Connectivity of Pulley Ridge With Remote Locations as Inferred From Satellite-Tracked Drifter Trajectories

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Abstract Using historical (1994–2017) satellite-tracked surface drifter trajectory data, we conduct a probabilistic Lagrangian circulation study which sheds light on the connectivity of Pulley Ridge with other locations in the Gulf of Mexico and adjacent areas. The analysis reveals that Pulley Ridge is connected with the North Atlantic, the Caribbean Sea, and most of the Gulf of Mexico. Preferred connecting pathways are identified and arrival times to potential reef sites computed. The study demonstrates the importance of Pulley Ridge as a source for neighboring regions like the Dry Tortugasa, the Florida Keys, Campeche Bank, and the east Florida coast as well as a self-recruitment area for species with short competence time. The study further suggests that the reefs in the Caribbean Sea, the Dry Tortugas, the western Florida Keys, and the West Florida Shelf can act as sources for Pulley Ridge, indicating the importance of Pulley Ridge as a central refugium for species in the Gulf of Mexico.
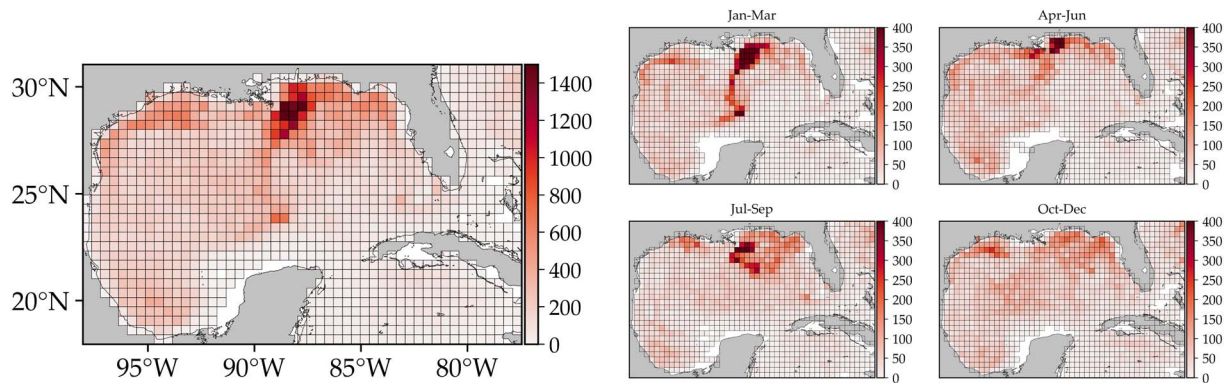
1. Introduction

Pulley Ridge is a mesophotic coral reef system in the Gulf of Mexico (GoM), located 80-m deep in the southwestern Florida shelf, and it is the deepest in continental U.S. waters (Reed, 2016). Far from the coast and surface, this coral reef is not impacted by coastal pollution and water temperature fluctuations that affect most shallow water reefs. It has been hypothesized that mesophotic coral reefs such as Pulley Ridge can be an important source of larvae for the more vulnerable shallow water reefs like the Dry Tortugas and the Florida Keys (Bongaerts et al., 2010; Semmler et al., 2016; Serrano et al., 2014). To protect those critical ecosystems, the GoM Fishery Management Council is considering the extension of the Florida Keys National Marine Sanctuary to Pulley Ridge (Baker et al., 2016; Reed, 2016).

Recent biophysical modeling work by Vaz et al. (2016) has provided a positive test for the above hypothesis by finding mesophotic–shallow coral reef connections by sporadic pulses of bicolor damselfish larvae settling in the Dry Tortugas and the Florida Keys, which supports the idea that Pulley Ridge can serve as a refugium for coral reef fauna and flora.

Despite the advancement of the understanding of how physical mechanisms drive the connections between Pulley Ridge and other reefs (Vaz et al., 2016), this knowledge is restricted to studies using hydrodynamic models, and there is a lack of direct measurements of connection pathways at large scales. The surface ocean circulation exerts first-order constraints on surface tracer transport, and in order to understand how different habitats are connected within the GoM, it is important to better understand the surface Lagrangian transport.

Here we examine the oceanographic connectivity of Pulley Ridge with remote locations using historical (1994–2017) satellite-tracked surface drifting buoy trajectory data. Additionally, we seek linkages between oceanographic and biological connectivity of the Pulley Ridge mesophotic reef, centering on surface dwelling pelagic larvae. Unlike prior use of drifter trajectory data in the study of connectivity (e.g., Carrillo et al., 2015; Lugo-Fernandez et al., 2001; Méndez-Jiménez et al., 2015), we consider a larger collection of drifters and further do not restrict attention to those drifters that happened to visit, or were deployed within, Pulley Ridge. In particular, a discrete transfer operator (Dellnitz et al., 2009; Froyland, 2001; Miron et al., 2017) is constructed using the totality of the drifter trajectories in the GoM to study its oceanographic connectivity in a statistical sense.

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Figure 1. Number of drifters per grid bin independent of the day over 1994–2017 (left) and regrouped by season (right). The finite grid used to construct a Markov-chain representation of the dynamics is shown in black.

In section 2, Pulley Ridge oceanographic connectivity is assessed from direct inspection of trajectories. The connectivity is then inferred using the transfer operator method in section 3. In section 4, we discuss the results from previous sections and the implications of habitat connectivity for the invasive lionfish (*Pterois volitans*), and two coral species: the great star coral (*Montastraea cavernosa*) and lettuce coral of the Agariciid group, which are considered because of their pelagic surface larval phase, their presence in Pulley Ridge (Reed et al., 2016), and the availability of genomic data for comparison. A summary and the conclusions are presented in section 5.

2. Direct Trajectory Inspection

We begin our assessment of the Pulley Ridge oceanographic connectivity with the rest of the GoM by directly inspecting drifter trajectories. The trajectories considered are taken from the large historical drifter database described in Miron et al. (2017), augmented with 16 drifters deployed recently within the Pulley Ridge neighborhood as part of the NOAA-funded Pulley Ridge Project (https:// coastalscience.noaa.gov/projects/detail?key=63). The historical data set combines surface drifters (undrogued, or 1–45-m drogued) from the NOAA Global Drifter Program (575; drogued at 15 m); the LAgrangian Submesoscale ExpeRiment (1002; drogued at 0.5 m); the Surface Current Lagrangian-Drift Program (523; drogued at 1 m); the Horizon Marine Inc.'s Eddy Watch program (441; drogued at 45 m); the Centro de Investigación Científica y de Educación Superior de Ensenada — Petróleos Mexicanos *Caracterización Metoceánica del Golfo de México* project (372; drogued at 45 m); the Grand LAgrangian Experiment (302; drogued at 1 m); the NOAA/Atlantic Oceanographic and Meteorological Laboratory South Florida Program (68; drogued at 1 m); drifters from the U.S. Coast Guard (30; drogued at 1 m) during LAgrangian Submesoscale ExpeRiment; and drifters deployed during the third GoM Ecosystems and Carbon Cruise (GOMECC-3; 23; drogued at 0.5 m).

Figure 1 in Miron et al. (2017) shows a *spaghetti* plot of trajectories from the historical database revealing a good spatial coverage of the GoM domain and adjacent portions of the Caribbean Sea and North Atlantic (this figure remains largely the same when the 16 drifters from the Pulley Ridge Project are included). Figure 1 shows that sampling is dense in space and also fairly well distributed across seasons. Ignoring time, about three drifters are found per kilometer squared on average. Exceptions are relatively small regions on the Yucatan Shelf, south of Cuba, and the Bahamas Bank, which have never been visited by any drifters. Gaps become more and more evident as time variability is considered. The time variability has been ignored in the analysis carried out by Miron et al. (2017) to maximize data coverage. We here follow Miron et al. (2017) and further note that a complete seasonal analysis might be possible but only if complemented with trajectories produced by an ocean model, which we do not pursue here.

There are more than 3,300 drifter trajectories since 1994 in the GoM, but only 74 drifters visit the Pulley Ridge area. Figure 2 shows a subset of these trajectories. They give an indication of the extent of possible surface connectivity with Pulley Ridge. Drifters that go through Pulley Ridge are seen to be coming from the Caribbean Sea and Yucatan area, the west Florida coast and shelf, the Florida Panhandle, the Dry Tortugas and the western Florida Keys, and Bay of Campeche. Drifters that pass through Pulley Ridge mainly reach the Dry Tortugas and the Florida Keys and the west and east Florida shelf.
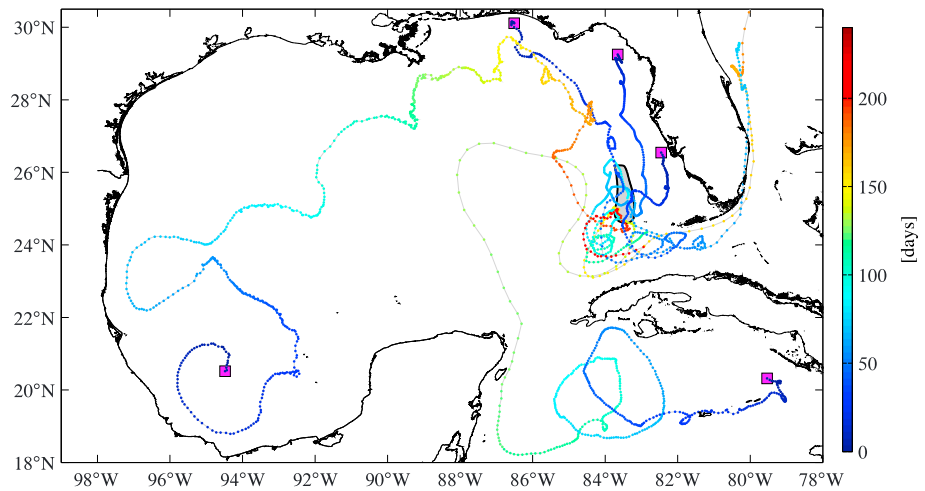
Figure 2. Satellite-tracked drifter trajectories highlighting some pathways from and to Pulley Ridge (gray area). The squares indicate the deployment positions.

Figure 3 shows the number of drifters which, starting on any day inside each of the 25-km-side boxes of a grid covering the domain, will visit Pulley Ridge within the next 6 months. Within the 6-month period, Pulley Ridge can be visited by drifters coming from most of the GoM. Note that the distribution of the drifters visiting Pulley Ridge is not uniform; more drifters originate on the West Florida Shelf than in the rest of the Gulf.

Table 1 shows the total number of drifters in each of the various regions indicated with numbers in Figure 3, the number of drifters that visit Pulley Ridge, and the time (median and range) it takes a drifter to get to Pulley Ridge from each of the regions. The regions were selected following prior work (Miron et al., 2017; Olascoaga, 2010). About 8% of the drifters from northwestern Florida shelf (region 4) visit the Pulley Ridge area. This accounts for 55% of the total drifters that have visited Pulley Ridge, thereby representing the main source for the region. About 3 % of the drifters from the Caribbean Sea (region 1) reach Pulley Ridge, which represents less than 3% of the total drifters that have visited Pulley Ridge. Another important characteristic is the high variability in the time it takes a drifter from any of the regions to reach Pulley Ridge. For instance, for a drifter originating in the Caribbean Sea, it can take as little as 15 days or as long as 4.5 months. Few drifters connect the Bay of Campeche (region 7) with Pulley Ridge, representing no more than 5% of the total number of drifters that have visited Pulley Ridge. The time the drifters take to connect these two regions is quite long
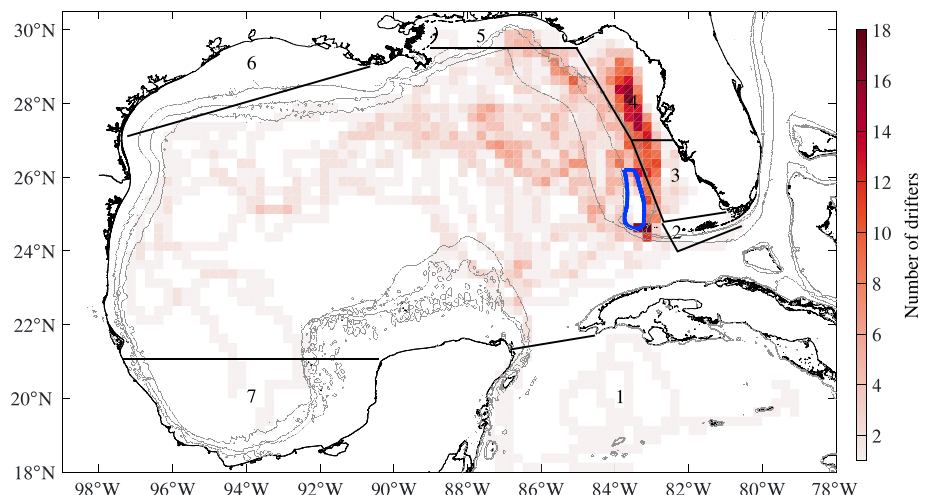
Figure 3. Number of drifters per 25-km-side box that starting on any day visit Pulley Ridge within the next 6 months. Gray curves correspond to the 50-, 100-, and 500-m isobaths. Regions 1–7 in Table 1 are indicated.

Table 1

Number of Drifters (of a Total Shown in Parentheses) That Have Visited Pulley Ridge After Passing Through Each of the Various Regions Indicated in Figure 3 and Corresponding Median Travel Time (Range in Parentheses)

Region #	# of drifters	Travel time (days)
1	2 (61)	75 (15–135)
2	5 (103)	18 (1.5–94)
3	21 (86)	5 (2–52)
4	41 (538)	15 (6–60)
5	9 (642)	39 (24–120)
6	1* (559)	129
7	4 (51)	171 (150–186)

*Drifter deployed on the shelf-break.

(more than 5 months). There is no evidence of direct connectivity with the interior of the Louisiana-Texas shelf (region 6). Only one drifter deployed on the shelf break was found to reach Pulley Ridge in about 4.3 months.

The high variability in connecting time with neighboring regions is revealed in Figure 4. The left panel in this figure shows the number of drifters per 25-km-side box that have gone through Pulley Ridge at any time. The middle (right) panel shows the minimum (maximum) time it takes the drifters to get to a given location after visiting the Pulley Ridge area (only boxes with more than three drifters were considered). The minimum and maximum time is taken since the drifter left the Pulley Ridge region. It can take a drifter from a few days to 2 months to travel from Pulley Ridge to the Dry Tortugas or the western Florida Keys. The upper Florida Keys and the east coast of Florida can be reached as fast as 1 week to as slow as a few months. Note also that the drifters can remain within (or nearby) Pulley Ridge for as long as 2 months or just for few days. The high variability in connecting and retention time can be related to the Loop Current position as well as the eddy activity in the area (Maze et al., 2015; Vaz et al., 2016).

To extend the above direct analysis of the drifter data beyond their strict spatiotemporal limits, a probabilistic approach that frames the action of the underlying Lagrangian dynamics at a coarse-grained level is presented in the next section.

3. Transfer Operator Approach

Let X be a domain on the surface of the ocean. Assume that tracer evolution in X is governed by an advection-diffusion process. A tracer δ-concentrated at position $x \in X$ at any time t evolves to some probability density $K(x, \cdot) \geq 0$ at time $t + T$. Normalizing so that the probability of getting somewhere from x is 1, namely, $\int_X K(x, y)dy = 1$ for all $x \in X$, $K(x, y)$ represents a stochastic kernel. A general initial tracer probability density $f(x) \geq 0$, $\int_X f(x)dx = 1$, evolves to

$$\mathcal{P}f(y) = \int_X K(x, y)f(x)dx. \tag{1}$$

Here $\mathcal{P}$ is a linear transformation of the space of densities $D(X) \subset L^1(X)$ to itself, a Markov operator known as the Perron-Frobenius operator or more generally a *transfer operator*. Markov operators defined by stochastic kernels and advection-diffusion equations are extensively discussed in Chapters 5.7 and 11.7 of Lasota and Mackey (1994), respectively.

Suppose that we are presented with tracer data in the form of trajectories of individual tracer particles, one can evaluate the action of $\mathcal{P}$ through a discretization of the Lagrangian dynamics using a Galerkin approximation referred to as Ulam's (1979) method. The Ulam method consists in partitioning the domain X into a grid of N connected boxes $\{B_1, \ldots, B_N\}$ and projecting functions in $D(X)$ onto a finite-dimensional space V_N approximating $D(X)$ and spanned by indicator functions on the grid. The discrete action of $\mathcal{P}$ on V_N is described by
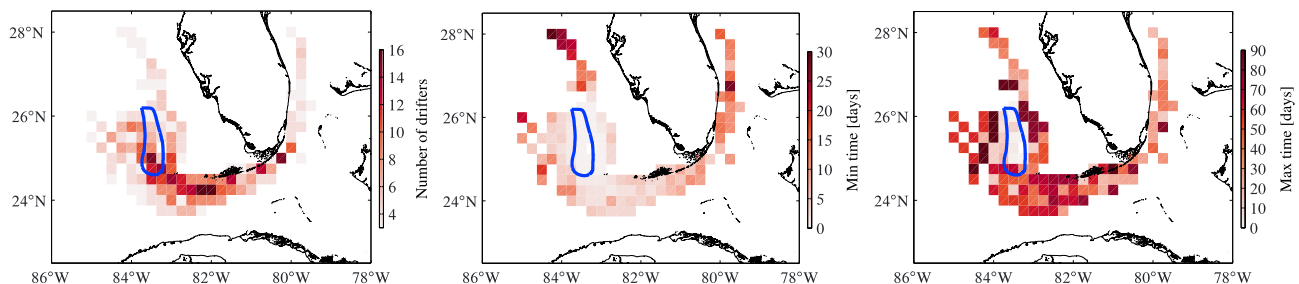
Figure 4. Number of drifters per 25-km-side box that have visited Pulley Ridge independent of the day (left) and minimum (middle) and maximum (right) time after visiting the Pulley Ridge area.
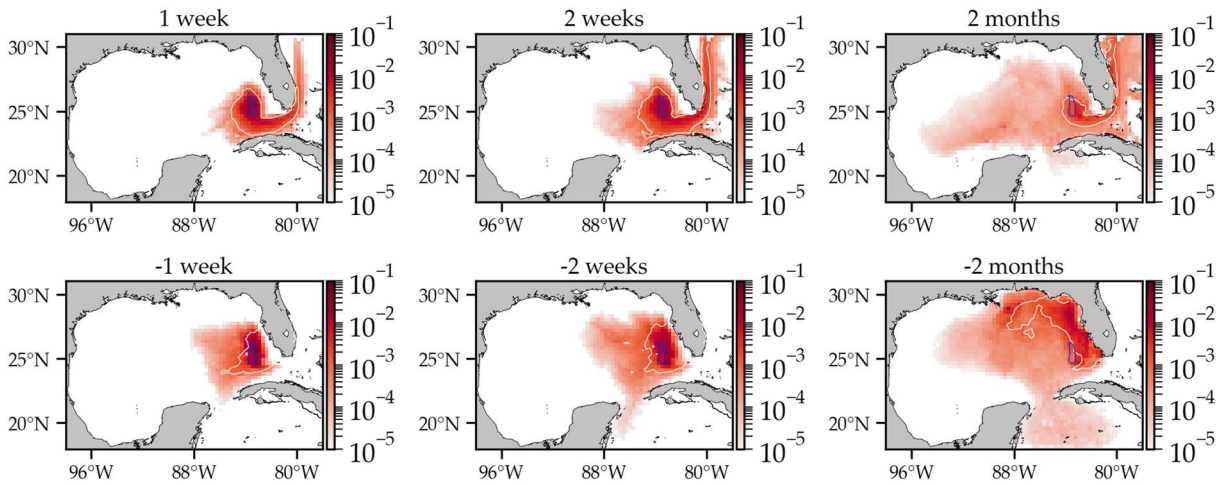
Figure 5. Forward (top) and backward (bottom) discrete drifter-data-based evolution of a tracer initially uniformly distributed over Pulley Ridge. On every frame, the 10^{-3} concentration is presented with a white contour line.

an $N \times N$ matrix P called a *transition matrix*. By considering a sufficiently large number of particles, we can estimate the entries of P as (e.g., Miron et al., 2017)

$$P_{ij} \approx \frac{\text{\# of particles in } B_i \text{ at any } t \text{ that evolve to } B_j \text{ at } t + T}{\text{\# of particles in } B_i \text{ at any } t}. \tag{2}$$

The matrix P defines a Markov-chain representation of the dynamics, with the entries P_{ij} equal to the conditional transition probabilities between boxes, which represent the states of the chain. The forward evolution of the discrete representation of $f(x)$, $\mathbf{f} = (f_1 \cdots f_N)$, is calculated under left multiplication, that is,

$$\mathbf{f}^{(k)} = \mathbf{f}P^k, \quad k = 1, 2, \dots . \tag{3}$$

The backward evolution is computed under left multiplication using P in (2) but with t replaced by $t - T$. We denote this transition matrix for backward evolution $\hat{P}$.

Note that the only time dependence in the exposition above is the duration of time T. We do not model variation of the advection-diffusion dynamics as a function of initial time. This statistical stationarity assumption, commonly made in turbulence studies (Orszag, 1977), has been considered in prior transfer operator analyses of drifter data (Maximenko et al., 2012; McAdam & van Sebillet, 2018; Miron et al., 2017). In particular, Miron et al. (2017) show that random reductions of the data set do not substantially affect the connectivity results.

Thus, following Miron et al. (2017), we construct the transition matrix P using 25-km-side boxes covering the GoM and 2-day-long drifter trajectory pieces, which may begin on any day (Figure 1). This box size choice guarantees reasonable individual box coverage. A transition time of $T = 2$ days is long enough to enable interbox communication. Moreover, there is negligible memory farther than 2 days into the past (LaCasce, 2008), so a Markov assumption is consistent with the above discretization. We note that while the above exposition assumes that the flow domain X is closed, the GoM domain is open. The only consequence of this is that P is substochastic, that is, $\sum_{j=1}^{N} P_{ij} < 1$.

Figure 5 shows the discrete drifter-data-based probabilistic evolution of a tracer initially distributed uniformly within Pulley Ridge, in both forward (top) and backward (bottom) time. The 10^{-3} concentration contour (white) is added to allow comparison with Figure 6. Note that one application of P ($\hat{P}$) corresponds to pushing forward (backward) an initial density by 2 days. As time advances, the tracer is drained out of the GoM (4%, 16%, and 65% after 1 week, 2 weeks, and 2 months, respectively) by the Loop Current through the Straits of Florida into the Gulf Stream. As it drains out of the GoM, the tracer reveals a connection between Pulley Ridge and the Florida Keys. This happens quite rapidly, within a period of less than a week. the Dry Tortugas and the western Florida Keys can be reached in ˜2 days. Note that a fraction of the tracer reaches the northern coast of Cuba. A small fraction of tracer is seen to be transported westward, which is the net effect of sporadic ring shedding from the Loop Current. This small tracer fraction reaches within 1 month or so the
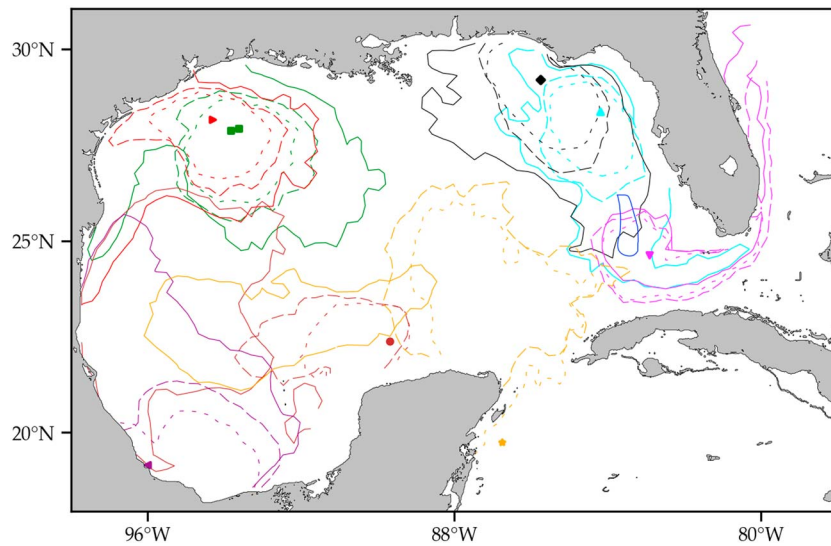
Figure 6. Isolines of 0.1% tracer concentration at 1 week (short dashes), 2 weeks (long dashes), and 2 months (solid). Tracer sources are located at Stetson Bank (red), East and West Flower Garden (green), Florida Middle Ground (cyan), Scorpions Reef (brown), Madison/Swanson Marine Reserve (black), Dry Tortugas (magenta), Veracruz (purple), and Mesoamerican Barrier Reef System (orange). After the 2-month period, 85% to 93% of the tracer concentration is bounded by those contour lines.

Campeche Bank, suggesting further connection of Pulley Ridge with this shelf. The backward time evolution shows the source of the tracer reaching Pulley Ridge. In the first 2 weeks, most of the tracer comes from the West Florida Shelf extending to the northern part. Within 1 month, the Florida Panhandle reaches the reef, while after 2 months, 2.1% of the initial tracer comes from the Caribbean Sea, and negligible amounts comes from the Atlantic Ocean. The tracers also comes from the eastern half of the GoM, covering a similar area to the eastern extended GoM (eeGoM) region presented in Miron et al. (2017).

Following the same methodology, we now push forward tracers initially located in some relevant ecological areas (e.g., Habitat Area of Particular Concern) within the GoM to investigate their oceanographic connections with Pulley Ridge. These areas were selected (from the list established by the GoM Fisheries Management Council) to be well distributed over the GoM in order to obtain a big picture of its connectivity (see a report by the Bureau of Ocean Energy Management [https://www.boem.gov/Essential-Fish-Habitat-Assessment/] and geographic information system data for most of the regions [http://sero.nmfs.noaa.gov/maps_gis_data/fisheries/gom/GOM_index.html]). In Figure 6, the contour lines correspond to 0.1% tracer density evolution starting from a 25-km-side box containing each of the ecological targeted areas after 1 week (short dashes), 2 weeks (long dashes), and 2 months (solid). Note that the source considered in the Mesoamerican Barrier Reef System is connected with both the western part of the GoM following the clockwise circulation and the Pulley Ridge area, the Florida Keys, and the North Atlantic through the Loop Current.

4. Discussion

While most marine species present a pelagic larval phase, their dispersal is regulated not only by the oceanographic transport but also largely by their own biological traits and available habitat in the case of benthic species. One notable behavior presented by the pelagic phase of several species is their capacity to change their buoyancy or to actively swim, occupying different vertical strata as they age, a behavior known as ontogenic vertical migration. The analysis presented here cannot capture this behavior, and results must then be interpreted as a first approximation of pelagic organisms motion in the oceans, particularly concerning the organisms that might occupy the first 10-m of the water column. In addition, other biological traits of the adult population influence the dispersal characteristics of their early stages, for instance, spawning seasonality. For this study, it was not possible to subsample our drifter data set to investigate seasonality patterns. Considering these limitations, below we discuss how the oceanographic connectivity might influence the distribution of the lionfish and two coral species (the great star and lettuce corals) found in Pulley Ridge.

The lionfish (*Pterois volitans*) is now present in the entire GoM, spawns all year round, and releases buoyant egg masses that float at the sea surface for about a week before larvae hatch (Morris et al., 2009). During this early stage, their dispersal is largely passive and thus can be approximately described by the drifters. Newly hatched larvae are hypothesized to leave the surface and undergo deep vertical migrations throughout their development, allowing the colonization from shallow water to mesophotic depths reefs. Indeed, numerous lionfish were observed to occupy red grouper holes on Pulley Ridge (Reed et al., 2016). Its typical larval duration falls in the range of 20–40 days (Ahrenholz & Morrist, 2010; Whitfield et al., 2002). In this case, the connection seems to be relatively fast stepping-stone (not continuous) within the Gulf (Schofield, 2010). This is corroborated by recent genomic analysis, which showed no genetic differentiation across the Atlantic coast of Florida, Caribbean Sea, and GoM (Pérez-Portela et al., 2018). Moreover, genetic data corroborated the colonization route of this invader from the Caribbean towards the GoM (Johnson et al., 2016). This pathway is supported by our findings (bottom right panel of Figure 5), which shows that the likelihood of transport from the Yucatan Straight towards Pulley Ridge at the lionfish pelagic duration is substantial. Following a stepping-stone pattern, larvae established at Pulley Ridge can then disperse toward both the Dry Tortugas and the Florida Keys, as well as toward the northern West Florida Shelf, as shown by our results.

Concerning the connectivity of the corals found at Pulley Ridge with the rest of the Gulf, lettuce coral (*Agaricia spp.*) is found in most of the Gulf but not in the West Florida Shelf and the Panhandle, and the great star coral (*M. cavernosa*) is not found in the northern West Florida Shelf nor in the Panhandle. These two species represent two distinct reproduction modes. *Agaricia spp* is a brooder (internal fertilization), releasing well-developed planulae which can start settlement within the first 24 hr in the water column, although in the absence of adequate subtract, some species of the genus can delay settlement by up to 42 days (Carlon & Olsont, 1993; VanMoorsel, 1983). Different agariciid corals spawn at distinct periods, and their planula also present distinct behavior and characteristics (Carlon & Olsont, 1993; VanMoorsel, 1983). The most common competency period for *Agaricia spp* is from 24 to 92 hr (Carlon & Olsont, 1993; Gleason & Wellingtont, 1995; Mavor, 1915), which is within the connectivity timescale between Pulley Ridge and the Dry Tortugas and the Florida Keys, but with a high likelihood of local recruitment, and not long enough to connect with the rest of the West Florida Shelf or the Panhandle area. This pattern is corroborated by a genetic analysis of Agariciid in Pulley Ridge and the Dry Tortugas, which registered no genetic flux between these regions (genetic distance based on the FST statistic = 0.0402, p value < 0.01; analyses performed following Drury et al., 2016). Contrastingly, *M. cavernosa* is a broadcaster spawner (external fertilization), releasing larvae which need about a week (Goodbody-Gringley et al., 2012) in the water column before achieving competency. The spawning of this species in South Florida is constrained in a small spawning season from July to September (Szmantl, 1991). Planula of a close broadcaster coral species (*Orbicella faveolata*) is initially highly buoyant (Holstein et al., 2016), which might allow larvae to reach the first 10 m of the water column. Broadcasting corals' planula are likely to remain long periods in the water column (around 100 days in lab experiments, Wilson & Harrisont, 1998). Thus, considering a possible settlement period from 1 week to few months, Pulley Ridge's larvae can reach the Southwestern Florida Shelf, as well as the Dry Tortugas and the Florida Keys (top panels of Figure 5). Moreover, it is evident (bottom-right panel of Figure 5) that planulae, originating on the north West Florida Shelf or the Panhandle area, can reach the Pulley Ridge region. However, other factors (e.g., behavior, habitat suitability, and water temperature) must be necessary for their successful settlement given the fact that *M. cavernosa* is not present in the north West Florida Shelf or the Panhandle area. Figure 6 highlights two possible pathways from the Caribbean Sea, to the Pulley Ride area or following the clockwise circulation to the western Gulf. Genetic analysis throughout the GoM and Caribbean has revealed that the species does not present genetic differentiation at shallow depths, including populations located at Flower Garden Banks (Goodbody-Gringley et al., 2012; Nunes et al., 2009; Serrano et al., 2014). However, there are patterns of genetic differentiation by depth (Brazeau et al., 2013; Serrano et al., 2014), which we are not able to address in our present study.

5. Summary and Concluding Remarks

In this paper, we have investigated possible oceanographic connectivity among Pulley Ridge and various regions in the GoM using a large set of satellite-tracked surface drifter trajectories. The surface pathways uncovered by the drifter trajectories constitute a first-order approximation for any surface ocean pollutant (e.g., spilled oil and toxic algae bloom), as well as for larval motion for species that have buoyant egg masses, such as lionfish (Morris et al., 2009), and broadcast spawners for which a fraction of larvae may reach the surface, such as the great star corals (Holstein et al., 2015; Wellington & Fittt, 2003).

The drifter trajectories revealed that Pulley Ridge can be a source of species with short settlement time for neighboring regions such as the Dry Tortugas, the Florida Keys, and the east Florida coast, but it can also be a source for remote regions such as Campeche Bank. The drifter data also suggested that Pulley Ridge can be connected with most of the GoM and the Caribbean Sea but because the larvae settlement time is in general smaller than the connecting time; only areas in the eastern GoM, Florida Straits, and northwestern Caribbean Sea (east of the Yucatan Peninsula and south of Cuba) could potentially be a source of larvae to Pulley Ridge.

The oceanographic connectivity results presented have the merit of relying exclusively on observed drifter trajectories. Their association with larval connectivity needs to be further assessed by biophysical modeling, whereby strategy of adults (e.g., spawning time and modality) is taken into account together with larval behavior (e.g., vertical motion during ontogeny, sinking behavior with turbulence and chemical cues, and orientation) and mortality. Accounting for these and other aspects such as settlement habitat is beyond the scope of the paper. Despite these restrictions, our study is an important step furthering the understanding of the oceanographic connectivity in the region, being the first one utilizing a large number of observations for this end.

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