Use of Larval Connectivity Modeling to Determine Settlement Habitats of Panulirus argus in The Bahamas as a Pre-cursor to Marine Protected Area Network Planning

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USE OF LARVAL CONNECTIVITY MODELING TO DETERMINE SETTLEMENT HABITATS OF *PANULIRUS ARGUS* IN THE BAHAMAS AS A PRE-CURSOR TO MARINE PROTECTED AREA NETWORK PLANNING

By

Karlisa A. Callwood

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USE OF LARVAL CONNECTIVITY MODELING TO DETERMINE SETTLEMENT HABITATS OF *PANULIRUS ARGUS* IN THE BAHAMAS AS A PRE-CURSOR TO MARINE PROTECTED AREA NETWORK PLANNING

Karlisa A. Callwood

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Caribbean spiny lobster (*Panulirus argus*) is a popular and heavily exploited seafood throughout its range. This species supports the primary fishery in many Caribbean countries, especially in the Bahamas, which reports the highest catches and where spiny lobster serves as the number one food export. *P. argus* possesses one of the longest pelagic larval durations of any marine species, ranging from 6-12 months. This allows for the possibility of long-range dispersal, which would make it difficult to determine if local adult populations originate from areas close-by or within the same countries/jurisdictions, thus presenting implications for conservation and management of the species. This project seeks to explore the policy implications of lobster larval dispersal in the Bahamas by examining the larval connectivity of locally spawned *P. argus* in order to determine the mean dispersal kernel and to identify hotspots of settlement within the area. A coupled biophysical model was used to simulate larval transport from scaled egg production of 47 release locations within the Bahamas. The model was initialized bi-weekly from April through May, the highest months of larvae production in the Bahamas, with each model run occurring for a maximum of 180 days. The dispersal kernel for the Bahamas was calculated to be an average of 100-300 km,
indicating that the larvae released within its boundaries typically settled there as well.
Due to the long pelagic larval duration, larval particles were able to travel extensive
distances, averaging trajectories covering distances of 4000 km and greater from the
source locations. Yet, those same larval particles still settled in locations within the
Bahamas, suggesting local retention, which varies from the common perception that
lobster in the Bahamas originate elsewhere. This knowledge can be used to assess and
perhaps reevaluate conservation and management strategies related to the Bahamian P.
argus fishery, including the implementation of MPAs and/or MPA networks, input and
output management controls, and other management tools.
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Chapter 1: Introduction

Caribbean spiny lobster (*Panulirus argus*) is a popular and heavily exploited seafood throughout most of its range. This species supports the primary fishery in many Caribbean countries (FAO 2006), especially in The Bahamas, which reports the highest catches and where spiny lobster is the number one food export (Ehrhardt *et al.* 2008). With one of the longest pelagic larval durations of any marine species, *P. argus* possess the possibility for long range dispersal, thus increasing the difficulty of determining the origins of local adult populations.

This thesis examines the larval connectivity of locally spawned *P. argus* within The Bahamas in order to determine the mean dispersal kernel and to identify hotspots of settlement within the area. Additionally it seeks to explore the policy implications of lobster larval dispersal in The Bahamas, including investigating the use of connectivity modeling as possible tool to assist in the optimization of MPA network planning for the economically important Caribbean spiny lobster.

1.1 Background

1.1.1 Caribbean Spiny Lobster

*Panulirus argus*, known commonly as the Caribbean or Florida spiny lobster, is a popular, and heavily exploited seafood. It constitutes the primary fishery in many Caribbean countries, and is probably one of the most economically important species, with fishery landings of approximately 35,665 metric tons in 2004 and comprising nearly 46% of the total catch for all spiny lobsters (FAO 2006). However, current fishery regulations of many Caribbean countries appear to be inadequate to protect local populations (Acosta 2002). Subsequently, marine reserves have been proposed as a
conservation and management tool to sustain productive *P. argus* fisheries (Bohnsack 1993).

*P. argus* inhabits tropical and subtropical waters of the Atlantic Ocean, Caribbean Sea and the Gulf of Mexico. It is distributed throughout the western Atlantic Ocean, from Brazil up to North Carolina, as well as Central America, Bermuda, and the Bahamas (Herrnkind 1980; Marx and Herrnkind 1986; Williams 1998). This species typically inhabits shallow waters and can be found in any habitat that offers them protection, such as on reefs, among rocks, and in seagrass beds. DNA analysis of the Caribbean spiny lobster indicates that there is a single stock structure (Silberman and Walsh 1994). This suggests high levels of gene flow due to long range larval dispersal throughout the Caribbean.

*P. argus* lacks the large pinching claws seen in other lobster species. As evidenced by their common name, the species is characterized by spines on the shell used for defense, a striped body, brown-gray in color, with yellow spots on the tail, use a second pair of antennae in sensory perception, and an average total body length of 20 cm (FAO Fisheries Synopsis 1991). If startled, *P. argus* will kick their tail rapidly to swim away backwards to safety. A primarily nocturnal animal, this organism hides in crevices and under ledges during the day. They are solitary until they reach their juvenile stage; at this point, they begin to congregate around more protective habitats in nearshore areas (Cascorbi 2004).

Caribbean spiny lobsters have a complex life cycle comprised of 4 phases. These are planktonic phyllosome larvae, swimming postlarval pueruli, benthic juveniles, and adults (Marx and Herrnkind 1986). Phyllosoma float in the upper 100 meters of the water
column for up to a year or more, until they settle to become pueruli. Pueruli molt to become juveniles when they encounter suitable inshore substrates such as mangrove roots or seagrass beds. Settlement is often triggered by physical and chemical cues from macroalgal rich hard-bottom, usual from the genus *Laurencia* (Butler *et al.* 1997). Although the benthic juveniles are primarily solitary, they begin to aggregate and migrate offshore where they eventually develop into adults (Marx and Herrnkind 1986).

*P. argus* spawning season occurs April through September in the southeast United States and throughout the year in the Caribbean. Females can produce 500,000 to 1.7 million eggs per spawning. Larvae can be carried for thousands of miles by currents until they settle in shallow nearshore areas among seagrass and algae beds (Marx and Herrnkind 1986). Pelagic larval duration for *P. argus* range from 6-12 months, with settlement triggered by physical and chemical cues produced by macroalgal rich hard-bottom and seagrass areas (Butler *et al.* 1997). The lengthy PLD of this species contributes to the high degree of larval connectivity in the Caribbean. As such, management of spiny lobster stocks must take into account the locations where the larvae are being recruited from, as any ecological issues in one region, as well as any management actions implemented in that region, may have considerable impacts on the stocks at another region.

1.1.2 The Bahamas *P. argus* Fishery

According to Cascorbi, *P. argus* “reaches its greatest abundance, fastest growth, and greatest fecundity” within the waters of The Bahamas (2004), so there is no surprise that the spiny lobster fishery in The Bahamas is one of the most important in the Caribbean
(Ehrhardt et al. 2008). This fishery is responsible for 2% of the Gross National Product of the country and 94% of the total value of its fisheries exports (CRFM Bahamas 2003).

The Bahamian lobster fishery is primarily artisanal, with the species harvested through several different methods, including spear, lobster hook, lobster traps, and casitas. Sometimes referred to as condos, the casitas – sheets of zinc placed on concrete blocks – are used to aggregate large numbers of lobsters for easy capture. Most of the landings in The Bahamas are just the tails, while the head and legs are wasted. Management regulations include gear restrictions, fishing seasons, size restrictions (minimum carapace length of 3.5 inches and tail length of 5.5 inches), and no-take of egg-bearing females. Although spear fishing tends to minimize the occurrence of bycatch, the use of the condos may cause the accidental spear and capture of egg-bearing females, as their tails cannot be viewed when within a casita. (Cascorbi 2004; Gittens 2004)

The high reproductive potential of the spiny lobsters in the Bahamas coupled with the relatively low-tech fishing methods has contributed to the stocks remaining better off when compared to other lobster fisheries. However, although the Bahamian fishery produces 5-6 million pounds of frozen tails per year, recent fishing mortality rates indicate that the stock biomass abundance has declined and that the stock is close to being fully exploited (Gittens and Braynen 2002). In fact, landings from each of the major Caribbean spiny lobster fisheries have decreased consistently from the mid-1990’s (Ehrhardt et al. 2008). Additionally, the introduction of the casitas method may have significant effects on the population, especially since there is little management or enforcement on where these units are placed and who can collect from them.
1.1.3 Marine Protected Areas and MPA Networks

The International Union for Conservation of Nature (IUCN) defines a protected area as “an area of land and/or sea especially dedicated to the protection of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means” (IUCN 1994). Over the past few decades, marine protected areas (MPAs) have emerged as a tool for protecting marine resources and managing the ways in which these resources are utilized. MPAs are being used in both fisheries management and biodiversity conservation to enhance ecosystem resilience, as well as to safeguard ocean resources for future generations. MPAs also help to achieve three main conservation objectives; they maintain essential ecological processes, preserve genetic diversity, and ensure sustainable use of ecosystems (Kelleher 1999).

Marine protected areas have a range of benefits, which can be grouped under three broad categories: ecological, socio-economic, and management. In terms of ecological significance, these areas conserve biodiversity, especially within critical habitats of threatened species (Kelleher 1999, IUCN-WCPA 2008). They protect critical spawning and nursery habitats (IUCN-WCPA 2008) and also serve as a safe haven for exploited species (Kelleher 1999) by offering areas protected from fishing. This aids in the creation of source populations for fisheries; these were previously found in “natural refuges” that were once too deep, remote, or dangerous to access (Roberts et al. 2001). These “natural refuges” no longer exist because as fishing capacity expanded, the refuges decreased. Another ecological benefit provided by MPAs is that they also protect the genetic diversity of exploited populations (Kelleher 1999). Furthermore, an MPA can
serve as a control site for scientific research or for aiding in the designing and evaluation of other protected areas (IUCN-WCPA 2008).

Marine protected areas also have a few socio-economic benefits as well. While there is an ecological advantage of protection from fishing, these areas can conversely enhance fisheries by increasing their productivity (Kelleher 1999). Many believe that areas in close proximity to MPAs will benefit from the spillover (IUCN-WCPA 2008) of the species gaining protection. A marine protected area also serves to protect not only cultural diversity, but attractive habitats and species that can define a community and influence its tourism industry (Kelleher 1999).

A major reason for the support of MPAs is that they can provide a tangible approach to an ecosystem level of management for both fisheries and conservation (Carr 2000). Because the definition of an MPA affords for varying degrees of protection, there exists a spectrum of management strategies that can range from areas of no entry, full protection, or multi-use (IUCN-WCPA 2008). And when used with other management tools, an MPA can offer the cornerstone of the strategy for marine conservation (IUCN-WCPA 2008).

Despite many of the benefits associated with the use of marine protected areas, there exist many issues with their implementation and functionality. MPAs only work if all of the users have a stake in their success (Kelleher 1999). If there are stakeholders who don’t see or understand the values associated with an MPA, then it is more than likely that enforcement within the MPA will be difficult. Also, most MPAs are isolated and less than 10 square kilometers (Roberts et al. 2001), which becomes problematic ecologically. However, while creating a large MPA would provide a solution to the
ecological conundrum, it becomes impractical in terms of economics and management (IUCN-WCPA 2008). For these and other reasons, it makes sense to convert from single marine protected areas to networks of MPAs that have some degree of connectivity.

Recently, the importance of the interconnectedness of marine habitats and their associated processes has highlighted the need for moving beyond individual MPAs to networks of MPAs, as it is the belief that such larger-scale approaches are necessary for the protection and conservation of these processes to be effective. The IUCN-WCPA defines a marine protected area network as “a collection of individual MPAs or reserves operating cooperatively and synergistically, at various spatial scales, and with a range of protection levels designed to meet objectives that a single reserve cannot achieve” (2008). A “network” implies that there is some sort of coordinated system in place. The areas must be linked on both a biological and administrative level, and reflect a consistent approach to their design, management, and monitoring (Roberts et al. 2001).

An MPA network can help maintain a functional marine ecosystem by encompassing temporal and spatial scales (IUCN-WCPA 2008) and creating protected areas that are linked by processes, especially larval transport (Roberts et al. 2001). Therefore, the composition and function of an MPA is highly dependent upon the strength of its interactions with other sites (Stoms et al. 2005), which serves to increase connectedness. Thus, the key factor for these networks to work well is dispersal (Roberts et al. 2001).

Establishing networks of several small to moderately sized MPAs may magnify the benefits provided by a single MPA, while also addressing some of the challenges of a single MPA. A network can increase the connectedness between protected and unprotected areas (Allison et al. 1998). It can also reduce the risk of anomalous effects
on a single reserve (Allison et al. 1998). And when truly effective, networks can protect large-scale processes, slow the loss of endangered species, and restore depleted fisheries (IUCN-WCPA 2008). In addition, a network is necessary to ensure biological connections are maintained between independent MPAs (Lafolley 2008).

1.1.4 Connectivity

Connectivity, described as “the degree of movement of organisms or processes” (Crooks and Sanjayan 2006), usually refers to the associations that occur between populations of marine organisms in different places. As defined by Sale et al., connectivity is “the demographic linking of local populations through the exchange of individuals among them as larvae, juveniles, or adults” (2005). The more movement and exchange there is, the more connectivity there is. If no connectivity exists, then the populations are isolated and referred to as closed populations. On the other hand, if there is high connectivity due to numerous exchanges, then the populations are considered to be open populations. As such, population connectivity plays a fundamental role in local and metapopulation dynamics, genetic diversity, and the resiliency of populations. It establishes the spatial scales over which a population is connected, as well as the primary scale over which population interactions and ecosystem dynamics occur (Cowen et al. 2006a).

Connectivity between populations in the marine environment is maintained primarily through larval dispersal, the spread of larvae away from a source to settlement site at the end of the larval stage (Pineda et al. 2007). The extent of this larval movement is important for determining the natural processes that limit population growth and resilience to disturbances (Cowen et al. 2006a). Species with wide dispersal capabilities
tend to be less susceptible to extinction because they have large ranges, multiple populations, and the potential for local recovery. On the other hand, species with less dispersal capabilities become subject to more local extinctions without the ability to regenerate their populations (Almany et al. 2009). Factors that can influence the scale of dispersal include pelagic larval dispersal, water currents, larval behavior, and the availability of suitable habitat for settling (Munday et al. 2009).

Larval dispersal is often described as dispersal kernels. Dispersal kernels describe the probability that a larva released from a particular location will disperse to another specific location with suitable habitat and settle successfully (Largier 2003). These kernels are continuous functions that represent the spatial distribution of dispersed larvae, and can vary in magnitude, width and displacement, symmetry, and spatially and temporally (Botsford et al. 2009).

Understanding the scale of connectivity becomes important for designing effective networks of MPAs (Munday et al. 2009). Connectivity helps to determine the optimal size and spacing of the areas for conservation and the potential for larval dispersal and recruitment to non-reserve areas. Theoretically, species will persist in an MPA as long as the spatial dimensions of the MPA are greater than the width of the determined dispersal kernel (Botsford et al. 2009). Connectivity can also have implications for how MPAs and networks of MPAs are managed (Cowen et al. 2006a), especially as it helps to exhibit the importance of adopting a metapopulation perspective in which the subpopulations, linked through dispersal, can serve as the management unit (Botsford et al. 2009).
1.1.5 Biophysical Modeling

The process of larval dispersal is intrinsically a biophysical problem. It involves interactions between biological traits of the larvae and physical properties of the environment operating on multiple scales (Cowen and Sponaugle 2009). Although horizontal transport of larvae has traditionally been attributed solely to advection in the direction of the flow, in recent years, larval behavior has emerged as having a considerable influence on the outcome of dispersal (Metaxas and Saunders 2009; Levin 2006; Kingsford et al. 2002). Therefore, a full understanding of population connectivity within the marine environment requires adequate comprehension of both the biological and physical process involved in dispersal and transport.

Biophysical models are increasingly being used as predictive tools for larval dispersal and for the general evaluation of the various factors responsible for larval transport. By coupling general circulation models with particle tracking models that can simulate larval transport, these models can be used as methods to quantify larval transport, assess the role of transport in regulating population connectivity, and evaluate the role of different biological and physical factors on dispersal (Metaxas and Saunders 2009). Development of these models entails using an interdisciplinary approach that will combine the larval biology of species of focus with the physical oceanography of the study area of focus.

The physical processes that affect larval dispersion involve both advection and diffusion properties of water circulation; the advection comes from the mean current velocity and direction, while the turbulent diffusion comes from instabilities generated by stochastic motion of the mean current. These physical factors are determined by
hydrodynamic processes, such as tidal currents, Ekman transport, density gradients, frontal structures, and vertical stratification. It is also important to note that these physical processes have the ability to limit larval transport at all spatial scales. (Cowen et al. 2006a; Pineda et al. 2007; Werner et al. 2007)

The biological processes within the biophysical model include those that influence offspring production, growth, development, and survival. Biological parameters that influence dispersion include spawning behavior, larval duration, larval mortality, and larval behavior such as vertical migrations, settlement behavior, and navigation. (Werner et al. 2007)

Two models are commonly used to simulate larval dispersion in marine organisms: eulerian and lagrangian models. Eulerian models are used to solve an advection diffusion equation while providing the spatial and temporal changes in larval concentrations. This model type is used primarily when knowledge of the biological parameters are limited. Lagrangian models, also known as individual-based models (IBMs), are used to capture individual particle pathways. This model is widely used to simulate dispersal by following the trajectories of a large number of particles with specific parameters. The use of IBMs allow for the parameterization of the biological variables (Cowen and Sponaugle 2009; Paris et al. 2007).

1.2 Significance

MPAs are a great idea on paper. They have the potential to contribute greatly to both management and conservation issues, especially as these areas are often seen as key components for the integrated management of marine areas as a way to influence sustainable development (Kelleher 1999). However, despite the many perceived benefits
of marine protected areas, the execution of this management strategy often fails to meet the intended and expected objectives. Many feel that there are too few MPAs to meet conservation goals, and that most of those MPAs are not effectively managed (Kelleher 1999). Additionally, their designs, implementations, enforcement, and evaluations have often been disorganized, thus failing to produce valuable evidence or data towards their effectiveness (Carr 2000). Furthermore, there is often a lack of a comprehensive theoretical framework to understand the population and community processes, as well as the biological and physical processes, that can affect their success (Kelleher 1999). All of these factors contribute to the push towards the use of MPA networks while utilizing additional tools, such as bio-physical models, to aid in their design.

*Panulirus argus* supports one of the most important fisheries throughout its range. However, landings of *P. argus* have declined over the past decade, resulting in a decrease in catch due to fishing pressures and changes or damage to their habitat (Eggleston *et al.* 2003). Although these lobsters are not currently considered to be threatened or endangered, they are recognized as an organism that could be in that position sometime soon (Cascorbi 2004). Because they are a highly sought after species, if high fishing pressures persist without proper management, *P. argus* populations could become at risk for decline. Understanding the population connectivity and local retention of *P. argus* is important for the conservation of this species and the management of this valuable fishery

1.3 Limitations

Optimizing the designs of MPAs is logistically difficult due to the many issues that might arise, whether they are ecological, political, cultural, or economic (Stockhausen
and Lipschius 2001). With MPAs, there are uncertainties as to the extent to which different areas are connected and how MPAs are impacted by dispersal patterns and migrations. As for lobsters, while the biology, ecology, and fishery dynamics of the juveniles and adults are well known (Goldstein et al. 2008), knowledge of the biological and population dynamics of the larval stages is quite limited. Understanding of connectivity is also poor, especially since it is difficult to quantify all the factors affecting dispersal in the water.

Using biophysical models does present some challenges as these models are often limited in their temporal and spatial resolution. They often cannot cover the entire spatial extent of the dispersal process or the full larval history of the focus species (Cowen and Sponaugle 2009). Additionally, the performance of these models is constrained because the parameterization of the both the physical and biological components can only be as good as estimates gained from field work (Metaxas and Saunders 2009).
Chapter 2: Statement of Problem and Objectives

The goal of this project is to explore the policy implications of *P. argus* in The Bahamas, by examining the larval connectivity of locally spawned individuals of the species. This will hopefully serve as the groundwork for later analyses that will consider how this information can be used to assess and perhaps reevaluate conservation and management strategies related to the Bahamian *P. argus* fishery, including the implementation and design of MPAs and/or MPA networks, input and output management controls, and other management tools. The specific objectives are to:

1. Calculate mean dispersal kernels for the sub-regions; and
2. Identify hotspots, i.e. locations of higher larval settlement within the Bahamas.
Chapter 3: Methods

3.1 Study Site

The Commonwealth of the Bahamas is an archipelago of over 700 islands and 2,400 uninhabited islets and cays (Figure 1). The 19 major islands of the Bahamas comprise a total area of 13,935 km². These islands and cays are spread over a shelf area of about 153,000 km² of shallower water and are located on 16 banks. Found 50 miles off the east coast of Florida, the Bahamas extend 760 miles from the coast of Florida on the north-west almost to Haiti on the south-east.

3.2 Connectivity Modeling System

This project utilizes the Connectivity Modeling System (CMS), which measures dispersal characteristics and marine population connectivity. CMS uses a parallel implementation of an IBM, specifically the BiOphysical Larval Tracking System (BOLTS), that features access to open model data using OPeNDAP and statistical interpolation of observations. CMS was developed to study complex larval migrations by simulating larval characteristics, such as larval movement, growth, and survivorship, while taking into account interactions with the pelagic physical environment and benthic habitats.
3.2.1 Model Setup

The biophysical model simulates dispersal and recruitment of larvae using a spatially explicit 3-dimensional IBM as described by Paris et al. (2007). This model links biological and physical modules to form a coupled biophysical IBM that allows the model to track individual larvae within a population as it interacts with the environment, and then produces probabilistic simulations of the larval trajectories and connectivity matrices.

The model is composed of several standalone modules that are coupled and parallelized (Figure 2). Individual larval particles are moved by the 3-D current (the oceanographic module), a specific behavior (the biological module), and turbulence. The base of the IBM tracking is a Lagrangian stochastic model (LSM) with a 4th order Runge-Kutta integration.

The ocean circulation module is an integration of archived velocities responsible for moving the larval particles. ROMS (Regional Ocean Modeling System), the generalized circulation model used for this project, has a domain that extends from the Grand...
Bahama and the Abacos in the north to the south of Turk and Caicos, with a resolution of 5 km (http://cassandra.rsmas.miami.edu:8080/thredds/dodsC/bah). The model has 25 vertical layers; the first 7 layers were utilized for this model.

Within the biological module, larval traits are simulated as a function of the development stage and settlement habitat. This includes parameters such as pelagic larval duration (PLD) and larval behavior, including vertical swimming capabilities. The biological module serves to stimulate larval movement, in addition to movement due to advection by the currents. A vertical matrix (Table 1) is included in the biological module to represent the ontogenic migration of the larval particles as they age. It contains a probability density function of larvae distribution with depth. The rows (j) represent depth layers and the columns (i) represent the time intervals. The value at each matrix point (j,i) depicts the percentage of larvae that should be found at that corresponding depth for that time interval.

The biological module is also responsible for releasing the individual larval particles. This information comes from the release file that contains the exact positions where each particle will spawn from. Each of these positions is located inside a polygon (see Seascape module below). Particle release information was obtained from the larval production supply data collected and calculated by the Coral Reef Targeted Research
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Table 2: Bahamas Habitat Polygons

The Polygon Release Numbers is how each polygon is identified in the model, while the Map ID corresponds to the polygon map (Figure 3). Longitude and latitude refer to the release locations within each polygon. Number of particles released has been scaled to make appropriate for model (in April, lobster’s in the Bahamas produce 250 million – 1.7 billion eggs per month per polygon, and 330 million - 2.3 billion in May (Butler et al. 2009).
The Particle Tracking Module uses a LSM that tracks the movements of individual particles offline. This is coupled to the seascape module, which quantifies the ecological interaction at the boundaries of habitat areas. The habitat areas are derived from remote sensing (Spalding et al. 2001; Andrefouet et al. 2004) in the form of polygons that extend throughout the spatial domain of the model (Figure 3), where each polygon corresponds to a specific location (Table 2). The polygons serve as a representation of major spawning and nursery lobster habitats in the model, describing the locations of both the source and recruitment areas. Additionally, an 18 km buffer was extended offshore of each polygon to account for the ability of *P. argus* larvae to sense coastal settlement habitats (Goldstein and Butler 2009). Together, the seascape module and the particle
tracking module traces the source location of the larval particles and provides habitat information to the particles at each time step. The polygons utilized in this model have a resolution of 50 km x 9 km.

The general algorithm for the code within the model involves 4 steps (Figure 4). Once the model is initialized, it reads the grid coordinates of the ocean model and the habitat polygons, as well as the biological information of the species. The larval particles are released based on inputs from the release file. The individual larval particles advance through the domain using the ocean model output frequency, followed by the input of individual larval behavior. If the larval particles are competent, their location is checked for the presence of suitable habitat that can capture it, and the particle is assumed to have successfully recruited. If it is not recruited, the particle will continue to disperse until it is recruited or until the model run for the number of days specified (see Table 3 for information on specific model parameters).

3.2.2. Model Output

The Connectivity Modeling System generates two types of outputs for each larval particle: trajectories and connectivity. The movement of every larval particle at the frequency specified within the model parameters generates a trajectory file that details the location of the model (through latitude and longitude), as well as the radial displacement (measured as a straight line between the larval particle’s initial position and its final position when the model run has completed) and the cumulative displacement (measured by the total distance the particle has traveled). The trajectory output also details the final status of the particle, indicating whether it is alive, dead, came too close to land, left the model area, or recruited to a polygon.
The second output describes the connectivity of the larval particles. The file generated contains information on the source and recruitment areas/polygons of each particle. This data is used to construct the connectivity matrix, which calculates the likelihood of larval exchange from one polygon to another. With this transition probability matrix, each matrix element describes the probability of an individual larva making the transition from its source habitat and successfully reaching the settlement stage in the destination habitat.

<table>
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<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
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<td>The total number of seconds that the particles are moving in the oceans</td>
<td>15552000 sec (180 days)</td>
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<td>hstep</td>
<td>Integration time step</td>
<td>1440 sec (24 min)</td>
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<td>tsout</td>
<td>The time interval after which information is added to the output file</td>
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<td>ckturb</td>
<td>Turbulence (a random kick is added to the velocities)</td>
<td>True: $2.5\times10^{-5}$ units</td>
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<tr>
<td>ckibio</td>
<td>Incorporates a probability matrix for vertical motion of the particles</td>
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<tr>
<td>chk_settlment</td>
<td>the time after which the larvae become competent to select an appropriate habitat</td>
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</tr>
<tr>
<td>chk_interval</td>
<td>Describes the amount of time between releases</td>
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Table 3: Description of model parameters.

Figure 4: Coupled Biophysical IMB (Paris et al. 2007)
Chapter 4: Results

The distance matrix (Figure 5) represents the distances between the different polygons. To create this matrix, the release locations of each polygon were used as end points to calculate the spatial lengths between all the polygons used in the model. From this matrix, it can be see that most of the polygons are within 300-500 km of each other. However, the 36th-38th polygons seem to be the furthest away from the other polygons, showing distances that span from 400 km to 800 km. These 3 polygons correspond to Map ID numbers 20, 21, and 22, the Cay Sal island group in the western Bahamas. The matrix also shows that the first 12 polygons are within 200 km of each other; these polygons correspond to the Grand Bahama, Bimini, and Andros islands. Additionally, these polygons are more than 600 km from the 27th-35th polygons, the islands of the
southeast Bahamas (Long Island, the Inaguas, Mayanagua, Crooked Island, Samana Cay, etc.).

The trajectories of the larval particles were used to calculate the total distances travelled by each of the particles that found a suitable polygon to settle in (Figure 6). In both runs, the particles traveled an average of 165 days before settlement to a polygon occurred. The number of particles that recruited increased with increasing distance from their source polygons for both the April and May runs. In each run, one maximum is evident, occurring at 3500-4000 km away from the source. However, the figure also demonstrates that more larval particles recruited in April overall. An examination of some of the particle trajectories (Figure 7) reveal that although many of the larval particles travel long distances, their displacements were much shorter. The particles that recruited tended to stay closer to their source locations. Figure 7 also demonstrates the tendency for some particles to travel outside of the domain.
The migration matrix (Figures 8) illustrates the probability of larvae originating from one polygon recruiting to another polygon after the appropriate pelagic larval duration. Both the April and May matrices indicate that only small quantities of the particles released in the Bahamas are being recruited within the Bahamas. This is confirmed by an analysis of the larval particles’ statuses for April and May (Figures 9), in which 49% and 60% of the particles, respectively, left the model area, while only 26% and 16% of the particles recruited to a polygon.

In the April run (Figure 8A), the migration matrix demonstrates that not many of the particles are recruiting to the first 15 polygons (see Table 2). It also indicates that most of the larvae are recruiting to the location where the 28th-38th polygons occur, and that there seems to also be some self-recruitment to that area, as well. There also appears to be some local retention occurring in the area where polygons 34 to 42 are located. The migration matrix for May (Figure 8B) also doesn’t demonstrate many particles recruiting to the first 15 polygons. This matrix also demonstrates possible local retention amongst polygons 28 to 35. Both matrices also show that there is generally less than a 30-40% probability that recruitment will occur in the Bahamas polygons, with only 10-12 matrix points (the red squares in Figures 8A and 8B) revealing a high probability or recruitment.

A closer look was taken at the areas showcasing possible locations of local retention.
Figure 8: Migration Matrices. A. April  B. May

Figure 9: Particle Status for larval releases. A. April  B. May
The dispersal kernels generated by the April and May runs (Figure 10) display a skewed distribution to the left, indicating a shorter dispersal kernel for this species in The Bahamas. The probability of survival is highest around 150-200 km for each run, suggesting the dispersal kernel for lobster in The Bahamas is an average of 100-300 km. However, the probability of surviving recruits is below 20%. The error bars also indicate a high variability in the dispersal kernel due to the varying distances between the polygons.

The areas suggesting local retention were examined closer for each run. In the April run, most recruitment is clustered around nine release locations: Long Island, Hogsty Reef, Samana Cay, Mira Por Vos Passage, Great Inagua East, Great Inagua West, Little Inagua, Mayagua, and Crooked Island Passage. The distance matrix for this group (Figure 11) indicates that the sites are within 100-300 km of each other, the same distance as the average dispersal kernel. The migration matrix (Figure 12A) identifies 2 instances where a high probability of recruitment occurs (red squares): when larval particles originate from Samana Cay and Great Inagua and recruit to Mira Por Vos Passage and
Mayanagua, respectively. Overall this migration matrix indicates that larvae from these 9 polygons are recruiting to the same polygons within this area. The average dispersal kernel for this area was calculated at 75-200 km (Figure 13A), which falls within the dispersal kernel for the entire Bahamas. However, the probability of surviving recruits has increased from 20% to 40%.

The May run shows a similar pattern of clustered recruitment in the same area. It also illustrates 3 cases where the probability of recruitment is high (Figure 12B). There is a
high probability of recruitment from both the Hogsty Reef and Samana Cay release locations to the Crooked Passage site, and there is also a high probability that larval particles released from the Mayaguana site will return to settle in the Mayaguana site. Also, similar to the April run, the average dispersal kernel for recruitment in this particular area is 100-200 km.

Figure 13: Dispersal Kernels: Southeast Bahamas Polygons
A. April. B. May.
Chapter 5: Conclusion

5.1 Summary of Major Findings

The dispersal kernel for *P. argus* in The Bahamas was calculated to be an average of 100-300 km, indicating that larvae spawned within these boundaries will typically settle there as well. However, both the dispersal kernel and the migration matrices also indicate that the probability of larval recruitment is less than 20%. These results are similar to those obtained by Butler *et al.* (2009).

Despite this outcome, while The Bahamas possesses numerous areas of suitable habitat for juvenile and adult *P. argus*, the results do indicate that many of the lobster originating from this area are leaving the domain. This is likely a function of the long pelagic larval duration characteristic of this species. Because the larvae are travelling for several months, they may have the opportunity to migrate to more distant locations not accounted for in the domain of the model (Figures 9 and 10); whether these particles are recruiting somewhere else or returning to The Bahamas remains to be seen. This is corroborated by Figure 6, which shows that the larval particles generally travelled distances of 3500-4500 km, with some particles reaching up to 7000 km. Yet, those same particles recruited within 300-800 km of the source locations.

According to Pineda *et al.* (2007), “long PLDs do not necessarily yield broad dispersal kernels, as larval behavior breaks the direct proportional relationship between PLD and dispersal distance.” By including behavioral traits, such as vertical migration, into the model, local recruitment was enhanced, allowing larvae to remain closer to their spawning sites (Butler *et al.* 2009; Paris *et al.* 2007; Paris and Cowen 2004). This is contrary to the long held belief that lobsters in The Bahamas are originating elsewhere in
the Caribbean, despite the idea that lobster populations in the Caribbean might be panmictic (a single population linked by widely dispersed larvae).

The Bahamian lobster fishery has started to exhibit declines in landings and mean size (Gittens and Braynen 2002). Historically, due to the size of The Bahamas and the remoteness of many of the islands, the fishery has been difficult to monitor, manage, and enforce. Not only does illegal harvesting by locals and foreigners occur, but additional conflicts also arise from the use of the casitas. But there hasn’t been much concern about the stock, as the locations of the source populations were believed to outside The Bahamas. However, if *P. argus* larvae are demonstrating local retention, then additional fishery controls would need to be implemented to protect the stocks. Limiting catches through quotas is a possibility; this would allow landings to be reduced to a level that will allow the stocks to recover. Nevertheless, a comprehensive stock assessment would need to be completed first.

Another option is to take an ecosystem-based approach to management by introducing zoning laws to protect the nursery areas and settlement habitats. This strategy could be especially useful in well connected areas, such as exhibited by the 8-9 habitat polygons in the southeast Bahamas. Placing a network of MPAs in this area, would afford some degree of protection for the varying stages of the lobster, ensuring that the population in this area could be self-sustaining.

Although the dispersal kernel does suggest local retention, there still exists the possibility for larval particles to travel outside The Bahamas and throughout the Caribbean. The large distances achieved by the particles’ trajectories allows for the opportunity for these larvae to travel to and settle almost anywhere. If the particles that
exited the model domain achieved the same trajectory distances, then this could have
great implications for Caribbean spiny lobster, as individuals within the metapopulation
could possibly travel throughout the range of the species.

This could further complicate the management of any *P. argus* fishery throughout the
Caribbean. An MPA network would need to be sufficiently large enough to cover the
entire range of the species. Additionally, as the smaller MPAs within the network would
be connected through the dispersal, where larvae produced at location A could supply a
fishery at location B, and vice-versa, different governments would need to work together
to ensure that each stock remained viable. The opportunity for scientists and managers
from different countries to come together in order to develop policies and strategies that
would benefit all the lobster fisheries in the Caribbean, as well as coordinating the
administration and implementation, would create a social network to complement the
already existing ecological one. Collaboration through the social networks may even
encourage countries to take a firmer stance on enforcement. These social and ecological
connections can also possibly impact international relations among many countries.

5.2 Future Work

Future work on this project would begin with expanding the range of the model,
allowing for the domain to include the entire Caribbean. With an expanded domain, the
particles that left the boundaries of The Bahamas could also be taken into account,
allowing for further examination into whether those particles will return to The Bahamas
or choose to settle within the jurisdictions of other countries. By incorporating these
changes into the model, the dispersal kernel for *P. argus* in can be determined throughout
the entire range of the species.
Another possibility will be to consider the impact of the increased use of casitas within the Bahamian lobster fishery. It would be interesting to determine what amount of the lobster catch is actually being obtained from casitas, and whether the casitas may lead to some biologically or ecologically significant impacts on the population. Identifying the major locations of the casitas would also be important, as this would allow for those habitats to be incorporated as polygons within the model.

Exploring the relationship between the ecological and social networks is also of interest. If ecological networks are optimized through long-range dispersal, what effect would this have on social networks? Could this work on lobster connectivity have a considerable influence on international relations or help with the establishment of bi- or multinational agreements?

Next, there is also interest in incorporating this data into decision support systems for marine resource management. One such system is the marine reserve planning tool, MARXAN, a model that provides decision support to the design of new reserves by identifying gaps in biodiversity protection, identifying areas to include in new reserve systems, and producing a number of different options that can meet both several objectives (Ball et al. 2009). With MARXAN, priority areas to be included within an MPA network can be identified by incorporating socioeconomics along with the connectivity. Often, socioeconomic factors are not included in the initial design or plan of marine protected areas or are considered secondary to biological factors (Klein et al. 2008). However, it is important that the design of MPAs must include some population models as well as predictions of the effects of implementing these MPAs. MARXAN can be used as a decision-support tool to identify those areas that will complement both
conservation and socioeconomic goals while taking into consideration the connectivity of the focal species. This will also allow for social, cultural, and legal implications of connectivity to be analyzed as an MPA network is designed, thus examining if MPAs that are optimal ecologically can also be optimal socioeconomically.
Works Cited


