

Title: The perfect storm: match-mismatch of bio-physical events drives larval reef fish connectivity between Pulley Ridge mesophotic reef and the Florida Keys

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Abstract:

Mesophotic coral reef ecosystems are remote from coastal stressors, but are still vulnerable to over-exploitation, and remain mostly unprotected. They may be the key to coral reefs resilience, yet little is known about the pattern of larval subsidies from deeper to shallower coral reef habitats. Here we use a biophysical modeling approach to test the hypothesis that fishes from mesophotic coral reef ecosystems may replenish shallow reef populations. We aim at identifying the spatio-temporal patterns and underlying mechanisms of larval connections between Pulley Ridge, a mesophotic reef in the Gulf of Mexico hosting of a variety of shallow-water tropical fishes, and the Florida Keys reefs. A new three-dimensional (3D) polygon habitat module is developed for the open-source Connectivity Modeling System to simulate larval movement behavior of the bicolor damselfish, *Stegastes partitus*, in a realistic 3D representation of the coral reef habitat. Biological traits such as spawning periodicity, mortality, and vertical migration are also incorporated in the model. Virtual damselfish larvae are released daily from the Pulley Ridge at 80m depth over 60 lunar spawning cycles and tracked until settlement within a fine resolution

(~900m) hydrodynamic model of the region. Such probabilistic simulations reveal mesophotic-shallow connections with large, yet sporadic pulses of larvae settling in the Florida Keys. Modal and spectral analyses on the spawning time of successful larvae, and on the position of the Florida Current front with respect to Pulley Ridge, demonstrate that specific physical-biological interactions modulate these “perfect storm” events. Indeed, the co-occurrence of 1) peak spawning with frontal features, and 2) cyclonic eddies with ontogenetic vertical migration, contribute to high settlement in the Florida Keys. This study demonstrates that mesophotic coral reef ecosystems can also serve as refugia for coral reef fish and suggests that they have a critical role in the resilience of shallow reef communities.

Highlights:

3 to 5 bullet points (max 85 characters each)

Mesophotic reefs can act as refugia for coral reef fish

Deep-shallow connections are modulated by physical mechanisms

Pulley Ridge mesophotic reef and Florida Keys shallow reefs are sporadically connected

Physical-Biological interactions influence deep-shallow connections

Keywords: (4 to 6)

Mesophotic reef, connectivity, larval transport, deep reef refugia hypothesis, biophysical mechanisms, mesoscale features

Contributors:

ACV designed and conducted experiments, analyzed data, wrote manuscript, CBP designed experiments, analyzed data, wrote manuscript, MJO designed experiment, analyzed data, wrote

manuscript, VHK provided ocean modeling data and analyses, contributed to manuscript writing, HK provided ocean modeling data and analysis, contributed to manuscript writing, JKR contributed to the benthic community surveys of Pulley Ridge, and manuscript writing.

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1. Introduction

Contemporary technological developments such as technical diving, remotely operated vehicles (ROV) and submersibles have allowed the exploration of previously undocumented warm-water coral reef habitat, found at greater depths and farther from the continent than their shallow-water counterparts (Armstrong *et al.*, 2006; Menza *et al.*, 2008; Lesser *et al.*, 2009; Kahng *et al.*, 2010). These mesophotic coral reef ecosystems (MCEs) occur at depths of 30 to >150m where light penetration is limited to approximately 10% of surface irradiance but still allows for photosynthetic corals and algae (Lesser *et al.*, 2009). Recent studies have demonstrated that mesophotic reefs are distributed over much larger areas than previously known, and are home to an abundant fauna and flora (Bare *et al.*, 2010; Bridge *et al.*, 2010; Kahng *et al.*, 2010; Baker *et al.*, 2016). Moreover, the latest evidence suggests that natural and anthropogenic disturbances may affect these regions differently than shallower reefs, in part because these ecosystems are located farther from shore and thus have less impact from anthropogenic stressors (Menza *et al.*, 2008; Bongaerts *et al.*, 2011, Baker *et al.*, 2016). Thus, MCEs can play a vital role in increasing the resilience of the more vulnerable shallow water reefs, particularly by the export of fish larvae and coral planulae, which aid the replenishment of disturbed populations. This role is termed as the “deep reef refugia hypothesis” (DRRH, Bongaerts *et al.*, 2011), and has prompted renewed interest in the study of mesophotic reefs. Despite MCEs importance for the conservation of degraded shallow habitat, the spatial characteristics and biophysical mechanisms underlying vertical connectivity of reef fishes are largely unknown (Tenggardjaja *et al.*, 2014; Holstein *et al.*, 2015, Puglise and Colin, 2016).

Pulley Ridge is located in the Gulf of Mexico approximately 250 km offshore of Florida (Fig. 1) and is known as the deepest mesophotic coral reef in continental U.S. waters (Reed, 2016). Photosynthetic zooxanthellate corals are common here along with an abundance of algae

at depths of 60 to 80 meters. A 346 km² area of the reef system is protected as the Pulley Ridge Habitat Area of Particular Concern (PR-HAPC) which is regulated by the Gulf of Mexico Fishery Management Council (GOMFMC) and prohibits bottom impacting fishing gear. Its reefs host more than 60 fish species, including a variety of shallow-water tropical fishes, such as *Thalassoma bifasciatum* (bluehead), *Stegastes partitus* (bicolor damselfish), and *Chromis enchrysurus* (yellowtail reef fish) (Halley *et al.*, 2005; Reed *et al.*, 2014).

The Florida Keys National Marine Sanctuary (FKNMS) which is approximately 60 km east of Pulley Ridge, is a stretch of islands, corals, seagrass and mangroves extending 200 miles along the Florida Keys. The region is the third largest coral barrier in the world, and was declared as a National Marine Sanctuary in 1990 (Suman *et al.*, 1990). The Sanctuary designation and management plan brought a degree of protection to the Florida Keys coral reefs from local anthropogenic actions, however, the region is still subject to both local and remote disturbances, including global warming and coral bleaching, which can lead to decline of coral coverage and fish assemblages. A better understanding of vertical connectivity is thus critical to determine if the boundaries of the Florida Keys National Marine Sanctuary should be extended to Pulley Ridge.

Available evidence from larval sampling, modeling studies, and genetic analysis, suggest horizontal connectivity among the shallower Florida Keys reefs for both vertebrates and invertebrate species (Limouzy-Paris *et al.*, 1997; Sponaugle *et al.*, 2012; Kough *et al.*, 2013). The question is whether such connections are also observed among reefs located on different depth strata, particularly between Pulley Ridge and the Florida Keys. Recent vertical connectivity studies for coral species showed genetic differentiation among different depths, with most export directed from shallow to deeper reefs (Serrano *et al.*, 2014; Prada and Hellberg, 2013), while other genet-

ic studies have found limited vertical connectivity for sessile species worldwide (Constantini *et al.*, 2011; Van Oppen *et al.*, 2011; Brazeau *et al.*, 2013), casting doubt upon the viability of the deep reef refugia hypothesis. Yet, these studies recognized that vertical connections are largely species- and location specific and that underlying biophysical mechanisms are still unknown. Biophysical modeling represents an ideal tool to the study of vertical connectivity patterns, allowing the investigation the relative importance of different processes (Paris *et al.*, 2007; Ayata *et al.*, 2010; Holstein, *et al.*, 2015). Moreover, it also overcomes the inherent limitations of synoptic sampling in a large study region.

Here we investigate the refugia hypothesis for reef fishes inhabiting the Pulley Ridge MCE. Our specific goals are to estimate the spatio-temporal scales of variability in larval connections from Pulley Ridge to the Florida Keys, and to unveil role of local oceanographic processes on successful export events. To address the complexities of simulating vertical larval transport, we add a submodule to the open-source Connectivity Modeling System (CMS, Paris *et al.*, 2013), representing the settlement habitat in three dimensions, and capitalize on accurate predictions by using a fine-resolution (~900m) ocean circulation model, the FKeyS-HYCOM (Kourafalou and Kang, 2012), while focusing on a species with known life history traits and widely distributed within our study region, the bicolor damselfish, *Stegastes partitus* (Sponaugle *et al.*, 2012). We also apply methods from dynamical system theory to identify physical structures underlying successful larval transport (Olascoaga *et al.*, 2010; Vaz *et al.*, 2013; Haller, 2015).

2. Methods

2.1. Study region

Our study region encompasses coral reefs habitats located in South Florida, a region characterized by a complex topography and unique ecosystems (Fig. 1a,b). The region abridges two distinct shelf areas, the broad Southwest Florida Shelf (SWFS) and the narrow Atlantic Florida Keys Shelf (AFKS). Connecting the two shelves is the deep region of the Straits of Florida. Of major importance for the local circulation it is the influence of the Loop Current, which enters the Gulf of Mexico through the Yucatan channel. The Loop Current originates the Florida Current when propagating through the Straits of Florida, and the Gulf Stream as it exits on the Atlantic Ocean (Weisberg and He, 2003; Kourafalou and Kang, 2012). Another important feature of the circulation is the downstream propagation of cyclonic mesoscale features, which are both locally and remotely generated (Lee and Williams, 1999; Kourafalou and Kang, 2012). The Loop Current influences particularly the outer region of the Southwest Florida Shelf, while the inner and middle regions are mostly influenced by wind stress and buoyancy fluxes induced by fresh-water discharge (Hetland *et al.*, 1999; Weisberg and He, 2003; Kourafalou *et al.*, 2009; Fig. 1a). The position and strength at which the Loop Current enters the Straits of Florida will also influence the Florida Current and its meandering front, changing the circulation over the Atlantic Florida Keys Shelf.

Our spawning and settlement grounds are spread from Pulley Ridge to the Upper Florida Keys (Fig. 1b). Spawning and settlement sites are represented by 51 discreet polygons (64 km^2), distributed along the water column from surface to 80m. Three distinct vertical strata are used in our simulations, as follows: i) shallow (0-20m, 32 polygons); ii) mid (20-40m, 15 polygons); and iii) deep (40-80m, 4 polygons). Due to the large extent of the reef tract, the Florida Keys is divided into four different regions: Western Keys (which includes Dry Tortugas and Marquesas Islands, 25 polygons), Lower Keys (10 polygons), Middle Keys (5 polygons), and Upper Keys (8

polygons).

2.2. Model description

To simulate the transport, connectivity and settlement of larvae originating from Pulley Ridge, we use the open-source Connectivity Modeling System (CMS, Paris *et al.*, 2013), a multi-scale Lagrangian implementation of an individual-based model (IBM) system, developed to investigate the physical and biological interactions surrounding the pelagic larval phase of marine organisms. Our multi-scale simulation relies on nested hydrodynamic models, which are three different implementation of the HYbrid Coordinate Ocean Model (HYCOM) covering the study domain with different horizontal resolutions capturing the spatial-temporal scales of circulation influencing larval dispersal in the region. The highest resolution model, 1/100 degrees (~900m), covers the Florida Keys (FKeyS-HYCOM, c.f. Kourafalou and Kang, 2012, 79-83.4°W 22.8-26.1°N). Daily hindcast from the GoM- and Global-HYCOM and 6 hourly for the FKeyS-HYCOM from 2004 to 2008 are used in the experiments.

The bicolor damselfish, *S. partitus*, has a wide distribution along the south Florida shallow and mesopelagic reefs, including the Pulley Ridge (Halley *et al.*, 2005; Reed *et al.*, 2014). The adult reproductive and larval of this species are well studied (Sponaugle and Cowen, 1996; Paris, 2001; Hixon *et al.*, 2012), and our model is able to reproduce successfully settlement levels measured *in situ* (Sponaugle *et al.*, 2012). Here, to properly represent vertical connections between shallow and mesophotic coral reefs, we develop a three dimensional (3D) version of the CMS seascape module described in Paris *et al.* (2013). This novel 3D seascape module allows CMS users to configure spawning and settlement areas at discrete depths; settlement only occurs if a larva is found within both vertical and horizontal boundaries of a polygon during its compe-

tency period (i.e., between its minimum and maximum pelagic larval duration or PLD).

We define three vertical strata encompassing from shallow water to mesophotic reefs (0 to 20m, >20m to 40m, and >40m to 80m). The 3D discrete polygons representing the spawning and settlement sites of *S. partitus* are obtained by combining a 2-dimensional (2D) map of reef locations with bathymetric projections from the 2 min NRL DBDB2 global data set. The reef locations were initially represented by 2D polygons (8km x 8km, as further described on Holstein *et al.*, 2014). By projecting each polygon boundary into the bathymetry, we verify if the 2D reef polygons have more than half of its area located on water throughout a strata depth (e.g. from 0 to 20m). If so, we use the 2D boundaries and the depth strata information to create a 3D polygon. The use of this criteria resulted in 51 3D polygons, distributed as follows: 32 in shallow depths (0-20m), 14 in mid depths (20-40m) and 5 deep polygons (40-80m), which include three polygons representing Pulley Ridge (Fig. 1b). Spawning occurs on a daily frequency at 51 sites, and the number of larvae released is scaled by *S. partitus* lunar cyclic spawning observed in Sponaugle *et al.* (2012), with a minimum and maximum of 100 and 1400 larvae released per site, respectively. Larvae are competent to settle 20 days after hatch and were tracked for a maximum PLD of 32 days following Sponaugle *et al.* (2012).

Specific traits of *S. partitus* larvae incorporated in the model are ontogenetic vertical migration (Paris and Cowen, 2004), and a daily mortality rate (Paris-Limouzy, 2001; Paris, 2009) measured *in situ*. Ontogenetic vertical migration is parametrized in CMS by a matrix of probabilities of Gaussian vertical distribution of larvae by age, where the center of mass and standard deviation of larval concentrations in the water column were parameterized with observations (Paris and Cowen, 2004). To account for the differences in depth between the spawning sites (<40 m on the Florida Keys and >60 on Pulley Ridge), we use two different vertical distributions (Supple-

mentary Information Table SI 1): 1) at shallow reefs the distributions of pre flexion larvae (less 10 days, Paris-Limouzy, 2001) were in the upper 20m of the water column, similar to those measured by Paris and Cowen (2004); at deeper reefs, pre-flexion larvae were in the lower 20m (i.e., 60-80m) of the water column, and were advected vertically by buoyancy alone. After reaching the flexion stage, all larvae OVM followed Paris and Cowen (2004). Daily mortality is given by an exponential decay function, representing the half-life of a spawning cohort (Paris 2009, Paris *et al.*, 2013). The full simulations include 1825 spawn events where more than 100 million larvae are tracked.

2.3. Characterization of connectivity

Throughout the simulation, CMS generates Lagrangian output for individual larva, *i.e.*, time and 3D coordinates, and connectivity output for each successful larva *i.e.*, its release site (i), settlement site (j), release and settlement time, and settlement depth. This output is used to generate sparse connectivity matrices (i,j). Since there is no information on larval production at each individual reef site (or reef polygon), the population connectivity is a row-normalized matrix representing the probability that a larva from a spawning site i arrives at a settlement site j (p_{ij}), while the content of the diagonal cell elements ($p_{i,j=i}$) represents the probability of self-recruitment (Paris *et al.*, 2007). Daily matrices are further computed to estimate the magnitude and temporal scales of the connections from Pulley Ridge to the Florida Keys.

The most common simulated larval pathways are represented by larval trajectories probability density function (PDF). These PDFs are computed from the CMS Lagrangian output by binning larval trajectories of successful settlers into a 0.05° by 0.05° grid. Larval PDFs trajectories are calculated for the initial dispersal period, or 10 days following spawning, and for the lar-

val competency period, or the last 12 days of dispersal when larvae are able to settle. Resulting PDFs are used to observe differences on larval pathways during the occurrence of distinct circulation conditions. To understand the spatial-temporal patterns of variation of the connectivity between Pulley Ridge, the Dry Tortugas and the Florida Keys, we employ spatial and temporal time series methods following Paris *et al.* (2002). These analyses are based on the joint output from the three spawning sites, or reef polygons, located on the Pulley Ridge (Fig. 1). We do not find significant difference by considering Pulley Ridge spawning sites individually or combined (results not shown), therefore we treat Pulley Ridge as a single polygon. First, we calculate the energy density spectra of the daily settlement of larvae spawned at Pulley Ridge by using a Fourier Fast Transform method (FFT) smoothed by a Hamming window with 365 points (i.e., one year). Second, the Empirical Orthogonal Functions (EOFs) of the daily anomalies of successful settlers spawned at Pulley Ridge are computed to obtain the major spatial and temporal patterns of settlement, following Paris *et al.* (2002). The EOFs are computed using the single value decomposition (SVD) method described by Emery and Thompson (2003).

2.4. Characterization of the flow

To aid the identification of physical mechanisms facilitating larval transport from Pulley Ridge to the Florida Keys, we employ Lagrangian methods, which allow the identification of physical mechanisms such as eddies, fronts and high turbulence. Of importance to larval dispersal is the characterization of the Hyperbolic Lagrangian Coherent Structures (LCSs), which are the most attracting or repelling material fluid lines of the flow (e.g., Haller, 2015). Attracting LCSs are particularly useful in this context: these structures act as attractors of particles, while also serving as barriers to transport in the cross LCS direction (Olascoaga *et al.*, 2010; Vaz *et al.*,

2013). The LCSs here are obtained by calculating Finite-time Lyapunov Exponents (FTLE, Haller, 2000; Haller, 2015), using the Eulerian velocity field from the FKeyS-HYCOM and GoM-HYCOM. The FTLEs are computed by simulating the dispersion of particle pairs over a time interval $[t_0, t_0+T]$, and the FTLE is proportional to the separation experienced by the particle pairs (Haller, 2000). Here, we are interested in finding the attracting LCSs, which act as aggregators of fluid material. Thus the velocity field (and particle dispersion) is integrated backwards ($T < 0$).

Broadly, ridges in FTLE fields tend to separate regions of the fluid presenting different dynamic activity. Fluid parcels found within a FTLE ridge tend to remain together as the flow evolves. Thus, the resulting maps can be used to characterize the underlying structures affecting larval transport in our study region, particularly 1) the presence of mesoscale activity and 2) the relative position of the Florida Current in relation to settlement grounds in Florida Keys.

In addition, a spectral analysis of the anomaly of the latitudinal position of the Florida Current front calculated at 83°W by Kourafalou and Kang (2012) is used to investigate the contribution of mesoscale variability on larval connectivity. The longitudinal incursions of the Loop Current displacement at 24.7°N are also quantified and correlated to the daily settlement time series, (where the Loop Current location defined as the 17 cm contour of SSH, Hetland *et al.*, 1999; Leben, 2005). Finally, the dispersal of larvae spawned on selected dates is tracked over time. Larval position is compared with both velocity fields and the Okubo-Weiss parameter calculated using the velocity fields integrated from 0 to 50m. The Okubo-Weiss parameter compares the relative vorticity and strain of the flow field, giving an indication of the presence of eddies (Kourafalou and Kang, 2012). In this paper, we limit our discussion to cyclonic mesoscale features occurring along the Loop Current and Florida Current front.

3. Results and Discussion

3.1. Connectivity between Pulley Ridge and the Florida Keys

The daily probabilistic matrix for larvae spawned at Pulley Ridge settling in the Florida Keys is shown in Figure 2. Larvae released at Pulley Ridge are exported to the Florida Keys reef tract, throughout all strata considered in the simulations, suggesting vertical transport. Connectivity of *S. partitus* larvae from Pulley Ridge to the Florida Keys is transient, whereby periods with high settlement alternate with periods with no settlement. In addition, these connections vary spatially and temporally (Fig. 2). During events where a large number of larvae successfully settle, most settlement occurs on reefs closer to Pulley Ridge, particularly Dry Tortugas and Marquesas Islands. Indeed, the probabilistic matrix for the entire study period (2004 to 2008) reveals that larvae released at Pulley Ridge present a high likelihood of settling at all strata the Western Florida Keys (Fig. 3). On the contrary, self-recruitment at Pulley Ridge is estimated around 30%, and its reefs appear to receive limited *S. partitus* larval subsidies from the Florida Keys. These results indicate that the region of Pulley Ridge might rely on local replenishment to support its population of *S. partitus*, or can receive additional larval subsidies from other regions not considered in this study, such as the shelf-break reefs located in the northern Gulf of Mexico.

3.2. Spatial and temporal scales of connectivity

The two-dimensional energy spectra of the daily probability of settlement quantify periodicity in connectivity (Fig. 4a). The elevated energetic peaks over some regions indicate larger settlement variability. A notable high energetic power spectra is found for settlement in the Western Keys, particularly in the upper 40 m reefs from the Dry Tortugas. Variability occurs at

high frequencies of periods equal or less than 30 days (Fig. 4a). These peaks reflect the lunar cycle periodicity of *S. partitus* spawning. The density spectra of the daily probability of settlers from Pulley Ridge also shows defined peaks, concentrated on the higher frequency band, which includes peaks at 7, 10, 15-16 and 28-30 days (Fig. 4b). Besides the peaks related to the spawning lunar cyclicity, clear peaks at 10 and 15 days are likely related to mesoscale eddy activity. Indeed, the spectral analysis of the anomaly of the latitudinal position of the Florida Current front reveals similar peaks at 28-30, 16, and 10 days, reinforcing the assumption the Florida Current underlays some of the observed variability in settlement. Other peaks of the Florida Current front are found at 60, 43, and 19 days (Fig. 4c).

The analysis of the spatial patterns of settlement will be referred hereafter as EOFs, while the temporal analysis of settlement patterns (or expansion coefficient, EC), will be referred as ECs. The first and second modes of the EOF explain together 72% of the settlement variability, with the first mode accounting for 43%, and the second mode for 29% (Fig. 5a). The magnitude of these 2 major EOF modes is larger over the shallow (<20m) and mid-depths (20-40m) of the Western Keys, corroborating expected high variability of settlement (Fig. 4a, 5a). The first EOF mode is positive throughout all reefs, with highest magnitude in the Marquesas reefs, both at shallow (< 20m) and mid-depths (20-40m). While the second EOF mode is also positive and peaks on the Western Keys, its higher magnitude occurs over the Dry Tortugas reefs. As expected, ECs' magnitudes are greater during peaks of larval export from Pulley Ridge. Specific settlement events are explained by distinct modes, as illustrated by two events highlighted on Fig. 5b.

The first EOF mode is related to settlement on the Marquesas Islands, while the second EOF mode is related to settlement on Dry Tortugas, as observed by the modes amplitudes over

the settlement grounds (Fig. 5a). These results were corroborated by relating specific settlement events dates (from Fig. 5b), with the probability of settlement showed on Fig. 2. Although EOFs are useful to represent patterns of a variable distributed over a large area for a long period, it is not always possible to relate individual EOF modes to specific physical processes. Here, the fact that different modes explain the variability of settlement peaks occurring at distinct geographical areas, suggests that separate physical mechanisms could regulate successful connections between Pulley Ridge and the Florida Keys. To evaluate this hypothesis, we investigate dispersal pathways and flow characteristics on these events. The following spawning dates are used in our analysis, since most of their settlement variance was explained by a EC mode (in chronological order): i) first mode: 8/28/2005, 11/24/2007, 12/1/2007; ii) second mode: 8/41/2004, 1/25/2005, 7/29/2005. In the following sections, results are shown from the following spawning events (as noted on Fig. 5b): E1 (12/1/2007) and E2 (1/25/2005).

3.3. Larval dispersal pathways and flow during high connectivity events

The dispersal pathways following spawning are highly variable, even for spawning days explained by the same mode (Fig. 6a,c). Generally, larvae spawned during events explained by the first mode are transported southward, and towards the Florida Keys, while larvae spawned during events explained by the second mode tend to be transported initially in the northwestern direction, towards the Southwest Florida Shelf. On both events, it is possible to observe a region of intense mixing in the Southwest Florida Shelf revealed by the LCSs (Fig. 6b,d). During E2, both the velocity fields and the LCSs show the Loop and Florida Currents flowing closer to the Pulley Ridge and the Florida Keys than during spawning events E1, when the Florida Current is located to the south of the Florida Keys. Also, on E2 a cyclonic eddy over the Dry Tortugas re-

gion is evident on the averaged velocity fields.

Distinct patterns of dispersal emerged during the settlement period (Fig. 7a,c). During their competency period, larvae spawned on events explained by the first mode were spread south of the Florida Keys (i.e., south of 24.4°N), particularly alongshore the Marquesas Islands and the Lower Keys. On the contrary, the pathways of the second mode settlers concentrate around the Western Florida Mid-Shelf and the Dry Tortugas region, mostly north of Pulley Ridge (i.e., latitude higher than 24.4°N , the average latitude of Dry Tortugas).

Averaged velocity fields and LCS also corroborate these findings. The LCSs fields calculated for settlement days of spawning events of the first mode (Fig. 7b) show the presence of mesoscale features, which propagate along the Straits of Florida and the Florida Keys. A concentration of attracting LCSs near the downstream reefs of the Western Keys is in agreement with high settlement expected on these reefs and dates (Figs. 2,5b). From the LCSs fields it was also possible to infer that the Florida Current was retreated to southern positions during event E1. Alternatively, attracting LCSs during settlement of larvae spawned during the second mode (Fig. 7c) are concentrated over the region of Dry Tortugas, and also distributed close to the Atlantic Florida Keys Shelf. The direction of these attracting LCSs are following the main curvature of the local bathymetry, indicative that the Florida Current is close to the reefs. Such circulation patterns are favorable for the retention of larvae over the Dry Tortugas and the Western Florida Keys.

During the spawning events that yield the highest settlement, the Loop Current was extending northward into the Gulf of Mexico (or at its "mature phase," Hetland *et al.*, 1999), as observed on Sea Surface Height maps (SSH, Fig. S1). However, no significant correlation between the time series of settlement and of the longitudinal incursions of the Loop Current was found for

the study period. The SSH fields also show that the configuration of the mesoscale circulation differs greatly between settlement events (Fig. S1). Indeed, during event E2, explained by the 2nd EOF mode, a cyclonic eddy sits on the Southwest Florida Shelf, to the northeast of Pulley Ridge right after spawning. But the SSH shows a cyclonic eddy near the Western Florida Keys for the events E1, which is explained by the 1st mode of the EOF.

3.4. Interactions of flow and biological traits shaping connectivity

The circulation patterns in the narrow Atlantic Florida Keys Shelf and in the broad Southwest Florida Shelf are influenced by both local and remote forcing, such as wind stress, buoyancy fluxes from the Mississippi river and watersheds on the Western Florida Shelf, the Loop Current and its front, meanders and associated eddies (Weisberg *et al.*, 2005; Kourafalou *et al.*, 2009; Kourafalou and Kang, 2012). Oceanic flows around the Florida Keys are primarily from west to east, and this is also the predominant downstream locations of settled larvae spawned at Pulley Ridge in our simulations. The regional averaged flow is dominated by the Florida Current, which originates when the Loop Current enters the Florida Straits. The position at which the meandering Florida Current front approaches the Florida Keys and the Atlantic Florida Keys Shelf varies seasonally and inter-annually (Kourafalou and Kang, 2012). Settlement peaks occur when the Florida Current front reaches a southern position near the western edge of the Florida Keys, therefore allowing remotely generated eddies to propagate along the reefs, aiding with entrapping and transporting larvae to settlement grounds. Both locally and remotely generated eddies can have their dissipation or growth enhanced by interactions with the topography of the Florida Straits, and by latitudinal variations of the Florida Current (Kourafalou and Kang, 2012). In our study we observed that the elongation of the cyclonic eddies as they

moved towards shallower bathymetry enhanced a counter current flowing along the Florida Keys, which further favored settlement. This is apparent in the trajectories of larval settlers during settlement on the event E1 (Dec/01/2007, Fig. 7a). Yet, the Florida Current front variability is not a good predictor of settlement. We found no significant correlation between the time series of the latitudinal variations of the Florida Current front (Kourafalou and Kang, 2012), and larval export from Pulley Ridge, up to a lag of 15 days (results not shown). This result corroborates with the transient nature of connections between Pulley Ridge and the Florida Keys, indicating that episodes of high connectivity resulted from rare optimal conditions created by a combination of physical and biological mechanisms. Connectivity would depend on a match-mismatch of favorable oceanographic conditions with the phenology of the target species. A match-mismatch hypothesis was put forward by Cushing (1969) between the food and the timing of first feeding for fish larvae. Here we find that the physical conditions present after spawning and during the early stages of larvae (about 10 days) are critical to realized connectivity and thus to reproductive success. Spawning timing with favorable physical conditions has been shown to play a fundamental role in various locations and species (Ayata *et al.*, 2009; Ayata *et al.*, 2010; Karnauskas, *et al.*, 2011; Vaz *et al.*, 2013).

Not only the remote circulation favors connectivity between Pulley Ridge and the Florida Keys, but local circulation mechanisms also play an important role. Circulation features occurring over the broad Southwest Florida Shelf were particularly important to enhance settlement on Dry Tortugas. Pulley Ridge is located on the outer shelf, where the interactions of the Loop Current, heat fluxes and shelf bathymetry create flows along the shelf break (Hetland *et al.*, 1999; He and Weisberg, 2003). Northward flows were observed at this region on the event explained by the second mode, such as Jan/25/2005 (E2). Larvae spawned at Pulley Ridge during north-

ward flow events are transported over the mid-shelf where a balance between buoyancy and wind-driven flows drives the transport (Weisberg *et al.*, 2005; Kourafalou *et al.*, 2009; Liu and Weisberg, 2012). Southward flows occur on the mid shelf during E2, aiding the dispersal of Pulley Ridge larvae towards Dry Tortugas. Once near Dry Tortugas, larvae benefit from the persistent eddy activity (Lee and Williams, 1999; Kourafalou and Kang, 2012) to be retained long enough, until they reach their competency period and settle.

The dispersal pathways revealed by the modeling outline the importance of the eddying flow for increasing connectivity, as per the initial work of Paris-Limouzy *et al.* (1997). This is indeed supported by the findings of energy peaks at frequencies related to mesoscale activity on the spectral analysis of daily settlement (Fig. 4a,b). It has been long suggested that eddies could aid reef fish settlement in the region, which has been confirmed by *in situ* observations (Lee *et al.*, 1992; Limouzy-Paris *et al.*, 1997; Lee and Williams, 1999; Sponaugle *et al.*, 2005). However, eddies occurring in the study region might have different origins (i.e., remotely or locally originated), do not present a clear temporal or spatial pattern, and vary in number, strength, and characteristics in scales from days to years (Kourafalou and Kang, 2012). In this context, the timing of spawning can be determinant on the outcome of a larval cohort and could also bring food to the larvae for better survival (Cushing 1969). This has also been suggested by *in situ* observations in South Florida (Sponaugle *et al.*, 2005) and in modeling studies for other regions presenting high eddy variability (Karnauskas *et al.*, 2011; Vaz *et al.*, 2013). The present study however, sheds a new light on this subject by exploring vertical connections. Here, we find that the co-occurrence of larval vertical migration and mesoscale circulation is not only an effective transport mechanism to connect fragmented coral reef habitat distributed over a large geographic region, but also to aid connections between reefs located at different depths. This result serves to

better understand the role of mesophotic reefs in increasing shallow water reefs resiliency. Moreover, our simulations indicate that populations of *S. partitus* at Pulley Ridge can be sustained by self-recruitment (Fig. 3). The region might also receive *S. partitus* larval subsidies from reefs outside of the study region, particularly other reefs in the Western Florida Shelf. This scenario deserves future investigation.

4. Summary and Conclusions

Our analyses allow the characterization of dispersal pathways of successfully settled larvae, and the identification of oceanographic mechanisms influencing vertical and horizontal connections between Pulley Ridge and the Florida Keys. In summary, the connection from Pulley Ridge to Dry Tortugas occurs via two main pathways: i) larvae are dispersed by the Florida Current flowing close to the Pulley Ridge latitude, and later recirculated over the Dry Tortugas (Fig. 6a) or ii) larvae are initially transported to the northeast of Pulley Ridge (Fig. 6c), then southward towards the Dry Tortugas (Fig. 7c). In both cases, cyclonic eddies over the Dry Tortugas enhanced settlement, which corroborated with high concentration of settling larvae trajectories in the region (Fig. 7a,c). This influence is evident on the animation of larval dispersal and evolution of the flow field as seen with FTLE, which is provided in the supplementary information (video S1).

Occasionally, the southward movement of the Florida Current Front allows the entrance of remotely generated cyclonic eddies (Fig. 7b). Larvae spawned at Pulley Ridge can be entrapped by these remotely generated eddies and transported over the shallower bathymetry of the Florida Keys. In this case, larvae reach the downstream reefs of the Western Keys during their competency period and predicted settlement increases (Fig. 7a). An example of a remotely gen-

erated cyclonic eddy facilitating transport between Pulley Ridge and Marquesas is available in the supplementary information (video S2). These connections depend on an unusual combination of circulation patterns related to the species phenology (the timing of peak spawning) and its larval traits (i.e., vertical migration and competency period).

The study of mesophotic reefs has gained attention due to their possible role as refugia for coral reef populations, however, the characteristics of deep-shallow connections are still poorly understood (Lesser *et al.*, 2009; Kahng *et al.*, 2014, Puglise and Colin, 2016). Most of the genetic studies to date focused on the vertical connectivity of sessile species, revealing distinct patterns across species and locations (Constantini *et al.*, 2011; Brazeau *et al.*, 2013; Kahng *et al.*, 2014, Serrano *et al.*, 2014). Remarkably, the 3-dimensional connectivity of coral reef fishes is currently unresolved, and only one study addresses simultaneously the vertical and horizontal connectivity of a damselfish species in the Pacific Ocean (Tenggadjaja *et al.*, 2014). Here, the implementation of a 3D seascape module for the individual-based model CMS, considering vertically defined strata, allows the simulation of complex patterns of vertical connections between mesophotic and shallow water reefs (Figs. 2,3). Our modeling results could provide the first mechanistic explanation of potential connections for coral reef fish, contributing to increasing the understanding of mesophotic systems (Menza *et al.*, 2008; Kahng *et al.*, 2014; Puglise and Colin, 2016). Connectivity matrices indicate that Pulley Ridge may export *S. partitus* larvae to shallow coral reefs of the Florida Keys Marine National Sanctuary, particularly to the Western Keys reefs. This suggests that the “deep reef refugia hypothesis” is also valid for coral reef fish living in these habitats. However, connections between the Pulley Ridge and the Florida Keys seem highly variable, mostly in time, fluctuating with local oceanographic conditions found during the spawning events.

We find that large, yet rare settlement events are modulated by the co-occurrence of a series of bio-physical processes, namely: 1) the timing of peak spawning with the proximity of the Florida Current front to the Pulley Ridge and Florida Keys reef tract; and 2) the presence of cyclonic eddies on the Southwest Florida Shelf and along the Florida Keys. The potential of these physical mechanisms to entrap and successfully transport larvae to settlement grounds is optimized by the ontogenetic vertical migration behavior (Paris and Cowen, 2004). Given that connections between these two coral ecosystems are rare and dependent on a “perfect storm” situation, the protection of the entire system could decrease disturbances and help maintain ecological connections.

Deep water reefs are known to be more resilient to most stressors affecting shallow water reefs (Bongaerts *et al.*, 2010, Baker *et al.*, 2016). Yet, their coral coverage has shown some decline in several locations (Bak *et al.*, 2005; Armstrong *et al.*, 2006; Menza *et al.*, 2007) and including Pulley Ridge HAPC (Reed *et al.*, 2014; Reed, 2016). Our results suggest that the protection of these environments from additional anthropogenic pressures could positively impact the Florida Keys and FKNMS, receiving larval fish subsidies from Pulley Ridge.

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