The Use of Vertical Distribution Data in the Identification of Potential Spawning Sites and Dispersal Pathways for Parrotfish (Genera *Sparisoma* and *Scarus*) within Territorial Waters of the U.S. Virgin Islands

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Large-bodied parrotfish populations (genera *Scarus* and *Sparisoma*) in the U.S. Virgin Islands (USVI) have declined due to overexploitation. An unanticipated consequence of population declines is macroalgal proliferation at the expense of coral growth, contributing to the degradation of reef complexity. Additionally, small-scale artisanal fisheries centered around parrotfish have collapsed or proceeded to catch smaller and smaller individuals. Previous management strategies have focused on the protection of adult stages of parrotfish through catch, size, and gear limits. However, the success of early life stages of these fish are just as important to the replenishment of their populations.

During early stages, larval fish have restricted swimming capabilities, thus their movements are largely controlled by oceanographic processes. The physical environment of the ocean varies with depth and larval fish are able to move vertically in the water column. Understanding differences in larval fish vertical distributions and the influence of varying oceanographic conditions on their horizontal movements is very important for accurate modelling of their dispersal pathways. Identification of species-specific vertical distributions can be used as representations of vertical movements in biophysical models to more accurately predict horizontal dispersal. Scaridae larvae (genera *Scarus* and *Sparisoma)* were collected in the USVI during National Oceanic and Atmospheric Administration (NOAA) Coral Reef Ecosystems Research (CRER) ichthyoplankton surveys during spring between 2007 and 2009 by the NOAA Southeast Fisheries Science Center (SEFSC) and Atlantic Oceanography and Meteorological Laboratory (AOML).

Vertically stratified ichthyoplankton samples were collected to identify depth-related differences in the abundance of Scaridae larvae. Differences in the vertical distribution of larval Scaridae ontogenetic stages were explored using an analysis of frequencies, and indicated that the greatest abundance of all ontogenetic stages of *Sparisoma* were found between 25 and 50 m. All ontogenetic stages of *Scarus* increased in abundance towards the surface. These patterns in vertical distribution of *Scarus* and *Sparisoma* larvae were used to develop probability matrices of vertical migration (PMVM) for a Backward-in-Time-Trajectory (BITT) model used to identify probable dispersal pathways and potential spawning habitat for Scaridae in and around the USVI.

The BITT model developed in the Connectivity Modelling System (CMS) framework was used to hindcast particles representing Scaridae larvae from CRER survey collection locations between 2007 and 2009 to potential spawning habitat. Model results indicated that the greatest abundance of larval recruits are transported into the USVI from spawning localities outside of the territory; and that an increase in larval retention within the territory occurred in 2009, during the passage of an anti-cyclonic eddy associated with the arrival of a freshwater plume originating from the Amazon River. The results from this study indicate that there is annual variability in dispersal pathways and spawning localities for larval scarids in the USVI, and that connectivity pathways and spawning sites for larvae of this genera are not spatially or temporally explicit. These results will improve our knowledge on the scale of larval dispersal and our understanding of factors impacting larval success in scarids. Thus, improving the decision support system used in the development of local and regional management to efficiently improve depleted stocks for this ecologically important and iconic Caribbean reef fish family.

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I understand that my thesis will become part of the permanent collection of the University of the Virgin Islands Library. My signature below authorizes release of my thesis to any reader upon request.

Kristen A. Ewen

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CONTRIBUTION OF AUTHORS

Kristen A. Ewen did the majority of the model construction, data analyses, and writing of this thesis. Major advisor Dr. Sennai Y. Habtes provided guidance, funding, and support throughout the project. Committee members Dr. Daniel M. Holstein, Richard S. Nemeth and Dr. Trika L. Gerard read several drafts of the thesis and provided beneficial feedback. Additionally, Dr. Trika L. Gerard, a lead researcher at the FORCES lab, provided the data on larval scarids used in the development of the model simulations in this study.

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Kristen A. Ewen

CHAPTER ONE: GENERAL INTRODUCTION

1.1 Territorial Significance of Parrotfish

Parrotfish (family Scaridae) are a family of herbivorous tropical reef fish which assume important ecological niches in nearshore reef communities. By intensively grazing macroalgae, scarids allow for the greater recruitment and growth of scleractinian corals, that are vital to maintaining reef ecosystem health and structure (Horn 1989; Streelman et al 2002; Venkataramani and Jayakumar 2006). During grazing, scarids also haphazardly ingest coral skeletons, resulting in the redeposition of calcium carbonate as newly bio-eroded materials, and reworked sediments (Bruggemann et al. 1996; Bellwood 1995). Reefs with grazing parrotfish show reduced levels of macroalgae on forereefs and assisted in coral recovery, delaying net reef erosion by approximately a decade (Kennedy et al. 2013). Beyond their ecological value, scarids have significant regional economic importance. Parrotfish are an iconic species on Caribbean reefs and their flamboyant colorations lead to increased participation in ocean-related tourism activities like SCUBA diving and snorkeling, which are a major driver of Caribbean island economies (Uyarra et al. 2009; Pittman et al. 2017). Additionally, parrotfish are a target of artisanal fisheries in the Caribbean, particularly the United States Virgin Islands (USVI) (Kojis and Quinn 2004; Toller and Tobias 2007; Thyresson et al. 2011). Making parrotfish in the USVI a valuable resource both economically and ecologically. Among island-scale artisanal fisheries, parrotfish were found to be traded at all market scales (local consumers to international buyers) for a multitude of purposes, and at a variety of sizes (Aswani and Sabetian 2010; Thyresson et al. 2011). This practice leaves no size refuge from harvest.

1.2 Scaridae Population Decline

Prior to the 1990's, waters of the USVI were relatively abundant with schools of large-bodied parrotfish and hosted spawning sites for grouper, snappers and parrotfish (Kadison et al. 2006; Randall and Randall 1963; Rodgers and Beets 2001). However, advancements in commercial fishing technology occurring in the 1980's led to the increased exploitation of reef fish, diminishing harvestable stocks across the Caribbean

(Jackson et al. 2001). Like many Caribbean islands, the USVI has depleted many of its large grouper and snapper fisheries (Causey et al. 2002; Nemeth 2005; Rodgers and Beets 2001). This has led the approximately 380 artisanal fishers in the region to resort to heavier harvesting of large herbivorous fish, including parrotfish (Tobias 1997). The change in the harvesting of fish from higher trophic levels to those in lower trophic levels in response to decreased fishery landings is a global phenomenon referred to as "fishing down the food chain" (Pauly et al. 1998). This decline in larger bodied predatory reef fish resulted in parrotfish becoming one of the most important reef fish species-groups harvested in the USVI, especially in St. Croix (Toller 2007).

Another response to the noticeable decline in catch rates from traps and other gear in the USVI waters was the development of a gill and trammel net fishery, by artisanal fishermen in St. Croix. The St. Croix fishery is historically larger than the fishery in St. Thomas and St. John. This method of net fishing accounts for a much larger percentage of annual landings of all species than traditional commercial fishing methods utilized in the USVI (Toller and Tobias 2007; SERO 2012). However, due to the placement of nets within migratory corridors between reefs, this method selectively targets large transient parrotfish species and they represent 88% of annual landings. This chronic removal of large individuals greatly impacts the reproductive output particularly in sex-changing species such as parrotfish (Rodgers and Beets 2001; Toller and Tobias 2007).

Concerns over declines in harvestable fish stocks led to the preparation of a Fishery Management Plan (FMP) for federal waters off Puerto Rico and the USVI in 1985. The plan called for more stringent amendments, including annual catch limits (ACL) and accountability measures (AMs), for overfished commercial stocks such as parrotfish of genera *Sparisoma* and *Scarus* (SERO 2012; Monaco et al. 2008). ACLs for the USVI were based on 85% of average parrotfish landings from 1999-2005. Puerto Rico and St. Thomas consistently fell below the recommended ACLs for parrotfish, however, St. Croix's ACL (240,000 lbs.) was exceeded by nearly double for 2006-2008 (402,744 lbs.) (SERO 2012). Agencies, including the National Oceanic and Atmospheric Administration (NOAA), Department of Planning and Natural Resources (DPNR), and Center for Biological Diversity (CBD), concerned with negative impacts to coral

ecosystems due to the decrease in scarid abundances sought to create a gill and trammel net buy-back program, establish minimum size limits (8" for red band parrotfish and 9" for all other parrotfish in St. Croix waters), and prohibited the harvest of blue (*Scarus coeruleus*), midnight (*Scarus coelestinus*), and rainbow (*Scarus guacamaia*) parrotfish in the US Caribbean (Rodgers and Beets 2001, Toller and Tobias 2007). Recent studies addressing the current state of scarids in the territory have identified a greater proportion of herbivorous fishes in comparison to large predatory species, however, the average sizes and overall populations continue to decline (Rogers and Beets 2001, Monaco et al. 2008) Additionally, large-bodied species of scarids in the Caribbean such as the blue, midnight, and rainbow parrotfish are now considered rare to locally extinct in the USVI (Rogers and Beets 2001).

1.3 Fisheries Independent Sampling

In the USVI, management decisions for harvested marine fisheries, including parrotfish, are derived from stock assessments. Stock assessments usually utilize diverse types of information including the estimation of abundance, to inform managers of the status of fisheries. However, in the USVI, these estimations of abundance are based on fishery dependent data, which focuses on the number of juvenile or adult fishes removed during commercial or recreational fishing activity (Habtes et al. 2014). To achieve effective management, all life history stages, especially vulnerable early life stages should be considered. During early stages (i.e. egg and planktonic larvae), successful growth and survival can contribute to a ten-fold difference in the number of recruits surviving to catchable size (Houde 2009). Thus, the success or failure of fish during these early stages strongly influences the abundance of year-classes recruited to the population which impact stocks and future fisheries harvest (Houde 2009).

Fishery-independent data collections utilize standard fishing techniques at established locations to forecast larval supply and recruitment (Ingram et al. 2010). To fill gaps in stock assessments, abundance data used in management should be a conjunction of fishery-independent and -dependent data to represent the entire life cycle (Maunder and Punt 2004). One of the most common forms of fishery-independent sampling are large scale systematic surveys focused on the collection of larval fish. Since

2007, the National Oceanic and Atmospheric Administration (NOAA) Atlantic Oceanography and Meteorological Laboratory (AOML) and Fisheries Oceanography for Recruitment, Climate, and Ecosystem Studies (FORCES) Lab have conducted these surveys in the US Caribbean. These annual Coral Reef Ecosystems Research (CRER) cruises are fisheries independent sampling surveys in the territorial waters of the USVI undertaken to address limitations in fisheries dependent data collection in this fisheries data-poor region. The CRER surveys routinely collect ichthyoplankton samples using S-10 neuston, Sub-surface Bongo, and Multiple Opening and Closing Net Environmental Sensing System (MOCNESS) sampling. In conjunction with ichthyoplankton observations in the upper 200 meters of the water column, Conductivity- Temperature-Depth (CTD) casts are conducted at each station measuring temperature, salinity, dissolved oxygen, chlorophyll, and colored dissolved organic matter (CDOM). A major focus of the research undertaken here is to develop recruitment indices for commercially important reef fish and improve stock assessments. This includes parrotfish of the *Scarus* and *Sparisoma* genera (Lamkin et al. 2009).

1.4 Ecology of Scaridae

The major genera of Scaridae in the Caribbean include *Scarus*, *Sparisoma* and *Cryptotomus.* Scaridae of the genera *Scarus* and *Sparisoma* are broadcast spawners which utilize a planktonic larva for population replenishment (Claydon, 2004; Farmer et al. 2017). Spawning is an essential life history event which heavily impacts fish stocks by controlling larvae abundances, early larval survival, and recruitment success (Farmer et al. 2017). During spawning, scarids have been observed to utilize pairs, harems, or large groups within home ranges all over reef habitats (Streelman et al. 2002). Additionally, 25% of the Scaridae family are known to form spawning aggregations (Claydon 2004). Aggregations are a group of conspecific fish gathered for the specific purpose of spawning at a predictable time in a particular space (Claydon 2004; Farmer et al. 2017). Scarids will migrate short distances and form aggregations annually, monthly, and, in some species, daily (Nemeth and Appeldoorn 2009). The locations of these spawning events are known as spawning sites. They are just as important as the act of spawning

because sites are chosen to optimize dispersal, minimize egg predation, maximize chances of larvae to find food, and increase the chances that settling larvae will be returned near the point of origin (Johannes 1978; Paris et al. 2007). However, these locations are also targets of heavy fishing due to the accessibility and ease of catching an abundance of large adult fish. In the USVI, many of the known spawning sites of scarids have already been depleted (Toller and Tobias 2007).

Due to the limited mobility of the eggs and fish larvae, they are subject to transport by physical oceanographic processes. The duration of this transport, based on the average duration of the scarid planktonic stage, is estimated to be between 28-53 days (Richards 2005). Following hatching (>25 hours) scarids of both genera grow and develop through several ontogenetic stages including pre-flexion, flexion and post-flexion, developing a functional tail as the notochord forms into the caudal fin (Richards 2005). Due to the functionality of a tail in latter ontogenetic stages, larvae are able to move via active swimming behaviors, and adjust their position in the water column vertically to locate food, avoid predation, and move into oceanographic features that enhance transport to ideal settlement habitats. Vertical migration is essential to reduce larval mortality due to the transport of currents and improve successful recruitment to natal reefs (Paris et al. 2007).

1.5 Larval Connectivity

Most bony coral reef fish such as Scaridae exchange individuals among geographically separated subpopulations during a larval pelagic stage, as adult stages have them confined within the borders of individual reefs (Pineda et al. 2007). This movement of larvae between populations is known as larval connectivity and is important for population replenishment (Cowen et al. 2006). Understanding the population connectivity, particularly the source and sink dynamics, of a meta-population is vital to interpreting how populations respond to natural and/or human disturbances, such as exploitation. Connectivity modelling can be used to further locate additional spawning sites, develop recruitment indices, and identify ecological bottlenecks between source and sink locations (Cowen et al. 2006).

The Connectivity Modeling System (CMS) is a probabilistic, multi-scale particle-tracking model using a stochastic Lagrangian framework coupled with a nested grid technique to approximate the migration and dispersal of marine organisms (Paris et al. 2013). Particles representing individual larvae are used in a simulation of complex larval migrations (Paris et al. 2005) and result in probability estimates of population connectivity (Cowen et al. 2006). Using where larvae move during their planktonic stage establishes the probability of connections/relationships existing between distant populations. These models can be modified to run particles forward-in-time (FITT) or backwards-in-time (BITT) to specifically answer ecological questions regarding the larval points of origin, settlement, and the pathways between over large spatial scales (Batchelder 2006).

To perform realistic dispersal simulations, the CMS requires biological features associated with the focal species and oceanographic features of the study area. Due to the relatively small size of early-stage larvae compared to the vast and complex three-dimensional fluid environment they are contained within, their trajectories are largely controlled by physical factors (i.e. currents, wind, eddies etc.) (Leis 1986; Cowen et al. 2007). To account for the variability in the oceanography of a region, archived ocean velocity data can be run in parallel to simulated larvae in CMS models. Using realistic parameters to design models, improves the strength and accuracy of the model outputs describing the dispersal and connectivity of focal species populations (Paris et al. 2013).

Larval behaviors can also impact the horizontal dispersal of larvae (Leis 1991). Pelagic larval duration (PLD) and larval ontogenetic vertical shifts are just two of the biological characteristics that play a significant role in larval dispersal (Paris et al. 2007). Variation in the length of the planktonic stage and depth of larvae, influenced strongly by controlling environmental conditions that change temporally and spatially, can impact directionality and magnitude of larval dispersal (Paris et al. 2007). To apply these species-specific parameters, biological modules for PLD and vertical distribution were activated in CMS simulations. Additional modules (i.e. mortality and turbulence) were turned on or off depending on their suitability regarding the larval ecology of the focal

species. In recent studies, species differences in vertical distribution of larvae associated with ontogenetic and diel vertical migration were found to exist in marine fish, and impact dispersal patterns, illuminating the importance of vertically discrete larval abundance matrices to the accuracy of connectivity models (Hare et al. 1999; Cowen et al. 2000).

This study was conducted to develop regional larval dispersal patterns and determine potential spawning sites for the genera *Scarus* and *Sparisoma* in the USVI using Lagrangian particle models, which incorporate empirical data collected during CRER ichthyoplankton surveys. Initially, vertical migration matrices were created from vertically stratified ichthyoplankton Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) tows. Identifying the vertical distribution of larvae at different ontogenetic stages provides realistic larval behaviors which may influence larval dispersal models. Backward-in-time-trajectory (BITT) larval dispersal models (hindcasting models) were created using location, date of collection and number of Scaridae collected during CRER cruises. These models will differentiate annual dispersal patterns, determine probable localities of spawning and improve our understanding of population connectivity. Identifying annual variability in larval abundances, survival and spawning localities will improve managers' abilities to establish effective spatial and temporal management.

CHAPTER TWO: DEVELOPMENT OF VERTICAL MIGRATION MATRICES USING VERTICAL DISTRIBUTION OF LARVAL PARROTFISH (GENERA *SCARUS* AND *SPARISOMA)* IN THE VIRGIN ISLANDS

Abstract

Most marine larvae undergo ontogenetic vertical migration, and descriptions of genera-specific vertical distribution can be used to describe these migrations. The vertical distribution of *Scarus* and *Sparisoma* larvae collected during CRER ichthyoplankton surveys surrounding the USVI during the spring of 2007-2009 were analyzed to develop depth discrete data for use in biophysical connectivity modelling. Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) tows were used to perform vertically stratified sampling for 25 m depth bins between 0-100 m. Differences in abundance among genera and ontogenetic stages in terms of depth bins were explored using an Analysis of Frequency (Chi-square). The greatest abundance of all ontogenetic stages of *Sparisoma* were represented in the 25-50 m bin and *Scarus* showed an increase in density towards the surface in all stages, especially pre-flexion individuals (3-7 days old). Vertical distributions of different life stages were used to develop stage-specific vertical migration matrices to aid in the development of realistic bio-physical larval dispersal models. These models can be used to improve the understanding of scarid recruitment patterns and establish appropriate temporal and spatial management to rebuild the stock.

2.1 Introduction

2.1.1 Vertical Migration

Marine larvae interact with a three-dimensional medium, resulting in both vertical and horizontal dispersal patterns (Leis 1991). While horizontal migration has been widely studied, little is known about vertical migrations of marine larvae (Leis and McCormick, 2002). Neilson and Perry (1990), described these vertical changes in depth as a structured response to endogenous mechanisms such as circadian rhythmicity or hormonal signaling, but were further controlled by environmental conditions such as light levels, prey and predator density, hydrological movements and turbulence. The most commonly described vertical distributions in marine larval fish are due to diel and ontogenetic

responses where larvae remain at or near the surface at night and/or during early ontogenetic stages (Oliver and Sabatés 1997).

2.1.2 Significance of Vertical Distribution in Larval Fish

Developing a clear understanding of vertical movement can be just as important as horizontal movement in understanding patterns in dispersal and connectivity in marine larvae (Leis 2007). During the planktonic stage, eggs and early-stage fish larvae, tend to drift due to their inability to control buoyancy or swim effectively under their own power. Horizontal movements of larvae are largely controlled by large-scale physical forces (i.e. wind, currents, temperature etc.) (Cowen and Sponaugle 2009). However, more developed larvae can move shallower or deeper in the water column using active swimming, to position themselves within more optimal oceanographic conditions (Cowen et al. 2006). Changes in depth by larvae also lead to changes in the extent of physical factors the larvae encounter and affect the horizontal dispersal of the larvae by impacting the directionality or velocity of their dispersal (Cowen et al. 2006). Dispersal models which incorporate the relationship between physical forces on the particular morphology and physiology of larvae provide more accurate representations of their distributions and horizontal movements. Realistic three-dimensional models of marine larval transport found that vertical migration profoundly impacts the directionality and velocity of the larvae, which increases the frequency of retention and avoids large bouts of larval mortality (Paris et al. 2007).

Larval dispersal models based on defined biological characteristics, rather than theoretical ones, provides realistic spatial scales of dispersal. Realistic spatial scales of larval dispersal particularly for commercially important species can aid in our understanding of factors affecting variability in their recruitment indices. The establishment of spatial management strategies, such as Marine Protected Areas (MPAs), which effectively protect spawning ground and settlement localities, or movement corridors can improve the stability of recruitment success. Protection throughout the entire life history of a species promotes increased larval dispersal and survivorship allowing for population rebound (Cowen et al. 2006).

2.1.3 Vertical Distribution of Family Scaridae

The increased harvest of parrotfish in the U.S. Virgin Islands (USVI) during the 1980's in response to the depletion of other commercial fisheries has led to the overexploitation of scarid populations in the region (Causey et al. 2002; Rodgers and Beets 2001; Tobias 1997). Following implementation of size and catch restrictions in 1990, the population did not rebound (Rogers and Beets 2001; Monaco et al. 2008). The reduction of recruitment into the territory may be a result of a bottleneck in stock replenishment at the larval stage due to high mortality or reduced larval abundance because of the chronic removal of reproductively active adults (Roberts 1997). An understanding of the vertical distribution of scarids can provide evidence of vertical migration behaviors to create realistic dispersal models to be used to identify the cause of these bottlenecks and where to focus management energy to improve the resource.

The National Oceanic and Atmospheric Administration (NOAA) Southeast Fisheries Science Center (SEFSC) has undertaken fisheries independent sampling surveys, especially in data-poor regions such as the USVI, to develop recruitment indices for commercially important fish. This includes parrotfish of the *Scarus* and *Sparisoma* genera. Since 2007, the NOAA SEFSC Atlantic Oceanography and Meteorological Laboratory (AOML) and Fisheries Oceanography for Recruitment, Climate, and Ecosystem Studies (FORCES) Lab have conducted annual Coral Reef Ecosystems Research (CRER) cruises. During these CRER cruises, scarid larvae were collected in vertically stratified ichthyoplankton samples using a MOCNESS.

Using MOCNESS data collected and enumerated on CRER cruises between 2007-2009, the vertical distribution of Scaridae was described in the USVI (Privoznik 2014). Scaridae larvae were found to be concentrated in the upper 50 m of the water column, rather than between 50-100 m (Privoznik 2014). Additionally, older larvae (later stages) were found in greater abundance at deeper depth bins than younger larvae, which was attributed to these larvae strategically positioning themselves for optimal settlement. Large abundances of younger larvae (early stages) at shallow depths indicate recent hatching from buoyant eggs (25-26 hours of age), which may indicate the proximity of their spawning locations (Richards 2005, Privoznik 2014).

A major focus of the research presented here is to use the vertical distribution of members of the Scaridae family described by Privoznik (2014), specifically highlighting differences between the *Scarus* and *Sparisoma* genera, to create vertical migration matrices to parametrize larval dispersal models. Identification of the frequencies of stage- or genus-specific larvae across their vertical distribution can assist in improving the precision of these biophysical models. Larval dispersal or connectivity models can be used to develop comprehensive management which incorporates the ecology at all life stages, rather than for just the adults. To create probability vertical migration matrices from the vertical distribution described for individuals of the Scaridae family collected during the 2007-2009 CRER ichthyoplankton cruises in the VI, the following objective and sub-objectives were explored:

Objective: To use vertical distributions of larval fish within the Scaridae family (*Scarus* and *Sparisoma*) collected within the USVI to create probability matrices of vertical migration (PMVM) to be used in realistic dispersal model development.

> **Sub-objective 1:** Identify differences in the frequency of larvae of each genus (*Scarus* and *Sparisoma)* within 25 m stratified depth bins from 100 m to 1m collected in territorial waters of the USVI.

> **Sub-objective 2:** Identify differences in the frequency of ontogenetic stages (pre-flexion, flexion, post-flexion) in 25 m stratified depth bins from 100 m to 1m for larvae of the *Scarus* and/or *Sparisoma* genera collected in territorial waters of the USVI.

2.2 Methods

2.2.1 Study Area

Located in the Northeast Caribbean Sea (18.3358° N, 64.8963° W), the U.S. Virgin Islands (USVI) are comprised of three major islands: St. Thomas (STT) (83 km^2), St. John (STJ) (52 km^2) and St. Croix (STX) (218 km^2). St. Thomas and St. John are joined by the Puerto Rican Shelf, a shallow water platform, which also connects them to

the neighboring island groups of Puerto Rico (PR) and the British Virgin Islands (BVI). St. Croix, located approximately 40 km south of St. Thomas, sits on an isolated narrow shelf separated from the other islands by the Virgin Islands Basin, which reaches depths of 4000 m.

National Oceanic and Atmospheric Administration (NOAA) scientists from the Southeast Fisheries Science Center (SEFSC) and the Atlantic Oceanographic and Meteorological Laboratory (AOML) aboard the research vessel Nancy Foster (NF) conducted CRER surveys from March to April in 2007, 2008 and 2009. These surveys lasted between two and three weeks and studied the biological and physical oceanography surrounding the USVI. Cruises occurred on 28 March-09 April 2007, 11-24 March 2008, and 07-20 April 2009. In 2007, surveys were conducted at stations based on a standardized grid at inshore, shelf break, and offshore stations in the waters south of the USVI and BVI, as well as exploratory stations in the Anegada Passage and the Leeward Islands. Additional stations were added in 2008 and 2009 to include areas of St. Croix, north of USVI and BVI and regions encompassing or near to meso-scale features in USVI waters, which impact larval dispersion (Fig. 1).

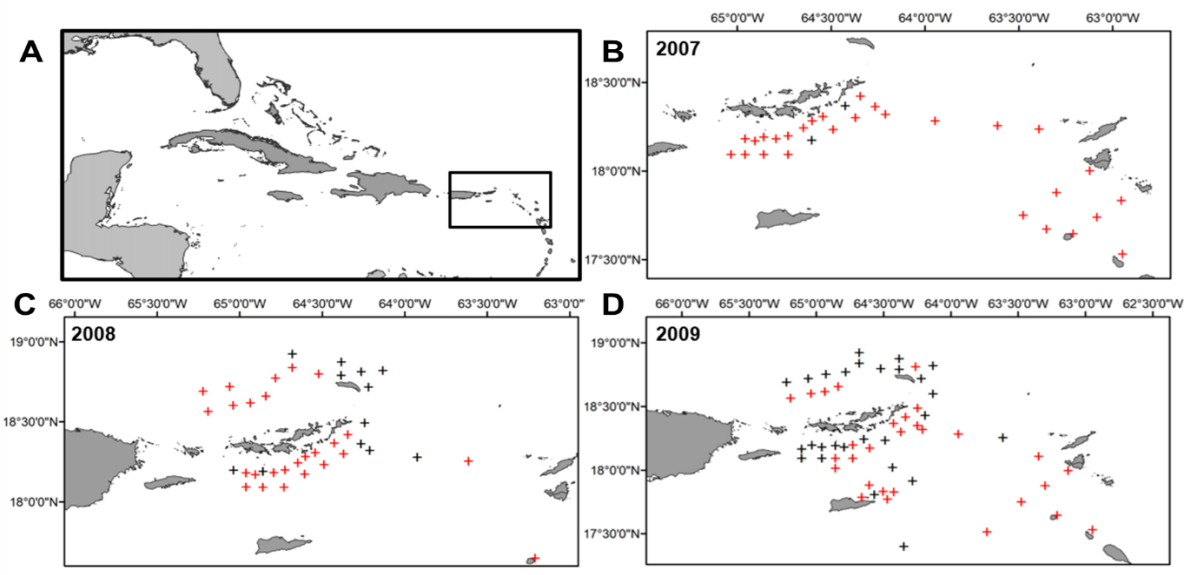

Figure 1 Study region of the USVI and PR inset on map of the Caribbean (a). CRER survey stations indicating MOCNESS sampling between 2007 and 2009. Each year is depicted in a different panel in chronological order left to right (b-d). Red crosses indicate stations where parrotfish species (*Scarus* and/or *Sparisoma*) were collected.

2.2.2 CRER Sampling Gear and Protocols

To understand the vertical distribution of Scaridae (*Sparisoma* and *Scarus*) in this study, only the vertically stratified samples of the CRER MOCNESS surveys were used (Table 1, Appendix A). Other ichthyoplankton sampling methods do not sample at discrete depths, making it impossible to develop data on vertical distribution.

Larval samples were collected by CRER scientists using a MOCNESS with five 0.505-micron mesh nets. At each station, five ichthyoplankton samples were collected between the surface and 125 m during a single MOCNESS tow within a circle of 0.5 mile radius around the station (Lamkin et al. 2009). The depth bins corresponding to each net are as follows: (1) 0-100 m, (2) 100-75 m, (3) 74-50 m, (4) 49-25 m and (5) 24 m sub-surface. A total of 476 MOCNESS samples were collected over the three years (Table 1). The mean volume of seawater filtered for samples from nets 2-5 between 2007 and 2009 was 384.8 ±122.6 m^3 while the mean volume filtered for net 1, collected as the MOCNESS was lowered to depth was 1388.17±194.7 m^3. Samples from net 1 were removed prior to data analysis due to the lack of a discrete depth bin. All nets were rinsed using filtered seawater and all plankton samples from each net were immediately preserved separately in 90% ethyl alcohol.

Table 1 Sampling information from MOCNESS stations during CRER Spring Ichthyoplankton Surveys within the Caribbean (2007-2009).

Year	Sampling Dates	Region Sampled	Number sampled stations	Net Type	Number of Tows	Number of *Scarus* Individuals	Number of *Sparisoma* Individuals	Average Vol. Filt. (m^3)
2007	30 March-07 April	17-18°N / 62-65°W	55	MOCNESS	100	222	1945	555.7±69.5
2008	11 March-24 March	17-19°N / 63-65°W	79	MOCNESS	159	173	1388	343.4±95.2
2009	08 April-20 April	17-19°N / 63-65°W	105	MOCNESS	217	192	1127	332.8±122.6

2.2.3 Laboratory Procedure

Larval fish collected from MOCNESS nets 2-5 during CRER surveys between 2007 and 2009 were identified to the family level by technicians at the FORCES Lab using a Leica MZ12.5 stereomicroscope and dichotomous identification keys (Lamkin et al. 2009). Members of the Scaridae family, distinguishable by long and continuous dorsal and anal fins with slender spines, a pointed snout and small terminal mouth, and a row of melanophores along the base of the anal fin (Richards 2005) were further identified to genus. Species within the Scaridae family are morphologically similar, with the exception of members of the genus *Sparisoma* which have a distinctive pigment on their gut which allows individuals to be distinguished from those of the *Scarus* genus (Richards 2005). However, DNA sequencing is required for identifications to the species level. Thus, for this study, only the genera with commercially exploited species, *Scarus* and *Sparisoma,* were used and the smaller species of the *Cryptotomus* genus were excluded.

Samples were placed into three stage categories indicating their level of development (i.e. pre-flexion, flexion, post-flexion) to examine possible ontogenetic differences in distribution. Stages were characterized by the development of the caudal (tail) fin. “Pre-flexion” or the pre-tail stage is indicated by a straight and pointed notochord. “Flexion” is identified by the notochord’s tip bending dorsally. “Post-flexion” includes the development of the caudal fin following the dorsal bending of the notochord (Miller and Kendall 2009; Richards 2005).

2.2.4 Data Anaylsis (Vertical Distibution)

An analysis of frequency was used to describe the vertical distribution of Scaridae to determine differences in frequencies at different depths. A Pearson’s Chi-Square Test of independence run in R studio was used to determine a relationship between genera and depth bin in terms of scarid count (n). This is to determine if there is variation between the two genera in terms of water column utilization. The same analysis was performed to determine whether there is a relationship between ontogenetic stage and depth bin for the abundance (No./m^3) of both *Scarus* and *Sparisoma*. This is to determine if there is a

difference in vertical distribution between development stages, indicating a potential of vertical migration behaviors. In all statistical analyses used, a significance level of $p < 0.05$ was used as the significance level above which we failed to reject the null hypothesis.

To increase the accuracy of dispersal models for scarids in the VI, probability matrices of vertical migration (PMVM) were constructed. These matrices statistically describe stage-specific probability density distributions identified by the analysis of frequencies in depth of scarids collected. These matrices represent patterns in the vertical distribution of scarids represented by ontogenetic vertical migration which occurs within the species and impacts the horizontal transport of the larvae. Each row (y) in the matrix represents a single 25 m depth bin from 1-100 m. Each column (x) corresponds to a duration of time the column is valid for which corresponds to the amount of time spent by the larvae within each ontogenetic stage (pre-flexion, flexion, post-flexion). Because specific durations of time for each stage are unknown the duration of each stage are estimations based on averaging pelagic larvae durations (PLD) of scarids reported in the literature (Table 2). These estimations of PLD by stage calculated for this study were similar to estimations used in bio-physical models describing *Sparisoma viride* dispersal from Holstein et al. (2014). Estimation of PLD have to be substituted for ontogenetic stage so the model can randomly choose the depth of a particle based on probability during each time-step in the model. The value at each point (x, y) refers to the percentage of larvae that can be found within each 25 m bin at that time interval. These percentages are based on stage-specific vertical distribution from the preceding analysis of frequency.

Table 2 Multi-species pelagic larval durations (PLD) for the genera Scaridae used in the estimation of the duration (days) of each larval ontogenetic stage.

Genus	Species	Stage	Duration	Citation	Duration Estimation (d)
Scarus	-	Hatch	25h	Randall and Randall (1963)	1
Sparisoma	*Sparisoma rubripinne*	Hatch	25h	Randall and Randall (1963)	1
Sparisoma	*Sparisoma viride*	Hatch	26h	Koltes, K. H. (1993)	1
Sparisoma	*Sparisoma viride*	Yoke stage	3	Koltes, K. H. (1993)	1-3
Sparisoma	-	Pre-flexion	?	-	3-7
Sparisoma	-	Flexion	?	-	7-34
Scarus	-	Post-flexion	28-53	Richards, W. J. (Ed.). (2005)	34-51
Scarus	-	Post-flexion	29-42	Ishihara and Tachihara (2011)	34-51
Sparisoma	-	Post-flexion	43- 55	Raventós and Macpherson (2001); Robertson and Warner (1978)	34-51
Other	*Bolbometopon muricatum*	Post-flexion	31	Lozano-Cortés, D. (2014)	34-51

2.3 Results

Scarid counts and densities from CRER stratified MOCNESS samples were used to describe the frequency of larvae in different depth bins in response to genera and ontogenetic stage. These frequencies were used to construct a PMVM to describe realistic larvae behavior used in the development of realistic dispersal models.

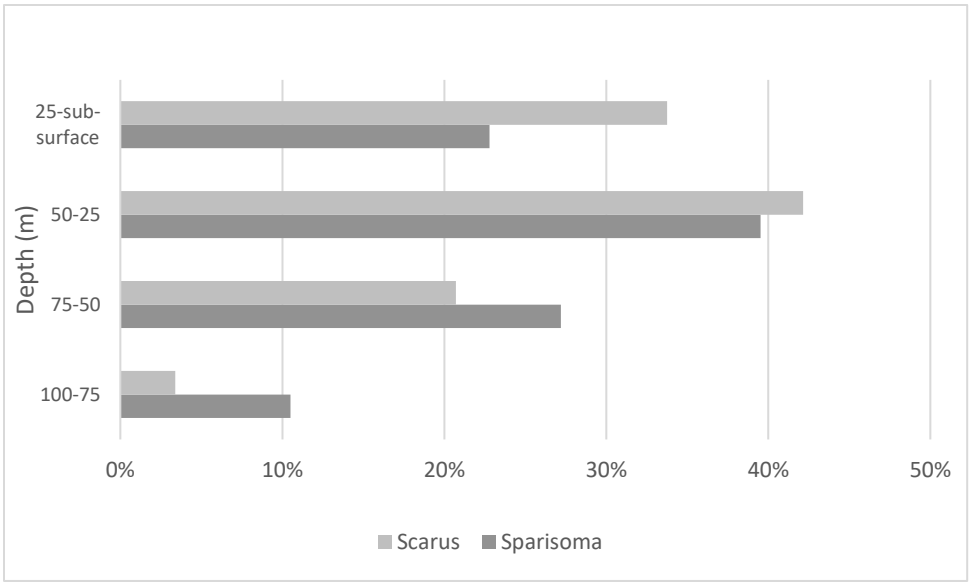

Figure 2 The proportion of *Sparisoma* and *Scarus* within 25m depth bins (0-100m) calculated from the number of *Scaridae* individuals in stratified MOCNESS samples during CRER surveys in the USVI between 2007 and 2009.

Both *Scarus* and *Sparisoma* spp. were most abundant in the 50-25 m depth bin (*Scarus* =42% and *Sparisoma*=40%) and least abundant in the 100-75m depth bin (Fig. 2). There was a significant relationship between genera and depth bin $\chi^2(3, N= 4786) = 59.2$, $p = <0.001$ (Table 3).

Table 3 Results of the chi-square test of independence indicating a significant association between the genera of larval Scaridae and depth (m), $\chi2(3) = 59.2$, $p = <0.001$.

	Value	**df**	**P-value**	**Sig.**
R Pearson Chi-Square (Count)	59.2	3	< 2.2E-16	< 0.001

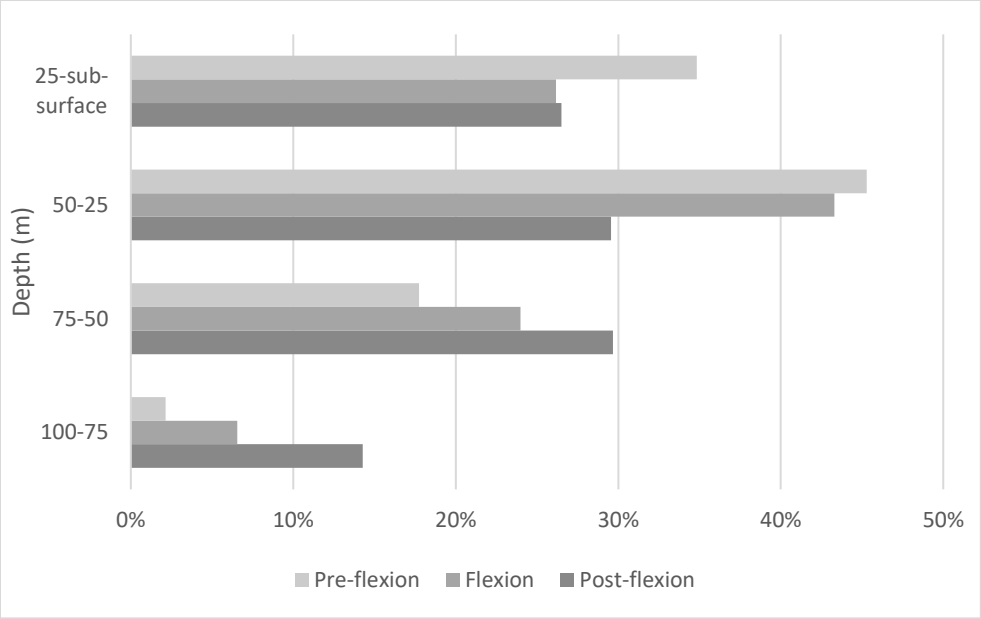

Figure 3 The proportion of *Sparisoma* ontogenetic stages within 25m depth bins (0-100m) calculated from larval fish abundance collected in stratified MOCNESS samples during CRER surveys in the USVI between 2007 and 2009.

The greatest proportion of *Sparisoma* larvae (35%) of all stages were collected in the 25-50 m depth bin (Fig. 3). Looking at stage specific proportions, post-flexion was represented equally in the 50-75 m and 25-50 m depth bins (30%), while the greatest proportion of flexion (43%) and pre-flexion (45%) was in the 25-50 m depth bin. There was a significant relationship between ontogenetic stage and depth bin $\chi^2(6, N= 4460) = 520.4$, $p = <0.001$ (Table 4).

Table 4 Results of the Chi-Square test of independence indicating a significant association between the ontogenetic stage (pre-flexion, flexion, & post-flexion) and depth (m) in *Sparisoma* larvae, $\chi2(6)$ N = 520.4, p = <0.001.

	Value	**df**	**P-value**	**Sig.**
R Pearson Chi-Square (Density)	520.4	6	< 2.2E-16	< 0.001

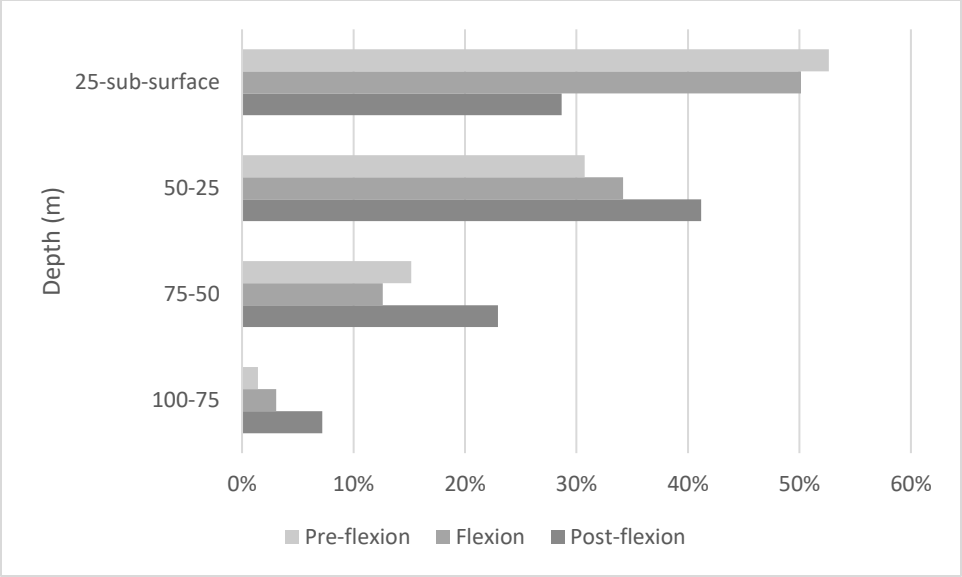

Figure 4 The proportion of *Scarus* ontogenetic stages within within 25m depth bins (0-100m) calculated from of larval fish abundance collected in stratified MOCNESS samples during CRER surveys in the USVI between 2007 and 2009.

The greatest proportion of *Scarus* larvae (42%) of all stages were in the sub-surface-25 m depth bin (Fig. 4). An analysis of stage specific proportions indicated the greatest proportion of post-flexion larvae was found in the 25-50 m depth bins (41%), while the greatest proportion of flexion (50%) and pre-flexion (53%) larvae was in the sub-surface-25 m depth bin. There was a significant relationship between ontogenetic stage and depth bin $\chi^2(6) = 104.9$, $p = <0.001$ (Table 5).

Table 5 Results of the Chi-Square test of independence indicating an association between ontogenetic stage (pre-flexion, flexion, & post-flexion) and depth (m) in *Scarus* larvae, $\chi 2(6) = 104.9$, $p = <0.001$.

	Value	**df**	**P-value**	**Sig.**
R Pearson Chi-Square (Density)	104.9	6	< 2.2E-16	< 0.001

The value at each point (x, y) in the probability matrices of vertical migration refers to the percentage of larvae that can be found within a particular 25 m depth bin at that time interval (Table 6). The percentages are based on the stage-specific vertical

distribution from preceding chi-squared tests (Tables 3-5). A high percentage of *Sparisoma* individuals were found in depth bins of 25- 50 m throughout all ontogenetic stages. *Scarus* remain in the 0-25 m depth bin during early stages, only dropping into deeper water later in development. Probabilities of vertical migration for fish eggs were included in the matrices because they do not follow the same vertical distribution as the other larval stages during the first three days, when the particles are still eggs or yoke stage. In addition, eggs are positively buoyant and unable to move, thus the probability of finding fish eggs is much higher at the surface than at depths greater than 1 m (Leis 1991).

Table 6 Probability matrices of vertical migration (PMVM) developed from abundance (No./m^{-3}) of (a) *Scarus* and (b) *Sparisoma* larvae in 2007-2009 CRER Survey MOCNESS samples. Matrices describe the frequency of larvae in each depth bin during different ontogenetic stages based on pelagic larval duration estimates for each stage (Table 2).

A. *Scarus*

Depth (m)	Age (days)			
	3	7	34	51
1	99	0	0	0
25	1	53	50	29
50	0	31	34	41
75	0	15	13	23
100	0	1	3	7

B. *Sparisoma*

Depth (m)	Age (days)			
	3	7	34	51
1	90	0	0	0
25	10	35	26	27
50	0	45	43	30
75	0	18	24	30
100	0	2	7	14

2.4 Discussion

Genera- and stage-specific vertical distributions of larval scarids were statistically significant, based on an analysis of frequencies using chi-square tests (Tables 3-5). Differences in vertical distributions as indicated by the chi-square test indicate the necessity to analyze differences in abundance and develop PMVM's (write the acronym for this out) for each genus separately. Vertical distributions described as frequencies provide valuable information to construct Probability Matrices of Vertical Migration

(PMVM) which reflect realistic genus-specific vertical larval movements that impact horizontal movements within dispersal models.

The vertical distribution of Scaridae in the USVI were previously described in Privoznik (2014) to be the result of ontogenetic vertical migration behaviors. Most marine larvae undergo ontogenetic vertical migration whereby they swim or adjust their buoyancy to move downward from the upper part of the water column to deeper layers or reversely, upward into the neuston (Leis and McCormick 2002), and scarids appear to be no different. Both *Scarus* and *Sparisoma* individuals were found in greater numbers in deeper in the water column during the post-flexion stage. As described in (Privoznik 2014), this is likely due to post-flexion being the final stage of their planktonic cycle and they are beginning their settlement towards a suitable reef system. The pre-settlement stage is when a larva leaves the pelagic environment to become closely associated with the bottom often dropping several meters out of the water column (Franco-Herrera et al. 2006). Additionally, the decrease in frequency of flexion and pre-flexion stages (<7 days old) as depth increased in *Scarus* is a result of increased buoyancy of *Scarus* eggs relative to that of *Sparisoma* (Koltes 1993). As *Scarus* hatch, their immobile pre-flexional stage would be in greater abundances at shallower depths than that of pre-flexion *Sparisoma* larvae (Leis 1991).

Beyond the ontogenetic controls on vertical distribution, ichthyoplankton are also largely controlled by environmental factors (i.e. light levels, prey and predator density, hydrological movements and turbulence) (Leis 1991; Olivar and Sabatés 1997). Thus, the patterns in vertical distribution for scarids in this study are also likely in response to the environmental conditions of the region. The dominant factors controlling ichthyoplankton in the USVI are likely seasonal food availability, predator abundance, hydrological movements and turbulence (Richards and Lindeman 1987).

During spring months, when CRER surveys are conducted, the sub-surface (upper 50 m) territorial waters of the USVI experience higher fluctuations in sea surface temperatures, lower salinity, and increased sunlight (Chérubin and Garavelli 2016). These conditions are optimal for the growth of planktonic communities (Lampert 1989). A large portion of these planktonic communities are photosynthetic organisms called

phytoplankton and remain in the photic zone (upper 80 m with the bulk of the distribution in depths less than 50 m) (Franco-Herreraet al. 2006) Predators of phytoplankton (zooplankton) are the primary prey of marine fish larvae (Richards and Lindeman 1987). Thus, the optimal conditions promoting phytoplankton abundance growth in spring and early summer leads to an increase in zooplankton and larval fish, including scarids within the photic zone (Armstrong and Singh 2012; Richards and Lindeman 1987). Zooplankton can also feed on larval fish. However, fully developed larval fish have swimming capabilities that can allow them to avoid predation, particularly in areas of more easily attainable prey such as phytoplankton (Fortier and Harris 1989). Increases in targeted predation due to a lack of alternative food sources may explain the decrease in abundances greater than 50 m. Turbulence is similarly shown to affect the vertical distribution of larval fish (Heath et al. 1988), and can affect distribution as a direct consequence of larval avoidance of regions with rougher or more turbulent conditions. Wind-driven turbulence may influence a theoretic ceiling above which larvae are not advected. Because 95% of wind-driven transport occurs in the upper 25 m, there is also likely a reduction in scarid larvae at the surface interface (Price et al. 1987). Similar avoidance responses have been observed in the presence of thermoclines, with the majority of larval avoidance responses being dependent on the magnitude of the difference in temperature at the interface. This avoidance may create a floor, restricting larvae to the mixed layer during spring months (March-June), with the formation of a thermocline at 50-60 m depth along the Puerto Rican shelf edge (Roger et al. 2008). These are all possible determinant factors contributing to the vast majority of scarid larvae being restricted to depths between 25 and 50 m in the waters of the USVI.

The collection of vertically discrete larval fish abundance during fisheries independent sampling provides a realistic understanding of stage-dependent migrations. Analysis of genera-specific and stage-specific vertical distributions allows the development of PMVMs (Table 6). These matrices are a way to statistically describe stage-specific probability density distributions with depth, and can be integrated into certain biophysical modeling systems. For example, the use PMVM's in the Connectivity Modeling System (CMS) can be used to produce more realistic larval trajectories. Using

realistic estimations of vertical distribution is an important biological characteristic in biophysical models because it greatly impacts the directionality and velocity of particle trajectories within the model (Bartsch and Backhaus 1988; Paris et al. 2007). A change in vertical position influences the environmental conditions (i.e. temperature, ocean circulation, wind-driven movement) experienced by larvae due to the variability in oceanographic conditions across depths (Doherty et al 1985). Without vertical distribution matrices, particles are often assumed to be at the surface and controlled by surface conditions. However, this would be an unrealistic assumption for scarid larvae, as data from CRER MOCNESS sampling indicate the majority of scarid planktonic duration is at depths above 50 m. These larval trajectories can then be used to understand population connectivity and network dynamics (i.e. source/sinks, upstream flow and self-recruitment; Roberts 1997). Understanding population connectivity is essential to the process of setting the appropriate scale for spatial management in reef fish stocks like scarids, and towards improving the understandings of recruitment indices and developing a comprehensive management plan based on the entire lifecycle of the stock (Privoznik 2014).

2.5 Conclusion

Previously described vertical distributions of scarids were used to develop PMVMs for the two genera (*Scarus* and *Sparisoma*) (Table 6). A better understanding of differences in scarid vertical distributions can inherently improve previous larvae dispersal and migration models which have unrealistically assumed either uniform vertical distribution, or an arbitrarily selected vertical distribution for these larvae (Williams et al. 1984; Doherty et al. 1985). Understanding differences in vertical distribution of ontogenetic stages for these genera can be useful in developing location-, species-, and stage-specific connectivity models. Developing precise connectivity models allows for better predictions of overall dispersal patterns to be used in the identification of areas that impact larval abundances and recruitment success for improvements in stock management.

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CHAPTER THREE: THE USE OF LARVAL DISPERSAL MODELS TO IDENTIFY POSSIBLE SPAWNING SITES FOR SCARIDAE (GENERA *SPARISOMA* AND *SCARUS*) IN THE VIRGIN ISLANDS.

Abstract

Large-bodied parrotfish populations (genera *Scarus* and *Sparisoma*) in the U.S. Virgin Islands (USVI) have declined due to overexploitation. Previous management designed to protect parrotfish populations focused efforts on the protection of the adult stages through catch, size, and gear restrictions. However, variability in survival and dispersal of the planktonic stage can greatly impact stock dynamics. A better understanding of larval connectivity pathways and the impact of environmental variability or factors inhibiting growth at different ontogenetic stages, is important in developing accurate decision support systems for use in more holistic management of harvested marine fish species. A bio-physical Lagrangian dispersal model was used to trace paths of Scaridae larvae back to potential spawning sites. The dispersal model developed in the Connectivity Modelling System (CMS) used regional circulation simulations and empirical data including locations, collection dates, and abundance of larvae from NOAA Southeast Fisheries Science Center's (SEFSC) Coral Reef Ecosystems Research (CRER) cruises, during spring between 2007 and 2009. The model outputs suggest that the greatest abundance of larval Scarids are transported into the USVI from spawning localities up current of the territory. However, in 2009 local spawning and an increase in retention were identified in the territory during periods associated with the passage of anti-cyclonic eddies related to the early arrival of a seasonal freshwater plume from the Amazon River. Understanding species-specific larval dispersal pathways and their variability can be used to increase the precision of spatial and temporal management to improve Scaridae stocks in the USVI.

3.1 Introduction

3.1.1 Background on Scaridae within the U.S. Virgin Islands

Since the 1990's, large-bodied parrotfish, family Scaridae (genera *Scarus* and *Sparisoma*), populations in the U.S. Virgin Islands (USVI) have declined due to targeted

fishing methods used in response to the decline in other commercially harvested larger predatory species of reef fish as a result of overexploitation (Smith et al. 2008). The decline in these herbivorous species contributes to the proliferation of macro-algae in coral reef ecosystems impacting coral recruitment and growth (Kennedy et al. 2013). Additionally, small-scale artisanal fisheries centered around scarids have collapsed or proceeded to catch smaller individuals in greater numbers furthering the exploitation of this family of fish (Toller and Tobias 2007; Kojis and Quinn 2004). Previously executed management strategies focused efforts on the protection of the adult stage through size limits, annual catch limits (ACLs), and species and gear restrictions. Populations of both genera, but especially *Scarus,* did not rebound in response to these enacted management strategies (Rogers and Beets 2001).

The ineffectiveness of previous management strategies may be due to a focus on only the adult stage, where early life history stages including eggs and larvae are equally as important to stock replenishment. This is because success or failure to disperse and recruit in the early stages, can lead to a 10-fold difference in number of recruits that survive to a catchable size (Houde 2009). Thus, the dynamics and variability in both early life history stages (planktonic and eggs) and adult scarids should be considered in the development of management strategies. Since 2007, the National Oceanic and Atmospheric Administration (NOAA) Atlantic Oceanography and Meteorological Laboratory (AOML) and Fisheries Oceanography for Recruitment, Climate, and Ecosystem Studies (FORCES) Lab have conducted surveys in the US Caribbean. These annual Coral Reef Ecosystems Research (CRER) cruises conduct fisheries-independent sampling surveys in the territorial waters of the USVI, an understudied region. A major focus of these surveys was to develop recruitment indices for commercially important reef fish to improve the understanding of stock assessments, including parrotfish of the *Scarus* and *Sparisoma* genera (Lamkin et al. 2009).

3.1.3 Scaridae Ecology

The family Scaridae contain three main genera within the Caribbean: *Scarus*, *Sparisoma* and *Cryptotomus*. However, the genera of *Scarus* and *Sparisoma* are the focus of this study because they include commercially important species (SERO 2012).

Spawning is an essential life history event in marine species, because it heavily impacts fish stocks by controlling larval abundances, early larval survival, and recruitment success (Farmer et al. 2017). Scarids (genera *Scarus* and *Sparisoma*) mate in pairs, harems, or large groups, often spawning monthly throughout the year in conjunction with lunar phases and/or tidal cycles, with peak spawning during summer months (Streelman et al. 2002). Additionally, 25% of the Scaridae family are known to form spawning aggregations with the majority of observation describing the activity occurring in the tropical Pacific (Colin and Bell 1991; Claydon 2004) and to a limited extent in the Caribbean (Randall and Randall 1963; Colin 1996). Aggregations are a group of conspecific fish gathered at a predictable time and place, for the purpose of spawning (Claydon 2004; Farmer et al. 2017). The locations of these spawning events are known as spawning sites. They are just as important as the act of spawning, because sites are chosen to optimize dispersal, minimize egg predation, limit starvation, and increase success of settlement on optimal habitat (Johannes 1978). However, these locations are also targets of heavy fishing due to the accessibility and ease of catching an abundance of large adult fish. In the USVI many of the scarid spawning aggregations have already been depleted or their locations remain unknown (Toller and Tobias 2007).

During spawning events, scarids produce eggs through broadcast spawning. After 25 hours, the eggs hatch, into a planktonic larva. These larvae then grow and develop through several ontogenetic stages including pre-flexion, flexion and post-flexion, at which point a functional tail is developed (Miller and Kendall 2009). The durations of this planktonic stage ranges from 28 to 53 days (Richards 2005). Due to the functionality of a tail in latter ontogenetic stages, larvae are able to develop active swimming behaviors and can adjust vertical positions in the water column to locate food, avoid predation, and move into oceanographic features which lead to ideal settlement habitats (Paris et al. 2007). During the post-flexion/pre-settlement stage, larvae will drop several meters in the water column in order to settle onto optimal habitat to continue to develop into a juvenile stage (Franco-Herrera et al. 2006).

Larval abundance from fisheries-independent CRER surveys, paired with Scaridae larval behaviors, can be used to develop realistic bio-physical connectivity

models. Connectivity modelling can be used to locate additional spawning sites, develop recruitment indices, and identify ecological bottlenecks between source and sink locations (Cowen et al. 2006).

3.1.2 Connectivity

The Connectivity Modeling System (CMS) is a probabilistic, multi-scale particle tracking model. The model uses a stochastic Lagrangian framework coupled with a nested grid technique to approximate the migration and dispersal processes of organisms in the ocean (Paris et al. 2013). The CMS models produces particle trajectories, these trajectories indicate larval transport and can be forward-in-time-trajectories (FITT) identifying settlement locations or backward-in-time trajectories (BITT) identifying spawning locations, depending on model parametrization (Batchelder 2006). Due to the vulnerability and impact on larval success of undocumented and/or unprotected spawning grounds of scarids, related to overexploitation, the identification of Scaridae spawning locations was a priority of this study (Aguilar-Perera 2006). Thus, BITT bio-physical models were used to identify larval dispersal and spawning localities. Additionally, the CMS is modular, which allows for augmentation that include more specific representations of particle behaviors (i.e. buoyancy, vertical migration, etc.). The CMS was used in this study over other similar software (i.e., ICHTHYOPS, and LTRANS) due to its ease-of-use and ability to couple biological (Scaridae-specific larval behavior) and physical factors to estimate dispersion and migration processes of scarid larvae (Paris et al. 2013).

3.1.3 Biological and Physical Characteristics Impacting Scaridae Larvae

Due to the relatively small size of larvae, their trajectory is largely controlled by physical factors (i.e. currents, wind, eddies etc.) (Leis 2007). Physical processes can have direct effects on larval transport and survival through physical movement (Cowen and Sponaugle 2009), but also indirectly impact optimal environmental conditions (i.e. light, temperature and currents) of the larvae resulting in endogenous vertical and horizontal movements (Cowen et al. 2006). To account for the variability in the oceanography of

the USVI, archived ocean circulation data from multiyear ROMS numerical simulations created by Chérubin and Garavelli (2016) were used in the CMS models to simulate dispersal pathways for scarid larvae.

The addition of biological attributes for larvae simulated as particles in biophysical models produce more realistic dispersal distributions based on species-specific information of the focal species (Cowen and Sponaugle 2009). Ontogenetic vertical migration and Pelagic Larval Duration (PLD) estimates are parameters which have been found to strongly impact the dispersal of larvae (Holstein et al. 2014, Bartsch 1988, Cowen et al. 2006). Planktonic larvae commonly undergo ontogenetic vertical migration, where the larvae actively swim or adjust their buoyancy to move up or down in the water column migrating towards oceanographic conditions ideal for growth, survival, retention and settlement (Paris et al. 2007). The interaction of biological responses and behaviors with the physical environment can serve to moderate dispersal and connectivity such that the outcomes are quite different from those predicted based on physics alone (Cowen et al. 2006). Using abundance data from vertically stratified MOCNESS samples of scarid larvae collected between 2007 and 2009, scarids were found to express genera-specific and ontogenetic stage-specific vertical distributions (Privoznik 2014). The genera-specific vertical distributions were included in the creation of probability matrices of vertical migration (PMVM) to statistically describe the ontogenetic vertical migrations for the genera. In addition to vertical migration behaviors, the PLD for scarids were included to further predict realistic estimates of scarid specific larval transport. The PLD determines the length of time a larva is suspended in the water column and largely constructs the spatial extent of larval dispersal (Paris et al. 2007). A long PLD can result in large-scale dispersal connecting distant populations, where larvae with a short PLD may recruit back to habitats near where they were spawned (Cowen et al. 2003).The PLD for Scarid species in the Atlantic is 28-53 days (Richards 2005) but to explore the impact of PLD on the horizontal distribution of scarids, multi-species PLD estimations for ontogenetic stages were used (Table 8). To evaluate the influence of PLD and vertical migration on the dispersal of larvae, simulations with and without PMVM and PLDs of 34 and 51 days were run.

Using the empirical data collected for Scaridae larvae during the CRER surveys (i.e. location, development stage, number and date), and congruent circulation models for the territory, larval origination points were identified through hindcasting. In addition, dispersal pathways and connectivity of the western Caribbean for *Scarus* and *Sparisoma* larvae were identified. Areas of high recurring probability can be used as indicators of spawning aggregation sites used by adults to establish cohesive and comprehensive management strategies. To determine the spawning localities, dispersal pathways. and recruitment patterns for the family Scaridae in the USVI the following objectives were explored:

Objective 1: Define the appropriate model framework for a Backward-in-Time-Trajectory (BITT) model for larval Scaridae (genera *Scarus* and *Sparisoma*) dispersal pathways within the territorial waters of the USVI.

Objective 2: Identify the dispersal pathways and potential spawning habitat for Scaridae (genera *Scarus* and *Sparisoma*) larvae within the territorial waters of the USVI.

3.2 Methods

3.2.1 Study Site

The U.S. Virgin Islands are comprised of three major islands: St. Thomas (STT; 83 km^2), St. John (STJ; 52 km^2) and St. Croix (STX; 207 km^2) located in the Northern Caribbean Sea. The coastlines of STX, STT and STJ are approximately 113, 85 and 80 km (Rogers et al. 2008). STT and STJ are connected to Puerto Rico and the British Virgin Islands (BVI) by an extensive shelf, known as the Puerto Rican shelf. The Puerto Rican shelf extends about 32 km north and 13km south of STT and STJ. The northern shelf edge slopes gradually to depths of over 300 m eventually dropping off into the Puerto Rican Trench (8,000 m). To the south, the slope is less gradual and abruptly drops to over 4,000 m. STX, about 40 km to the south of STT, is on a separate platform. STX's platform is much smaller than the Puerto Rican shelf and extends less than 5 km from

shore, except for a small extension to the east end of the island, known as Lang Bank. The deepest part of territorial waters in the USVI is the Virgin Islands Basin that separates STT and STJ from STX with depths of nearly 4,200 m. The bathymetry of the Virgin Islands supports vast habitats and features, including fringing, bank-barrier, patch, spur and groove reefs, algal ridges, and a submarine canyon (Rogers et al. 2008) (Fig. 5).

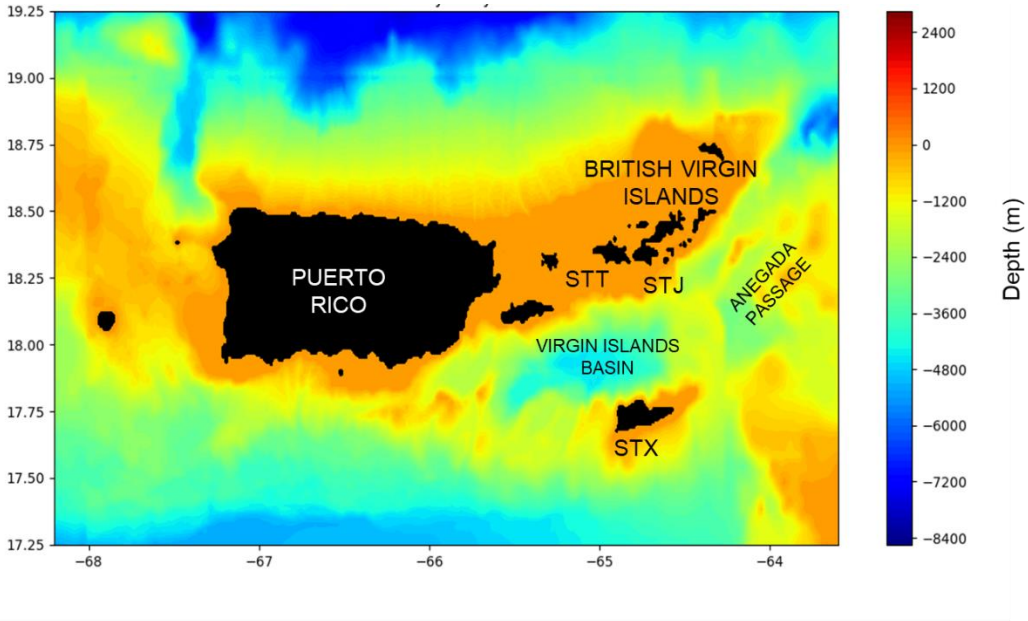


Figure 5 Bathymetry of the northwestern Caribbean, surrounding the USVI. The bathymetry data was derived from the National Geophysical Data Center using 2-minute Gridded Global Relief Data (ETOPO2) v2.

Currents in the upper level of the Caribbean Sea flow on average west to northwest. This includes the weak Antilles Current which flows along the northern side of the Puerto Rican shelf and the stronger Caribbean Current which flows westward through the center of the Caribbean Sea (Lamkin et al. 2009). This circulation is heavily controlled by the trade winds (Chérubin and Garavelli 2016). However, the Virgin Islands confer unique oceanography in the region during the arrival of Orinoco or Amazon freshwater plumes which move gyres and eddies from the northeast into the region surrounding the USVI and PR (Johns et al. 2014). As meso-scale features (i.e. eddies and gyres) move into the northern Caribbean (Virgin Islands) complex physical features (i.e. bathymetry, coastlines and shelf-slope) of the Virgin Islands can impact the variability in the strength and longevity of eddy systems (Chérubin and Garavelli 2016)

(Fig. 5). The complex coastline of the islands especially along the eastern and western ends of STX can modify the vorticity of mesoscale features, allowing these features to increase in strength and persist longer within USVI waters (Chérubin and Garavelli 2016). Where there are islands on the Puerto Rican plate, the lateral friction from shallow shelves reduces the strength and duration of these dynamic eddies (Chérubin and Richardson 2007). This introduction of meso-scale features causes annual and seasonal variability in circulation in the northern Caribbean (Lamkin et al. 2009; Chérubin and Garavelli 2016), and strongly affect larval dispersal pathways and survivability.

NOAA SEFSC and AOML scientists aboard the research vessel Nancy Foster (NF) conducted 2-3 week CRER surveys of biological and physical oceanography surrounding the USVI from March to April in 2007, 2008 and 2009. Cruises occurred on 28 March-09 April 2007, 11-24 March 2008, and 07-20 April 2009. In 2007, surveys were conducted at stations based on a standardized grid at inshore, shelf break, and offshore stations in the waters of the U.S. and British Virgin Islands, as well as exploratory stations in the Anegada Passage and Leeward Islands. Using adaptive sampling, which utilizes satellite imagery, habitat models, and ship-based, flow-through/hull mounted sensors, additional stations were added in 2008-2009 to include areas of St. Croix, north of St. Thomas/St. John and locations where mesoscale circulation features were present. Historic stations are stations sampled annually chosen as part of the standard grid or were added to address new research incentives (Fig. 6).

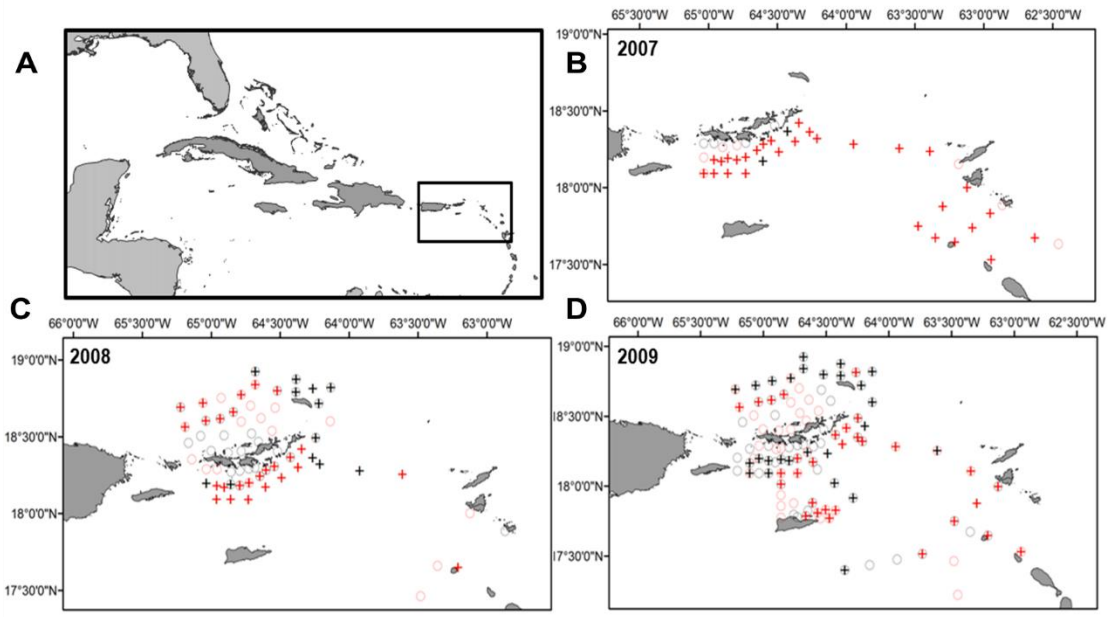


Figure 6 Study region of the USVI and PR inset on map of the Caribbean (a). CRER survey stations indicating MOCNESS (+) and Bongo (○) sampling between 2007 and 2009. Each year is depicted in a different panel in chronological order left to right (b-d). Symbols highlighted in red are where parrotfish species (Scarus and/or *Sparisoma*) were collected.

3.2.2 Data Collection

Ichthyoplankton samples were collected during CRER surveys in 2007, 2008, and 2009 using Subsurface Bongo and MOCNESS tows (Table 7, Appendix A). MOCNESS tows were conducted obliquely from 100 m to the surface in 25 m increments for each net and occurred in a short radius around the station. The sampling used a MOCNESS with five 0.505 mm mesh nets, depth bins include: (1) 0-100 m, (2) 100-75 m, (3) 74-50 m, (4) 49-25 m and (5) 24 m sub-surface. Cod-ends attached at the base of each net collected separate ichthyoplankton samples at stratified depths. The Subsurface Bongo consisted of two circular 0.505-micron nets, towed obliquely, with a 45° wire angle (vessel speed of approximately 2 knots), approximately 5 m below the surface. The volume of water passing through the net was measured by a mechanical flowmeter mounted off-center in the net mouth of the Bongo and by an electronic flowmeter centered on the frame for the MOCNESS. Each net filtered approximately 500 m^3 of seawater, and samples were preserved in 90% ethyl alcohol (Lamkin et al. 2009).

Table 7 Stations from CRER spring ichthyoplankton surveys within the Caribbean (2007-2009).

Year	Sampling Dates	Region Sampled	Number sampled stations	Net Type	Number of Tows	Number of *Scarus*	Number of *Sparisoma*	Average Vol_Filt (m^3)
2007	30 March-07 April	17-18°N / 62-65°W	55	MOCNESS	100	222	1945	555.7±69.57
		17-18°N / 62-65°W	55	Bongo	11	24	71	555.4±325.5
2008	11 March-24 March	17-19°N / 63-65°W	79	MOCNESS	159	173	1388	343.4±95.2
		17-19°N / 63-65°W	79	Bongo	50	57	164	648.6±100.0
2009	08 April-20 April	17-19°N / 62-65°W	105	MOCNESS	217	192	1127	333.6± 122.6
		17-19°N / 62-65°W	105	Bongo	97	236	663	575.5±136.5

3.2.3 Larval Fish Taxonomy

Larval fish collected during the CRER cruise were later identified to family taxonomic level by technicians at the FORCES Lab using a Leica MZ12.5 stereomicroscope and dichotomous identification keys (Lamkin et al. 2009). Samples containing a member of Scaridae, distinguishable by long and continuous dorsal and anal fins with slender spines, a pointed snout and small terminal mouth and a row of melanophores along the base of the anal fin were removed, analyzed and enumerated from corresponding samples for site specific larval abundances. Samples were placed into three categories indicating their level of development (i.e. pre-flexion, flexion, post-flexion) to examine possible ontogenetic differences in distribution. Stages were characterized by the level of development in the caudal fin (tail). “Pre-flexion” individuals have a straight and pointed notochord. In the “flexional” stage the notochord’s tip bends dorsally, while “Post-flexion” larvae are identified by the formation of a functional tail (Miller and Kendall 2009).

3.2.4 Early Life History

The Scaridae family is morphologically identical, except for a distinctive gut pigment of the *Sparisoma* members separating *Scarus* from *Sparisoma.* However, DNA-sequence analyses are required for identifications to the species level (Richards 2005). Thus, for this study we used only commercially important genera *Scarus* or *Sparisoma* excluding the species within the Scaridae family which have smaller individuals that are not commercially havrvested (*Cryptotomus*).

Although members of the Scaridae family are similar morphologically, they vary in important life history behaviors and characteristics. For example, Scaridae egg characteristics have been well documented (Richards 2005), for both of the genera of *Scarus* and *Sparisoma*, that are the focus of this study. These two species have been found to have different physiology including buoyancy and shape. According to Richards (2005), *Scarus* spp. produce 2.5 - 3.0 mm long spindle shaped eggs. *Sparisoma* spp. produce spherical, 0.6 -1.1 mm in diameter, negativity buoyant eggs (Leis 1991).

However, beyond observed egg characteristics, information on early development of Scaridae larvae is limited to brief descriptions (Richards 2005).

3.2.5 Use of Empirical Data from CRER Surveys

The model simulations created in this study are based on empirical data from CRER ichthyoplankton surveys, rather than theoretical assumptions. Abundances of larvae released in the models are based on number of scarid larvae caught at each station. Survey station locations (latitude and longitude) where individual *Sparisoma* and/or *Scarus* larvae were collected are the starting position of the larvae in the model (Appendix A). The duration each larva is run for in the model is based on the ontogenetic stage of the collected larvae (categorized by FORCES technicians). Each stage is interpreted as an estimation of time the larvae spends within each stage based on PLDs in the literature (Table 8). Additionally, dates of collection from these surveys for each larva, were used to run congruent oceanographic simulations. Thus, the particles representing individual larva experienced realistic physical factors which occurred during the days of dispersal within the model between 2007 and 2009. Using fisheries-independent surveys allows for more realistic and accurate model simulations of larvae, allowing hindcasting from known collection sites to potential spawning locations when integrated into the Connectivity Modeling System (CMS).

3.2.6 The Connectivity Modeling System Simulations

In conjunction with ichthyoplankton samples, CRER surveys collected temperature, salinity, chlorophyll, CDOM via a CTD and the ship's flow-through system; water velocity, bathymetry and regional circulation using the ship's hull-mounted acoustic doppler current profiler (ADCP), depth sounders and Lagrangian surface drifters. However, due to the spatial limitations of this oceanographic data, a multi-year Regional Ocean Modeling System (ROMS) simulation for the northwest Caribbean created by Chérubin and Garavelli 2016 was used in this study. The ROMS is a three-dimensional numerical oceanic model intended for simulating currents, ecosystems, biogeochemical cycles, and sediment movement in various coastal regions. The Chérubin and Garavelli 2016 simulation used ROMS-AGRIF climatologies, consisting of three

embedded simulations on nested grids allowing for one-way forcing from parent to child grids at each time step. The parent grid encompasses the northeastern Caribbean including the USVI and adjacent islands (14–23°N, 71–61°W). Additional nested grids (child grids) were comprised of two different horizontal resolutions, the first encompassing the USVI and BVI at 1 km resolution, and the second grid encompassing St. Thomas alone at resolution of 330 m. The water column for all three grids was discretized into 25 layers using two topographic datasets the Global Topography dataset (GTOPO 30), and the National Geophysical Data Center Coastal Relief Model. Archived ocean circulation data from these realistic simulations for model year 2007-2009 and four vertical layers ((1) 100-75m, (2) 75-50m, (3) 50-25m and (4) 25m- sub-surface) were used in this study (Chérubin and Garavelli 2016). Dates of release during model simulations were the date of collection from CRER surveys (Table 7).

Starting position of the particles released in the model for individual larvae were the standard latitude and longitude of the station where the scarid larvae were collected during CRER surveys (Appendix A1). To investigate the network dynamics of scarid larval dispersal in the USVI, the CMS multi-scale biophysical model was used (Paris et al. 2013). Using the backward tracking (hindcasting) module, larval transport of scarids was reversed to determine particle origin (potential spawning locations) within the USVI during Spring between 2007 and 2009. The hindcasting parameterizing creates backwards-in-time model (BITT) simulations by reversing the velocity field. To calculate the backward trajectories used in the module the daily nested grid files of current velocity and Sea-surface Temperature (SST) from the end of the time interval are read first and the sign of the velocity components (U, V and W) for the particles are flipped (Socolofsky et al. 2015).

Due to a small sample size each instance of scarid larvae that was collected was multiplied ten-fold, creating a total of 53,580 particles representing *Sparisoma* individuals, and 9,040 particles representing *Scarus* individuals released in simulations between 2007 and 2009. The duration that particles remained in the model were based on the ontogenetic stage of the larvae identified by FORCES technicians. Durations of each

stage are unknown, so were estimated based on an average PLD of Scarids from the literature (Table 8). Thus, pre-flexion, flexion and post-flexion simulations were run for different durations of time based on the estimations for each stage. Similar estimations of PLD duration by stage were used in Holstein et al. (2014) bio-physical model describing *Sparisoma viride* larvae dispersal.

Table 8 Multi-species pelagic larval durations (PLD) for Scaridae used in the estimation of the duration (days) for each ontogenetic stage.

Genus	Species	Stage	Duration	Citation	Duration Estimation (d)
Scarus	-	Hatch	25h	Randall and Randall (1963)	1
Sparisoma	*Sparisoma rubripinne*	Hatch	25h	Randall and Randall (1963)	1
Sparisoma	*Sparisoma viride*	Hatch	26h	Koltes, K. H. (1993)	1
Sparisoma	*Sparisoma viride*	Yoke stage	3	Koltes, K. H. (1993)	1-3
Sparisoma	-	Pre-flexion	?	-	3-7
Sparisoma	-	Flexion	?	-	7-34
Scarus	-	Post-flexion	28-53	Richards, W. J. (Ed.) (2005)	34-51
Scarus	-	Post-flexion	29-42	Ishihara and Tachihara (2011)	34-51
Sparisoma	-	Post-flexion	43- 55	Raventós and Macpherson (2001); Robertson and Warner (1978)	34-51
Other	*Bolbometopon muricatum*	Post-flexion	31	Lozano-Cortés, D. (2014)	34-51

For each genus, a total of 48 unique simulations were conducted. Preliminary simulations used only the influence of horizontal and vertical diffusion to represent random turbulent diffusion for passive particles. The rate of horizontal and vertical diffusion is based on recommendations of North et al. (2009); with a vertical diffusion of 0.05 (m^2/s) and horizontal diffusion rate of 0.0103 (m^2/s) within the first nested grid and 0.002 (m^2/s) for the second nested grid. Additional simulations used the same rate of diffusion but, biological modules were turned on to determine the influence of a range of PLDs, ontogenetic vertical migration (PMVM), and differences in origin location on larval trajectories. For each model year (2007-2009), ontogenetic stages of each genus were run as either passive with a PLD of 51 or 34 days or with PMVM with a 51or 34 day PLD (Table 9).

Table 9 Parameterization characteristic for Connectivity Modeling System (CMS) Backwards in Time Trajectory (BITT) model simulations. Numbers of particles run in each simulation are in parenthesis based on the number of larvae caught for each genus during CRER surveys multiplied 10-fold. Locations of the starting position of particles are described in Appendix A1.

Genus	Number of Particles (x10)	Year	Stage	Duration of Simulation (days)	Transportation Type
Scarus 904	(9040)	2007 (2460)	Pre-flexion (1090)	7	Vertical Migration
					Passive
			Flexion (250)	21 or 34	Vertical Migration
					Passive
			Post-flexion (1120)	34 or 51	Vertical Migration
					Passive
		2008 (2300)	Pre-flexion (1070)	7	Vertical Migration
					Passive
			Flexion (110)	21 or 34	Vertical Migration
					Passive
			Post-flexion (1120)	34 or 51	Vertical Migration
					Passive
		2009 (4280)	Pre-flexion (2480)	7	Vertical Migration
					Passive
			Flexion (780)	21 or 34	Vertical Migration
					Passive
			Post-flexion (1020)	34 or 51	Vertical Migration
					Passive
Sparisoma 5358	(53580)	2007 (20160)	Pre-flexion (7820)	7	Vertical Migration
					Passive
			Flexion (1270)	21 or 34	Vertical Migration
					Passive
			Post-flexion (11070)	34 or 51	Vertical Migration
					Passive
		2008 (15520)	Pre-flexion (3190)	7	Vertical Migration
					Passive
			Flexion (3190)	21 or 34	Vertical Migration
					Passive
			Post-flexion (11710)	34 or 51	Vertical Migration
					Passive
		2009 (17900)	Pre-flexion (6960)	7	Vertical Migration
					Passive
			Flexion (810)	21 or 34	Vertical Migration
					Passive
			Post-flexion (10130)	34 or 51	Vertical Migration
					Passive

The PLD of a larva refers to the amount of time spent in the water column during their planktonic stage. A multi-species average PLD of 34 and 51 days, calculated from the literature for Scaridae was used in this study. The influence of larval PLD was included by extending the TimeMax of the CMS to 51 days (4,406,400 seconds) for a long PLD or shortening the TimeMax to 34 days (2,937,600 seconds) for a shorter PLD. A PLD of 34 days had a shorter flexional (21 days) and post-flexional stage (34 days) based on averaging duration estimations, where a PLD of 51 days used the maximum estimated duration of all stages. Altering the TimeMax alters the amount of time the particle remains in the water column which could impact dispersal pathways and origins of larvae.

The results from Chapter 2 indicate differences in the vertical distribution of different ontogenetic stages of the *Scarus* and *Sparisoma* genera. These differences in the vertical distribution of ontogenetic stages, were used to develop a PMVM to simulate ontogenetic vertical migration during CMS simulations (Table 8). In this simulation, the influence of observed distributions of larvae in the water column due to ontogenetic migrations was included as the probability of an individual larvae of a given ontogenetic stage found at a specific depth. This data was developed using stage and depth-specific probability density distributions from abundance data collected by MOCNESS during NOAA CRER surveys between 2007 and 2009. Particles (i.e. virtual larvae) were stochastically moved vertically through four timesteps based on PLD estimations for each ontogenetic stage (3, 7, 34, 51 days), following a probability density function distributed over the 5 layers (1 m, 25 m, 50 m, 75 m, 100 m) based on observed vertical distribution of developmental stages of larvae in the field.

Table 10 Probability matrices of vertical migration (PMVM) developed from frequency of (a) *Scarus* and (b) *Sparisoma* larvae in 2007-2009 CRER Survey MOCNESS samples. Matrices describe the probability of larvae in each depth bin during different ontogenetic stages based on duration estimations for each stage (Table 8).

A. *Scarus*

Depth (m)	Age (days)			
	3	7	34	51
1	99	0	0	0
25	1	53	50	29
50	0	31	34	41
75	0	15	13	23
100	0	1	3	7

B. *Sparisoma*

Depth (m)	Age (days)			
	3	7	34	51
1	90	0	0	0
25	10	35	26	27
50	0	45	43	30
75	0	18	24	30
100	0	2	7	14

3.2.7 Data Analysis

From CMS outputs, the positions of larval scarids at each time-step (ts) (ts=3600 seconds), were turned into trajectory plots for each simulation. From these trajectories, the position of the particle at the final timestep in the simulation was used to determine the latitude and longitude associated with the particles, referred to hereafter as their terminal position. The terminal position in our BITT simulations represents the starting position or the origin of an individual larvae referred to as the location of origin (LO).

To develop an appropriate model framework for scarid larval dispersal, pertinent ecological parameters were explored using heatmaps created in ArcMap 10.5.1. The Create Fishnet tool was used to construct a polygon grid over point features (LOs). Then the Spatial Join tool was used to count the number of events falling (LOs) within each grid polygon to create weighted polygons. Grid polygons within the study area which contained zeros for the number of events, were removed prior to analysis. Using the hotspot analysis (Getis-Ord Gi* statistic) z-scores and p-values were created for each weighted polygon which described the features with either high or low values cluster spatially. For statistically significant positive z-scores, the larger the z-score is, the more

intense the clustering of high values (hot spot). Simulations comparing PLDs of 51d and 34d used a two-way T-test assuming equal variance to compare the area of hotspots. The area of hotspots for simulations with PMVM and without PMVM were compared using a Paired T-test. Greater variation in hotspots indicates the BITT models sensitivity to parameter variation.

To identify possible scarid spawning aggregation's sites within the VI, dispersion probability maps were developed using the LOs of 51d PLD and vertical migration simulations (51d+PMVM simulations were found to best represent larval scarid dispersal and were used in proceeding analysis. See results). LOs represent areas of origin for the particles within the BITT model. The greater number of particles originating from one location means it is a habitat or location which host an abundance of reproductive individuals creating spawning sites. Thus, potential spawning sites were identified by binning LOs within a 1000 by 1000 m raster of the northeastern Caribbean (14–23°N, 71–61°W) in ARCMap 10.5.1. A probability density function was assigned to each grid cell using the total number of pixels within each grid cell divided by the total number LO pixels in the model boundaries. Probabilities within each grid cell, were converted by the feature to point tool in ARCMap 10.5.1 which creates a feature class containing points generated from the representative locations of input features. Points representing probabilities of spawning sites were centered in each grid cell. The centering of these points resulted in nearshore points appearing on-land during analysis. In this study areas with points containing probabilities > 0.02 were considered to be potential spawning sites for scarids.

To identify source dynamics, retention potentials and spawning sites of scarids in the USVI, particles with LOs within the territorial boundaries of the USVI were analyzed. Due to the overlap in the Exclusive Economic Zones (EEZ) (200 nautical miles from shore) of the Virgin Islands (BVI and USVI), territorial boundaries were used to focus on resource exchange of the USVI only. Territorial water boundaries defined as 3 nautical miles from shorelines of main islands as well as off-shore cays were overlaid in ARCMap 10.5.1. LOs from 51d+PMVM simulations were plotted in ARCMap 10.5.1 on

the OpenStreetMap Basemap with territorial boundaries. The abundance of LOs within territorial boundaries were counted using the select by location tool in ARCMap 10.5.1 and compared to the abundance of LOs outside of territorial boundaries. Post-flexion scarid larvae are near settlement after 51 days. Thus, post-flexion larvae with a PLD of 51 days, which were collected within the territory with LOs also within territorial waters were considered to be retained, because these larvae were recruited back to their area of origin (Holstein et al. 2014). Thus, the proportion of retention is defined within this study as the proportion of only post-flexion larvae surveyed in territorial boundaries with LOs also within territorial boundaries.

3.3 Results

3.3.1 Parameter Sensitivity

BITT dispersal simulations were run for the post-flexion larvae of each genus (*Scarus* and *Sparisoma*) during model years in 2007, 2008, and 2009 with either a short (34 days) or long (51 days) PLD to determine the influence of PLD on larval dispersal and retention (six simulations per genera). Heatmaps developed from simulations of post-flexion larvae, run with a 34d and 51d PLDs, strongly overlapped. The difference between a 51d PLD and a 34d PLD is approximately 17 days, however, a two-sample T-test assuming equal variance found there was no statistical difference in the area of hotspots for either *Scarus* (p-value =0.99) or *Sparisoma* (p-value =0.74) model simulations.

To determine the influence of vertical migration on larval dispersal and LOs of scarids, BITT dispersal simulations with passive particles or vertical migration (species-specific PMVM) were run for each genus (*Scarus* and *Sparisoma*) during 2007, 2008, and 2009 model years. Not only was there a significant difference in area of hotspots (*Sparisoma* p-value= 0.047 and *Scarus* p-value= 0.046) but the frequency, shape and distance between hotspots varied between vertical migration and passive particle simulations (Fig. 7 and 8). The average distance between hotspots which are constructed based on simulations with and without-vertical migration was ~13.8 km for *Sparisoma*

(Fig. 7) and ~25.8 km for *Scarus* (Fig. 8). This distance in hotspots reflects a difference between simulations when PMVM were integrated. Hotspots using vertical migrations were also more unified and cylindrical in composition, highlighting more specific locations (Fig. 7). Hotspots using passive particles were disorganized and often expansive due to low densities of LOs making up the distribution of the hotspots (Fig. 7 and 8).

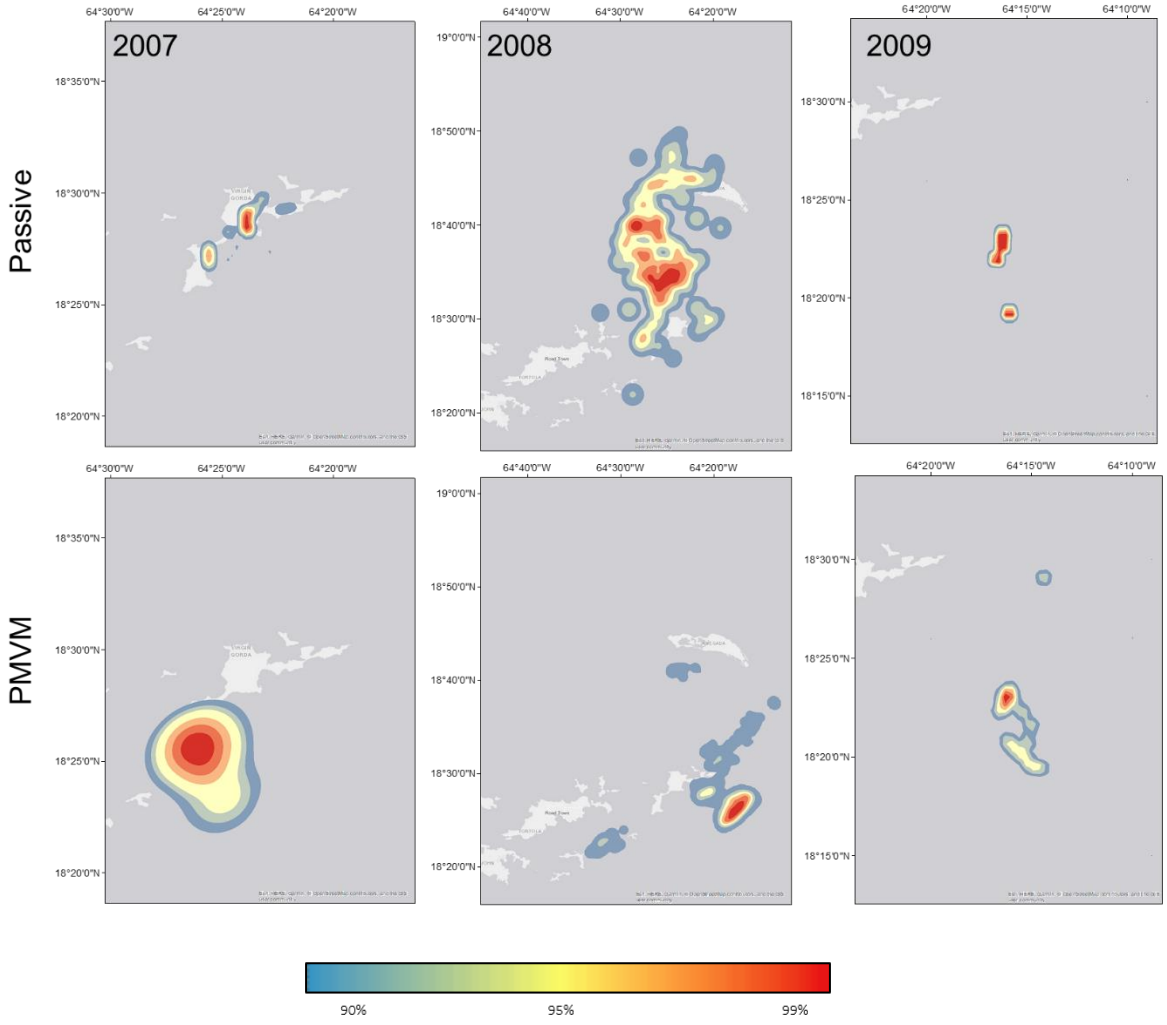


Figure 7 Heatmap analysis of the distribution of 51d PLD *Sparisoma* larvae without PMVM (top panels) and with (bottom panels) for model years 2007, 2008 and 2009 (left to right). Percentages of LO densities represented by contours using a Kernel Density Estimation (KDE).

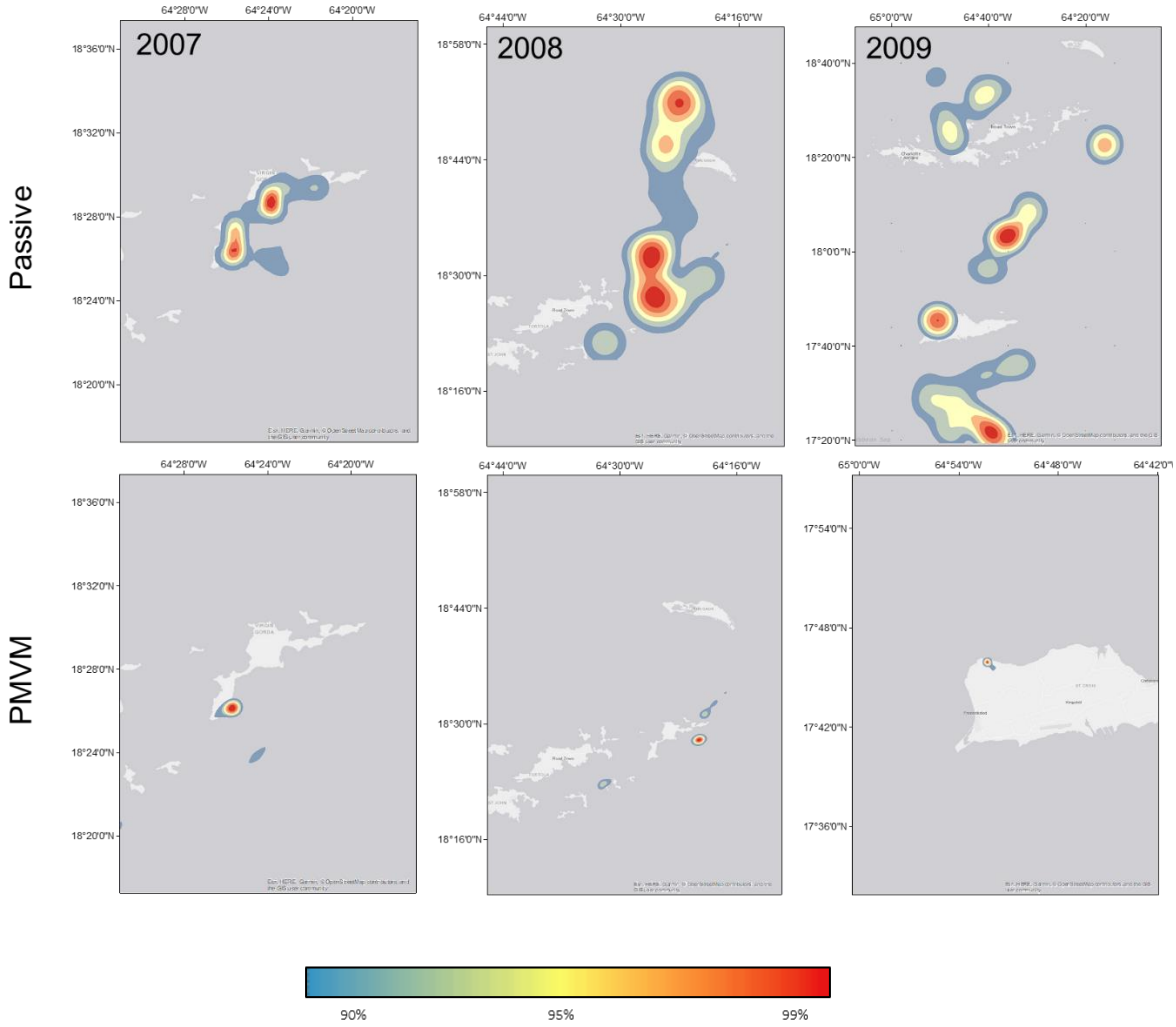


Figure 8 Heatmap analysis of the distribution of 51d PLD *Scarus* larvae with PMVM (top panels) and without (bottom panels) for model years 2007, 2008 and 2009 (left to right). Percentages of LO densities represented by contours using a Kernel Density Estimation (KDE).

The complete overlap of the simulation outputs using 51d and 34d PLD's indicates that there is little to no difference in the effect of a long and short PLD on dispersal and spawning site of the larvae. Thus, either simulation could be used in describing spawning sites and dispersal, but simulations run with a 51d PLD were used in the remaining analysis, to anaylze the full extent of dispersal of the larvae. Model simulations with the added parameter of vertical migration were significantly different from passive simulations with hotspots varying in size, area and distance. Thus, indicating larvae behavior (vertical migration) as an important factor that influences dispersal. Simulations with the combination of vertical migration behaviors and a 51d PLD (51d +PMVM simulations) were used in the remaining analysis to depict realistic behaviors of scarids to determine accurate dispersal and spawning sites.

3.3.2 Scaridae Larval Dispersal

Using the BITT (51d +PMVM) simulations, particle position at each timestep (ts=3600) in the simulation, were used to determine the trajectories and dispersal pathways of *Sparisoma* and *Scarus*.

In 2007, the dispersal pathways of larvae for both genera followed the southern extent of the Puerto Rican shelf, moving along the southern shelf edge by currents originating in the Anegada Passage transporting particles from sites of origin in the BVI (Virgin Gorda, Peter Island and Anegada) and the Anegada Passage (Fig. 9 and 10). Spawning locations extended to the northern extent of the Anegada passage. Indicating that larvae had traveled as far as 129.91 km in 51 days along the shelf prior to entering USVI waters.

In 2008, particles for both genera followed similar dispersal pathways as those from the 2007 model year. In addition to the similar transport seen in 2007, a large majority of particles traveled from origin sites along the northern edge of the Puerto Rican shelf to the north of St. Thomas (commonly referred to as the north drop) which continues east of STJ terminating within BVI territorial waters. These particles moved in

a cyclonic manner and were transported over 251.50 km in 34-51 days reaching speeds of 0.08 m/s (Fig. 9 and 10).

In 2009, particles followed more erratic dispersal patterns. Particles representing *Sparisoma* larvae originated directly south (25 km) of the southern bank of STX in waters west of the Saba Bank and along the north drop of STT and STJ (65.6-64.5°W). Particles originating south of STX moved northward into the Virgin Islands Basin where they remained recirculating within a cyclonic eddy which transported the particles into nearshore waters of STT and STJ (Fig. 9 and 10). Indicating that larvae traveled as little as 60 km in 34-51 days. Potentially, perpetuating the exchange of larvae from STX spawning sites to STJ/STT connecting larval dispersal pathways throughout the USVI. The particles which originated along the North Drop of STT were transported in a single circular pattern moving east to west along the northern shelf with inputs of larvae from locations to the northwest of the northern Puerto Rican shelf edge and outside of model boundaries north of Puerto Rico (PR) (Fig. 9 and 10). Particles representing *Scarus* larvae had similar trajectories to *Sparisoma* larvae in model year 2009. These particles originated from the southern bank of STX west of the Saba Bank. However, *Scarus* particles originated from further south (40 km) than that of *Sparisoma* and in greater quantities. Additionally, unlike particles in *Sparisoma* simulations, *Scarus* larvae collected in the USVI had little advectition from spawning sites in the northern extent of the USVI portion of the Puerto Rican shelf or PR.

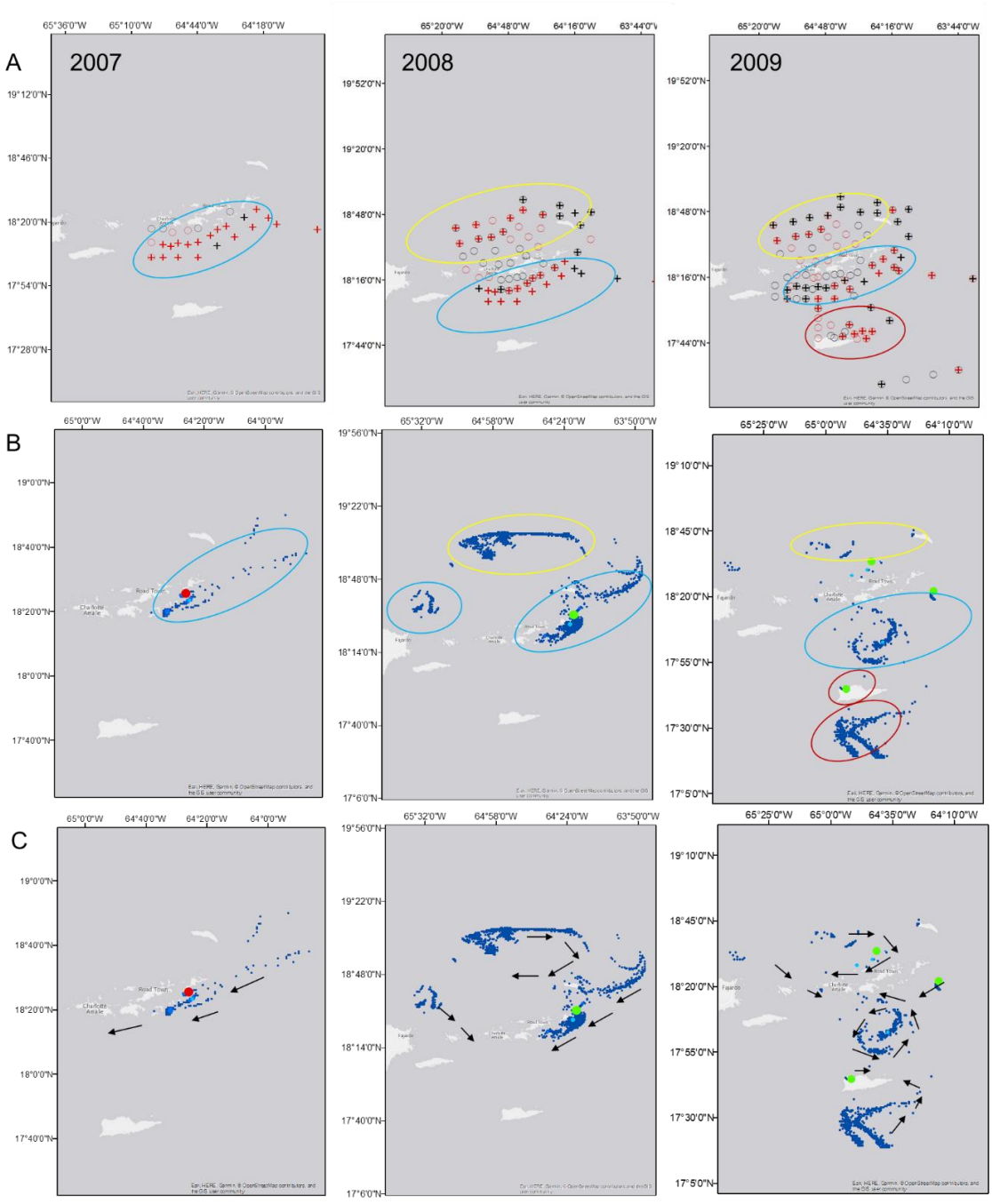


Figure 9 *Sparisoma* larval dispersal pathways in the USVI for 2007, 2008 and 2009 (left to right). (a) CRER survey stations where scarid larvae were captured. (b) Location of origin (spawning site) of *Sparisoma* from BITT model hindcasting. (c) Direction of larval dispersal pathways. Colored circles indicate general survey and dispersal regions: (blue) southern Puerto Rician shelf, (yellow) northern Puerto Rician shelf and (red) St. Croix.

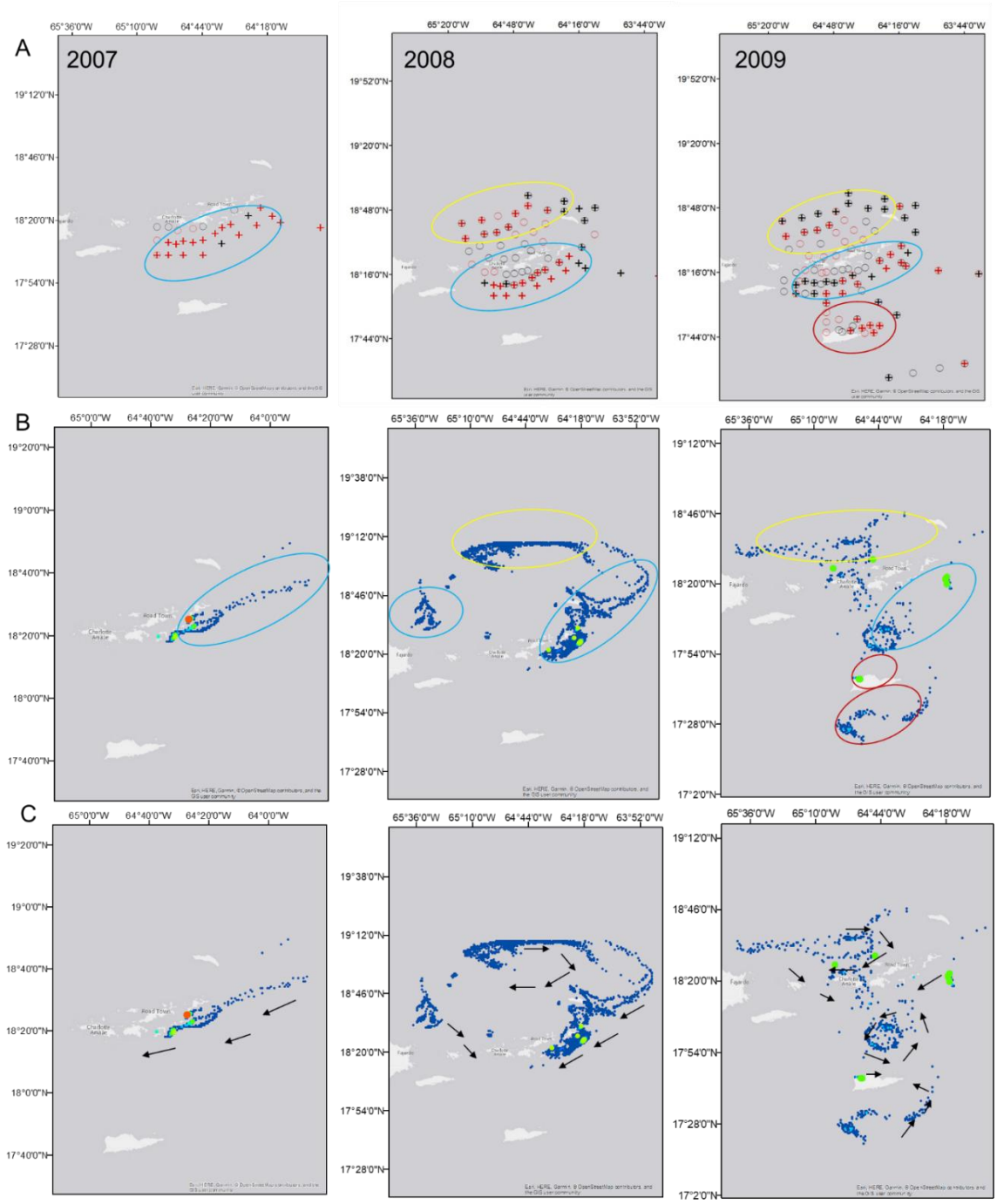
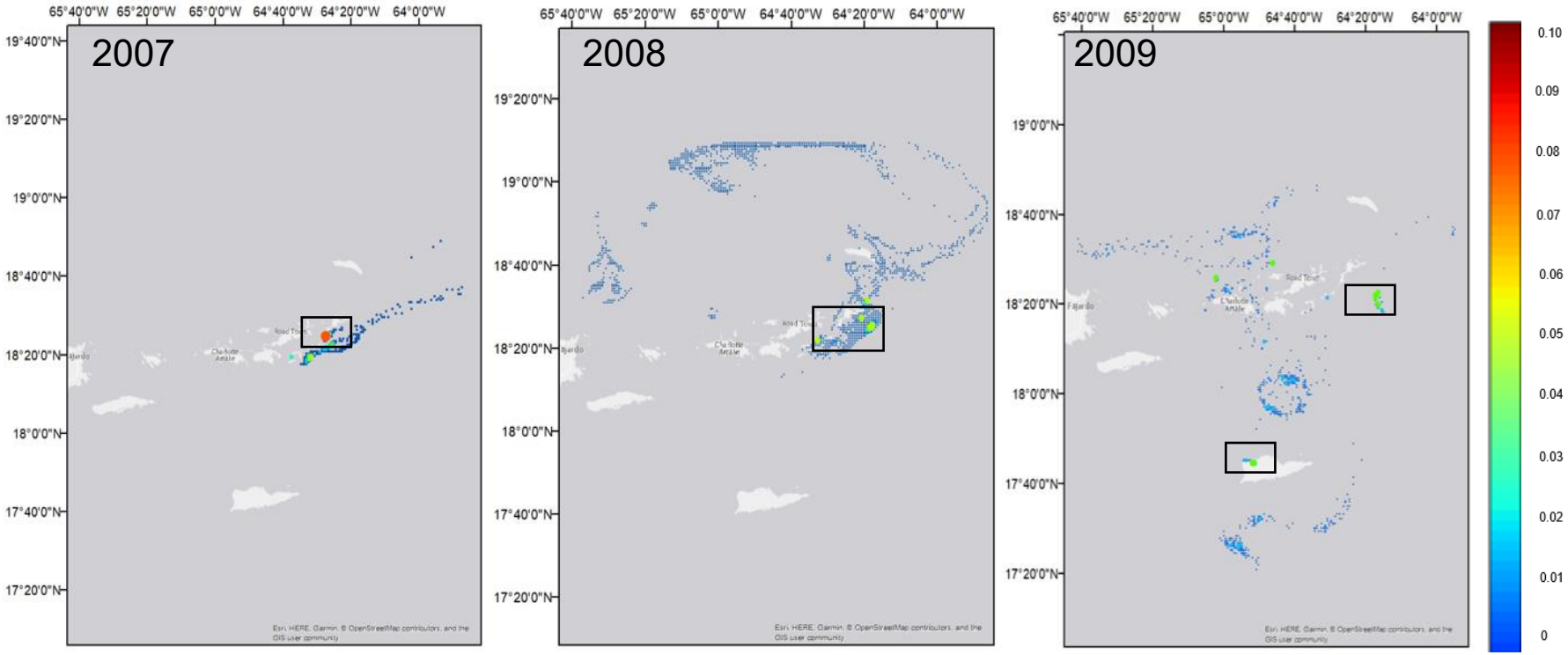


Figure 10 *Scarus* larval dispersal pathways in the VI for 2007, 2008 and 2009 (left to right). (a) CRER survey stations where scarid larvae were captured. (b) Location of origin of *Scarus* (spawning site) from BITT model hindcasting. (c) Direction of larval dispersal pathways. Colored circles indicate general survey and dispersal regions: (blue) southern Puerto Rician shelf, (yellow) northern Puerto Rician shelf and (red) St. Croix.

3.3.3 Distribution of Potential Spawning Sites

The results from the CMS BITT simulations highlighted inter-annual differences in the transport of each genera. The distribution of larval LO's from 2007-2009 were used to describe the probability of potential spawning sites for *Sparisoma* (Fig. 11) and *Scarus* (Fig. 12) within the Virgin Islands.

The nearshore areas of the British Virgin Islands hosted a high probability of potential spawning sites during the 2007 model year. The areas with the greatest probability of containing a spawning site was an area south of the Salt Island Passage along the shelf edge (0.06) and Crooks Bay and Stoney Bay of Virgin Gorda (0.07) (Fig. 11). Particles which did not terminate at these high probability sites continued along the Puerto Rican shelf edge until tapering out into the Anegada passage. In 2008, high probability sites (>0.05) were still found around the island of Virgin Gorda; however, they were found 13 km to the east of Taylor's Bay and reef systems northeast of Pajaros Point. These high probability sites, unlike the nearshore shallow localities identified in 2007, were located among deeper (40 m) reef systems (Fig. 11). Particles which did not terminate at these high probability (>0.05) sites moved in a cylindrical pattern beyond the northern shelf edge of the Virgin Islands. In 2009, high probability sites were still found east of Virgin Gorda at the eastern extent of the Puerto Rican shelf, however, additional high probability sites were identified off the northwest coast of STX within Annaly and Davis Bays. A few sporadic sites within the northern shelf of STT have a probability as high as 0.02 (Fig. 11). Several particle trajectories also suggest they originated from within the Virgin Islands Basin and beyond the southern bank of STX, likely from the Saba Bank outside of model boundaries.


2007
2008
2009
65°40'0"W
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65°0'0"W
64°40'0"W
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19°40'0"N
19°20'0"N
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18°40'0"N
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17°40'0"N
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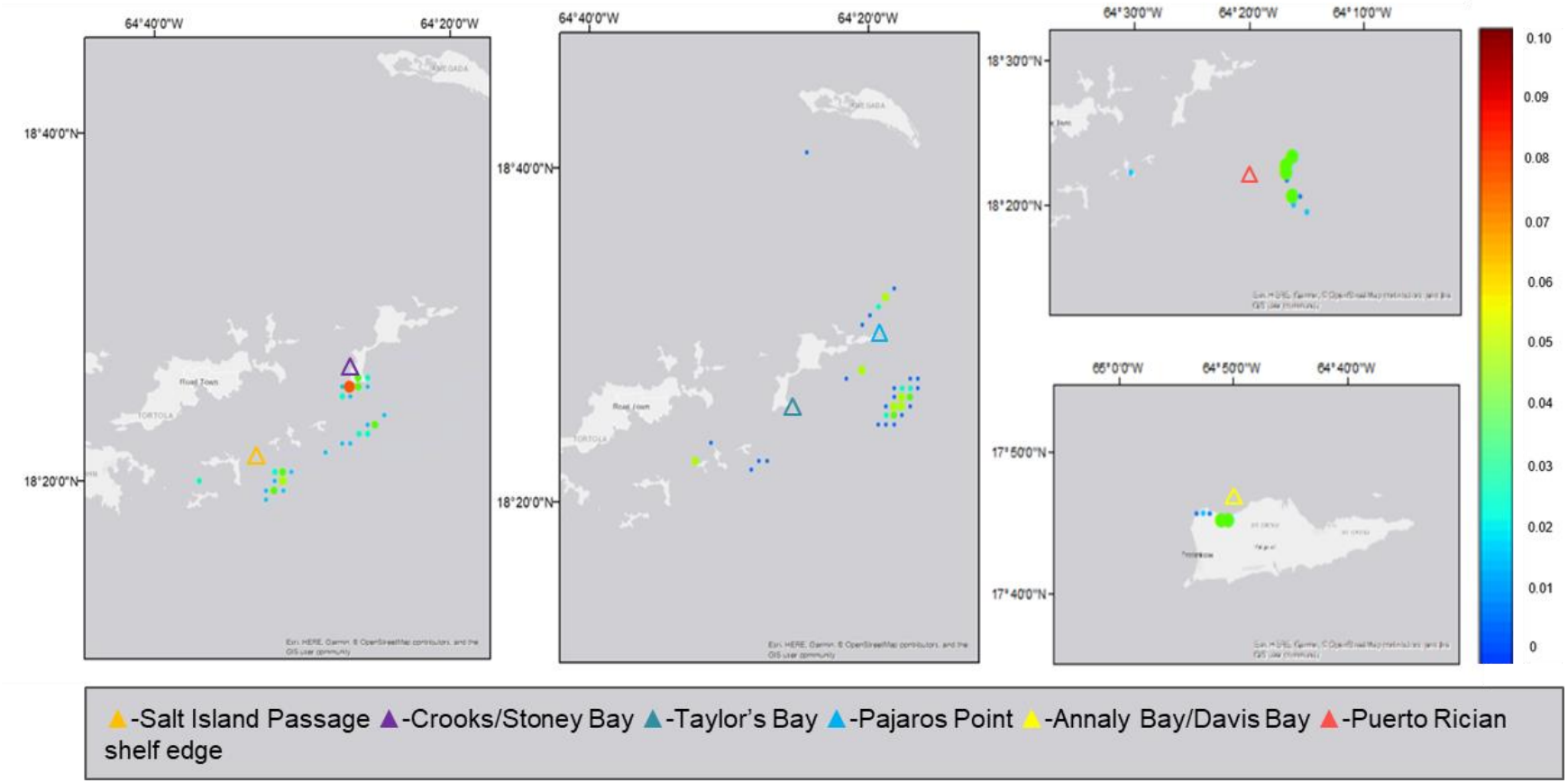
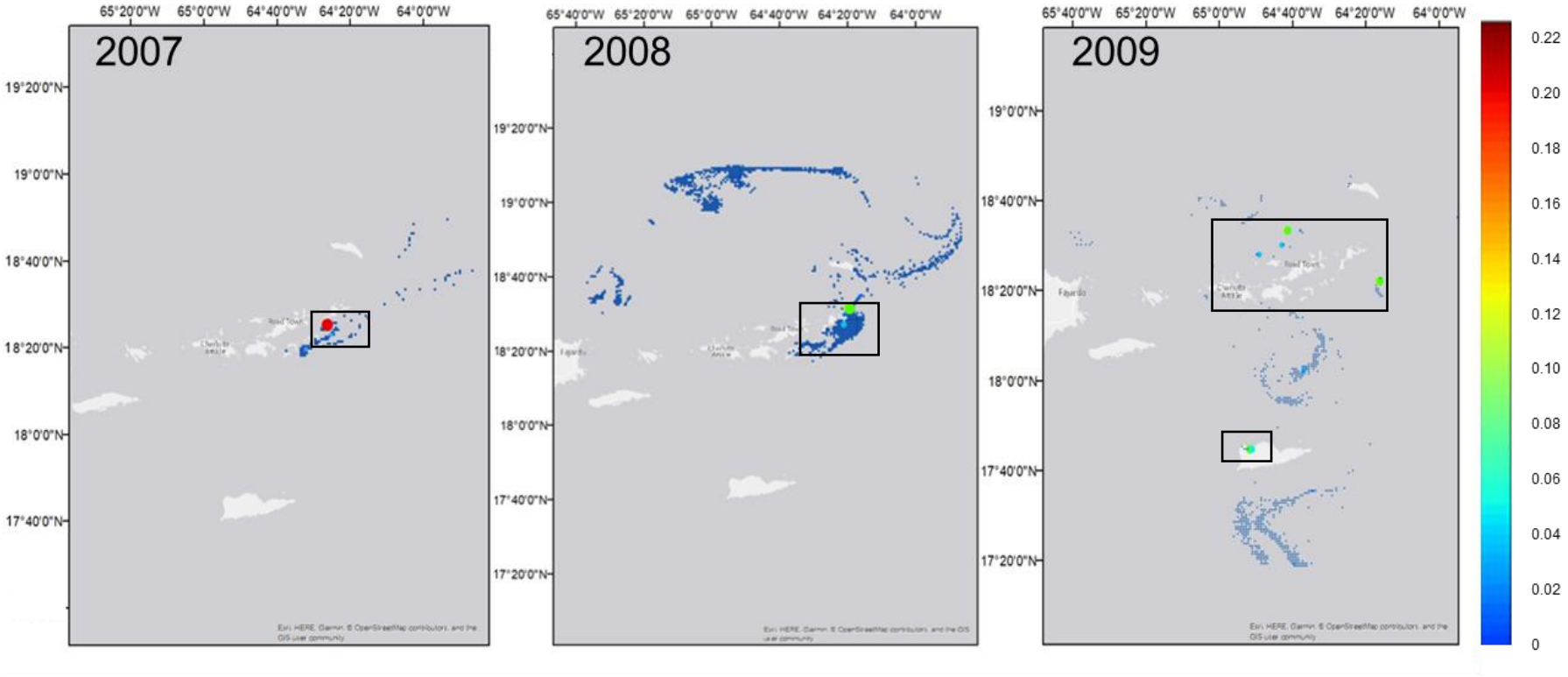


Figure 11 Distribution of probable spawning sites for *Sparisoma* in the waters surrounding the USVI for 2007, 2008, and 2009 (left to right). Scales represent the spawning site probability density function, calculated by binning LOs from the CMS BITT model into a 1000 m by 1000 m grid and dividing by total LOs within model boundaries. All levels of probability are projected (top). Smaller-scale map depicts areas of highest probability (>0.02) (bottom).

In 2007, high probability spawning sites for *Scarus* occurred within Cooper Mine's Point (0.14) and Taylor's Bay (0.22) in Virgin Gorda (Fig. 12). Particles which did not terminate at these high probability sites, split and tapered out east of Anegada along the Puerto Rican shelf edge. In 2008, high probability sites (0.06) were present north of Virgin Gorda extending to Herman's reefs (Fig. 12). Additional sites of spawning activity extended into the northern shelf of STT and tapered out east of Puerto Rico following a pattern of cyclonic transport. In 2009, the highest probability of spawning sites were in shallow reef systems in Annaly Bay of the northwest coast of STX, 13 km southeast of Taylor's Bay, Virgin Gorda, and within a pocket of deep water 8 km north of Little Jost Van Dyke with probabilities between 0.03-0.06. The waters off STX seems to be a particularly important region for *Scarus* larval dispersal pathways within the territory, while *Sparisoma* larvae spawning habitat occur in greater abundances of high probability locations in the BVI (Fig. 12). Like *Sparisoma* in 2009, *Scarus* larvae also originating from within the Virgin Islands Basin and also from beyond the southern bank of STX, likely from the Saba Bank, which is well outside of the boundaries of our model.


2007
2008
2009
65°20'0"W
65°0'0"W
64°40'0"W
64°20'0"W
64°0'0"W
19°20'0"N
19°0'0"N
18°40'0"N
18°20'0"N
18°0'0"N
17°40'0"N
17°20'0"N
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0.12
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0

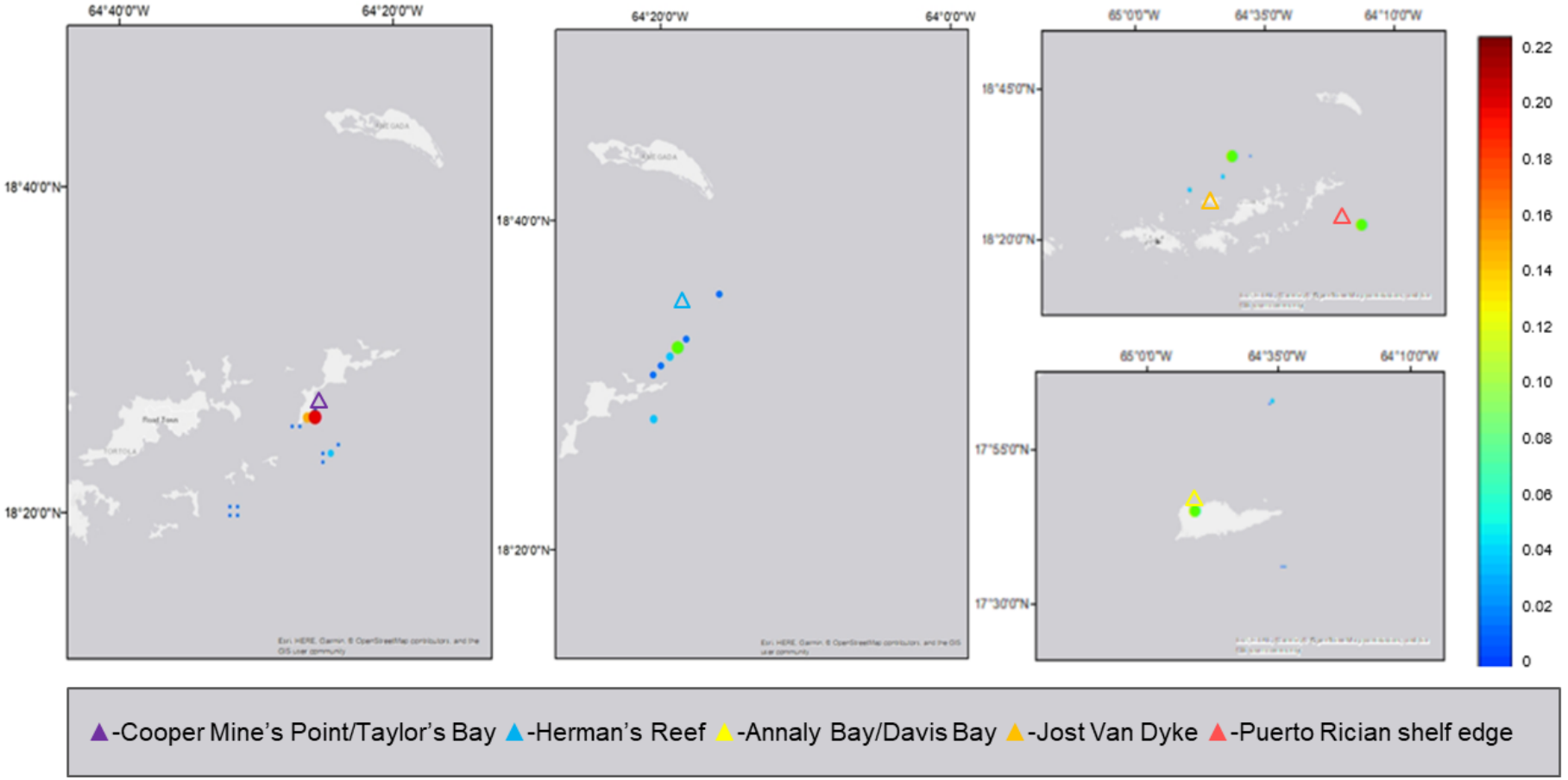

Figure 12 Distribution of probable spawning sites for *Scarus* larvae in the waters surrounding the VI for 2007, 2008 and 2009 (left to right). Scales represent the spawning site probability density function, calculated by binning LOs from the CMS BITT model into a 1000 m by 1000 m grid and dividing by total LOs within model boundaries. All levels of probability are projected (top). Smaller-scale map depicts areas of highest probability (>0.02) (bottom).

3.3.4 USVI Dispersal, Spawning Sites and Retention

Particles representing scarid larvae, did not terminate within USVI territorial boundaries during 2007 or 2008 (Fig. 13). Thus, spawning sites were also not identified within the USVI territorial waters, limiting the potential for retention dynamics during the two model years. However, in 2009 particles representing both *Sparisoma* and *Scarus* did terminate within territorial water and indicated localities of spawning and potential retention within territorial boundaries of the USVI (Fig. 13).

In 2009, larvae of both genera were hindcasted from stations located in the Virgin Islands Basin and Lang Bank into the Pillsbury Sound, the passage between STT and STJ, and from the northwest stations of STX to the shoreline of Annaly Bay, STX. Additional particles in the *Sparisoma* model run were advecte from the western extent of the model north of Puerto Rico (71°W) into territorial waters along the northwest shelf of STT and from stations in the BVI between Tortola and Jost Van Dyke into territorial waters north of Congo Cay north of STT. 14% of the LOs or spawning sites for *Sparisoma* occurred in the territorial waters of the USVI, occurring within Pillsbury Sound, the Leeward Passage, the north bank of STT and the northwest coast of STX. The highest probability sites appear off the northwest coast of STX. A small number of sporadic sites within the northern shelf of STT (7 km north) and 4 km north of Congo Cay, have probabilities of containing spawning sites as high as 0.02 (Fig. 13). For *Scarus*, 13% of LOs or probable spawning sites occurred in the territorial waters of USVI. These probable spawning sites occurred in similar locations as *Sparisoma* but in lower frequencies except for in STX. Spawning sites were identified south of Savanna Cay, northwest of STT and STJ, Pillsbury sound, and northwest STX. The highest probability sites (0.042) for *Scarus* were in shallow reef systems in Annaly Bay of the northwest coast of STX.

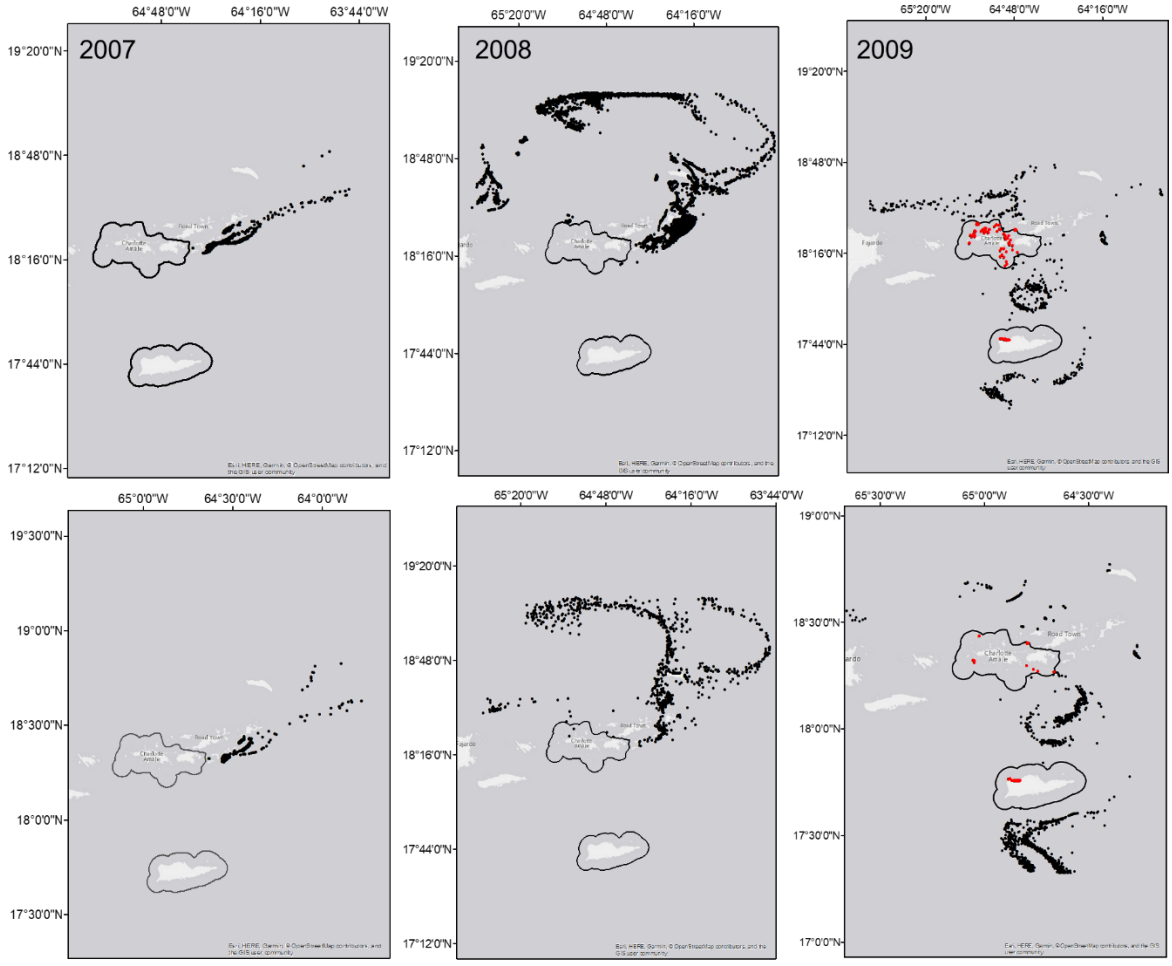

Figure 13 Distribution of BITT model particle origination points inside (black dots) and outside (red dots) of USVI territorial waters for *Sparisoma* and *Scarus (top and bottom)* larvae from 2007, 2008 and 2009 (*left to right*). Boundaries of USVI territorial waters (3 nautical miles from shorelines) are delineated by solid black lines.

With the occurrence of probable spawning sites within the USVI in model year 2009, we explored potential retention using the positions of LOs and the corresponding collection station to determine if particles remained in their area of origin with a PLD of 51 days. 5% of simulated *Sparisoma* particles (n=43) stayed within model boundaries and indicated retention within the USVI (Table 11). Retention occurred in particles from stations on the northwest shore of STX which were spawned within Annaly Bay and from STX stations spawned in Pillsbury Sound and the Leeward Passage. For *Scarus larvae,* retention accounted for 10% of particles (n= 190) (Table 11). The majority of these

particles spawned within STX's territorial boundaries along the northwest coast and were also collected at a station at the northwest edge.

Table 11 The proportion of LOs and the percentage of retention of the *Sparisoma and Scarus* particles within the territorial boundaries (3 nautical miles) for the USVI.

Genera	2007	2008	2009	Retention (2009)
Sparisoma	0	0	14%	5%
Scarus	0	0	13%	10%

3.4 Discussion

CMS BITT models were used to run simulations with different combinations of ecological parameters to determine the most appropriate simulation to estimate the dispersal of scarid larvae in the USVI. Using simulations with a combination of PMVM and a 51d PLD for both genera, dispersal pathways and potential spawning sites were identified. The dispersal patterns and spawning sites in this study are not discrete nor does this study identify every existing spawning site for parrotfish in the Northern Caribbean. Instead, this study identifies important biological and physical processes which impact larval dispersal pathways and identifies annual variability in spawning site success and retention.

3.4.1 Parameter Sensitivity

Running simulations with variations in specific parameters tests the sensitivity of the modeling system (CMS) to determine which attributes of scarids are essential to produce realistic dispersal models. BITT simulations were run using estimations of PLDs for ontogenetic stages including PLDs of 34 and 51days. The 17 day difference in PLD had very little impact on the spatial range of LOs for larval scarids. The similarities in dispersal and LO between a long and short PLD may be explained by the physical oceanography of the USVI and specific larval behaviors. The circulation, bathymetry and shelf-slope of the USVI manipulates current flow to encourage movement from deeper reef systems into nearshore systems (Chérubin et al. 2011). These currents are typically

fast moving at the shelf edge but slow within coastal areas. Thus, larvae were likely moved quickly in preliminary ontogenetic stages covering greater distances, but during their post-flexion stage (~17 day difference in PLD) preceding settlement, they were caught within the slower across-shelf currents closing gaps between LOs of PLD 34 days and 51 days. Broadcast spawners including scarids target these oceanographic patterns to improve survival of larval and settlement in optimal locations (Chérubin et al. 2011; Paris et al. 2013). Model simulations with the added parameter of vertical migration matrices were significantly different from passive simulations. Hotspots from model simulations with PMVM varied in size, area and distance from passive simulations. Passive particles only experience surface circulation and wind driven movement, where active particles move both vertically and horizontally in response to environmental and ontogenetic factors (Leis 1991). Vertical migration in the water column influence larvae horizontal transport, as current speed and direction often changes with depth (Fortier and Leggett 1983). Running passive particles can overestimate locations of recruitment and spawning leading to nine-fold differences between estimated and actual locations (Cowen et al. 2006). Thus, simulations with vertical migrations were used to identify genera-specific LOs over the arbitrary patterns of passive particle LOs.

3.4.2 Larval Dispersal and Spawning Sites of the VI

BITT model simulations indicated that the dispersal of larval scarids which estimate spawning localities varied annually in both the *Scarus* and *Sparisoma* genera. However, dispersal patterns in 2007 and 2008 revealed relativity constant flow of larvae from spawning sites in the BVI into the USVI. In model year 2009, dispersal pathways occurred intra-territorially (USVI) which revealed inconsistent dispersal pathways and spawning site locations from previous years.

In the 2007 model year, larvae dispersal pathways occurred primarily along the Puerto Rican shelf edge, south of the BVI. This dispersal is a result of currents from the Anegada passage transporting larvae from the BVI into the USVI through an upstream transport dynamic. Additional transport likely occurred from offshore, onto inshore reefs by tidal currents and upwelling (Chérubin et al. 2011). The majority of larvae collected in

2008 originated in the BVI following similar transport as in 2007 via shelf induced currents. However, several spawning sites (LOs) occurred at greater distances from their collection sites than in 2007. Particles terminated north of Virgin Gorda and in some cases larvae traveled in a large circular pattern north of the Puerto Rican shelf covering a maximum of 251.50 km in 34-51 days moving at speeds of 0.08 m/s. Caribbean reef species as planktonic larvae generally move between 10-100 km (Cowen et al. 2006; Kitchens et al. 2017). This increase in speed is likely due to large current systems found along the shelf edge of the Puerto Rican Trench (0. 22 m/s) (Tucholke and Ewing 1974). Other high speed currents including the Loop Current, which transports water into the Gulf of Mexico through the Yucatan Channel, has been shown to impact the distance of larval transport. With speeds reaching 1 m/s, the Loop Current (Vukovich and Maul 1985) has been observed to transport larvae 200 to 880 km from their spawning areas within 14–17 days (Kitchens et al. 2017). Even with the slight differences in transport speeds, distributions of scarids in the region for 2007 to 2008 were similar

In 2007-2008 model years, Virgin Gorda was identified to be a spawning hotspot for both scarid genera. This is probably due to Virgin Gorda being most directly upstream from USVI. Thus, even though larvae are being spawned in multiple other locations in the region, larvae from this location are most likely to end up in USVI waters. Similar patterns were described in Roberts (1997) where a general increase in the density of juvenile scarids occurred off Anegada (the easternmost reefs) through the lower BVI to the shallow STJ sites where they were most abundant. This depicts a consistent larval dispersal pathway for 2007 and 2008 from spawning sites in the BVI following downcurrent flow leading to the the largest recruitment to the USVI.

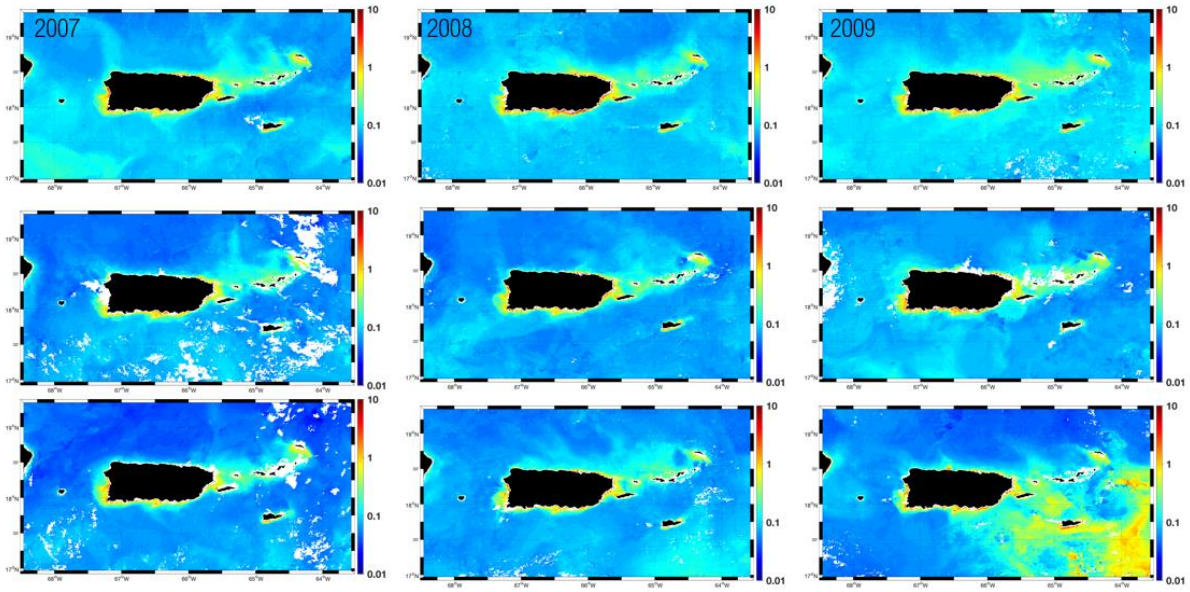

Figure 14 Seven day composite images of chlorophyll-a (chl-*a*) concentration (in mg m^3) derived from the MODIS Terra satellite sensor for the second week in months January-May (top to bottom) for survey years 2007-2009, produced by the USF IMaRS. All map coordinates are 8–21°N, 77–58°W.

Larval scarid dispersal during 2009 was inconsistent with the patterns exhibited in 2007 and 2008. The dispersal of particles between the islands of the USVI and the retention of larvae within the territory in 2009 is likely in response to the appearance of the Amazon River plume arriving in early spring (April), several months earlier and farther to the north than is normally observed in the area (John et al. 2014). Satellite images of the weekly means of Chl *a* from January-May of 2009 show the formation of a mesoscale eddy formation in the Virgin Islands Basin between STT and STX, as a result of surface salinity changes, which did not occur in 2007 or 2008 (Fig. 14). The Amazon River water was delivered to the Caribbean by advection of a North Brazilian Current (NBC) ring. As it entered the Caribbean Sea, it spread to the north and northwest. This transport explains the increase in larvae originating south of the STX southern shelf, it is likely larvae from the Saba Bank being advected west before being caught in the cyclonic eddy moving the larvae into the Virgin Islands (Fig. 15). Similar inconsistencies in annual dispersal patterns occurred in *T. bifasciatum* in STX and other larval fish in the eastern Caribbean during 2009. These differences were attributed to a variability in the flow of trans-Caribbean eddies during the 2009 model year (Chérubin and Garavelli 2016

and Johns et al. 2014). Thus, similar mesoscale events such as eddy formation in the western Caribbean, which caused inconsistent dispersal of other shorefish larvae (*T. bifasciatum;*Chérubin and Garavelli 2016), may also account for the same inconsistencies in the dispersal of scarids.

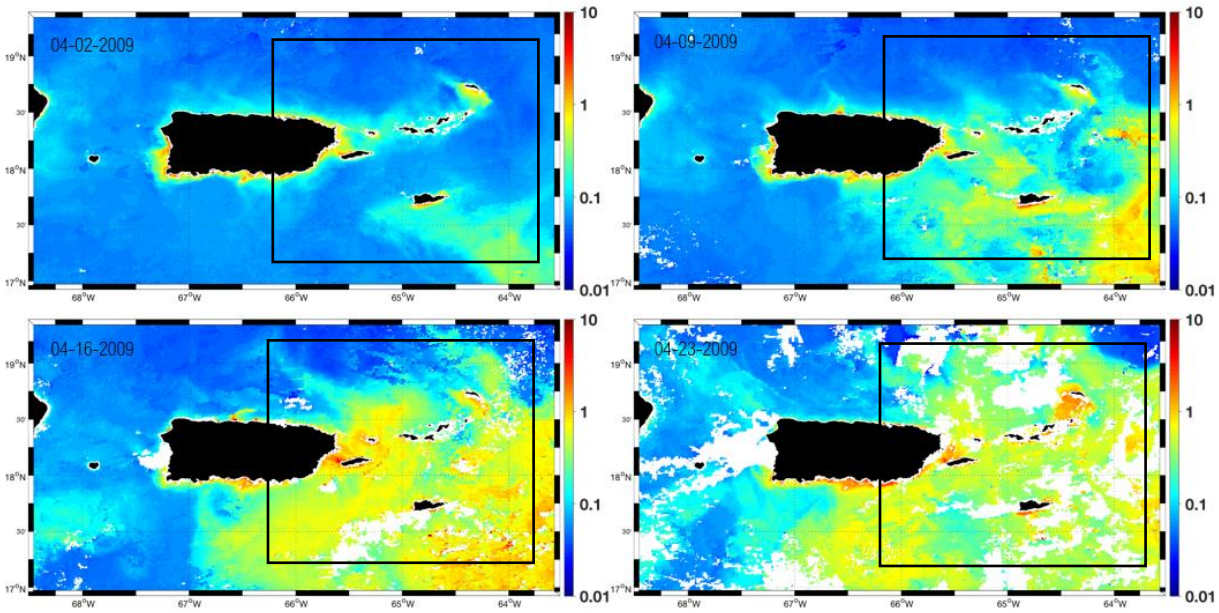

Figure 15 Seven day composite images of chlorophyll-*a* (chl-*a*) concentration (in mg m^3) composite images derived from the MODIS Terra satellite sensor for April 2- April 23, 2009, 2009, produced by the USF IMaRS. All map coordinates are 8–21°N,77–58°W. The black rectangle shows the cruise study area, 17–19°N, 66–62°W.

3.4.3 Territorial Dispersal, Spawning Sites and Retention

In 2007 and 2008, scarid larval dispersal occurred outside of territorial boundaries of the USVI in areas of the BVI and Anegada Passage. These dispersal pathways indicated that all spawning sites for larvae caught in CRER ichthyoplankton surveys also occurred outside of territorial boundaries. However, in 2009 the dispersal that occurred in the USVI indicated local spawning and retention.

In 2009, scarid larvae were transported intra-territorially, from the southern bank along STT/STJ to Lang Bank STX and from south of STX and the Saba Bank into STT and STJ. Also, a portion of scarid particles remained along the northwest shoreline of

STX. These differences in dispersal also highlighted an appearance of probable spawning sites within the USVI waters. The majority of these spawning sites did not retain larvae, but instead larvae were dispersed outside of the territory. However, spawning sites in STX's Annaly Bay and Davis Bay did indicate local spawning and retention for both *Scarus* and *Sparisoma*. This retention is likely a result of the movement of the mesoscale eddy system impacting dispersal since it was found to increase recruitment by 70% in *T. bifasciatum* (Chérubin and Garavelli 2016). The nearshore shallow reef habitat in these bays is optimal settlement habitat for scarids in both genera (Streelman et al. 2002). Thus, to reduce the risk of larval mortality off the STX shelf and to encourage recruitment to these optimal locations, scarids likely spawned in areas and at times which utilize currents that would retain larvae. Similar spawning behaviors have been seen in red hind, *Epinephelus guttatus*, in the USVI where spawning occurred spatially and temporally to encourage onto-shelf recruitment (Cherubin et al. 2011, Nemeth et al. 2008).

3.4.4 Data Limitations

Dispersal patterns and spawning localities from this study cannot be used as comprehensive accounts of scarid larval dispersal or spawning due to the differences in sampling effort and regional coverage between model years. Although NOAA CRER surveys began in 2007, sampling only occurred within territorial waters of STT and STJ. It wasn't until 2009 when sampling included the territorial waters surrounding the north side of STX. Since STX was only sampled in 2009 we don't have a consistent record of the dispersal patterns around STX. The only dispersal patterns for STX were simulated in 2009 and based on the inconsistences in STT and STJ dispersal pathways during this model year, it may not be representative of characteristic larvae dispersal for STX. To improve the overall understanding of the territories connectivity additional sampling years which include all historical sampling sites in both STX and STT/STJ would be appropriate. Additional model years, (beyond 2009) should also be analyzed to improve our understanding of the connection between large climatological events (i.e. mesoscale eddies and freshwater plumes) and dispersal patterns.

To truly understand patterns in dispersal pathways in species that spawn year round, CRER surveys should be conducted seasonally, outside of late winter (February) to early summer (June), to understand seasonal variable in larvae dispersal and larval success. Since most scarids reach peak spawning in late summer and early fall (July and August) (Robertson and Warner 1978), CRER surveys should especially collect ichthyoplankton sample during this time period to improve our sample sizes and understanding of dispersal patterns during this peak time.

Finally, these localities do not represent every spawning aggregation that may exist. Spawning aggregations of scarids have been documented throughout the Caribbean in addition to those observed in the USVI: *Sparisoma rubripinne*, Randall and Randall (1963) Reef Bay, STJ, *Sparisoma rubripinne* Ruffo (2006) Reef Bay and Coral Bay STJ, and unknown spp. Kadison et al. (2006) Hind Bank STT (not apparent in the current study). This may be a result of the models only using individuals caught at offshore sites, meaning larvae from near-shore spawning aggregations are not transported via mesoscale features or transported offshore. Another explanation is that there is an upstream connection from USVI spawning sites to PR which is not accounted for due to the spatial extent of the BITT model and the lack of samples collected in PR. Additional sites and months should be surveyed for scarid larvae around Puerto Rico to use in BITT models to complete our understanding of larval scarid connectivity in the USVI and Eastern Caribbean and to expand our understanding of the upstream flow of recruits.

3.5 Conclusion

Due to the lack of population replenishment after the implementation of size limits and catch restrictions, other management strategies must be employed to limit the further decline of the scarid population and reduce the consequences of algal growth and artisanal fishery collapse. To improve the population status of scarids in the USVI, both *Sparisoma* and *Scarus*, larval abundances and variability in survival should be focused upon.

A biophysical Lagrangian BITT particle model developed in the CMS was used to simulate the larval transport of scarids in the USVI. The first step was to validate the biological parameters used in the model. The difference in pelagic larval durations did

not significantly impact the dispersal and the origin of the larvae. In addition, running passive particles compared to those with vertical migration attributes presented significantly different origins for the larvae. Thus, species-specific vertical migration and a 51d PLD was used in the final model framework to identify and display dispersal patterns based on realistic oceanographic conditions experienced by the larvae. BITT simulations with the validated biological parameters were used to create dispersal trajectories and identify spawning sites for larvae from the *Sparisoma* and *Scarus* genera annually between 2007 and 2009. Annual dispersal followed similar patterns controlled by shelf-currents, with small variations among genera. In 2009, larval dispersal for both genera occurred intra-territorially where particles were moved between the territorial waters of STX and STT/STJ in response to cyclonic eddies formed by the leading edge of a freshwater plume originating Amazon River. Cyclonic eddies during 2009 also led to a 5-10% level of retention within territorial waters of STX, STT and STJ, and retained larvae through cyclonic wake flows. Improved networks of connectivity based on larval dispersal pathways and spawning sites identified in this study, can be used to inform management about dispersal patterns for scarids.

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CHAPTER FOUR: GENERAL CONCLUSION

In the U.S. Virgin Islands parrotfish (family Scaridae) are an important commercial fishery, with the majority of all parrotfish commercial landings in the Caribbean caught in St. Croix waters. To manage the resource and reduce continued exploitation of parrotfish the Caribbean Fishery Management Council (CFMC) approved several policies and regulations applying prohibition of targeted gear (gill and trammel nets) and the catch of vulnerable species. Additional Amendments were applied to implement annual catch limits (ACLs) and accountability measures (AMs) for overfished commercial stocks. In 2006, the ACL's of Puerto Rico and St. Thomas ACL were set at 52,737 and 42,500 lbs, respectively, and the much larger St. Croix fishery had an ACL 240,000 lbs. Landings remained below estimated ACL for St. Thomas and Puerto Rico, however, St. Croix's reliance on parrotfish in commercial fisheries resulted in continued landings of 402,744 lb between 2006 and 2008, almost double the ACL (SERO 2012). The purpose of this study was to define the spatial and temporal dynamics of dispersal, spawning sites and recruitment patterns for the parrotfish genera *Scarus* and *Sparisoma*. The results of this study provide a more holistic view of the parrotfish population dynamics and informs managers of the factors and variability in the "critical" early stages of commercial species which provide for the success of future stocks.

The results of this study suggest that parrotfish populations would benefit from island-specific instead of genera-specific management. Previous studies have found related species and regions often benefit from similar management (Holstein et al. 2014). In the region surrounding STT and STJ *Scarus* and *Sparisoma* populations were found to experience low self-recruitment and have high source diversity dynamics meaning their larvae come from a diversity of spawning locations. This is emphasized in all model years, with little to no retention and the large number of probable spawning sites being located in the British Virgin Islands. This type of source-sink relationships between the BVI and the USVI would be better managed by providing maintenance for upstream populations in the BVI's, because local management would likely benefit recruitment in other areas (Holstein et al. 2014; Roberts 1997). However, in STX, using previous studies

of reef fish larva dispersal to fill sampling gaps in 2007 and 2008, populations seem to have high self-recruitment due to small-shelf features and relative isolation (Chérubin and Garavelli 2016 and Chérubin and Richardson 2007). This type of network benefits from maintenance of local adult reproductive populations within the region (Holstein et al. 2014). Thus, it is important that management focuses efforts on areas of local retention (ex. northwest end of STX discussed in this study) to avoid overfishing in essential self-recruitment and spawning areas. This supports the CFMC regulation to lower the STX ACL below average catch limits since self-recruiting populations can often appear stable when they are actually near collapse (Bonfil 2005). Understanding larval population connectivity and dynamics can also be used to assist the scale and determine the appropriateness of spatial management for a species.

Due to the distance of dispersal (some particles originating from 10-100 km from their origin) and the annual variability in retention and spawning site success of scarids, suggests that scarids are not spatially explicit. Scarids, unlike snappers and grouper species which travel long distances to aggregate in the same exact spawning location annually or bi-annually, would not likely benefit for spatial management such as 'Spawning Special Management Zones' (SMZs) (Farmer et al. 2017). This is because spawning grounds vary slightly annually (and likely monthly and daily), thus, strict boundaries may only protect a small portion of the population during any given time. Instead, managers' focus should be on what separates high probability spawning localities from low probability spawning habitats. Providing broader regulations, such as MPAs which protect successful spawning sites may be a more successful dynamic for the scarid population and culturally in the Virgin Islands (SERO 2012).

This study also infers the importance of fisheries-independent data. Fisheries-independent surveys provide not only the distribution of parrotfish stocks, but when paired with connectivity modeling it can be used to describe connectivity pathways identifying the entire pathway from spawning to possible settlement, including where larvae are being retained. Thus, small island communities like the USVI can focus limited resources on fisheries-independent surveying to capture necessary information on

stocks of commercially important species rather than based on incomplete, unreliable or biased fisheries-dependent stock assessments alone. Management based on the entire lifecycle of scarids from fishery-independent surveys will hopefully improve regulations and protections to effectively replenish stocks of this economically and culturally significant family of reef fish.

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Appendix A

Table A1 List of CRER Scaridae abundances organized by year, date, cruise code, lat/lon, station and gear.

Year	Date	Cruise	Latitude	Longitude	Station	Gear	Number of Scarus	Number of Sparisoma
2007	3/30/2007	NF0705	18.0933	-65.0333	10	Bongo	0	0
2007	3/30/2007	NF0705	18.0933	-65.0333	10	MOCNESS	1	3
2007	3/30/2007	NF0705	18.1967	-65.0333	9	Bongo	1	5
2007	3/30/2007	NF0705	18.2883	-64.9583	11	Bongo	2	0
2007	3/31/2007	NF0705	18.0933	-64.9583	13	MOCNESS	1	3
2007	3/31/2007	NF0705	18.0933	-64.8583	17	MOCNESS	2	3
2007	3/31/2007	NF0705	18.1700	-64.9050	14	MOCNESS	1	3
2007	3/31/2007	NF0705	18.1817	-64.9583	12	MOCNESS	0	0
2007	3/31/2007	NF0705	18.1817	-64.7933	18	MOCNESS	3	10
2007	3/31/2007	NF0705	18.1917	-64.8583	16	MOCNESS	10	38
2007	3/31/2007	NF0705	18.2650	-64.8967	15	Bongo	3	6
2007	3/31/2007	NF0705	18.2767	-64.7933	19	Bongo	5	101
2007	3/31/2007	NF0705	18.2917	-64.7283	20	Bongo	3	19
2007	4/1/2007	NF0705	18.0933	-64.7283	22	MOCNESS	3	83
2007	4/1/2007	NF0705	18.1733	-64.6033	23	MOCNESS	0	38
2007	4/1/2007	NF0705	18.1983	-64.7283	21	MOCNESS	0	7
2007	4/1/2007	NF0705	18.2433	-64.6467	24	MOCNESS	4	19
2007	4/1/2007	NF0705	18.2833	-64.6000	26	MOCNESS	2	64
2007	4/2/2007	NF0705	18.2333	-64.4883	27	MOCNESS	7	81
2007	4/2/2007	NF0705	18.3000	-64.3700	29	MOCNESS	2	75

2007	4/2/2007	NF0705	18.3067	-64.5433	28	MOCNESS	0	1
2007	4/4/2007	NF0705	18.3200	-64.2100	35	MOCNESS	15	12
2007	4/4/2007	NF0705	18.3633	-64.2650	34	MOCNESS	32	13
2007	4/4/2007	NF0705	18.4217	-64.3433	32	MOCNESS	0	185
2007	4/5/2007	NF0705	18.2367	-63.3917	39	MOCNESS	22	37
2007	4/5/2007	NF0705	18.2550	-63.6133	38	MOCNESS	1	28
2007	4/5/2007	NF0705	18.2833	-63.9450	37	MOCNESS	0	0
2007	4/6/2007	NF0705	17.7500	-63.4767	46	MOCNESS	70	42
2007	4/6/2007	NF0705	17.8783	-63.2983	45	MOCNESS	0	167
2007	4/6/2007	NF0705	18.0017	-63.1217	44	MOCNESS	4	27
2007	4/6/2007	NF0705	18.1533	-63.1833	42	Bongo	0	26
2007	4/7/2007	NF0705	17.6333	-62.4583	55	Bongo	23	234
2007	4/7/2007	NF0705	17.8867	-62.8667	51	Bongo	8	239
2007	(blank)	NF0705	18.2883	-65.0333	8	Bongo	3	51
2007	(blank)	NF0705	18.3667	-64.4250	30	MOCNESS	17	354
2007	(blank)	NF0705	18.4050	-64.5183	31	Bongo	1	42
2008	3/11/2008	NF0805	18.1972	-65.0360	2	MOCNESS	1	2
2008	3/11/2008	NF0805	18.2880	-65.0345	1	Bongo	0	5
2008	3/12/2008	NF0805	18.0917	-64.8588	11	MOCNESS	0	0
2008	3/12/2008	NF0805	18.0923	-64.9600	6	MOCNESS	0	0
2008	3/12/2008	NF0805	18.1700	-64.9050	7	MOCNESS	0	0
2008	3/12/2008	NF0805	18.1812	-64.9598	5	MOCNESS	1	2
2008	3/12/2008	NF0805	18.1818	-64.7935	12	MOCNESS	0	0
2008	3/12/2008	NF0805	18.1900	-64.8580	10	MOCNESS	2	6

2008	3/12/2008	NF0805	18.2775	-64.7932	13	Bongo	0	0
2008	3/12/2008	NF0805	18.2885	-64.9572	4	Bongo	0	0
2008	3/13/2008	NF0805	18.0915	-64.7303	16	MOCNESS	0	0
2008	3/13/2008	NF0805	18.1730	-64.6055	17	MOCNESS	0	0
2008	3/13/2008	NF0805	18.1992	-64.7245	15	Bongo	0	0
2008	3/13/2008	NF0805	18.1992	-64.7245	15	MOCNESS	0	0
2008	3/13/2008	NF0805	18.2332	-64.4892	21	MOCNESS	0	2
2008	3/13/2008	NF0805	18.2435	-64.6475	18	MOCNESS	13	4
2008	3/13/2008	NF0805	18.2828	-64.6015	20	MOCNESS	0	0
2008	3/14/2008	NF0805	18.2998	-64.3705	23	MOCNESS	0	0
2008	3/14/2008	NF0805	18.3068	-64.5420	22	MOCNESS	3	43
2008	3/14/2008	NF0805	18.3625	-64.2648	28	MOCNESS	0	0
2008	3/14/2008	NF0805	18.3668	-64.4257	24	MOCNESS	0	5
2008	3/14/2008	NF0805	18.4200	-64.3442	26	MOCNESS	0	0
2008	3/15/2008	NF0805	18.2547	-63.6132	32	MOCNESS	0	0
2008	3/16/2008	NF0805	17.4612	-63.4820	35	Bongo	0	0
2008	3/16/2008	NF0805	17.6588	-63.3585	34	Bongo	0	0
2008	3/20/2008	NF0805	17.6482	-63.2093	38	MOCNESS	0	0
2008	3/20/2008	NF0805	18.0025	-63.1228	39	Bongo	0	0
2008	3/21/2008	NF0805	18.4927	-64.2425	48	MOCNESS	0	5
2008	3/21/2008	NF0805	18.6007	-64.1368	49	Bongo	0	15
2008	3/22/2008	NF0805	18.5382	-64.5588	59	Bongo	10	6
2008	3/22/2008	NF0805	18.6200	-64.6387	60	Bongo	13	8
2008	3/22/2008	NF0805	18.6880	-64.5368	58	Bongo	1	13

2008	3/22/2008	NF0805	18.7017	-64.7148	61	Bongo	1	3
2008	3/22/2008	NF0805	18.7167	-64.2192	51	MOCNESS	0	6
2008	3/22/2008	NF0805	18.7898	-64.3853	53	MOCNESS	0	0
2008	3/22/2008	NF0805	18.7988	-64.5202	55	MOCNESS	0	2
2008	3/22/2008	NF0805	18.8128	-64.2633	52	MOCNESS	0	0
2008	3/22/2008	NF0805	18.8200	-64.1330	50	MOCNESS	0	0
2008	3/22/2008	NF0805	18.8390	-64.6800	57	Bongo	0	0
2008	3/22/2008	NF0805	18.8390	-64.6800	57	MOCNESS	0	0
2008	3/22/2008	NF0805	18.8740	-64.3837	54	MOCNESS	0	0
2008	3/23/2008	NF0805	18.4073	-65.0012	74	Bongo	0	0
2008	3/23/2008	NF0805	18.5042	-65.0767	75	Bongo	6	22
2008	3/23/2008	NF0805	18.5982	-64.7817	65	Bongo	4	7
2008	3/23/2008	NF0805	18.6035	-65.0382	73	Bongo	0	1
2008	3/23/2008	NF0805	18.6035	-65.0382	73	MOCNESS	0	0
2008	3/23/2008	NF0805	18.6178	-64.9348	71	MOCNESS	2	2
2008	3/23/2008	NF0805	18.6603	-64.8403	64	Bongo	0	2
2008	3/23/2008	NF0805	18.6603	-64.8403	64	MOCNESS	0	2
2008	3/23/2008	NF0805	18.7202	-65.0597	72	Bongo	0	1
2008	3/23/2008	NF0805	18.7202	-65.0597	72	MOCNESS	1	11
2008	3/23/2008	NF0805	18.7520	-64.9275	63	Bongo	3	75
2008	3/23/2008	NF0805	18.7728	-64.7823	62	Bongo	1	4
2008	3/23/2008	NF0805	18.7728	-64.7823	62	MOCNESS	0	3
2008	3/24/2008	NF0805	18.3522	-65.1402	79	Bongo	0	1
2008	3/24/2008	NF0805	18.4588	-65.1650	78	Bongo	9	175

2008	3/24/2008	NF0805	18.5642	-65.1900	77	Bongo	0	30
2008	3/24/2008	NF0805	18.5642	-65.1900	77	MOCNESS	8	51
2008	3/24/2008	NF0805	18.6917	-65.2217	76	Bongo	1	25
2008	3/24/2008	NF0805	18.6917	-65.2217	76	MOCNESS	23	81
2008	(blank)	NF0805	17.2326	-63.4541	36	Bongo	1	8
2008	(blank)	NF0805	17.8860	-62.8678	37	Bongo	7	55
2008	(blank)	NF0805	18.1818	-64.7935	12	Bongo	5	114
2008	(blank)	NF0805	18.1900	-64.8580	10	Bongo	0	15
2008	(blank)	NF0805	18.2435	-64.6475	18	Bongo	7	241
2008	(blank)	NF0805	18.2707	-64.8573	9	Bongo	2	29
2008	(blank)	NF0805	18.2786	-63.9233	31	MOCNESS	0	2
2008	(blank)	NF0805	18.2828	-64.6015	20	Bongo	0	1
2008	(blank)	NF0805	18.2910	-64.7273	14	Bongo	0	0
2008	(blank)	NF0805	18.2988	-64.6830	19	Bongo	0	0
2008	(blank)	NF0805	18.3068	-64.5420	22	Bongo	7	70
2008	(blank)	NF0805	18.3208	-64.2117	29	MOCNESS	11	118
2008	(blank)	NF0805	18.3668	-64.4257	24	Bongo	3	12
2008	(blank)	NF0805	18.3962	-64.8782	69	Bongo	0	8
2008	(blank)	NF0805	18.4037	-64.5185	25	Bongo	0	4
2008	(blank)	NF0805	18.4058	-64.7832	68	Bongo	2	0
2008	(blank)	NF0805	18.4662	-64.6568	67	Bongo	0	5
2008	(blank)	NF0805	18.4927	-64.2425	48	Bongo	8	20
2008	(blank)	NF0805	18.5078	-64.9067	70	Bongo	0	3
2008	(blank)	NF0805	18.5205	-64.7077	66	Bongo	0	0

2008	(blank)	NF0805	18.6178	-64.9348	71	Bongo	9	22
2008	(blank)	NF0805	18.7167	-64.2192	51	Bongo	5	26
2008	(blank)	NF0805	18.7898	-64.3853	53	Bongo	13	17
2008	(blank)	NF0805	18.7988	-64.5202	55	Bongo	31	23
2008	(blank)	NF0805	18.8200	-64.1330	50	Bongo	6	27
2008	(blank)	NF0805	18.8740	-64.3837	54	Bongo	5	23
2008	(blank)	NF0805	18.9233	-64.6805	56	Bongo	4	78
2008	(blank)	NF0805	18.9233	-64.6805	56	MOCNESS	1	11
2009	4/8/2009	NF0903	18.0933	-65.1083	6	Bongo	0	0
2009	4/8/2009	NF0903	18.1650	-65.1083	5	Bongo	0	0
2009	4/9/2009	NF0903	18.0933	-65.1083	6	MOCNESS	0	0
2009	4/9/2009	NF0903	18.0933	-64.9583	13	MOCNESS	0	4
2009	4/9/2009	NF0903	18.1650	-65.1083	5	MOCNESS	0	3
2009	4/9/2009	NF0903	18.1700	-64.9050	14	Bongo	0	3
2009	4/9/2009	NF0903	18.1817	-64.9583	12	MOCNESS	0	2
2009	4/9/2009	NF0903	18.2650	-64.8967	15	Bongo	0	0
2009	4/9/2009	NF0903	18.2700	-64.8583	16	Bongo	0	0
2009	4/9/2009	NF0903	18.2883	-65.0333	8	Bongo	0	1
2009	4/9/2009	NF0903	18.2883	-64.9583	11	Bongo	0	0
2009	4/10/2009	NF0903	18.0150	-64.8583	19	MOCNESS	0	0
2009	4/10/2009	NF0903	18.0933	-64.8583	18	Bongo	1	20
2009	4/10/2009	NF0903	18.0933	-64.8583	18	MOCNESS	0	4
2009	4/10/2009	NF0903	18.1817	-64.7933	20	MOCNESS	0	2
2009	4/10/2009	NF0903	18.1917	-64.8583	17	Bongo	1	0

2009	4/10/2009	NF0903	18.1917	-64.8583	17	MOCNESS	18	151
2009	4/10/2009	NF0903	18.3967	-64.8783	23	Bongo	0	0
2009	4/10/2009	NF0903	18.4067	-65.0017	24	Bongo	0	0
2009	4/10/2009	NF0903	18.4067	-64.7817	22	Bongo	0	0
2009	4/10/2009	NF0903	18.4583	-65.1650	26	Bongo	0	2
2009	4/10/2009	NF0903	18.5050	-65.0750	25	Bongo	4	4
2009	4/10/2009	NF0903	18.5650	-65.1900	27	Bongo	0	1
2009	4/10/2009	NF0903	18.5650	-65.1900	27	MOCNESS	4	12
2009	4/10/2009	NF0903	18.6917	-65.2217	28	Bongo	2	0
2009	4/11/2009	NF0903	18.4667	-64.6567	37	Bongo	3	19
2009	4/11/2009	NF0903	18.5217	-64.7083	36	Bongo	1	1
2009	4/11/2009	NF0903	18.5383	-64.5600	38	Bongo	0	0
2009	4/11/2009	NF0903	18.5983	-64.7817	35	Bongo	0	0
2009	4/11/2009	NF0903	18.6017	-65.0383	30	MOCNESS	0	0
2009	4/11/2009	NF0903	18.6167	-64.9350	32	MOCNESS	0	0
2009	4/11/2009	NF0903	18.6183	-64.6367	39	Bongo	0	0
2009	4/11/2009	NF0903	18.6567	-64.8367	34	MOCNESS	0	0
2009	4/11/2009	NF0903	18.6917	-65.2217	28	MOCNESS	2	5
2009	4/11/2009	NF0903	18.7000	-64.7133	40	Bongo	8	17
2009	4/11/2009	NF0903	18.7200	-65.0600	29	MOCNESS	10	2
2009	4/11/2009	NF0903	18.7533	-64.9283	33	MOCNESS	6	2
2009	4/11/2009	NF0903	18.7717	-64.7817	41	Bongo	15	11
2009	4/11/2009	NF0903	18.7717	-64.7817	41	MOCNESS	2	9
2009	4/11/2009	NF0903	18.9233	-64.6800	42	Bongo	2	5

2009	4/11/2009	NF0903	18.9233	-64.6800	42	MOCNESS	0	4
2009	4/12/2009	NF0903	18.7200	-64.2200	50	MOCNESS	1	0
2009	4/12/2009	NF0903	18.7917	-64.3833	48	MOCNESS	0	0
2009	4/12/2009	NF0903	18.7983	-64.5200	46	MOCNESS	0	0
2009	4/12/2009	NF0903	18.8133	-64.2617	49	MOCNESS	0	0
2009	4/12/2009	NF0903	18.8200	-64.1317	51	MOCNESS	0	0
2009	4/12/2009	NF0903	18.8400	-64.6800	43	Bongo	0	0
2009	4/12/2009	NF0903	18.8400	-64.6800	43	MOCNESS	0	0
2009	4/12/2009	NF0903	18.8750	-64.3833	47	MOCNESS	0	0
2009	4/12/2009	NF0903	18.9233	-64.6800	42	MOCNESS	0	1
2009	4/13/2009	NF0903	18.1733	-64.6033	60	MOCNESS	0	0
2009	4/13/2009	NF0903	18.2333	-64.4883	57	MOCNESS	0	0
2009	4/13/2009	NF0903	18.3000	-64.3700	55	MOCNESS	0	0
2009	4/13/2009	NF0903	18.3667	-64.4250	56	MOCNESS	0	0
2009	4/13/2009	NF0903	18.4300	-64.1917	53	MOCNESS	0	0
2009	4/13/2009	NF0903	18.4867	-64.2467	54	MOCNESS	0	0
2009	4/13/2009	NF0903	18.6000	-64.1317	52	Bongo	0	0
2009	4/13/2009	NF0903	18.6000	-64.1317	52	MOCNESS	0	0
2009	4/13/2009	NF0903	18.8200	-64.1317	51	MOCNESS	0	0
2009	4/15/2009	NF0903	18.0933	-64.7283	66	Bongo	1	4
2009	4/15/2009	NF0903	18.0933	-64.7283	66	MOCNESS	5	50
2009	4/15/2009	NF0903	18.1983	-64.7283	65	Bongo	2	2
2009	4/15/2009	NF0903	18.1983	-64.7283	65	MOCNESS	11	2
2009	4/16/2009	NF0903	18.2433	-64.6467	67	Bongo	0	0

2009	4/16/2009	NF0903	18.2433	-64.6467	67	MOCNESS	0	0
2009	4/16/2009	NF0903	18.2550	-63.6133	74	Bongo	1	16
2009	4/16/2009	NF0903	18.2550	-63.6133	74	MOCNESS	0	1
2009	4/16/2009	NF0903	18.2833	-63.9450	73	Bongo	11	33
2009	4/16/2009	NF0903	18.2833	-63.9450	73	MOCNESS	0	0
2009	4/16/2009	NF0903	18.3200	-64.2100	71	MOCNESS	0	0
2009	4/16/2009	NF0903	18.3500	-64.2483	70	MOCNESS	0	0
2009	4/16/2009	NF0903	18.4167	-64.3367	68	Bongo	0	0
2009	4/16/2009	NF0903	18.4167	-64.3367	68	MOCNESS	4	21
2009	4/17/2009	NF0903	17.5317	-62.9467	82	Bongo	0	3
2009	4/17/2009	NF0903	17.5317	-62.9467	82	MOCNESS	0	1
2009	4/17/2009	NF0903	17.6467	-63.2100	81	MOCNESS	3	3
2009	4/17/2009	NF0903	17.7500	-63.4767	79	MOCNESS	0	1
2009	4/17/2009	NF0903	17.8783	-63.2983	78	MOCNESS	0	0
2009	4/17/2009	NF0903	17.9967	-63.1283	77	MOCNESS	0	0
2009	4/17/2009	NF0903	18.1083	-63.3467	76	Bongo	0	0
2009	4/17/2009	NF0903	18.1083	-63.3467	76	MOCNESS	0	0
2009	4/18/2009	NF0903	17.2233	-63.4500	83	Bongo	1	2
2009	4/18/2009	NF0903	17.4000	-64.3500	88	MOCNESS	7	3
2009	4/18/2009	NF0903	17.4650	-63.4817	84	Bongo	9	20
2009	4/18/2009	NF0903	17.4767	-63.9333	86	Bongo	55	53
2009	4/18/2009	NF0903	17.5150	-63.7317	85	Bongo	1	3
2009	4/18/2009	NF0903	17.5150	-63.7317	85	MOCNESS	0	0
2009	4/18/2009	NF0903	17.7717	-64.4717	92	Bongo	0	0

2009	4/18/2009	NF0903	17.7717	-64.4717	92	MOCNESS	0	0
2009	4/18/2009	NF0903	17.8283	-64.4233	91	Bongo	0	0
2009	4/18/2009	NF0903	17.8283	-64.4233	91	MOCNESS	0	0
2009	4/18/2009	NF0903	17.9150	-64.2850	89	MOCNESS	5	33
2009	4/18/2009	NF0903	18.0217	-64.4333	90	MOCNESS	24	81
2009	4/19/2009	NF0903	17.7683	-64.5467	95	Bongo	15	39
2009	4/19/2009	NF0903	17.7867	-64.6617	99	MOCNESS	1	7
2009	4/19/2009	NF0903	17.8083	-64.5683	96	Bongo	0	1
2009	4/19/2009	NF0903	17.8083	-64.5683	96	MOCNESS	2	2
2009	4/19/2009	NF0903	17.8317	-64.5033	94	Bongo	0	0
2009	4/19/2009	NF0903	17.8317	-64.5033	94	MOCNESS	1	1
2009	4/19/2009	NF0903	17.8783	-64.7583	102	Bongo	0	9
2009	4/19/2009	NF0903	17.8817	-64.6067	97	MOCNESS	0	4
2009	4/20/2009	NF0903	17.7750	-64.8583	103	Bongo	2	55
2009	4/20/2009	NF0903	17.8583	-64.8583	104	Bongo	5	13
2009	4/20/2009	NF0903	17.9367	-64.8583	105	Bongo	0	1
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2009	(blank)	NF0903	17.6733	-63.3517	80	Bongo	0	3
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2009	(blank)	NF0903	17.7783	-64.7300	100	Bongo	0	1
2009	(blank)	NF0903	17.7867	-64.6617	99	Bongo	0	5
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2009	(blank)	NF0903	17.8817	-64.6067	97	Bongo	0	8
2009	(blank)	NF0903	17.9150	-64.2850	89	Bongo	0	2
2009	(blank)	NF0903	17.9967	-63.1283	77	Bongo	0	1
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2009	(blank)	NF0903	18.1100	-65.2067	1	Bongo	0	38
2009	(blank)	NF0903	18.1183	-64.5700	61	Bongo	1	15
2009	(blank)	NF0903	18.1733	-64.6033	60	Bongo	6	1
2009	(blank)	NF0903	18.1817	-64.9583	12	Bongo	1	16
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2009	(blank)	NF0903	18.1967	-65.0333	9	Bongo	1	26
2009	(blank)	NF0903	18.1967	-65.0333	9	MOCNESS	0	58
2009	(blank)	NF0903	18.2033	-65.2067	2	Bongo	29	72
2009	(blank)	NF0903	18.2683	-65.1083	4	Bongo	7	5
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2009	(blank)	NF0903	18.2833	-64.6000	59	Bongo	1	6
2009	(blank)	NF0903	18.2917	-64.7283	64	Bongo	0	19
2009	(blank)	NF0903	18.2983	-64.6817	63	Bongo	0	8
2009	(blank)	NF0903	18.3067	-64.5433	58	Bongo	2	35
2009	(blank)	NF0903	18.3200	-64.2100	71	Bongo	9	58

2009	(blank)	NF0903	18.3500	-64.2483	70	Bongo	1	10
2009	(blank)	NF0903	18.3667	-64.4250	56	Bongo	0	2
2009	(blank)	NF0903	18.4050	-64.5183	62	Bongo	7	11
2009	(blank)	NF0903	18.4867	-64.2467	54	Bongo	18	94
2009	(blank)	NF0903	18.5067	-64.9067	31	Bongo	8	59
2009	(blank)	NF0903	18.6017	-65.0383	30	Bongo	1	26
2009	(blank)	NF0903	18.6100	-64.4633	45	Bongo	0	3
2009	(blank)	NF0903	18.6167	-64.9350	32	Bongo	0	1
2009	(blank)	NF0903	18.6567	-64.8367	34	Bongo	0	4
2009	(blank)	NF0903	18.6883	-64.5367	44	Bongo	3	74
2009	(blank)	NF0903	18.7200	-65.0600	29	Bongo	12	29
2009	(blank)	NF0903	18.7533	-64.9283	33	Bongo	6	24
2009	(blank)	NF0903	18.7917	-64.3833	48	Bongo	5	18
2009	(blank)	NF0903	18.7983	-64.5200	46	Bongo	3	20
2009	(blank)	NF0903	18.8133	-64.2617	49	Bongo	40	89
2009	(blank)	NF0903	18.8200	-64.1317	51	Bongo	0	0
2009	(blank)	NF0903	18.8750	-64.3833	47	Bongo	0	0