

Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling

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ABSTRACT: The potential linkages among Cuba and geographically associated northwestern Caribbean locations were examined through simulated transport of snapper larvae for 5 harvested snapper species. The analyses are based on a coupled biophysical model incorporating realistic, intra-annual varying currents from a single year (1984), a Lagrangian stochastic scheme, and larval behaviors to find settlement habitat. Sequential runs centered on peak spawning months and lunar phases estimated the degree to which each spawning event contributes larvae to distant populations or to neighboring populations on the complex Cuban shelf. Results suggest that considerable levels of self-recruitment (ca. 37 to 80% total recruitment) structure Cuban snapper populations, in particular, those from the southern and north-central regions. The northern snapper populations exported larvae to the southern Bahamas, specifically to Cay Sal Bank (ca. 11 to 28% total recruitment), while, for more distant locations, the import of larvae from Cuba was negligible depending on the species. Regional oceanographic regimes for cubera, dog and gray snappers and site utilization (e.g. shelf geomorphology) for mutton snapper caused most within-species recruitment variability. However, a small lag in peak spawning times contributed significantly to high recruitment variability among species. Active virtual larvae stand a better chance of reaching settlement habitat, whereas spatial distribution of recruitment is similar but less structured (i.e. homogeneous low abundance) for passive larvae. This modeling approach produces spatio-temporal predictions of larval pathways with explicit measures of variance. Further, it allows for the quantification of relative levels of connectivity, a component needed in the design of marine reserve networks.

KEY WORDS: Spawning aggregations · Larval transport · Recruitment · Biophysical modeling · Connectivity · Marine reserve network · Lutjanidae · Cuba

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INTRODUCTION

A broad range of marine organisms concentrate the release of eggs and larvae by forming spawning aggregations during limited periods of time (e.g. lobster, octopus, horseshoe crab). Several snapper (Perciformes: Lutjanidae) species have adopted this particular spawning strategy (Carter & Perrine 1994, Domeier & Colin 1997, Domeier et al. 1997, Lindeman et al. 2000, Heyman et al. 2001). Historically, large groups of snappers have converged to spawn at specific sites on

the insular shelf of Cuba (Claro & Lindeman 2003). Knowledge of these concentrated spatial and temporal patterns provides an excellent template to examine patterns of egg and larval transport. The snapper family includes several of the Caribbean's most economically important reef fishes. With 18 species utilizing a wide array of habitats, snappers are also ecologically important as predators and agents of trophic exchange among differing communities (Parrish 1989).

Snappers are the principal finfish fishery in Cuba, with the lane snapper *Lutjanus synagris* being the

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primary fishing target and having the highest landings in the Golfo de Batabanó in the southwest of Cuba (Claro et al. 2001a). Mutton snapper *L. analis* catches rank second, with the largest catches on the northeastern coast. Both of these areas may have key spawning aggregation sites for these respective species. Large decreases in catches from as early as 1975 have been reported and may be attributed to overfishing of spawning aggregations (Claro & Lindeman 2003).

Reproduction in snappers can vary intra-specifically across differing spatial and temporal scales (Grimes 1987, García-Cagide et al. 2001). In Cuba, snapper spawning aggregations typically occur at the shelf edge and promontories, but there can be some variability in within-site spawning locations and timing depending on the species and area of the island (Claro & Lindeman 2003). Single or multiple sites may be used by several species simultaneously or on differing seasonal spawning schedules. Spawning by individual species occurs during a narrow window in time (usually 1 to 3 mo) associated with lunar phases that can vary among species. Considerable information on the larval biology of snappers has also accumulated (Laroche 1977, Borrero et al. 1978, Rabalais et al. 1980, Leis 1987, Potthoff et al. 1988, Clarke et al. 1997, Riley et al. 1995, Drass et al. 2000, Pauly et al. 2000, Lindeman et al. in press). Planktonic larval durations (PLDs) in snappers range from approximately 20 to 35 d (Lindeman et al. 2000). However, the mean PLD (e.g. ca. 30 d) does not appear to differ widely among the species targeted in this study.

A fundamental attribute of informed management of over-exploited reef fishes is the understanding of population connectivity (Warner & Cowen 2002). Such information is also significant to the design of marine protected areas (Palumbi 2003). Snappers may require particular protection, since they are highly vulnerable to fishing activities during spawning (Lindeman et al. 2000, Luckhurst 2002). Thus, information on the potential larval pathways likely to occur from specific spawning aggregations can serve to guide reserve design to ensure maximum population replenishment. However, only studies that incorporate accurate information on spawning locations, currents, physical forcing, and larval behaviors can make such predictions (Mora & Sale 2002).

Utilizing a high-resolution ocean circulation model (see Cowen et al. 2000), we modeled larval trajectories for several species of snapper emanating from known spawning sites on the Cuban shelf. Using differing larval-behavior scenarios (e.g. passive and active), we developed a range of likely transport outcomes under varying winds and currents associated with seasonal conditions. We structured these model runs to address the following questions: (1) What is the relative level of

larval retention and transport within and off primary Cuban archipelagos? (2) What distant populations receive spawning products generated from various Cuban spawning locations and at what relative percentages? (3) To what degree do variations in measures of larval traits influence the prior 2 analyses?

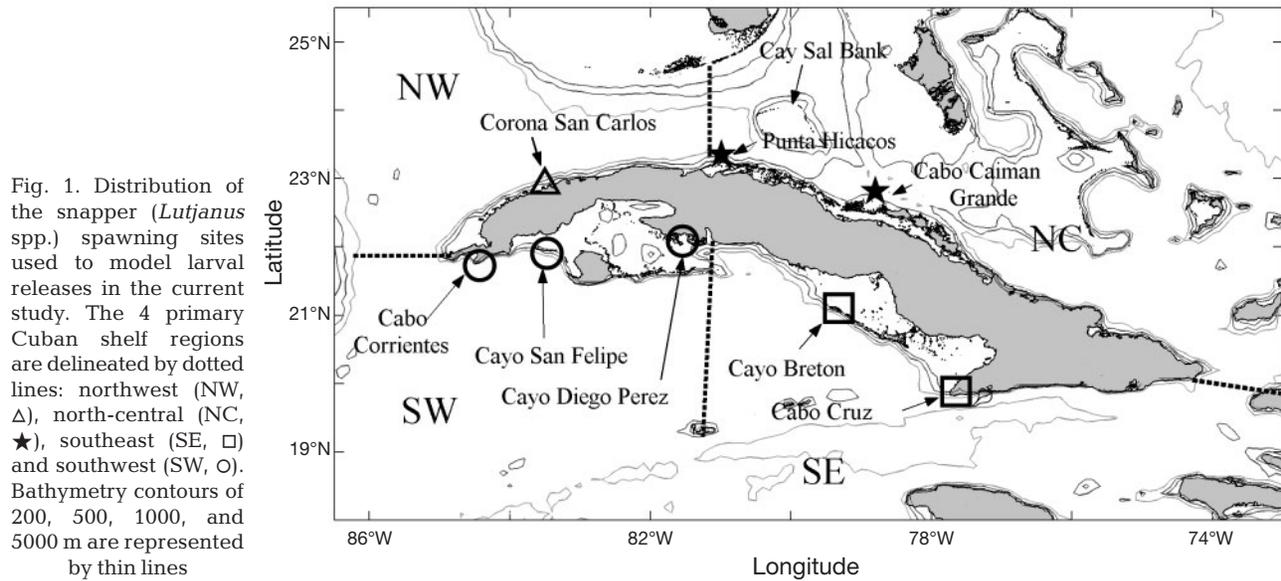
METHODS

Cuban shelf geomorphology and spawning sites.

Cuba has the largest insular shelf in the Caribbean. The geomorphology of the Cuban shelf is also distinct, in that it has several large, shallow shelf areas surrounded by fringing keys and reefs forming a series of lagoons, while the shelf edge is abrupt and formed by a series of submerged terraces (Claro et al. 2001b). The shelf contains 4 relatively wide regions separated by long stretches of narrow shelf areas. The wide shelf areas typically have long lines of keys offshore that form large leeward lagoons. The wide shelf areas occur in these regions: northwest (NW), north-central (NC), southeast (SE) and southwest (SW) Cuba (Fig. 1).

Twenty-one spawning aggregation sites of snapper and grouper species on the insular shelf of Cuba were reported by Claro & Lindeman (2003). Five commercially and ecologically important snapper species were examined in this study: mutton snapper *Lutjanus analis*, lane *L. synagris*, dog *L. jocu*, cubera *L. cyanopterus*, and gray *L. griseus* snappers. The sites used as particle release sites are listed in Table 1. Six major spawning aggregation sites were selected for the mutton snapper (1 in the NW and the SE, 2 in the SW and the NC) as well as for the lane snapper (2 each in the SE, SW, and NC). The cubera, dog, and gray snappers were treated as a species complex, because they often share both locations and peak spawning times; for this species complex, 4 major spawning aggregation sites were selected (1 each in the NW and the SW, and 2 in the SE).

Transport model and larval trajectories. To compute a range of likely larval transport outcomes under varying winds and currents associated with seasonal conditions, a biophysical transport model was developed using velocity fields of the high-resolution (1/12° grid ~9 km mesh) Miami Isopycnal Coordinate Ocean Model (MICOM, <http://micom.rsmas.miami.edu/oceanmodeling/>) forced by true daily winds of the European Center for Medium-Range Weather Forecasts (ECMWF). Here, we present results from the year 1984, which was the first year available with high temporal and spatial resolution. MICOM uses bottom topography from a digital terrain data set with 5' latitude–longitude resolution (ETOPO5) and a coastal boundary set at the 20 m isobath. To extend the geo-



graphical range toward shallow coastal areas, MICOM velocities were extrapolated from the interior into coastal regions within a 5 to 35°N and 55 to 90°W domain. Individual-based larval trajectories were simulated by coupling the resulting circulation model to a Lagrangian stochastic model (LSM, see Paris et al. 2002). Species-specific reproductive information, larval-behavior estimates, and availability of settlement habitat were introduced as parameters to produce the most realistic larval-trajectory conditions that current information allows (Cowen et al. 2003, see below).

The model output reflected the nested characteristics of the actual particles (or virtual larva) releases. In

particular, spawning production (SP) was simulated using sequential runs centered on peak spawning months and lunar phases. From each of the release sites described above, we modeled 6 releases of 1000 eggs site⁻¹ species⁻¹. This spawning event of 6000 particles site⁻¹ species⁻¹ was partitioned in 3 releases mo⁻¹ at peak lunar spawning times for 2 mo (see Table 1), with 3 d intervals in between each release sequence within each month (see Fig. 2 as an example of a single time release). These fine-scale release patterns were based on available information on the reproductive biology of these species (García-Cagide et al. 2001, Claro & Lindeman 2003).

Table 1. *Lutjanus* spp. Major spawning aggregation sites by region and timing of spawning for *L. synagris* (lane), *L. analis* (mutton), *L. cyanopterus* (cubera), *L. griseus* (gray), and *L. jocu* (dog). *: peak spawning months (adapted from Claro & Lindeman 2003). Shelf region abbreviations are explained in Fig. 1

Shelf region	Spawning site	Coordinate	Species	Spawning peak	Moon
SE	Cabo Cruz	19° 49' 24" N, 77° 44' 36" W	Lane	Jun	Before full
			Mutton	May*–Jun	Full to 7 d after
	Cayo Bretón	21° 07' 36" N, 79° 31' 24" W	Cubera & Gray	Jul*–Aug	Full
			Cubera	Jul–Aug	Full
SW	Cayo Diego Pérez	22° 02' 00" N, 81° 30' 25" W	Dog	Jul*–Aug	Full
			Lane	Jun*–Jul	Before full
	Cayo San Felipe	21° 55' 00" N, 83° 36' 00" W	Lane	May*	Before full
			Mutton	May–Jun*	Full to 6 d after
			Mutton	May–Jun*	Before full
Cabo Corrientes	21° 44' 43" N, 84° 32' 05" W	Cubera & Dog	Jul*–Aug	Full to 6 d after	
		Mutton	Jul*–Aug	Full	
NW	Corona de San Carlos	22° 54' 24" N, 83° 36' 12" W	Mutton	May–Jun*	Full to 6 d after
			Cubera & Gray	Jul*–Aug	Full
NC	Punta Hicacos	23° 17' 00" N, 81° 05' 00" W	Mutton	May–Jun*	Full to 6 d after
	Cayo Mono	81° 05' 00" W	Lane	May–Jun*	Before full
	Cayo Caimán Grande	22° 45' 12" N, 78° 52' 48" W	Mutton	May–Jun*	Full to 6 d after
			Lane	May–Jun*	Before full

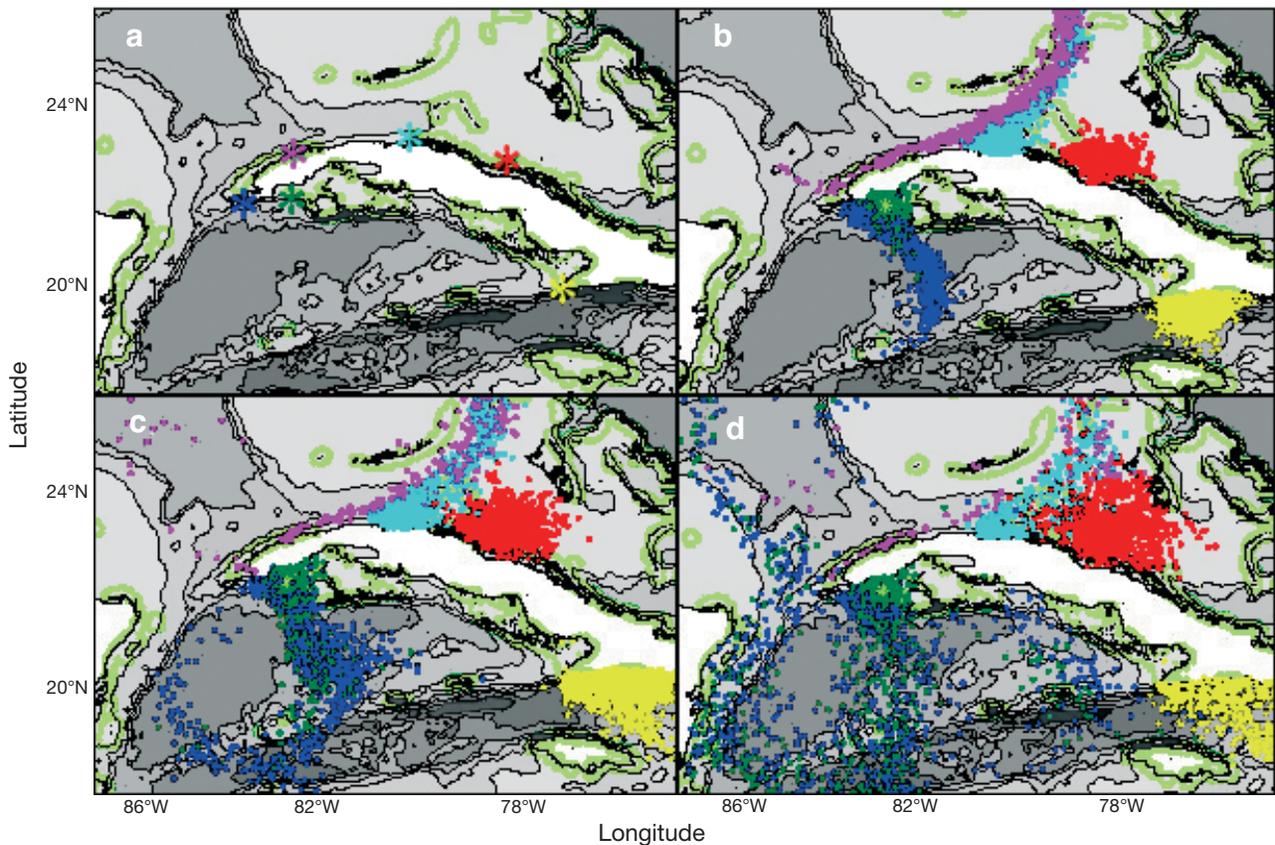


Fig. 2. *Lutjanus analis*. Spatial distribution of virtual larvae at (a) Day 1, (b) Day 7, (c) Day 14, and (d) Day 30 after the first day of simulated spawning events of mutton snapper from the 4 Cuban ecoregions: SW: Cabo Corrientes (blue) and Cayos San Felipe (green); NW: Corona de San Carlos (magenta); NC: Punta Hicacos (cyan) and Cayo Caimán Grande (red); SE: Cabo Cruz (yellow). In these images, larval transport is passive and the retention zone for snapper larvae is set within 9 km of suitable settlement habitat (delineated in light green)

Successful larval recruitment was measured by the number of larvae reaching a suitable habitat at the end of a 30 d larval period (Lindeman et al. 2000) with a series of larval-behavior scenarios (see below). Successful recruitment was calculated as the percent of virtual larvae recruiting from the total number released per spawning event (e.g. 6000 site⁻¹ species⁻¹ post-mortality). Levels of recruitment reported here were scaled by natural mortality occurring during the larval pelagic period, which typically ranges between 0.1 and 0.5 d⁻¹ (Houde 1989, Paris-Limouzy 2001). For example, a spawning event of 6000 individuals (total number of released particles per spawning event) is the equivalent of an initial SP of ~6 million eggs after applying a 0.21 daily natural mortality rate for 30 d. Successful recruitment refers strictly to supply of larvae to settlement habitat and does not include post-settlement processes. Within-region recruitment (or local recruitment) refers to virtual larvae that self-recruited within the same Cuban region; among-region recruitment (or regional recruitment) signifies

virtual larvae that recruited to other regions within Cuba; and export recruitment designates export of larvae outside Cuba, while total recruitment represents both recruitment within Cuba (i.e. within-region and among-region recruitment) and outside Cuba (export recruitment).

Larval-behavior components. Larval behavior is based on probable biophysical retention mechanisms (i.e. ontogenetic vertical migration into low-flow regions; Paris & Cowen 2004) as well as sensory capabilities (Kingsford et al. 2002). These traits served to define a retention zone (RZ) for pelagic larvae of which the boundaries correspond to the probable extent of the biophysical mechanisms experienced by reef fish larvae (see Sponaugle et al. 2002) and were set within 9 to 18 km of suitable settlement habitat. Suitable habitat was identified via remote sensing and associated maps (i.e. Reefs at Risk in the Caribbean; <http://marine.wri.org>), transferred to a Geographic Information System (ArcView GIS 3.3) and buffered with a sensory zone (e.g. 9 km). Lagrangian trajectories were imported into the resulting

recruitment habitat to count larvae falling within the RZ as a post-process described below.

During ontogeny, flexion of the larval notochord allows for formation of the caudal fin and increased swimming ability (Fisher et al. 2000). Therefore, the timing of notochord flexion represented a benchmark for the onset of active behavior in the model. Information on the size and/or age of notochord flexion is available for 6 species of lutjanids from 3 genera; the flexion initiates between 3.8 and 4.7 mm (= 9 to 12 d post hatching) in 4 species of *Lutjanus* (R. Claro & K. C. Lindeman unpubl. data). Flexion is subsequently completed between 4.8 and 6 mm (= 14 to 18 d post hatching), and therefore the onset of active behavior of the virtual larvae in the model was set at Day 14. In the model, an active virtual larva stops as its trajectory intercepts a RZ and is retained for the remainder of the larval duration before recruiting successfully. Otherwise, it continues its trajectory until the end of the PLD. Mortality at the end of the transport scenario occurs at 100% for simulated larvae that are outside the RZ after 30 d. In contrast, passive virtual larvae can only recruit at the end of the PLD. To evaluate the role of the onset of active behavior on the outcome of larval transport, a sensitivity analysis was carried out, whereby simulated larvae were subjected to a range of active scenarios. Active behavior was started as early as Day 7 after initial particle release and as late as the end of the pelagic duration (i.e. Day 30).

Statistical analysis. A hierarchical analysis of variance or nested ANOVA (Underwood 1981, Sokal & Rohlf 1995) on the number of successful recruits produced by each of the spawning events was used to detect variability contributed by different spatial scales (region, site effects), spawning time (species effect), and larval behavior (onset of active behavior effect) simulated in the model. Analyses were done independently with 2 data sets (i.e. recruitment within Cuba and export recruitment) at 2 different levels. For recruitment within Cuba, nested ANOVA was first performed for all recruits then separated by individual species. For export recruitment, nested ANOVA was performed for all recruits, and then separated by receiving countries. Analyses were performed using BIOMstat (version 3.2, Applied Biostatistics, Setauket).

RESULTS

Recruitment patterns within Cuba

Most of the spawning aggregations simulated in Cuba supplied larvae to their own region, with among-region recruitment in Cuba being lower than recruitment within the source region. The exception was mut-

ton snapper larvae released from NW Cuba, which were mostly a source of recruits to the NC region (Fig. 3). Inter-specific differences in spatial recruitment were evident, even though there were only small lags

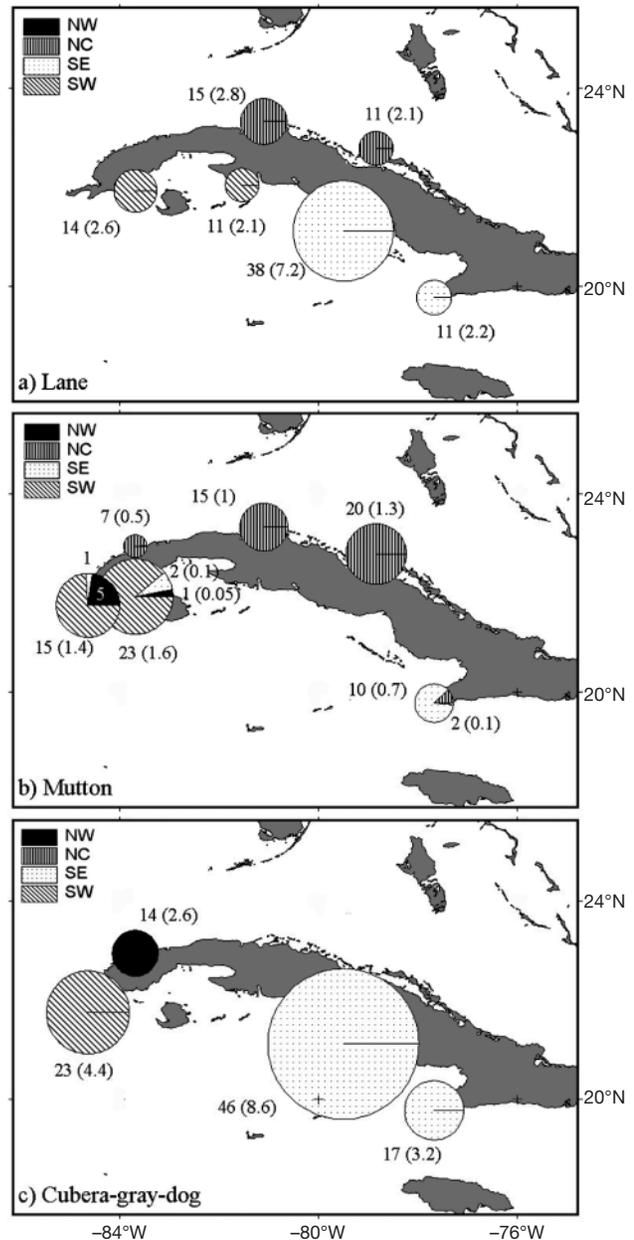


Fig. 3. *Lutjanus* spp. Composition of recruitment within the 4 regions of Cuba from spawning sites utilized by (a) lane, (b) mutton, and (c) cubera-gray-dog complex snappers. Each pie represents a spawning aggregation site and its fraction of recruits to each of the four eco-regions; the size of the pie is proportional to its contribution to total recruitment within Cuba (pie size range = 7 to 46%). Recruitment is also indicated in parentheses as the fraction of the simulated spawning production (10^{-3} SP). Values are from simulations using MICOM year 1984 with the onset of larval behavior set at Day 14

Table 2. *Lutjanus* spp. Estimated recruitment levels (% simulated spawning production) for all sites combined within Cuba and its ecological provinces and to neighboring countries from the spawning aggregation of snappers in Cuba for the MICOM year 1984. Note that Colombia is represented by islands in the Nicaragua–Jamaica Bridge and that Cay Sal Bank is the major receiving region of the Bahamas. Numbers in parentheses are the proportion of total recruitment (within Cuba + export). The assumption in simulating larval transport here is that the onset of larval behavior is at 14 d after spawning. Shelf region abbreviations as in Fig. 1

Species	In Cuba		By Cuban region		Export out of Cuba	By country		Total
	Within regions	Among regions						
Mutton	5.1×10^{-3} (36.7%)	1.7×10^{-3} (12.2%)	NW	0.4×10^{-3}	7.1×10^{-3} (51%)	Bahamas	3.94×10^{-3}	13.9×10^{-3}
			NC	2.9×10^{-3}		Cayman	0.87×10^{-3}	
			SE	0.9×10^{-3}		Mexico	0.85×10^{-3}	
			SW	2.6×10^{-3}		Hispañola	0.51×10^{-3}	
						Honduras	0.24×10^{-3}	
						Colombia	0.20×10^{-3}	
						Florida	0.18×10^{-3}	
						Belize	0.16×10^{-3}	
Lane	19.1×10^{-3} (79.9%)	0 (0%)	NW	0	4.8×10^{-3} (20.1%)	Bahamas	2.75×10^{-3}	23.9×10^{-3}
			NC	5.0×10^{-3}		Cayman	0.77×10^{-3}	
			SE	9.4×10^{-3}		Hispañola	0.39×10^{-3}	
			SW	4.7×10^{-3}		Jamaica	0.38×10^{-3}	
						Mexico	0.24×10^{-3}	
						Colombia	0.13×10^{-3}	
						Honduras	0.08×10^{-3}	
						Belize	0.04×10^{-3}	
Cubera –gray–dog	11.9×10^{-3} (43.6%)	7.1×10^{-3} (26%)	NW	2.6×10^{-3}	8.4×10^{-3} (30.8%)	Bahamas	4.94×10^{-3}	27.3×10^{-3}
			NC	0		Cayman	1.26×10^{-3}	
			SE	11.9×10^{-3}		Jamaica	0.79×10^{-3}	
			SW	4.4×10^{-3}		Hispañola	0.60×10^{-3}	
						Florida	0.29×10^{-3}	
						Colombia	0.25×10^{-3}	
						Mexico	0.22×10^{-3}	
						Honduras	0.02×10^{-3}	

in spawning schedules. The southern regions (SE and SW) received a large majority of the recruitment of snappers within Cuba, which contributed largely to overall recruitment (e.g. 25 to 60%, Table 2). The NW region received the least amount of recruits for all species. However, since suitable recruitment habitat in the NW is approximately 3 to 4 times smaller than that of the NC, if recruitment was scaled by area, the levels of recruitment in the NW may be similar to those of the NC region.

It was also clear that some regions produced more recruitment than others (Figs. 3 & 4). For example, the SE sites contributed to most of the recruitment within Cuba of the lane snapper and the cubera–dog–gray species complex, mostly via self-recruitment (within-region), while the SW and NC sites were more important for mutton snapper recruitment over all regions. Compared with the other regions, the NW was consistently a poor source of larvae within Cuba for all the species. There were also site differences within a region (Fig. 3), where some sites contributed more to local recruitment than others (e.g. SE region: Cayo Breton produced more self recruits than Cabo Cruz for both mutton and 3 cubera–gray–dog snappers).

Small-scale temporal variability represented by differing monthly spawning peaks (see Table 1) significantly drove large variability in recruitment within

Cuba among species (Table 3a). Recruitment patterns at the species level were mostly attributed to regional (large-scale oceanographic) effects for the cubera–gray–dog snapper complex and to a lesser extent for the lane snapper, while individual sites (small-scale geomorphologic effects) were associated with most of the variability in recruitment for the mutton snapper (Table 3b).

Recruitment patterns outside of Cuba

Simulations indicated that export to other countries from Cuba typically ranged from 1 to 3 orders of magnitude lower than recruitment within Cuba. The exception was the Bahamas, where total exports represented 20 to 51% of total recruitment (Table 2). Because of their proximity, sites from the NC region were nearly 50% connected to the southern Bahamas, and may contribute to an important part of the replenishment of mutton and lane snapper populations at Cay Sal Bank (Fig. 5). There were significant inter-specific differences in the amounts of export (Table 4a). For the mutton snapper, sites from the SW region showed some connectivity to Mexico (6%), Cayman Islands (6.2%), and to a lesser extent to Honduras (2%) and Belize (1.2%), while populations in Hispañola

Table 3. *Lutjanus* spp. Nested ANOVA analyses testing the effect of geographical and biological factors on simulated recruitment levels within Cuba (a) with 'region' as primary factor and (b) with 'species' as primary factor, during the MICOM year 1984 for *L. synagris* (lane; LA), *L. analis* (mutton; MU), and the *L. cyanopterus*–*L. griseus*–*L. jocu* complex (cubera–gray–dog; CU). ANOVA significance levels: * $p < 0.05$. Note that the 'species' effect is driven by differences in site selection and timing of spawning in the model

Source	df		MS	F_s	p-value	% explained
(a) Region						
Region	3		2 123 444.4	4.56	0.088	12.01
Site/region	4		465 596.3	0.43	0.787	0
Species	16		1 089 481.8	2.13	0.022	24.1*
Onset of behavior	48		511 164.2	–	–	63.89
(b) Species						
Region	3	LA	1 710 828.3	1.39	0.368	8.4
		MU	169 505.6	0.55	0.674	0
		CU	2 918 148.2	4.98	0.078	40.1
Site/region	4	LA	376 334.4	0.94	0.466	0
		MU	1 225 448.1	1.65	0.210	16.33
		CU	586 523.6	0.97	0.452	0
Onset of behavior	16	LA	742 248.4	–	–	75.27
		MU	185 283.3	–	–	82.03
		CU	605 961.1	–	–	59.9

(3.6%) and in the eastern Bahamas (2%) were more connected via sites in the SE zone. Despite the proximity of the Florida Keys to the NW sites, none of the spawning aggregations seemed to contribute much to the Florida Keys snapper populations; the largest level of estimated connectivity was 1% for the cubera–gray–dog complex (Fig. 5).

Sensitivity analysis of larval-behavior scenarios

Sensitivity analysis was performed on the onset of active behavior and on the sensing distance (RZ around settlement habitat). The number of larvae that recruited within their source region (i.e. within-region recruitment) decreased significantly with the delay of active behavior, while the width of the RZ did not have a significant effect on recruitment levels (Fig. 6a). Although delay in the onset of behavior and, to a lesser extent, smaller range in sensing capability decreased the levels of recruitment, these factors had little effect on the spatial distribution of recruitment and on dispersal distances (Fig. 6b). Similarly, the export levels decreased considerably with delay of active behavior, especially for nearby locations (e.g. Cay Sal Bank, Bahamas; Fig. 6c). When exports were scaled by area of recruitment habitat, onset of larval behavior was an important factor for Cay Sal Bank

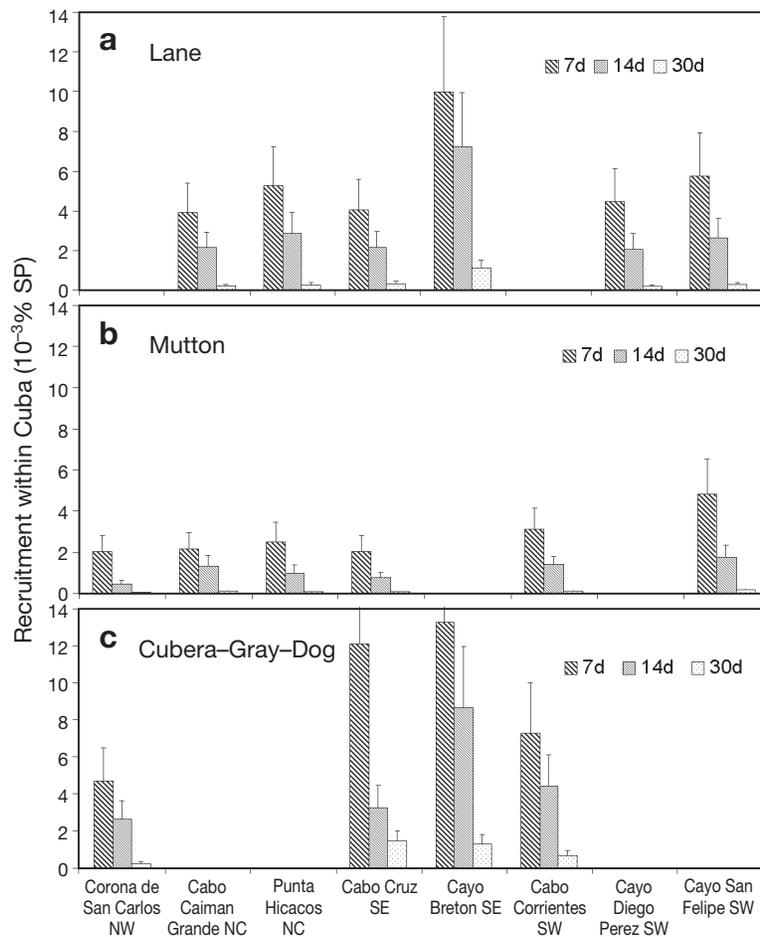


Fig. 4. *Lutjanus* spp. Recruitment production from modeled spawning aggregation sites utilized by (a) lane, (b) mutton, and (c) cubera–gray–dog complex snappers. Changes in recruitment are a function of the onset of active behavior simulated in the larval transport model at 7, 14 and 30 d. SP: spawning production

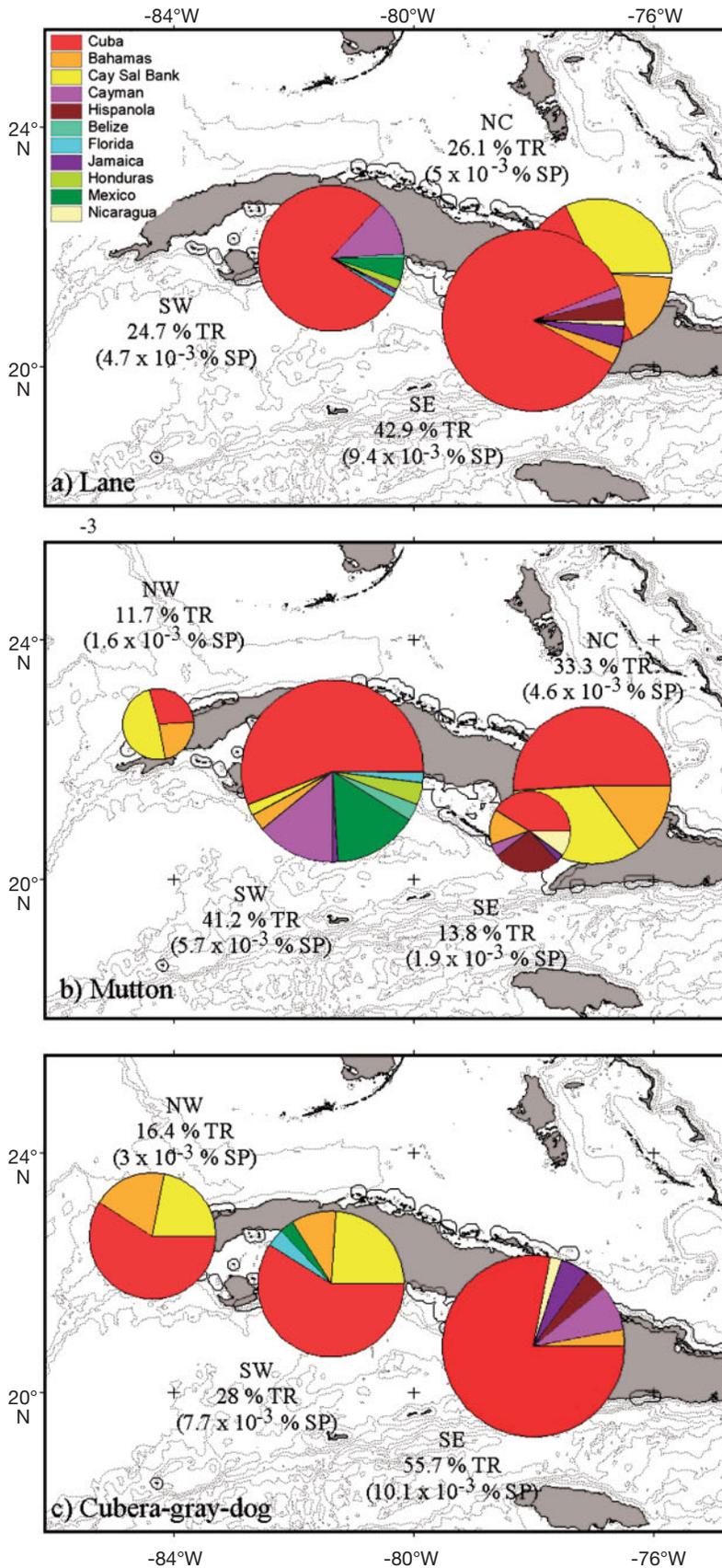


Fig. 5. *Lutjanus* spp. Total recruitment (TR = within Cuba + export) produced from spawning aggregations of (a) lane, (b) mutton, and (c) cubera–gray–dog complex snappers grouped by the 4 primary shelf regions of Cuba. Each pie represents a region and its fraction of recruits to Cuba and receiving countries; the size of the pie is proportional to its contribution to TR. TR is also indicated in parentheses as the fraction of the simulated spawning production (% SP); TR from all regions for lane, mutton, and cubera–gray–dog complex snappers is 29.3×10^{-3} , 13.9×10^{-3} , and 27.3×10^{-3} %, respectively (Table 2). Onset of larval behavior is set at Day 14. Shelf region abbreviations as in Fig. 1

only (Fig. 6d). For the Cayman Islands, the export levels were low but consistent for the early onset of active behavior (Days 7 and 14) and decreased strongly when larvae were passive until the end of the pelagic phase. For all species, the onset of larval behavior notably contributed to variability in recruitment within Cuba for the year examined (Table 4a). This component was less important when considering recruitment to other countries, except for Cay Sal Bank (Bahamas), which is in close proximity to the northern regions of Cuba (Table 4b).

DISCUSSION

Larval transport

Modeling approaches that integrate hydrodynamic models, biological traits, and settlement habitats have only recently been applied to research on larval dispersal and recruitment (e.g. Werner et al. 2001, James et al. 2002, Cowen et al. 2003). The above analyses are based on a coupled biophysical model integrating simulated currents to a biologically relevant Lagrangian stochastic component. The biological component reproduces turbulence and allows virtual larvae to have individual paths and larval sensory capabilities. Fine-scale control of larval trajectories is further generated by incorporating informed estimates of species-specific life-history traits (i.e. spawning schedules, site selection, and PLDs) and suitable recruitment habitat into the biophysical model. This modeling approach estimates the extent to which each spawning event contributes larvae to distant popu-

Table 4. *Lutjanus* spp. Nested ANOVA analyses of the effects of geographical and biological factors on simulated (a) total export levels from Cuba and (b) export levels partitioned by countries during the MICOM year 1984 for *L. synagris* (lane), *L. analis* (mutton), and *L. cyanopterus*–*L. griseus*–*L. jocu* (cubera–gray–dog) complex snappers in the Bahamas (BA), Florida (FL), Mexico (ME), Jamaica (JA), Cayman Islands (CA), and Belize (BE). ANOVA significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

(a) Total export levels						
Source	df		MS	F_s	p-value	% explained
Region	3		109 833.2	0.35	0.790	0
Species	8		313 114.8	3.10	0.038	51.2*
Onset of behavior	12		101 092.2	–	–	48.8
(b) Partitioned export levels						
Source	df	Country	MS	F_s	p-value	% explained
Region	3	BA	15 864.1	0.320	0.811	0
	3	FL	3 854.8	6.171	0.018	62.9*
	3	ME	40 180.2	3.204	0.083	41.8
	3	JA	33 286.7	4.789	0.034	51.6*
	3	CA	75 415.0	1.903	0.208	20.5
	3	BE	888.2	2.965	0.097	39
Species	8	BA	49 609.6	2.733	0.057	46.4
	8	FL	624.6	58.56	0.0001	35.9***
	8	ME	12 539.0	45.06	0.0001	55.7***
	8	JA	6 950.7	5.428	0.005	33.3**
	8	CA	39 631.9	5.859	0.0034	56.4**
	8	BE	299.5	40.39	0.0001	58.1***
Onset of behavior	12	BA	18 154.5	–	–	53.6
	12	FL	10.7	–	–	1.2
	12	ME	278.3	–	–	2.5
	12	JA	1 280.6	–	–	15.1
	12	CA	6 764.8	–	–	23.2
	12	BE	7.4	–	–	2.9

lations or to neighboring populations. For the first time, we were able to estimate the relative contribution of the different spawning aggregations to local and regional recruitment, and the degree to which these aggregations export recruits to downstream populations at variable distances.

These results provide only limited support for substantial long-distance advection from Cuba and reinforce mounting evidence (Jones et al. 1999, Cowen et al. 2000, Swearer et al. 2002) that local retention provides a significant replenishment source. For example, 36.5 to 80% of the estimated total recruitment generated by the snapper spawning aggregations of the Cuban archipelagos is of local origin (Table 2). The levels of self-recruitment for Cuba estimated in this study are of the same order of magnitude of those previously observed in Barbados (Paris & Cowen 2004), which is an area of high retention for locally spawned coral reef fish larvae (Cowen & Castro 1994). The contribution of snapper recruits exported to other countries was a relatively small fraction of the total spawning production during the model period. These results agree with predictions of Lindeman et al. (2001) based

on oceanographic information and biological traits of snappers and grunts. In the present study, simulated export recruitment was 1 to 3 orders of magnitude lower than levels of recruitment observed in other places in the Caribbean (Cowen et al. 2003; Fig. 6) and than levels of simulated recruitment within Cuba, with the exception of exports to Cay Sal Bank in the Bahamas (Fig. 5).

Distant populations that received a small fraction of exported spawning products included those at the Cayman Islands (e.g. mutton and cubera–dog–gray complex); Mexico, which benefited from the mutton snapper spawning aggregations of SW Cuba due to the presence of an anticyclonic eddy during MICOM year 1984; Jamaica and Hispanola, each of which received recruits of the cubera–dog–gray complex. Despite its relatively close proximity, the Florida Keys did not receive a significant number of recruits from the NW or the SW regions of Cuba. The most probable cause of such recruitment patterns for larvae originating from the NW spawning sites may be difficulties in crossing the strong Florida Current front during its period of maximum transport (Lee & Williams

1999) and an absence of frontal eddies (Limouzy-Paris et al. 1997). Snapper larvae originating from the SW sites would typically sustain high mortality before reaching the Florida reef track via the Loop Current pathway when its northward intrusion into the Gulf of Mexico is high.

Model validation

Hierarchical ANOVA, which has previously been used to classify processes that determine the distribution of early life-history stages of marine fishes (e.g. Sullivan et al. 2002), served in this study to emphasize the importance of species-specific effects in modeling larval transport (i.e. spawning strategies, onset of larval behavior). In particular, the timing of spawning influenced spatial recruitment patterns significantly, and early onset of larval behavior increased recruit probability both within Cuba and to distant populations. The quasi-passive behavior scenario produced such low levels of recruitment that detection of any possible spatial variation in recruitment level is lim-

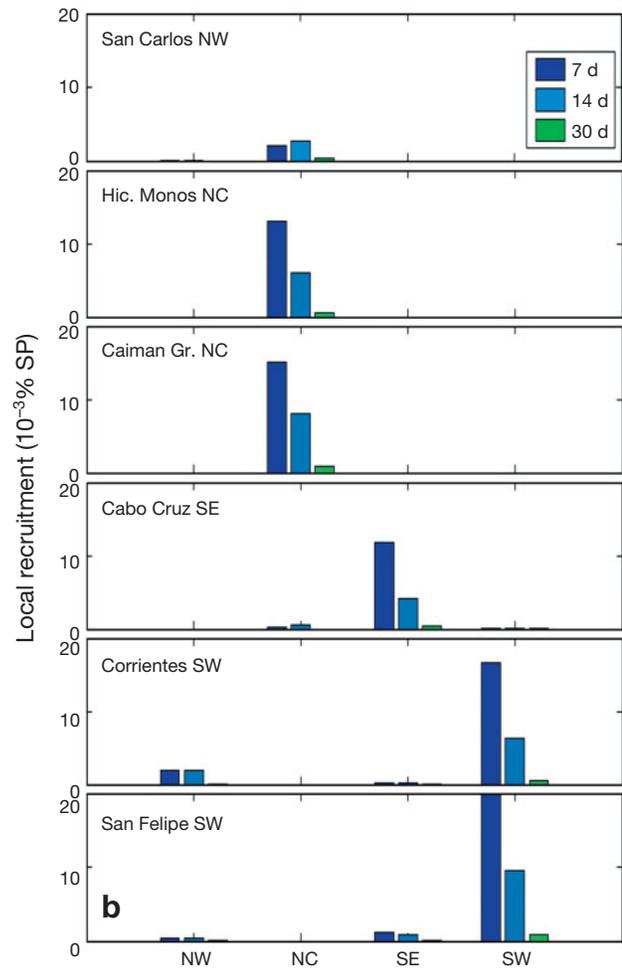
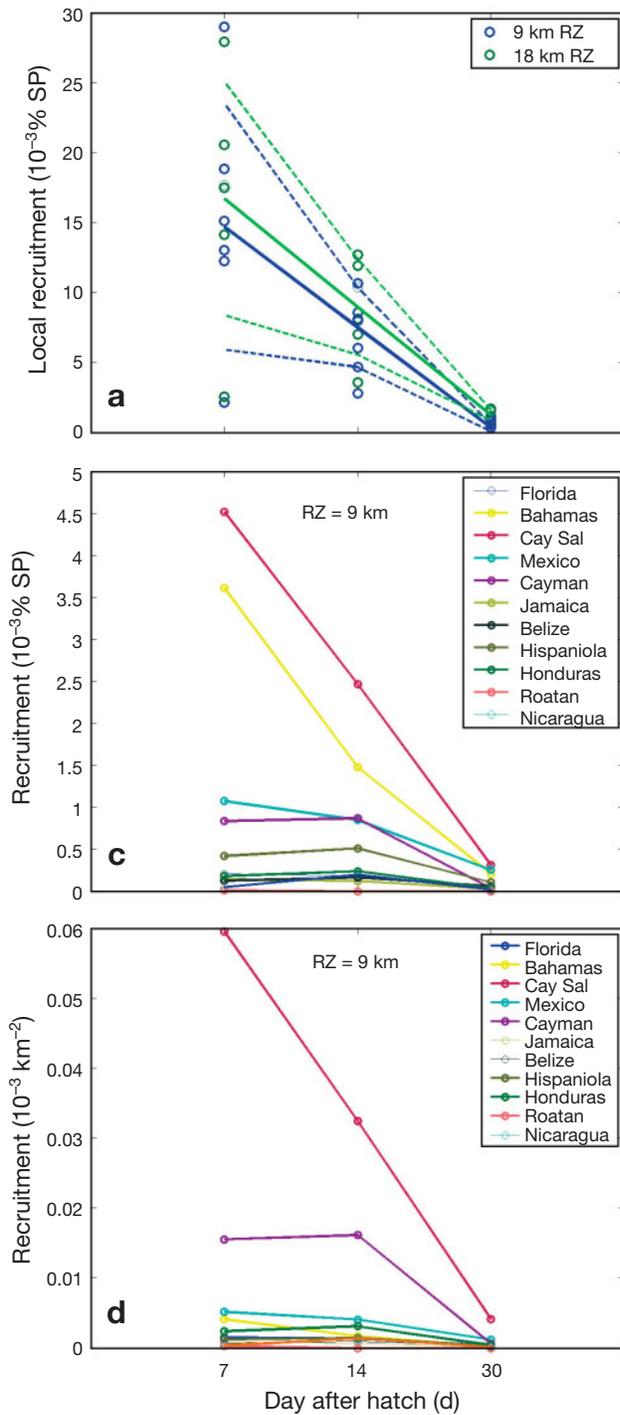


Fig. 6. *Lutjanus analis*. Sensitivity analyses of the effects of various larval behavior modes (i.e. sensory threshold distance, onset of active behavior during ontogeny) on levels and spatial distributions of recruitment in dispersal simulations for mutton snapper in Cuba. (a) Levels of local recruitment as a function of onset of active behavior (onset at 7, 14 and 30 d) and of sensing distances from suitable settlement habitat (retention zones = 9 and 18 km). Dotted lines represent 95 % confidence intervals around the mean. (b) Spatial distribution of within-region and among-region recruitment in Cuba as a function of the onset of active behavior. (c) Proportion of the simulated spawning production from Cuba exported to neighboring countries as a function of the onset of active behavior. (d) Exports scaled by suitable settlement habitat in neighboring countries as a function of the onset of active behavior. Shelf regions abbreviations as in Fig. 1

ited. As one might anticipate, we found that biological factors caused much of the recruitment variability among species, while regional differences in recruitment resulted from distinct oceanographic regimes around insular Cuba. The products of our coupled model were validated by (1) comparison of the predicted larval trajectories and their variance with satellite-tracked oceanic drifters released in the region

(Fig. 7), and (2) the estimated recruitment levels generated by active larval behavior with those observed at Barbados (see Cowen et al. 2003). However, there are some limitations in this modeling approach, mostly because ocean models typically do not resolve coastal circulation well, and knowledge of larval behavior for snappers, as in most marine fishes, is limited to higher taxonomic levels (e.g. family and genus; Powles 1977,

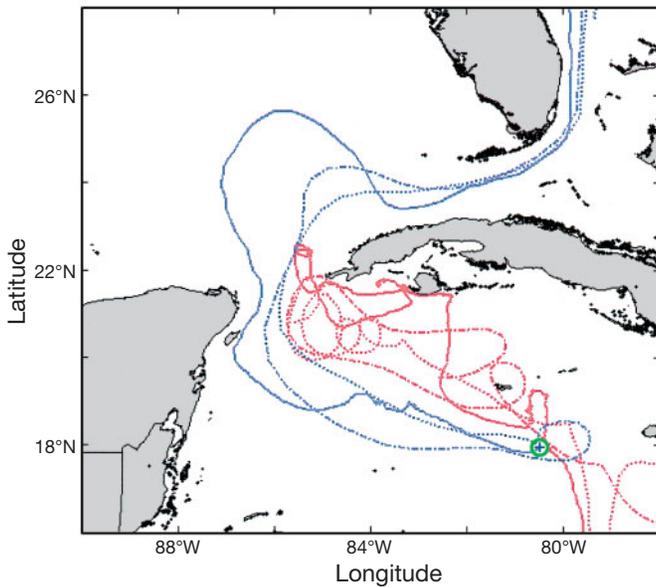


Fig. 7. Comparison of 2 drifter trajectories (solid lines) from the Global Lagrangian Drifter Database (GDL, http://db.aoml.noaa.gov/cgi-bin/db/Bin/init_applet.x?gld+GLDKRIG-GUI.class) south of Cuba with simulated drifters (dashed and dotted lines) using MICOM/ECMWF velocity fields. Note that 1 drifter passes through the Yucatan channel into the Florida Straits, while the other returns to southwest Cuba. The green circle with a blue cross represents the deployment location of the real float (solid blue lines) and the corresponding release of the virtual floats (dotted blue lines) in the model

Leis 1987, Cowen 2002). These factors caused uncertainty in the estimated trajectories that we recognized and minimized in several manners. First, to resolve the circulation beyond the ocean model limits (i.e. 20 m isobath), MICOM velocities were spatially smoothed from the interior during the interpolation scheme. This scheme provided a first approximation for the coastal circulation, but the interpolation reduced oceanic eddy variability. We compensated by adjusting the variance of the turbulent velocity in the stochastic scheme to reproduce the observed IAS float trajectories (Fig. 7). To approximate the influence of larval behaviors, we developed RZs for virtual larvae which are located in shallow areas (see 'Methods') and are based on empirically derived proportions of coral reef fish larvae retained near the coastal environment (e.g. Paris & Cowen 2004). In future work, extrapolating velocities from the ocean model boundary to the shoreline without modifying velocities in the interior, or nesting a diffusive coastal boundary to the existing velocity field, should enhance accuracy of the transport (C. B. Paris & A. Srinivasan unpubl. data).

In addition, improvements will be achieved by use of ocean models with larger coastal extent and with the development of mesoscale coastal models that include detailed topography and tidal forcing. Comparisons of

Atlantic inflow to the Caribbean Sea between observations and MICOM in the Florida Straits (NW region) and the Yucatan Channel (SW region) agree well, but the mean total transport (from the surface to bottom) from MICOM model years 1979 to 1986 in the Old Bahama Channel is slightly towards the east (i.e. -0.7 Sv; Z. Garraffo, RSMAS, pers. commun.), while transport derived from observations is towards the west (i.e. $+1.9$ Sv; Atkinson et al. 1995). However, observed westward flow was prominent in the deeper layers (250 to 435 m), while near-surface (50 m), along-channel currents reversed during the 12 mo time series (variance = 1400, mean currents = 2.6 cm s^{-1} , Atkinson et al. 1995), flowing mostly toward the Straits of Florida from November to March and mostly eastward from April to October throughout the snapper spawning season. In addition, when comparing MICOM surface velocities (i.e. mixed layer) to *in situ* drifters, the mean simulated velocity in this region does not statistically differ from the observations (see Garraffo et al. 2001, their Fig. 4d). Discrepancies of transport in the Old Bahama Channel could have created inaccuracy in the levels of exchange between the NC region and Cay Sal Bank, with the potential to underestimate local recruitment from Cayo Caimán Grande. The larval-behavior component is based on the assumption that competent larvae can be retained near coastal regions (i.e. recruitment zones) and recruit if their trajectory intercepts a suitable settlement habitat. Once fully operational in the study region, ocean models of higher vertical resolution and shallow extent (e.g. HYCOM; <http://hycom.rsmas.miami.edu>) will enable the incorporation of active behavior where vertical migration into stratified currents could be directly implemented to simulate observed behavior (see Paris & Cowen 2004). These challenges warrant strong consideration, yet the results presented here represent relatively robust estimators of sources of variability and proportions of recruitment within Cuba and among adjacent countries.

Spawning aggregations and management

Variation in the timing and location of spawning among snapper species leads to significant recruitment variability in both space and amplitude. For example, the SE region was a source of recruits for lane and cubera–gray–dog complex snappers recruiting within Cuba, while the SW was a larger source for mutton snappers recruiting within Cuba (Fig. 3). Both of the spawning sites utilized by the cubera–gray–dog snapper complex produced similar recruitment within Cuba, while Cayo Bretón produced significantly more lane snapper recruits within Cuba than Cabo Cruz.

Spawning aggregations of lane and cubera–gray–dog complex snappers strictly generated local recruitment within source archipelagos, with no transport to other Cuban regions. However, high local recruitment was not observed for the mutton snapper spawning aggregations from the SW and NW regions, which exported recruits to the NW and the SE regions, and to the NC region, respectively (Fig. 3). The lane and mutton snapper spawning aggregations from Punta Hicacos in the NC region produced comparatively similar levels of self-recruitment. However, aggregations at Caimán Grande in the same region generated twice as many mutton snapper recruits than lane snapper.

These results identify major source populations and some of their probable recruitment sites (sinks), which may warrant protection, such as the lane snappers that aggregate in Cayo Bretón. A full-scale study of temporal variability (e.g. several years of model runs) is needed to better estimate this variation and to optimize conservation advice for management options. For example, a recent study of dispersal from a Florida mutton snapper aggregation using drifter vials for 2 consecutive years showed that, although the spread of dispersal was similar, regions of concentrated returns differed (Domeier 2004). Additional sources of variability in production and recruitment, such as differences in the number of spawners among sites should also be considered. For example, the lane snapper population spawning in Cayo Bretón is much smaller than in Diego Pérez (R. Claro unpubl. data) and a higher larval survival percentage of may be needed to produce a similar number of recruits.

Disappearance of large spawning aggregations has largely been attributed to overfishing (Sadovy 1996, Domeier & Colin 1997, Beets & Friedlander 1999) and habitat loss (Koenig et al. 2000). Loss of these centers of production may affect recruitment to both local and downstream populations. Such impacts could be particularly significant at spawning sites used by multiple species through the year (Lindeman et al. 2000). The present study suggests that most of the snapper spawning aggregations in Cuba may be largely self-recruiting, with the exception of the NW region. The low retention in the NW is consistent with lower historical catches and the geomorphology of the narrow shelf in this region (Claro et al. 2001a,b), and these populations could export a significant proportion of their spawning production. For example, sustainability of the snapper populations in the southern Bahamas, particularly at Cay Sal Bank, may depend in part on spawning aggregations from the northern regions of Cuba. In addition, a small fraction of lane snapper larvae from the SW spawning sites can be entrained in a transitory anticyclonic gyre towards Mexico. But in this particular case, export from Cuba may be too

low to contribute significantly to the replenishment of these snapper populations.

Interconnected marine reserve networks have been suggested as one strategy for preserving coral-reef fishery systems (Lubchenko et al. 2003, Sale & Ludsin 2003). One key concern in designing such a reserve network is whether the reserves are appropriately placed and sized to maximize the replenishment of targeted species both within and outside the reserve boundaries via larval dispersal (Sale et al. 2005). Information on the potential larval pathways likely to occur from specific spawning aggregation sites can guide reserve design for improved effectiveness in ensuring population replenishment. The integrated modeling employed here produces spatio-temporal predictions of larval pathways with explicit measures of variance and allows the quantification of relative recruitment levels, thus representing a powerful tool to assist the design of marine reserve networks.

These results suggest that Cuban snapper populations are structured by considerable levels of local recruitment, and therefore the sustainability of these populations may largely depend on the conservation of spawning aggregations, in particular those of the southern archipelagos. Most of the spawning aggregations were largely self-recruiting, but also did export a small number of larvae to other regions. Both temporal variability (e.g. lag in spawning timing) and spatial variability (e.g. differential site utilization) among species lead to significant recruitment variability. Yet, inter-annual oceanographic variability also plays a significant role in larval linkages (Cowen et al. 2003). The integrated modeling in this study reinforces the need for further examination of how dispersal and recruitment vary inter-annually with oceanographic regimes and develops new opportunities for accomplishing this and associated tasks.

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