns of larval dispersal from Cuban spawning aggregations suggest support for management policies that recognize considerable intra-region connectivity.

Consistency in connection pathways

We used MNR to assess consistency in the spatial probabilities of exchange from Cuban ecoregions to other Caribbean nations and within Cuba. The dynamic currents shaping dispersal patterns caused high variability in projected settlement magnitude,

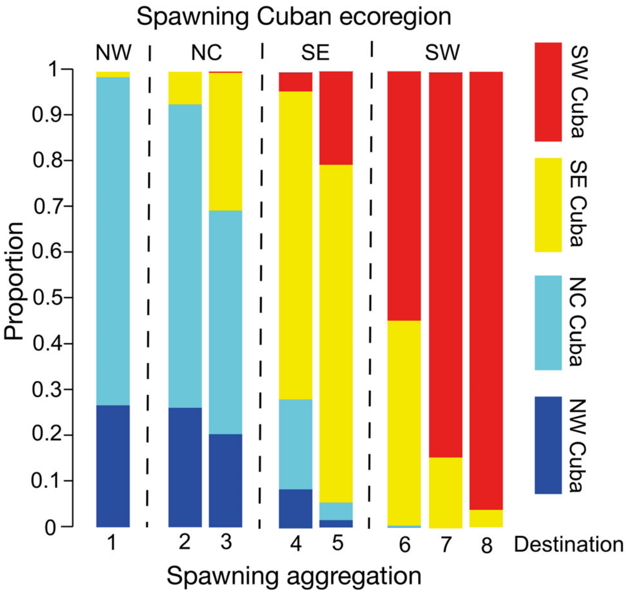

Fig. 7. Mean larval snapper *Lutjanus* spp. exchange within Cuban ecoregions (NW, NC, SE, and SW; see Fig. 1) predicted by a multinomial logistic regression model (MNR). The proportion of Cuban settlement to each ecoregion was predicted by the best-ranked MNR and averaged over the 10 yr simulation; MNR included nominal factors spawning aggregation (*x*-axis, 8 levels) and year (10 levels), and modeled settlement to Cuban ecoregions (4 levels)

yet connections were highly predictable. On broader scales (Caribbean-wide dispersal), our MNR results suggest that the proportion of spawned larvae reaching major settlement destinations outside Cuba can be predicted for each Cuban shelf region (Fig. 4A). However, the linkages between individual spawning aggregations and Cuban ecoregions were not as clearly supported by MNR predictions. Thus, ensemble biophysical simulations using repeated spawning seasons become more important as the spatial scales of connections are reduced. These results further suggest that spawning periodicity controls spatial connections (Kough & Paris 2015) and that storage effects may indeed be important for species that aggregate to spawn over short periods of time.

Variability in the northwest Caribbean Sea on both seasonal and annual cycles can affect settlement success and larval pathways (Qian et al. 2015); thus, it is not surprising that connection pathways are not identical in every year (Figs. 2 & 3). Despite variability in the Caribbean currents, it is possible to project larval settlement when both adult spawning strategy and larval traits are encoded (Sponaugle et al. 2012, Kough et al. 2013). Here, our results show consistency and demonstrate predictability in the destinations of modeled larval dispersal (Figs. 2–4), but not in magnitude, similar to Sponaugle et al. (2012). We recognize that even a time series spanning 10 yr is not long enough to capture any number of physical oceanographic variations at annual and multi-annual scales. Such variations could have multiple effects on biophysical features of connectivity that could impact the survival of eggs, early larvae, and late larvae. This suggests that additional iterations of this work could have value at 5 to 10 yr intervals.

Few studies have compiled data on modeled larval connectivity over ocean basin and decadal scales. James et al. (2002) used a 20 yr simulation of depth-integrated currents (i.e. 2D transport) to model idealized reef fish larval transport around the Great Barrier Reef and noted high inter-annual variability in self-recruitment, suggesting that connectivity predictions should be based on replicated spatial and temporal estimates. In the Baltic Sea, Berglund et al. (2012) assembled a 25 yr time series of modeled Lagrangian larval oyster connectivity to optimize MPA placement. At least 10 yr of connectivity were required to place MPAs as well as the average network from the full experiment (Berglund et al. 2012). Our findings further underscore the importance of extended temporal replication in larval connectivity modeling by showing how the mean and variance of linkages decreased as more years of simulation were included (Fig. 6). As a compromise between overweighting rare dispersal events and properly including consistent trends, at least 5 yr of biophysical modeling should be performed to minimize prediction variances (Fig. 6).

Species-specific use of spawning sites, spawning times, and ontogenetic vertical migrations combine to retain most larvae within Cuban waters, despite current variability. Those species with spawning aggregations may experience more variability in dispersal over their life histories, due to periodic seasonal events such as tropical storms or hurricanes, making biological traits an important control over uncertain dispersal (Snyder al. 2014, Donahue et al. 2015). Different conditions can cause the relative success or decline of different age-classes of the same species at the same sites (Bolle et al. 2009). These changes can be attributed to factors including population cycles, growth conditions, and post-settlement processes (van der Veer & Witte 1999). Therefore, variability in the environment and the ecology of a species, especially during early life history, can cause cohort resonance (Botsford et al. 2014). Our model focused exclusively on larval transport and did not include post-settlement or other demographic processes. However, it is notable that the process of larval dispersal from Cuban aggregations was consistent between years, especially since other studies have suggested stochasticity driving connectivity in less-complicated current systems, such as on the west coast of the United States (Siegel et al. 2003, Harrison et al. 2013). Given the PLD of snapper and the spatial scales of the majority of our connections, it is likely that the species using spawning aggregations in Cuba in this study select for mesoscale and sub-mesoscale features as in other systems (Karnauskas et al. 2011, Vaz et al. 2013, Donahue et al. 2015).

Model comparisons

This study updated and reinforced most findings of the biophysical model used in Paris et al. (2005) to describe Cuban snapper spawning aggregations. That earlier work did not have the capacity of 3D ocean circulation models (and thus vertical larval movements), yet still captured many of the same patterns. Indeed, without access to the vertical resolution of the currents, Paris et al. (2005) took a pattern-oriented modeling approach (POM; Grimm et al. 2005) to simulate larval retention mechanisms observed over scales of 15 to 20 km due to downward migration of larvae within stratified currents (Paris & Cowen 2004). They further carried out sensitivity analyses on the timing of the mechanism throughout the larval duration and on the distance from suitable settlement habitat from which retention could occur. Their probabilistic simulations produced both the major connections and the divisions between regions evident in the advanced replicates presented here. Overall, we found that most predicted connections from that initial work remain plausible, but that dispersal into Mesoamerica is less probable according to our more analytically advanced results from a longer time series. In addition, we used a PLD range that included an upper estimate of 40 d for the species (Denit & Sponaugle 2004). Incorporating a longer PLD and not directly imposing mortality rates is a more conservative approach to projecting retention because it expands the potential dispersal kernel of the modeled larvae. Mortality is often calculated as a rate over time; thus, a longer PLD in the absence of mortality could facilitate highly improbable distant connections at the maximum PLD. Our results showed no spatial difference in the distribution of larval ages (i.e. the locations where larvae arrived early were the same as those where the larvae arrived late; see Fig. S3 in the Supplement at www.int-res.com/articles/suppl/m550p175_supp/), suggesting that including a mortality rate would not remove these connections. These modifications compared to Paris et al. (2005) are notable, in that we still saw high within-archipelago retention, reinforcing our results in regards to the scales of retention. We also found that each Cuban region exchanged larvae with at least one other Cuban region for each of the species, though most of the settlement into each region originated from spawning within that region. This demonstrates that place-based and other management actions are relevant at both within- and between-region scales inside Cuba.

Potential implications for management

The placement and effectiveness of existing Cuban MPAs and other management tools relative to major spawning aggregation areas is of considerable interest, and is complicated by the sheer number of aggregation sites, species, managed areas, and underlying bio-physical complexity. Only 2 of the spawning sites examined were within Cuban MPAs, but long-term effectiveness is uncertain since heavy fishing pressure occurs on pre-spawning, migratory individuals before they enter areas that are nominally protected. These questions are highly complex, not uniform across regions, and require additional study. To illustrate, the 4 Cuban regions we examined are considered below in terms of aggregations, prominent species connectivity patterns, and current management tools.

The 3 spawning sites examined in SW Cuba, the region with highest catches of lane snapper, showed high levels of local retention within-region, but the sites were distant (e.g. more than 200 km between Cayo Corrientes and Cayo Diego Perez), and there were substantial differences among site geomorphology and circulation. Some larvae from Cayo Corrientes and Cayo San Felipe probabilistically advect to the NW region of Cuba, the Bahamas, and Florida — relatively more than from Cayo Diego Perez on the east side of the large Golfo de Batabano. In addition, fishery statistics (Ministerio de Industria Pesquera unpubl. data) show large differences in the sizes of spawning aggregations for lane snapper (e.g. nominally very high in Diego Perez, few in San Felipe, and none in Cayo Corrientes); all of these areas require more detailed surveys. The spawning site at Cayo Corrientes is within the Peninsula de Guanahacabibes National Park, but pre-spawning mutton snapper are fished outside while migrating to the spawning site. The MPA has some enforcement, which may help to maintain the population size in the western part of the region. An important diving resort, Maria la Gorda, is near the spawning site and helps reinforce spawning protections.

In SE Cuba, which is the second most important region for lane snapper (800 to 1000 mt in the 1950s to 1970s, approximately 250 to 400 mt more recently; Claro et al. 2009), the 2 spawning sites studied showed high levels of local retention within the source region. The spawning site at Cabo Cruz is close to, but not inside the Desembarco del Gramma National Park. This is one of the most important spawning sites for lane snapper in the region. Protection of spawning aggregations at this site may be fundamental for the maintenance of lane snapper in this area, due to the absence of known aggregations of this species that could similarly replenish the region. Dispersal could also be international, to SW Cuba and, notably, to countries south and east of Cuba, such as the Cayman Islands and Jamaica. Considering that the shelf area of these islands is relatively small and that lane and mutton snapper populations are quite large in the SE region of Cuba, the export of larvae from Cuba may be important in maintaining some populations of snapper species in these countries.

On the NC coast (the region with the highest catches of mutton snapper), the spawning site at Cayo Caimán is within the recently created Los Caimanes National Park. However, several snapper species are heavily fished during migration to the spawning site while still outside the reserve. Further to the east, Cayo Mono near Punta Hicacos is an important spawning site for mutton snapper. As with most spawning aggregations in Cuba, the site is heavily fished. Both of these NC sites showed high recruitment within the source region and also considerable recruitment to NW Cuba and the Bahamas. The primary known aggregation site in NW Cuba, Corona de San Carlos, showed intermediate recruitment within its source region with some transport to the Bahamas and Florida, and also to SW Cuba via the Cuban Countercurrent, south around Cabo San Antonio. This site is not protected outside of catch quotas and size limits, which are probably not highly effective.

For all regions, temporal closures of primary aggregation sites before and during peak spawning seasons may also be effective and deserve management consideration. This conclusion reached in Paris et al. (2005) with a single year simulation is reinforced by using varying oceanographic regimes and finding that regional self-recruitment still rules.

CONCLUSIONS

Ocean currents are dynamic, with annual and climatic cycles — yet most fisheries management plans are not. Biophysical modeling can identify and scale consistency in larval transport patterns, identify resilience in connections, and appropriately describe population processes that are relevant for conservation and management (Karnauskas et al. 2013). Even when ocean circulation models are available for only short or non-ideal lengths of time, biophysical modeling can provide an important first look at dispersal that can be examined later through complementary techniques and/or over an expanded temporal scale. Revisiting this system in the future as higher resolution circulation models and specialized ichthyoplankton datasets become available will be important to further validate our results. This study offers further support for integrating biophysical models of larval dispersal that take into account adult spawning strategies and larval traits and behavior into research on the ecology and management of marine organisms. Our work reinforces initial findings that settling larvae from Cuban snapper spawning aggregations are largely retained within Cuban regions. While the magnitude of settlement varies annually, the spatial arrangement of major patterns of connectivity is relatively predictable and consistent; thus, management plans can be improved in these systems by including modeled connectivity pathways from spawning aggregations.

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