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# Population Connectivity and Larval Dispersal of Caribbean Spiny Lobster

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UNIVERSITY OF MIAMI

POPULATION CONNECTIVITY AND LARVAL DISPERSAL OF CARIBBEAN  
SPINY LOBSTER

By

Andrew Sebastian Kough

A DISSERTATION

Submitted to the Faculty  
of the University of Miami  
in partial fulfillment of the requirements for  
the degree of Doctor of Philosophy

Coral Gables, Florida

August 2014

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POPULATION CONNECTIVITY AND LARVAL DISPERSAL OF CARIBBEAN  
SPINY LOBSTER

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Population Connectivity and Larval Dispersal  
of Caribbean Spiny Lobster

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Studies of movement, fundamental to most life on earth, become complicated in the ocean. Many marine organisms have a complex lifecycle with a larval phase, giving them vast dispersal potential from powerful ocean currents while obscuring direct observation by virtue of their minute size. These research challenges are beginning to be circumvented through biophysical modeling of larval transport. Modeling simulates the potential pathways of larvae, but not fine-scale spatial movements. Despite their small size, larvae actively participate in their dispersive journey, detecting and responding to environmental cues. Orientation behavior has a great impact on a larva's survival and journey, and links dispersal and settlement.

A thorough examination of larval movement encompasses two scales: investigating small-scale orientation behavior *in situ* and broad dispersal through modeling. Comprehensive studies spanning a range of spatial scales are rare, thus there is a knowledge gap between modeling dispersal and studying behavioral ecology. This dissertation bridges the gap by addressing both scales of movement for the Caribbean spiny lobster, *Panulirus argus*, and asking: what are the consequences of larval lobster movement?

Caribbean larval movement and connectivity were explored using Lagrangian stochastic modeling of larval dispersal. The first focus was on how variation in modeled biological traits impacted connectivity networks, to provide a template for setting up and evaluating future models of larval dispersal. Any linkage of modeled larvae between two habitat sites was defined as a connection. Connections were rare in time, associated with mesoscale features in both time and space, and vertical migration behavior increased the stability of connections. Next a dispersal model was parameterized, validated with observed average monthly settlement at multiple sites, and used to determine the probabilistic larval connectivity of lobster; translating connectivity into fisheries management strategy. The majority of larval exchanges cross international boundaries, and management scenarios focused on international exchange yielded the most settlement potential. However, self-recruitment still dominated in some areas. Management scenarios focused on preserving connectivity from self-recruitment caused a near universal increase in modeled larval settlement across the Caribbean. Simulations including behavior and realistic spawning biology performed best when compared with empirical data. Modeled pelagic nurseries were identified that entrained lobster larvae across age classes, and may be important features for conservation.

Previous studies suggest that as a larva moves towards appropriate settlement habitat, it is exposed to environmental cues including sound, odor, pressure, and light. If, when, and how a settling larva integrates this information to influence its journey remains a mystery. The Drifting In Situ Chamber (DISC) allows glimpses into this process; while imbedded in the ocean current it simultaneously observes the environment, and quantifies the orientation behavior of larvae. This study deployed this new instrumentation in a

novel manner, investigating the orientation behavior preceding settlement of postlarval lobsters *in situ* and nocturnally for the first time. Postlarvae oriented differently relative to the tide. During ebb tide postlarvae oriented using partial compensation into the current and towards the shore, potentially facilitating transport towards settlement habitat. Postlarvae may orient using the wind while at the surface, using a seabreeze as a compass to swim towards settlement habitat.

Investigating the specific movement patterns during settlement and the far-flung dispersal of a species throughout its range gives this study a comprehensive examination of marine larval movement ecology over multiple spatiotemporal scales. The dynamics of spiny lobster dispersal throughout the Caribbean are necessary information for managing an internationally important fishery. Understanding the cues that guide the postlarvae of lobster, and likely a broad range of other species, into settlement habitat is important to better conserve nursery habitats.

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## **CHAPTER 1. GENERAL INTRODUCTION**

### *Movement Ecology*

Almost all life on earth moves at one time or another, whether as a seed buried deep in the gut of a bird hitch-hiking a ride to a permanent home, or as a highly mobile albatross that only stops flying during occasional breeding bouts. With resources and conditions varying across the earth, movement is often the only solution in the struggle to thrive or perish for a species or individual to feed, breed, or grow. The essential nature of movement for life has not been ignored by scientists; roughly 26,000 studies have been published on some aspect of movement (Holyoak et al. 2008) and the search for a unified theory of movement is ongoing (Holden 2006). Movement ecology is a term being applied to the “random, biomechanical, cognitive, and optimal” (Nathan et al. 2008) paradigms of researching movement. Simply put, these are the roles of outside processes (e.g., physical environment, chance encounters), the physical abilities to move and to navigate, and the internal conditions that determine the need for movement. Very few studies have taken an integrated approach to address how such processes interact to dictate the movement of the same organism (Holyoak et al. 2008).

Studies in the ocean are under-represented in movement ecology (Holyoak et al. 2008). In the marine realm, life seems on the edge to terrestrially based humans. As a mammal that raises resource demanding broods, planktonic dispersal seems like an alien process. Spawning directly into the ocean, not providing lasting protection or resources, and letting offspring fend for themselves adrift in the seas appears to be a futile effort with success driven by luck, yet most marine animals have a planktonic lifestage. Marine

populations have long been viewed as “open” (Roughgarden 1985; Roberts 1997; Shanks and Eckert 2005; Sale 2004) with long distance dispersal (LDD) of larvae in powerful currents considered commonplace. The LDD paradigm has been shifting over the past decade, and the marine literature now recognizes a continuum of larval planktonic dispersal including LDD and local replenishment (Kinlan et al. 2005; Cowen et al. 2006). As researchers have endeavored to describe larval dispersal they have discovered that larvae are not passive particles, and actively swim and navigate in the ocean (Leis et al. 1996; Fisher et al. 2000; Paris and Cowen 2004; Gerlach et al. 2007; Paris et al. 2013a).

Similarly in the terrestrial literature LDD has long been challenging to identify, and its role in forming populations and dispersal networks has been underappreciated (Higgins et al. 2003; Levin 2003). Recent advances in modeling have caused a surge of interest in LDD (Trakthenbrot et al. 2005; Nathan 2006; Wright et al. 2008). Thus, marine dispersal provides an opportunity to simultaneously examine multiple paradigms of movement. The conflict and compromise between larval mediated movements and wide-scale advection sets the stage for an interdisciplinary study of larval movement, with findings relevant across the field of movement ecology.

### *Challenges of Studying Larvae*

The size of the ocean and the potential dispersive range relative to the size of the organism being examined is a hurdle for empirical studies examining marine dispersal (Steneck et al. 2007). For empirical studies, new techniques have been developed to assess dispersal and the role of larval behavior (Leis 2007). For example, direct larval tracking can be accomplished, using chemical and genetic markers. The otoliths of fish can be impregnated with certain isotopes or tetracycline, which gives animals a

permanent marker (Jones et al. 1999; Almany et al. 2007; Saenz-Agudelo et al. 2011). If these individuals are then recovered they can be definitively identified as self-recruits or dispersers, if found at distant locations. However the recovery rate is low even in organisms with short pelagic larval durations (PLD). Such tagging techniques can only describe recruits that return to the same site, giving such studies a very limited scope for species with broad dispersal abilities. When coupled with microsatellite markers, artificial markers and parentage analysis have demonstrated a connectivity network on the scale of 10s of km (Planes et al. 2009; Almany et al. 2013) but not over the distances interlinking most marine metapopulations (Cowen et al. 2006; Holstein et al. 2014).

The regionally differing elemental compositions found throughout the ocean have been used to identify where larvae matured by using the concentrations of Mn, Mg, Sr, Ba, or Pb found within an organisms shell or otolith (Swearer et al. 1999; Thorrold et al. 2001; Becker et al. 2007; Hamilton et al. 2010; Carson et al. 2010). The validity of this technique when confronted with a huge potential range is unknown, as these studies focused in on limited areas within a bay or the runoff and coastal area around an island. Having a wide population range (such as comprehensively throughout the Caribbean) means that a broad variety of elemental signatures are likely to be encountered and specific paths are unlikely to be definitively identified.

Even newly developed techniques do not work when the subject lacks hard markable structure, is ubiquitous across a wide range, or has a lengthy pelagic larval duration. Massive mortality comes with pelagic larval dispersal (Houde and Bartsch 2008; Cowen et al. 2000; Paris 2009), thus actively marked recruits are rarely recovered. Moreover, studies of connectivity have concentrated on fish with short larval durations and

extremely restricted habitat requirements, such as anemonefish (Jones et al. 1999; Almany et al. 2007; Saenz-Agueldo et al. 2012). More mortality occurs over longer pelagic periods, and the likelihood of recapture decreases as PLD increases, thus the efficiency of marking techniques rapidly decreases with longer PLDs (Cowen et al. 2006). Additionally, the concentration and uptake of an isotopic signature on large and externally brooded clutches is unknown for most invertebrates (Kingsford et al. 2002). Importantly, even when an origin and an endpoint are definitely identified, the proximate steps making up the larval path remain unknown. Fortunately there are other methods of describing larval dispersal.

### *Biophysical Modeling*

Biophysical modeling provides researchers with a tool that can resolve potential pelagic trajectories, which cannot be addressed through conventional field techniques. An individual-based coupled biophysical model uses ocean currents from circulation models in conjunction with a movement algorithm to model particle transport through the ocean. These particles can be given the properties of eggs, larvae, or adult organisms. Ultimately such models simulate the likely paths of larval dispersal and can be used to build connectivity networks. When tagging or marking larvae is either logistically or financially impossible, coupled biophysical models have become the norm for connectivity studies (For review: Metaxas and Saunders 2009; Jones et al. 2009). Computing power limited the realism of early circulation models, so researchers often used mean current velocities and with lower spatial resolution (Roberts 1997; James et al. 2002; Armsworth 2001). Biophysical models have drastically improved since their initial conception, and can now accurately predict and portray the spatiotemporal patterns of

larval settlement (Paris et al. 2007; Sponaugle et al. 2012; Hidalgo et al. 2011). Today's models function across many spatial scales and assimilate real time data, bringing a new level of realism to simulated circulation and dispersal (Paris et al. 2013b). Further advances now portray the vital biological traits of larvae, making the 'bio' portion of biophysical modeling potentially more robust (Metaxas and Saunders 2009; Butler et al. 2011; Staatterman et al. 2012). However, the data used to parameterize such behaviors risk biasing the model and successful simulations require detailed data and hypothesis-based tuning (Brickman 2009; Pelc et al. 2012; Simons et al. 2013). In addition, large scale simulations relevant to commercially important species are missing.

#### *Assessing Behavior In Situ*

Larvae feed, grow, swim, hunt, and evade predators as they disperse in the sea and new observational tools are needed to resolve small-scale larval movements. Indirect assessment methods have been used to examine how environmental cue manipulation can alter recruitment. Bolstering odor (Browne and Zimmer 2001) or sound (Jeffs et al. 2003; Simpson et al. 2004; Simpson et al. 2007) cues at a habitat patch can enhance recruitment, but the underlying behavior guiding the movement itself is not resolved. *In situ* examination of late stage larval behavior in fish by divers using SCUBA has demonstrated the importance of larval behavior to recruitment, (Leis et al. 1996; Bellwood and Stobutzki 1998; Irisson and Lecchini 2008) but may introduce observer bias and interference. Building upon direct observations of larval fish, researchers have also deployed binary choice chambers at sea to examine specific cues especially sound and chemical cues (Tolimieri et al. 2000; Jeffs et al. 2003; Leis and Lockett 2005; Lecchini et al. 2005; Radford et al. 2007). However, some question the validity of these



experiments that test larval reactions to sound cues (Egner 2004; Mann et al. 2007). Additional *in situ* work to examine how larvae react to cues for orientation and navigation is encouraged (Leis 2007). New technologies (e.g., free-floating chambers) for observing larval orientation behavior while minimizing observer bias have been developed (Paris et al. 2008; Irisson et al. 2009), used to describe larval fish reactions to odor and light (Paris et al. 2013a; Berenshtein et al. 2013), and compared favorably with *in situ* observations (Leis et al. 2014). Still, work conducted within such chambers using subjects other than fish larvae and during the night is virtually non-existent.

### *Spiny Lobster*

The Caribbean spiny lobster, *Panulirus argus*, is found throughout the tropical Western Atlantic. Like most marine organisms *P. argus* has a complex lifecycle: adults dwell on coral reefs where they reproduce, spawn, and release larvae that mature in the pelagic zone. The planktonic larvae (phyllosomata) go through 10 different stages over the course of 5-12 months post hatching (Goldstein et al. 2008; Lewis 1951) and are fierce mesoplanktonic predators (Fitzgibbon et al. 2013). A combination of laboratory studies and oceanic trawls elucidated the diurnal and ontogenic vertical migration of the phyllosomata which changes after about three months when the older and larger larva descend to deeper depths (Butler et al. 2011). The postlarval (puerulus) stage is morphologically and behaviorally distinct from earlier phyllosome stages, and occurs after metamorphosis over the shelf break (McWilliam and Phillips 2007; Phillips and McWilliam 2009). Like other panulirid lobster postlarvae (Phillips and McWilliam 1986; Lemmens 1994; Jeffs and Holland 2000), the postlarval stage of *P. argus* is capable of rapid sustained swimming (Calinski and Lyons 1983), and because it does not feed, it

uses lipid energy stores (Jeffs et al. 1999; Wilkin and Jeffs 2011) to power onshore swimming to back-reef vegetated settlement habitat (Herrnkind and Butler 1986; Butler et al. 2006). Postlarval onshore arrival is remarkably precise, occurring most months, at night with the rising tide during the new moon (Acosta et al. 1997). Juveniles and adults display gregarious behavior for mutual predatory defense (Childress and Herrnkind 1996) and actively avoid unhealthy individuals (Behringer et al. 2006) as they mature over a range of habitats including mangroves, seagrass, and coral reefs (Acosta and Butler 1997).

Worth one billion US\$ annually, *P. argus* is the most valuable fishery throughout the Caribbean Sea (Ehrhardt 2010). Commercial, recreational and artisanal fishers in many Caribbean nations are therefore dependent on the proper management of the spiny lobster. The lobster fishery is fully or over-exploited in most of its range, making the establishment of appropriate management techniques an international fisheries priority (Cruz and Bertelsen 2008). In addition, lobsters attract a rabid recreational harvest, bringing in revenue from tourism and maintaining their value in the public eye as cultural icons (Eggleston et al. 2003; Parsons and Eggleston 2005).

A life history demanding adept sensory behavior, coupled with economic and cultural value, makes *P. argus* the ideal research species in marine movement ecology. The potentially conflicting needs for settlement at appropriate habitat and dispersal may be addressed through behavior and other larval life history traits, and are especially important in species with extended larval durations (Bradbury and Snelgrove 2001). The lengthy pelagic larval duration of spiny lobsters culminating in the puerulus stage pairs

broad dispersal potential with a specialized stage for swimming and navigation. Since spiny lobster larvae are extreme dispersers, they are ideal research subjects.

### *Dissertation Scope*

Using the Caribbean spiny lobster as a focal species, my dissertation aims to describe larval dispersal and the role of larval behavior over multiple scales. Spiny lobster larval dispersal probably defines the maximum population connectivity through larval dispersal because *P. argus* have long PLDs approaching the extreme of all known Caribbean species. Ultimately my dissertation makes use of an extreme disperser with economic and cultural value to explore Caribbean larval connectivity.

My first chapter examined how variation within modeled biological traits impacted connectivity networks, which provided a template for setting up and evaluating Lagrangian stochastic models of larval dispersal. Next I parameterized, validated, and used a dispersal model to determine the probabilistic larval connectivity of lobster in the Caribbean. This translated connectivity into fisheries management strategy, while providing a guide to parameterize larval dispersal models. The goal of my final chapter was to describe the environmental cues that guide *P. argus* postlarvae to settlement habitat, thus directly connecting larval dispersal to ecological processes. Abstracts are at the start of each chapter on the title page, and the major goals of each chapter follow.

### ***Chapter 2: Connectivity through time and space: frequent rarity and biological control.***

The first goal was to assess how often connections among Caribbean reef habitat locations occur in time. The influence of release interval on the modeled connectivity network was investigated and compared between three species with different PLDs (coral

5 days; fish 30 days; lobster 152 days). The temporal patterns which emerged in the variance of connections among locations through time were then examined using empirical orthogonal functions. Peaks of variance were found at annual, seasonal, and biweekly temporal scales for all three modeled species. A changing spatial scale of connection was used to identify distances with predictable connections and the distance of LDD in each species. Finally, OVM behavior was included in the model to see how spatiotemporal patterns changed.

***Chapter 3: Larval connectivity and the international management of fisheries.***

The goal of this chapter was to see if a Lagrangian stochastic model of larval dispersal for Caribbean spiny lobster could be constructed using primarily open source data and tools, and then to verify the model with empirical data from independent sources. The influence of biological parameterization on the model verification was also investigated. The connections and dispersal pathways across the Caribbean were then identified and modeled lobster larval connectivity was translated into potential fisheries management strategy.

***Chapter 4: In situ swimming and orientation behavior of spiny lobster (*Panulirus argus*) postlarvae.***

I modified scientific instrumentation developed to study larval fish behavior to examine spiny lobster postlarvae orientation *in situ*. Next, I investigated which environmental conditions changed postlarval orientation to search for cues that postlarvae could use to swim towards settlement habitat.

## CHAPTER 2. CONNECTIVITY THROUGH TIME AND SPACE: FREQUENT RARITY AND BIOLOGICAL CONTROL

In the marine environment many populations exist as discrete pieces of habitat linked through larval dispersal into a larger network. Coupled biophysical Lagrangian stochastic models (LSM) are common tools to study marine networks that model connections, here defined as larval exchanges among locations. However, many LSM studies are restricted to a small sample in time which does not capture the temporal complexity of the marine environment. I described connectivity and variance through time, examined how biology influences connectivity networks through time, and identified the spatial scales of predictability using LSM in a complex Caribbean-wide network. I used three representative Caribbean species to investigate connectivity through time: a short PLD (5 days – the octocoral *Anthielloorgia elisebeathe*), a medium PLD (30 days – the bicolor damselfish *Stegastis partitus*), and a long PLD (152 days – the Caribbean spiny lobster *Panulirus argus*). All representative species were based on available parameterizations that include OVM behavior. Many organisms spawn periodically and release eggs or larvae over a range of frequencies. Here, I define the time between sequential spawning events as the release interval and define any linkage of modeled larvae between two habitat sites as a connection. I investigated how changing release interval affected the connectivity network. As the release interval increases (i.e., releases occur less often) the number of connections decreases, the average time with connection decreases, and the average probability of the remaining connections increases. Overall, the most common connections were those that were rare in time, which suggested the seemingly paradoxical finding of “frequent rarity.” Frequent rarity emerged

in simulations of all three different species. Empirical orthogonal function analysis identified peaks in the temporal patterns of variance in settlement.

Connections were examined from local to Caribbean-wide spatial scales, and the variance captured in the first 10 EOF modes peaked at spatiotemporal scales consistent with mesoscale features. This modeling work demonstrated how spawning relates to temporal features and spatial scales, that most connections occur occasionally, and the impacts of restricted spawning time on the connectivity network. In addition, I found that simple ontogenic vertical migration behavior acted as a biological control and stabilized dispersal by increasing the amount and predictability of connections through time.

**Background:**

In the marine environment many populations exist as discrete pieces of habitat linked through larval dispersal into a larger connectivity network (Hanski 1998; Cowen et al. 2006). Here I define a connection as any modeled larval exchange between two habitat sites. Many studies describing connectivity are only able to collect and quantify arriving larvae during a subsample of the year (Harrison et al. 2012; Coles et al. 2011; Almany et al. 2007; Jones et al. 2005). However pulses of larvae arrive in a stochastic (Siegel et al. 2008) and unpredictable manner (Eggleston et al. 1998) because there is variability in spawning time over the year even within species (Bertelsen and Matthews 2001), and because the currents in coastal systems are highly variable (Paris et al. 2002; Siegel et al. 2003). In fact, in an area with variable prevailing currents, changing spawning time can drive speciation (Carson et al. 2010). The uncertainty surrounding the timing of larval pulses suggests that studies restricted to a snapshot in time may not adequately describe demographic connectivity.

Management and conservation efforts modify recruitment environments. Many habitats are managed as multi-use areas that allow and encourage both recreational and commercial activities and correspondingly require a variety of species to be replenished. Natural cycles fluctuate seasonally. The environment for larvae can be more or less favorable through the year following changes in food availability, temperature, predator abundance, species composition, and available habitat (Bauer et al. 2014; Nunn et al. 2012; Butler and Herrnkind 1994; Lipicus et al. 1997). Human impacts such as sound and light pollution (Longcore and Rich 2004) freshwater outflow (Santos et al. 2011), and boat disturbances (Hallac et al. 2012) modify the environment for arriving larvae and may vary seasonally. Other impacts, such as oil spills (Carls et al. 2010), can negatively influence wide swaths of coastal and pelagic habitat.

Despite their small size, larval behavior and physiology during dispersal are key elements controlling connectivity networks. Traits such as ontogenic vertical migration (OVM; Paris and Cowen 2004; Pineda 2007; Butler et al. 2011), mortality (Cowen et al. 2000), horizontal swimming (Staaterman et al. 2012), spawning phenology (Paris et al. 2005; Karnaskas et al. 2011), reproductive population sizes (Kough et al. 2013), variable growth parameters (Feng et al. 2011), and pelagic larval duration (PLD; Shanks et al. 2009; Simmons et al. 2013) can all dramatically influence connectivity networks. By investigating connectivity patterns through time, we gain insight about biological processes that interact with a changing physical environment.

The ideal tool to examine connectivity through time operates over large scales in both time and space. Lagrangian stochastic individual based models of larval transport (LSM) couple oceanographic circulation models with biological characteristics within a

flexible framework to describe dispersal over many spatiotemporal scales (Werner et al. 2007; Staaterman and Paris 2013). The surge of studies using LSM in the past decade attests to their availability and power as hypothesis testing tools (Miller 2007; Leis 2011; Peck and Hufnagel 2012). The goal of these LSMs is to probabilistically describe linkages between locations by moving particles in a virtual ocean following rules assigned to the physical environment, specific biological traits, and variability from unresolved subscale turbulence.

Using LSM modeling, my goals are to examine how often in time larval connections occur, assess the impact of larval release interval, and to identify temporally and spatially predictable patterns. In addition, by using three species with scientifically described OVM, I can investigate the impact of such behavior on connectivity through time. Using the Caribbean Sea, an ocean basin with complex geophysical composition, as my study location gives results meaningful to management and biology.

## **Methods**

### *Species parameterization*

I modeled larval transport among reefs throughout the Caribbean using an open source LSM, the Connectivity Modeling System (Paris et al. 2013), coupled with four years of open access HyCOM ocean circulation models (Table 1). Three different PLDs indicative of those common to the Caribbean were used to determine if patterns in time were driven by the geophysical environment or by the biology of the modeled dispersal. I selected a short PLD (5 days – the octocoral *Anthielloorgia elisebeathe*), a medium PLD (30 days – the bicolor damselfish *Stegastis partitus*), and a long PLD (152 days – the Caribbean spiny lobster *Panulirus argus*) based on available parameterizations that



include OVM behavior (Figure 2.1; Paris and Cowen 2004; Butler et al. 2011; Lasker et al. 2012).

### *Habitat*

The spatial extent of the simulation was a representation of coral reef habitat from around the Caribbean subdivided into 22 bioregions (Cowen et al. 2006). I used data from the Millennium Coral Reef Mapping Project (Andrefout et al. 2004) to define the locations of coral reef habitat within each bioregion. An 8×8 km grid was placed over the reef habitat (Holstein et al. 2014), and grids that did not overlap the ocean circulation model's landmask were used to represent the larval release (grid centroid) and larval settlement locations for the CMS, yielding 1682 coral reef habitat locations (Appendix A).

### *Release interval*

Setting a uniform but periodic (i.e. weekly, monthly, annually) larval release interval, as is often done in LSM, may be a faulty assumption. This may be inappropriate from a biological perspective because spawning often varies over small spatial scales (DiFranco and Guidetti 2011). Importantly, releasing larvae throughout a simulation, rather than on just a few days, is analogous to increasing sample size and may better capture variability through time. I used a daily larval release interval, corresponding to the daily forcing of the HyCOM model (Bleck et al. 2002) and lower than the mean Lagrangian decorrelation timescale (Dutkiewicz et al. 1993). Having larval releases on each day of the simulation allowed me to subsample through time to compare networks created with different release intervals.

To quantify the impact of release interval I used a stratified random resampling approach through time. The simulation was split into segments of a given time period: from daily through monthly. Each segment had a single day chosen at random and the connectivity matrices from chosen days were combined and used as the data for each release interval.

#### *Release magnitude*

A different release magnitude was selected for each PLD that saturated the mean connections in the network. The network was considered saturated when increasing the daily release magnitude no longer appreciably increased the mean number of connections throughout the simulation (Figure 2.2). This method follows the recommendation of Brickman and Smith (2002) to use a suite of runs to examine the variability of a single outcome (i.e. the number of connections). In a preliminary simulation, a single random habitat location from each of 22 the bioregions was run throughout the simulation for releases spanning four orders of magnitude and for each simulated species. Analogous to the work of Simons et al. (2013), the release magnitude that captured 95% of the asymptotic connections in the preliminary experiment was ultimately used in the full experiment (Table 2.1). Having a saturated larval release meant that changes to the network when subsampled through time were not due to differences in release magnitude. Each day was a complete and independent probabilistic run.

#### *Daily connection activity*

Larvae that settled in the model are used to describe connections. I define a connection existing between two habitat locations if at least one modeled larva starts at one habitat location and then settles at the second. Modeled larval connections between

habitat locations yielded a four-year timeseries of daily connectivity matrices. These matrices were then used to show connection activity for each habitat location as both a source (connections originating from the location; exports) and a sink (connections with the location as a destination; imports). Connection activity at each location was calculated as the amount of larvae received or donated on a particular day divided by the total amount of larvae received or donated over the entire simulation at that habitat location. Thus connection activity demonstrates when and where larvae were settling in the simulation. Matrices of connection activity were sorted through time (along the X-axis) by placing the highest probability days in each habitat location on the left. Next, the matrices were sorted through habitat (along the Y-axis) by placing the highest probabilities at the top. Sorting created surfaces of connection activity throughout a simulation, transforming a stochastic pattern into an underlying smooth spatiotemporal surface that can visualize Caribbean-wide trends (Figures 2.3-2.8; Appendix B).

#### *Empirical orthogonal function analysis*

I conducted empirical orthogonal function (EOF) analysis on the matrices of daily source and sink connections to better explain variation in settlement through habitat locations and time. The EOF formulation followed Paris et al. (2002). The spatial scale of variability was explored by restricting connectivity to a range of distances. The distances used went from 0 km (local recruitment) through 2000 km using a step of 10 km. Connections that occurred at or closer than the distance being examined were used in the EOF. The variance within the first 10 modes of the EOF was considered relative to the total variance. I plotted the power density spectrum (PDS) to show peaks of variance in each spatially restricted simulation (Figure 2.12-2.17). These show the spatial scale at

which variance through time could be explained and the important frequencies in the simulation. This information can be used to potentially identify oceanographic features which may cause settlement patterns.

## **Results**

### *Daily connection activity*

Spatiotemporal surfaces demonstrate where and when connection activity was higher (red areas in Figures 2.3-2.8) or lower (blue areas in Figures 2.3-2.8) than expected, assuming that settlement was consistent throughout the simulation. Connection activity occurred over at least 33% of the spatiotemporal surface (Table 2.2). Connection surfaces for sinks were smaller than connection surfaces for sources. As PLD increased, the successful export of larvae increased in both space and time but the successful import of larvae decreased, enlarging the export surface and shrinking the import surface. Thus longer PLDs created more patchy import environments. However, including OVM increased the amount of time where connections occurred, as both a source and as a sink across species (Table 2.2).

### *Frequent rarity*

To show spatially specific connections throughout time, the daily connectivity matrices were transformed into binary matrices. I noted only the presence or absence of a connection on any given day, regardless of connection strength. Summing together these binary matrices across simulation time describes how often a specific connection occurred in time. I found that the most common connections were those that were rare in time, regardless of PLD and OVM (Figure 2.9). The settlement from these occasional connections made up the majority of settlement in each of the simulations (Figure 2.20).

### *Release interval*

The impact of each release interval was assessed by looking at changes in the number of connections (Figure 2.10), probability of connections that occur (Figure 2.11B), and the average connection time through the simulation (Figure 2.11C). As the release interval increases (i.e., releases occur less often) the number of connections decreases, the average time with connection decreases, and the average probability of the remaining connections increases. Therefore the network becomes made up of mostly higher probability connections and fewer rare events.

### *Empirical orthogonal functions*

Temporal patterns had some consistency among species. The octocoral scenario PDS was characterized by a series of sharp peaks at yearly, biweekly, weekly, and once per 5 days. However, when pooled the top 10 modes of the EOF for octocoral only described up to 15% of the variance. The biweekly peak was the strongest signal in imports and was enhanced in both imports and exports by OVM. Variance in imports had an asymptote at spatial scales of up to 200 km with the strongest peak biweekly. The annual peak was the most important at local spatial scales for exports. Contrary to all of the other scenarios, OVM behavior decreased the explainable variance within exports for octocoral, although it enhanced seasonal and biweekly signals. The damselfish and lobster scenarios were dominated by peaks that occurred on seasonal to annual timescales. For both fish and lobster scenarios, more variance can be explained in the timeseries of exports than of imports, and the lobster simulation had considerably more attributable variation. For damselfish, OVM behavior increased variance captured at spatial distances of 70-100km. At this spatial scale, there had previously been little

variance attributable to major peaks. The increase was associated with seasonal peaks (90-180 days). On the time scale of 2 weeks there was a peak which was strongest for connections occurring within 200km. There were peaks that may be related to mesoscale features in both space (10s to 100s of km) and time (weeks to months) for all three modeled species.

#### *Connection and settlement distances*

The spatial scale of connection differs among modeled species. I examined the distances over which possible connections (i.e., a connection that occurred at least once in the simulation) and probable connections (i.e., connections out of total connections) were made from to define long distance dispersal (LDD; here defined as dispersal distances >90% of all settlers). Probable connections (Figure. 2.19) occurred over smaller spatial scales than possible connections (Figure. 2.18) in each species. There was agreement between when variance reached an asymptote in the EOF analysis of exports and the distance defined as LDD in probable connections for coral and fish (400km and 700km, respectively). I also examined how LDD varied with time of the year, by considering the frequencies that I had previously identified in the EOF analysis. When LDD existed, I then plotted out the spawning month with the maximum LDD and identified relevant seasonal patterns conducive to LDD across the Caribbean (Figure 2.21). Strikingly, a late summer through fall spawning season for lobsters created the most LDD almost comprehensively throughout the Caribbean. This timing matches the secondary spawning peak of spiny lobsters in many regions through the Caribbean (Kough et al. 2013). Fish and corals had seasonal LDD with similar spatial grouping as previously identified Caribbean bioregions (Cowen et al. 2006).

## Discussion

The theme of my work investigating connections through time was the seemingly paradoxical finding of frequent rarity. Across a wide range of PLDs, the most common larval connection events among populations were those that were rare in time (Figure 2.9), suggesting that infrequent and stochastic connections in time dominated Caribbean larval transport. Larval exchange occurs throughout the spatiotemporal surfaces that I constructed (Table 2.2). The modeled connectivity network was a patchwork of many occasional events in time at each habitat location, and settlement from occasional events outnumbered more persistent and probable connections. Despite the rarity of specific connections, larval exchange itself was ubiquitous and occurred on every day of the simulation.

Defining what a connection is within the context of this work is important. Previous works have coupled LSM output with population models to give a biologically relevant definition to a connection (Cowen et al. 2000). However, this is only possible when quality data exist on the life history and population sizes of the organism in question. In this work I have taken a theoretical approach to look at how probable connections are through time, while not assigning a particular value (e.g., 1 modeled larva = 700 larvae settling at a site) to a connection. By having a connection simply be a modeled larva that settles at a habitat location, and by saturating the experiments to model all possible connections, the model captures when any connection may occur including improbable events. Such improbable events should be described as they can build genetic structure (LeRoux et al. 2014), and contribute to long-lived species persistence (e.g., coral colonies that live for hundreds of years need a single larva to

become established). In addition, some populations of fish have dominant year classes when settling larvae encounter extremely favorable conditions. Thus an improbable and occasional pulse of larvae can create a cohort within a fishery, and becomes important for management.

If frequent rarity characterizes modeled connectivity networks, then the release interval used becomes critical. As I increased the release interval from daily to monthly, the simulation captured less than a third of the previously modeled connections. Thus the more often larvae were released, the more connected the network became. This occurred across PLDs, with a more precipitous fall with the longer PLDs. Larger release intervals captured the most probable connections, which may explain past work suggesting that the long-term connectivity patterns predicted by a LSM using a restricted release interval were relatively stationary in time (Berglund et al. 2012). Including OVM behavior in the simulations yielded more connections over longer release intervals. In addition, increasing the release interval removed mostly rare events. Thus if a researcher is interested in rapidly assessing the major connections among populations, a monthly release interval may be adequate for a multiyear simulation depending on PLD. However, if the release interval is going to be infrequent, the role of behavior becomes accentuated. These simulations indicate that inclusion of behavior in connectivity modeling is indeed paramount, as others have indicated (Paris et al. 2005; Butler et al. 2011; Staatterman et al. 2012), but even more so if computational strength is lacking and the larval release interval is therefore infrequent.

The implications of frequent rarity for management of larval dispersal on a demographic timescale are striking. It is unlikely that the majority of the connections in a



network can be forecast in time without detailed empirical data and high-resolution models, prohibiting real-time management and conservation strategies. Frequent rarity is a direct result of the geophysical environment, because LSM use the best available scientific knowledge to describe both the ocean circulation and spatial arrangement of habitat. Physical processes such as fronts and eddies, which pool oceanic larvae from diverse origins and age-classes and deliver them as a pulse to a restricted spatiotemporal location, can cause unpredictability through time (Siegel et al. 2003; Siegel et al. 2008; Vaz et al. 2013; Harrison et al. 2013). However, previous works have not incorporated realistic three-dimensional larval migrations, and discounted the role of behavior as a control on dispersal (Harrison et al. 2013). My results support the concept of connections being made from a diverse set of source habitat, and delivered in pooled pulses to sink habitat.

In previous works LSM has successfully captured empirically observed biophysical patterns in connectivity networks. Connections appeared spatially stable yet most larval connections were occasional and driven by the geophysical environment. In other words the pathways of exchange in the network were consistent, although when they occurred varied. The empirical data required to verify model performance is costly to obtain over broad scales, and therefore studies with large spatial domains must restrict comparisons to smaller areas with available data. Studies have verified model performance using comparison with mean larval fish densities (Hidalgo et al. 2012; Vikebo 2011), direct observations of larval cohorts at sea (Paris and Cowen 2004), settling fish larvae in light traps (Sponaugle et al. 2012), monthly trends from lobster postlarval collectors (Feng et al. 2011; Kough et al. 2013), and annual trends from settled

lobster observations (Incze et al. 2010). Thus, the coupled biophysical LSM used in marine dispersal research are of sufficient quality to recreate complex and temporally unstable environments, making them valuable tools for protecting and understanding marine environments.

Marine protected areas (MPAs) are promoted as conservation tools for marine ecosystems, yet they must simultaneously serve species across a range of lifestyles (Holstein et al. 2014). Our investigation into the role of larval release frequency in connectivity networks can be applied to theoretical MPA design to determine how much habitat must be protected depending on how often a particular animal spawns, and the length of its PLD. A steep decline in connections occurs as habitat space decreases and release interval increases (Figure 2.21). If management wants to target a particular threshold of connections to provide replenishment in the face of extraction or as a safety net to disturbances, then the specific quantities of habitat to protect can be estimated (Figure 2.21). It is important to note that the connections in my model require additional information about spawning populations and habitat capacities to become meaningful for management. The connections investigated in this study are better suited to examine theoretical geophysical and biological interactions.

Our finding of frequent rarity leads to a biologically important question: how do dispersing animals optimize their spawning efforts in an unpredictable environment? Adding simple OVM behavior increased the amount of time in a simulation with connections, making connections more common. Accordingly, including information on larval movement reduced stochasticity in larval connections and suggested biological control on dispersal in animals with a larval pelagic phase. Vertical movements are likely

driven by feeding as both a predator and prey (Murphy et al. 2011), by physical ocean concentration features (Greer et al. 2013), and by the need to maintain optimum physiological conditions (Nunn et al. 2012). I show that an additional benefit may be increasing the stability of reproduction through time. This is especially important when spawning occurs on an occasional basis. Often the variability of crucial spawning times is great at scales < 10s of kilometers (DiFranco and Guidetti 2010), or tied to a particular physical phenomenon (Karnaskas et al. 2011). Vertical movement behavior is an additional biological control on dispersal, increasing the amount of time with successful connections in an otherwise highly stochastic environment.

I have modeled and quantified stochastic imports and exports of larvae over a broad spatiotemporal range. Some patterns of larval export may be attributed to mesoscale features, as explainable variance was highest over spatial scales of hundreds of kilometers and temporal scales of weeks to months (Paris et al. 2002; Lindo-Atichati et al. 2012). Thus models of marine dispersal need to have sufficient resolution to capture these processes. The recurring pattern of peaks on a biweekly basis may explain the cycle over which many marine creatures spawn. Tides are at a maximum during syzygy, which occurs on a biweekly basis with both the new and the full moon. In addition, tropical winds may oscillate with a similar periodicity (Viltard et al. 1997). The OVM behavior used in the model accentuated these peaks, suggesting that there may be multiple biological traits selecting for biweekly periodicity.

Frequent rarity in the imports drives the stochasticity of the system. Rare dispersal events in the terrestrial literature have long been challenging to identify, their role in connectivity networks has correspondingly been underappreciated, and there is

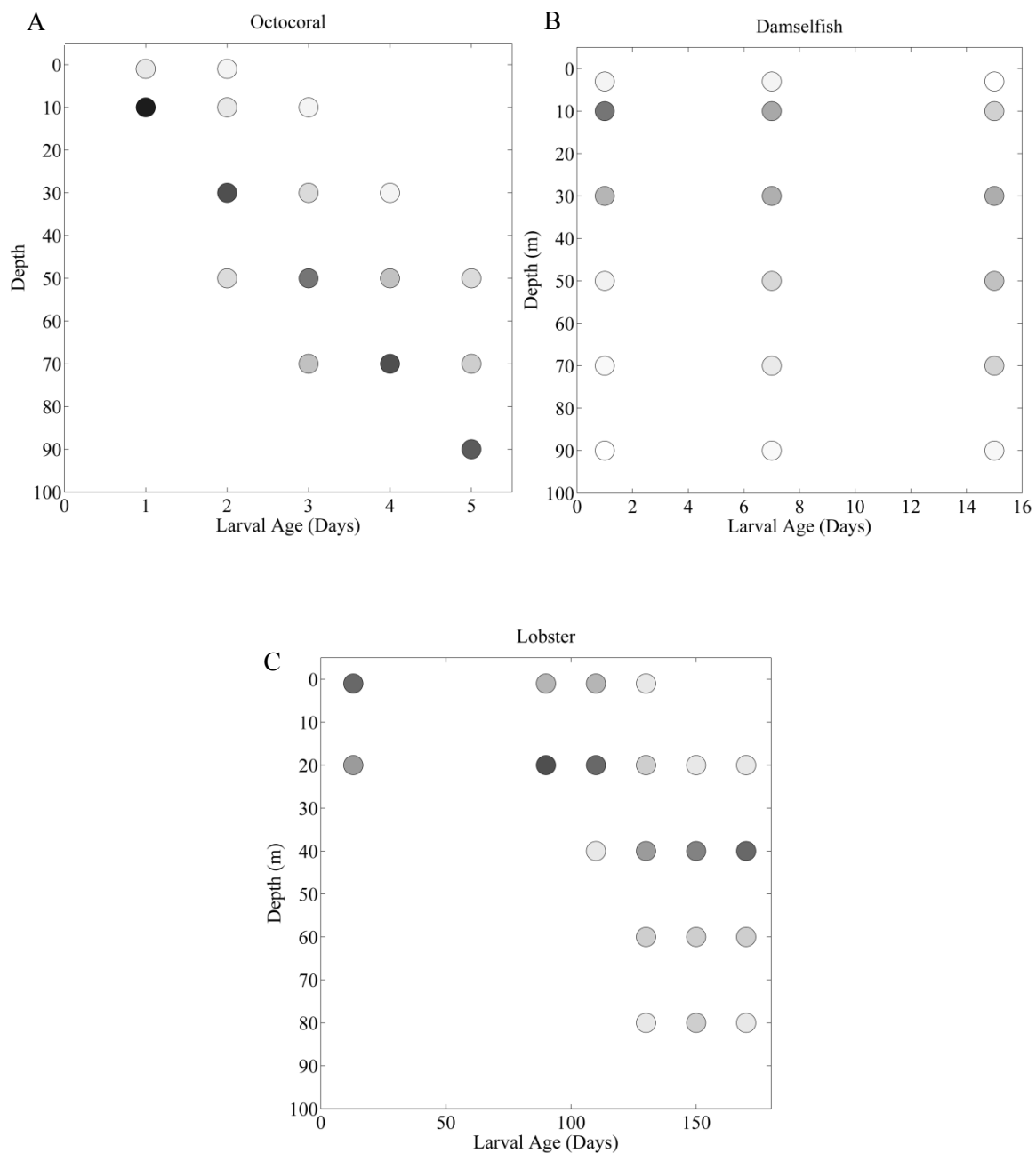
likely disconnection between frequency and importance in dispersal (Higgins et al. 2003; Levin et al. 2003; Nathan 2006). We provide the hypothesis that marine networks modeled for a diverse range of species are similarly ripe with rare events. Thus across a variety of ecosystems the importance of rare events suggests that resilience and connectivity through time need to be viewed with the understanding that stochasticity is a natural and critical component of distant spread, especially in passive dispersal. Modeled biology increases stability and predictability, and may offer potential control to marine species with larval dispersal.

**Table 2.1. Model parameterization.**

<b>Input</b>	<b>Value</b>
horizontal diffusivity	5m <sup>2</sup> /s
integration timestep	2700s
PLD octocoral	5d
PLD damselfish	30d
PLD lobster	152d
daily release coral	50 larvae per location
daily release damselfish	100 larvae per location
daily release lobster	500 larvae per location
HyCOM Global Data Assimilated, resolution	1/12°
HyCOM Global Data Assimilated, output time	daily currents
HyCOM GoM, resolution	1/25°
HyCOM GoM, output time	daily currents

Scenario	Passive Coral	OVM Coral	Passive Damselfish	OVM Damselfish	Passive Lobster	OVM Lobster
Any Export Connection Activity	60.09%	66.06%	69.44%	73.32%	83.51%	85.98%
Any Import Connection Activity	50.02%	61.24%	40.17%	49.73%	33.19%	45.64%
Higher than Expected Export Connection Activity	43.26%	42.94%	33.12%	33.29%	32.20%	36.10%
Higher than Expected Import Connection Activity	26.51%	29.82%	14.37%	17.38%	11.01%	17.02%

**Table 2.2. Activity within spatiotemporal surfaces across scenarios.** The connection activity as both sources (export) and sinks (import) for simulations with (OVM) and without (passive) behavior. The expected connection activity for each habitat location is a uniform distribution of connections throughout simulation time.

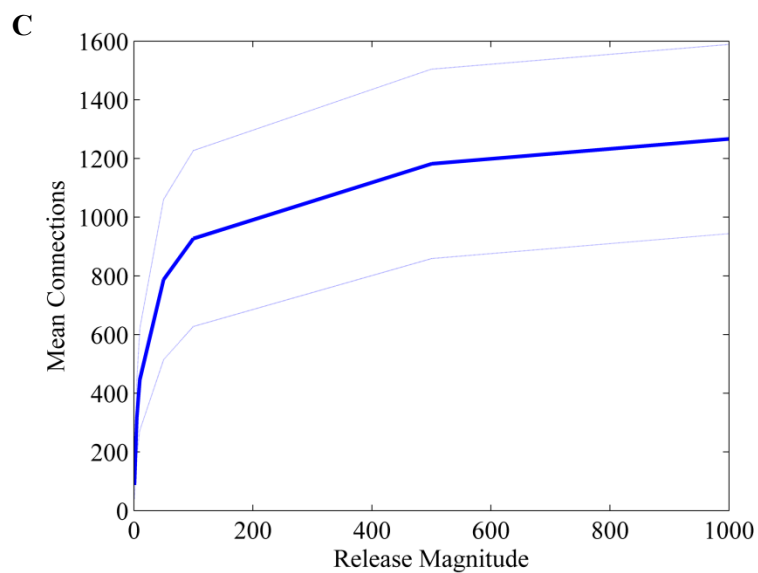
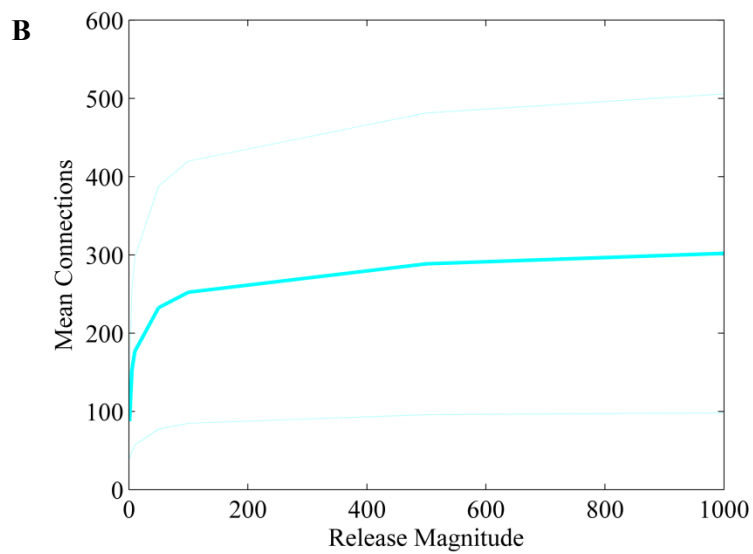
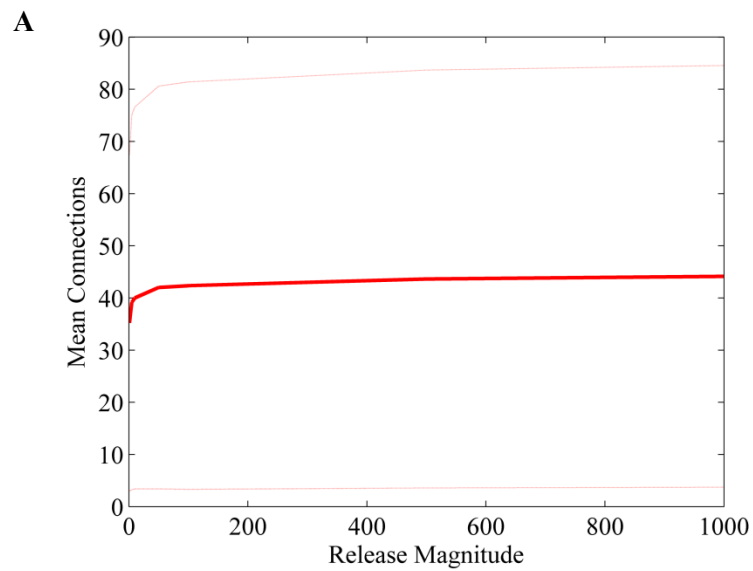


**Figure 2.1. The ontogenic vertical migration schemes used in the model.** The times throughout ontogeny where modeled larval coral (A), damselfish (B), and lobster (C) had their distribution modified through the water column. Darker circles indicate depths with higher percentages of modeled larvae of each age. Each age class sums to 100%.

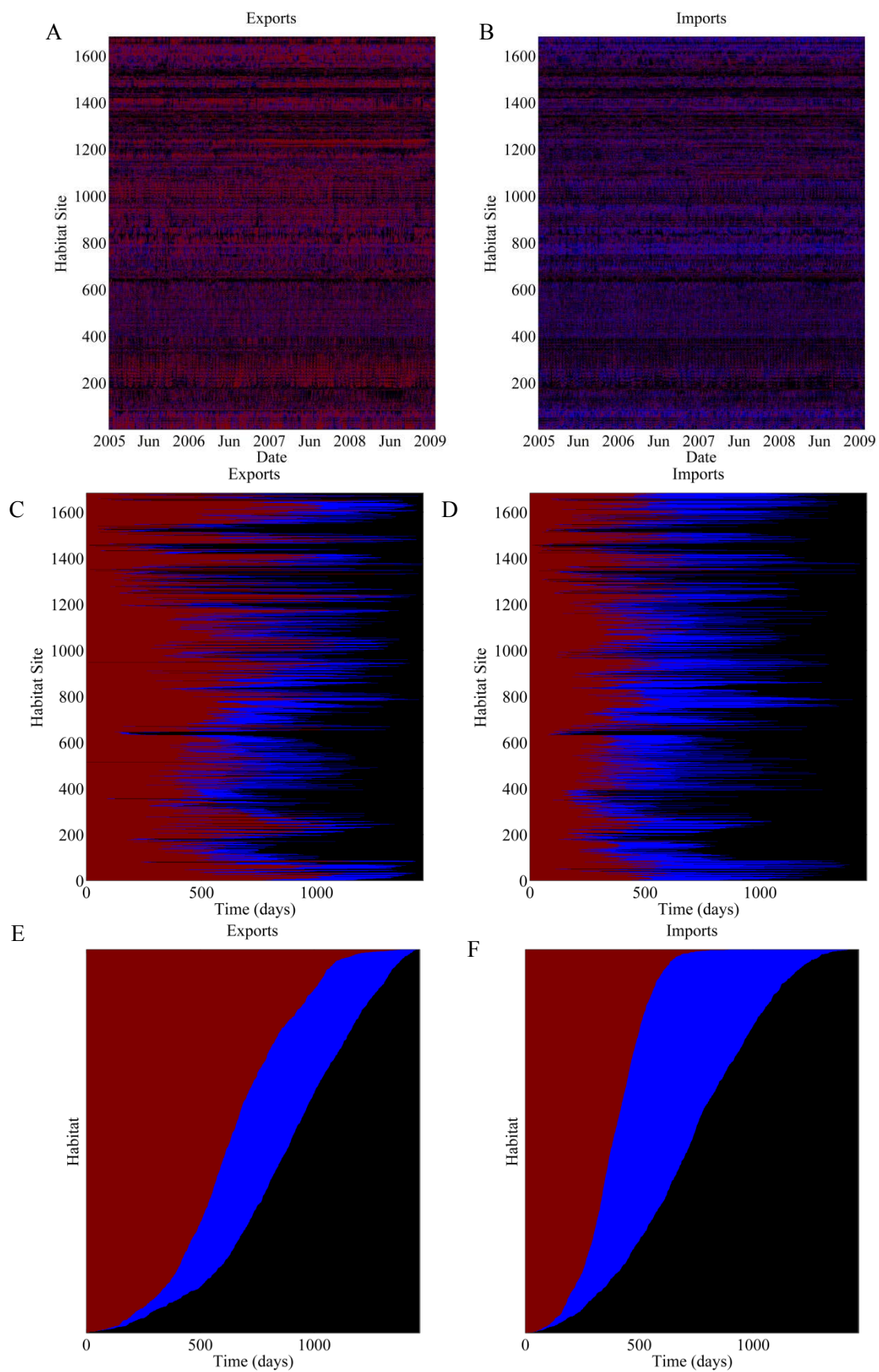
**Figure 2.2. Saturating the release magnitude for different pelagic larval durations.**

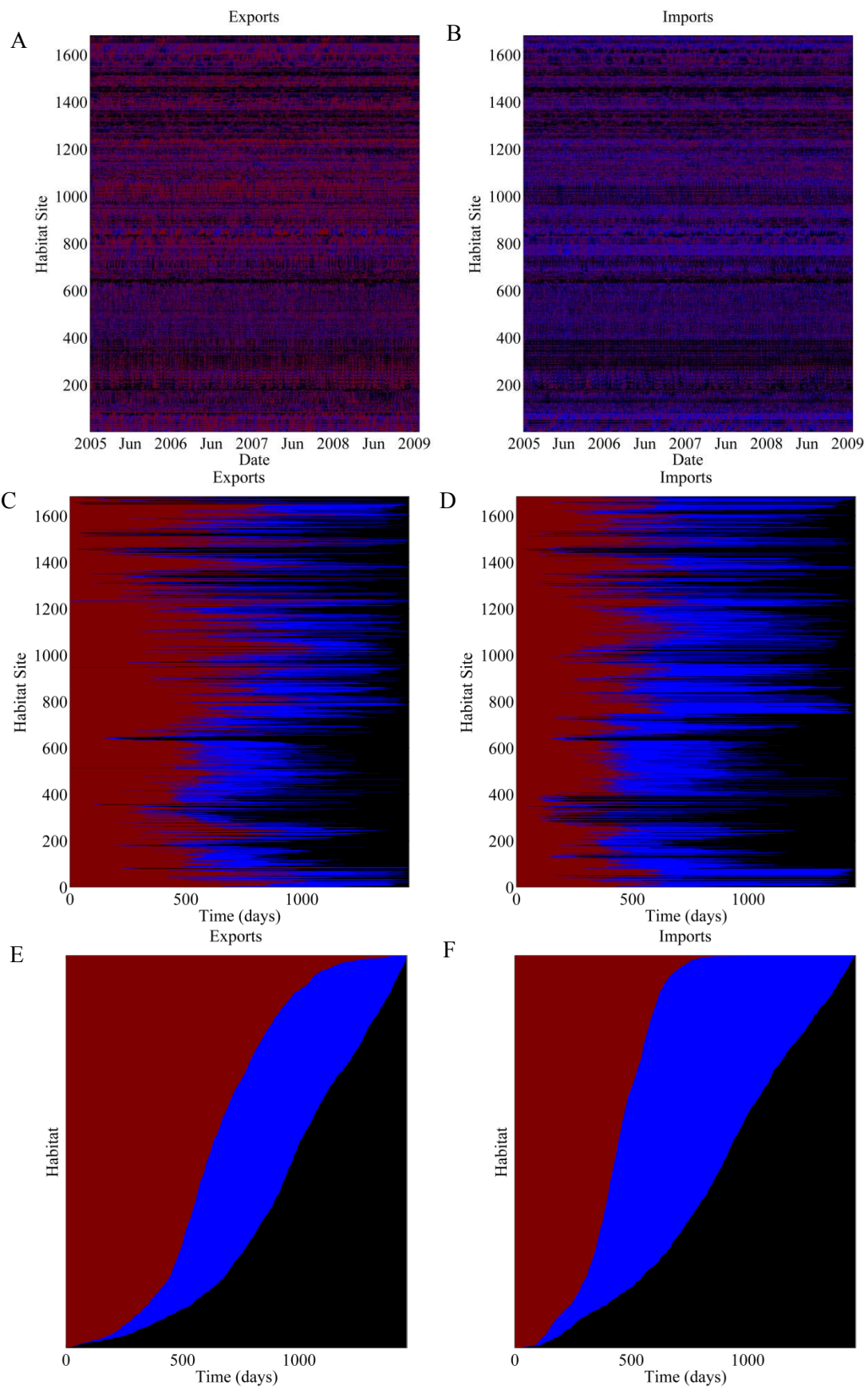
From each of 22 Caribbean bioregions, a single habitat location was picked at random and used to test the sensitivity of the simulation to release magnitude. Daily releases of 1, 5, 10, 50, 100, 500, and 1000 larvae were carried out for the entire simulation period using each of three PLDs, and the average number of connections ( $\pm$ SD) was plotted. Asymptotic values were then used for the release magnitude throughout the Caribbean for each PLD. A (red): the 5 day PLD octocoral simulation. B (cyan): the 30 day PLD damselfish simulation. C (blue): the 152 day PLD lobster simulation.

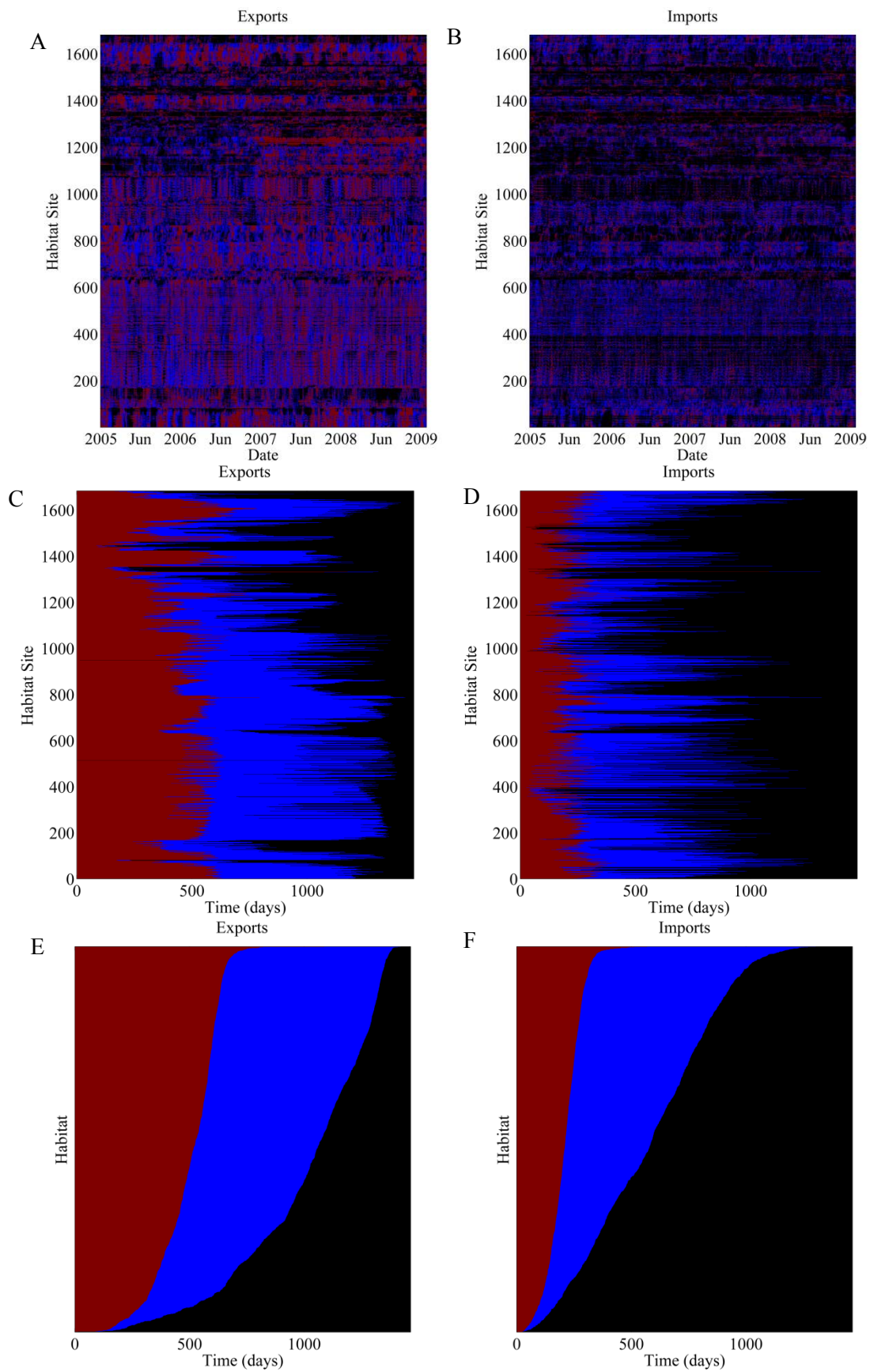




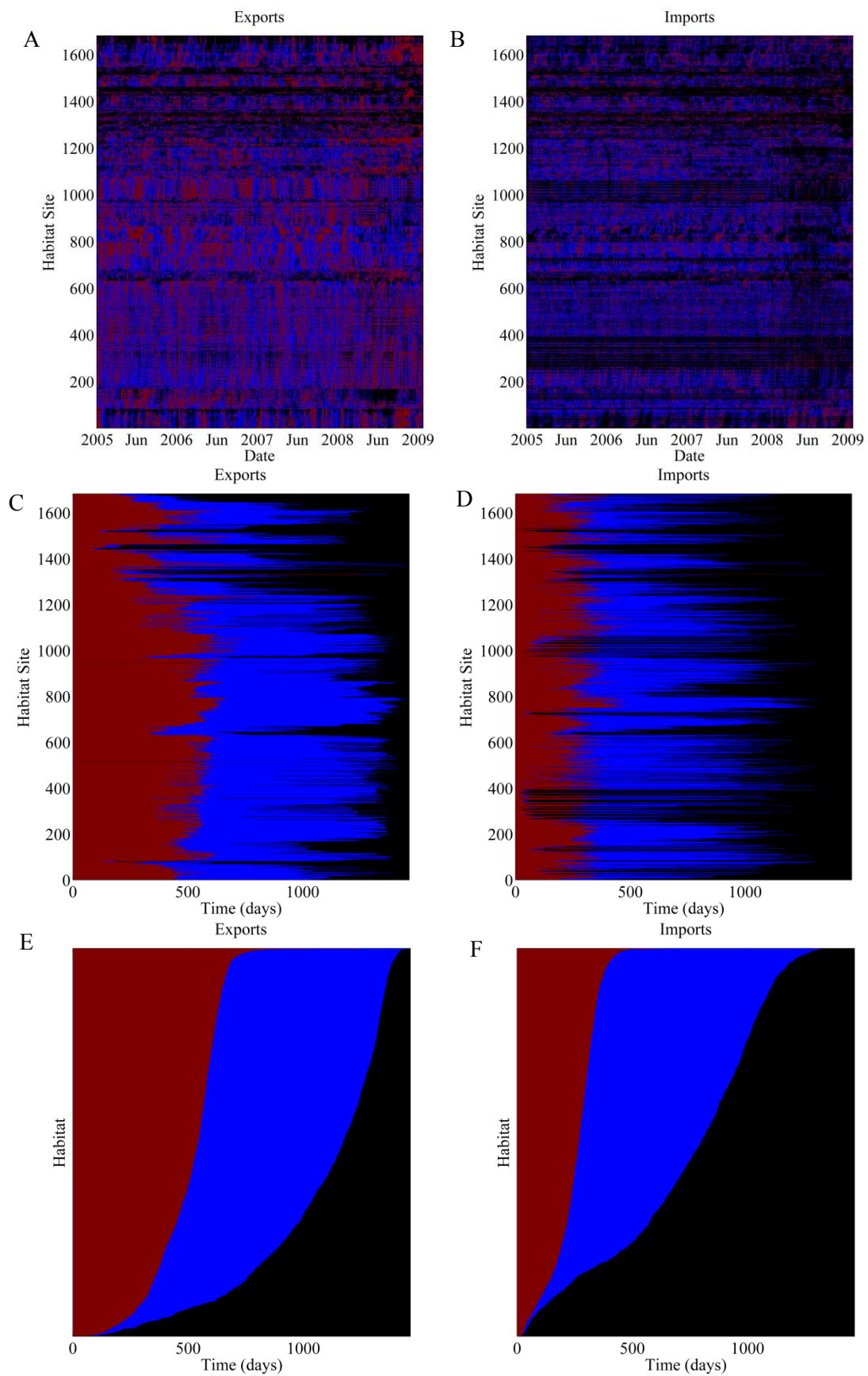
**Figures 2.3 – 2.8. Visualizing connections through time and space.** Matrices of the daily probability of exporting connections as a source or receiving a connection as a sink at each habitat site through the simulation. The probability matrices as a source (a) and as a sink (b) sorted through time with the highest probability days on the left (source c & sink d), and then sorted across habitat with the highest probabilities at the top (source e & sink f) to make a surface of connection activity through space and time. The matrices were categorically colored to demonstrate deviation from constant activity (e.g., for each habitat location, . Red indicates days with higher than expected connection activity, and blue indicates days with lower than expected connection, while black indicates no connection. Figure 2.3 passive coral. Figure 2.4 OVM coral. Figure 2.5 passive damselfish. Figure 2.6 OVM damselfish. Figure 2.7 passive lobster. Figure 2.8 OVM lobster.

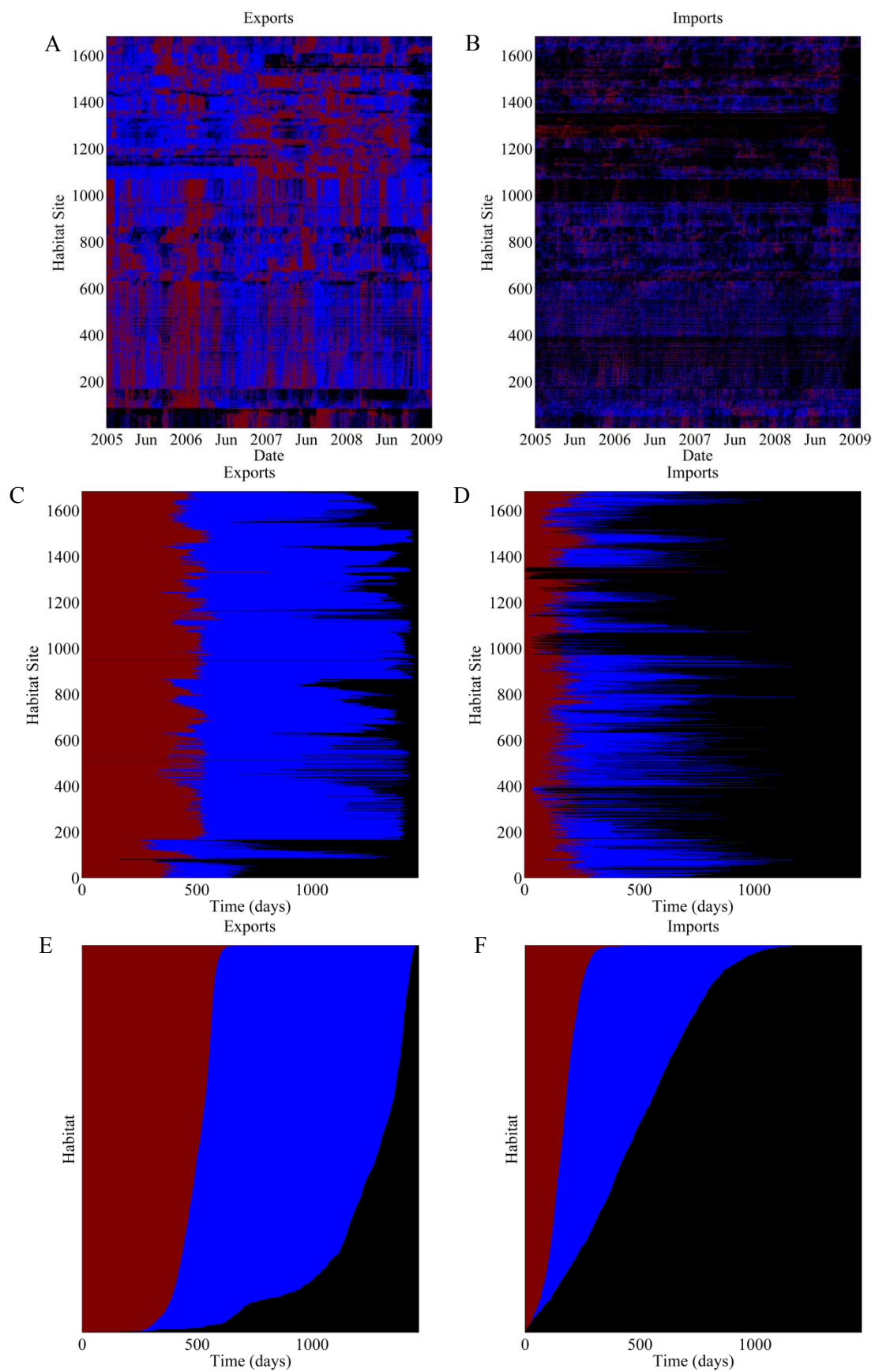


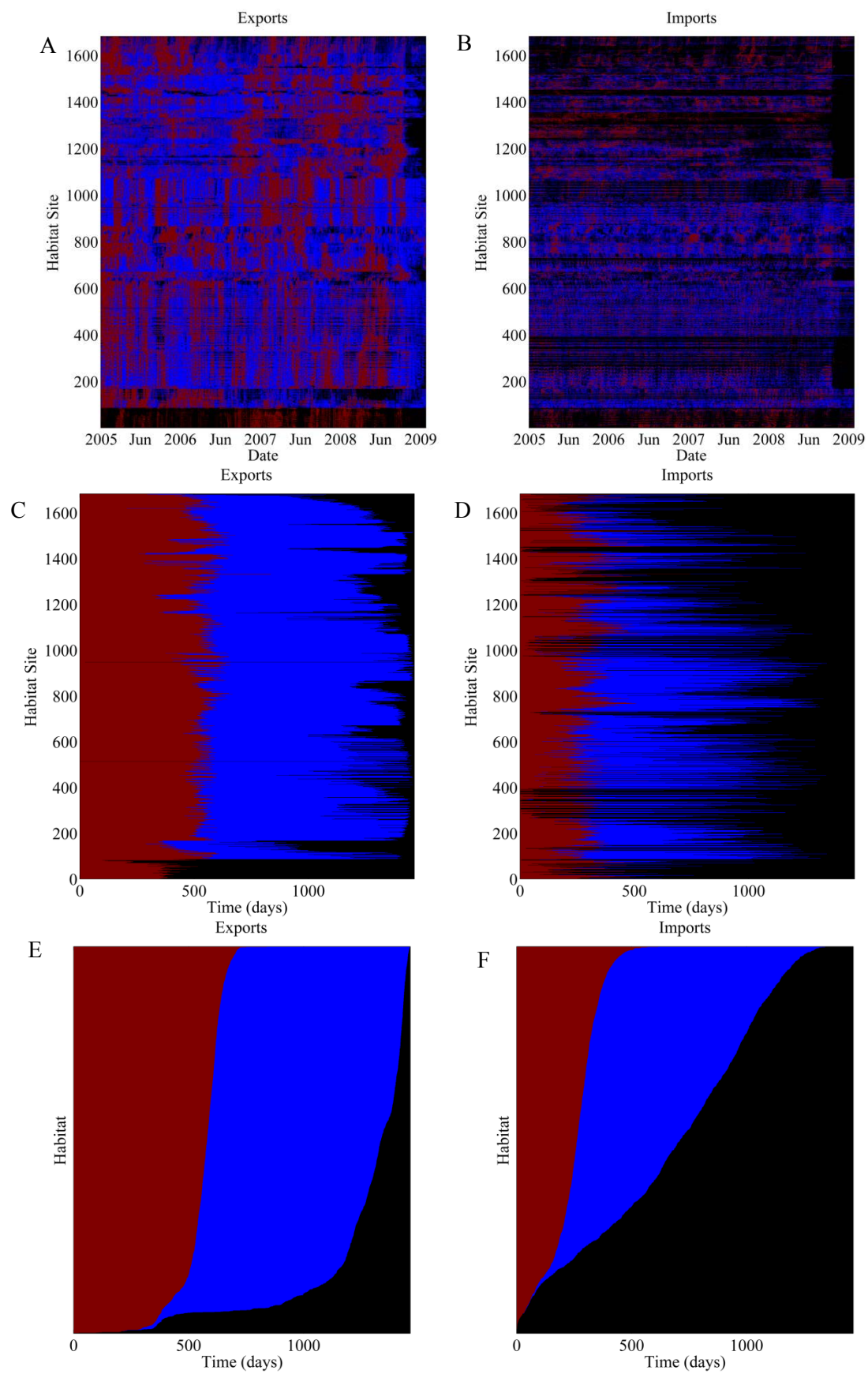




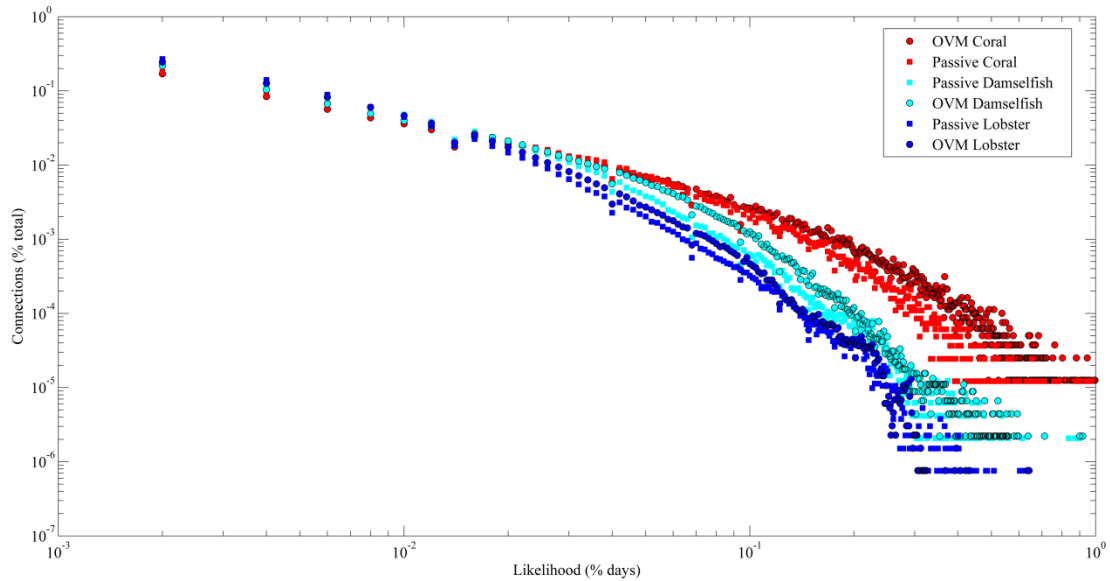




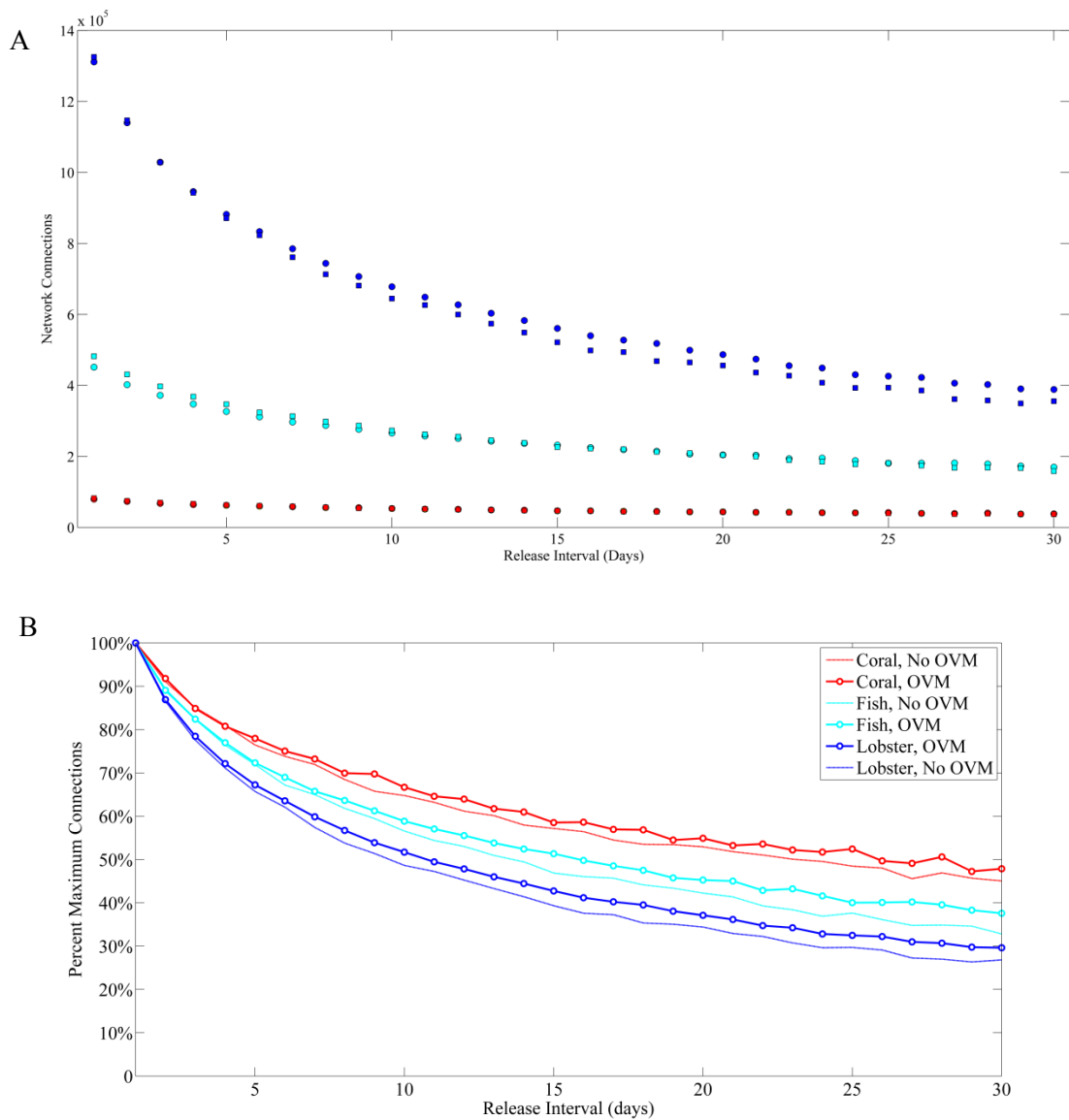




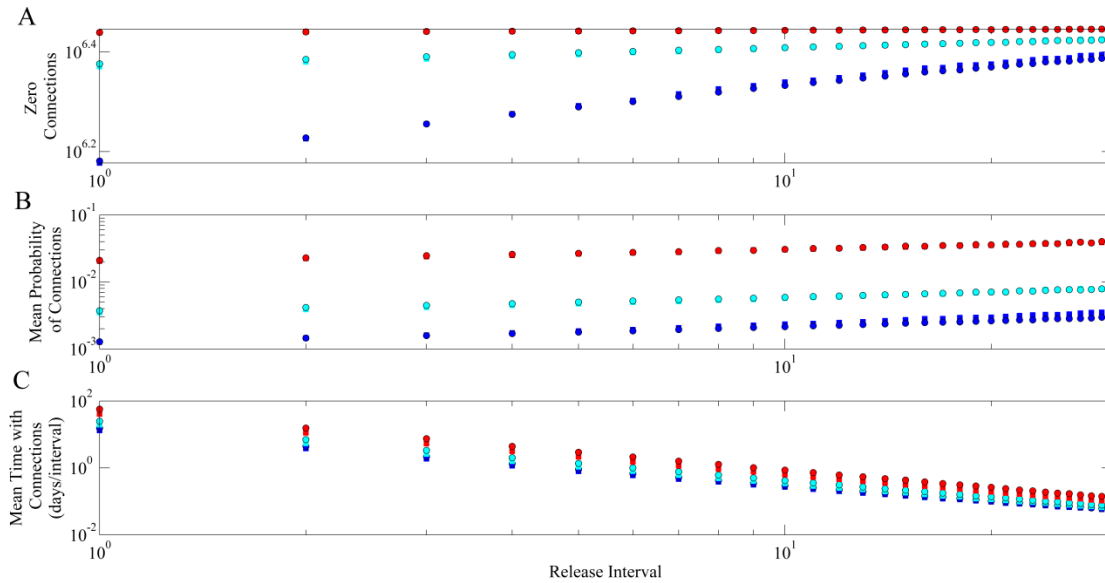




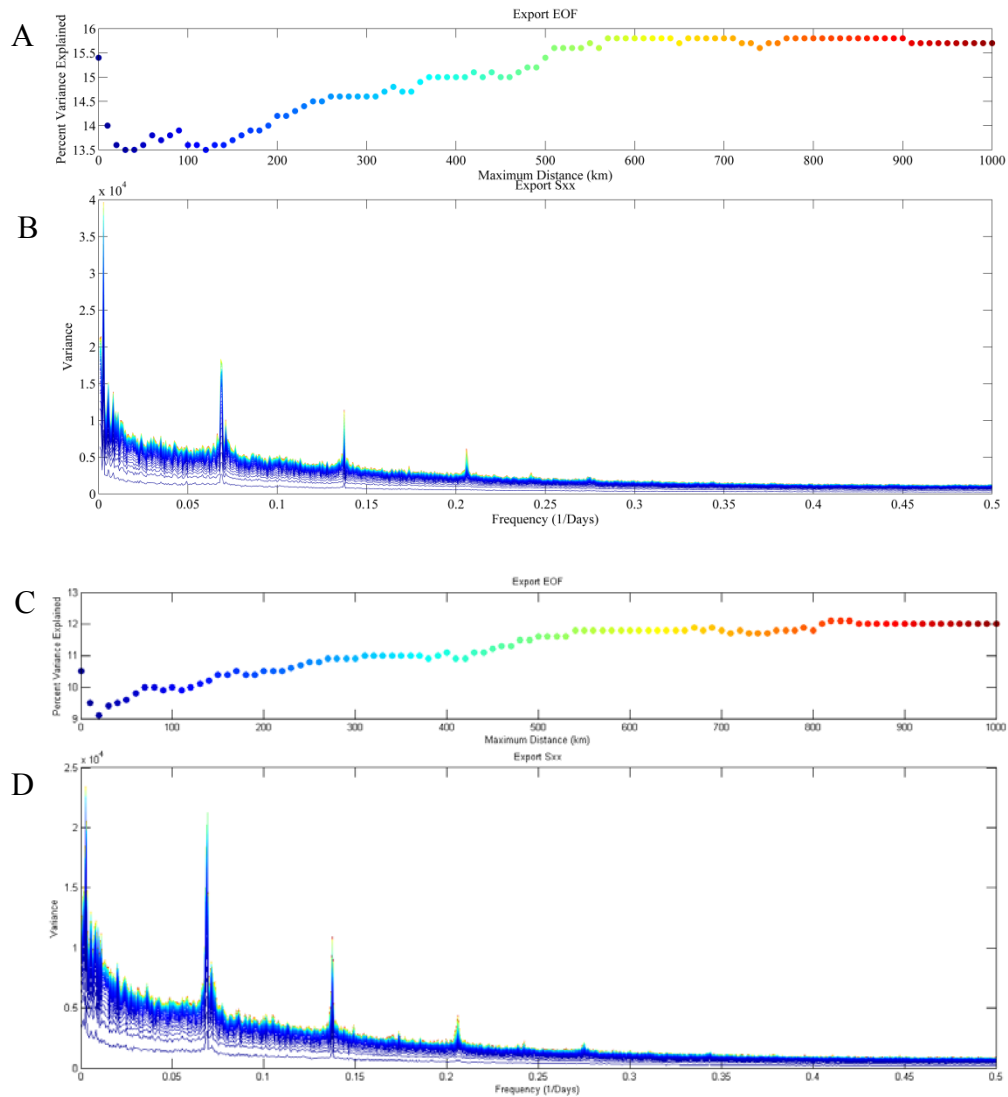
**Figure 2.9. Frequent rarity in time across pelagic larval durations.** Each point is derived from a histogram of connections through time, using bins of 0.2% of the total simulation time. Results using different PLDs were normalized to show the likelihood as a percent of time on the x-axis, and connections as a percent of the total unique connections on the Y-axis. Most connections (higher percent of the total connections, top of Y-axis) were unlikely in time (small percent of time, left on X-axis). Note the log-log scale.



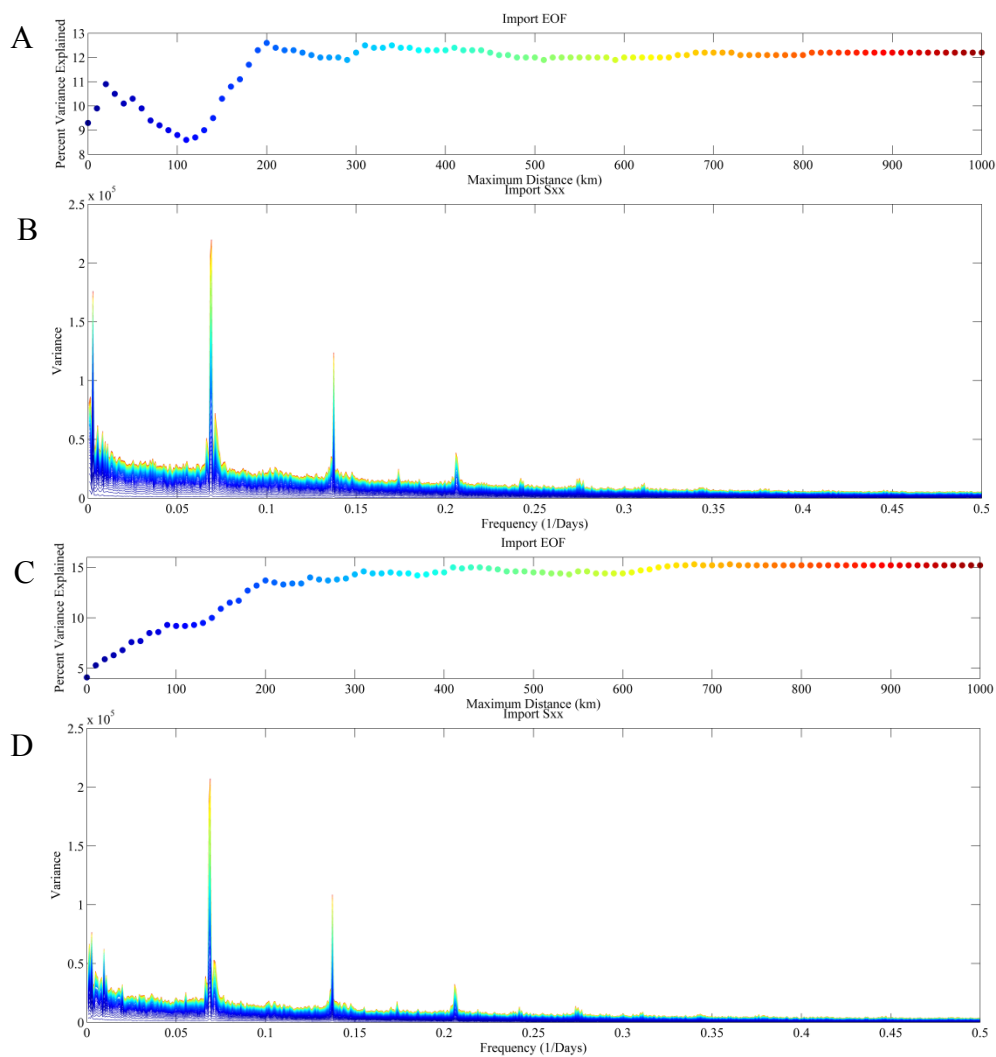
**Figure 2.10. Release interval alters network connections.** The release interval was systematically reduced for simulations of coral (red), fish (cyan), and lobster (blue), with OVM behavior (solid or circles) or without behavior (dashed or squares). The network connections are the total connections in the network, regardless of strength (A). The percent of maximum connections (B) shows the decline relative to the release interval that yielded the most network connections (release interval = 1 day).



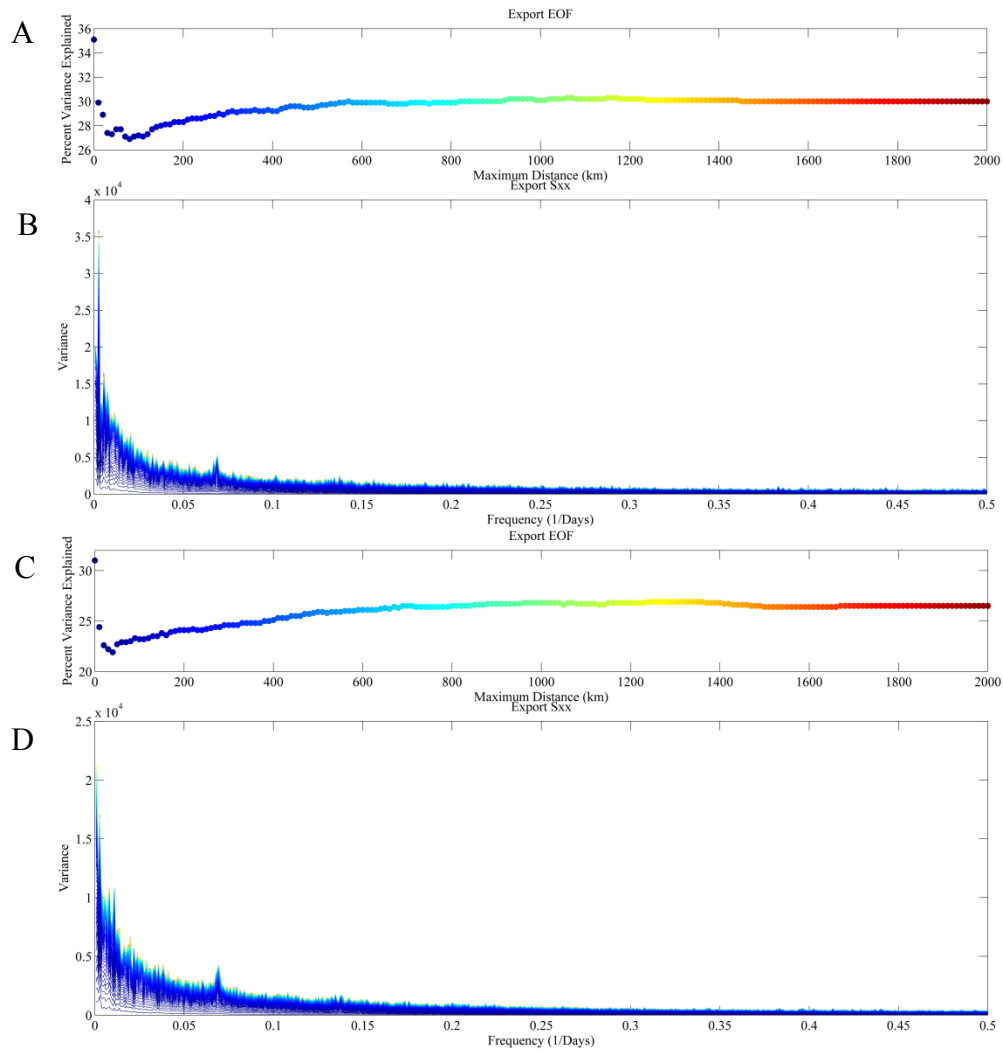
**Figure 2.11. Release interval changes zero connections, probability of connections, and time with connections** The amount of connections that do not exist (A) increases as release interval increases across a range of species (red:coral, cyan:fish, blue:lobster). For each connection, the mean probability of connections is the average of non-zero connection probabilities from the corresponding highest frequency release interval (B). As release interval increases, the mean probability of connections which are made increases, as fewer rare events are captured. The mean time that connections exist through a simulation decreases as release interval increases (C). Note the log-log scale.



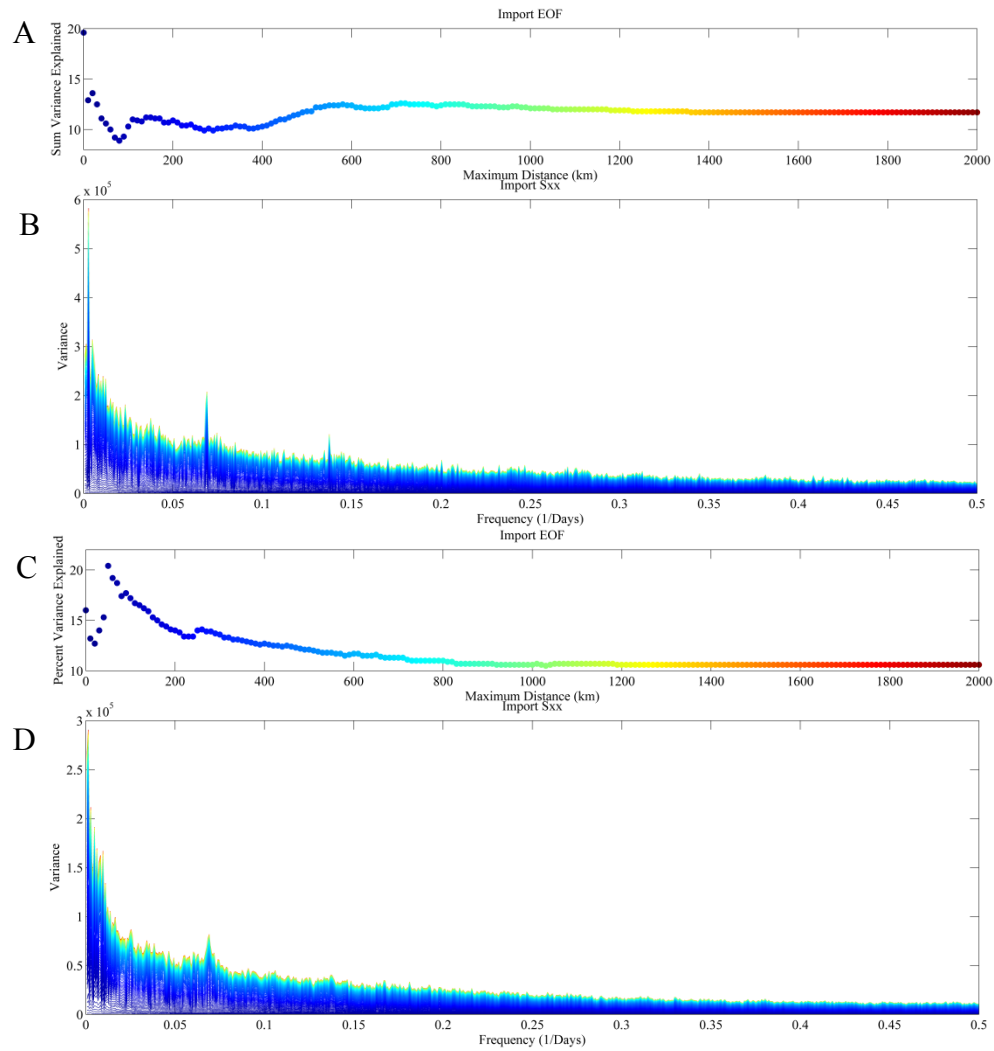
**Figure 2.12. Variance through time across habitat for exports in the octocoral simulation.** The percent of variance explained by the first 10 modes of the empirical orthogonal function of the timeseries of connections as a source over habitat locations. Connections were constrained over an increasing spatial scale (shown in color), changing the network from local through greater than 1000km. The corresponding power density spectrum shows the periodicity of trends in the timeseries. Passive: A&B. OVM: C&D.



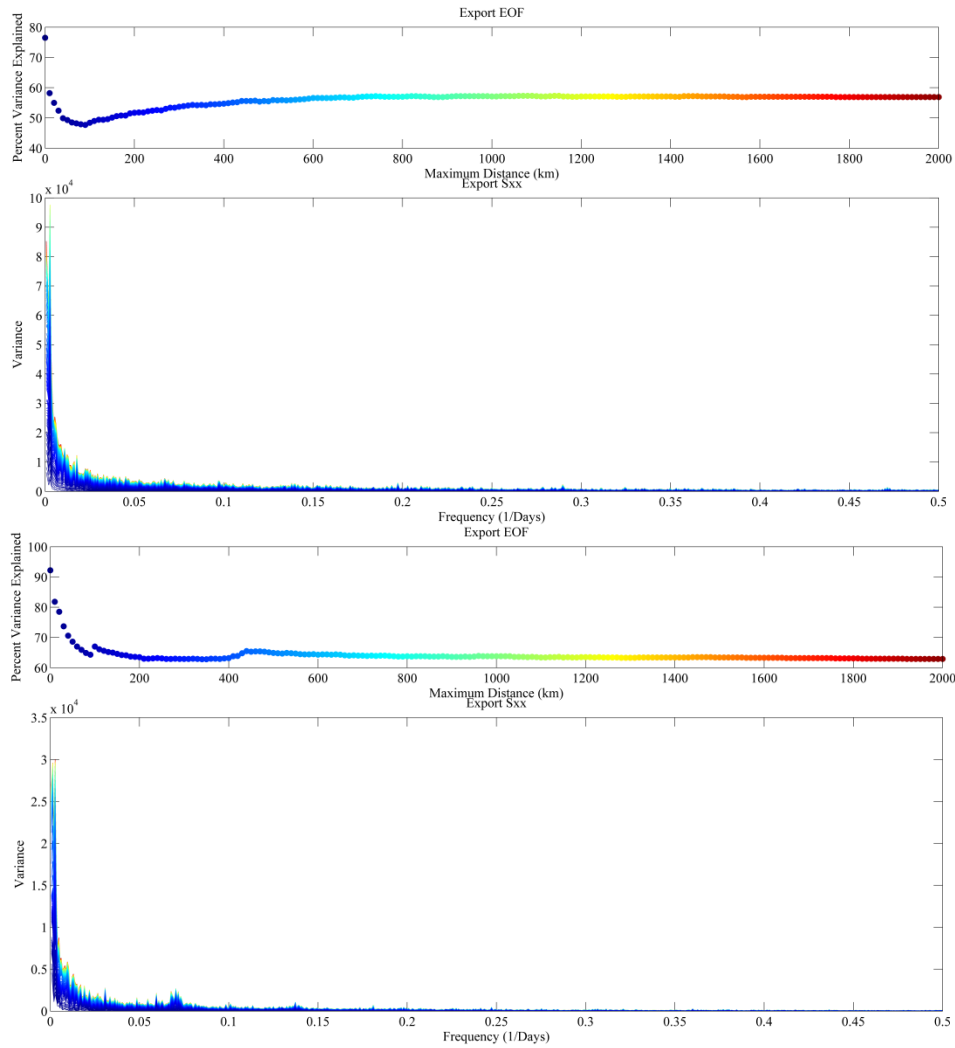
**Figure 2.13. Variance through time across habitat for imports in the octocoral simulation.** The percent of variance explained by the first 10 modes of the empirical orthogonal function of the timeseries of connections as a sink over habitat locations. Connections were constrained over an increasing spatial scale (shown in color), changing the network from local through greater than 1000km. The corresponding power density spectrum shows the periodicity of trends in the timeseries. Passive: A&B. OVM: C&D.



**Figure 2.14. Variance through time across habitat for exports in the damselfish simulation.** The percent of variance explained by the first 10 modes of the empirical orthogonal function of the timeseries of connections as a source over habitat locations. Connections were constrained over an increasing spatial scale (shown in color), changing the network from local through greater than 2000km. The corresponding power density spectrum shows the periodicity of trends in the timeseries. Passive: A&B. OVM: C&D.

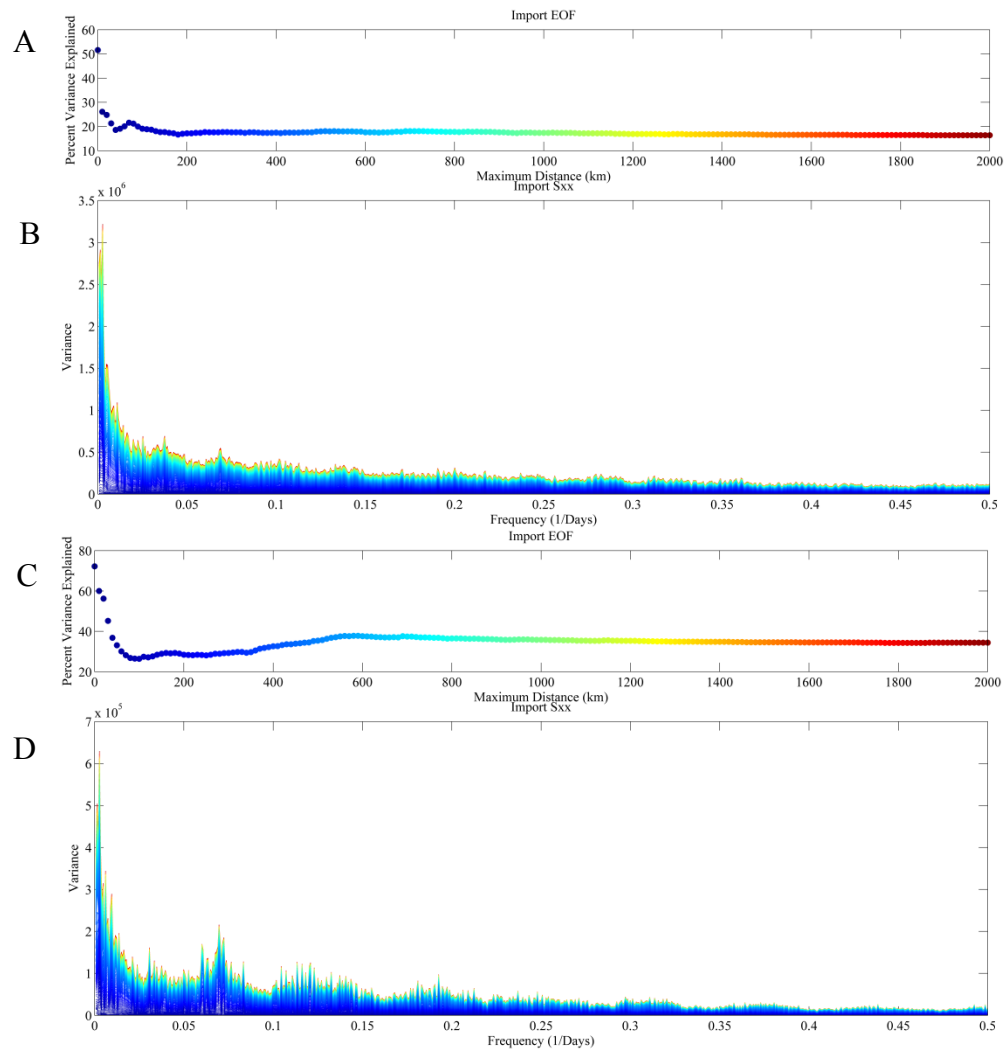


**Figure 2.15. Variance through time across habitat for imports in the damselfish simulation.** The percent of variance explained by the first 10 modes of the empirical orthogonal function of the timeseries of connections as a sink over habitat locations. Connections were constrained over an increasing spatial scale (shown in color), changing the network from local through greater than 2000km. The corresponding power density spectrum shows the periodicity of trends in the timeseries. Passive: A&B. OVM: C&D.

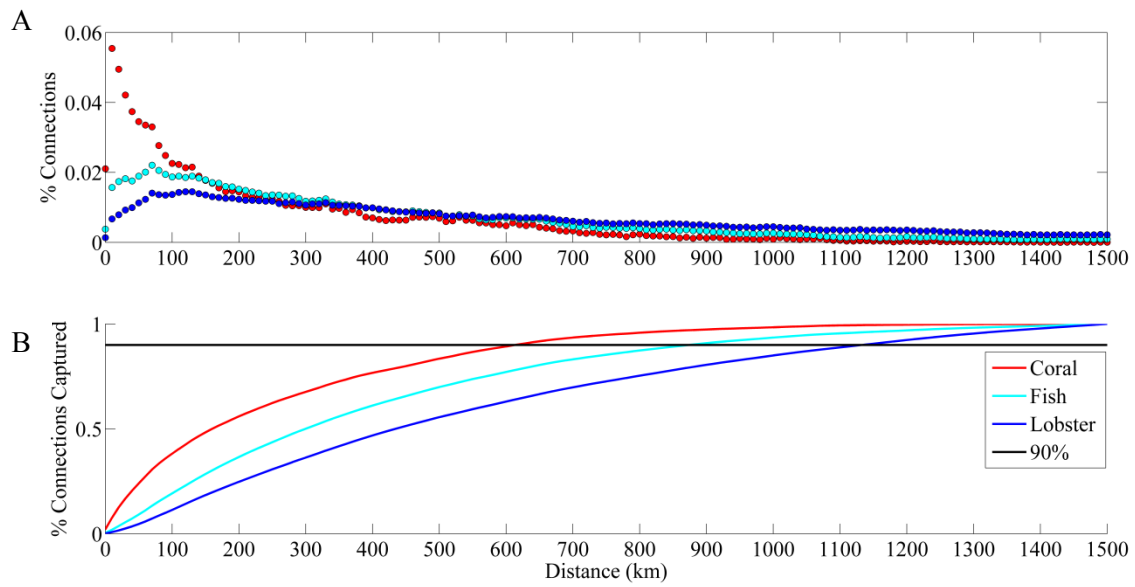


**Figure 2.16. Variance through time across habitat for exports in the lobster simulation.** The percent of variance explained by the first 10 modes of the empirical orthogonal function of the timeseries of connections as a source over habitat locations. Connections were constrained over an increasing spatial scale (shown in color), changing the network from local through greater than 2000km. The corresponding power density spectrum shows the periodicity of trends in the timeseries. Passive: A&B. OVM: C&D.

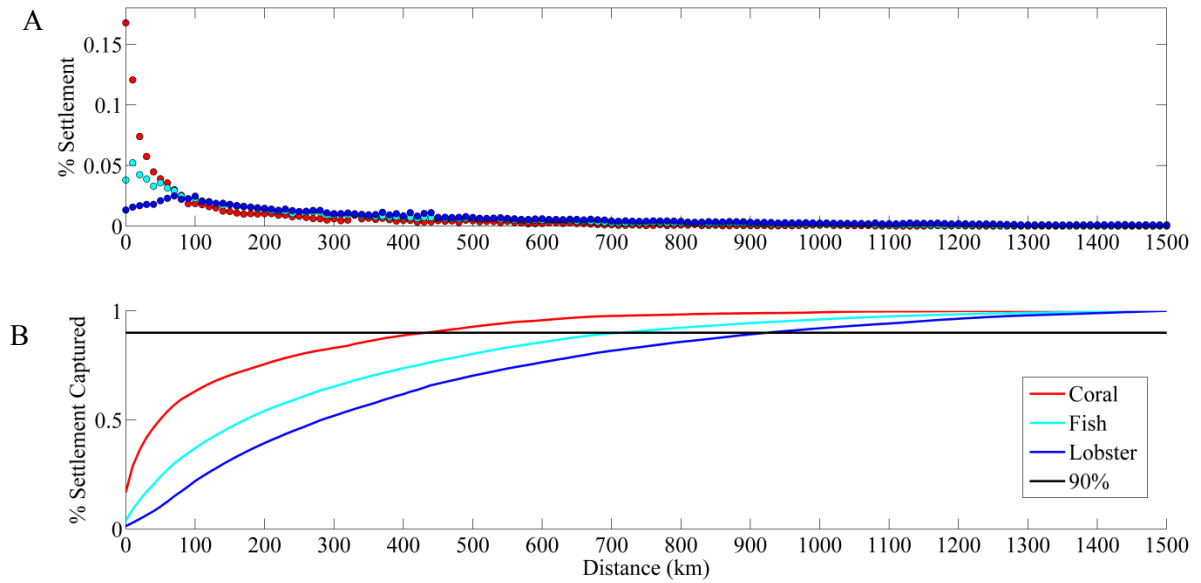




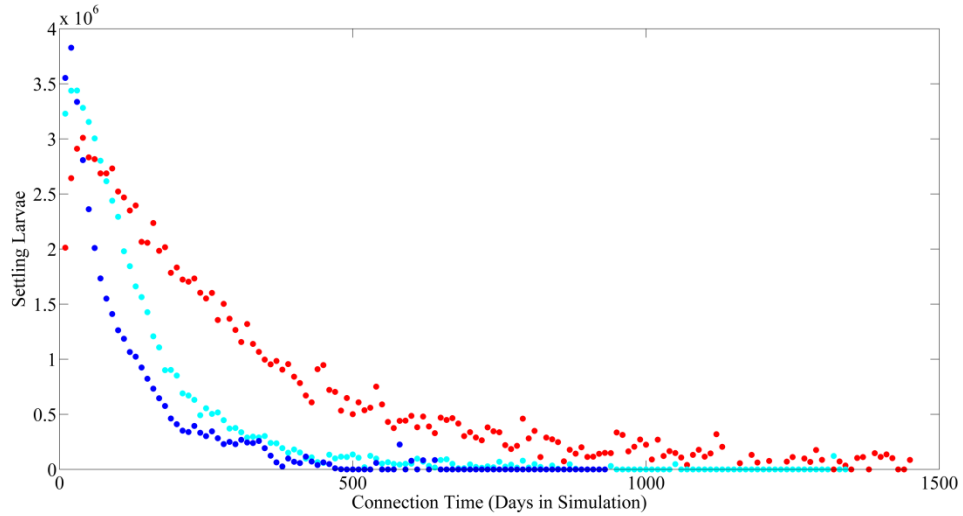
**Figure 2.17. Variance through time across habitat for imports in the lobster simulation.** The percent of variance explained by the first 10 modes of the empirical orthogonal function of the timeseries of connections as a source over habitat locations. Connections were constrained over an increasing spatial scale (shown in color), changing the network from local through greater than 2000km. The corresponding power density spectrum shows the periodicity of trends in the timeseries. Passive: A&B. OVM: C&D.



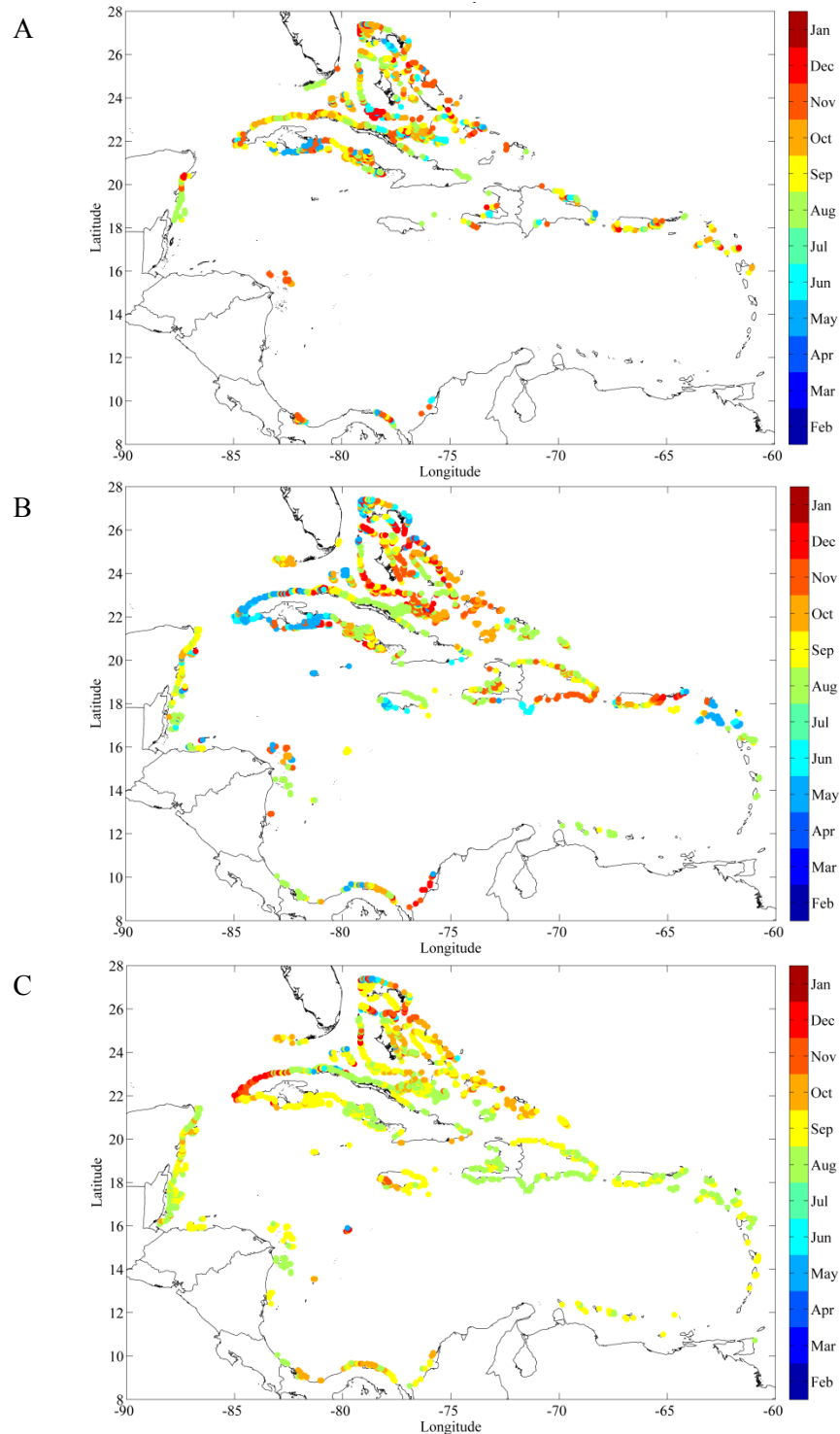
**Figure 2.18. Spatial scales of connection.** For three simulations (red = coral; cyan = fish; blue = lobster) the percentage of the total connections regardless of connection probability (A) and the cumulative percent of all connections occurring at increasing spatial scales (B).



**Figure 2.19. Spatial scales of settlement.** For three simulations (red = coral; cyan = fish; blue = lobster) the percentage of the total recruits (A) and the cumulative percent of all settlers occurring at increasing spatial scales (B).

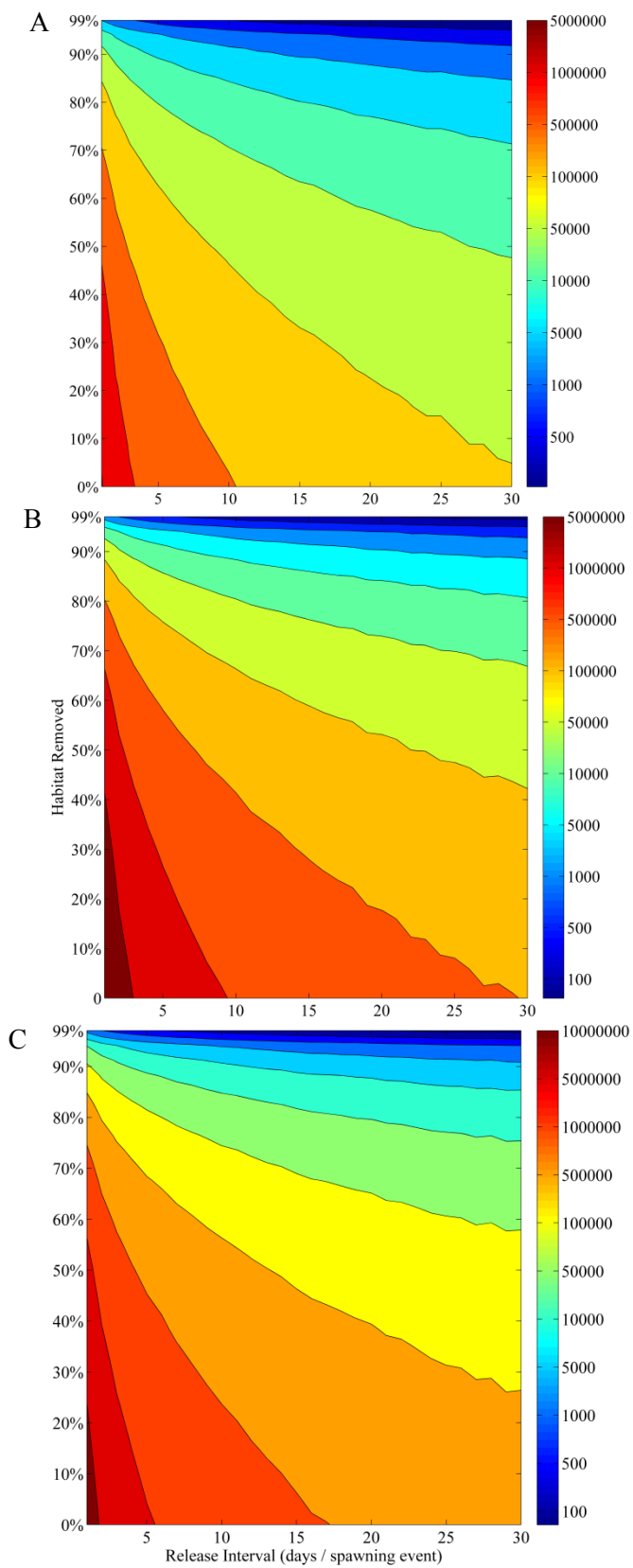


**Figure 2.20. Modeled larval settlement and connection time.** For three simulations (red = coral; cyan = fish; blue = lobster) the number of larvae which settled, and how much time the connection causing the settlement occurred. Larger amounts of larvae settled in the more occasional connections.



**Figure 2.21. Seasonal patterns of maximum long distance dispersal.** Recruitment was pooled by month for four years of simulations to identify favorable long distance dispersal spawning periods. In locations that generated long distance dispersal, bubbles were plotted and colored by the month with the most. Coral (A), fish (B), and lobster (C) had separate scales of long distance dispersal: 400km, 600km, 900km respectively.

**Figure 2.22. Reduction in spawning frequency and habitat.** The number of connections made irrespective of probability throughout a four year simulation for three different species (A: coral; B:fish; C:lobster) shown relative to decreases in both release interval and habitat removal. Habitat was reduced with a step of 3%. Connections are the average of 1000 random habitat removals of habitat at each release interval.



### **CHAPTER 3. LARVAL CONNECTIVITY AND THE INTERNATIONAL MANAGEMENT OF FISHERIES**

Predicting the oceanic dispersal of planktonic larvae that connect scattered marine animal populations is difficult, yet crucial for management of species whose movements transcend international boundaries. Using multi-scale biophysical modeling techniques coupled with empirical estimates of larval behavior and gamete production, the spatiotemporal patterns of larval supply were predicted and empirically verified to describe the Caribbean-wide pattern of larval connectivity for the Caribbean spiny lobster *P. argus*, an iconic coral reef species whose commercial value approaches \$1 billion USD annually. These results provide long sought information needed for international cooperation in the management of marine resources by identifying lobster larval connectivity and dispersal pathways throughout the Caribbean. Dispersal pathways entrained lobster larvae across age classes, and this concentration was related to current strength. Finally, an outline is provided for how large-scale fishery management could recognize the metapopulation structure by incorporating "larval credits" and considering the establishment of pelagic larval sanctuaries.



## Background

The lifecycle of most marine animals includes a dispersive planktonic larval stage lasting hours to months that connects scattered populations. Therefore, knowledge of larval connectivity is crucial for understanding population dynamics and sustainably managing marine taxa whose biogeographic distributions rarely coincide with political boundaries. Recent studies of larval connectivity employing natural or artificial tags (Becker et al. 2007; Almany et al. 2007; Hamilton et al. 2010), biophysical modeling (Cowen et al. 2006; Paris et al. 2005; Hidalgo et al. 2011), tracking larval patches (Paris and Cowen 2004), and genetic analysis (Planes et al. 2009; Saenz-Agudelo et al. 2011) have revealed surprising levels of population self-recruitment, eclipsing the long-held paradigm that marine populations are largely "open" and dependent upon an exogenous supply of larvae (Roughgarden 1985; Roberts 1997). As compelling as these findings are, the ability to predict the actual dispersal of larvae from spawning grounds to nurseries remains a rare exception. This chapter describes how an empirically parameterized biophysical model provides estimates of larval supply and may be used to pinpoint larval origins, destinations, and pathways for one of the Caribbean's most valuable marine species - the spiny lobster, *Panulirus argus*.

The Caribbean spiny lobster is a ubiquitous inhabitant of coral reefs and shallow tropical seas in the tropical West Atlantic. Commercial fishermen and recreational divers in over 30 Caribbean nations harvest lobsters, a resource valued at nearly \$1 billion USD annually (Ehrhardt et al. 2010). Like most marine animals, *P. argus* has a complex life cycle: adults inhabit coral reefs where they spawn, their planktonic larvae (phyllosoma) mature in the open sea and engage in diurnal and ontogenetic vertical migration during

dispersal before returning to coastal nurseries in shallow, vegetated habitats (Lipcius 1994). Given the long pelagic larval duration (PLD) of this species (5-9 months; Goldstein et al. 2008), larvae potentially disperse among lobster populations throughout the Caribbean (Ehrhardt 2005). Genetic analyses support the hypothesis of a single "pan-Caribbean" lobster metapopulation (Silberman et al. 1994; Naro-Maciel 2011; Diniz et al. 2005), indistinguishable within the Caribbean but distinct from a closely related species off the coast of Brazil (Tourinho et al. 2012).

Frequent and widespread dispersal of larvae can mask genetically distinct subpopulations, whereas demographic connectivity - the frequent (i.e., weeks to years) exchange of individuals within a metapopulation - is a fundamental ecological process relevant to the management of marine fisheries and protected areas (Kritzer and Sale 2004). Studies of demographic connectivity have largely focused on taxa with short PLDs (e.g., bivalves and reef fish) and though valuable scientific contributions, they likely bias our understanding of connectivity at the larger spatial scales most important for marine resource management (Pelc et al. 2010). Yet, empirical evidence of demographic connectivity among distant (>1000 km) populations is virtually undetectable given current tagging methods and genetic techniques (Lowe and Allendorf 2010; Waples et al. 2008). For this less tractable circumstance, biophysical modeling is a fast and affordable tool that is unhindered by the PLD of target species; moreover it permits the evaluation of hypothetical management strategies on larval connectivity within marine metapopulations (Botsford et al. 2009).

To identify the origins, destinations, and dispersal corridors of spiny lobster larvae within and among Caribbean nations, this study used an open source, multi-scale

coupled biophysical larval transport model (Paris et al. 2013) built from an earlier configuration of a Lagrangian individual-based model (Paris et al. 2002). The model has four components: 1) a GIS-based benthic module representing habitat for lobster spawning and recruitment, 2) a physical oceanographic module (Figure 3.1) containing daily 3-D current velocities from an array of hydrodynamic models, 3) a larval biology module depicting larval life history characteristics, and 4) a Lagrangian stochastic module that tracks the trajectory of individual larvae. The model was parameterized with data on spatiotemporal patterns of spiny lobster spawning and planktonic larval behavior, and then verified the model by comparing simulation results with empirical data on the spatiotemporal patterns of larval supply at four sites in the Caribbean (Muller and Matthews, FWC; Briones-Fourzan et al. 2009). Compared to other larval dispersal models created for spiny lobsters (Sotckhausen and Lipcius 2001; Griffin et al. 2001; Chiswell and Booth 2008; Rudorff et al. 2008; Briones-Fourzan et al. 2008) this model uses the highest resolution, three-dimensional oceanographic circulation models and also larval behavior, both of which affect dispersal trajectories. The objectives were to employ this modeling system to investigate: (a) the demographic connectivity of spiny lobster larvae among Caribbean nations, (b) the international patterns of larval imports and exports, and (c) the relevancy of connectivity in designing Caribbean-wide networks of marine protected areas (MPAs). An unanticipated phenomenon also emerged from modeling results: the predicted existence of pelagic larval nursery areas.

## **Methods**

Focusing on the Caribbean's most valuable fishery resource as a model system, larval dispersal was investigated through the use of an open-source coupled biophysical

larval transport model, specifically parameterized using empirical data collected for *P. argus* (Table 3.1). The model adheres to the recommended practices for Lagrangian biophysical modeling laid forth in North et al. (2009), while also incorporating empirical data for biological parameterization. Empirical estimates of spawning population (this study), laboratory and field observations of larval vertical migration in the water column (Butler et al. 2011), and postlarval sensory behavior (Goldstein and Butler 2009) were used to parameterize the early life history traits of *P. argus*. Each of four submodules was specifically parameterized for spiny lobster larvae.

#### *Lagrangian stochastic module*

The Lagrangian stochastic module drives the coupled biophysical Connectivity Modeling System (CMS). It uses a 4th order Runge-Kutta integration scheme (Paris et al. 2013) in both time and space to improve the accuracy of simulated larval trajectories as is best practice (Brickman et al. 2009). For each particle, the next position along the trajectory was calculated during each integration time-step of 2700 seconds, comparable to a previous experiment using spiny lobster that used a time-step of 4500 seconds (Butler et al. 2011). The trajectories resulting from the modeled time-step and turbulence are smooth and relatively free of artifacts. Submesoscale turbulent movement was accounted for with stochastic turbulent diffusion during each time-step, calculated by multiplying a random number between 0 and 1 by the square root of twice the diffusivity coefficient ( $0.1\text{m}^2/\text{s}$ ) divided by the time-step (Paris et al. 2013). Simulations ran starting daily from January 1, 2004 until December 31, 2007, tracking larval flow for over 4 years.

### *Physical oceanographic module*

The physical oceanographic module contains the various oceanographic models that provide the currents with which to move larvae (Figure 3.1). These currents vary as depth changes from the surface down to 100 m, which is the likely maximum depth utilized by lobster phyllosoma (Butler et al. 2011). A hierarchy of ocean circulation models are nested offline in the physical oceanographic module, allowing a Caribbean-wide simulation scale (-100:-55 degrees longitude West and 8:32 degrees latitude North) while not compromising resolution in areas with advanced local circulation models. Four different ocean circulation models were nested together for this study: 1/12 degree HYCOM + NCODA Global Hindcast Analysis provided the base, followed by the higher resolution HYCOM + NCODA Gulf of Mexico 1/25° Analysis (GOM10.04) (HyCOM Consortium), a 1/24th degree ROMS model of the Bahamas, and the fine scale 900 meter resolution FLKeys-HYCOM (Kourafalou et al. 2012).

### *GIS-based benthic module*

The GIS-based benthic module determines where larvae can settle and the location, quantity, and timing of larval release. It is directly coupled to the particle tracking module and is accessed during each integration time step. It consists of 261 habitat sites (polygons - vector GIS data) that are a combination of settlement habitat and a sensory envelope reflecting the threshold at which lobster postlarvae can detect and move to settlement habitat (APPENDIX C). Further information on polygon theory is in Paris et al. (2007). The 18km sensory envelope for this study was constructed based on the sensory abilities of spiny lobster postlarvae (Goldstein and Butler 2009). Postlarvae are the highly mobile, non-feeding, settlement stage of spiny lobsters and are capable of

detecting nursery habitat cues over similarly long distances (Jeffs et al. 2005). Lobster benthic habitats were delineated based on data from the Millennium Reef Project (Andréfouët et al. 2004). Larvae were released from the nearest non-land location to the center of each habitat site.

### *Spawning input*

The daily timing and magnitude of lobster spawning and thus larval release from each habitat site was estimated as a function of lobster density, sex ratio, size, and fecundity. First, the relative abundance of adult lobsters within each Caribbean country was estimated from FAO fishery landing statistics and an independent mail survey. Data was gathered from the top 10 lobster fishing nations that make-up 95% of the fishery in the Caribbean. This assumed that the FAO (2006) fishery landing statistics are an indicator of relative adult lobster abundance due to the overexploited nature of spiny lobster fisheries. However, these are fishery dependent data with unknown bias (e.g., under reporting of total catch). These data on the relative abundance of lobsters were then supplemented by a mail survey distributed to lobster scientists and fishery managers with intimate knowledge of their local jurisdiction. These data sources provided fine-scale resolution of the timing of spawning, the sex ratio, and the size-structure of adult male and female lobsters, which was used to determine fecundity (Bertelsen and Matthews 2001) per habitat site.

The larval production per habitat site per day proportional to the total annual egg production in the Caribbean (Figure 3.2A) was scaled using these data. These estimates of total *P. argus* egg production per year in the Caribbean were then divided into monthly patterns of spawning for each region based on the FAO and survey data (Figure 3.2B).

The total spawned per month and site was further divided into each day because *P. argus* does not spawn synchronously. Finally, these empirical estimates were scaled so as to restrict the annual release of particles in the model to approximately 40,000,000; of which 38,000,000 were distributed to the 10 countries representing 95% the fishery and the remaining 2,000,000 particles distributed equally throughout the rest of the habitat sites with less accurately known lobster population structure. The annual value of 40,000,000 particles was found a priori to saturate movement paths in the model, after accounting for mortality (Figure 3.3). The end result was a daily release of larvae that varied in magnitude proportional to the total fishery, constructed with the local size, population, and spawning patterns when known for each of the 261 habitat sites.

A modified pattern was used to test for idealized MPA placement, which assumed that each habitat site could hold the same climax population size and have the same reproductive potential. This had timing structured as in the original release, but allocated an equal number of particles to each site, rather than scaling population size based on survey and fishery data.

#### *Larval biology input*

The larval biology module accounts for the early life history traits of spiny lobster including PLD, larval competency period, and ontogenetic vertical migration. Lobster larvae display distinct patterns of vertical distribution throughout ontogeny, which greatly alters which currents they are exposed to and therefore their dispersal. To reproduce this behavior, CMS assigns larvae probabilistically to different depth bins. In the present simulations, individual larvae may reside during each time-step within one of five depth ranges (0-20m, 20-40m, 40-60m, 60-80m, and >80 m) with an age-dependent probability.

During each time step, the depth bin is assigned randomly from the age-specific distribution (Butler et al. 2011). However, larvae are not allowed to travel more than one depth bin per time step. Older larvae (>3 months old) have a higher chance of being deeper than younger larvae. These probabilities were determined through a combination of plankton trawls and laboratory experiments described in another study (Butler et al. 2011). The mean PLD of lobster larvae was observed to be ( $\pm 1$  SD)  $174 \pm 22$  d, based on data from laboratory rearing of *P. argus* from egg to postlarval stage (Goldstein et al. 2008). Larvae in the model metamorphose to postlarvae within a competency period (152 to 196 d) and postlarvae are recorded as ‘settled’ if they enter a benthic nursery habitat site (habitat module) within this competency period; if suitable habitat was not encountered within the competency period they ‘die’ and are removed from the simulation.

#### *Mortality input*

Mortality is a key parameter in biophysical modeling (Hood and Bartsch 2008). There is no evidence that vertebrate plankton mortality rates are similar to that of invertebrate plankton, however there is growing evidence that mortality changes throughout ontogeny for both coral (Graham et al. 2008) and fish (Paris 2009). To impose mortality, a half-life function was used to reflect varying survivorship as a function of larval duration. There are no known mortality rates for *P. argus* phyllosoma, thus an estimate was used for another spiny lobster (*P. cygnus*) from Feng et al. (2011), based on trawl surveys that had diminishing returns of later stage larva (Rimmer and Phillips 1979), suggesting abundance based mortality of 85-90%. The cumulative



mortality imposed on the larva in the model in this study is  $\approx$  ca. 90%, including advective mortality resulting from not reaching settlement habitat.

## **Results**

### *Model Verification*

Two independent sets of empirical data on postlarval lobster settlement that were not used in the parameterization of the model (Muller and Matthews, FWC, Marathon, Florida, USA; Briones-Fourzan et al. 2008) were subsequently used to evaluate the final coupled system's performance. The model was compared against the monthly patterns of *P. argus* postlarval arrival at two sites in both Mexico and Florida, corresponding to four separate habitat polygons (sites) in the model (Figure 3.4). The simulated pattern of monthly arrival of postlarval lobsters was significantly correlated ( $p < 0.05$ ) with observed postlarval recruitment at two of the four sites and captured the peak in seasonal recruitment at all four sites (Figure 3.4). The correlation was not robust when the peak month of postlarval abundance was removed for Puerto Morales ( $n=11$ ,  $R=0.1849$ ,  $p = 0.5863$ ), nor for Bahia de Ascension ( $n=11$ ,  $R=0.5248$ ,  $p=0.0974$ ). The model shows the fall peak in postlarval arrival in the Florida Keys, but does not show the spring peak (Figure 4, Long Key and Big Munson). When run without biology, the model did not capture the pattern at any of the habitat sites ( $p > 0.05$ ; Figure 3.5).

### *Connectivity Matrices*

The simulations reveal distinct flows of long-lived spiny lobster larvae among some regions of the Caribbean and pockets of larval retention within others (Figure 3.6). Probabilistic imports and exports of larvae from each of 261 sites show that the majority of larval exchanges transcend international boundaries, when summarized by country

(Figure 3.7). Nonetheless, domestic connectivity (i.e., self-recruitment of lobsters within a country) still dominates larval recruitment in some areas. For example, lobster populations in the Bahamas, Cuba, Nicaragua, and Venezuela are largely self-recruiting, whereas those in the Cayman Islands, Columbia, Honduras, Jamaica, Panama, and Puerto Rico depend largely on larval subsidies from outside their borders.

#### *Imbalanced International Exchange*

Much like international trade, large disparities between larval imports and exports among countries abound in the simulations. Imbalances in the international exchange of lobster larvae were identified by removing model predictions of domestic connectivity from the total larval supply and then compared the remaining difference in larval subsidies received and subsidies donated to the pan-Caribbean larval pool (Figure 3.8). This analysis reveals which countries harbor lobster populations that sustain populations elsewhere. The eastern Bahamas, southern Cuba, Dominican Republic, Nicaragua, and Venezuela export far more lobster larvae than those areas receive from the international community. In contrast, the western Bahamas, Cayman Islands, northern Cuba, Columbia, Florida Keys, Jamaica, and Panama are regions whose lobster populations receive more larvae from outside their boundaries than they donate to the Caribbean larval pool.

#### *Connectivity and Marine Reserve Networks*

Networks of MPAs have been proposed as a solution to ensure that demographic connectivity is maintained among marine animal metapopulations, with a recommendation that on average 20-30% of the coastal seas be set aside as MPAs (Gaines et al. 2010). The model was used to explore this recommendation specifically

for spiny lobster in the Caribbean by designating various model sites as hypothetical MPAs and evaluated different networks of sites as if they were the sole sources of lobster larvae for the Caribbean (Table 3.2). Five MPA network scenarios were evaluated in simulations in which 40 habitat sites were designated as MPAs and selected in one of five ways: (1) Random: 40 sites individually and randomly selected from all those in the Caribbean, (2) Stratified Random: two randomly selected sites from each of 20 countries, (3) Local Recruitment: top two self-recruiting sites per country, (4) Long Distance Dispersal: top forty sites in Caribbean in terms of successful international export, and (5) Maximum Export: top forty sites in Caribbean with export imbalanced exchange (Figure 3.8). For these simulations larval production from each habitat site was fixed and uniform (unlike the realistic and variable production used in the first set of simulations), which removed the effect of differences in local population size and focused on the effect of spatial arrangement of MPAs on biophysical connectivity networks.

The geographical location and connectivity characteristics of sites selected as MPAs altered patterns of spiny lobster dispersal and settlement (Table 3.2). Sites selected at random (scenarios 1 and 2; bootstrapped 1000 times to create a distribution) produced less successful larval connectivity than sites selected based on their merit as international (scenarios 4 and 5) or domestic (scenario 3) larval exporters. Simulations focusing on preserving domestic connectivity caused a near universal increase in larval recruitment across the Caribbean, although smaller than the ideal internationally managed scenario. These results, which take into consideration complex patterns of connectivity for a species with long-lived larvae, add specificity to generalized recommendations concerning the proportion of protection necessary to sustain marine fishery resources.

### *Pelagic Larval Nurseries*

An unexpected pattern in larval distribution within the open ocean also appeared in the simulations. When the oceanic pathways travelled (i.e., sum of PLD spent in each oceanic locale) by successfully settling larvae were examined, in contrast to the paths taken by larvae that are eventually lost from the system, zones emerged that could be described as “pelagic larval nurseries”. That is, regions in the open Caribbean Sea where lobster larvae from around the Caribbean spend much of their planktonic existence before later settling into coastal benthic nurseries. These larval nurseries include relatively large regions offshore of Nicaragua, southern Cuba, and the central Bahamas as well as smaller areas north of Cuba and southeast of Hispaniola (Figure 3.9). The role of larval behavior in creating these pelagic nurseries was evaluated by conducting an additional simulation without ontogenetic vertical migration (OVM), thus simulating passive larval dispersal. The segregation between the regions of concentration was accentuated when larvae drifted passively (Figure 3.9), indicating that the larval nursery zones were governed primarily by physical oceanographic features, not OVM behavior specific to spiny lobsters. Thus, these pelagic larval nurseries are potentially relevant to the pelagic retention of other Caribbean species, not just spiny lobster.

### *Larval density*

Larval density through different age classes was investigated to identify how stationary pelagic nurseries were. Simulated larval positions were recorded every 10 days, which is approximately the molting schedule for *P. argus* (Goldstein et al. 2008). Two scenarios were used: one with the ontogenetic vertical migration behavior observed in lobster phyllosomata and one treating the larva as passive particles. A random

subsample of 2 million larvae was used from each scenario, reducing computational demands and creating comparable datasets. The locations of animals in each age class were analyzed separately to assess data clustering. Rather than examining clustering over the entire dataset at once, data was gridded to see how clustering occurred on a biologically relevant scale. The scale was determined by taking the resolution of available current data and then doubling it to insure coverage over areas with low current data resolution in HyCOM, but high resolution in the multi-scale CMS. The grid size was a third of a degree (Figure 3.10).

Clustering in each age class of each scenario in each grid cell was determined by using the local Moran's I statistic. Data was analyzed using MATLAB code developed by Felix Hebel (2006), which calculates the local Moran's I value using a moving window of a fixed size across a matrix. The matrix was weighted (W) by the larva within the given grid (i) proportional to the total larva within all grids (j).

$$W_i = \frac{Larva_i}{\sum_j Larva}$$

Clustering was examined across age classes for both scenarios, and was examined again after subsampling the scenarios and targeting individuals of particular fates. Two fates were considered: successful settlers, and unsuccessful animals.

The local Moran's I analysis showed clustering present in each of the scenarios and with both fates. Clustering was apparent within the first 10 days and, surprisingly, was maintained throughout each of the simulations. The general trend was clustering through the core of the Caribbean, a region here defined as following the Caribbean current from the coast of Venezuela up around Cuba, and through the Straits of Florida.

A few spots of particularly high concentration, throughout each of the scenarios, included the Southwestern coast of Cuba, outside of the Bay of Batabano, and near the Colombian archipelago off of the Nicaraguan Rise. In addition, the Bahamas demonstrated consistent clustering throughout and increased densities in the Northeast, especially when all animals were considered.

### *Larval age*

To determine if the prevalence of larvae at any given grid could be predicted by the age of the larvae, a geospatially weighted regression between probability and age was performed in ArcGIS 10.1. The geographically weighted regressions demonstrate that a relationship exists between age and probability (Figures 3.11-3.14). The probability of encountering animals increases as they age in places with larger circles that trend towards blue. This relationship holds in most of the Caribbean for the OVM scenario (Figures 3.13 and 3.14). For the scenario without behavior, there is less of a relationship, and a very different pattern especially for settling larvae (Figures 3.11 and 3.12).

### *Current Strength*

The strength of the ocean current likely has a large role in driving larval concentration. To explore this hypothesis the total kinetic energy (TKE) of the base ocean circulation model (1/12° HyCOM) was evaluated over the course of the experiment. TKE is a simple metric of current strength and movement within an area. Using the top 100 meters, TKE was formulated at the scale of the native grid (1/12°) by adding together the absolute value of the u,v, and w components of the current, integrating over depth, and summing through simulation time:

$$TKE = \sum_{beginning}^{end} \int_{surface}^{bottom} (|u| + |v| + |w|)$$

The TKE from the native grid scale was then adjusted to a scale of interest by using a Delaunay interpolation scheme (TriScatteredInterp in MATLAB using a linear interpolation method) to fit the data to the coarser one-third degree grid (Figure 3.10). The geospatially weighted regression tracks the relationship well in areas within a specific band of energy. When the TKE is either too low or too high, the relationship breaks down. It should be noted that the best fit belongs to the most realistic and desired scenario (red line; Figure 3.15), suggesting that OVM allows concentrations of larvae to persist through the simulation, even in areas with strong currents.

## Discussion

Managing marine fisheries organisms as if they were constrained within geopolitical boundaries is not working as fisheries worldwide are in decline (Beddington et al. 2007; Pauly 2009). For example, in regions where the spiny lobster *P. argus* are most abundant and thus heavily fished, adult stocks have declined by 30% or more over the past two decades despite spirited management (Chavez 2009; Ehrhart and Fitchett 2010). For many species, an approach to fisheries management that acknowledges dispersal dynamics with estimates of larval connectivity is needed and now possible.

When MPAs were used to protect specific locales that tend to export larvae internationally, those simulations yielded the highest successful settlement of larvae throughout the Caribbean (Table 3.2). Certain regions contribute greatly to the wider Caribbean larval pool (Figures 3.7 and 3.8), so maintaining the health of adult lobster spawning stocks in those countries should be an international priority. Perhaps one

strategy for doing so, similar to the trade of “carbon credits” outlined in article 6 of the Kyoto protocol (United Nations 1998), would be to assign each nation “larval credits” based on regional larval export production. Nations that absorb disproportionately more larvae from the international larval pool bear an ethical responsibility and financial incentive to assist in the preservation of lobster spawning stocks in other areas best suited for exporting larvae. Such non-traditional management strategies are likely to be met with skepticism and their implementation difficult, considering the political and economic realities of international agreements and the needs of local artisanal fishermen (Smith et al. 2009). Still, the best scientific evidence derived from genetic research (Silberman et al. 1994; Naro-Maciel 2011; Diniz et al. 2005), fisheries analysis (Chavez and Chavez-Hidalgo 2013), and modeling studies such as this one suggest that lobster stocks in the Caribbean are linked across geopolitical boundaries by larval connectivity, and should be managed accordingly.

Just as preserving pathways between habitat fragments is essential for sustaining many terrestrial species, including carnivores such as the Asian tiger (Wikramanayake et al. 2011), intact connectivity corridors for marine organisms may be needed. This study’s results suggest that open ocean larval corridors are regions that regularly entrain, concentrate, and nurture pelagic larvae while on their ontogenetic journey to coastal habitat (Figure 3.9; Figures 3.11-3.14). For example, the prevailing Caribbean current that snakes through the Caribbean Basin is a “graveyard” for larval lobsters in the model, presumably because its high mean flows entrain and then wash larvae into the North Atlantic where few will survive (Figure 3.9). This stands in contrast to the view that larvae harness strong currents to successfully disperse long distances (Roberts 1997).



Perhaps the deep diurnal and ontogenic vertical migrations of lobster larvae enable them to pass beneath surface boundary currents and escape being swept away by strong currents, aiding their retention within certain areas of the Caribbean. Behavior allowed settling larvae to maintain concentrations of older larvae in areas of the ocean even with strong currents (Figure 3.15). Simulations with and without larval behavior indicated that the identified pelagic nursery zones were stable and likely maintained by oceanographic features. Thus findings for *P. argus* are likely to be robust despite differences in larval origins, destinations, and avenues of dispersal that invariably differ among taxa with dissimilar dispersive traits (Largier 2003). If so, then the existence of pelagic nurseries for larvae as predicted model has implications beyond lobsters and may constitute oceanic “essential fish habitat” (National Oceanographic Atmospheric Administration 2002). Protection of these open ocean larval habitats from potentially deleterious processes (e.g., pollution from oil spills, coastal runoff, and vessel discharges) may be considerations for the long-term sustainability of lobster populations and other species.

Although an adequate flow of larvae among sub-populations is crucial for the sustainability of marine resources, larvae reaching a site does not necessarily equate to successful recruitment. The transition from pelagic larva to benthic juvenile and on to adulthood is dependent on a variety of post-settlement processes (Stockhausen and Lipcius 2001; Pineda et al. 2009), many of which are site-specific and not accounted for in this model that assumed homogeneous and static habitat quality. Whereas larval supply and later recruitment are correlated for some species of spiny lobster and in some areas (Ehrhardt and Fitchett 2010; Phillips 1986; Caputi et al. 1995), unsuitable nursery habitats decouple the relationship between larval supply and juvenile recruitment in

others (Lipcius 1997; Butler and Herrnkind 1997). The integration of biophysical larval dispersal models with spatially-explicit and dynamic depictions of benthic habitat conditions that drive benthic population dynamics (Butler 2003; Butler et al. 2005) are a logical next step in the development of predictive large-scale metapopulation models.

Verification of models lends credence to their results. Whereas the backbone of coupled bio-physical models is ocean circulation models whose physical dynamics have been validated and peer reviewed, the biological predictions of larval dispersal models should also be verified (Metaxas and Saunders 2009). This study's verification of the model predictions is based on correlations between model predictions and empirical observations of recruitment into relatively small *ca.*  $\approx 50\text{km}^2$  habitat patches following the dispersal of larvae over thousands of kilometers during their 5-9 month PLD. There is precedent for using postlarval collector seasonal settlement trends to verify a Lagrangian model (Feng et al. 2011), and predictable seasonal patterns are vital for fishery management. Correlating the spatial concentration of observed pelagic larval or juvenile patches with modeled outputs has been done in other studies constrained to smaller spatial scales (Paris and Cowen 2004; Hidalgo et al. 2012; Incze et al. 2010; Vikebo et al. 2011), but may be prohibitively costly and difficult to do throughout the Caribbean-scale of the model in this study.

Sensitivity analyses of some parameters for which empirical data are lacking or based on laboratory studies (e.g., mortality, PLD, age of competency) could potentially improve the accuracy of the model (Paris et al. 2005). For example, a run without biology did not capture the seasonal recruitment pattern (Figure 4.5), suggesting that additional biological parameterization could further improve model performance. For

example, Briones-Fourzan et al. (2008) used stochastic perturbations of a particle backtracking simulation to investigate potential origins of postlarvae arriving on the Mexican Quintana Roo coast, without having data on OVM. In comparison with their findings, the results of this study suggest diminished larval supply to Mexico from the Lesser Antilles Caribbean Islands and the Venezuelan corridor, while increasing the supply of larva from Central America and Hispaniola (Figure 3.16). This was expected since the vertical migratory behavior of the actively moving larva increases retention (Butler et al. 2011). A simulation conducted without larval OVM nor adult population structure did not capture the seasonal recruitment pattern evident in the empirical data, and is more similar to the connectivity described in Briones-Fourzan et al. (2008), suggesting that additional biological parameterization can further improve model performance.

Advances in computing, genetics, and oceanographic remote sensing are yielding tools useful in addressing questions about the connectivity of marine metapopulations that were unfathomable only a decade ago. The dispersal of long-lived larvae is a complex function of temporally unstable hydrodynamics and ontogenetically variable larval behavior. Therefore models that do not capture these essential system traits or whose results are not verified with empirical data will be misleading. Management of marine resources should benefit from new tools such as biophysical modeling that quantify larval connectivity and can thus be used to guide policy. For example the establishment of MPA networks in ecologically relevant areas that maximize larval production and the connectivity among disparate populations will maximize population viability in both self-recruiting regions as well as those regions dependent upon larvae

from elsewhere. The findings of this study with respect to spiny lobster connectivity in the Caribbean suggest that international management agreements that recognize the existence of marine metapopulations, focus on rebuilding and sustaining adequate spawning stocks (Steneck et al. 2009; Chavez 2009), and protect sensitive coastal and pelagic nurseries (Cruz and Bertelsen 2009) represent a scientifically sound policy for sustainable management of many marine resources.

**Table 3.1. Parameterization of the Biophysical Model.**

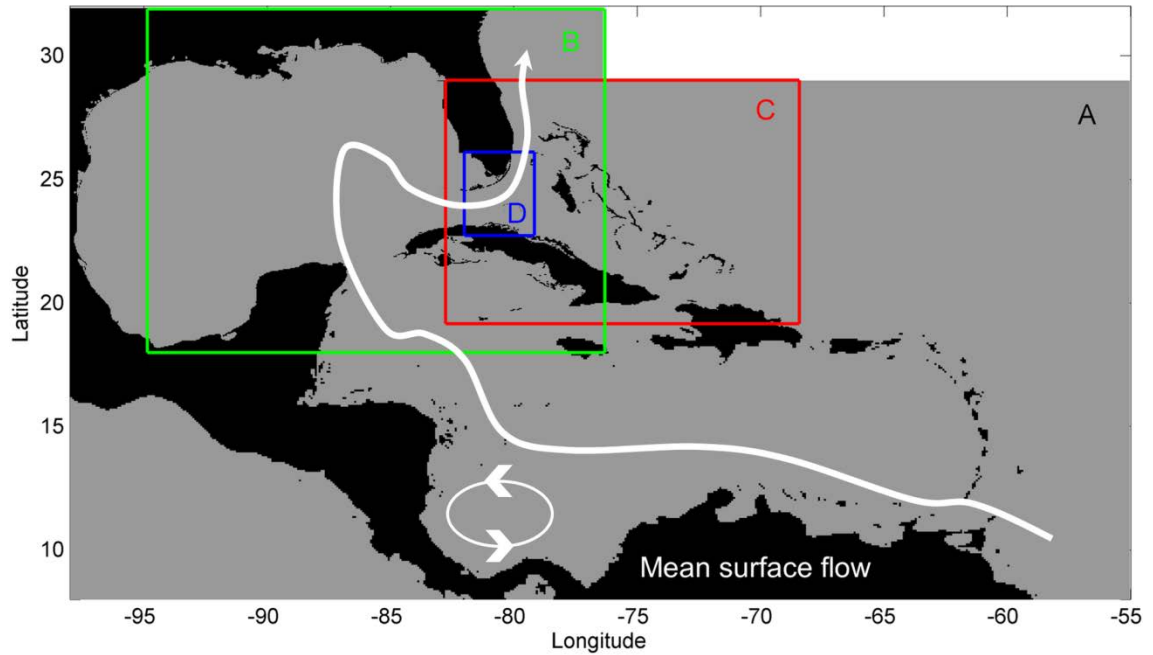
The data used to parameterize each module of the model, along with specific references to sources.

Module	Trait	Source
Habitat	Benthic Habitat	Andréfouët et al. 2004
Habitat	Polygon Theory	Paris et al. 2005
Habitat	18km Postlarval Sensory Buffer	Goldstein and Butler 2009
Habitat	Adult General Abundance	FAO 2006
Habitat	Adult General Abundance	CRTR survey
Habitat	Spawning Timing	CRTR survey
Habitat	Size Based Fecundity	Bertelsen and Matthews 2001
Ocean	Base Hydrodynamic Nest/Layer 1	HYCOM + NCODA Global 1/12°
Ocean	Hydrodynamic Nest/Layer 2	HYCOM + NCODA Gulf of Mexico 1/25°
Ocean	Hydrodynamic Nest/Layer 3	Bahamas ROMS simulation (Cherubin 2013)
Ocean	Hydrodynamic Nest/Layer 4	HYCOM-FLKeys
Biology	Max Pelagic Larval Duration (196 days)	Goldstein et al. 2008
Biology	Competency (152 days)	Goldstein et al. 2008
Biology	Mortality (half-life of 80 days)	Maximum possible while still maintaining saturation (Figure 3.3)
Biology	Vertical Migration Behavior	Butler et al. 2011
Lagrangian	Biophysical Approach and algorithms	Paris et al. 2013
Lagrangian	Time-step (2700 seconds)	Increased resolution from Butler et al. 2011
Lagrangian	Horizontal Diffusivity (0.1 m <sup>2</sup> /s)	Okubo 1971
Lagrangian	Vertical Diffusivity (0.0005 m <sup>2</sup> /s)	Ledwell 1993
Lagrangian	Annual particles released (40 million)	(Figure 3.3) and methods

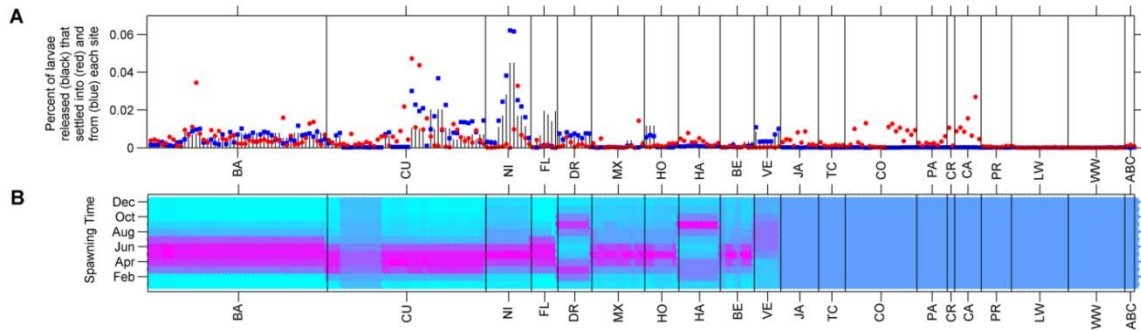
**Table 3.2 Strategies for selecting marine protected areas.**

Five MPA network scenarios were evaluated in simulations in which 40 habitat sites were designated as MPAs and selected in one of five ways: (1) *Random*: 40 sites individually and randomly selected from all those in the Caribbean, (2) *Stratified Random*: two randomly selected sites from each of the 20 countries, (3) *Self-Recruitment*: the top two self-recruiting sites per country, (4) *Long-distance Dispersal*: the top forty sites which successfully export larvae internationally in the Caribbean (5) *Maximum Export*: the top forty sites throughout the Caribbean with export imbalanced exchange (Figure 3.8). The random sites are the averages of 1000 random selections (MATLAB rand function). In each case, an equal number of larvae were released so the difference between scenarios is where the larvae were released from.

	Random	Stratified Random	Long- distance Dispersal	Maximum Export	Self- Recruitment
Total Settled	2188330	214646	403889	289080	274940
Average per site	838	822	1547	1107	1053



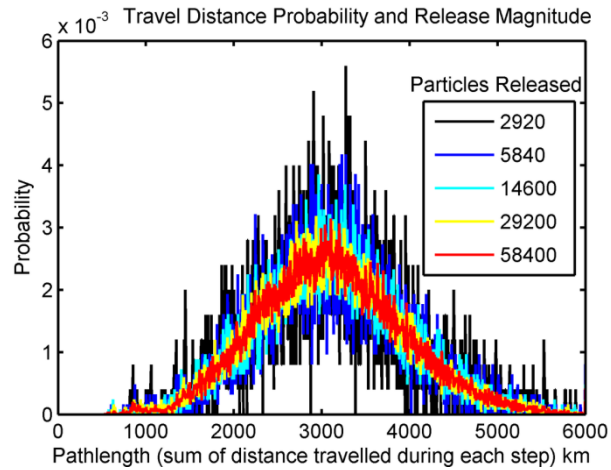
**Figure 3.1. The hierarchy of nested circulation models used in the study and the conceptual mean Caribbean flow.** The ocean circulation models used in reverse order of priority for use by the Lagrangian tracking module with their horizontal resolution and vertical depth bins in meters. A) HyCOM Global  $1/12^\circ$ : 0, 10, 20, 30, 50, 75, 100; B) GOM-HyCOM  $1/25^\circ$ : 0, 5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 90, 100; C) Bahamas ROMS  $1/24^\circ$ : 0, 2, 4, 8, 10, 20, 30, 40, 50, 55, 60, 80, 100; D) FLK-HyCOM  $1/100^\circ$ : 0, 5, 10, 30, 50, 75, 100. Mean surface flow after Fratantoni (1996).



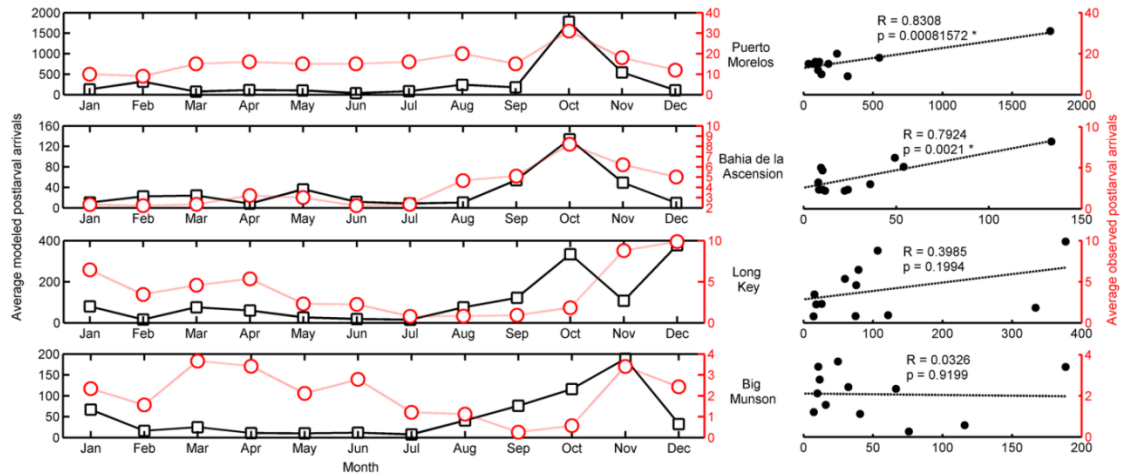
**Figure 3.2. Simulation larval release, settlement, and seasonality.**

The details of the timing and magnitude of the simulated releases and the larvae received at each habitat site ( $n=261$ ). The annual release (black lines), the larvae successfully received (red circles), and larvae donated (blue squares) at each habitat site as a percentage of the total (A). The annual timing of spawning at each site (B). The monthly effort increases from cyan to a peak of spawning occurring in red for locations with dynamic reproductive seasons. A uniform spawning pattern was used in locations that did not have empirical data on spawning time.

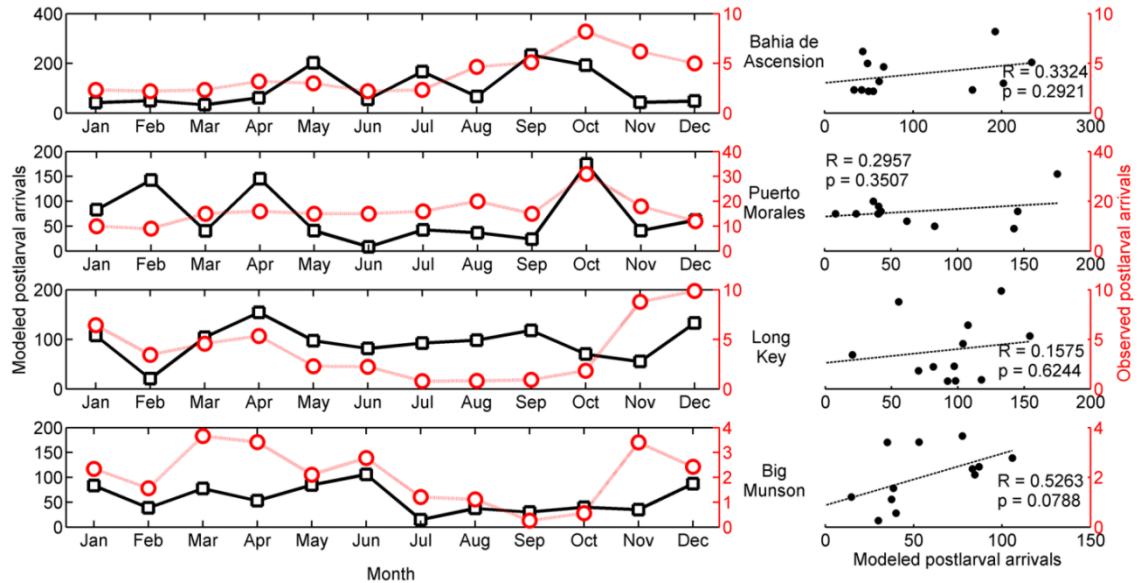




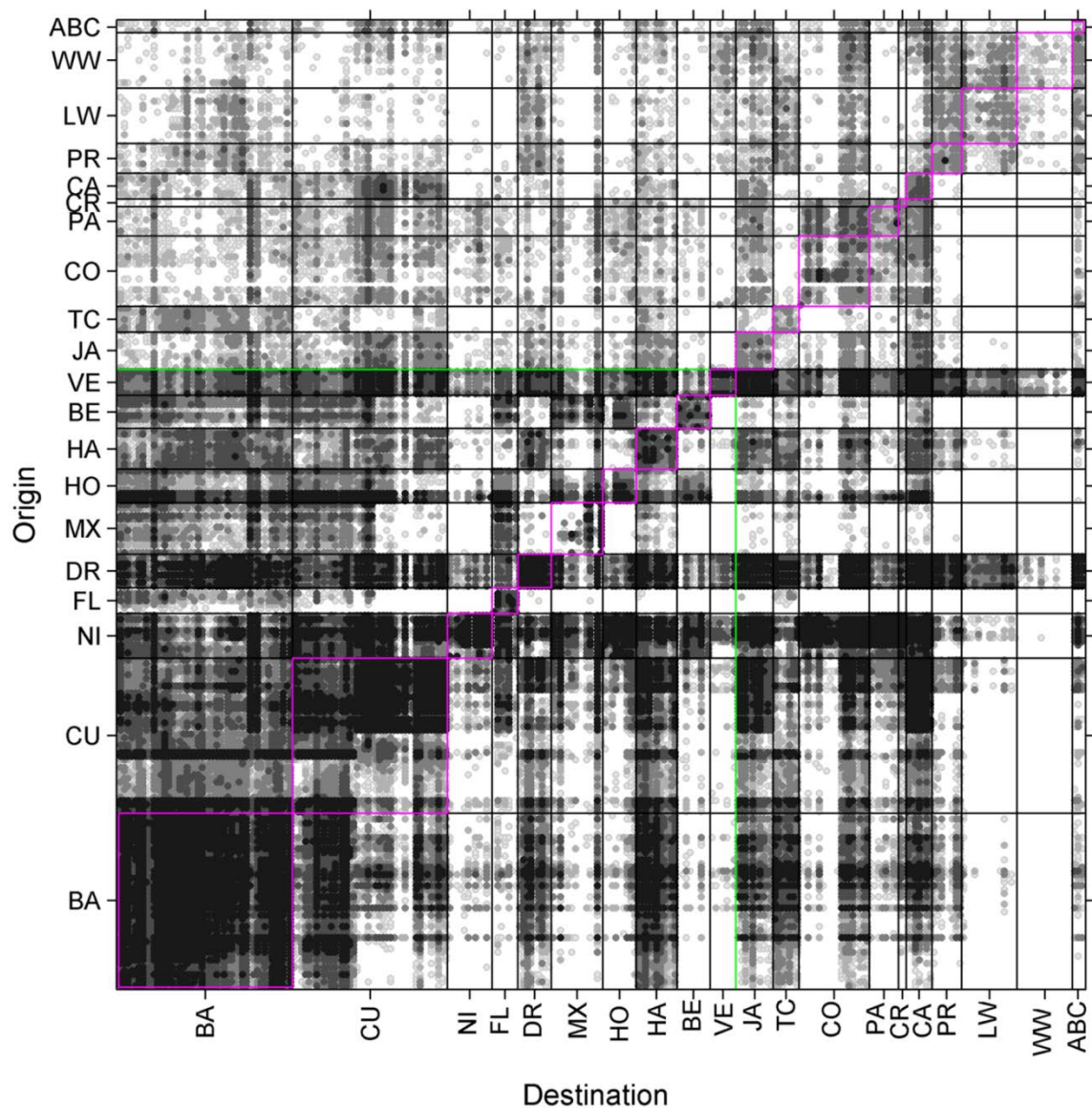
**Figure 3.3. Larval release magnitude and movement pathlength.** The probability of dispersal distances for larval releases from a central Caribbean release location ( $-68^{\circ}\text{W}, 14^{\circ}\text{N}$ ). The X-axis is the pathlength (sum of distances moved during each time-step) traveled by each larva binned into 5km increments, and the Y-axis is the probability. The number of larvae released (over 4 years of daily releases) increases in color from black to red and yellow. The smoother curves in red and yellow reflect the stochastic saturation, and suggest the proper number of larvae needed to release daily to probabilistically describe potential lobster larvae dispersal. These values reflect the number of larvae from a single site with no mortality, and had to be multiplied to account for each site and for mortality.



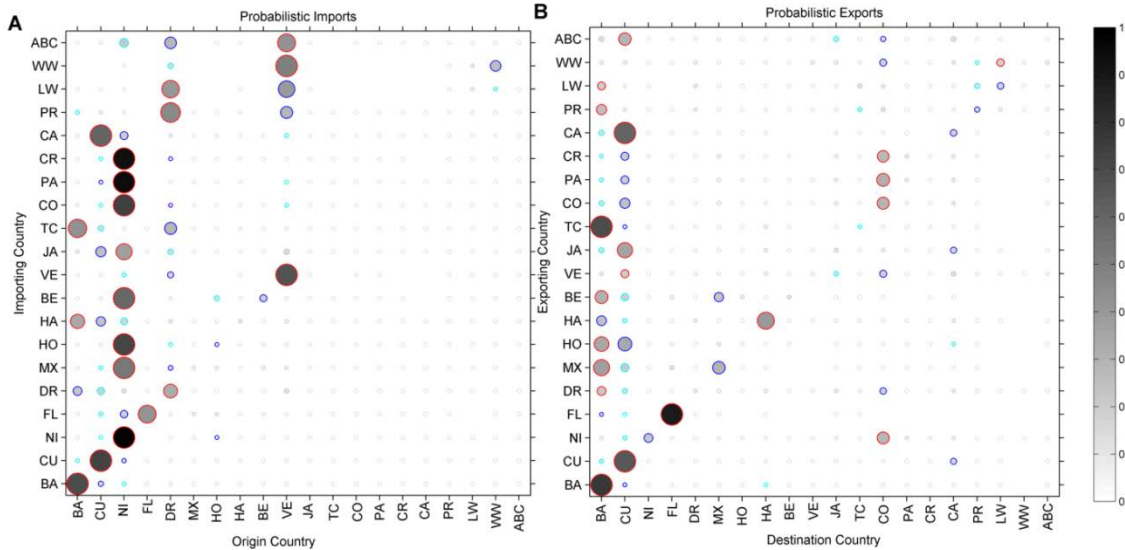
**Figure 3.4. The seasonal pattern of observed postlarval arrival compared to model predictions.** A comparison of the actual coastal arrival of *P. argus* postlarvae (red) as compared to model predictions (black) over four years at four different locations (Mexico: Bahia de Ascension, Puerto Morales; Florida: Long Key, Big Munson). The Florida observations are of average postlarval arrivals per collector from 2004-2008. The Mexican observations are averages from Briones-Fourzan et al. (2008). The correlation between the modeled and the observed arrivals was significant ( $p < 0.05$ ) for Bahia de Ascension and Puerto Morales. The model also predicted the appropriate peak month of settlement in three locations, suggesting that the model can capture the temporal pattern of arriving larvae.



**Figure 3.5. The seasonal pattern of observed postlarval arrival compared to modeled predictions, without considering population structure.** A comparison of the actual coastal arrival of *P. argus* postlarvae (red) as compared to modeled predictions (black) over four years at four different locations (Mexico: Bahia de Ascension, Puerto Morales; Florida: Long Key, Big Munson). The Mexican observations are averages from Briones-Fourzan et al. (2008). The Florida FWC observations are of average postlarval arrivals per collector from 2004-2008 (Muller and Matthews, Marathon, FL). The model parameterization ignored seasonal reproductive characteristics and population sizes. There was no significant ( $p < 0.05$ ) correlation between the modeled and the observed arrivals for any site, highlighting the importance of using spatially and temporally explicit biological knowledge of reproduction in population modeling.



**Figure 3.6. Connectivity matrix of spiny lobster (*P. argus*) larvae.** A simple matrix showing the number of larva migrating from place to place in a coupled biophysical model. The origin of each larval connection is from the left (rows) and the destination of the larvae is at the bottom (column). Domestic connectivity (recruits that settled into their origin nation) follows the diagonal. The strength of connections among sites is a percentage of the total larval exchanged, and the grey shades represent five quantiles. The top 10 lobster fishery nations are separated by the green box.

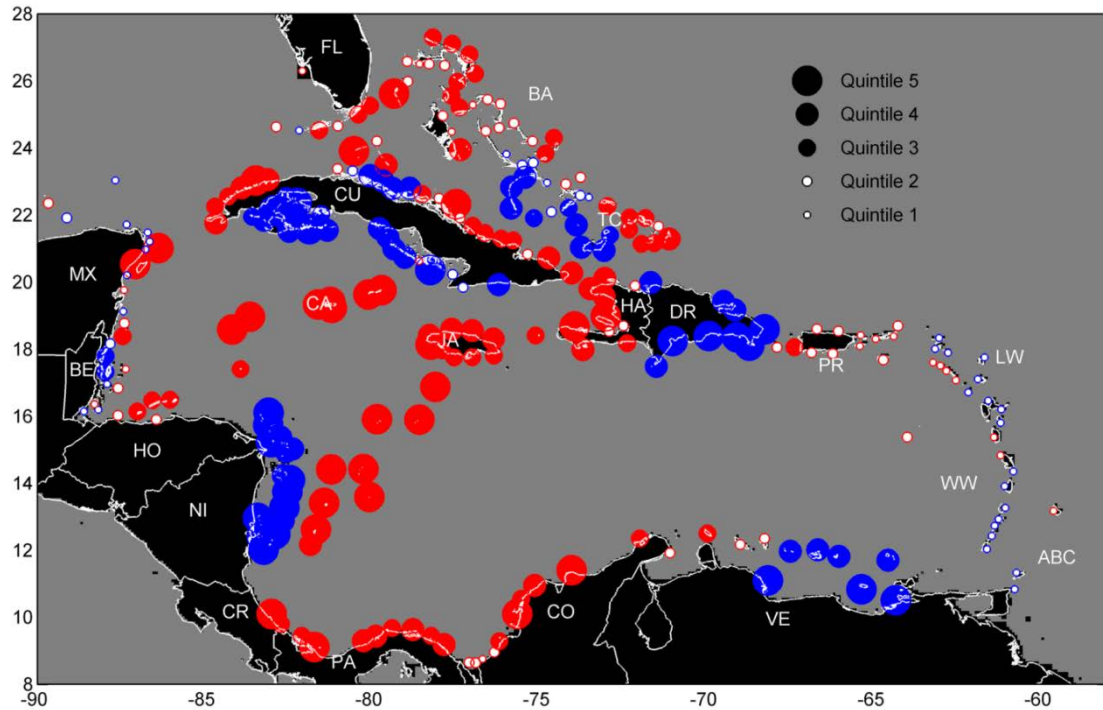


**Figure 3.7. Probabilistic imports (A) and exports (B) of spiny lobster (*P. argus*) larva grouped by political boundaries.** The probability for each instance is computed as:

$$P_{ij} = P_j / \sum_1^n P_i$$

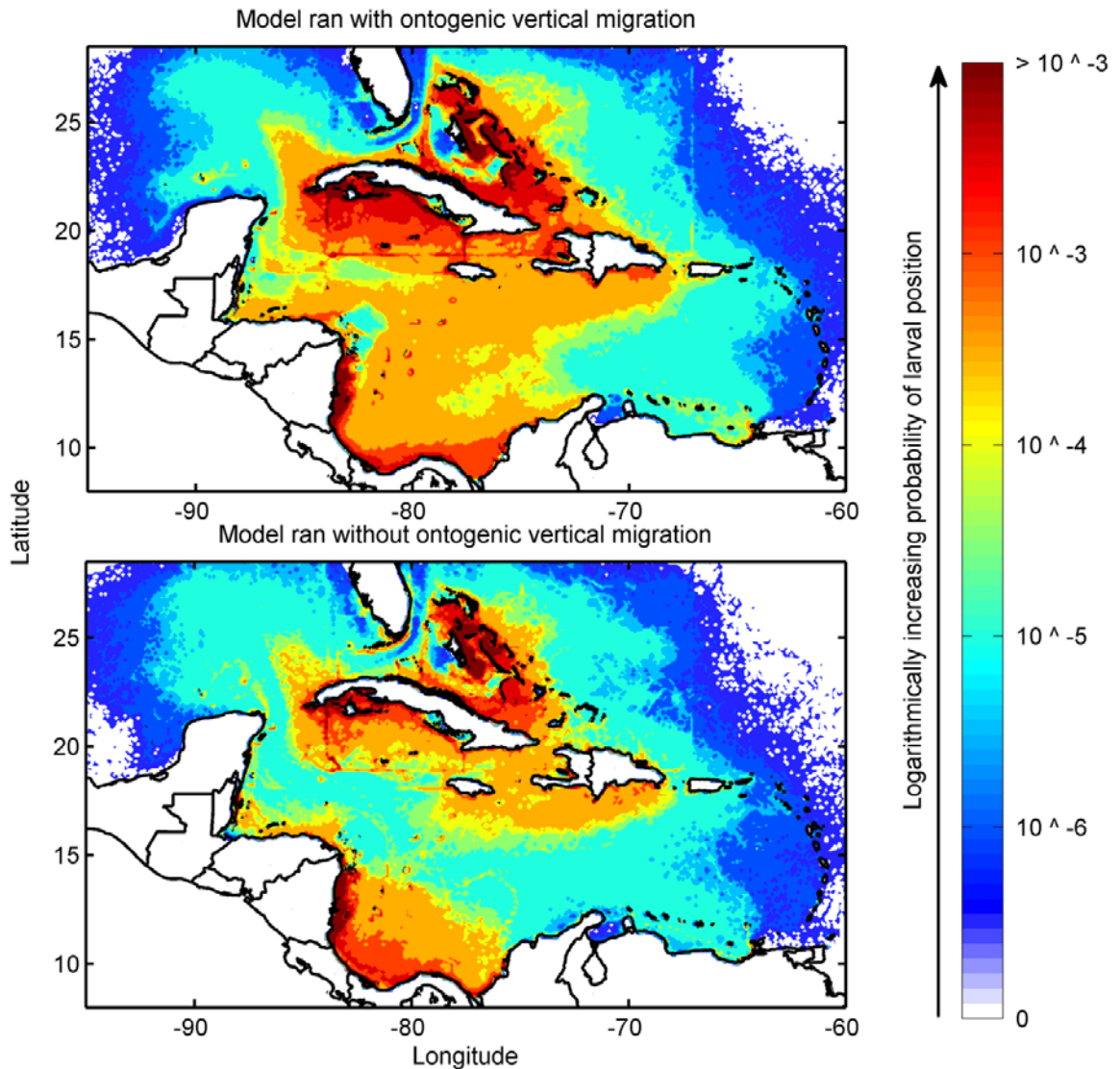
where  $i$  = the country importing (A) or exporting (B),  $j$  = the origin (A) or the destination (B) country, and  $n$  = all countries. The size and shade of grey of the bubble represent the normalized probability, increasing with size and darkness. The three highest probabilities in each scenario are also colored in red, blue, and cyan, respectively. The results are from four years of Caribbean-wide lobster larval dispersal simulations among 261 habitat sites distributed into 39 countries whose abbreviations are:

BA = Bahamas; CU = Cuba; NI = Nicaragua; FL = Florida; DR = Dominican Republic; MX = Mexico; HO = Honduras; HA = Haiti; BE = Belize; VE = Venezuela; JA = Jamaica; TC = Turks and Caicos; CO = Columbia; PA = Panama; CR = Costa Rica; CA = Cayman Islands; PR = Puerto Rico; LW = Leeward Islands (10 countries); WW = Windward Islands (9 countries); ABC = Aruba, Bonaire, and Curacao.

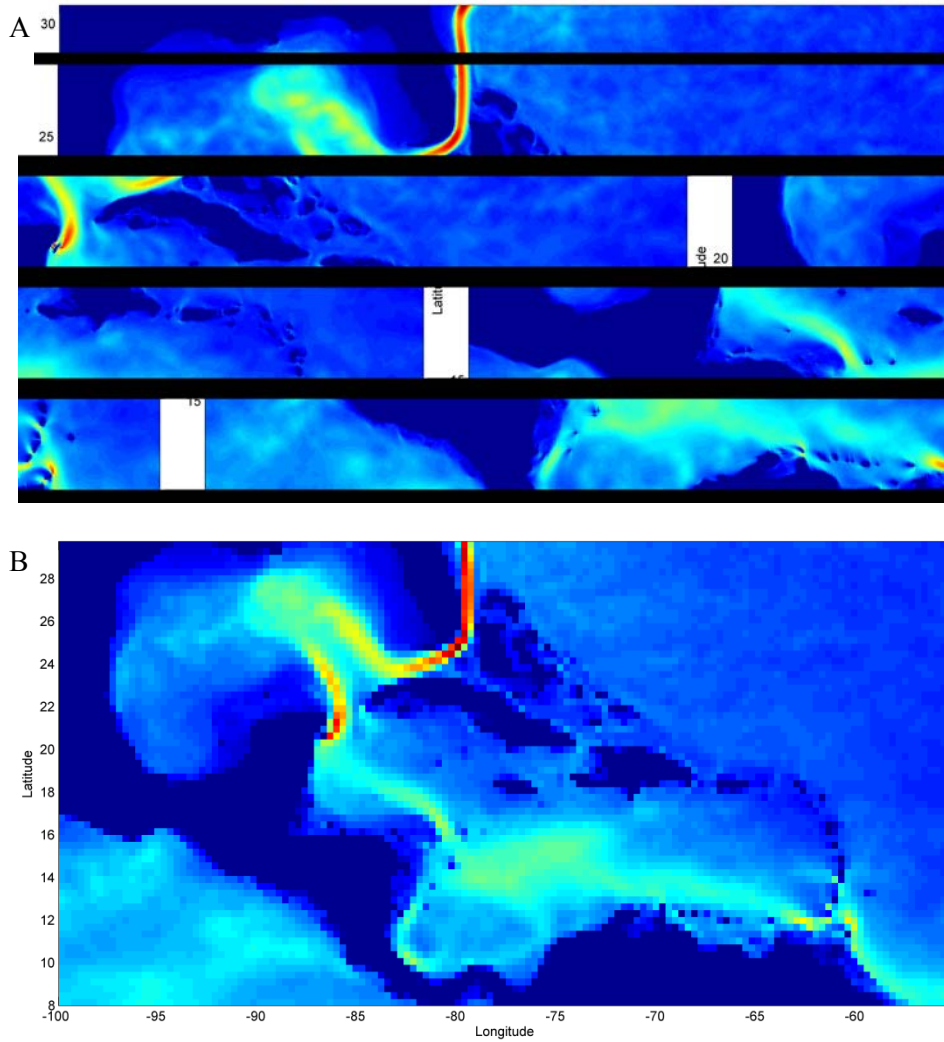


**Figure 3.8. International larval exchange of spiny lobster (*P. argus*) larvae.** The difference between larval exports and imports at a site ( $n=261$ ), after removing self-recruitment. The size of the circle depicts the relative magnitude of the difference, grouped into 5 quintiles. The direction of the difference is shown as blue for positive (more larval exports) and red for negative (more larval imports).



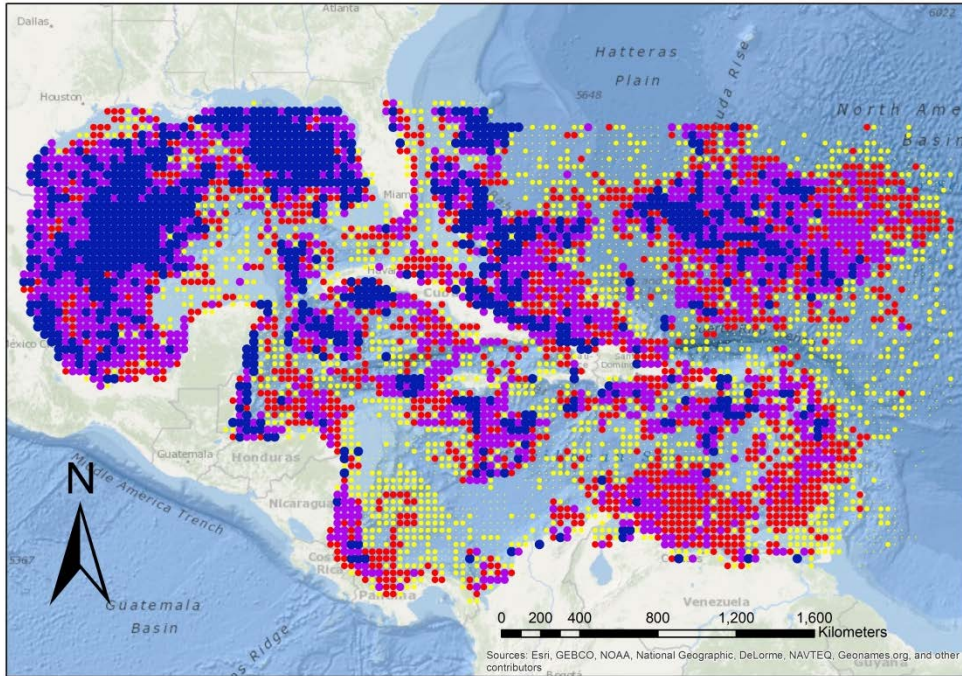


**Figure 3.9. Probabilistic modeled spiny lobster (*P. argus*) larval concentrations.** The probability density distributions represent pelagic nursery habitat within the Caribbean Sea for successfully recruiting spiny lobster larvae. The output location was recorded on a ten day frequency and added into a  $0.1^{\circ} \times 0.1^{\circ}$  gridcell. Blue areas were relatively devoid of successfully dispersing larvae; warmer colored regions had more larval trajectories pass through them, increasing logarithmically from blue to red. The most important pelagic nursery zones for larvae are represented in red-orange. The areas of highest mean flow through the Caribbean represent a distinct, inter-linked larval ‘graveyard’. Simulations were conducted with (A;  $n = 54,186,756$  larval locations) and without (B;  $n = 68,675,786$  larval locations) ontogenic vertical migration.

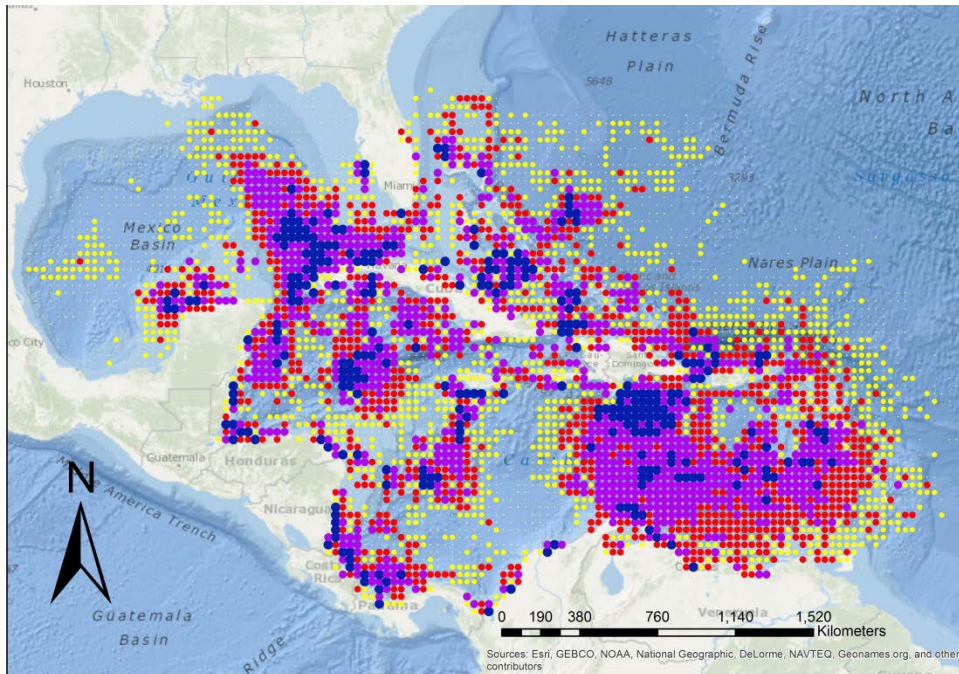


**Figure 3.10. Rescaling the native HyCOM grid to a coarser resolution.** A Delaunay interpolation scheme was used to transform the native HyCOM output (A) to a  $1/3^\circ$  grid (B). Color shows the TKE of the model over 5 years, with warmer color having higher TKE.

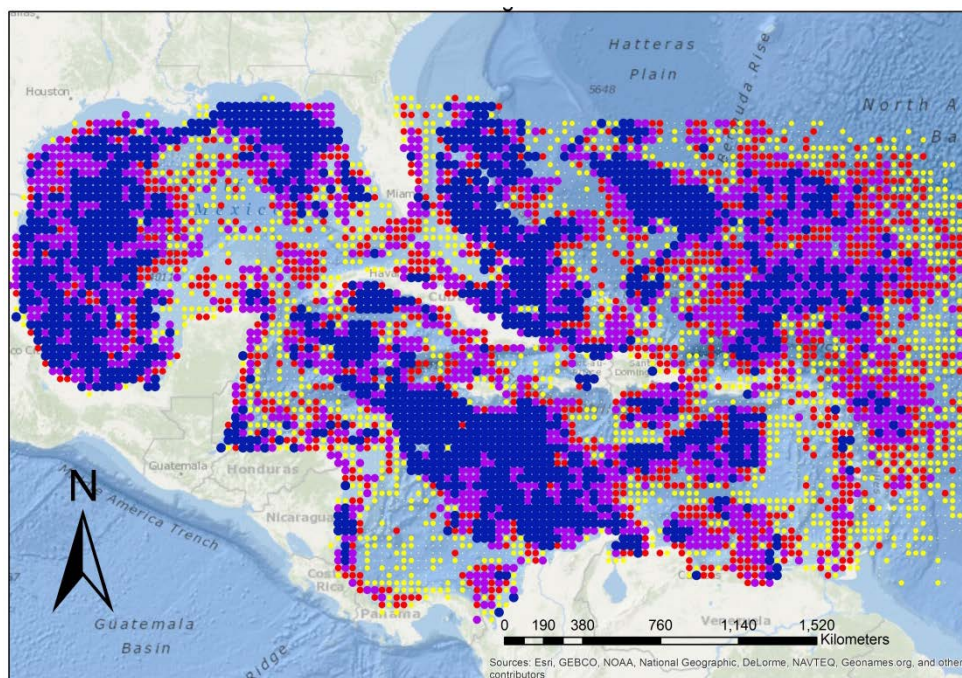




**Figure 3.11. Geospatially weighted regression of age and concentration for larval lobsters that had no OVM and did not settle.** The  $R^2$  value of the regression between 19 age classes and associated densities in each  $1/3^\circ$  bin was then plotted over the Caribbean. Color and size indicated the  $R^2$  value: 0.01-0.09; 0.09-0.275; 0.275-0.465; 0.465-0.676;  $>0.676$ .

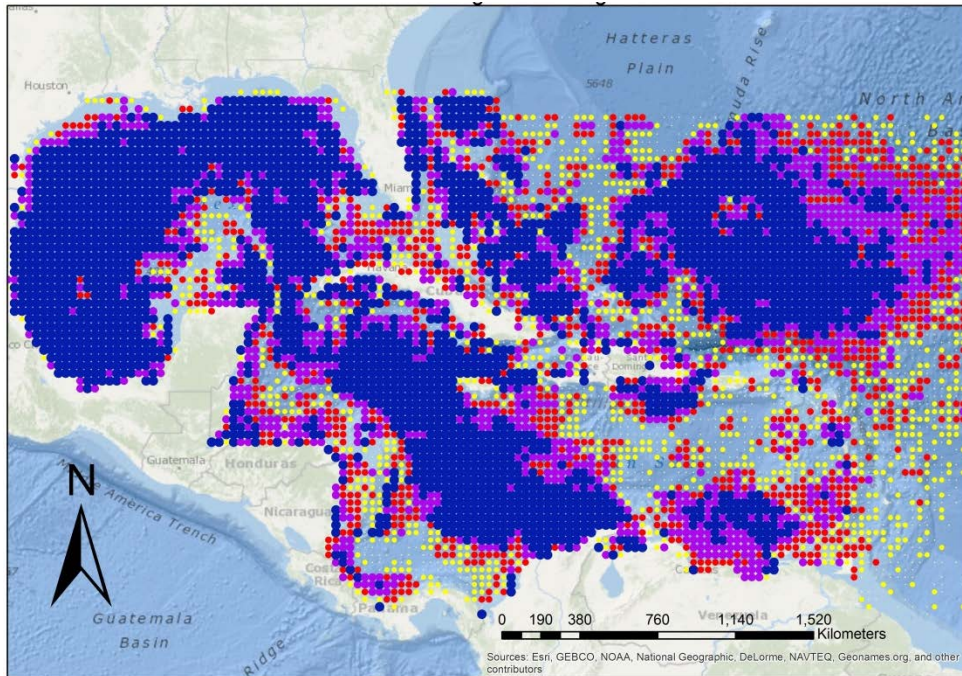


**Figure 3.12. Geospatially weighted regression of age and concentration for larval lobsters that had no OVM and settled.** The  $R^2$  value of the regression between 19 age classes and associated densities in each  $1/3^\circ$  bin was then plotted over the Caribbean. Color and size indicated the  $R^2$  value: 0.01-0.09; 0.09-0.275; 0.275-0.465; 0.465-0.676; >0.676.

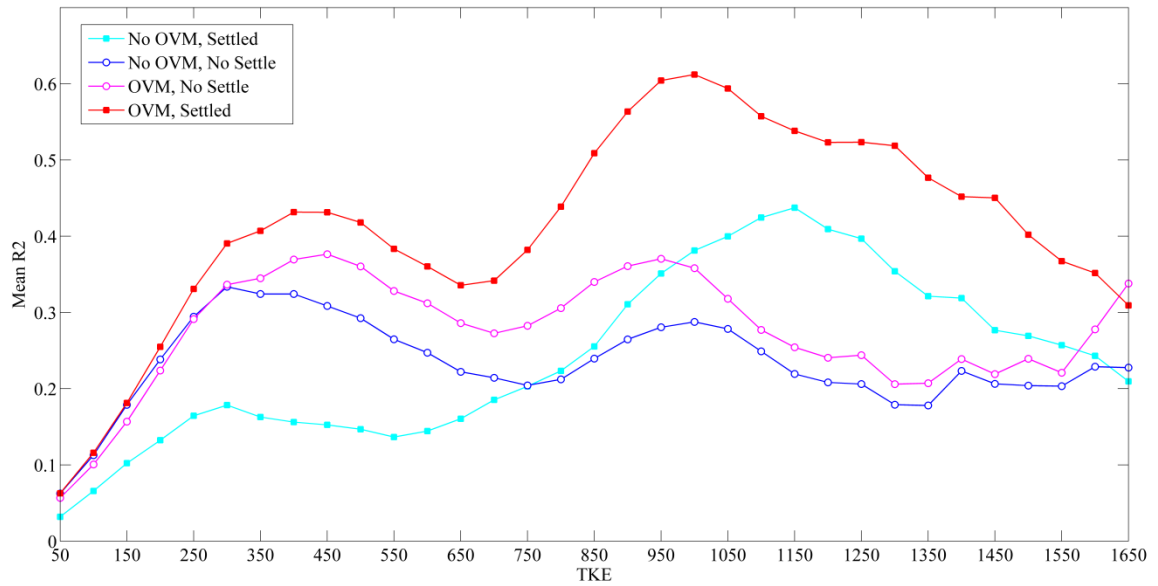


**Figure 3.13. Geospatially weighted regression of age and concentration for larval lobsters that had OVM and did not settle.** The  $R^2$  value of the regression between 19 age classes and associated densities in each  $1/3^\circ$  bin was then plotted over the Caribbean. Color and size indicated the  $R^2$  value: 0.01-0.09; 0.09-0.275; 0.275-0.465; 0.465-0.676; >0.676.

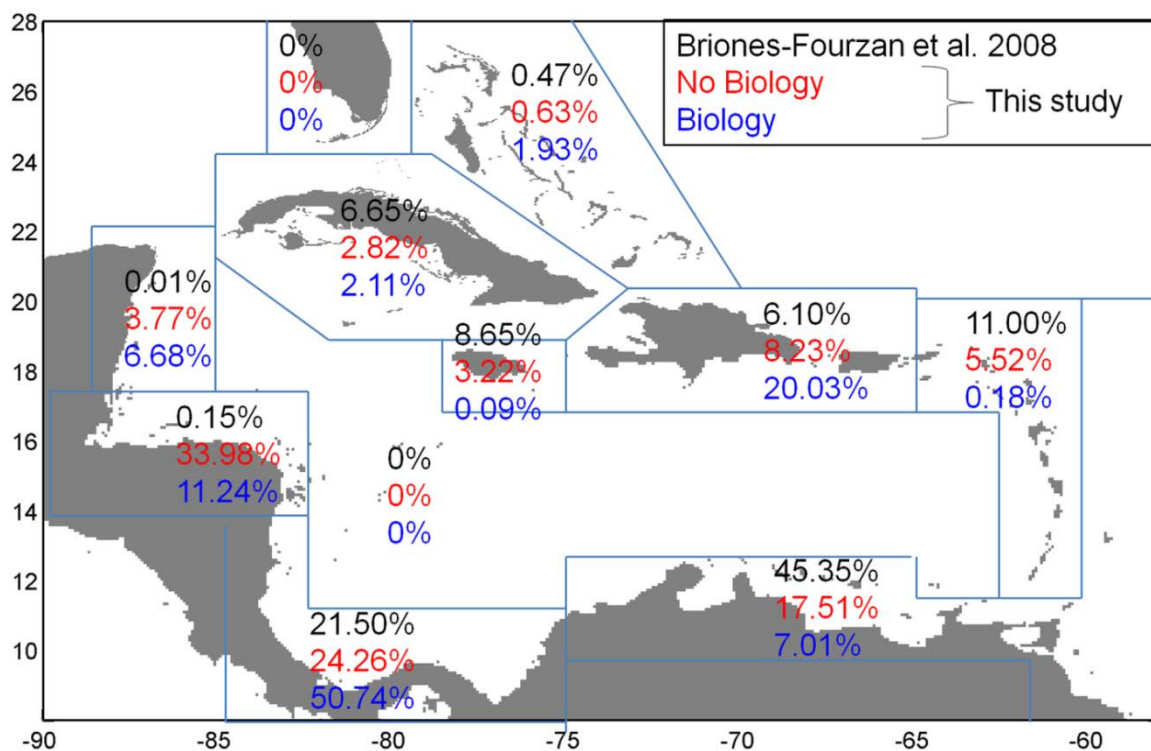




**Figure 3.14. Geospatially weighted regression of age and concentration for larval lobsters that had OVM and settled.** The  $R^2$  value of the regression between 19 age classes and associated densities in each  $1/3^\circ$  bin was then plotted over the Caribbean. Color and size indicated the  $R^2$  value: 0.01-0.09; 0.09-0.275; 0.275-0.465; 0.465-0.676; >0.676.



**Figure 3.15. Comparing the mean  $R^2$  value from larval density and age, with the current strength.** A geospatially weighted regression between larval age and larval density was carried out using a grid of  $1/3^\circ$  across the Caribbean and the  $R^2$  value was kept for each grid. TKE, a relative measure of current strength, was obtained over the same grid. Average  $R^2$  values were obtained by dividing TKE into bins of 50.



**Figure 3.16. A comparison of possible larval sources to the Mexican Quintana Roo coast between two Lagrangian individual based models.** The origins of larvae that arrived to habitat on the Quintana Roo coast during April, May, September, and October. Results from Briones-Fourzan et al. (2008) are averages between their figures 10 and 11. Results from this study, using a simulation with passive larvae released equally in magnitude and timing from around the Caribbean (red), and another incorporating vertical migration behavior and larvae released based on reproductive biology (blue).

#### **CHAPTER 4. *IN SITU* SWIMMING AND ORIENTATION BEHAVIOR OF SPINY LOBSTER (*PANULIRUS ARGUS*) POSTLARVAE**

Larval dispersal is common in benthic marine organisms, but the environmental cues guiding the final larval stages to settlement habitat remain largely unknown. The Caribbean spiny lobster (*Panulirus argus*) spend 5 to 12 months at sea as pelagic phyllosome larvae before transitioning into rapidly swimming and non-feeding puerulus postlarvae. The rapidly swimming and non-feeding puerulus postlarvae of *P. argus* are specialized to seek settlement habitat making them an ideal model for studying orientation behavior during the transition to benthic environments. This study observed the swimming orientation of *P. argus* in the open ocean during all hours of the day and across tidal phases using a circular behavioral arena deployed at sea. Contrary to only nocturnal activity during laboratory observations, swimming and orientation occurred during both the day and the night in open waters ca. 6-8 km offshore in the Florida Straits. Individual postlarvae swam directionally with similar accuracy in all hours. The mean orientation direction was significantly different with tidal phase. Postlarvae oriented to the southeast ( $163.5^\circ$ ) during flood tide, and to the southwest during ebb flow ( $225.1^\circ$ ), placing them on a shoreward trajectory. Postlarval behavior was circatidal, and during ebb tide innate swimming behavior beneficial to finding settlement habitat was triggered. Postlarvae also oriented relative to the wind, potentially using the sea breeze to orient towards the coast. A change in behavior tied to ubiquitous coastal signals is a strategy likely used by other pelagic larvae searching for a benthic home.

## Background

How, why, when, and where animals move is the focus of the emerging field of movement ecology (Nathan et al. 2008), which also examines how the internal state of the animal and external environmental conditions drive movement. The ocean is underrepresented in studies of movement (Holyoak et al. 2008), perhaps because dispersal within the marine realm is different than most terrestrial systems. Rather than dispersing as adults, many marine organisms have a bipartite lifecycle, where adults are sessile or sedentary but spawn massive numbers of planktonic larvae that disperse in the sea. Dispersing larvae connect populations of species that live in patches of benthic habitat separated by vast expanses of ocean. Larval behavior can increase the odds of finding discrete settlement habitats, and may mitigate mortality caused by passive advection from ocean currents that move larvae away from desired habitat (Paris et al. 2005; Cowen et al. 2006; Butler et al. 2011). Successful dispersal within an interconnected metapopulation is crucial for species with an “open” connectivity pattern (Myrberg and Fuiman 2002), yet the behaviors governing how larvae disperse are underdescribed (Kingsford et al. 2002).

The postlarval stage of the Caribbean spiny lobster, *Panulirus argus*, is ideal for studying behavior and coastal orientation. The final pelagic stage of the spiny lobster is the puerulus postlarva (hereafter called postlarva), which is a strikingly different postlarval stage, both morphologically and behaviorally, from earlier phyllosomes. Spiny lobster postlarvae do not feed (Lemmens 1994; Jeffs et al. 1999) yet may swim tens to perhaps a hundred kilometers over several weeks to find settlement habitat (Rimmer and Phillips 1979; Jeffs and Holland 2000; Phillips and Melville-Smith 2005; Goldstein et al.



2008; Fitzgibbon et al. 2013). This journey starts near the shelf break, where postlarvae likely metamorphose from phyllosomes (McWilliam and Phillips 2007; Phillips and McWilliam 2009), and ends at a variety of shallow settlement habitats (Butler et al. 2006). In the laboratory, spiny lobster larvae and postlarvae respond to a diverse array of environmental cues including light (Ziegler et al. 2010; Lecchini et al. 2010), chemical odors (Butler and Herrnkind 1991; Goldstein and Butler 2009), pressure (Goldstein and Butler 2009), and salinity (Field and Butler 1994; Acosta et al. 1997; Goldstein and Butler 2009). Spiny lobsters also support a valuable commercial and recreational fishery in tropical and subtropical oceans around the world (Cruz and Bertelsen 2008; Ehrhardt et al. 2011), giving further significance to research into the behavioral drivers of their recruitment and transition from the pelagic environment.

Linking directional cues with larval orientation behavior *in situ* is logistically challenging, so researchers have relied on studies of larval choice using behavioral chambers or traps in the ocean (Stobutzki and Bellwood 1998; Tolimieri et al. 2000; Radford et al. 2007) and the laboratory (Boudreau et al. 1993; Atema et al. 2002; Goldstein and Butler 2009; Lecchini et al. 2010). However, the binary response in a choice chamber does not demonstrate how larvae use proximate cues to alter their path and does not provide detailed information on individual movements. *In situ* observations made from small boats (Phillips and Olsen 1975; Calinski and Lyons 1983; Cobb et al. 1989) or by scuba diving or snorkeling (Shanks 1995; Leis and Carson-Ewart 1998) provide snapshots of larval swimming behavior. Inconspicuous nocturnal studies of behavior are rare (Stobutzki and Bellwood 1998; Fisher and Bellwood 2003), owing to the difficulty of observing the movements of small, often translucent, larvae in an

unobtrusive manner in the dark. However, the simultaneous examination of both environmental signals and the larval responses to these signals is now possible using emerging technologies such as the Drifting *In situ* Chamber (DISC; Paris et al. 2008). The DISC observes and quantifies larval behavior in the open ocean while minimizing any “observer bias” (Irisson et al. 2009). Observing the behavior of animals *in situ* as they navigate is the next necessary step to describe how they search for appropriate settlement habitat.

The goal of this study was to determine the directionality of spiny lobster postlarval swimming by observing *in situ* orientation within a DISC deployed off the coast. Crucial to this goal was the development of a new module for the DISC that enabled the first *in situ* nocturnal study of proximate postlarval behavior (Figure 4.1). Research focused on behavior across time of the day and tidal phases to determine if postlarvae use these predictable signals to orient towards coastal habitats. It was hypothesized that spiny lobster postlarvae would swim only during the night, and that spiny lobster postlarvae would orient shoreward.

## **Methods**

### *The Drifting In Situ Chamber*

The Drifting *In situ* Chamber (DISC) is a novel Lagrangian research platform for observing and quantifying the orientation behavior of marine larvae in the open ocean (Figure 4.1; Paris et al. 2008; Paris et al. 2013). The DISC is a cylindrical behavioral framework (1.2m height x 0.4m diameter) made of clear acrylic that is transparent to fine scale turbulence, light, and sound. The DISC is attached to a surface float using low-drag kite line. A clear monofilament bridal centers the line above the DISC. A subsurface

buoy attached 1m beneath the surface acts as a shock absorber and dampens the effect of waves. The DISC can be coupled with environmental sensors to allow simultaneous observation of larvae in conjunction with proximate (sound, temperature, light, wind) and distant (celestial, magnetic) cues in a natural setting. In the present study, a light and temperature pendant (HOBO model UA-002-64) was attached to the DISC and real-time wind data was obtained from a nearby weather station (FWYF1). The temperature pendant was accurate within 0.53° C, and measured relative light levels, which was appropriate for detecting differences between trials. The DISC was set adrift at sea with an individual postlarva, and postlarval movement was recorded using an imaging system.

Nocturnal observations with the DISC were possible because the chamber was rigged with underwater flashlights and a GoPro Hero camera with the infrared (IR) filter removed (Figure 4.1). Each flashlight bulb was replaced with a 315 mW LED with a peak wavelength of 850nm, making the flashlights IR. Four lights were mounted on top of the DISC to illuminate the chamber, and one pointed up to illuminate a compass.

#### *Study site, environmental conditions, and postlarval collection*

The DISC was deployed in water between 40 and 160 meters deep starting *ca* 1 km southeast of Fowey Rocks (25.591 N, -80.097 W), which is the northern-most extent of the Florida Keys Reef Tract (Figure 4.2). Deployments of the DISC were designed to sample across both the diel cycle and across tides (Figure 4.4). The timing of tides for Fowey Rocks was predicted using the *t\_tide* package for MATLAB and *xtide* harmonics (Pawlowicz et al. 2002). Wind data were available from the NOAA Fowey Rocks station FWYF1, at a frequency of once every 10 minutes (NOAA, National Data Buoy Center, Stennis Space Center, MS, USA 39529).

Spiny lobster postlarval availability varies monthly; lobsters only arrive during certain months of the year in sufficient quantities for our experimental studies (Acosta et al. 1997, Acosta and Butler 1999). The timing of their arrival, during nocturnal flood tides in the first quarter moon, posed a tradeoff in our sampling. Animals were elected to be tested as soon as possible after collection to minimize any physiological or behavioral changes from confinement. However, this reduced the sample size during nocturnal ebb tide and daytime flood tide conditions due to logistical and temporal constraints.

Plankton were collected from Bear Cut, the largest natural tidal inlet into Biscayne Bay, with tidally driven currents in excess of 100 cm/s during flood tide (Fiechter et al. 2006), which are used by incoming postlarvae to travel into the bay (Forward and Tankersley 2001). Spiny lobster postlarvae were caught during nocturnal rising tides using 1m diameter, 750  $\mu$ m mesh size, channel nets during the first quarter moons of September 2012, October 2012, and February 2013. Animals were held in static, natural seawater-filled buckets in the laboratory at 16° to 19°C and received a complete water change daily. All animals were used within 72 hours of collection from the plankton. Some individuals were held after testing to observe the timing of pigmentation on the edge of the carapace, which did not develop for at least 6 days post-capture ( $N=14$ ), similar to previous works (Goldstein et al. 2008, Goldstein and Butler 2009).

#### *Tethering and deployments*

Postlarval lobsters were attached to tethers before being tested in the DISC. The tether was a 12 cm piece of 1kg test fly fishing tippet with a loop tied at one end. To attach the tether, a postlarva was removed from the water and its dorsal carapace was

lightly dried with a paper towel. Using a fine point applicator, a drop of superglue was placed on the center of the dorsal carapace and the tether was attached. The glue was allowed to dry (<1min), and each postlarva was returned to an individual container of new seawater to prevent tangling. No mortality or noticeable damage was associated with any tethering operations ( $N = 104$ ), and tethered animals retained after use metamorphosed into juveniles without mortality ( $N = 14$ ). After the completion of a trial, the tether was gently removed and the animal was released.

Experiments were carried out in seas forecast to be < 1.5 meters and wind < 15 knots during September 2012, October 2012, and February 2013. During each DISC deployment, a tethered postlarva was attached to a weighted line in the center of the DISC structure at a focal point 42cm from a GoPro camera (Figure 4.1d). The tether is the only restraint on the postlarva that prevents it from swimming off into the ocean. By attaching the postlarva to a weighted line suspended in the middle of the DISC framework, the animal had a full range of movement on its tether without being able to physically touch any portion of the DISC. Additionally, the only potentially detectable lateral structures that could influence the physical environment experienced by the postlarvae were the clear acrylic posts of the instrument. The DISC was deployed at two distances from the surface: shallow (3m) and deep (25m). During September 2012 and October 2012 it was deployed at 3m from the surface, and each individual postlarva was used only once. Based on wave theory (Dean and Dalrymple 1991), it is approximated that the influence of the dynamic pressure is less than 1% of the surface wave height at 25m depth with a wave period of 4 seconds. Recent work has suggested that Stokes drift decays even more rapidly, and is negligible at a depth on the order of the mean

significant wave height (Tamura et al. 2012). Thus a second experimental depth of 25m was added in February 2013 to deploy the DISC at a depth conservatively beneath most of the orbital wave motion. The same postlarvae were used in both depth treatments in February 2013, with a randomized order between shallow and deep treatments. For all deployments, once the DISC was in the water, the boat was driven upwind and the engine was turned off. Deployments lasted 15 minutes before the DISC was retrieved.

### *Image processing*

Data were processed using DISCUS software, which digitizes the location of the postlarva throughout each deployment using the camera images (Irisson et al. 2009). The suite of instruments on the DISC (camera, HOBO temperature and light meter, GPS, electronic tri-axial compass) was synchronized in time for further analysis. The deployment time protocol from earlier studies with the DISC was followed (Irisson et al. 2009; Paris et al. 2013): the first 5 minutes of each 15 minute deployment were treated as acclimation time and were not analyzed.

### *Movement Analysis*

The position of the postlarva relative to the camera, and the bearing of the compass relative to the camera were used to create a series of positions for individual larva relative to cardinal directions with a resolution of one position every 2 seconds. The postlarvae alternated between swimming forward to the extent allowed by the tether, and a cessation in swimming causing momentary drifting. Postlarvae actively modified their orientation by swimming, and did so throughout the deployments. If a postlarva was clearly not swimming (the tether was not taut, or the postlarva's antennae were not forward) or not visible in an image, that position was omitted. The DISC rotated slowly

throughout each deployment, and custom software corrected for this rotation (Irisson et al. 2009). The resulting positions were used to describe the mean bearing of each postlarva. A Rayleigh's test was used to test significant directionality (i.e., whether the postlarva was keeping a significant bearing).

Circular statistics were carried out at the individual (first order) and population level (second order). Because each set of postlarval positions (projected as a vector from the center of the behavioral chamber) was unequal in size, due to unique gaps corresponding with occasional picture frames of unclear position or non-swimming behavior, only the mean bearings of significantly directional individuals were retained and reported for use in second order circular statistics. All movement statistics were performed using the package Circular (Lund and Agostinelli 2011) in R. Accuracy (the length of the mean vector, Rayleigh's  $r$ ) comparisons were assessed using a Welch's two sample t-test in Matlab. DISC rotation, temperature, wind speed, current speed, and light intensity during trials were compared using Welch's two sample t-tests in Matlab to justify pooling data between months and seasons.

## **Results**

### *Postlarval orientation relative to the DISC*

The design of the DISC provides no frame of reference to the subject within it. Just like any other circular arena, the DISC is symmetrical from the point of view of the postlarva. However, one of the strengths of the DISC, that is absent in most other behavioral arenas, is its ability to rotate while locked in the current. This rotation allows the disentanglement of movement relative to the DISC (the point of view of the camera) and movement relative to a cardinal reference point. In other words, if a postlarva was

orienting, then it should have corrected for the rotation of the DISC and held a constant direction. Alternatively, did the larva rotate with the DISC? While exploring the data, directional statistics were separately calculated for both the point of view of the camera, and from the perspective of a cardinal direction. However, ultimately all of the data was presented together as justified in the following paragraphs and figures.

To support inclusion of all of the behavioral data, the data is presented graphically and statistically to describe the relationships therein. The data is divided by tidal phase to be consistent with rest of the study. To determine if tethered postlarvae were behaving in a biased manner, the Rayleigh's values of the movement relative to the DISC versus movement relative to cardinal directions were compared. Postlarvae that had larger Rayleigh's  $r$  when considered relative to the camera, and therefore the DISC, are denoted as "Camera," and those that had a greater Rayleigh's  $r$  relative to a cardinal reference as "Cardinal". Using this established technique (Paris et al. 2008; Irisson et al. 2009; Paris et al. 2013) in 39 out of 55 shallow water deployments the postlarvae oriented more directionally in a cardinal reference (i.e. were "Cardinal"), suggesting that the DISC provided little frame of reference to tethered postlarvae.

The decision to pool the data was justified by visually examining the data (Figure 4.3) and through statistical tests showing no change in direction. When comparing between rising tide "Cardinal" postlarvae and rising tide "Camera" postlarvae using a Watson two test of homogeneity, there was not a significant difference in mean direction ( $U^2 = 0.1027$ ;  $U_{crit} = 0.187$ ;  $\alpha = 0.05$ ;  $N1 = 12$ ;  $N2 = 21$ ). The same conclusion is reached when comparing falling tide "Cardinal" postlarvae and falling tide "Camera" postlarvae ( $U^2 = 0.0379$ ;  $U_{crit} = 0.187$ ;  $\alpha = 0.05$ ;  $N1 = 4$ ;  $N2 = 18$ ). Considering just



the “Cardinal” postlarvae meets the assumptions of a Watson-Williams test and there is a significant difference in direction between rising and falling tides ( $F = 9.1016$ ;  $p = 0.0046$ ;  $N_{\text{rising}} = 21$ ;  $N_{\text{falling}} = 18$ ). Increasing the sample size by using all of the data gives a more comprehensive picture of how changes in the physical environment could be altering the postlarval behavior.

### *Accuracy*

The accuracy (the length of the mean vector, Rayleigh’s  $r$ ) of postlarval movement was the strength, or directionality, of individual postlarval swimming. The accuracy was similar across multiple environmental measures including the hour of the day, the tidal phase, the water temperature, the wind speed, the current speed, and the light intensity (Figure 4.4). The mean accuracy was not significantly different between ebb and flood tide during shallow (Welch’s two sample t-test:  $N_1=22$ ,  $N_2=33$ ,  $P = 0.1291$ ) or deep deployments (Welch’s two sample t-test:  $N_1=7$ ,  $N_2=11$ ,  $P = 0.1291$ ).

### *Swimming direction, shallow treatment:*

Postlarvae swam in a significantly directed manner ( $N=55$ ; Figure 4.5) during deployments 3m from the surface. During ebb flow the mean population direction of postlarvae was towards the southwest ( $225.1^\circ$ ) and thus toward coastal environments, whereas during flood tides the mean population direction was towards the southeast ( $163.5^\circ$ ) and thus toward the open ocean (Table 4.1; Figure 4.5). The mean directions of postlarvae were normally distributed (Watson’s test for the von Mises distribution:  $U^2=0.0625$ ,  $N = 55$ ,  $\text{Alpha} = 0.05$ ,  $U_{\text{crit}}=0.079$ ), and met the assumptions for parametric statistics. Population orientation was in significantly different directions depending on tidal phase (Watson-Williams test:  $F = 13.0506$ ,  $N_1 = 22$ ,  $N_2=33$ ,  $P = 0.000674$ ).

### *Swimming direction, deep treatment*

The deep treatment results were considered separately from the shallow results, as a supplement to the main experiment. Directional postlarvae ( $N = 18$ ) were observed in the deep treatment (Table 4.1; Figure 4.6). The direction of postlarval orientation differed with tidal phase (Watson two-test of homogeneity:  $U^2 = 0.2301$ ,  $N1 = 7$ ,  $N2 = 11$ ,  $\alpha = 0.05$ ,  $U_{\text{crit}} = 0.187$ ). The mean population direction was heuristically similar to the shallow treatments during ebb tide, but postlarvae did not orient directionally during flood tide. The accuracy of the postlarval swimming direction in the deep treatments did not change with hours of the day, tidal phase, wind speed, current speed, temperature, or relative light (Figure 4.4).

### *Swimming Direction and Current:*

Postlarvae partially oriented into the prevailing flow during both ebb and flood tide, and their bearing with respect to the direction of the current was considered (Table 4.1; Figure 4.6a,b,e,f). Swimming directions with respect to current are given in degrees clockwise from the direction that the DISC (a Lagrangian drifter locked in the current) travelled. The mean directions of postlarvae with respect to drift during shallow deployments swimming were normally distributed (Watson's test for the von Mises distribution:  $U^2=0.028$ ,  $N = 55$ ,  $\text{Alpha} = 0.05$ ,  $U_{\text{crit}}=0.079$ ) and significantly different depending on tide (Watson-Williams test:  $F = 16.755$ ,  $N1 = 22$ ,  $N2= 33$ ,  $P = 0.000146$ ). Deep deployments were similar to shallow deployments during ebb tide with respect to the current (Figure 4.6a,e), but the animals maintained no significant direction during deep deployments during flood tide (Figure 4.6f).

### *Swimming Direction and Wind*

The bearing of swimming postlarvae were considered with respect to concurrent wind direction because the wind is a major force shaping the dynamics of the upper ocean, and detailed empirical data on the wind was available in proximity to the study site. Swimming directions with respect to wind are given in degrees clockwise of the direction from which the wind blew (Table 4.1; Figure 4.6c,d,g,h). The orientation directions of postlarvae with respect to wind during shallow deployments were not normally distributed (Watson's test for the von Mises distribution:  $U^2=0.1287$ ,  $N = 55$ ,  $\text{Alpha} = 0.05$ ,  $U_{\text{crit}}=0.066$ ) and were significantly different depending on tide (Watson two-test:  $U^2 = 0.3512$ ,  $N1=22$ ,  $N2=33$ ,  $\text{alpha} = 0.05$ ,  $U_{\text{crit}} = 0.187$ ). Deep swimming direction with respect to wind was not normally distributed and was not significantly different depending on tide (Watson two-test:  $U^2 = 0.1031$ ,  $N1=7$ ,  $N2=11$ ,  $\text{alpha} = 0.05$ ,  $U_{\text{crit}} = 0.187$ ). The only time that postlarvae oriented with the wind was during shallow ebb tide deployments (Figure 4.6c), during all other times they oriented upwind.

### *Environmental Conditions:*

Having a similar physical environment between tides lets the changes in orientation direction be attributed to circatidal behavior. The DISC was used as a Lagrangian drifter to assess the true current direction and speed. A change in current direction was not anticipated to be associated with tide because the tidal current at Fowey Rocks is categorized as weak and variable, indicating a current of less than 0.25 knots (Jena Kent *pers comm*, NOAA, Center of Operational Oceanographic Products and Services). Confirming this, there was no significant difference between the direction of the current during ebb or flood flow during shallow deployments (Watson-two test of

homogeneity:  $U^2 = 0.0513$ ,  $N1 = 22$ ,  $N2 = 33$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ) or deep deployments (Watson-two test of homogeneity:  $U^2 = 0.1579$ ,  $N1 = 7$ ,  $N2 = 11$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ). The wind direction was onshore and was significantly different between tides during shallow (Watson-two test of homogeneity:  $U^2 = 0.2959$ ,  $N1 = 22$ ,  $N2 = 33$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ) but not deep deployments (Watson-two test of homogeneity:  $U^2 = 0.1579$ ,  $N1 = 7$ ,  $N2 = 11$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ) prompting the consideration of orientation relative to the physical environment (Figure 4.6). The wind speed was not significantly different between tides during shallow (Welch's two sample t-test:  $N1=22$ ,  $N2=33$ ,  $P = 0.6619$ ) or deep (Welch's two sample t-test:  $N1=7$ ,  $N2=11$ ,  $P = 0.2496$ ) deployments, nor was the current speed different between tides during shallow (Welch's two sample t-test:  $N1=22$ ,  $N2=33$ ,  $P = 0.3471$ ) or deep deployments (Welch's two sample t-test:  $N1=7$ ,  $N2=11$ ,  $P = 0.1619$ ).

Postlarval swimming data were pooled between two seasons to robustly compare across tides. Although temperature differed with season (Table 4.2), because orientation accuracy did not change with water temperature (Figure 4.4d), the decision to pool data between seasons remains appropriate. The relative light level that animals experienced in the DISC during the day was similar (Table 4.2). The direction from which the wind blew (Watson two-test:  $U^2 = 0.875$ ,  $N1=35$ ,  $N2=20$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ), the wind speed, and the current speed were significantly different between the fall deployments and the spring deployments (Table 4.2). However, there was no relationship between the current speed and the wind speed (Figure 4.7), the current direction remained constant, and the DISC rotated in a similar manner during both seasons, supporting our decision to pool the data. In addition, the orientation of postlarvae relative to the physical

environment during each deployment was compared (Figure 4.6) to account for any changes in behavior driven by differences in the season or physical environment.

### **Discussion:**

The *in situ* observations of the swimming behavior of spiny lobster postlarvae provide compelling evidence that postlarvae actively orient and swim during both day and night. Previous laboratory work suggested that spiny lobster postlarvae only swam during the night. This difference in swimming behavior between laboratory and field studies demonstrates the enduring merit of *in situ* behavior experiments (Waterman 1988) and is an important piece of information to include in biophysical models of larval lobster transport and settlement (Butler et al. 2011; Kough et al. 2013), since rapid horizontal swimming can alter modeled dispersal patterns (Staaterman et al. 2012). Continuously swimming during the day and the night may reduce the metabolic cost of the larval journey to benthic habitat, and increase available energy stores crucial for surviving the first juvenile molt and successful settlement (Wilkin and Jeffs 2011; Fitzgibbon et al. 2013). In addition, these results show that spiny lobster postlarvae oriented differently and directionally depending on tidal phase, which indicates that pelagic postlarvae adjust their movement towards the coast in response to cues associated with tide. The swimming behavior that was observed during ebb tide would place pelagic postlarvae near the coast and settlement habitat (Figure 4.5).

Multimodal cues are associated with tide and could be used by postlarvae. In areas of strong tidal current, such as the channels leading into Biscayne Bay, lobster postlarvae harness flood tide transport at the surface to move further inland (Acosta et al. 1997). However, in the study area a reaction to the tidal current is unlikely because the

deployments took place in a weak and variable tidal current offshore of the reef tract and at least 8 km from a channel into the bay. In these experiments, the DISC did not drift with respect to tidal phase, but instead drifted with the strong, northward flowing Gulf Stream (Figure 4.2). Additionally, the theory of relativity suggests that tested postlarvae are unable to detect the direction of the current because the DISC is imbedded within the current. Temperature gradients could be established with the tide. Lobster postlarvae arrive into settlement habitat year round in Florida (Acosta et al. 1997; Yeung et al. 2001), thus swimming behavior towards coastal environments should operate independently of temperature. Supporting this contention, no difference in swimming accuracy with temperature was found (Figure 4.4). Salinity gradients may also vary with tide. Spiny lobster postlarvae have been shown to have altered metamorphic responses (Fields and Butler 1994) and behavioral aversion (Goldstein and Butler 2009) to extreme salinity changes, but show no significant preference within the moderate gradients (Goldstein and Butler 2009) expected 6-8 km offshore. Sound has been suggested as a potential navigational cue for decapod postlarvae (Radford et al. 2007), yet sound from a multiyear study at two sites in Florida does not vary with the tide (E Staaterman, *unpublished data*). There is an endogenous reaction to the tide. Young (stage I) *P. argus* larvae have a twilight vertical migration pattern mediated by a combination of endogenous rhythm and behavioral response to changing light levels (Ziegler et al. 2010). The periodicity of the endogenous rhythm is imprinted by the hatching location of the larvae, and could be quite different from the local conditions if larvae travel long distances (Briones-Fourzan et al. 2008; Butler et al. 2011; Kough et al. 2013). Additionally, there is no proposed physiological mechanism for how an endogenous cue

could become directional, unless the tide acts as a switch, triggering innate behavior (Forward and Tankersley 2001) that requires another cue to act as a compass.

These results suggest that odor is not followed by spiny lobster postlarvae to find settlement habitat. Previous works suggest that chemical cues may play an important role in postlarval settlement (Butler and Herrnkind 1991; Goldstein and Butler 2009).

Additionally, juvenile and adult spiny lobsters can track or avoid chemical signals from food sources (Reidenbach and Koehl 2011), predators (Berger and Butler 2001) and conspecifics, both healthy (Zimmer-faust et al. 1985; Butler et al. 1999) and diseased (Behringer et al. 2006; Anderson and Behringer 2013) likely by using an infotaxis strategy (Vergassola et al. 2007) since odor is transported more by turbulent advection than by diffusion over scales useful for distant navigation (Atema et al. 2002; Moore and Crimaldi 2004). Such infotaxis is unlikely in these experiments because the DISC was locked into a water parcel, and drifted with it over the course of a deployment. Thus animals constrained to the DISC are unable to actively map an odor stimulus.

The most plausible response to odor cues in the study is a simple change in swimming behavior with either the presence or absence of an odor. If chemical signals from the tide were responsible for the change in swimming direction, then large variation in the accuracy of the postlarvae over the tide would be anticipated, corresponding with changes in the frequency of encountering advectively transported odor. The highest accuracy would be expected when the tidal current is strongest, propelling turbulently advected chemicals offshore, and maximizing encounters with nearshore-flavored eddies. However, little variation in accuracy can be attributed to the time into the tidal phase (Figure 4.4b). Still, a chemical cue could trigger another innate behavior beneficial to

finding settlement habitat (Paris et al. 2013). Nearshore specific odors that are advected offshore could activate an internal clock or other instinctive behavior that causes the specific swimming directionality that we observed. In the future, clock-shifting postlarvae by a full tidal cycle could disentangle the presence of an internal clock, and perhaps which cues align the clock. However, keeping postlarvae within the lab for an extended time could cause changes related to settlement, and fundamentally alter postlarval behavior causing a tradeoff in the ability to describe the clock and artificial swimming behavior. This study can only speculate on what signal (s) could be resetting or triggering the internal clock because experimental animals were collected from a tidal channel, and they could already be instilled with circatidal behavior. If experimental animals had imprinted to a settlement location before collection, then they may have exhibited homing behavior. However, homing does not account for the switch in bearing associated with the tidal cycle and fails to explain why some postlarvae oriented towards their capture location, while others oriented away from it.

Stokes drift, or particle transport due to orbital motion, has been suggested as a mechanism that would enhance onshore transport of spiny lobster postlarvae (Feng et al. 2011). However, the primary evidence suggesting passive hydrodynamic orientation and transport stems from correlations between settlement indices and physical phenomena, and not from observations (Jeffs et al. 2005). It is challenging to relate these findings to Stokes drift, since the study vessel was not rigged to collect empirical measurements of the specific wave periodicity, direction, or mean height. However if the lobster postlarvae were using Stokes Drift or orbital motion to ascertain and maintain a bearing, the deeper deployments would have had lower accuracy and no population direction



because wave related motion rapidly decreases with depth (Tamura et al. 2012). The average accuracy for deep deployments was significantly higher, suggesting that postlarvae are actually better at maintaining a bearing without Stokes drift. The results cannot rule out Stokes drift as a compass for orientation, but the deep treatment suggests that other cues are also involved.

Animals reliably arrive in Florida Bay using tidal stream transport, but to get far enough onshore to harness the tidal current, using the wind may be an adaptive strategy. The mean wind during deployments came from the east and southeast, blowing towards shore (Table 4.1). Results suggest that while in the top layer of the ocean, where wind driven currents are at a maximum, lobster postlarvae adjust their bearing relative to the wind and tide. When the bearing of the postlarvae was considered with respect to the wind during deep deployments, there was not a significant difference between tides. However, during the shallow deployments the bearing of the postlarvae with respect to the wind was significantly different and nearly reversed depending on tidal phase. While within the top 3 meters of the ocean during ebb tide lobster postlarvae oriented with the wind, surfing towards the shore. No physiological mechanism for how the lobsters could detect the wind is known, but they are directional with respect to the wind which suggests that they can detect it.

These results suggest that the tides act as a proximal cue, possibly via an internal clock mechanism, informing the animal to modify its orientation. Across tidal phases, a southward cardinal orientation would prevent strong advection via the Florida Current, and surfing with the wind would direct postlarvae towards the coast. An analogous situation with respect to the current occurs off Lizard island in Australia, where

populations of reef fish innately swim in a consistent direction during the daytime (Leis and Carson-Ewart 2003). The complex flow patterns in the Caribbean Sea do not contain a single straight-forward current system for which a larva, such as *P. argus*, with such an extended planktonic stage could have an adaptive strategy. However, maintaining a bearing could help a postlarva simply keep a course that would increase encounters with settlement habitat. A swimming direction could be maintained by using multimodal cues including celestial, wind, acoustic, or magnetic cues. Results suggest that the cue that lobster postlarvae use does not change over the course of the day, based on their relatively constant accuracy of swimming direction (Figure 4.4). In addition, trials at 25 m depth had similar directional results to shallow deployments at 3 m during ebb tide. This shows that a cue is available further from the surface, which suggests magnetic orientation as found in adult spiny lobster (Lohmann et al. 1995, Boles and Lohmann 2003). Cue manipulation *in situ* will be necessary to elucidate the nature of the sensory signals. Altering the magnetic field, using speaker playback, or isolating a particular chemical signature from tidal effluent, and then exposing postlarvae in a naturally devoid environment are approaches possible with the DISC in future experiments.

Observing lobster postlarvae in the open ocean using a novel framework is not without caveats. The use of a tethering system could create unnatural swimming behavior (Peterson and Black 1994) and the depth changes involved with a deployment could trigger barokinesis as observed in both crustaceans (Tankersley et al. 1995) and fish larvae (Huebert 2008). If postlarvae descend to lower depths during the day, as inferred from observations in the laboratory (Calinski and Lyons 1983, Booth and Phillips 1994, Jeffs and Holland 2000) and rare trawl catches (Ritz 1972, Phillips and Pearce 1997),

then the tether and fixed depth of the DISC could prevent them from doing so, forcing them to swim presumably in a descending manner. However, a significant horizontal swimming component was observed in this study. The similar swimming directions for postlarvae at 25m depth and 3m depth during ebb tide suggest that the horizontal swimming behavior may be uniform through the top of the water column (Figure 4.5 and 4.6). Also, lobster adults and postlarvae have been successfully used in a variety of tethering experiments examining predation (Acosta and Butler 1999; Mills et al. 2008; Butler and Lear 2009, Behringer and Butler 2009), and orientation (Lohmann et al. 1995, Jeffs and Holland 2000; Lozano-Alvarez et al. 2002; Boles and Lohmann 2003). This body of work suggests that tethering is a valid option for assessing lobster ecology and behavior. For the present experiments, this was confirmed by snorkelers observing the behavior of tethered postlarvae in the DISC, noting that postlarvae were swimming forward to the extent allowed by the tether (Figure 4.1b). As part of our protocol to avoid bias from tethering we only recorded postlarvae that were actively swimming. This caused our data to be made up of only directional data, and including inactive positions may have yielded different results.

Partially upstream orientation was observed in spiny lobster postlarvae, which is typically only common near the goal of a long distance journey. This is because the metabolic costs of sustained swimming against flow are considerable (reviewed in Chapman et al. 2011). Animals that demonstrate upstream orientation include those with powerful rheotactic responses such as salmon, and other diadromous species that use tidal stream transport to transition between habitats (Moore et al. 1998; Forward and Tankersley 2001; Gibson 2003; Trancart et al. 2012). The present study found that

lobster larvae used “partial compensation” (Chapman et al. 2011), swimming at an angle that could increase their chances of reaching settlement habitat. The metabolic cost of swimming followed by the additional energetic cost of metamorphosis may be a limiting factor in spiny lobster dispersal and survival (Jeffs et al. 1999; Jeffs et al. 2005; Wilkin and Jeffs 2011). Wilkin and Jeffs (2011) also noted that by swimming continuously throughout the day and night the metabolic cost would be reduced, although daytime swimming was not thought to occur and the present study is the first to document it. Comparisons between the projected paths of lobsters orienting during ebb and flood tide demonstrates that lobsters are better positioned to reach nearshore using the observed ebb flow orientation (Figure 4.5).

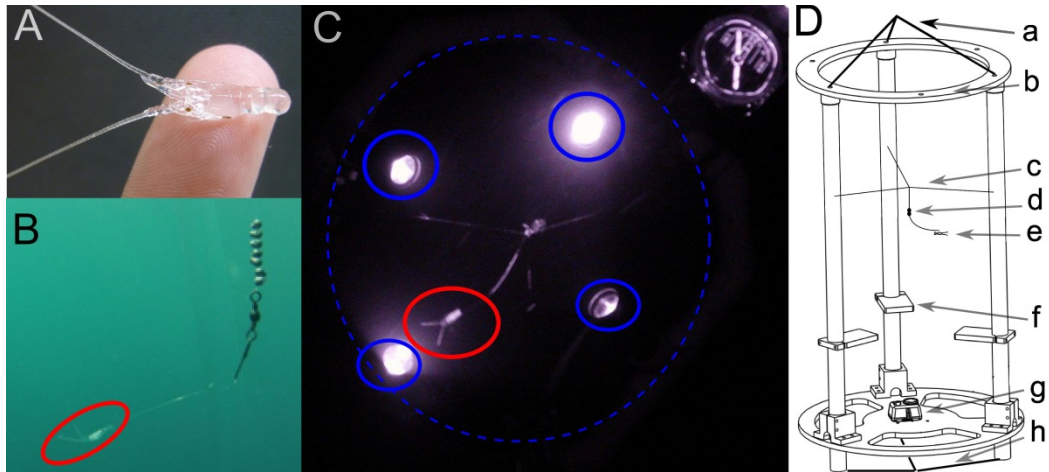
The tide is a signal from shallow settlement habitat that is available to dispersing larvae transitioning out of their pelagic phase. A tidally-mediated switch in swimming behavior would be beneficial not only to spiny lobster postlarvae, but to a multitude of other pelagic larvae seeking a benthic home. The next step is to discover the cues that larvae can use as a compass to maintain directionality during the day, night, and throughout other variable environmental conditions. Emerging technologies such as the DISC can be used to systematically discover, describe, and quantify both larval behaviors and the environmental cues driving them. Understanding how larvae resolve environmental characteristics to change their orientation during recruitment is fundamental knowledge. If recruiting larvae across taxonomic groups use a compass it suggests that it is an evolutionary requirement for marine dispersal with a larval phase.

**Table 4.1. Mean population directional data during DISC deployments of spiny lobster postlarvae.** The track of the DISC (a Lagrangian drifter) gave the current direction and the NOAA weather station FWYF1 gave wind direction. The postlarval swimming directions are the population means during DISC deployments of different tides and depths. The Rayleigh's  $r$ ,  $p$ -value, and direction are given for each variable. The postlarval swimming directions relative to the wind and the current are in degrees clockwise of the environmental variable, rather than in a cardinal reference frame. Statistically significant population directions are bold.

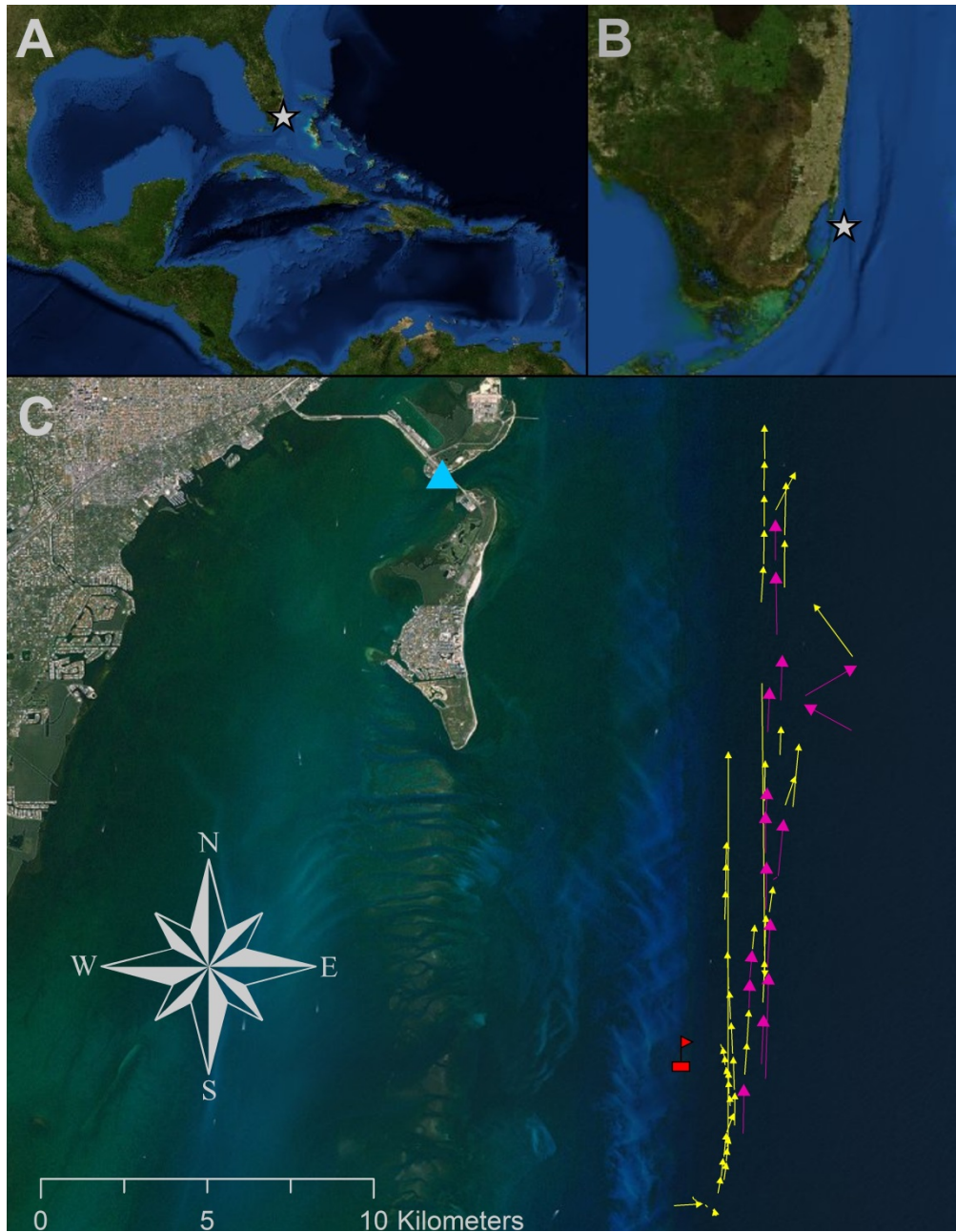
Variable	Depth (m)	Tide	n	r	p	Direction
Current Direction	3	Ebb	22	0.9531	<0.0001	<b>355.8°N</b>
Current Direction	3	Flood	33	0.8866	<0.0001	<b>358.2°N</b>
Current Direction	25	Ebb	7	0.9975	<0.0001	<b>6.5°N</b>
Current Direction	25	Flood	11	0.9997	<0.0001	<b>1.7°N</b>
Postlarval Swimming Direction	3	Ebb	22	0.5983	<0.0001	<b>225.1°SW</b>
Postlarval Swimming Direction	3	Flood	33	0.5596	<0.0001	<b>163.5°SSE</b>
Postlarval Swimming Direction	25	Ebb	7	0.9743	<0.0001	<b>214.4°SW</b>
Postlarval Swimming Direction	25	Flood	11	0.3454	0.053	166.1°SSE
Direction Facing Wind	3	Ebb	22	0.7502	<0.0001	<b>105.6°E</b>
Direction Facing Wind	3	Flood	33	0.5917	<0.0001	<b>121.9°SE</b>
Direction Facing Wind	25	Ebb	7	0.9969	<0.0001	<b>160.1°SSE</b>
Direction Facing Wind	25	Flood	11	0.307	0.0761	134.9°SE
Swimming Direction Relative to Current	3	Ebb	22	0.5781	<0.0001	<b>226.4°</b>
Swimming Direction Relative to Current	3	Flood	33	0.5353	<0.0001	<b>154.2°</b>
Swimming Direction Relative to Current	25	Ebb	7	0.9662	<0.001	<b>207.9°</b>
Swimming Direction Relative to Current	25	Flood	11	0.3439	0.0538	166.5°
Swimming Direction Relative to Wind	3	Ebb	22	0.4352	0.0017	<b>126.1°</b>
Swimming Direction Relative to Wind	3	Flood	33	0.4326	0.0002	<b>10.3°</b>
Swimming Direction Relative to Wind	25	Ebb	7	0.9689	<0.0001	<b>54.2°</b>
Swimming Direction Relative to Wind	25	Flood	11	0.8494	<0.0001	<b>19.9°</b>

**Table 4.2. Seasonal differences sampled by the DISC.** Fall deployments were done in September and October of 2012 (n=35), while the spring deployments occurred in February of 2013 (n=20). Temperature and light intensity were sampled with a Hobo probe. Total rotation is the sum of compass movement (pathlength of the compass headings) throughout a DISC trial. Maximum displacement is the circular range (minimum arc containing all of the headings) of the compass headings during a DISC trial. Comparisons were made using a Welch's two-sample t-test in MATLAB with an alpha of 0.05.

<b>Variable</b>	<b>Fall mean (<math>\pm</math>SD)</b>	<b>Spring mean (<math>\pm</math>SD)</b>	<b>p value</b>
Temperature ( $^{\circ}$ C)	29.09 $\pm$ 0.65	24.88 $\pm$ 0.91	<b>&lt;0.001</b>
Relative Light intensity (Lux)	15,810 $\pm$ 9,407	15,698 $\pm$ 7,880	0.9769
Wind speed (m/s)	4.36 $\pm$ 1.52	6.76 $\pm$ 2.02	<b>&lt;0.001</b>
Current speed (m/s)	0.52 $\pm$ 0.38	0.89 $\pm$ 0.42	<b>&lt; 0.01</b>
Total rotation ( $^{\circ}$ )	1,011 $\pm$ 319	1,114 $\pm$ 167	0.1889
Maximum displacement ( $^{\circ}$ )	140 $\pm$ 92	155 $\pm$ 91	0.5862

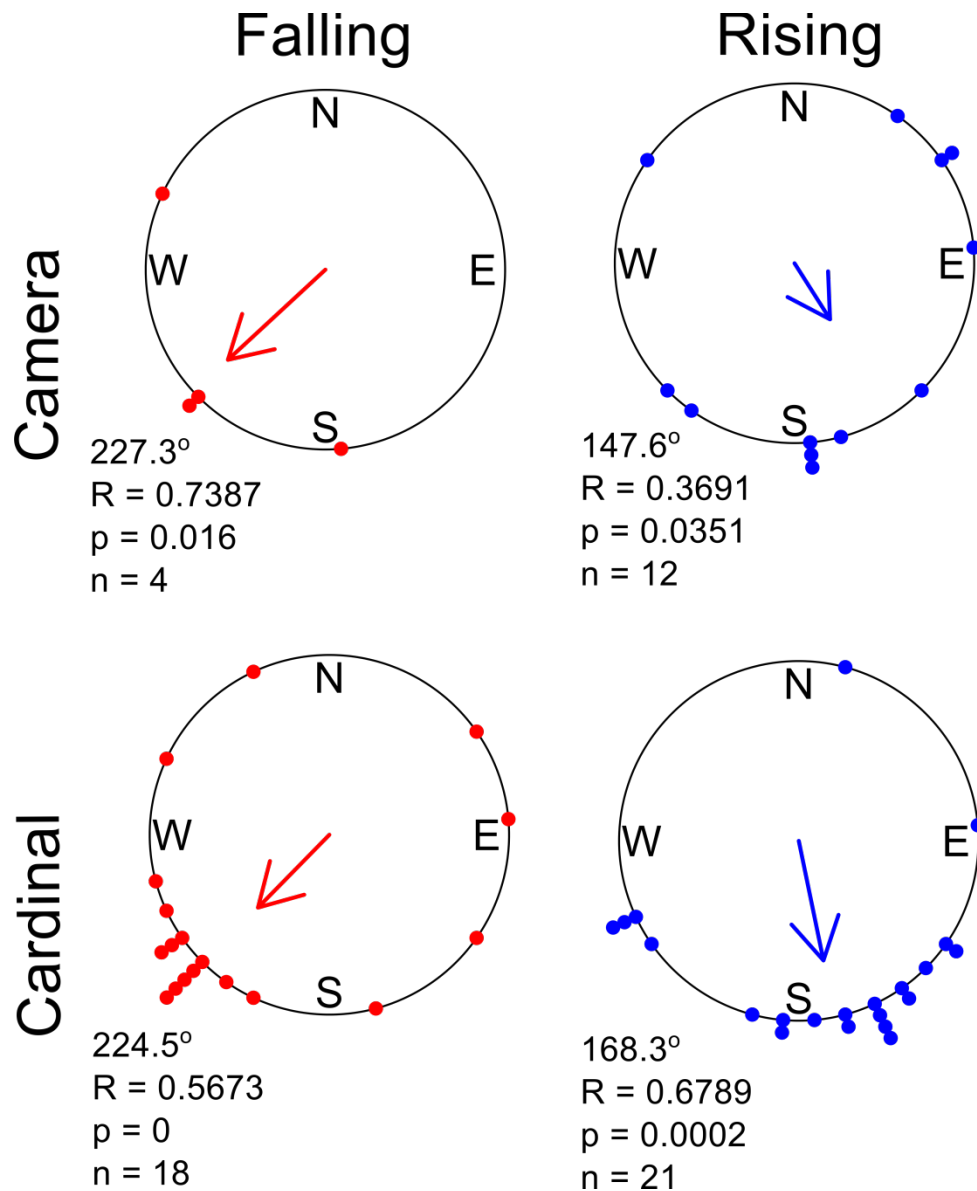


**Figure 4.1. Tethering spiny lobster postlarvae.** Panel A: A spiny lobster, *Panulirus argus*, postlarva on a human finger for scale. Panel B: a tethered postlarva (highlighted in red) swims forward by beating its pleopods and holding its antennae out in front of it. Panel C: a sample image from the camera looking up at a tethered lobster postlarva illuminated by the removable infrared lighting rig (highlighted in blue) during the night. Panel D: the DISC is engineered from clear acrylic using an orientation with no frame of reference design. a) attached to surface line; b) top frame; c) monofilament between posts; d) weighted clip at focal point of camera; e) tethered postlarva; f) compass; g) camera and HOBO on bottom frame; h) clip that attaches to drogue.

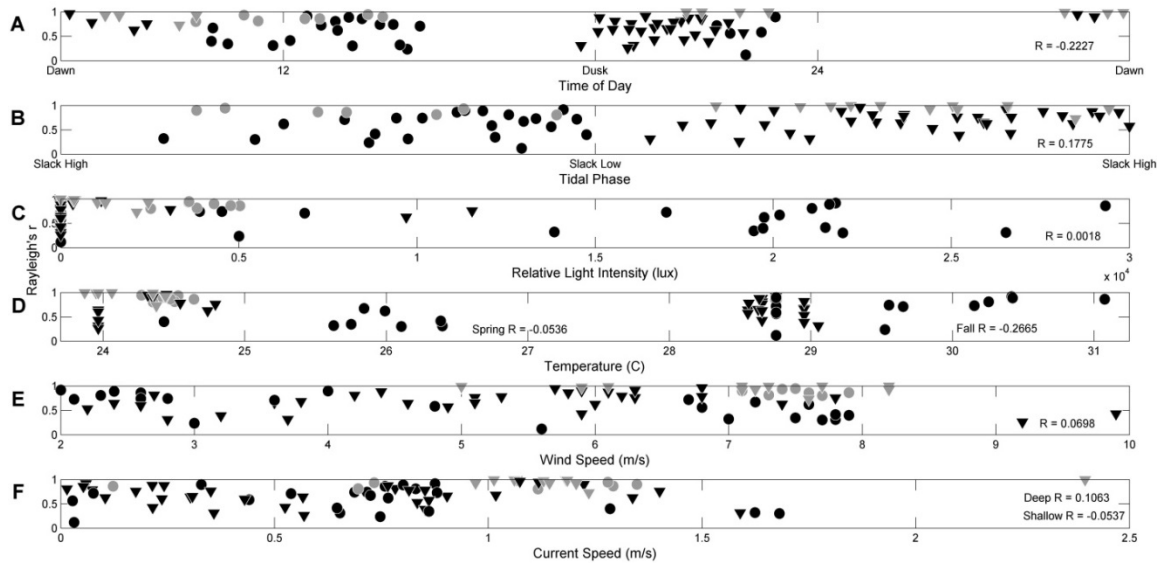


**Figure 4.2. The study area for the DISC deployments.** Deployments occurred in the Caribbean Sea (A) off the coast of Florida (B). The paths of deployments (C) at 25 m ( $N = 18$ ) from the surface are in purple, and deployments 3 m ( $N = 55$ ) from the surface are in yellow. Fowey Rocks is the red icon, and the location where lobsters were collected from the plankton is the cyan icon.

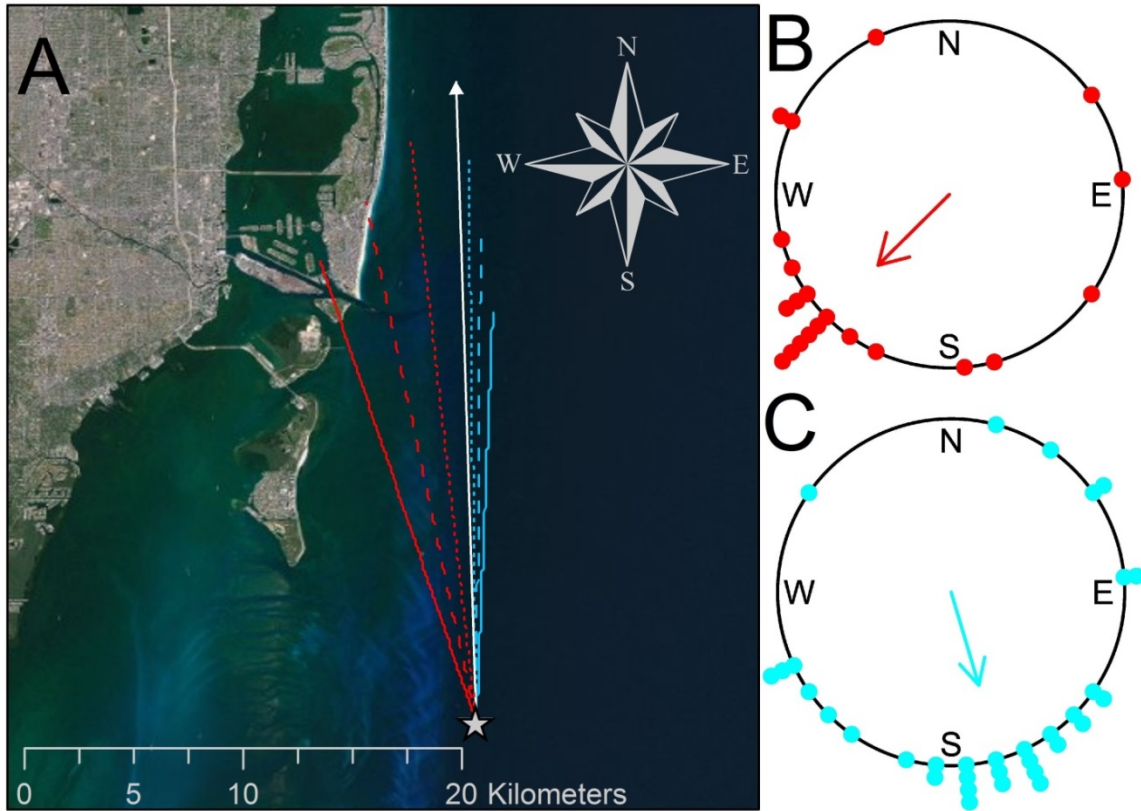




**Figure 4.3. Reference frame comparisons of postlarval swimming directions in the DISC.** To determine if tethered postlarvae were behaving in a biased manner, Rayleigh's values of the movement with a frame of reference to the DISC versus movement relative to cardinal directions are compared. Postlarvae that had larger Rayleigh's  $r$  when considered relative to the camera are denoted as "Camera," and those that had a greater Rayleigh's  $r$  relative to a cardinal reference as "Cardinal".



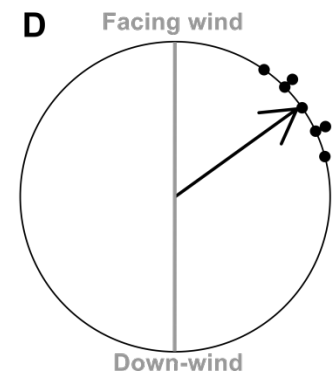
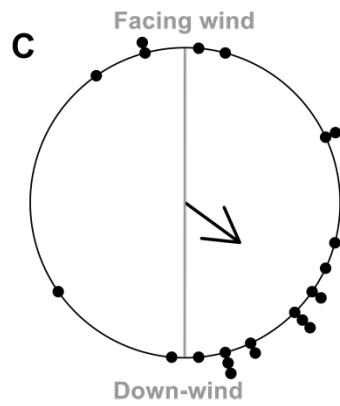
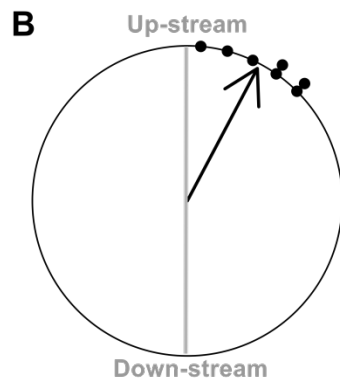
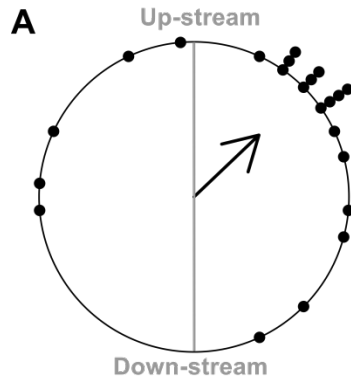
**Figure 4.4. Accuracy of postlarval swimming direction changing with the environment.** Postlarvae swimming behavior was tested in the DISC at 3m (black) or 25m (grey) from the surface across the tidal phases and hours of the day. The Rayleigh's  $r$  value (Y-axis) of the mean postlarval swimming direction indicates the strength of the directionality and higher  $r$  values indicate more accuracy. Instances of ebb tide are circles and instances of flood tide are triangles. The accuracy of postlarval orientation was compared over the time of the day (A), the tidal phase (B), the relative light intensity (C), the temperature (D), the wind speed (E) and the current speed (F). Spearman's  $R$  was used to test for any correlations across sampled conditions and no correlation was significant (all  $P > 0.05$ ). Correlations were separated by season in C (temperature changed with season), and by depth in F (currents were faster deeper).



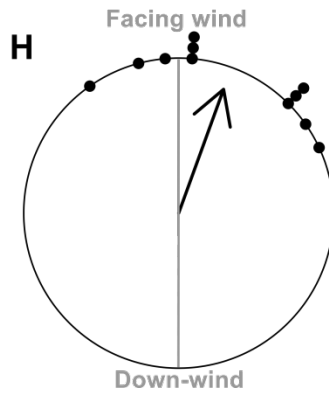
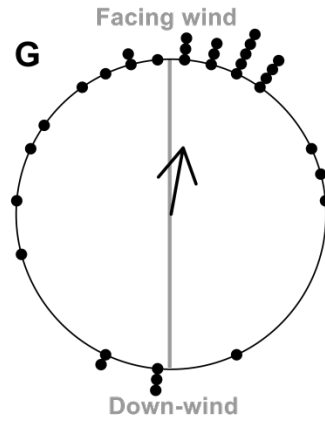
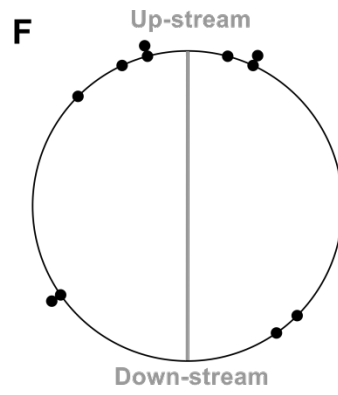
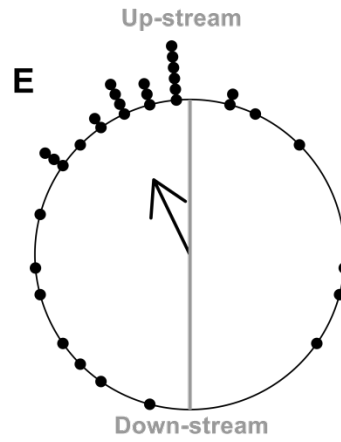
**Figure 4.5. The consequences of postlarval swimming.** Panel A shows 6.5 hours (a tidal cycle) of modeled swimming in the mean observed currents (white arrow;  $358^{\circ}\text{N}$ , at a speed of  $0.82\text{ m/s}$ ), starting from the mean center of DISC deployments (grey star) at  $3\text{m}$  from the surface. Swimming trajectories were calculated through vector addition of the swimming of the postlarva along with the mean observed current speed and direction. The swimming direction is the mean observed in either ebb (B, red, Rayleigh's  $r = 0.598$ ) or flood tide (C, cyan, Rayleigh's  $r = 0.560$ ). Each bubble corresponds with an individual postlarva's swimming direction (B, C). Modeled transport paths are based on three swimming speeds for each tidal direction:  $10$ ,  $20$ , and  $30\text{ cm/s}$  (dotted, dashed and solid respectively). Drift without swimming behavior is the white line. If lobster postlarvae continued the swimming behavior that was observed in the DISC trials, the animals orienting with the ebb tide may reach shore.

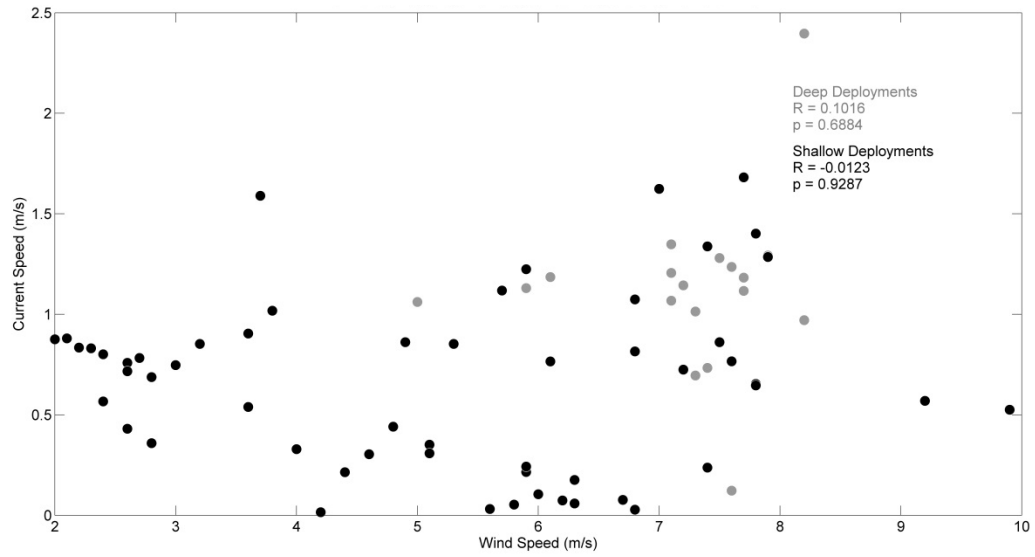
**Figure 4.6. Spiny lobster postlarval *in situ* swimming directions with respect to the current and wind.** The mean swimming direction of each individual postlarva within the DISC is indicated by a bubble. For significantly directional populations, the length of the arrow is Rayleigh's  $r$  value, relative to a maximum of 1. Swimming directions are given in degrees clockwise facing the current (A,B,E,F) or the wind (C,D,G,H). Shallow deployments were 3m from the surface (A,C,E,G) and deep deployments were 25m from the surface (B,D,F,H). Columns separate trials by the tide; ebb tide is the left (A,B,C,D) and flood tide is the right (E,F,G,H).

### Ebb Tide



### Flood Tide





**Figure 4.7. The DISC (a Lagrangian drifter) travels independently of the wind.** The current speed obtained from the GPS track of the DISC is plotted against the concurrent wind speed obtained from NOAA station FWYF1. There is no significant correlation ( $p > 0.05$ ) using Spearman's ranked correlations in either deep (gray) or shallow (black) deployments.

## CHAPTER 5. CONCLUSIONS

The connectivity of spiny lobster at the Caribbean scale has attracted attention for decades, yet drawing conclusions is challenging and has been the subject of debate (Lyons 1986; Briones-Fourzan 1994; Acosta et al. 1997; Cruz et al. 2001; Ehrhardt 2005; Cruz and Bertelsen 2008; Briones-Fourzan et al. 2008). The role of extremely local self-seeding in lobster is a contention supported by Ehrhardt and Fitchett (2010) following correlations between models of local spawning and models of postlarval recruitment, however most work supports pan-Caribbean connectivity. A highly variably downstream flow of larvae harnessing the powerful Caribbean boundary currents has been the prevailing point of view for decades, especially in Florida where evidence was based on erratic puerulus arrivals (Herrnkind and Butler 1993) and lengthy pelagic larval durations (Lewis 1951). A lack of genetic structure throughout the Caribbean found by Silberman et al. (1994) and confirmed by Naro-Murciel et al. (2011) gives this theory further credence (although South American populations were not sampled). Ongoing work (Truelove et al. *in prep*) using a more comprehensive sampling scheme suggests that there is some limited population structure in the Caribbean, and finds agreement between calculated genetic distances and network distance in the model described in chapter three. This gives empirical support to the connectivity findings of the model using a different approach. A decreased dispersal range in lobster due to deep larval vertical migratory behavior may contribute to this structure (Butler et al. 2011), and the modeled pathways linking together the Caribbean contain higher densities of larvae when behavior was included (Kough et al. 2013).

My work provides an updated model of the linkages between Caribbean spiny lobster populations. Traditional fishery models struggle to portray spiny lobster fisheries because of the high variability in recruitment, the variety of gears used, inconsistent fishery data, and other factors (Medley and Ninnes 1997; Cruz and Adriano 2004), so some scientists have turned to individual based modeling. Several previous IBM studies of Caribbean spiny lobster larval connectivity (Briones-Fourzan et al. 2008; Rudorff et al. 2009) have used only surface currents for advection, not accounted for larval behavior, not appropriately accounted for differences in local spawning population abundance or size structure, nor had a realistic periodicity of spawning. Other work used an improved model construct, including behavior that moved larvae into more realistic currents, yet still had a limited scope in space (13 spawning areas concentrated between Belize and Mexico) and time (only 2 spawning events) leaving much room for improvement (Butler et al. 2011). Models of Caribbean spiny lobster have also not been validated outside of general circulation model performance. The modeling work in this dissertation addressed these needs from both theoretical (chapter two) and functional (chapter three) perspectives.

Before applying a tool to explore questions concerning an economically important fishery, the strengths and limitations of the model were tested using a variety of species across spatiotemporal scales. A general concept in statistics is that both precision and accuracy are increased as sample size increases, leading to a closer approximation of the true population mean. However, much previous LSM work has not placed emphasis on continuously releasing larvae and exhaustively sampling time. My finding that most connections are rare in time and variability in matrices depends on release interval is



therefore relevant to future LSM studies. Networks constructed from occasional releases were a stochastic draw from the overall connectivity pattern, which has important implications for connectivity modeling.

The modeling effort in chapter three contributes to the Caribbean spiny lobster connectivity debate, and provides fresh insight on how the metapopulation is structured, crucial information for an internationally valuable commercial and artisanal fishery. These data provide an example and blueprint for how larval transport models can be implemented in future work and with other species. The study demonstrates the importance of incorporating biology into dispersal models. Basic research on both population structure and larval biology were essential components for LSM. The modeling results did not mesh with puerulus arrival time series unless the model included both OVM and realistic spawning time and population structure.

Whereas LSM modeling is a powerful and established tool for testing hypotheses about marine dispersal, there are several assumptions that go along with using it. For example, the general ocean circulation models (GOCM) available today still do not capture the sub-mesoscale activity that plays a vital role in larval journeys. Thus, there is a mismatch between the currents larvae experience, and the currents captured in GOCM. The stochastic component of LSM accounts for sub-mesoscale dynamics in dispersal models, and must fill this role until such dynamics are better understood and capable of being incorporated in a GOCM. In addition, properly portraying nearshore dynamics and tides requires an extremely high resolution GOCM. The GOCMs used did not include the tides, although the Florida Keys HyCOM and Bahamas ROMS had sufficient resolution to do so. The lack of realistic nearshore dynamics made the habitat polygons and

associated buffer crucial. However, the choice of lobster as a model organism reduced the need for nearshore realism. The ability for lobster postlarvae to swim towards shore even while in a pelagic environment (a notion supported in chapter four) reduces the need for highly realistic nearshore dynamics; postlarvae that are transported to pelagic environment adjacent to coasts (and within habitat sites used in the model) likely swim the remainder. Finally, LSM should only be used to describe probabilistic connections; the precise amount of transport, or number of animals, is only possible to describe when population and spawning estimates are well defined. It is important to acknowledge these caveats and to use LSM to address only hypotheses that are feasible within a GOCM construct.

The largest caveat to the modeling portion of this dissertation is the temporal scale of the entire simulation. The total simulation length was restricted to 5 years. Although this is clearly an important and relevant timescale for an exploited species, such as lobster which take 2 years to become mature, it may not be relevant for genomics. Genetic changes could be the result of a single extreme dispersal event on a decadal scale or even longer scale (LeRoux et al. 2014), which is beyond the scope of this study. A 30 year timescale would be more appropriate for lobster and fish, as it would capture the upper echelon of lifespans. Unfortunately GOCM are not trivial to develop, especially for such a long time period, which is why this study relied on publicly available and verified models. The GOCM (1/12° HyCOM and 1/25°GoM HyCOM) output required to run the simulation is being updated for another 4 years (2010-2013), and will be used with future work stemming from this dissertation. Although this almost doubles the available

GOCM data and the total simulation time, it still does not cover the optimal temporal scale.

Another caveat concerns the resolution of model inputs. In chapter two, the ideal setup to explore alterations of release frequency and PLD would have been to treat them as continuous variables. As that is not possible in the current CMS framework, steps were chosen for each manipulation. However, by using a logical set-up, this caveat turned into an advantage. By choosing distinct steps that corresponded with the attributes of known species, it gave more meaning to the experiment itself, rather than purely a theoretical approach. In chapter three, survey and fishery data on stock sizes, abundances, and spawning times sometimes did not have high resolution through an entire country or bioregion. In such cases when only lower resolution data was available, they may not be as realistic because such population traits vary greatly in space (DiFranco and Guidetti 2010). However, this was also a study based on a large body of survey data, and is a good use of “data of opportunity”. The results demonstrate that even though the resolution of the population structure may be coarse, it still improves the model by enhancing comparison with observed postlarval settlement (Figure 4.4).

Empirical *in situ* measurements of larval density are important yet costly data to collect, and would have improved the model validation. If collected in a manner that allows direct comparison among locations, such data would either support the modeling results, or suggest that LSM is not an appropriate tool to use for hypotheses outside of connectivity. The prohibitive cost of pelagic sampling campaigns makes these data a “pipe dream”, especially in today’s funding environment. Although such data would be valuable, it would also require an inordinately large amount of coordination and many

ships to facilitate. The stochasticity that emerged within the second chapter also suggests that generalized patterns may be more meaningful than time-limited observations. Thus, the model capturing the mean settlement to multiple habitat sites (Figure 4.3) is powerful support for the proper parameterization and performance of the connectivity model.

There is a continuum of different larval dispersal potentials within marine species. Broad dispersal potential and the strength of pre-settlement navigation behavior should be intrinsically linked. An organism is expected to be adept at finding and swimming to nursery habitat from a greater distance if its pelagic journey covers more ground. Caribbean spiny lobsters are extreme dispersers from a larval dispersal perspective. Not only due to the dispersal modeled in this dissertation, but also because of they are a generalist species with flexible nursery habitat requirements. Spiny lobsters are broadly dispersed, can settle into a variety of habitats, and display innate swimming behavior beneficial to finding the coast. These traits make lobster postlarval sensory behavior pertinent to understanding settlement behavior of other benthic marine species with a planktonic larval phase.

The sensory behavior described in chapter four that potentially leads to enhanced settlement should not be unique to spiny lobsters. The wind and tide are cues not exclusive to lobster; they are widely available to many organisms in the ocean and their study merits attention with other settling larvae. However, the compass mechanism used by lobster postlarvae can only be surmised without further field and laboratory experiments. Further experimentation is logistically and financially expensive, yet a protocol has now been established for fieldwork. The compass used by lobsters is available independent of celestial signals, can guide orientation at multiple depths

including beneath surface cues, and is available throughout the tidal phase. A magnetic compass could function in such a manner, and is supported by other work with adult and juvenile lobsters (Lohmann et al. 1995; Boles and Lohmann 2003). Multiple compasses seem likely, especially because lobsters oriented significantly relative to the wind and current (current may also alter electric fields and be a compass sense; Paulin 1995). These findings support efforts to pioneer techniques in night research as well. Many biological and physical cues continue under the shroud of darkness when most larval settlement occurs, yet *in situ* larval orientation and navigation studies are often constrained to daylight hours. The imaging system developed in chapter four has already been used with a variety of larval fish in addition to lobsters, and has proven to be adaptable and flexible.

The key findings from this dissertation apply to a diverse array of marine species. The modeled presence of pelagic larval nurseries has broad implications. These nurseries were amplified by larval behavior, and remain relatively stationary through larval development time, suggesting that they are an important phenomenon for conservation. Anthropogenic activities such as deep sea oil exploitation and trash disposal may degrade their quality and have negative implications for any species or animals which become entrained in proximity. Discovering exactly what senses larvae use when seeking settlement grounds, and how they may therefore be impacted by potential anthropogenic changes, is a necessary step in protecting orientation from pelagic towards benthic habitats. Once the cues guiding settlement are better understood, conservation efforts could be optimized to maximize recruitment for lobster fisheries and for other organisms affected in the same ways. Steps could also be taken to fix anthropogenic damage to cues

that have been heavily impacted (e.g., silent ships or light reduction laws), and help revive declining recruitment. Understanding the cues and spaces demanded by larval biology is one step towards mitigating the growing human footprint on the ocean.

The Caribbean spiny lobster has unequivocal value as a fishery, cultural icon, and ecosystem component. It also proves to be a model scientific species, and a meaningful subject for studying dispersal across broad spatiotemporal scales. Modeled Caribbean lobster populations are linked over large distances and on a demographically relevant timescale, requiring international cooperation for their proper management. The vast larval dispersal potential also yields postlarval pueruli specialized for navigation, and suited for experiments over short spatiotemporal scales. Using novel *in situ* experiments, it was found that these postlarvae orient on a circatidal basis, even many kilometers offshore. Their behavior facilitates orientation towards shore using the wind during ebb tide. Using both LSM and *in situ* experiments, this dissertation has covered a multi-scale examination of the connectivity and behaviors driving lobster larval dispersal.

#### *Dissertation as Haiku*

Studying dispersal, using multiple methods, across space and time scales.

Unless larvae swim, most connections are fleeting: frequent rarity.

Lobster larvae move, linking the Caribbean. Demand alliances!

Postlarval swimming, bearings changing with the tide, the wind points towards home.

Valued fishery, iconic marine species, best research subject.

## WORKS CITED

- Acosta CA, Butler MJ (1999) Adaptive strategies that reduce predation on Caribbean spiny lobster postlarvae during onshore transport. *Limnol Oceanogr* 44:494–501.
- Acosta CA, Matthews TR, Butler MJ (1997) Temporal patterns and transport processes in recruitment of spiny lobster (*Panulirus argus*) postlarvae to South Florida. *Mar Biol* 129:79–85.
- Acosta CA, Butler MJ (1997). Role of mangrove habitat as a nursery for juvenile spiny lobster, *Panulirus argus*, in Belize. *Mar Freshwater Res* 48:721-727.
- Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science* 316: 742-744.
- Almany GR, Hamilton RJ, Bode M, Matawai M, Potuku T, Saenz-Agudelo P, Planes S, Berumen M, Rhodes KL, Thorrold SR, Russ GR, Jones GP (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Curr Biol* 23:1-5.
- Anderson JR, Behringer DC (2013) Spatial dynamics in the social lobster *Panulirus Argus* in response to diseased conspecifics. *Mar Ecol Prog Ser* 474:191–200.
- Andréfouët S, Muller-Karger FE, Robinson JA, Kranenburg CJ, Torres-Pulliza D, et al. (2004) In: 10th ICRS. Global assessment of modern coral reef extent and diversity for regional science and management applications: a view from space. Okinawa, Japan: Japanese Coral Reef Society pp. 1732-1745.
- Armsworth PR (2001) Directed motion in the sea: efficient swimming by reef fish larvae. *J Theor Biol* 210: 81-91. doi:10.1006/jtbi.2001.2299
- Atema J, Kingsford MJ, Gerlach G (2002) Larval reef fish could use odour for detection, retention and orientation to reefs. *Mar Ecol Prog Ser* 241:151–160.
- Atema J (1995) Chemical signals in the marine environment: dispersal, detection, and temporal signal analysis. *Proc Nat Acad Sci USA* 92: 62-66.
- Atema J (2012) Aquatic odor dispersal fields: opportunities and limits of detection, communication and navigation. In: *Chemical Ecology in Aquatic Systems* (Eds Christer Bronmark and Lars-Anders Hansson) Oxford Univ. Press
- Barta A & Horváth G (2004) Why is it advantageous for animals to detect celestial polarization in the ultraviolet? Skylight polarization under clouds and canopies is strongest in the UV. *J Theor Biol* 226: 429-37. doi:10.1016/j.jtbi.2003.09.017

- Bauer RK, Gräwe U, Stepputtis D, Zimmermann C, Hammer C (2013) Identifying the location and importance of spawning sites of Western Baltic herring using a particle backtracking model. *ICES J Mar Sci*. DOI:10.1093/icesjms/fst163
- Becker B, Levin L, Fodrie F, McMillan P (2007) Complex larval connectivity patterns among marine invertebrate populations. *Proc Natl Acad Sci USA* 104: 3267-3272.
- Beddington JR, Agnew DJ, Clark CW (2007) Current problems in the management of marine fisheries. *Science* 316: 1713-1716.
- Behringer DC, Butler MJ, Shields JD (2006) Avoidance of disease by social lobsters. *Nature* 441:441421–441421.
- Behringer DC, Butler MJ (2009) Disease avoidance influences shelter use and predation in Caribbean spiny lobster. *Behav Ecol Sociobiol* 64: 747–755.
- Bellwood DR & Stobutzki IC (1998) Nocturnal orientation to reefs by late pelagic stage coral reef fishes. *Coral Reefs* 17: 103-110.
- Berger DK, Butler MJ (2001) Octopuses influence den selection by juvenile Caribbean spiny lobster. *Mar Freshw Res* 52:1049–1053.
- Berglund M, Jacobi MN, Jonsson PR (2012) Optimal selection of marine protected areas based on connectivity and habitat quality. *Ecol Model* 240: 105-112.
- Bertelsen RD, Matthews TR (2001) Fecundity dynamics of female spiny lobster (*Panulirus argus*) in a south Florida fishery and Dry Tortugas National Park lobster sanctuary. *Mar Freshwater Res* 52: 1559-1565.
- Bleck R (2002) An oceanic general circulation model framed in hybrid isopycnal-cartesian coordinates. *Ocean Modeling* 4: 55-88
- Boles LC, Lohmann KJ (2003) True navigation and magnetic maps in spiny lobsters. *Nature* 421:60–63.
- Booth JD, Phillips BF (1994) Early Life History of Spiny Lobster. *Crustaceana* 66: 271–294.
- Botsford LW, White JW, Coffroth MA, Paris CB, Planes S, Shearer TL, Thorrold SR, Jones GP (2009) Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs*. DOI: 10.1007/s00338-009-0466-z
- Boudreau B, Bourget E, Simard Y (1993) Behavioral responses of competent lobster postlarvae to odor plumes. *Mar Biol* 117:63–69.



- Bradbury IR & Snelgrove PRV (2001) Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behaviour and advective processes in determining spatial pattern. *Can J Fish Aqua Sci* 58: 811-823.
- Brickman D, Ådlandsvik B, Thygesen UH, Parada C, Rose K, et al. (2009) Particle Tracking in Modelling physical–biological interactions during fish early life (North EW, Gallego A, Petitgas P, eds.) ICES Cooperative Research Report 295: pp 9-13.
- Briones-Fourzan P (1994) Variability in postlarval recruitment of the spiny lobster *Panulirus argus* (Latreille, 1804) to the Mexican Caribbean Coast. *Crustaceana* 66:326-340.
- Briones-Fourzan P, Candela J, Lozano-Alvarez E (2008) Postlarval settlement of the spiny lobster *Panulirus argus* along the Caribbean coast of Mexico: patterns, influence of physical factors, and possible sources of origin. *Limnol Oceanogr* 53:970–985.
- Browne KA & Zimmer RK (2001) Controlled field release of a waterborne chemical signal stimulates planktonic larvae to settle. *Biol Bull* 200: 87-91.
- Butler MJ, Lear JA (2009) Habitat-based intraguild predation by Caribbean reef octopus *Octopus briareus* on juvenile Caribbean spiny lobster *Panulirus argus*. *Mar Ecol Prog Ser* 386: 115–122.
- Butler MJ, Paris CB, Goldstein JS, Matsuda H, Cowen RK (2011) Behavior constrains the dispersal of long-lived spiny lobster larvae. *Mar Ecol Prog Ser* 422: 223–237.
- Butler MJ, MacDiarmid AB, Booth JD (1999) The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. *Mar Ecol Prog Ser* 188: 179–191.
- Butler MJ, Dolan T, Hunt JH, Herrnkind WF, Rose K (2005) Recruitment in degraded marine habitats: a spatially-explicit, individual-based model for spiny lobster. *Ecol App* 15: 902-918.
- Butler MJ, Steneck RS, Herrnkind WF (2006) Juvenile and adult ecology. In: *Lobsters: Biology and Management, Aquaculture and Fisheries*. (ed. BF Phillips). Blackwell Publishing, Oxford, pp. 263–309.
- Butler MJ, Herrnkind WF (1991) Effect of benthic microhabitat cues on the metamorphosis of pueruli of the spiny lobster *Panulirus argus*. *J Crustac Biol* 11: 23–28.
- Butler MJ, Herrnkind WF (1997) A test of recruitment limitation and the potential or artificial enhancement of spiny lobster populations in Florida. *Can J Fish Aquat Sci* 54: 452-463.

- Butler MJ (2003) Incorporating ecological process and environmental change into spiny lobster population models using a spatially-explicit, individual-based approach. *Fisheries Res* 65: 63-79.
- Butler MJ, Herrnkind WF, Hunt JH (1997) Factors affecting the recruitment of juvenile spiny lobsters dwelling in macroalgae. *Bull Mar Sci* 61:3-19.
- Calinski MD, Lyons WG (1983) Swimming behavior of the puerulus of the spiny lobster *Panulirus argus*. *J Crustac Biol* 3: 329–335.
- Caputi N, Brown RS, Chubb CF (1995) Regional prediction of the western rock lobster, *Panulirus cygnus*, commercial catch in Western Australia. *Crustaceana* 68: 245-256.
- Carls MG, Rice, SD, Hose JE (2010) Sensitivity of fish embryos to weathered crude oil: Part I. Low-level exposure during incubation causes malformations, genetic damage, and mortality in larval pacific herring (*Clupea pallasii*). *Environ Toxicol Chem* 18:481–493
- Carson HS, López-Duarte PC, Rasmussen L, Wang D, Levin LA (2010) Reproductive timing alters population connectivity in marine metapopulations. *Curr Biol* 20:1926-31. doi:10.1016/j.cub.2010.09.057
- Chapman JW, Klaassen RHG, Drake VA, Fossette S, Hays GC, Metcalfe JD, Reynolds AM, Reynolds DR, Alerstam T (2011) Animal orientation strategies for movement in flows. *Curr Biol* 21: 861–870.
- Chavez EA (2009) Potential production of the Caribbean spiny lobster (*Decapoda, Palinura*) fisheries. *Crustaceana* 82: 1393-1412.
- Chavez EA, Chavez-Hidalgo A (2013) Pathways of connectivity amongst Western Caribbean spiny lobster stocks. *Proc 12th Intl. Coral Reef Symp.*
- Childress MJ, Herrnkind WF (1996) The ontogeny of social behaviour among juvenile Caribbean spiny lobsters. *Animal Behav* 51:675-687.
- Chiswell SM, Booth JD (2008) Sources and sinks of larval settlement in *Jasus edwardsii* around New Zealand: where do larvae come from and where do they go? *Mar Ecol Prog Ser* 354: 201-217.
- Cobb JS, Wang D, Campbell DB, Rooney P (1989) Speed and direction of swimming by Postlarvae of the American Lobster. *Trans Am Fish Soc* 118: 82–86.
- Cole VJ, McQuaid CD, Nakin MDV (2011) Marine protected areas export larvae of infauna, but not of bioengineering mussels to adjacent areas. *Biol Conserv* 144: 2088-2096.
- Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311: 522–527.

- Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? *Science* 287: 857-859.
- Cowen RK, Paris CB, Olson DB, Fortuna JL (2002) The role of long distance dispersal versus local retention in replenishing marine populations. *Gulf and Caribbean Research Supplement*, 1-10.
- Cruz R, Bertelsen RD (2008) The spiny lobster (*Panulirus argus*) in the wider Caribbean : a review of life cycle dynamics and implications for responsible fisheries management. *Proc Gulf Carib Fish Inst* 61: 433-446
- Cruz R, Adriano R (2004) Use of a fishery independent index to predict recruitment and catches of the spiny lobster. *NAGA WorldFish Center Quarterly* 27 (1).
- Cruz R, Diaz E, Baez M, Adriano R (2001) Variability in recruitment of multiple life stages of the Caribbean spiny lobster, *Panulirus argus*, in the Gulf of Batabano, Cuba. *Mar Freshw Res* 52: 1263-1270.
- Dean RG, Dalrymple RA (1991) *Water wave mechanics for scientists and engineers*. Teaneck, NJ : World Scientific.
- DiFranco A, Guidetti P (2011) Patterns of variability in early-life traits of fishes depend on spatial scale of analysis. *Biol letters* 7:454-6. doi:10.1098/rsbl.2010.1149
- Diniz FM, Maclean N, Ogawa M, Cintra IHA, Bentzen P (2005) The hypervariable domain of the mitochondrial control region in Atlantic spiny lobsters and its potential as a marker for investigating phylogeographic structuring. *J Mar Biotechnol* 7:462-473.
- Dutkiewicz S, Griffa A, Olson DB (1993) Particle diffusion in a meandering jet. *J Geophys Res* 98: 487-500
- Duffy JE (1996) Eusociality in a coral reef shrimp. *Nature* 381:512-514.
- Eggleston DB, Lipcius RN, Marshall LS, Ratchford SG (1998) Spatiotemporal variation in postlarval recruitment of the Caribbean spiny lobster in the central Bahamas: lunar and seasonal periodicity, spatial coherence, and wind forcing. *Mar Ecol Prog Ser* 174: 33-49.
- Eggleston D, Johnson E, Kellison G, Nadeau D (2003) Intense removal and non-saturating functional responses by recreational divers on spiny lobster *Panulirus argus*. *Mar Ecol Prog Ser* 257: 197-207. doi:10.3354/meps257197
- Egner SA (2004) Auditory sensitivity of the sergeant majors (*Abudefduf saxatilis*) from post-settlement juvenile to adult. University of South Florida.

- Ehrhardt NM (2005) Population dynamic characteristics and sustainability mechanisms in key Western Central Atlantic spiny lobster, *Panulirus argus*, fisheries. *Bull Mar Sci* 76: 501-525.
- Ehrhardt NM, Puga R, Butler MJ (2011) Implications of the ecosystem approach to fisheries management in large ecosystems. The case of the Caribbean spiny lobster. In: Fanning L, Mahon R, McConney P (Eds) *Towards Marine Ecosystem-Based Management in the Wider Caribbean*. The Netherlands: Amsterdam University Press, pp. 425.
- Ehrhardt NM, Fitchett MD (2010) Dependence of recruitment on parent stock of the spiny lobster, *Panulirus argus*, in Florida. *Fisheries Oceanography* 19: 434-447.
- Feng M, Caputi N, Penn J, Slawinski D, de Lestang S, Weller E, Pearce A (2011) Ocean circulation, Stokes drift, and connectivity of western rock lobster (*Panulirus cygnus*) population. *Can J Fish Aquat Sci* 68:1182-1196.
- Fiechter J, Steffen KL, Mooers CNK, Haus BK (2006) Hydrodynamics and sediment transport in a southeast Florida tidal inlet. *Est Coast Shelf Sci* 70: 297-306.
- Field JM, Butler MJ (1994) The influence of temperature, salinity, and postlarval transport on the distribution of juvenile spiny lobsters, *Panulirus argus* (Latreille, 1804), in Florida Bay. *Crustaceana* 67: 26-45.
- Fisher R, Bellwood DR (2003) Undisturbed swimming behaviour and nocturnal activity of coral reef fish larvae. *Mar Ecol Prog Ser* 263: 177-188.
- Fisher R, Bellwood DR, Job SD (2000) Development of swimming abilities in reef fish larvae. *Mar Ecol Prog Ser* 202: 163-173.
- Fitzgibbon QP, Jeffs AG, Battaglione SC (2013) The Achilles heel for spiny lobsters: the energetics of the non-feeding post-larval stage. *Fish Fisheries DOI: 10.1111/faf.12018*
- Food and Agriculture Organization (2006) Fifth regional workshop on the assessment and management of the Caribbean spiny lobster. Available: <ftp://ftp.fao.org/docrep/fao/010/a1518b/a1518b00.pdf> Accessed 2013 Jan 1.
- Forward RB, Tankersley RA (2001) Selective tidal-stream transport of marine animals. *Oceanogr Mar Biol Annu Rev* 39: 305-353.
- Fratantoni DM (2001) North Atlantic surface circulation during the 1990's observed with satellite tracked drifters. *J Geophys Res* 106: 22067-22093.
- Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing marine reserve networks for both conservation and fisheries management. *Proc Natl Acad Sci USA* 107: 18286-18293.

- Gardiner JM, Atema J (2010) The function of bilateral odor arrival time differences in olfactory orientation of sharks. *Curr Biol* 20:1187-91. doi:10.1016/j.cub.2010.04.053
- Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. *Proc Nat Acad Sci USA* 104: 858-863.
- Griffin DA, Wilkin JL, Chubb CF, Pearce AF, Caputi N (2001). Ocean currents and the larval phase of Australian western rock lobster, *Panulirus cygnus*. *Mar Freshw Res* 52: 1187–1199.
- Gibson RN (2003) Go with the flow: tidal migration in marine animals. *Hydrobiologia* 503:153-161.
- Goddard SM, Forward RB (1991) The role of the underwater polarized light pattern , in sun compass navigation of the grass shrimp, *Palaemonetes vulgaris*. *J Comp Physiol A* 169: 479-491.
- Goldstein JS, Butler MJ (2009) Behavioral enhancement of onshore transport by postlarval Caribbean spiny lobster (*Panulirus argus*). *Limnol Oceanogr* 54:1669–1678.
- Goldstein JS, Matsuda H, Takenouchi T, Butler MJ (2008) The complete development of larval Caribbean spiny lobster (*Panulirus argus*) in culture. *J Crustac Biol* 28:306–327.
- Graham EM, Baird AH, Connolly SR (2008) Survival dynamics of scleractinian coral larvae and implications for dispersal. *Coral reefs* 27: 529-539.
- Greer AT, Cowen RK, Guigand CM, McManus M, Sevadjan JC, Timmerman AHV (2013) Relationships between phytoplankton thin layers and the fine-scale vertical distributions of two trophic levels of zooplankton. *J Plankt Res* 0: 1-18.
- Hallac DE, Sadle J, Pearlstine L, Herling F, Shinde D (2012) Boating impacts to seagrass in Florida Bay, Everglades National Park, Florida, USA: links with physical and visitor-use factors and implications for management. *Mar Freshw Res* 63: 1117-1128.
- Hamilton SL, Casellea JE, Malone DP, Carr MH (2010) Incorporating biogeography into evaluations of the Channel Islands marine reserve network. *Proc Natl Acad Sci USA* 107: 18272-18277.
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41-49.
- Harrison CS, Siegel DA, Mitarai S (2012) Filamentation and eddy-eddy interactions in marine larval accumulation and transport. *Mar Ecol Prog Ser* 472: 27-44.
- Herrnkind WF, Butler MJ (1986) Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. *Mar Ecol Prog Ser* 34: 23-30.

Herrnkind WF, Butler MJ (1993) Settlement of spiny lobster, *Panulirus argus* (Latreille, 1804), in Florida : pattern without predictability? *Crustaceana* 67:46-64.

Hidalgo M, Gusdal Y, Dingsør DE, Hjermann D, Ottersen G, Stige LC, Melsom A, Stenseth NC (2011) A combination of hydrodynamical and statistical modeling reveals non-stationary climate effects on fish larvae distributions. *Proc R Soc B*. DOI: 10.1098/rspb.2011.0750

Higgins SI, Nathan R, Cain ML (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* 84:1945-1956.

Holden C (2006) Inching toward movement ecology. *Science*:313 779 & 782.

Holstein DM, Paris CB, Mumby PJ (2014) Consistency and inconsistency in multispecies population network dynamics of coral reef ecosystems. *Mar Ecol Prog Ser* 499:1-18.

Holyoak M, Casagrandi R, Nathan R, Revilla E, Spiegel O (2008) Trends and missing parts in the study of movement ecology. *Proc Nat Acad Sci USA* 105: 19060-5. doi:10.1073/pnas.0800483105

Houde E, Bartsch J (2008) Mortality in Modelling physical–biological interactions during fish early life (North EW, Gallego A, Petitgas P, eds.) *ICES Cooperative Research Report* 295: pp 27-42.

Huebert KB (2008) Barokinesis and depth regulation by pelagic coral reef fish larvae. *Mar Ecol Prog Ser* 367:261-269.

Incze L, Xue H, Wolff N, Xu D, Wilson C, Steneck R, Wahle R, Lawton P, Pettigrew N, Chen Y (2010) Connectivity of lobsters (*Homarus americanus*) populations in the coastal Gulf of Maine: part II. Coupled biophysical dynamics. *Fisheries Oceanography* 19: 1-20.

Irisson JO, Lecchini D (2008) In situ observation of settlement behaviour in larvae of coral reef fishes at night. *J Fish Biol* 72: 2707-2713. doi:10.1111/j.1095-8649.2008.01868.x

Irisson JO, Guigand CM, Paris CB (2009) Detection and quantification of marine larvae orientation in the pelagic environment. *Limnol Oceanogr Meth* 7: 664–672.

James MK, Armsworth PR, Mason LB, Bode L (2002) The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. *Proc Biol Sci Royal Soc* 269: 2079-86. doi:10.1098/rspb.2002.2128

- Jeffs AG, Willmott ME, Wells RMG (1999) The use of energy stores in the puerulus of the spiny lobster *Jasus edwardsii* across the continental shelf of New Zealand. *Comp Biochem Physiol A* 123:351–357.
- Jeffs AG, Holland RC (2000) Swimming behaviour of the puerulus of the spiny lobster, *Jasus edwardsii*. *Crustaceana* 73:847–856.
- Jeffs AG, Montgomery JC, Tindle C (2005) How do spiny lobster post-larvae find the coast? *NZ J Mar Freshw Res* 39:605–617.
- Jeffs A, Tolimieri N, Montgomery JC (2003) Crabs on cue for the coast : the use of underwater sound for orientation by pelagic crab stages. *Mar Freshw Res* 54: 841-845.
- Jones GP, Millicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature* 402: 802-804.
- Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28: 307-325. doi:10.1007/s00338-009-0469-9
- Karnaskas M, Cherubin LM, Paris CB (2011) Adaptive significance of the formation of multi-species fish spawning aggregations near submerged capes. *PLoS ONE* 6: e22067.
- Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J (2002) Sensory environments, larval abilities and local self-recruitment. *Bull Mar Sci* 70:309–340.
- Kinlan BP, Gaines SD, Lester SE (2005) Propagule dispersal and the scales of marine community process. *Diversity Distrib* 11:139-148.
- Kough AS, Paris CB, Butler MJ (2013) Larval connectivity and the international management of fisheries. *PLoS ONE* 8:e64970.
- Kough AS, Paris CB, Staaterman E (2014) *In situ* swimming and orientation behavior of spiny lobster (*Panulirus argus*) postlarvae. *Mar Ecol Prog Ser* 504: 207-219.
- Kourafalou VH, Kang H (2012) Florida Current meandering and evolution of cyclonic eddies along the Florida Keys Reef Tract: Are they interconnected? *J Geophys Res*: doi:10.1029/2011JC007383
- Kritzer JP, Sale PF (2004) Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries* 5:131-140. DOI: 10.1111/j.1467-2979.2004.00131.x
- Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. *Ecol Appl* 13: S71-S89.

- Lasker HR, Paris CB, Kough AS, Porto I, Cherubin LM (2012) Oral presentation at the 12th International Coral Reef Symposium, Cairns, AUS. 7/13/2012.
- Le Roux JJ, Strasberg D, Rouget M, Morden CW, Koordom M, Richardson DM (2014) Relatedness defies biogeography: the tale of two island endemics (*Acacia heterophylla* and *A. koa*). *New Phytologist*. doi: 10.1111/nph.12900
- Lecchini D, Shima J, Banaigs B, Galzin R (2005) Larval sensory abilities and mechanisms of habitat selection of a coral reef fish during settlement. *Oecologia* 143: 326-34. doi:10.1007/s00442-004-1805-y
- Lecchini D, Mills SC, Brie C, Maurin R, Banaigs B (2010) Ecological determinants and sensory mechanisms in habitat selection of crustacean postlarvae. *Behav Ecol* 21:599–607.
- Leis JM, Carson-Ewart BM (1998) Complex behavior by coral-reef fish larvae in open-water and near-reef pelagic environments. *Environ Biol Fish* 53:259–266.
- Leis JM, Carson-Ewart BM (2003) Orientation of pelagic larvae of coral-reef fishes in the ocean. *Mar Ecol Prog Ser* 252:239–253.
- Leis JM (2007) Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Mar Ecol Prog Ser* 347:185-193. doi:10.3354/meps06977
- Leis JM, Lockett MM (2005) Localization of reef sounds by settlement stage larvae of coral-reef fishes (*Pomacentridae*). *Bull Mar Sci* 76: 715-724.
- Leis JM, Sweatman HPA, Reader SE (1996) What the pelagic stages of coral reef fishes are doing out in blue water: Daytime field observations of larval behavioural capabilities. *Mar Freshw Res* 47:401-411.
- Leis JM, Paris CB, Irisson JO, Yerman MN, Siebeck UE (2014) Orientation of fish larvae in situ is consistent among locations, years and methods, but varies with time of day. *Mar Ecol Prog Ser* 505:193-208.
- Lemmens JWTJ (1994) Biochemical evidence for absence of feeding in puerulus larvae of the Western rock lobster *Panulirus cygnus* (Decapoda: *Palinuridae*). *Mar Biol* 118:383–391.
- Levin SA (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Annu Rev Ecol Evol Syst* 34:575-604.
- Lewis JB (1951) The phyllosoma larvae of the spiny lobster *Panulirus argus*. *Bull Mar Sci* 1(52).



- Lindo-Atichati D, Bringas F, Goni G, Muhling B, Muller-Karger FE, Habtes S (2012) Varying mesoscale structures influence larval fish distribution in the northern Gulf of Mexico. *Mar Ecol Prog Ser* 463: 245-257.
- Lipcius RN, Stockhausen WT, Eggleston DB, Marshall LS, Hickey B (1997) Hydrodynamic decoupling of recruitment, habitat quality and adult abundance in the Caribbean spiny lobster: source–sink dynamics? *Mar Freshw Res* 48: 807-815.
- Lipcius RN, Cobb JS (1994). In: Phillips BF, Cobb JS, Kittaka JK, editors. *Spiny lobster management*. Oxford, UK : Fishing news books, pp. 1-30.
- Lohmann KJ, Pentcheff ND, Nevitt GA, Stetten GD, Zimmer-faust RK, Jarrard HE, Boles LC (1995) Magnetic orientation of spiny lobsters in the ocean: experiments with undersea coil systems. *J Exp Biol* 198:2041–2048.
- Longcore T, Rich C (2004) Ecological light pollution. *Front Ecol Environ* 2:191-198.
- Lowe WH, Allendorf FW (2010) What can genetics tell us about population connectivity? *Mol Ecol*. DOI: 10.1111/j.1365-294X.2010.04688.x
- Lozano-Alvarez E, Carrasco-Zanini G, Briones-Fourzán P (2002) Homing and orientation in the spotted spiny lobster, *Panulirus guttatus* (Decapoda, Palinuridae), towards a subtidal coral reef habitat. *Crustaceana* 75: 859–873.
- Lund U, Agostinelli C (2011) Package: “Circular” in R. Available at: <https://r-forge.r-project.org/projects/circular/> Accessed: 17, Sep 2013
- Lyons WG (1986) Problems and perspectives regarding recruitment of spiny lobsters, *Panulirus argus*, to the South Florida Fishery. *Can J Fish Aqua Sci* 43:2099-2106.
- Mann D, Casper B, Boyle K, Tricas T (2007) On the attraction of larval fishes to reef sounds. *Mar Ecol Prog Ser* 338: 307-310. doi:10.3354/meps338307
- Marshall DJ, Monro K, Bode M, Keough MJ, Swearer S (2010) Phenotype-environment mismatches connectivity in the sea. *Ecol Lett*. doi: 10.1111/j.1461-0248.2009.01408.x.
- McWilliam PS, Phillips BF (2007) Spiny lobster development: mechanisms inducing metamorphosis to the puerulus: a review. *Rev Fish Biol Fisheries* 17:615-632.
- Medley PA, Ninnes CH (1997) A recruitment index and population model for spiny lobster (*Panulirus argus*) using catch and effort data. *Can J Fish Aqua Sci* 54: 1414-1421. doi:10.1139/f97-027
- Metaxas A, Saunders M (2009) Quantifying the “bio-” components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. *Biol Bull* 216: 257-272.

Meyer-Rochow VB (1975) Larval and adult eye of the western rock lobster (*Panulirus longipes*). Cell Tissue Res 162: 439-57.

Mills DJ, Johnson CR, Gardner C (2008) Bias in lobster tethering experiments conducted for selecting low-predation release sites. Mar Ecol Prog Ser 364: 1–13.

Miller TJ (2007) Contribution of individual based coupled physical biological models to understanding recruitment in marine fish populations. Mar Ecol Prog Ser 347:127-138.

Mishra M, Jeffs A, Meyer-Rochow VB (2006) Eye structure of the phyllosoma larva of the rock lobster *Jasus edwardsii* (Hutton, 1875): How does it differ from that of the adult ? Invert Reprod Develop 49:213-222.

Moore A, Ives S, Mead TA, Talks L (1998) The migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts in the River Test and Southampton Water, southern England. Hydrobiologia 371:295-304.

Moore P, Crimaldi J (2004) Odor landscapes and animal behavior: Tracking odor plumes in different physical worlds. J Mar Syst 49:55–64.

Muller R, Matthews T, FWC collector data 2005-2009, (FWC, Marathon, FL 33001 USA).

Murphy HM, Jenkins GP, Hamer PA, Swearer SE (2011) Diel migration related to foraging success in snapper *Chrysophrys auratus* larvae. Mar Ecol Prog Ser 433:185-194.

Myrberg AA, Fuiman LA (2002) The sensory world of coral reef fishes. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, p 123–148.

Nathan R (2006) Long-distance dispersal of plants. Science 313: 786-788.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) Movement research. Proc Nat Acad Sci USA 105: 19052–19059.

Naro-Maciel E, Reid B, Holmes KE, Brumbaugh DR, Martin M, DeSalle R (2011) Mitochondrial DNA sequence variation in spiny lobsters: population expansion, panmixia, and divergence. Mar Biol 158: 2027-2041.

National Oceanographic Atmospheric Administration (2002) Fishery conservation and habitat. Available: <http://www.habitat.noaa.gov/pdf/efhregulatoryguidelines.pdf>. Accessed: 2012 Jun 18.

- North E, Schlag Z, Hood R, Li M, Zhong L, Gross T, Kennedy V (2008) Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. *Mar Ecol Prog Ser* 359: 99-115. doi:10.3354/meps07317
- North EW, Gallego A, Petitgas P, Adlandsvik B, Bartsch J, et al. (2009) Manual of recommended practices for modeling physical – biological interactions during fish early life history. ICES Cooperative Research Report 295.
- Nunn AD, Tewson LH, Cowx IG (2012) The foraging ecology of larval and juvenile fishes. *Rev Biol Fisheries* 22:377-408.
- Paris CB, Cowen RK, Lwiza KMM, Wang DP, Olson DB (2002) Objective analysis of three-dimensional circulation in the vicinity of Barbados, West Indies: Implication for larval transport. *Deep Sea Res* 49: 1363-1386.
- Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef larvae. *Limnol Oceanogr* 49: 1964-1979.
- Paris CB, Cowen RK, Claro R, Lindeman KC (2005) Larval transport pathways from Cuban snapper (*Lutjanidae*) spawning aggregations based on biophysical modeling. *Mar Ecol Prog Ser* 296: 93–106.
- Paris CB, Guigand CM, Irisson JO, Fisher R, Alessandro E (2008) Orientation with no frame of reference ( OWNFOR ): A novel system to observe and quantify orientation in reef fish larvae. In: Grober-Dunsmore R, Keller B (eds) *Caribbean connectivity: Implications for marine protected area management*. Silver Spring, MD: NOAA, p 54-64.
- Paris CB, Atema J, Irisson JO, Kingsford MJ, Gerlach G, Guigand CM (2013) Reef odor: a wake up call for navigation in reef fish larvae. *PLoS ONE* 8: e72808.
- Paris CB, Helgers J, Van Sebille E, Srinivasan A (2013) The Connectivity Modeling System: A probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. *Environ Modell Softw*. DOI: 10.1016/j.envsoft.2012.12.006
- Paris CB (2009) Fate of reef fish larvae through ontogeny: advection or true mortality? Theme Session T: Death in the sea, Proceedings of the 2009 Annual Science Conference, September 21-25 2009, Berlin, ICES CM 2009/T:13, pp. 22
- Parsons D, Eggleston D (2005) Indirect effects of recreational fishing on behavior of the spiny lobster *Panulirus argus*. *Mar Ecol Prog Ser* 303: 235-244. doi:10.3354/meps303235
- Paulin MG (1995) Electroreception and the compass sense of sharks. *J Theor Biol* 174:325-339.

- Pauly D (2009) Beyond duplicity and ignorance in global fisheries. *Scientia Marina* 73: 215-224.
- Pawlowicz R, Beardsley B, Lentz S (2002) Classical tidal harmonic analysis including error estimates in MATLAB using T\_TIDE. *Comput Geosci* 28:929–937.
- Peck MA, Hufnagl M (2012) Can IBMs tell us why most larvae die in the sea? Model sensitivities and scenarios reveal research needs. *J Mar Sys* 93:77–93
- Pelc RA, Warner RR, Gaines SD, Paris CB (2010) Detecting larval export from marine reserves. *Proc Natl Acad Sci USA* 107: 18266-18271.
- Peterson CH, Black R (1994) An experimentalist's challenge: When artifacts of intervention interact with treatments. *Mar Ecol Prog Ser* 111:289–297.
- Phillips BF, Olsen L (1975) Swimming behaviour of the puerulus larvae of the Western rock lobster. *Aust J Mar Freshwat Res* 26:415-417.
- Phillips BF, Pearce AF (1997) Spiny lobster recruitment off of Western Australia. *Bull Mar Sci* 61:21-41.
- Phillips BF, Melville-Smith R (2005) Sustainability of the western rock lobster fishery: a review of past progress and future challenges. *Bull Mar Sci* 76:485–500.
- Phillips BF, McWilliam PS (2009) Spiny lobster development: where does successful metamorphosis to the puerulus occur?: a review. *Rev Fish Biol Fisheries* 19:193-215.
- Phillips BF (1986) Prediction of commercial catches of the western rock lobster *Panulirus cygnus* george. *Can J Fish Aquat Sci* 43:2126-2130.
- Pineda J, Reynolds NB, Starczak VR (2009) Complexity and simplification in understanding recruitment in benthic populations. *Popul Ecol* 51: 17–32.
- Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a network of marine protected areas. *Proc Natl Acad Sci USA* 106: 5693-5697.
- Puebla O, Bermingham E, McMillan WC (2012) On the spatial scale of dispersal in coral reef fishes. *Mol Ecol*. DOI: 10.1111/j.1365-294X.2012.05734.x
- Radford CA, Jeffs AG, Montgomery JC (2007) Directional swimming behavior by five species of crab postlarvae in response to reef sound. *Bull Mar Sci* 80: 369–378.
- Reidenbach MA, Koehl MAR (2011) The spatial and temporal patterns of odors sampled by lobsters and crabs in a turbulent plume. *J Exp Biol* 214:3138–3153.

- Rimmer DW, Phillips BF (1979) Diurnal migration and vertical distribution of phyllosoma larvae of the Western rock lobster *Panulirus cygnus*. Mar Biol 124:109–124.
- Ritz, DA (1972) Factors affecting the distribution of rock lobster larvae (*Panulirus longipes cygnus*) with reference to variability of plankton net catches. Mar Biol 13: 309-317.
- Roberts CM (1997) Connectivity and management of coral reefs. Science 278: 1454-1457.
- Roughgarden J, Iwasa Y, Baxter C (1985) Demographic theory for an open marine population with space-limited recruitment. Ecology 66:54-67.
- Rudorff CA, Lorenzetti JA, Gherardi DF, Lins-Oliveira JE (2009) Modeling spiny lobster larval dispersion in the Tropical Atlantic. Fish Res 96: 206-215.
- Saenz-Agudelo P, Jones GP, Thorrold SR, Planes S (2011) Connectivity dominates larval replenishment in a coastal reef fish metapopulation. Proc R Soc B. DOI: 10.1098/rspb.2010.2780
- Sale PF (2004) Connectivity, recruitment variability, and the structure of coral reef fish communities. Integr Comp Biol 44:390–399.
- Santos RO, Lirman D, Serafy JE (2011) Quantifying freshwater-included fragmentation on submerged aquatic vegetation communities using a multi-scale landscape ecology approach. Mar Ecol Prog Ser 427: 233-246.
- Shanks AL (1995) Orientated swimming by megalopae of several Eastern North Pacific crab species and its potential role in their onshore migration. J Exp Mar Biol Ecol 186:1-16.
- Shanks AL, Eckert GL (2005) Population persistence of California current fishes and benthic crustaceans: a marine drift paradox. Ecolog Mono 75:505-524.
- Shanks AL (2009) Pelagic larval duration and dispersal distance revisited. Biol Bull 216: 373-385.
- Siegel DA, Kinlan BP, Gaylord B, Gaines SD (2003) Lagrangian descriptions of marine larval dispersion. Mar Ecol Prog Ser 260: 83-96.
- Siegel DA, Mitarai S, Costello CJ, Gaines SD, Kendall BE, Warner RR, Winters KB (2008) The stochastic nature of larval connectivity among nearshore marine populations. Proc Nat Acad Sci USA 105:8974-8979.
- Silberman JD, Sarver SK, Walsh PJ (1994) Mitochondrial DNA variation and population structure in the spiny lobster *Panulirus argus*. Mar Biol 120: 601-608.

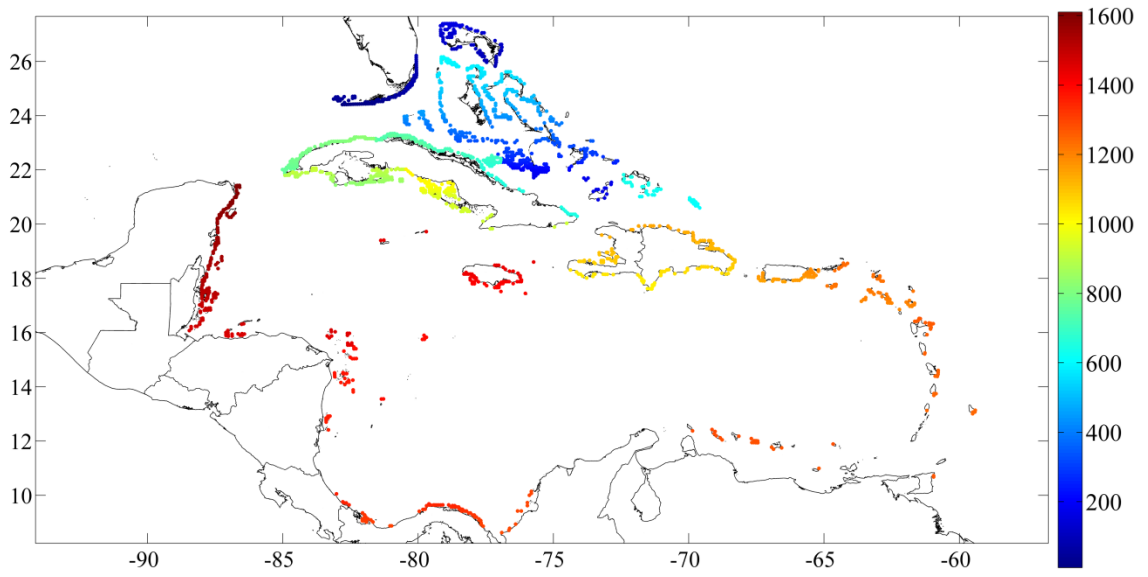
- Simons RD, Siegel DA, Brown KS (2013) Model sensitivity and robustness in the estimation of larval transport: a study of particle tracking parameters. *J Mar Sys* 119:19-29.
- Simpson SD, Jeffs A, Montgomery JC, McCauley RD, Meekan MG (2007) Nocturnal relocation of adult and juvenile coral reef fishes in response to reef noise. *Coral Reefs* 27: 97-104. doi:10.1007/s00338-007-0294-y
- Simpson SD, Meekan MG, McCauley RD, Jeffs A (2004) Attraction of settlement-stage coral reef fishes to reef noise. *Mar Ecol Prog Ser* 276:263-268. doi:10.3354/meps276263
- Smith MD, Lynham J, Sanchirico JN, Wilson JA (2009) Political economy of marine reserves: understanding the role of opportunity costs. *Proc Natl Acad Sci USA* 107: 18300-18305.
- Sponaugle S, Paris CB, Walter KD, Kourafalou V, d'Alessandro E (2012) Observed and modeled larval settlement of a reef fish in the Florida Keys. *Mar Ecol Prog Ser* 453: 201-212
- Staaterman E, Paris CB, Helgers J (2012) Orientation behavior in fish larvae: a missing piece to Hjort's Critical Period Hypothesis. *J Theor Biol* 304:188–196.
- Staaterman E, Paris CB (2013) Modeling larval fish navigation: The way forward. *ICES J Mar Sci*. doi: 10.1093/icesjms/fst103.
- Steneck RS, Paris CB, Arnold SN, Ablan-Lagman MC, Alcala AC, Butler MJ, McCook LJ, Russ GR, Sale PF (2009) Managing outside the box: coalescing connectivity networks to build resilience in coral reef ecosystems. *Coral Reefs* 28: 367-378.
- Stobutzki IC, Bellwood DR (1998) Nocturnal orientation to reefs by late pelagic stage coral reef fishes. *Coral Reefs* 17:103–110.
- Stockhausen WT, Lipcius RN (2001) Single large or several small marine reserves for the Caribbean spiny lobster? *Mar Freshw Res* 52: 1605-1614.
- Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402: 799-802.
- Tamura H, Miyazawa Y, Oey L (2012) The Stokes drift and wave induced-mass flux in the North Pacific. *J Geophys Res* 117 doi:10.1029/2012JC008113.
- Tankersley RA, McKelvey LM, Forward RB (1995) Responses of estuarine crab megalopae to pressure, salinity and light: implications for flood-tide transport. *Mar Biol* 122:391-400.

- Thorrold SR, Latkoczy C, Swart PK, Jones CM (2001). Natal homing in a marine fish metapopulation. *Science* 291:297-9. doi:10.1126/science.291.5502.297
- Tolimieri N, Jeffs AG, Montgomery JC (2000) Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. *Mar Ecol Prog Ser* 207:219–224.
- Tourinho JL, Sole-Cava AM, Lazoski C (2012) Cryptic species within the commercially most important lobster in the tropical Atlantic, the spiny lobster *Panulirus argus*. *Mar Biol* 159: 1897-1906.
- Trankhtenbrot A, Nathan R, Perry G, Richardson D (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity Distrib* 11:173-181.
- Trancart T, Lambert P, Rochard E, Daverat F, Coustillas J, Roqueplo C (2012) Alternative flood tide transport tactics in catadromous species: *Anguilla anguilla*, *Liza ramada*, and *Platichthys flesus*. *Estuar Coast Shelf Sci* 99:191-198.
- United Nations (1998) Kyoto protocol to the United Nations framework convention on climate change. Available: <http://unfccc.int/resource/docs/convkp/kpeng.pdf>. Accessed 2013 Jan 1.
- Ugolini A, Talluri P, Vannini M (1989) Astronomical orientation and learning in the shrimp *Palaemonetes antennarius*. *Mar Biol* 103: 489-493.
- Vaz AC, Richards KJ, Jia Y, Paris CB (2013) Mesoscale flow variability and its impact on connectivity for the island of Hawai'i. *Geophys Res Lett* 40:332-337.
- Vergassola M, Villermaux E, Shraiman BI (2007) 'Infotaxis' as a strategy for searching without gradients. *Nature* 445:406-409.
- Vikebø FB, Ådlandsvik B, Albretsen J, Sundby S, Stenevik EK, Huse G, Svendsen E, Kristiansen T, Eriksen E (2011) Real-time ichthyoplankton drift in northeast Arctic cod and Norwegian spring-spawning herring. *PLoS One*. doi:10.1371/journal.pone.0027367
- Viltard A, de Felice P, Oubuin J (1997) Comparison of the African and 6-9 day wave-like disturbance pattern over West-Africa and the tropical Atlantic during summer 1985. *Meteorol Atmos Phys* 62: 91-99
- Waples RS, Punt AE, Cope JM (2008) Integrating genetic data into management of marine resources: how can we do it better? *Fish and Fisheries* 9: 423–449.
- Warrant E, Dacke M (2010) Visual orientation and navigation in nocturnal arthropods. *Brain, behavior and evolution* 75: 156-73. doi:10.1159/000314277

- Waterman TH (2006). Reviving a neglected celestial underwater polarization compass for aquatic animals. *Biol Rev Cambridge Phil Soc* 81: 111-5.  
doi:10.1017/S1464793105006883
- Waterman T (1988) Polarization of marine light fields and animal orientation. *Soc Phot Optic Instr Eng* 925:431-437.
- Werner FE, Cowen RK, Paris CB 2007. Coupled biological and physical models: Present capabilities and necessary developments for future studies of population connectivity. *Oceanogr* 20: 54-69.
- Wikramanayake E, Dinerstein E, Seidensticker J, Lumpkin S, Pandav B, Shrestha M, Mishra H, Ballou J, Johnsingh AJT, Chestin I, Sunarto S, Thinley P, Thapa K, Jiang G, Elagupillay S, Kafley H, Pradhan NMB, Jigme K, Teak S, Cutter P, Aziz A, Than U (2011) A landscape-based conservation strategy to double the wild tiger population. *Conservation Letters* 00: 1 -9.
- Wilkin JL, Jeffs AG (2011) Energetics of swimming to shore in the puerulus stage of a spiny lobster: Can a postlarval lobster afford the cost of crossing the continental shelf? *Limnol Oceanogr Fluids & Environments* 1:163–175.
- Wright JS, Trakhtenbrot A, Bohrer G, Detto M, Katul GG, Horvitz N, Muller-Landau HC, Jones FA, Nathan R (2008) Understanding strategies for seed dispersal by wind under contrasting atmospheric conditions. *Proc Nat Acad Sci USA* 105: 19084-19089.
- Yeung C, Jones DL, Criales MM, Jackson TL, Richards WJ (2001) Influence of coastal eddies and counter-currents on the influx of spiny lobster, *Panulirus argus*, postlarvae into Florida Bay. *Mar Freshw Res* 52:1217–32.
- Ziegler TA, Cohen JH, Forward RB (2010) Proximate control of diel vertical migration in phyllosoma larvae of the Caribbean spiny lobster *Panulirus argus*. *Biol Bull* 219:207–219.
- Zimmer-faust RK, Tyre JE, Case JF (1985) Chemical attraction causing aggregation in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. *Biol Bull* 169:106–118.



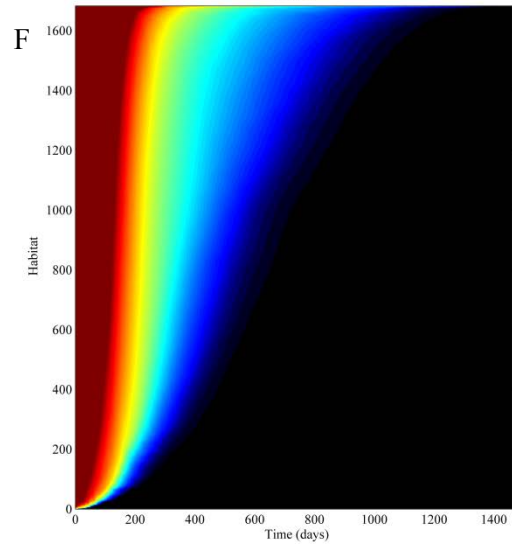
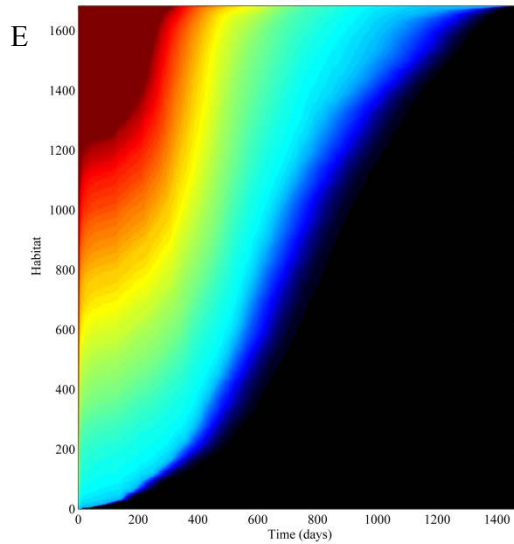
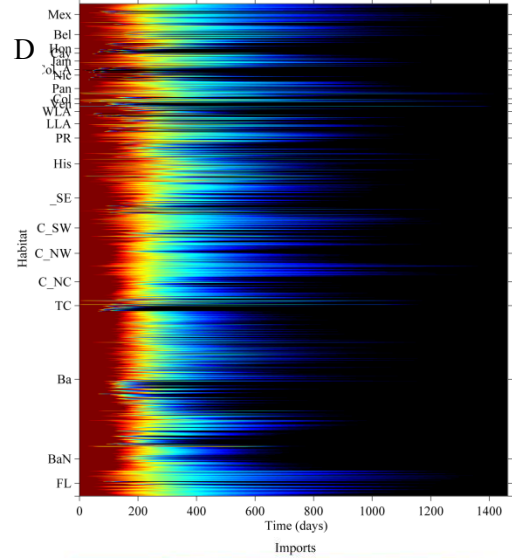
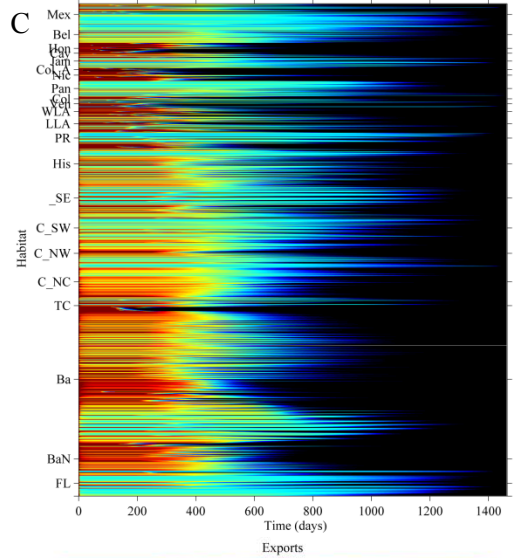
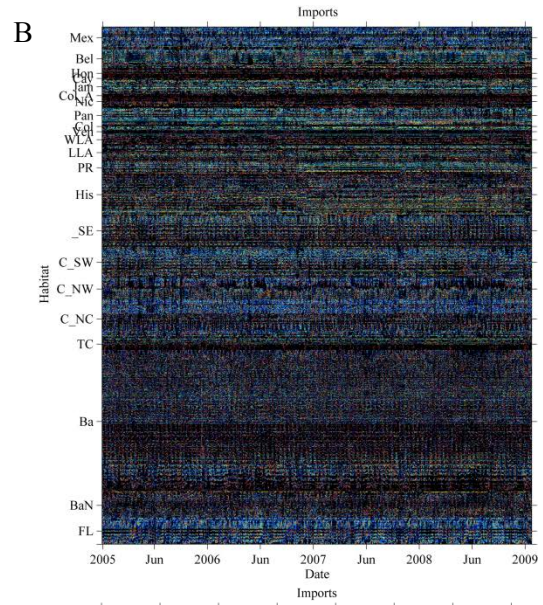
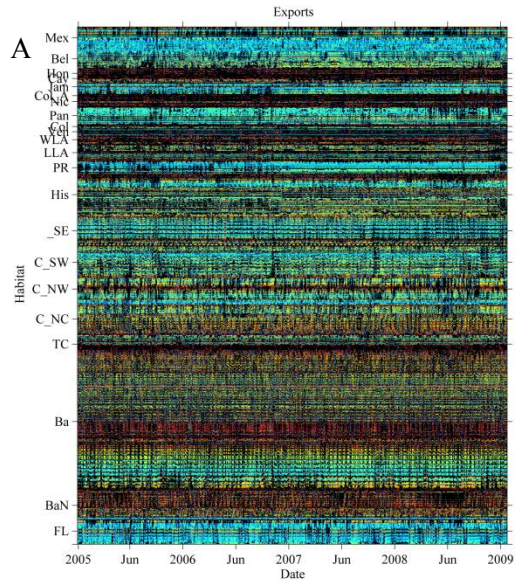
APPENDIX A: Map of habitat used in chapter 2.

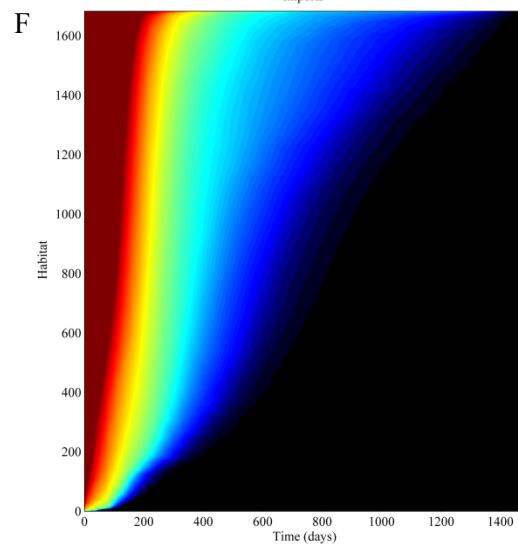
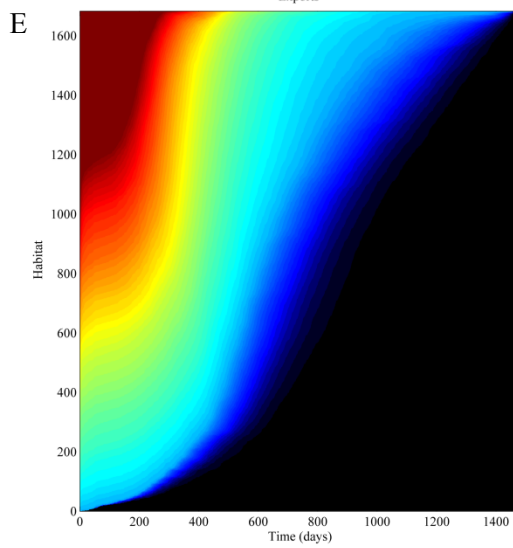
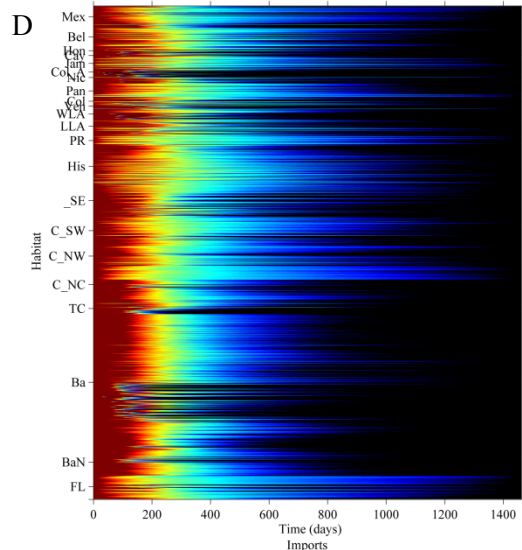
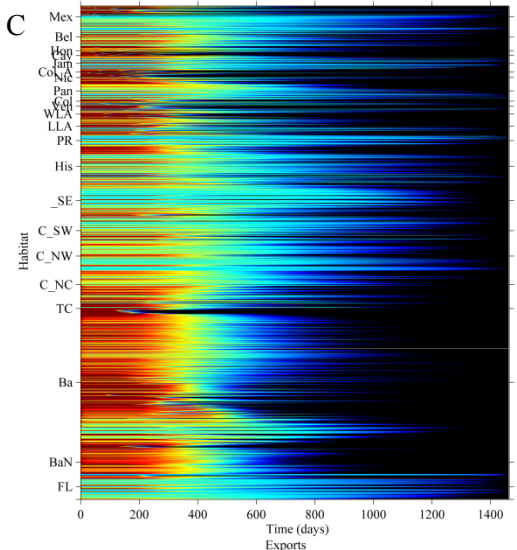
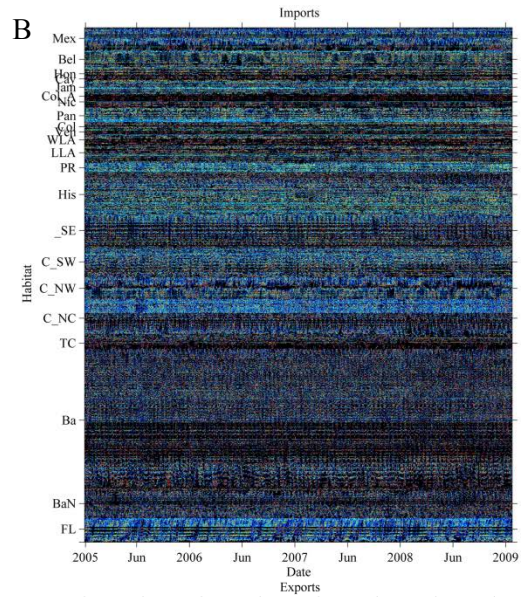
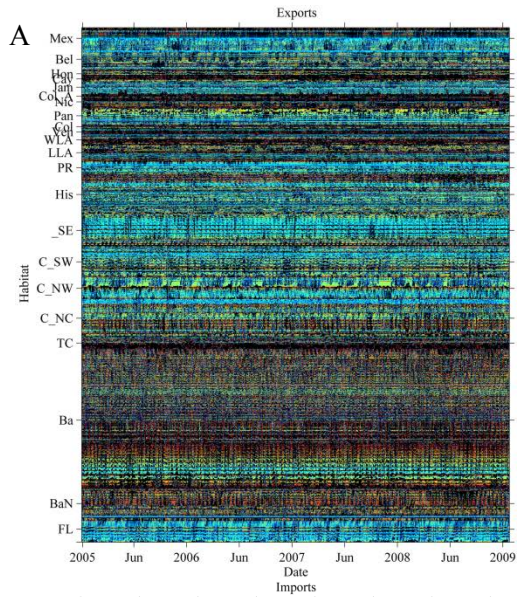


The centroids of the 8×8 km square reef habitat locations used in the simulations. Color is used to identify location numbers, corresponding to the position of habitat in the rows of the connectivity matrices (Figure 2.3 – Figure 2.8).

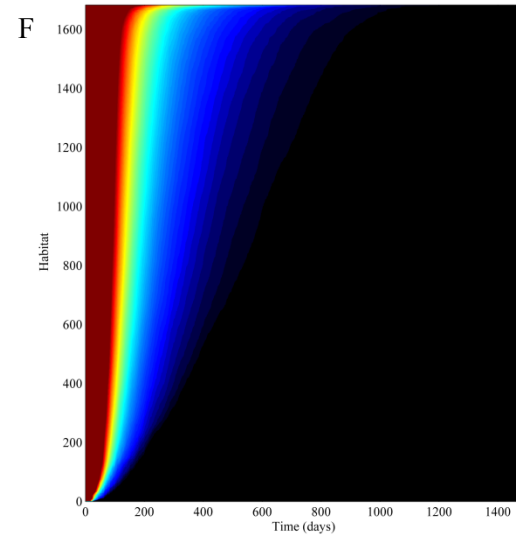
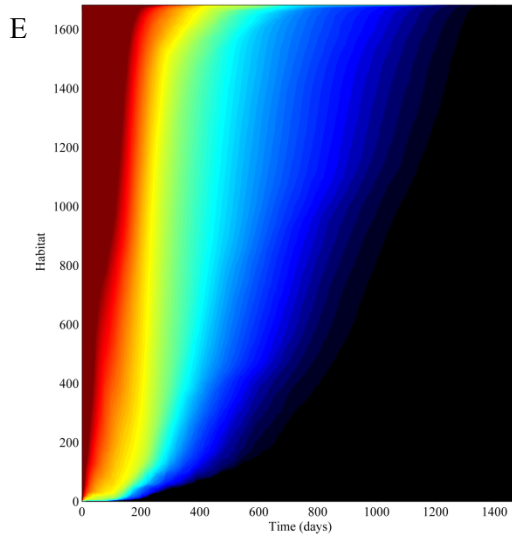
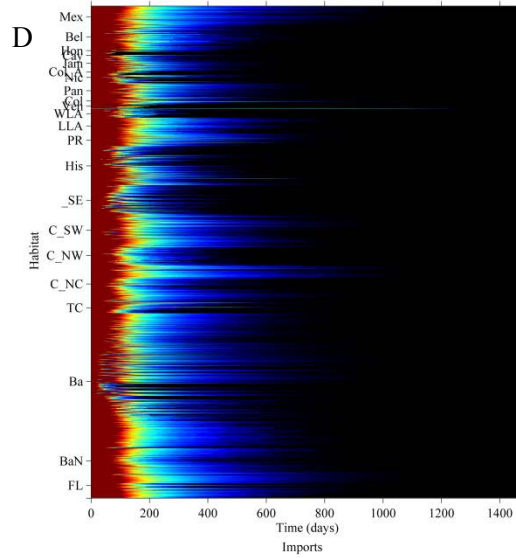
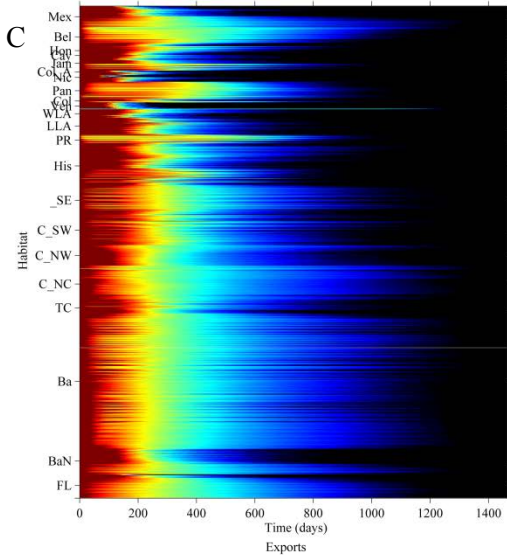
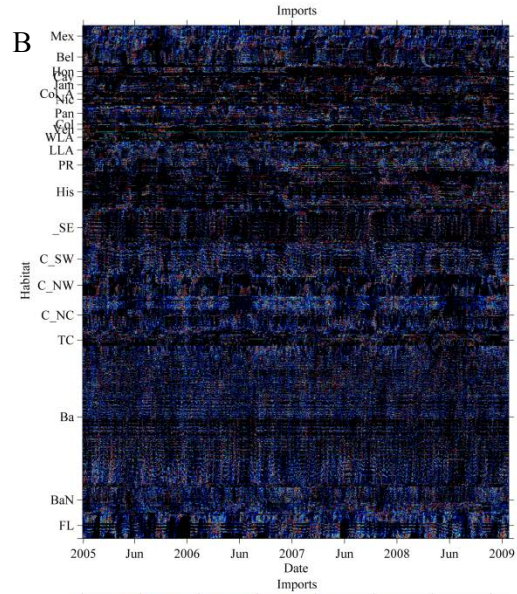
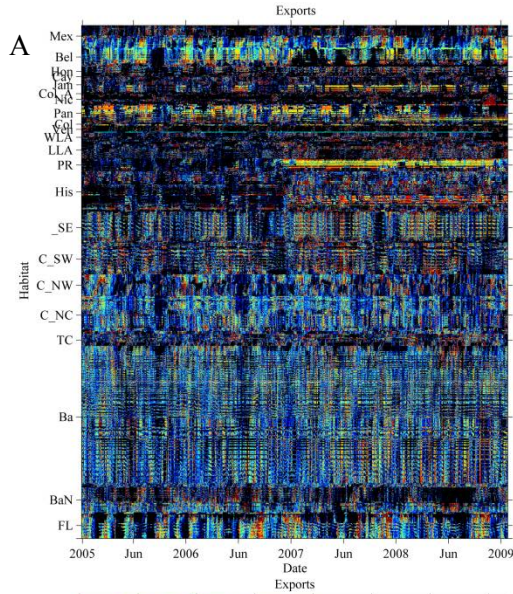
#### APPENDIX B:

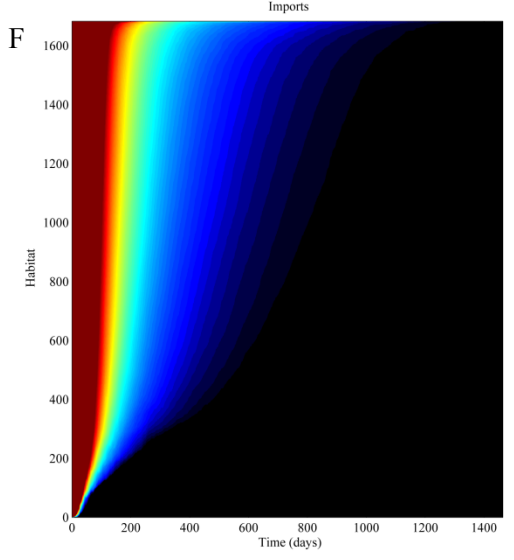
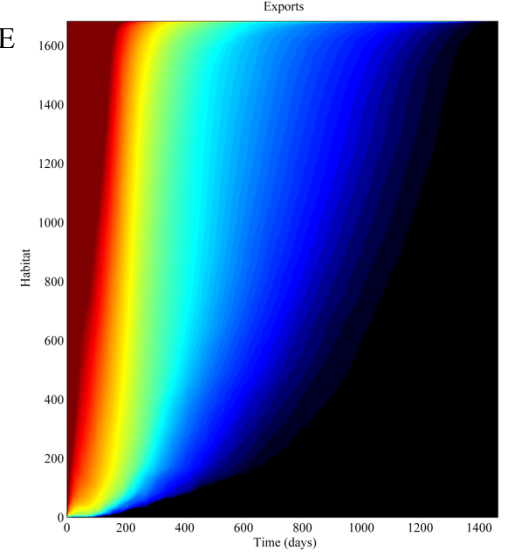
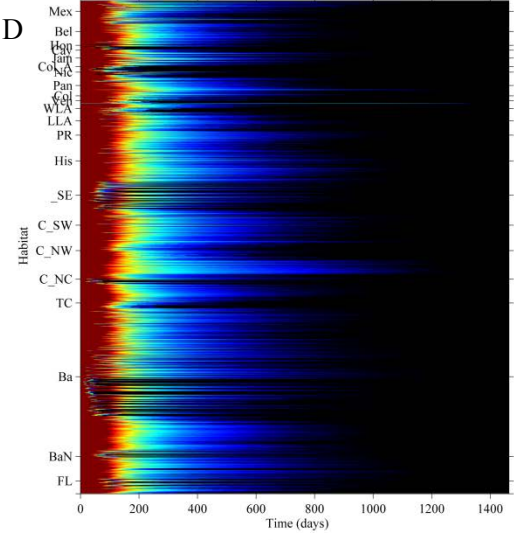
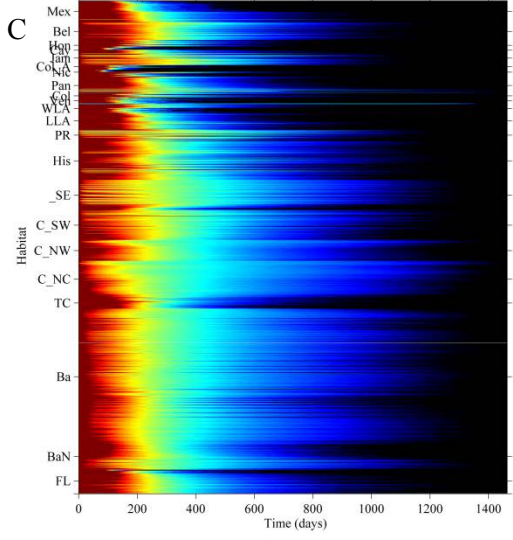
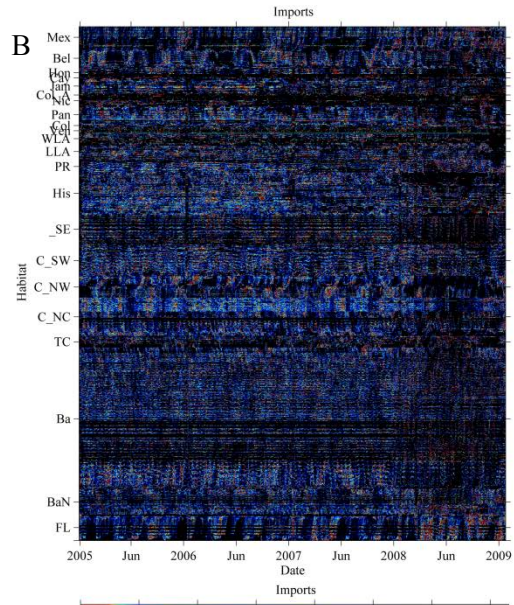
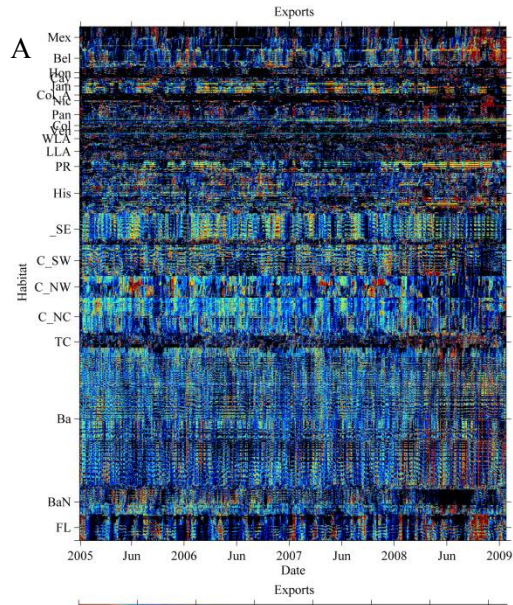
**Visualizing connections through time and space.** Matrices of the daily probability of exporting connections as a source or receiving a connection as a sink at each habitat site through the simulation. The probability matrices as a source (a) and as a sink (b) sorted through time with the highest probability days on the left (source c & sink d), and then sorted across habitat with the highest probabilities at the top (source e & sink f) to make a surface of connection activity through space and time. These are the same matrices as in Figures 2.3-2.8, but are not categorically colored and have more detail as to the magnitude of individual connections. The matrices were colored to demonstrate deviation from constant activity through space and time. Equal export or import activity on each day of the simulation would create a cyan line for a habitat site. Rows that deviate from a solid cyan line are patchy in time. Redder hues indicate days with higher connection activity, and bluer hues indicate days with lower connection, while black indicates no connection. Figure B.1 passive coral. Figure B.2 OVM coral. Figure B.3 passive damselfish. Figure B.4 OVM damselfish. Figure B.5 passive lobster. Figure B.6 OVM lobster.



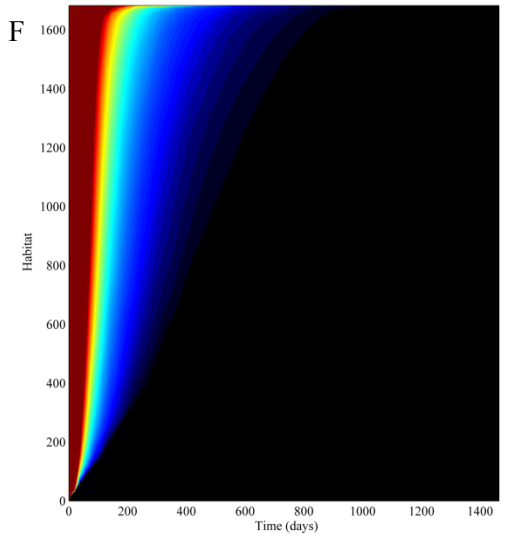
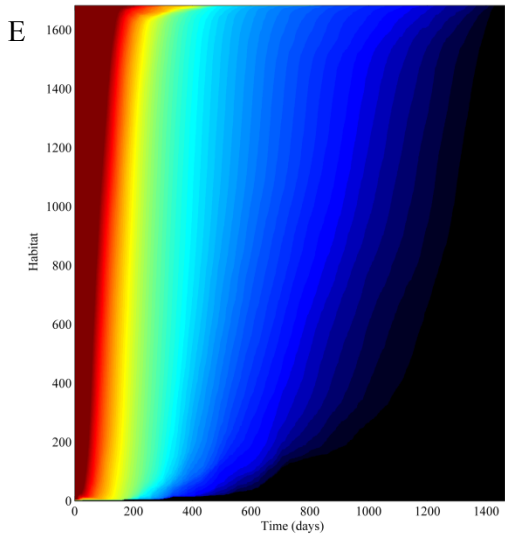
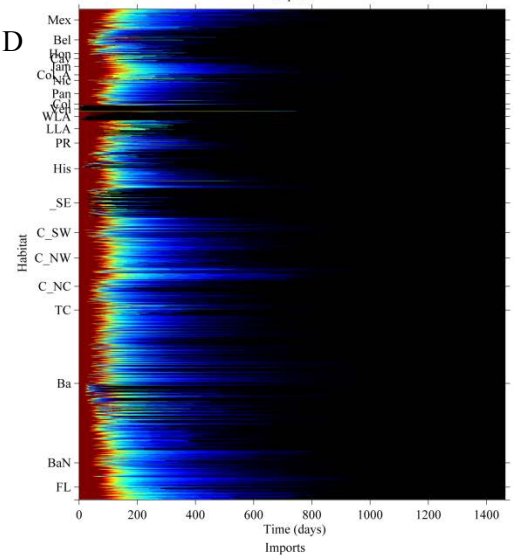
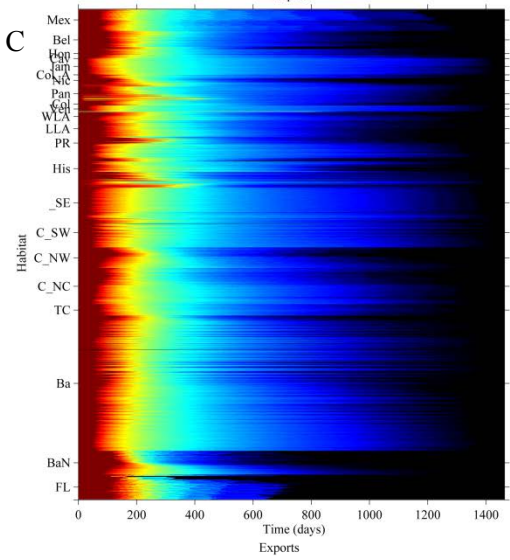
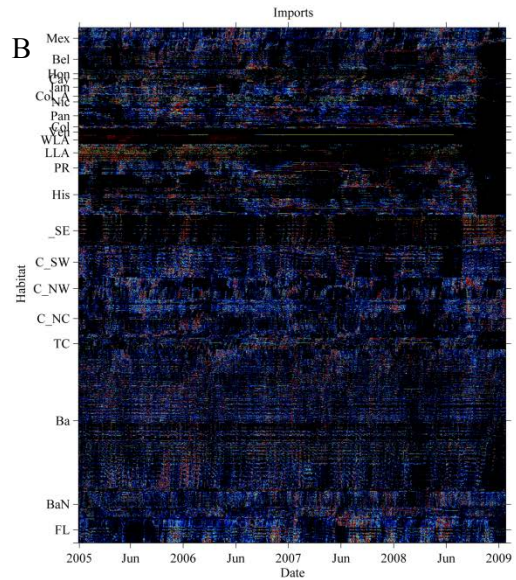
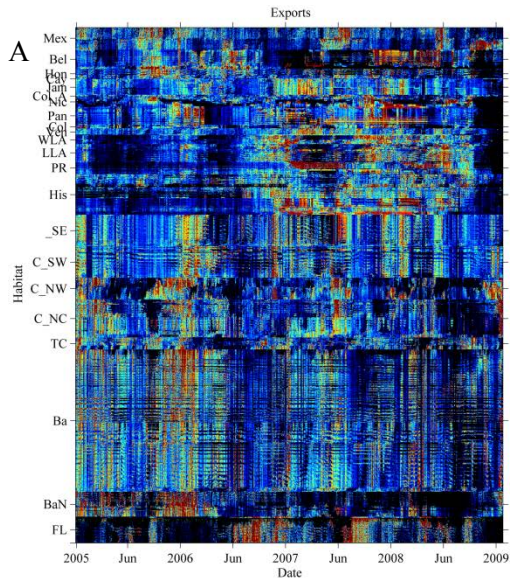


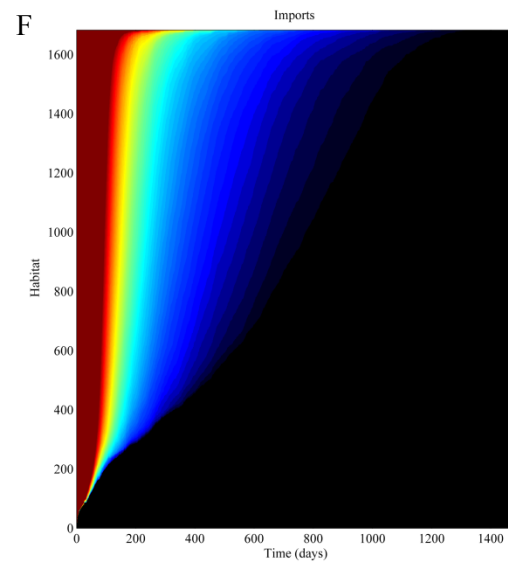
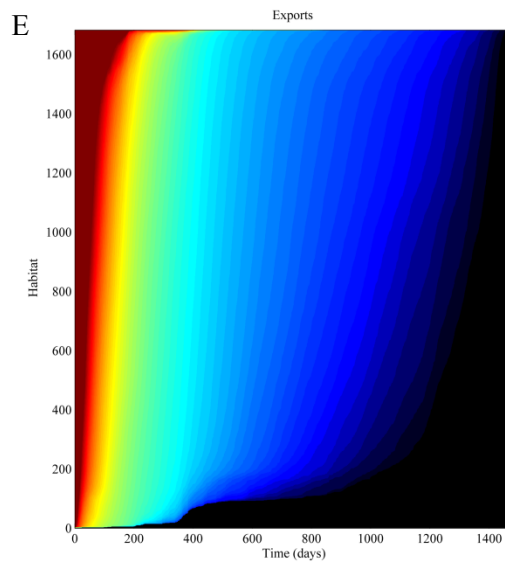
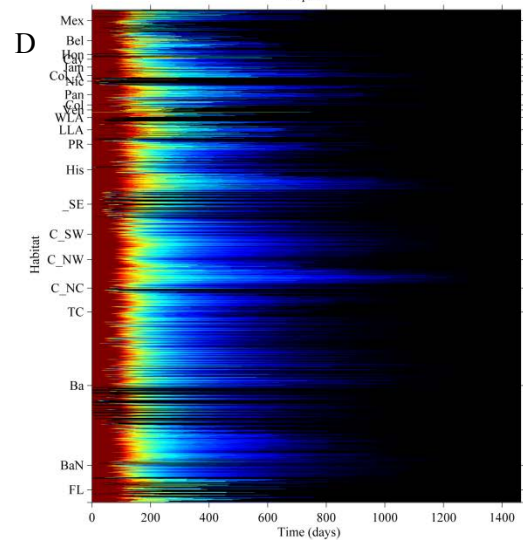
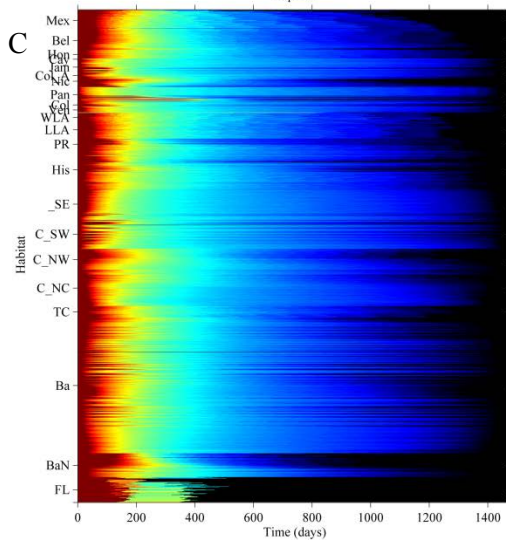
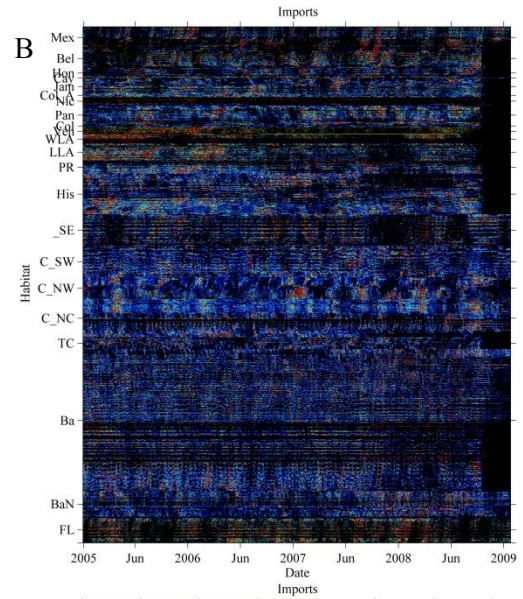
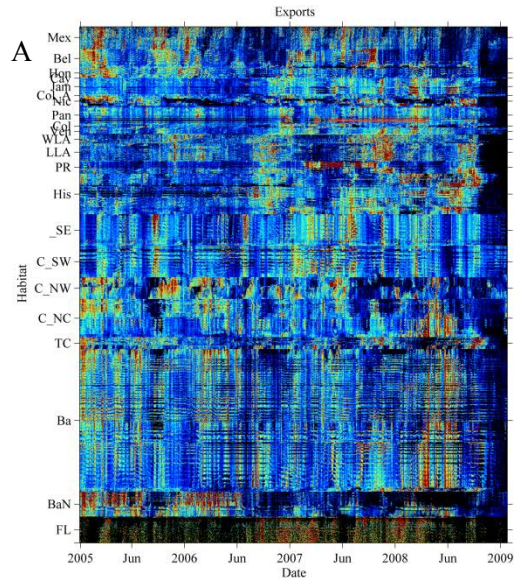






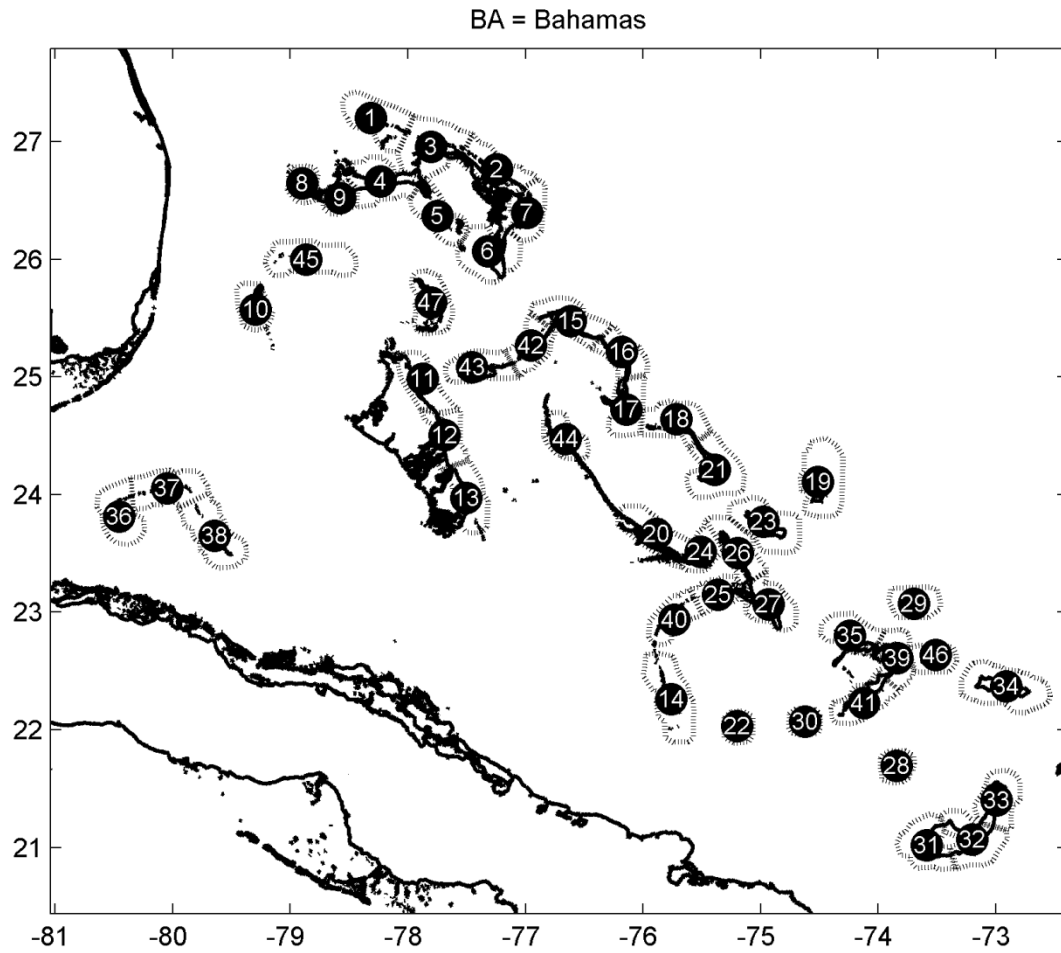


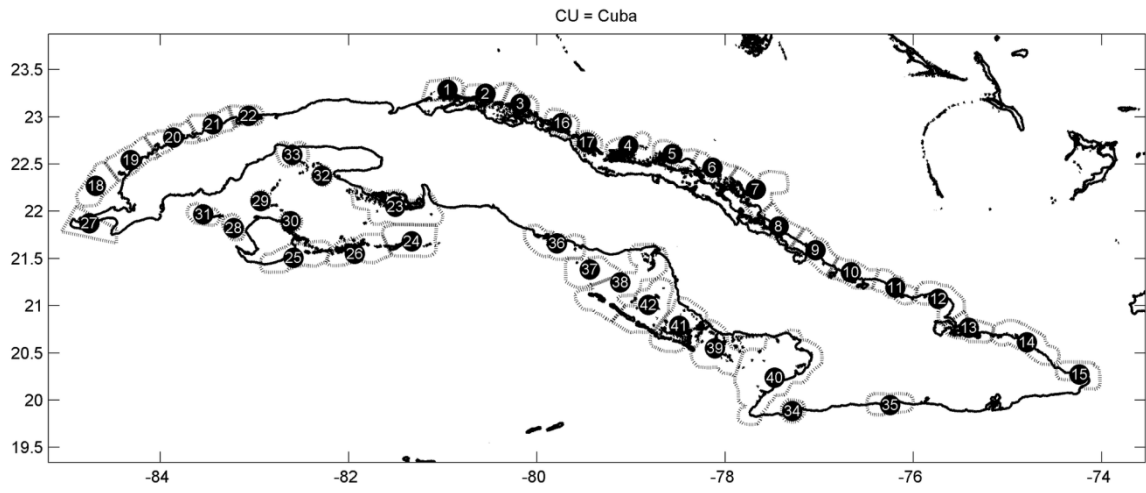




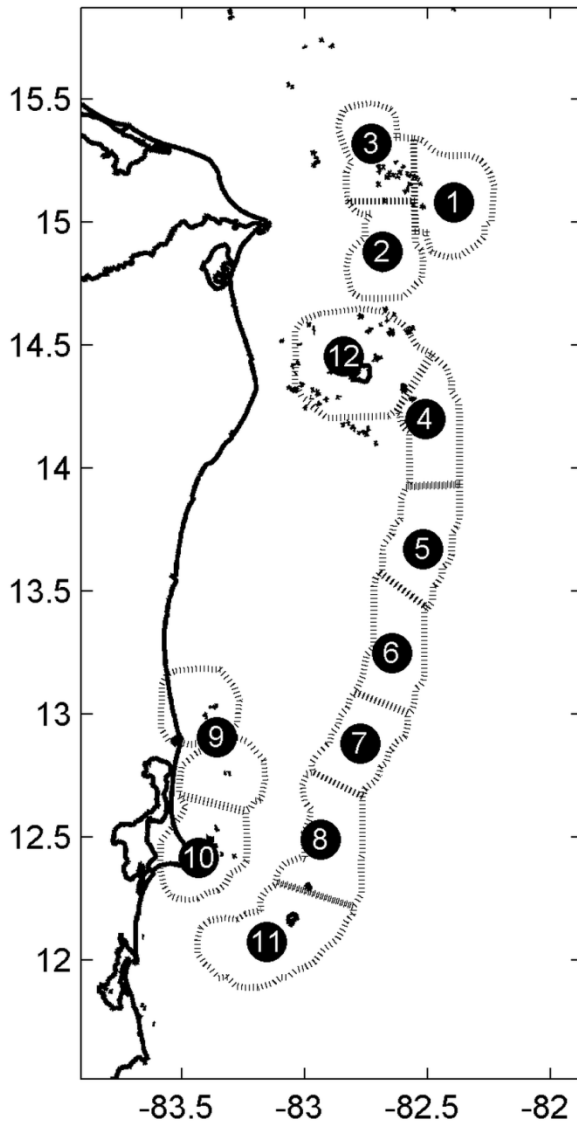


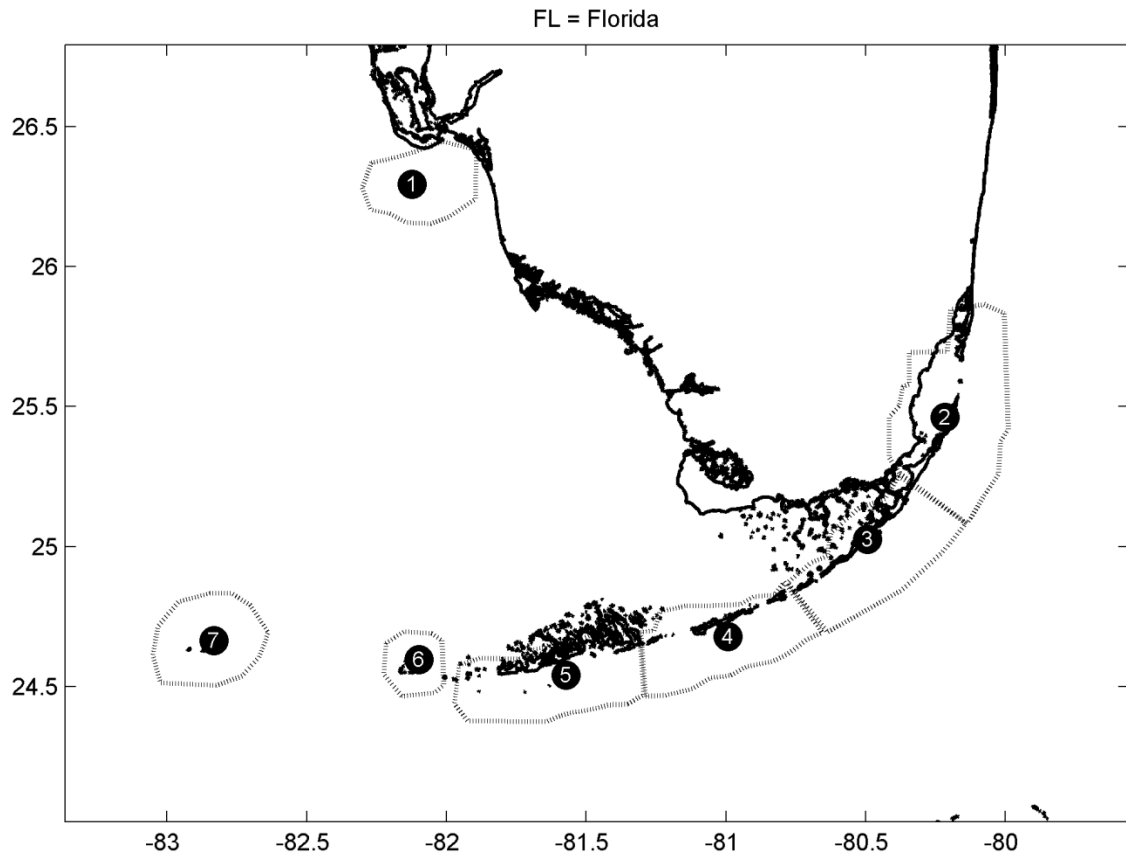
APPENDIX C: Maps of habitat used in chapter 3, listed with the largest populations first and numerically ordered by position within the connectivity matrix (Figure 3.5).



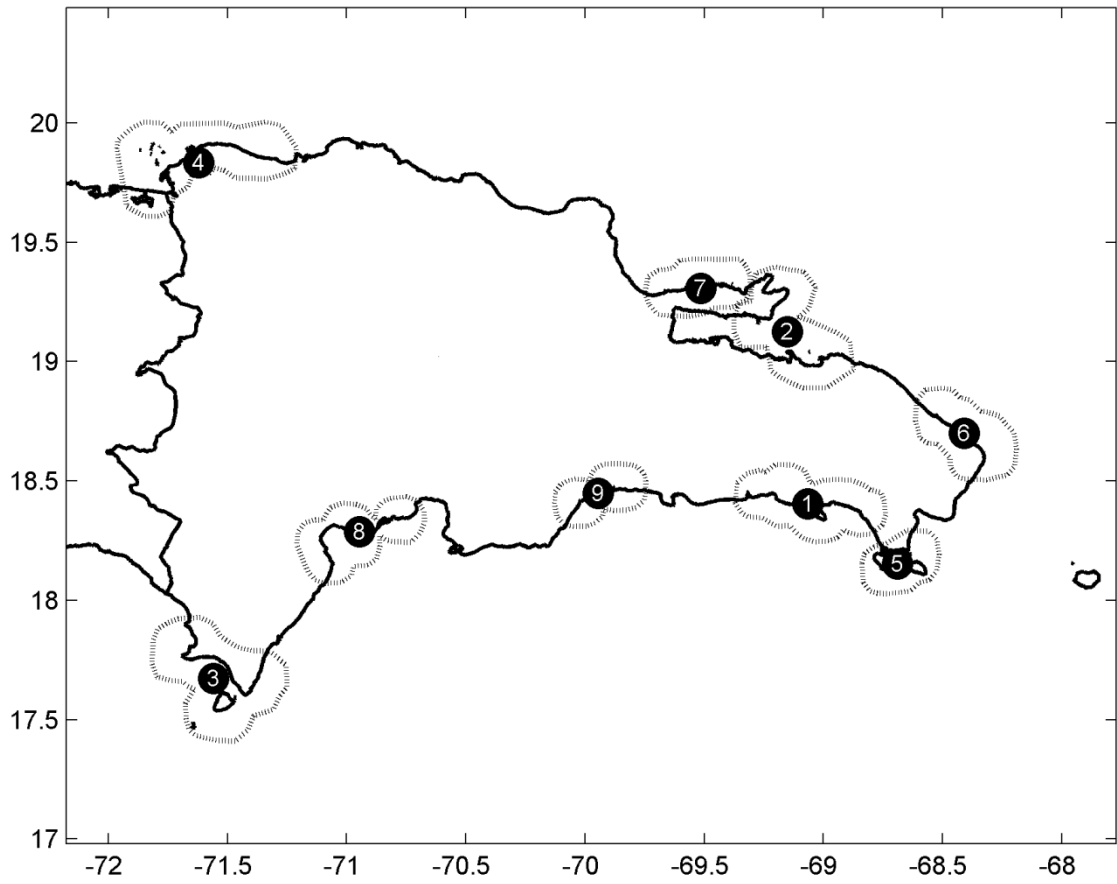


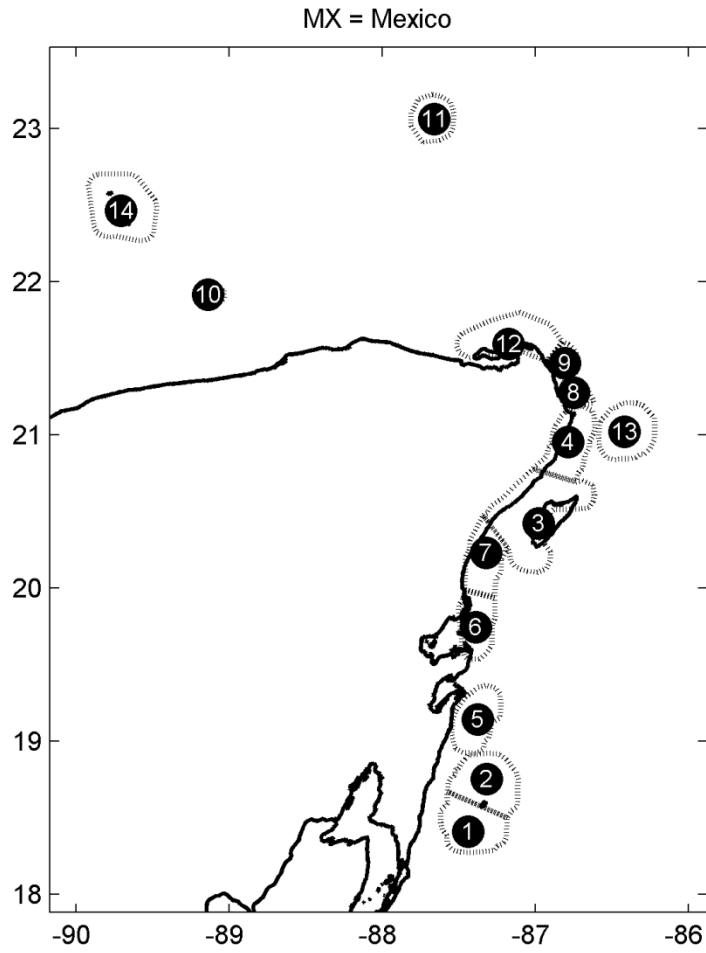
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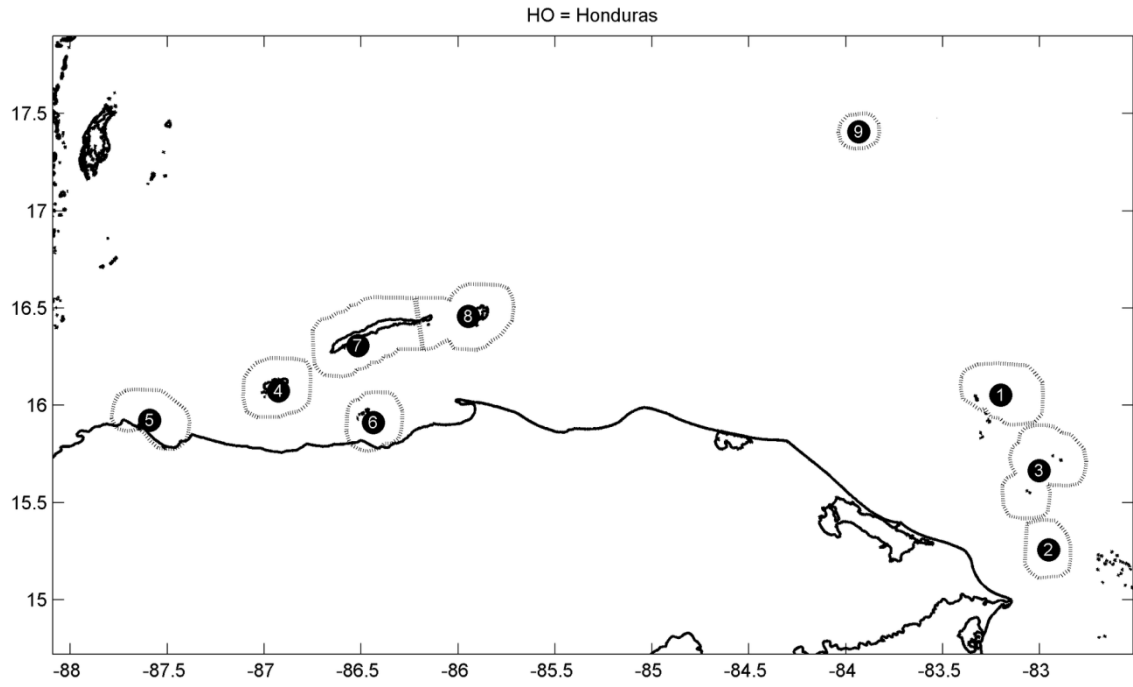


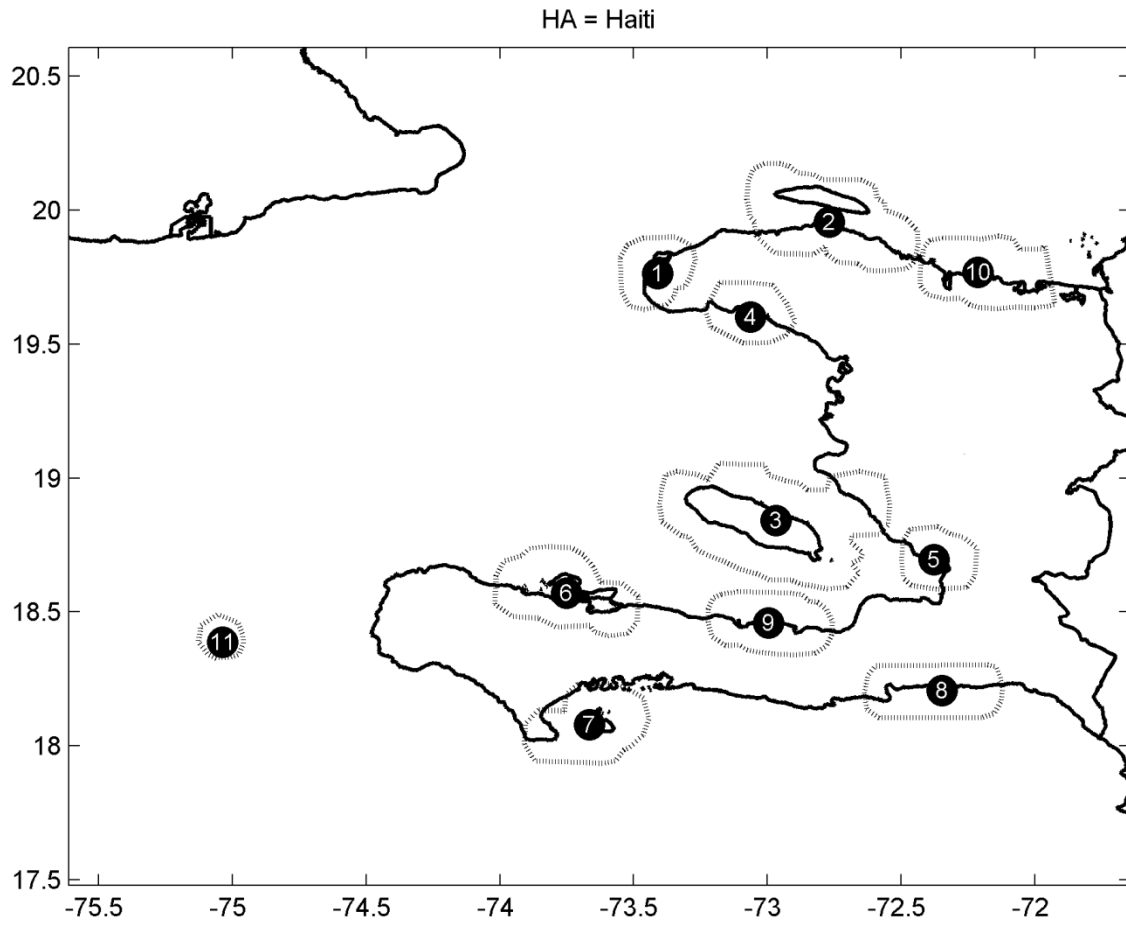


DR = Dominican Republic

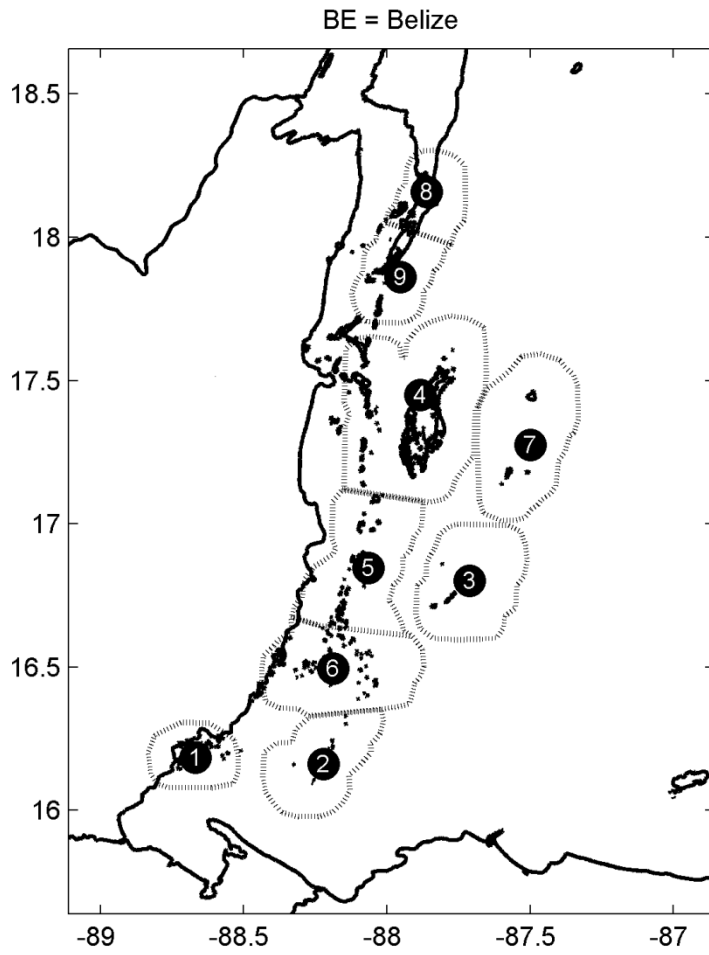


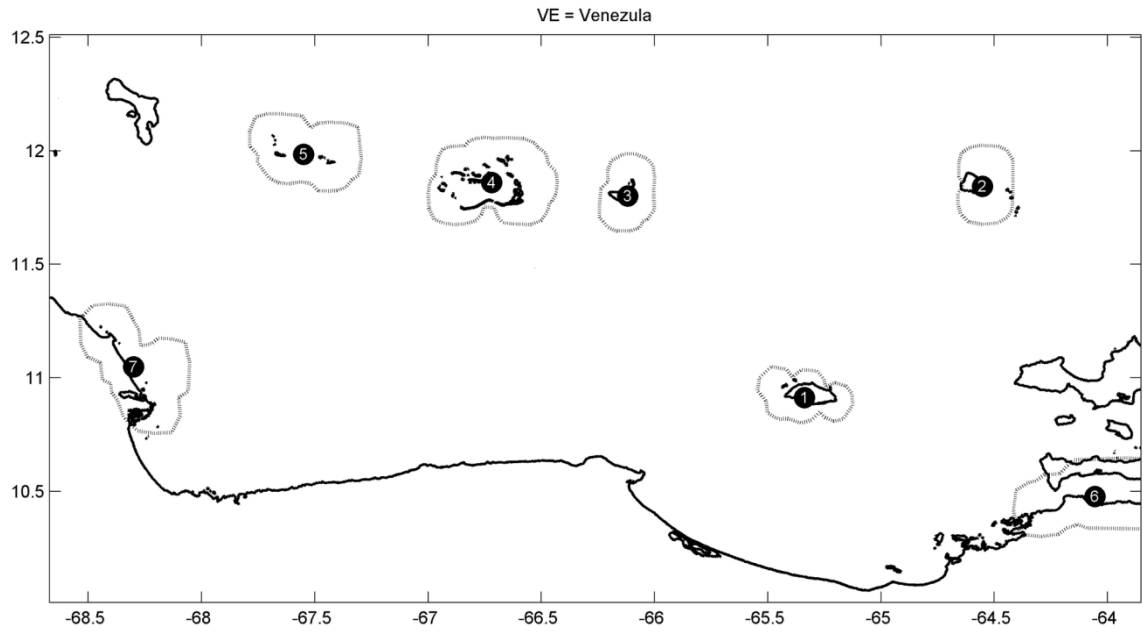


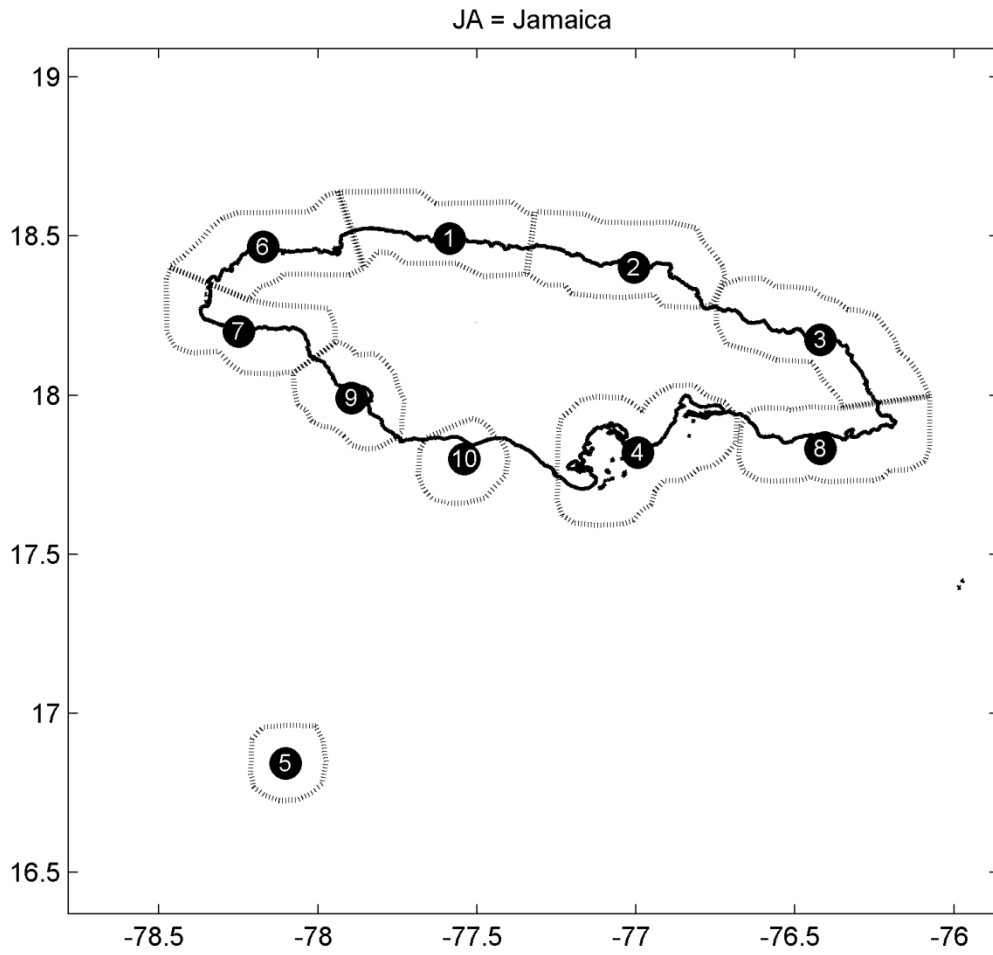




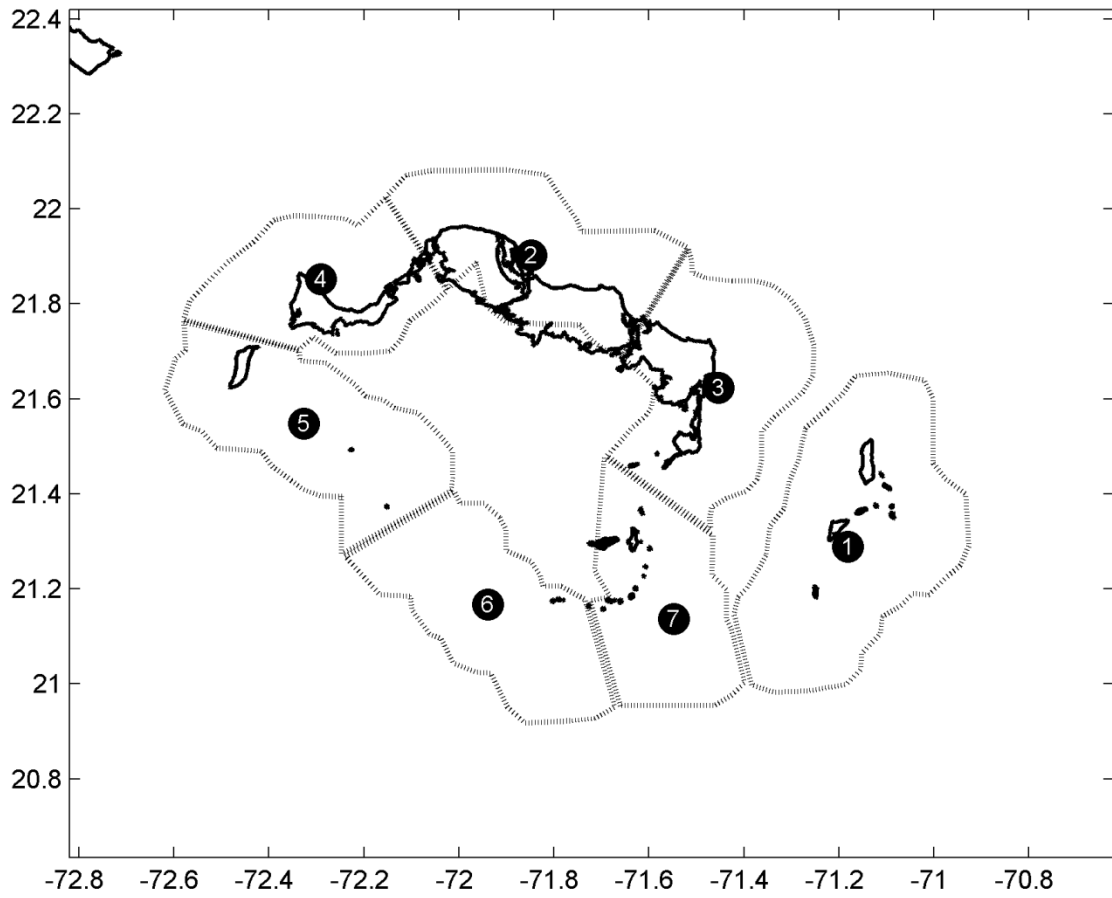




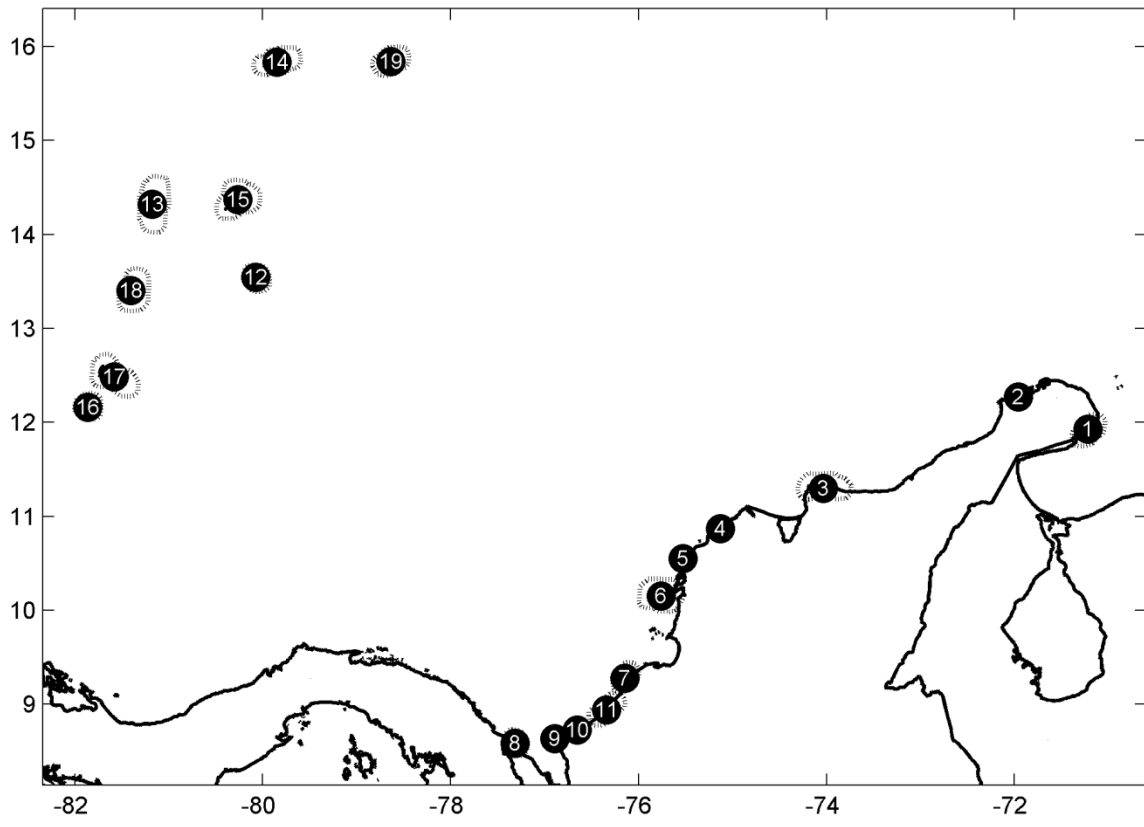


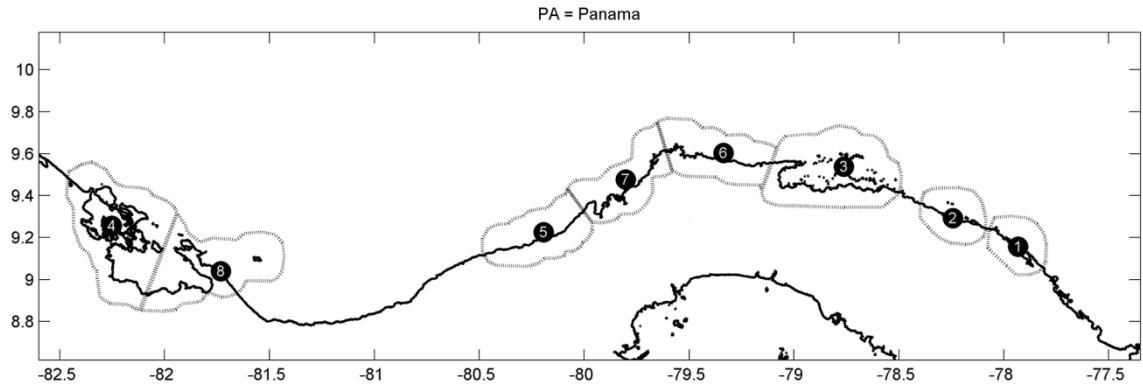


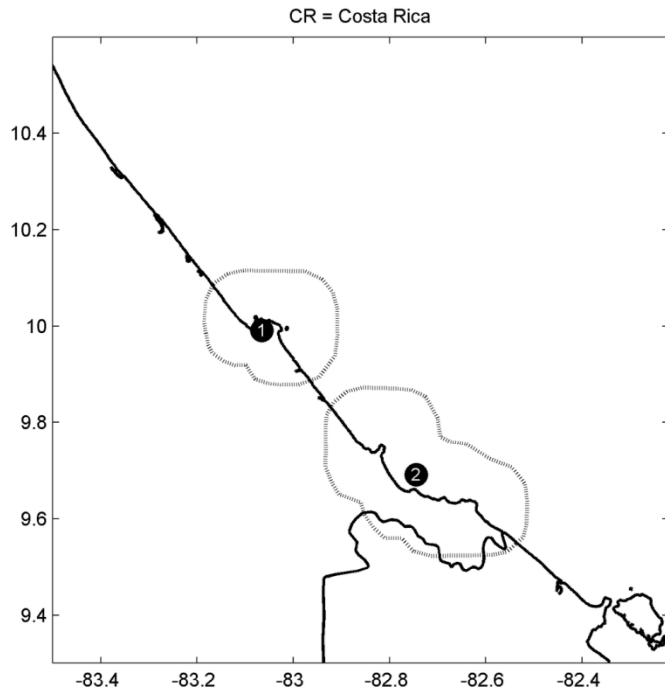
TC = Turks and Caicos

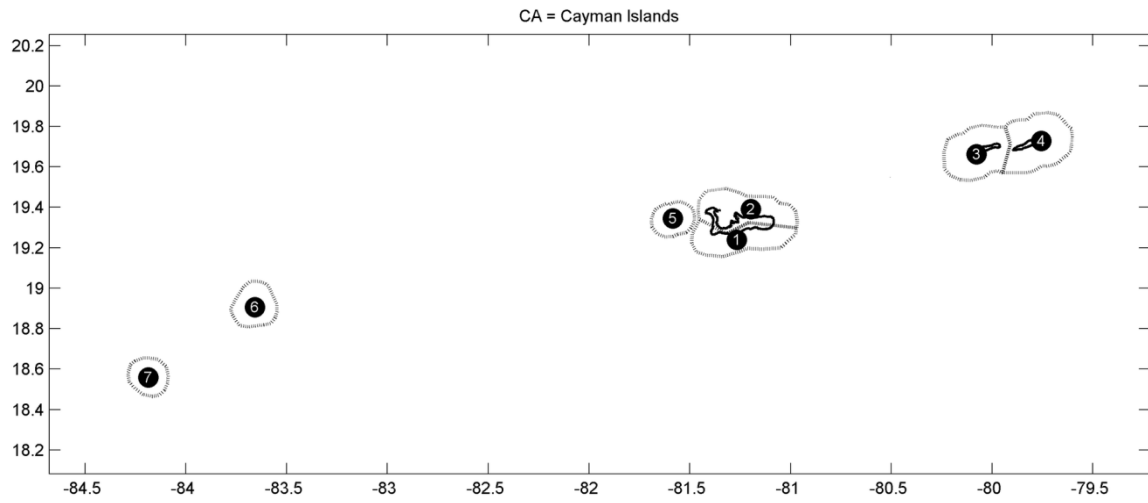


CO = Colombia

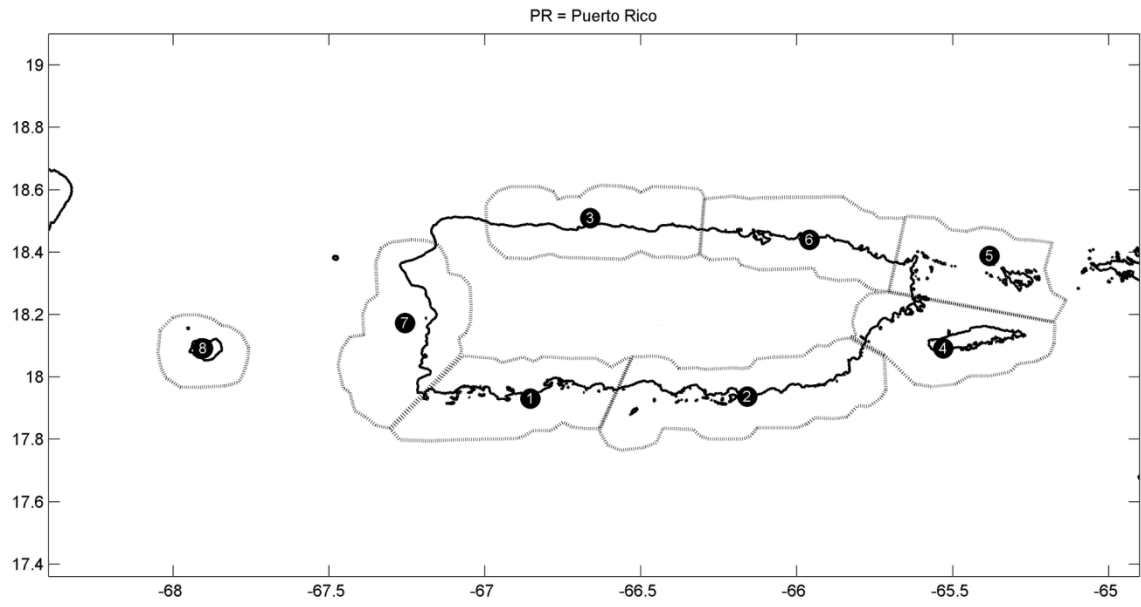


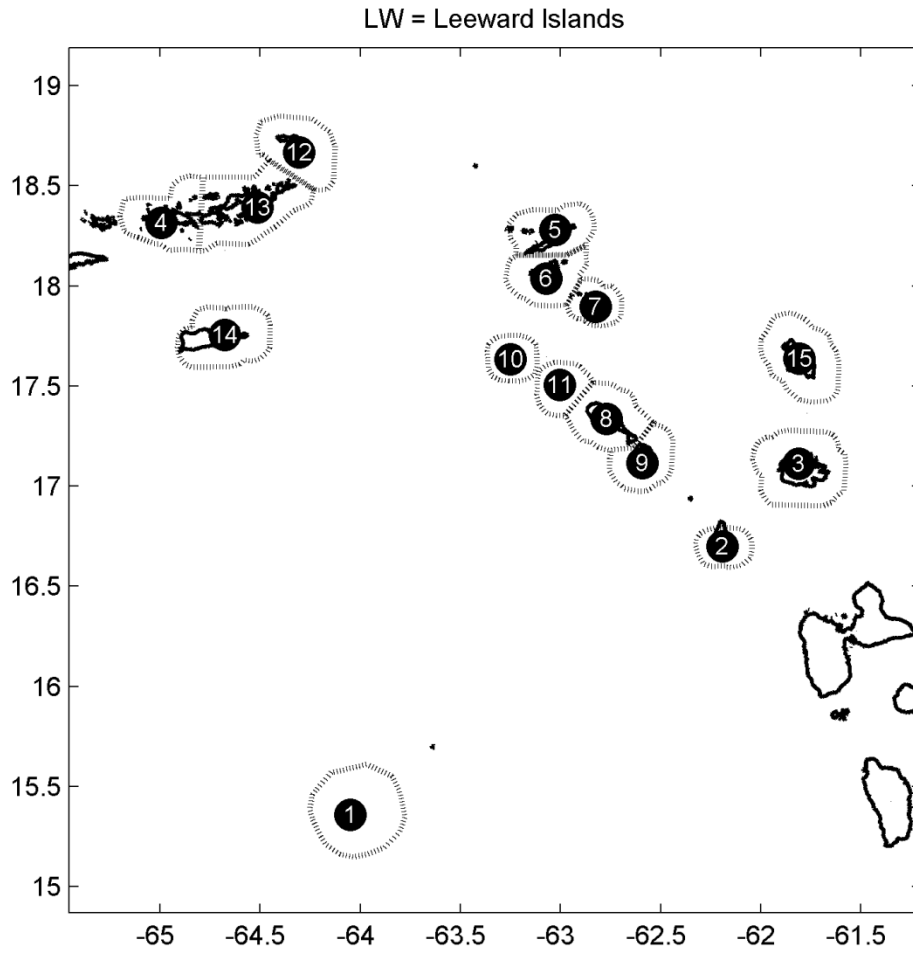












WW = Windward Islands

