Condos and Connectivity: Developing an Interdisciplinary Approach to Guide Caribbean Spiny Lobster (*Panulirus argus*) Fisheries Management Within the Bahamas

Las Casitas y la Conectividad: Desarrollando un Enfoque Interdisciplinario para Informar el Manejo Pesquero de la Langosta (*Panulirus argus*) en las Bahamas

Condos et Connectivité: Développement D'une Approche Interdisciplinaire comme Outil D'Information pour la Gestion de Pèches de la Langouste (*Panulirus argus*) dans les Bahamas

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ABSTRACT

Caribbean spiny lobster (*Panulirus argus*) is a heavily exploited seafood throughout its range. Its long pelagic larval duration and thus potential for long-range dispersal increases the difficulty in determining the origins of local populations and impairs management. Spiny lobster supports the primary fishery in The Bahamas. In addition, the use of condos (or casitas) as a fishing method has increased in recent years. Yet, the combination of the ecological, social, and management implications of condo usage have not been fully evaluated. Here we present an interdisciplinary approach and assess how this novel strategy can assist in the difficulties of designing sustainable management for spiny lobster in The Bahamas. Emphasis is placed on the integration of anthropological and biophysical modeling techniques, providing an example of how these merged tools can help understand ecological processes while assisting management decisions. Simulations of larval dispersal for Bahamian spiny lobster populations indicate dispersal distances (or dispersal kernel) of 200 - 400 km, with a 25% probability of successful settlement. Surveys and semi-structured interviews of Bahamian fishers revealed five popular areas for condo placement. Further connectivity assessments of these locations indicate higher rates of settlement success for four sites. Two of these locations demonstrated a narrower dispersal kernel, suggesting self-recruitment. However, the three remaining locations appear to depend on subsidies from other spiny lobster populations throughout the Caribbean. These differences in connectivity suggest each location be evaluated individually to determine spatially-dependent management actions, and to effectively develop and implement condo-related policies that will be supported by local communities.

KEY WORDS: Caribbean spiny lobster, *Panulirus argus*, connectivity, interdisciplinary methods, The Bahamas, fisheries management

INTRODUCTION

Dynamics within marine populations have important considerations for fisheries management. Most of these populations are not isolated, instead existing within complex ecosystems that involve impacts from biological, physical, chemical, and geological forces, as well as from humans. This variability makes it challenging to provide adequate management for fisheries resources. As many worldwide fisheries continue to decline or struggle to maintain sustainability, we must reevaluate traditional management tools and how these tools can be improved to provide for effective fisheries management strategies.

Many marine populations are spatially distributed metapopulations (assemblages of local populations that inhabit spatially distinct habitat patches within a landscape (Sanchirico and Wilen 2005). This increases the difficulty in predicting outcomes from implemented management scenarios, as there tends to be an incomplete understanding of the spatial characteristics involved and how they operate (Kritzer and Sale 2004). The result is a mismatch between natural spatial scales and appropriate scales of management. As such, for successful management to occur, fisheries managers need to be cognizant of the spatial scales that characterize dispersal processes and align management scales appropriately (Botsford et al. 1997, Palumbi 2004, Kaplan 2006). This highlights the importance for not only understanding the processes of connectivity, but also for incorporating connectivity within proposed management strategies.

Caribbean spiny lobster (*Panulirus argus*) is a popular and heavily exploited seafood throughout most of its range. The species supports the primary fishery in many Caribbean countries (FAO 2006), where it is harvested both commercially and recreationally, and is valued at nearly $1 billion US dollars annually (Ehrhardt et al. 2010). This is especially true in The Bahamas, which reports one of the highest catches and where spiny lobster is the number one food export (Ehrhardt et al. 2009).

Understanding population connectivity and local retention of spiny lobster is important for the conservation and management of the valuable fishery it supports. However, the ability for wide-range dispersal, due to its pelagic larval dispersal (PLD) of 5 - 9 months (Ehrhardt 2005), increases the difficulty in determining the origins of local adult populations and can complicate management. Despite the long-range potential of this species, findings have indicated high proportion of spiny lobster offspring settle relatively close to their spawning sites (Black 1993, Butler et al. 2005). Yet, several studies have also provided evidence that connectivity patterns do exist among spiny lobster populations throughout the Caribbean and may have implications for the species' management (Chavez 2012, Kough et al. 2013).

One of the core challenges to connectivity is determining overall how connectivity contributes to issues of conservation and management (Bode et al. 2012). Since connectivity implies that local processes and populations may be dependent on processes occurring elsewhere (Grober-Dunsmore and Keller 2009), local management initiatives may be ineffective for providing adequate protection or localized benefits. Additionally, if connectivity across large spatial scales is indeed the case, there is no doubt that these populations are also crossing political boundaries along their journey, allowing for decisions made in one country to possibly impact ecosystems elsewhere. It may be necessary to increase the scale of management to account for these issues. However, development of management strategies to ensure sustainability of entire ecosystems is complex and will require more interdisciplinary work than what is currently being done.

Exploration of the impacts of these connections, whether local or distant, is imperative, especially for countries like The Bahamas, where spiny lobster is an important commodity and management of the fishery is difficult. Attempts at managing this species must take into account the recruitment locations of the larvae, where the larvae settle, how far the adults move and where they end up. Identifying the spawning and settling sites will help provide fishery managers a better perspective of the areas that should be considered for protection locally or those areas abroad that can lead to cooperation between nations to promote effective use and management of the resource.

In recent years, The Bahamian spiny lobster fishery has seen an increase in the use of condos (referred to as “casitas” throughout the Caribbean; Figure 1), artificial habitats used to aggregate lobsters in large numbers for easy capture (Lozano-Álvarez et al. 1991, Sosa-Cordero et al. 2008). The Bahamas is one of many Caribbean nations using condos condos to concentrate lobsters in order to boost production in the fishery and meet the increased market demand (Baisre 2000, Cruz and Phillips 2000, Eggleston et al. 1992, Losada-Tosteson and Posada 2001, Briones-Fourzán et al. 2000, Deleveaux and Bethel 2002). Condos have also effectively created additional spiny lobster habitat, especially in The Bahamas, where the structures tend to be placed in locations with sandy or grassy bottoms instead of near reefs, the ecological habitat of choice for adults.

While the use of condos has increased greatly throughout Caribbean spiny lobster fisheries, the ecological, social, and management implications of their use have not been fully evaluated. Condo studies have focused on their design (Briones-Fourzán et al. 2000, Cruz and Phillips 2000, Sosa-Cordero et al. 1998, Nedimyer et al. 2001, Seaman 2000, Losada-Tosteson and Posada 2001, Sherman et al. 2001), stock assessments and population enhancement (Ley-Cooper et al. 2011, Behringer and Butler 2006, Cruz and Borda 2013); disease transmission (Behringer et al. 2012, Lozano-Alvarez et al. 2008, Briones-Fourzan et al. 2012, Candia-Zulbaran et al. 2012, Cruz Quintana et al. 2012, Huchin-Mian et al. 2013), impacts on juvenile populations (Arce 1997, Eggleston et al. 1992, Smith and Herrnkind 1992, Childress and Herrnkind 1994), suitability as additional habitat in areas lacking adequate natural refuges (Miller 1982, Briones et al. 1994, Spanier and Zimmer-Faust 1988, Eggleston et al. 1990, Spanier 1994, Mintz et al. 1994, Butler and Herrnkind 1997, Sosa-Cordero et al. 1998, Briones-Fourzan and Lozano-Alvarez 2001), and their influence on lobster predation (Mintz et al. 1994, Butler and Herrnkind 1997, Sosa-Cordero et al. 1998, Behringer and Butler 2006, Eggleston et al. 1990, Eggleston and Lipcius 1992, Briones-Fourzan et al. 2007, Lozano-Alvarez et al. 2009). Few studies have focused on the impact of condos on lobster fisheries and their management (Cruz and Phillips 2000, Briones-Fourzan et al. 2000, Losada-Tosteson and Posada 2001, Henderson and Cote 2011, Ley-Cooper 2013) and even fewer have assessed the role of condos on dispersal characteristics (Eggleston and Lipscius 1999) or how these characteristics might influence management of the fishery and vice-versa (Ley-Cooper et al. 2014, Gonzalez and Wehrtmann 2011). Additionally, to date, none of these studies have incorporated anthropological methods to determine how condo use might impact dispersal and ultimately spiny lobster fishery management.

Figure 1. Condos being prepped for the 2013 - 2014 spiny lobster season in Spanish Wells.

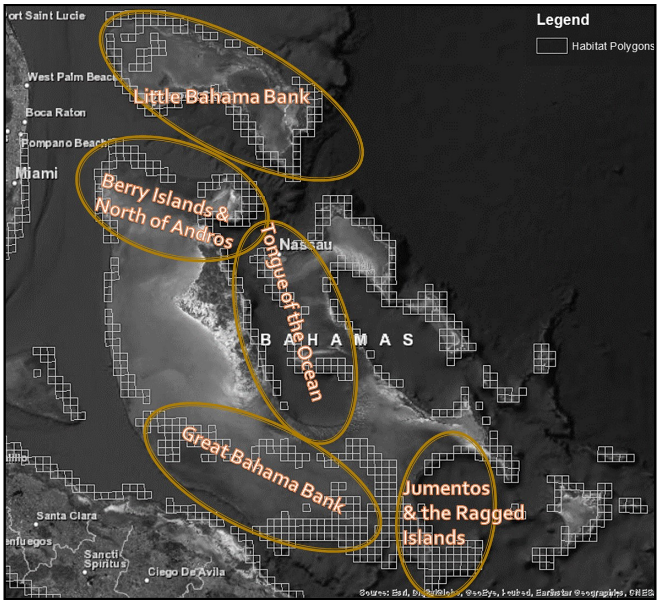
With these factors in mind, there is a need to not only determine natural patterns of connectivity, but to learn how to sustain these patterns (McCook et al. 2009) while also protecting the population, especially in the face of changing perspectives and fishing strategies, such as the increased use of condos. As the construction and addition of these structures continue to occur, so too do the questions and concerns about their impacts on the species and the fishery, and what those impacts mean for sustainable management. Moreover, development of management strategies to ensure sustainability of an entire, and potentially Caribbean-wide ecosystem, will be difficult without utilizing interdisciplinary approaches. While biophysical models have been used to evaluate management strategies based on connectivity (Kough *et al.* 2013; Botsford *et al.* 2009), coupling these spatially explicit models with additional tools, such as anthropological research and social science methods, can aid in the assessment of some of the aforementioned challenges, allowing for management decisions based on a range of factors (ecological, social, economic, etc.) to result in the design of appropriate, more holistic, strategies.

The purpose of this study is to examine the sustainability of the Bahamian spiny lobster fishery based on the dispersal characteristics of Caribbean spiny lobster. Emphasis is placed on modeling lobster connectivity to predict the spatial scales over which the lobster travel within, and beyond, The Bahamas, and then coupling the connectivity results with anthropological data gathered from Bahamian fishers. This pairing of data allowed for the examination of how these two methodologies can be used to predict locations that might either help to optimize condo placement or identify those locations requiring additional management considerations.

METHODS

Surveys

In the summers of 2011, 2012, and 2013, surveys were administered in The Bahamas to spiny lobster fishers. The surveys were conducted in person on several of the islands with major lobster fishing settlements, including New Providence Island, Grand Bahama, Abaco, Andros, Long Island, and Spanish Wells. Utilizing the snowball method (Singleton and Straits 2010), fishers were identified through recommendations from local contacts, approaching individuals on fishing docks, boats, or markets, and requesting contact information for additional individuals at the end of each interview. The survey contained 125 questions and included a variety of topics around general demographics and fishing practices, including the use of condos. Each survey lasted 45 minutes to 2 hours, based on the amount of additional anecdotal information fishers were willing to provide. For those individuals who expressed concern over the time commitment required, semi-structured interviews (Singleton and Straits 2010) were conducted, following the general format of the surveys; these interviews were typically 20 - 30 minutes. At the end of each survey, fishers were shown a map of The Bahamas (Figure 2) highlighting the habitat areas used as polygon habitats within the connectivity model. Fishers were asked to identify locations on the map where they have either deployed condos or fished from condos. While exact locations were not given by any fisher, they were able to provide general locations for condos.



Source: Esri, DigitalGlobe, GeoEye, i-cubed, Earthstar Geographics, CNES

Figure 2. Bahamas Polygon Map. Circles indicate the five locations identified by Bahamian fishers as the top condo placement locations.

Connectivity Modeling System

The open-source coupled biophysical model of Lagrangian transport, the Connectivity Modeling System (CMS; Paris et al. 2013), simulated the probabilistic connections between spiny lobster populations around the Caribbean. The CMS enables seamless multiscale nesting between general ocean circulation models to maximize the temporal and spatial resolution of ocean currents. The CMS has been verified against empirical data and successfully described the ocean dispersal of fish larvae (Spounagle et al. 2012), lobster larvae (Kough et al. 2013), and oil plumes (Paris et al. 2012). In addition, the performance of HyCOM has been verified and it is a widely used and powerful general ocean circulation model (Chassignet et al. 2007, Bleck 2002). The 3D currents within the top 100 m of both the Global HyCOM and the higher-resolution Gulf of Mexico HYCOM were used for larval transport simulations of spiny lobster.

Spiny lobsters spawn at the edge of coral reef habitats around the Caribbean and settle on a variety of habitats, including the hard-bottom algal beds in proximity to reefs. In these simulations, appropriate habitat for both spawning and settlement was contained within 3202 sites at coral reef locations (Holstein et al. 2014). Spawning occurred daily from the centroid of each 8 km x 8 km reef site. The magnitude of spawning, 500 larvae per site per day, was enough to saturate potential connections and probabilistically describe dispersal (Kough and Paris 2015). Lobster larvae spend a long time as planktonic wanderers; advances in aquaculture have given an estimate of between 5 and 9 months for spiny lobster PLD (Goldstein et al. 2008). In the simulation, lobster larvae reached competence at 152 days and were no longer tracked after 196 days. During their pelagic journey, lobster larvae have ontogenetic vertical migration and daily vertical migration. The ontogenetic vertical migration described through larval collection trawls and laboratory experimentation (Butler et al. 2011) was included in the simulation. (See Table 1 for a summary of CMS parameters.)

Table 1. Summary of CMS parameters

Oceanography:	1/12 degree Global HyCOM + data assimulation. 1/25 degree HyCOM Gulf of Mexico.
Horizontal diffusion:	15m^2/s for Global, 10m^2/s for GoM
Integration Timestep:	2700s
Spawning Timespan:	1/1/2004 through 12/31/2008
Habitat:	3202 sites consisting of 8x8 km polygons overlaid on Caribbean coral reef habitat
Competency:	152 days
Maximum dispersal time:	196 days
Spawning Frequency:	daily
Spawning Magnitude:	500 larvae per site per day
Vertical Migration:	ontogenetic migration

Data Analysis

The likelihood of larval exchange between any two sites in the network are represented using a probability matrix. Paths of exchange from an origin location ("i") follow a row in the matrix to each other habitat location ("j"), which are the columns. The probability (probability of dispersal from "i" to "j") was obtained by dividing export (larvae with an origin in "i" that settled in "j") by the total export (sum of all successfully settling larva with an origin in "i"). Distances between habitat sites were calculated using the haversine great circle formulation using the coordinates of each site's centroid. Mean dispersal distances were calculated by combining the probability of dispersal with a distance matrix and therefore represent a Euclidean distance rather than a path length. The spatial scales of larval linkage were calculated by subsampling and counting unique connections or tabulating probabilities in 100 km bins from 0 through 4500 km away from each habitat site. Betweenness centrality is a measure of how important a given habitat location is to the entire connectivity network. It was formulated by calculating how many times a given habitat location is involved in the most probable pathway of larval exchange between any other two locations in the network. The inverse of the probability matrix was used as an edge weight, to assess the shortest distance (in units of connection probability) between two locations. Calculations were made using the BGL Toolbox developed by Gleich (2006). The betweenness centrality was normalized to the maximum of the sampled network to place habitat sites into logical tiers.

Betweenness centrality and three other connectivity factors were used to help determine the importance of individual habitat polygons in terms of the role they play in maintaining connectivity of the local spiny lobster population: betweenness centrality - sites with the highest number of shortest paths passing through them and serve as important connectors for the entire population network; diversity of connections - sites with the highest number of unique incoming connections with other sites and serve as important sinks, as they provide the opportunity for distant populations to subsidize local ones; self-recruitment - the probability a site will export larvae back to itself, providing the potential for these habitats to be both good sinks and sources; and successful settlement of larvae - the percent of larvae exported from a site that settle successfully anywhere within the network, representing habitats that may represent good sources. Roberts et al. (2006) and Salm et al. (2006) affirm that resilient source populations can provide larvae to revive other depleted populations. However, those sites that function solely as sources must have substantial self-replenishment to persist, especially while subsidizing other areas (Jones et al. 2007). There have been arguments made that those populations functioning mostly as sinks must rely on larvae from elsewhere in order to persist, and therefore should be considered low conservation priorities (Almany et al. 2009). While these sinks may not be able to replenish other populations like sources can, they may be important for genetic diversity, especially if they receive larvae from multiple sources. Additionally, if sinks respond in different ways than sources to environmental changes, including them in reserve networks can contribute to population resilience and persistence, especially if those responses are positive. Isolated populations also have high conservation values, especially when they harbor endemic species and/or unique assemblages (Jones et al. 2002, Perez-Ruzafa et al. 2006, Roberts et al. 2006). The low connectivity that creates the isolation also contributes to less resilient populations. This places isolated populations at greater risks of both extinction and inbreeding (Reed 2005), placing further importance on protecting their habitats.

Using this as guidance, a rating system was implemented to evaluate the four connectivity factors listed above, with the intention of creating a system for determining which areas should be evaluated further for additional management considerations. Habitats examined within the connectivity model received a rating from 1 through 10 within betweenness centrality, diversity of connections, and successful settlement, with 10 indicating the habitat should be considered a high priority for closing to fishing and 1 indicating the habitat should have the least consideration for closure. Individual data from the betweenness centrality, diversity of connections, and successful settlement analyses were entered into ArcGis for comparison, followed by combination of the data through a raster analysis to provide a final ranking (with scores between 3 to 30) to help identify those locations potentially most suitable for marine protected areas. Self-recruitment within the habitats was examined separately, as a high propensity for this ability may not necessarily suggest the habitat should be closed, particularly when examined in isolation. For this parameter, a 10 indicates the habitat has high levels of self-recruitment. Once the final ranking for each habitat was determined, it was compared against the self-recruitment rating to determine an appropriate course of action. This analysis was coupled with the results obtained from the survey data to provide recommendations for spatial management of the Bahamian spiny lobster fishery.

RESULTS

Of the 3,202 habitat polygons identified throughout the Caribbean and used within the CMS model, 848 are within The Bahamas. During interviews, fishers identified 44.7% of the polygons (n = 379) as locations where they have either placed or fished from condos. Survey responses to the question, *Where in The Bahamas is the best place to catch lobster*, returned a variety of answers; however, the most frequent responses were Cay Lobos (n = 12), the Great Bahama Bank (n = 10), the Tongue of the Ocean (n = 9), the Jumentos (n = 7), the Little Bahama Bank (n = 6), the Berry Islands (n = 6), the Ragged Islands (n = 6), and Cochinos (n = 6). These responses where coupled with the locations identified on the habitat map to delineate five main areas of condo placement and use within The Bahamas (Figure 2): the Little Bahama Bank (LBB), the Berry Islands and North of Andros (BI), the Tongue of the Ocean (TOTO), the Great Bahama Bank (GBB), and the Jumentos and Ragged Island Chain (JRI).

Exchange between Spiny Lobster Populations

Caribbean Wide — The simulations reveal connections between lobster populations within The Bahamas and other areas throughout the Caribbean (Figure 3). Despite these international connections, the lobster populations within The Bahamas have a high probability for self-recruitment, signifying domestic connectivity.

The dispersal kernel (DK) for the spiny lobster population throughout the entire Caribbean (Figure 4) indicates the probability of survival for the population is highest between 200 - 400 km, with approximately 13% of recruits settling successfully. Those populations originating within The Bahamas exhibit a similar dispersal kernel distance (Figure 5); however the probability of survival at this distance was doubled (25%).

Within the Bahamas — We took a closer examination of the connectivity in the five popular condo locations identified by the Bahamian fishers. These habitats also demonstrated local and international connections, with populations within TOTO dominated by self-recruitment. The DKs for these areas were similar to The Bahamas as a whole (Figure 5), with LBB and TOTO populations demonstrating narrower kernel distances, and GBB populations demonstrating a wider DK. Differences are also apparent in the probabilities of successful recruitment, with the populations originating in the GBB decreasing their probability of recruits to 17%, while populations within the other four areas increased their recruit survival rate. TOTO demonstrated the highest probability of successful recruitment at 36%.

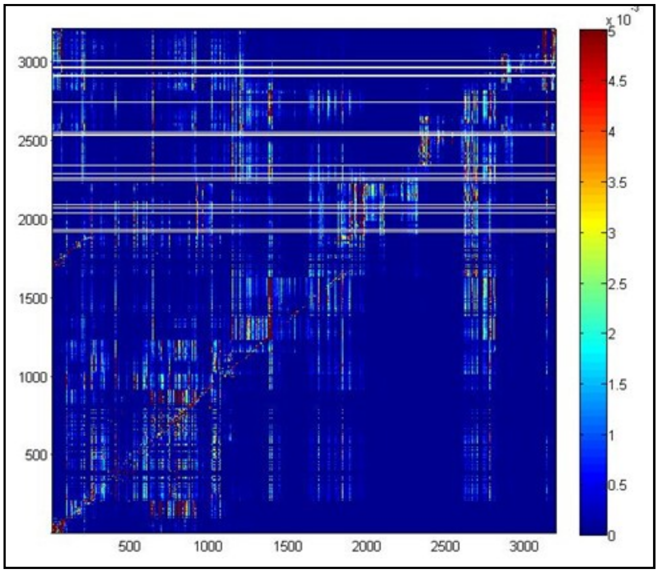


Figure 3. Connectivity Matrix: Caribbean.

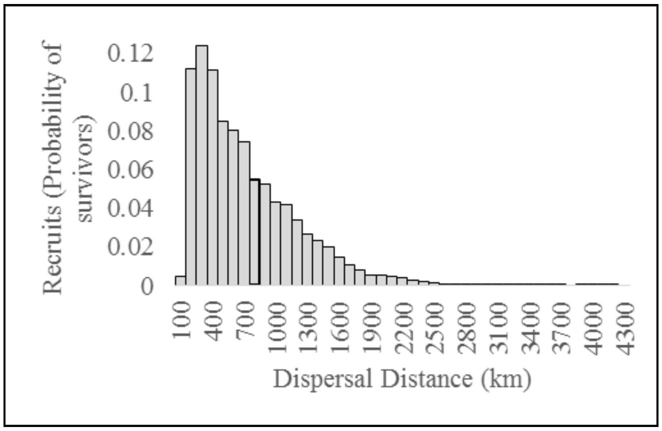


Figure 4. Dispersal Kernel: Caribbean.

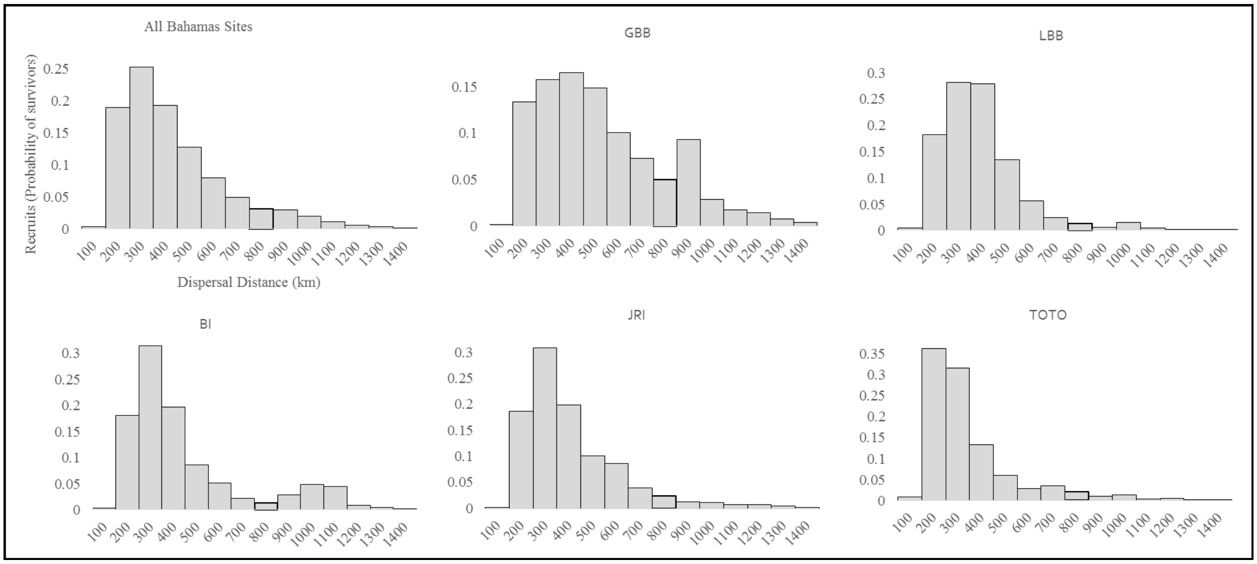


Figure 5. Dispersal Kernel: Bahamas and the 5 Popular Condo Areas.

Spatial Scales of Linkages

Betweenness centrality, diversity of connections, self-recruitment, and successful settlement were used to help determine the importance of individual habitat polygons in terms of the role they play in maintaining connectivity of the local spiny lobster population. Habitats within The Bahamas demonstrated betweenness centrality scores ranging from 0 to 452,005, the highest score for the entire Caribbean, almost 450% greater than the next highest score of 82,227 in Jamaica. Sites within GBB and BI show high potentials for serving as important connectors for habitats within the Caribbean-wide network (Figure 6A). The quantity of unique incoming connections also has a wide range for Bahamian habitats, starting from only 4 connections and reaching to 2,746 connections, again, the greatest for all the sites in the Caribbean. Over 70% of the habitats displaying high levels of connections from other sites all throughout the Caribbean are within The Bahamas, with areas in LBB and BI receiving larvae through the largest number of unique links (Figure 6B). The percent of successful settlement of exported larvae from polygon habitats within The Bahamas ranges from 0.5% to 50.4%. Despite not having the highest proportion of habitats with successful settlers in the Caribbean, over 80% of Bahamas habitats have a successful settlement rate of 20% or higher, with the LBB, BI, TOTO and JRI producing the best settlers (Figure 6C). The probability of self-recruitment within The Bahamas ranges from 0 to 0.1257, with 80% of the sites receiving some level of returned larvae. Medium to Higher rates of self-recruitment are demonstrated in BI, TOTO, and the southern areas of GBB (Figure 6D).

Final Ranking Scores for habitats — Each Bahamian habitat polygon was assigned a score of 1 to 10 within the 4 factors, with a 10 indicating there should be higher considerations for further management actions (such as closing to fishing and/or condo placement) within a habitat and a 1 indicating the area should have less considerations for management actions. Figure 7A describes the final ranking scores for each of the habitat polygons based on a combination of the individual scores for betweenness centrality, unique incoming connections, and percent of successful settlers, with 30 being the highest score possible. (Self-recruitment was left out, allowing each habitat to be evaluated on a case by case basis, as the level of self-recruitment may not necessarily dictate a closed vs open area in every scenario.) Habitat polygons with scores greater than 20 should have the highest consideration for additional management, such as fishing closures, once self-recruitment is assessed; polygons with scores between 15 - 20 should have medium consideration for additional management; and scores below 15 should have low considerations for additional management.

Most of the polygon habitats in The Bahamas fall under the "medium priority" for closing (Figure 7B), suggesting other factors should be evaluated before a final decision is made on whether to impose new management scenarios. This is true for the five main fishing areas as well, with the exception of LBB, where 63% of the habitats obtained a rating for low consideration. Each of these popular areas also contain some sites with a high priority rating (n = 144), ranging from 4% in LBB to 40% in the GBB. Of these sites 65% (n = 94) are currently locations where condo placement occurs in each of the five areas except for the LBB.

DISCUSSION

The connectivity simulations indicate larval exchange does occur between Caribbean spiny lobster populations. Although the DK is narrow, at only 200 - 400 km, many particles successfully traveled longer distances, at times reaching beyond 4,500 km. This allowed for many of these connections to cross international lines, a result similar to those obtained by Kough et al. (2013). Probabilistic exports and imports of larvae originating from and settling within

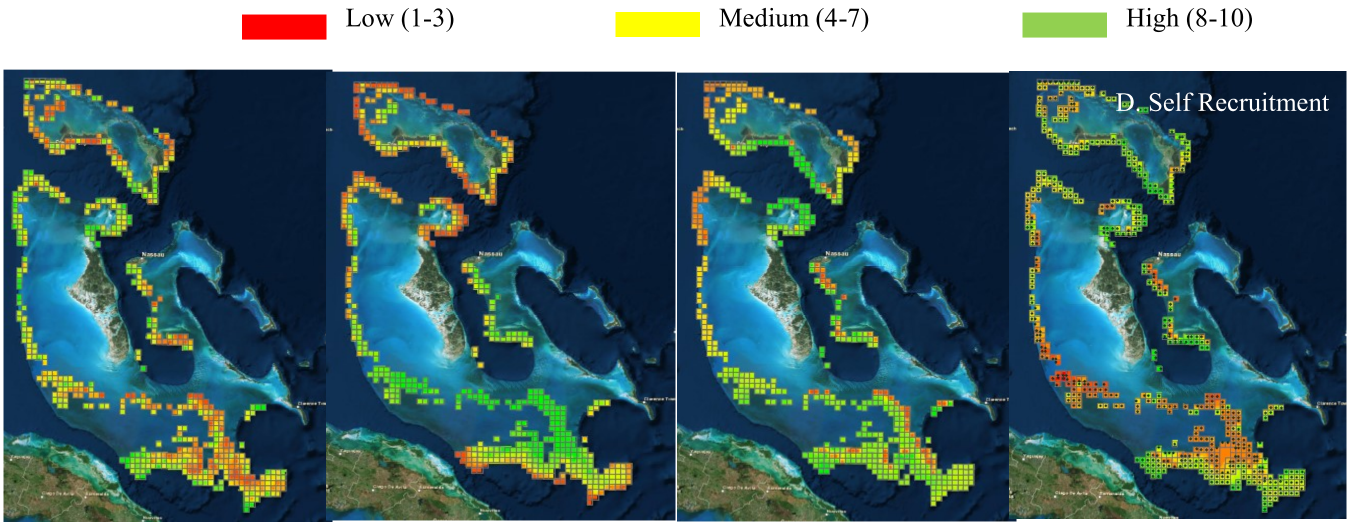


Figure 6. Individual Habitat Rankings Based on Connectivity Factors: Habitats were ranked from 1 to 10, with 10 indicating a high level for that factor. A. Betweenness Centrality B. Diverse Connections C. Successful Settlement D. Self-Recruitment

The Bahamas, respectively, demonstrate that exchanges between populations in The Bahamas and other countries also occur. Despite this, The Bahamas does tend to retain most of its larval exports with a higher probability for survival than when compared to Caribbean-wide populations, suggesting that lobster spawned within The Bahamas settle and thrive there as well.

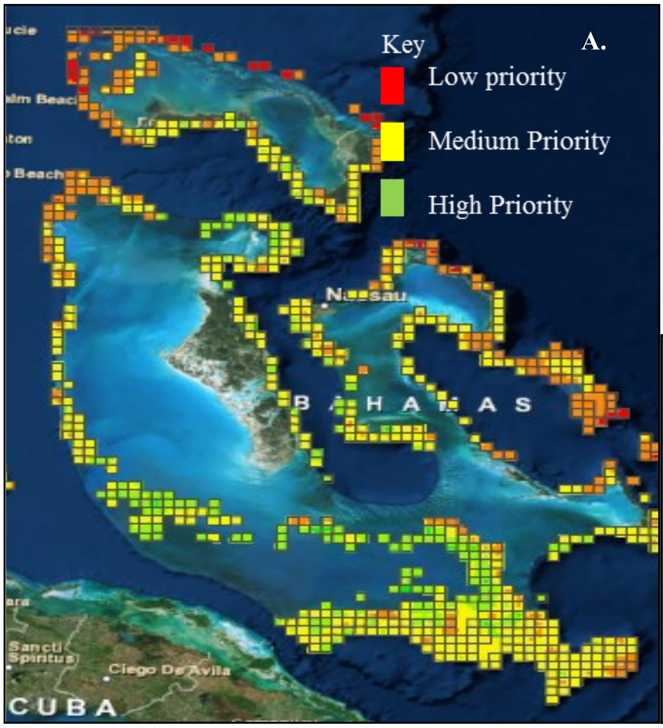
Although Bahamian fishers deploy condos all over the Bahama Bank, five main areas emerged as clear favorites for most of the fishers. These areas (the Little Bahama Bank, the Berry Islands and North of Andros, the Tongue of the Ocean, the Great Bahama Bank, and the Jumentos and Ragged Island Chain) encompass a variety of habitats, including those critical to the attraction of the pueruli at the end of the larval journey and to the survival of the juveniles (Gittens 2004). Examining the probabilistic imports and exports for these areas highlights their connections to other local areas within The Bahamas, as well as to populations elsewhere in the Caribbean. With similar dispersal kernels to the one obtained for The Bahamas population as a whole, these areas are also exhibiting high levels of domestic connectivity for the region, with each site demonstrating greater rates of recruit survival, with the exception of the GBB area. This data suggests these areas have some importance for maintaining the populations that support the Bahamian spiny lobster fishery.

Based on fisher responses, the majority of habitat polygons in each of the popular fishing areas are most likely hosting condos as well. This is especially prevalent in the JRI, BI, and TOTO areas, where over 95% of the habitat polygons were also identified as condo locations. This may have important implications for how these sites are managed when the percentage of condos present in the areas are weighed against the areas' importance for sustaining both the population and the fishery. The creation of protected areas may be an option to achieve this. Two of the factors that can influence the placement of reserve locations are the identification of source/sink and isolated populations (Jones et al. 2007), which can be extrapolated from the connectivity factors examined here.

It was revealed that GBB had the most sites with high betweenness centrality, followed by the BI area, suggesting these locations may have importance for securing connections between the populations within The Bahamas and across the entire Caribbean network. As such, it may be best to limit habitats in these areas to intense fishing, as this may impact how individuals in the population move throughout the network. However, this is complicated by the presence of high quantities of condos in these locations, as 100% and 61% of the habitat polygons in the BI and GBB, respectively, are also preferred condo placement areas.

LBB and BI have the most habitats within the top 10% for diverse connections (greater than 2500 unique linkages with other sites Caribbean wide). The high number of unique incoming connections to these areas indicates these populations can be subsidized by others from various locales, ensuring a level of maintenance for the population and also potentially the sustainability of fishing operations within these areas. As such, these areas should have lower priorities for closure. While a large percentage of the LBB habitats (68%) are already condo sites, there may be additional habitats here that can possibly accommodate condos, especially if condo placement is limited in other highly popular areas.

This may be the case for TOTO. Although there are 27% of sites with 1000 or more unique connections, none of the habitats in TOTO fell in the top 10% for connection diversity. Despite this, TOTO was the one area displaying high levels of self-recruitment, with 29% of its habitats demonstrating a probability for self-



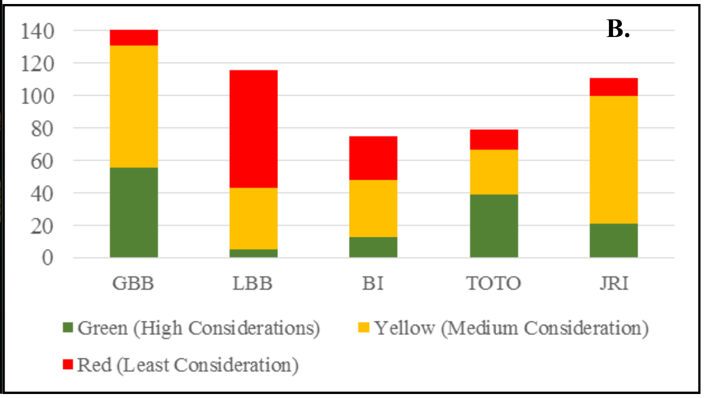


Figure7. Final Management Priorities. Based on a combination of the individual scores from the assessment of the connectivity factors. A. Individual Habitat Rankins B. Quantify of habitats within each category for area.

recruitment of 0.01 to 0.12, compared to the 4 - 7% of habitats in the other four areas displaying a self-recruitment probability greater than .01. As such, TOTO habitats may have some importance for helping to maintain Bahamas populations. A closer examination of the larval exchange occurring between TOTO and the rest of the network reveals strong connectivity with other Bahamas sites, but relatively low connectivity with other Caribbean habitats. This is supported by TOTO's DK, which is narrower than the DK's for the rest of the Bahamas), and has the highest probability of successful recruits (36%). These characteristics aid in further substantiating the notion that TOTO may be a self-sustaining system essential to the success of the Bahamian spiny lobster population.

LBB and BI also possessed the most habitats with the highest rates of larval particles that successfully settled somewhere within the network, followed by TOTO and JRI. This suggests lobsters being spawned in these areas are more likely to find suitable habitat at the end of their larval journeys, not only contributing to the strength of the ecological network, but to the sink populations as well. Limiting harvesting and/or the deployment of condos in these important source locations may be one suitable management option for these areas based on their potential as nursery habitats. Currently, none of the LBB habitats identified as potentially important nurseries, those along the south-east edge, were identified as popular condo locations. As such, there may be little disagreement if a management decision is made to close or impose harvesting limitations in these areas. However, the opposite is true for the BI nurseries, where 100% of the habitats are also condos sites. This may cause some contention should any limitations be imposed.

Self recruitment within the GBB ranges from low in the northern and western areas, to high along the southern edge of the bank. Coupled with the southern area's great potential as an important population connector, the habitats in this location may be good candidates for closure, allowing the area as a whole to serve as a safe haven for both Bahamian and Caribbean-wide spiny lobster populations. These southern habitats are also locations where condo placement is extremely popular; however, based on fisher interviews, the western edge is not currently a first choice for condo placement. It may be best to encourage fishers to place more condos in these habitats as a compromise for potentially losing what is considered "prime" condo space in the southern GBB.

TOTO demonstrates high levels of successful settlement, as well as some diversity of connections with other habitats throughout the network. Factoring in its ability for high levels of domestic connectivity (higher than all the other habitats in The Bahamas), especially along the northern edge, TOTO habitats may be significant sites for supporting the Bahamian spiny lobster population and the fishery, with the potential for helping to subsidize the habitats in the other Bahamian areas. Despite this, the level of unique incoming connections to TOTO may not be enough to help subsidize the area should the population it supports collapses. This is a potential threat as interviews indicate harvesting in this area, particularly through the use of condos, is high, suggesting the increased potential for the harvesting of juveniles based on the connectivity factors explored. As such, it is suggested the entire TOTO area be closed to fishing and condos, allowing this area to serve primarily as a nursery.

Despite having one the highest average rates of successfully settling larvae, suggesting some importance as a nursery, JRI is not an area that serves as an important connector of habitats, nor does it have much importance in terms of diversity of connections. Condo usage in this area is also extremely popular, as a high percentage of fishers mentioned placing or using condos all throughout this region. Therefore, it is suggested this area remains open. Managers may want to consider the potential for closing some of the habitats along the southern edge that demonstrate higher rates of successful settlement; however, since self-recruitment is not particularly high in JRI, it is likely these larvae are leaving the Bahamas and settling elsewhere throughout the Caribbean (which may provide some additional opportunities for collaborative management amongst different countries sharing these populations). Couple this with the popularity of the area by local fishers and the closing of other popular areas, it may be best to leave this area as is.

BI also had a medium consideration for closing due to a large number of habitats demonstrating importance for betweenness centrality and successfully settling larvae, but not for unique connections. Domestic connectivity for the entire area is average, with higher levels seen in the habitats surrounding the eastern edge, around the Berry Islands group. Further examination of this section reveals it also has a higher consideration for closing when compared to the western portion. This suggests limiting fishing within the eastern part of this area might be best, allowing it to serve as a spawning and linking site that helps to facilitate the movement of larvae throughout the local and Caribbean-wide network. More fishing can be encouraged in the western section along the bank, where most of the connectivity factors have low importance and where condo placement tends to be favored.

Lastly, LBB was the only area to receive a low consideration for closing. It has relatively low betweenness centrality and diversity of connections, with average rates of larvae with successful settlement. However, high levels of self-recruitment are evident along the southeast edge. Most of this southern area also has a medium consideration for closing, which should be a viable option as condo placement along this edge is not as popular as in the northern and western regions of this smaller bank. Despite the low consideration rating for the area as a whole, closing the eastern section may be a good choice, as fishers may not oppose this decision.

Managing the Bahamian Spiny Lobster Fishery for Connectivity

The resolution of connectivity has important implications when trying to gain a fundamental understanding of the structure and dynamics of these populations or when trying to determine the appropriate scales at which to implement management strategies (Sale et al. 2010). If larvae are mostly retained at local scales, as may be the case for Bahamian spiny lobster populations, then local management alone can be effective; yet, if larvae disperse beyond those scales, as is also the case for Bahamian spiny lobster populations, management will need to scale up appropriately to be effective. This is one of the fundamental issues that continues to plague connectivity research, especially for species like lobster with long PLDs.

Ecosystem based management will be key to managing for connectivity within The Bahamas, where multiple factors are in play. Through the identification of the functional factors within ecosystems, including humans, managers can begin to assess how best to maintain the connections between all the possible networks. When these connections are severely impacted or broken through population loss or decline, the overuse or destruction of key habitats, or drastic changes in resource use and/or user behavior, the ability for these systems to recover while still continuing to provide valued ecological utilities will also decline (Steneck et al. 2004, Hughes et al. 2005). Understanding how all these factors intersect is imperative; this work demonstrates that creating links between various methodologies may serve as one strategy to help achieve this. dditionally, mapping connectivity patterns will assist with the identification of key management priorities and partnerships that can be created between managers and local fishers, and between The Bahamas and other countries. Furthermore, an overall awareness of connectivity, especially the potential for it to highlight how management decisions and the resulting human reactions in one location can lead to consequences, either positive or negative, in another location, provides an added boon for bolstering not only the use of social connectivity and networks, but for integrating ecosystem based management that has the capability to span the range of the Caribbean spiny lobster both within The Bahamas and throughout the Caribbean.

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