

Faculté des bioingénieurs

Investigating the transmission of the Stony Coral Tissue Loss Disease among coral reefs in the United States Virgin Islands

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Abstract

Over the last eight years, the Stony Coral Tissue Loss Disease (SCTLD) has spread in the Caribbean and the Gulf of Mexico, leading to significant losses in coral cover and diversity. In the United States Virgin Islands (USVI), it has now become the greatest threat for shallow coral reefs (0 - 30m), even beyond climate change. In addition, the disease has recently been observed at low mesophotic depths (30 - 60m), thereby threatening the refuge potential of upper mesophotic coral ecosystems (UMCEs) for shallow species. However, the causative agent for this outbreak is currently unknown. Here we show how a three-dimensional high-resolution biophysical model coupled with a SIR epidemic model can characterize the potential causative agent(s) of the disease and its vector(s). Based on these findings, we assess the extent to which UMCEs are threatened by the spread of the SCTLD. We assume the disease agents to be transported within different materials (coral mucus, dead tissues, and/or suspended sediments) presenting specific buoyancy behaviors. The results of our simulations emphasize the importance of the disease vectors buoyancy on its propagation pattern. In particular, we find that the SCTLD may be transported by negatively buoyant materials referring to fine silts, and we conclude that the UMCEs are likely to be affected by the spread of the disease. Calibration of our epidemiological model with species-specific parameters gives a mean transmission time of 6.0 days, with a basic reproduction number above 1.1. This study follows a new connectivity-based approach to understand the spread of the SCTLD in the USVI, particularly between shallow coral reefs and UMCEs. More generally, this method could bring some insights into the characterization of other marine disease vectors and could provide a valuable complement to field experiments to support the management of coral disease outbreaks.

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List of acronyms

DRRH Deep Reef Refugia Hypothesis

ECMWF European Center for Medium-Range Weather Forecasts

ENSO El Niño Southern Oscillation

GEBCO General Bathymetric Chart of the Oceans

HYCOM Hybrid-Coordinate Ocean Model

IBM Individual Based Model

LPT Lagrangian Particle Tracker

MCE Mesophotic Coral Ecosystem

NAO North Atlantic Oscillation

NEMO Nucleus for European Modelling of the Ocean

NOAA NCCOS National Oceanic and Atmospheric Administration's National Centers for Coastal Ocean Science

OGCM Ocean General Circulation Model

ROMS Regional Ocean Modeling System

ROV Remotely Operated Vehicle

SCTLD Stony Coral Tissue Loss Disease

SIR Susceptible-Infectious-Recovered

SLIM Second-generation Louvain-la-Neuve Ice-Ocean Model

TCRMP Territorial Coral Reef Monitoring Program

UML Upper Mixed Layer

USCROMS United States Caribbean Regional Ocean Modeling System

USVI United States Virgin Islands

VI-CDAC Virgin Islands Coral Disease Advisory Committee

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1 Introduction

1.1 Coral reef ecosystems in peril

Of all ecosystems on Earth, coral reefs are of the most productive and biologically diverse (Moberg and Folke 1999). Warm-water corals are known to shelter about one quarter of marine biodiversity, i.e. more than 830,000 species (R. Fisher et al. 2015; Buddemeier, Kleypas, and Aronson 2004) including fishes, algae, sponges, corals, etc. Even though they cover less than 0.2% of the ocean floor (Costanza and Limburg 1997), they benefit to hundreds of millions of people for their livelihood (Moberg and Folke 1999) and provide a huge range of ecosystemic services including fisheries, cultural services (recreation and tourism), regulating services like coastal protection and provisioning services (building materials) (Woodhead et al. 2019). Estimations of their economic value have reached US\$375 billions per year throughout more than 100 countries (Moberg and Folke 1999; Hoegh-Guldberg 2004; Hoegh-Guldberg et al. 2017).

Light-dependent (or warm-water) corals are mainly found in two biological provinces: the Indo-Pacific basin, which accounts for about 85% of the world's reefs and the Atlantic basin, of which the Caribbean region is the best studied area (Buddemeier, Kleypas, and Aronson 2004). The term "coral reefs" actually refers to the association between limestone formations in tropical and subtropical regions and hard corals, also called scleratinians or reef-building corals (Kleypas, Buddemeier, and Gattuso 2001). These organisms consist of a symbiotic association between animals called polyps and single-cell microalgae called zooxanthellae (*Symbiodinium spp.*) living within the polyps' tissues. Polyps are used as a shelter and an anchor point for the microalgae that, in response, offer a part of their photosynthetic products to sustain the animal. Thanks to this hybrid combination, hard corals are able to feed as animals and to benefit from photosynthesis at the same time, thereby increasing their potential for survival. However, this property prevents warm-water coral species from colonizing deep ($>150\text{m}$) habitats where the light input is insufficient for the zooxanthellae. Indeed, most of the coral reef ecosystems that have been studied are located in shallow waters (depth $<30\text{m}$) (Menza, Kendall, and Hile 2007) and this proximity to the surface makes them particularly vulnerable to many stress factors.

The last 30-50 years have witnessed a dramatic increase in coral mortality and reef degradation, caused by both anthropogenic and natural factors (Pandolfi et al. 2003). This "coral reef crisis" has lead to a decline of about 50% of warm-water corals (National Academies of Sciences and Medicine 2019) for the past decades in tropical regions and has been well documented, especially in the Caribbean (Riegl and Dodge 2008). Pressures on coral reefs can be divided in nonclimatic and climatic stresses that are connected by synergistic interactions (Buddemeier, Kleypas, and Aronson 2004). Nonclimatic stresses are mainly linked to anthropogenic actions at local scales whereas climatic ones are related to global-scale climate changes that are most of the time an indirect consequence of human pressures on the environment (see Table 1, retrieved from Buddemeier, Kleypas, and Aronson 2004).

Table 1: Stress factors applied on coral reefs in tropical regions. * G = global, R = regional, L = local.

Stress factor	Scale*			Description
	G	R	L	
<i>Nonclimatic</i>				
Overharvesting	X	X	X	Commercial and recreational fishing.
Nutrient loading		X	X	Land use: agriculture, sewage and runoff.
Invasive species/diseases		X		Increased competition and debilitation by parasites, predators or diseases.
Sedimentation		X	X	Land use: agriculture, construction, erosion and runoff.
Coastal alteration		X	X	Alteration of circulation patterns and land-ocean coupling.
Commercial and incidental destruction		X	X	Transportation, tourism, mining and dredging.
<i>Climatic</i>				
Coral bleaching		X	X	Chronic bleaching events due to a change in ocean state variables.
Temperature increase	X	X		Transient high-temperature episodes.
Reduced calcification	X			Carbonate ion decrease due to ocean acidification.
Ocean/atmospheric circulation change		X		Specific predictions are difficult.
El Niño S.O.	X	X		Linkage to climate change uncertain; major factor in acute temperature stress.
Storm frequency and intensity increase		X	X	Major factor in land-ocean coupling.

Coral bleaching is the usual response of coral organisms following an acute stress event induced by a change in ocean state variables: temperature, light intensity, salinity, acidity and others. However, bleaching is most of the time associated to warming events. This response consists in a separation between the coral and its zooxanthellae, breaking the symbiotic association and making the white calcium carbonate skeleton appear. As a result, corals cannot benefit from photosynthesis anymore and will die within weeks if symbiosis is not restored. Even though this process remains reversible for a couple of weeks or months if better conditions are brought back, the recovering process is long and brings vulnerability to coral reef ecosystems by reducing the coral reproductive capacities, growth and disease resistance (Hoegh-Guldberg 1999). As the effects of nonclimatic factors are more and more described, protection and management measures are progressively taken by policy makers so as to mitigate the direct consequences of anthropogenic stressors at local scales. On the other hand, as climate change will increase in the next decades (IPCC 2021), local-scale thermal refugia will disappear, coral bleaching events will become more frequent and coral populations will continue to decrease, leading to a dramatic loss in effective ecosystemic services (Hoegh-Guldberg 1999; Sheppard 2003; Dixon et al. 2022).

1.2 A glimmer of hope: the deep reef refugia hypothesis

Despite the extent of the threats to coral reefs, an important discovery gives some hope to coral reef survival. Thanks to the development of Remotely Operated Vehicles (ROVs) and rebreather technologies over the past three decades, scientists have been able to dive deeper in the ocean to explore new marine habitats, and have discovered a totally new set of coral reefs, sometimes living far from the coast: the Mesophotic Coral Ecosystems (MCEs). MCEs are defined as "light-dependent corals and associated communities typically found at depths ranging from 30-40m and extending to over 150m in tropical and subtropical regions" (Puglise et al. 2009; Hinderstein et al. 2010). They are mostly populated with the same types of organisms that are typically associated with shallow coral reefs but also contain unique species, specific to their depths. As a result, they can be considered as both middle-depth extensions of coral reefs and unique ecosystems of their own. The correspondance between shallow and deeper species implies the possible existence of a vertical connectivity between shallow and mesophotic coral ecosystems. MCEs are present throughout the world (see Fig. 1), with a particularly large density in the Western Atlantic.

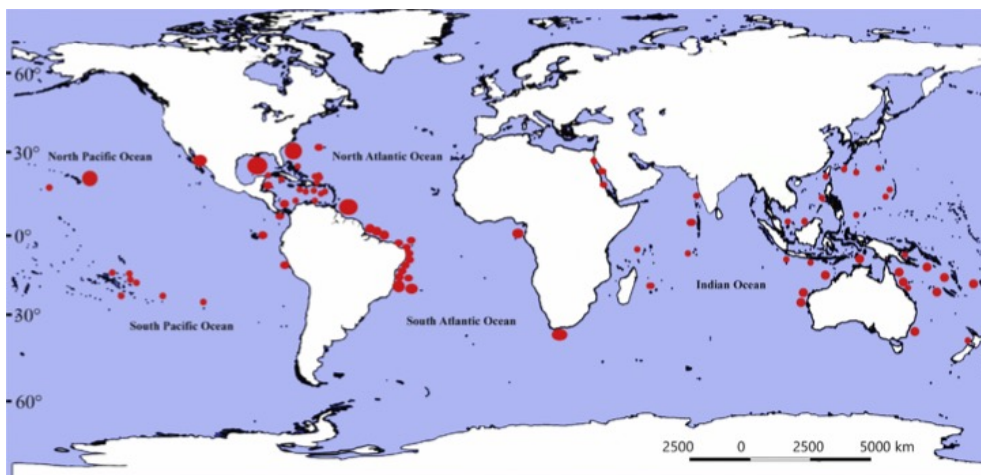


Figure 1: Mesophotic coral ecosystems (MCEs) worldwide. Circle size indicates the number of MCEs in the region. Sources: mesophotic.org, Baker et al. 2016; Turner et al. 2017; Soares, Tavares, and Carneiro 2018

Since MCEs are largely understudied compared to their shallow counterparts (Menza, Kendall, and Hile 2007), there is still little awareness of their importance among policy makers and resource managers. However, MCEs might be fundamental to tackle the rapid decrease in several shallow coral populations throughout the world. Indeed, there is a common understanding that MCEs may undergo climatic and nonclimatic disturbances in a totally different extent from shallow reefs. Due to the the vertical and sometimes horizontal distances that separate MCEs from the coast, stress factors happen to be weaker than those experienced by shallower reefs (Baker et al. 2016; Loya, Puglise, and Bridge 2019). As MCEs are located further away from the coast and at greater depth, sediment plumes dilute, physical impacts of storms are diminished, pressure from chronic coastal pollution is decreased, heat exchanges are smaller, and so on.

As a result, Glynn (1996) and Bongaerts et al. (2010) proposed the Deep Reef Refugia Hypothesis (DRRH), which states that deep reef areas:

- (1) **are protected or dampened from disturbances that affect shallow reef areas.**
- (2) **can provide a viable reproductive source for shallow reef areas following disturbance.**

Basically, the hypothesis states that MCEs could both act as a well protected genetic bank for several coral species, and serve as a consistent larval source that could help repopulate shallow reefs after major stress events. The presence of an effective connectivity inside coral metapopulations could strongly enhance their resilience and therefore, increase their chances of survival in the future.

While it is appealing, the DRRH has also been criticized. This hypothesis seems to consider MCEs as reproductive refugia that could provide larval supplies in any circumstances during the future decades. However, growing global warming might soon affect mesophotic depths as well. Mesophotic coral ecosystems are not totally protected from heatwaves and thermal stress events as they happen to show a smaller resilience to temperature increase than shallow reefs (Smith et al. 2016). As a result, even though deep habitats benefit from cooler environments, the coral species that they host may be more susceptible to temperature increase and may be impacted by thermal stress in the same way as shallow reef ecosystems. Indeed, thermal stresses can penetrate to mesophotic depths in some places in the World like in the Great Barrier Reef and in the Western and Central Pacific Islands (Frade et al. 2018; Venegas et al. 2019), implying that climate changes could be threatening all warm-water coral metapopulations, whatever their depth. This casts doubts on the ability of MCEs to thrive during future challenging periods and continue to play a role of reproductive sources.

Other arguments have been put forward and state that the reproductive capabilities of coral communities might be limited at mesophotic levels. As light inputs decrease with depth, MCEs are progressively energetically limited, which could lead to smaller growth rates and reproductive performances and could question their potential to supply larvae to other coral populations. Actually, little is yet known about reproduction rates of mesophotic corals and collecting data might display an heterogeneous pattern, as those rates could vary depending on the coral species or the study area. However, encouraging results have already been found for *Orbicelle faveolata* and *Porites astreoides* (a broadcasting and a brooding species of depth-generalist stony corals) in the US Virgin Islands, stating that mesophotic communities of those species could act as important larval sources for shallower communities, provided that vertical exchanges are viable (Holstein et al. 2015; Holstein, Smith, and Paris 2016).

Precisely with regard to vertical exchanges, another point to clarify is the existence and the scope of vertical connectivity between coral communities living at different depths. Recent studies have evaluated the potential connectivity for multiple coral species by means of statistical analyses or biophysical modelling and have found a subsidy to shallow areas by mesophotic larvae, hence confirming the DRRH (Holstein et al. 2016; Semmler, Hoot, and Reaka 2017). More

data sharing the conclusions drawn by those studies would be welcome, as vertical connectivity has so far only been assessed in very few locations. However, the current knowledge seems to be supportive of the idea that the DRRH could bring hope in the survival of shallow coral reef ecosystems. In this framework, species overlap between shallow and mesophotic communities has become an important indicator and could provide new insights into the understanding of coral resilience (Montgomery et al. 2021).

In terms of species distribution, MCEs regroup some specific coral species that cannot be found at shallow depths, and shallow reefs contain species that did not colonize greater depths (Semmler, Hoot, and Reaka 2017). This non-negligible discrepancy between shallow and deep species implies that even if more facts and data could entirely support the DRRH, mesophotic coral ecosystems would still have a limited potential to act as deep refugia. However, despite discussions regarding this hypothesis, MCEs are most important for the conservation of both shallow and mesophotic coral ecosystems and regional reef diversity (Soares et al. 2020). In addition to that, many MCEs have yet to be discovered, particularly in regions that have been understudied like in the "coral triangle" (Indonesia, Philippines, Papua New Guinea and Solomon Islands where MCEs are numerous, see Fig. 1), Polynesia, Micronesia, as well as in the large banks of the central Indian Ocean (Baker et al. 2016).

The Caribbean and the Gulf of Mexico are among the regions that have been the most documented so far and where the DRRH has begun to be assessed. Indeed, they host many mesophotic coral ecosystems (see Fig. 1). However, those areas have recently been hit by several coral disease outbreaks causing a significant decline in coral cover (Aronson and Precht 2001; Miller et al. 2009; Alvarez-Filip et al. 2019). The black and white band diseases were the first to be reported, followed by the white plague and other bacterial infections and fungal diseases like aspergillosis (Richardson and Aronson 2000). Even though these epidemics appeared to spread mainly inside shallow coral reefs, a recent outbreak called the Stony Coral Tissue Loss Disease (SCTLD) that is now considered to be the largest coral disease on record happen to be able to reach upper mesophotic coral reefs (30-60m) and could now be the greatest threat to upper MCEs survival, even before climate change (Brandt et al. 2021). Knowing that upper mesophotic corals are the ones whose species correspond the most to shallow ones, SCTLD is therefore increasingly endangering the refuge potential of mesophotic corals and the whole conservation of susceptible warm-water coral species of the Caribbean.

1.3 The stony coral tissue loss disease: a threat for shallow and mesophotic reefs

The first observations of SCTLD cases were reported near the coast of Miami-Dade county (Florida) in 2014. They were initially described as white plague as its gross morphologic features are most similar to those of SCTLD. However, the persistence, the extent of the spread and number of species affected by SCTLD are higher than for any coral disease outbreak that has been recorded to date (Meiling et al. 2021). Over the last seven years, the disease expanded

through the Floria Reef Tract and then reached the Mexican Caribbean, Jamaica, the United States Virgin Islands (USVI), the Turks and Caicos Islands and it has now spread throughout the entire Caribbean basin where it has led to dramatic loss in coral cover and diversity (Alvarez-Filip et al. 2019; Estrada-Saldívar et al. 2020; Brandt et al. 2021). During the 2015-2017 period, the progression speed was evaluated to 7-10 km per month but this figure has been reduced to 2.5 km per month since 2018 (*Case Definition* 2018).

Practically, SCTLD appears as (multi)focal areas of acute to subacute tissue loss distributed basally, peripherally or both (*Case Definition* 2018). Tissue loss generally appears on the edge of a colony (though it can begin as patches or blotches), progresses at a rate of 3-4 cm/day and is characterized by the exposition of a white intact skeleton (Fig. 2). The corresponding pathogens have not been identified clearly yet but it is likely that the infections imply several microbial community shifts with species such as *Rhodobacterales spp.* and *Rhizobiales spp.* (Meyer et al. 2019; Rosales et al. 2020). A few antibiotic treatments have been tested with kanamycin and ampicillin but have not led to consistent conclusions (*Case Definition* 2018) whereas treatments with amoxicillin seem to be a rather efficient tool for halting disease lesions on several coral species affected by SCTLD (Neely et al. 2020).

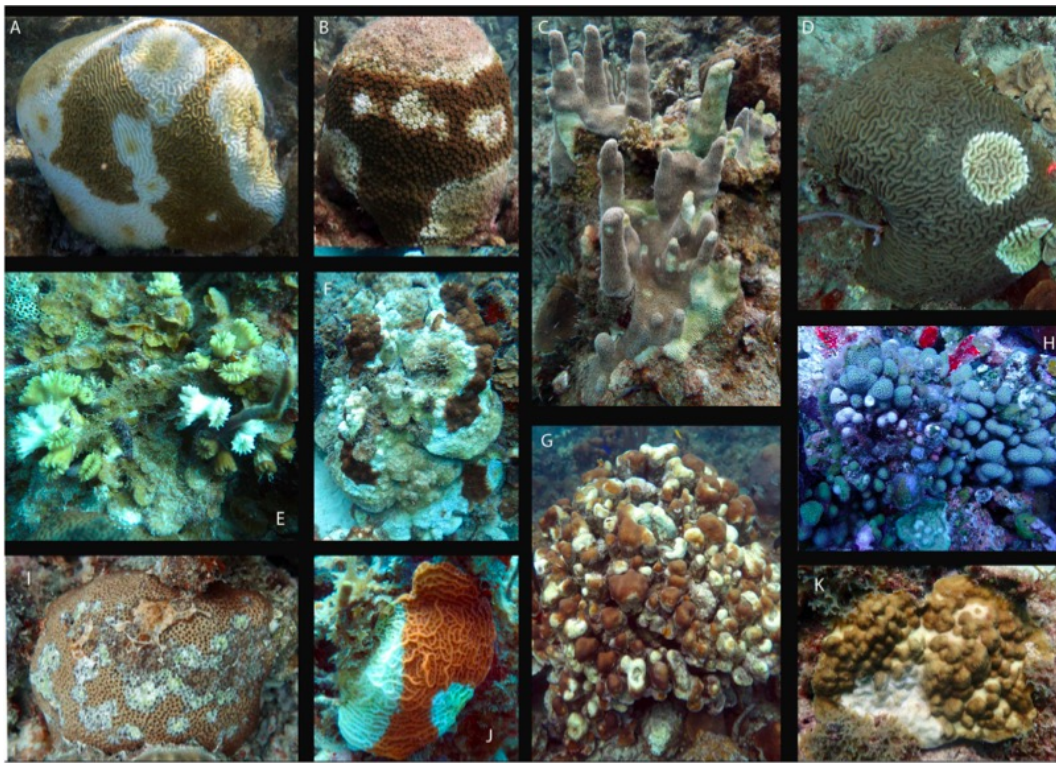


Figure 2: Images of SCTLD-affected colonies of coral multiple species. Image credits: panel (A) J. Townsend, panel (B–K) M. Brandt. Retrieved from Brandt et al. 2021.

Coral species have been categorized in 4 groups according to their susceptibility to SCTLD, which takes into account both the average duration before onset of tissue loss and the associated mortality rate. General information about this classification can be found in Table 2 where non-exhaustive examples of typical species are also given. In total, at least 23 species of scleractinian corals are affected, 8 of which are highly susceptible ones (*Case Definition* 2018).

Table 2: Categories of susceptibility to SCTLD (*Case Definition* 2018)

Category	Description	Typical species
Highly susceptible	First affected during an outbreak and total mortality within 1 week to 2 months.	<i>M. meandrites</i> , <i>D. stokesii</i> , <i>C. natans</i>
Intermediately susceptible	Affected a month after highly susceptible species. Lower numbers show disease signs.	<i>Orbicella spp.</i> <i>M. cavernosa</i>
Low susceptible	Rarely affected	<i>P. astreoides</i> , <i>P. porites</i> , <i>A. palmata</i>
Presumed susceptible	Insufficient data to be categorized	<i>Agaricia spp.</i> , <i>M. angulosa</i>

In parallel, it has been shown that SCTLD may not follow the diversity-disease hypothesis stating that high species diversity tends to show lower disease prevalence, which implies that more diverse reefs may be more vulnerable. This characteristic was validated for both epidemic (areas affected for 2-6 months where propagation is still fast) and endemic zones (areas affected for more than 9 months where disease shows signs of slowdown) and is important to understand how SCTLD can change coral structure and communities among reefs (Costa et al. 2021). In this case, coral reefs which overall structure mainly relies on highly susceptible species or on high diversity show high risk of mortality and fast degradation.

The transmission of SCTLD can be operated through direct contact or indirectly through the ocean currents, implying that water can potentially function as a disease vector (Aeby et al. 2019). As a result, water currents, more particularly in the middle layer where currents speeds are significantly smaller than at the surface (Muller et al. 2020; Dobbelaere et al. 2020), may have been a fundamental driver of the disease expansion since 2014. However, due to the recent appearance of the disease, still very few studies developed oceanic modelling efforts in order to reproduce and predict the propagation of SCTLD in the Caribbean region. Dobbelaere et al. 2020 used a coupled epidemio-hydrodynamic model in order to better understand the spread of the SCTLD through the Florida Reef Tract. This thesis aims to use a similar approach for the United States Virgin Islands (USVI).

The main reason to focus on the USVI is that they are one of the best studied area in the Caribbean region when it comes to both shallow and mesophotic coral ecosystems (Rogers et al. 2008; Turner et al. 2017). Singularly, the extent of MCEs (204 km²) exceeds by a factor of 3 the surface covered by shallow reefs (71 km²), displaying an important potential for horizontal and especially vertical exchanges. Nevertheless, this potential makes these islands a region rather vulnerable to the propagation of SCTLD, including down to mesophotic habitats.

1.4 Objectives of this thesis

This master thesis aims to investigate the transmission of the SCTLD among both shallow and mesophotic coral reefs in the USVI. The main objective is to bring an answer to the following questions:

- **How can we characterize the potential causative agent(s) of the SCTLD and its vector(s) ?**
- **To what extent are the upper mesophotic coral ecosystems of the USVI threatened by the spread of the SCTLD ?**

To answer those questions, we define intermediate milestones that allow us to build an integrated modelling sequence.

As the dispersion of the pathogen agents is mainly supported by water currents, the first step of the sequence consists in simulating the hydrodynamics in the USVI basin for the period of onset of the disease. In this framework, we use the 3D version of the ocean model SLIM.

After that, we simulate the spread of the disease vectors with different buoyancy behaviours with SLIM's transport model. The resulting potential connectivity matrices are used to study the exchanges inside the coral reef network, especially between shallow and mesophotic reefs.

Finally, we rely on a simple SIR epidemiological model to simulate the spread of the disease inside the study area. The comparison between the simulated and the observed spreads allows us to characterize the disease vector(s).

All the steps needed to achieve these goals are described in the Materials and Methods section. We then present our results and discuss their implications.

2 Materials and Methods

2.1 Area of interest: the United States Virgin Islands

In this section, a summary of geographical, physical and biological characteristics of the USVI will first be given, after which a description of the spread of SCTLD for the 2019-2021 period will be addressed.

2.1.1 Geographical, physical and biological situation

The USVI are part of the Virgin Island Archipelago and are composed of about 50 islands. The three biggest are St Thomas (91 km²), St John (54 km²) and St Croix (216 km²) (Fig. 3). The latter is located in the Caribbean Sea, about 55 km south of the former two and separated from them by the Anegada-Jungferd Passage that extends down to 4000m to form the Virgin Islands Trough (Smith et al. 2019). St Thomas and St John are located on the Puerto Rican shelf and are thereby connected to Puerto Rico and the Spanish Virgin Islands to the west and to the British Virgin Islands to the east. The Puerto Rican shelf marks the limit between the western Atlantic Ocean and the Puerto Rican Trench, whose depth reaches 8400m.

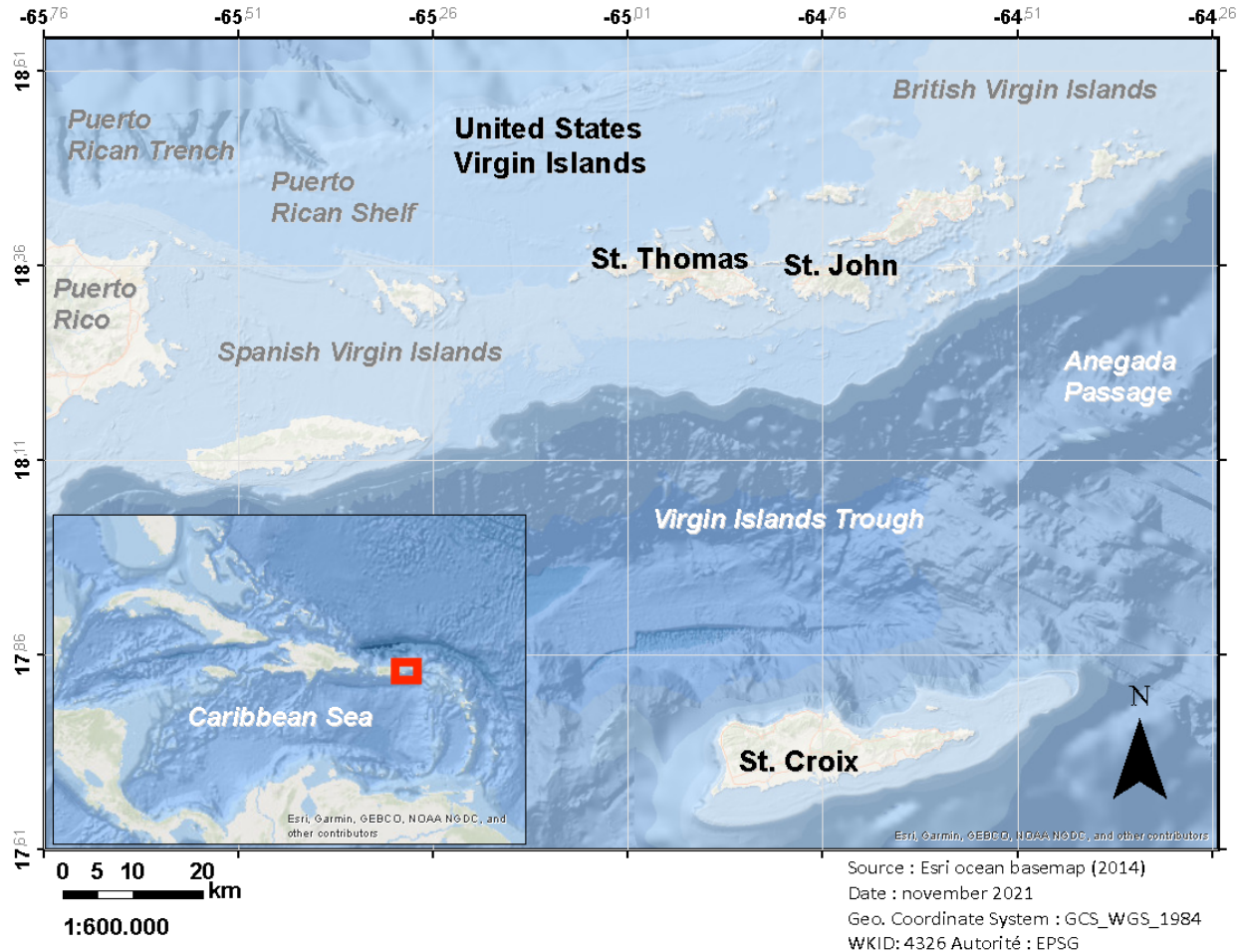


Figure 3: United States Virgin Islands and geographical environment

Speaking about their geology, the three major islands have a mountainous topography and are tectonically active, which can generate local tsunamis (Hubbard et al. 2008; Watlington 2006). However no recent volcanic activity has been recorded. The USVI present a tropical climate with weakly defined wet and dry seasons and are also strongly impacted by hurricanes and tropical storms (Chollett et al. 2012). They particularly suffered from the passage of hurricanes Hugo in 1989, Marilyn in 1995, and Irma and Maria in 2017. Even though intense periods of heavy rain often cause sediment plumes of eroded soil to extend up to several kilometers offshore, there are very few areas giving freshwater entries into the marine environment (Smith et al. 2019).

The oceanographic settings of the region can be described in two zones : surface and mesophotic-depths levels. The USVI surface waters are characterized by warm temperatures, high salinity and increased water clarity (Chollett et al. 2012). These waters show regularly changing circulation patterns according to rainfall and mesoscale eddies influenced by the extension of the Amazon and Orinoco river plumes coming from the south (Hu et al. 2004). The surface circulation is mainly northward due to the Ekman transport (Olbers, Willebrand, and Eden 2012), perpendicularly to strong easterly trade winds. In addition, the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) play the role of large-scale oceanic drivers that modify the strength and directions of the prevailing winds.

On the other hand, the mesophotic-depths waters do not always undergo the same circulation patterns, according to the depth of the Upper Mixed Layer (UML) defined as the area to the pycnocline (an abrupt seawater density change). Their physical characteristics can be similar to the ones of surface waters if the UML is deep enough to include mesophotic depths and to homogenize physical conditions with wind-induced vertical mixing. Smith et al. 2019 explain how fluctuations in the UML can impact ocean features. During the oceanographic warm season (June-November), the UML is rather shallow because of calm winds and due to the effect of riverine eddies from the Amazon and rainfall that create vertical gradients of salinity: the pycnocline is at 30-40m and surface and mesophotic layers are decoupled. During the milder season (December-May), the UML extends to 80-90m and creates rather homogeneous conditions for habitats established down to these depths. The reasons of this mixing are increased winds, salinity and turbulence, but also diminished temperatures.

MCEs in the USVI show an impressive heterogeneity in geomorphology, stony coral abundance and dominant species. The USVI marine environment is composed of horizontal banks on the insular shelf and steep slopes and walls along shelf edges (Smith et al. 2019). According to the environment type in which coral ecosystems develop, community compositions and density can vary drastically: from about 4% cover in hard bottoms to high scleractinian coral abundance (about 20%) in other habitats (Smith et al. 2016). The major coral species vary a lot with depth: star coral (*Orbicella*) are dominant in the upper mesophotic zone whereas sheet and scroll corals (*Agaricia*) are the most abundant on steep slopes from the lower levels. The intermediate zone (45-60m) often consists of low stony coral cover hard bottoms, colonized by microalgae, sponges, octocorals and antipatharians.

Since the 1970s, USVI have been an important area for research on coral reefs. Before the 1990s, this area hosted many shallow-water research studies, but there was yet little awareness of MCEs south of St Thomas and St John. Beets and Friedlander 1999 conducted habitat observations, giving the first indications that shallow-water species predominated at mesophotic depths. Subsequently, the first permanent monitoring site for MCEs was established in 2003, in the context of the Territorial Coral Reef Monitoring Program (TCRMP) at depths of 38m and 41m. Seven additional MCE sites were added between 2009 and 2011, making these islands one of the most extensively monitored MCE location globally.

2.1.2 Progression of the SCTLD through the islands

In January 2019, SCTLD was first identified in the Flat Clay monitoring location, near the coast of St Thomas. Brandt et al. 2021 studied the progression of the outbreak through the northern USVI (area around St Thomas and St John) during the 18 following months. A part of their work is summarized in Fig. 4. This figure shows the first detection dates of several monitoring locations around the two major islands. In parallel to these results, a progression map containing data up to May 2021 can be found at <https://www.vicoraldisease.org/sctld-disease-tracking> (last check on June 2022).

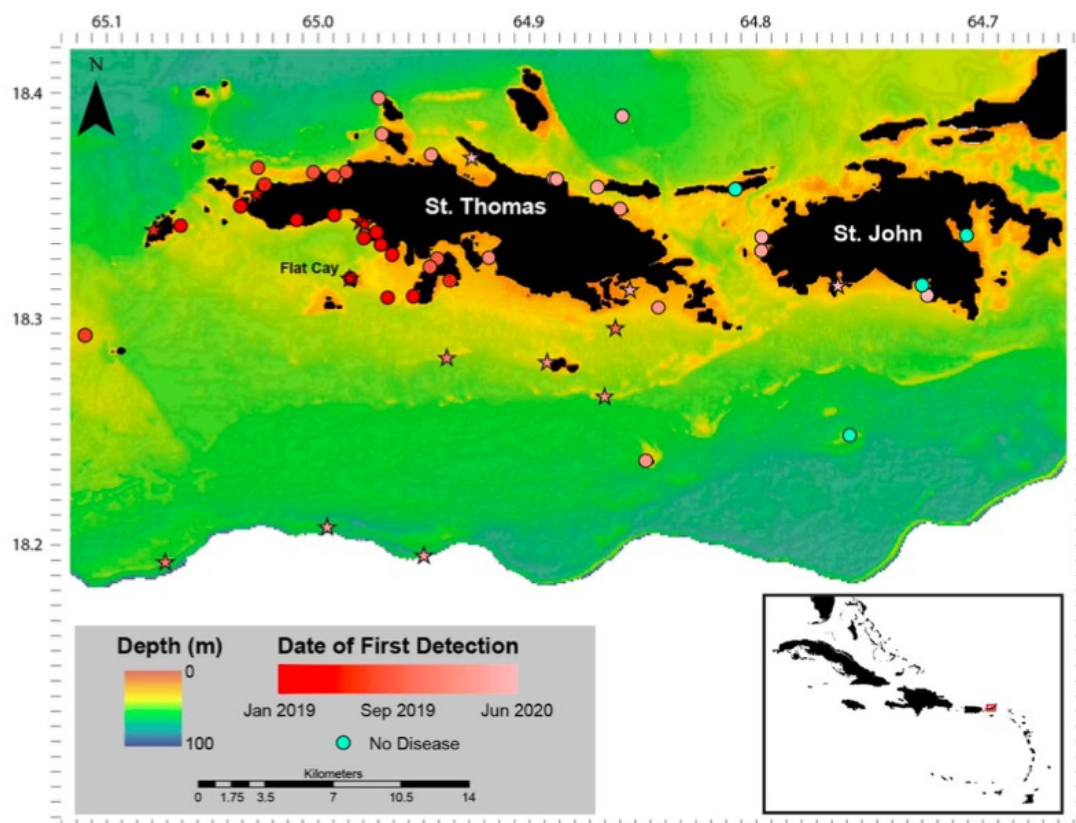


Figure 4: Sentinel monitoring locations and date of first detection of SCTLD around St Thomas and St John (U.S. Virgin Islands) between January 2019 and June 2020. Sites that are long-term monitoring locations part of the Territorial Coral Reef Monitoring Program are indicated as stars. The Flat Cay (FC) monitoring location where SCTLD was first detected is indicated with a label. Retrieved from Brandt et al. 2021.

What emerges from their work is that the spread of SCTLD around the northern USVI has been rapid and unrelenting. In contrast to many other coral diseases that have displayed a spatially or temporally limited expansion, SCTLD has not shown signs of slowdown yet and keeps emerging on new reefs. The disease's activity does not seem to follow seasonal cycles either. The extension pattern happens to be linear from reef to reef through time and from its first location of appearance near St Thomas. Even though the majority of coral reef ecosystems infected with SCTLD are found in shallow waters (<30m), observations from multiple mesophotic coral reef sites indicate that the disease is able to affect corals at depths up to at least 40m. As a result, Brandt et al. 2021 suggest that upper mesophotic reef habitats in the USVI do not represent a refuge from SCTLD.

When added to other events that have lately reduced coral cover, such as coral bleaching events, acute events (tropical storms) or chronic events (coastline developments), SCTLD presents a unique and catastrophic threat and may decimate what remains of the USVI's coral reef ecosystems. In addition, the great potential for deep refuge in the area is also threatened now that SCTLD is known to affect upper mesophotic coral reefs. In parallel, the outbreak also reached the southern island of St Croix in August 2020 (Fig. 5) and has now extended among almost all shallow coral reefs in the area. It is of the uttermost importance to produce an immediate response in order to avoid the dramatic decrease in coral diversity that has taken place in Florida (where the outbreak started). Walton, Hayes, and Gilliam 2018 evaluated the impacts to about 50% decline in coral density (95% of which concerning highly-susceptible species) and about 60% reduction in living coral tissues in this region.

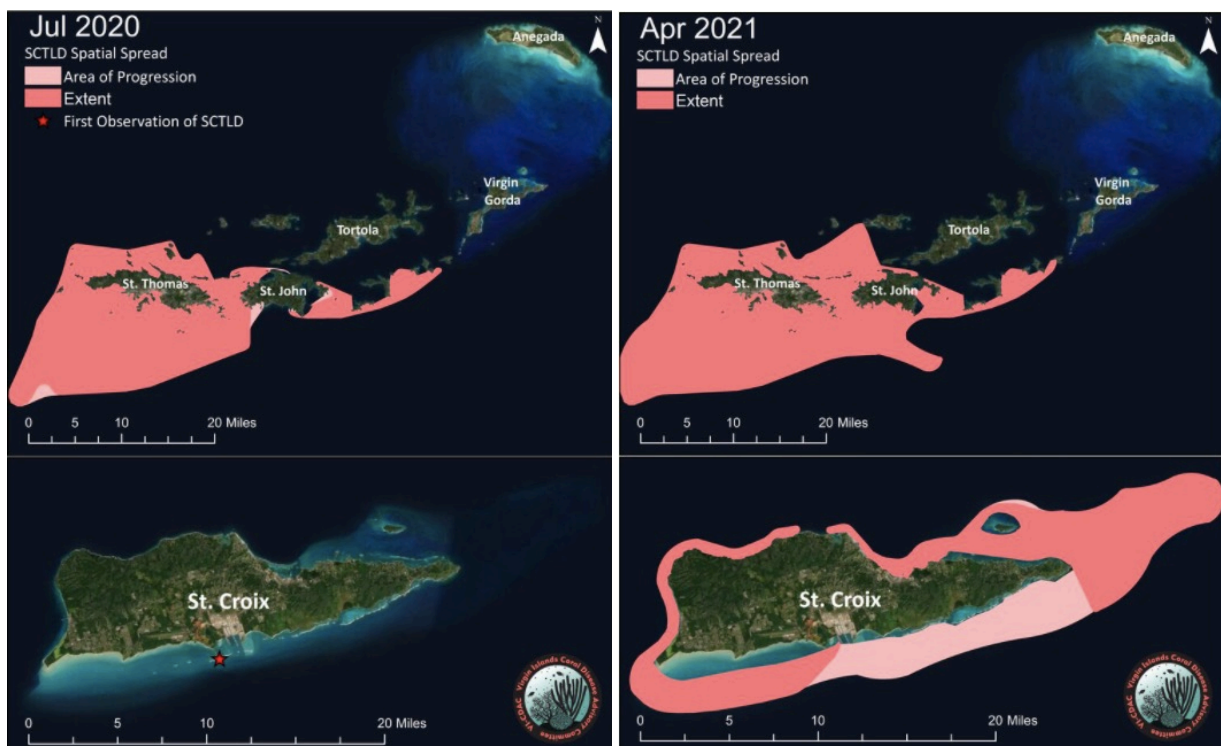


Figure 5: Tracking of the SCTLD in the northern and southern USVI between July 2020 and April 2021. Source: VI-CDAC 2022

2.2 General approach

In order to investigate the transmission of the SCTLD among both shallow and mesophotic coral reefs in the USVI, a three-step biophysical modelling approach is proposed. This sequence, along with the main tools it requires, is illustrated in Fig. 6 and is described step by step in the following sections.

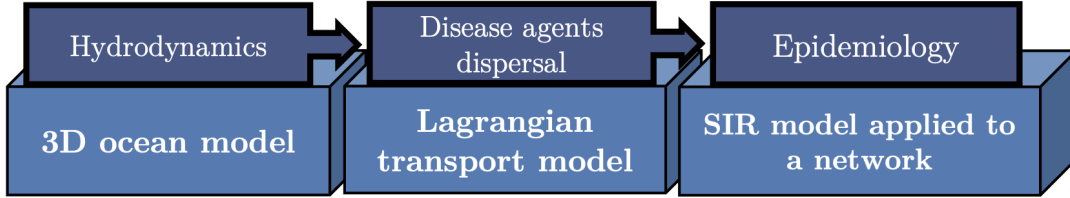


Figure 6: Modelling sequence and associated tools

First of all, we choose to set a modelling approach to address the epidemiological issue taking central stage in this master thesis. Models are commonly used in animal epidemiology as they provides a wide range of applications that cannot be handled by other means (Garner and Hamilton 2011). Modelling allows us to better understand disease processes by trying to reproduce them and by assessing the impacts of several hypotheses and parameters on the transmission patterns. It can also provide advice on risks associated with emerging threats and helps evaluate control strategies at various scales. In addition, modelling is particularly useful in situations where it is impractical to conduct experimental or field studies, as it is the case for coral disease outbreaks, especially at mesophotic depths where standard scuba diving becomes impossible. The use of epidemiological models as main decision tools remains however controversial. The management of the COVID-19 pandemic surely is the best current example of certain large economic and health failures, despite forecasting efforts involving excellent modelers and sophisticated tools (Ioannidis, Cripps, and Tanner 2022). It is also important to remember that models are just one tool for providing technical advice and that they should never be considered in isolation from field studies and experimental data. Nonetheless, many successful outbreak management programs (Ebola, influenza and smallpox for instance) have been put up in several years thanks to epidemiological modelling (Dembek, Chekol, and Wu 2018), which reinforces our decision to use this approach.

Following this choice, an upstream modelling sequence (hydrodynamics & transport model) is therefore established to provide the connectivity analysis needed to run the epidemiological model. In fact, biophysical modelling is one of the two most used approaches to study coral connectivity. Alongside many examples of modelling sequences (Lequeux et al. 2018; Gary et al. 2020; Wang et al. 2020), genetic assessment is also a very common method for this purpose (Huang et al. 2018; Studivan and Voss 2018). It is even possible to combine the two methods (Bracco et al. 2019). Nevertheless, since field sampling cannot be carried out as part of this master thesis, the modelling approach is thus preferred to the genetic assessment.

As the exchange of pathogen agents is mainly supported by water currents, the first step of the sequence thus consists in simulating the hydrodynamics in the USVI basin. Considering the steep and deep bathymetry of the region, a 3D baroclinic ocean model is therefore needed for this purpose. As a result, it is decided to use SLIM3D, the 3D baroclinic version of the multi-scale Second-generation Louvain-la-Neuve Ice-Ocean Model (SLIM). SLIM is developed at UCLouvain and relies on the Discontinuous Galerkin finite element method to solve the ocean dynamics governing equations on an unstructured mesh. This discretization allows the user to reach a very good level of detail in critical areas while compensating in other parts of the domain. In the present case, more computational resources are focused near coral habitats and near the coast, thereby providing a higher level of detail in the area where the SCTLD is spreading. The resolution is also refined in places with steep bathymetry, allowing us to deal with the complex bathymetry field of the USVI. On the vertical axis, SLIM is able to combine z and σ layers in order to reach a high resolution near the surface while properly approximating the bathymetry gradient where it is needed.

In a second step, the resulting currents are used in combination of SLIM's transport model to simulate the dispersal of the pathogen vector. The transport model is an object-based Lagrangian Particle Tracker (LPT) that is able to give its particles a specific behavior derived from life history traits and buoyancy characteristics. In the case of vectors of SCTLD agents, the virtual particles are released continuously over coral reefs during the simulated period and are considered to lose mass at a constant rate. If these particles are brought over other reefs, the amount of mass that they lose can land on these neighbouring reefs and start to infect them. The contact between coral reefs and the infectious mass is the starting point of the disease transmission process. The outputs of these simulations are connectivity matrices that can be interpreted as large graphs describing the probability of disease exchanges between reefs. They are later analyzed with graph theory algorithms and spatial metrics.

The last step of the process involves an epidemiological model relying on the connectivity matrices produced in the previous step. This model is composed of simple SIR (Susceptible - Infectious - Recovered) equations describing the evolution of sound, diseased and killed coral populations. In this model, susceptible reefs are exposed to infection through contact with the infectious mass that is lost during the dispersal of the disease agents, or through direct contact with infected reefs. These infected reefs are later killed by the disease with a given mortality rate. Different sensitivity analyses are also conducted to assess the impact of the SCTLD agents buoyancy and other model parameters on the epidemiological results.

More generally, the modelling sequence used in this master thesis aims to simulate the spread of the SCTLD as it arrives in the islands and to compare the results with field observations. This comparison allows us to characterize the disease vector(s). In addition, we assess the potential for upper MCEs to be reached by pathogen agents by studying the connectivity inside the coral reef network, especially between shallow and mesophotic reefs.

2.3 Study area

In the scope of this master thesis, the study area only includes the southern part of the USVI and is therefore mainly focused on the island of St Croix. Two main reasons can be pointed out for this spatial restriction. First, the presence of the Virgin islands Trough south of the Puerto Rican shelf (see Fig. 7) and the steep bathymetry surrounding the islands make it a particularly complex region over which modelling calls for substantial computational and time resources that exceed those at our disposal. In addition, as the SCTLD has already reached both sub-regions at the time of writing, the investigation of the exchanges of disease agents inside each of them appears to have priority over the study of the exchanges between these areas. Given the distance between them, it seems reasonable to study each sub-region separately. The second reason is that the spread of the SCTLD near St Croix has been less studied than around St Thomas and St John, where the disease is now considered as endemic and where signs of its passage are ubiquitous. Several recent studies (Brandt et al. 2021; Costa et al. 2021) have indeed focused on the northern part of the islands, not only because it witnessed the first infection cases in the USVI, but also because it contains more monitoring facilities and because the steep slopes of the coast of St Croix make field sampling rather impractical. As mentioned earlier, modelling can be particularly useful in situations where experimental investigations are harder to conduct. The present biophysical modelling approach is thus rather well adapted for the case of the southern USVI and could help bring more insights on the dispersal processes acting in this region.

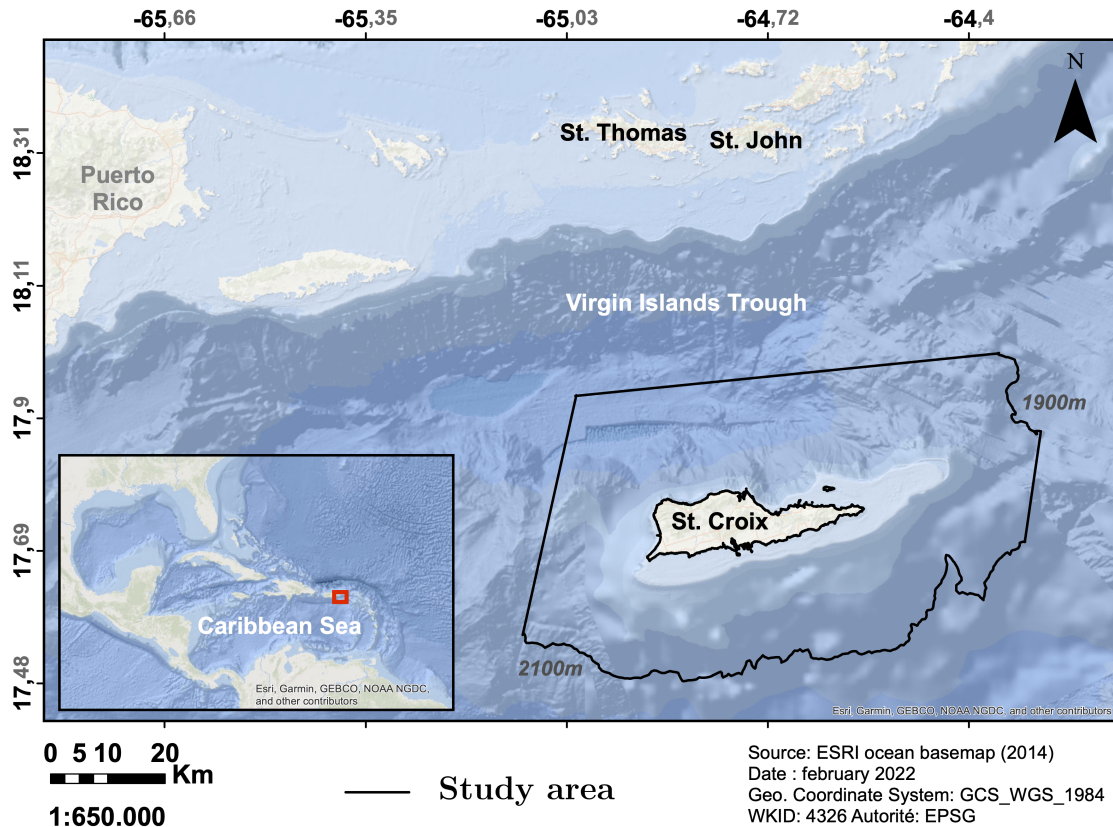


Figure 7: Area of study and boundaries of the computational domain ($\sim 3700\text{km}^2$ land included)

The outer limits of the domain are defined by two isobaths (1900m and 2100m depth in the east and south respectively, see Fig. 7) and 3 straight lines that are drawn through the open ocean. A distance of minimum 20km to the coast is ensured at every point of the borders to avoid too much dependence of the simulated currents on boundary conditions. The model covers an area of about 3700 km², land included. Coastlines are provided by OpenStreetMap¹.

As an exhaustive inventory of coral reefs in the area is virtually impossible to obtain, a coral habitat map is produced based on estimates of different seabed categories, retrieved from the National Oceanic and Atmospheric Administration's National Centers for Coastal Ocean Science (NOAA NCCOS)². Four benthic habitats are then regrouped into one reef extent of 45.82 km²: hardbottoms, aggregate reefs, patch reefs and scattered corals & rocks. In order to better reproduce the propagation of the infection front inside the broadest reefs, the habitat map is divided into 450 × 450m square sub-reefs (Fig. 8). A filter is then applied to only keep sub-reefs that are larger than the minimal resolution of the hydrodynamics model (see section 2.4.2). As a result, sub-reefs with a surface area smaller than 0.02 km² (corresponding to ~140m squares) are discarded. Finally, each sub-reef is associated to a given depth based on the vertical position of its centroid (more information about the bathymetry used is given in section 2.4.2). Sub-reefs with centroids located below 150m depth are then discarded as well. This last step allows us to remove habitats which would not be suitable for MCEs. In total, of the 547 sub-reefs composing the coral habitat map, 446 are located in shallow waters (0 - 30m depth) and 101 are mesophotic (30 - 150m depth). The corresponding distribution is represented in Fig. 9.

Several values have actually been tested for the size of the square sub-reefs, as well as for the filter applied afterwards. The present values (450m - 0.02 km²) were kept because they allowed us to keep a good level of representativeness of all the covered areas around St Croix. As a matter of fact, other combinations of values would (partially) remove certain patches of reefs that should be represented in the final coral habitat map. It was also necessary to use a filter that corresponded to the resolution of the hydrodynamics model in order to avoid omitting certain sub-reefs in the particles dispersal simulations.

A few assumptions directly emerge from the use of this coral habitat map:

- All sub-reefs ranging from 0 to 150m depth are populated by corals. This implies a certain continuity in coral populations along the vertical axis, which may overestimate connectivity pathways between shallow and mesophotic reefs and thus disease dispersal. It can be noted that the vertical extent of each sub-reef is not only defined by the position of its centroid, but also by the bathymetry below the extent of each square.
- Coral cover is homogeneous over the entire area. Again, this assumption may result in overestimations of the horizontal connectivity between reefs and of disease dispersal. Higher coral density involves higher probabilities of (in)direct contacts and thus higher infection rates.

¹<https://osmdata.openstreetmap.de/data/coastlines.html>

²<https://coastalscience.noaa.gov/project/benthic-habitat-mapping-puerto-rico-virgin-islands>

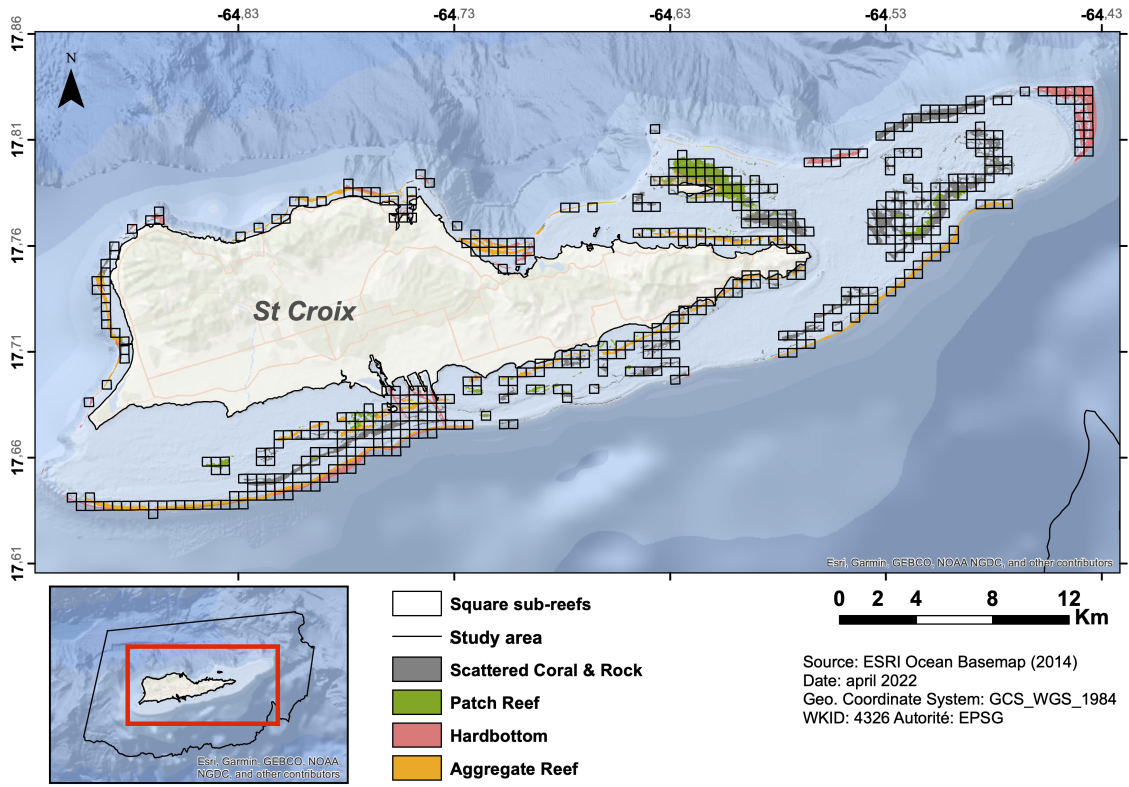


Figure 8: Coral habitats around St Croix and their division on $450 \times 450\text{m}$ sub-reefs. Habitats defined here are composed of hard bottoms, patch and aggregate reefs, as well as scattered corals and rocks.

- Spatial variability linked to species distribution is not taken into account. The presence of species that are more or less susceptible to infection is thus not specified in this approach.

The global consequences of such assumptions are that we can only claim to compute a potential coral connectivity that may be higher than that observed on the field, even though the distribution of susceptibilities to SCTLD is not identified and could play a non-negligible role in the disease propagation rate. This will be later discussed in section 4.

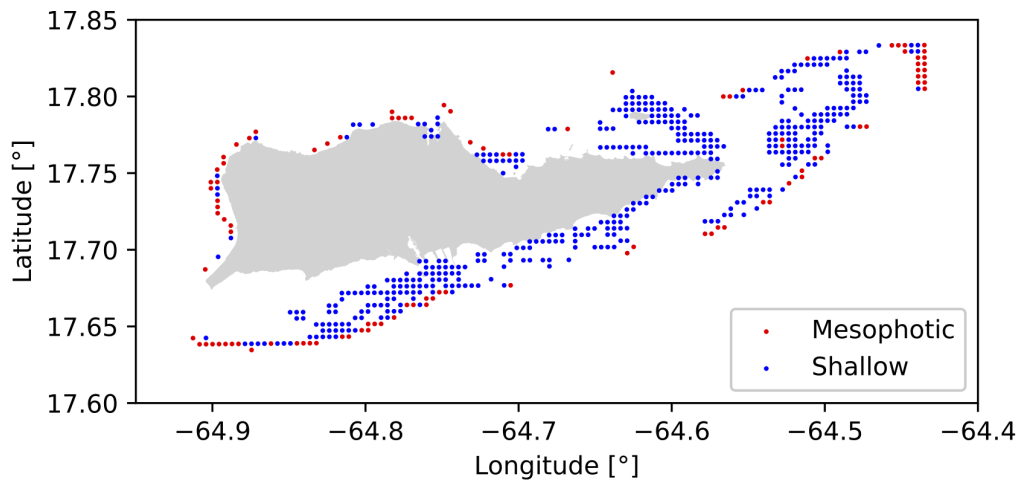


Figure 9: Distribution of shallow (0 - 30m depth) and mesophotic (30 - 150m depth) sub-reefs in the study area. Out of 547 sub-reefs, 446 are shallow and 101 are mesophotic.

2.4 Hydrodynamics

As mentioned before, the hydrodynamics in the area of interest are simulated thanks to the 3D baroclinic version of the Second-generation Louvain-la-Neuve Ice-Ocean Model (SLIM3D, <https://www.slim-ocean.be/index.php/slim3d/>). Ocean currents, as well as other variables such as temperature, salinity and surface elevation are computed by solving the ocean circulation governing equations under the hydrostatic and Boussinesq approximations on an unstructured mesh. The present subsection is based on the work of Vallaeys 2018 and describes the mathematical model that is used, along with its numerical implementation. Forcing with the outputs of a Regional Ocean Modeling System (ROMS) model and validation process for the hydrodynamic simulations are detailed hereafter.

2.4.1 Mathematical model

Domain

The domain on which the three-dimensional hydrostatic equations are applied is denoted as Ω . It is defined by three coordinates: x and y represent the horizontal dimensions of a local planar projection of the Earth's surface (such as UTM), while z is the vertical coordinate of the position vector $\mathbf{x}$ (see Fig. 10). The domain is limited by three types of boundaries: the fixed lateral boundaries (Γ_l), the bottom boundary (Γ_b) and the moving top surface boundary (Γ_s). Lateral boundaries can either be closed if they correspond to the coastline, or open if they are located in the ocean. The bottom boundary Γ_b corresponds to the seafloor, i.e. $z = -h(x, y)$, where $h(x, y)$ is the bathymetry. Finally, The top boundary Γ_s corresponds to the time dependent free surface height ($z = \eta(t, x, y)$) defined with respect to a reference surface layer $\Gamma_{s,0}$ ($\eta = 0$) corresponding to a sea at rest. The total water depth is $H(t, x, y) = h(x, y) + \eta(t, x, y)$.

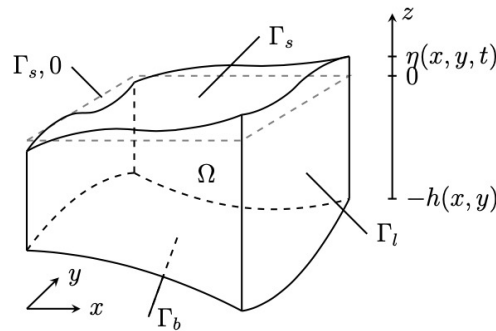


Figure 10: Sketch of the 3D domain Ω defined by its boundaries Γ . The top surface Γ_s is the only moving boundary. Source: Delandmeter 2017.

Model assumptions

Two main assumptions are included in the mathematical model: the hydrostatic hypothesis and the Boussinesq approximation. The former states that the gravitational force that is

applied on a fluid is compensated by the vertical component of the pressure gradient force in experiments. In other terms, the weight of the water column laying above is balanced by the upward force resulting from the difference of pressure this water column generates. The Navier-Stokes vertical momentum conservation equation therefore reduces to:

$$\frac{\partial p}{\partial z} = -\rho g, \quad (2.1)$$

where $p(t, x, y, z)$ is the pressure [$N.m^{-2}$], g is the mean Earth gravitational acceleration [$m.s^{-2}$] and $\rho(t, x, y, z)$ is the density [$kg.m^{-3}$]. When integrating from z to η , it yields:

$$\begin{aligned} p &= p_a + \int_z^\eta \rho g \, dz, \\ &= p_a + g\rho_0(\eta - z) + g \int_z^\eta (\rho - \rho_0) \, dz, \end{aligned} \quad (2.2)$$

where $p_a(t, x, y)$ is the atmospheric pressure [$N.m^{-2}$], $\rho_0 = 1027 \, kg.m^{-3}$ is the constant reference density and $\rho(t, x, y, z) - \rho_0$ is the density deviation.

The Boussinesq approximation, used in particular in the field of oceanic circulation, ignores density differences (i.e., $\rho - \rho_0 \ll \rho_0$) in the momentum equation except in the gravity term. Gravity is indeed assumed to have a sufficiently large magnitude to make the specific weight of the fluid significant.

Equations

The three-dimensional hydrostatic equations are solved on the domain Ω in order to retrieve the temporal sequence of six hydrodynamic variables (see Table 3). In total, five governing equations and one supplementary equation for the computation of the density can be described.

Table 3: Description of the computed variables

Variable	Description	Units
$\mathbf{u}(t, \mathbf{x})$	Horizontal velocity field	[$m.s^{-1}$]
$w(t, \mathbf{x})$	Vertical velocity component	[$m.s^{-1}$]
$\eta(t, x, y)$	Sea surface elevation	[m]
$S(t, \mathbf{x})$	Salinity	[$g.kg^{-1}$]
$T(t, \mathbf{x})$	Temperature	[°C]
$p(t, \mathbf{x})$	Hydrostatic pressure	[$N.m^{-2}$]

Momentum equation

This equation is based on the momentum conservation principle stating that, within a domain, the change in the system momentum is proportional to the action of the forces applied on this system:

$$\begin{aligned}\mathbf{P}(t) &= \int_{\Omega(t)} \rho \mathbf{v} dV \\ \frac{d}{dt} \mathbf{P}(t) &= \mathbf{F}^c + \mathbf{F}^d\end{aligned}\tag{2.3}$$

where the momentum of the system $\mathbf{P}(t)$ is equal to the sum of the contact $\mathbf{F}^c$ and distance $\mathbf{F}^d$ forces. The 3D velocity $[m.s^{-1}]$ is denoted as $\mathbf{v}$. When developing equation (2.3), we obtain:

$$\frac{\partial \mathbf{u}}{\partial t} + \nabla_h \cdot (\mathbf{u}\mathbf{u}) + \frac{\partial w\mathbf{u}}{\partial z} = \nabla_h \cdot (\nu_h(\nabla_h \mathbf{u})) + \frac{\partial}{\partial z} \left(\nu \frac{\partial \mathbf{u}}{\partial z} \right) - f \mathbf{e}_z \wedge \mathbf{u} - \frac{1}{\rho_0} \nabla_h p, \tag{2.4}$$

where ∇_h is the horizontal gradient operator (see Eq.[2.5]), $\mathbf{e}_i$ is the unitary vector in direction i , $\nu(t, x, y, z)$ is the vertical eddy viscosity $[m^2.s^{-1}]$, f is the Coriolis factor $[s^{-1}]$ (see Eq.[2.6]) and $\nu_h(t, x, y, z)$ is the horizontal viscosity $[m^2.s^{-1}]$ (see Eq.[2.7]). The left terms represent the total temporal derivative of the momentum whereas the right terms correspond to the sum of the different forces. The contact force (2 first terms) is the shear stress generated by the velocity gradient. The distance forces are the Coriolis force (third term) and the action of gravity as a pressure gradient (last term, see Eq.[2.8]).

$$\nabla_h = \mathbf{e}_x \frac{\partial}{\partial x} + \mathbf{e}_y \frac{\partial}{\partial y}, \tag{2.5}$$

$$f = 2\Omega \sin \Phi, \tag{2.6}$$

where $\Omega = 7.292 \times 10^{-5} [rad.s^{-1}]$ is the rotation rate of the Earth and Φ is the latitude.

$$\nu_h = \alpha \Delta^2 \sqrt{2 \left(\frac{\partial u}{\partial x} \right)^2 + 2 \left(\frac{\partial v}{\partial y} \right)^2 + \left(\frac{\partial v}{\partial x} + \frac{\partial u}{\partial y} \right)^2} \tag{2.7}$$

The horizontal eddy viscosity $\nu_h(t, x, y, z)$ follows the model of Smagorinsky: α is a non-dimensional constant coefficient and Δ^2 is the surface of the horizontal section of the three-dimensional mesh element (Smagorinsky 1963).

Pressure equation

The last term of Eq.[2.4] can be calculated thanks to the pressure equation described here. Following the hydrostatic hypothesis and Eq.[2.2] we can derive an expression for the horizontal gradient of pressure. As the pressure is only dependent on the atmospheric pressure p_a , the height of fluid above $(\eta - z)$ and its own density ρ , the horizontal gradient of pressure is a function of the horizontal gradient of these 3 variables. When applying the the operator ∇_h and dividing by ρ_0 , we obtain:

$$\frac{1}{\rho_0} \nabla_h p = \frac{1}{\rho_0} \nabla_h p_a + g \nabla_h \eta + \frac{g}{\rho_0} \nabla_h \int_z^\eta (\hat{\rho}(S, T) - \rho_0) dz, \tag{2.8}$$

where $\hat{\rho}(S, T)$ is the density calculated with the state equations from Jackett et al. 2006.

Continuity equation

The continuity equation relies on the mass conservation law stating that the variation of mass contained in the domain Ω is equal to the mass flow going through its surface:

$$\frac{d}{dt}M(t) = \frac{d}{dt} \int_{\Omega} \rho d\Omega = 0, \quad (2.9)$$

with $M(t)$ the mass of the system. The local form of the previous equation writes:

$$\frac{\partial \rho}{\partial t} + \nabla \cdot (\rho \mathbf{v}) = 0 \quad (2.10)$$

The Boussinesq approximation considers non-compressible fluids, which is a reasonable assumption for water. This equation can therefore be written as:

$$\rho \nabla \cdot \mathbf{v} = 0, \quad (2.11)$$

and finally,

$$\nabla_h \cdot \mathbf{u} + \frac{\partial w}{\partial z} = 0 \quad (2.12)$$

Salinity and temperature equations

Both salinity (Eq.[2.13]) and temperature (Eq.[2.14]) are expressed in the form of advection-diffusion equations. **Blue** terms in the equations are related to the advection part whereas terms in **red** correspond to the diffusion part:

$$\frac{\partial S}{\partial t} + \nabla_h \cdot (\mathbf{u}S) + \frac{\partial wS}{\partial z} = \nabla_h (\kappa_h \nabla_h S) + \frac{\partial}{\partial z} \left(\kappa \frac{\partial S}{\partial z} \right) + S_{rel}, \quad (2.13)$$

$$\frac{\partial T}{\partial t} + \nabla_h \cdot (\mathbf{u}T) + \frac{\partial wT}{\partial z} = \nabla_h (\kappa_h \nabla_h T) + \frac{\partial}{\partial z} \left(\kappa \frac{\partial T}{\partial z} \right) + T_{rel}, \quad (2.14)$$

where $\kappa_h(t, x, y, z)$ and $\kappa(t, x, y, z)$ are respectively the horizontal and vertical diffusivities [$m^2.s^{-1}$]. It must be pointed out that the vertical eddy viscosity ν and diffusivity κ are determined with the κ - ϵ turbulence closure model GOTM (General Ocean Turbulence Model) (Karna et al. 2012) with Canuto A stability functions (Canuto et al. 2001). This κ - ϵ turbulence model allows us to account for the time-space evolution of vertical turbulent fluxes. In addition, the choice of adapted stability functions defines the model's ability to properly predict the mixed layer deepening. Canuto A stability functions have proved to perform well in the case of SLIM3D (Karna et al. 2012). On the other hand, the horizontal diffusivity κ_h is defined by the parameterization of Okubo 1971:

$$\kappa_h = c \Delta^{1.15} \quad (2.15)$$

where c is the Okubo coefficient and Δ is the mesh size.

The last terms of equations [2.13] and [2.14] are surface relaxation terms that are added to force the computed values towards the salinity and temperature provided by an Ocean General Circulation Model (OGCM), such as Nucleus for European Modelling of the Ocean (NEMO) or Hybrid-Coordinate Ocean Model (HYCOM). The reason for these implementations is that SLIM3D is currently lacking proper heat and salinity fluxes at the surface. More details about relaxation are given in subsection 2.4.2. The salinity relaxation term can be described as follows:

$$S_{rel} = \frac{\max((z_s + z), 0)}{z_s \tau_s} (S_{OGCM} - S) \quad (2.16)$$

where z_s is the thickness of the surface layer, z is the vertical level of computation, τ_s is the relaxation time and S_{OGCM} is the reference surface salinity. The same calculation principle applies to T_{rel} as well. Relaxation is therefore maximal at surface, linearly decreases with depth until $z = -z_s$ and vanishes underneath.

External mode

The surface elevation $\eta(t, x, y)$ is predicted with an external 2D mode relying on the depth-averaged velocity $\bar{\mathbf{u}}(t, x, y)$ given by the depth-averaged shallow water equations:

$$\frac{\partial \eta}{\partial t} + \nabla_h \cdot (H \bar{\mathbf{u}}) = 0, \quad (2.17)$$

$$\begin{aligned} \frac{\partial \bar{\mathbf{u}}}{\partial t} + (\bar{\mathbf{u}} \cdot \nabla_h) \bar{\mathbf{u}} = & - \frac{g}{\rho_0 H} \int_{-h}^{\eta} \left(\nabla_h \int_z^{\eta} (\rho - \rho_0) dz \right) dz - \frac{1}{\rho_0} \nabla_h p_a - g \nabla_h \eta - f \mathbf{e}_z \wedge \bar{\mathbf{u}} \\ & + \frac{1}{H} \nabla_h \cdot (H \nu \nabla_h \bar{\mathbf{u}}) + \frac{\tau_s - \tau_b}{\rho H} + \mathbf{F}_{\mathbf{u}'}, \end{aligned} \quad (2.18)$$

where $\tau_s(t, x, y)$ and $\tau_b(t, x, y)$ are respectively the surface wind stress and bottom friction stress [$N.m^{-2}$] and $\mathbf{F}_{\mathbf{u}'}(t, x, y)$ gathers all the depth-averaged momentum contributions of the velocity deviations $\mathbf{u}' = \mathbf{u} - \bar{\mathbf{u}}$.

Boundary conditions

Boundary conditions differ according to the type of boundaries they are applied on. Closed lateral boundaries (Γ_l , land barriers) are imposed to be impermeable:

$$\mathbf{u} \cdot \mathbf{n}_h = 0, \quad (2.19)$$

where $\mathbf{n}_h(x, y) = (n_x, n_y)$ is the horizontal unit vector, normal to Γ_l . Top (Γ_s) and bottom (Γ_b) boundary layers are also subject to imposed impermeability conditions:

$$w + \mathbf{u} \cdot \nabla_h h = 0, \quad \mathbf{x} \in \Gamma_b \quad (2.20)$$

$$w - \frac{\partial \eta}{\partial t} - \mathbf{u} \cdot \nabla_h \eta = 0, \quad \mathbf{x} \in \Gamma_s \quad (2.21)$$

In addition, surface wind $\tau_s(t, x, y)$ and bottom friction $\tau_b(t, x, y)$ stresses take part in top and bottom slip conditions:

$$\nu \frac{\partial \mathbf{u}}{\partial z} = \frac{\tau_b}{\rho_0}, \mathbf{x} \in \Gamma_b \quad (2.22)$$

$$\nu \frac{\partial \mathbf{u}}{\partial z} = \frac{\tau_s}{\rho_0}, \mathbf{x} \in \Gamma_s \quad (2.23)$$

τ_s is computed with the law of the wall, assuming a logarithmic profile of velocity parameterized by the constant bottom roughness length z_0 . Boundary conditions on open lateral boundaries (open ocean) are defined by the outputs of other hydrodynamics models (see section 2.4.2).

2.4.2 Numerical model

Model discretization

The governing equations are solved numerically with the discontinuous Galerkin finite element method on an unstructured mesh. Unlike structured grids, the unstructured meshes have a variable resolution that allows us to refine the elements size in areas of particular interest while coarsening it in other parts of the domain. This process is essential to optimize computing resources allocation and is especially important to find a good balance between precision and workload of the hydrodynamics model. One big advantage of the discontinuous Galerkin method is that it doesn't require the continuity of the numerical solution between neighbouring elements. As a result, the three-dimensional domain can be divided into many local subsets that are handled in parallel. The use of concurrent programming (also called parallel programming) is vital to considerably reduce time resources needed for the simulations. Until recently, mesh generation was performed with the GMSH software (Geuzaine and Remacle 2009). However, Remacle and Lambrechts 2018 developed a faster and more robust tool, mainly based on shapefiles as inputs. This tool is now integrated in the *seamsh* Python library³, which is used for the generation of the present 3D mesh.

The first step of the generation process is to create the horizontal mesh of the study area. This 2D unstructured mesh is later extruded over several vertical layers to form the 3D mesh. As explained in section 2.3, the domain is delimited by 2 isobaths (2100m and 1900m depth to the south and east respectively) linked by 3 straight lines drawn over the open ocean. The choice to follow isobaths is motivated by the need to minimize abrupt bathymetry changes on the boundaries in order to avoid numerical issues during the computations. However, it is also necessary to space out the limits of the domain from the coast to avoid too much influence of the boundary conditions on the simulated currents, especially near coral reef habitats that are the main object of interest in this study. As the hydrodynamics models that we use to force SLIM have a resolution of at most 10km (more details below), a spacing of 20km is chosen to ensure a good relaxation level. As a result, and given the local bathymetry, closing the domain boundaries is achieved more easily by drawing straight lines rather than following other isobaths around the island.

³<https://jlambrechts.git-page.immc.ucl.ac.be/seamsh/>

In the present case, the 2D mesh is refined near the coast, where currents are more complex and influenced by the topography, near coral habitats since they are the main object of interest, and finally in areas where the bathymetry gradient is high, i.e. mostly near the edges of the island's plateau. Steep areas are included in the refined regions in order to satisfy the consistency Haney (1991) criterion defined below. The resulting mesh is presented in Fig. 11. It is composed of 21'699 triangles with minimal and maximal resolutions of $\sim 200\text{m}$ and $\sim 1.6\text{km}$ respectively.

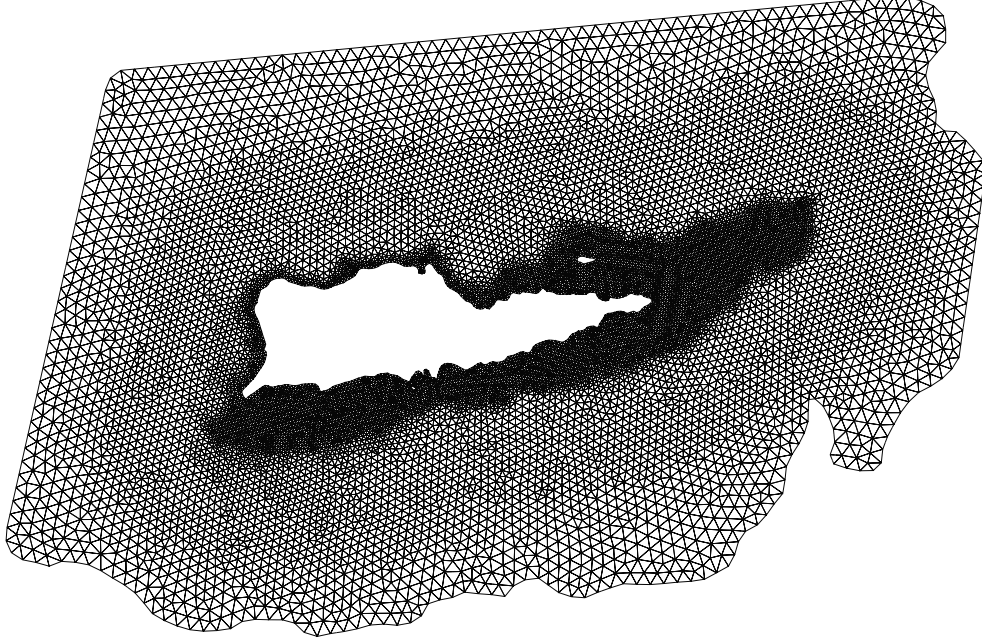


Figure 11: 2D surface mesh composed of 21'699 triangles refined near the coast, reefs and steep areas. Minimal resolution is $\sim 200\text{m}$ and maximal resolution is $\sim 1.6\text{km}$.

The extrusion of the surface mesh is executed on a combination of 2 types of vertical layers: z -layers that are parallel to the surface and σ -layers that follow the bathymetry. These two types are illustrated in Fig. 12. Contrary to z -layers that are placed at fixed depths, σ -layers display a variable vertical spacing, according to the evolution of the bathymetry, and tend to become more and more parallel towards the surface. As a matter of fact, they provide a more realistic representation of the ocean bottom. However, these layers are also less numerically stable and can lead to hydrostatic inconsistency and numerical errors in areas with a highly variable bathymetry. To avoid such numerical issues for a finite difference scheme, Haney 1991 defined a consistency criterion relying on a few different features of the 3D grid:

$$\left| \frac{\sigma}{h} \frac{\partial h}{\partial x} \right| \Delta x < \Delta \sigma, \quad (2.24)$$

which is equivalent to

$$\frac{\Delta h}{h} < \frac{\Delta \sigma}{\sigma}, \quad (2.25)$$

with σ the vertical coordinate in the σ -layers system, $\Delta\sigma$ the vertical grid interval, Δx the horizontal grid interval and Δh the difference of bathymetry between two neighbouring nodes of the bottom layer.

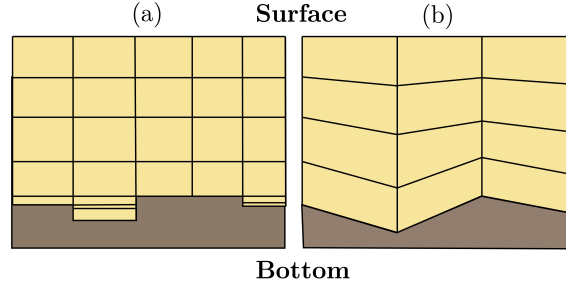


Figure 12: Illustration of (a) z -layers and (b) σ -layers in yellow. The corresponding approximation of the seabed is shown in brown.

Satisfying the Haney criterion is a sufficient condition to have a stable scheme. Practically, it ensures that every node in every σ -layer is located above/below the neighbours of its corresponding node in the layer just below/above. In regions with large bathymetry gradients, compliance with this criterion is achieved either with a high resolution on the horizontal, i.e. small horizontal grid intervals (Δx) or with a coarse resolution on the vertical, i.e. few σ -layers (high $\Delta\sigma$). Fig. 13 explains how the choice of $\Delta\sigma$ and Δx is important for that condition. Stability of the scheme is ensured when the bottom layer ($\sigma = -1$) stays below the n^{th} layer within a grid interval (a). Numerical errors start to take place if the vertical resolution becomes higher, that is $\Delta\sigma \downarrow$ (b), or if the horizontal resolution is reduced, that is $\Delta x \uparrow$ (c). It must be noted that the extrusion process includes a preliminary step of bathymetry smoothing. This step is used to restrict the bathymetry gradient to a defined maximal percentage so as to lower the occurrence of instabilities.

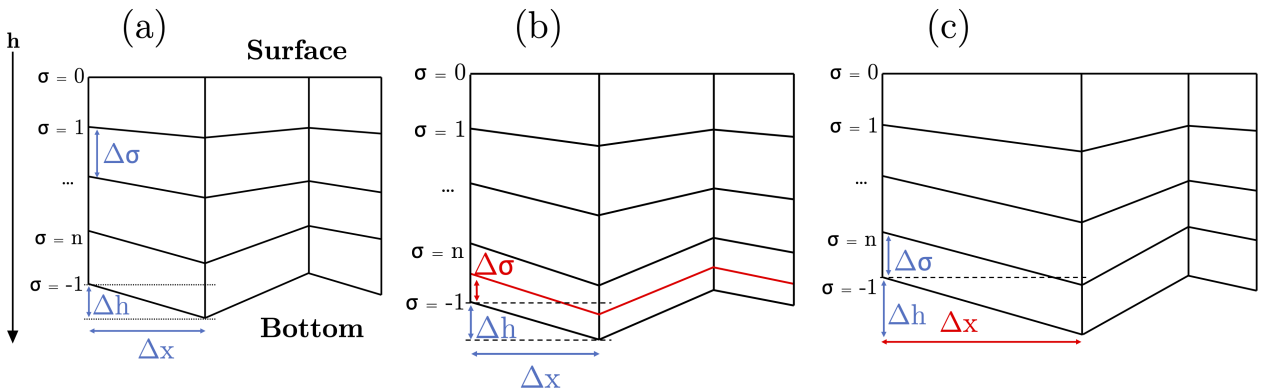


Figure 13: Illustration of Haney consistency criterion. Case (a) provides a stable scheme whereas the others give rise to numerical inconsistency: (b) low $\Delta\sigma$, (c) high Δx .

In the present case, the final 3D mesh is the result of the extrusion of the surface mesh on a combination of 10 σ -layers near the surface with a maximum depth of 150m and 8 z -layers at greater depths (200, 300, 400, 500, 700, 1000, 2000, 3000, 4000m). Here, σ -layers are used with

a relatively high vertical resolution over the first 150m in order to produce a good hydrodynamics near coral reef habitats. z -layers are used with a coarser resolution as less information is needed below this threshold. The 3D mesh is represented in Fig. 14 with different perspectives. Fig. 15 illustrates the use of different layer types with different resolutions along the vertical axis.

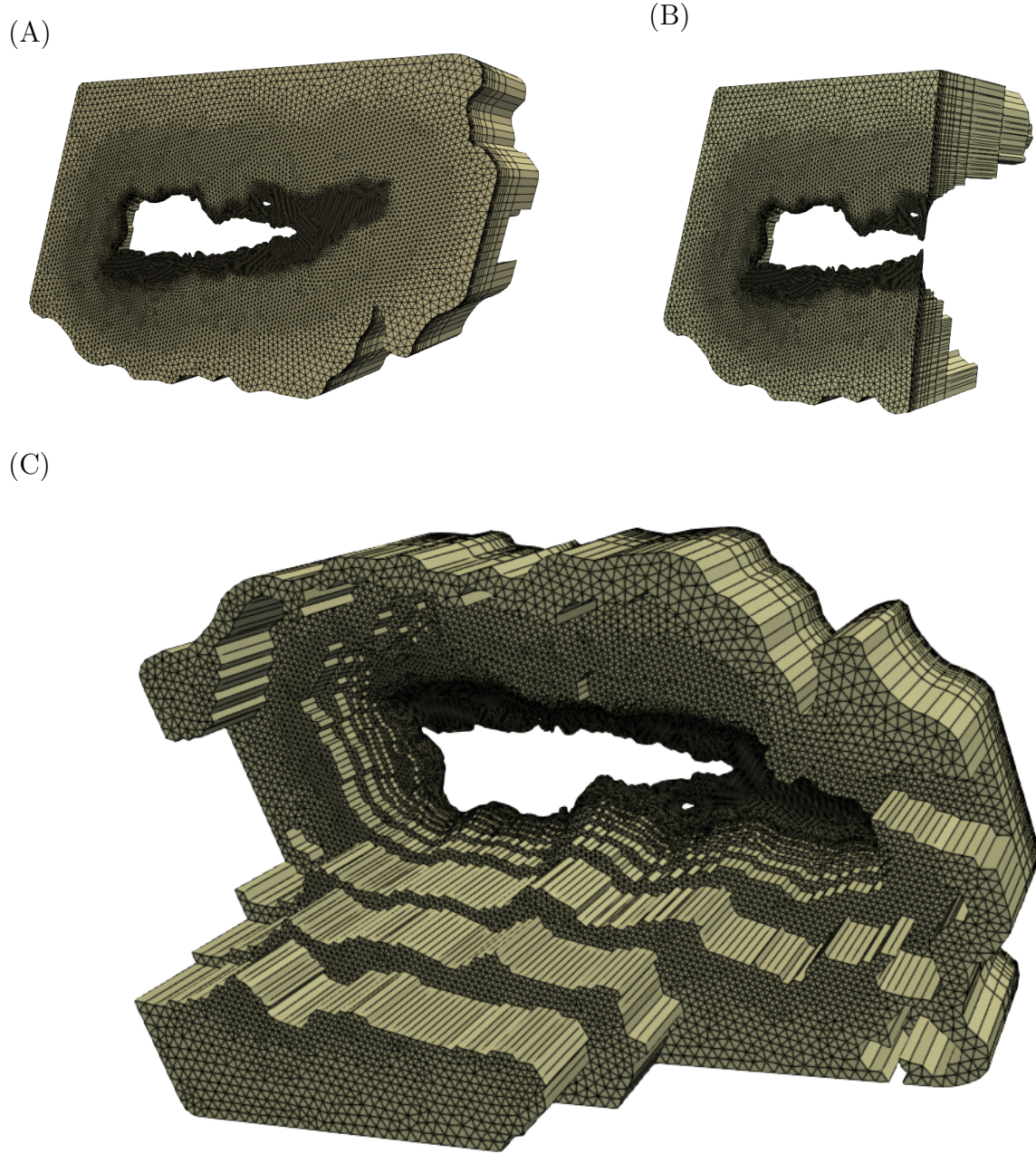


Figure 14: 3D mesh composed of $\sim 2.85 \times 10^5$ prisms refined near the coast, reefs and steep areas. It combines 10 σ -layers near the surface and 8 z -layers at greater depths. (A) Perspective front view, (B) western part of a meridional cross section, and (C) Flipped bottom view. The vertical scale has been multiplied by 10 for visualization purpose.

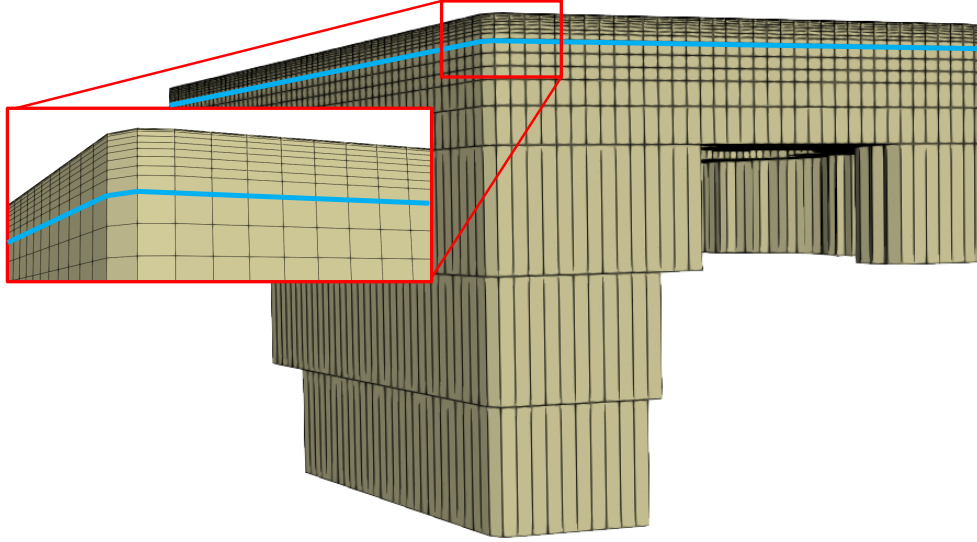


Figure 15: Vertical layers of the 3D mesh (northwestern view). The blue line represents the upper boundary of the first z -layer at 200m depth. Vertical scale has been multiplied by 10 for visualization purpose.

Forcings and initial conditions

External forcings corresponding to the main drivers of water circulation are essential to simulate realistic behaviours of the ocean currents. Both initial conditions and time-dependent boundary conditions are therefore needed for the hydrodynamic model to initiate and maintain the simulations. Such forcings include the wind, the tides and the large scale circulation and density gradients, determined by several ocean variables. Contrary to stationary external forcings that were described in the mathematical parameterization of SLIM3D (see section 2.4.1), such as the Coriolis force, gravity and bottom friction, time-dependent forcings are retrieved from different models and measurements. This sub-section aims to describe the sources of the data that is used in the hydrodynamics simulations.

The bathymetry is the only condition specific to the seabed. In this master thesis, we decide to combine two data sources. The first one is a mid-resolution bathymetry with 15 arc-seconds intervals ($\sim 450\text{m}$) coming from the General Bathymetric Chart of the Oceans (GEBCO)⁴. The second one is a 10m-resolution dataset from the NOAA, obtained with lidar measurements, which covers only a subset of the study area (see Fig. 34 in Appendix). It can be noted that the region covered by this high-resolution bathymetry includes all coral habitats (shallow and mesophotic) listed in the habitat map. These two datasets are combined thanks to a buffer area of 5000m along which a smooth transition from one source to the other is achieved.

The open lateral boundaries are provided with several large-scale ocean circulation variables, such as u , v , η , S and T . As part of this master thesis, and thanks to the help of Dr. Sonaljit Mukherjee (University of the Virgin Islands), we have been granted access to the United States Caribbean Regional Ocean Modeling System (USCROMS) simulation outputs for 2019 and

⁴https://www.gebco.net/data_and_products/historical_data_sets/#gebco_2019

2020. USCROMS is an ocean modeling system based on the larger ROMS architecture and focuses on Puerto Rico and the US Virgin Islands. The ocean variables of interest are computed on an orthogonal curvilinear grid with 32 σ -layers and with spatial and temporal resolutions of 2km and 1 hour respectively. More information about USCROMS can be found below.

Finally, 3 drivers are needed for the closed surface boundary. The wind and atmospheric pressure forcings are retrieved from the ERA5 (ECMWF Reanalysis 5th Generation) dataset⁵, produced by the European Center for Medium-Range Weather Forecasts (ECMWF). Wind stress is expressed as wind speed at 10m above the sea surface with two horizontal components. Spatial and temporal resolutions are of 31km on a standard regular grid and 1 hour respectively. The last surface forcing is related to astronomical tides. In the present study, tidal velocity and elevation are already included in the outputs of the USCROMS simulations and are therefore not retrieved separately.

Apart from the forcings that are used throughout the simulations, initial conditions also need to be established all over the domain at the beginning of the computations. Salinity and temperature initial values are extracted from USCROMS data whereas current velocities and surface elevation are set to 0. As a result, a spin up phase is necessary for these variables to slowly converge towards realistic and dynamically-balanced values.

US Caribbean ROMS

As mentioned above, the major data source used to produce the initial and boundary conditions for the hydrodynamics simulations is the USCROMS model. This section aims to describe the main features of this model, based on the work of Mukherjee et al. 2022.

The USCROMS is a split-explicit primitive equation ocean modeling system based on the ROMS AGRIF (ROMS with Adaptive Grid Refinement in Fortran) architecture. Ocean currents and variables are computed by solving the Navier-Stokes equations with a hydrostatic mode on an orthogonal curvilinear grid with 32 σ -layers. Bathymetry is retrieved from the 1km-resolution ETOPO dataset⁶ and is smoothed using a 2D Gaussian filter in order to avoid numerical inconsistency. One particularity of the model is its nested structure including a 2km-resolution parent grid that holds 2 separate 330m-resolution nested grids covering St Thomas and St Croix respectively. As part of this master thesis, only the 2km parent grid data is used. Climatological forcing data is taken from the Mercator Daily Global Physical Bulletin with a 1/12° resolution (~ 9.3 km). Atmospheric forcings comprise 6-hourly wind stress from CER-SAT⁷ and hourly heat flux data from the PIRATA⁸ mooring station. Tidal forcing is retrieved from the OTIS Python package⁹.

⁵<https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5>

⁶<https://ngdc.noaa.gov/mgg/global/etopo1sources.html>

⁷https://resources.marine.copernicus.eu/product-detail/WIND_GLO_WIND_L4_REP_OBSERVATIONS_012_006/INFORMATION

⁸<https://www.pmel.noaa.gov/gtmba/pmel-theme/atlantic-ocean-pirata>

⁹https://pytmd.readthedocs.io/en/stable/user_guide/output_otis_tides.html

Model validation

Even though it is one of the most important part in the modeling process, no consistent validation step could be applied on the present hydrodynamics results. Validation is usually achieved by comparing the outputs of the simulations, i.e. the simulated ocean currents and variables, with field data collected in situ or with the outputs of other larger models. Analyzing the kind of discrepancies found between reference and simulated data is then useful to identify what processes/trends/parameterizations would need to be implemented/modified in the model to provide the desired level of realism.

Reliable monitoring agencies that are typically referred to in ocean modeling validation are the National Data Buoy Center from the NOAA¹⁰ for salinity, temperature and currents direction and magnitude, or the European Commission Joint Research Center (ECJRC)¹¹ for sea surface elevation. However, as no ocean data could be retrieved for the area around St Croix for the 2019-2020 period in both sources, no comparison was actually possible.

However, two small qualitative validation measures are provided (Fig. 16). First, we verify the behaviour of the UML (salinity and temperature) at a small depth spot, south of the island. As the hydrodynamics are simulated during the warm season (August-November), we expect to observe a rather shallow mixed layer. Then, we also ensure that the stratification of temperature and salinity profiles are preserved through time and that no unexpected vertical mixing is introduced by the model. The two profiles are checked at a great depth spot, north of the island, where a mixed layer can develop above a stratified one.

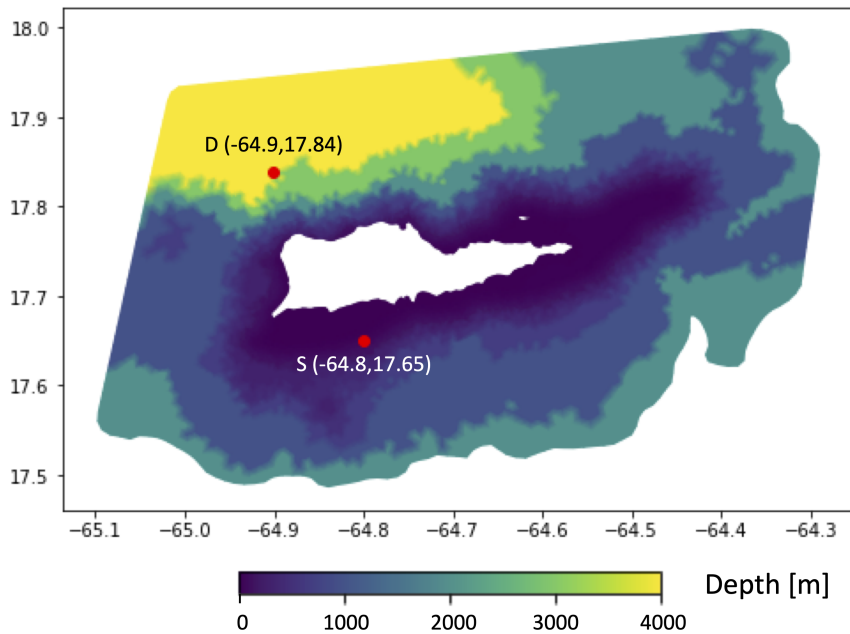


Figure 16: Location of validation points in the study area: (D) Great depth spot, and (S) shallow water spot. The displayed bathymetry corresponds to the layers of the 3D mesh.

¹⁰<https://www.ndbc.noaa.gov/>

¹¹<https://webcritech.jrc.ec.europa.eu/SeaLevelsDb>

2.5 Circulation of the pathogen agents

This section describes the transport model used to simulate the spread of SCTLD agents vectors, along with its implementation, as well as the analysis that is conducted on the resulting connectivity matrices. In addition, a clustering of the coral sub-reefs by depth range is provided. This depth stratification allows us to specifically study the potential connectivity between shallow and mesophotic coral reefs.

2.5.1 Lagrangian Particle Tracker

The second step of the biophysical modeling approach consists in simulating the dispersal of virtual SCTLD agents on the hydrodynamics previously produced. This process is achieved by using a Lagrangian Particle Tracker (LPT, also called a Lagrangian Transport Model) directly integrated within SLIM3D. The operating principle of such an Individual Based Model (IBM) is to follow the course of individual objects while assigning them biological or physical behaviours that influence their trajectories and their interactions with other entities. The outputs of this model are connectivity matrices quantifying the pairwise interactions between the different starting and transit points of the particles.

In the context of SCTLD agents dispersal, virtual particles represent the agents vectors like infected pieces of coral tissues, coral secretions or sediments that are carried away from one reef to another by water currents. It must be noted that one virtual particle does not effectively represent one piece of tissue or one sedimentary particle, but instead a bunch of pieces with a given mass and buoyancy behaviour. Starting and transit points of these particles are the square sub-reef polygons shown in Fig. 8. During their journey, the agents vectors continuously lose a certain amount of infectious mass, thereby releasing SCTLD agents on the neighbouring reefs over which they are transported. As a result, connectivity matrices are used to quantify the exchanges of infectious materials between source and sink reefs in the entire study area.

The 3D position of the particles is computed with an advection-diffusion equation in Lagrangian form. Blue terms in the equations are related to the advection part whereas terms in red correspond to the random diffusion:

$$d\mathbf{X}(t) = (\mathbf{u} + \nabla \cdot \mathbf{K}) dt + \sqrt{2\mathbf{K}dt} \cdot \mathbf{R}(t), \quad (2.26)$$

where $\mathbf{X}(t)$ is the time-dependent 3D position vector, $\mathbf{u}$ is the total particle velocity (current velocity + buoyancy velocity), $\mathbf{R}(t)$ is a vector of random numbers with zero mean and unit variance, and $\mathbf{K}$ is the turbulent diffusivity tensor, which writes:

$$\mathbf{K} = \begin{bmatrix} \kappa_h & 0 & 0 \\ 0 & \kappa_h & 0 \\ 0 & 0 & \kappa \end{bmatrix}, \quad (2.27)$$

First, the advection term of Eq.[2.26] can be interpreted as the deterministic component of the particles' motion, obtained by the combination of the 3D hydrodynamic velocity with the particles' own vertical buoyancy velocity. Due to the spatial variability of the turbulent diffusivity $\mathbf{K}$, the term $\nabla \cdot \mathbf{K}$ needs to be added to this deterministic part in order to include a mean drift in the particles displacement. This correction drift is used to prevent accumulations of particles in regions of low diffusivity (Grawe and Wolff 2010). On the other hand, the diffusion term is used to represent the stochastic part of the particles' motion. It corresponds to a random walk with an average step length of $\sqrt{2\mathbf{K}dt}$, used to account for the mixing effect of subgrid-scale flow features in an ocean with turbulent diffusion. The deterministic part of Eq.[2.26] is solved numerically with a 4th order Runge-Kutta scheme whereas the second part is solved with a 1st order Euler scheme. The Runge-Kutta scheme provides an estimate slope computed as the weighted average of four preliminary estimates and is particularly convenient to account for the curvature of the velocity field, which is an important feature when proceeding with a three-dimensional model.

2.5.2 Implementation

The implementation of this model is based on the approach of Dobbelaere et al. 2020 and is adapted for three-dimensional modelling. Practically, virtual particles are released continuously every 4 hours at random locations inside the 547 sub-reef polygons ($450 \times 450\text{m}$) during monthly simulations. The seeding height of one particle is set to one meter above the reef at its given location. Once seeded, these particles acquire a state composed of their polygon of origin and of a mass that they loose at a constant rate γ as they are moved. The value of γ is chosen so as to give them a half-life of 30 days. The three possibilities for an individual to disappear from the system are (1) by being seeded below 150m depth, or (2) by entirely losing its mass, or (3) by being carried out of the computational domain. Once individuals are removed from the system, they stop being tracked and are erased.

Due to limited computational and time resources, the seeding density of the particles is set to 3 individuals/km². Unfortunately, this value cannot lead to robust results, since choosing a low seeding density brings some variability in the outputs of the transport simulations. Consequently, the monthly potential connectivity matrices that are produced by the LPT are less representative than expected. To bypass this problem, we decide to execute each monthly simulation several times and to use the average of their resulting connectivity matrices.

These matrices are the main output of the transport model and give the probabilities of exchange of pathogen agents between reefs. When particles are brought over a reef polygon during their displacement, the amount of infectious mass that they lose at each time step can interact with this reef and start to infect it. The only condition for such an interaction to take place is that the particles must be located at most 10m above the reef at a given time step. This condition reflects the possibility that vertical turbulence and mixing will bring the infectious mass closer to the reef with an arbitrary range of 10m, which thus allows the infection process to occur. Subsequently, successful infectious mass exchanges are recorded in monthly potential connectivity matrices, whose entries are denoted C_{ij} . The matrix rows correspond to the source

sub-reefs i (where the particles originate) and the columns correspond to the destination reefs j (where they successfully release infectious materials). Finally, the monthly potential connectivity matrices are summed to produce the total potential connectivity matrices, which are then normalized by dividing all entries of row i by the total amount of mass seeded on polygon i during the entire period of simulation. The normalized matrices are denoted $\tilde{C}$. Their entries correspond to the probability that disease agents produced on sub-reef i settle on sub-reef j during the entire simulated period. The choice of 10m as the maximal range of vertical turbulence effects in this model is discussed in section 4.

Sensitivity analysis

As mentioned above, all particles are subject to a vertical constant buoyancy velocity in addition to the 3D velocity that they are given by the water currents. Even though the major hypothesis is that they remain within the water column (Dobbelaere et al. 2020; Muller et al. 2020), no precise buoyancy behaviour has been identified for SCTLD agents-carrying vectors yet. As a result, three types of buoyancy behaviour are considered in the present study: positive (surface-seeking), negative (bottom-seeking) and neutral (zero buoyancy velocity). All LPT simulations and subsequent analyses are therefore carried out for these 3 behaviours.

2.5.3 Connectivity analysis

A connectivity matrix can be interpreted as a large graph whose nodes are coral sub-reefs and whose edges are connectivity pathways to other sub-reefs. The strength of the pathway between reefs i and j is proportional to the probability given in the entry C_{ij} of the matrix. As a result, the outputs of the transport model can be analyzed with graph theory tools. Following the approach of Dobbelaere et al. (2020), five potential connectivity measures are used to interpret the computed graphs. They are described in the following subsection. In addition, as we want to investigate the transmission of the SCTLD between shallow reefs and MCEs, we also compute these five indicators for specific subgraphs composed of clusters of sub-reefs, based on their depth. This clustering is described in the second subsection.

Indicators

The first indicator is the **weighted connectivity length** (WCL). It gives the average distance successfully traveled by the disease agents released over one sub-reef. In other words, it determines the average range of impact of one sub-reef regarding the transmission of the disease. For a sub-reef i , it writes:

$$WCL_i = \frac{\sum_j \tilde{C}_{ij} L_{ij}}{\sum_j \tilde{C}_{ij}}, \quad (2.28)$$

where L_{ij} is the horizontal distance between source reef i and destination reef j .

The **out-degree** (OD) is a measure of the overall potential for a reef to spread the disease in the network. Its value is proportional to the number of non-zero entries of a row in the non-normalized potential connectivity matrix, as well as to the quantity of disease agents sent to the network by the corresponding reef:

$$OD_i = \sum_j \delta(C_{ij}, 0) \sum_j C_{ij}, \quad j \neq i \quad (2.29.1)$$

where

$$\begin{cases} \delta(x, y) = 1, & \text{if } x \neq y \\ \delta(x, y) = 0, & \text{if } x = y \end{cases} \quad (2.29.2)$$

The third indicator is complementary to the out-degree, as it measures the relative likelihood of successful spread of the disease from one reef to the others. Practically, the **fraction exchanged** (FE) corresponds to the fraction of disease agents released over a reef that successfully settles on other reefs:

$$FE_i = \sum_j \tilde{C}_{ij}, \quad (2.30)$$

It can be noted that the FE strictly depends on the amount of infectious mass successfully sent to the network, contrary to the OD that is also influenced by the number of different outgoing connections.

The **self-recruitment** (SR) is used to measure the isolation of a reef in the network and corresponds to the relative likelihood of unsuccessful spread of the disease to other reefs. It is calculated as the fraction of disease agents settling on reef i that originates from reef i :

$$SR_i = \frac{C_{ii}}{\sum_j C_{ji}}, \quad (2.31)$$

Finally, the last indicator is sort of the opposite of the out-degree, as it measures the overall potential for a reef to import the disease from other reefs in the network. This fifth indicator is called the **in-degree** (ID) and is calculated as follows:

$$ID_i = \sum_j \delta(C_{ji}, 0) \sum_j C_{ji}, \quad j \neq i \quad (2.32)$$

where $\delta(C_{ji})$ refers to the same function as described in Eq.[2.29.2].

These five metrics can be computed for each reef in the network and for each transport model simulation with a given buoyancy behaviour. Their statistical and spatial distributions can help us identify which reefs can be good disease importers or exporters. For instance, good disease exporters will have a relatively high out-degree or fraction exchanged, whereas good importers will show a high in-degree and a low self-recruitment. However, one must be cautious when interpreting the self-recruitment. Due to its relative nature, a high SR could still be related to a large amount of exogenous materials reaching the reef, even though this quantity would be proportionally small compared to the total mass settling on this reef.

Slicing in depth ranges

In order to specifically identify the exchanges between shallow and mesophotic reefs, the network of coral reefs is divided into several subsets according to the depth of its polygons. Figure 17 shows the distribution of the 547 sub-reefs in depth intervals of 10m based on the position of their centroid, along with their classification in 3 categories: shallow (0 - 30m depth), upper mesophotic (30 - 60m) and lower mesophotic (60 - 150m). We decide to distinguish the upper mesophotic reefs from the lower ones to be able to study the connectivity patterns between categories that are more likely to share common species (i.e. shallow - upper mesophotic or upper - lower mesophotic). Spatial distribution of the 3 types of sub-reefs is presented in Fig. 18.

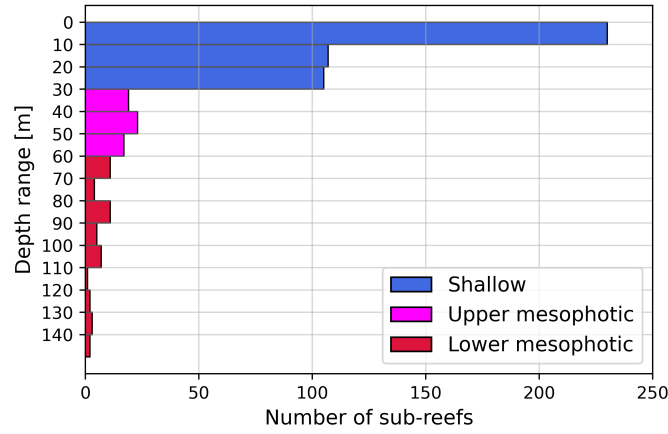


Figure 17: Distribution of the 547 sub-reef polygons in depth ranges of 10m and classification in 3 categories: 446 are shallow, 55 are upper mesophotic and 46 are lower mesophotic.

Consequently, the indicators presented above can be computed from restricted (non-)normalized connectivity matrices that are only composed of the entries corresponding to certain sub-reef categories. As each coral reef subset can be considered either as the source reefs or the sink reefs, the same connectivity analysis can thus be conducted for the 9 possible pairs of categories.

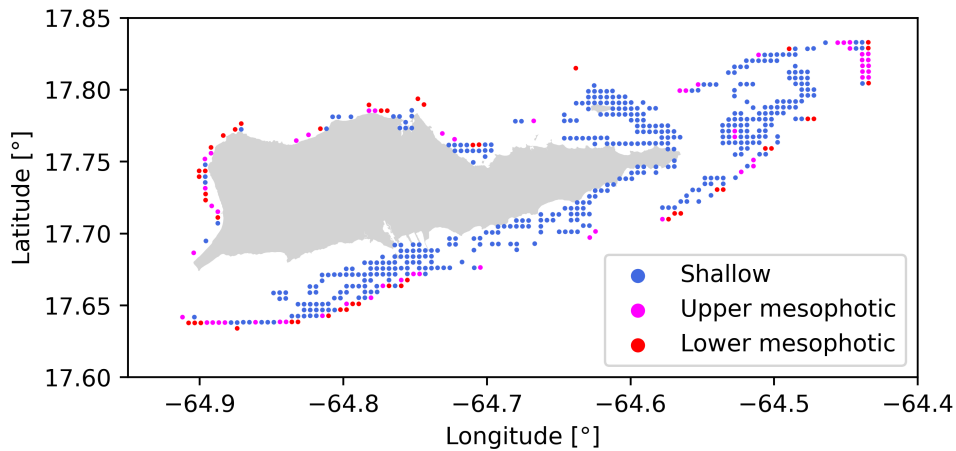


Figure 18: Spatial distribution of shallow (0 - 30m depth), upper mesophotic (30 - 60m) and lower mesophotic sub-reefs (60 - 150m) in the study area.

2.6 Epidemiology

The last step in the biophysical modelling approach is the application of a SIR model to the previously produced coral reef network to simulate the spread of the SCTLD within it. To do so, we rely on the epidemiological model proposed by Dobbelaere et al. (2020) and adapt it to the three-dimensional case. The present section describes the equations governing this model, as well as its calibration and initialization with field-derived parameters. The comparison of the results with field observations is detailed in the last part of this section.

2.6.1 SIR equations

The spread of the SCTLD around the island of St Croix is simulated with a connectivity-based SIR model. Susceptible-Infectious-Recovered (SIR) models are one of the most standard kind of epidemiological models and provide a foundation for many other kinds of more complex tools (Kermack and McKendrick 1927; Satsuma et al. 2004). Conceptually, they allow us to follow the transmission of a disease inside a given population by studying the evolution of 3 individuals compartments: susceptible (S), infected/infectious (I) and recovered/removed (R). Once susceptible individuals are affected by the disease, they are moved to the infectious compartment and start infecting other susceptible individuals until they are removed from the system, either through death or through recovery. Such models usually rely on the hypothesis of an homogeneous and well-mixed population to be valid. It can be noted that natural births and deaths can also be included in a SIR model, even though they are not considered here as they are assumed to balance each other.

Regarding the application of a SIR model for the SCTLD, we account for the spatial heterogeneity of the coral reefs around St Croix by considering the fractions of susceptible (S_j), infectious (I_j) and removed (R_j) individuals for each sub-reef j in the network. As mentioned in section 1.3, the SCTLD may display a contagious mode of transmission while being carried out from one reef to the other by different disease vectors (dead tissues, mucus, sediments) (Aeby et al. 2019; Muller et al. 2020). The probabilities of interaction between affected and susceptible reefs can thus be represented by the entries of the connectivity matrices produced with the transport model. In addition, for each sub-reef j and at any time, the following relations hold: $0 < S_j, I_j, R_j < 1$ and $S_j + I_j + R_j = 1$. The evolution of these fractions through time is described by 3 governing differential equations:

$$\begin{aligned}\frac{dS_j}{dt} &= -\beta \sum_i \frac{A_i}{A_j} I_i \tilde{C}_{ij} S_j - \beta'(I_j) S_j I_j \\ \frac{dI_j}{dt} &= \beta \sum_i \frac{A_i}{A_j} I_i \tilde{C}_{ij} S_j + \beta'(I_j) S_j I_j - \sigma I_j \\ \frac{dR_j}{dt} &= \sigma I_j\end{aligned}\tag{2.33}$$

where A_i is the area of reef polygon i [km^2], $\tilde{C}_{ij}$ is the entry corresponding to the reef pair (i, j) in the normalized connectivity matrix $[-]$, σ is the mortality rate [day^{-1}] and β and $\beta'(I_j)$ are the inter- and intra-reef disease transmission rates respectively [day^{-1}].

Eqs. [2.33] clearly state that an infection process can only take place between a pair of reefs (i,j) if there is a non-zero probability of disease agents exchange in the entry $\tilde{C}_{ij}$. However, once a sub-reef has been reached by the disease, intra-reef transmission slowly takes over. This part of the equations is dependent on the fractions of susceptible (S_j) and infectious (I_j) individuals from sub-reef j , but also on the transmission rate $\beta'(I_j)$ as a function of I_j . This function accounts for coral resistance to the disease and writes:

$$\beta'(I_j) = \frac{\beta'_0}{2}(1 + \tanh [(I_j - I_0)/\tau]), \quad (2.34)$$

where I_0 is a threshold on the infected population above which intra-reef transmission becomes significant, τ is a measure of the interval over which the transition from low to high transmission occurs, β'_0 is the maximal intra-reef transmission rate (equal to β in this case) and $\tanh$ is the hyperbolic tangent.

Practically, this function has the shape of a smooth step function that reaches β'_0 when I_j reaches the chosen threshold I_0 . Therefore, intra-reef transmission becomes significant with a rate β'_0 when I_j approaches I_0 . A larger value of the threshold results in a greater resistance of the corals to the disease and ends up to a slower spread of the infection inside one sub-reef.

2.6.2 Calibration

In order to find relevant field-derived values for the transmission (β'_0) and mortality (σ) rates of Eqs [2.33], we fit our model to SCTLD prevalence observations from 6 permanent monitoring sites in the lower Florida Keys. As no quantitative observations of the spread of SCTLD are available for the USVI, we calibrate our model with data collected between May 2018 and December 2019, when the disease was propagating south of Florida. This data was shared with us by Dr. Erinn M. Muller (Mote Marine Laboratory). In May 2018, three focal reef sites were established in the Lower Keys. All coral colonies > 10 cm in size were then mapped inside two $10\text{m} \times 10\text{m}$ quadrats within each site. At first, when no infection case was observed, each coral was given geospatial coordinates, identified to species and maximum diameter was noted. After that, each site was visited every two to three weeks for rapid assessments to determine whether SCTLD was present. The first affected corals were found in October 2018. Detailed surveys during which corals were assessed for visual signs of SCTLD were conducted until December 2019. Prevalence of apparently healthy, diseased and dead corals, as well as corals of unknown state, were then compiled for each time period.

As the coral species distribution in the USVI is different from the one in Florida, we decide to fit our parameters to prevalence data corresponding to the most represented species in our study area. Table 4 shows the relative abundance and the frequency of occurrence of the 6 most common stony coral species in 52 stations around St Croix, as reported by Fisher et al. (2014). This set of species involves different kinds of susceptibilities to SCTLD and reaches a total relative abundance of 67.8%. As the other 32.2% can be attributed to many other more dispersed species, we thus consider this set to be representative of the entire area. Considering the resulting average susceptibility, we expect our transmission and mortality rates to be slightly higher than for the Florida Keys, i.e. $\beta'_0 \geq 1/6.45$ and $\sigma \geq 1/6.99$ (Dobbelaere et al. 2020).

Table 4: Frequency of occurrence [FO] (percent of stations where a species was observed) and relative abundance [RA] (contribution of each species to the total stony corals documented) of 6 stony coral species around St Croix (52 stations, 2062 corals). Source: Fisher et al. 2014.

Stony coral species			St Croix	
Name	Acronym	Susceptibility to SCTLD	FO [%]	RA [%]
<i>Porites astreoides</i>	PAST	Low	80.8	15.0
<i>Pseudodiploria strigosa</i>	PSTR	High	90.4	13.5
<i>Siderastrea siderea</i>	SSID	Intermediate	78.8	12.9
<i>Montastraea cavernosa</i>	MCAV	Intermediate	67.3	12.7
<i>Orbicella annularis</i>	OANN	Intermediate	30.8	8.9
<i>Orbicella faveolata</i>	OFAV	Intermediate	59.6	4.8
Total			67.8	

Unfortunately, as *P. astreoides* and *O. annularis* are not documented in the SCTLD prevalence dataset, we decide to create two additional time series based on simple assumptions. First, we assume that *O. annularis* has exactly the same behaviour as *O. faveolata*. The prevalence data of *O. faveolata* is thus shared for these two species and accounts for a relative abundance of 13.7%. This assumption seems acceptable since both species share the same genus and are equally susceptible to the disease. Secondly, *P. astreoides* is simply assumed to show no sign of infection or death linked to SCTLD. As a matter of fact, *P. astreoides* is one of the few species to display a low susceptibility to the disease and is rarely or not affected during outbreaks (*Case Definition* 2018). This second assumption seems thus acceptable as well. The prevalence data averaged over the 6 monitoring sites in the Lower Keys for the 4 documented species is presented in Fig. 19.

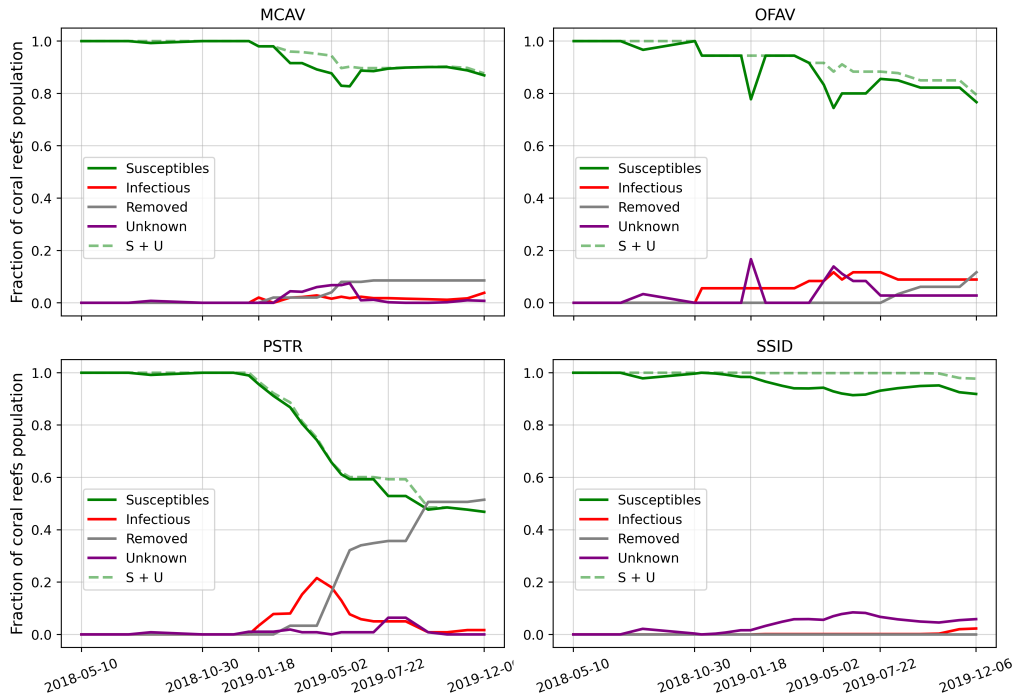


Figure 19: SCTLD prevalence observations averaged over 6 monitoring sites in the Lower Keys (Florida) for 4 stony coral species (acronyms are given in Table 4).

Since our model cannot be calibrated with data related to corals with unknown state (purple lines in Fig. 19), we decide to consider them as healthy. This assumption seems rather small since the Unknown data mainly contributes to the time series with small peaks that do not seem to interact with the evolution of Infectious or Removed series. Instead, these peaks mostly bring undesirable and well marked discontinuities in the Susceptibles series. As a result, we add the Unknown data of the 4 documented species to the corresponding Susceptibles data (green lines, sums are shown in dashes). Subsequently, we average the 6 time series with respect to the relative abundance of their species and normalize the results by the total relative abundance (67.8%). This last step gives us one single sites- and species-averaged time series for healthy, diseased and dead corals that are representative of our study area.

As proposed by Dobbelaere et al. (2020), to relate our calibration step with the compiled data, we simplify Eqs. [2.33] to a single-reef SIR model:

$$\begin{aligned}\frac{dS}{dt} &= -\beta'_0 SI \\ \frac{dI}{dt} &= \beta'_0 SI - \sigma I \\ \frac{dR}{dt} &= \sigma I\end{aligned}\tag{2.35}$$

Eqs. [2.35] give a reasonable approximation of the evolution of the disease on reefs where intra-reef transmission has already overtaken the inter-reef one. Indeed, due to the low entries in the normalized connectivity matrix $\tilde{C}_{ij}$, intra-reef transmission becomes the dominant mechanism as soon as $I_j \geq I_0$. As a result, it is possible to estimate the ratio β'_0/σ by matching the modeled fraction of susceptible corals remaining after the disease activity has stopped (S_∞) with observations. A standard property of a SIR model is that:

$$S_\infty - \frac{\sigma}{\beta'_0} \log(S_\infty/S(t=0)) = 1\tag{2.36}$$

where the initial fraction of susceptible individuals ($S(t=0)$) is set to $1 - I_0$. We can also interpret the ratio β'_0/σ as the basic reproduction number R_0 , defined as the average number of secondary cases produced by one infected individual introduced into a population of susceptible ones (Keeling and Rohani 2011). This indicator is commonly used in epidemiological models to determine if an emerging infectious disease can spread in a population ($R_0 > 1$) or not ($R_0 < 1$) and to determine what proportion of this population should be immunized (with vaccination for instance) to eradicate this disease. R_0 is thus calculated for the present case to express β'_0 in terms of σ . Finally, σ is calibrated to best reproduce the species-averaged time series.

2.6.3 Initialization

To solve Eqs. [2.33], initial fractions of susceptible (S_{j0}), infectious (I_{j0}) and removed (R_{j0}) corals are needed for each sub-reef j . The first observations of SCTLD-affected corals around St Croix were located near the southern coast of the island between August and September 2020 (Brandt et al. 2021). More precisely, they were found in the surroundings of Ruth Island

(VI-CDAC 2022). According to the division of our coral habitat map, we find that two sub-reef polygons are located in this area (Fig. 20). As a result, we decide to assign them an initial fraction of infectious individuals of 0.1, i.e. $(S_{j0}, I_{j0}, R_{j0}) = (0.9, 0.1, 0)$, while the other 545 polygons are assumed to be fully healthy at the beginning of the simulation, i.e. $(S_{j0}, I_{j0}, R_{j0}) = (1, 0, 0)$.

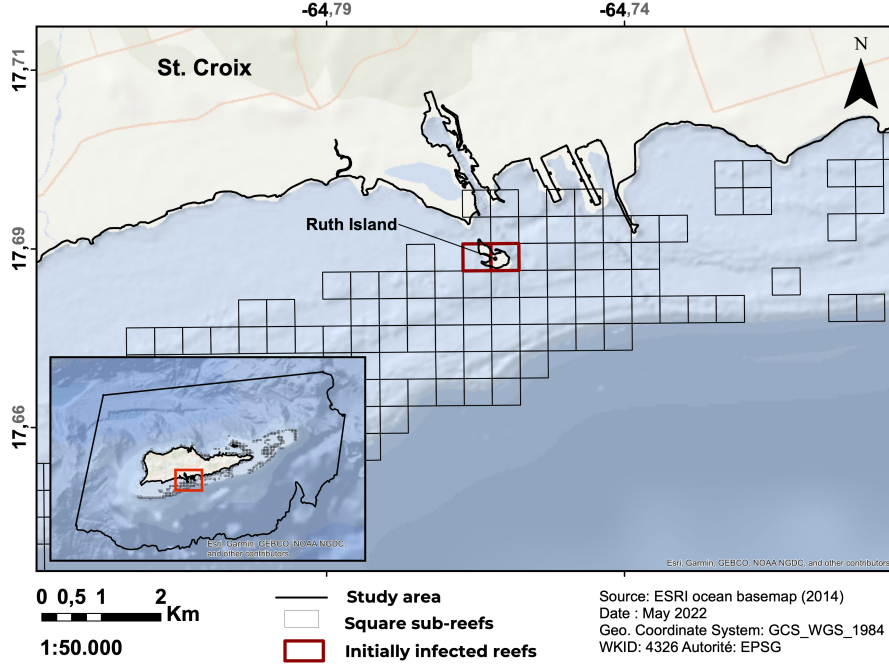


Figure 20: Location of the sub-reefs that are initially infected in the epidemiological simulations.

2.6.4 Comparison with field observations

In the absence of quantitative data describing the spread of the SCTL D among coral reefs around St Croix, we assess the quality of the epidemiological results by comparison with monthly extent diagrams (similar to those shown in Fig. 5) shared by the Virgin Islands Coral Disease Advisory Committee (VI-CDAC). These diagrams provide the area of progression and the current extent of the disease, based on field surveys for each month between January 2019 and June 2021. In order to visually assess the correspondence between the results of the modelling process and these observations, we compute the convex hulls of the sub-reef polygons according to different criteria regarding their proportion of infectious and removed individuals. The convex hulls are computed with the Graham Scan algorithm at different time steps to produce snapshots that can be directly compared with the extent diagrams.

3 Results

In this section, we present the results related to the 3 steps of our biophysical modeling approach. First of all, we comment the outputs of the hydrodynamics model. Then, we focus on the results of the connectivity analyses for the different buoyancy behaviors. Finally, we address the results of the epidemiological model.

3.1 Hydrodynamic model

First, we assess the quality of the salinity and the temperature of the water. To do so, we verify the behaviour of the UML at a small depth spot (64.80°W 17.65°N), and we check the stratification of their profiles at a greater depth spot (64.90°W 17.84°N). The period of simulation extends from August 1 to October 30, 2020. However, the first 10 days of the simulation are not taken into account to produce the following results. This choice is made to account for a spin-up phase of the model (cfr section 2.4.2).

Figure 21 shows the temperature and salinity means and standard deviations over the simulated period. The temperature curve appears to be quite stable through time, whereas the salinity shows a standard deviation that progressively decreases with depth. Both mean curves are quite stable over the first 5 meters and then follow a slight slope.

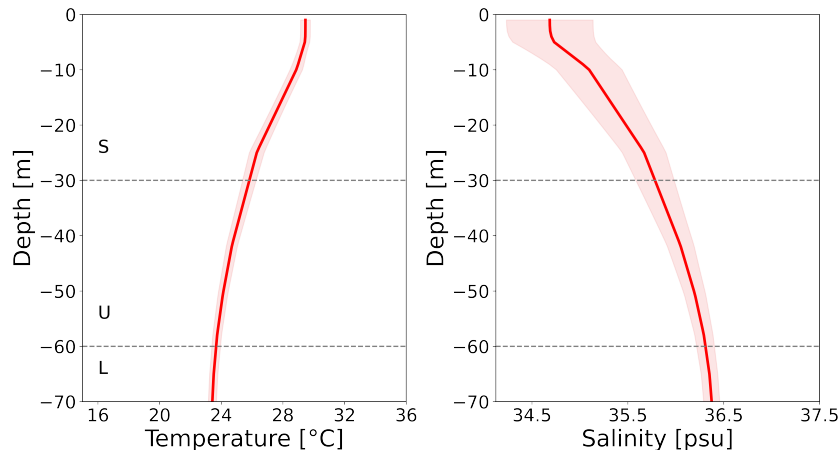


Figure 21: Temperature and salinity profiles at 64.80°W 17.65°N. The red curve represents the average over the simulated period. The pink area shows the standard deviation. Dashed lines separate the shallow depths (S) from the upper mesophotic (U) and lower mesophotic (L) ones.

Figure 22 highlights the stable stratification of both temperature and salinity profiles during the entire period of simulation. These profiles are presented over a depth range of 500m. While temperature slowly decreases with depth, salinity is minimum at the surface and displays a maximum range around 100m. We can observe that both profiles are dotted with slight peaks that tend to be more consequent with depth. However, these small peaks do not seem to disturb the global stratification in both cases. It can be noted that the salinity stratification is high near the surface and lower in depth.

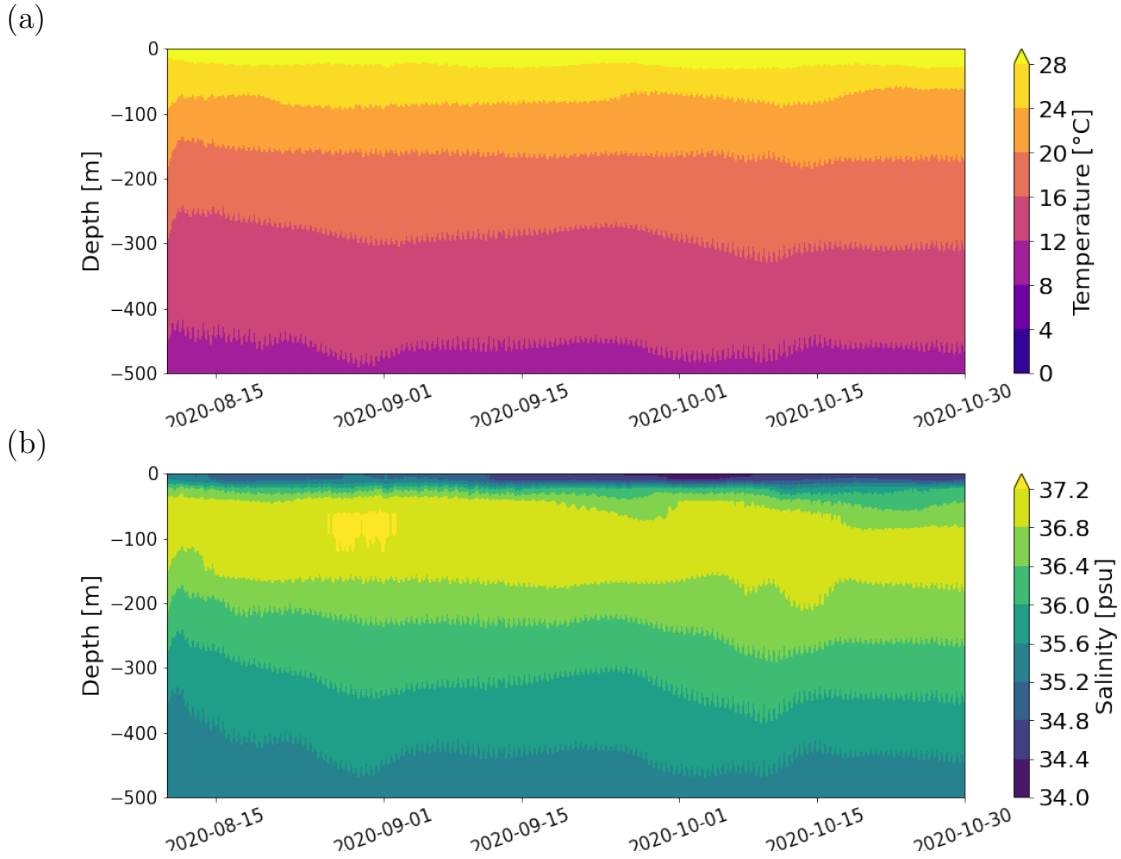


Figure 22: Temperature (a) and salinity (b) profiles through time at 64.90°W 17.84°N.

In a second step, we present the main circulation patterns around St Croix. Figure 23 shows the horizontal velocity field at the surface, averaged over the entire period of simulation. We can observe that the leading currents in the area come from the southeast and hit the southern coast of the island. The circulation is then divided into a western component, highlighted by arrow A, and an eastern component, highlighted by arrow B. The first one is redirected to the west and is later joined by the currents coming from the north of St Croix to form a recirculation eddy, highlighted by arrow C. This eddy is about the same size as the island ($\sim 30\text{km}$) and is clearly distinguished by the very weak currents ($< 0.025\text{m.s}^{-1}$) in its center. On the other hand, the second component is slightly redirected to the east before rapidly turning west to follow the north coast of the island. More generally, it can be noted that the average currents at the surface are relatively slow. The fastest ones are located in the path of arrows A and B and reach 0.2m.s^{-1} .

Figure 24 shows the averaged horizontal velocity field at 60m depth. At this depth, only two circulation features stand out in the study area. We can observe that they start from opposite sides of the island, and then turn clockwise around it. The first one is highlighted by arrow A and heads northwest with currents having an average speed of 0.08m.s^{-1} . The other one is highlighted by arrow B and heads eastward before sloping southwards. The currents in the turn reach 0.14m.s^{-1} . It can be noted that the circulation patterns in depth are totally different from the ones at the surface for the eastern part of the area. However, for the western part, it is possible to find some similarities between the two schemes.

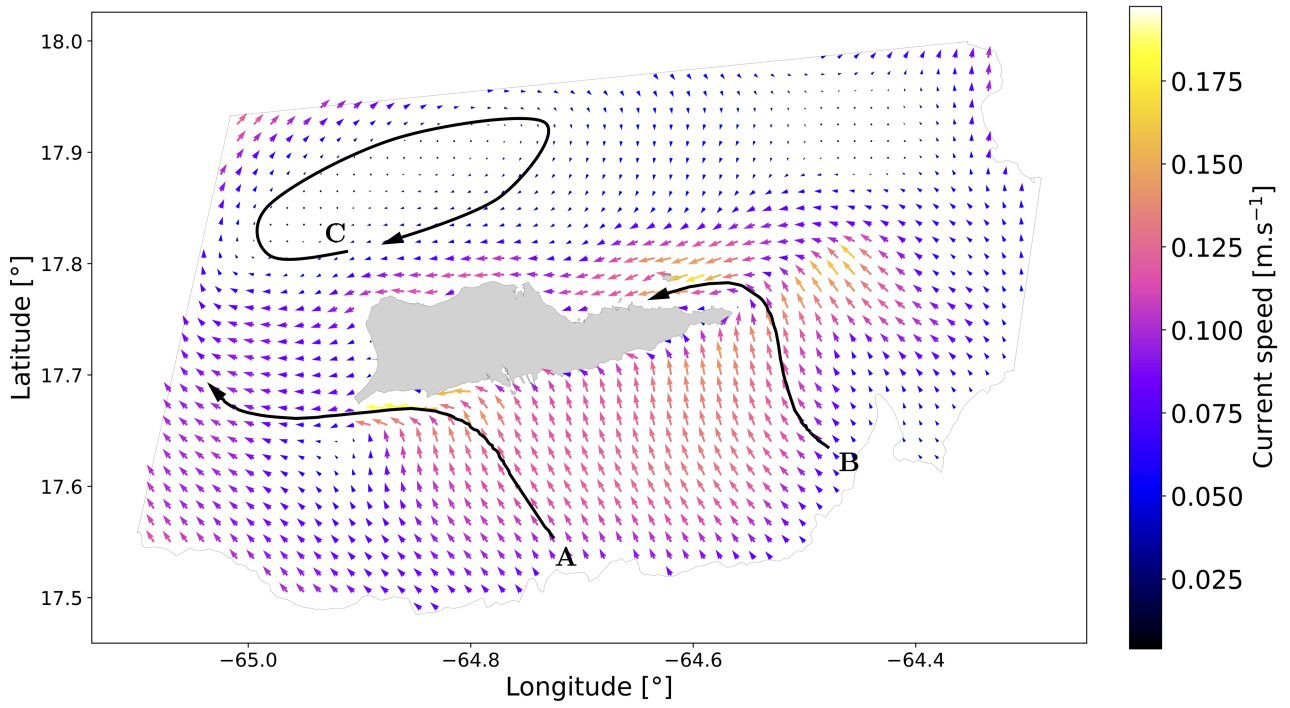


Figure 23: Average horizontal velocity field at the surface of the study area over the simulated period. The large black arrows are added to highlight the main circulation patterns around St Croix.

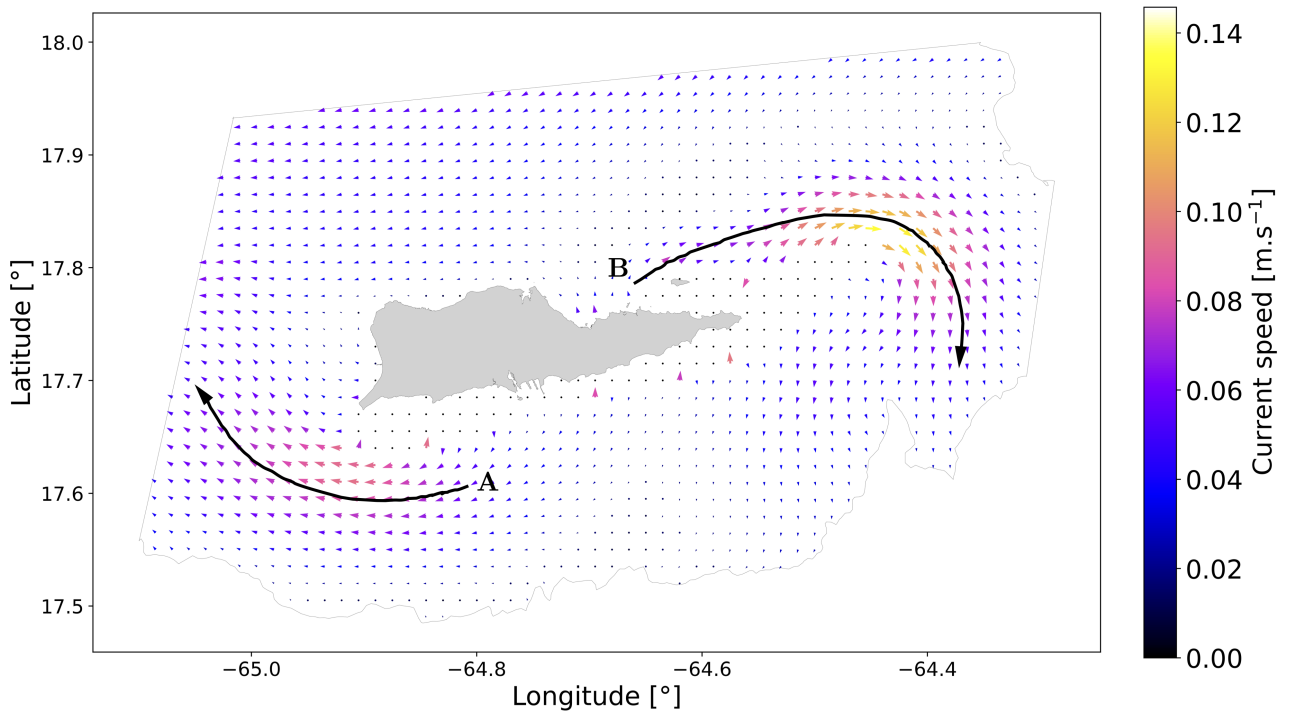


Figure 24: Average horizontal velocity field at 60m depth over the simulated period. The large black arrows are added to highlight the main circulation patterns around St Croix.

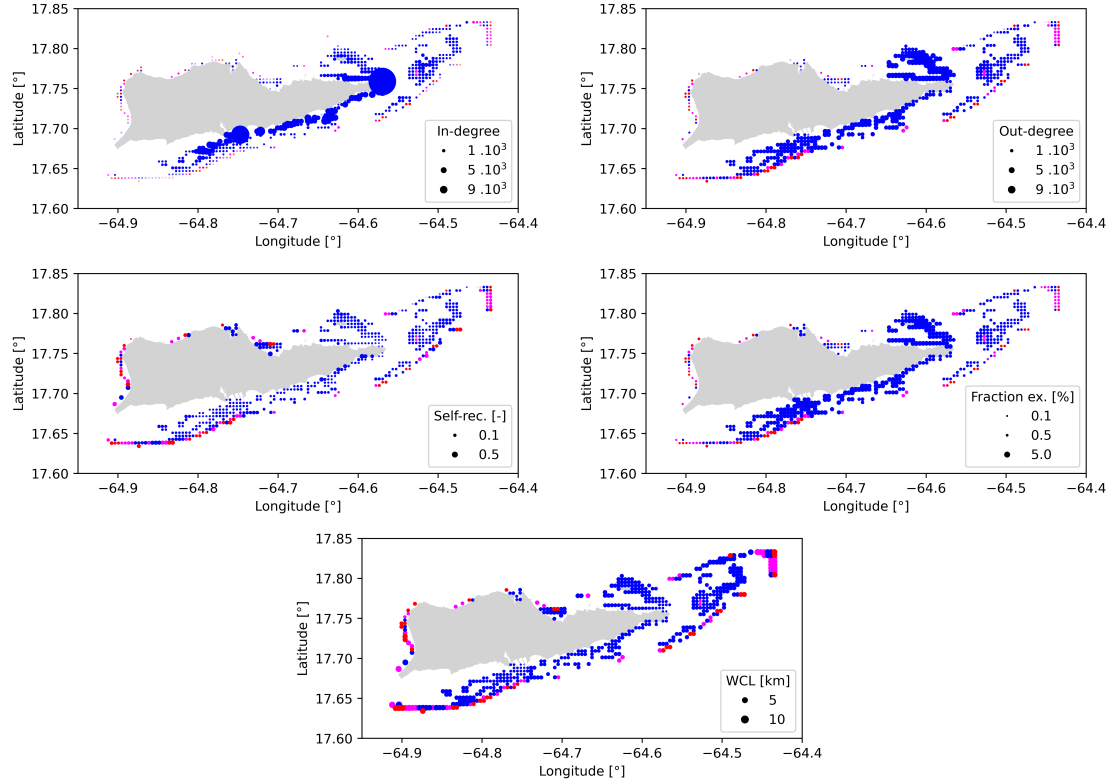
3.2 Coral reef connectivity

In this section, we present the results of the connectivity analysis conducted on the coral network. It must be noted that this analysis is carried out for 5 buoyancy velocities of the disease vectors: -25, -10, 0, +10, and +25 [m.day^{-1}]. However, we choose to omit the results associated to a velocity of +10 m.day^{-1} because of their high similarity to those computed with a buoyancy of +25 m.day^{-1} . These results can be found in appendix B.

The statistical distribution of our 5 connectivity indicators for the 5 buoyancy velocities is presented in Figure 27. What rapidly stands out of these boxplots is that the velocity of -25 m.day^{-1} displays a much larger out-degree (OD) and fraction exchanged (FE) than the four other behaviours. It can also be noticed that these two indicators present several high outliers for a buoyancy of -10 m.day^{-1} . The differences between the 3 other distributions are very small. The in-degree (ID) is also marked by a higher distribution for -25 m.day^{-1} compared to the others. In particular, there is a large gap of a factor 8 between the mean and median, indicating the presence of several important outliers. We can also notice several outliers for +25 m.day^{-1} . On the other hand, the differences between the distributions associated to the 5 buoyancy velocities are smaller for the self-recruitment (SR) and weighted connectivity length (WCL). Regarding the self-recruitment, it can be noticed that negative velocities display smaller medians, as well as more flattened distributions. On the other hand, the WCL is minimal for neutrally buoyant materials and slowly increases with the absolute value of the velocity. Distributions are comparable for buoyancy velocities with the same absolute value.

The spatial distribution of these 5 indicators computed over the entire period of simulation is presented in Figures 25 and 26. The same properties as those highlighted for the statistical distributions can be identified in these graphs. First, the OD and FE are significantly higher for all sub-reefs in the network in the case a buoyancy of -25 m.day^{-1} (Fig. 25(a)). The few outliers associated to -10 m.day^{-1} can also be seen near the eastern tip of the island in Fig. 25(b). Regarding the ID, we can easily identify the huge outliers of the distribution associated to -25 m.day^{-1} . These reefs are located along the southern coast of the island, as well as on its eastern tip. As noticed before, several important outliers are also identified for +25 m.day^{-1} at the same locations (Fig. 26(b)). As these reefs have an important ID, they display a smaller SR. However, the spatial distribution of the SR is rather comparable for all buoyancy velocities. Finally, we can observe that the WCL is rather low for 0 m.day^{-1} (Fig. 26(a)) and that it tends to increase for certain reefs for the other buoyancy behaviours. It is interesting to notice the differences in their locations according to the buoyancy. For instance, the reefs displaying a higher WCL for -10 m.day^{-1} (Fig. 25(b)) are located north and northeast of the island, whereas certain reefs south of the island begin to stand out for -25 m.day^{-1} . In addition, these reefs south of the island display the highest WCL in the network for a buoyancy velocity of +25 m.day^{-1} .

(a)



(b)

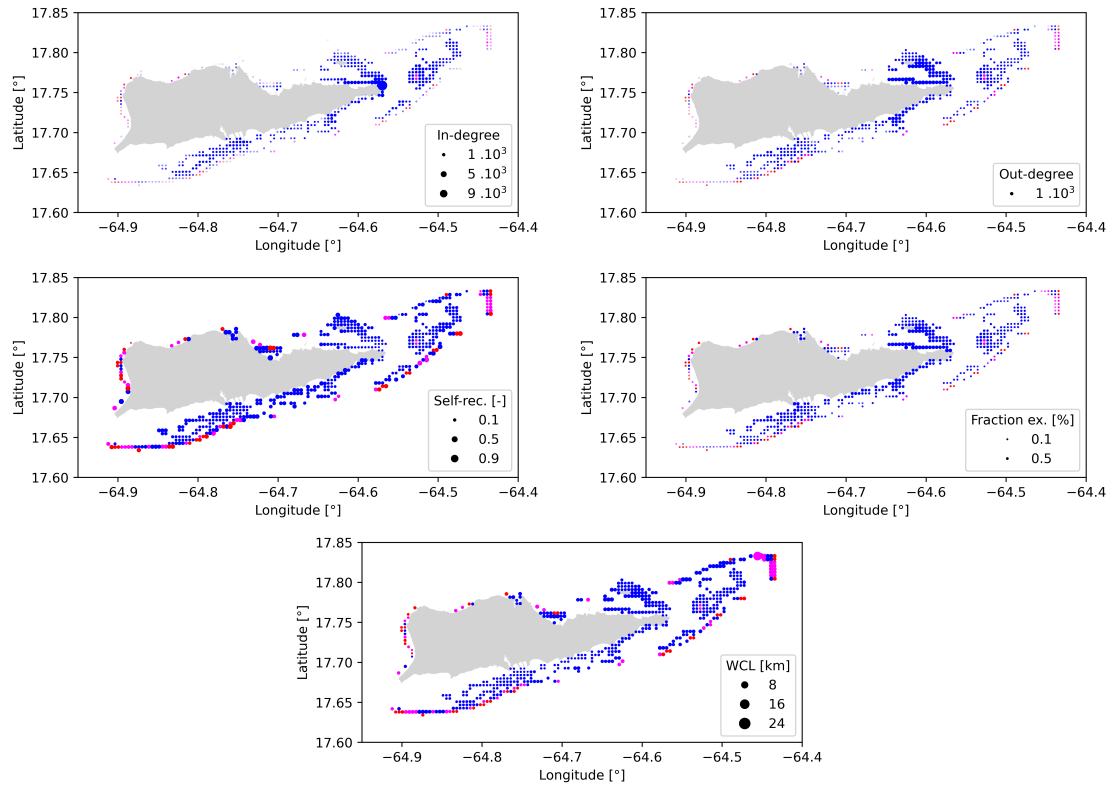
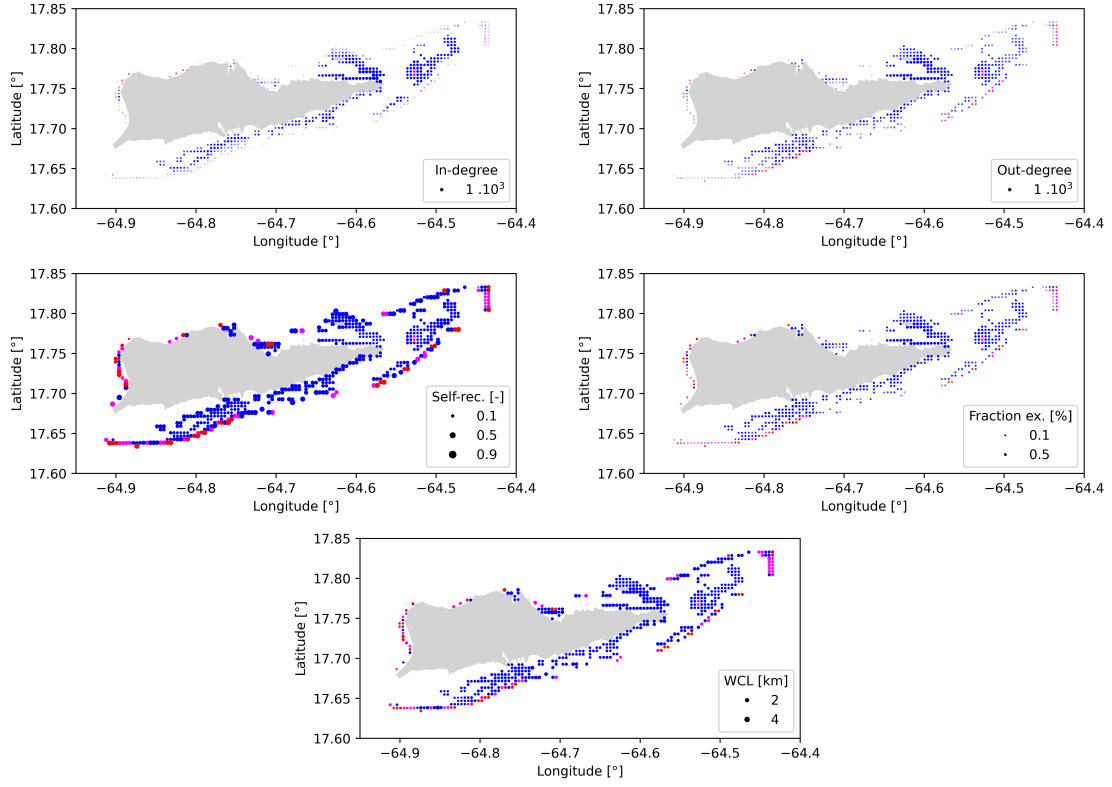


Figure 25: Spatial distribution of the 5 connectivity indicators computed for each sub-reef over the simulated period for a buoyancy of the particles of (a) -25 m.day^{-1} , and (b) -10 m.day^{-1} .

(a)



(b)

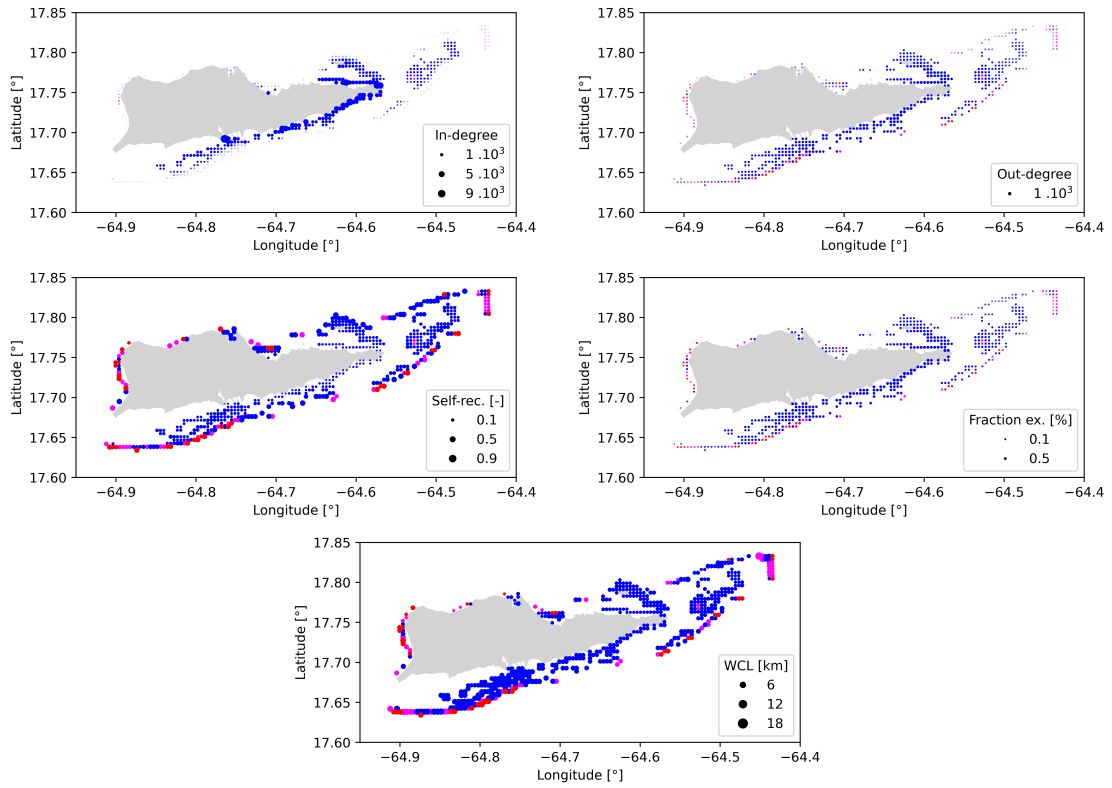


Figure 26: Spatial distribution of the 5 connectivity indicators computed for each sub-reef over the simulated period for a buoyancy of the particles of (a) 0 m.day^{-1} , and (b) $+25 \text{ m.day}^{-1}$.

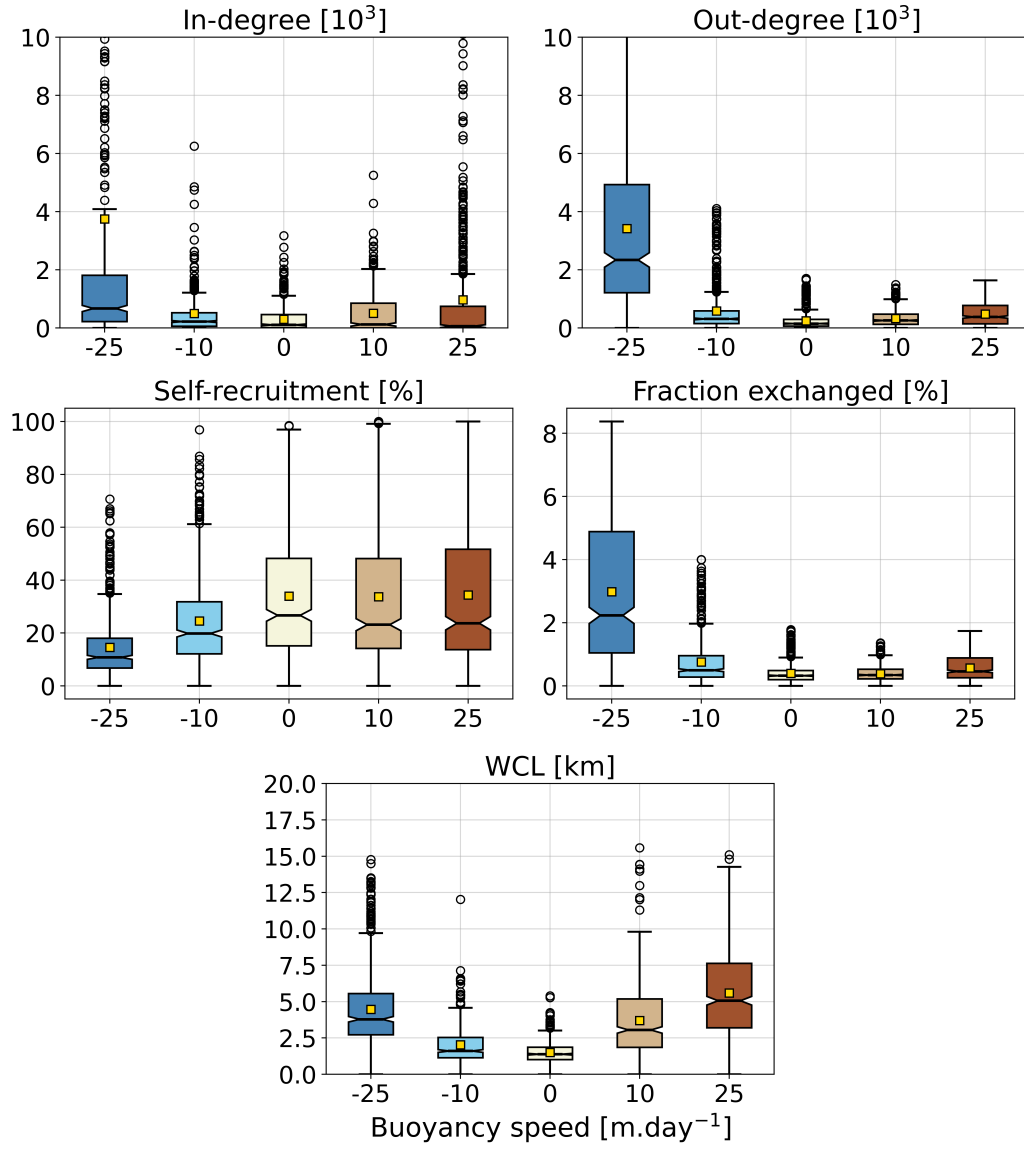


Figure 27: Statistical distribution of the 5 connectivity indicators computed for each sub-reef and for the 5 buoyancy behaviors over the simulated period. Mean values are indicated by yellow squares.

In order to investigate the exchanges between shallow and mesophotic coral reefs, we compute the same indicators between 3 different clusters of sub-reefs (*cfr* section 2.5.3). We show the means of these indicators computed between each pair of clusters in the matrices presented in Figures 28 and 29. It must be noted that these matrices have been scaled to the highest value found among all buoyancy velocities. To refer to a specific connectivity, we will use a code made of two letters. For instance, when addressing the exchanges of infectious materials originating from shallow reefs (S) and reaching upper mesophotic reefs (U), we will use the code SU. The first letter represents the cluster from which the particles originate (referring to the lines of the matrices), and the second one represents the cluster with which these particles interact (referring to the columns).

What appears clearly in these matrices is that the in-degree (ID), out-degree (OD), and fraction exchanged (FE) display significantly higher values for the horizontal connectivity between shallow reefs (SS exchanges) than for any other pair of clusters. This observation can be made for all buoyancy velocities. We can also notice that mesophotic reefs are able to connect with shallow reefs, even though these connections have a lower intensity than those of the SS exchanges. Indeed, the OD and FE corresponding to the US and LS exchanges present non-negligible values, especially for a buoyancy velocity of -25 m.day^{-1} . However, these are one-way connections, as there seems to be no SU nor SL exchanges in the network for these two indicators. The only exchanges originating from shallow reefs and reaching mesophotic reefs can be found in the ID computed for negative buoyancy velocities (Fig. 28). Even though it is difficult to perceive them due to the scaling of the matrices, SU and SL exchanges display non-zero values for both negative velocities. Regarding the horizontal connectivity of each of the 3 clusters, we can once again observe that SS exchanges have a much greater intensity than UU or LL ones, no matter which buoyancy behaviour. Finally, vertical connectivity between mesophotic reefs (UL and LU exchanges) also happens to be very limited in every situation.

The distribution of the self-recruitment (SR) reflects very well the observations made for the connectivity of the entire network. First, it must be pointed out that the SR can only be computed for horizontal exchanges (SS, UU, and LL), by definition. For all buoyancy velocities, the SR of shallow reefs is lower than the ones of both mesophotic clusters, reaching 20-40%. In most cases, the SR of lower mesophotic reefs is highest in the network and reaches 60-70%.

The weighted connectivity length (WCL) is the indicator whose distribution is the most variable according to the buoyancy velocity. For a velocity of -25 m.day^{-1} , the highest values can be found for SL exchanges, with a mean distance of about 12 km. The SU, US, and UL exchanges also score relatively high with average distances of about 8-10 km. On the other hand, horizontal exchanges (SS, UU, and LL) display the lowest mean WCL with values ranging from 0 to 4 km. As for both -10 m.day^{-1} and 0 m.day^{-1} , the distribution of the WCL is very similar to that of -25 m.day^{-1} , excepted that the mean values are almost all smaller than before. Quite apart from that, the distribution for positive velocities shows a maximum WCL of 12km for US exchanges, as well as a high score for LS ones. All connections originating from shallow reefs are rather limited and only reach 6 km at best.

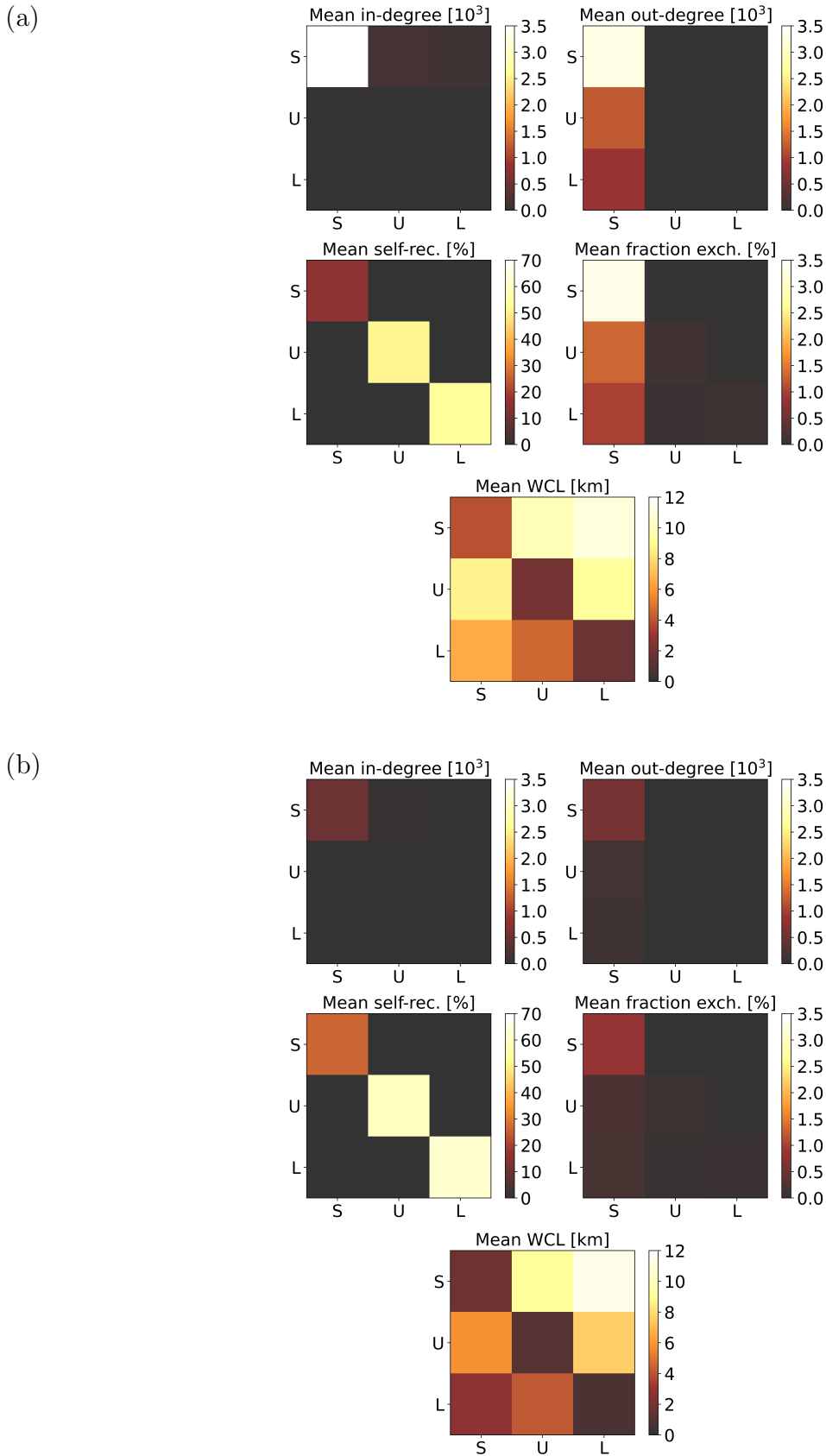
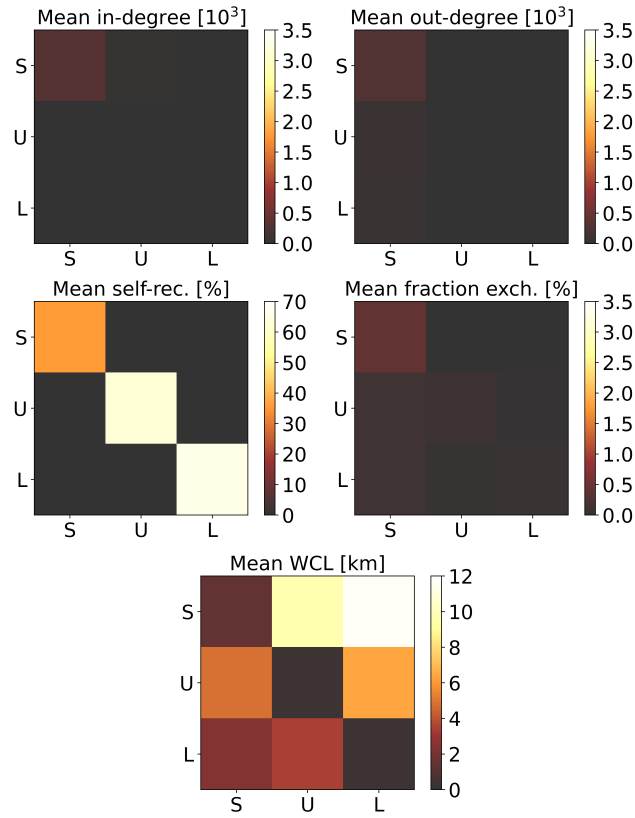


Figure 28: Mean values of the 5 connectivity indicators computed between the 3 clusters of sub-reefs over the simulated period. The clusters consist in (S) shallow, (U) upper mesophotic, and (L) lower mesophotic reefs. Source reefs correspond to the lines of the matrices, whereas sink reefs correspond to their columns. (a) Buoyancy = -25 m.day^{-1} , and (b) -10 m.day^{-1} .

(a)



(b)

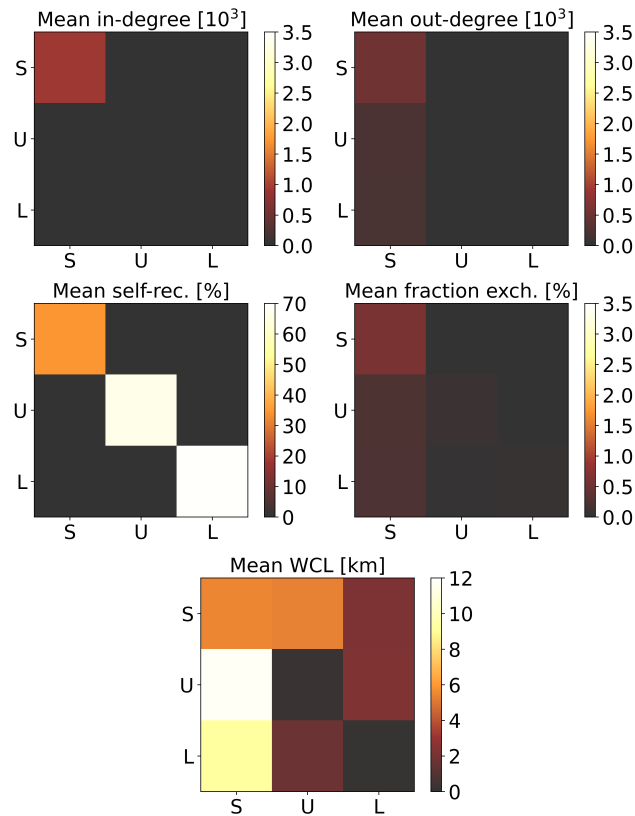


Figure 29: Mean values of the 5 connectivity indicators computed between the 3 clusters of sub-reefs over the simulated period. The clusters consist in (S) shallow, (U) upper mesophotic, and (L) lower mesophotic reefs. Source reefs correspond to the lines of the matrices, whereas sink reefs correspond to their columns. (a) Buoyancy = 0 m.day⁻¹, and (b) +25 m.day⁻¹.

3.3 Epidemiology

In this section, we first address the calibration of the epidemiological model with species-specific data collected in the Florida Keys. Then, we present the simulated spread of the SCTLD around St Croix for the different buoyancy behaviors of the disease vectors.

3.3.1 Model calibration

As the observed fraction of susceptible individuals after a year of disease activity (S_∞) reaches 80.7%, we obtain a basic reproduction number $R_0 = \beta'_0/\sigma = 1.111$ with the help of Eq. [2.36]. Using this ratio, we can express the mortality rate σ in terms of the transmission rate β'_0 and finally find the best value to fit with the compiled prevalence data. In this framework, we assume that the disease activity started on August 17, 2018 with an initial infected population $I_0 = 10^{-4}$. As a result, we find the best-fitting simulated curves with $\sigma = \frac{1}{6.66} \text{ day}^{-1}$ and $\beta'_0 = \frac{1}{5.99} \text{ day}^{-1}$. Comparison between the observations and the simulated curves produced with Eq. [2.35] is shown in Figure 30. The parameters are tuned to best fit the observed Susceptibles curve. We can see that our model performs well, as it is able to reproduce its evolution accurately. However, the observed Infectious and Removed curves are not reproduced with the same quality. Our model overestimates the fraction of removed (dead) individuals by 3-5%, and clearly underestimates the proportion of infectious individuals throughout the simulated period. In fact, the simulated Infected curve fails to take off as the observations suggest (around 2019-05-02), and constantly remains at a very low level.

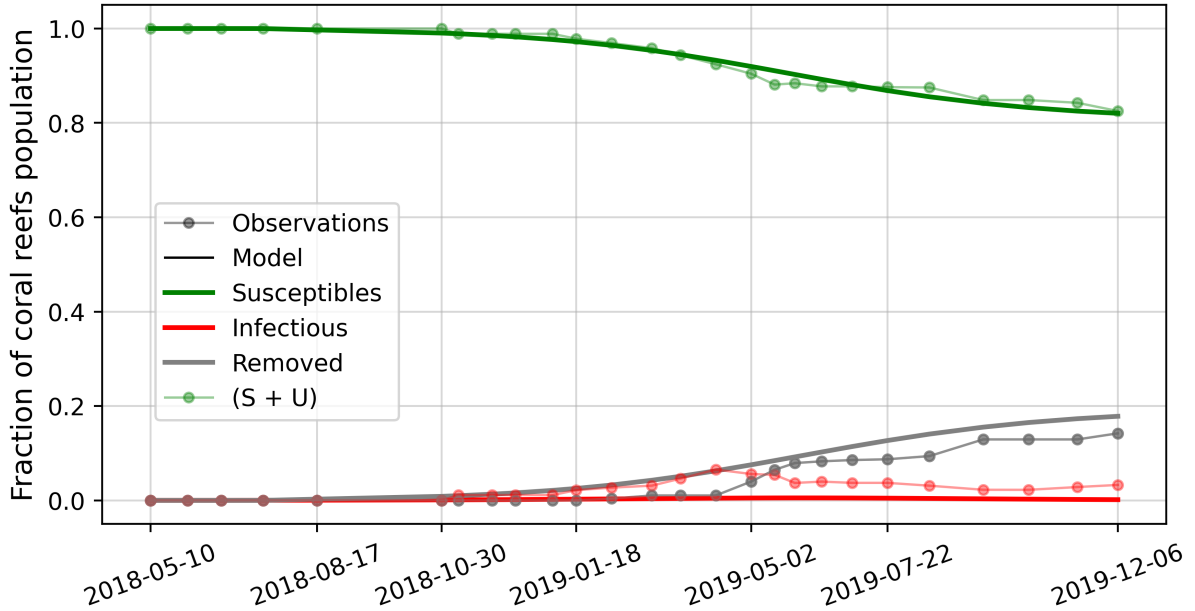


Figure 30: Calibration of the model based on hypothetical SCTLD prevalence data averaged over 6 stony coral species (PAST, PSTR, SSID, MCAV, OANN, OFAV) and weighted by their relative abundance around St Croix. The Susceptibles curve (green) is calibrated to the sum of the observations related to Susceptibles and Unknown individuals (S+U).

3.3.2 Spread of the disease

As for the connectivity analysis, we only present the results associated to 4 buoyancy velocities. The results of the epidemiological simulations carried out for a buoyancy of $+10 \text{ m.day}^{-1}$ can be found in appendix B. The simulated spreads of the SCTL D around St Croix are presented in Figures 31 and 32. The convex hulls showing respectively the areas where intra-reef transmission is significant, and the area where the disease is present (*cfr* section 2.6.4), are computed based on the thresholds $I > 10^{-6}$ and $R > 10^{-6}$.

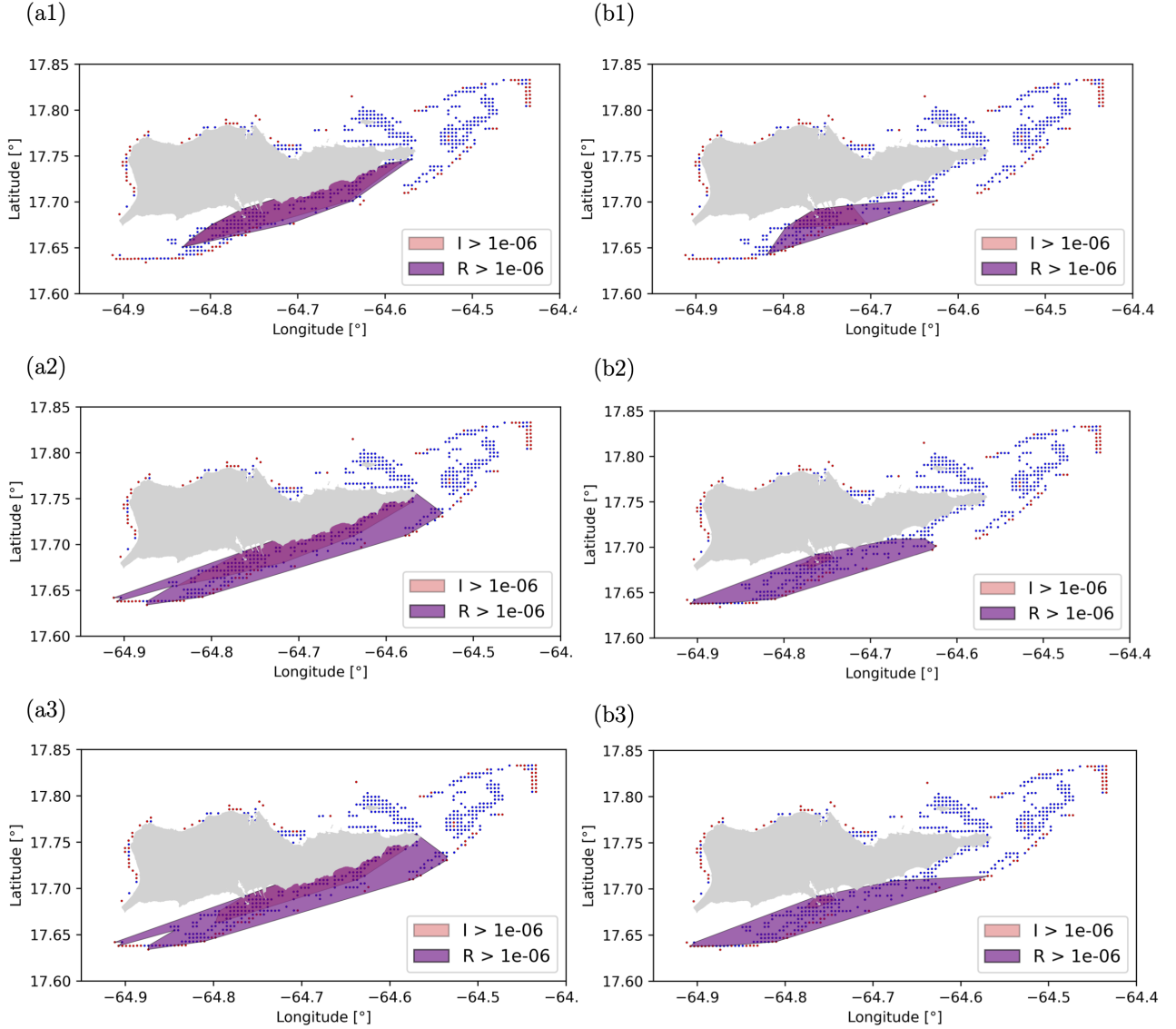


Figure 31: Simulated spread of the SCTL D among the sub-reefs around St Croix for a buoyancy of the particles of (a) -25 m.day^{-1} , and (b) -10 m.day^{-1} . The pink convex hull shows the area where intra-reef transmission is significant. The violet hull shows the current extent of the disease. Snapshots on (1) 2020-08-30, (2) 2020-09-30, and (3) 2020-10-30.

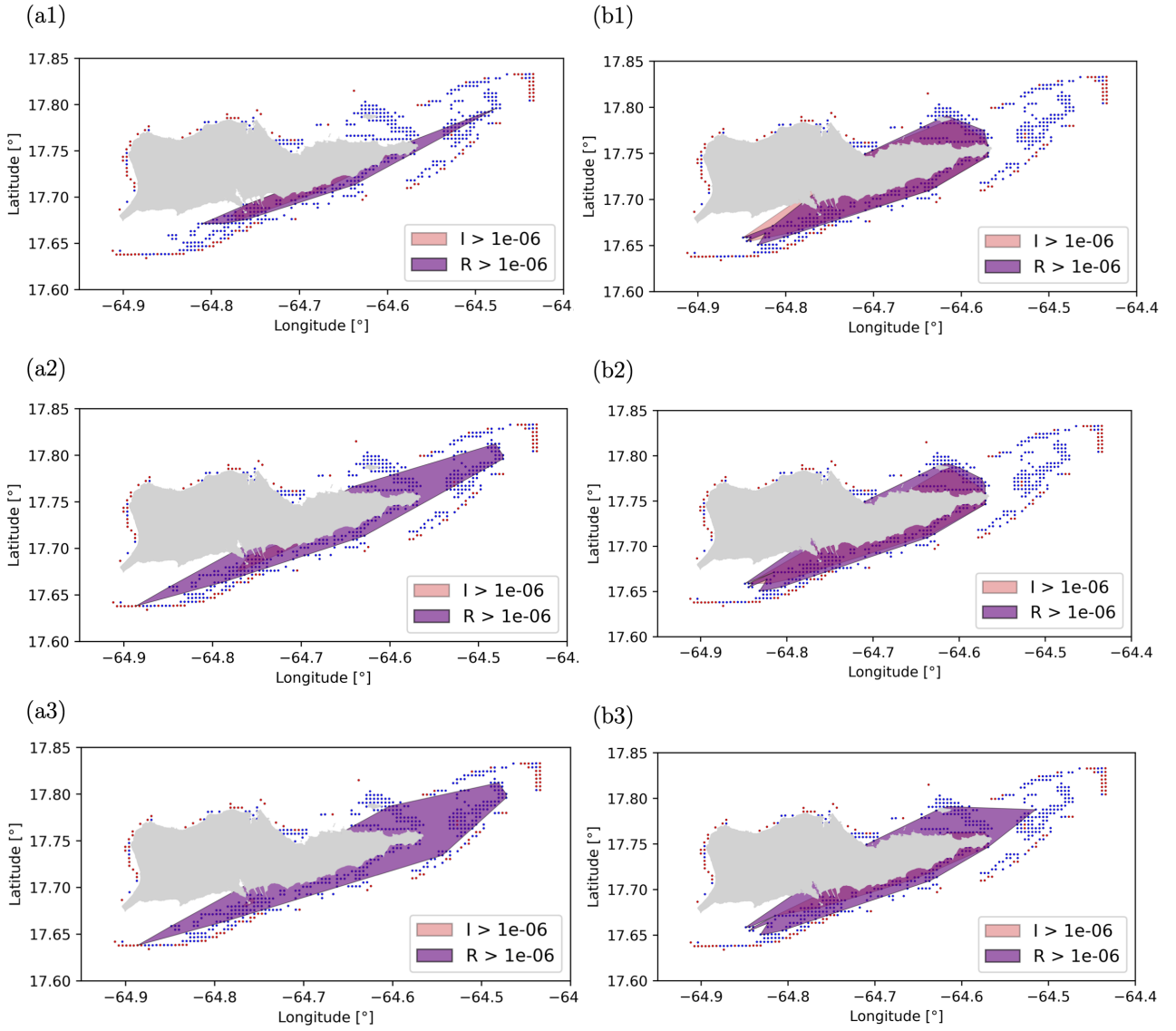


Figure 32: Simulated spread of the SCTLD among the sub-reefs around St Croix for a buoyancy of the particles of (a) 0 m.day^{-1} , and (b) $+25 \text{ m.day}^{-1}$. The pink convex hull shows the area where intra-reef transmission is significant. The violet hull shows the current extent of the disease. Snapshots on (1) 2020-08-30, (2) 2020-09-30, and (3) 2020-10-30.

We can notice that the simulated spreads produced with negative buoyancy velocities (Fig. 31) extend towards the southwest of the island, whereas the spreads associated to positive velocities (Fig. 32(b)) extend to the northeast of the island. On the other hand, neutrally buoyant disease vectors seem to support a propagation pattern that extend both southwest and northeast, following a narrower path. Unsurprisingly, mesophotic reefs seem to be reached by the SCTLD only when its spread is supported by negatively buoyant vectors. In almost all cases, the reefs located in the eastern part of the southern coast of St Croix are reached by the disease rapidly after its start. An interesting feature that can be pointed out is that positively buoyant vectors seem to be able to spread the disease up to the north coast of the island without infecting the reefs located to the east (Fig. 32(b)).

4 Discussion

In this section, we discuss the implications of the results of each step of the biophysical modeling sequence, as well as their limitations.

4.1 Validation of the hydrodynamics

As we cannot provide a quantitative validation of SLIM3D's outputs, it is difficult to assess the quality of the hydrodynamics produced around St Croix. However, it can be noted that the use of USCROMS data as the main forcing is an asset for this master thesis. The fact that this model has been specifically calibrated and validated for the northern Caribbean region gives us confidence in the results we obtained for the area around St Croix. In addition, the observed salinity and temperature profiles at different locations in the study area provide comforting results.

First, we can identify a UML of about 30-40m, which is an expected behaviour for the warm season (June-November) in the region (Smith et al. 2019). The salinity curve presented in Figure 21 shows a reduced temporal variability below this depth, which is the sign of a stable layer decoupled from the one above. In addition, Figure 22(b) shows a significant stratification of salinity in the first 30-40m at a greater depth spot, which is also typical of a short UML. As expected in the USVI waters, these profiles show high salinity and temperature values near the surface, as well as a slow decreasing trend with depth (Chollett et al. 2012).

Secondly, the leading currents represented in Figure 23 correspond to the northward currents caused by the wind-driven circulation in the region (Olbers, Willebrand, and Eden 2012). These currents are an extension of the North Equatorial Current crossing the Atlantic Ocean and are part of the North Atlantic Gyre. The mesoscale eddy highlighted by arrow C in the same figure is produced by the redirection of these leading currents due to their encounter with St Croix. The fact that our hydrodynamic simulations are able to represent this eddy is comforting, especially as it takes place close to the northwestern boundary of the computational domain. In particular, Limer, Bloomberg, and Holstein (2020) have shown that such eddies could have a major impact on coral connectivity pathways.

In conclusion, the qualitative validation carried out for the hydrodynamics suggests that our model is able to reproduce the main oceanic features observed in the region. Obviously, the addition of quantitative *in situ* measurements would be valuable to truly assess the accuracy of our simulations. In the absence of validation data for the perimeter of St Croix, we could for instance evaluate the performance of SLIM3D with USCROMS forcings by validating the hydrodynamics produced for the northern USVI during the same period of simulation.

4.2 Coral reef connectivity around St Croix

Our analysis of the simulated infectious agents exchanges through the coral reef system around St Croix clearly shows that the buoyancy of disease agents has a significant impact on the connectivity patterns. Our results suggest that infectious exchanges are more likely to occur with negatively buoyant material rather than with neutrally or positively buoyant one. However, we find that both global and vertical connectivity are very sensitive to the settling velocity of negatively buoyant particles, which was taken in a range of values up to 25 m.day^{-1} . Regarding the infectious exchanges between shallow coral reefs and MCEs, we suggest that negatively buoyant disease vectors represent a non-negligible threat for upper mesophotic reefs. Based on several connectivity indicators, we however expect the propagation of the SCTLTD among MCEs to be much more localized and slower than among shallow coral reefs.

Based on the statistical and spatial distributions of our 5 connectivity indicators, we find that the disease import and export potentials of coral reefs are much higher for a velocity of -25 m.day^{-1} than with any other behaviour. On the one hand, we know that the out-degree (OD) and fraction exchanged (FE) are two indicators quantifying the export potential of the reefs. In Figure 27, the means of these two metrics associated to -25 m.day^{-1} are respectively about an order of magnitude and about 5 times larger than those of the 4 other velocities. The export potential of coral reefs is therefore increased with similar proportions. Surprisingly, the differences between the distributions of the 4 other velocities are quite smaller. In addition, both indicators display many outliers for a speed of -10 m.day^{-1} , and that these outliers tend to overlook the other distributions. We thus conclude that the reefs' export potential is higher when they release negatively buoyant vectors, with a high sensitivity to the fall velocity up to -25 m.day^{-1} . On the other hand, we know that the self-recruitment (SR) and in-degree (ID) are used to quantify the import potential of the reefs. A low SR reflects a higher proportion of interaction with external materials, whereas a higher value of this indicator is associated to a higher isolation of the reefs. Once again, negative velocities stand out of the lot with smaller medians (up to 30%) and more flattened distributions (up to 60%), meaning that the reefs are less isolated with these behaviours. However, the distributions of the ID suggest that the import character of the reefs is only increased for -25 m.day^{-1} , as well as for a few outliers associated to $+25 \text{ m.day}^{-1}$. In particular, we observe a gap of a factor 8 between the mean and the median of the ID for -25 m.day^{-1} . This result reflects the presence of several large importers in the network that significantly increase the mean of the distribution. Finally, the weighted connectivity length (WCL) gives the average disease-vector connection length for each sub-reef. This indicator is minimum with neutrally buoyant materials and increases with both positive and negative speeds. This result is expected for positive speeds, as the disease vectors tend to be more often transported near the surface by the stronger wind-driven circulation (Olbers, Willebrand, and Eden 2012). However, the outcome is rather surprising for negatively buoyant materials as the ocean middle and bottom layers are usually less energetic than the surface layer.

To explain these results, it is important to remember that we assumed that a disease vector can transfer disease material to a reef if it is less than 10 m above that reef as it travels over. This 10m threshold parameter hence defines a range above the reefs out of which the deposition of infectious mass is impossible when particles pass over them (*cfr* section 2.5.2). Consequently, infectious exchanges are more likely to occur with negatively buoyant vectors. Due to their constant fall in the water, they tend to be more often within the range of interaction of the reefs, which increases their chances of infecting them. As a result, negatively buoyant materials are substantially favoured to provide a higher connectivity in the coral reef network. Unfortunately, this threshold must be chosen arbitrarily, as the processes of infectious material exchanges between the vector and the reefs have not been clearly identified yet (Aeby et al. 2019; Muller et al. 2020; Dobbelaere et al. 2020; Meiling et al. 2021).

On the other hand, the sensitivity of connectivity to the fall velocity can be explained by looking at the spatial distribution of the indicators. First, we can observe that a higher fall velocity simply implies a higher export potential for all reefs in the network by comparing the graphs of Figure 25(a) and (b). The out-degree and fraction exchanged of all sub-reefs are consistently higher for a buoyancy of -25 m.day^{-1} than for -10 m.day^{-1} . However, the explanation is a bit more subtle for the import potential of the reefs. Indeed, the in-degree presented in Figure 25(a) shows a far more heterogeneous spatial distribution. We can observe that only several dozens of sub-reefs along the southern coast and on the eastern tip of the island display an important ID in case of a high fall velocity. All these reefs happen to be located in shallow areas, many of them being easily identified as major importers. What causes this heterogeneity is that particles rapidly fall to the seafloor when they are released in shallow waters. After that, they somewhat get stuck on the reefs and exchange a high amount of infectious mass over time, giving birth to these super importers near the coast. However, this effect is not always as important with a lower fall velocity, as the particles are carried away by the currents before settling on the seafloor of the shallow areas. This explains why the shallow sub-reefs in Figure 25(b) display far smaller in-degrees at the same locations.

That being said, it should be noted that our results are only representative of coral connectivity at the end of summer 2020. The dispersal patterns of disease vectors may be highly dependent on oceanographic conditions, as well as on their inter-annual variability, even more in the USVI that is a high-frequency hurricane region (Chollett et al. 2012; Foster et al. 2013). In addition, the progressive effects of climate change may also alter considerably the ocean circulation patterns, thereby impacting coral connectivity (Munday et al. 2009; Hoegh-Guldberg et al. 2017; Qihua et al. 2022).

In a second step, we find that negatively buoyant disease vectors represent a non-negligible threat for upper mesophotic reefs. Based on the statistical distribution of our indicators computed between each pair of reef clusters (*cfr* section 2.5.3), we suggest that MCEs are likely to be affected by the spread of the disease. As expected, the mean out-degree, fraction exchanged and in-degree computed for a buoyancy velocity -25 m.day^{-1} (shown in Figure 28(a)) are significantly higher than for the other behaviours. It can be noted that all matrices shown in Figures 28 and 29 are scaled to the highest values found among all velocities. For all matrices, shallow-

shallow (SS) exchanges¹² display higher values than for any other pair of clusters. This result is not surprising given the fact that shallow reefs are much more clustered together, whereas mesophotic reefs are much more distant in the network. We can also observe that both upper and lower mesophotic reefs are able to reach the shallow ones, whether for positive or negative velocities. However, the intensity of these connections are much lower than for SS exchanges.

Apart from that, we are mostly interested in the shallow-mesophotic (SU and SL), as well as the mesophotic-mesophotic (UU, UL, LU, LL) exchanges. First, we can observe that SU and SL exchanges are almost non-existent for all velocities. This result is expected for positive velocities, as positively buoyant materials are rather unlikely to infect mesophotic reefs. Nevertheless, certain SU and SL exchanges become visible in the mean in-degree computed for a velocity of -25 m.day^{-1} . These exchanges can also be perceived for -10 m.day^{-1} , even if the scaling of the matrices makes this much more difficult. Even though their intensity is much weaker than the SS exchanges, this indicates us that we cannot neglect the fact that localized infection processes might take place between shallow and mesophotic reefs, provided negatively buoyant vector support the transmission of the disease. In addition, we must recall that the present connectivity is calculated during the warm season, when the UML is rather shallow (Chollett et al. 2012). It might be possible that the extension of the UML to mesophotic depths during the milder season reinforces these SU and SL exchanges, thereby favouring the transmission of the disease to these depths. Considering the horizontal connectivity between mesophotic reefs, we find once again that the exchanges are rather limited compared to the SS ones, for all velocities. This result suggests that, if infection processes were to occur between shallow and mesophotic reefs, the propagation in the mesophotic network would be much slower than the one observed among shallow reefs.

On the field, several cases of diseased corals have already been identified at mesophotic depths. Brandt et al. (2021) observed SCTLD-affected corals at multiple mesophotic reef sites in the northern USVI and suggest that upper mesophotic reef habitats in this area do not represent a refuge from SCTLD. Williams, García-Sais, and Sabater-Clavell (2021) have assessed the prevalence of the disease at a mesophotic site near Puerto Rico, and have found that the severity of the infections is likely to have severe and long-lasting effects on coral communities. The present study shows that the transport of infected negatively buoyant materials inside the water column threatens the upper mesophotic reefs in St Croix. To have a better idea of the extent of the threat, we suggest to extend our approach to several years of simulation, as this would allow us to take into account the inter-annual variability of the oceanographic conditions on the calculation of the coral network connectivity.

¹²we use the term "exchanges" to refer to 3 indicators: out-degree, fraction exchanged, and in-degree.

4.3 Spread of the SCTLD

Of all our epidemiological simulations, those that best reproduce the observed spread of SCTLD around St Croix involve vectors with negative buoyancy. In particular, we find that the patterns of disease spread between August and November 2020 simply cannot be explained by neutrally or positively buoyant materials. To relate our results to the identified potential disease vectors, we suggest that disease transmission was supported by the dispersal of fine silts eroded around the reefs and transported into the water column. This study supports the hypothesis that sediments play a major role in the transmission of the SCTLD in epidemic areas, and calls for a better understanding of their impact on the disease transmission patterns.

Based on both the simulated spread of the disease and the oceanic conditions in the period of simulation, it is clear that the most probable disease vectors are subject to a negative buoyancy. First, we compare the results presented in section 3.3.2 with the observed spread represented in Figure 33(a). The main spreading pattern that we consider for this comparison is the southwestern path taken by the disease, starting from Ruth Island in early August 2020. This path follows a flattened U-shaped trajectory during the first two months and goes up to the northwest to join the western coast of the island in late November. Even though our comparison stops in late October when our simulations end, we can notice that the spread of the disease goes on to the northwestern coast of St Croix during the following months (VI-CDAC 2022). In addition, we can notice the emergence of another diffusion point of the disease in October. This second point is located north of the island, near Christiansted Harbor, and might have given the start for the infection of the whole eastern part of the area in the following months (VI-CDAC 2022). Given the distance with the initial propagation point, and given the environment in which it emerged, it could be assumed that its appearance was caused by human action and might not be related to the transmission occurring south of the island. Infected waters transported inside the ballast of a ship have indeed been hypothesized several times as being responsible for the first infection cases observed in the USVI (Shore and Caldwell 2019; Staletovitch 2020; Costa et al. 2021). Consequently, we will not focus on this second diffusion point.

Considering the simulated spread of the disease with different buoyancy behaviours, we rapidly see that the spreading pattern mentioned above can only be found in the "disease foot-prints" obtained with negatively buoyant particles. Figures 31(a) and (b) are the only ones to show infected reefs located south of St Croix, including along the path of observations, at the end of October. In contrast, the extents produced with neutrally and positively buoyant vectors are mostly directed towards the northeast of the island. We also find that all extents are rather consistent with the mean ocean currents presented in section 3.1. Neutrally and positively buoyant materials are carried out by the surface currents, highlighted by arrows A and B in Figure 23. A part of them are redirected to the west where they find no shallow reefs to infect (A), while the other part goes up the southern coast and even interacts with reefs on the north coast (B). On the other hand, negatively buoyant particles follow the course of arrow A in Figure 24 that carries them out along the path where real observations of SCTLD-affected

corals were made. This process is illustrated more clearly in Figure 33(b), where arrows 1 and 2 show the propagation of the disease during the period of simulation and arrow 3 shows the expected evolution for one additional simulated month. In the same figure, we can observe that the convex hulls showing the presence of the disease also extend eastward, which has not been observed. These discrepancies might be caused by several factors, including the fact that our model relies on the potential connectivity of the network, which tends to overestimate the exchanges between reefs (*cfr* section 4.4). In addition, we do not claim to provide an exact picture of the spread of the disease, but only to identify transmission pathways informing us of the possible course taken by different types of disease vectors. Finally, it can be noted that the extents produced with a buoyancy of -10 m.day^{-1} provide results that better correspond to the observations compared to those produced with a buoyancy of -25 m.day^{-1} . Given the limited sensitivity analysis provided for the buoyancy velocities, we suggest that the spread of the SCTLD in late summer 2020 is likely to have been supported by negatively buoyant materials showing a fall velocity of a similar order of magnitude.

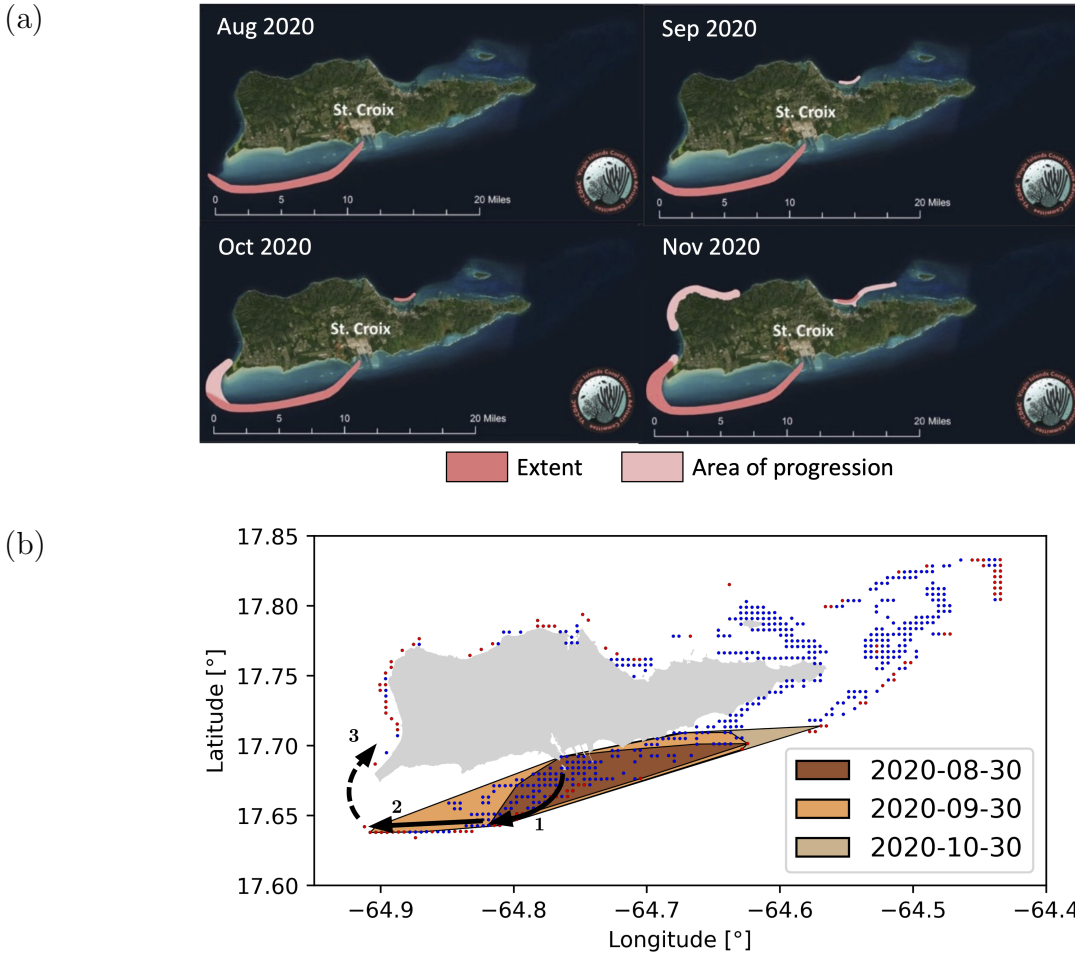


Figure 33: Observed (a) and simulated (b) spread of the SCTLD around St Croix in late summer 2020. In the observations figure, the extent corresponds to the area where SCTLD-affected corals can be found in a given month. The area of progression shows the difference with the extent of the next month. The simulated spread shows the convex hulls of presence of the disease for a buoyancy velocity of -10 m.day^{-1} . Arrows A, B and C are added to highlight the elements of comparison with the observations. Source (a): VI-CDAC.

Among the identified potential vectors of the SCTLD, we find that fine sediments best correspond to the range of fall velocity highlighted by our simulations. Shore and Caldwell (2019) have listed many potential mechanisms of coral disease transmission that could apply to the case of the SCTLD. This list can be split in three categories: direct transmission, vector-borne transmission (where vector relates to living organisms), and water-borne transmission. This last category involves several mechanisms, including the transmission by free living pathogens, by free-floating (a)biotic vectors, or by dislodged pieces of infected coral tissues. Water-borne transmission is currently considered as one of the most likely mechanism explaining the spread of SCTLD. Aeby et al. (2019) carried out aquaria-based experiments, showing that the SCTLD could be transmitted to healthy colonies through the water column. Muller et al. (2020) suggest a contagious mode of transmission of the disease and have shown that the middle layer or the bottom boundary layer of the ocean may be the vertical location in which transmission occurs. Dobbelaere et al. (2020) support these latter results by emphasizing the importance of mean barotropic currents in the transmission of the SCTLD in the Florida Reef Tract. Finally, Rosales et al. (2020) suggest that the causative agents of the SCTLD could be transported within fine sediments, such as silts, especially in epidemic areas, i.e. where the disease has been spreading for less than one year. The importance of sediments as a vector of SCTLD agents is also emphasized by Studivan et al. (2022), who conducted a successful *ex situ* transmission assay with two methods of sediment inoculation. Fine sediments are easily eroded around coral reefs in shallow areas and can be transported inside the water column by the ocean currents. In this context, we try to relate our results with the fall velocity of different types of sediments. The particle settling velocities can be computed thanks to the formulas proposed by Soulsby (1997) and adapted for extremely fine grain sizes by MacDonald et al. (2006):

$$w_s = \begin{cases} \frac{\nu}{D} \sqrt{107.33 + 1.049 D_{gr}^2} - 10.36, & D_{gr} \geq 0.672 \\ \frac{\nu}{D} 0.0077 D_{gr}^2, & D_{gr} < 0.672 \end{cases} \quad (4.1)$$

where $\nu [m^2s^{-1}]$ is the kinematic viscosity of the fluid, $D [m]$ is the sediment grain size and D_{gr} is a dimensionless sediment grain size. Table 5 gives typical ranges of fall velocity of 4 types of sediments, based on Eq. [4.1] and characteristic diameter ranges. As we found a fall velocity in the order of 10 m.day^{-1} (10^{-4} m/s), we can associate the disease vectors to fine silts. This finding supports the assertions of Rosales et al. (2020) and Studivan et al. (2022) and indicates that sediments may have an important role in the transmission of pathogens associated with SCTLD lesions.

Table 5: Typical range of fall velocity (W_s) and diameter (D) for different types of sediments. Source: MacDonald et al. 2006

Sediment	D [mm]	W_s [m/s]
Silts	0.01 - 0.06	0.00005 - 0.0024
Fine sand	0.07 - 0.12	0.0032 - 0.009
Medium sand	0.13 - 0.5	0.01 - 0.07
Coarse sand	0.5 - 1	0.07 - 0.12

4.4 Limitations and perspectives

This master thesis follows a new three-dimensional modelling approach to characterize the spread of the SCTL D. As with all modelling studies, it is subject to many assumptions and limitations. Here we discuss the most important of them and we try to identify the key aspects that could be improved in the future.

First, we base our connectivity analysis on a coral habitat map that overestimates the number of coral reefs in the study area. We built this map based on estimates of different seabed categories by assuming that the whole extent is fully covered by coral reefs. As a result, we implement a certain continuity in the coral distribution that may not be representative of the real conditions. In addition, it can be noted that this assumption has an impact on the whole modelling sequence. Improving the quality of this habitat map should certainly be considered in future studies.

Given the limited time and computational resources, we were constrained to implement a low seeding density in the the Lagrangian transport model. As explained in section 2.5.2, the results of our simulations are thus subject to a non-negligible variability. To bypass this effect, we ran each simulation 3 times and based the subsequent analyses on the average of their results. For further improvement, we suggest to increase the number of these repetitions so as to average out a greater part of the variability associated with the stochastic part of the Lagrangian transport model.

The arbitrary threshold of 10m chosen to limit the range of infectious depositions in the particle tracker represents one of the biggest assumption in this master thesis. Given that we want to assess the differences between multiple buoyancy velocities for the disease vectors, we suggest to carry out a robust sensitivity analysis on this parameter to evaluate its impact on the network connectivity.

Concerning the limitations of the epidemiological model, we could first try to improve the performance of the calibration step, especially for the Infectious and Removed populations. In particular, the simulated dynamics of the disease underestimates the proportion of infectious organisms, which can have a significant impact on the transmission patterns of the disease. We believe that these discrepancies are related to the simplicity of the SIR model and the calibration equations. On the other hand, the transmission parameters found in this thesis are comparable to the ones found by Dobbelaere et al. (2020) for the Florida Reef Tract. Strong similarities in the behaviour of the SCTL D between the US Virgin Islands and Florida are also supported by Meiling et al. (2021). As a further improvement, we consider to develop a more complex epidemiological model implying a new compartment dedicated to pathogens, such as the one described by Tien and Earn (2010).

Another thing to point out is that by restricting our approach to the surroundings of St Croix, we neglect the exchanges that might occur with the neighbouring islands. Some aspects of coral connectivity in the region may therefore be overlooked. We suggest to reproduce the approach on a broader region, including for instance the northern USVI, the British Virgin

Islands and Puerto Rico. In addition, extending the approach over a longer period would allow us to try to reinforce our conclusions. In this framework, we could get more insights into the characterization of the disease agents, as well as concerning the threat to upper MCEs.

Furthermore, we could try to provide an additional sensitivity analysis on the infection threshold I_0 used in the epidemiological model. Such an analysis has been carried out by Dobbelaere et al. (2020) and has highlighted the importance of this parameter in the simulated transmission rates of the SCTLD.

Finally, we could try to take into account the inter-species variability of susceptibility to the SCTLD in the epidemiological model. For now, we simulate the spread of the disease inside a network in which all elements display the same mean susceptibility, which is far from real conditions. With further development, we could consider different categories of susceptibility and vary their proportion from reef to reef. We could then correlate the susceptibility distribution with the observed species distribution on the field.

5 Conclusion

Eight years after the first cases of infection in Florida, the causative agent(s) of the Stony Coral Tissue Loss Disease and their potential vector(s) are still poorly understood. However, the SCTLD is now considered as the largest coral disease outbreak on record and has been observed at multiple mesophotic coral reef sites in the Caribbean. The aim of this study was to characterize the potential vector(s) of the disease by reproducing its propagation dynamics in the southern USVI in late summer 2020, by means of a biophysical modeling approach. In addition, we evaluated the potential for upper mesophotic reefs to be reached by the disease.

The first step of this approach consisted in simulating the hydrodynamics around the island of St Croix between August and October 2020. Considering the steep and deep bathymetry of the region, we used the 3D baroclinic multi-scale ocean model SLIM3D. This model simulates the three-dimensional ocean circulation on an unstructured mesh whose resolution can be adapted locally to represent fine-scale topographical features in coral reef areas. The resulting currents were then used in combination of SLIM's biophysical Lagrangian transport model to simulate the dispersal of different pathogen vectors displaying specific buoyancy velocities. The simulated exchanges of infectious material were subsequently recorded in potential connectivity matrices. The last step of the approach involved an epidemiological model made of Susceptible-Infectious-Recovered equations relying on these connectivity matrices to simulate the spread of the SCTLD in the coral reef network. The simulations were then compared to field observations to determine which type of vector was the most probable to have started the epidemic. Finally, a connectivity analysis of the coral network allowed us to assess the extent to which disease transmission processes could occur between shallow and upper mesophotic reefs.

This biophysical modeling approach allowed us to answer the two research questions identified at the beginning of the thesis:

How can we characterize the potential causative agent(s) of the SCTLD and its vector(s) ?

Our simulations best reproduced the observed spread of the SCTLD with negatively buoyant vectors displaying a settling velocity of about 10 m.day^{-1} . In particular, we found that neutrally and positively buoyant vectors were unable to explain the transmission patterns of the disease between August and November 2020. By relating our results with the identified potential disease vectors, we found that the disease transmission is likely to have been supported by the dispersal of fine silts eroded around the reefs and transported inside the water column. We therefore support the hypothesis that sediments play a major role in the transmission of the SCTLD in epidemic areas. In addition, we call for a better understanding of their impact on the disease transmission patterns.

To what extent are the upper mesophotic coral ecosystems of the USVI threatened by the spread of the SCTLD ?

Our connectivity analyses showed that negatively buoyant vectors represent a non-negligible threat for upper mesophotic reefs. Based on several connectivity indicators, we however expect the propagation of the SCTLD among MCEs to be much more localized and slower than among shallow reefs. In addition, we found that the buoyancy of the particles has a significant impact on the connectivity patterns of the network. In particular, we showed that coral connectivity presents a high sensitivity to the settling velocity of the particles, which was taken in a range of values up to 25 m.day^{-1} .

Taking a step back, we identified several limitations and perspectives of this study. A substantial improvement of the approach could be provided by gathering more information about the spatial distribution of coral species in the area. This would allow us to build a more representative coral habitat map, and would help us integrate more inter-species variability of susceptibility to the SCTLD in the epidemiological model. This very model could also be further developed by integrating new components dedicated to the pathogens. Finally, we could conduct a few additional sensitivity analyses along the modeling sequence.

This study also has several implications. The connectivity-based method used in this master thesis could bring some insights into the characterization of other marine disease vectors and could provide a valuable complement to field experiments to support the management of coral disease outbreaks. In addition, it could help investigate the importance of infectious exchanges between shallow and mesophotic coral reefs in other areas.

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Appendices

A. Bathymetry

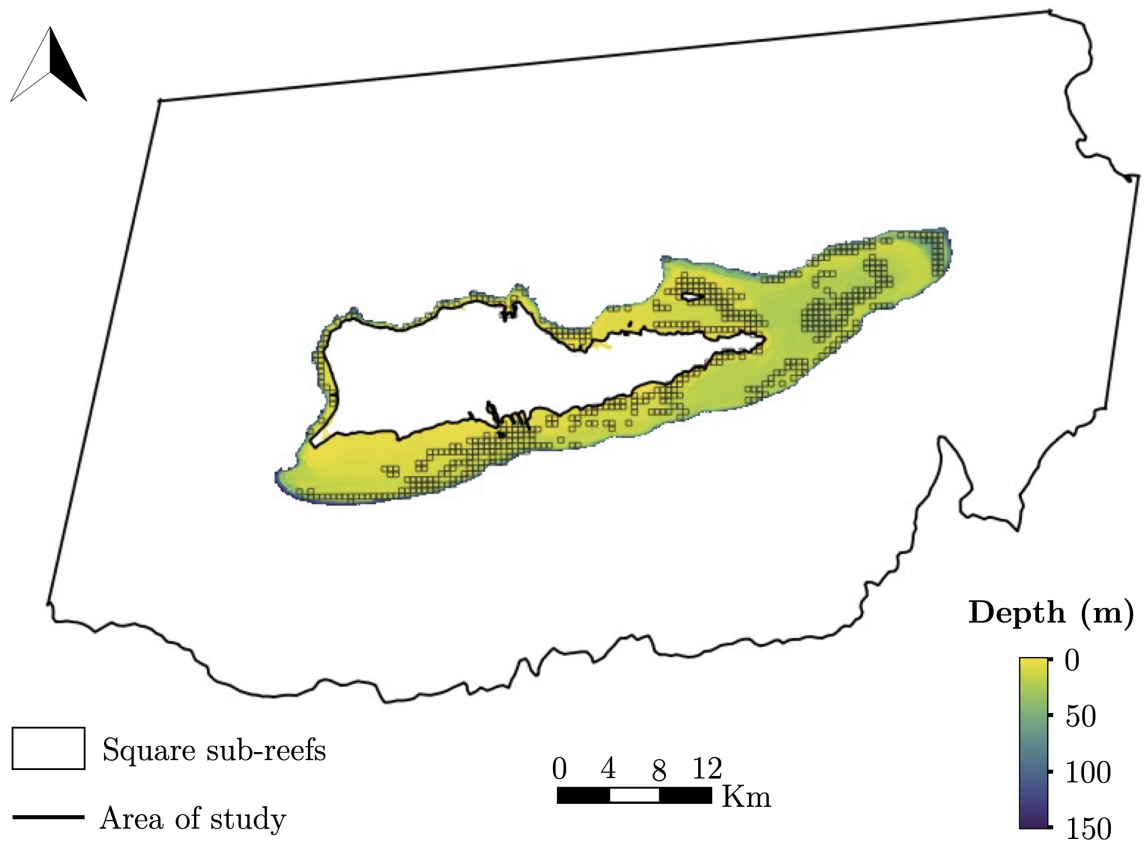


Figure 34: Extent of the high-resolution (10m) bathymetry dataset from the NOAA obtained by lidar measurements.

B. Results for a buoyancy behavior of $+10 \text{ m.day}^{-1}$

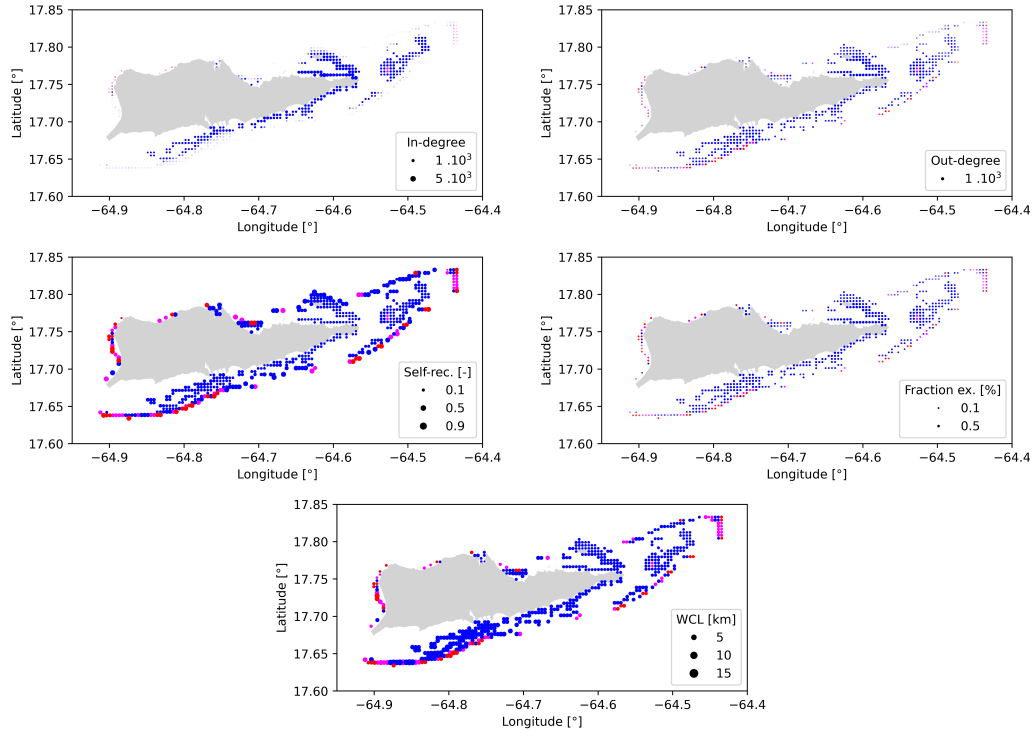


Figure 35: Spatial distribution of the 5 connectivity indicators computed over the simulated period for a buoyancy of the particles of $+10 \text{ m.day}^{-1}$.

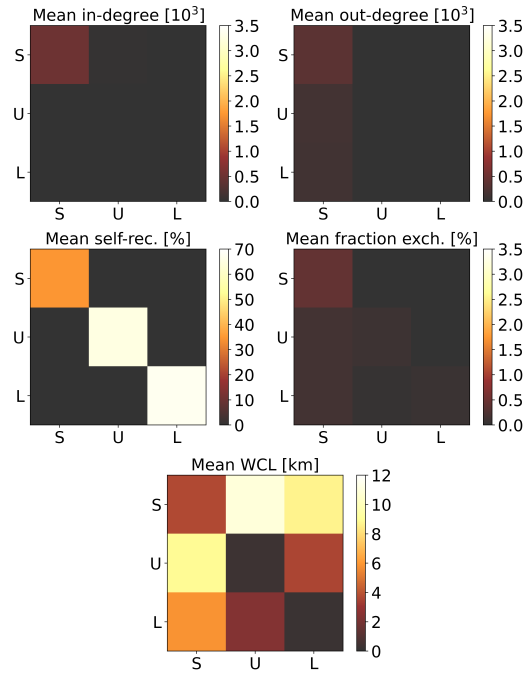
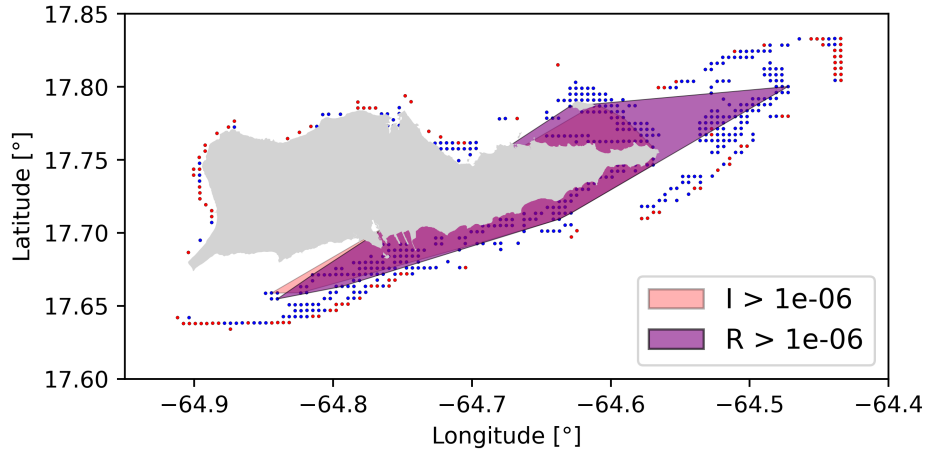
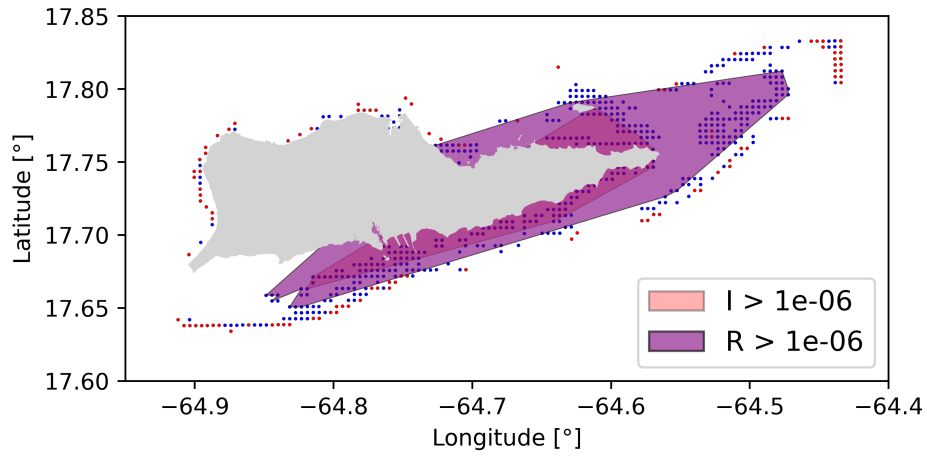


Figure 36: Mean values of the 5 connectivity indicators computed between the 3 clusters of sub-reefs over the simulated period. The clusters consist in (S) shallow, (U) upper mesophotic, and (L) lower mesophotic reefs. Source reefs correspond to the lines of the matrices, whereas sink reefs correspond to their columns. Buoyancy = $+10 \text{ m.day}^{-1}$.

(a)



(b)



(c)

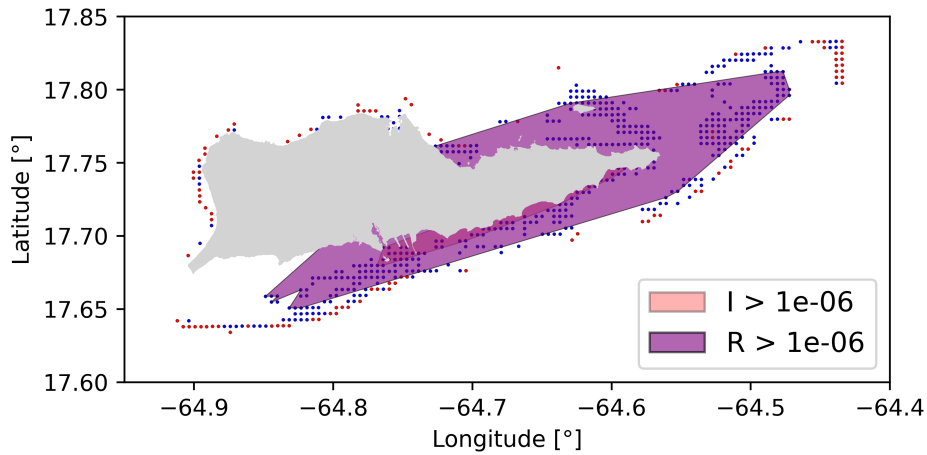


Figure 37: Simulated spread of the SCTLD among the sub-reefs around St Croix for a buoyancy of the particles of $+10 \text{ m.day}^{-1}$. The pink convex hull shows the area where intra-reef transmission is significant. The violet hull shows the current extent of the disease. Snapshots on (a) 2020-08-30, (b) 2020-09-30, and (c) 2020-10-30.

Investigating the transmission of the Stony Coral Tissue Loss Disease among coral reefs in the US Virgin Islands

Colin Scherpereel

Over the last eight years, the Stony Coral Tissue Loss Disease (SCTLD) has spread in the Caribbean and the Gulf of Mexico, leading to significant losses in coral cover and diversity. In the United States Virgin Islands (USVI), it has now become the greatest threat for shallow coral reefs (0 - 30m), even beyond climate change. In addition, the disease has recently been observed at low mesophotic depths (30 - 60m), thereby threatening the refuge potential of upper mesophotic coral ecosystems (UMCEs) for shallow species. However, the causative agent for this outbreak is currently unknown. Here we show how a three-dimensional high-resolution biophysical model coupled with a SIR epidemic model can characterize the potential causative agent(s) of the disease and its vector(s). Based on these findings, we assess the extent to which UMCEs are threatened by the spread of the SCTLD. We assume the disease agents to be transported within different materials (coral mucus, dead tissues, and/or suspended sediments) presenting specific buoyancy behaviors. The results of our simulations emphasize the importance of the disease vectors buoyancy on its propagation pattern. In particular, we find that the SCTLD may be transported by negatively buoyant materials referring to fine silts, and we conclude that the UMCEs are likely to be affected by the spread of the disease. Calibration of our epidemiological model with species-specific parameters gives a mean transmission time of 6.0 days, with a basic reproduction number above 1.1. This study follows a new connectivity-based approach to understand the spread of the SCTLD in the USVI, particularly between shallow coral reefs and UMCEs. More generally, this method could bring some insights into the characterization of other marine disease vectors and could provide a valuable complement to field experiments to support the management of coral disease outbreaks.