

École polytechnique de Louvain

Modelling larval dispersal and coral connectivity in the Florida Reef Tract during hurricane Irma

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Academic year 2018–2019

Master [120] in Civil Engineering

Abstract

The Florida Reef Tract (FRT) is the third largest barrier reef in the world and lies at the southern end of Florida. Because of diseases, human activities and climate change, coral health and populations have declined in the last decades. In order to determine which coral reefs should be given the most attention to inhibit the destruction of the FRT, several studies focusing on coral connectivity were carried out. With this aim in mind, we studied the hydrodynamics of the FRT thanks to SLIM, a finite-element model solving shallow-water equations on an unstructured grid. We also used a Lagrangian particle tracker to follow coral larvae of two species: *Montastrea Cavernosa* (MC) and *Acropora Cervicornis* (AC). This tracker then provided us with a connectivity matrix, a square matrix of which each element gives the number of larvae that were seeded by a reef i and recruited by a reef j . We also used graph theory tools to treat this matrix and to identify connectivity properties of the FRT. In this study, we continued the work of Frys (2017) and Béchet and Verstraeten (2018) and investigated the impact that a hurricane could have on connectivity in the FRT. Florida is indeed subjected to increasingly more frequent and intense hurricanes. If the damage sustained by the corals are rather well documented, the changes in connectivity and the perspectives for coral development are not. We can indeed imagine that a hurricane is sufficiently strong to modify the larval dispersal in such a way that new connections between reefs are created. On the contrary, a hurricane might also cut off vital connections between reefs and have dramatic consequences on the coral network. To evaluate the impact of hurricanes, we focused on hurricane Irma, which made landfall on the FRT on 10 September 2017. It appeared that MC spawning season started on the same day and ended on 12 September. Since Irma had vanished from the area on 12 September, we could compare the larval dispersal and the resulting connectivity patterns between the larvae seeded on 10 and 12 September. Furthermore, we compared the total MC's connectivity with the connectivity of AC, which spawned a month before MC. AC's larval dispersal was thus barely impacted by Irma. The comparison between the connectivity properties of these two species showed that a hurricane similar to Irma would mainly affect the westernmost reefs of the FRT. These reefs indeed become greater suppliers of the network, but do no longer recruit many larvae. For that reason, protective measures affecting these reefs could be useful to face hurricanes comparable to Irma. Apart from these reefs, the scattered islands of the Florida Keys look sufficiently dense to hold back larvae from being sent away by the hurricane. The majority of the reefs thereby shows similar properties with and without hurricane conditions. Moreover, it appears that if a hurricane crosses the FRT during the spawning season, it will most likely enhance the diversification of the network. The different reefs will indeed benefit from the new connections enabled by the hurricane and combine their usual connections with the new ones to constitute a large and diverse cluster of reefs.

Acknowledgments

First of all, I would like to thank my supervisor Emmanuel Hanert. He kept supportive and enthusiastic all along the year, even when I faced major issues and did not achieve any progress for several weeks. I have never heard of any other supervisor who sees his thesis students two times a week. Honestly, I could not think of a better framework. I would also like to thank my co-supervisor, Eric Deleersnijder for the marine hydrodynamics background he gave me.

I would also like to thank Antoine Saint-Amand and Thomas Dobbelaere for the precious and tedious work they delivered for me. Without them, I would still be struggling with the preprocessing of the data. My thanks also go to Valentin Vallaeys and Jonathan Lambrechts for giving me some advice regarding the use of SLIM, with a different point of view.

I also thank Jessica, Nicolas, François and especially Noé for the mutual support all over the year and I wish them good luck with the writing and the oral presentation.

And finally, I express my deepest thanks to my family and lover who gave me the highest support when I needed it the most.

List of Acronyms

AC	<i>Acropora Cervicornis</i>
FC	Florida Current
FRT	Florida Reef Tract
HYCOM	HYbrid Coordinate Ocean Model
LC	Loop Current
LPT	Lagrangian Particle Tracker
MC	<i>Montastrea Cavernosa</i>
MPA	Marine Protected Area
NOAA	National Oceanic and Atmospheric Administration
SCC	Strongly Connected Components
SLIM	Second-generation Louvain-la-Neuve Ice-ocean Model
TAPPY	Tidal Analysis Program in PYthon
UCL	Université Catholique de Louvain
WCL	Weighted Connectivity Length
WFS	West Florida Shelf

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1 Introduction

1.1 The Florida Reef Tract

Located along the southern and eastern coasts of Florida, the Florida Reef Tract (FRT) is known as the third largest barrier reef in the world, after the Great Barrier Reef and the Belize Barrier Reef. It extends roughly over 580 km from the Dry Tortugas National Park to the north of West Palm Beach (Florida Department of Environmental Protection, n.d.). It is located just north of the Florida Strait, which links the Gulf of Mexico to the Atlantic Ocean.

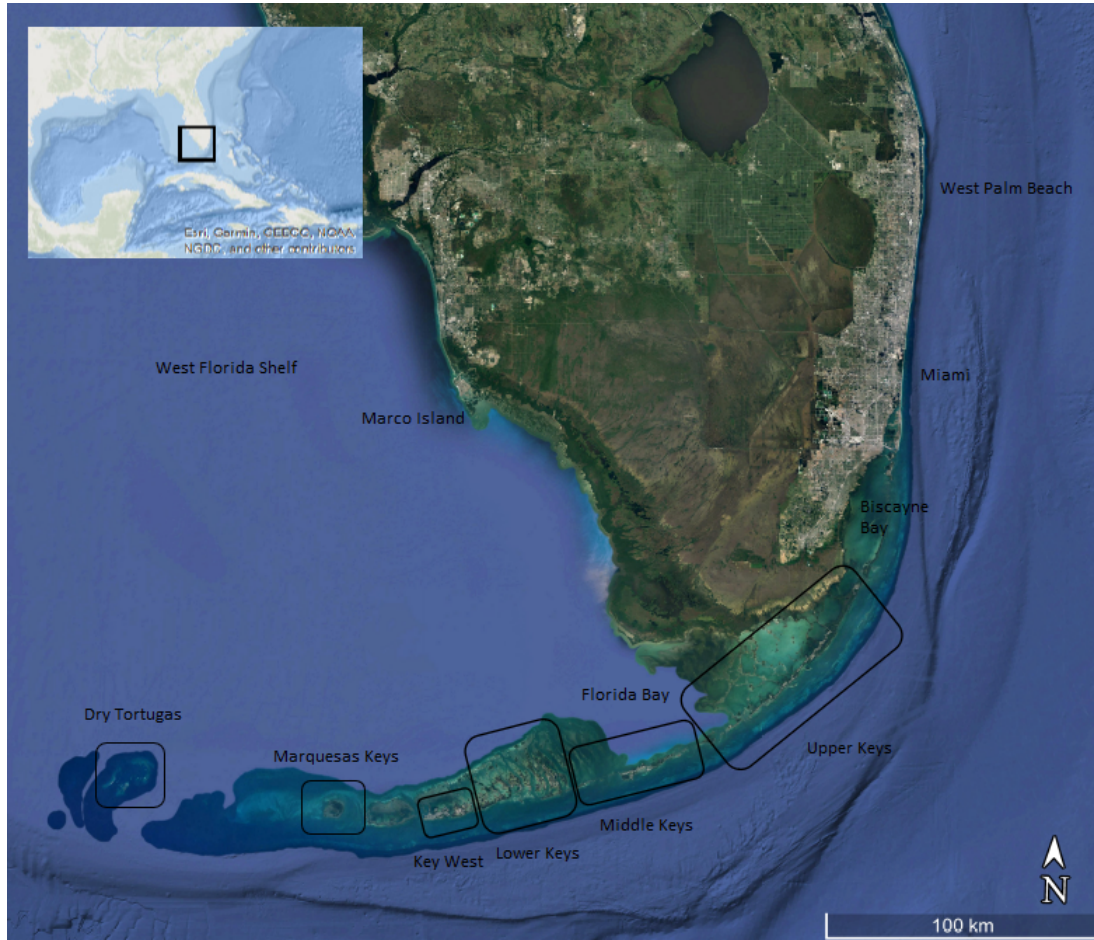


Figure 1: The Florida Reef Tract extends from the Dry Tortugas, west of the Florida Keys, to the north of West Palm Beach, on the eastern coast of Florida.

Coral reefs constitute one of the most diverse ecosystems in the world, supporting more species per unit area than any other marine environment. Worldwide, this includes 4000 fish species and 800 coral species (NOAA National Ocean Service Education, n.d.). Besides, coral reefs may also act as a barrier against waves and prevent coasts from erosion. Ferrario et al. (2014) even showed that reefs were able to reduce the energy of the waves by 97 % on average and that coral reefs restoration projects would in general be significantly cheaper than equivalent breakwaters construction projects in term of energy reduction. Furthermore, apart from fisheries and tourism benefits, corals are deeply studied for medicinal purposes. Among others, they are indeed promising regarding reconstructive bone

surgery applications or anti-cancer and anti-inflammatory properties (Florida Museum, n.d.).

Coral reefs usually form in tropical shallow water regions. They are part of the *anthozoa* class along anemones and gorgonians. Two categories exist, but the stony corals represent the majority of coral species. Actually, more than 45 stony coral species can be found along the FRT whereas 35 species of octocorals (including sea fans, sea whips and soft coral species) also exist (Florida Department of Environmental Protection, n.d.). Most of the time, they develop thanks to the symbiosis of coral individuals, called polyps, with algae known as zooxanthellae (NOAA's Coral Reef Information System (CoRIS), n.d.). Corals provide metabolic waste consisting in nutrients needed for the photosynthesis and protect the algae from environmental threats. In exchange, the algae produce oxygen and compounds that stony corals use to build their calcium carbonate skeleton. As a matter of fact, zooxanthellae bring 90% of the organic material they produce through photosynthesis to the coral (NOAA's Coral Reef Information System (CoRIS), n.d.). In case of separation of the algae from the coral, the latter undergoes many difficulties to thrive.

Darwin (1842) highlighted three reef structures throughout the world: atolls, barrier reefs and fringing reefs. The latter is the most common structure and is characterised by reefs developing directly along the shoreline. Barrier reefs are very similar, but form at a greater distance from the shore. Finally, atolls consist in oval or circular structures around a submerged volcanic island (NOAA's Coral Reef Information System (CoRIS), n.d.).

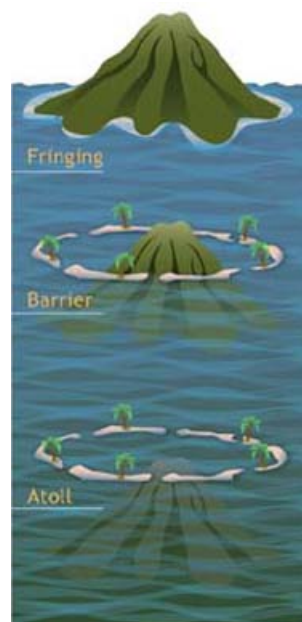


Figure 2: Darwin's reefs structures. Image credit: NOAA's Coral Reef Information System (CoRIS) (n.d.).

Florida reefs resemble barrier reefs the most, but are very close to the shore such that they are usually referred to as bank reefs (Florida Department of Environmental Protection, n.d.). Since these reefs present the highest species diversity, they constitute the best destination for divers and snorkelers. In the FRT, we can find such reefs from Miami to the Dry Tortugas (Florida Museum, n.d.). Elkhorn, star and brain corals are the

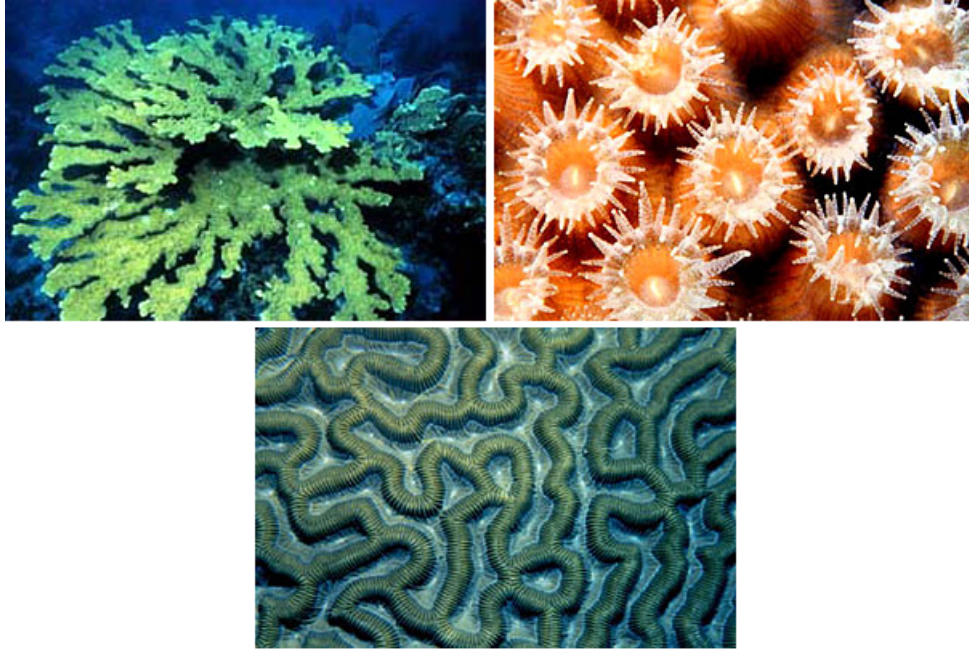


Figure 3: The three most common coral types in the FRT: elkhorn coral (upperleft), star coral (upperright) and brain coral (center). Image credit: Florida Museum (n.d.).

most frequent species in these reefs. Moreover, the FRT also contains patch reefs. These form in shallow waters ($3 - 6\text{ m}$) and are delimited by a sandy ring. Star and brain large colonies are very common in patch reefs.

Unfortunately, coral reefs are subjected to many threats. First of all, they can suffer from diseases. Black band disease is caused by a bacteria, but results from a stressing environment as well. It is responsible for the death of entire coral colonies within a few months (Florida Museum, n.d.). The cause of white band disease is still uncertain, but its effects are dramatic. 95 % of *Acropora* corals in the FRT were killed in a five year period because of this disease (Florida Museum, n.d.). Of course, human activities have a huge impact on coral health. Alongshore development activities cause erosion of the land such that sediments run off land and increase the water turbidity, decreasing the available light for zooxanthellae. Besides, nutrients also flow into the FRT waters, easing the development of algae which eventually smother corals (Florida Museum, n.d.). Overfishing of large reef fish, grazing on algae responsible for the smothering of corals, is another cause of corals depletion. Finally, even if the touristic sector tries to limit its impact on the reefs, tourists and boats can be harmful to the corals by touching and harming the polyps.

An indirect impact of human people on corals health manifests through climate change. For example, the increase of water temperature or of carbon dioxide concentration in the ocean can lead the corals to stress and expel the zooxanthellae. Consequently, corals lose their colour as the photosynthetic pigments present in the algae are responsible for most of corals coloration (Marshall, Schuttenberg, & West, 2006). This phenomenon is worldly known as bleaching. However, unlike a common idea, bleaching does not mean death. Corals are able to recover when the stressing factor comes back to normal. Meanwhile, they are certainly way more fragile against diseases and other threats, though (Precht, Gintert, Robbart, Fura, & van Woessik, 2016).

Finally, storms and hurricanes, increasingly more frequent and intense due to climate change, can have a huge impact on coral reefs development. First of all, storms drive large volumes of fresh water into the ocean, causing a sudden decrease in salinity, leading the coral to stress. They can also damage habitats located on the shore, resulting in the release of sediments polluting the water and increasing its turbidity (Florida Museum, n.d.). Fast winds can also result in strong waves and break large reef structures (NOAA's Coral Reef Information System (CoRIS), n.d.). Accordingly, Gardner, Côté, Gill, Grant, and Watkinson (2005) determined that the coral cover of impacted sites could decrease dramatically (up to 17 % in average for hurricanes in the period 1980-2001 in the Caribbean) in the year following a hurricane, depending on the hurricane intensity.

Hopefully, coral diversity seems not affected by the intensity of hurricanes (Rogers, 1993). In fact, abundant species on a reef sometimes suffer more damage than scarce ones, even leading to an increase in diversity.¹ This is particularly the case for reefs that are rarely impacted by storms since a prominent species would often have developed. If this species is vulnerable against storms, diversity will rise.

Nevertheless, Manzello et al. (2007) showed storms could definitely have a positive impact on bleached corals recovery. A usual effect of a hurricane passage is indeed a decrease in sea temperature, caused by wind-forced vertical mixing. This temperature decrease depends on the distance with the track, but can reach up to 5°C (Manzello et al., 2007).

Unfortunately, recovery between two hurricanes has become increasingly more difficult since the latter are more frequent and intense than in the past. Besides, threats, and especially new anthropogenic threats like pollution and acidification of the oceans, act in synergy with hurricanes and tend to inhibit past recovery properties of the network (Gardner et al., 2005).

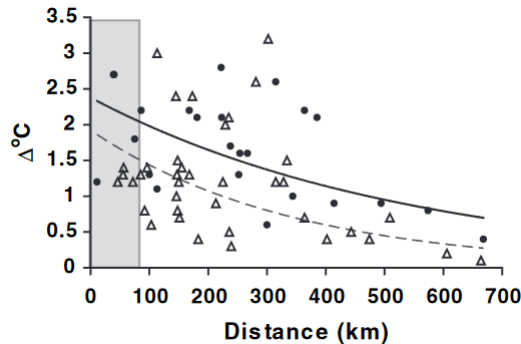


Figure 4: Decrease in water temperature with the distance to the hurricane track, assessed for the Florida Reef Tract in the period 1998-2005. Filled circles stand for sites located left of storm tracks whereas open triangles stand for sites being on the right of the tracks. The solid line is a regression line for sites being on the left of tracks. The dashed line is then the regression line for sites being on the right of the tracks. The shaded box indicates the range of physical damage swath. Image credit: Manzello et al. (2007)

¹Diversity being defined as the number of species weighted by their relative abundance (Rogers, 1993). For example, we can use the Shannon-Weaver measure of the diversity: $H' = -\sum p_i \ln(p_i)$ where p_i is the proportion of the number of individuals of one species relative to the total number of individuals on a reef.

1.2 Water circulation

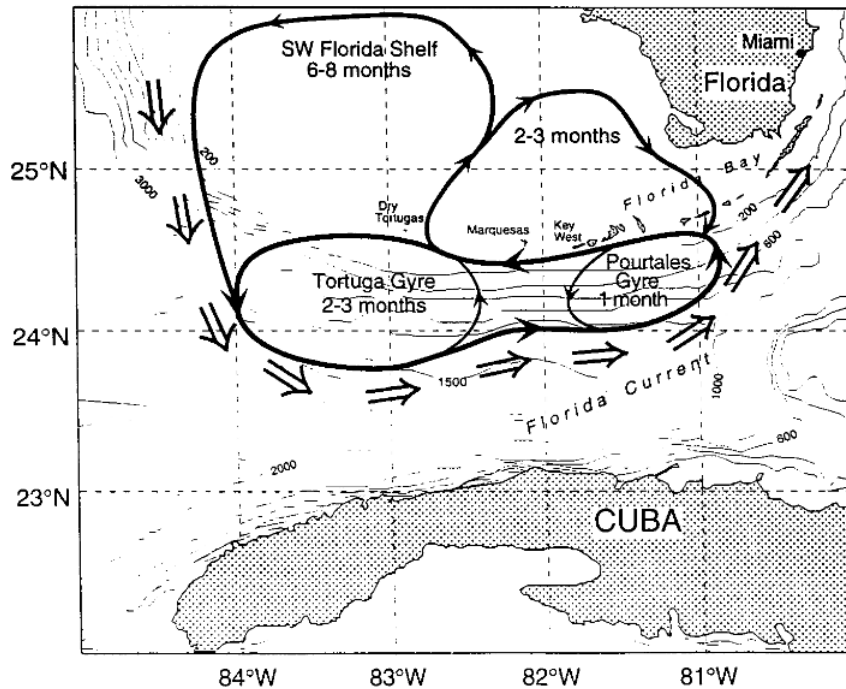


Figure 5: Most important current patterns in the Florida Keys. Recirculation patterns are indicated with their typical time scale. Larval dispersal will be strongly influenced by these patterns. Image credit: Lee and Williams (1999).

The Florida Keys present several current patterns, all of them having different time scales. Two main trends can be highlighted depending on the position. On one hand, water circulation in the nearshore region, including Hawk Channel, is mainly determined by tidal and wind forcings. On the other hand, seaward of the reef tract, the currents are mostly influenced by wind forcings and the Florida Current (FC), associated to eddies and gyres through the keys (Lee & Williams, 1999).

The FC firstly circulates west to east through the Florida Strait, bounded by the Florida Keys to the north and by Cuba to the south. After that, it runs alongside the eastern coast of Florida, south to north. Near Cape Hatteras, in North Carolina it then joins the Gulf Stream.

The FC takes most of his transport from the Loop Current (LC), a warm water current circulating in a loop in the Gulf of Mexico and coming from the passage between Cuba and the Yucatan Peninsula. These warm waters precisely consist in the first reason for coral reefs presence and such marine life in the Florida Keys (Florida Keys National Marine Sanctuary, n.d.). These warm water fluxes are also responsible for the formation of baroclinic eddies running along the FRT. The STACS project measured the volume transport going through the Florida Strait in 1982-1984 thanks to undersea cables, Pegasus profiles and mooring stations. In average, this transport reaches $30.5 Sv$ and has a standard deviation of about $\pm 3 Sv$, but is subjected to a strong seasonal variability with maxima of $40 Sv$ and minima of $20 Sv$ (Schott, Lee, & Zantopp, 1988).

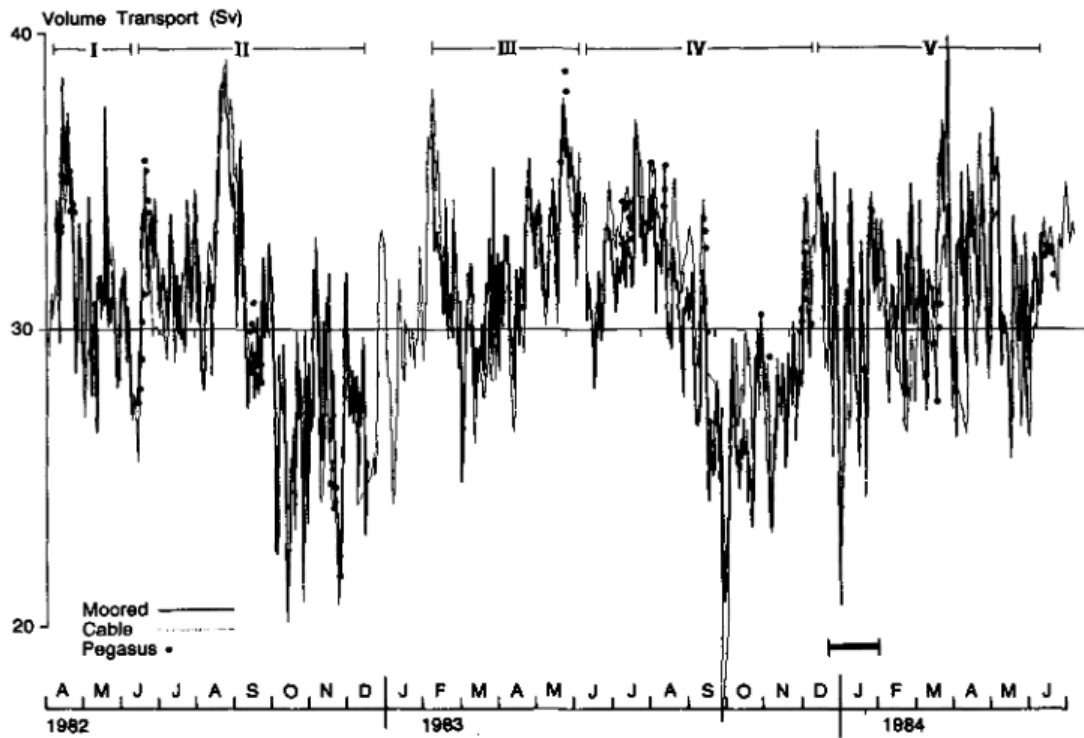


Figure 6: Volume transport in Sv measured by the STACS project in the period 1982-1984 in the Florida Strait. Image credit: Schott et al. (1988).

1.3 Coral connectivity

Corals are all able to reproduce sexually and asexually and can be either gonochoristic (unisexual) or more commonly, hermaphroditic. As far as asexual reproduction is concerned, polyps bud off their parent polyp and fall onto the ground to start a new colony (NOAA National Ocean Service Education, n.d.). This happens when the coral reaches a certain size and becomes vulnerable to strong wave action, like for *Acropora Cervicornis* (AC), we study here. When it comes to sexual reproduction, the majority of them are broadcast spawners. This means they release a huge number of male or female gametes into the water. The eggs and sperm then join to form larvae called planulae. Sometimes, like in Florida, this spawning event occurs on a synchronized basis for each species. For instance, considering both species we will study hereafter, all AC larvae in 2017 were released from 10 August to 12 August whereas *Montastrea Cavernosa* (MC) larvae are supposed to have spawned from 10 September to 12 September. Hurricane Irma passing over Florida at the same time, proper conditions for precise observations were indeed not fulfilled (Figueiredo J., personal communication, 23 October 2018).

A large number of larvae is thus released and will be distributed over a wide geographical area, following the currents pointed out in Fig. 5. Thanks to the FC, larvae can be transported over long distances along the outer shelf of the Florida Keys. They can also be retained in one of the recirculating gyres so that local recruitment is also a possibility. This is mainly the case in the inner shelf of the Florida Keys. After a few days, larvae become able to swim and to settle on reefs. They are said to be competent. Eventually, post-settlement processes (inability to settle because of a lack of place for instance) will

reduce the final number of larvae that were effectively recruited by a reef (Thomas et al., 2014). We can then express the connectivity between two reefs as the number of exchanges of effectively recruited larvae (Cowen, Gawarkiewicz, Pineda, Thorrold, & Werner, 2007). However, connectivity being still a vague concept, we must pay attention to the exact definition we use. In this study, as we use a numerical modelling approach, which does not take post-settlement processes into account, connectivity will only refer to *potential connectivity*, i.e. the number of exchanged larvae between two reefs, considering that all settled larvae are recruited. Moreover, we will consider here that the number of released larvae is proportional to the size of the reef. We thus consider that only one species covers all reefs, we neglect the coral cover of these reefs and we assume the net egg production ability does not vary in space (Thomas et al., 2014). These three last assumptions are really strong, but are necessary to develop a sufficiently simple system, mainly focused on larval dispersal.

Because of all the threats mentioned in section 1.1, we assist to a severe reduction of world coral populations. In Florida, the National Oceanographic and Atmospheric Administration (NOAA) set up a Coral Reef Conservation Program, involving the creation of Marine Protected Areas (MPAs) and measures to restore viable coral populations, among other things (National Oceanic and Atmospheric Administration, n.d.-b). The program especially implies breeding corals onshore in nursery labs with the aim of implanting them, when sufficiently developed, on the most strategic reefs (National Oceanic and Atmospheric Administration, n.d.-b). In order to determine which reefs are the best suited to receive these bred corals, numerical simulations using Lagrangian particle tracking of the larvae can be used (Werner, Cowen, & Paris, 2007).

Hydrodynamic numerical models can thus be used to study larval dispersal. Afterwards, graph theory tools can be used to assess the connectivity between reefs. Some models were developed to study larval dispersal for different species and different regions of the world like CMS (Paris, Helgers, van Sebille, & Srinivasan, 2013) or Ichthyop (Lett et al., 2008). Both models read hydrodynamic data from structured-grid ocean models and then use an Individual Based Model (IBM) approach to derive connectivity (Thomas et al., 2014).

Structured-grid models are very widely used for such studies. For example, HYbrid Coordinate Ocean Model (HYCOM) is a general 3D circulation model that we partly use in this study. In the Gulf of Mexico, its spatial resolution reaches $1/25^\circ$, making it unable to catch small-scale information about larval dispersal (Crowder & Diplas, 2000). Consequently, Frys (2017) and Béchet and Verstraeten (2018) used SLIM (Second-generation Louvain-la-Neuve Ice-ocean Model), an unstructured-grid finite element hydrodynamic model, to simulate the hydrodynamics in the Florida Reef Tract and then to track the larvae thanks to a Lagrangian particle tracker. Since the spatial resolution of this model varied from 100 m to 15 km , it was able to capture small-scale features without losing performance in time. The present thesis continues their work.

1.4 Hurricanes

1.4.1 Hurricanes in southern Florida

Tropical cyclones are organized systems of clouds and thunderstorms rotating, counter-clockwise in the Northern Hemisphere. Their formation depends on the coexistence of several factors among which warm waters and a warm moist atmosphere.

Depending on their location, their name might change. The word cyclone is used when it concerns systems located in the Southern Pacific or in the Indian Ocean. In the Western Pacific, they are often referred to as typhoons whereas in the Atlantic Ocean and in the Eastern Pacific, they are called hurricanes, named after *Hunraken*, the Mayan storm god (National Oceanic and Atmospheric Administration, n.d.-a).

The appellation hurricane also depends on the maximum speed of the wind, though. As far as winds up to 61 km/h are concerned, the system is only a tropical depression. From 61 km/h to 117 km/h , we talk about a tropical storm. Above the latter speed, the storm becomes a hurricane. And if the winds reach maximum speeds above 178 km/h , the system is even called a major hurricane (National Hurricane Center, n.d.-c). Hurricanes can then be classified according to their sustained wind speed along the Saffir-Simpson scale, which assesses the potential property damage (National Hurricane Center, n.d.-a). Category 1 and 2 hurricanes need preventive measures while higher categories (up to 5) consist in major hurricanes with dramatic or catastrophic damage.

The hurricane season in the Atlantic Basin, which includes the Atlantic Ocean, the Caribbean Sea and the Gulf of Mexico, starts on 1 June and ends on 30 November (National Hurricane Center, n.d.-c). As illustrated on Fig. 7, the peak of the season generally happens in September. For each month of the hurricane season, the National Hurricane Center also determined the average origin and path we could expect. These tracks are of course highly variable, but can help the concerned areas take preventive measures when a hurricane is likely to pass over them. Fig. 8 suggests that the passage of a hurricane on the FRT is very likely during high season, particularly in October.

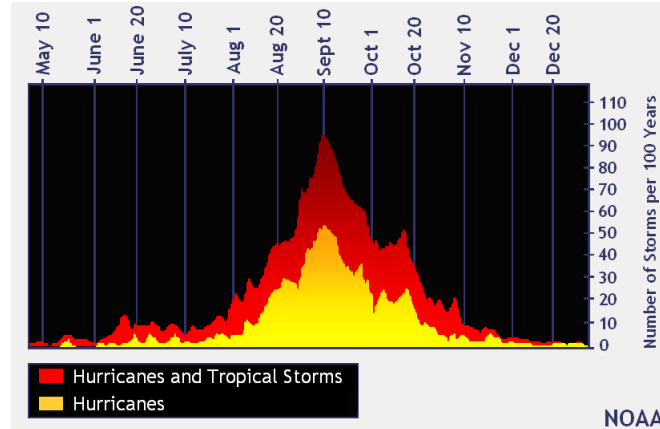
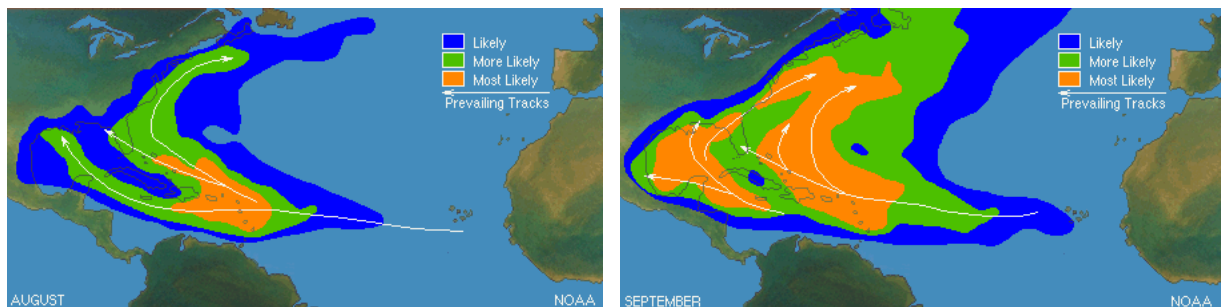


Figure 7: Hurricane season based on a hundred years analysis. Image credit: National Hurricane Center (n.d.-c).



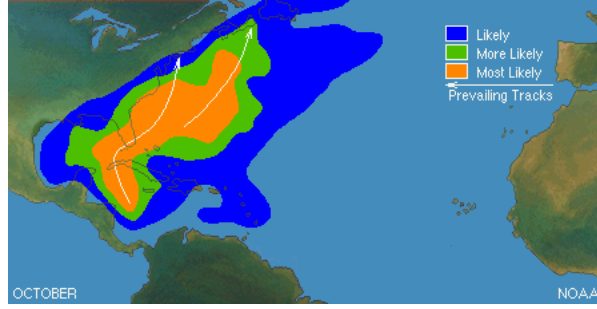


Figure 8: Likely origins and tracks for the three most dense months in terms of hurricane occurrences. The level of likeliness can be likely (blue), more likely (green) or most likely (orange). Image credit: National Hurricane Center (n.d.-c).

Finally, we can look at the frequency of hurricanes in Florida, and especially on the southern coast, where most coral reefs are found. In the period 1900-2010, the coastal Florida counties underwent several hurricanes. Counties on the southern coast were the most impacted zones by both hurricanes and major hurricanes. For example, the counties of Monroe and Miami-Dade, including the Florida Reef Tract waters, were respectively hit by 15 and 14 major hurricanes in that period. Fig. 11 and Fig. 12 give the return periods of hurricanes and major ones. We see that the southern counties, and thus the Florida Reef Tract, are the most likely counties to be hit by hurricanes. All these figures show us that hurricanes are rather common in Florida and especially where we find coral reefs the most. Consequently, the impact of a hurricane on the larval dispersal should be investigated.

Schulman and Bermingham (1995) indeed showed that episodic events like hurricanes could be non negligible regarding larval dispersal and reefs connectivity. Although hurricanes could be blamed for cutting-off existing and vital connections for the network, they also might create new connections between reefs and enhance the development of the network, because of their strong winds and the water elevation changes they produce. Furthermore, such episodic events could increase the gene flow between coral populations, i.e. the transfer of genetic variations between two distinct coral populations. Accordingly, inbreeding would be reduced whereas genetic diversity would be improved, making the coral populations stronger against diseases and other threats. Finally, we can expect the hurricanes to send larvae away from traditional settlement spots, colonizing new spaces and creating development possibilities for the network in the following years.

In this study, we will focus on hurricane Irma, which struck Florida in September 2017.

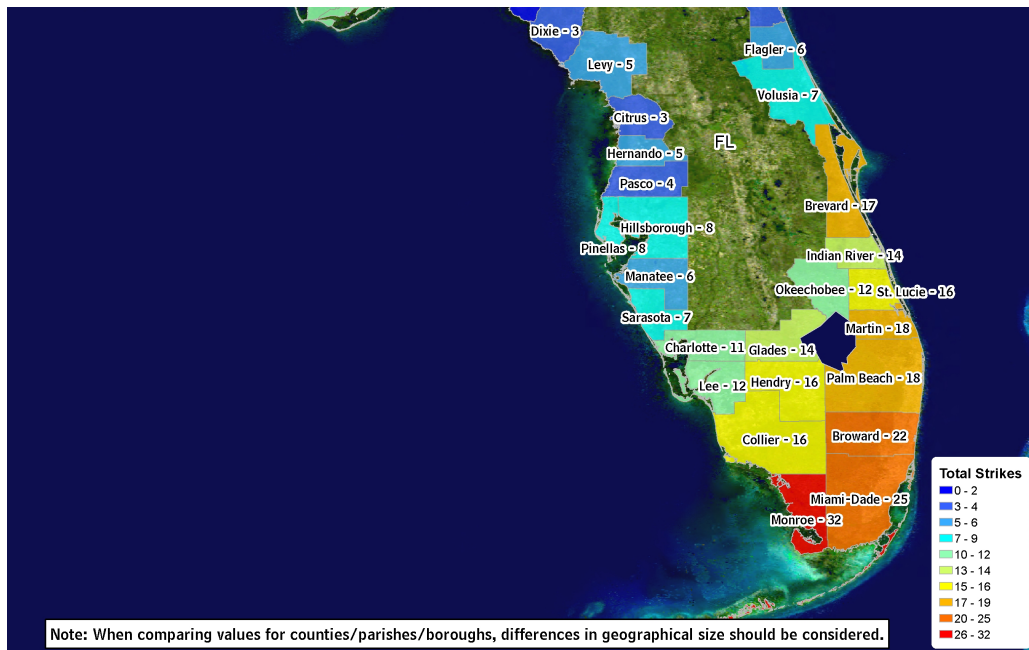


Figure 9: Total number of hurricane strikes on Florida counties in the period 1900-2010. Monroe and Miami-Dade counties, covering the FRT, at the southern end of Florida peninsula count the most strikes in that period. Image credit: National Hurricane Center (n.d.-c).

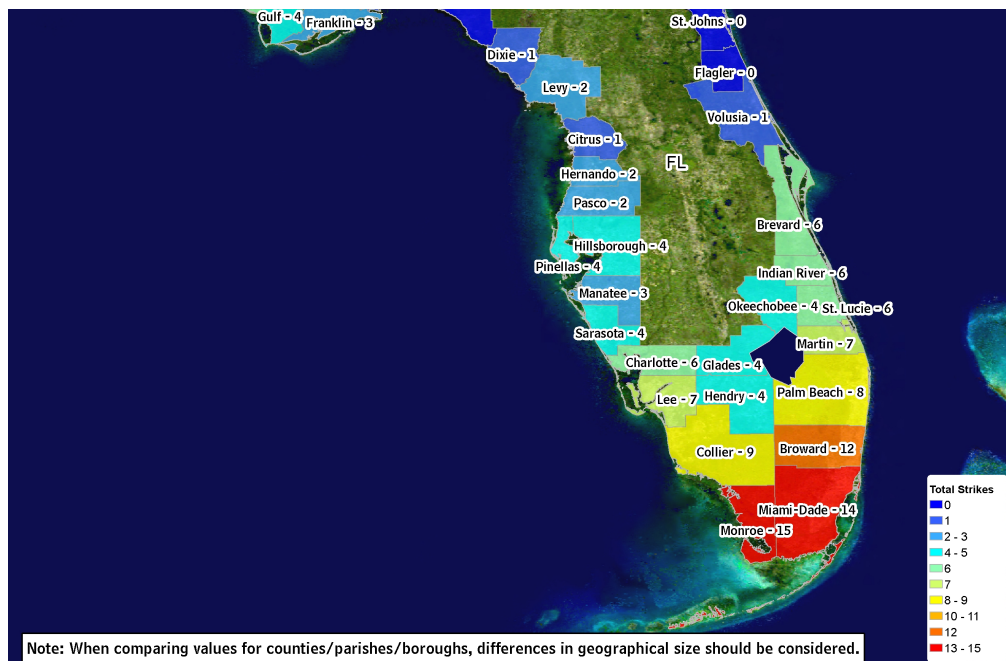


Figure 10: Total number of major hurricane strikes on Florida counties in the period 1900-2010. Monroe and Miami-Dade counties, covering the FRT, at the southern end of Florida peninsula count the most strikes in that period. Image credit: National Hurricane Center (n.d.-c).

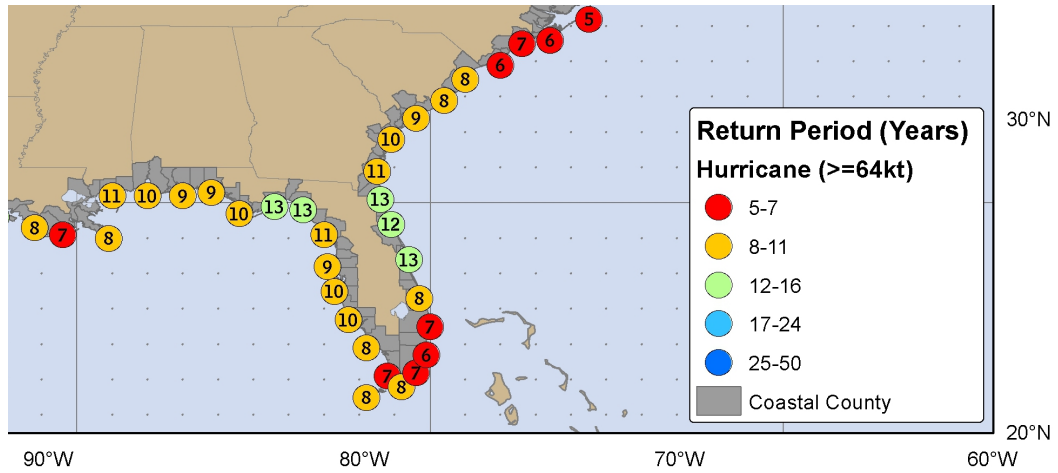


Figure 11: Return periods of hurricanes in Florida. The return periods of hurricanes in the FRT area are amongst the lowest ones on the eastern and southern coasts of the United States. Image credit: National Hurricane Center (n.d.-c).

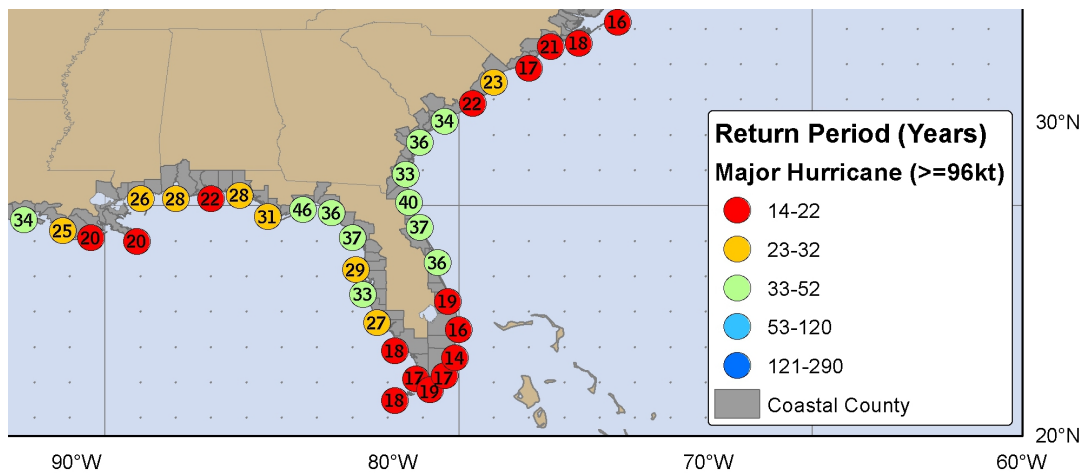


Figure 12: Return periods of major hurricanes in Florida. The return periods of major hurricanes in the FRT area are amongst the lowest ones on the eastern and southern coasts of the United States. Image credit: National Hurricane Center (n.d.-c).

1.4.2 Hurricane Irma

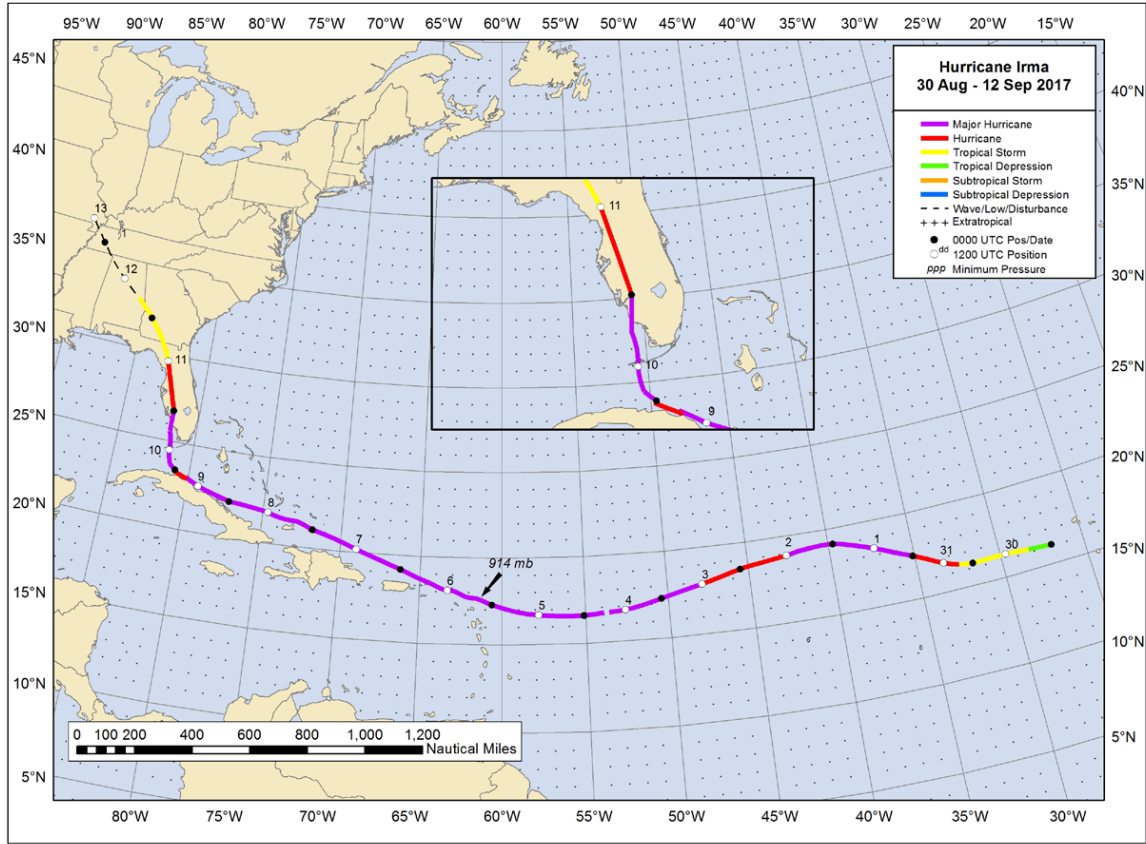


Figure 13: Best track positions for Hurricane Irma from 30 August to 13 September. Before getting through mainland, Irma crossed the Lower Keys on 10 September. Image credit: Cangialosi et al. (2018).

Hurricane Irma originated in Cap Verde waters on 27 August 2017 as a tropical wave. By 6 September, when it made landfall on Barbuda in the Caribbean Sea, it had grown as a Category 5 hurricane on the Saffir-Simpson scale, reaching maximum wind speeds around 287 km/h and minimum pressure of 914 mbar (Cangialosi et al., 2018). In the following days, Irma's intensity decreased, hitting the American Virgin Islands, the Bahamas and Cuba among other islands. On 9 September, Irma had become a Category 2 hurricane. However, by crossing the Florida Strait, the warm waters helped the hurricane to reintensify so that it grew up as a Category 4 hurricane once again. It then made landfall on Cudjoe Key in the Florida Keys on 10 September at 1 p.m., with winds reaching 213 km/h and minimum pressure of 931 mbar . On 7:30 p.m., Irma had lost intensity and made its last landfall on Marco Island, Florida. Because of vertical shear due to land roughness, the hurricane eventually weakened while heading for northwestern Florida, Georgia, Alabama, Tennessee and finally Missouri where it dissipated on 13 September.

Although the Caribbean islands suffered the most in terms of direct deaths, i.e. drownings, lightning strikes or wind-related events, the death toll in Florida, direct and indirect combined reaches the number of 84 (Cangialosi et al., 2018). In Florida alone, 6 million

people were evacuated. Due to heavy rains, floods, strong winds and storm surges among other factors, Florida and especially the Florida Keys, suffered from high material damage as well. According to the Federal Emergency Management Agency (FEMA), 25 % of the buildings in the Florida Keys were completely destroyed, 65 % were highly damaged while 90 % were impacted (Cangialosi et al., 2018). As a matter of fact, Irma took the fifth place on the list of the most damaging tropical cyclones in the United States of America, with a bill of approximately \$50 billion (National Hurricane Center, 2018).



Figure 14: Irma made seven landfalls among which two in Cudjoe Key near Sugarloaf Key (left) and in Marco Island (right). Image credit: Cangialosi et al. (2018).

Regarding corals, the damage were obviously unequally distributed over the entire FRT. Three zones of the outer belt were defined by the NOAA according to the level of damage (NOAA, 2018). It appears corals located south of Cudjoe Key sustained the highest damage. We can also notice that corals located east of Irma's center were affected on a way longer distance and to a larger extent than those located west of it.

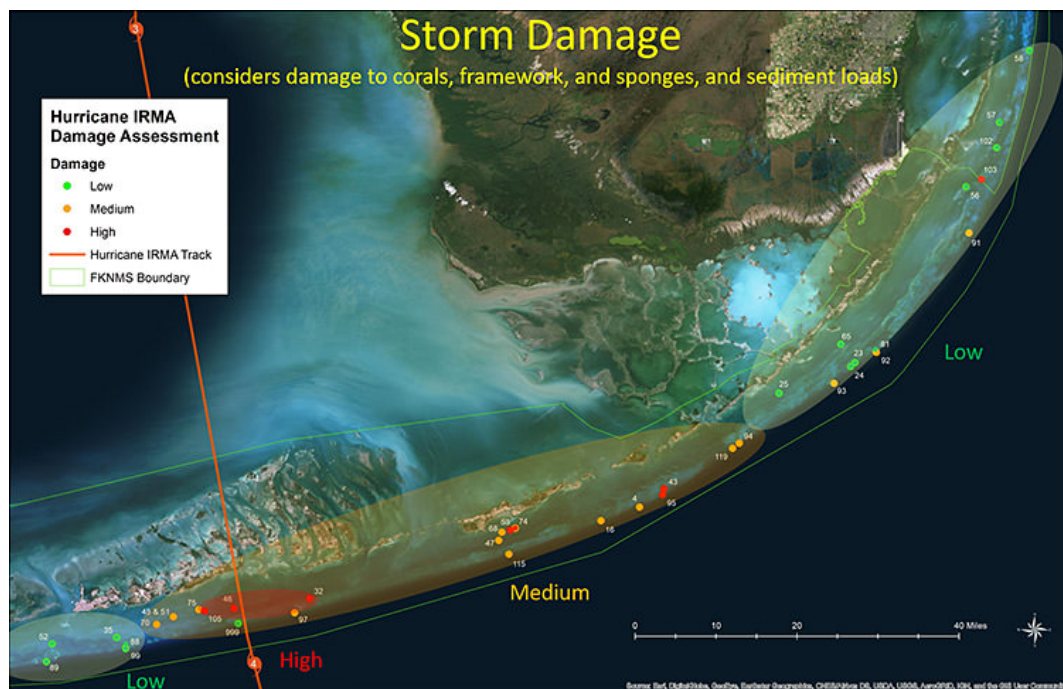


Figure 15: Spatial distribution of damage inflicted to corals on the outer belt of the FRT. Three zones can be defined. Lower and Middle Keys sustained the heaviest damage. Image credit: NOAA (2018).

1.5 Objectives

As previously mentioned, this thesis follows Frys (2017) and Béchet and Verstraeten (2018). These two theses led to the determination of connectivity matrices in the FRT for several years and two coral species: *Acropora Cervicornis* and *Montastrea Cavernosa*. They also identified important reefs in the coral development network that would constitute good candidates for protection and restoration projects.

Nevertheless, both theses were lacking hurricanes in their model, even though they are rather frequent in the area as we showed earlier on. Apart from forcing strong wave action breaking large-sized corals and cooling the water temperature, hurricanes could also be responsible for deep changes in larval dispersal and consequently, in connectivity. On one hand, as mentioned by Paris (2010), strong winds and sea level rise could lead to the creation of new connections between reefs and change local connectivity patterns. Hurricanes, as brief disturbances, could also be sufficient to drive planulae away from their traditional paths and make them colonize new spaces. Even though the latter seems rather unlikely on a short timescale, gene flow variations could benefit the whole network. Paris (2010) judges the likeliness of these favorable impacts on connectivity rather low, though. On the other hand, the intensification of hurricanes will surely contribute to habitat loss and fragmentation, leading the path for a likely decline in connectivity in the affected areas. Hurricanes might indeed cut off existing vital connections and possibly have dramatic consequences for the survival of coral populations in the FRT. Besides, the increase in frequency of such disturbances will most likely result in a raising variability of the connectivity patterns in the future.

The first step of this thesis consists in defining an unstructured mesh, bounded by coasts and open boundaries as well. The size of the elements of the mesh should depend both on the distance to the coasts and on the bathymetry. We want a finer resolution nearby coasts, and especially those of the Florida Keys where we find the majority of coral reefs.

Next, we will run the hydrodynamics of our domain, using four external forcings: tides, large circulation patterns, winds and pressures. Unlikely Frys (2017) and Béchet and Verstraeten (2018), we will use the conservative form of the shallow water equations. High wind speeds combined with low pressures in the area of the hurricane will indeed lead to significant water level variations across the domain. In shallow water areas, the whole water column could even be dried off and then become wet again. This phenomenon, that we also identify in estuary regions because of tides for example (de Brye et al., 2010; Gourgue et al., 2009; Pham Van et al., 2011), is known as wetting-drying. In order to avoid dividing any quantity by a negative water depth H , we must use the conservative form of the shallow water equations. By comparing the difference of the total water column height and the bathymetry with a threshold value, we can assess if a cell becomes dry. Finally, we must also change the wind parameterisation used by Frys (2017) and Béchet and Verstraeten (2018). The wind drag stress exerted on the water surface was indeed proportional to a drag coefficient linearly increasing with the wind speed at 10 m above the sea level (Smith & Banke, 1963). In hurricane conditions, this parameterisation needs to be revised since it leads to an overestimation of the drag force (Letchford & Zachry, 2009).

This simulation will be performed from 5 August to 10 November. This period actually covers the spawning seasons of the two coral species studied by Frys (2017) and Béchet

and Verstraeten (2018), *Montastrea Cavernosa* and *Acropora Cervicornis* respectively. In fact, the latter spawned roughly a month before hurricane Irma struck the FRT whereas MC spawning nights occurred during the passage of the hurricane. We can thus expect large differences in larval dispersal patterns.

These dispersal patterns will be determined thanks to a Lagrangian particle tracker, able to record the path of a larva and to identify both seeding and recruiting reefs. The connectivity between all reefs can then be determined under the form of a connectivity matrix. Afterwards, graph theory tools will be used to assess the impact of the hurricane on MC's connectivity. After applying the same tools to AC, we will compare the connectivity patterns of AC and MC. Thanks to this comparison, we will determine the extent of Irma's influence over the connectivity in the FRT. In particular, we will identify the reefs that could benefit from protection or restoration measures when subjected to a hurricane similar to Irma. Finally, the main objective of this thesis is to determine whether a brief but strong disturbance, like a hurricane, is sufficient to significantly modify the connectivity in the FRT, whatever the species and the spawning season.

2 Simulation of the hydrodynamics

This study was realised thanks to the above-mentioned SLIM model, developed at the Université Catholique de Louvain (UCL) and successfully applied to several places in the world like the Scheldt Estuary-Sea (de Brye et al., 2010), the Great Barrier Reef (Lambrechts et al., 2008) or the Mahakam River-Lake-Delta (Pham Van et al., 2011) for instance. All information about any SLIM project can be found on the dedicated website.²

SLIM is a multi-scale hydrodynamic model of the land-sea continuum. It can be used in 1D for river networks, in 2D for shallow barotropic flows or in 3D when the vertical structure can not be omitted (SLIM - Second-generation Louvain-la-Neuve Ice-ocean Model, n.d.). It also contains modules such as a Lagrangian particle tracker and an Eulerian transport model able to simulate the dynamics of tracers. Whatever the version of SLIM, the model can be used on unstructured meshes, letting the possibility to the user to refine the mesh where it is needed the most, like near coasts or reefs. Thanks to this adaptative mesh, a lot of computational cost can be spared. Solving the equations is performed spatially thanks to a Discontinuous Galerkin finite element method.

In this paper, we will use SLIM2D with a wetting-drying module since the hurricane is expected to be responsible for strong water elevation variations. We shall also use the Lagrangian particle tracker to follow larvae once they are released and to determine where they settle.

2.1 Generation of an unstructured mesh

The use of an unstructured mesh lets us focus on zones of interest by increasing the resolution where it is needed. In our case, we wanted the resolution to be dependent of the bathymetry and of the distance to the coasts as well. For that purpose, we used three bathymetry data sets. The coarsest one, but which has the largest spatial coverage, was extracted from the ETOPO1 1 Arc-Minute Global Relief Model released by the National

²<https://www.slim-ocean.be>

Geophysical Data Center (NGDC) (Amante & Eakins, 2009). As its name suggests, this data set has a spatial resolution of 1 arc-minute. A more precise bathymetry data set, focused on Florida with an approximate horizontal resolution of 90 m was retrieved from National Geophysical Data Center (2001). The last one, that has a horizontal resolution of 30 m , concerned a part of the Florida Keys and of the West Florida Shelf (WFS) (Adcroft, 2013). For all points of the domain, we always considered the most precise bathymetry data set it was located in.

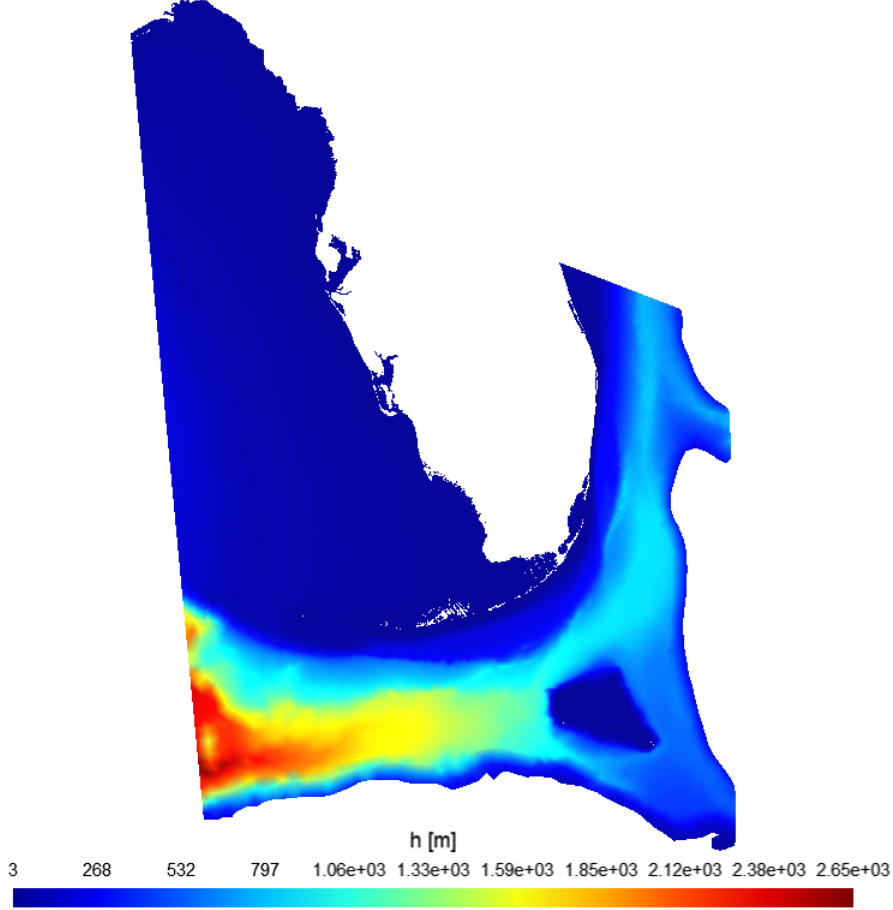


Figure 16: Bathymetry of our domain once the three data sets were merged.

The bathymetry criterion was as follows:

$$s_0 = \alpha \sqrt{h} \quad (1)$$

where $h = \min(3000, \max(5, -h))$ since the bathymetry h is negative in the data. Taking the maximum between 5 m and $-h$ meant to avoid any infinitely small elements in the vicinity of coasts. The minimum between the latter and 3000 m aimed at keeping the largest elements at a constant and manageable size. Eventually, it was an even larger value than the maximum bathymetry value (2650 m) interpolated in our domain. According to our own desires only, the α coefficient was chosen to be 250.

The second criterion computed the element size s_i according to the distance to the coasts. After delimiting our domain with closed and open boundaries in the Geographic

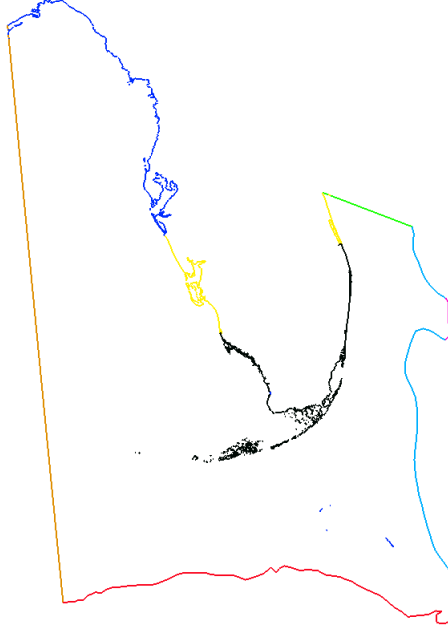


Figure 17: Tags associated to the boundaries of the domain. Dark: Florida Keys and nearby coasts; yellow: transition zone coasts; dark blue: northwest Florida and Cay Sal Bank atoll; brown: open boundary to the Gulf of Mexico; red: Cuba; purple: eastern open boundary to the Atlantic Ocean; light blue: Great Bahama Bank and Little Bahama Bank taken as a closed boundary; green: northern open boundary to the Atlantic Ocean.

Information System (GIS) QGIS (QGIS Development Team, 2019), we tagged the coasts in function of their importance in the domain (Fig. 17).

For each point of the domain, we computed the distance to the closest coast d_i . In function of the coast tag, we used a linear interpolation to impose the element size, knowing that s_i would be 10 km maximum for all tags and 100 m , 500 m , 900 m , 7 km and 7.8 km minimum for elements closer to the Florida Keys, to the so-called transition zone coasts, to northwest Florida and Cay Sal Bank atoll, to the Bahamas and to Cuba respectively. Finally, we took the minimum between s_i and s_0 for all elements, except for the ones located closer to Cuba or the Bahamas for which we only considered the distance to the coasts criterion. We indeed wanted to avoid small elements along those coasts, as there were no reefs along them that interested us. Moreover, the bathymetry gradient is very sharp near those coasts. Using the bathymetry criterion there would have caused big differences in adjacent element sizes and difficulties for the solver to converge. On the contrary, a shelf sea lies to the West of Florida, the West Florida Shelf, avoiding any strong bathymetry gradient and such convergence problems. Eventually, we created a domain counting 1.75 million elements.

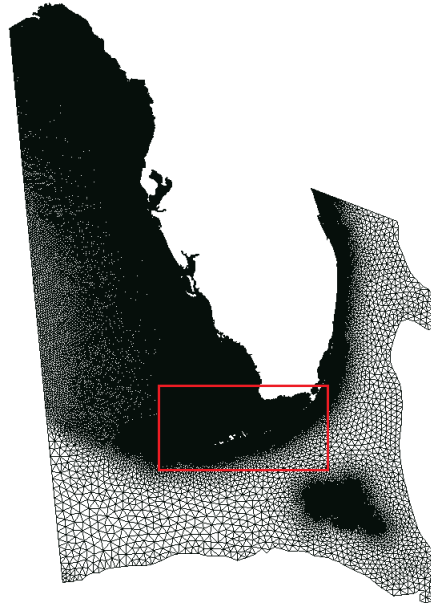


Figure 18: Entire mesh composed of approximately 1.75 million elements. The resolution is close to 100 m in the Florida Keys, along Florida's coasts, in the WFS and in Cay Sal Bank because of the closeness to the shores of the elements or due to the low bathymetry. Nevertheless, the resolution on the WFS could be a bit coarser without affecting the accuracy of the results. Their high resolution is due to the very low bathymetry on that plateau.

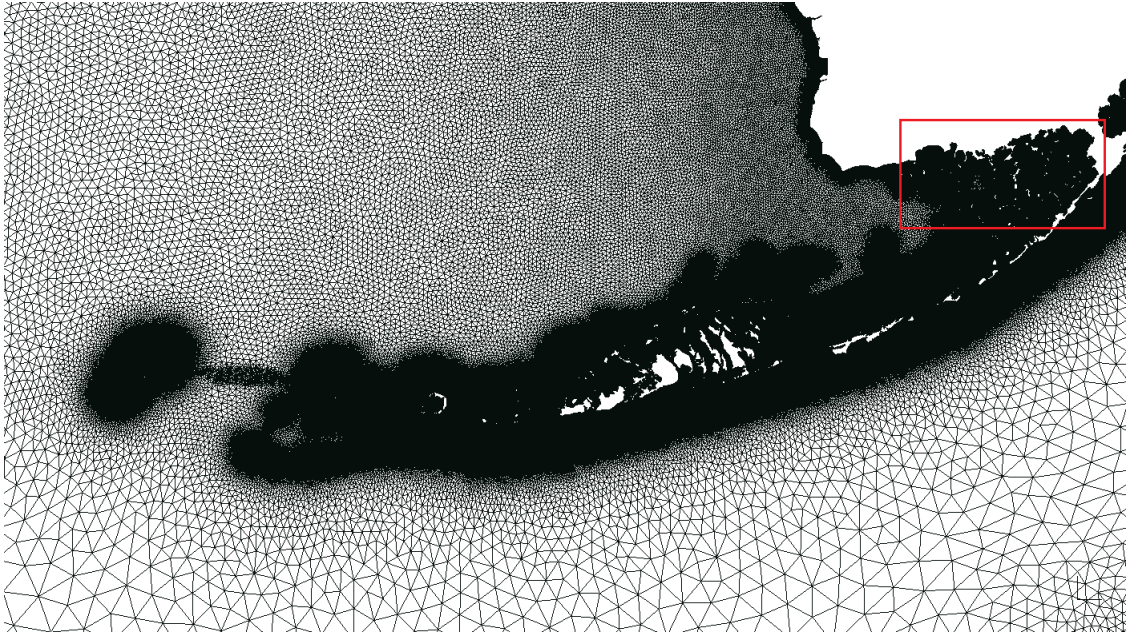


Figure 19: Zoom on the red framed area on Fig. 18. It corresponds to the Lower and Middle Keys where most coral reefs lie.

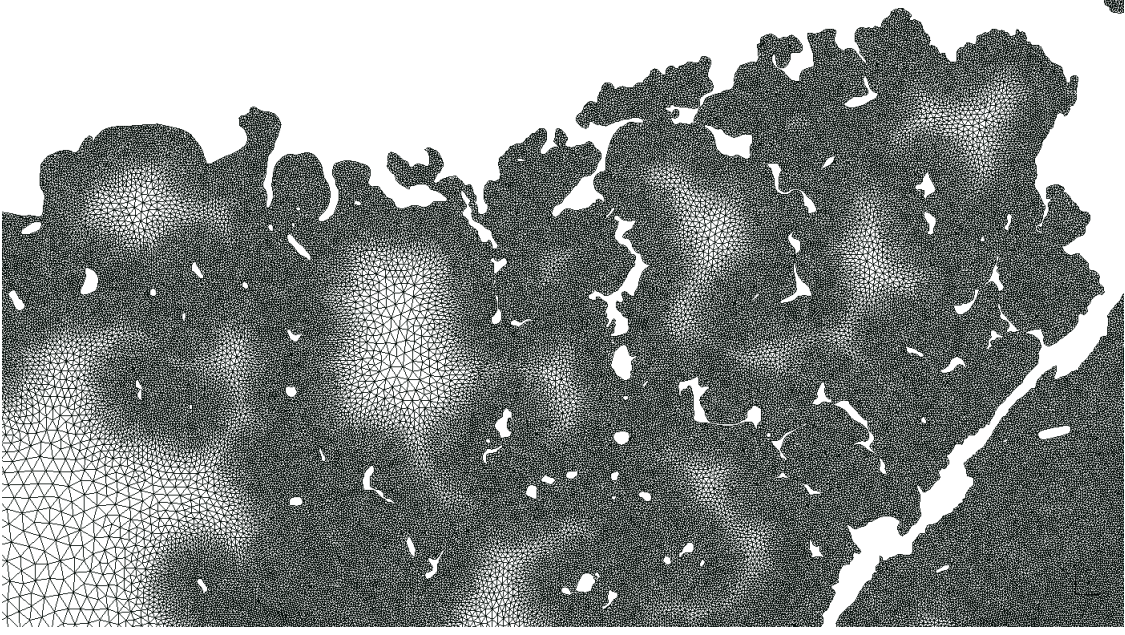


Figure 20: Zoom on the red framed area on Fig. 19. We can distinguish very precisely all the islands and peninsulas in the area as the elements in this zone have a minimal 100 m size.

2.2 Hydrodynamic model

As mentioned before, we used the two-dimensional barotropic version of SLIM, which solves the depth-averaged Navier-Stokes equations, assuming that the water density is constant. As explained hereafter, some cells might turn dry because of the hurricane. In order to avoid the velocities to be undefined in these cells, we will use the conservative form of the equations. These equations indeed treat the transport instead of the velocity, which is better here since the transport in dry cells is defined and is zero because of the zero water depth. These so-called shallow water equations write this way:

$$\frac{\partial H}{\partial t} + \nabla \cdot (\mathbf{U}) = 0 \quad (2)$$

$$\begin{aligned} \frac{\partial \mathbf{U}}{\partial t} = & -\nabla \cdot \frac{\mathbf{U}\mathbf{U}}{H} - g\nabla \frac{|H|H}{2} - f\mathbf{e}_z \times (\mathbf{U}) - \frac{H}{\rho} \nabla p + gH\nabla h - g \frac{|\mathbf{U}|\mathbf{U}}{C^2 H^2} + \frac{\tau}{\rho} \\ & + \nabla \cdot (H\nu(\nabla \mathbf{u})) - C_s \frac{|\mathbf{U} \cdot \nabla H| \mathbf{U}}{H^2} + \gamma(\mathbf{U}_* - \mathbf{U}) \end{aligned} \quad (3)$$

where h is a water depth reference level, η is the water elevation regarding this reference level, $H = h + \eta$ is the total water column depth, $\mathbf{u}$ is the depth-integrated velocity vector, $\mathbf{U} = H\mathbf{u}$ is the transport, g is the gravitational acceleration, f is the Coriolis factor, $\mathbf{e}_z$ is a unit vector pointing vertically upwards, ρ is the water density, p is the atmospheric pressure, C is the Chézy bottom stress-coefficient, τ is the surface wind stress vector, ν is the water kinematic viscosity, C_s is the numerical slope stress coefficient, γ is a nudging relaxation parameter and $\mathbf{U}_* = H\mathbf{u}_*$ where $\mathbf{u}_*$ is the sum of tidal velocities and depth-averaged velocities of HYCOM. The last two terms of equation (3) were added by Frys (2017) to deliver better results and will be discussed in section 2.3. Since the simulations are rather long and the spatial resolution can be very fine in some areas,

an explicit time stepping scheme is not appropriate. We thus use here an implicit Euler one.

As mentioned earlier on, the hurricane should cause non negligible water elevation changes. Some very shallow-water elements could thus turn dry and then turn wet once again. This phenomenon is called wetting-drying and must thus be included in our model to avoid negative water depths. Several versions of wetting-drying algorithms were implemented in SLIM, but the one described in this document was only recently developed. For that reason, no paper currently describes it. We will not discuss its performance, as Le et al. (n.d.) is to do so in the next few months, but we will explain its principle.

The goal of the algorithm is to solve major problems arising when H becomes zero. First of all, in a situation identified by Vater, Beisiegel, and Behrens (2015) as a flooding-type situation, the discretization can lead to nonphysical elevation gradients. Secondly, the fluid depth must always remain positive. And finally, ill-conditions arise when the water velocity is computed by $\mathbf{u} = (H\mathbf{u})/H$ and the water depth approaches zero.

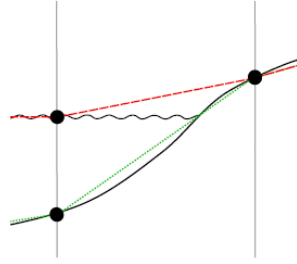


Figure 21: The real water surface and bottom topography are figured by the solid wavy black line and the ascending black curve respectively. The green dotted straight line represents the discretized bottom topography while the red dashed one stands for the discretized water surface. As the influx point on the left lies below the dry point on the right, a nonphysical elevation gradient appears.

To tackle these issues, Vater et al. (2015) proposed to define a parameter $f = \max_{x \in I_i} H(x) - \max_{x \in I_i} h(x)$ and to compare it to a threshold value ϵ under which the cell is considered to be dry, I_i being the considered cell and x the nodes of this cell. However, in partially dry cells, when one node at least has a non zero depth, a gravitational flux crosses the wet-dry interface. This flux then may be the cause for unbalanced in-cell distributions of η (Le et al., n.d.). A blending parameter α is thus introduced in order to limit these unbalanced processes. It ranges from 0 (dry) to 1 (wet):

$$\alpha = \min \left(1, \max \left(0, \frac{f - \epsilon}{4\epsilon} \right) \right) \quad (4)$$

where ϵ was chosen to be equal to $0.15 m$.

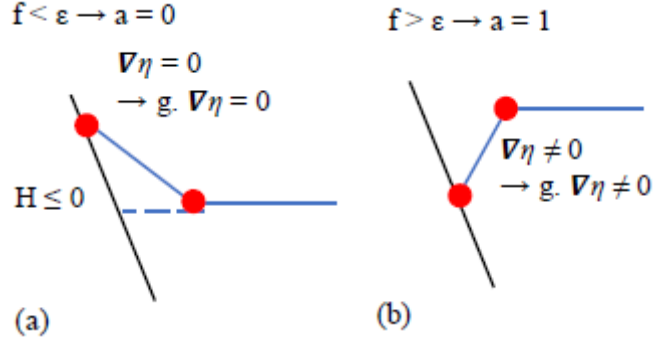


Figure 22: The bottom bathymetry is in black, the water surface in blue, the water depth in a dry cell in dashed blue and the cell nodes in red. a stands for α . a) The cell is dry, the water depth is considered to be zero on all nodes and there is no gravitational flux term across the wet-dry interface. b) As $f > \epsilon$, the cell is not (at least completely) dry and there is a water elevation gradient leading to a gravitational flux term across the wet-dry area. Image credit: Le et al. (n.d.).

Finally, to avoid the ill-conditions mentioned before when computing the water velocity $\mathbf{u} = (H\mathbf{u})/H$, the algorithm simply uses an $\tilde{H} = \max(H, \epsilon)$ for each term with H at the denominator. The equations used to simulate the hydrodynamics in our domain and taking wetting-drying processes into account are:

$$\frac{\partial H}{\partial t} + \nabla \cdot (\mathbf{U}) = 0 \quad (5)$$

$$\begin{aligned} \frac{\partial \mathbf{U}}{\partial t} = & -\nabla \cdot \frac{\mathbf{U}\mathbf{U}}{\tilde{H}} - g\nabla \frac{|H|H}{2} - f\mathbf{e}_z \times (\mathbf{U}) - \frac{H}{\rho}\nabla p + gH\nabla h - g\frac{|\mathbf{U}|\mathbf{U}}{C^2\tilde{H}^2} + \frac{\tau}{\rho} \\ & + \nabla \cdot (H\nu(\nabla\mathbf{u})) - C_s\frac{|\mathbf{U} \cdot \nabla H|\mathbf{U}}{\tilde{H}^2} + \gamma(\mathbf{U}_* - \mathbf{U}) \end{aligned} \quad (6)$$

A few parameterisations still need to be detailed, though. The Chezy bottom-stress coefficient C is taken as $\frac{h^{1/6}}{n}$ where n is the manning coefficient. In this study, we will consider $n = 0.025 m^{-1/3}/s$ everywhere, like de Brye et al. (2010) suggested it for seabed. Unlike Frys (2017) and Béchet and Verstraeten (2018), we will not use a different value for n on reefs, as the current version of the wetting-drying module of SLIM can only manage a constant coefficient.

The surface wind stress τ follows the theoretical formula found in Cushman-Roisin and Beckers (2006):

$$\tau = \rho_{air}C_D||\mathbf{u}_{10}||\mathbf{u}_{10} \quad (7)$$

where ρ_{air} is the air density, C_D is the drag coefficient and $\mathbf{u}_{10}$ is the wind speed 10 m above sea level. In usual conditions, i.e. wind speeds inferior to 12.5 m/s approximately, conventional parameterisations, like the one proposed by Smith and Banke (1963), give reasonable results (Moon, Ginis, Hara, & Thomas, 2007). The majority of SLIM's models were based on that parameterisation:

$$C_D = 0.001(\alpha + \beta||\mathbf{u}_{10}||) \quad (8)$$

where $\alpha = 0.63$ and $\beta = 0.066 \text{ s/m}$ (Smith & Banke, 1963). This parameterisation is thus linear with the wind speed. In high wind conditions, the drag coefficient would thus be very high as well. Before Powell, Vickery, and Reinhold (2003), this parameterisation was used in hurricanes forecasting systems and numerical simulations as no observations were available to confirm/refute it. Data available for wind speed inferior to hurricane speeds (33 m/s) were thus extrapolated. However, Powell et al. (2003) observed with GPS sondes that the drag coefficient levels off around 33 m/s and then even decreases with increasing wind speeds. Donelan (2004) set up an experiment in hurricane conditions and reached the same conclusion. This drag coefficient saturation could be attributed to the formation of sea foam and spray by breaking waves, maybe leading to the formation of a slipping sea surface and a decrease in aerodynamic roughness and drag (Powell et al., 2003). Makin (2005) then proposed a theoretical parameterisation that is consistent with Powell's observations. Nevertheless, the physical phenomenons behind the drag coefficient decrease are not very well understood. Moon et al. (2007) thus proposed a simple wind friction parameterisation with a levelling off drag coefficient based on theory and numerical studies. The latter does not show a decreasing phase after the cap, though.

Moon's parameterisation makes use of a roughness length z_0 , widely used in other wind parameterisations to which he compares his results. For low wind speeds, the Charnock's formulation of this roughness length gives good results (Charnock, 1955):

$$z_0 = \frac{z_{ch} u_*^2}{g} \quad (9)$$

where $z_{ch} \simeq 0.0185$ is the constant Charnock coefficient, $u_* = \sqrt{\frac{\tau}{\rho}}$ is the wind shear velocity and g is the gravitational acceleration. This relation can be used in combination with the logarithmic wind profile which determines the wind speed 10 m above sea level:

$$u_{10} = \frac{u_*}{\kappa} \ln \frac{10}{z_0} \quad (10)$$

where $\kappa = 0.4$. Using polynomial fitting, we can express the shear velocity and the roughness length in function of u_{10} (Moon et al., 2007):

$$u_* = 0.001 u_{10}^2 + 0.028 u_{10} \quad (11)$$

$$z_0 = \frac{0.0185}{g} (0.001 u_{10}^2 + 0.028 u_{10})^2 \quad (12)$$

As we said earlier, this formulation gives reasonable results for low wind speeds. According to Moon et al. (2007), they are valid up to 12.5 m/s . When the wind speed rises above 12.5 m/s , Moon et al. (2007) propose an empirical relation for the roughness length:

$$z_0 = \frac{(0.085 u_{10} - 0.58)}{1000} \quad (13)$$

For both wind speed ranges, the drag coefficient can be estimated thanks to the following relationship:

$$C_D = \kappa^2 \left(\ln \frac{10}{z_0} \right)^{-2} \quad (14)$$

Equation (7) can then be used to compute the stress exerted by the wind on the sea surface, in the same way as the Smith and Banke formulation. Moon et al. (2007) compared

their formulation with conventional ones implemented in the Geophysical Fluid Dynamics Laboratory hurricane prediction model, which is used by the U.S. National Hurricane Center. They identified the saturation effect of increasing wind speeds on C_D highlighted by Powell et al. (2003).

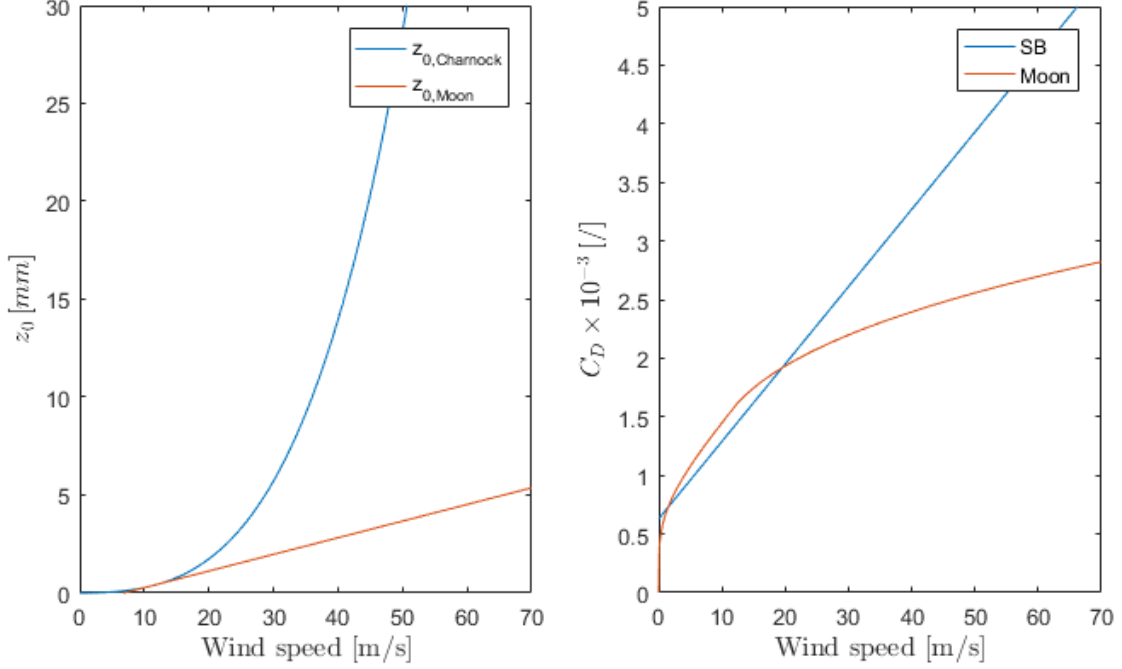


Figure 23: Left: Comparison of the roughness length between Charnock's and Moon's formulations. Right: Comparison of the drag coefficient C_D between Smith and Banke's and Moon's formulations. The right panel shows that Moon's parameterisation gives a higher drag coefficient for low wind speeds, but then levels off for high wind speeds like Powell's observations.

If we compare the wind stress τ obtained by Moon et al. (2007) with Smith and Banke (1963), a significant difference appears when wind speed increases (Fig. 24). The formulation of the latter must thus be rejected for high wind speeds.

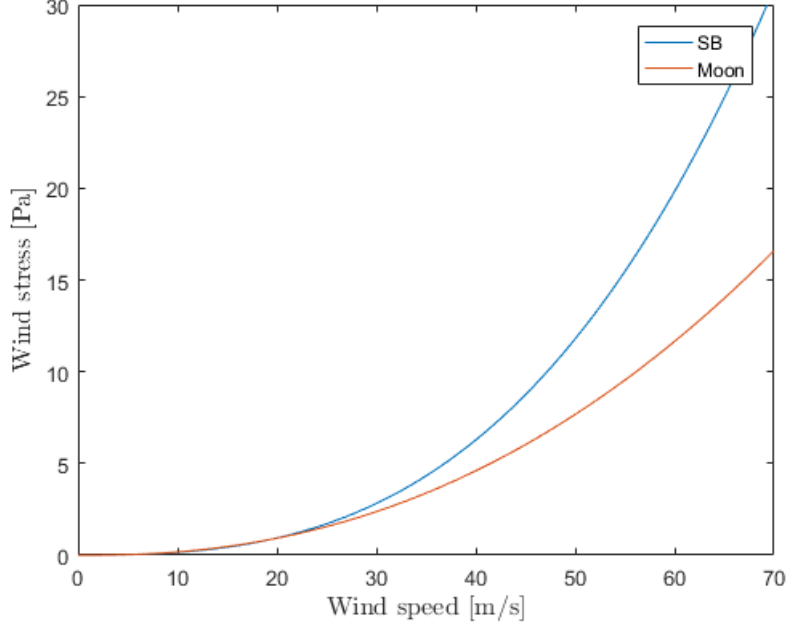


Figure 24: Comparison between wind stress versus wind speed for Smith and Banke (1963) (blue) and Moon et al. (2007) (orange). For high wind speeds, the formulation of Smith and Banke (1963) overestimates the stress exerted by the wind on sea surface.

Regarding the last dissipative term, we used the Smagorinsky parameterisation to modelise the viscosity ν (Smagorinsky, 1963):

$$\nu = (\tilde{C}_s \Delta)^2 \sqrt{2 \left(\frac{\partial u}{\partial x} \right)^2 + 2 \left(\frac{\partial v}{\partial y} \right)^2 + \left(\frac{\partial u}{\partial y} + \frac{\partial v}{\partial x} \right)^2} \quad (15)$$

where $\tilde{C}_s = 0.1$ is the Smagorinsky coefficient (Lambrechts et al., 2008), Δ is the local mesh element size, the couple (x, y) is the couple of Cartesian coordinates in the horizontal plan whereas u and v stand respectively for the components of the depth-integrated velocity vector $\mathbf{u}$.

2.3 Model forcings

The implementation of equations (5) and (6) needs to use four external time-dependent forcings: winds, pressures, tides and global circulation currents. The winds are directly requested by the surface wind stress term in equation (6). Although the pressure term is usually neglected in low wind speeds conditions, the hurricane conditions of this simulation force us to take the atmospheric pressures into account. A hurricane is indeed characterised by a low pressure zone at its center. The strong pressure gradient over a short distance, responsible for high wind speeds, can thus not be neglected. Tides are not taken into account by SLIM unless we add them as boundary conditions. And finally, SLIM is not able to reproduce some large circulation processes like the FC. Because of that, the use of another model is also needed at the boundary. Tides and large circulation processes are also used for the relaxation term of equation (6), but this term was only added to the equations for the accuracy of the model. All these data were measured and established on a structured grid. Consequently, they need to be interpolated on our unstructured grid.

The winds used for the entire simulations are measured 10 *m* above the sea surface. These data were extracted from the National Operational Model Archive and Distribution System (NOMADS) project of the National Centers for Environmental Prediction (NCEP) (Saha et al., 2010). Regarding Irma, we combined two data sets. High resolution wind data were retrieved from Powell, Houston, Amat, and Morisseau-Leroy (1998) whereas the track of the hurricane, including the track of the center position, the maximum wind sustained and the minimal pressure, was obtained through Landsea and Franklin (2013). After interpolating the wind data and merging them if needed, the resulting interpolated data could be used in equation (7).

The pressure data were obtained through Saha et al. (2010) as well. As mentioned before, the pressure is often neglected in numerical simulations, at least by most SLIM modellers. The reason is that the pressure gradient is very low in low wind speeds conditions, making it negligible. In high wind speeds conditions, such as storms and hurricanes, the pressure term can not be neglected, though. A quick dimensional analysis indeed shows us that the pressure term is higher than a tenth of the wind stress term and thus non negligible when:

$$\frac{H}{\rho} \frac{\Delta p}{\Delta L} \geq \frac{1}{10} \frac{\tau}{\rho} \quad (16)$$

$$\frac{10}{1000} \frac{\Delta p}{50000} \geq \frac{1}{10} \frac{10}{1000} \quad (17)$$

$$\Delta p \geq 50 \text{ mbar} \quad (18)$$

where $H \simeq 10 \text{ m}$ is the order of the bathymetry in the FRT, $\rho = 1000 \text{ kg/m}^3$ is a reference value for the water density, $\Delta L \simeq 50 \text{ km}$ is the approximate radius of Irma's eye and $\tau = 10 \text{ Pa}$ is the order of magnitude of the wind stress exerted for medium to strong wind speeds. As the pressure difference between the conventional atmospheric pressure and the minimal recorded pressure is even higher than that pressure difference, it appears the pressure term can indeed not be neglected. To assess the wind speed above which the pressure term can not be neglected, we can use the relationship between wind and pressure proposed by Atkinson and Holliday (1977):

$$u_{10} = 12.41(1010 - p_a)^{0.644} \quad (19)$$

where p_a is the atmospheric pressure in *mbar*. This formulation is consistent with our observation since it gives $u_{10} = 206.9 \text{ km/h}$ for the minimal pressure recorded in the FRT $p_a = 931 \text{ mbar}$ (as a reminder 213 km/h maximum were recorded). To reach a pressure difference of 50 mbar between 1 atm and the atmospheric pressure, the winds must be higher than $u_{10} = 173.32 \text{ km/h}$, i.e. considering almost major hurricanes conditions. However, if we use the same procedure in deep waters, Δp needs to be lower to be significant. For $H \simeq 2000 \text{ m}$, we obtain $\Delta p = 25 \text{ Pa}$, leading to a wind speed limit above which the pressure is significant of $u_{10} = 98.63 \text{ km/h}$. In such deep waters, the pressure term should thus be included for storm conditions. Nevertheless, the wind stress is not the dominant momentum term in deep waters. In this case, a comparison of the pressure term with the gravity term is a better idea:

$$\frac{H}{\rho} \frac{\Delta p}{\Delta L} \geq \frac{gH}{10} \frac{\Delta h}{\Delta L} \quad (20)$$

$$\Delta p \geq \frac{\rho g}{10} \Delta h \simeq 3 \text{ bar} \quad (21)$$

where $\Delta h \simeq 300 \text{ m}$ is a bathymetry difference that can be found for a horizontal $\Delta L = 50 \text{ km}$ distance in deep areas of the Florida Strait. Of course, no hurricane would ever produce such a pressure difference. The pressure term in deep waters could thus be neglected.

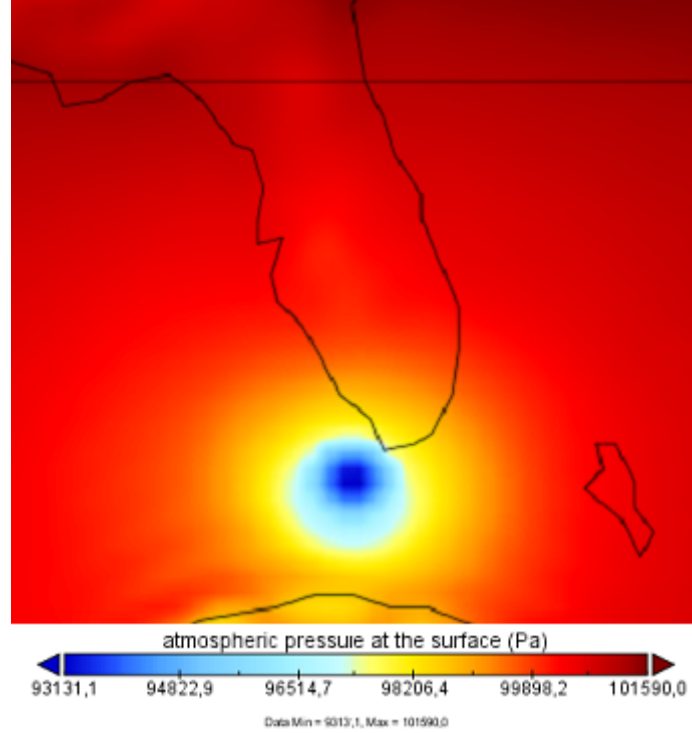


Figure 25: Pressure data on 10 September 1 p.m. when Irma struck Cudjoe Key. The radius of the eye is 50 km wide (Saha et al., 2010).

In fact, the decrease in atmospheric pressure causes a sea water rise where the hurricane is the strongest. The importance of this pressure-related sea rise is quite weak in comparison with the rise caused by wind waves, though (National Hurricane Center, n.d.-b).

The tidal forcing data are recovered thanks to the OSU TOPEX/Poseidon Global Inverse Solution tidal model (Egbert & Erofeeva, 2002). The latter gives us the amplitude and phase of the main tidal components on a $1/4^\circ$ resolution grid.

Finally, large circulation current data are retrieved from HYCOM (Hycom, n.d.). In the Gulf of Mexico, HYCOM offers a $1/25^\circ$ resolution grid. Actually, HYCOM is a 3D hydrodynamic model. Since this study uses a two-dimensional approach, leaving barotropic processes aside, we need to compute a depth-integrated velocity for each point of the domain. Because of that, we will not be able to reproduce large-scale eddies in a proper way with SLIM. The 2D velocity and the water elevation are then added to tidal velocities

and elevations respectively and then imposed at all open boundaries.

Nevertheless, imposing HYCOM and tides at the boundaries looks not sufficient to reproduce large scale currents in the inner domain, especially when the depth-averaging hypothesis is not very relevant, i.e. in deep waters. For that reason, we will use a relaxation parameter γ to drive SLIM's results towards HYCOM's ones. The large scale circulation term is given by:

$$F_c = \gamma(\mathbf{U}_* - \mathbf{U}) \quad (22)$$

where $\mathbf{U}_* = H\mathbf{u}_*$ and $\mathbf{u}_*$ is the sum of the tidal velocities and the depth-averaged velocities of HYCOM. The parameter γ corresponds to the inverse of the relaxation time τ , defined to be longer than the timescale of the main tidal component (Le Bars et al., 2016). The Florida Keys constituting our zone of major interest, we wanted the influence of HYCOM and tides on SLIM to be zero there, except for the propagation of the boundary conditions. Consequently, the γ parameter must be zero in that area.

The nudging coefficient γ consists in the addition of two terms: $\gamma_{depth}(h)$ and $\gamma_{dist}(d)$. The first one grows linearly between 50 m and 300 m while the latter is function of the distance d to the closest open boundary.

$$\gamma_{depth} [s^{-1}] = \begin{cases} 0 & \text{if } h \leq 50 \text{ m} \\ 10^{-7} \times h & \text{if } 50 \text{ m} < h \leq 300 \text{ m} \\ 3 \times 10^{-5} & \text{if } h > 300 \text{ m} \end{cases} \quad (23)$$

$$\quad (24)$$

$$\gamma_{dist} [s^{-1}] = \begin{cases} \frac{10^5 - d}{10^{10}} & \text{if } d \leq 100 \text{ km} \\ 0 & \text{otherwise} \end{cases} \quad (25)$$

$$\quad (26)$$

Finally, $\gamma(h, d) = \gamma_{depth}(h) + \gamma_{dist}(d)$. The projection of the nudging coefficient over our domain is presented in Fig. 26

Apart from the nudging term, we also added a slope friction term $C_s \frac{|\mathbf{U} \cdot \nabla H| |\mathbf{U}|}{\bar{H}^2}$ to the usual expression of the conservative momentum equation. It was inspired by Döös (2004), developed by Frys (2017) and aims at obtaining better results in areas with a high bathymetry gradient. The usual dissipation parameterisations were indeed developed for flat bottom applications. However, several studies have showed that a rough topography was responsible for an important part of the total dissipation (Döös, 2004). In combination with the Chézy-Manning-Strickler term, this slope friction term increased the dissipation only in steep areas. Even if Döös (2004) determined that $C_s = 26$ would lead to the best results, Frys (2017) experimented different values and got better results with $C_s = 5$. As we work on the same region of the world and since we use the same model, we will use his value.

2.4 Validation of the hydrodynamics

In order to get a reliable larval dispersal, we first had to validate the hydrodynamics of our model. To do so, we exported our results on 13 validation points shown on Fig. 27.

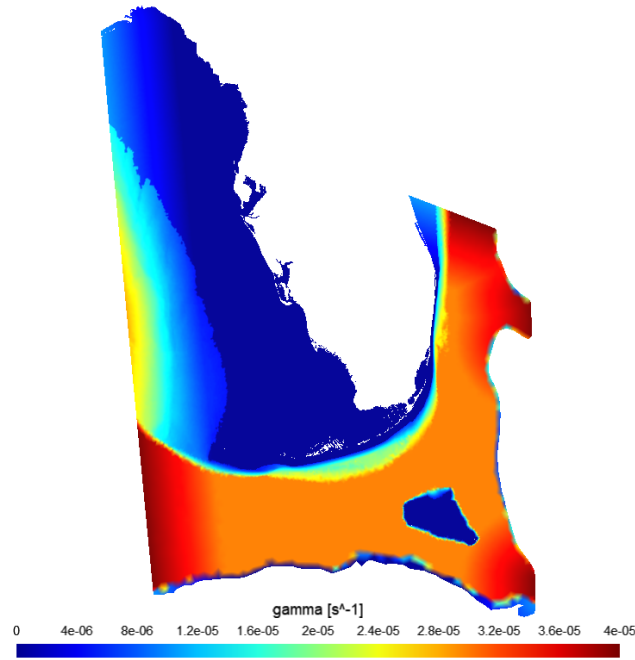


Figure 26: Nudging coefficient γ projected on the mesh. It is maximum at deep-waters open boundaries and zero in shallow waters like the FRT.

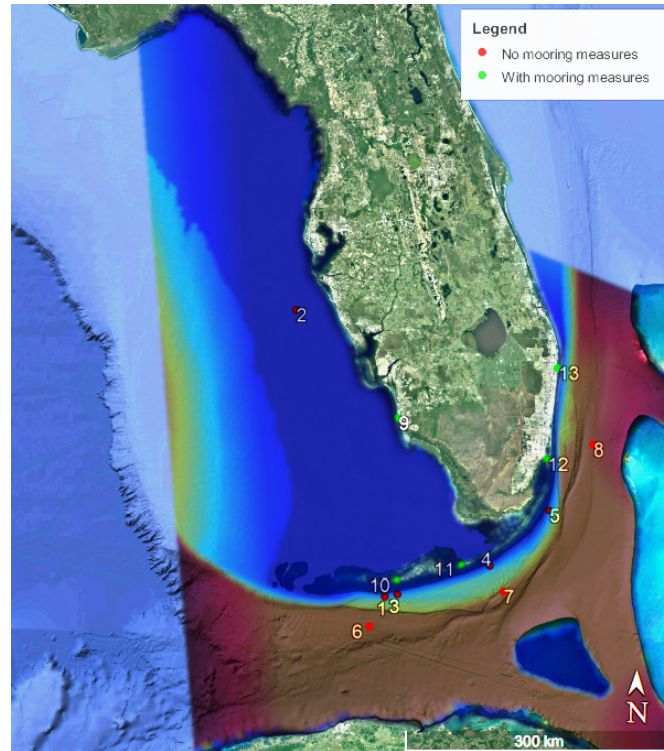


Figure 27: The nudging parameter is projected on the validation points map used to validate our model. Point 8 is located in a deep water zone where the nudging coefficient is rather high. Same remark for points 6 and 7, but to a lesser extent. The results of all the other points should not be affected much by the nudging term. Most of them are located along the FRT or seawards as it is the zone where most corals lie and through which most larvae are transported.

Even if the model solves the shallow water equations under the conservative form, we divided the computed transport $\mathbf{U}$ by the water depth $\tilde{H}$ to treat velocities on an understandable scale and we exported their components for all validation points at each hour. We also exported the water elevation for all these points. Furthermore, we also interpolated HYCOM’s results at these points and we exported their temporal evolution, both for elevation and for velocity components. We did the same with TOPEX/Poseidon and the sum of HYCOM and TOPEX/Poseidon.

Moreover, we also retrieved water level measures from the NOAA (National Oceanic and Atmospheric Administration, n.d.-c). These data were available for alongshore points only, though. Consequently, we were only able to compare the water elevation measures with our model for points 9, 10, 12 and 13. Even if we had observations for point 11 at that period, SLIM did not manage to provide proper results in elevation at this point. Sadly, we did not find any measures regarding velocities.

2.4.1 Water elevation validation

Frys (2017) and Béchet and Verstraeten (2018) used TAPPY to carry out a harmonic analysis of SLIM and to compare it to the measures (Cera, 1991). TAPPY actually splits the signal in all the different tidal components. By comparing each tidal component of the measures with the simulation results, it computes an error both in velocity and phase. However, in our case, hurricane Irma leads the simulated water level to significant variations from the usual tidal evolution. For that reason, TAPPY would not be able to break down the signal into appropriate tidal components and would deliver poor results.

Consequently, we will omit the Irma period from our harmonic analysis. We will actually realise two analyses. The first one will deal with the first 35 days of the simulation, before that Irma’s impact on the water elevation of our validation points becomes significant. Besides, we will also omit the first 7 days of these 35 days to let the model spin up. The second analysis will extend from 13 September to 10 November, i.e. after the passage of Irma till the end of the simulation. For a four day period around the hurricane, we will thus leave the harmonic analysis aside and simply compute the Root Mean Square Error (RMSE) between the two signals.

Validation point	SLIM mean amplitude [m]	SLIM maximum amplitude [m]	Mooring mean amplitude [m]	Mooring maximum amplitude [m]	RMSE [m]	Mooring proportion [%]
9	0.39	1.18	0.5	1.48	0.34	23.29
10	0.14	0.47	0.24	0.74	0.17	30.59
12	0.14	0.41	0.29	1.03	0.26	25.45
13	0.26	0.51	0.32	0.73	0.22	30.55

Table 1: RMSE calculation between mooring measures and SLIM simulations from 9 to 13 September. The last column gives the ratio between the RMSE and the maximum amplitude of the mooring timeseries.

Table 1 shows rather large differences in maximum amplitude between SLIM and mooring measures for all validation points. Of course both SLIM and mooring maximum amplitudes occur during the passage of the hurricane. It looks our model underestimates

the water elevation changes caused by the hurricane. It is particularly the case for validation point 12. The focuses on Irma's passage for the 3 other validation points with mooring measures are given in Appendix A. Even if the peak amplitude looks underestimated by SLIM, the simulation results seem to be in phase with the observations.

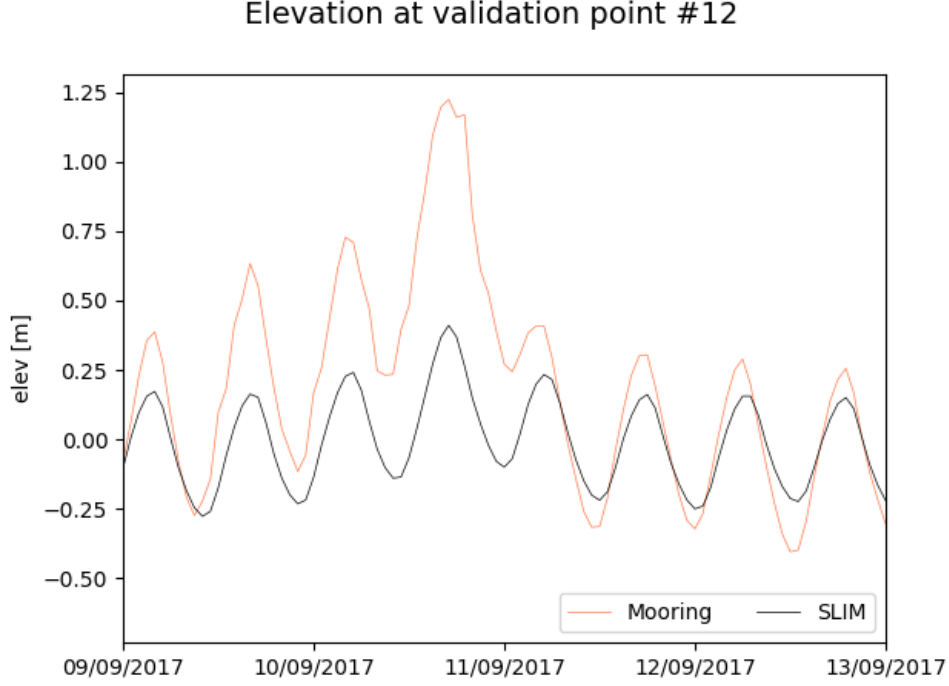


Figure 28: Comparison of the water elevation temporal evolution between SLIM and the mooring measures from 9 to 13 September at validation point 12.

Let us now compare the harmonic analyses of SLIM with mooring measures for a longer period, when no major disturbance is in progress. For all the four tables presented here and in Appendix A, the 10 most important tidal components in terms of amplitude of the observations can be found. The contributions from one component can be more important for a point and less important for another. The rank of a component in amplitude contribution can vary among the four points. The relative error in amplitude corresponds to the ratio between the absolute error in amplitude and the measured amplitude of the concerned tidal component. The phase lag is computed in comparison with the theoretical equilibrium tidal phase. Since the pre-Irma period delivered worse results than the post-Irma period, we will present the former. For each mooring station, the difference between pre-Irma and post-Irma periods were limited to roughly 10 % of the relative amplitude error of the first tidal component, though. We present here the analysis results for the worst point (12) and the best one (13) in terms of relative error. The results of points 9 and 10 can be found in Appendix A.

Tidal compo- nent	Amplitude [cm]				Phase [$^\circ$]		
	Values		Errors		Values		Errors
	Measures	SLIM	Absolute	Relative [%]	Measures	SLIM	Absolute
M2	28.46	17.29	-11.17	-39.25	39.36	50.62	11.26
N2	5.52	3.35	-2.17	-39.31	314.96	132.1	-182.86
S2	3.73	2.43	-1.3	-34.85	99.59	101.91	2.31
O1	3.16	1.7	-1.46	-46.2	101.83	268.51	166.68
MSf	2.42	2.24	-0.18	-7.44	40.3	55.99	15.69
K1	2.23	1.1	-1.13	-50.67	95.58	347.93	252.65
M6	1.16	0.6	-0.56	-48.28	169.94	242.54	72.59
ν 2	1.08	0.66	-0.42	-38.89	76.5	253.62	177.13
K2	1.01	0.66	-0.35	-34.65	95.45	272.33	176.89
L2	0.8	0.48	-0.32	-40	3.13	180.1	176.97

Table 2: TAPPY harmonic analysis for validation point 12 from 12 August to 8 September. This table is limited to the 10 most predominant tidal components in terms of observation amplitude.

Tidal compo- nent	Amplitude [cm]				Phase [$^\circ$]		
	Values		Errors		Values		Errors
	Measures	SLIM	Absolute	Relative [%]	Measures	SLIM	Absolute
M2	40.99	34.22	-6.77	-16.52	12.2	16.45	4.26
N2	7.95	6.64	-1.31	-16.48	314.45	314.63	0.18
S2	4.51	4.5	-0.01	-0.22	75.88	69.06	-6.82
O1	4.39	1.78	-2.61	-59.45	66.46	297.38	230.92
K1	3.56	3.57	0.01	0.28	50.81	0.54	-50.27
MSf	2.21	1.73	-0.48	-21.72	284.38	94	-190.37
ν 2	1.56	1.3	-0.26	-16.67	76	76.16	0.16
K2	1.23	1.22	-0.01	-0.81	95.04	94.9	-0.13
P1	1.18	1.18	0	0	90.28	131.67	-177.83
L2	1.15	0.96	-0.19	-16.52	2.69	2.66	-0.03

Table 3: TAPPY harmonic analysis for validation point 13 from 12 August to 8 September. This table is limited to the 10 most predominant tidal components in terms of observation amplitude.

The results of point 12 are undoubtedly disappointing. The relative error between SLIM and the observations is at least 34.85% for the four main tidal components. Besides, the 39.25% error on the first component is quite concerning, as the amplitude of this component is more than five times the one of the second component. Although the second and fourth components are almost fed with a 180° phase shift between the observations and the simulations results, the first component shows at least a low phase error. Looking at Fig. 29, such errors are not surprising.

Even though the relative error stays rather high for the two main components, point 13 shows a closer match between SLIM and the measures. Here again, the first component is equivalent to more than five times the second in terms of measured amplitude and its relative error is still 16.52 %. The phase error between SLIM and the observations is excellent for the three first components. Fig. 30 indeed shows better results than Fig. 29.

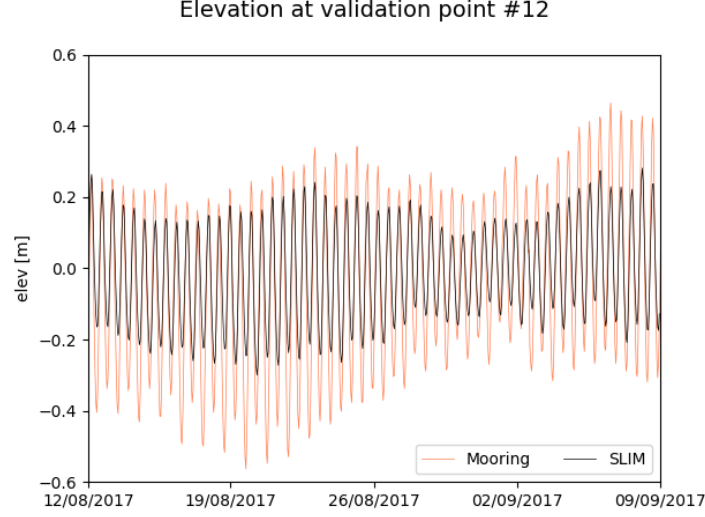


Figure 29: Comparison of the water elevation temporal evolution between SLIM and the mooring measures from 12 August to 8 September at validation point 12.

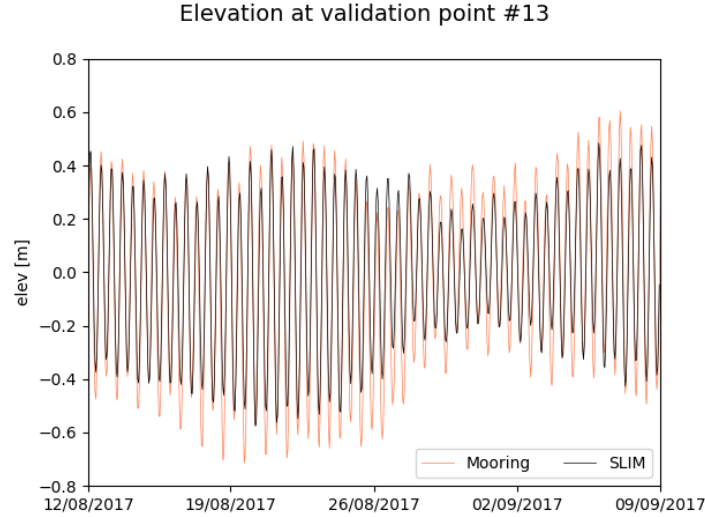


Figure 30: Comparison of the water elevation temporal evolution between SLIM and the mooring measures from 12 August to 8 September at validation point 13.

Eventually, the wetting-drying phenomenon due to the hurricane is limited. We considered that a cell was dry when $f < \epsilon = 0.15 \text{ m}$. It appears that such a condition is only occurring along the coast between Marco Island and Florida Bay, i.e. where there is not any coral reef (Fig. 32). Water depths inferior to ϵ are found on 10 September from 3

p.m. till 7 p.m., right before Irma's last landfall on Marco Island (Fig. 31). However, the hurricane is still responsible for strong water elevation changes, as simulation and observations showed it. Figures 33 and 34 indeed show that the water level drops under 1 m over quite a large distance seawards, and in the northeastern Lower Keys. The absence of water surrounding the top of large reef structures might make them stress or be damaged by the strong winds. However, this model does not treat such considerations and maintains the same coral cover through the whole simulation.

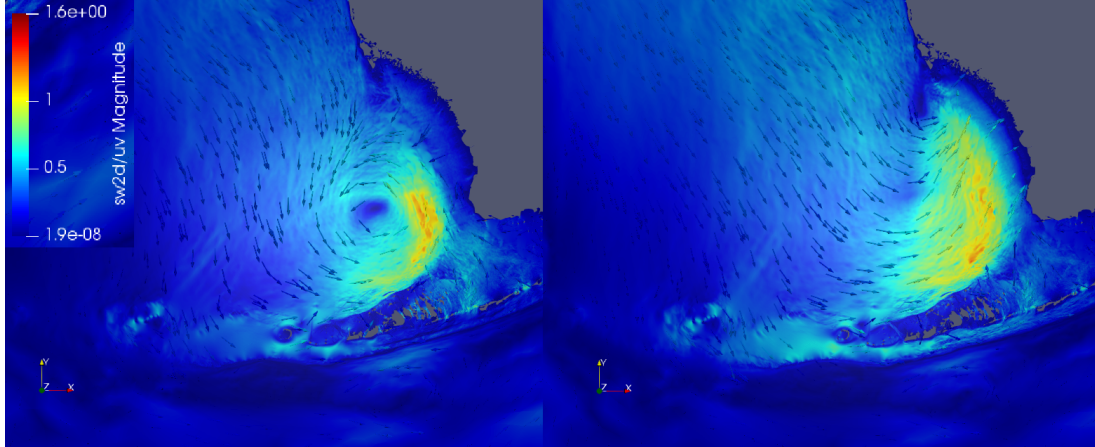


Figure 31: Water velocities on 10 September between 3 p.m. and 6 p.m. The hurricane is about to strike Marco Island.

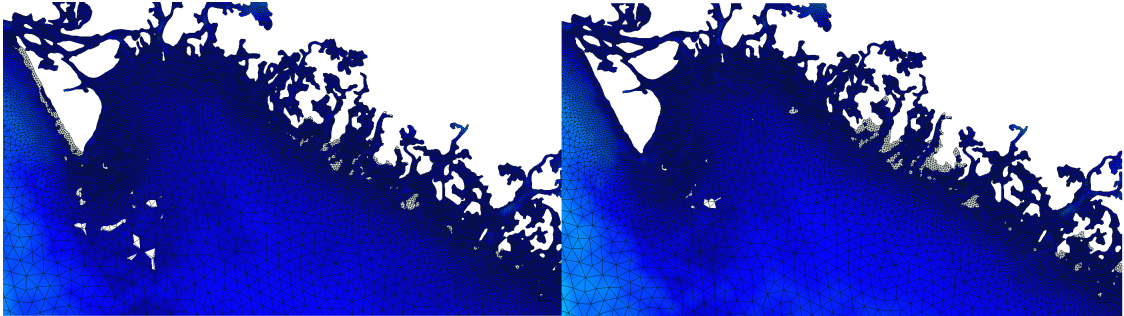


Figure 32: Water level near Marco Island on 10 September from 4 p.m. till 6 p.m. White cells correspond to the dry ones where $f < \epsilon = 0.15 m$. Only a few cells show this condition.

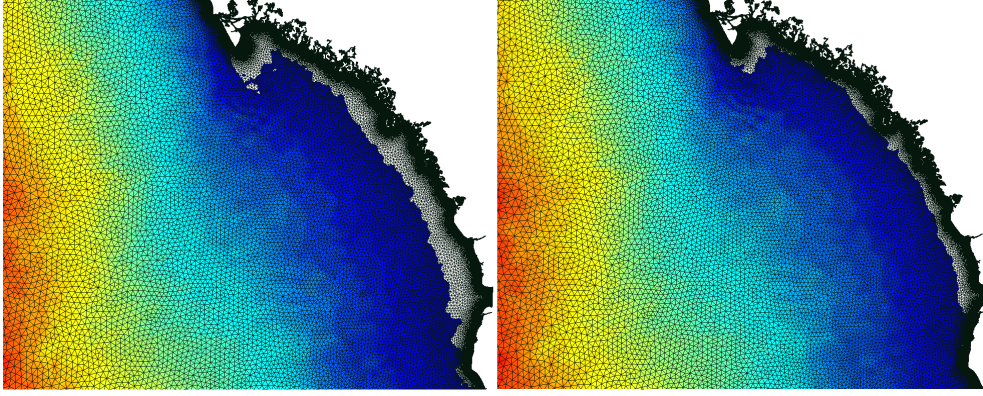


Figure 33: Water level along the coast between Marco Island and Florida Bay on 10 September from 4 p.m. till 6 p.m. White cells correspond to the ones with $H < 1\text{ m}$. A lot more cells show such a significant water level change than those of Fig. 32.

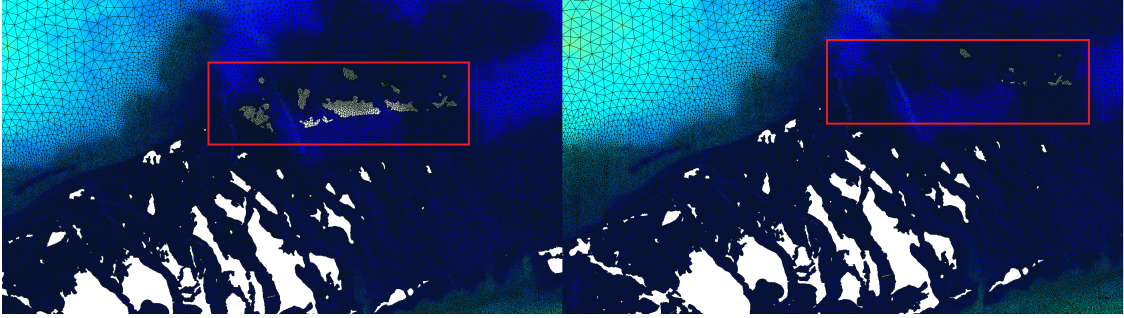


Figure 34: Water level in the northeastern Lower Keys on 10 September from 3 p.m. till 6 p.m. White cells correspond to the ones with $H < 1\text{ m}$. A small area (framed in red) is subjected to such a water level drop. Some coral reefs are located very close to it.

In conclusion, SLIM looks to follow the same tendencies as the mooring measures and is mostly in phase with the observations. Nevertheless, the error between the simulations results and the measures is significant for all the points, especially for point 12. Validation point 13 shows the lowest error and the best phase match with the observations. Regarding the management of the hurricane, it appears SLIM underestimates the peak amplitude in all cases. Yet, the phase looks good. The wetting-drying phenomenon seems to be limited. According to our model, the reefs do not see the water surrounding them drop to zero. Nevertheless, we saw that SLIM underestimated the water level rise due to the hurricanes. It is thus highly possible that the water level drop gets also underestimated.

2.4.2 Water velocity validation

By comparing our results with the HYCOM model, we can assess their relevance, depending on the location of the considered validation point. Unlike the water elevation validation, we will present timeseries going on the whole simulation period. Unfortunately, we do not have any measures for that period. We will plot both velocity amplitude and direction of the currents. In all graphs, black corresponds to SLIM, red to HYCOM and blue to the sum of HYCOM and tides, obtained via TOPEX/Poseidon. The direction graphs give the direction taken by the current at the validation point for the whole simulation. The first point of the simulation lies in the middle of the polar graph. Then, the distance to the center of the cir-

cle linearly increases with time. The last point of the simulation lies on the edge of the circle.

Points 1, 3 and 6 are located south of Key West, in an area characterised by the presence of circulating baroclinic eddies. Even if the nudging coefficient is rather strong for point 6, so that the amplitude follows the great tendencies, it does not match with the sum of HYCOM and tides perfectly. Looking at the directions of the currents, we see that both HYCOM and the sum of HYCOM and tides are mostly directed eastwards, but sometimes turn counterclockwise in other directions. The reason for this is the presence of eddies that SLIM is not able to reproduce because of its two dimensional limitations. Velocity amplitudes and directions for points 1 and 3 are given in Appendix A.

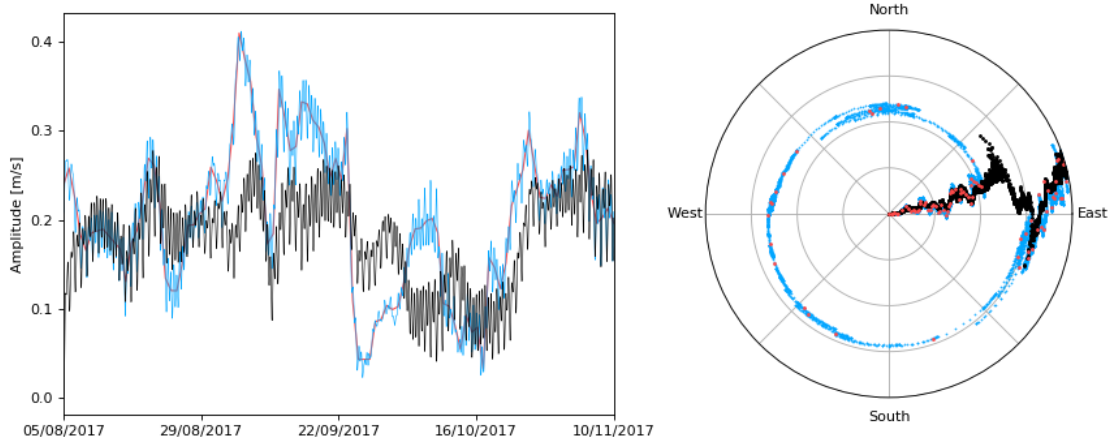


Figure 35: Left: water velocity amplitude. Right: water velocity direction. Validation point 6.

Validation point 2 lies in the WFS. Even if the nudging is zero here because of the low bathymetry, SLIM velocities are quite close to HYCOM's. This point is heavily impacted by hurricane Irma. We clearly observe a peak in velocity amplitude. Nevertheless, the peak amplitude of SLIM is far below HYCOM's. However, HYCOM does not take account for the cap reached by the wind drag coefficient and overestimates the wind-related momentum flux. On the contrary, this model uses a wind drag parameterisation more suited to storm conditions. HYCOM currents are mainly directed from the southeast to the northwest. SLIM and tides vary more in direction and match pretty well. Tides are applied as a boundary condition and there is no obstacle between the open boundary to the Gulf of Mexico and validation point 2. Moreover, velocity amplitude is rather low, except for the hurricane period, because of the high friction induced by the bottom being close to the water surface. The amplitude of the tides is thus sufficient to influence much the simulations results, in amplitude and in direction.

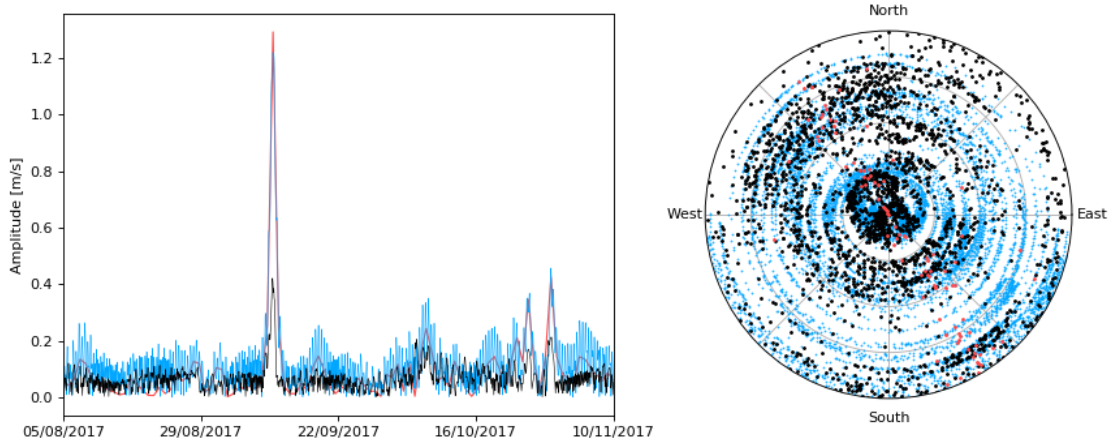


Figure 36: Left: water velocity amplitude. Right: water velocity direction. Validation point 2.

As we could expect it, SLIM looks the closest to HYCOM for validation point 8, the only point where the nudging coefficient is almost maximum. The velocity tendency is the same, even though there are some differences in amplitude. This point is not on the path of the hurricane and does not seem to be affected by Irma. Regarding directions, we recognize the northerly pattern of the Florida Current when it turns north after facing the Bahamas.

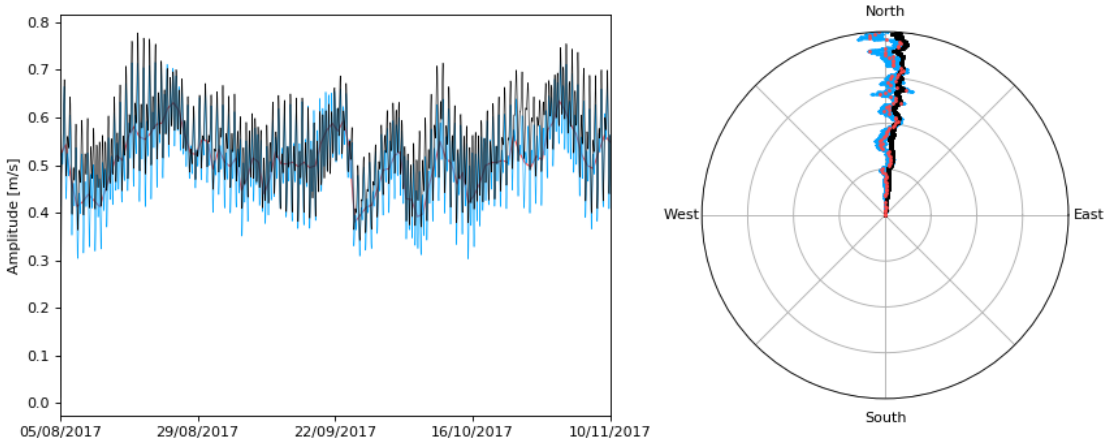


Figure 37: Left: water velocity amplitude. Right: water velocity direction. Validation point 8.

Validation points 9 to 13 are located in harbours or are very close to the shore. Consequently, the comparison with HYCOM and TOPEX/Poseidon is pointless since these two models have a spatial resolution way too coarse to depict the hydrodynamics properly near shores. The velocity amplitude computed by SLIM is very low for all these points. Like point 2, this can be explained by the proximity of the bottom to the surface. The amplitude and direction graphs of these points can be found in Appendix A.

To conclude about velocity validation, we can say that SLIM is more relevant than

HYCOM and TOPEX/Poseidon in shallow regions, particularly along shores. HYCOM and TOPEX/Poseidon data sets are both too coarse to represent properly the hydrodynamics near coasts. They usually overestimate the velocity amplitude. Our goal concerning the hydrodynamics accuracy in coastal areas, where most coral reefs lie, is thus achieved.

We were also able to recognize velocity peaks during the passage of the hurricane, even near shores, where HYCOM was not able to do so. As our wind drag parameterisation is based on a capping drag coefficient instead of one increasing linearly with wind speed, SLIM might be more reliable than HYCOM that surely overestimates the wind stress exerted by the storm on the water. This assumption needs to be validated by observations, though.

Unfortunately, SLIM does not reproduce large scale circulation patterns very well unless a strong nudging coefficient is applied. In deep water areas, the use of HYCOM is absolutely necessary.

Moreover, the use of a depth-integrated water velocity inhibits the capacity of the model to reproduce circulating eddies along the Florida Keys. We reckon these eddies should be important regarding larval dispersal, though. Their absence in the numerical model is thus quite a strong drawback.

2.5 Limitations

Unfortunately, our model suffers from some limitations. The major simplification of our model is certainly the averaging of the velocity over the water column. Doing so does not let us take into account 3D features like upwelling and baroclinicity. Nevertheless, this hypothesis was necessary to ensure a sufficient horizontal resolution capable of solving the hydrodynamics close to reefs with a reasonable accuracy. The aim was indeed to be able to simulate the larval dispersal near reefs with precision. Consequently, we used a relaxation parameter nudging our model towards HYCOM results in deep waters. The validation of SLIM in these areas is thus not very relevant since it does not criticize HYCOM's accuracy.

Our model is also limited, especially in strong wind conditions, for it does not take waves into account. In shallow waters, like the FRT, where the depth-integrated velocity is close to the surface velocity, the effect of waves on surface currents should not be omitted. Perrie, Tang, Hu, and DeTracy (2003) indeed reckoned that the waves-induced currents could be responsible for roughly 40 % of the current velocity in strong wind conditions like storms. Yet, these observations were concerning wind fields reaching 30 m/s maximum. Besides, Perrie et al. (2003) highlights the relationship between increasing winds, increasing waves and increasing waves impacts on currents. In our hurricane conditions, we can thus imagine that the influence of waves on surface currents becomes far from negligible. Furthermore, our model does not include wave-breaking effects that affect the direction of surface drift and consequently, larval dispersal (Melsom, 1996). Besides, breaking waves result in the formation of sea spray, which is responsible for a non negligible momentum flux with the atmosphere. For major hurricanes conditions, Andreas and Emanuel (2001) estimated that the sea spray momentum flux can even equal the wind drag momentum flux. Nevertheless, the use of a depth-integrated model in deep waters would not let us assess the impact of the waves on the currents properly. It indeed mainly concerns surface currents. The mean velocity over the entire water column would not be much affected by the waves. Besides, regarding water elevation, the wind driven components of storm surges are far way more important than pressure driven components (National Hurricane Center, n.d.-b). In hurricane conditions, sea level rise is thus highly underestimated.

3 Particle tracking

3.1 Model equations

Now we know the velocities of our currents, we can move on to the larval dispersal study. For that purpose, we will use the method described by Thomas et al. (2014), mathematically developed by Dimou and Adams (1993), discussed by Spagnol et al. (2002) and used both by Frys (2017) and Béchet and Verstraeten (2018). This method consists in a Lagrangian random walk formulation of the advection-diffusion equation. The numerical equation used to track particles then writes this way:

$$\mathbf{x}_{n+1} = \mathbf{x}_n + \mathbf{v}_n \Delta t + \frac{\mathbf{R}_n}{\sqrt{r}} \sqrt{2K \Delta t} \quad (28)$$

$$\mathbf{v}_n = \left(\mathbf{u}_n + \frac{K}{h} \nabla h + \nabla K \right) |_{x_n} \quad (29)$$

where $\mathbf{x}_{n+1}$ and $\mathbf{x}_n$ correspond to the particle position vectors at time iterations $n + 1$ and n respectively. $\mathbf{v}_n$ is the marching velocity vector and is composed of the depth-integrated horizontal water velocity $\mathbf{u}_n$ computed by SLIM, of the horizontal diffusivity K and the water depth h . Finally, $\Delta t = 900 \text{ s}$ is the time step whereas $\mathbf{R}_n$ is a two-dimensional random numbers vector with a zero mean and a r variance such that $\frac{\mathbf{R}_n}{\sqrt{r}}$ is a random numbers vector with unit variance.

As explained by Spagnol et al. (2002), the use of the marching velocity $\mathbf{v}_n$, instead of the depth-integrated velocity $\mathbf{u}_n$ solely, drives particles towards areas of increasing depth and diffusivity, avoiding accumulation of particles in regions with low depth and diffusivity.

The last term of equation (28) is a stochastic term aiming at representing the turbulent movements of particles. Accordingly, the influence of this term on $\mathbf{v}_n$ rises where the horizontal diffusivity K is high.

The diffusivity K is computed thanks to the formula proposed by Okubo (1971) and rests on the coefficient values calibrated by Andutta, Ridd, and Wolanski (2011) for the Great Barrier Reef:

$$K = \alpha \Delta^{1.15} \quad (30)$$

where $\alpha = 0.041 \text{ m}^{0.85}/\text{s}$ and $\Delta [m]$ is the local element size. In this way, the diffusivity was really simply characterised and emphasised the greater range of unresolved water motions for large elements than for small ones.

3.2 Biological parameters

The model described hereabove does not care about the larva's species. It only runs the larval dispersal based on the hydrodynamics and on some stochastic features. As our model aims at studying living organisms, we can include several parameters to it to better represent the behaviour of each larval species. Since we eventually want to compare connectivity patterns for two species, we will describe these biological parameters both for *Acropora Cervicornis* (Béchet & Verstraeten, 2018) and for *Montastrea Cavernosa* (Frys,

2017).

Before describing life history traits corresponding to both species, we must identify the reefs concerned by the two spawning events. For that purpose, we retrieved a map with the location of all coral reefs in the FRT (Florida Fish and Wildlife Conservation Commission-Fish and Wildlife Research Institute, 2016). By interpolating these data on our mesh, we were able to assign an index to each reef. In total 1817 reefs were identified. In comparison, Frys (2017) and B  chet and Verstraeten (2018) only counted 996 reefs. The interpolation of the reef map on our mesh looks to be more accurate.

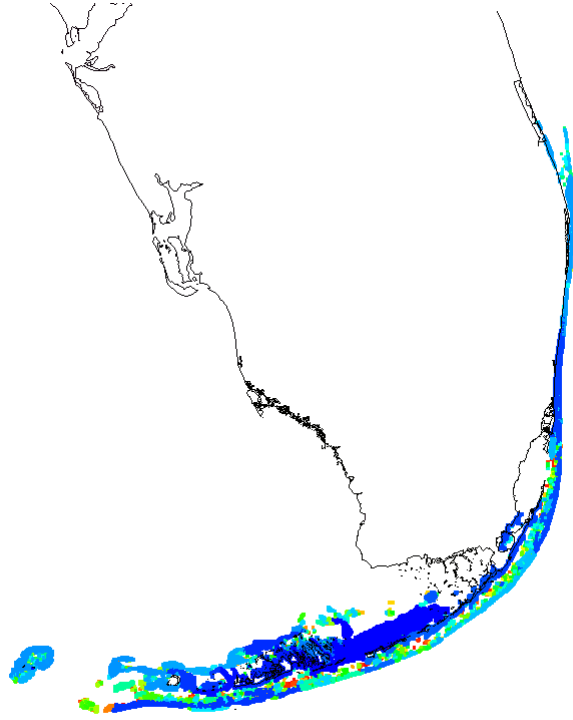


Figure 38: Florida Reef Tract interpolated on our mesh. An index ranging from 1 to 1817 was assigned to each reef. For visibility reasons, only the boundaries of the mesh were printed. It turns out that the largest reefs were assigned with the lowest indices, corresponding to blue color.

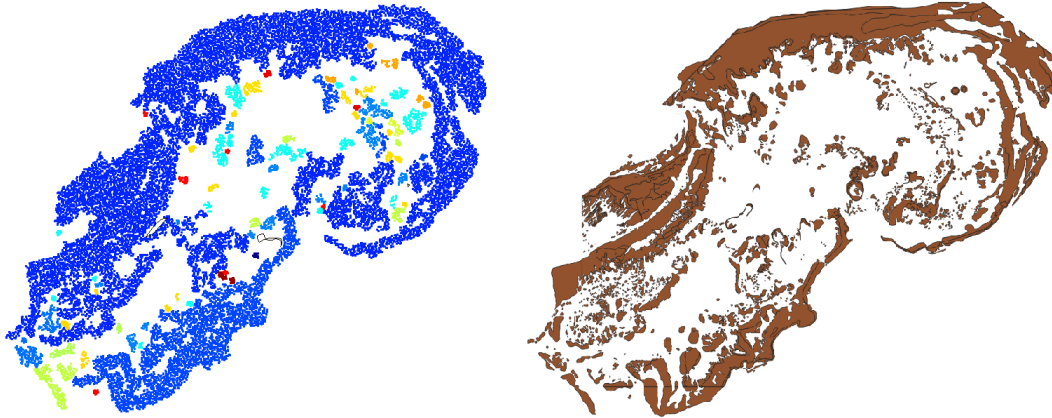


Figure 39: Comparison between the Dry Tortugas interpolated on our mesh (left) and the TIFF map retrieved thanks to Florida Fish and Wildlife Conservation Commission-Fish and Wildlife Research Institute (2016) (right). On the left, each point corresponds to a particle seeded by the reef with the same color. Thanks to the fine horizontal resolution of elements near reefs, the interpolation of the map is really conclusive.

Because of a lack of information concerning the total coral cover on these reefs and especially the cover for the two studied species, we made a very simplifying hypothesis. We indeed imposed the coral cover of each species to 100 %, which is obviously a nonsense since many other species live on those reefs and the reefs are far from being entirely covered by corals. We then imposed a spawning density proportional to the reef size for each species of $100 \text{ larvae}/\text{km}^2$, with a minimum number of 25 larvae released on each reef. Since three spawning nights are considered for each species, the maximum number of seeded larvae will occur after two days simulation. However, this maximum number does not match with the total number of seeded particles, for some larvae die between two spawning nights. The total number of larvae released by both species reaches 4.7×10^6 larvae. After three spawning events, the number of larvae caps at 4.08×10^6 for MC and at 4.4×10^6 for AC. Nevertheless, the results obtained hereafter must be taken relatively to the concentration in released larvae. This thesis is more about a qualitative analysis than a quantitative one.

Larvae are living organisms and consequently have some abilities, but die if they did not manage to find a proper recruiting reef. After a few days, larvae are able to settle onto a reef. They are said to be competent. Based on the experiments of Connolly and Baird (2010), the dedicated SLIM module grants the larvae a constant competency acquisition rate. After a certain period, the larvae also gradually lose their competency. However, we only fixed a time limit beyond which larvae were no longer competent. The post-competency processes are indeed badly known. When larvae have become competent, they can change their buoyancy and sink down to settle on a reef. As settlement conditions are rather complex and badly documented, we made the hypothesis that the larvae will settle on the first reef they encounter when competent, even if this simplifies the reality a lot.

Finally, larvae may die on their way to a recruiting reef. SLIM models the larval mortality according to a Weibull law, proposed by Connolly and Baird (2010) and Figueiredo, Baird, and Connolly (2014). Omitting predation processes because of a lack of information, the

model is characterised by a high mortality in the beginning of the simulation, decreasing with time. The implemented law requests 2 parameters and is written as follows:

$$f(t|\nu, \lambda) = \mu \exp(-\lambda t)^\nu \quad (31)$$

$$\mu = \nu \lambda (\lambda t)^{\nu-1} \quad (32)$$

where, ν is a shape parameter, λ is the inverse of a scale parameter and μ is the mortality rate. In the particular case $\nu = 1$, the Weibull distribution becomes equivalent to an exponential distribution, with a constant mortality rate. When $\nu < 1$, the mortality rate decreases with time whereas it increases when $\nu > 1$. For AC, we will use $\lambda = 0.06 \text{ days}^{-1}$ and $\nu = 0.64$ like B  chet and Verstraeten (2018). When it comes to MC, we will use the exponential law used by Frys (2017) after Kuba (2016) with a constant mortality rate and a $\lambda = 0.067 \text{ days}^{-1}$.

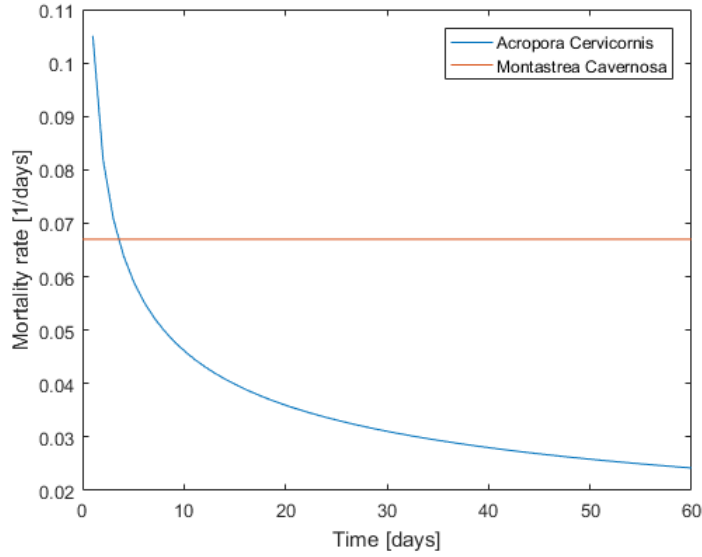


Figure 40: Comparison of mortality rates μ of the Weibull distributions. The mortality rate of AC ($\nu = 0.64$ and $\lambda = 0.06 \text{ days}^{-1}$) tends to infinity at the beginning and decreases as larvae age. The one of MC ($\nu = 1$ and $\lambda = 0.067 \text{ days}^{-1}$) is constant over time and equals λ .

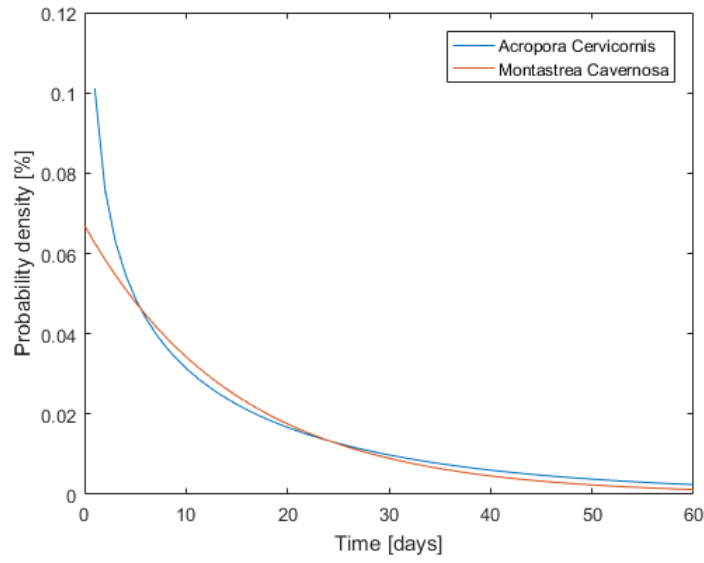


Figure 41: Comparison of Probability Density Functions of the Weibull distributions. For AC, mortality probability tends to infinity at the beginning and decreases as larvae age. For MC, mortality probability is maximum (6.7 %) at the beginning and decreases as larvae age.

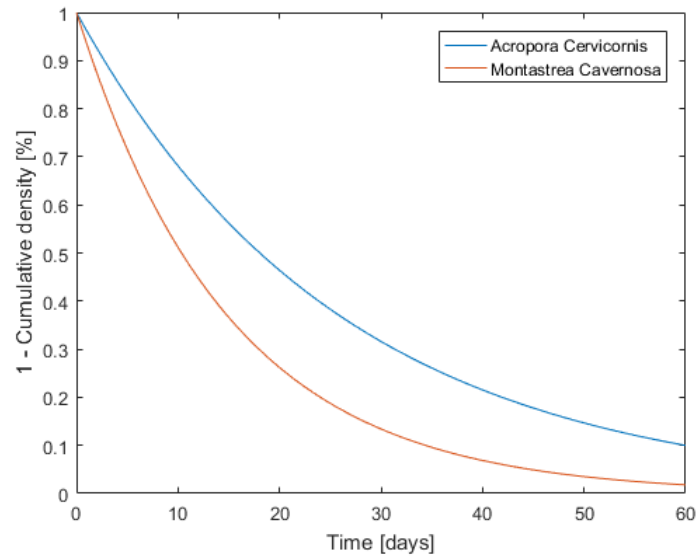


Figure 42: Comparison of Cumulative Density Functions of the Weibull distributions. It appears that 95 % of dead particles after 60 days die after 50.52 days and 40.33 days for AC and MC respectively. After 60 days, 9.99 % of all AC released larvae are still alive according to Weibull whereas it only reaches 1.8 % for MC.

Species	Competency start date	Competency acquisition rate [%/day]	Competency time limit [days]	Weibull λ parameter	Weibull ν parameter
<i>Acropora Cervicornis</i>	5.13	0.065	100	0.06	0.64
<i>Montastrea Cavernosa</i>	3.8	0.064	100	0.067	1

Table 4: Summary of competency and mortality requested parameters by SLIM’s particle tracking module.

Figures 43 and 44 give the evolution of the state of the particles with time. All proportions are computed relative to the total number of larvae released. Since one third of that total is released one day after the beginning of the simulation and another third two days after the beginning, we observe jumps in the total number of particles alive. Whatever the elapsed time since the beginning of the simulation, mortality is non zero and this explains the decrease in alive particles between two spawning events. Furthermore, as mortality immediately affects some particles, the maximum number of particles simultaneously alive is lower than the total number of seeded particles. In MC’s case, which admits a constant mortality rate, the *alive* curve is parallel to the Weibull theoretical cumulative distribution function curve until some larvae become competent and settle. The mortality implemented in the model indeed does not apply to settled particles. That is why the final proportion of particles *alive and settled* is far way superior than the proportion of undead particles according to the Weibull curve. The same conclusion can be drawn for AC, even though the slope of the *alive* curve is not parallel to the corresponding Weibull law. This can be explained by the spawning delays and the higher initial mortality rates.

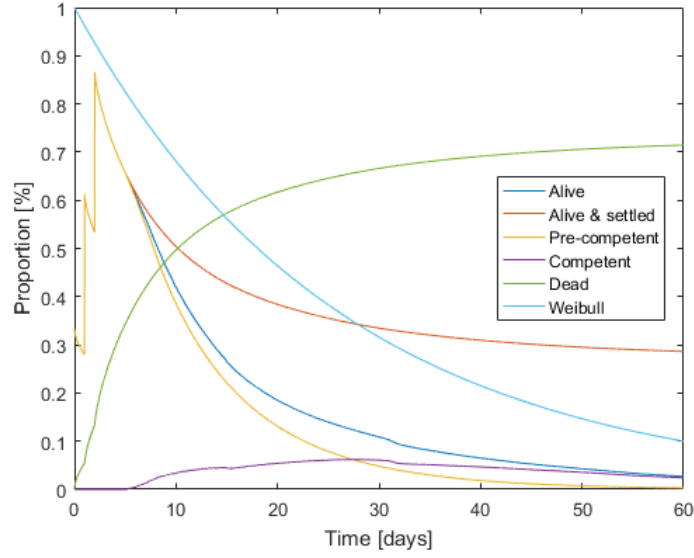


Figure 43: Particles state evolution for AC. After a brief pre-competency period (5.13 days) during which the larvae may only survive or die, mortality decreases and competency increases. After 60 days simulation, only 2.7 % of the total number of seeded particles are still alive. However, 25.94 % of the total number of seeded particles have settled. Accordingly, 71.45 % are dead. Furthermore, 88.99 % of all alive particles are competent. The ratio of competent larvae over the total number of seeded particles caps after 27.42 days and then decreases slowly.

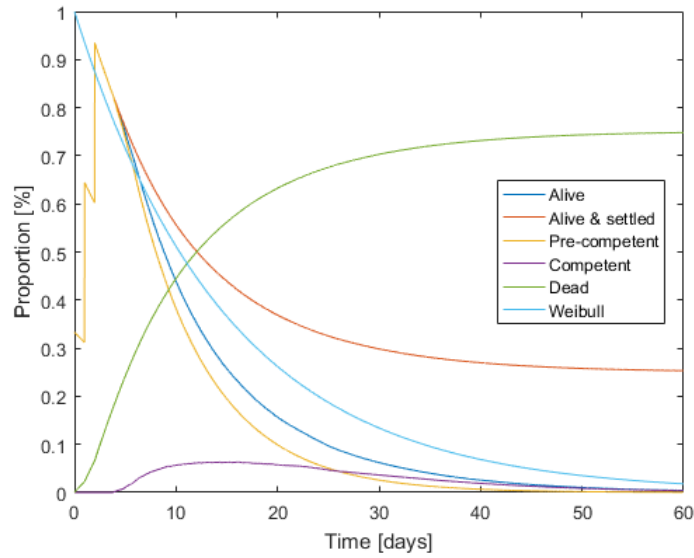


Figure 44: Particles state evolution for MC. After a brief pre-competency period (3.8 days) during which the larvae may only survive or die, mortality decreases and competency increases. After 60 days simulation, only 0.43 % of the total number of seeded particles are still alive. However, 24.89 % of the total number of seeded particles have settled. Accordingly, 74.82 % are dead. Furthermore, 89.2 % of all alive particles are competent. The ratio of competent larvae over the total number of seeded particles caps after 16.15 days and then decreases slowly.

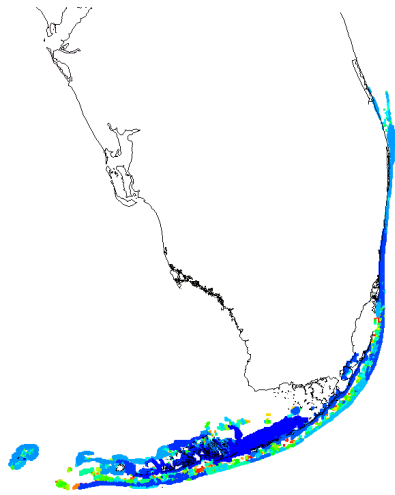
Regarding the considered production density of larvae, the 60 days duration of the simulation looks relevant, for almost no particles are still able to settle in the end. Whatever their competency and mortality properties, the two species show settlement results of the same order. We can also notice that the proportion of AC competent particles barely reaches 5.6 % of the total number of seeded particles when hurricane Irma strikes Cudjoe Key (10 September around 1 p.m.). By the time the hurricane affects the larval dispersal, 23.23 % of the total number of seeded planulae has already settled, i.e. 89.56 % of the final settlement proportion. The impact of the hurricane on AC's dispersal and connectivity is thus very limited. On the contrary, Irma passes over the FRT between two spawning nights of MC. By that time, coral larvae have not developed their competency ability yet. Irma will thus have influence over the whole connectivity pattern of larvae seeded before its passage. The comparison between the connectivity patterns of MC larvae seeded before and after Irma's passage is thus relevant to determine the changes to connectivity caused by the hurricane. The comparison of connectivity patterns of MC and AC can then be used to identify the extent of the impact of the hurricane on MC's connectivity.

3.3 Larval dispersal

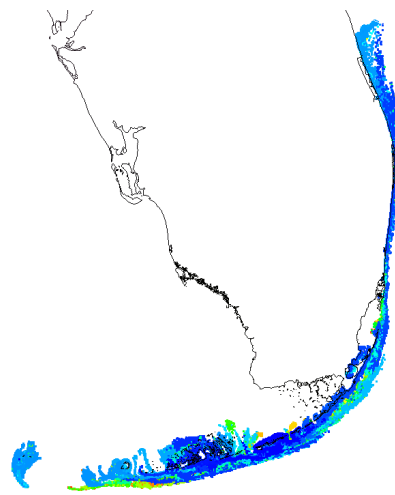
Two simulations were run, one for each coral species. The spawning events did not occur simultaneously for the two species. Therefore, the impact of the hurricane on their dispersal is very different. For both species, we will limit our presentation of the larval dispersal to the 50 first days of the simulation, as the amount of larvae still implied in the simulation by then only represents a tiny fraction of the total amount of larvae seeded. Furthermore, we will have a look at the zone of the FRT that is subjected to the largest impact of the hurricane for each species.

3.3.1 *Acropora Cervicornis*

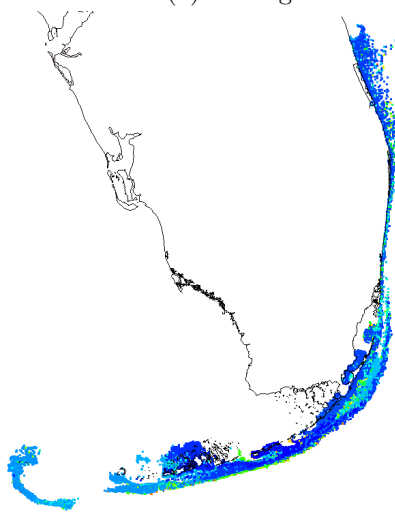
AC's particle tracking simulation started on 10 August and ended on 8 October. Fig. 45 shows two tendencies. On one hand, coral larvae seeded in the inner shelf and in the Dry Tortugas are retained for a moment in their spawning region, especially in the Lower Keys. After some time, they would cross the Keys and go south to meet the Florida Current. On the other hand, the larvae seeded on the outer belt are immediately transported along the Keys by the strong Florida Current. Consequently, those particles, along with the ones that have crossed the Keys, head northeast and then north, following the curvature of the FRT. Yet, since the Upper Keys lie in the region where the curvature of the FRT is the strongest, we see that the Florida Current and the transported larvae detach from that region and then get back to the FRT in front of Biscayne Bay. The larvae seeded in the Upper Keys thus mainly stay in the vicinity of their origin reefs. This detachment can be seen on Fig. 45c.



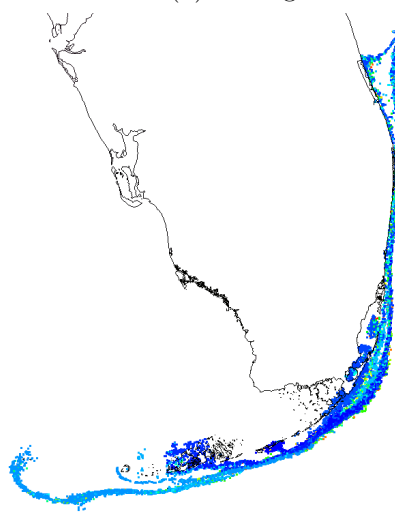
(a) 10 August



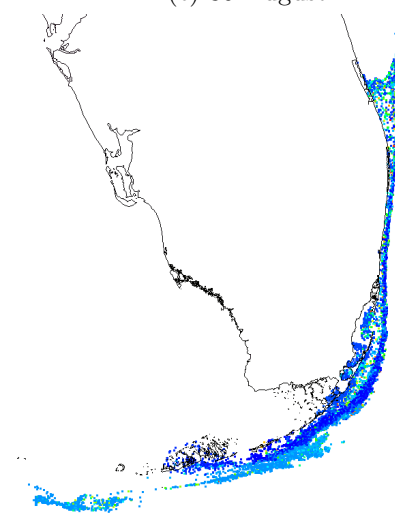
(b) 20 August



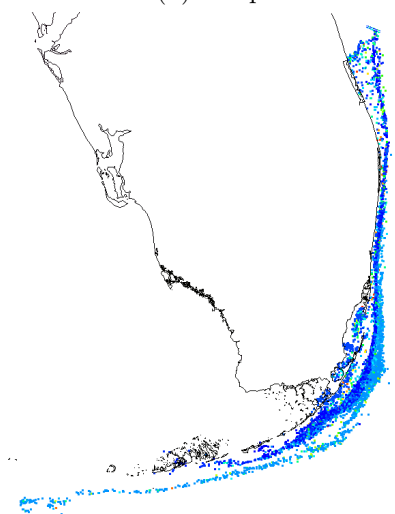
(c) 30 August



(d) 9 September



(e) 19 September



(f) 29 September

Figure 45: *Acropora Cervicornis*' larval dispersal.

As soon as Irma crosses the Florida Strait and comes in the vicinity of the FRT, the strong winds lead to the formation of a mesoscale eddy near the FRT (Fig. 47). Turning anti-clockwise, this eddy goes against the FC along the FRT. Consequently, the larvae are driven back southwest along the outer belt of the FRT. After Irma made landfall on Cudjoe Key and moved north, this return current ceases and the particles go back northeast, though. Nonetheless, the wind-driven eddy formed along the outer belt does not dissipate once Irma crosses the Keys. Yet, its radius decreases a lot and its center moves southwest. Accordingly, it is no longer able to drive planulae back southwest and to influence larval dispersal. It appears that this eddy dissipates on 11 September 2 a.m. This eddy is the only one detected by our model since it is not able to reproduce baroclinic eddies caused by warm waters exiting the Loop Current, neither eddies caused by the structure of the FRT and highlighted by Lee and Williams (1999).

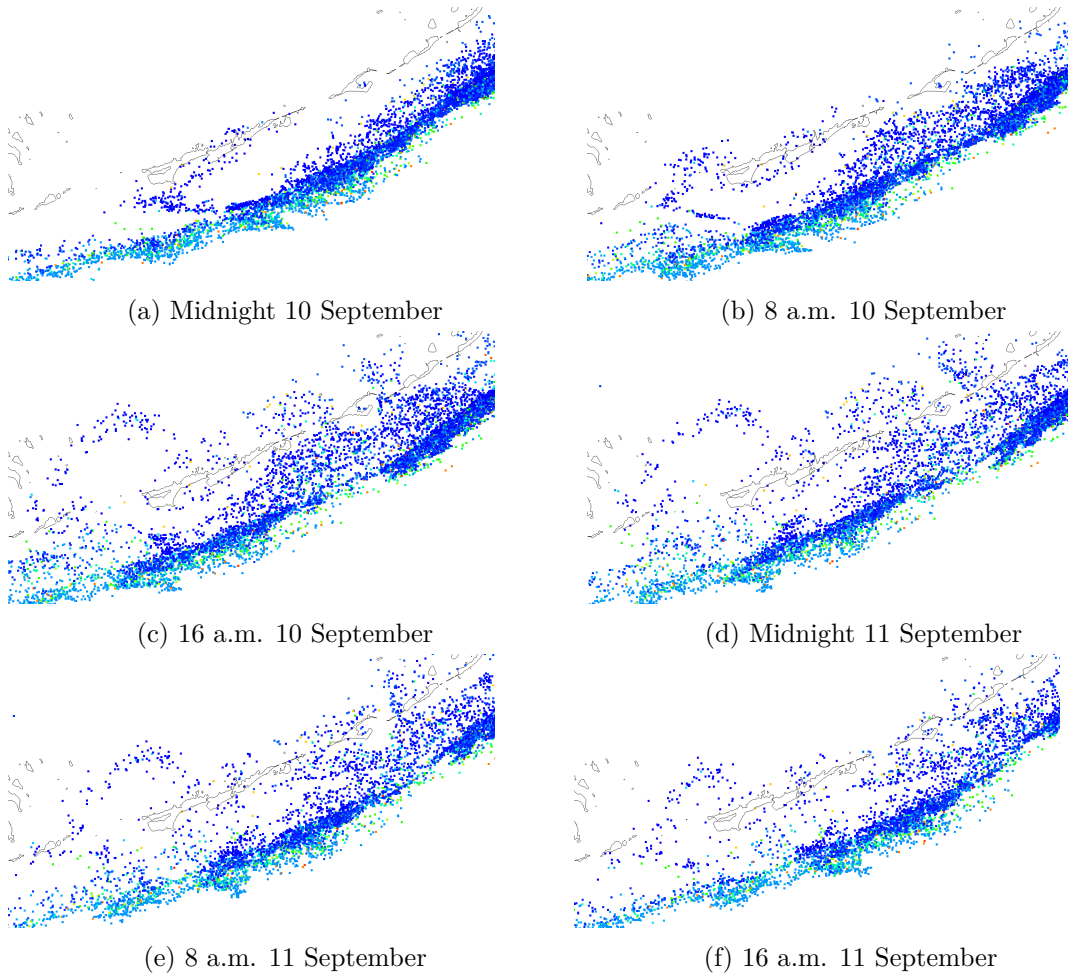


Figure 46: Irma's disturbance on AC's larval dispersal. Focus on the Middle Keys in the vicinity of Vaca Key. Larvae from the Upper and Middle Keys are driven southwestwards and cross the Middle Keys northwards. After Irma's influence diminishes, the larvae go back seawards.

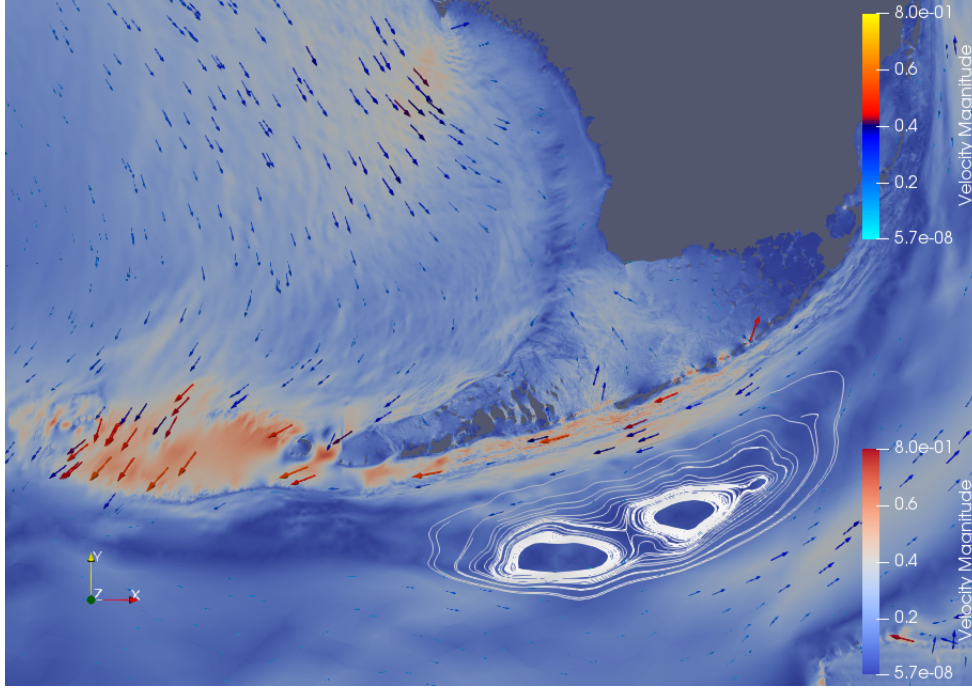


Figure 47: The Irma-driven eddy along the outer belt of the FRT is responsible for the return of larvae southwest along the FRT. Screenshot taken on 10 September 6 a.m. The streamlines of the eddy are printed in white in order to better visualize it.

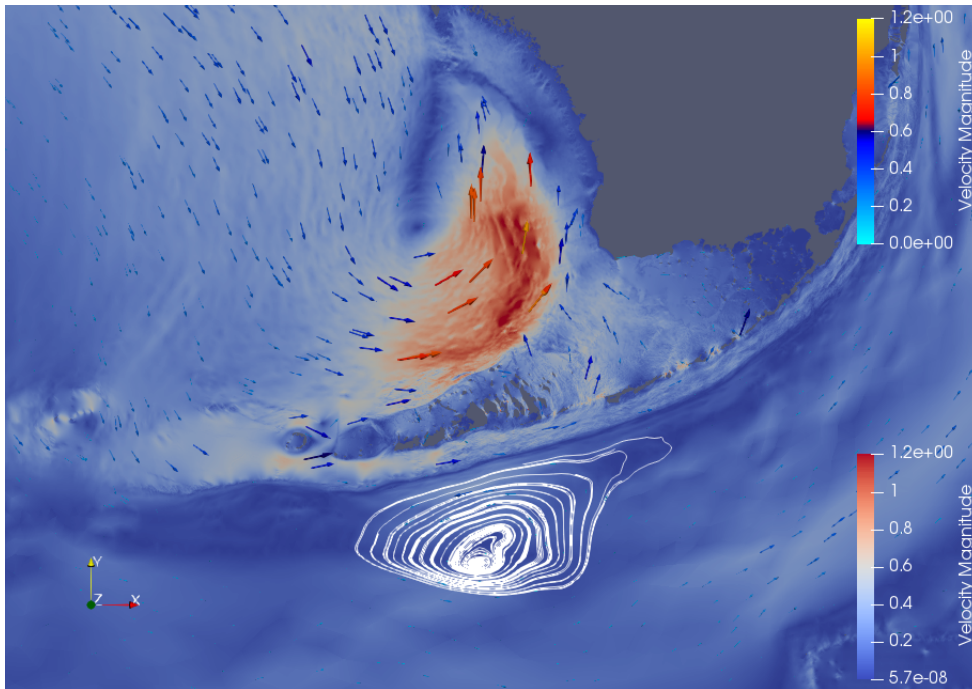


Figure 48: The Irma-driven eddy along the outer belt of the FRT has not yet dissipated after Irma crossed the FRT. Screenshot taken on 10 September 4 p.m. Its radius decreased much and the center moved southwest, south of Key West. Irma can be highlighted north of the Lower Keys.

3.3.2 *Montastrea Cavernosa*

The larval dispersal for *Montastrea Cavernosa* is strongly impacted by Irma. Fig. 50 and 51 show the larval dispersal on a 50 day period for larvae seeded on 10 and 12 September respectively. One third of the particles is released each day at midnight from 10 to 12 September. Irma is thus utterly dominant regarding early larval dispersal for the larvae seeded on 10 September. The strong wind-induced currents indeed drive larvae far away from their origin in a short period of time (Fig. 49). Its influence is still noticeable for the larvae seeded on 11 September. However, the larval dispersal has come back to normal on 12 September, the hurricane crossing Alabama.

By comparing Fig. 50 and 51, we can notice that the hurricane introduces some dispersal tendencies that are not present for the particles seeded on 12 September. First of all, it immediately drives planulae seeded in the Dry Tortugas southwest of them. These larvae will then cross the passage between them and the Marquesas Keys more quickly and follow the Florida Current. The majority of these larvae will not be able to settle on its origin reefs, with consequences on connectivity as we will see later on. Moreover, once they have gone southwest and are redirected eastwards, they will travel mostly off the FRT, at least until Biscayne Bay. They will not be able to settle on the FRT until that point either. We can make the same remark for the Marquesas Keys, but to a lesser extent regarding future settlement. On the contrary, Irma pushes larvae seeded in the Lower Keys northwards and then eastwards, driving a significant amount of particles into Florida Bay. As for the Middle Keys and inner Upper Keys, larvae are mainly driven north and east respectively. Accordingly, larvae will have more time to settle on their origin or neighbouring reefs. They will indeed not immediately cross the Keys southwards but will go back and forth. As we could see it with AC, the wind-driven eddy drives the particles seeded along the outer belt of the FRT southwest. Furthermore, this movement results in the transfer of particles coming from the Upper Keys into the inner shelf of the Middle Keys and Florida Bay. Finally, the southwestward movement imparted by the hurricane to the larvae looks to cease in the vicinity of Biscayne Bay, where the Florida Current is strong enough to drive planulae northwards, despite the strong winds. However, when the particles are pushed back to the northeast, Irma tends to increase the velocity of the water along Biscayne Bay so that larvae seeded in the area get subjected to a strong transport northwards. After the passage of the hurricane, the general dispersal trend is to cross the Keys southwards and to follow the Florida Current northeastwards, likewise AC. Nevertheless, early October sees the return of larvae seeded in the Dry Tortugas and southwest of the Marquesas Keys that were not too distant from their origin. The larvae located south of the Marquesas Keys will move north and be retained there till the end of the simulation. However, the planulae in the south of the Dry Tortugas will cross them and go north into the West Florida Shelf for an important part. As there are no coral reefs there, they will eventually die. This migration of the larvae from the south to the north is very clear for the larvae seeded on 12 September. As the hurricane drove the larvae quicker away from their origin in that area, the proportion of locally seeded larvae that is subjected to these northward currents is lower for larvae seeded before the passage of Irma. Nonetheless, this effect can be observed on Fig. 50 from 10 October. These currents can be explained by rather strong northwestward winds over the area in early October, partially due to hurricane Nate crossing the Gulf of Mexico from the Yucatan Channel to Louisiana. If such winds had taken place right during the spawning season like they did for Frys (2017) and Béchet and Verstraeten (2018), the larval dispersal would have been much affected. The Dry Tortugas and the Marquesas Keys would most likely not have

supplied the rest of the FRT as much as they did in our simulations. Some of the most remarkable conclusions of our work would not have taken place.

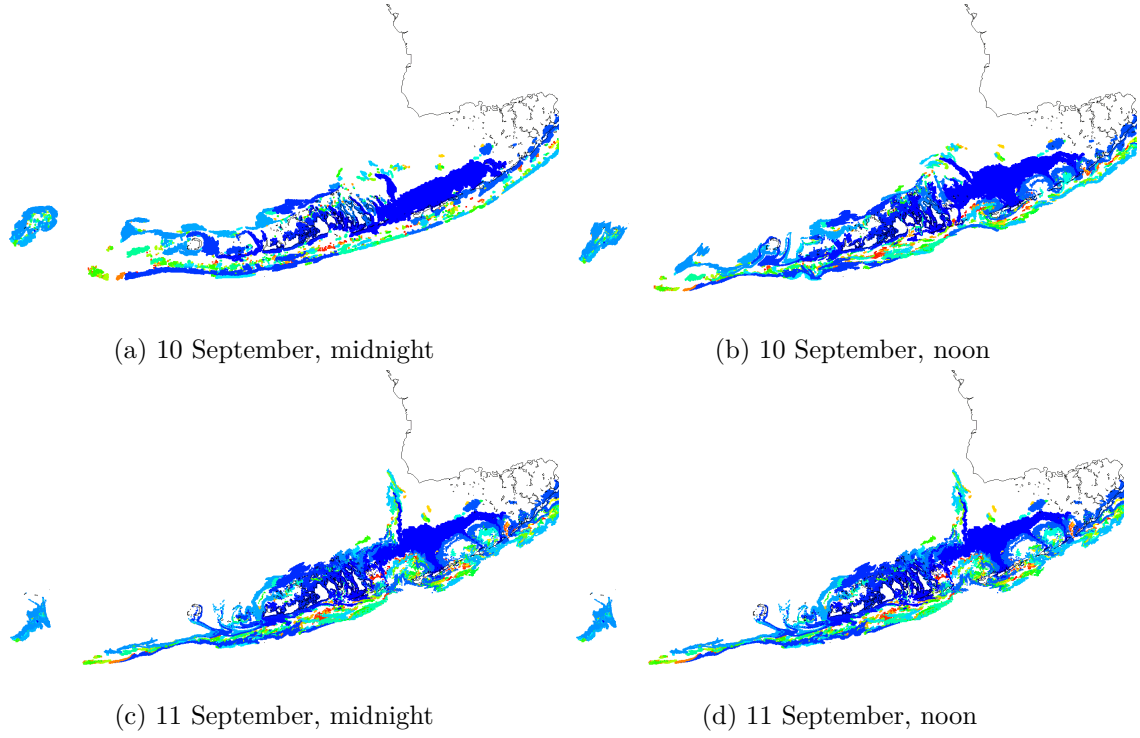
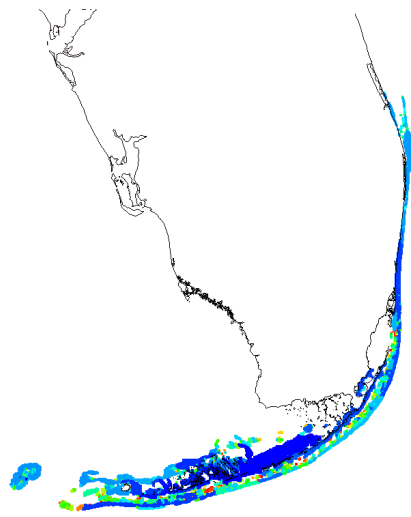
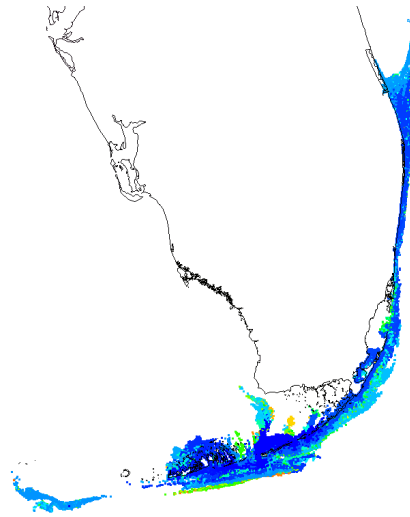


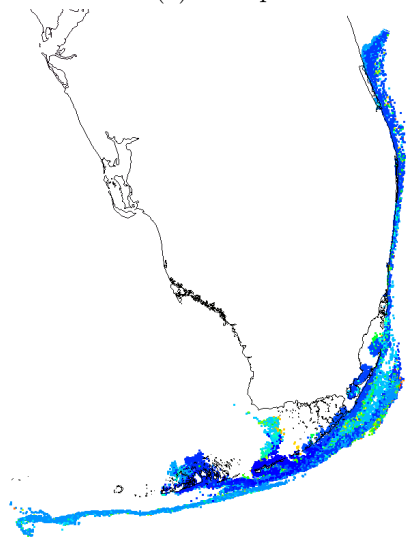
Figure 49: Irma's disturbance on MC's larval dispersal. Focus on the FRT from the Dry Tortugas to the beginning of the Upper Keys. We observe a southern and then eastern transport of the larvae seeded in the Dry Tortugas and the Marquesas Keys. Moreover, we notice a displacement of larvae seeded in northern Lower Keys to the northeast of the Lower Keys and their accumulation in Florida Bay. Finally, we point out an important flux of larvae coming from the Middle and Upper Keys in Florida Bay through Hawk Channel. These larvae will remain in Florida Bay for a while, before crossing Hawk Channel in the opposite direction.



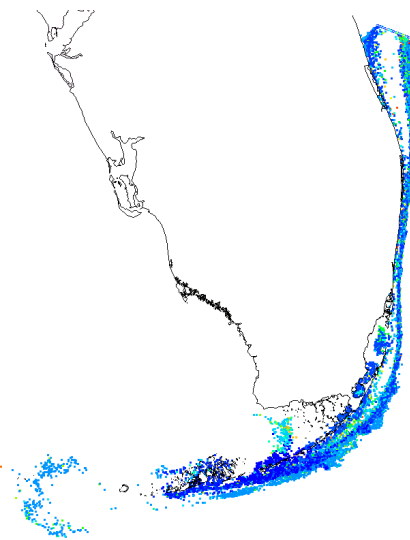
(a) 10 September



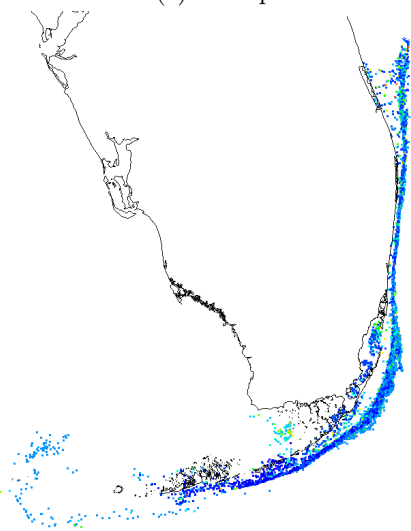
(b) 20 September



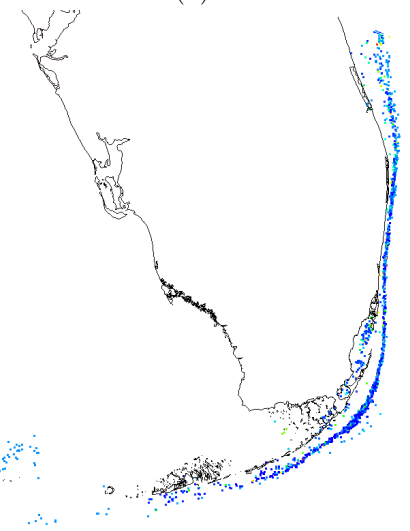
(c) 30 September



(d) 10 October

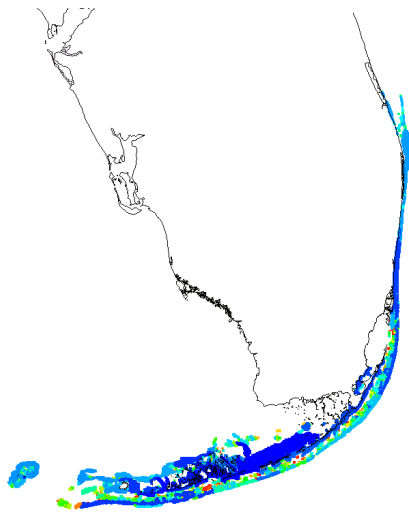


(e) 20 October

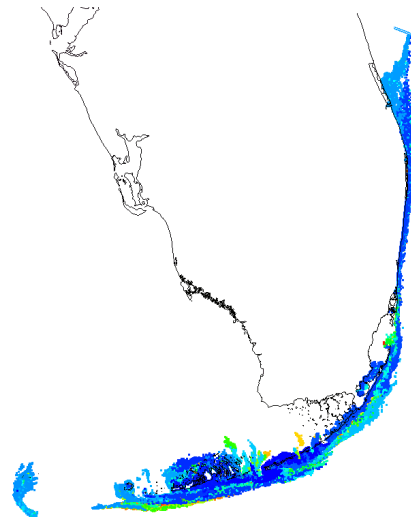


(f) 30 October

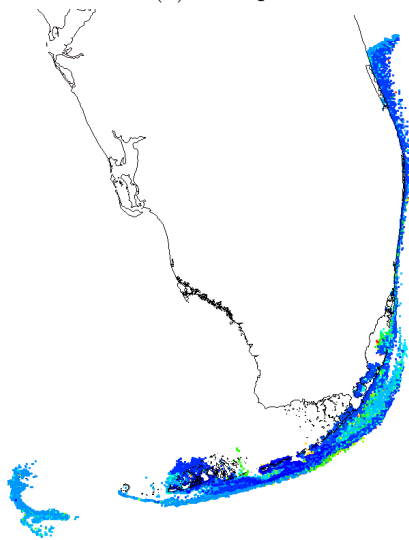
Figure 50: Dispersal of MC's 10 September larvae.



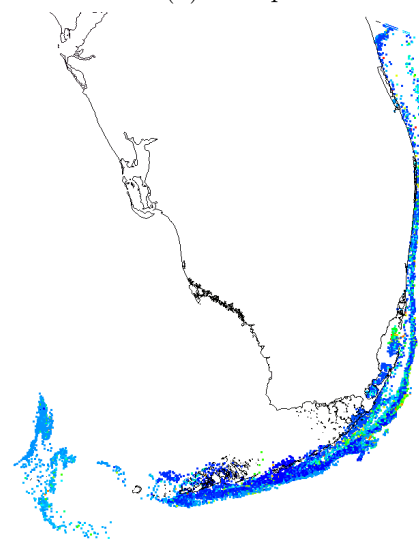
(a) 12 September



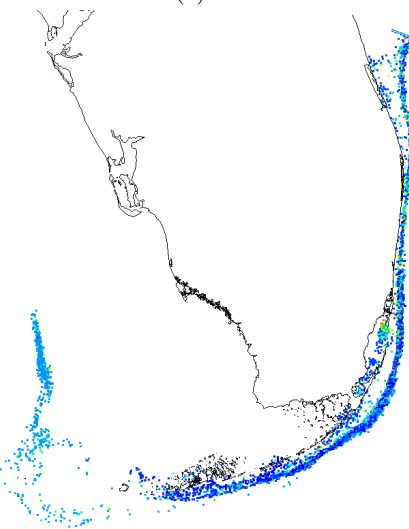
(b) 22 September



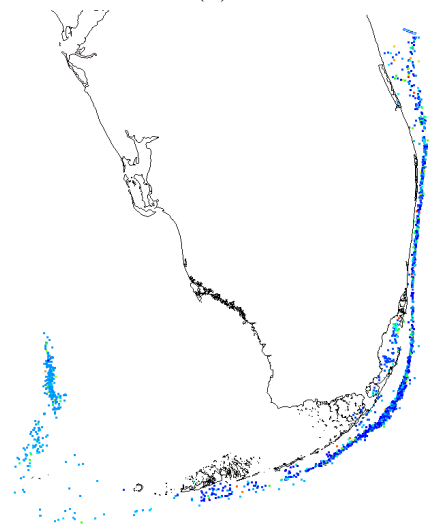
(c) 2 October



(d) 12 October



(e) 22 October



(f) 1 November

Figure 51: Dispersal of MC's 12 September larvae.

Fig. 50 and 51 suggest that the hurricane is responsible for a significant acceleration of the water currents and for a quick transport of the larvae away from their origin. We can then wonder how far these larvae are likely to be sent by such a hurricane and the consequences on the distance to their origin at the end of the simulation. On Fig. 52, we plotted the histograms of the distance to the center of the origin reefs of the larvae after one and fifty days. Yet, we must admit that these histograms are only based on still alive larvae and do not take settled larvae into account either. The width of the sample thus shrinks with time. Larvae that were sent off the FRT and transported by the FC over long distances might be overrepresented. Nevertheless, it remains a good indicator of the tendencies regarding larval dispersal. We must also notice that the initial distance to the center of the origin reef of a larva is usually non zero and can even reach 55.72 km at most. Some reefs indeed correspond to very long and stretched strips of coral, like north of Biscayne Bay or south of the Marquesas Keys. This explains the large distances already covered after one day. The median initial distance to the center of the origin reefs of the larvae is limited to 3.9 km , though.

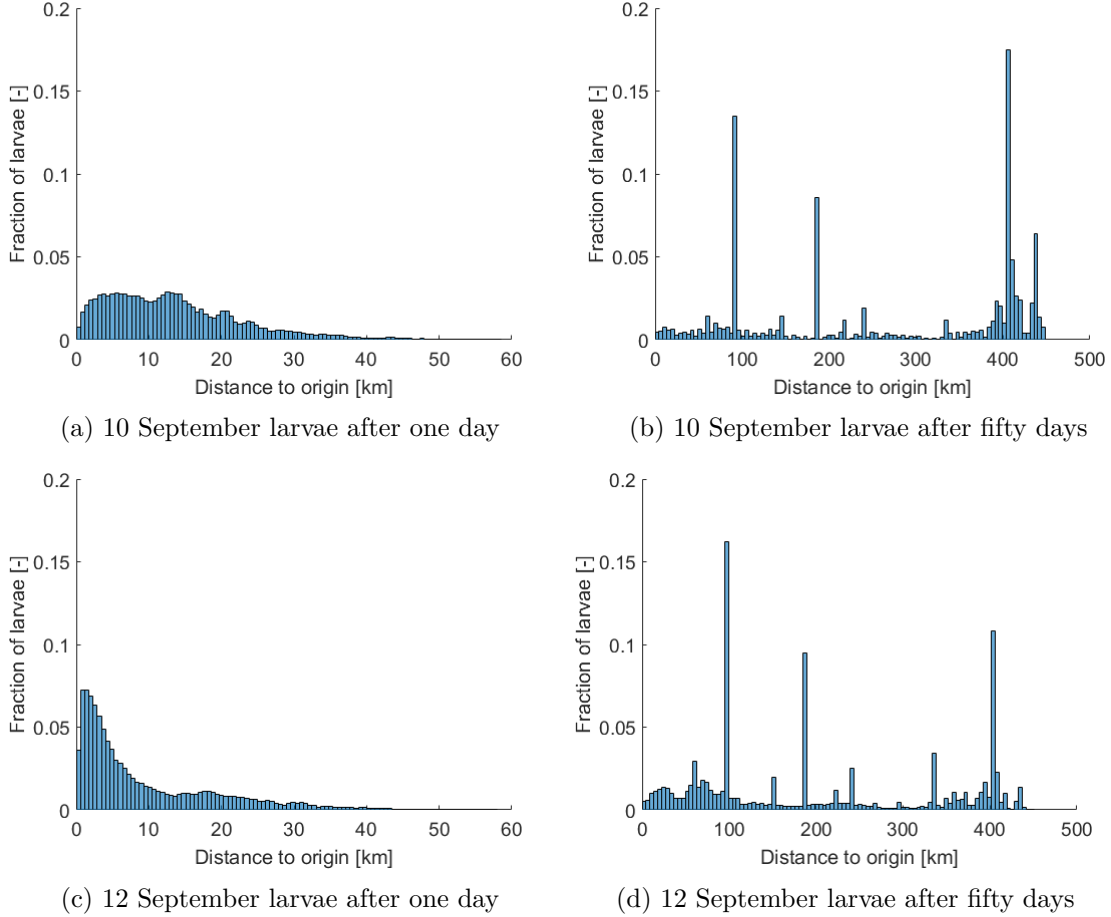


Figure 52: Comparison of the distributions of the distance to the origin between larvae seeded on 10 and 12 September after one day and fifty days. The larvae seeded on the first spawning night have globally crossed a longer distance in one day than the larvae seeded on the third night. After fifty days, a larger fraction of the larvae seeded on 10 September than those seeded on 12 September has reached long distances (roughly 400 km).

In comparison with Fig. 52c, Fig. 52a shows that a large fraction of the larvae was already driven rather far away from its origin after one day. By then, the median distance to the center of the origin reefs is 12.06 km for the 10 September larvae and 5.29 km for the 12 September larvae. After fifty days, it is interesting to note that 3 intervals (around 100 km , 190 km and 400 km) shine out for larvae of both spawning nights. Nevertheless, 10 September larvae look to be further away than 12 September larvae from the origin reefs. For the former, the median distance to the center of the origin reefs is 334.19 km whereas it only reaches 189.04 km for the latter. Furthermore, we can subtract the median initial distance to the median distance after one day and compute the ratio of that result over the median distance after fifty days. For larvae seeded on the first spawning night, we obtain 2.44% while we get 0.74% for the larvae seeded on the last spawning night. Based on this very simple analysis, we can thus say that the influence of the first day on the final larval dispersal is threefold with the hurricane. Moreover, if we again subtract the median initial distance to the center of the origin reefs to the median distance after one day simulation, it appears that the distance covered by the larvae seeing Irma's influence after one day is almost 6 times larger than the median distance covered by 12 September larvae after one day.

4 Connectivity study with graph theory tools

After running the Lagrangian particle tracker, we did a statistical analysis of the outputs thanks to graph theory tools. This analysis is based on three files exported from SLIM. First of all, the particle tracking module of SLIM gave us connectivity matrices as outputs at each time step. Each element C_{ij} of this matrix corresponds to the number of larvae released from reef i and recruited by reef j . It is thus a 1817 square matrix. In this study, we will only consider the last matrix computed by SLIM. Beside the connectivity matrix, we will also use the seeding matrix. Each element S_i of it corresponds to the total number of larvae released from each reef i . And finally, we will need a third matrix $\mathbf{X}$ containing the latitudes and longitudes of all reefs. In fact, the location of the reef concerns the center of the interpolated reef on our mesh.

In the connectivity matrices described hereabove, the C_{ij} elements between two large reefs can be way higher than those between small ones, even if the latter are strongly connected. The connection will have more weight in the first case than in the second one. For that reason, it might be interesting to consider disproportional measures of connectivity between reefs. We can do this by normalizing the connectivity between two reefs i and j either by the number of larvae released from reef i or by the total number of larvae recruited by reef j . As a clustering method used in this study follows the first approach, it is the one that we will consider in all our connectivity normalizations and can be written as:

$$\tilde{C}_{ij} = \frac{C_{ij}}{S_i} \quad (33)$$

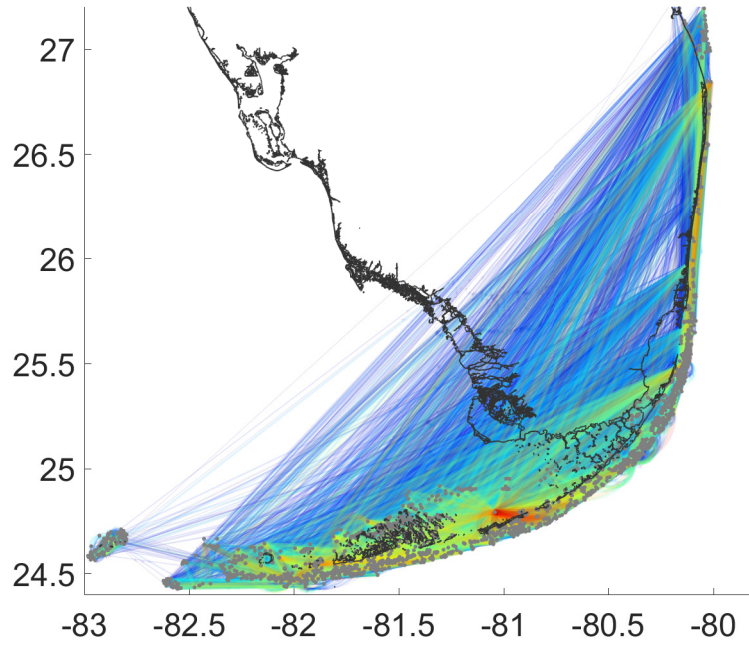


Figure 53: Connectivity matrix of *Acropora Cervicornis* projected on the FRT map.

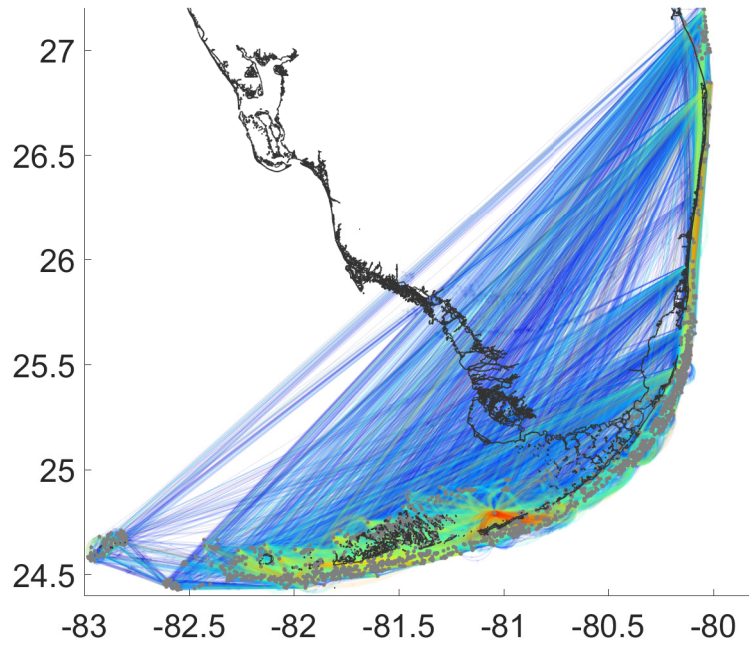


Figure 54: Connectivity matrix of *Montastrea Cavernosa* projected on the FRT map.

Fig. 53 and 54 present the spatial projection of the connectivity matrices of AC and MC respectively. A connection is represented as a straight line from one node to another, or by a curve to distinguish two nodes really close to each other. In that way, we can easily

represent long distance connections. The color and the width of a connection are related to the weight of the connection. The more larvae transit through that connection, the higher the wavelength of the color and the wider the line.

We can directly make some remarks that should be confirmed later on. First of all, it looks like the Dry Tortugas have many more connections, especially long ones, for MC than for AC. Secondly, both species show their highest connection density in Vaca Reef, the largest reef in the FRT. We also see that MC counts fewer weighty connections from the Marquesas and Lower Keys to the Upper Keys than AC does.

4.1 Connectivity indices

The following indices were developed by Thomas et al. (2014) and Frys (2017) and used again by Béchet and Verstraeten (2018). All the definitions are thus directly extracted from their work.

The **local retention** of a reef expresses the proportion of larvae, released from it and that settled on it, with respect to the total number of larvae seeded by the same reef:

$$\lambda_i = \frac{C_{ii}}{S_i} \quad (34)$$

If the local retention is high for a reef, its ability to replenish itself is high too. As far as each reef is concerned, a high local retention is preferable. However, a high local retention leads to a lower proportion of larvae sent to other reefs. High local retention would thus be interesting for reefs rather isolated from the network and having few ingoing and outgoing connections.

Self recruitment is the ratio between the number of recruited larvae that were released from the same reef and the total number of larvae that settled on that reef:

$$\sigma_j = \frac{C_{jj}}{\sum_i C_{ij}} \quad (35)$$

This indicator compares the number of larvae recruited by a reef that were released from the same one with the number of larvae received from the other reefs. A strong self recruitment capacity indicates that the reef is rather independent from the network. It does not give any information about its importance for the network, though. Being good at self recruiting can thus be seen as favorable for the reef since it does not rely much on other reefs and the damages they could sustain. However, in a long term perspective, it is not very good since it will cause a lower diversity and lead to a decrease in reproductive abilities.

The **proportion settled** is the proportion of larvae that settles on any other reef than the source:

$$P_i^{settled} = \frac{\sum_{j \neq i} C_{ij}}{S_i} \quad (36)$$

As each j is different from i , the local retention is not included in this information. It indicates the capacity of a reef to supply other reefs with larvae.

The **proportion lost** is the proportion of larvae that were neither recruited by the seeding reef nor by any other reef. It indicates how many larvae never settled:

$$P_i^{lost} = \frac{S_i - \sum_j C_{ij}}{S_i} = 1 - P_i^{settled} - \lambda_i \quad (37)$$

The **weighted connectivity length** (WCL) measures the average distance between a source reef and all the sinks where larvae settle. Each connection C_{ij} is weighted by the radial distance L_{ij} between the centres of the source and the sink reefs that we can obtain through the position matrix $\mathbf{X}$:

$$WCL_i = \frac{\sum_j C_{ij} \times L_{ij}}{\sum_j C_{ij}} \quad (38)$$

The WCL can be seen as the characteristic length scale of connectivity between reefs (Thomas et al., 2014).

The **betweenness** describes the usefulness of a reef i to create a connection between two other reefs. It helps us determine which reefs can be seen as hubs in the network. The idea is to measure how often a reef appears on the shortest path from a reef A to a reef B :

$$B_i = \sum_{A, B \neq i} \frac{n_{AB,i}}{N_{AB}} \quad (39)$$

where $n_{AB,i}$ is the number of shortest paths linking A and B going through i whereas N_{AB} is the total number of shortest paths linking A and B . The shortest paths are computed thanks to the *centrality* function of Matlab[®]. This function can be used with a *betweenness* argument and a *cost* parameter which describes the attractiveness of a connection. If the cost is low, the connection is attractive. In our case, the cost corresponds to the inverse of the connectivity between two reefs $1/C_{ij}$ or $1/\tilde{C}_{ij}$ in case of a study of the normalized connectivity.

The **source-sink index** of a reef i corresponds to the difference between all exported larvae with all settled larvae on the source/sink reef, normalized by all larvae exported from/settled on that same reef:

$$N_i = \frac{\sum_j C_{ij} - \sum_i C_{ij}}{\sum_j C_{ij} + \sum_i C_{ij}} \quad (40)$$

This index lets us know whether a reef is mostly an exporter ($N_i = 1$) or an importer ($N_i = -1$). However, it lacks an important information. It indeed does not give us any information about the number of reefs implied in these connections. Actually, it is more interesting for an importer to receive many larvae from many reefs than many larvae from a single one, for diversity and robustness reasons. This problem is solved using the following index.

The **PageRank** index was created by Google[®] to assess the importance of a web page (Page, Brin, Motwani, & Winograd, 1999). If many websites point to the concerned web page, it is considered as an important page. Moreover, if these links are coming from websites which are themselves abundantly referenced by other websites, it makes the final web page even more important. The simplified version of the PageRank index R_u of a web page u can be written as:

$$R_u = c \sum_{v \in B_u} \frac{R_v}{N_v} \quad (41)$$

where c is a normalizing factor, B_u is the number of pages pointing to u and N_v is the number of links from v . We can then easily apply this index to the coral connectivity concept. Reefs can indeed be seen as web pages whereas the connectivity between two reefs corresponds to the number of links.

In this study, we will compute both the **Outgoing PageRank** π^{out} and the **Incoming PageRank** π^{in} indices. A high π^{out} would constitute a reef providing larvae to many reefs which then keep on providing larvae to many other reefs. Such a reef would thus be part of a development process leading to a sufficiently diverse network. In the same perspective, π^{in} can be used to mix quantity and quality incoming information. It identifies reefs that are supplied by many reefs which are themselves supplied with larvae coming from many reefs. A high π^{in} actually indicates good robustness and resilience capacities. Such a reef would indeed be less affected by a disease coming from one single reef.

Like the betweenness index, the PageRank is computed via the Matlab[®] function *centrality*, but with the argument *pagerank*. It is also important to notice that these PageRank indices are calculated without self-referencing connections.

4.2 Protection and restoration indices

We can use the indices defined in section 4.1 to determine if a reef is a good larvae exporter, importer or if it is quite isolated from the network. We can also combine these indices to highlight which reefs could be considered for protective and restoration measures. As a reminder, one goal of this study is indeed to determine on which reefs polyps should be outplanted to increase the resilience of the FRT.

On one hand, we can define the **PageRank protection index** of a reef i as the indicator aiming at assessing if that reef needs protection, i.e. if it exports many larvae, but receives few:

$$\pi_i^{out-in} = \frac{\pi_i^{out} - \pi_i^{in}}{\pi_i^{out} + \pi_i^{in}} \quad (42)$$

Since its normalization, this index ranges from -1 to $+1$. In the first case, it means the reef imports a lot more than it exports. It does not need protective measures since it is resilient by itself. Besides, it is not very important for the network. In the second case, the reef exports way more than it imports. For his network importance, this reef should receive protection.

On the other hand, a **PageRank restoration index** can be defined. It helps us identifying the reefs that both import and export many larvae. In that case, they would be resilient by themselves once restored, but important for the network as well. This index is a product:

$$\pi_i^{out \times in} = \pi_i^{out} \times \pi_i^{in} \quad (43)$$

In this way, the index will request both high importing and exporting capacities to reach high values.

4.3 Reef clusters

Finally, we can use the connectivity matrices to highlight reef clusters in the FRT, i.e. parts of the network whose reefs are always connected to all other reefs, sometimes via other reefs, in the two directions. This definition of clusters corresponds to the Strongly Connected Components method used by both Frys (2017) and Béchet and Verstraeten (2018). In order to avoid tiny clusters of only two nodes connected exclusively to one another, we will filter the clusters and keep only the ones that are constituted by at least 3 nodes. For example, doing so for AC reduces the number of clusters from 921 to 8. However, an important drawback of this method is that the strength of the connections is not taken into account. For that reason, we will also consider this method for *demographically significant* connections. In other words, this means we will only keep clusters for which the ratio $\frac{C_{ij}}{S_i} > 10^{-3}$.

The study of reef clusters is essential to get a clear and simple view on the entire network behaviour. It indeed helps us understand which zones are linked with each other and what consequences a perturbation, like a disease for example, could produce. On one hand, only one cluster covering the entire FRT could be seen as positive. Theoretically, genetically diverse coral individuals could thus be transferred from one place to another and could thereby increase the diversity of all coral reefs. Accordingly, diseases could be less effective. On the other hand, a single cluster might rely upon only a few central hubs (identified by the betweenness index) of which an important part of the connections make use. In case of a very local perturbation damaging these hubs, the whole dispersal process could be much impacted with dramatic consequences on connectivity and the development of coral reefs. Furthermore, one single cluster is not only able to send larvae all across the FRT, but also to transmit diseases from Palm Beach to the Dry Tortugas. The more complex a system is, the more fragile it is against significant perturbations (P. Servigne and R. Stevens, 2015). A good clustering objective could be the millenary equilibrium found by the FRT before human intervention on the environment.

4.4 Irma's impact on connectivity

In the following sections, we will try to determine the impact of hurricane Irma on connectivity. For that purpose, we will first analyze the connectivity differences for MC larvae seeded on 10 and 12 September. The hydrodynamics will indeed be the same after the passage of the hurricane. If the hurricane has no influence at all, the connectivity matrix should be really close, as there is only a two day time delay. Obviously, we expect the hurricane to be determinant, for it occurs at the very beginning of the larval dispersal and thereby influences the whole dispersal. Afterwards, we will compare connectivity patterns between AC and MC to assess the global impact of a brief disturbance on the connectivity in the FRT. For concision purposes, we will only present here the connectivity indices showing the most striking differences. The other useful indices can be found in Appendix B. In order to follow some structure, we will present the different indices in the order they were defined in section 4.1.

4.4.1 Differences between MC larvae seeded on 10 and 12 September

In this section, we will compare the graphs produced for MC larvae seeded on the first night of spawning with the ones based on larvae seeded during the third night. Irma will indeed impact much the larval dispersal for the former, but not for the latter. We will not

consider larvae from the second spawning night since the hurricane has still some influence on the hydrodynamics. We want to compare two extreme cases. Most of the time, we will present the graphs corresponding to the first night, to the last one and to the difference between the former with the latter. These index differences should help us highlight the most important changes that result from the hurricane.

At first, let us have a look at the projection of the difference between the connectivity matrices of the larvae seeded on 10 and 12 September. This should help us understand the information given by all the computed indices discussed hereafter. Fig. 55 shows that the vast majority of connections varies by only 25 larvae approximately. Irma's real impact is only felt by a minority of connections. Fig. 56 only displays the connections that are deeply influenced by the hurricane. We can highlight some trends. Irma tends to increase long distance connections between the Marquesas Keys and the eastern coast of Florida. We can expect a rise in WCL for these reefs. We also notice that Irma enhances the connections between the Lower Keys and Vaca Reef. Its incoming PageRank index should increase. There is also a rise in connection density between the northern Lower Keys and the southern ones. Same remark for the northern Upper Keys and reefs near Palm Beach. Finally, it appears that Irma strengthens the connection between the northern Dry Tortugas and the southern Marquesas Keys. On the contrary, Irma looks to decrease the connection density within the Dry Tortugas and the Marquesas Keys. We can also blame Irma for weakening the outgoing connections of Vaca Reef towards the outer Middle Keys. Its outgoing PageRank index should decrease. Nevertheless, all these observations are purely qualitative and it is highly possible that one weighty connection, going against these trends, changes the expected result.

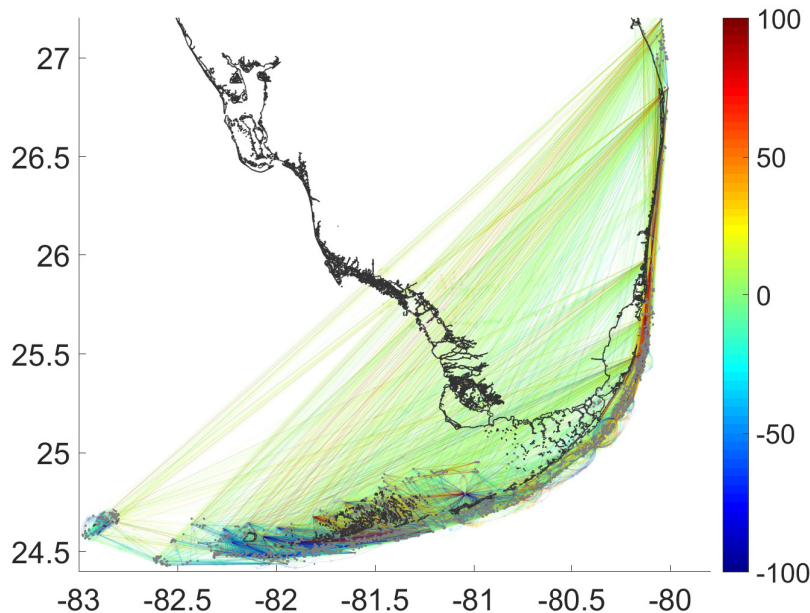


Figure 55: Projection of the difference between the connectivity matrices of larvae seeded on 10 and 12 September. Positive values represent connections that are created or at least strengthened by the hurricane whereas negative ones correspond to deleted or weakened ones. The color bar is cropped at 100 larvae in each direction for readability reasons.

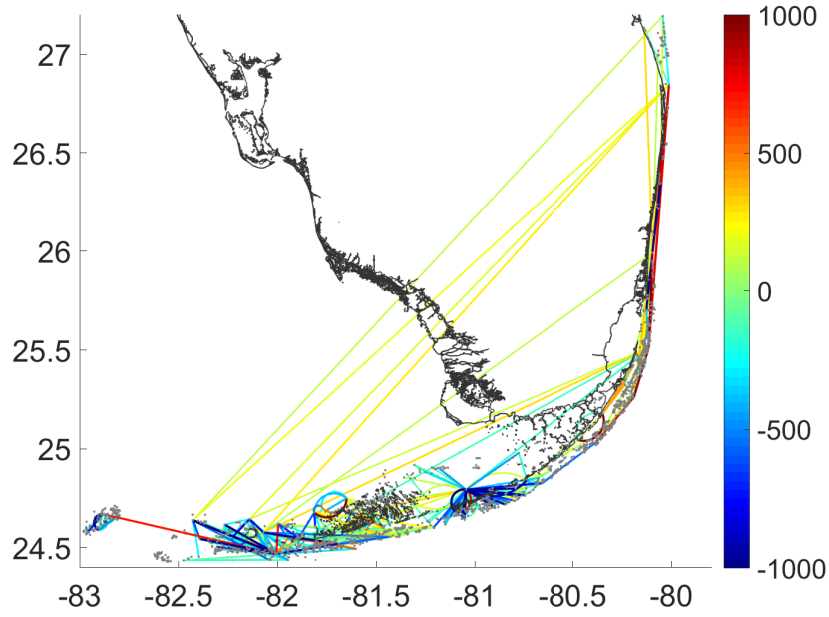


Figure 56: Projection of the difference between the connectivity matrices of larvae seeded on 10 and 12 September. Now, the connections with a difference inferior to 100 larvae are disregarded to better grasp the most striking differences. The color bar is still cropped at 1000 larvae in each direction.

Let us now consider local retention. The absolute difference between the larvae seeded before and after the passage of the hurricane is quite limited. Fig. 57 indeed shows that the vast majority of reefs has a local retention inferior to 5% in both conditions.

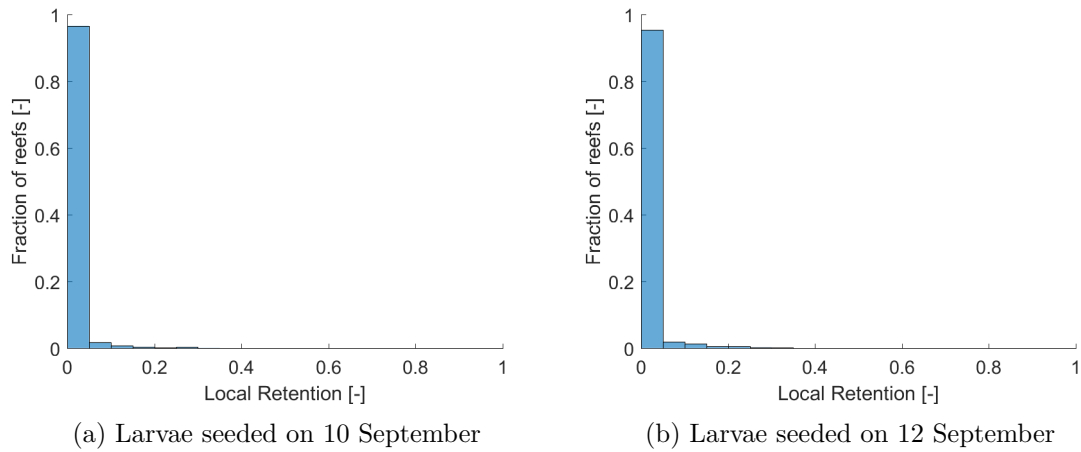


Figure 57: Comparison of the local retention histograms between the larvae seeded on 10 and 12 September. In both situations, an overwhelming majority of reefs shows a very low local retention.

The majority of locally retained larvae lies in the Lower and Upper Keys. In the first case, the dense spatial distribution of islands retains larvae locally. In the second one, the high curvature of the FRT results in the detachment of the FC. Locally seeded larvae

are thereby mainly subjected to tidal and local currents. Local retention looks limited almost everywhere, though. The highest value encountered being 31.37 % and 34.49 % for the larvae seeded on the first and last night respectively. It looks like Irma has mostly a negative impact. Since the FC does not much impact the Upper Keys because of its detachment there, the locally seeded larvae are driven southwestwards to the Middle Keys by the hurricane. They will then cross back Hawk Channel once Irma disappears, but will join the FC and will not come back over their origin reefs. The local retention is thus rather low there. We can also notice that the local retention decreases with the hurricane in the Dry Tortugas, the Marquesas Keys and in Key West. This can be explained by the fact that almost all larvae are immediately driven towards the outer belt in that area. Afterwards, the FC transports them along the FRT, so that they will not be able to settle on their origin reefs, apart as from early October thanks to the northwestward winds, but to a lesser extent since the vast majority of larvae will be dead by then. On the contrary, we see that Irma increases a bit the local retention in the Lower and Middle Keys. We explain this by the back and forth movements of the water due to the hurricane that leave more time to the larvae to locally settle.

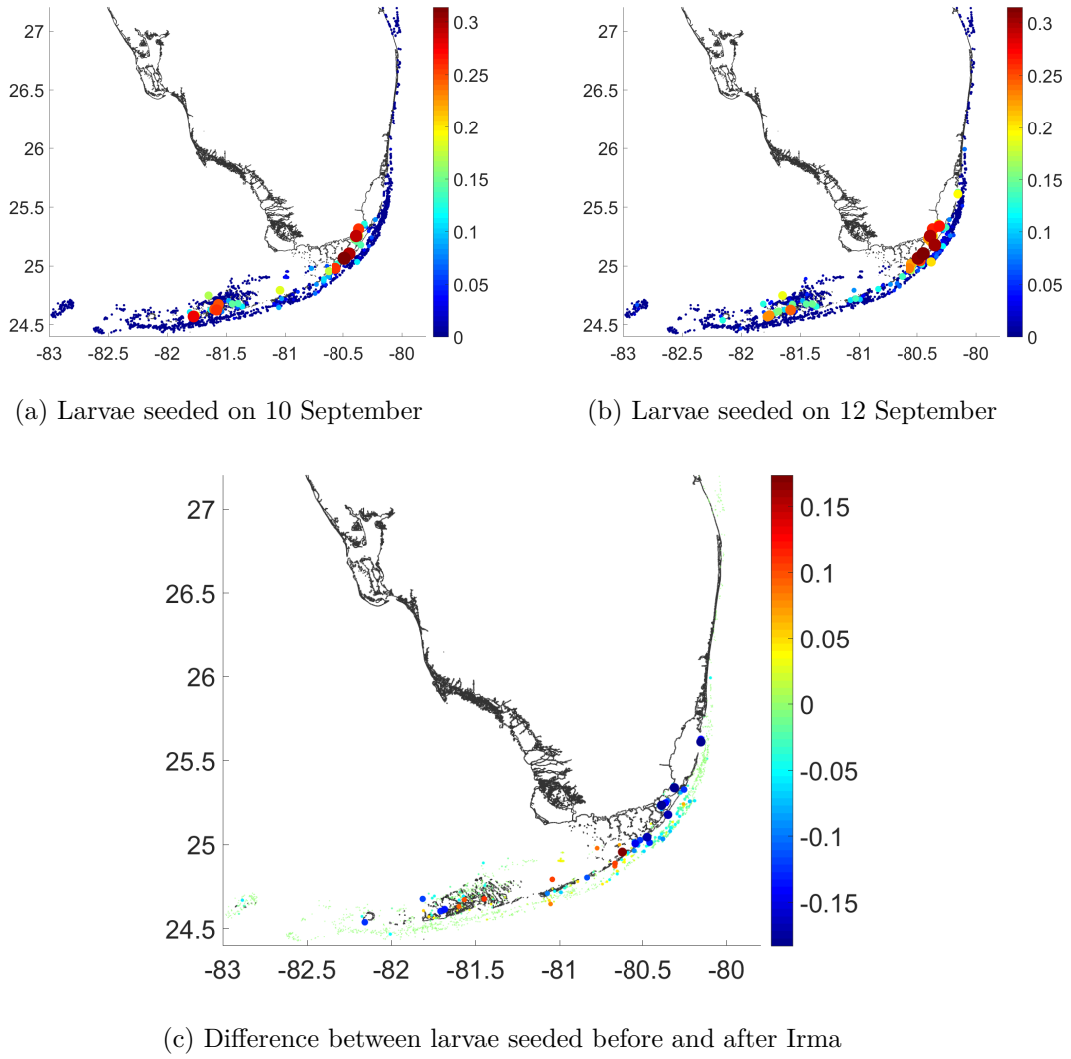


Figure 58: Comparison of the local retention between the larvae seeded on 10 and 12 September. Irma looks to impact it negatively in Key West, in the Marquesas Keys, in the Dry Tortugas and above all, in the Upper Keys.

Self recruitment is somewhat related to local retention. Here again, most reefs show a very limited self recruiting capacity (see Fig. 98 in Appendix B). The indices of the two situations are the highest in the Lower and Upper Keys. Nonetheless, self recruitment shows larger differences than local retention. Like local retention, self recruitment is negatively impacted by Irma in the Marquesas Keys. The larvae that will eventually settle there can not be the locally seeded ones since they were pushed southwards. Besides, self recruitment also decreases with Irma in the northeastern Lower Keys. Planulae are indeed transported northeastwards by the hurricane and will then transit through Florida Bay. The larvae settled on those reefs mainly come from more southern Lower Keys. Finally, since Irma pushed the larvae of the inner Upper Keys a bit more eastwards, larvae do not quickly cross Hawk Channel and remain longer in Florida Bay, thereby settling locally.

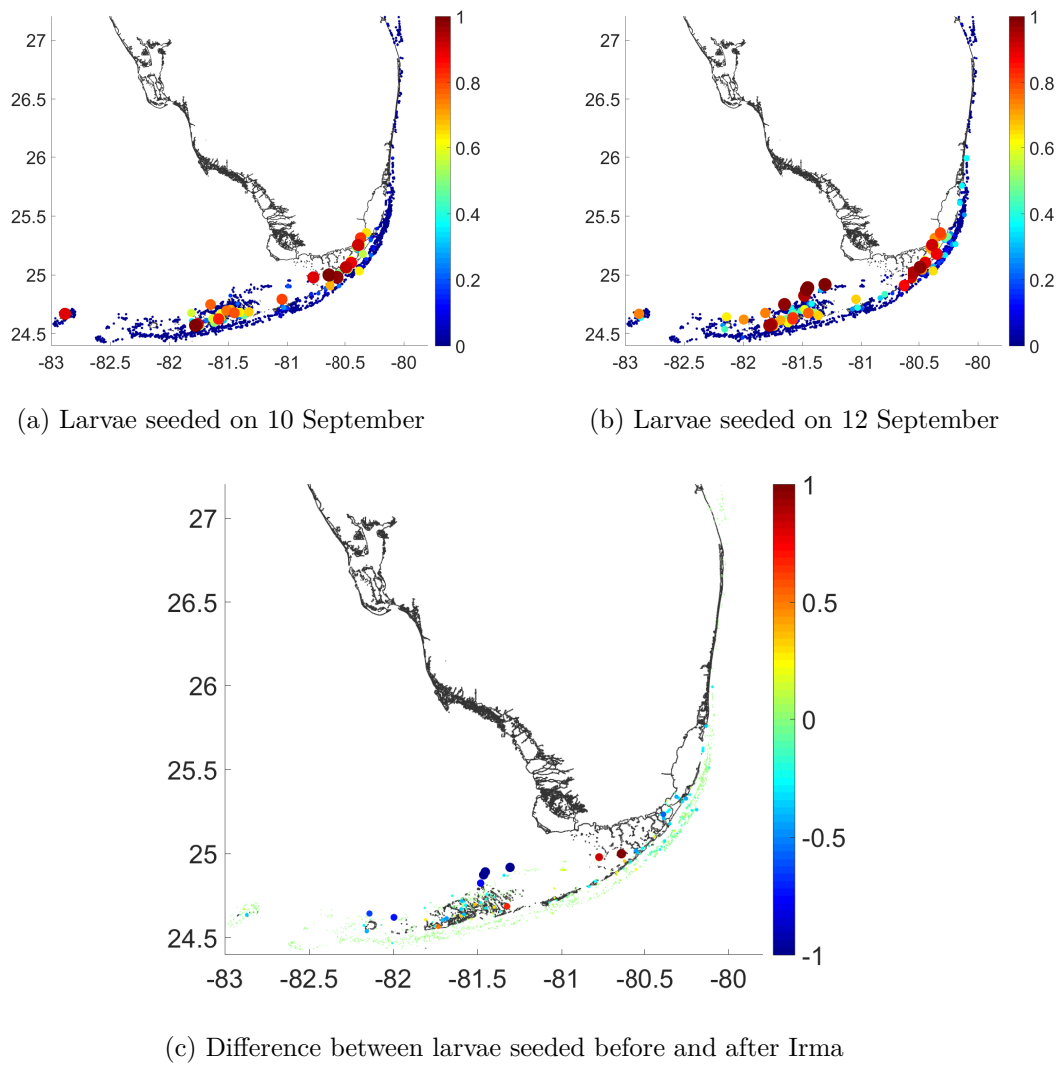


Figure 59: Comparison of self recruitment between the larvae seeded on 10 and 12 September. Irma looks to impact it negatively in the Marquesas Keys and in the northeastern Lower Keys, but positively in the inner Upper Keys.

In both conditions, the reefs providing the best settlement proportions are found in the Lower and Upper Keys. The maximum proportion levels at 52.05 % and 51.89 % for the larvae seeded on the first and last night respectively. However, the larvae from the third night present higher proportions of settlement on western reefs than those from the first night. The difference between the two graphs highlights the trends mentioned before. We observe that the Dry Tortugas, the Marquesas Keys and Key West show low settlement proportions. After moving their larvae southwestwards, the currents drive them eastwards, but not close enough to the reefs for an important part. The more western the reefs, the least they will supply the FRT with larvae. Since the western reefs are not continuously exposed to northwestward winds after the passage of Irma, the larvae seeded on 12 September show a greater settlement proportion than the ones obtained by Frys (2017) and Béchet and Verstraeten (2018). A similar conclusion can be drawn regarding northeast Lower Keys when subjected to Irma. In this case, the larvae are taken away from the reefs and then migrate through Florida Bay without encountering many reefs. For that reason, the settlement proportion is lower than for larvae seeded on 12

September. Planulae seeded after the hurricane will indeed settle locally or southwards in the Lower Keys. On the contrary, Irma looks to act positively on the outer belt of the Middle and Upper Keys. An important amount of larvae will indeed cross Hawk Channel and stay for a moment in the Middle Keys, giving plenty opportunities to settle. In both cases, the reefs located on the east coast of Florida are characterised by a low settlement proportion. These reefs are indeed supplied with larvae thanks to the strong Florida Current, flowing northwards. The currents are mainly unidirectional as we can see on Fig. 37. The only possibility for the larvae is to settle on the northern reefs near Palm Beach. However, this is where the reefs are the scarcest and thus the settlement probability the lowest. Moreover, the larvae seeded at the northern end of the FRT exit the network before becoming competent. The proportion of lost larvae can be found in Appendix B.

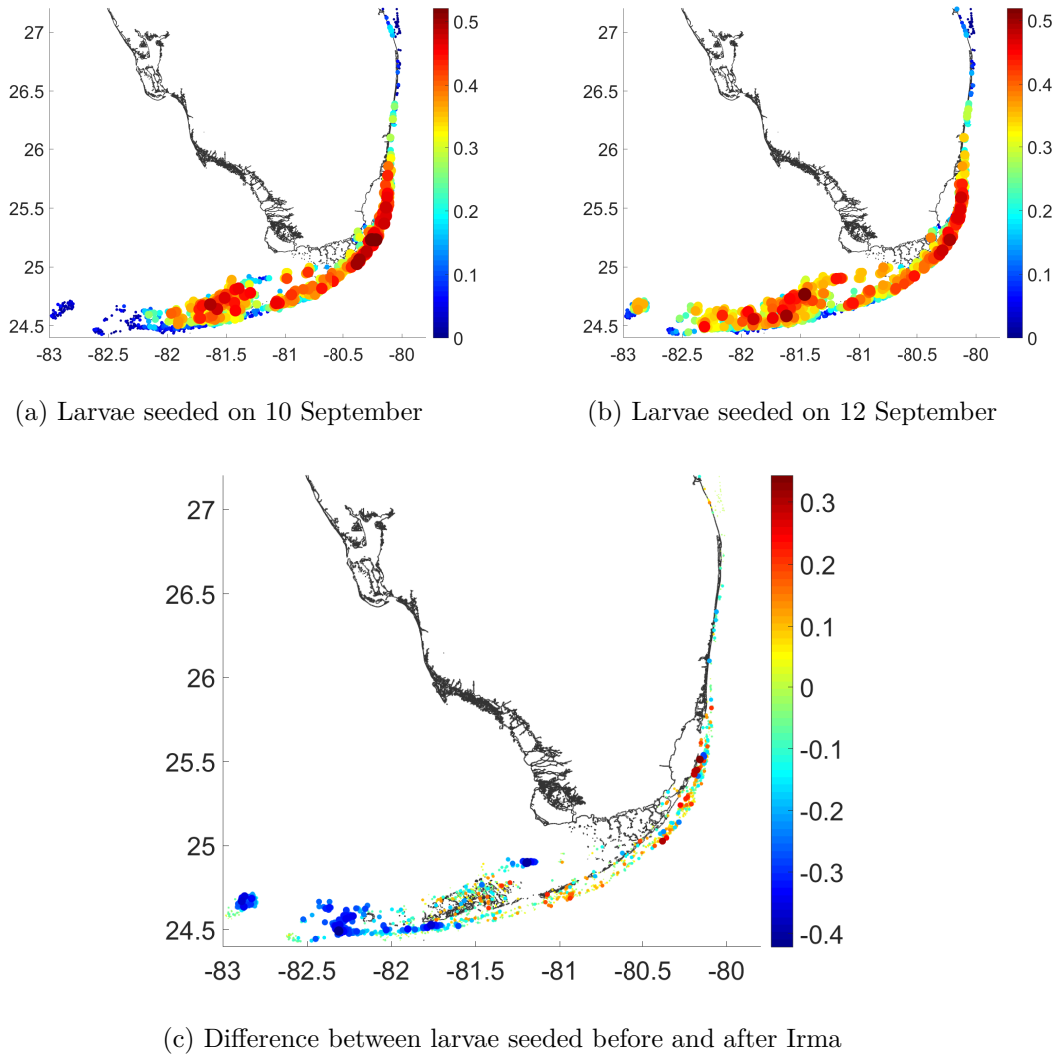


Figure 60: Comparison of the proportion of settled larvae between the larvae seeded on 10 and 12 September. Irma looks to impact it negatively in all the reefs located west of Key West and in the northeastern Lower Keys. However, it increases the proportion of settled larvae coming from the outer belt of the Middle and Upper Keys, but to a lesser extent.

In a more general perspective, Fig. 61 shows that Irma negatively impacts the settlement

of larvae. The first interval with settlement proportion up to 5 % counts more than 20 % of the reefs for the larvae seeded before Irma. This interval is the most populated one. On the contrary, the first interval only reaches roughly 7 % of the total number of reefs for the larvae seeded on 12 September. The highest fraction of reefs is to be found in the interval ranging from 30 % to 35 % of settlement proportion. The mean settlement proportion of reefs jumps from 21.68 % for the larvae seeded on 10 September to 25.53 % for the ones seeded two days later. Regarding the settlement proportion of larvae, which includes self recruitment as well, a similar observation can be made. The 22.62 % mean proportion of 10 September larvae indeed becomes 26.96 % for the 12 September larvae. In conclusion, Irma not only modifies the spatial distribution of settlement proportion, but also diminishes it in terms of reefs and larvae. The complementary histogram of lost proportion can be found in Appendix B (Fig. 99).

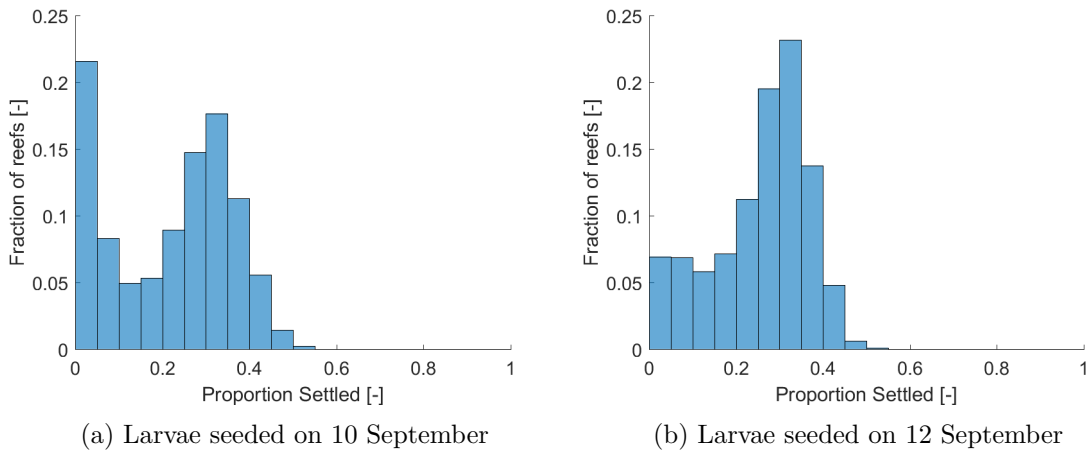


Figure 61: Comparison of the settlement proportion histograms between the larvae seeded on 10 and 12 September. The first interval counts many more reefs for larvae seeded on 10 September than for those seeded two days later. The seventh interval ranks first for the latter and second for the former.

The inspection of the weighted connectivity length (WCL) index adds some information to the previous conclusions. In the westernmost reefs of the FRT, we can clearly see that the WCL is way higher for the larvae seeded on the first night than for the ones seeded on the third one. The maximum WCL is 401.95 *km* and 369.71 *km* for the former and the latter respectively. This lets us conclude that the larvae seeded in the western end of the FRT will supply reefs that are located way further away with Irma's influence. We indeed observed that the larvae were taken too much to the south to be able to settle on the Lower and Middle Keys. Actually, they will only be able to settle once the FC redirects them northwards in the vicinity of Biscayne Bay. Such a high WCL is interesting in terms of diversity. It indeed means that larvae will settle on genetically different coral reefs. Nevertheless, it is important to notice that the high WCL reached in the west of the FRT is not very relevant in that sense, since the proportion of settled larvae is extremely low in that area. In fact, the WCL of the westernmost reefs concerns only very few larvae.

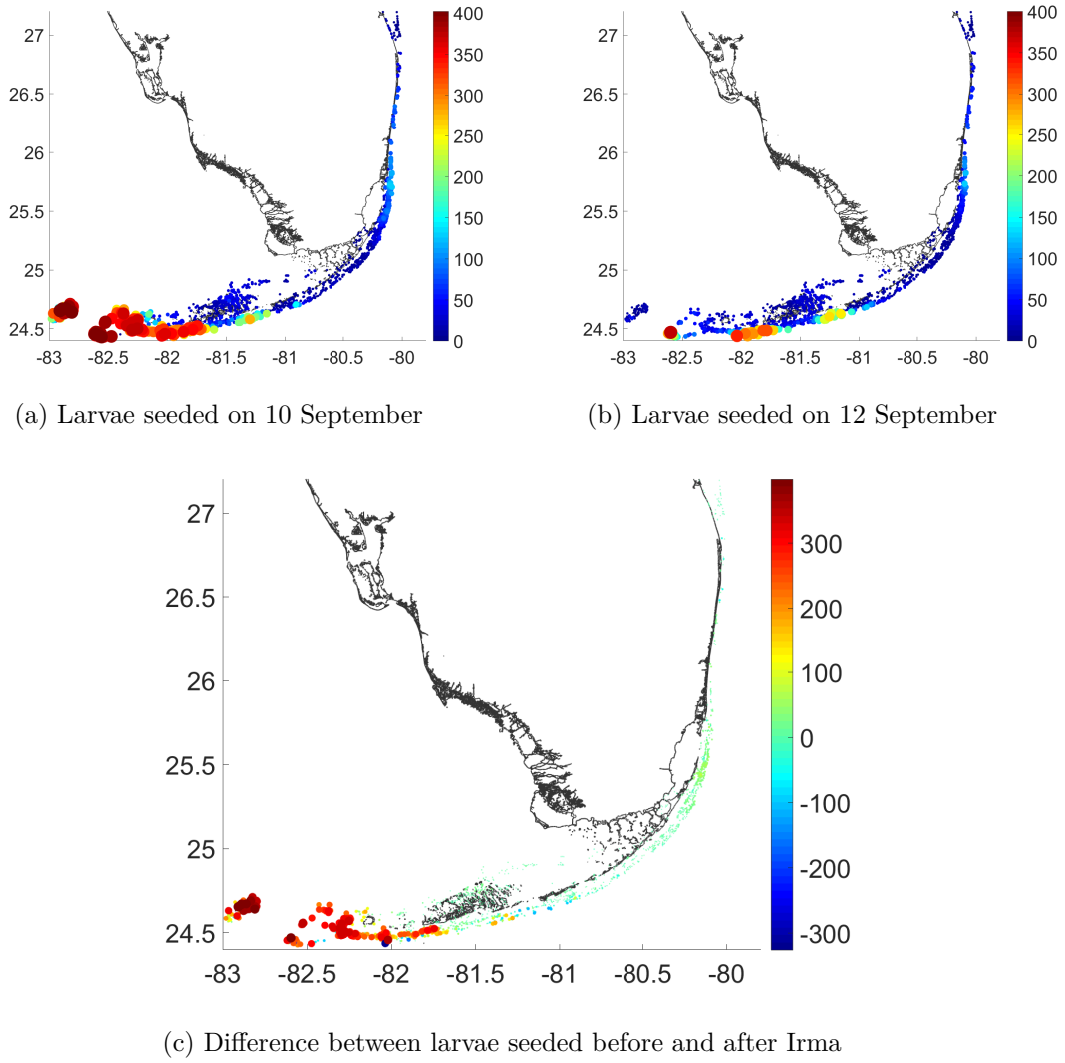


Figure 62: Comparison of the weighted connectivity length between the larvae seeded on 10 and 12 September. Irma raises the value of the WCL drastically in the westernmost reefs of the FRT.

A look at the histograms also gives us additional information. Even though, the fraction of reefs presents an exponential decay with the WCL for the two situations, the mean WCL of the 10 September larvae (75.5 km) is more than the double of the mean of the 12 September larvae (36.31 km). As mentioned earlier, the westernmost reefs of the FRT act as outliers, with a WCL far above the mean in the case of larvae seeded before Irma especially. The difference in the median WCL is less contrasting, even if it shows the same trend. Larvae from the first night have a 30.04 km median while those from the last night have a median of 21.78 km .

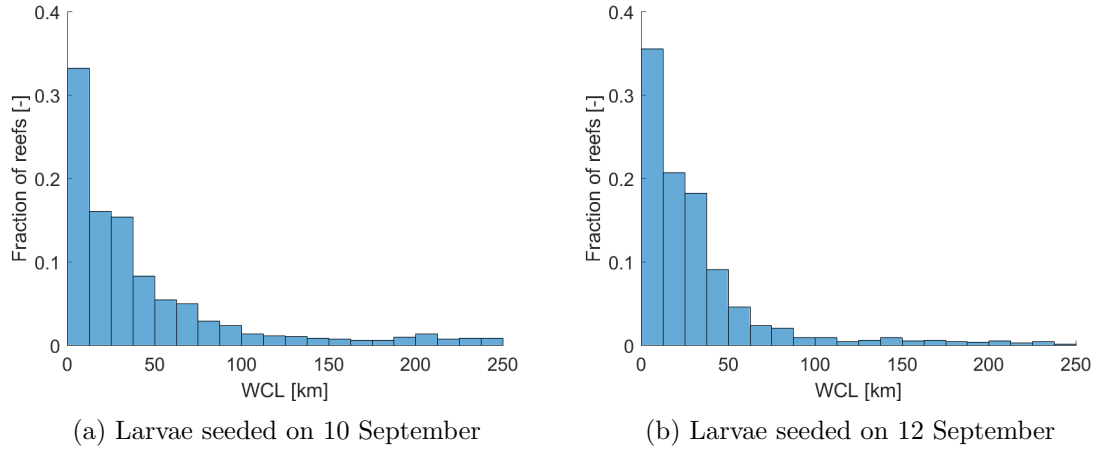


Figure 63: Comparison of the WCL histograms between the larvae seeded on 10 and 12 September. The exponential decay of the fraction of reefs with the WCL is observed in both conditions. The mean and median WCL are higher for the larvae impacted by Irma, though.

When it comes to analyzing the betweenness, we do not really need to compute the difference between the two situations since they are quite similar. Both conditions indeed show a maximum betweenness in Vaca Reef, like Frys (2017) and Béchet and Verstraeten (2018) pointed out. Moreover, Fig. 65 shows the hotspots in terms of betweenness. It appears the most central hubs in the network are mainly located in the western Lower Keys, Key West and in the Upper Keys in both cases. The situation without impact of the hurricane also highlights hotspots in the Middle Keys, beside Vaca Reef. Vaca Reef is a very important reef in the FRT as it counts 301 and 294 incoming and outgoing connections respectively for the larvae seeded on 10 September. Regarding the larvae seeded during the third night, these connections numbers decrease a bit, but stay very high with 258 and 265 incoming and outgoing connections respectively. As a matter of fact, Vaca Reef is the largest coral reef in the FRT. Since we imposed a constant seeding density for all reefs, Vaca Reef is also the largest seeder with 3.6×10^5 larvae seeded in each case, i.e. 8% of the total number of particles seeded. Nevertheless, it is important to notice that the coral cover on this reef is estimated to range between 0 and 10% (Florida Fish and Wildlife Conservation Commission-Fish and Wildlife Research Institute, 2016). The resulting connectivity associated with that reef is thus most likely overestimated. Once again, the results obtained in this thesis must be taken with precaution and used more qualitatively than quantitatively.

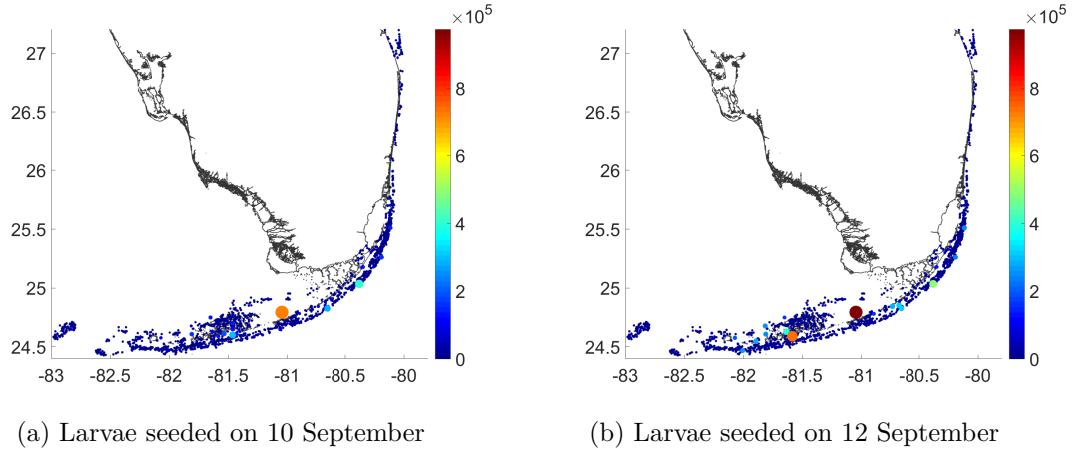


Figure 64: Comparison of the betweenness between the larvae seeded on 10 and 12 September. Vaca Reef appears as the most central hub in both situations.

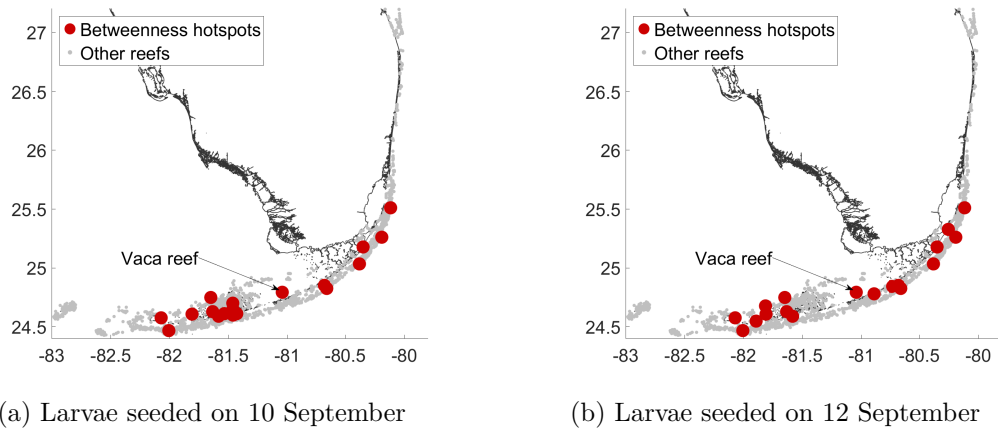


Figure 65: Comparison of the betweenness hotspots between the larvae seeded on 10 and 12 September. In general, both situations show the same hotspots zones.

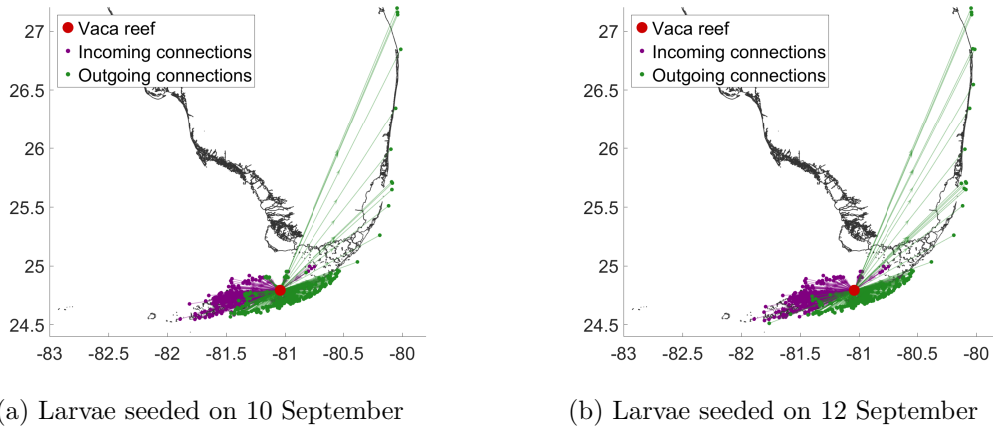


Figure 66: Comparison of all the incoming and outgoing connections of Vaca Reef between the larvae seeded on 10 and 12 September. In both cases, Vaca Reef admits a very important number of incoming and outgoing connections with links to almost the entire FRT, except for the Dry Tortugas and the Marquesas Keys.

The source-sink index varies a bit with and without the hurricane. In the first case, the sinks are mostly located on the outer belt of the Middle Keys and past Biscayne Bay to the north. In the second case, we can add the south of the Lower Keys, Key West and the Marquesas Keys to these zones. Looking at the difference between the two graphs, it appears that the south of the Dry Tortugas turns from a sink to a source. The Dry Tortugas larvae do not have enough time to become competent and to settle on the southern part of them, as they are driven southwards by the hurricane. Moreover, due to their isolation and the unidirectional FC, they cannot receive any larvae from other reefs of the FRT. All the Dry Tortugas reefs thus turn into sources when Irma passes over the FRT. The same phenomenon is observed regarding the south of the Marquesas Keys. While they are receiving larvae from the northerly Marquesas Keys without the hurricane, they only act as a supplier with the hurricane. A bit surprisingly, the southwest of the Marquesas Keys is a less important source with the hurricane than without it. This can be explained by the low settlement proportion of that zone even without the hurricane. The low incoming and outgoing connectivities of these reefs indeed make them sensitive to a slight change in settlement proportion. Finally, we can remark that the index of reefs located northeast of the Lower Keys in Florida Bay decreases for 10 September larvae. The northeastern part of the Lower Keys indeed provides those reefs with a significant amount of larvae. We should also notice that recirculating eddies along the FRT, that are not reproduced by our model, should increase the number of larvae received by upstream reefs and thereby lead to a decrease in recruited larvae for downstream reefs. These eddies should most likely have a significant impact on the source-sink index.

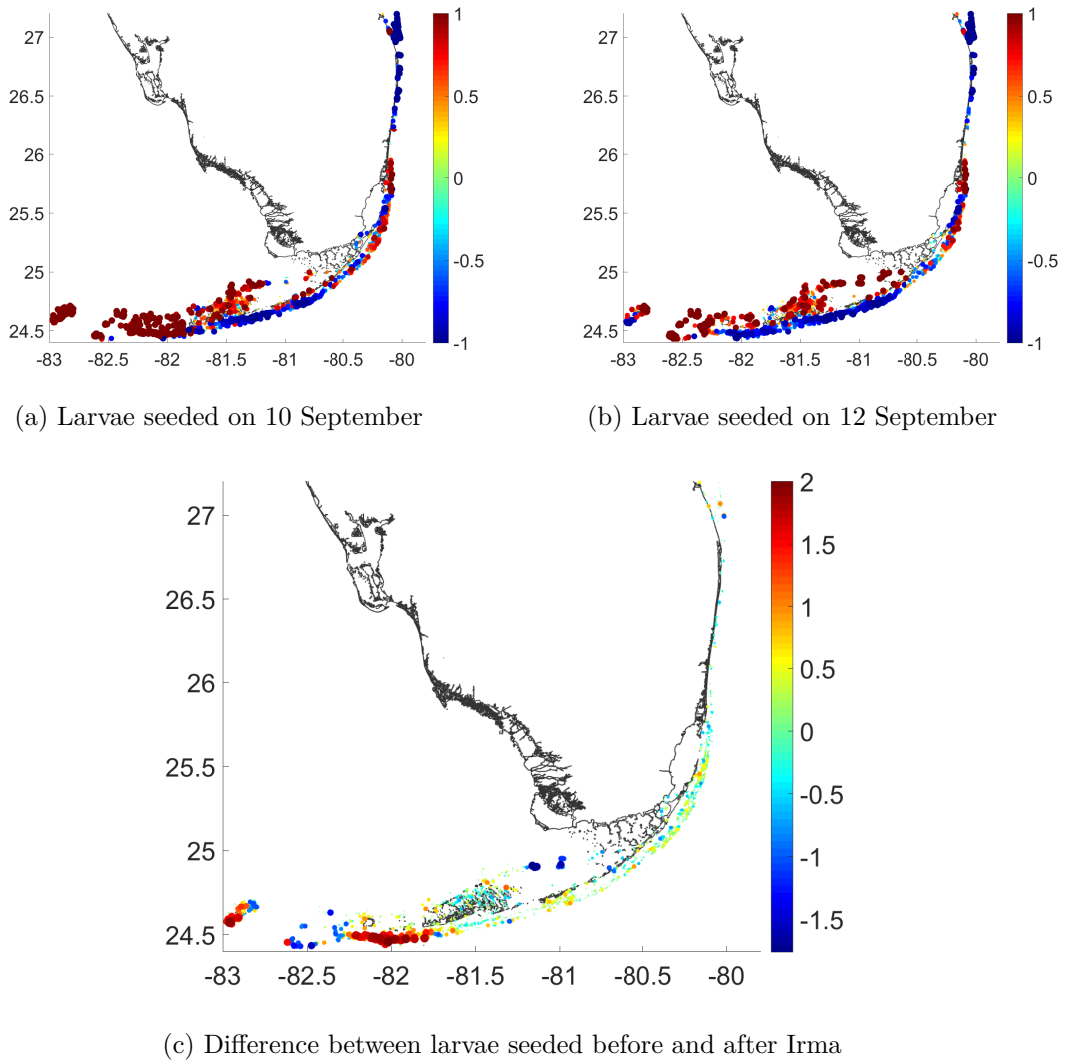


Figure 67: Comparison of the source-sink index between the larvae seeded on 10 and 12 September. The southern Dry Tortugas and Marquesas Keys as well as south Key West tend to be sources whereas the southwestern Marquesas Keys and the reefs located northeastwards to the Lower Keys show a lower source-sink index with the hurricane.

Whatever the situation, the outgoing PageRank shows close results. The reefs that will end up taking part the most to the diversification of the network lie in the outer belt of the Upper Keys, in the northern Dry Tortugas and especially in the north of the Lower Keys. The influence of the hurricane is once more discernible, though. Fig. 69 points out some changes in outgoing PageRank hotspots. We see that the south of the Dry Tortugas is no longer a hotspot, as larvae are transferred too much to the south at first. The Marquesas Keys also lose some supplying importance to the advantage of the Lower Keys. Vaca Reef because of its size, its high seeding capacity and its central position is an important supplier in both situations as well.

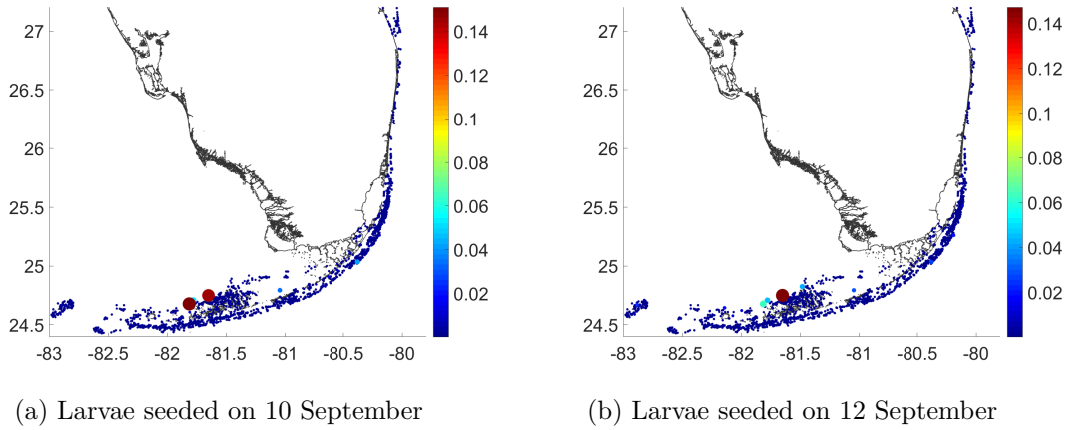


Figure 68: Comparison of the outgoing PageRank between the larvae seeded on 10 and 12 September. The northwestern Lower Keys stand out from the other reefs as the best suppliers for the network.

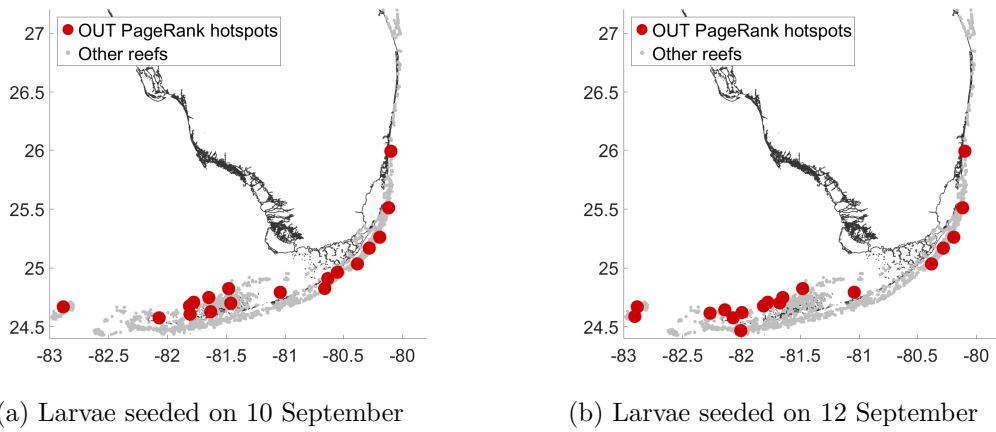


Figure 69: Comparison of the outgoing PageRank hotspots between the larvae seeded on 10 and 12 September. The best suppliers lie in the Lower and Upper Keys. The strongest difference between the larvae seeded during the first and third nights is the displacement of some of the best suppliers from the Marquesas Keys to the Lower Keys for 10 September larvae.

The reefs receiving the most diversified flux of larvae are of course located on the east coast of Florida. The Florida Current indeed sweeps many larvae along the whole FRT towards its north end. Incoming PageRank hotspots once more illustrate the tendencies pointed out earlier on. The Dry Tortugas and the south of the Marquesas Keys admit few settled larvae from 10 September, as the larvae passing there are not competent yet.

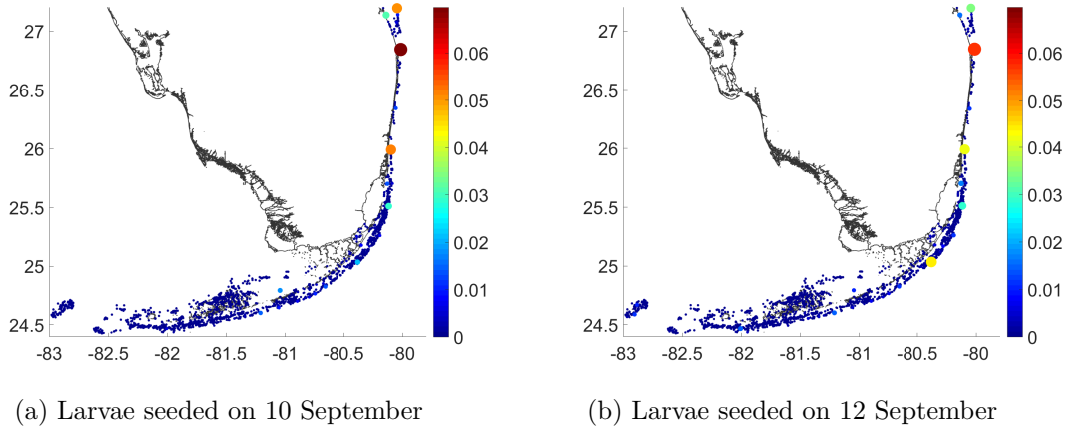


Figure 70: Comparison of the incoming PageRank between the larvae seeded on 10 and 12 September. The east coast of Florida appears to embrace the reefs receiving the most diversified flux of larvae.

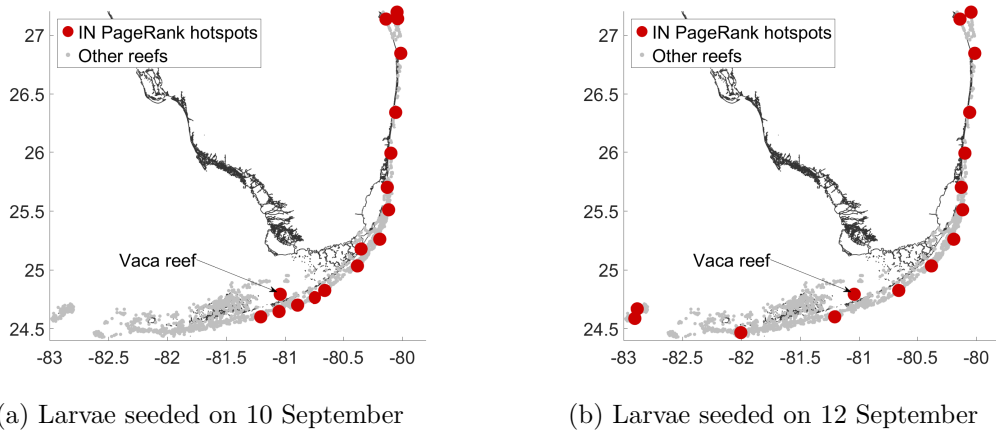


Figure 71: Comparison of the incoming PageRank hotspots between the larvae seeded on 10 and 12 September. Both conditions show similar situations, but the larvae seeded on 12 September also admit reefs with a diversified flux in Key West and in the Dry Tortugas.

The aim of the PageRank protection index is to determine which reefs should receive protective measures because of their vulnerability and their provider role. The present analysis is carried out for a particular hurricane. This index thereby indicates reefs that may be worth protecting in this very particular context. Nevertheless, we must keep in mind that another hurricane might have a different path and different intensities, leading to different wind-induced currents and thus to different connectivity properties.

Looking at Fig. 72, we notice that the inner Keys and the north of the Dry Tortugas should receive protection measures in a usual situation. When Irma passes over the FRT, some reefs in the Upper Keys and the south of the Dry Tortugas are to be added to this list. Of course, it makes no sense to remove the reefs with a negative difference index from it. Only the positive values of the difference index should be considered. The outer reefs of Key West and the Lower Keys, for which Frys (2017) obtained a high index, could also be considered. Nonetheless, as mentioned before, the southern Dry Tortugas do not have a high proportion of settled larvae seeded before Irma's passage. Therefore, it might be

more interesting to favour the Upper Keys rather than the southern Dry Tortugas when it comes to protective measures, even though the PageRank protection index in the former is lower than in the latter.

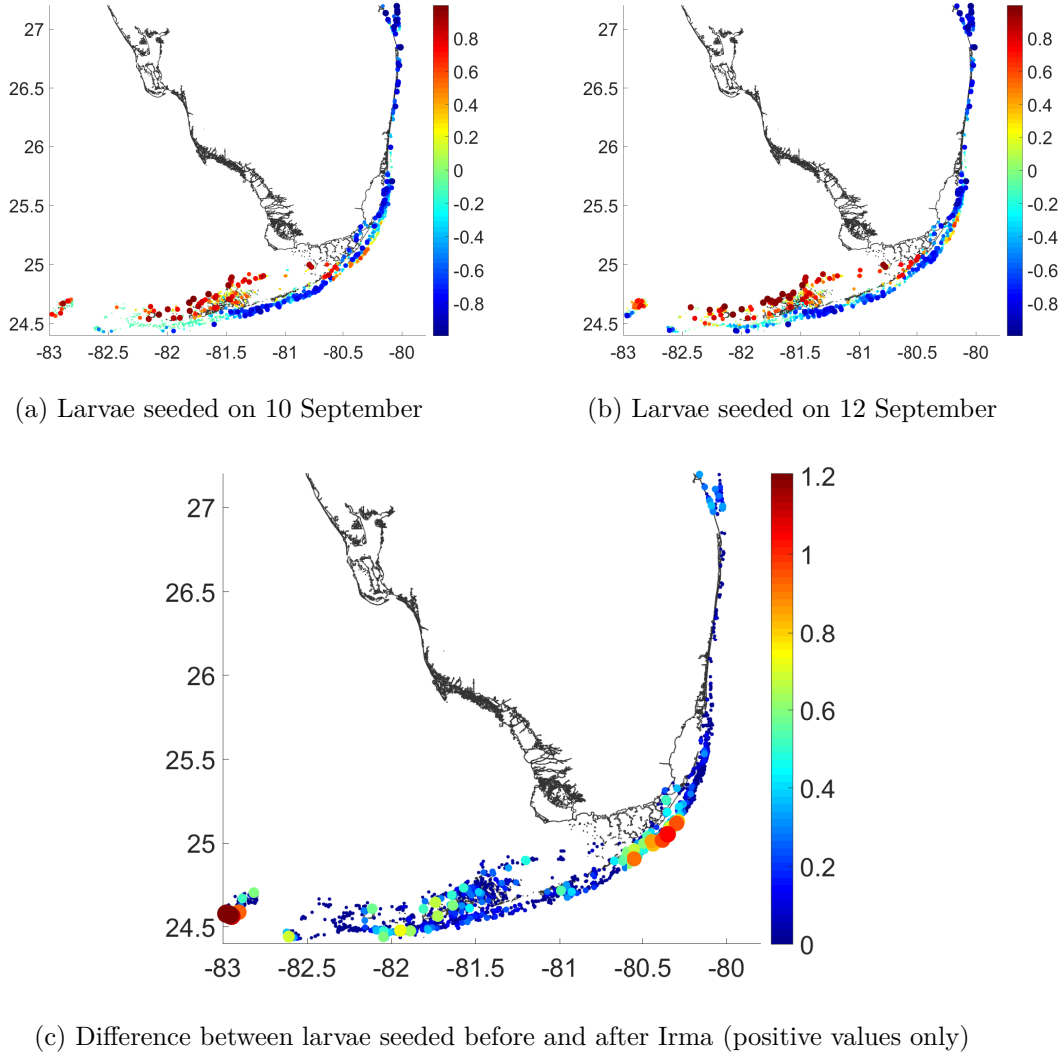


Figure 72: Comparison of the protection PageRank index between the larvae seeded on 10 and 12 September. The hurricane showcases the southern Dry Tortugas and the Upper Keys as additional reefs to protect.

Likewise the PageRank protection index, the PageRank restoration index of the larvae seeded before the hurricane should be thought as a complementary indicator to the one computed without the hurricane. It seems that two reefs stand out from the others in both situations: Vaca Reef and Key Largo. These two reefs were also listed amongst the ten betweenness and outgoing PageRank hotspots, for both situations. However, the care given to Vaca Reef should rise with Irma. Fig. 74 also shows that several other reefs should be regarded as well. This figure shows very similar results. The most interesting reefs regarding restoration are mainly to be found in the Upper Keys and on the east coast of Florida. Some of them can also be found in the Middle Keys, in the northwestern Lower Keys and in Key West. The principal difference between the situation with and without the hurricane is that Irma leads to focus on the Upper Keys and to abandon the Dry

Tortugas. However, as explained earlier on, it makes no sense to leave restoration sites aside. The principal information of this investigation is thus that the Upper Keys should receive special attention in Irma's case.

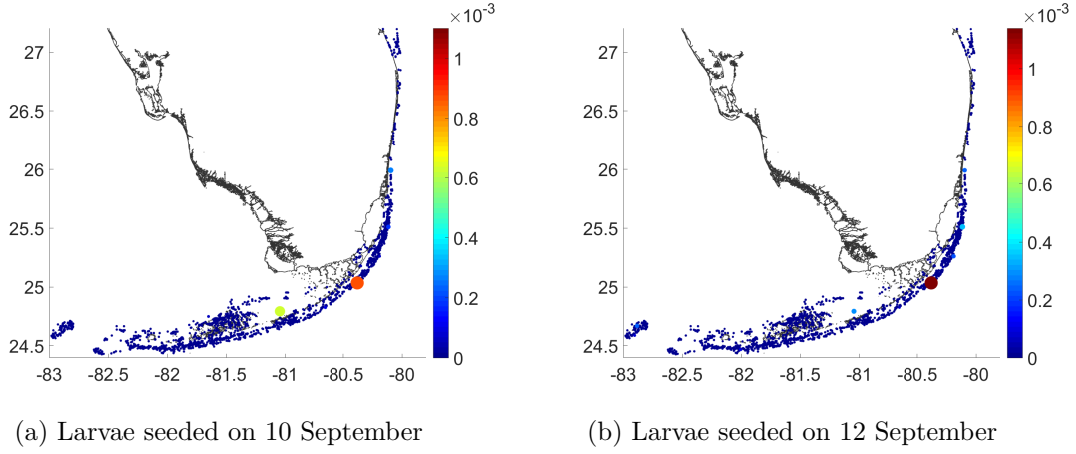


Figure 73: Comparison of the PageRank restoration index between the larvae seeded on 10 and 12 September. Vaca Reef and Key Largo shine out as the best spots to implement restoration measures in both situations.

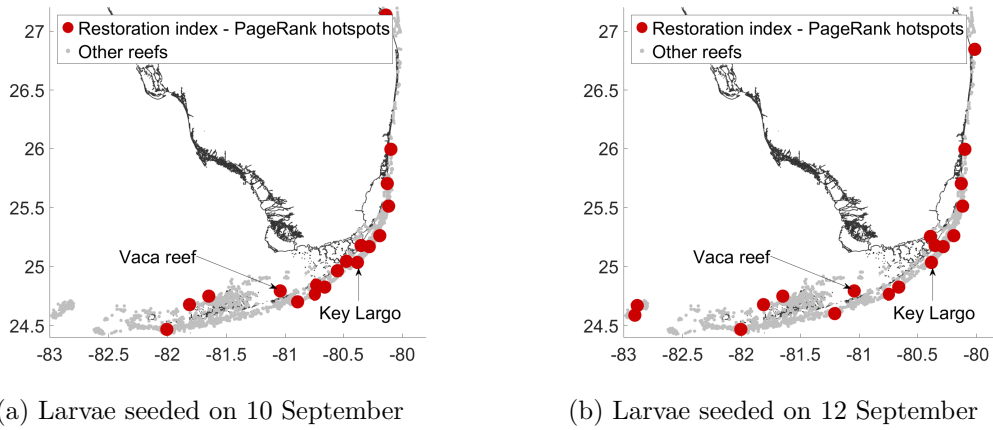


Figure 74: Comparison of the PageRank restoration index hotspots between the larvae seeded on 10 and 12 September. Irma's passage increases the attention that should be affected to the Upper Keys.

Finally, we can have a look at the clusters of reefs constituted thanks to the SCC method. Fig. 75 gives very similar results with and without the hurricane. A huge cluster embraces almost the whole FRT in both cases, except the noteworthy exception of the western Marquesas Keys for 10 September larvae. Within this large cluster, we find a little one lying over a few reefs in the inner Upper Keys. Both situations also have a third cluster in the Dry Tortugas, even if the larvae seeded before the hurricane do not encompass the northern Dry Tortugas in it, as the northern reefs have almost no incoming connections with the southern Dry Tortugas. Without the passage of the hurricane, the SCC method also gives 3 more clusters on the east coast of Florida, but little ones that have nothing to compare with the most important one. Fig. 76, that excludes demographically

unsignificant reefs, gives more contrasting results. The larvae seeded before Irma now count 7 clusters while the larvae seeded after it count 13 clusters. In both conditions, a large cluster extends over the Upper and Middle Keys. 3 and 4 clusters respectively lie in the Lower Keys and little clusters lie in the northern Upper Keys, Biscayne Bay and in Florida Bay for the larvae seeded on 10 September. The strongest difference between the two can be found in the western Keys. The Dry Tortugas, the Marquesas Keys and the south of Key West were identified as undemographically significant for the larvae seeded before the passage of the hurricane. The reason for this is of course the transport of the northern larvae southwards at the very beginning of the larval dispersal. Because of that, southern larvae will never be able to settle northwards and to create bidirectional connections.

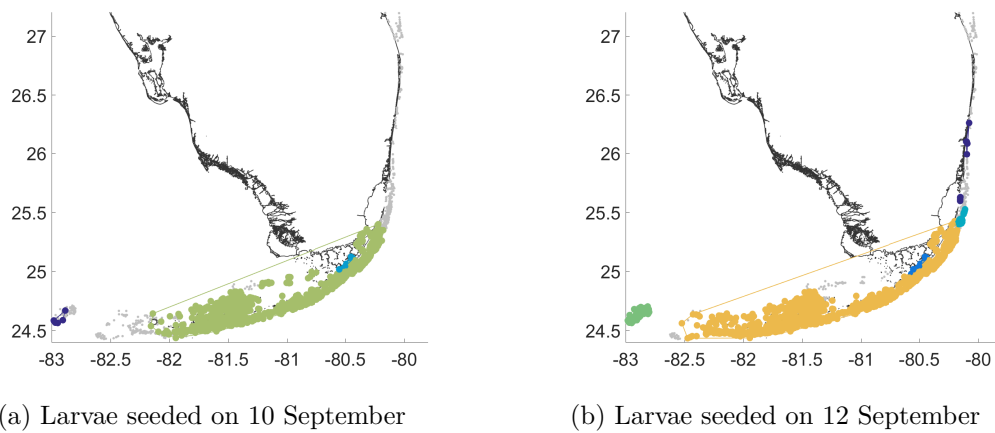


Figure 75: Comparison of the clusters determined thanks to the SCC method between the larvae seeded on 10 and 12 September. One large cluster stands out in each case. The one of the larvae seeded on 10 September is shorter in the west, though.

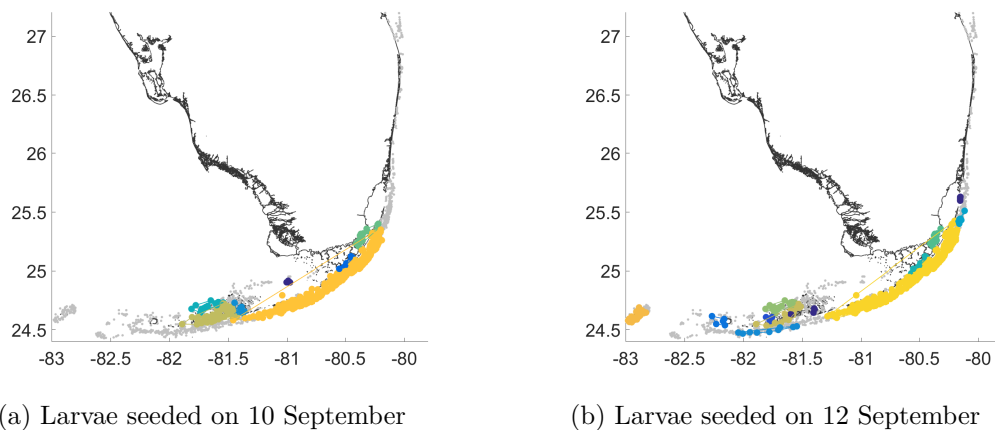


Figure 76: Comparison of the demographically significant clusters determined thanks to the SCC method between the larvae seeded on 10 and 12 September. The Dry Tortugas, the Marquesas Keys and Key West are excluded from the demographically significant clusters for larvae seeded before Irma's passage.

4.4.2 Comparison between *A. Cervicornis* and *M. Cavernosa*

Most of the time, we will present the graphs corresponding to all MC larvae, to the MC larvae seeded on 12 September, to AC and to the difference between MC and AC. For each index, we will proceed in the following way. By keeping a look on the results obtained in section 4.4.1, we will try to discern the extent of Irma's impact on MC's connectivity. At first, we will compare the total MC's connectivity with the connectivity of MC larvae that are free from Irma's influence, i.e. those seeded on 12 September. Afterwards, we will compare the connectivity of AC larvae with MC larvae seeded after the hurricane. This should highlight common connectivity features that do not rely on seasonal fluctuating forcings, like winds for example. Finally, we will subtract AC's considered index to MC's one. If a difference between the two species is spotted and if larvae seeded on 10 and 12 September also show different results, we will attribute this difference to the hurricane. If larvae seeded on 10 and 12 September show similar results, the difference between MC and AC must be imputed to another factor than the hurricane. This methodology should help us determine if a strong but brief disturbance, like any hurricane, is able to deeply affect the connectivity in the FRT, whatever the species and its spawning season.

The comparison of the local retention and self recruitment indices between MC and AC show only limited differences. They can be found in Appendix B (Fig. 101 and 102). The settlement proportion gives more interesting information. By comparing Fig. 77a and 77b, we can notice that the decrease in settlement proportion in the Marquesas Keys and in the Dry Tortugas for all MC larvae can be imputed to Irma, except for the most western reefs of the Marquesas Keys. As Fig. 77b and 77c display similar values in these areas, we can conclude that a brief disturbance like Irma is capable of sufficiently modifying the settlement proportion over there. The westernmost reefs of the FRT show the sparsest coastal environment. For that reason, the effect of a disruption is felt to a greater extent, as coasts are not able to act as barriers against fluctuating currents. B  chet and Verstraeten (2018) indeed showed in their interannual study of the FRT connectivity that the Marquesas Keys and the Dry Tortugas showed the greatest standard deviation and coefficient of variations for most indices. Even without a storm, these reefs are the most likely to show differences. The introduction of a hurricane will thus emphasize these differences. And since climate change will cause more frequent and intense hurricanes, the variability of the connectivity in these areas is expected to increase in the future.

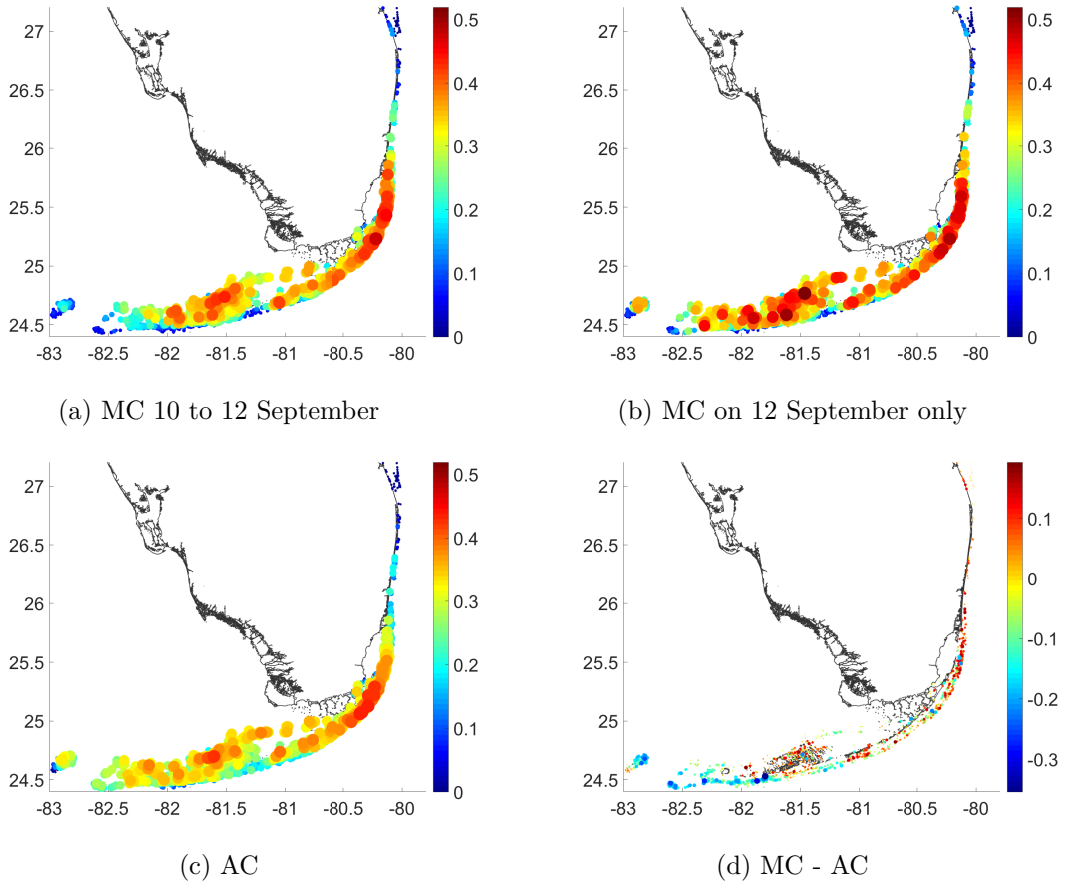


Figure 77: Comparison of the settlement proportion between AC and MC.

The study of the WCL highlights a counterintuitive observation. The total MC's WCL index shows higher values in the southwestern Marquesas Keys than the index computed for the larvae seeded on 12 September only. Moreover, the WCL of the latter is even more important than the one of AC. The difference between MC and AC can thus be only partially imputed to Irma. Nevertheless, the southern Dry Tortugas have a WCL way more important with AC than with MC, even when the hurricane blows the larvae southwards and then transports them eastwards very quickly. This surprising result can be related to the high coefficient of variation determined by Béchet and Verstraeten (2018) in this area. The settlement proportion in the Dry Tortugas is quite low such that a single long distance connection can be determinant on the WCL, even if this connection only concerns a few particles.

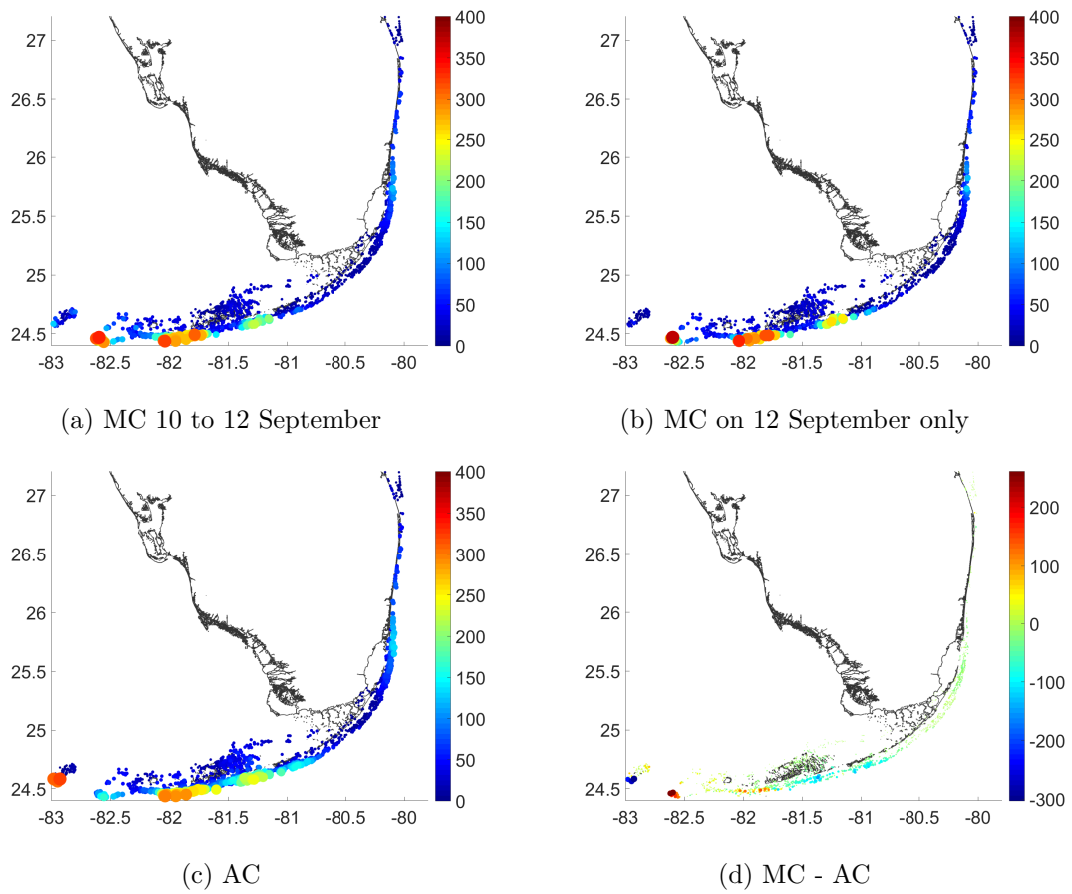


Figure 78: Comparison of the WCL between AC and MC. The westernmost reefs show the most striking differences. Even though the WCL increase in the southwestern Marquesas Keys can be put on Irma, the WCL decrease in the southern Dry Tortugas is very surprising.

Regarding betweenness, the major difference between MC and AC is certainly the displacement of the principal hub. For MC, Vaca Reef is dominant whereas Key Largo shines out for AC. These two hubs are listed amongst betweenness hotspots for both species, though. Another difference concerns the hotspots. While MC hotspots are concentrated in the Keys and mainly in the Lower Keys, AC hotspots are found in the Upper Keys, Key West, the Marquesas Keys and the Dry Tortugas. Apart from Vaca Reef that remains an important hub because of its high spatial coverage, no single AC hotspot lies in the Middle and eastern Lower Keys. As explained earlier on, the larval dispersal from the western reefs is more variable and this can maybe explain these differences.

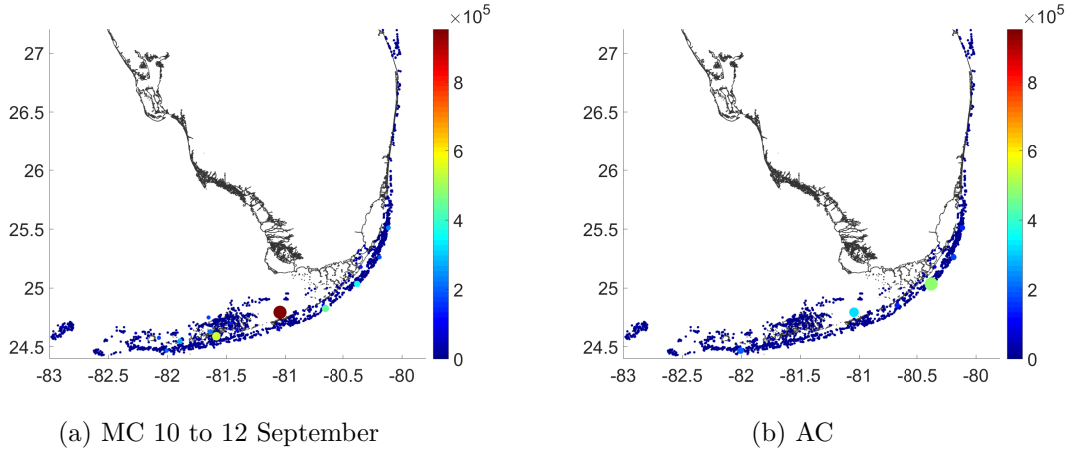


Figure 79: Comparison of the betweenness between AC and MC. MC and AC do not have the same principal hub.

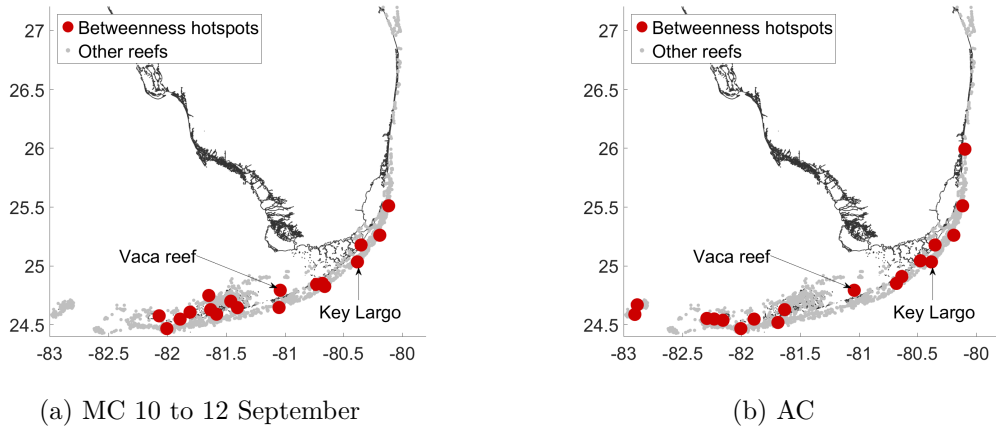


Figure 80: Comparison of the betweenness hotspots between AC and MC. AC has more hotspots in the western reefs, including the Dry Tortugas. Vaca Reef and Key Largo are on the list of the ten most important hubs for both species.

All the previous observations lead to the following result. The difference in PageRank protection index between MC and AC shows that the south of the Dry Tortugas could possibly be provided with more protective measures to cope with a hurricane similar to Irma. The latter indeed turns the southern Dry Tortugas in an important source (see Fig. 104) while it does not receive many larvae from the northern part of the archipelago. It is thus no longer resilient enough. Even though Irma has its own track and its own temporal evolution, the isolation of the Dry Tortugas, their sparse spatial distribution in comparison with the rest of the FRT and the unidirectional Florida Current make them vulnerable against hurricanes in a general way. On the contrary, Irma does not cause a significant increase in the PageRank restoration index, except for Key Largo (see Fig. 109 in Appendix B). PageRank restoration hotspots remain the same for both species, though. We should also notice that these results partially differ from the ones of Frys (2017) and Béchet and Verstraeten (2018). These two studies indeed obtained high protection indices on the outer belt of the Lower Keys. On the contrary, the northwestward winds blowing over the Dry Tortugas and the Marquesas Keys made these reefs insignificant sources and

thus not suited to protective measures. As this study only concerns one single spawning season for each species, their conclusions regarding protection and restoration measures should be taken into account as well.

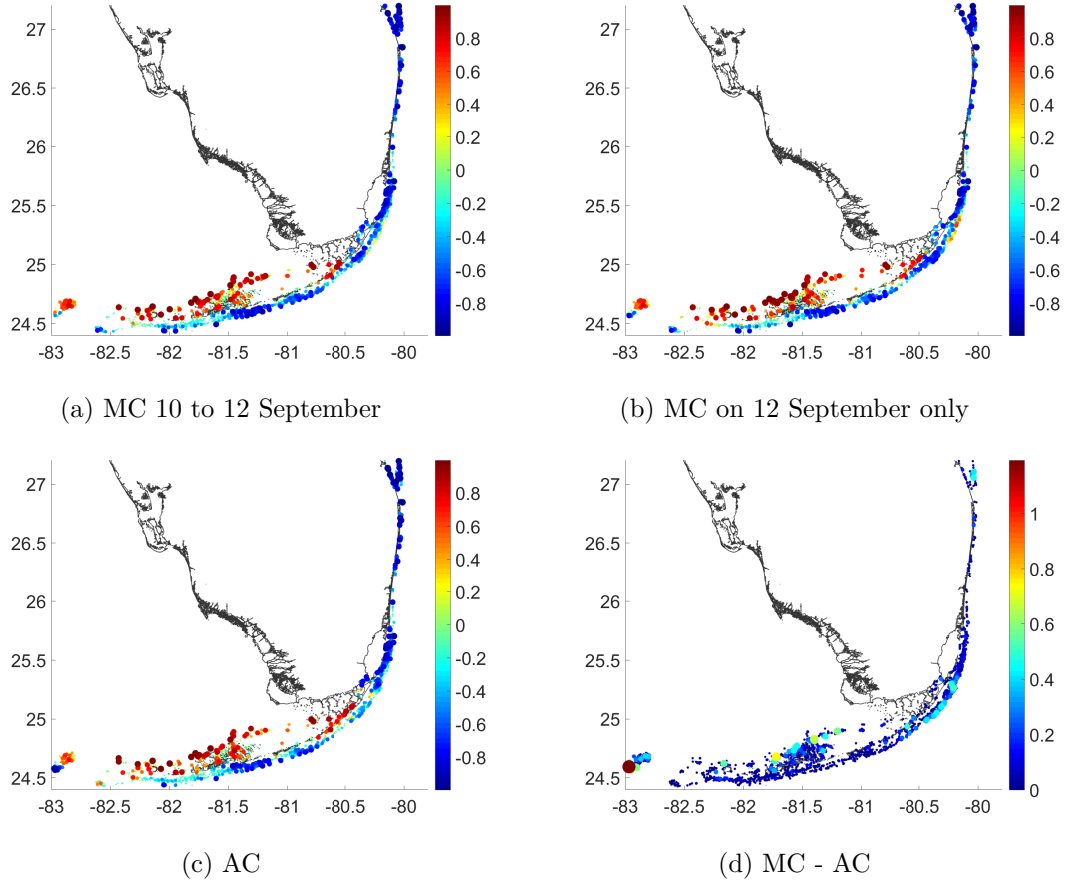


Figure 81: Comparison of the PageRank protection index between AC and MC. The southern Dry Tortugas appear to need more protective measures in the case of a hurricane similar to Irma.

Finally, the comparison of clusters made with the SCC method brings additional information. We see that the main cluster identified in Fig. 75a and 75b now embraces all the Keys, apart from the northeastern extremity in front of Biscayne Bay. Since the hurricane modifies the larval dispersal, the resulting main cluster corresponds to the union of the two clusters highlighted for the two situations. Moreover, it creates new connections and can turn unidirectional connections occurring without the hurricane into bidirectional ones and integrate them to the main cluster. Hurricane Irma contributes to the diversification of the FRT. Aside from this main cluster, MC still shows 3 little clusters on the eastern coast of Florida and another one in the Dry Tortugas. However, regarding demographically significant connections, we see that the south of the Marquesas Keys is not embedded in any cluster whereas it was present for the larvae seeded on 12 September (Fig. 76b). The share of the larval dispersal influenced by the hurricane is too high to consider the connections in this area to be demographically significant. On the contrary, we notice the presence of the Dry Tortugas in the clusters, in spite of their absence in Fig. 76a.

AC clusters show a different pattern. The largest cluster extends from Biscayne Bay

to the Lower Keys only. The Lower Keys, Key West and the Marquesas Keys then form another cluster while the eastern and northern Lower Keys, the south of the Marquesas Keys, the Dry Tortugas, some reefs in the Upper Keys and the northernmost Upper Keys form 6 other clusters. When it comes to demographically significant connections, the clustering counts even more subdivisions and is characterised by a significant shrinkage of the main cluster. The different clustering pattern of AC in comparison with MC can not be imputed to Irma. As a matter of fact, AC shows clusters rather similar to the demographically significant ones of MC. We thus suppose that a few connections linking the different parts of the Lower and Marquesas Keys with the rest of the Keys admit only a few larvae. If these connections are cut off due to the hydrodynamics or keep only one direction, the cluster breaks apart. The same phenomenon certainly applies to the clusters when considering only demographically significant connections. The shrinkage of the main cluster can be attributed to the lower importance of Vaca Reef in the case of AC. We indeed see on Fig. 84 that the outgoing connections of Vaca Reef in the western direction are much scarcer for AC than for MC. If the few connections happen to be demographically insignificant, the other reefs might not be able to maintain the connection with the western Keys. Furthermore, since almost all larvae seeded in the Middle Keys cross Hawk Channel and then follow the Florida Current northeastwards, no bidirectionnal connections are created and the Middle Keys, among which Vaca Reef, get excluded from the demographically significant clusters. Since the radius of curvature of the FRT is the strongest in the Upper Keys, we can expect the detachment of the Florida Current from the FRT in that area. The inner currents of the Upper Keys might thereby be dominant and enable bidirectional connections and the formation of a local cluster. AC shows a different clustering pattern than MC, not because of the hurricane, but because of the fragile connections linking the different regions of the Keys and the particular hydrodynamics during AC's spawning season.

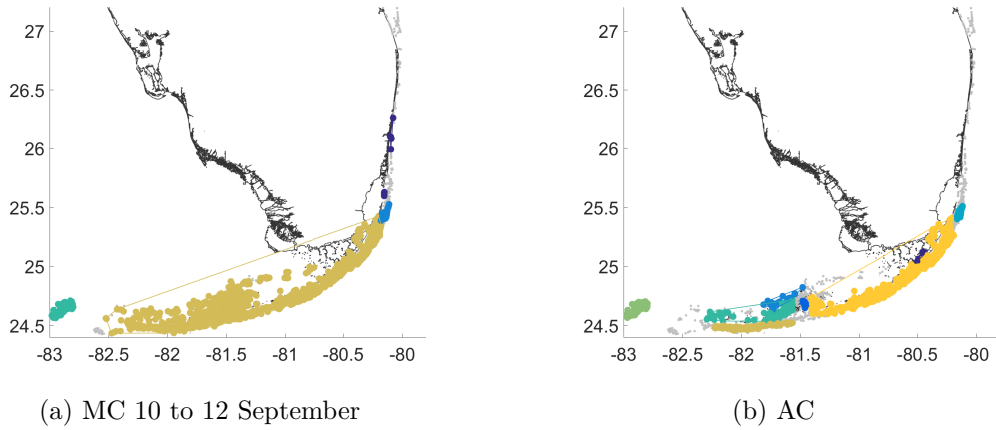


Figure 82: Comparison of the clusters between AC and MC. AC shows several clusters in the Keys while MC shows only one main cluster.

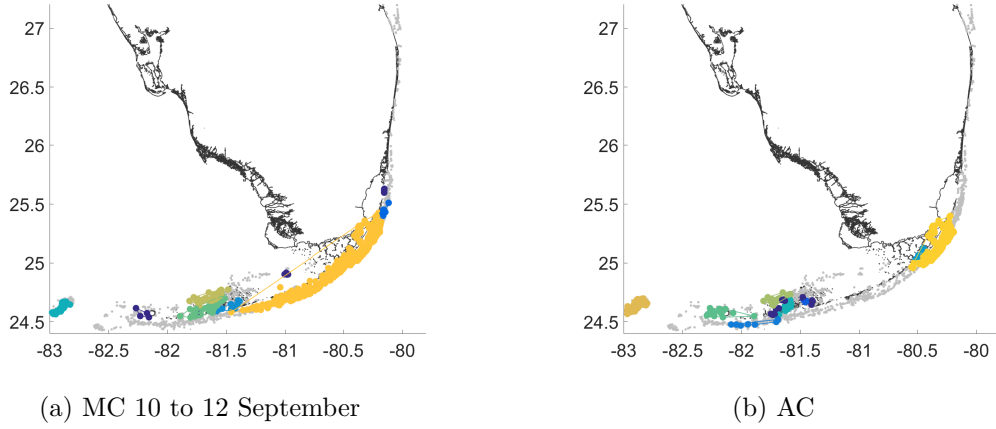


Figure 83: Comparison of the demographically significant clusters between AC and MC. AC is characterised by a shrinkage of its main cluster. This is certainly due to the exclusion of Vaca Reef from it.

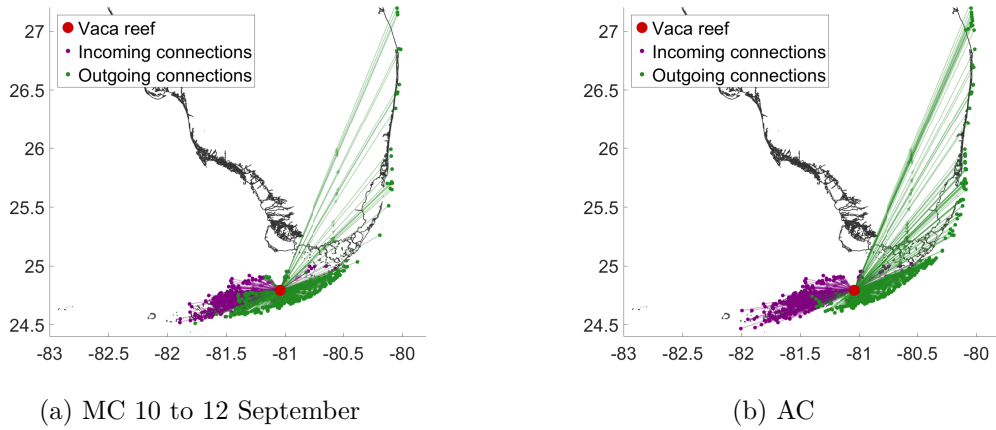


Figure 84: Comparison of the incoming and outgoing connections of Vaca Reef between AC and MC. MC counts 338 incoming connections and 346 outgoing connections. AC has less incoming connections (328), but more outgoing connections (350). Although AC has approximately as many connections as MC, it looks like Vaca Reef sees fewer outgoing connections with western reefs for AC than for MC. If the remaining connections happened to be demographically insignificant, it could explain the shrinkage of AC's main cluster observed on Fig. 83b.

5 Conclusion

In this thesis, we investigated the impact of hurricane Irma on coral connectivity in the Florida Reef Tract thanks to numerical simulations. For that purpose, we used SLIM, a hydrodynamic model using a Discontinuous Galerkin finite-element method. Besides, we used a Lagrangian particle tracker to study the larval dispersal of two coral species: *Acropora Cervicornis* (AC) and *Montastrea Cavernosa* (MC). Finally, we used graph theory tools to determine the connectivity differences between the two species and the extent of Irma's impact on their connectivity. It appeared that its influence mostly concerned westernmost reefs on the FRT. We also highlighted a positive impact on diversity for

MC larvae that were seeded simultaneously with its passage on the FRT. Eventually, our methodology could be extended to similar hurricanes crossing the FRT. Further details about the former and our results are given below.

First of all, we had to build a mesh. In order to grasp small-scale flow features along reefs with the highest precision, we built a 2D unstructured mesh with a minimal element size of 100 *m*.

We then used the 2D version of SLIM to solve the conservative shallow-water equations on our mesh. In order to take account for the strong hurricane winds, we had to switch from the usual Smith and Banke (1963) wind stress parameterisation to the one proposed by Moon et al. (2007). Moreover, we used the wetting-drying module of SLIM to cope with the strong water level variations caused by the hurricane. We ran this model from 5 August to 10 November to cover the spawning season of the two aforementioned coral species. It appeared that our model underestimated the water level rise due to the hurricane. Moreover, elevation validation, through a harmonic analysis comparing our results to mooring buoys measures, delivered rather poor results. The water velocity could not be validated with measures, but was compared to HYCOM. The simulation results seemed relevant, but they showed that our model was unable to reproduce baroclinic eddies along the FRT. Yet, these eddies are important regarding connectivity since they are able to drive larvae upstream, increasing the weight of incoming connections in the western part of the FRT. It would be worth comparing these velocity results with real observations, particularly during the hurricane.

AC spawned a month before that hurricane Irma made landfall on Cudjoe Key on 10 September at 1 p.m and on Marco Island at 7:30 p.m. At the moment of the first landfall, only 5.6 % of all AC larvae were still alive. Consequently, AC's larval dispersal was barely influenced by the hurricane. On the contrary, MC's spawning nights extended from 10 to 12 September. The dispersal of the larvae seeded on the first night was thus highly impacted by hurricane Irma whereas the larvae seeded on 12 September did not see its influence. We used the Lagrangian particle tracker of SLIM to track the dispersal of the larvae, seeded in hurricane condition or not. For each species, we ran a 60-day simulation that provided us with a square connectivity matrix giving the number of larvae involved in all connections between reefs. It appeared that Irma drove the larvae of the Dry Tortugas and of the Marquesas Keys southwestwards, off the FRT. They were then transported by the Florida Current at a high pace and sometimes eventually joined the FRT near Biscayne Bay. The hurricane also transported the larvae seeded in the northern Lower Keys northeastwards, increasing the concentration of larvae transiting through Florida Bay. Finally, Irma led to the formation of a wind-induced eddy along the FRT and to the resulting flux of larvae from the Upper Keys into the Middle Keys.

Afterwards, we used graph theory tools to better identify Irma's consequences on the connectivity in the FRT. Because of its strong winds, the hurricane produced a significant acceleration of the water currents. In general, the larvae were driven away from their origin reefs more quickly. The consequence is a global decrease in local retention and self recruitment, especially in the Dry Tortugas and in the Marquesas Keys where the coastal density is too low to hold back larvae. These larvae were sent so far away from the FRT that they hardly managed to get back to it in the vicinity of Biscayne Bay. Consequently, the settlement proportion decreased while the WCL increased. Nevertheless, it is interesting to note that AC's WCL admits higher values in the southern Dry Tortugas than MC larvae seeded before the passage of the hurricane. Since the southern Dry Tortugas have one of

the lowest settlement proportion of the FRT, we understand that the WCL will easily be influenced by the few larvae recruited far away from their origin. Béchet and Verstraeten (2018) indeed showed that the Dry Tortugas admitted one of the largest WCL variability of the FRT. Again, the low coastal density in the western reefs can not prevent the larvae from being sent away by a hurricane. Provided the hurricane passes east of the Marquesas Keys, the larvae will most likely follow the same path as MC larvae seeded before Irma, i.e. south until they meet the Florida Current. In case of a hurricane passing west of the Dry Tortugas, we can expect that the settlement proportion of the western reefs decreases much more, as the larvae would be driven northwards where no coral reefs lie. This is actually what happened in October 2017, when hurricane Nate crossed the Gulf of Mexico.

Protection and restoration measures should be taken based on several years and conditions, with and without hurricanes. The reefs that should benefit from them must act as important suppliers at some point. Our study emphasized the southern Dry Tortugas as additional reefs that might receive protection measures to resist to a hurricane similar to Irma, that is crossing the FRT in the Lower Keys from south to north and during the spawning season of a coral species. If other studies showed that similar features arose for other hurricanes with the same particular conditions or not, those reefs could thus receive protection measures, along with the northern Dry Tortugas and the inner Keys. Whether there is a hurricane similar to Irma or not, the Dry Tortugas, Vaca Reef and Key Largo should be considered as the priority reefs to restore. In fact, a hurricane comparable to Irma only increases the attention that should be affected to Key Largo. Studies investigating the impact of other hurricanes on restoration measures could be useful.

Finally, it appears that Irma is slightly beneficial for the FRT in terms of diversification. The clusters result from the superimposition of the clusters formed by each third of the seeded larvae, more or less influenced by the hurricane. Although it might destroy seeding reefs, a fast-moving hurricane would not affect the whole larval dispersal. Consequently, corals would benefit from the dispersal patterns of each spawning night and the diversity would increase. However, a hurricane impacting the FRT over a longer period than Irma, by crossing it from east to west instead of south to north for example, would affect the dispersal of all spawning nights. Corals should thus only cope with the connections enabled by such a hurricane. Some features of the network could thus not be fulfilled. For instance, there might be no settled larvae on the Dry Tortugas and the northwestern Marquesas Keys at all, with dramatic consequences for these areas. Moreover, the hurricane can act too strongly on certain parts of the network, making their bidirectional connections demographically insignificant. Furthermore, the higher fragmentation of AC's network shows that only a few reefs act as rather fragile bidirectional connections between different parts of the network. If the amount of larvae they receive or send drops for some reason, the clusters might break apart. Béchet and Verstraeten (2018) highlighted both types of network for AC, depending on the considered year. In all cases, the Dry Tortugas form their own cluster, because of their isolation. We can also find at most two main groups of clusters in the Keys: one organised around the Lower and Marquesas Keys and one in the Upper Keys.

Of course, it is important to keep our hypotheses and the limits of our model in mind when considering the obtained results. We left baroclinic processes aside on a voluntary basis, in order to model small-scale features near reefs. As mentioned before, the recirculating eddies along the FRT could actually increase incoming connections of the upstream reefs and have a significant impact on the connectivity patterns.

The effect of waves, especially during the hurricane, was also disregarded because of

time constraints. Nonetheless, the waves are expected to significantly change the hurricane-driven currents and thus connectivity results for MC larvae seeded on 10 September. Moreover, the hydrodynamics validation did not give really satisfying results regarding elevation, especially during the hurricane. More advanced investigation in that field could be useful. The comparison of velocity results with measures could also be interesting, particularly to validate the new wind stress parameterisation used in this study.

The ecological model is also quite simplified. The consideration of egg-production and post-settlement processes would definitely enhance our model. Moreover, the spatial distribution of coral species and their coral cover would have a huge impact on final connectivity results. The most striking example is Vaca Reef, the largest reef in the FRT and which is one of the most important hubs of the network, but for which the coral cover only reaches 10 % at most. We should also remember that the production density was arbitrarily determined. The present results must be analysed qualitatively and not quantitatively. Besides, the model does not consider long-distance larval exchanges with the Western Caribbean, even though the gene flow over hundreds of kilometers is rather restricted for *Acropora* and *Montastrea* coral groups (Hemond & Vollmer, 2010).

Furthermore, our model aims at determining the impact of a hurricane on the larval dispersal of coral reefs, but relies on untouched reefs. The two spawning nights following the hurricane certainly seeded way fewer larvae than the first night did. To cope with this fact, the production density of all impacted reefs could have been lower on 11 and 12 September than on 10 September, but that would have assumed that all reefs were evenly damaged by the hurricane, which is far from the reality (NOAA, 2018). Be that as it may, we can safely assume that the larvae seeded on 10 September certainly had a greater impact on MC's connectivity than what we obtained because of the damages sustained by the reefs after Irma's passage.

Last but not least, this study only focuses on one single hurricane. The conclusions that we derived were thus obtained for very particular timing, track and wind velocity field.

Beside all its limits, our model highlights several tendencies that are likely to arise with other hurricanes in the future. By taking into account hurricanes that are similar to Irma and others that are not, we could determine which connectivity features could be expected for any type of hurricane in the FRT. We could then maybe identify which connectivity properties are the most likely to develop because of increasingly more frequent hurricanes. Based on these properties, we could really determine which reefs would be worth protecting and/or restoring to resist to the hurricanes of the future. We would thus be able to enlarge the MPAs to the reefs that are the most vulnerable against hurricanes. Nevertheless, it would be worth updating the coral cover between two hurricanes events, taking destruction and recovery of the reefs into account. We can indeed expect the connectivity pattern to change with time, as some connections related to the most vulnerable reefs are likely to become insignificant. Eventually, our model could also be used to assess the connectivity of strongly different coral species and even of other living organisms like fish or crustaceans.

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Appendix A - Validation of the hydrodynamics

Validation of the elevation

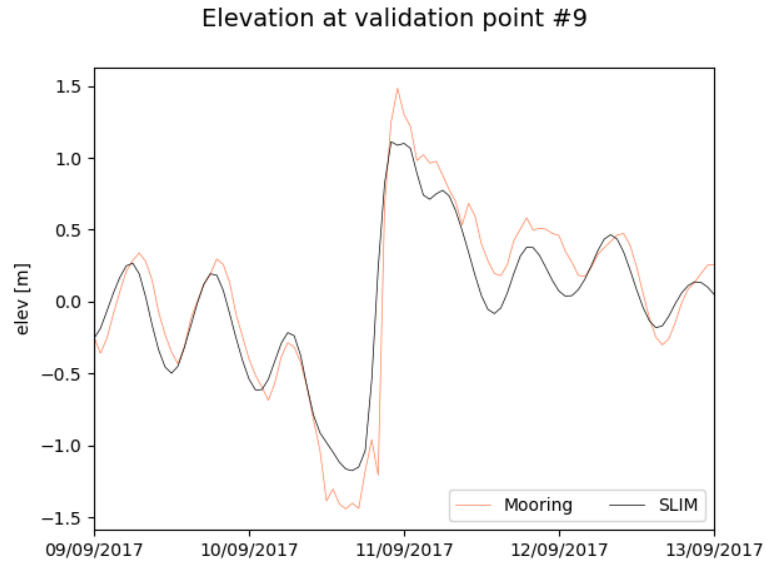


Figure 85: Comparison of the water elevation temporal evolution between SLIM and the mooring measures from 9 to 13 September at validation point 9. Like for point 11, SLIM underestimates the elevation changes due to the hurricane.

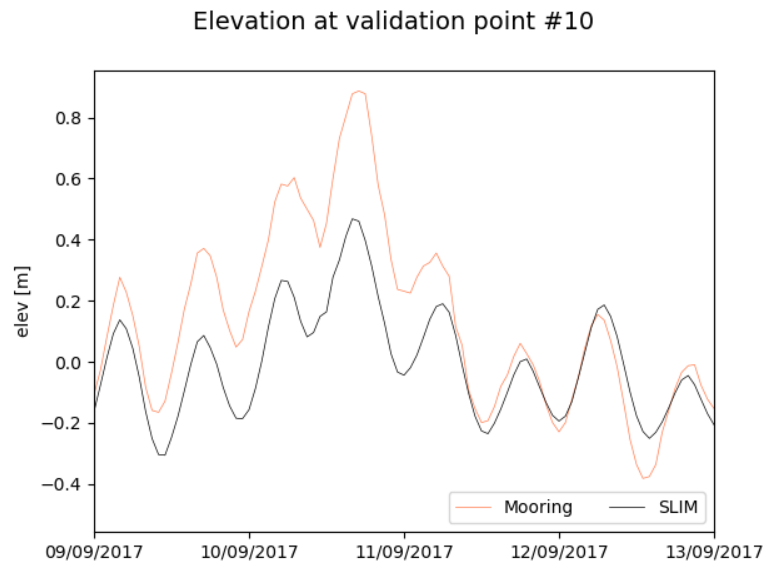


Figure 86: Comparison of the water elevation temporal evolution between SLIM and the mooring measures from 9 to 13 September at validation point 10. Like for point 11, SLIM underestimates the elevation changes due to the hurricane.

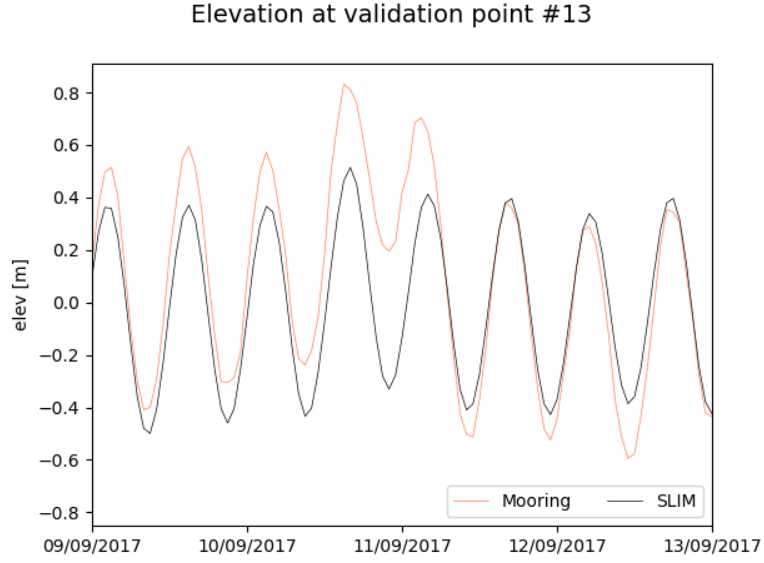


Figure 87: Comparison of the water elevation temporal evolution between SLIM and the mooring measures from 9 to 13 September at validation point 13. This point being located on the east coast of Florida, the influence of Irma is felt to a way lesser extent. The amplitude peak is inferior to the ones of the other points.

Tidal component	Amplitude [<i>cm</i>]				Phase [°]		
	Values		Errors		Values		Errors
	Measures	SLIM	Absolute	Relative [%]	Measures	SLIM	Absolute
M2	26.53	21.47	-5.06	-19.07	142.25	113.09	-29.16
O1	11.79	8.8	-2.99	-25.36	181.77	216.29	34.52
K1	9.06	5.84	-3.22	-35.54	215.06	211.96	-3.1
S2	7.51	7.03	-0.48	-6.39	180	138.15	-41.85
MSf	5.8	3.39	-2.41	-41.55	75.22	87.83	12.6
N2	5.15	4.17	-0.98	-19.03	135.51	133.435	-2.07
P1	3	1.93	-1.07	-35.67	128.7	312.07	183.37
Q1	2.29	1.71	-0.58	-25.33	261.92	270.69	8.8
K2	2.04	1.91	-0.13	-6.37	90.28	272.93	182.65
M4	1.66	0.38	-1.28	-77.11	117.82	125.33	7.51

Table 5: TAPPY harmonic analysis for validation point 9 from 12 August to 8 September. This table is limited to the 10 most predominant tidal components in terms of observation amplitude.

Tidal compo- nent	Amplitude [cm]				Phase [$^{\circ}$]		
	Values		Errors		Values		Errors
	Measures	SLIM	Absolute	Relative [%]	Measures	SLIM	Absolute
M2	17.58	15.14	-2.44	-13.88	65.68	73.42	7.73
O1	8.94	7.02	-1.92	-21.48	169.14	208.48	39.34
K1	6.83	4.53	-2.3	-33.67	185.68	209.88	24.2
MSf	4.53	1.65	-2.88	-63.58	1.43	31.42	29.99
S2	4.02	3.9	-0.12	-2.99	107.81	100.06	-7.75
N2	3.41	2.94	-0.47	-13.78	132.45	132.73	0.28
P1	2.26	1.5	-0.76	-33.63	306.48	129.12	-177.35
Q1	1.73	1.36	-0.37	-21.39	106.9	272.06	165.16
K2	1.09	1.06	-0.03	-2.75	272.42	272.28	-0.16
M4	0.72	0.06	-0.66	-91.67	249	164.6	-84.4

Table 6: TAPPY harmonic analysis for validation point 10 from 12 August to 8 September. This table is limited to the 10 most predominant tidal components in terms of observation amplitude.

Validation of the velocities

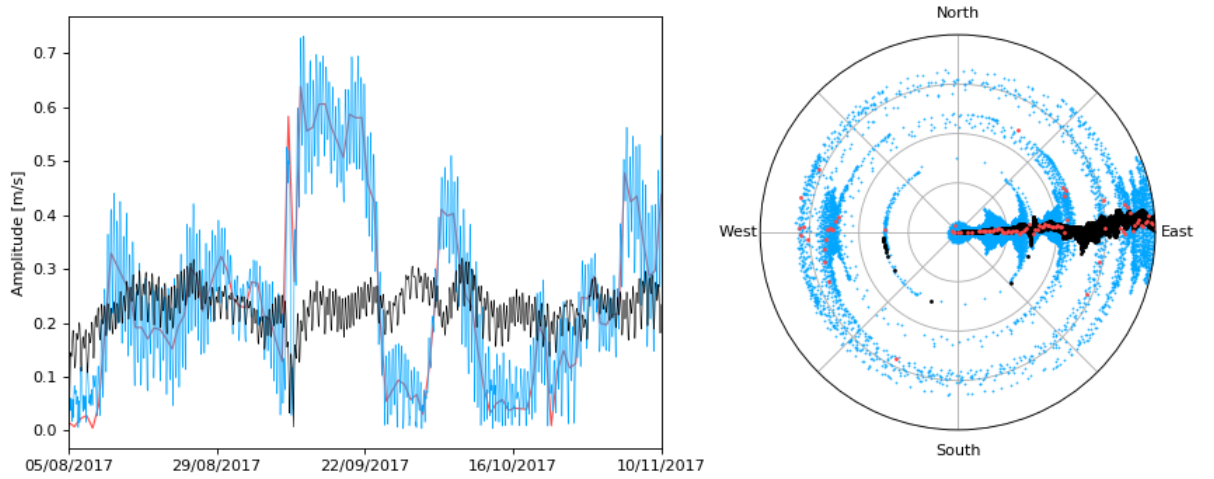


Figure 88: Left: water velocity amplitude. Right: water velocity direction. Validation point 1. The easterly directed Florida Current is well depicted by SLIM. However, it does not look to reproduce the circulating eddies.

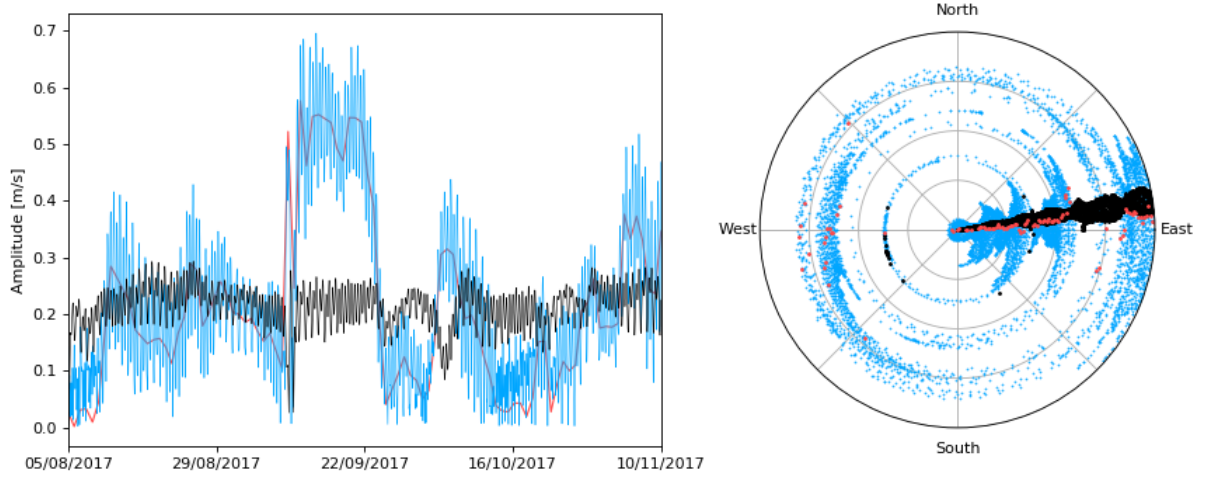


Figure 89: Left: water velocity amplitude. Right: water velocity direction. Validation point 3. The easterly directed Florida Current is well depicted by SLIM. However, it does not look to reproduce the circulating eddies.

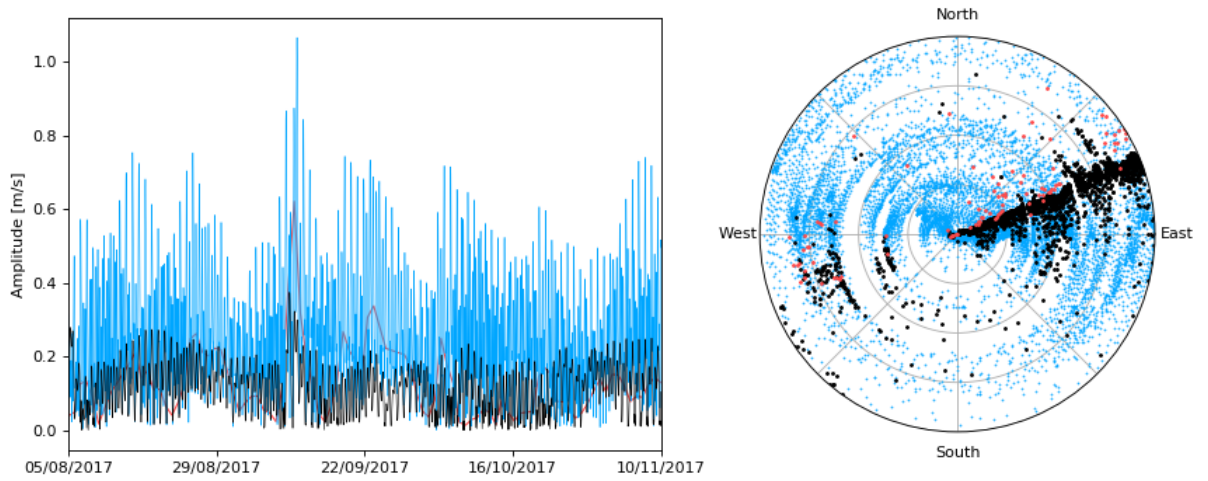


Figure 90: Left: water velocity amplitude. Right: water velocity direction. Validation point 4. The easterly directed Florida Current is well depicted by SLIM. Like for point 2, the amplitude of the tides is comparable or even superior to the residual current. Tides are thus sufficient to lead to some direction fluctuations.

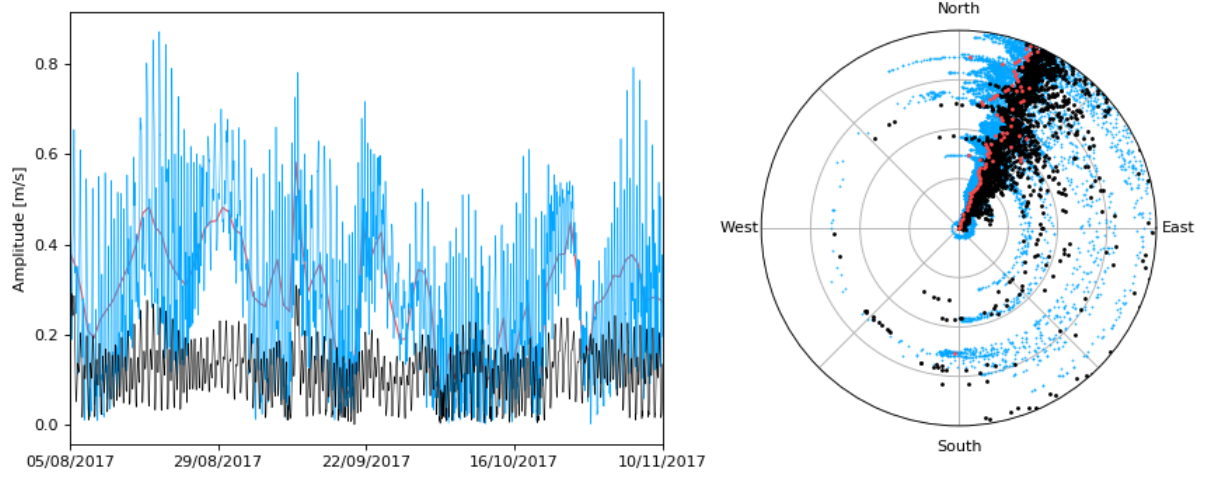


Figure 91: Left: water velocity amplitude. Right: water velocity direction. Validation point 5. The easterly directed Florida Current is well depicted by SLIM. Like for point 2, the amplitude of the tides is comparable or even superior to the residual current. Tides are thus sufficient to lead to some direction fluctuations.

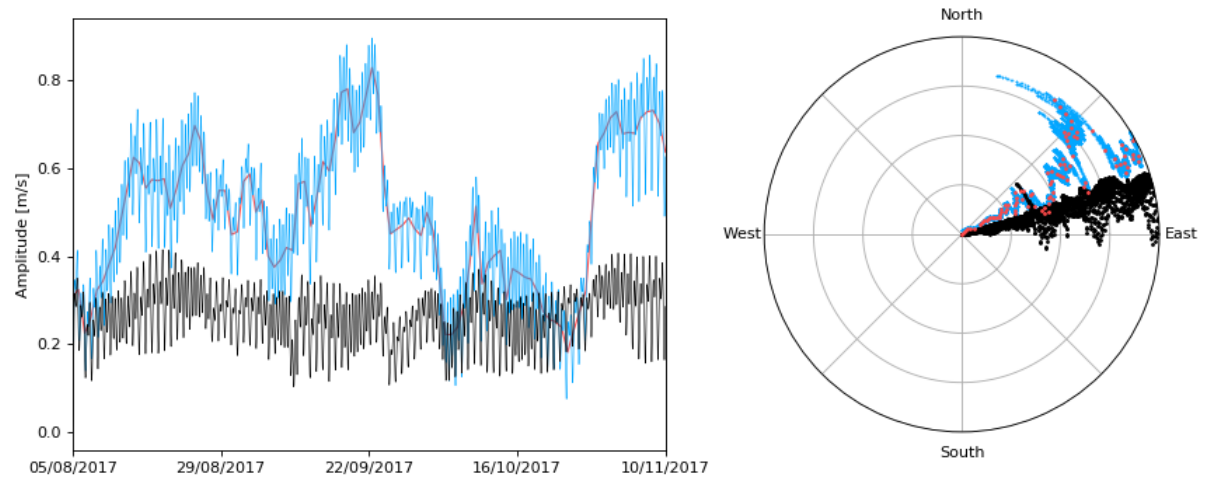


Figure 92: Left: water velocity amplitude. Right: water velocity direction. Validation point 7. Despite the rather high nudging coefficient, SLIM is not as close as we could have expected to HYCOM regarding velocity amplitude. Concerning directions, we point out a slight angle between HYCOM's tendency and SLIM's one. Eddies seem to be completely dissipated now. The currents follow almost only the Florida Current.

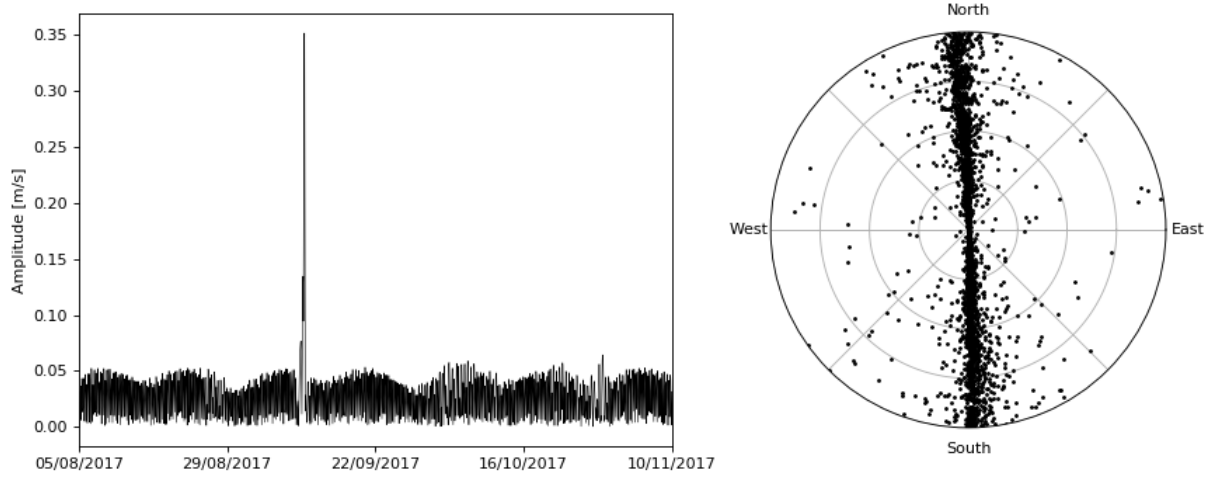


Figure 93: Left: water velocity amplitude. Right: water velocity direction. Validation point 9. Except for the hurricane period, the amplitudes are very low.

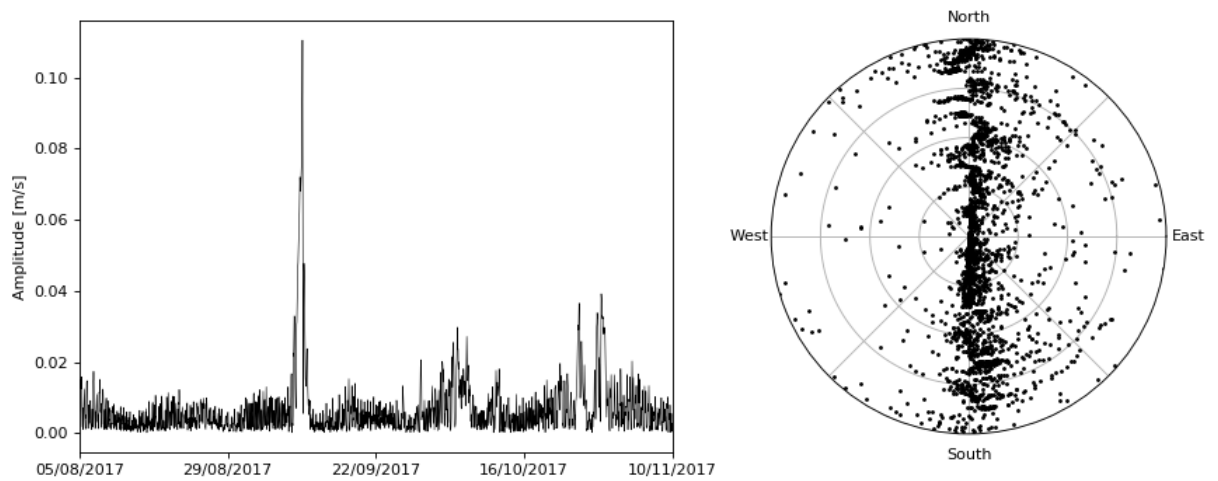


Figure 94: Left: water velocity amplitude. Right: water velocity direction. Validation point 10. Except for the hurricane period, the amplitudes are very low.

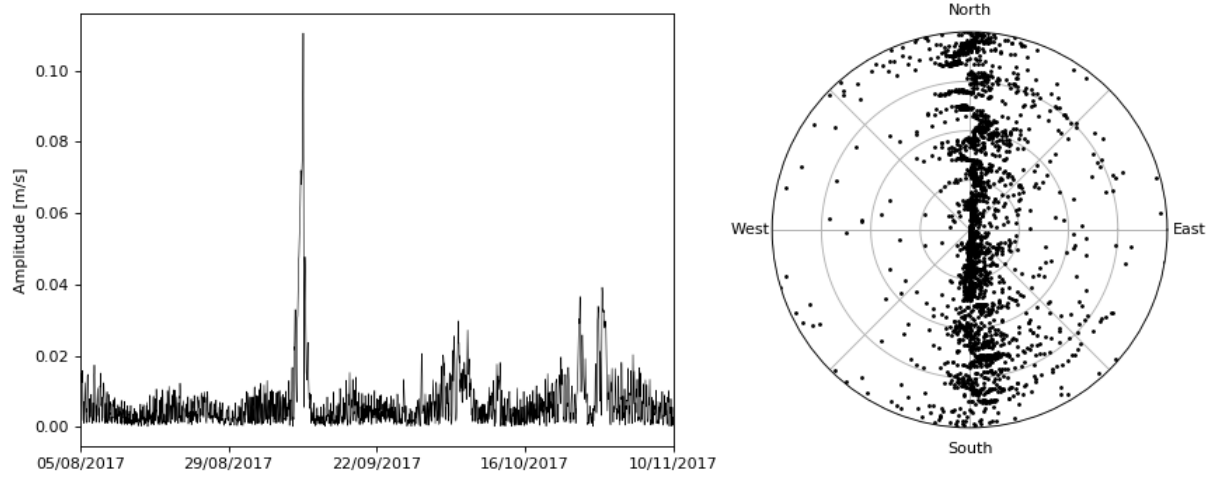


Figure 95: Left: water velocity amplitude. Right: water velocity direction. Validation point 11. Except for the hurricane period, the amplitudes are very low.

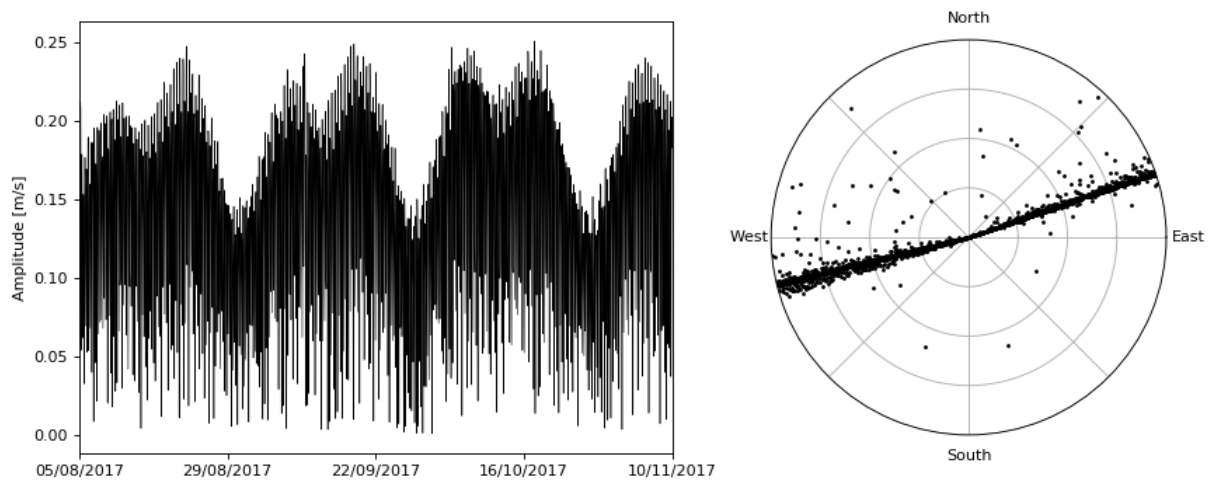


Figure 96: Left: water velocity amplitude. Right: water velocity direction. Validation point 12. The hurricane does not affect the amplitude profile.

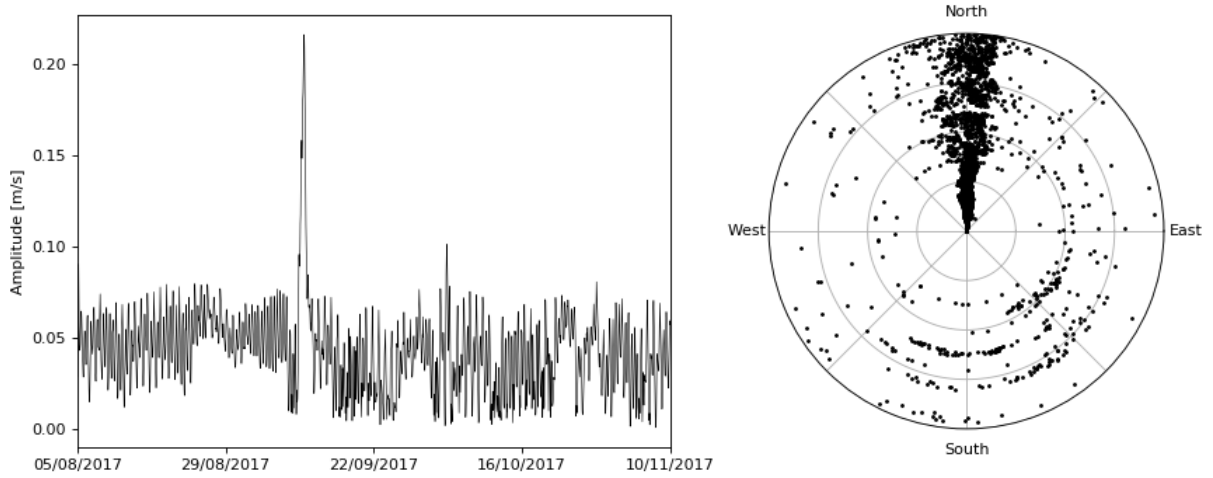


Figure 97: Left: water velocity amplitude. Right: water velocity direction. Validation point 13. Except for the hurricane period, the amplitudes are very low. The influence of the hurricane is detected, even if it was not the case in elevation. This can be explained by the very low amplitude reached anytime but during the hurricane.

Appendix B - Connectivity graphs

Differences between *M. Cavernosa* larvae seeded on 10 and 12 September

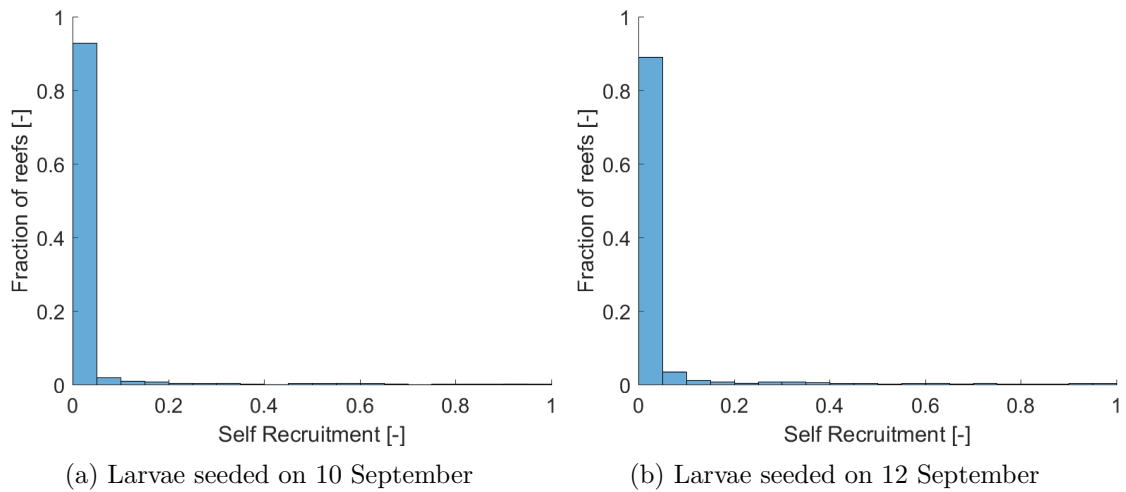


Figure 98: Comparison of the self recruitment histograms between the larvae seeded on 10 and 12 September. The vast majority of reefs has a very low self recruiting capacity.

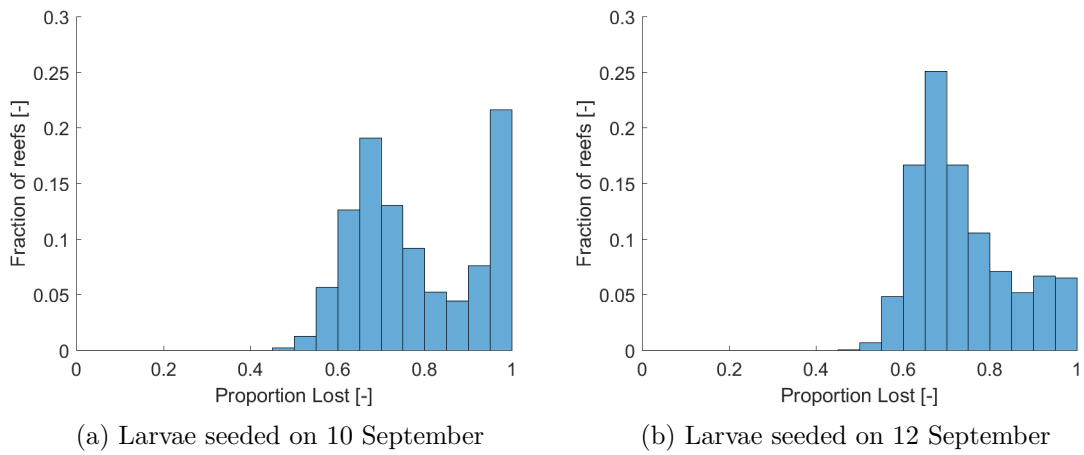


Figure 99: Comparison of the proportion of lost larvae histograms between the larvae seeded on 10 and 12 September. This histogram of course shows the same tendencies as Fig. 61, but in opposite direction.

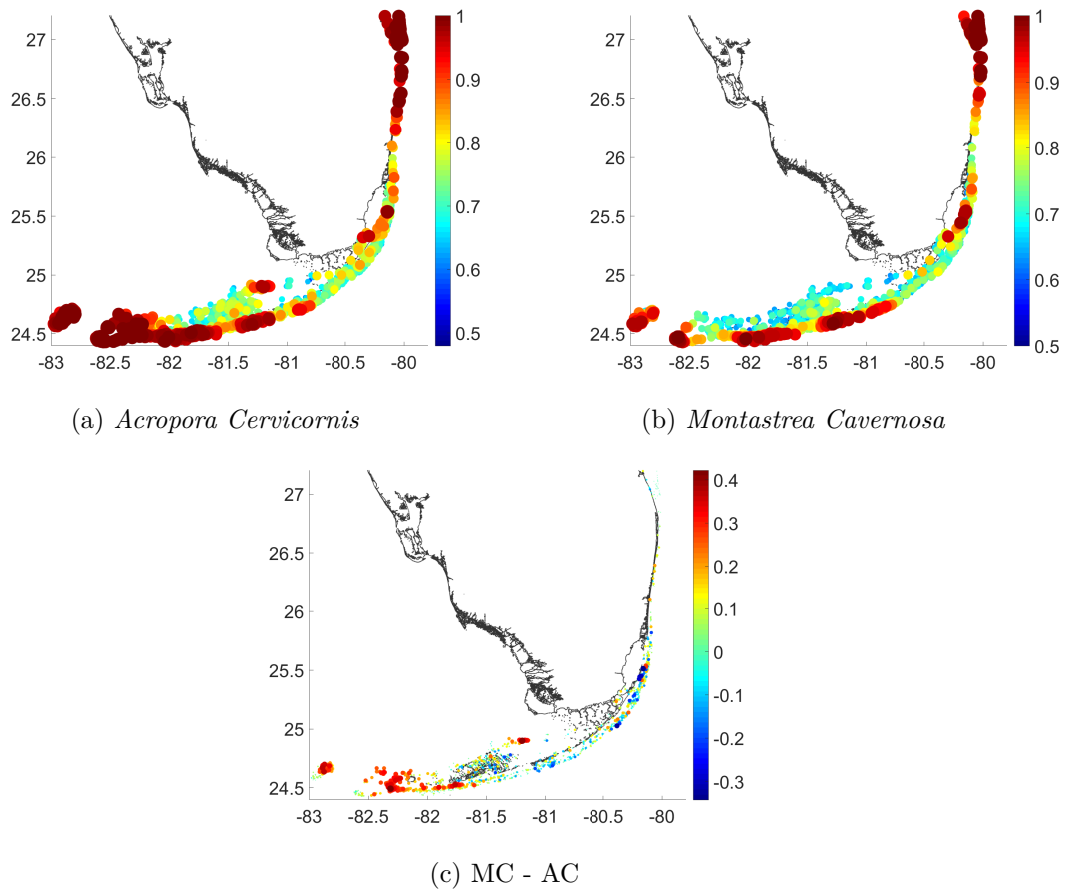


Figure 100: Comparison of the proportion of lost larvae between 10 and 12 September. Irma looks to impact it negatively in the northern Dry Tortugas, in the Marquesas Keys and in the northeastern Lower Keys, but positively in the Upper Keys.

Comparison between *A. Cervicornis* and *M. Cavernosa*

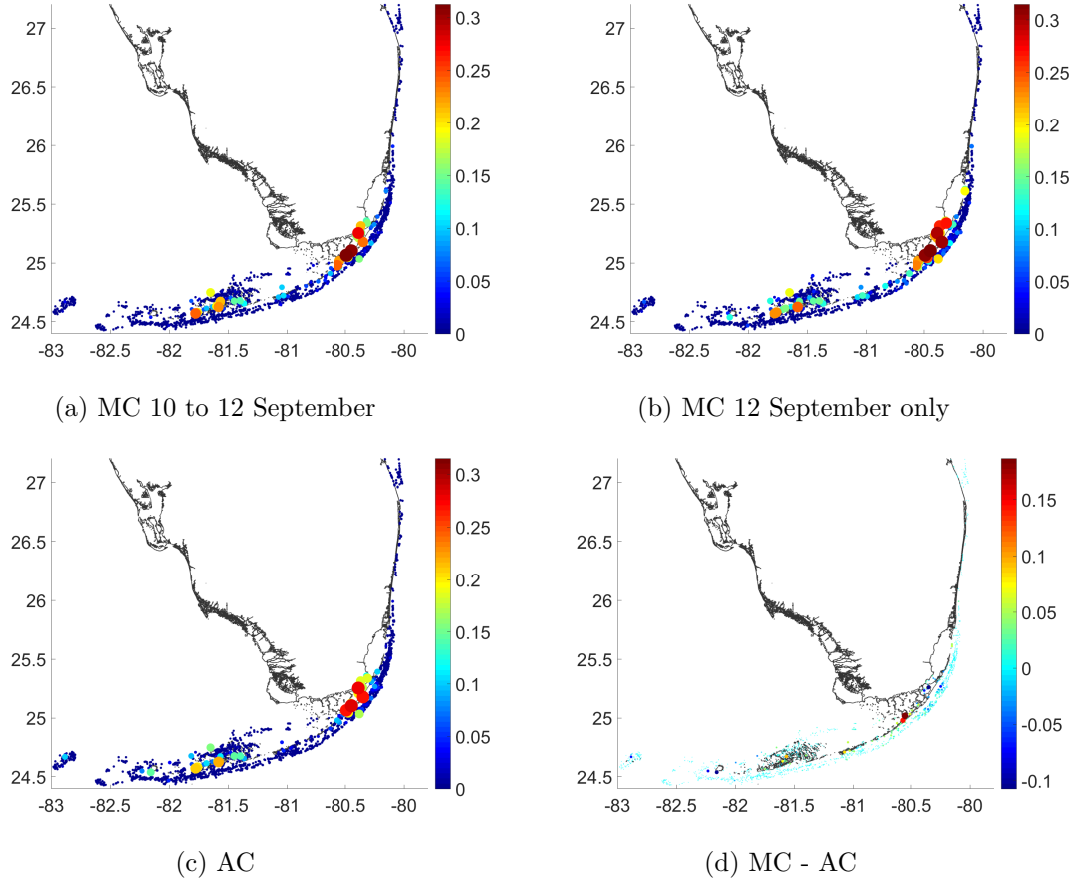


Figure 101: Comparison of the local retention between AC and MC. The negative difference in local retention in the Marquesas Keys and in the Dry Tortugas can be attributed to the hurricane, as the third night of MC has an index value similar to AC. Yet, the reason for the increase in local retention in the inner Upper Keys is more difficult to figure out.

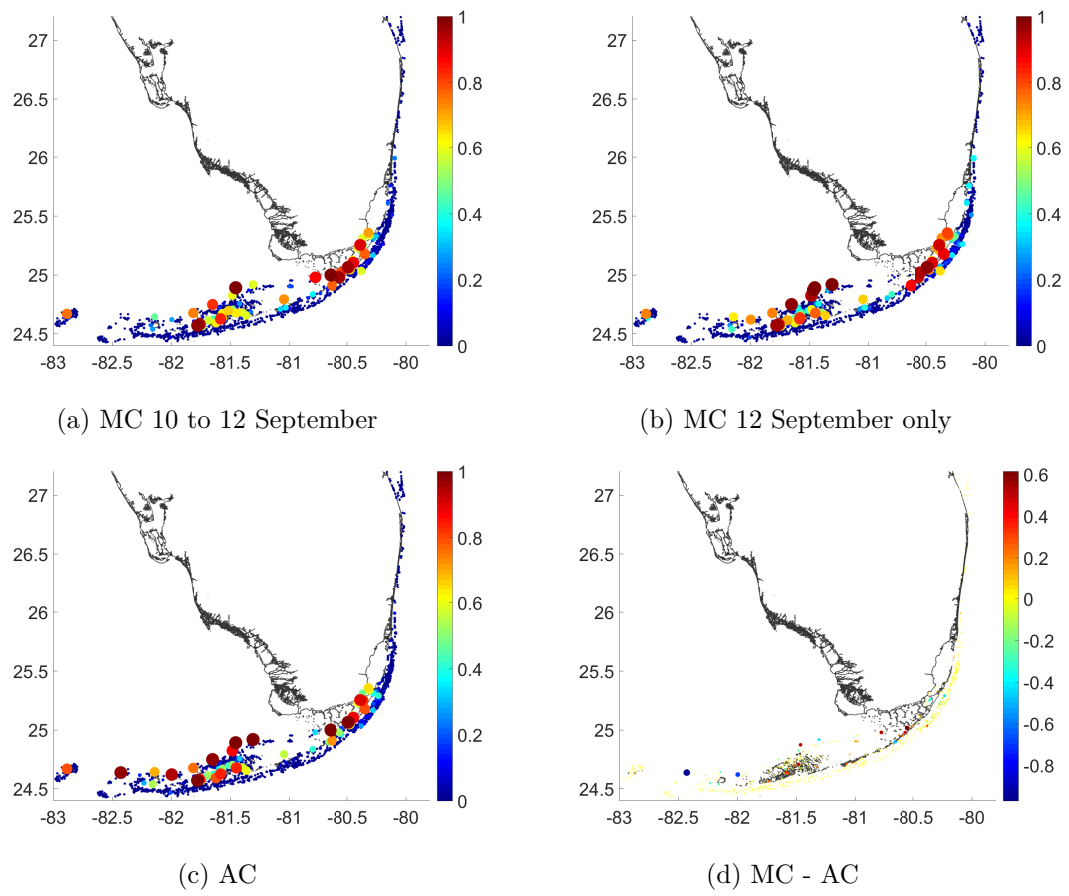


Figure 102: Comparison of the self recruitment between AC and MC. The strongest difference in self recruitment comes up in the west of the Marquesas Keys. Yet, Irma can not be blamed for this negative difference.

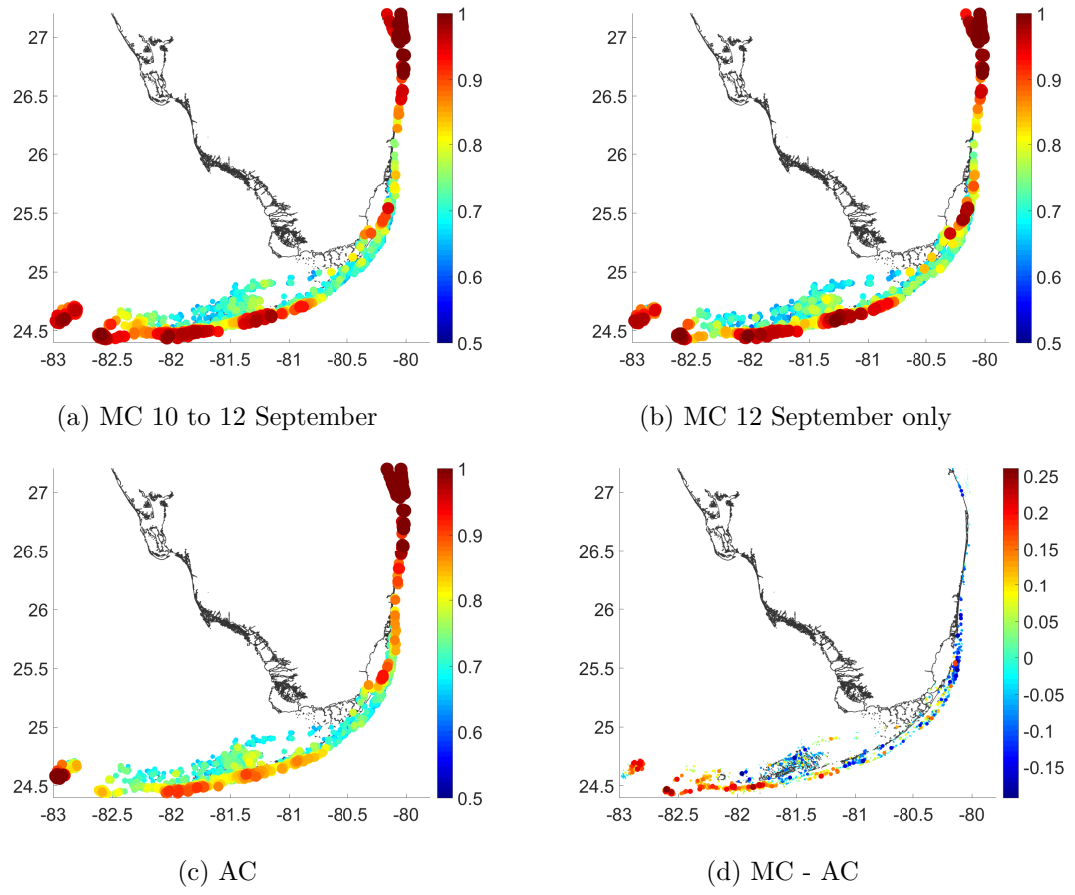


Figure 103: Comparison of the proportion of lost larvae between AC and MC.

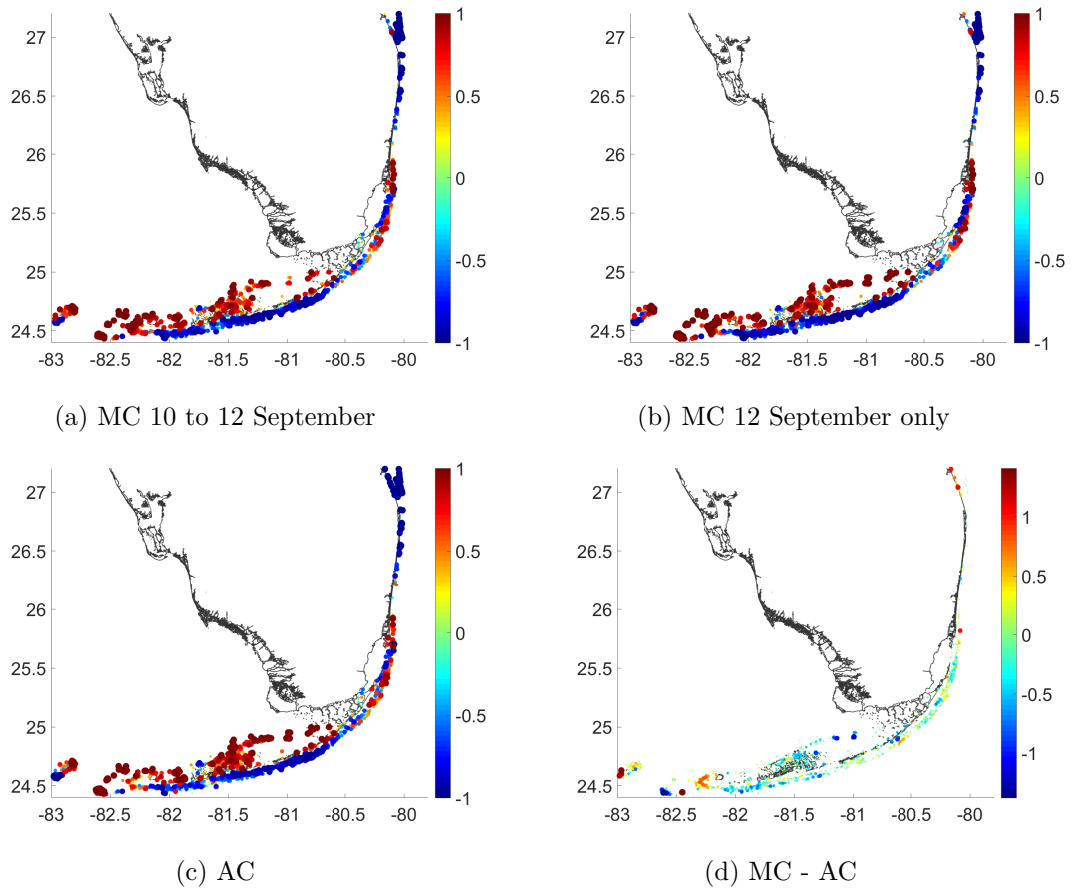


Figure 104: Comparison of the source-sink index between AC and MC. The southern Dry Tortugas turn into sources, partly because of Irma.

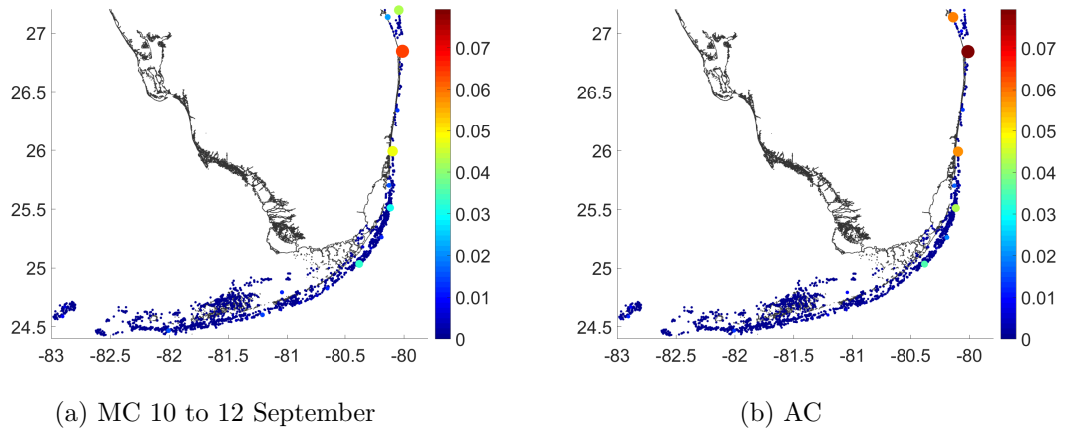
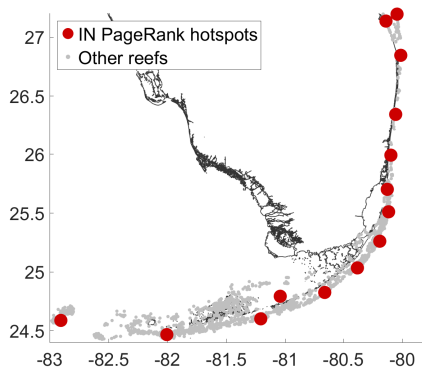
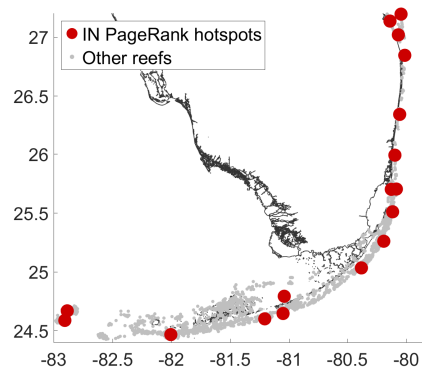


Figure 105: Comparison of the incoming PageRank between AC and MC. The two species show very close results.

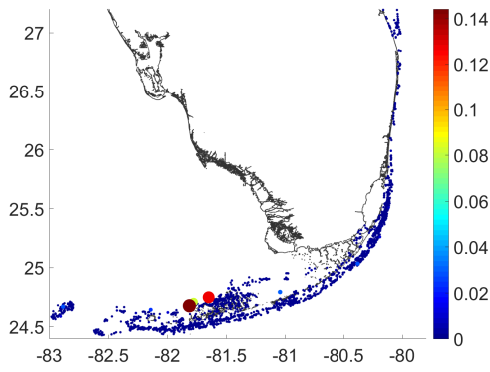


(a) MC 10 to 12 September

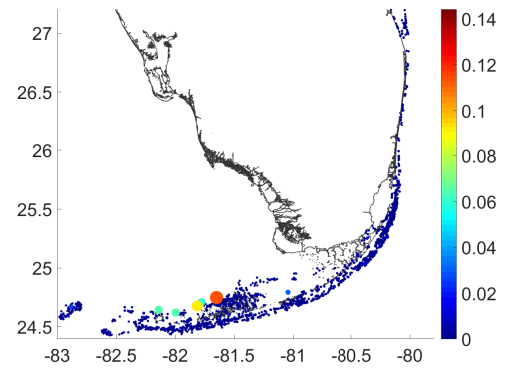


(b) AC

Figure 106: Comparison of the incoming PageRank hotspots between AC and MC. Even if the Dry Tortugas are more represented in the hotspots for AC than MC, the two species have similar results.

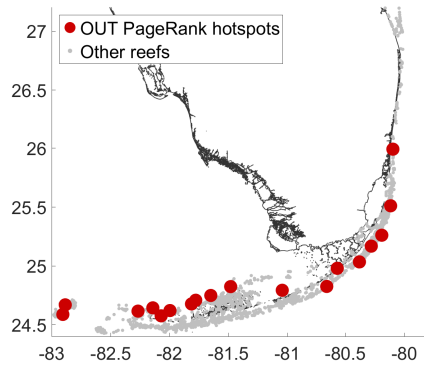


(a) MC 10 to 12 September

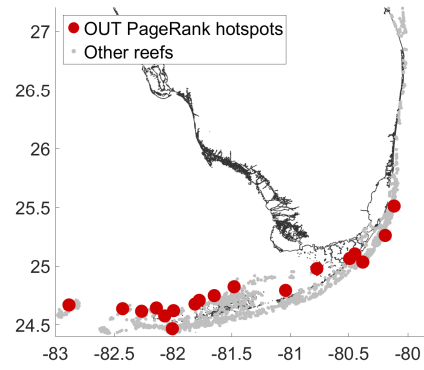


(b) AC

Figure 107: Comparison of the outgoing PageRank between AC and MC. The two species show very close results.

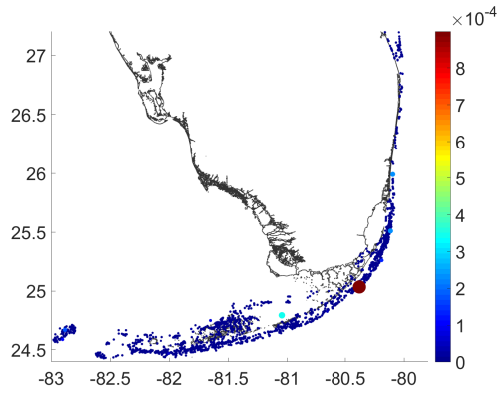


(a) MC 10 to 12 September

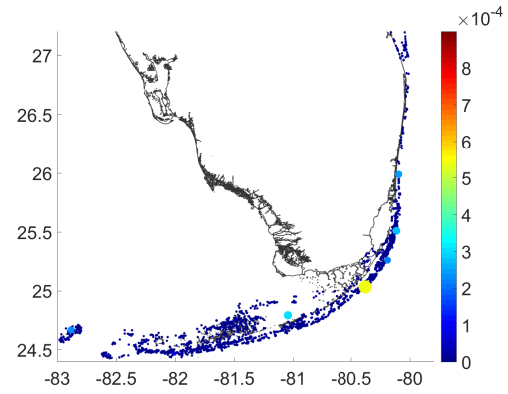


(b) AC

Figure 108: Comparison of the outgoing PageRank hotspots between AC and MC. The hotspots look very similar as well.

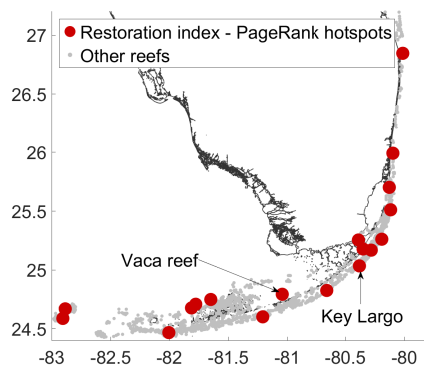


(a) MC 10 to 12 September

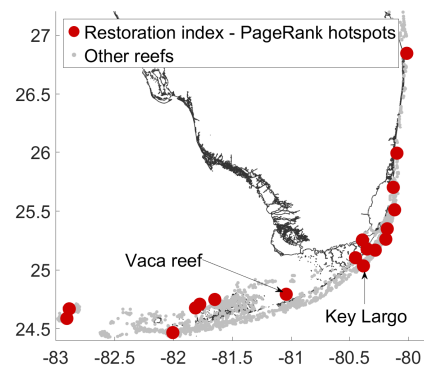


(b) AC

Figure 109: Comparison of the PageRank restoration index between AC and MC. Both species present similar results.



(a) MC 10 to 12 September



(b) AC

Figure 110: Comparison of the PageRank restoration hotspots between AC and MC. The hotspots look very similar as well.

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