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Spatial Ecology of Great Barracuda (*Sphyraena barracuda*) around Buck Island Reef National Monument, St. Croix, U.S.V.I.

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Spatial ecology of great barracuda (*Sphyraena barracuda*) around Buck Island Reef
National Monument, St. Croix, U.S.V.I.

A Thesis Presented

by

SARAH L. BECKER

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

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Spatial ecology of great barracuda (*Sphyraena barracuda*) around Buck Island Reef
National Monument, St. Croix, U.S.V.I.

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ABSTRACT

SPATIAL ECOLOGY OF GREAT BARRACUDA (*SYPHRAENA BARRACUDA*)
AROUND BUCK ISLAND REEF NATIONAL MONUMENT, ST. CROIX, U.S.V.I.

MAY 2016

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Marine protected areas (MPAs) are increasing in popularity as a tool to manage fish stocks through conservation of entire habitats and fish assemblages. Quantifying the habitat use, site fidelity, and movement patterns of marine species is vital to this method of marine spatial planning. The success of these protected areas requires that sufficient habitat is guarded against fishing pressure. For large animals, which often have correspondingly large home range areas, protecting an entire home range can be logistically challenging. For MPAs to successfully protect large top predator species, it is important to understand what areas of a home range are especially important, such as breeding and feeding grounds. New technologies, such as acoustic telemetry, have made it possible to track marine animal movements at finer spatial and temporal scales than previously possible, better illuminating these spatial use patterns. This study focused on the movement patterns of great barracuda ($n=35$), an ecologically important top predator, around Buck Island Reef National Monument, a no-take MPA in St. Croix, U.S.V.I. managed by the National Park Service. As developing standardized methods for acoustic

telemetry is still a work in progress, the first half of this study focuses on determining appropriate tools for generating home range size estimates for great barracuda and analyzing ecological parameters driving these results. The second half of this study focused on the use of network analysis to look at spatial divisions within individual home ranges and to compare individual to population level spatial patterns, as well as to generate a relative estimate of population density within the park. Barracuda within the park demonstrated high site fidelity to individual territories, but at the population level they consistently used all habitats within the array. Core use areas within home ranges were evenly distributed throughout all habitats monitored by the acoustic array, although movement corridors were detected along high rugosity reef structures. Greater population densities within the park indicate that density dependent behaviors may be influencing habitat use within the park, and suggest that barracuda are contributing high levels of top down pressure through predation within the park boundaries.

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CHAPTER 1

MARINE SPATIAL PLANNING FOR SUBTROPICAL COASTAL ECOSYSTEMS: MOVEMENT ECOLOGY AND HABITAT CONNECTIVITY USING ACOUSTIC TRACKING OF A PREDATORY FISH

Marine protected areas are increasingly being used as a tool to protect essential fish habitats in order to increase fish diversity and abundance, and have support as a means to achieve ecosystem-based fisheries management (Pikitch et al. 2004, Douvère 2008). This shift from single stock management is grounded in the concept of ecosystem based management, in which maintaining sustainable populations of target species is inextricably linked to conserving the habitats and species assemblages within which they exist (Pauly et al. 2002, Airame et al. 2003, Pikitch et al. 2004). Spatial closures or restrictions are seen as one way to approach this complex management strategy. The amount of area under marine protection has burgeoned in recent years, driven in part by the 2006 Convention for Biological Diversity which led to a global commitment to protect >10% of the ocean by 2020 (Spalding et al. 2013). It is intuitive that decreasing fishing pressure within a determined area would lead to increased fish biomass. In closures that are appropriate in scope, location, and enforcement, science often agrees (Allison et al. 1998, Murawski et al. 2000, Roberts et al. 2001, Pauly 2002, Halpern 2003, Lester et al. 2009). Disagreements lie in how to accurately define what constitutes

an appropriate parameter across ecologically heterogeneous, socioeconomically complex, and often politically un-inclined coastal territories (Murawski et al. 2005, Heupel et al. 2006, Claudet et al. 2010, Suuronen et al. 2010, Farmer et al. 2011, De Santo 2013, Edgar et al. 2014). Ecological information is far from the only consideration required to implement and enforce spatial closures. Conservation needs must be carefully balanced with human interests, which are often complicated by socio-economic disparities and a history of tension over control of resources (De Santo 2013). Despite this, data on marine species provides the backbone for generating sustainable policy, and therefore fine-tuning the ability to accurately quantify spatial ecology and movement patterns of mobile animals is necessary to simultaneously achieve conservation goals.

Defining appropriate closures from an ecological perspective requires an understanding of the interplay between life histories, spatial ecology, and trophic interactions of diverse species assemblages (Gerber et al. 2003). There can be great variation among marine species in spatial use of habitats and migratory-residency patterns (Palumbi 2004). Variation in home range size and site fidelity leads to many combinations of temporal differentiation in habitat use for needs such as feeding, spawning, or nursery grounds (Burke 1995, Mumby et al. 2004, Meyer et al. 2007, Luo et al. 2009, Kimirei et al. 2011). High trophic-level predator populations have been shown to often be heavily impacted by fishing pressure, and consequently rebound with properly implemented MPAs (Pauly 1998, Micheli et al. 2004). However, predator species may be less likely to be fully associated with specific benthic habitats, which are an easily surveyed variable often used to define and protect critical fish habitats (Block et al. 2005, Letessier et al. 2015). MPA efficacy for mobile predators therefore depends heavily on

understanding complex activity spaces and determining home range areas, site fidelity, residency times within different habitats and management areas, including temporal variation. Understanding ecological motives (for example feeding or spawning) and environmental cues (for example time of day, lunar cycles, or season) driving these behaviors allows managers to determine appropriate spatial and temporal protection strategies.

Due to data gaps regarding home range and residency patterns of many marine species, particularly large predators, protected areas are often based on broad assumptions regarding the spatial ecology of marine animals. Thus, the actual conservation benefits of many marine protected areas remain unquantified (Heupel et al. 2006, Farmer et al. 2011). Acoustic telemetry, a technology for tracking movements of marine animals, has increased opportunities to quantify the spatial ecology of marine animals, including their home range size, residency patterns, and habitat use at a finer scale than previously possible (Heupel et al. 2006, Cooke 2008, Hussey et al. 2015). One way acoustic telemetry works is by mooring fixed receiver stations throughout a study area. These arrays can either take the form of positioning systems – which use overlapping coverage to triangulate location data for a detection – or in the form of broad scale arrays, in which there is no overlapping coverage and each receiver station functions as an independent node of detection. Tags that emit ultrasonic pings with a unique digital code are attached to or implanted within target species. Pings within the detection range of the receiver are recorded and logged. Receivers are periodically downloaded and movement patterns of tagged animals can be reconstructed via analysis of these logged detection histories. Acoustic telemetry has provided great opportunities

for increased understanding of the spatial ecology of marine species, however, analytic techniques have not kept pace with the recent proliferation of acoustic tracking studies (Heupel et al. 2006, Ledee et al. 2015).

To make best use of the opportunities acoustic telemetry provides, there has been increasing effort in recent years by researchers to develop standardized methods that are appropriate to the node – based study design of many broad scale acoustic arrays (Hedger et al. 2008, Jacoby et al. 2012a, Finn et al. 2014, Ledee et al. 2015). Tools used for many other forms of telemetry have been applied to acoustic telemetry studies, but there is increasing concern that depending on receiver array configuration, input data may be too coarse to produce reliable results (Hedger et al. 2008). Additionally, due to gaps in receiver coverage of a study site, individual tags within a single study may produce datasets of highly variable consistency of detection frequencies. For all of these reasons, choices regarding both study design and data analysis can have large impacts on the way results are interpreted. Ironing out these issues is vital in order for this technology to provide the insights needed to improve the capacity to implement ecologically-based spatial management strategies.

This study brings these two areas of research together by using acoustic telemetry to examine movement patterns of great barracuda (*Sphyraena barracuda*) in a MPA in the U.S. Virgin Islands. Buck Island Reef National Monument is a no-take MPA managed by the National Park Service located on the Northeastern coast of St. Croix, U.S.V.I. This park was created by Presidential Proclamation 3443 in 1961 as a mixed-use area, and was increased from the original 3.56 km² to its current size of 77 km² and converted to a no-take zone in 2001. Parts of the original park were designated as no-

take, making it one of the first no-take reserves in the Caribbean (Costa et al. 2012). This area encompasses a variety of shallow water habitat types ranging from highly rugose coral reefs to sand and seagrass flats. The park includes a steep shelf drop off and roughly two thirds of its area is dominated by deep water coral and pelagic habitat (Costa et al. 2012). All receivers used in this study were anchored in shallow water habitats. To the east and south, BIRNM borders St. Croix East End Marine Park, a multiuse MPA managed by the territorial government. To date, no studies assessing movement patterns of fish have been published within these park systems. This study is part of a larger collaboration conducting tracking studies on many species, with the goal of eventually combining individual species movement ecology with analysis of species interactions within a spatial framework.

Great barracuda are a large piscivorous fish, considered an apex predator to high mesopredator depending on age class, body size, and presence of other top predator species (Ceccarelli and Ayling 2010, Mumby et al. 2012). They are found worldwide in nearshore tropical and subtropical waters (De Sylva 1963). Males mature at 1-2 of age and females at 2-4 years (Kadison et al. 2010). Patterns of juvenile recruitment indicate offshore spawning during the summer months, but aggregation sites have yet to be documented (Kadison et al. 2010). Great barracuda are considered common in these habitats and populations are assumed to be in good standing, but little research has been conducted. Juveniles have been found to occupy calm inshore estuaries and lagoons, while adults are found farther offshore across all benthic habitat types (De Sylva 1963, Blaber 1982, Kadison et al. 2010). Great barracuda can also be found in deep pelagic water and there is evidence of broad population connectivity with little genetic

differentiation among global populations (Daly-Engel et al. 2012). Observations of nearshore habitat use indicate selective use of mangroves during the rainy season, but non-selective or random use during the rest of the year, demonstrating seasonal patterns but less habitat affiliation than lower trophic level predators (Faunce and Serafy 2008). The only other movement tracking study to date shows high variation in site fidelity and residency patterns at a study site in Eleuthera, The Bahamas (O'Toole et al. 2011).

High trophic level predators form a key ecological group for maintaining the balance in trophic relationships within fish assemblages (Meyer et al. 2007, DeMartini et al. 2008, Boaden and Kingsford 2015). Large predators are often more mobile, with movement patterns defined by highly migratory behavior, making defining spatial extent of MPAs prohibitively large and difficult to define (Block et al. 2005, Letessier et al. 2015). As abundant, large predators with limited habitat preference, barracuda populations could have a large top down influence on fish community structure across broad swaths of warm coastal oceans. Impacts of spatial closures on barracuda populations remains unstudied, but given predator resurgence in MPAs, predation pressure could be increased within protected areas (Pauly et al. 1998, Micheli et al. 2004). It is important, therefore, to gain an understanding of home range areas and site fidelity, habitat use patterns, and population densities of this species.

The objectives for my thesis research were to generate home range size estimates, determine the degree of site fidelity of individual fish to these core use areas, understand individual and population level patterns of habitat use, and generate a relative population density estimate for BIRNM. Quantifying these parameters will fill in much needed data

gaps regarding the spatial ecology of great barracuda. Additionally, understanding residency patterns and home ranges of target species allows managers to assess the viability of existing spatial closures or base future spatial management strategies on strong ecological groundings. In order to meet these ecological objectives, it was first necessary to determine the appropriate analytical methods.

Chapter 2 addressed methodological questions. I assessed to what degree analytic method choice influenced the size of home range estimates for the study population. Additionally, I looked at whether strength in detection histories influenced these same results, as well as the ability to determine ecological drivers of home range size, in this case body size. Once appropriate methodological parameters were set, I used this analysis to generate estimates of the size and location of home range territories. In Chapter 3, I used the methods and detection history strength parameters determined as appropriate in Chapter 2 to expand on the home range assessments, looking more closely at site fidelity, habitat use, and key activity spaces for individuals and across the study population. I followed up on this by generating comparative population densities between BIRNM and a second study site in Culebra, Puerto Rico. I also validated our home range analysis through generating a generalized linear model that analyzes benthic habitat type, season, and fish individuality as drivers of observed spatial patterns.

Through looking at these two foci, I hope to look at how movement patterns of this species and management are overlapping to drive barracuda population dynamics, which will give insight into the top down pressures being exerted within the park, as well as provide tools for future managers to assess populations using acoustic telemetry data. Generating accurate data on the spatial ecology of marine species forms the groundwork

for generating ecologically relevant and successful conservation policies (Palumbi 2004). However, ecological relevance is just one step in a complex decision making framework that leads to the creation of policy (Airamé et al. 2003, Pikitch et al. 2004). Through this study I worked to fine tune analytic methods to increase confidence in the ecological results, and took the initial steps to quantify the movement patterns of this ecologically important top predator. More work is needed on other trophic levels and species interactions (much of which is currently being undertaken by project collaborators) but this study forms the first step in examining these spatial variables within this historical protected area.

CHAPTER 2

INFLUENCE OF ANALYTICAL TOOLS AND DETECTION HISTORY ON QUANTIFYING SPATIAL ECOLOGY OF A NEARSHORE PREDATORY FISH

2.1 Abstract

As marine protected areas expand globally, filling data gaps regarding the spatial ecology of marine species has become increasingly important. Tracking technologies such as acoustic telemetry aim to provide this vital information through providing data that make possible individual based models that can illuminate complex movement patterns. Before this potential can be realized, analytic methods must be standardized and the effects of study design on results rigorously analyzed to validate the accuracy of ecological interpretations. This study assessed the role of analytic method choice on ecological conclusions derived from an acoustic telemetry array in the US Virgin Islands. Results of core use area estimates of great barracuda ($n=35$) in Buck Island Reef National Monument, U.S.V.I. generated by three analytical methods were compared. In addition, the impact of variation in detection history on the ability to interpret results was modeled. Analysis using kernel density estimators (KUD), dynamic Brownian bridge movement models (DBBMM), and network analysis indicated that these fish show high site fidelity but also undergo wide ranging exploratory movements. Comparisons among techniques showed similar results for KUD and DBBMM, which both under estimated area in comparison to network analysis. Generalized linear models analyzing each method

showed that detection history greatly impacts home range area estimates and confounded the ability to analyze ecological relationships. Utilization distributions identify high use areas, while network analysis placed higher emphasis on movement corridors and links between core and peripheral use areas. As marine protected areas increase in relevance and expand to include the conservation of mobile species, it is important that methods to evaluate their effectiveness do not smooth over complex spatial-temporal patterns. The inclusion of network methods in routine spatial assessments may help illuminate patterns previously unconsidered using conventional home range analysis.

2.1.1 Key words: Acoustic telemetry, home range, marine protected areas, great barracuda, analytical tools

2.2 Introduction

In recent decades, fisheries management has shifted from purely stock management towards adopting ecosystem based principles (Pikitch et al. 2004), with increasing emphasis on spatial frameworks such as the creation of marine protected areas (MPAs; Pauly et al. 2002, Airame et al. 2003, Douvère 2008). The 2006 Convention for Biological Diversity led to a global commitment to protect >10% of the ocean by 2020 (Spalding et al. 2013), leading to a surge in MPA establishment, but to be successful this shift necessitates understanding of species spatial ecology within managed areas. The spatial ecology of an animal is influenced by traits such as life-stage and ontogeny that interact with benthic habitat, population dynamics, species interactions, and physical environmental variables that can vary temporally (Polis et al. 1997). While this boon in

MPA establishment is broadly seen as a conservation success (Allison et al. 1998, Lester et al. 2009, Cressy 2011), the actual net benefits that MPAs have on the ecosystems and human populations within and surrounding them is variable (Claudet et al. 2010, De Santo 2013, Edgar et al. 2014).

Cumulative research on MPA efficacy has shown that when implemented correctly, reducing fishing pressure typically leads to increased fish abundance (Allison et al. 1998, Murawski et al. 2000, Roberts et al. 2001, Pauly 2002, Halpern 2003, Lester et al. 2009). What defines correct implementation is harder to establish. Quantitative assessments are needed to determine whether decreasing fishing pressure in designated zones will automatically result in healthier ecosystems (Heupel et al. 2006, Farmer et al. 2011). Trophic dynamics, fish assemblage structure, and the history and type of harvest in a region may all impact how an ecosystem recovers after fishing pressure is reduced or eliminated (Murawski et al. 2005, McClanahan et al. 2007, Lester et al. 2009, Claudet et al. 2010). In addition, geographic and socioeconomic factors also play a huge role in the success of MPAs (Murawski et al. 2005, Suuronen et al. 2010, Edgar et al. 2014). In some cases, if an MPA does not cover adequate or accurate essential habitats for target species, closing of non-relevant areas will lead to greater concentration of fishing effort in adjacent habitats (Murawski et al. 2005, Suuronen et al. 2010). If target habitats are misidentified – or if spatial closures are based on political feasibility rather than ecological research - managers run the risk of merely shifting or even intensifying fishing pressure while simultaneously “meeting” conservation goals by increasing the percent of space under protection (Suuronen et al. 2010).

Recent studies show a global trend of MPAs failing to adequately protect biodiversity, despite their potential (Edgar et al. 2014, Klein et al. 2015). Failure is defined as the lack in overlap between species range and MPA boundaries, or the lack of difference between fish populations in MPAs and adjacent fished habitat due to improper enforcement or planning (Edgar et al. 2014, Klein et al. 2015). A necessary assumption in planning effective MPAs is that established range data for species is accurate and comprehensive. Large-scale assessments of MPA efficacy rely on data on species home ranges modeled as static core use areas (Pressey et al. 2007), however, movement studies reveal that many marine species demonstrate dynamic and shifting habitat preferences that vary temporally on scales ranging from life-span ontogenetic shifts (Mumby et al. 2004, Kimirei et al. 2011) to diel foraging migrations (Burke 1995, Meyer et al. 2007, Luo et al. 2009). Traditional assessment of MPA efficacy states that for MPAs to successfully protect marine species, coverage must protect enough area that the probability that the focal species will be outside protection for enough time to be harvested is minimized (Edgar et al. 2014). More recently, MPAs have been targeting the conservation of mobile species whose home ranges cannot be fully protected, in which case the goal has shifted towards the protection of essential habitat for ecological functions such as spawning or feeding (Runge et al. 2014, Pérez-Jorge et al. 2015). Thus, MPA failure is possible because species cross over MPA boundaries due to inadequate reserve extent, or a lack of data regarding use of adjacent habitats during limited movements away from core home range, such as to hunt or spawn (Bolger et al. 2008, Buler and Moore 2011, Runge et al. 2014).

Gathering the information needed to successfully implement ecosystem-based spatial management requires building a nuanced understanding not just of the target area or habitat type, but also of the interrelationships between species, adjacent habitats and regional networks of ecosystems and metapopulations (Crowder and Norse 2008). This can be a very complex task and may not initially be realistic in a management decision making timeline (Tallis et al. 2010). Metrics that summarize spatial use, such as home range utilization distributions or area estimates, can be used to approximate cumulative activity space of an individual or population (Kie et al. 2010). These metrics can be very useful as a planning tool, but must be applied carefully so that broad summaries are not excluding nuances in habitat use vital to a target species' life history (Powell 2000, Kie et al. 2010). Highly mobile species in particular may prove challenging to summarize with simple metrics, as spatial closures may aim to target areas of specific ecological relevance, rather than cover entire home ranges (Buler and Moore 2011, Runge et al. 2014). Additionally, even for species whose movement patterns are well represented by traditional home range estimators, many marine species that MPAs seek to conserve currently lack comprehensive home range estimates.

Obtaining accurate data on the movements and spatial use of marine species is made challenging by the inaccessibility to consistent unbiased sampling designs at the correct ecological scale. Tracking of movements using telemetry is valuable in quantifying habitat use within and between habitat types for adult fish, allowing for long term data sets on residency and migration patterns (Heupel et al. 2006, Hussey et al. 2015). Acoustic telemetry is a relatively new method, and it is rapidly increasing in popularity (Cooke 2008, Hussey et al. 2015), however methods for analyzing the often

vast quantities of data are still catching up with the technology's prolific use and application (Heupel et al. 2006, Ledee et al. 2015). Methods used to estimate activity space rely on data that remains as coarse as the spatial scale of the array design, or alternately, draws from coarse scale data to make broad interpolations (Hedger et al. 2008, Ledee et al. 2015). Kernel utilization density (KUD) remains one of the most widely used and popular methods to predict core activity space using telemetry data (Kie et al. 2010, Jacoby et al. 2012). While these metrics can provide valuable data, there is concern that these interpolation methods may be less accurate for broad scale acoustic telemetry (Hedger et al 2008). These arrays generate data that is spatially limited to the range of the acoustic receiver. Datasets take the form of repeated detections at few locations. In contrast, the telemetry methods KUDs have traditionally been used for, such as GPS collars, produce a large number of unique positions that can then be interpolated from with greater accuracy (Hedger et al. 2008, Ledee et al. 2015).

Recently, there has been a greater emphasis on developing ways in which to more deeply utilize acoustic telemetry datasets by exploring the use of analyses that incorporate temporal sequences of detections to quantifying movements, rather than viewing raw detections as unique data points (Jacoby et al. 2012). For instance, Dynamic Brownian bridge movement models (DBBMM) are an alternate utilization density method to KUD that takes movements between receivers as the input, interpolates intermediate points between these two detections, and then bases density estimates off of the interpolated points (Horne et al. 2007). This method addresses gaps in receiver coverage and temporal relationships between detections, primary concerns regarding use of KUD in acoustic telemetry analysis. Network analysis takes a completely different

approach from both utilization density estimators and quantifies the relationships between nodes (points) and edges (connections between points) (Jacoby et al. 2012, Jacoby, Croft, & Sims 2012, Finn et al. 2014). It has been used for analyzing neural networks, social networks, and increasingly, spatial networks. The format is well suited to the interconnected array of individual receivers that often constitutes a broad scale acoustic array, but its potential is only recently being explored.

As activity space estimates often have direct repercussions for management decisions, it is important for conservation that these estimates are accurately representing ecological drivers. Currently there are a diversity of methods used to estimate the same parameters, thus it is important to understand whether and under what conditions there are variations in the estimates produced by disparate analytical methods. I sought to investigate how data quality and methodological choice influenced estimates of core activity space of great barracuda tagged with transmitters within an extensive acoustic telemetry receiver array deployed in a marine protected area in the U.S. Virgin Islands. Specifically, I compared utilization density methods described above, kernel utilization density estimation and dynamic Brownian bridge movement models to one another and to metrics identifying core activity spaces using network analysis. Comparisons were made by identifying receivers within the core use area of individual animals (Ledee et al. 2015). The size of individual activity spaces were compared among methods and modelled in relation to detection history and body size (Kramer and Chapman 1999).

2.2.1 Objectives

My objectives for this study were to generate activity space estimates for great barracuda within BIRNM using telemetry data generated from a passive, broad scale acoustic array. In order to better understand ecological results drawn from activity space estimates, these objectives took two major paths; comparing estimation methods and determining the role of method choice and variation in detection frequency on resulting area estimates, as well as generating cumulative activity space estimates for a year of tracking data. Specifically, I aimed to compare home range results from two utilization density methods; KUD, a traditional home range estimator, and Dynamic Brownian Bridge Movement Models, which take into account movement between location sites, as well as compare these results to central activity spaces indicated by network analysis. Following the methods comparison I aimed to assess the impact of strength of detection history on home range size estimates, as well as the ability to detect ecological drivers of home range, in this case body size through generalized linear models. Lastly, once the impacts of method choice and detection history were taken into account, I sought to generate home range estimates for individual fish within the study population.

2.3 Methods

2.3.1 Study site and array design

Buck Island Reef National Monument (BIRNM) is a MPA managed by the U.S. National Park Service. BIRNM is located on the northeastern shelf of St. Croix (Fig. 2.1). In 2001, management shifted from multiuse to no-take and the original park boundaries were greatly expanded to over 19,000 acres. To date, no studies have been done

quantifying fish species home ranges, habitat use, and connectivity among habitat structures within and adjacent to the park.

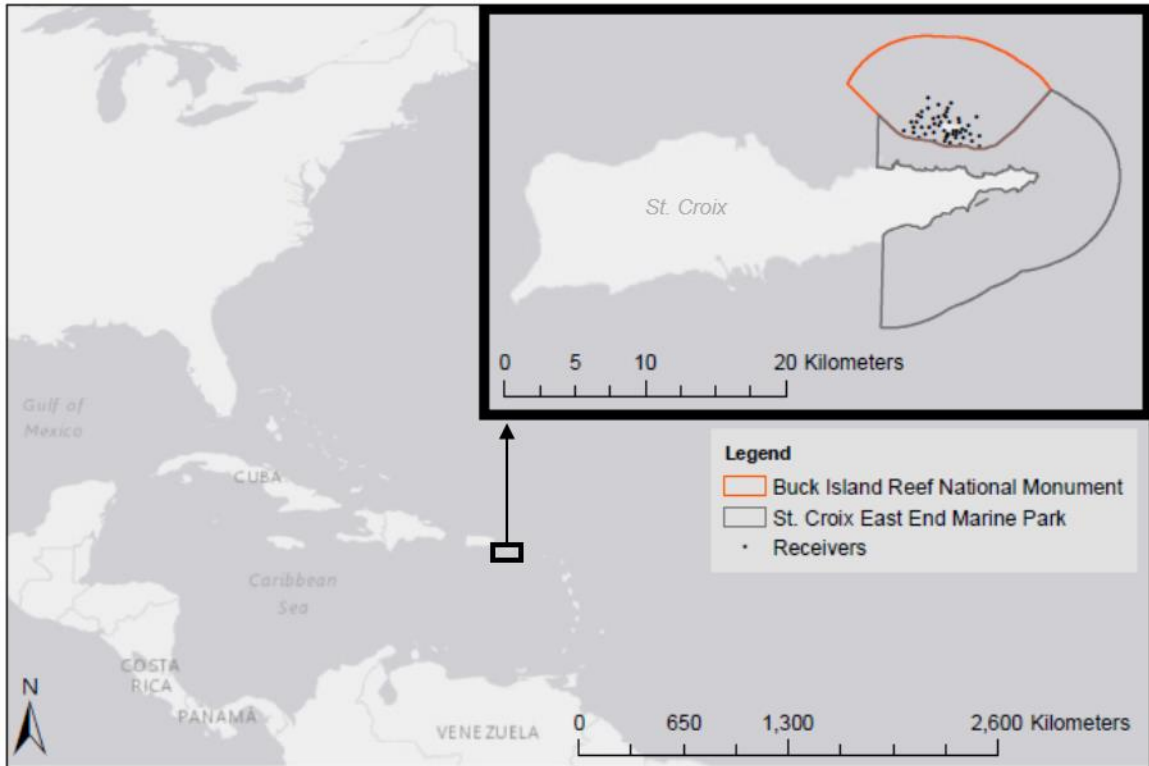


Figure 2.1: Location of Buck Island Reef National Monument, adjacent protected areas, and receiver array placement within the park.

BIRNM is composed of a shelf habitat containing various shallow water habitats and deeper waters overlying a drop off towards an oceanic trench. An extensive linear reef protects the southeastern coastline. Inside these reef structures lie calm lagoons. High rugosity linear and patch reefs are interspersed with colonized hard bottom and spur and groove reef to the north and west. Sandy flats and seagrass occur to the south and west. Habitat types are highly interwoven in a patchy mosaic pattern (Costa et al. 2012).

This study uses passive detection of tagged barracuda using fixed, autonomous acoustic receivers (VR2W 69 kHz VEMCO Inc, Nova Scotia, Canada) deployed as part of a collaborative research effort. A total of 52 acoustic receivers were anchored semi-

permanently throughout the shallow water habitats of the park. Anchors included cement blocks in hard-bottom habitats and 3 foot, 6 inch diameter blade sand screws where sand was deep enough to accommodate. Sites were chosen based on proximity to other receivers, with the intention of avoiding overlapping ranges and providing equal coverage among the various benthic habitats (Fig. 2.2). Range of detection of an acoustic signal by a fixed receiver can be influenced by bottom structure, depth, and a myriad of other environmental factors such as suspended particulate matter, background noise, currents, turbidity, wave height, and weather and can vary from several meters to upwards of 100 meters, depending on placement and conditions (Kessel et al. 2013). Range testing calculating maximum detection range and probability of detection at a scale of distances was conducted by NPS and USGS employees in the BIRNM array. Preliminary analysis indicated that the average range where 50% of detections are detected is approximately 125 meters (Thomas Selby USGS, personal communication).

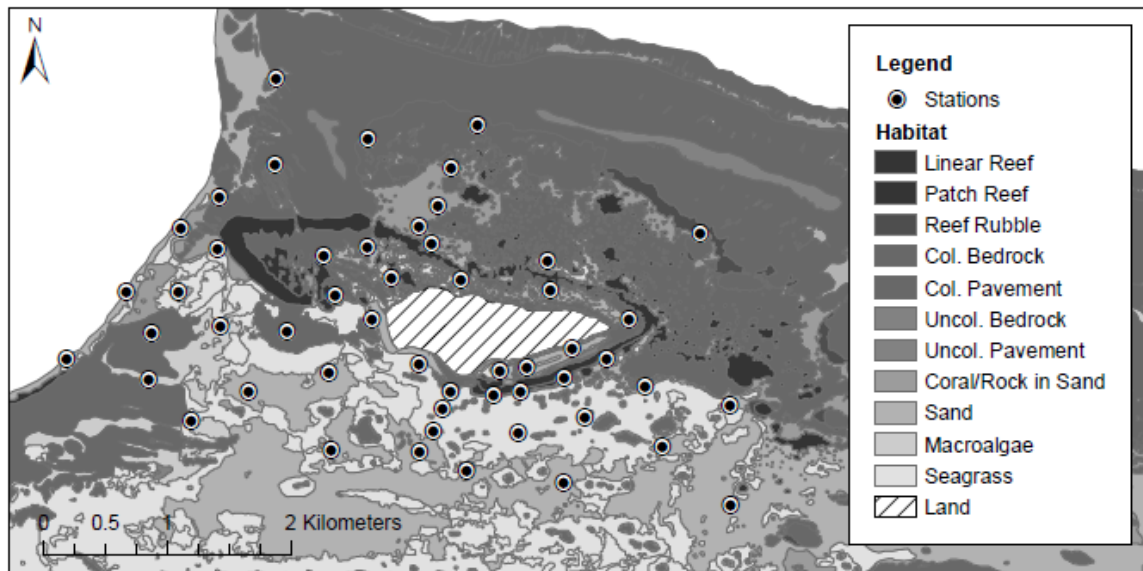


Figure 2.2: Location of receiver stations within the shallow water section of BIRNM. Benthic habitat shapefiles were generated by NOAA Biogeography Branch.

2.3.2 Barracuda capture and tagging

Great barracuda were captured by trolling with medium action 10-50 lb recreational fishing gear and artificial lures rigged with brightly colored plastic 1” diameter tubing and 2 9/0 circle hooks (O’Toole et al. 2011). Fishing effort data was collected by timing trolling and recording gear type and number of hooks. All capture sites were marked with a GPS waypoint. Upon capture, the fish were evaluated visually, looking for hook damage, other recent injuries, normal swimming, and ability to maintain equilibrium in order to determine if health was adequate to support a tag.

Depending on size class, barracuda (n = 35) were tagged with either a V16 (16 by 54mm, 8.1 grams) or V13 (13 by 36mm, 6 grams) standard VEMCO acoustic transmitters programmed to ping randomly between 60-180 seconds for the duration of the battery life, ranging from 1299 days for V13 to 3650 days for V16. Fish selected for tagging were placed into a 204.4 L Rubbermaid tote measuring 108 by 54.3 by 45.7 cm of seawater. The anesthetic MS222 diluted to a 10g/L concentration stock solution was slowly added to tote to induce stage 4 anesthesia (O’Toole et al. 2011, FAU IACUC Guidelines 2014). Fish were determined to be sufficiently dosed for surgeries at the onset of slowing of gill movement and loss of full equilibrium. Anesthetized fish were held in a supine position with gills submerged while an incision was cut with a #10 blade carbon steel sterile disposable scalpel just off the central mid-line between the pelvic and anal fins. Acoustic tags disinfected with 70% isopropyl alcohol were then surgically implanted into the body cavity. Incisions were closed with Ethicon polydioxanone monofilament sterile absorbable FS-1 24mm reverse cutting needle sutures (Model PDS*II), using 2-3 simple interrupted sutures. Halfway through the surgery, fresh seawater was added to the

cooler to dilute the anesthetic and begin the recovery process. Total length and fork length was measured. Time and length of procedure was recorded for all aspects of the capture and surgery. Fish were allowed to recover and monitored in ambient seawater until normal swimming patterns are observed before being released back into the study area from which they were captured (Friedlander and Monaco 2007, O'Toole 2011). Small fish were recovered in a floating mesh pen (4' x 6', 2.5 cm mesh size) to isolate them from predators, while fish too large for the pen (and less at risk for predation) were lowered over the side of the boat and held facing into the current until strong enough to swim normally. No more than four fish from a given capture site were tagged on a single tagging trip to ensure adequate distribution of tagged animals throughout the array and across habitat types and to avoid tag collisions. All capture and tagging methods were approved under IACUC #2013-0031 (University of Massachusetts Amherst).

2.3.3 Data management, filtering, and analyses

Acoustic data was filtered in R version 3.2.2 (R Core Team 2015) and VUE (VEMCO Inc, Halifax, NS) software to remove false detections caused by tag collisions and interference from background noise. Biologically unlikely movement patterns that would indicate the death of a tagged fish or another event that would invalidate data from that transmitter were also removed. Any fish that recorded more than three consecutive weeks of transmissions at a single receiver was presumed to have died or shed its tag in the vicinity of that receiver.

For all analyses the same dataset was used, spanning from July 2014-July 2015 providing a full year of data after last fish in this study was tagged. I calculated the time

between each detection, and removed any detections that occurred less than 55 seconds apart. The nominal delay in transmission was set to an average frequency of 120 seconds, randomly ranging from 60-180 seconds. I allowed detections that strayed five seconds or less in order to not falsely remove detections that could be real and due to clock drift or tag irregularities. Short ping rates due to echoes or simultaneous detections were considered to not be representative of actual great barracuda location data. All analysis was conducted in R version 3.2.2 (R Core Team 2015).

2.3.3.1 Kernel density estimation (KUD)

KUD estimates were conducted for all 32 fish present in the dataset spanning from July 2014-July 2015. Grid size was set to approximately 50 by 50 meters, and the smoothing parameter was set at 125 meters, which corresponds to the average 50% contour for receiver detection range in this array. I standardized the area over which the utilization distribution was calculated to include the entire array. In order to allow the KUD to run on acoustic telemetry data, which included many points at the same location, each data point was randomly assigned a location within the 50% cut off in detection range for that receiver (125m).

2.3.3.2 Dynamic Brownian bridge movement models (DBBMM)

A DBBMM framework differs from KUD, which uses single point location data, by employing movements between two locations as the data input. I created movement matrices in which each line of data indicates a movement between two receivers and used this as the model input. All models were run using the move package (Kranstauber &

Smolla 2015). DBBMM interpolates intermediate points between detections and generates a density surface based on these. I set the interpolation time to be 120 seconds, to replicate the average ping rate, and set the location error to be 125 meters, based on the average receiver detection range.

2.3.3.3 Home range estimation

For both utilization density methods, I calculated contour lines representing where on the density surface fifty percent and ninety-five percent of density probabilities occurred. I then calculated the area falling within each of these contour lines in order to generate core and general use area estimates, which I later used to compare these two utilization density methods, as well as to compare utilization density methods to network analysis.

2.3.3.4 Network analysis

Network analysis uses different metrics to assess the association between nodes – points in a network – and edges – the connections between those nodes. Recently, this method has begun to be used to analyze broad scale acoustic telemetry arrays (Jacoby et al. 2012, Finn et al. 2014, Ledee et al. 2015). I created networks of receivers for each fish, with each node representing an individual receiver and each edge a movement of the fish from one receiver to another. I used the igraph package (Csardi & Nepusz 2006) to assign centrality to metrics for each node in each individual fish array (Ledee et al. 2015). I assessed centrality based on degree. This metric represents the number of edges connected to a single node, including self-loops, when an animal was detected

consecutive times at the same receiver. Centrality degree should, therefore, be broadly comparable to utilization density methods estimating frequency of use. I used degree ranks to create spatially referenced plots in order to visualize activity spaces for individual fish.

2.3.3.5 Core and General use receiver identification

In addition to using utilization density to define home range areas, I also used the fifty percent contours to define core use receivers (CUR) in order to compare utilization density estimation methods with network analysis (Ledee et al. 2015). The 50% area was used to look at core areas, since for many of the fish the 95% areas lay outside the array, leading to greater confidence in the 50% estimates for model comparison. For network analysis, degree metrics were used to assign core use receivers for each fish. Receivers were rank ordered by degree value and all receivers that fell below the 50% were identified. Numbers of core use receivers (CUR) were compared to numbers of receivers that fell within the utilization density generated 50% contour lines in order to compare overlap between approaches.

2.3.3.6 Model comparisons

Normality tests indicated non-normally distributed data. Additionally, detection data indicates movements from one receiver to another, which automatically violates the assumption of independence of data. Therefore, randomization tests were used to test for significant differences between results of the various methods. Area estimates at both

fifty and ninety-five percent contour areas were tested against each other. CUR identified by KUD and DBBMM were tested against CUR identified by NA.

2.3.3.7 Impact of variation in detection history on activity space estimates

Several generalized linear models were created to assess drivers of home range size and centrality ranking generated by the comparison methods. The models examined how estimates generated by each method were being influenced by fish size as indicated by fork length, as well as strength of datasets, as indicated by mean number of detections per week. Fish size has been shown to be a driver of home range size (Kramer and Chapman 1998). Strength of detection histories was highly variable for the individual great barracuda. I included mean weekly detections as a parameter in the model to examine to what degree the data limitations as opposed to barracuda ecology were influencing patterns. The generalized linear models tested these two covariates and their interaction for each of the three methods. For the first two models (DBBMM core area and KUD core area estimates) I used the gamma distribution with a log link, and for the last (NA CUR estimates) I used the Poisson distribution with a log link. For all models the predictor variables include fish fork length, average number of detections per week, and the interaction between length and detections. Conditional plots generated using the R package VisReg were used to more closely examine the relationship between body size and detection history within the interaction term (Breheny and Burchett 2015).

2.4 Results

2.4.1 Activity space estimation

While barracuda had detections on many or all receivers, both utilization distribution methods show steep distribution surfaces dominated by relatively small activity spaces (Table 2.1). Fifty percent home range estimates were very small for both utilization distribution models, between 0.1 to 0.2 km² for each method. Ninety-five percent home range areas were much larger for both estimates and were more variable across the two methods compared to fifty percent estimates. KUD showed a mean of 1.39 km² and DBBMM showed more than twice that, with a mean of 3.69 km². Results from the CUR analysis for both utilization density methods as well as centrality degree network analysis show comparable numbers for KUD and DBBMM, but noticeably larger numbers of core receivers as defined by network analysis (Table 2.1). For these estimates, CUR generated by KUD and DBBMM again appear to be fairly similar, albeit slightly greater for DBBMM. However, estimates are much larger for CUR estimates generated using network analysis.

Table 2.1: Summary statistics for estimation of home range and activity space. Home range area estimates include core (50) and general (95) area estimates for both kernel utilization density (KUD) and dynamic Brownian bridge movement models (DBBMM). Core use estimates include the number of core use receivers generated by KUD, DBBMM, and network analysis (NA). All estimates used to generate these summary statistics can be found in Appendix J.

	Home range area estimates (km ²)				Core use estimates (# receivers)		
	KUD_50	DBBMM_50	KUD_95	DBBMM_95	CUR_KUD	CUR_DBBMM	CUR_NA
Mean	0.208	0.202	1.389	3.690	2.313	3.0313	6.813
Median	0.130	0.145	0.941	1.368	1.5	2	7

2.4.2 Methods comparison

Visual comparison of plots from KUD, DBBMM, and network analysis indicated that there is agreement across methods in predicting location and size of home range territories. All methods show broad use of the array, with general use areas encompassing large swaths of receivers across all habitat types and core use areas that are found across all habitat types and overlap spatially with the territories of neighboring barracuda (Fig 2.3).

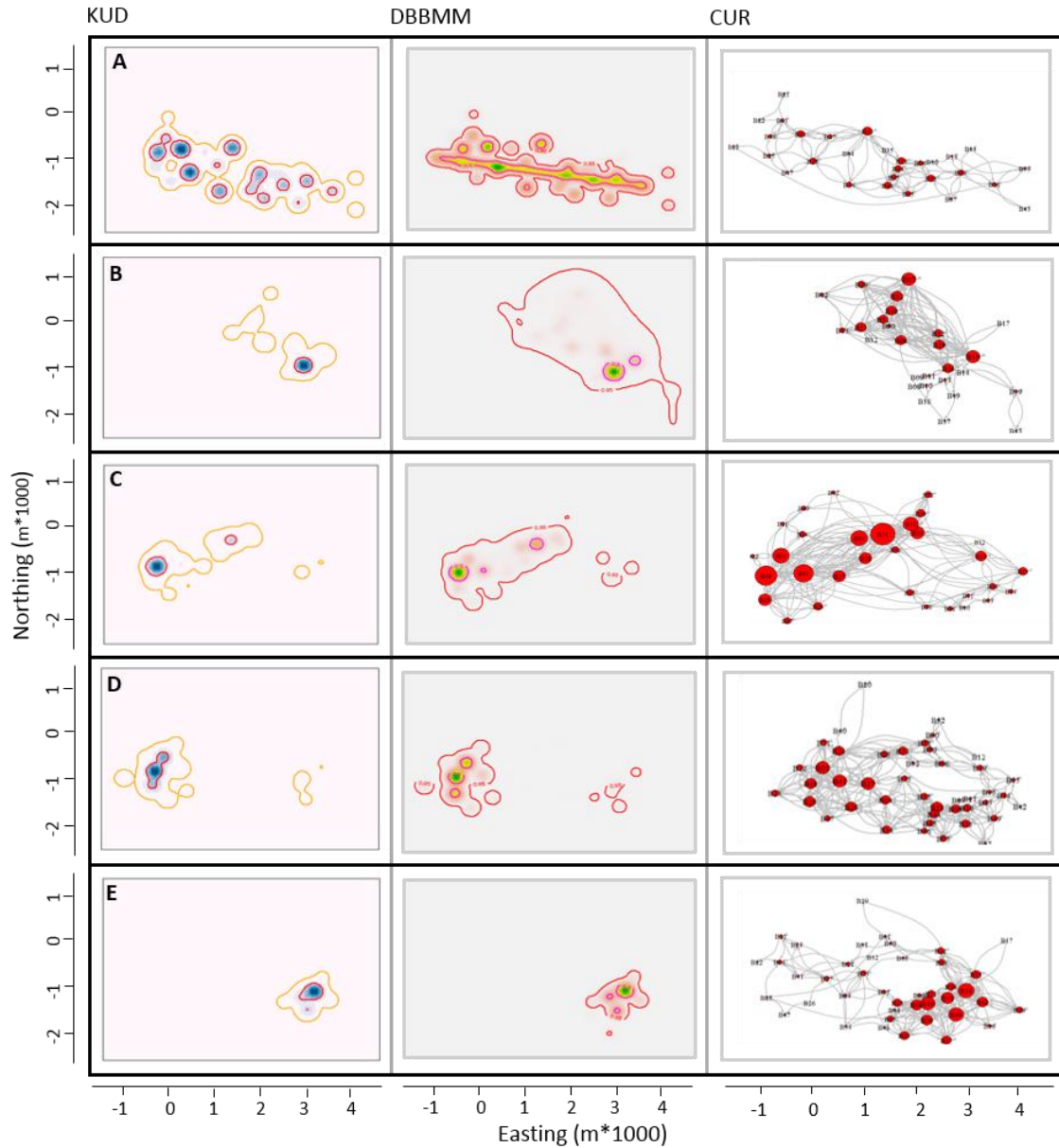


Figure 2.3: Comparison between three different methods of estimation of activity space (KDE, DBBMM, and NA, respectively) for five example barracuda; A-E. A: Tag 24551, 812 detections; B: Tag 24555, 7,645 detections; C: Tag 24554, 13,282 detections; D: Tag 26799, 51,276 detections; E: Tag 26800, 106,074 detections.

2.4.2.1 Randomization permutation tests

Results from the randomization permutation tests validated the trends shown by the summary statistics of utilization density and CUR comparisons (Table 2.2). There is

no significant difference between estimates at the utilization density fifty percent estimates, but a significant difference is observed at ninety-five percent. Plotting observed/ expected detection ratios against area estimates for both utilization distribution methods showed a pattern of decreasing area estimates with increasing detection histories (Figure 2.4). The difference between estimates by the two utilization distribution methods, as well as the overall variability in estimated area also decrease with increasing detection histories (Figure 2.4). When examined more closely by plotting KUD and DBBMM results against each other, and then looking at the residuals residuals for the two utilization distribution methods against mean detections per week, it is apparent that as detection histories increase, residuals decrease (Figure 2.5). Therefore, as detection histories increase, the differences in area estimates between KUD and DBBMM decrease.

Table 2.2: Significance tests between KUD and DBBMM at the 50th percentile (core home range), 95th percentile (general home range), as well as between the number of CUR generated by each method. CUR tests conducted between KUD and DBBMM, KUD and NA, and DBBMM and NA. Significance was determined using permutation tests without replacement. Significant values are highlighted in bold.

TEST	p(value)
KUD_50:DBBMM_50	0.904
KUD_95:DBBMM_95	0.0091
KUD_CUR:DBBMM_CUR	0.999
KUD_CUR: NA_CUR	<0.001
DBBMM_CUR:NA_CUR	<0.001

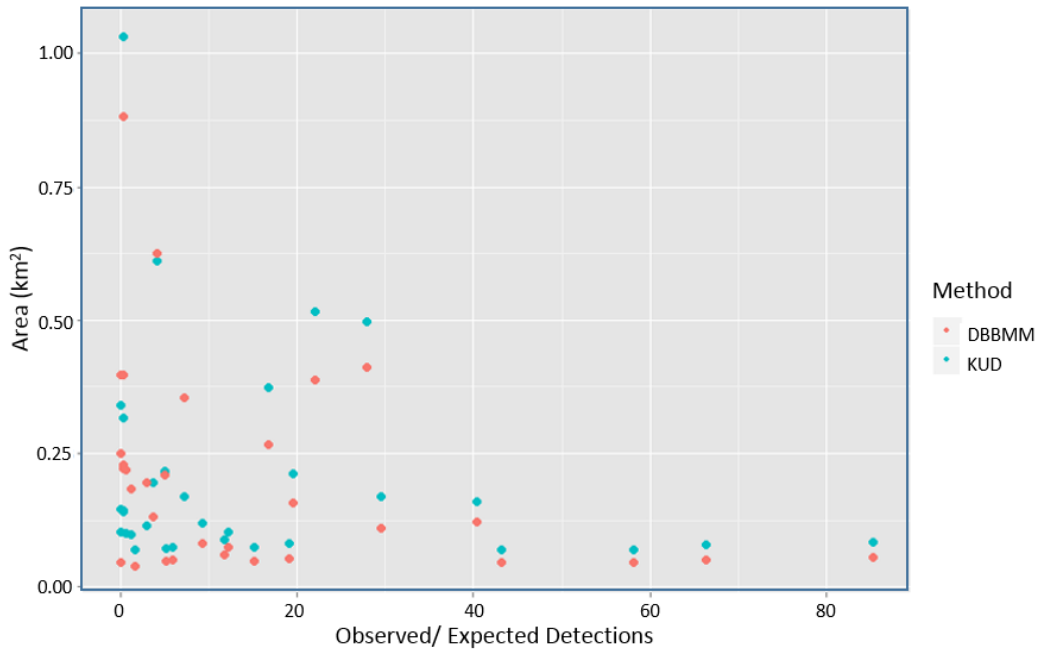


Figure 2.4: Core use area estimates for DBBMM and KUD plotted against observed/expected detections ratio.

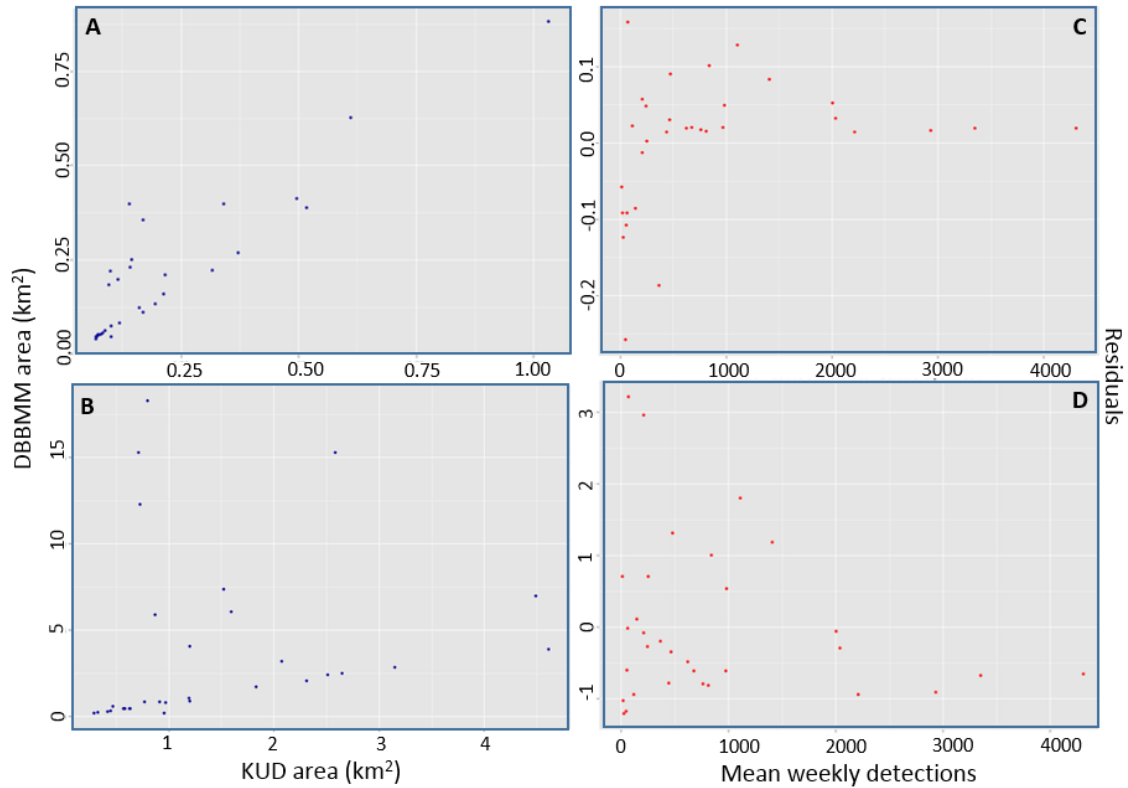


Figure 2.5: Scatterplot of KUD and DBBMM area estimates for 50th (A) and 95th (B) percentiles. Residuals of linear regressions run on each scatterplot, plotted against mean weekly detections for 50th (C) and 95th (D) percentile area estimates.

2.4.2.2 Generalized linear models

There were variations among the three models regarding which variables were significant but agreement as to whether relationships between model parameters and core use area estimates (the dependent variable) were positive or negative (Table 2.2). The model with KUD as the dependent variable showed no significant predictor variables, however, DBBMM did, despite there being no significant difference shown between these two methods in the randomization tests. CUR also had a significant relationship between detection history strength and home range size. This model however, also showed the interaction between detection history and body size as significant, warranting

closer examination of this relationship. All models, including KUD (although the relationship was not significant in that case), showed negative relationships for the detection history variable. As detection histories increased, the home range size decreased. Fork length showed a negative relationship across all models, however none found this variable alone significant.

Table 2.3: Outputs from three generalized linear models examining influence of mean weekly detection rates (Dets/Week), body size (Fork length) and the interaction between these two terms on core use area estimates generated by kernel utilization densities (KUD), dynamic Brownian bridge movement models (DBBMM) and network analysis centrality-degree ranking of core use receivers (CUR). KUD and DBBMM generate area estimates at the 50th percentile contour of density plots, and CUR generates number of receivers in the top 50th percentile for centrality-degree rankings. For KDE and DBBMM, a gamma distribution with a log link was used, whereas a Poisson distribution with a log link was used for the CUR model.

	KUD	DBBMM	CUR
	estimate, standard error, significance levels: *0.05, **0.005, ***0.0005		
Intercept	-0.74(+/-1.342)	-0.30(+/-1.19)	2.44(+/- 0.61)***
Dets/week	-0.0024(+/-0.002)	-0.0028(+/-0.0013)*	-0.002(+/-0.0007)*
Fork length	-0.0078(+/-0.016)	-0.012(+/-0.014)	-0.0069(+/-0.0071)
Dets/week: FL	0.000025(+/-0.00002)	0.000027(+/-0.00002)	0.000019(+/-0.000008)*

When plotted separately in conditional plots with fixed detection history values, the input of body size on the interaction of fork length and detections per week was positive across all models, and significant for the CUR model (Table 2.3). Detection history strength initially clouds the relationship, but when strong detection histories are observed a strong positive relationship between fork length and home range size exists (Figure 2.6). This relationship is shown by the randomization testing to be significant just for CUR, but the trend of a positive relationship between body size and home range for

high detection history individuals is shown across all models, but is hidden by the numbers of low detection history great barracuda that do not display this relationship.

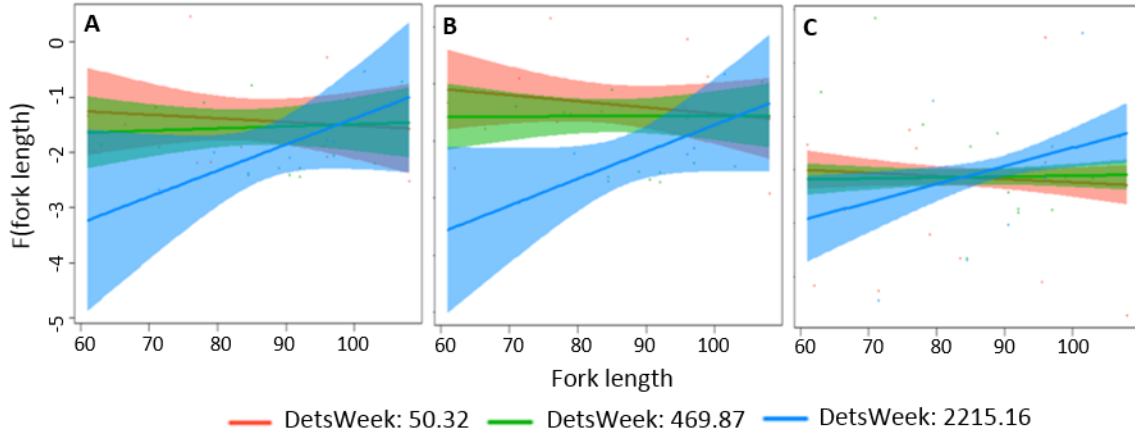


Figure 2.6: Conditional plots showing the relationship between barracuda fork length and home range area as a function of fork length, with detections segregated by detection history for each of the three generalized linear models. A) KUD_50 as dependent variable; B) DBBMM_50 as dependent variable; and C) CUR as dependent variable. Fork length is plotted on the x axis, and the contribution of fork length into the interaction is plotted in log scale on the y axis. The relationship is plotted separately for 3 fixed values of mean weekly detections (DetsWeek), a low value shown in red, a moderate value shown in green, and a high value shown in blue.

2.5 Discussion

Utilization distribution methods indicated that barracuda are predominantly utilizing small, overlapping territories at the detection scale of the acoustic array. Individual fish have unique core areas of use and they frequently return to these areas after not being continuously detected. Of the 33 observed fish, 27 were detected on a large number of receivers, but had a majority of detections occurring on a much smaller subset. Barracuda appear to display high site fidelity to small core use areas, but periodically demonstrate broad movements throughout surrounding areas, making

barracuda an ideal species for testing analytical techniques since they display periods of residence and higher mobility.

2.5.1 Activity space estimation and method comparison

The two utilization distribution methods predicted very similar values using 50% area estimates, but showed significantly different results at the 95% level, with DBBMM predicting values with an average twice as high as the KUD. Comparison of utilization density plots and area estimates showed that a handful of fish have ninety-five percent DBBMM predictions many times the KUD estimates. These extreme values are primarily driving the overall difference. Individual fish that show the highest discrepancies are those with comparatively weak detection histories. While functioning very similarly when detection histories were high, DBBMM estimate larger areas compared to KUD when detection histories are low. Differences between data input and model algorithms, which for DBBMM use movements between receivers to interpolate intermediary points (Horne et al. 2007) means that estimates for individual fish with fewer detections would base distribution surfaces on a higher ratio of interpolated intermediary points compared to true detections, leading to a loss of true movements informing the model and the expectation individuals have strayed farther. Thus, low detection history primarily drives differences between utilization distribution methods.

The number of CUR predicted by both utilization distributions were similar, but network analysis using the centrality degree metric predicted significantly more CUR, thus utilization distribution methods estimate central activity spaces significantly smaller than network analysis. Since location input data from broad scale acoustic telemetry for

utilization distributions – especially KUD – is limited, these methods are magnifying the effect of high value receivers, concentrating density estimates. Utilization distribution methods, while useful for showing high use areas, are limited in identifying less frequently used areas, at least for a fish displaying periodic movements, like great barracuda. Less commonly used spaces may still be vital to an animal's ecology; many species demonstrate periodic use of vital spawning, nursery, and feeding grounds that might be outside their typical resident territory (Burke 1995, Nemeth et al. 2006, Starr et al. 2007, Meyer et al. 2007, Luo et al. 2009). Network analysis ranked receiver use metrics in relation to other receivers rather than interpolating across intermediate areas, and thus appears to be quantifying receivers as more highly valuable to an animal's activity space than utilization densities. These findings indicate that the method of choice can significantly impact estimates of core area use for great barracuda in the study population.

2.5.2 Variability in detection history on ecological interpretations

Generalized linear models were employed to look at the effects of strength of detection history and fish size on core activity space estimates, as well as to look at the impact of the interaction between these two predictor variables. The results were varied across the three models, but trends indicating a negative correlation between strength of detection history and home range size were consistent across all models and significant in two of the three models. When detection histories were more consistent, predicted home range size was smaller. Greater detection histories identify fish whose resident activity space is captured within the array and therefore the bulk of detections are fully contained

within small, frequently used territories. The lowest mean weekly detections are indicative of the acoustic array containing only exploratory movements. Thus, area estimates become based on widely spread movements indicating a large core use area, when the reality is the core resident territory lies outside the array.

Body size (fork length) was not a significant predictor across any of the models, despite previous research indicating size as a driver of home range size for reef associated species (Kramer and Chapman 1998). The interaction between fork length and detection history was only significant when modeling network analysis defined core use receivers, and estimate values indicated that this interaction is not driving home range size positively or negatively. However, when the regression relationships are evaluated at different mean weekly detections, there is a positive relationship between fork length and home range size for fish with strong detection histories across all models. While a relationship exists for fish with stronger detection histories, this trend is masked in the full dataset. Thus, detection histories in the study not only influenced predictions of home range size, but also the interpretation of the role of body size. The results indicate that it is important to examine how variation in the strength of detection histories within a given dataset might be contributing to the potential to make erroneous conclusions regarding ecology.

2.5.3 Management implications

Estimates of movement patterns are implemented widely to inform planning decisions regarding spatial management of marine and aquatic ecosystems (Kie et al. 2010). The methods comparison results indicate that method choice can influence the size

of predicted core activity areas as well as affect the ability of researchers to detect ecologically valuable but infrequently used activity spaces such as spawning grounds or feeding areas (Burke 1995, Nemeth et al. 2006, Starr et al. 2007, Meyer et al. 2007, Luo et al. 2009), and identify important ecological relationships. Great barracuda in this study appear to be territorial and show strong site fidelity rather than having highly dispersed movements, indicating that individuals whose core use area during the one year study period is completely encompassed within the acoustic array and thus the marine reserve. Utilization density methods strongly highlight these core use areas but smooth out complexities, thus leading to the risk of failing to identify movement corridors or peripheral areas of use. Network analysis also ranks these core areas as highly central, but also displays wide ranging forays outside core areas, identifying significantly greater numbers of receivers as having high centrality than shown by utilization distribution methods.

For the conservation of mobile predators, the effectiveness of MPAs may lie in their ability to protect specific ecologically valuable habitats, rather than attempting to cover large and unpredictable home ranges (Hooker et al. 2011, Runge et al. 2014). The great barracuda in this study appear to occupy a middle ground between residency and mobility, given their high site fidelity paired with larger ranging movements, proving to be an informative species on which to compare how these methods summarize activity space. Variability between methods will likely be highly dependent on the movement patterns and life history of the study species. The discrepancies between the complexities of movement patterns shown by utilization distributions versus network analysis demonstrate the potential of network analysis in identifying movement corridors and

peripheral use areas (Ledee et al. 2015). More analysis is needed to understand the ecological function of these movement patterns, but as MPAs become more widely applied as a conservation tool for mobile as well as resident species, it is increasingly important to develop tools to identify ecologically vital areas rather than only closing off areas with the highest density of use (Hooker et al. 2011).

Detection histories have the potential to greatly influence the interpretation of results. It is intuitive that poor detection histories may lead to spurious results and many studies have corrected for this by rejecting fish whose datasets are not robust enough for analysis (Ledee et al. 2015). There is currently no *a priori* method for determining what constitutes a sufficient detection history, something that will vary by species, array design and specific research question. The relationship shown in the data between detection histories and home range size demonstrate the importance in determining a specific cut off point based on individual data prior to analysis. Without taking detection histories into account, it would appear that some of the fish use much larger areas than others, and inconsistently. The only other acoustic telemetry study focusing on great barracuda indicates just this pattern; the presence of both resident and transient populations (O'Toole et al. 2011). For this dataset, it seems that the fish whose home ranges appear much larger and infrequent are in fact animals whose core home range lies outside the array. So while these animals are indeed resident and transient to the array, this interpretation indicates that the patterns demonstrated are consistent across the population and not indicative of behaviorally unique sub-groups. There was an additional impact of variable detection histories on identifying ecological patterns, in this case the relationship

between fish size and home range size. Failure to account for detection histories risks misidentifying patterns as of ecological origin.

I anticipate varied results if the same approaches are applied to other study species, geographic areas, and array configurations, as much of the noise in telemetry data is highly dependent on these study specific factors. However, the presence of these patterns within this study demonstrate the importance of careful analysis regarding the impact of methodological choice and detection history as a critical part of the process of analysis of acoustic telemetry data.

2.6 Conclusion

While useful in identifying core use areas, utilization distribution methods are less well suited to identifying movement corridors and peripheral use areas from acoustic telemetry datasets. Network analysis shows potential in filling this missing link. Sporadic use or rapid movements through larger areas may generate fewer detections than resident behavior, but repeated use provides ecological information about a mobile species movements that can inform management. Analyses that smooth out less frequent detections ignore a vital asset of acoustic telemetry data: the ability to use temporal patterns in the data to tease apart drivers for observed movements. As MPAs are created with the conservation of mobile species in mind, it is important to identify movement corridors among ecologically valuable territories. Regardless of method choice, variability in detection histories heavily influenced home range area results, and confounded the ability to determine the influence of the ecological parameter of fork length in this study. As tools to analyze acoustic telemetry continue to be fine-tuned, it is

important to move towards standard approaches for linking fish movements, developing array designs and integration of findings into spatial management frameworks.

CHAPTER 3

NETWORK ANALYSIS INDICATES SPATIAL DIFFERENTIATION AND SITE FIDELITY IN INDIVIDUAL TERRITORIES AMONG A BARRACUDA POPULATION AROUND BUCK ISLAND REEF NATIONAL MONUMENT, ST. CROIX, U.S.V.I.

3.1 Abstract

Top predators play a crucial role in fish communities, shaping population structure through predation pressure. Examining associations of movement patterns with benthic habitat and environmental drivers can reveal ways in which top down pressure intersects with habitat complexity and productivity to influence community structure within and among marine ecosystems. This study assesses the extent to which benthic habitat is a driver of great barracuda ($n = 17$) home range territory choice within an acoustic array located in Buck Island Reef National Monument, U.S.V.I. and compares population densities within this marine reserve to a similar un-fished acoustic array in Culebra, Puerto Rico. Network analysis was used to generate centrality rankings and receiver communities for individual fish and patterns were assessed for individuals and across the study population. A zero-inflated Poisson generalized linear model was created to assess the role of benthic habitat type, seasonal patterns, and fish individuality in driving the observed daily detection frequencies. High variation exists among individuals

regarding habitat characteristics and location of home range territories. Benthic habitat appears to have little influence on home range location, although movement corridors were detected more frequently along high rugosity reef habitat. Increased catch per unit effort values in comparison to Culebra suggest that the marine park may be increasing great barracuda population density. The high site fidelity, widespread use of all habitat types, and relatively dense populations indicate that barracuda are likely playing an important ecological role within the park through predation.

3.1.1 Key words: Great barracuda, network analysis, habitat use, population density, spatial communities

3.2 Introduction

Understanding how predator patterns in habitat use are influenced by environmental and biological parameters can help elucidate links among population, community and ecological structure and dynamics. Large marine predators are currently at low densities compared to the past as a result of overfishing (Myers and Worm 2003, Heithaus et al. 2008). Catch data and ecosystem modeling have shown that historical fisheries focused on higher trophic level species, shifting over time towards lower trophic levels (Pauly 1998) and consequently altering ecosystem functioning including a loss of migratory biomass (Nuttall et al. 2010). Large bodied predators are often less clearly tied to benthic habitat than smaller species (Block et al. 2005, Letessier et al. 2015), instead occupying home ranges large enough to encompass multiple habitat types or management areas (McNab 1963, Kramer and Chapman 1998, Meyer et al. 2007a). Many studies

verify movements of large predators across habitat boundaries (Humston et al. 2005, Meyer et al. 2007a, Meyer et al. 2007b, Clark et al. 2009, Murchie et al. 2013). When the scale of closures is appropriate to ecological needs, top predator populations impacted by fishing pressure have been shown to rebound with the implementation of MPAs (Micheli et al. 2004).

Fishing pressure that disproportionately targets one species or trophic level can lead to the alteration of food webs and trophic relationships of fish communities (Hixon and Carr 1997). For example, variation in population density has been shown to impact a wide variety and life history traits, population dynamics, and behaviors in many different fish species (Sanchez Lizaso et al. 2000, Meyers 2001) including life history parameters such as life span, growth, mortality, rate of maturation, and timing of reproductive developments or events (Stearns and Crandall 1984). Thus, changes in fishing pressure, both through increased harvest in unprotected areas as well as the establishment of marine protected areas (MPAs) after a history of harvesting, can lead to changes in population density and body size of certain species which then influence population ecology or management strategies (Beverton and Holt 1957, Hastings and Botsford 1999). Due to the wide variety of impacts that shifts in density can have on inter and intra-species interactions and population dynamics, it is very important to incorporate density parameters into analyses of spatial ecology.

Great barracuda have been shown through genetic studies to have some traits that closely resemble reef-associated species, but others that indicate large pelagic migrations, potentially occupying a middle ground between reef-associated and pelagic behavior (Daly-Engel et al. 2012). Efficacy of MPAs for mobile predators is highly dependent on

understanding home range and residency patterns (Letessier et al. 2015). Increased understanding of home range size and site fidelity can improve assessments of MPA efficacy and lead to improvements in future planning based on more accurate quantifications of spatial use (Meyer et al. 2007a, Afonso et al. 2009, Letessier et al. 2015). The only study to date on movement ecology for adult great barracuda shows high variability in habitat choice, residency, and site fidelity, thus highlighting the need for further research examining adult habitat use (O'Toole et al. 2011). Due to their size and predation rates these populations could exert strong predation pressure on lower trophic level species (Meyer et al. 2007a). Top down influences based on predator density have been shown to impact fish community structure (DeMartini et al. 2008, Boaden and Kingsford 2015), although it is acknowledged that other ecological variables such as habitat complexity (Beukers and Jones 1998) can vary this impact.

Use of spatial management strategies will lead to heterogeneous density of target species across protect and unprotected areas, again based on residence and dispersal (spillover, etc) and catchability of fishing gears. High trophic level species (Hixon and Carr 1997, Meyer et al. 2007a) and high predator density (DeMartini et al. 2008, Boaden and Kingsford 2015) have been demonstrated to exert impact fish community structure, mediated through other ecological variables such as habitat complexity (Beukers and Jones 1998). Thus, understanding predator patterns in habitat use and density, as influenced by environmental, biological and anthropogenic parameters can help elucidate links among population, community and ecological structure and dynamics that inform management.

Tracking of movements using acoustic telemetry is valuable in for quantifying habitat use within and between among habitat types for adult fish, allowing for long term data sets on residency and migration patterns (Heupel et al. 2006, Hussey et al. 2015). Assessing movement patterns can show spatial and temporal variation in spatial use, and can reveal patterns of connectivity among habitat types and management areas. Understanding how populations associate with benthic habitat patterns and prey assemblages can improve management efforts by strengthening managers' ability to make ecological inferences based on easily surveyed variables. Additionally, increased understanding of home range size and site fidelity can improve assessments of MPA efficacy and lead to improvements in future planning based on more accurate quantifications of spatial use (Meyer et al. 2007a, Afonso et al. 2009, Letessier et al. 2015).

For this study, I examined movement patterns and relative population densities of great barracuda (*Sphyraena barracuda*) through acoustic tracking and catch per unit effort (CPUE) surveys. Great barracuda have been shown through genetic studies to have traits that resemble reef-associated species and large pelagic migrations suggesting a middle ground between reef-associated and pelagic behavior (Daly-Engel et al. 2012). Adults utilize all nearshore habitats, but the specifics of habitat use remain relatively unknown (De Sylva 1963, Blaber 1982, Kadison et al. 2010), with one study indicating seasonal variation in use patterns of certain habitats, but also large spans of time in which habitat use appeared random (Faunce and Serafy 2008). Great barracuda are known to utilize a variety of nearshore habitat types throughout their life histories, moving from inshore estuaries to reefs and open water as they mature, and are believed to spawn in

offshore aggregations throughout the summer months (De Sylva 1963, Blaber 1982, Kadison et al. 2010). The only study to date on movement ecology for adult great barracuda shows high variability in habitat choice, residency, and site fidelity, thus highlighting the need for further research examining adult habitat use (O'Toole et al. 2011). Adult great barracuda exist at a high trophic position in coastal ecosystems and, as large predators that eat indiscriminately, may exert a significant influence on fish community structure (Blaber 1982, Kadison et al. 2010). Barracuda were considered abundant throughout most of the subtropical and tropical world (De Sylva 1963), but while still considered common, the current status of this species in comparison to historical numbers is not known. Ease of capture via angling and high rates of bycatch in recreational fisheries as well as some direct targeting make this species potentially vulnerable to fishing pressure (Springer and McErlean, 1961; de Sylva, 1963; Villareal et al., 2007, O'Toole et al. 2010). Understanding whether this large predator is demonstrating residency concentrated within a marine reserve, as well as assessing whether population densities are elevated in comparison to similar unprotected habitats, could reveal ways in which the exclusion of fishing pressure could be impacting top predator population recovery as well as prey fish community structure through top-down pressure.

3.2.1 Objectives

In order to accomplish my broad goal quantifying the movement patterns of great barracuda within BIRNM in order to better understand great barracuda ecology and make management recommendations to the National Park Service, I used the same dataset from

Chapter 2, but only focused on the 17 best detection histories. My specific objectives were to use network analysis to define spatial patterns from broad scale acoustic telemetry datasets by using two community algorithms to define receiver communities for individual fish. Once results for individual great barracuda were complete, I aimed to summarize and map community results as well as CUR rankings from Chapter 2 for all the study population to assess differences in individual versus population level patterns. In addition to analyzing spatial patterns through network analysis, I wanted to examine underlying drivers of these patterns by generating relative catch per unit effort (CPUE) levels within this marine park and a similar receiver array in Culebra, Puerto Rico in order to determine relative population density levels within the park as well as by building a predictive generalized linear model was built to try to assess drivers of daily detection frequencies. Finally, I aimed to analyze all of these combined results in order to determine define individual and population level site fidelity and habitat use.

3.3 Methods

3.3.1 Study site and array design

Buck Island Reef National Monument (BIRNM) is a MPA managed by the U.S. National Park Service. BIRNM is located on the northeastern shelf of St. Croix (Fig. 3.1). In 2001, management shifted from multiuse to no-take and the original park boundaries were greatly expanded to over 19,000 acres. To date, no studies have been done quantifying fish species home ranges, habitat use, and connectivity among habitat structures within and adjacent to the park.

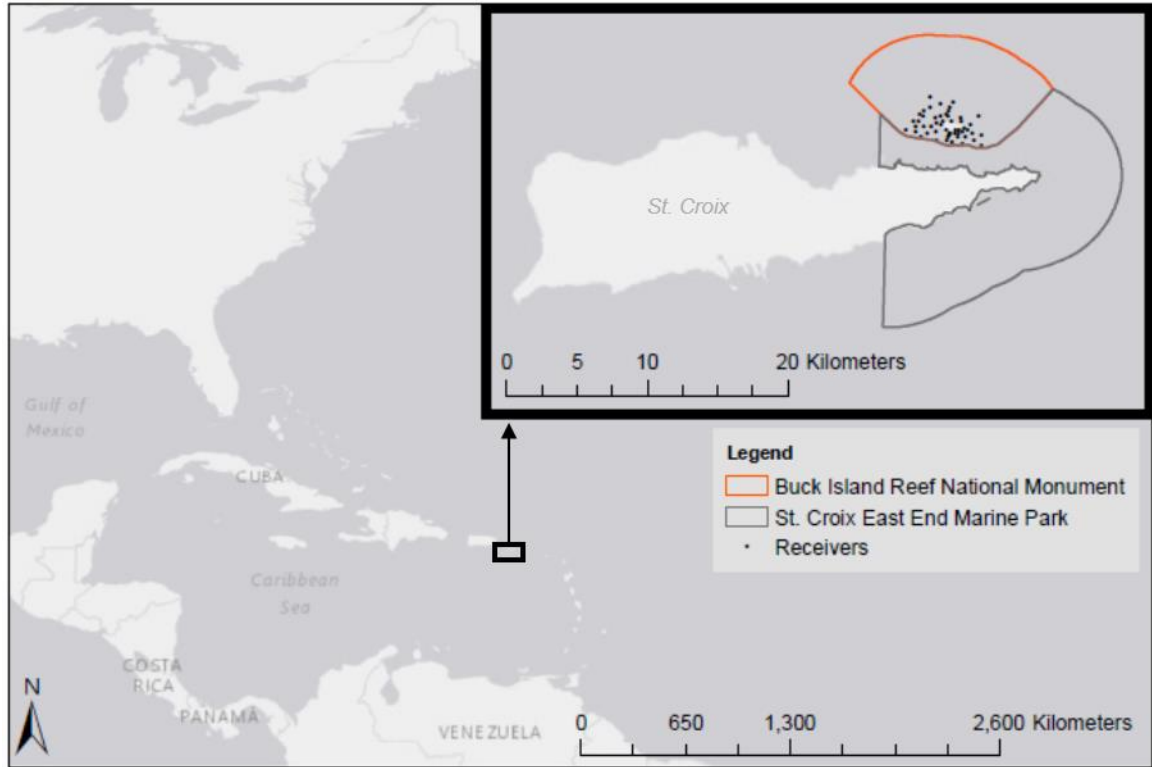


Figure 3.1: Location of Buck Island Reef National Monument, adjacent protected areas, and receiver array placement within the park.

BIRNM is composed of a shelf habitat containing various shallow water habitats and deeper waters overlying a drop off towards an oceanic trench. An extensive linear reef protects the southeastern coastline. Inside these reef structures lie calm lagoons. High rugosity linear and patch reefs are interspersed with colonized hard bottom and spur and groove reef to the north and west. Sandy flats and seagrass occur to the south and west. Habitat types are highly interwoven in a patchy mosaic pattern (Costa et al. 2012).

This study uses passive detection of tagged barracuda using fixed, autonomous acoustic receivers (VR2W 69 kHz VEMCO Inc, Nova Scotia, Canada) deployed as part of a collaborative research effort. A total of 52 acoustic receivers were anchored semi-permanently throughout the shallow water habitats of the park. Anchors included cement blocks in hard-bottom habitats and 3 foot, 6 inch diameter blade sand screws where sand

was deep enough to accommodate. Sites were chosen based on proximity to other receivers, with the intention of avoiding overlapping ranges and providing equal coverage among the various benthic habitats (Fig. 2.2). Range of detection of an acoustic signal by a fixed receiver can be influenced by bottom structure, depth, and a myriad of other environmental factors such as suspended particulate matter, background noise, currents, turbidity, wave height, and weather and can vary from several meters to upwards of 100 meters, depending on placement and conditions (Kessel et al. 2013). Range testing calculating maximum detection range and probability of detection at a scale of distances was conducted by NPS and USGS employees in the BIRNM array. Preliminary analysis indicated that the average range where 50% of detections are detected is approximately 125 meters (Thomas Selby, USGS, personal communication).

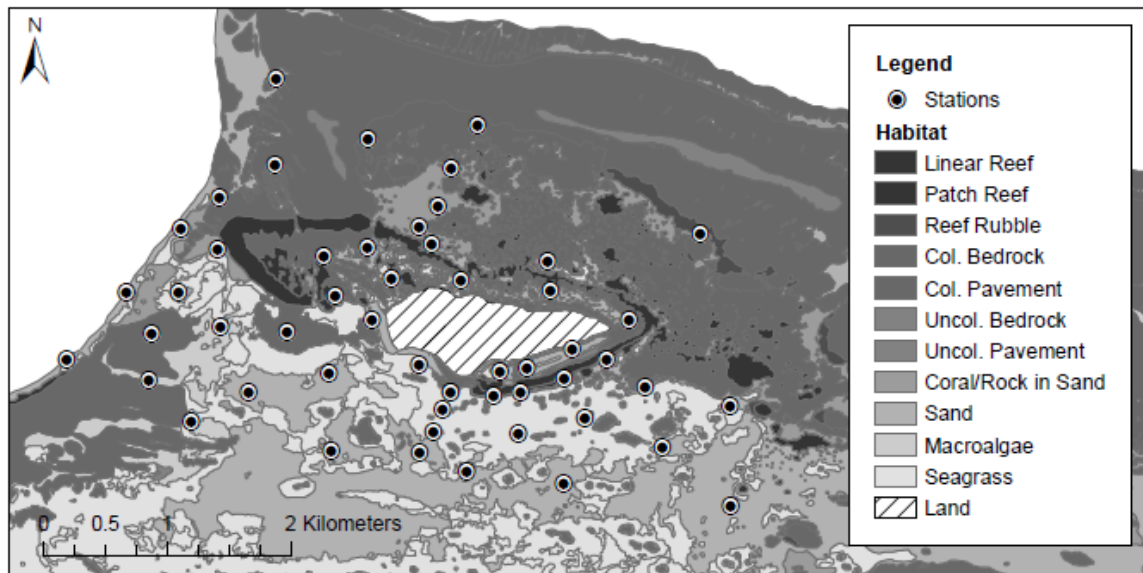


Figure 3.2: Location of receiver stations within the shallow water section of BIRNM. Benthic habitat shapefiles were generated by NOAA Biogeography Branch.

Culebra is approximately 27 km east of Puerto Rico and is comprised of mostly mountainous terrain. There is significant terrestrial conservation land on Culebra and the

surrounding islands in the form of a wildlife refuge run by the Fish and Wildlife Service, including protection of coastal terrestrial habitats. The Luis Peña Channel No-Take Natural Reserve (LPCNR), an MPA established in 1999, is located on the southwest coast of the island. The benthic habitat surrounding Culebra represents a wide range of habitat types. The area to the northeast of the island is dominated by reef, rubble, and colonized hard-bottom, and is exposed to greater wave action and currents. The southwest side of the island is more protected from currents and wave action and is dominated by seagrass beds. There are two large bays located on the east and southeast sides of the island, dominated by seagrass, sandy flats, and mangroves.

3.3.2 Barracuda capture and tagging

Great barracuda were captured by trolling with medium action 10-50 lb recreational fishing gear and artificial lures rigged with brightly colored plastic 1” diameter tubing and 2 9/0 circle hooks (O’Toole et al. 2011). Fishing effort data was collected by timing trolling and recording gear type and number of hooks. All capture sites were marked with a GPS waypoint. Upon capture, the fish were evaluated visually, looking for hook damage, other recent injuries, normal swimming, and ability to maintain equilibrium in order to determine if health was adequate to support a tag.

Depending on size class, barracuda (n = 35) were tagged with either a V16 (16 by 54mm, 8.1 grams) or V13 (13 by 36mm, 6 grams) standard VEMCO acoustic transmitters programmed to ping randomly between 60-180 seconds for the duration of the battery life, ranging from 1299 days for V13 to 3650 days for V16. Fish selected for tagging were placed into a 204.4 L Rubbermaid tote measuring 108 by 54.3 by 45.7 cm

of seawater. The anesthetic MS222 diluted to a 10g/L concentration stock solution was slowly added to tote to induce stage 4 anesthesia (O'Toole et al. 2011, FAU IACUC Guidelines 2014). Fish were determined to be sufficiently dosed for surgeries at the onset of slowing of gill movement and loss of full equilibrium. Anesthetized fish were held in a supine position with gills submerged while an incision was cut with a #10 blade carbon steel sterile disposable scalpel just off the central mid-line between the pelvic and anal fins. Acoustic tags disinfected with 70% isopropyl alcohol were then surgically implanted into the body cavity. Incisions were closed with Ethicon polydioxanone monofilament sterile absorbable FS-1 24mm reverse cutting needle sutures (Model PDS*II), using 2-3 simple interrupted sutures. Halfway through the surgery, fresh seawater was added to the cooler to dilute the anesthetic and begin the recovery process. Total length and fork length was measured. Time and length of procedure was recorded for all aspects of the capture and surgery. Fish were allowed to recover and monitored in ambient seawater until normal swimming patterns are observed before being released back into the study area from which they were captured (Friedlander and Monaco 2007, O'Toole 2011). Small fish were recovered in a floating mesh pen (4' x 6', 2.5 cm mesh size) to isolate them from predators, while fish too large for the pen (and less at risk for predation) were lowered over the side of the boat and held facing into the current until strong enough to swim normally. No more than four fish from a given capture site were tagged on a single tagging trip to ensure adequate distribution of tagged animals throughout the array and across habitat types and to avoid tag collisions. All capture and tagging methods were approved under IACUC #2013-0031 (University of Massachusetts Amherst).

3.3.3 Data management, filtering, and analyses

Acoustic data was filtered in R version 3.2.2 (R Core Team 2015) and VUE (VEMCO Inc, Halifax, NS) software to remove false detections caused by tag collisions and interference from background noise. Biologically unlikely movement patterns that would indicate the death of a tagged fish or another event that would invalidate data from that transmitter were also removed. Any fish that recorded more than three consecutive weeks of transmissions at a single receiver was presumed to have died or shed its tag in the vicinity of that receiver.

For all analyses the same dataset was used, spanning from July 2014-July 2015 providing a full year of data after last fish in this study was tagged. I calculated the time between each detection, and removed any detections that occurred less than 55 seconds apart. The nominal delay in transmission was set to an average frequency of 120 seconds, randomly ranging from 60-180 seconds. I allowed detections that strayed five seconds or less in order to not falsely remove detections that could be real and due to clock drift or tag irregularities. Short ping rates due to echoes or simultaneous detections were considered to not be representative of actual great barracuda location data. All analysis was conducted in R version 3.2.2 (R Core Team 2015).

Detections were grouped into frequency of detections per receiver, per day. Based on results from Chapter 2 that indicate low detection frequencies can lead to spurious interpretation of results, I rejected any dataset showing less than 5% of possible detections. This filtering left a total of 17 great barracuda for use in this model.

3.3.3.1 Spatial community plots

Results from Chapter 2 indicate rough partitioning of barracuda activity space into highly used core areas and general use areas with infrequent but repetitive use patterns. Building off previous work using network analysis to identify community relationships between network nodes (Finn et al. 2014), I have used similar methods to look at spatial communities for individual fish, rather than identifying community relationships among populations. Finn et al. (2014) define communities as groups of nodes that have a stronger relationship to one another than to the rest of the nodes in the network, and there are several algorithms used to determine how to divide network relationships into community groups, many of which were tested for usefulness in analysis of acoustic telemetry array network models by Finn et al (2014). Using the igraph package (Csardi & Nepusz 2006), I generated networks for individual fish with receivers as nodes and movements between them as edges weighted by the number of movements connecting each receiver pair. These networks were used in Chapter 2 to generate centrality rankings for receivers, indicating high and low use areas within the array. Using these matrices I applied two of the algorithms tested by Finn et al. (2014); Fast-Greedy and Walk-Trap. Fast-Greedy works by hierarchically dividing receivers into groups based on similarity in detection patterns (Clauset et al., 2004; Newman and Girvan, 2004), while Walk-Trap uses random walk models and identifies groups of receivers where movements get trapped in a loop based on probabilities weighted by the strength of interconnections (Pons and Latapy, 2006). Each node (receiver) within the community was assessed for the number of in-degree links (links to nodes within the community module) and out-degree links (links to nodes outside the module). Wilcoxin

rank sum tests were employed to test for significance among different groups by indicating whether the community has significantly more links within, indicating a positive community (Finn et al. 2014). Conversely, a group of receivers that demonstrate significantly greater connections to receivers outside their community is an anti-community (Finn et al. 2014).

Communities were plotted both as non-spatially referenced and spatially referenced plots, with edges weighted by number of movements between nodes, and nodes weighted by numbers of connecting edges. Spatially referenced plots demonstrate along what lines spatially proximate receivers are being divided amongst communities and make direct comparisons to spatial variables such as benthic habitat type more intuitive. They also give a visual representation of movement patterns, as edges laid out in this context begin to approximate spatial paths within the array, indicating general use patterns. For example, a great barracuda that shows very high residency to a small core area may show a pattern resembling spokes on a wheel, while a highly mobile roaming predator could show large repeated loops or a tangled web of lines (Finn et al. 2014). Cumulative maps were made that summarize centrality values, number of times a receiver was included in a core use area, and summing station values for significant communities, positive significant communities, and significant anti-communities for all analyzed fish. For community membership maps, any receiver present in a positive significant community was assigned a value of 1, an anti-community member received a value of -1, and no significant membership a value of zero. Tag-station matrices for both algorithms were populated with these values, and summed by station. Station values could indicate a commonly used positive area (high positive value), highly used anti-

community (negative value), or an area with neutral use generated either by lack of use, or variability in use areas between individuals, leading to a smoothing out of spatial patterns on a population level.

3.3.3.2 Predictive habitat models

NOAA Biogeography has conducted extensive mapping of the benthic habitat in and surrounding Buck Island Reef National Monument (NOAA Biogeography Team 2001). Shapefiles generated by NOAA of fine scale benthic habitat were imported into ESRI ArcGIS (ESRI ArcGIS 10.2, 2013) and converted to raster files for use in R. These raster files were used to generate kernel density estimates of each habitat type around each receiver, categorizing the array by proximity to and density of habitats within detection range, which was estimated to be 50% detection at 125 meters, based on range testing conducted by USGS researchers (Thomas Selby, USGS, personal communication). All habitat density values were normalized. These density results were merged with detection data for all fish at each receiver. To select which habitat variables to incorporate in the model, each habitat type (sand, seagrass, macroalgae, mangrove and linear reef) was tested against daily detections at each bandwidth (100 m, 200 m, 300 m, 400 m, 500 m, 750 m, 1000 m, 1250 m, and 1500 m) distance from the receivers. These were tested using a negative binomial model, which looked at each possible detection (average of 720 per day) as a trial, and whether or not a detection was heard as a positive or negative response. AIC was run for each habitat type to identify which bandwidth was the best predictor of detections. This process identified seagrass 750 m, sand 1000 m, macroalgae 1500 m, mangrove 1500 m, and linear reef 300 m as the most appropriate

predictors to include. These variables were then tested for collinearity and sand and mangrove variables were dropped. After this, all variables showed variable inflation factors lower than three, and were considered appropriate for use in the final model. The final variables included seagrass 750 m, linear reef 300 m, and macroalgae 1500 m, season (hurricane, spring, and winter) and tag as fixed categorical predictors, and interactions between season and tag, tag and seagrass, and season and seagrass. Hurricane season was defined as July-October, winter was November –February, and spring was March-June. The final model was a zero-inflated Poisson generalized linear model with frequency of detections per day per station as the response variable.

3.3.3.3 Catch per unit effort

To estimate relative population density compared to Culebra, Puerto Rico, I calculated a standardized CPUE rate based on randomized trolling surveys (Kimura 1981, Alcala 1988, Kaunda-Arara and Rose 2004). I hypothesized that the marine park would have greater densities of barracuda than unprotected waters, and this might impact home range size and habitat use (Kramer and Chapman 1999, Abesamis and Russ 2005). Trolling surveys were conducted using the same gear as for capture, but with lures modified by removing the hooks. Straight line transects with start points and direction of travel randomized using random number generators in ArcGIS were conducted, running for 15 minutes or until an obstacle was encountered. Transects were timed, number of strikes were counted, and waypoints were taken to quantify rate and location of capture. I used a depth stratified random sampling design, beginning transects within three depth strata: 1-7 m, 7-14 m, and 14-21 m. These sites were compared using permutation

randomization tests to determine whether there was a statistically significant difference in strike rates, and therefore population densities, between the two sites.

3.4 Results

3.4.1 Spatial communities

The Fast-Greedy algorithm separated the array into 5.82 mean communities per fish when results for individual fish were summarized across the study population. Once significance testing was conducted, the average number of significant communities per fish was 1.65. Arrays for all great barracuda included multiple significant communities, along with receivers that although included in activity space, were not used with enough frequency and regularity to be included in significant communities. The majority of significant communities were positive, with more connections to receivers within the community than outside of it. Although in the minority, there were several significant anti-communities as well, one each for tags 26796, 26793, and 24556. Community detection results, plotted as spatially referenced receivers colored by community membership, show all receiver communities for each fish as spatially proximate to one another (Fig 3.3). Significant communities had on average greater numbers of receivers with higher ratios of in versus out connections than non-significant communities. Positive communities and anti-communities occurred with similar frequency (mean of 2.65 positive versus 2.71 anti), but significant communities were much more frequently positive than anti (25 versus 3) (Table 3.1).

Walk trap algorithms showed mean number of communities of 5.58, and significant communities of 1.41. On average, significant communities contained greater

numbers of receivers than non-significant communities. Overall, this algorithm generated anti-communities more frequently than positive communities (mean of 3.17 per fish versus 1.76), but with the exception of two communities for fish 26793, all other significant communities (22 total) were positive. Walk-trap showed less variation than Fast-Greedy in its community assignments. This algorithm either broke receiver use per fish into smaller numbers (compared to Fast-Greedy) of positive communities or alternately, divided the array into larger numbers of anti-communities (Table 3.2).

Both algorithms defined on average between one and two significant communities, which is consistent with the heavy core use areas and infrequent exploratory movements that home range network analysis identified in Chapter 2. However, significant communities defined by both algorithms included more receivers on average than indicated by CUR defined by network analysis. The Fast-Greedy algorithm also frequently indicated two significant communities, indicating a third non-specific pattern of movement. Walk-trap also on average predicted greater than one significant (and therefore greater than two overall) receiver communities, as opposed to CUR and GUR groups assigned by centrality metrics from chapter one, which assume two basic use areas: core and general (Table 3.3). Spatial community plots for individual fish show spatially proximate groups of receivers that correspond both with intensity of use, shown by weight of edges connecting receiver nodes, as well as with broad benthic habitat zones (Fig.3.3).

Table 3.1: Fast-Greedy summary statistics, showing number of communities, mean number of receivers per community, mean in connections per community, mean out connections per community. Significant communities are summarized for these same values, and in addition for mean p-value, and the number of positive, anti, and neutral communities per fish, and the percent of the time that each community was positive.

Communities								Significant communities					
	#	Receivers	In-links	Out-links	Pos	Anti	NA	#	Receivers	In-links	Out-links	P-value	% Pos
26802	6	4.67	21	5	4	1	1	2	9.5	51	6.5	0.001	100
26801	7	5.14	30.86	24.57	3	3	1	2	8	63	15	0.018	100
26800	5	8.4	43.2	23.2	3	2	0	2	13.5	78	27	0.0044	100
26799	8	5.5	32.25	17	3	5	0	2	15.5	106	20.5	>0.001	100
26798	4	7.5	35.5	8.5	2	1	1	1	23	118	13	>0.001	100
26797	5	5.8	31.2	14.4	2	2	1	2	11	67	15	0.0012	100
26796	11	4.36	19.091	20.91	4	6	0	2	10	42	27	0.011	50
26793	5	10.4	80.4	68.4	2	3	0	2	15.5	118	70.5	0.014	50
24785	5	6	28.8	14.4	1	3	1	1	22	118	20	>0.001	100
24784	5	5.4	27.2	16	2	3	0	2	11	60	16.5	0.0019	100
24780	6	4.17	17.67	7	4	2	0	2	10	47	11.5	0.003	100
24779	4	3.5	16	7.5	3	1	0	1	9	48	12	0.0012	100
24776	2	4.5	14	4	1	0	1	1	7	24	4	0.0037	100
24556	10	3.6	13.8	18.4	3	7	0	3	7	28.67	20.67	0.014	66
24554	8	3.88	17.5	20.5	2	6	0	1	11	60	18	>0.001	100
24550	5	4.2	14.4	8.4	4	1	0	1	8	28	10	0.022	100
173	3	2.67	8.67	3.33	2	0	1	1	4	16	3	0.02	100
Mean	5.82	5.28	26.56	16.56	2.65	2.71	0.41	1.65	11.47	63.1	18.25	0.01	92.12

Table 3.2: Walk trap summary statistics, showing number of communities, mean number of receivers per community, mean in connections per community, mean out connections per community. Significant communities are summarized for these same values, and in addition for mean p-value, and the number of positive, anti, and neutral communities per fish, and the percent of the time that each community was positive.

Communities								Significant communities					
	#	Receivers	In-links	Out-links	Pos	Anti	NA	#	Receivers	In-links	Out-links	P-value	% Pos
26802	1	28	156	0	1	0	0	1	28	156	0	>0.001	100
26801	11	3.27	20.91	14.36	3	6	2	2	10.5	95	49.5	0.0015	100
26800	5	8.4	58	8.4	5	0	0	2	15	127	10	0.005	100
26799	7	6.29	43.14	13.14	3	2	2	3	12.33	94	24	>0.001	100
26798	1	30	176	0	1	0	0	1	30	176	0	>0.001	100
26797	15	1.88	7.38	6.88	1	10	5	1	9	68	28	0.0063	100
26796	6	8.17	65.67	7.67	6	0	0	3	13.67	122.67	10.67	0.012	100
26793	27	1.89	8.59	18.89	1	26	0	2	5	30	69	0.015	0
24785	1	30	216	0	1	0	0	1	30	216	0	>0.001	100
24784	14	1.93	8.29	7.14	1	10	3	1	26	78	26	0.0014	100
24780	1	25	148	0	1	0	0	1	25	148	0	>0.001	100
24779	1	14	94	0	1	0	0	1	14	94	0	>0.001	100
24776	1	9	36	0	1	0	0	1	9	36	0	>0.001	100
24556	1	36	322	0	1	0	0	1	36	322	0	>0.001	100
24554	1	31	304	0	1	0	0	1	31	304	0	>0.001	100
24550	1	21	114	0	1	0	0	1	21	114	0	>0.001	100
173	1	8	36	0	1	8	36	0	8	1	0	0	100
Mean	5.6	15.52	106.7	4.5	1.41	19.03	130.4	12.8	19.03	1.76	3.18	0.71	94.12

Table 3.3: Network analysis summary statistics, including number of CUR using centrality rankings, comparison CUR for KUD and DBBMM, Walktrap and Fast-Greedy significant communities and mean receivers per significant community. Number of days detected (DaysOut), mean detections per week (DetsWeek) and fork length (FL) were also included for comparison and reference.

Tag	CUR	Core area (KUD)	Core area (DBBMM)	WT significant	WT receivers	FG significant	FG receivers	Days Out	Dets per week	Fork length
26802	8	0.10	0.074	1	28	1	4	332	679.44	103
26801	9	0.52	0.39	2	10.5	1	8	364	1111.038	107
26800	10	0.16	0.12	2	15	1	11	364	2039.88	97
26799	10	0.21	0.16	3	12.33	3	7	364	986.077	71
26798	14	0.082	0.053	1	30	1	7	361	976.18	89
26797	9	0.17	0.11	1	9	1	9	270	2007.57	96
26796	15	0.17	0.35	3	13.67	2	10	364	368.81	63
26793	12	0.5	0.41	2	5	2	11	364	1411.52	101.5
24785	9	0.079	0.051	1	30	1	22	364	3352.96	79.5
24784	7	0.084	0.056	1	26	2	15.5	364	4311.13	90.5
24780	6	0.074	0.048	1	25	2	10	363	765.43	90.5
24779	5	0.089	0.061	1	14	2	11	348	625.7	92
24776	3	0.071	0.046	1	9	1	23	364	2937.54	84.5
24556	8	0.37	0.27	1	36	2	15.5	364	846.87	85
24554	8	0.22	0.21	1	31	2	13.5	364	255.42	61
24550	5	0.12	0.081	1	21	2	8	364	469.87	97
173	3	0.072	0.048	1	8	2	9.5	117	812	84.5
mean	8.29	0.18	0.15	1.41	19.03	1.65	11.47	340.88	1409.26	87.76

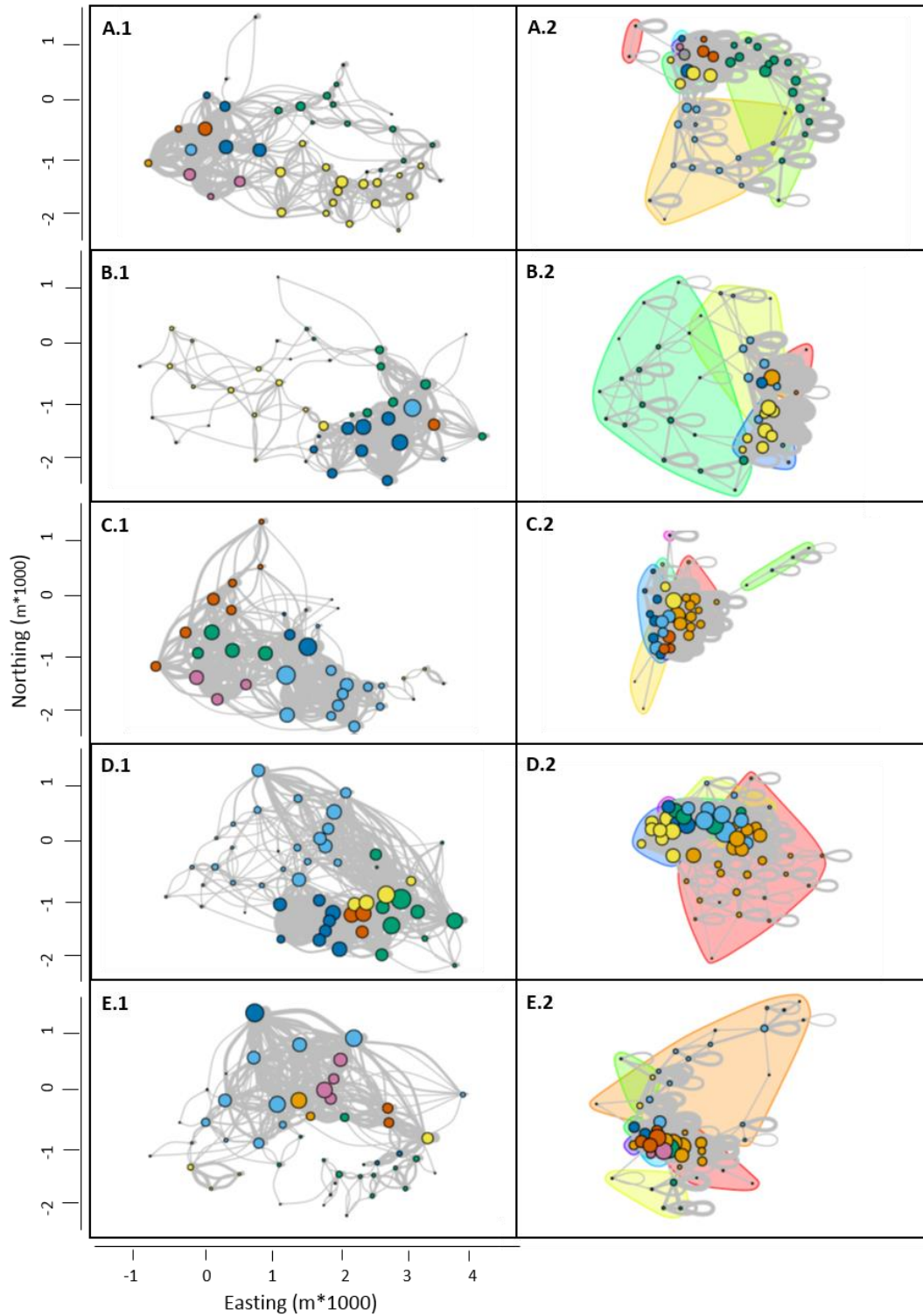


Figure 3.3: Community membership plots for 5 example fish (A-E), showing both spatial (1) and non-spatial results (2) generated using the Fast-Greedy algorithm. A: Tag 26799, 51,276 detections; B: Tag 26800, 106,074 detections; C: Tag 26801, 57,774 detections, D: Tag 26793, 73,399 detections; E: Tag 26796, 19,178 detections.

Location of individual home range core areas was highly variable across the study site, as shown in Chapter 2, so individual fish's spatial plots cover unique use areas. Cumulative maps show higher centrality values and CUR inclusion across linear reef and seagrass (Fig.3.4). Significant community and positive community counts both show fairly uniform values across stations, with slightly higher numbers shown around rugose areas and southern seagrass and colonized pavement flats (Fig.3.5, 3.6).

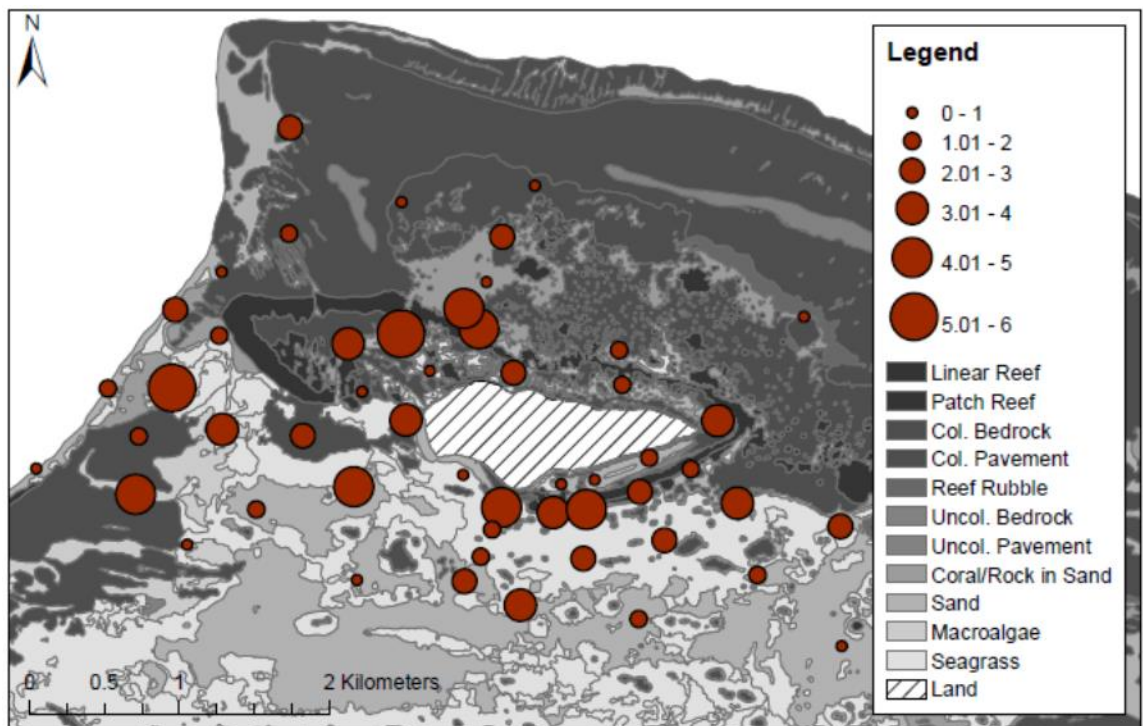


Figure 3.4: Sums for all fish in the study population for presence of receiver stations in a core use area (CUR) determined by centrality rankings through network analysis.

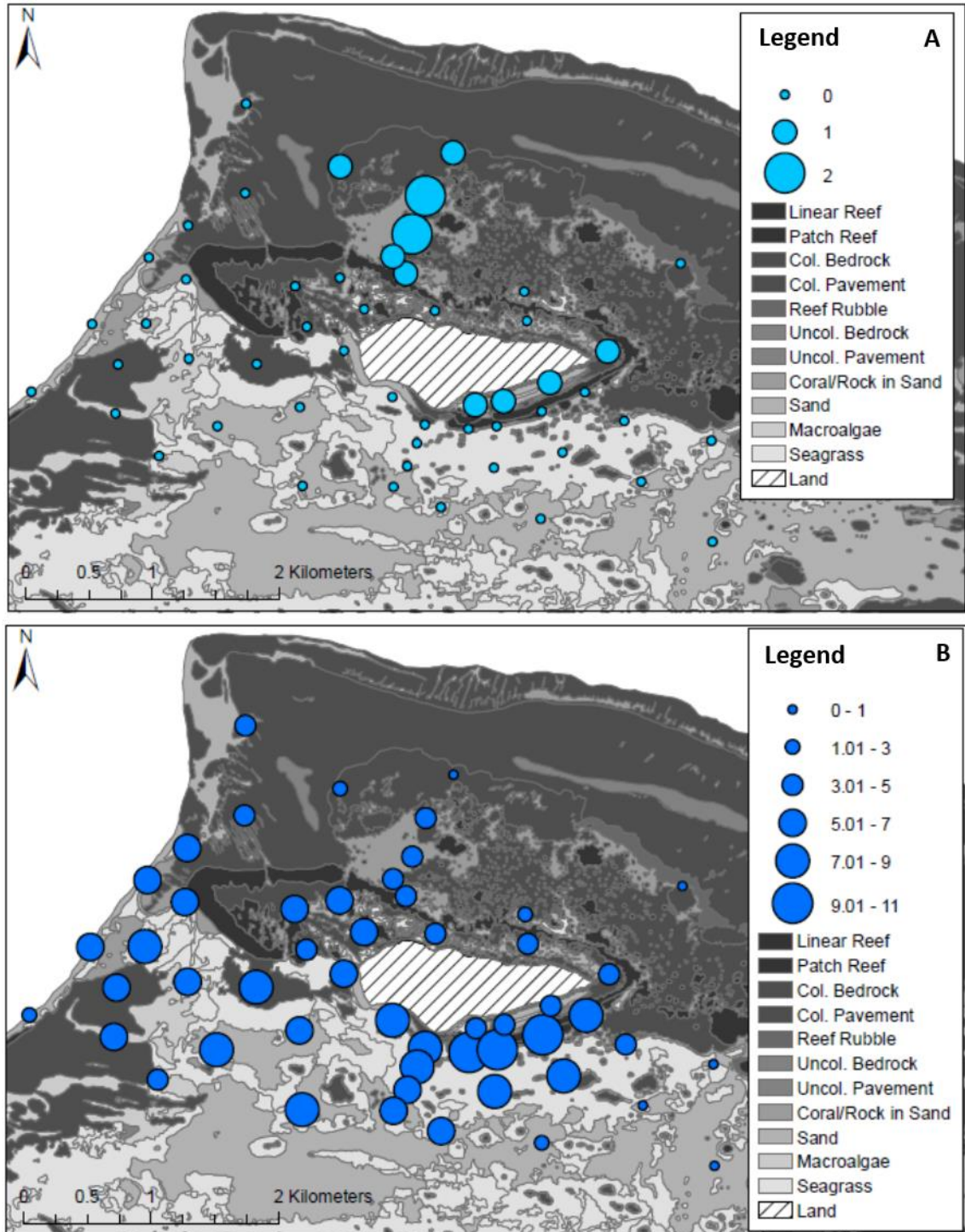


Figure 3.5: Spatial community sums for all fish in the study population for presence in a significant anti-community (A) or positive community (B), generated by the Fast-Greedy algorithm.

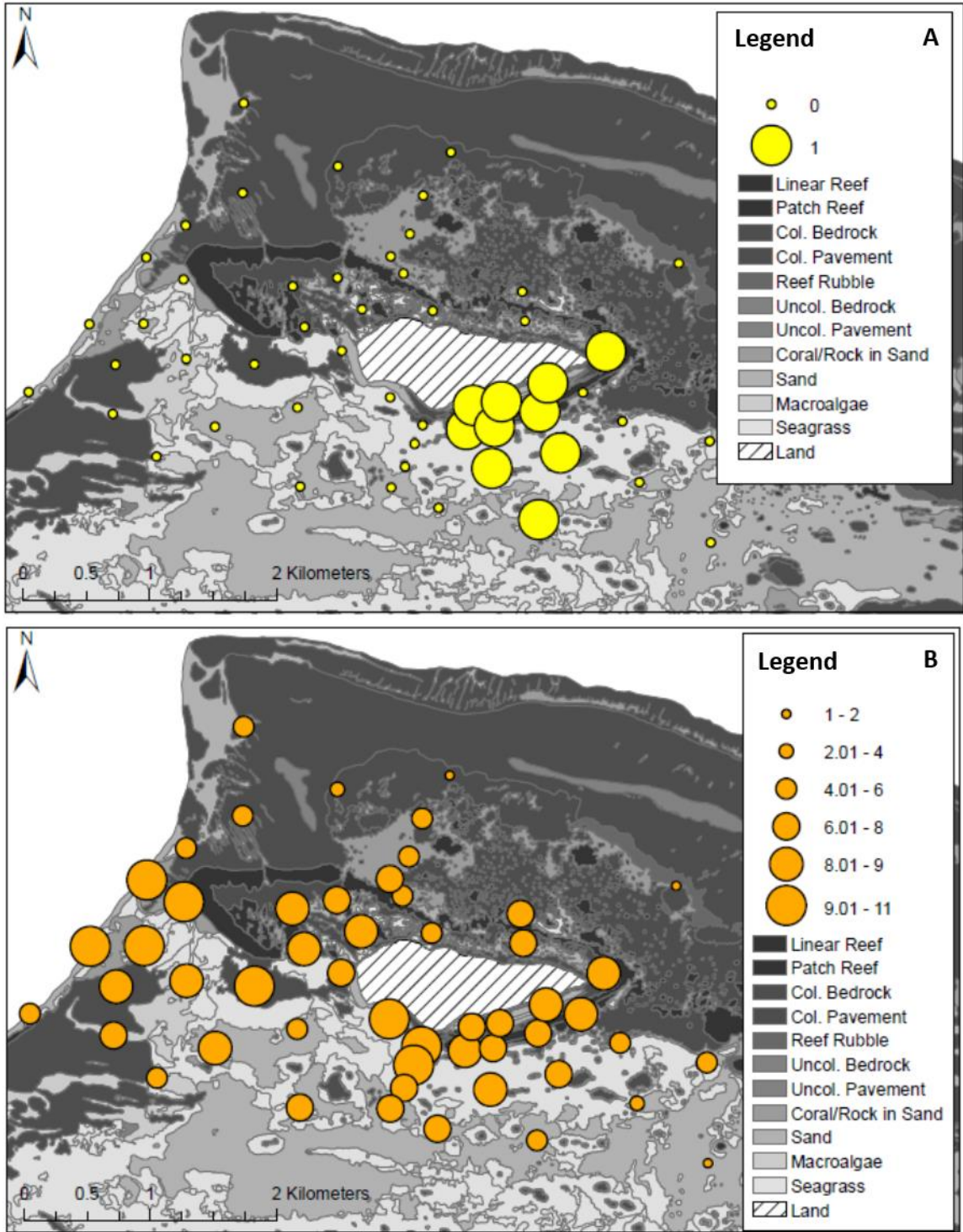


Figure 3.6: Spatial community sums for all fish in the study population for presence in a significant anti-community (A) or positive community (B), generated by the Walktrap algorithm.

Anti-community sums highlight two areas within BIRNM with repeated designation as anti-communities, both highly rugose (Fig.3.5, 3.6). However, numbers even for these sites are low, with no more than two fish indicating these areas as an anti-community. Positive communities on the other hand, showed values as high as 11 fish out of 17 (Tables 1-3).

3.4.2 Catch per unit effort

CPUE randomization tests showed a statistically significant difference between BIRNM and Culebra, for both randomized surveys and tagging effort records. The permutation test for the randomized surveys resulted with a p-value of 0.005, while the test of tagging effort had a p-value of <0.001 . These low p-values indicate that it is extremely unlikely that the large differences in CPUE shown by the surveys at both site could have occurred due to chance. Since I used CPUE as a relative indication for population density, these results suggest large a difference in the abundance of great barracuda between the sites, with greater densities occurring in BIRNM.

3.4.3 Habitat models

The model results showed all variables and most interactions as highly significant, with the exception being for several specific tag interactions. Therefore, habitat type, season, tag ID, as well as interactions between tag ID and season, tag ID and seagrass, and seagrass and season were all shown to be important drivers of daily detection frequency. Since no single parameter appears more significant than others, no one habitat type or season stood out as being more important to detection frequency. Residual plots

indicated that there was variation in drivers of daily detection rates that was not explained by the model. When residuals for habitat density were separated by season and tag, it was clearly visible that the model could predict the detection patterns of some tags more accurately than others (Fig.3.7). Predicted and observed values plotted by tag and station again show that for most tags and stations, the model was over-predicting detections (Fig.3.8).

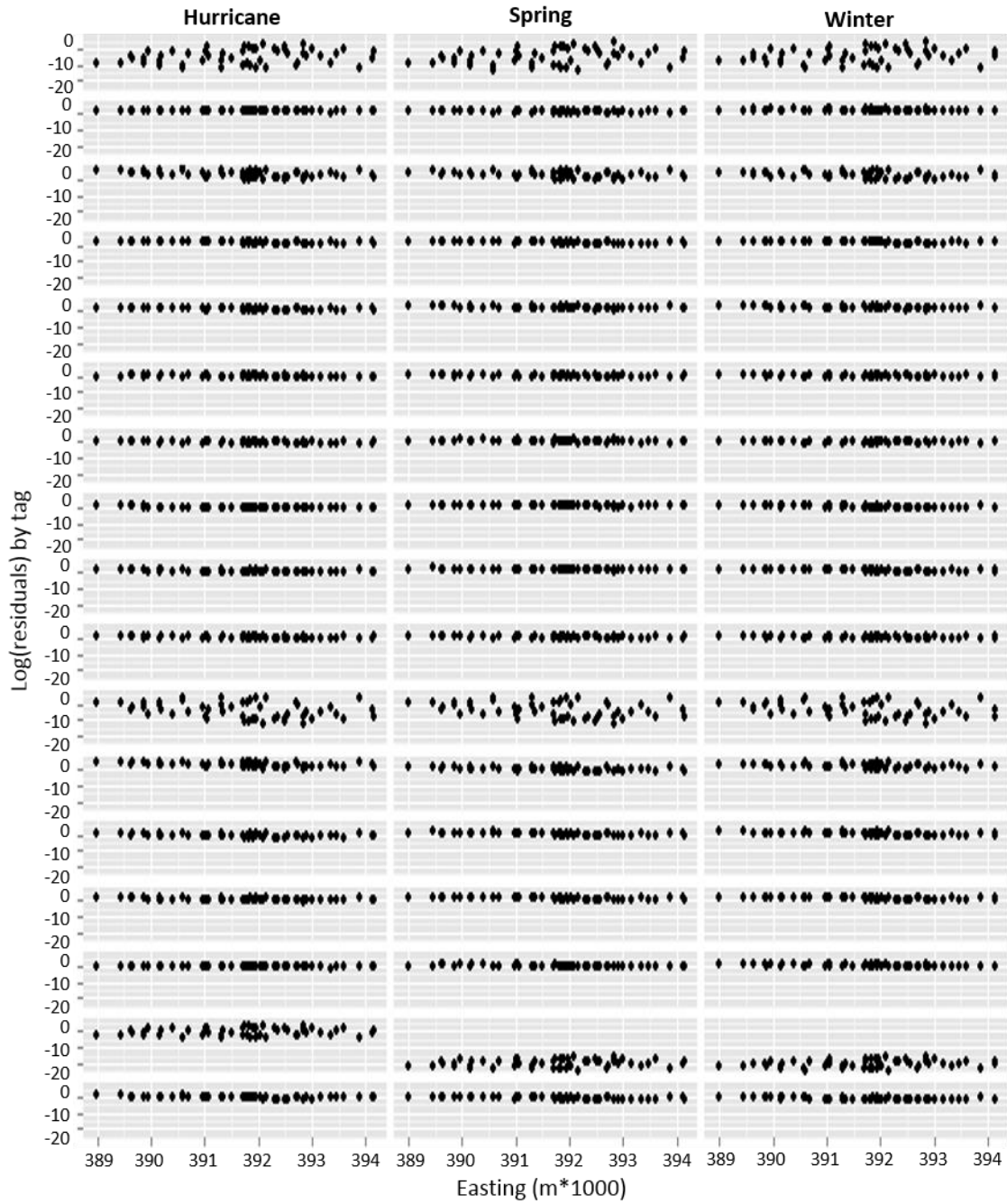


Figure 3.7: Residual values for generalized linear Poisson model, divided by season and tag for Easting location.

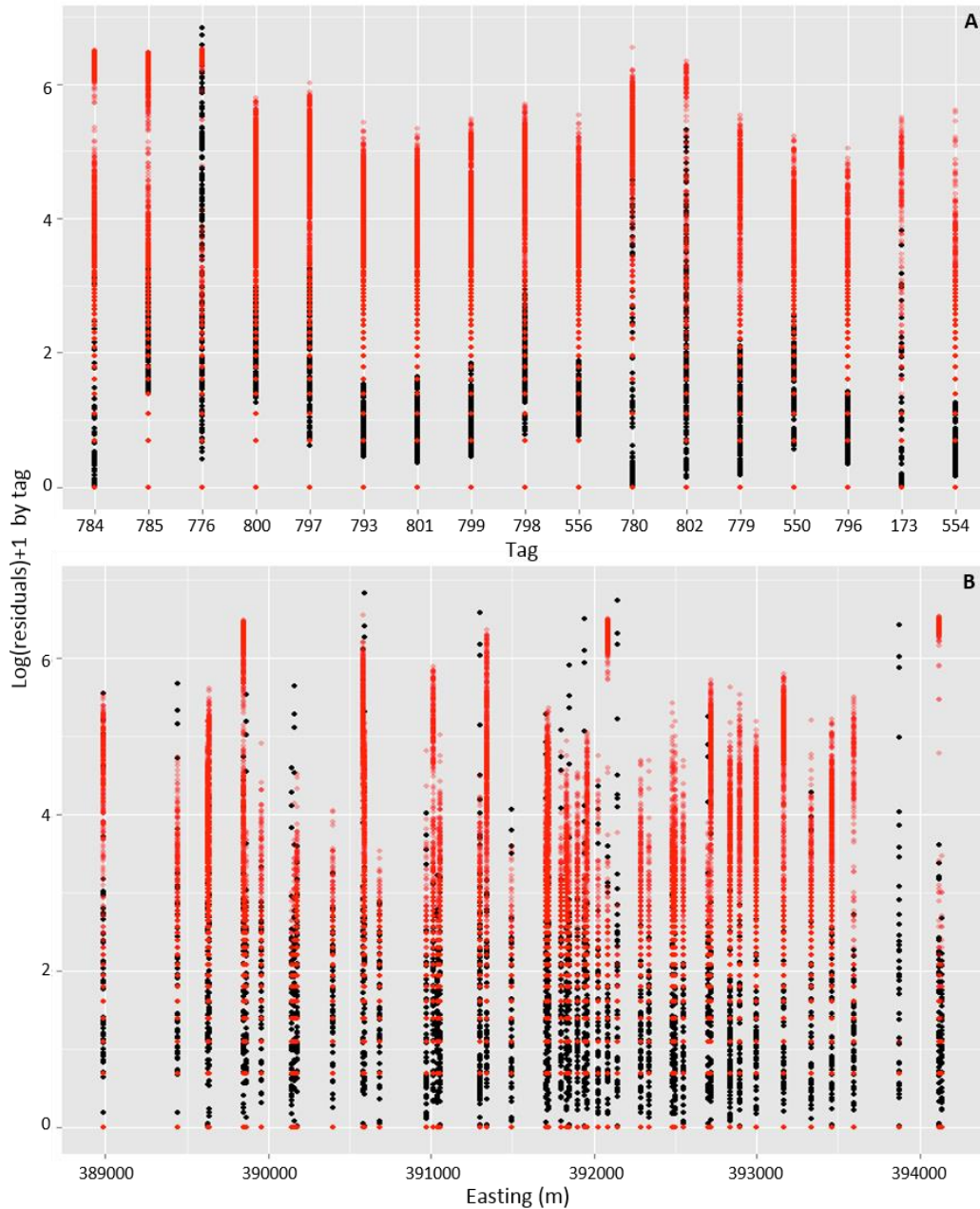


Figure 3.8: A) Predicted (red) versus observed (black) daily detection frequencies divided by tag as estimated by the generalized linear Poisson model. B) Daily detection frequencies divided by station.

3.5 Discussion

Network analysis centrality rankings and spatial community assignments showed high variation in location of home ranges among individual great barracuda, but high use

areas demonstrated relatively evenly dispersion across the array for the study population. Greater than two significant communities indicated some temporal variation in movement patterns. Variation among individuals was high, but across the study population there was no strong spatial pattern in centrality rankings or presence in a significant community across the array. This indicates a degree of individual-level niche partitioning among individuals, potentially to avoid competition for resources (Ostfeld 1990). Even at the population-level there was little indication of great barracuda preference for a specific type of benthic habitat. Daily detection frequencies were equally influenced by all habitat types and seasons, and individual tags were a significant driver of detection patterns in the generalized linear Poisson model. The array was evenly used at the population-level including individual partitioning, despite the presence of multiple spatial communities indicating temporal variation in spatial use. Highly elevated relative densities within BIRNM may be influencing spatial use patterns of individual partitioning and lack of habitat preference (Vincent et al. 1994, Kramer and Chapman 1999, Absamis and Russ 2005).

3.5.1 Centrality metric and spatial community plots

Centrality metrics designating core and general use areas highlight areas of frequent and infrequent use within the barracuda's activity space. Core areas indicated by network analysis were defined by using a 50% and 95% cut off, similar to contour lines for the utilization density analysis (Chapter 2). Network analysis (Chapter 2) predicted larger areas of frequently used space compared to utilization distribution methods, and was able to highlight frequently travelled pathways between parts of the array.

Algorithms subdivided the array and assigned community membership into multiple significant groups, with a “leftover” group. Even when looking at only statistically significant communities, the array was divided into more than two groups on average, indicating a complexity of spatial use patterns greater than described by a framework using utilization densities and core and general use areas.

Significant communities of great barracuda most frequently were positive. This means that receivers had more connections to receivers within the community module than to receivers outside (Finn et al. 2014). Positive communities can be thought of as destinations within a total activity space (Finn et al. 2014). They could be a resident territory, or a feeding or spawning ground where a fish might travel to and remain for a duration of time long enough to generate frequent connections between receivers within that space (Burke 1995, Mumby et al. 2004, Meyer et al. 2007, Luo et al. 2009, Kimirei et al. 2011, Finn et al. 2014). The presence of, on average 1.5 significant resident communities, the bulk of which were positive, indicates that within an individual great barracuda’s activity space there are multiple resident use areas. Highly mobile animals, or ones that showed high differentiation in habitat would have movement patterns that generated a greater number of communities (Finn et al. 2014). More than one significant community indicated some temporal differentiation in the movement patterns may exist, consistent with demonstrated seasonal patterns in previous studied (Faunce and Serafy 2008).

There were several significant anti-communities present, although greatly outnumbered by positive communities. These anti communities represent groups of receivers that have more connections to receivers outside their community than within it.

These communities can be thought of as transit hubs, or places that a fish frequently passes through to get to another destination, and are indicative of movement corridors. If a species were highly mobile, their networks would be dominated by anti-communities. While walk-trap in particular generated many non-significant anti-communities, the infrequency (but presence) of significant anti-communities indicates that these individuals are demonstrating site fidelity within their set activity space, and that larger exploratory movements are not consistent enough to register as significant within the algorithms. The presence of these communities at all, even though not statistically significant, indicates that while not frequent enough to generate a significant number of links between receivers, mobile as well as resident movement patterns were commonly displayed within the study population. These patterns of residence and potential for high mobility are consistent with genetic studies indicating characteristics of great barracuda common to both reef-associated as well as pelagic species (Daly-Engel et al. 2012).

Network analyses were generated for individual fish and also summarized across the study population to identify areas of the array that were more frequently included as core use territories or significant communities. Superimposing these results onto benthic habitat maps demonstrated little pattern for resident use areas (positive communities). Two highly rugose reefs were indicated as significant movement corridors (anti-communities), one of which was found in the northern part of the array, an area shown to have poor detection ranges (Thomas Selby, USGS, personal communication). Therefore, this area may naturally generate sporadic detection histories that could make this area appear to be a movement corridor due to frequent missed detections. The other anti-community, on the south side of the island within a shallow lagoon, has been shown to

have adequate detection range, providing greater confidence that the area is a movement corridor. The even spread of the positive community membership counts show that as a whole population, BIRNM great barracuda appear to be widely using all habitat types, with individual variation based on location of resident use areas. This type of individual differentiation of space is reflective of intraspecific spatial niche differentiation driven by food availability and population density (Hixon 1980, Ostfeld 1990). Barracuda may be dividing up spatially to limit competition for resources and prey (Quevedo et al. 2009).

3.5.2 Catch per unit effort

It is important to mention that this study was conducted in a no-take MPA and results might vary in non-protected areas. The CPUE is indicative of a higher population density of great barracuda in BIRNM than the coastal waters surrounding Culebra. Density can have wide ranging impacts on ecology and community interactions, through altering the balance in trophic relationships and food webs as well as through influencing a number of different life history parameters (Stearns and Crandall 1984, Vincent et al. 1994, Kramer and Chapman 1999, Absamis and Russ 2005). This initial comparison between sites demonstrates that densities of barracuda within the MPA would be higher than in openly fished waters. While there is not at this point direct evidence showing that this is due to a difference in fishing pressure, these results are consistent with many other studies that have demonstrated higher abundance of a top predator in no-take MPAs (Micheli et al. 2004). Increasing densities leading to population level shifts in preferential habitat use to all available space has been demonstrated in a number of ecological systems (Vincent et al. 1994). Therefore, the elevated densities observed at BIRNM in

comparison to Culebra are consistent with homogenous habitat use patterns at the population-level documented through network analysis.

3.5.3 Habitat models

The habitat model did not address all the possible environmental and physical variables that could influence detection frequency. The lack of parsimonious explanatory variables in the model is consistent with the apparent disregard for benthic habitat shown in the community significance plots. Habitat type and season were significant at influencing detection frequency, including many significant interactions. Widespread significance of nearly all the variables, save for a couple non-significant variables driven by individual tag variability, could indicate that I am missing the true drivers of movement. Certainly adding in additional variables looking at temporal variation of environmental variables could be beneficial. However, the lack of specific highlighted drivers in the model indicates that individuals in the study population are not more likely to use one habitat over another and that barracuda movements are not highly associated with benthic habitat or season, and that individual behaviors or territories are just as likely to influence habitat choice.

3.6 Conclusion

Great barracuda within the study population were shown to occupy unique, overlapping territories throughout the array, with individuals showing high site fidelity to small resident use areas but also using wide swaths of the array in less frequent but repeated movements at apparently random directions. Population level use of the array

shows no preference for specific benthic habitat types in regards to resident area choice, but spatial community identifications indicate some temporal differentiation in spatial patterns, consistent with previous research indicating seasonal variability in spatial patterns but with habitat use dominated by non-selective behaviors (Faunce and Serafy 2008). While resident use areas were evenly distributed, movement corridors were clustered along high rugosity reef habitats. This could either be due to more consistent roaming along preferential reef habitats (Heithaus et al. 2002), or could alternately be indicative of necessary paths of travel around very shallow reef systems. In order to extrapolate from these spatial patterns towards greater understanding of ecological and management implications of these results, it is necessary to relate these findings to more general themes of habitat connectivity, trophic dynamics, and species interactions (Gerber et al. 2003).

Highly resident behaviors and high density demonstrated in this study, combined with known trophic position and predation strategies of great barracuda (De Sylva 1963, Ceccarelli and Ayling 2010, Mumby et al. 2012) mean that great barracuda within the study population are likely generating high and temporally consistent top down pressure on the rest of the fish community (Sih 2005). Residency patterns through all habitat types, combined with broad but infrequent use of the rest of the array shows that these impacts of top down pressure are likely being applied across all habitat types and also suggests that this species might be an important vector of predation-driven connectivity across habitat boundaries (Polis et al. 1997, Quevedo et al. 2009). Whereas some large predators must be highly mobile to access productive foraging sites (Jorgensen et al. 2009), site fidelity and high rates of residency have been shown to indicate sufficient

resource availability within a core use space (Wittmer et al. 2006, Knip et al. 2012). The habitat generalist behavior demonstrated by the study population appears fairly unique within subtropical coastal fish communities to great barracuda (Faunce and Serafy 2008). Given the importance of apex predators in structuring communities (Friedlander and DeMartini 2002, Heithaus et al. 2008) this indicates that barracuda are ecologically influential in driving community dynamics within the study site.

The even use of the array for resident core territories regardless of benthic habitat is a pattern sometimes indicated in animal populations existing at high densities, even among species that at low population densities show habitat preferences (Ostfeld 1990, Vincent et al. 1994). This pattern, combined with elevated population densities in comparison to Culebra could be indicative of the MPA leading to increased density of this top predator within the park boundaries. High rates of residency combined with elevated density results suggest that the park may be at a scale beneficial to great barracuda population resurgence. MPAs have often been shown to increase top predator biomass, especially for fish easily impacted by fishing pressure (Pauly 1998, Micheli et al. 2004), which great barracuda are likely to be given their high rates of bycatch in a variety of recreational and commercial fisheries (Springer and McErlean, 1961; de Sylva, 1963; Villareal et al., 2007, O'Toole et al. 2010, Brownscombe et al. 2014). High rates of residency are more amenable to successful protection through spatial closures (Kramer and Chapman 1999). It has been suggested that high rates of density-dependent modification of home range size or habitat use would compound the effect of spatial closures from fishing pressure on population resurgence (Kramer and Chapman 1999). The scale of BIRNM appears effective for increasing great barracuda biomass. However,

success in increasing fish biomass as a whole depends on the spatial ecology of other species in the fish community, and the intersection between trophic dynamics and spatial patterns (Gerber et al. 2003).

CHAPTER 4

ECOLOGICAL AND MANAGEMENT IMPLICATIONS FOR BARRACUDA HABITAT USE AND SITE FIDELITY PATTERNS AROUND BUCK ISLAND REEF NATIONAL MONUMENT

Developing accurate assessments of the spatial ecology of marine species is a vital step in developing ecologically sustainable management policies (Gerber et al. 2003, Palumbi 2004, Murawski et al. 2005, Douvère 2008, Edgar et al. 2014). While ecological considerations are only one step in the complex process of marine spatial planning, which must balance societal needs and political viability with ecological justifications for conservation (De Santo 2013), the groundwork for successful policy remains sound science (Gerber et al. 2003, Palumbi 2004, Murawski et al. 2005, Edgar et al. 2014). Many MPAs to date are based around large assumptions regarding spatial use of target species since historically it has been difficult to generate accurate estimations of home range, residency and habitat use (Heupel et al. 2006, Cooke 2008, Hussey et al. 2015). Range estimates have often been assumed to be static, and density of use across activity space consistent (Pressey et al. 2007). However, the proliferation of acoustic telemetry studies, which have made tracking movements in marine systems viable on a finer scale than previously possible, have indicated that there is often high variability in temporal patterns and density of use across many species home range areas (Burke 1995, Mumby

et al. 2004, Meyer et al. 2007, Luo et al. 2009, Kimirei et al. 2011). These finer scale understandings of habitat use, and the degree to which these variables intersect with trophic dynamics, species interactions and drive connectivity across habitat boundaries depicts a vastly more complex view of habitat use across species assemblages than is usually able to be considered in spatial management planning (Leslie and McLeod 2007). Increasingly, scientists and managers are realizing that in order to tailor spatial closures towards the conservation of larger animals, which often have correspondingly larger home range areas, it is vital to form a better understanding of this temporal and spatial variation in use in order to target protection towards specific areas used for feeding, spawning, or nursery grounds and other undefined movements, if full ranges cannot be protected (Runge et al. 2014, Pérez-Jorge et al. 2015).

Through this study, I sought to address these issues for the spatial management of top predators by analyzing the movement patterns and habitat use of great barracuda within the Buck Island Reef National Monument (BIRNM) no-take protected area managed by the National Park Service in St. Croix, U.S.V.I. As standardized analytic methods for acoustic telemetry are still being perfected, I first focused on assessing the impact of analytic method choice and variability in detection histories on home range estimates. The results from this work are summarized in Chapter 2. For Chapter 3, I then used the results from this research to inform further work looking at home range, site fidelity, spatial differentiation in use patterns, and habitat use of animals with detection histories deemed sufficient for analysis by previous work in Chapter 2. In addition, I compared population densities within BIRNM to a similar fished array in Culebra, Puerto Rico to generate an estimate of relative population densities inside the reserve. In

combination, this work aims to quantify activity space estimates of great barracuda within BIRNM and to understand the implications that observed rates of residency, size of core use areas, and habitat use patterns for this study population have on ecosystem ecology and spatial management within the study site.

Results from the methodological comparison show that both KUDs, a traditional utilization density based home range estimator (Kie et al. 2010, Jacoby et al. 2012), as well as DBBMM, a more complex utilization density method that incorporates movements between points (Horne et al. 2007) tend to underestimate core activity spaces and smooth out peripheral use areas in comparison to network analysis based methods. KUDs and DBBMM may be helpful in indicating high use area, but accuracy may vary based on the scale and density of receiver arrays, detection history, life history and the movement patterns of the study species. For barracuda in this study site, which displayed high site fidelity to unique core use areas but also sporadically roamed through large areas of the array, both utilization distribution methods oversimplified and excluded areas. For the conservation of larger and potentially more mobile species, it is important to be able to identify movement corridors and ecologically relevant peripheral use areas (Runge et al. 2014, Pérez-Jorge et al. 2015), which for this study were more readily identifiable using network analysis. For all methods, variability in detection history was a major driver of home range size estimation and also confounded the ability to detect a relationship between body size and home range size, which became apparent when data was analyzed only for fish with good detection histories. This highlights the need for close examination of the impacts of detection variability when using acoustic telemetry to try to identify ecological drivers of spatial patterns.

Once appropriate methods and detection histories were determined for this dataset, additional analysis conducted in chapter three demonstrated that individuals have unique home ranges to which they show strong site fidelity, but on a population level there appeared to be consistent use of the full array. Network analysis dividing the array into spatial communities indicates that individual barracuda have several distinct areas within their activity space with significantly different use patterns. Significant receiver communities were predominantly associated with positive communities, which indicate a core use area. Positive communities were evenly distributed across the array. There were several significant anti communities as well, indicating movement corridors, which were consistently distributed around high structure reef habitats. Network analysis methods consistently showed even distribution of core resident territories. This indicates partitioning of space into individual territories, potentially to avoid competition for resources (Hixon 1980, Ostfeld 1990, Quevedo et al. 2009).

Even spread of core use areas across the array, independent of benthic habitat type was reinforced both by habitat models as well as CPUE-based relative population density results. The generalized linear model showed no benthic habitat or seasonal predictors showing a greater impact on detection frequencies, with all variables being highly significant. Tag individuality was also highly significant, which was consistent with the unique territories indicated by the home range analyses in chapter two. Previous work with other species has shown preferential habitat use for low population density species switching to even spatial distributions at higher densities (Vincent et al. 1994), and the high relative populations shown by the CPUE comparison are consistent with this prediction. This displayed disregard for benthic habitat is unusual for fish species in these

habitats, most of which are shown to demonstrate specific habitat preferences (Faunce and Serafy 2008).

This study is the first to document the level of site fidelity and small core use areas for great barracuda. The relative high population densities combined with high degree of site fidelity and even spread of habitat use suggests that these barracuda are likely a highly influential driver of top down pressure within this park through heavy predation rates (Friedlander and DeMartini 2002, Sih 2005, Heithaus et al. 2008). Robust populations of top predators are often shown within marine protected areas, with higher trophic levels showing rapid rebounds from fishing pressure (Pauly 1998, Micheli et al. 2004). There are concerns among some that rebounding predator populations could lead to size-based competition and top heavy predation pressure on fish communities whose overall productivity has declined to the point of being unable to sustain pre-harvest levels of high trophic level species (Mumby et al. 2007, McClanahan et al. 2007). However, high top predator biomass is often seen as a sign of a healthy, recovering system due to the observed dominance of apex predators in reefs in uninhabited areas (Stevenson et al. 2007).

Precision in methodological choice and analysis are inextricably intertwined with the ability to interpret the ecological influence of these high density, highly resident top predators within BIRNM. Our methodological results in Chapter 2 indicated the influence both method choice and detection history can have on the ability to accurately interpret ecological results, which form the scientific framework driving effective ecosystem based management (Gerber et al. 2003, Palumbi 2004, Murawski et al. 2005, Douvère 2008, Edgar et al. 2014). Great barracuda functioned as an ideal species on which to examine

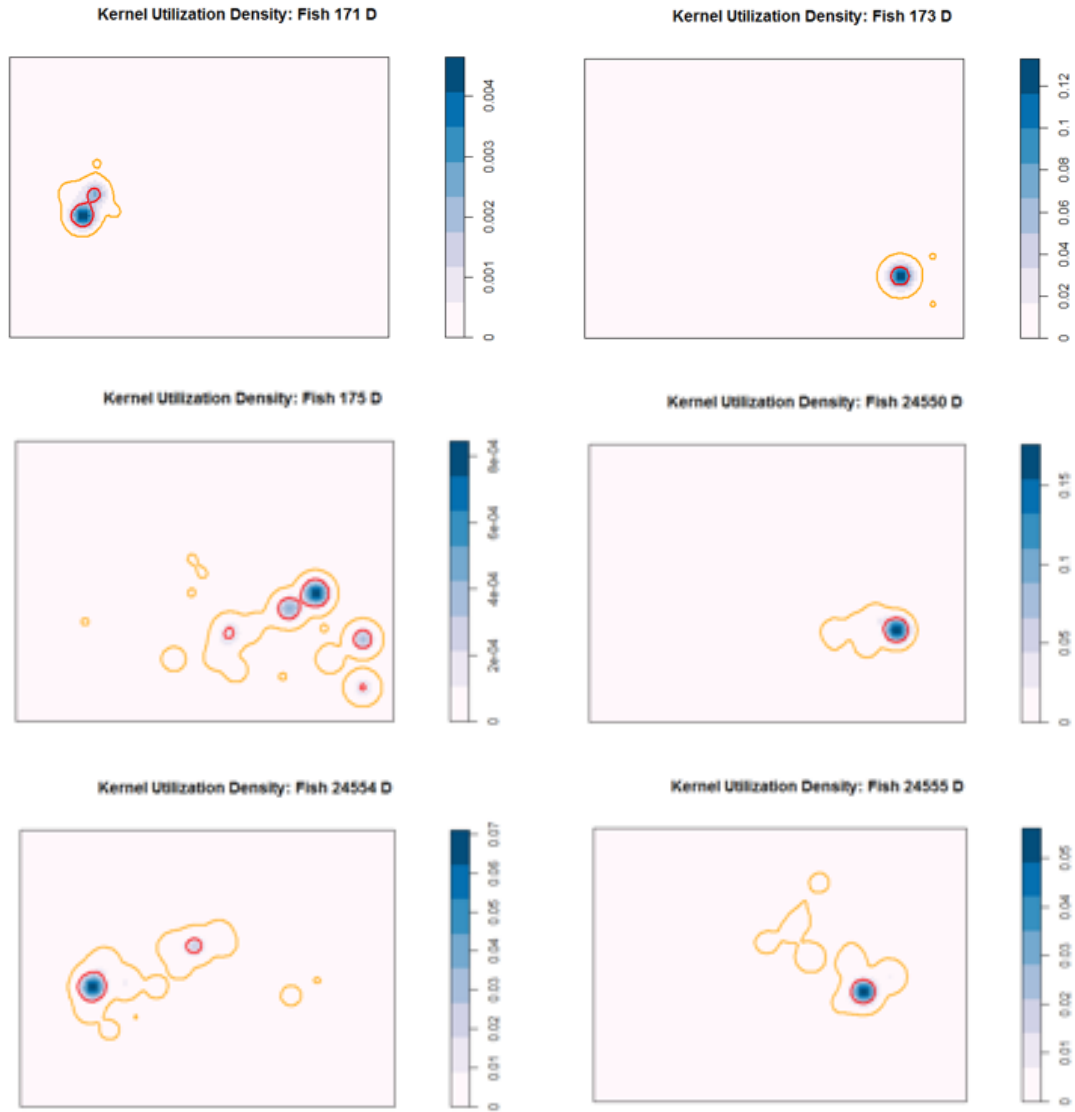
the impacts of various methods of home range estimation on different movement patterns since the study population demonstrated two unique movement behaviors: residence to core areas combined with wide-ranging exploratory movements. Based on these results it appears that utilization density methods appear more useful in acoustic telemetry studies utilizing finer scale array systems, or for highly resident species, whereas network analysis was more successful in identifying mobile movement patterns. The ability to interpret the acoustic telemetry datasets that make much of this fine scale tracking work possible is inextricably tied to continuing to improve on creating appropriate and standardized methods of analysis in order for these datasets to be able to answer the ecological and management questions they seek to answer. The correct interpretation of these results is necessary to determine efficacy of existing marine parks and to plan future closures based on ecological realities, which is tantamount to the ability of these MPAs to live up to their much-lauded conservation potential.

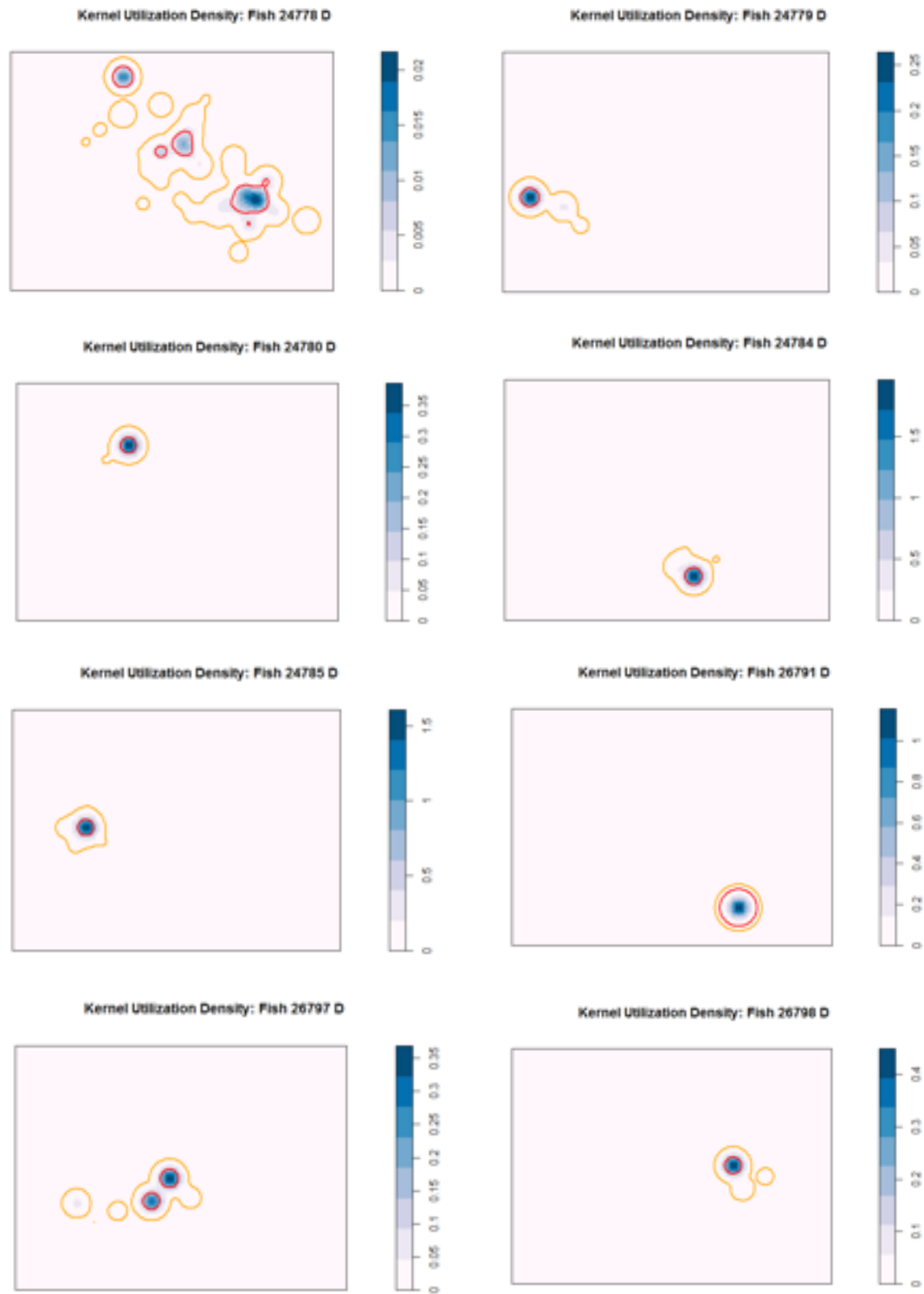
Given the demonstrated high residency rates (which make it more likely that the scale of the MPA will be sufficient), even use showing great barracuda presence in all habitats, as well as demonstrated elevated densities, BIRNM appears to be successful at increasing barracuda biomass. Given that BIRNM is not designed solely as a great barracuda reserve, the broad management implications of this thesis are tied to the ecological role that this species plays in overall ecosystem dynamics and how this could be taken into consideration for ecosystem-based management. Overall success of this MPA at creating a robust fish community across all trophic levels necessitates additional research linking together the spatial and trophic ecology of this species – great barracuda – together with additional research analyzing the movements, population levels, and

species interactions across the full fish community. Future work that this thesis paves the way for includes further examining the role of density dependence on habitat use patterns and home range by developing a comparison study with Culebra, Puerto Rico and comparing great barracuda spatial ecology to those of other trophic level species within BIRNM. Many collaborators on this study are currently involved in tracking and analyzing movement data of many other fish, turtle, and invertebrate species within BIRNM. This study forms the groundwork for analysis of future datasets within this array, and ideally will lead to future comparative studies.

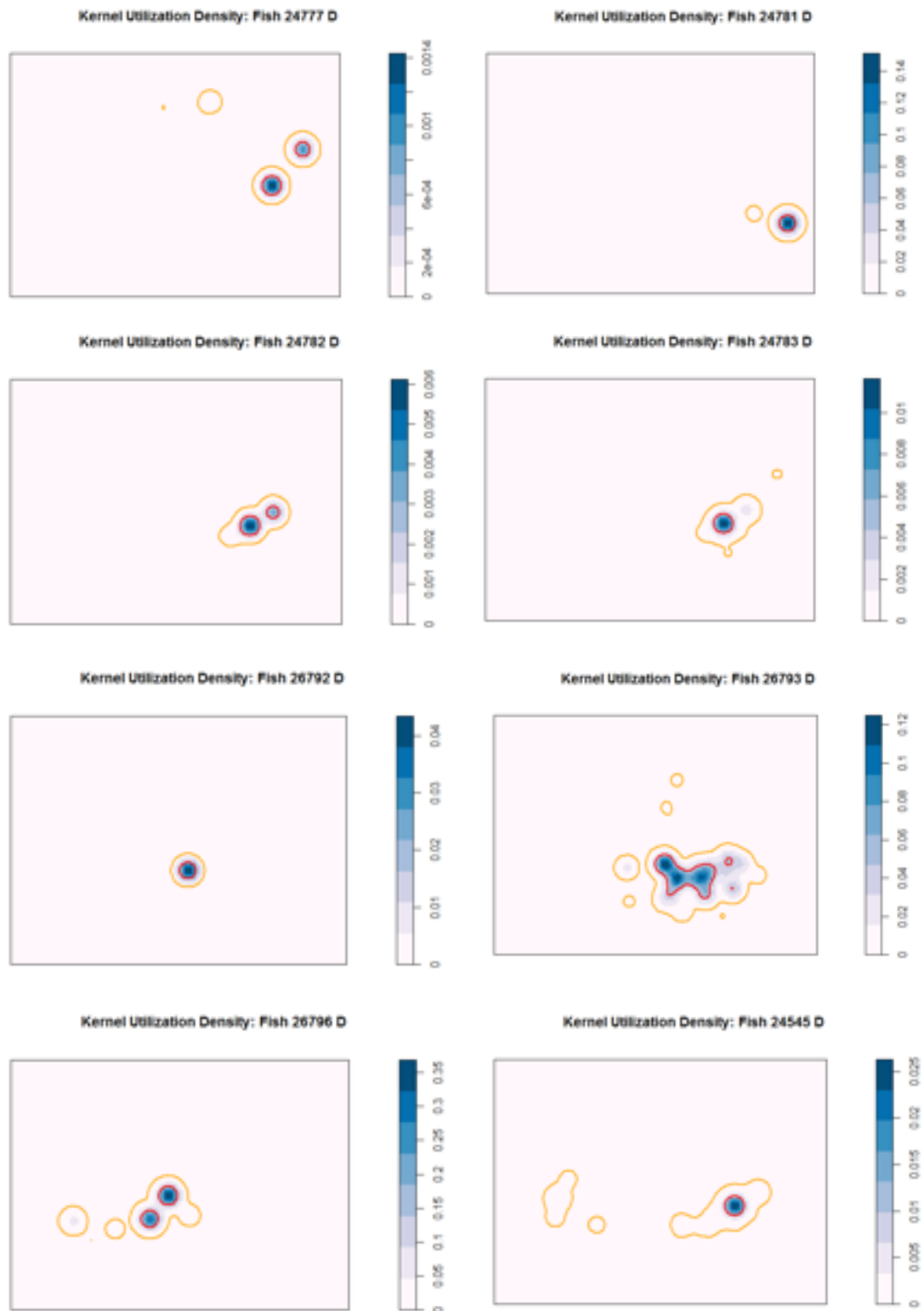
APPENDIX A

SUPPLEMENTAL FIGURES: KERNEL UTILIZATION DENSITY ESTIMATES

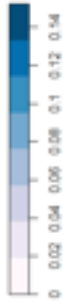
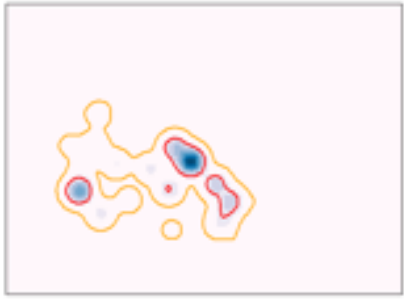




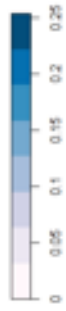
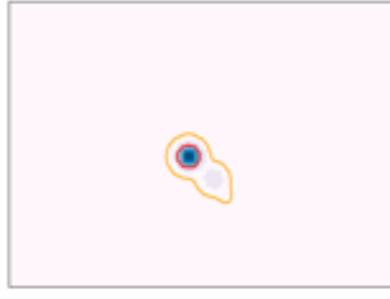




Kernel Utilization Density: Fish 26801 D



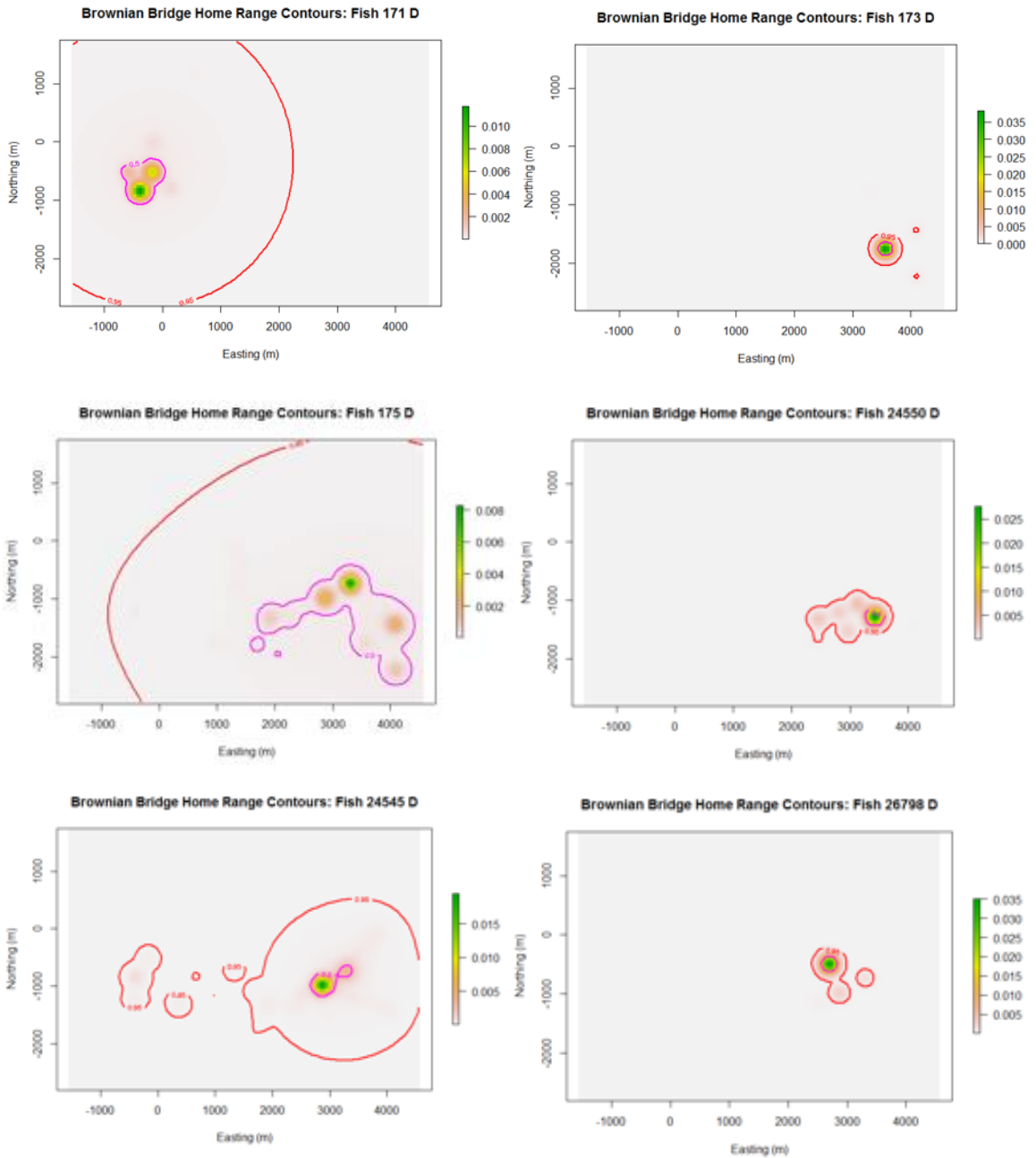
Kernel Utilization Density: Fish 26802 D

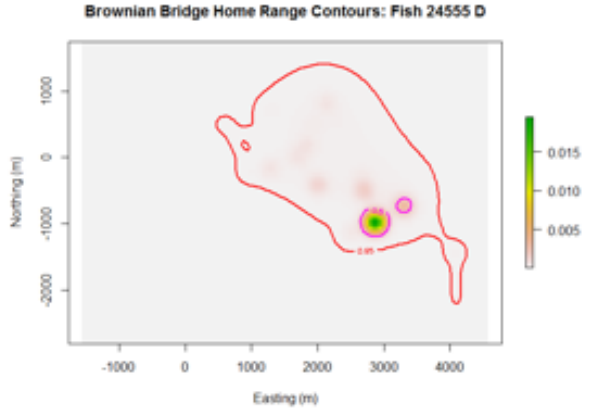
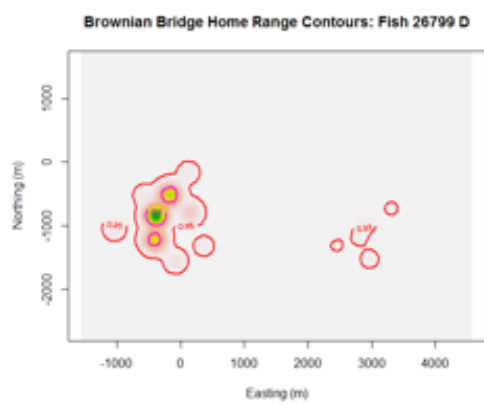
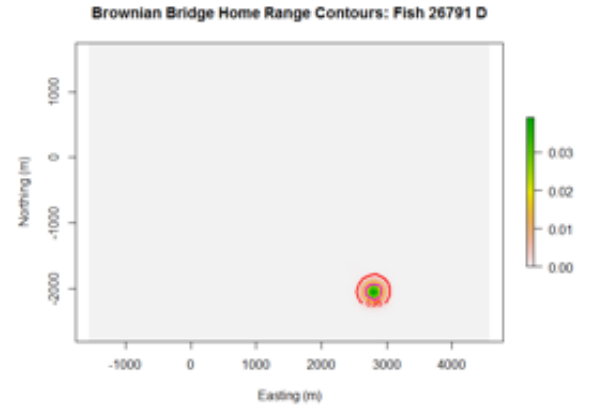
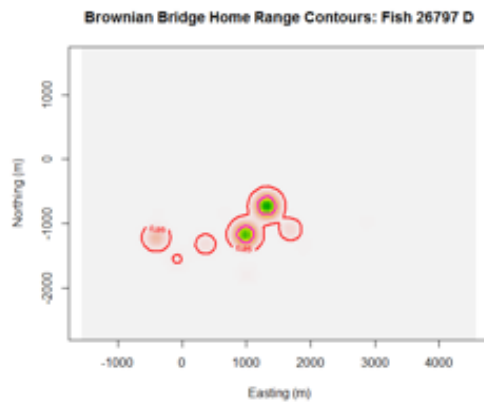
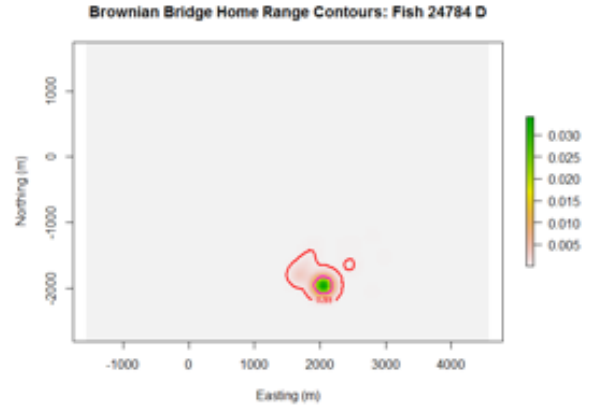
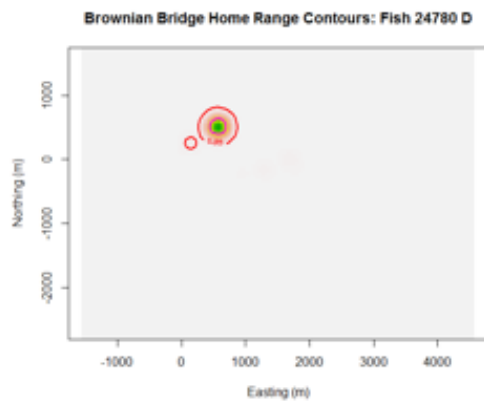
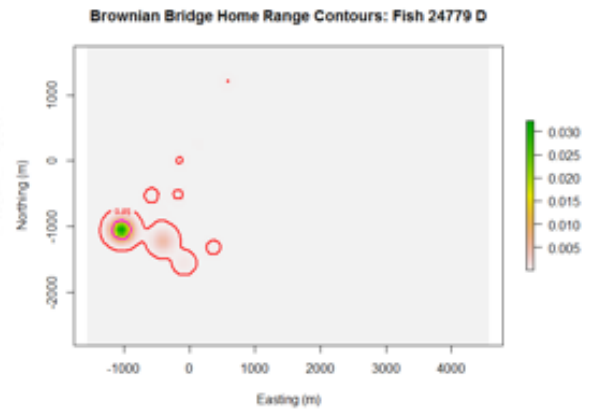
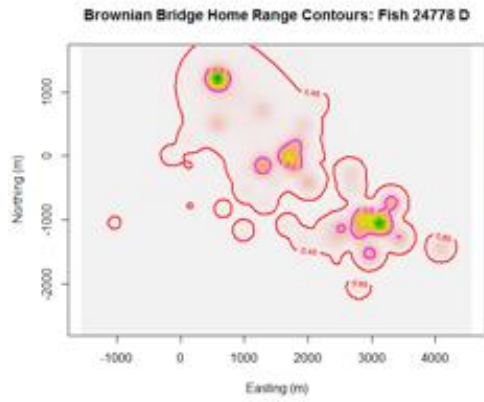


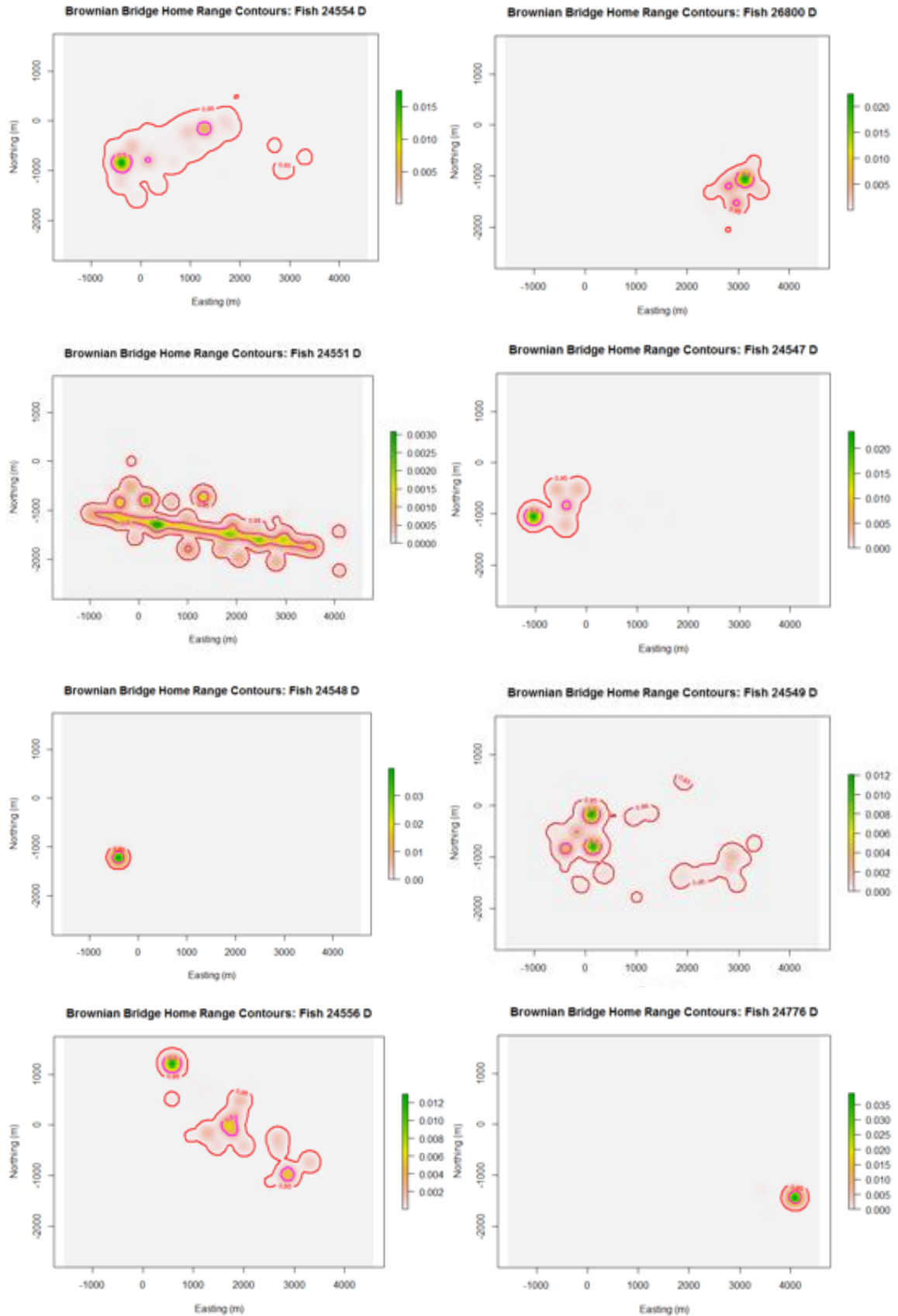
APPENDIX B

SUPPLEMENTAL FIGURES: DYNAMIC BROWNIAN BRIDGE MOVEMENT

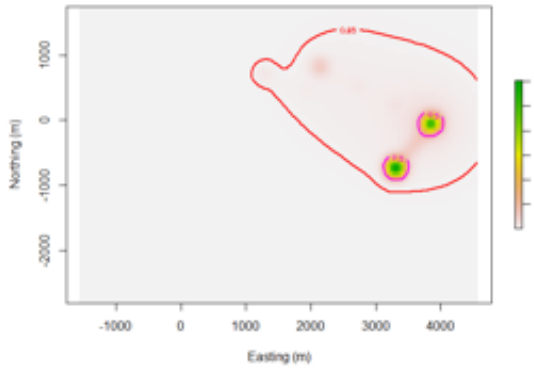
MODELS



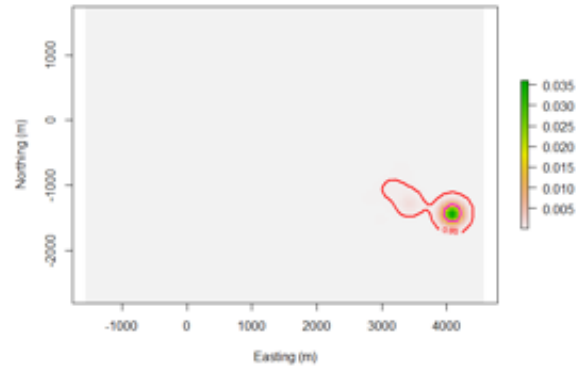




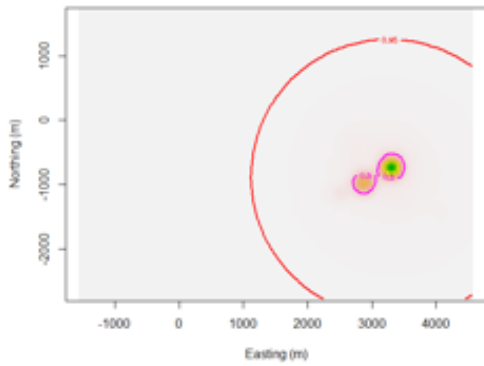
Brownian Bridge Home Range Contours: Fish 24777 D



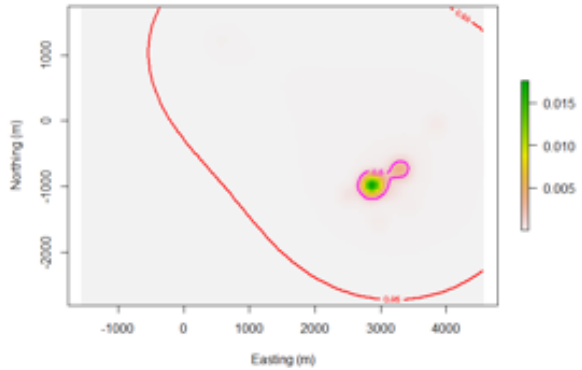
Brownian Bridge Home Range Contours: Fish 24781 D



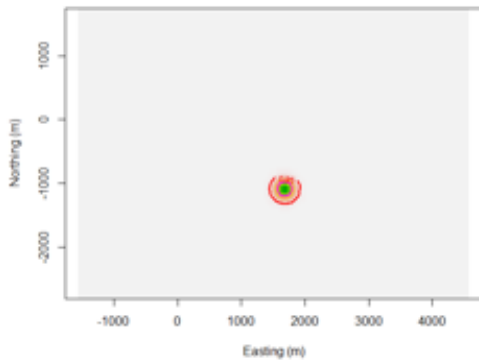
Brownian Bridge Home Range Contours: Fish 24782 D



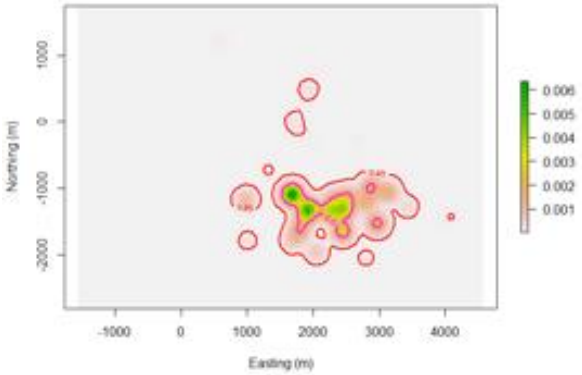
Brownian Bridge Home Range Contours: Fish 24783 D



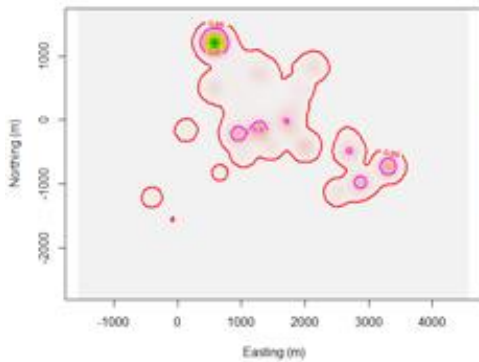
Brownian Bridge Home Range Contours: Fish 26792 D



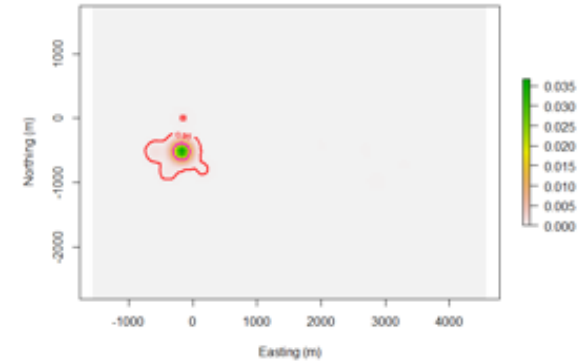
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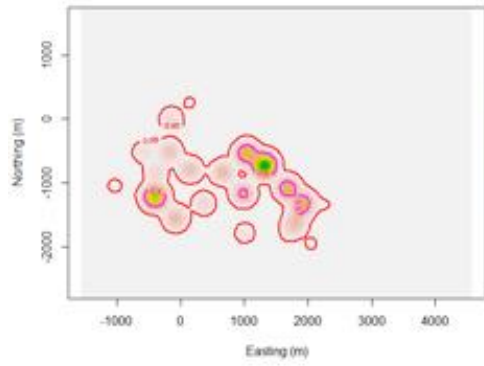
Brownian Bridge Home Range Contours: Fish 26796 D



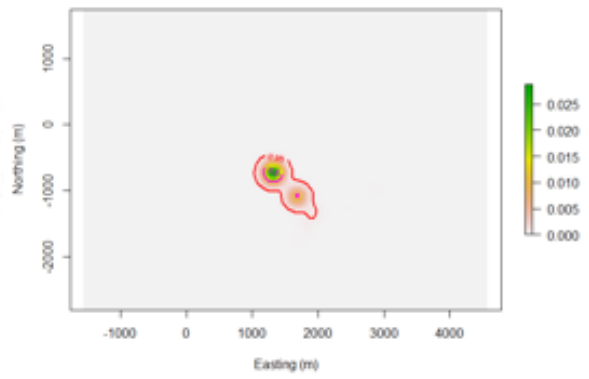
Brownian Bridge Home Range Contours: Fish 24785 D



Brownian Bridge Home Range Contours: Fish 26801 D

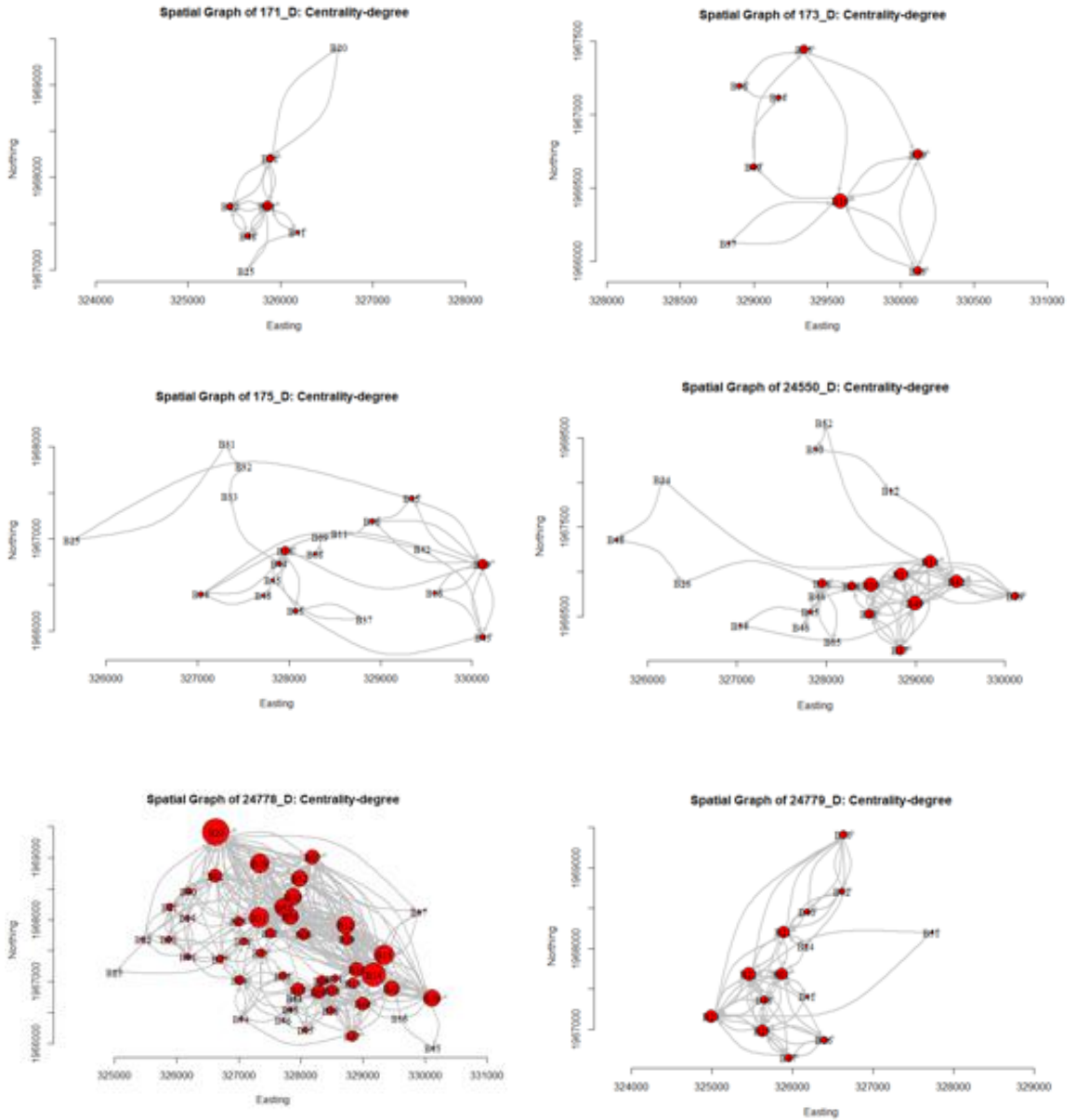


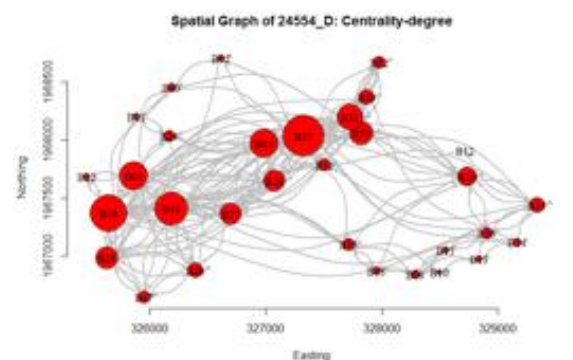
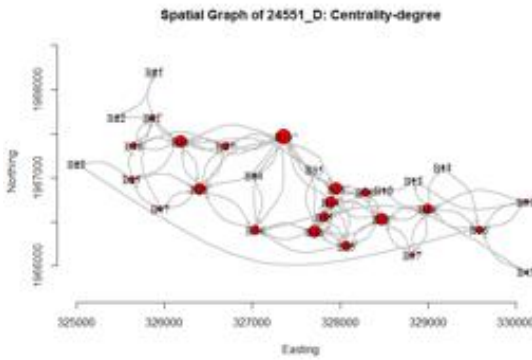
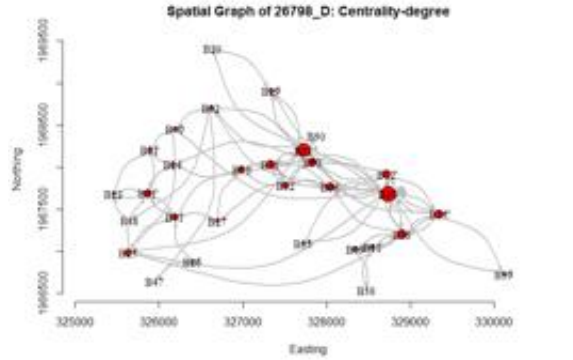
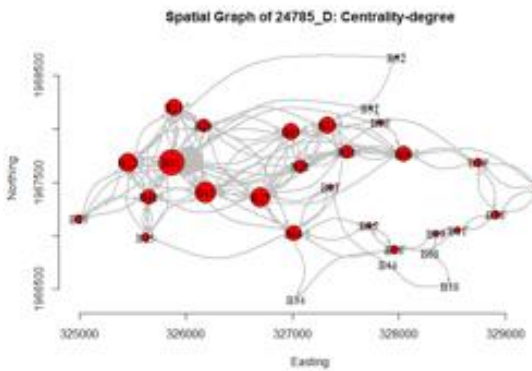
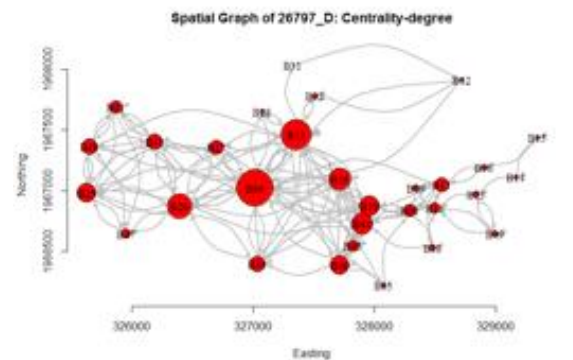
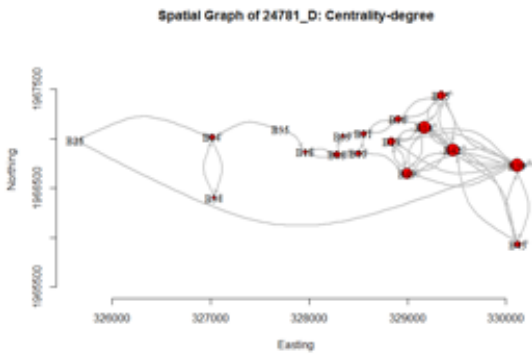
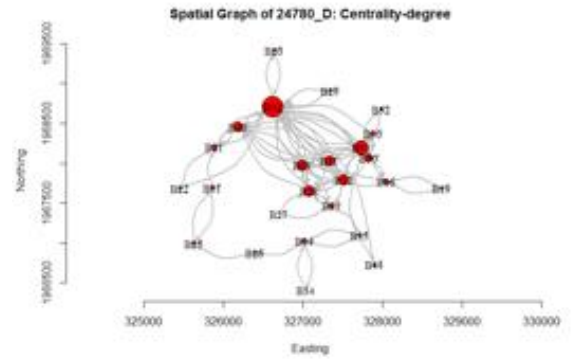
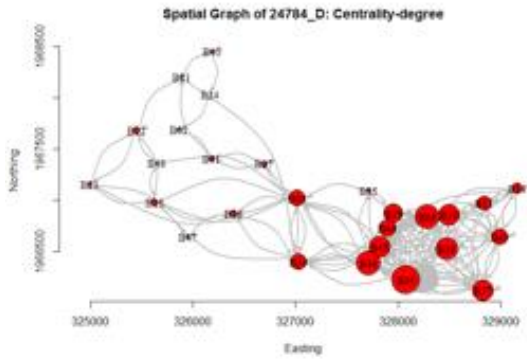
Brownian Bridge Home Range Contours: Fish 26802 D

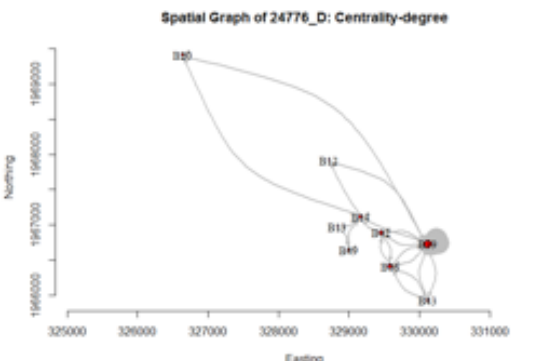
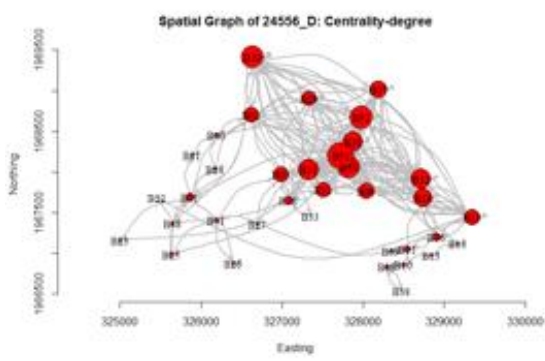
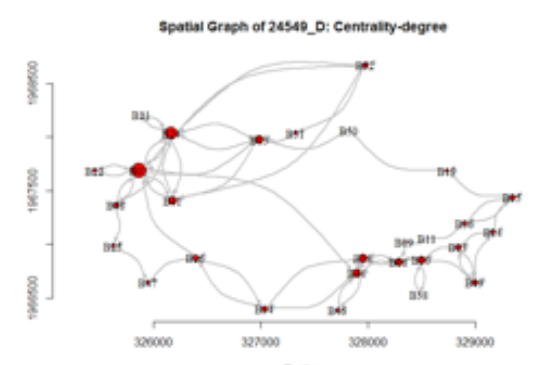
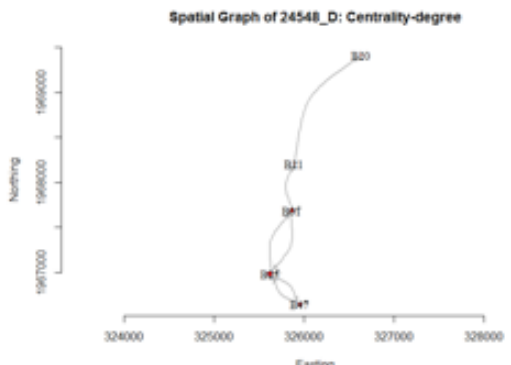
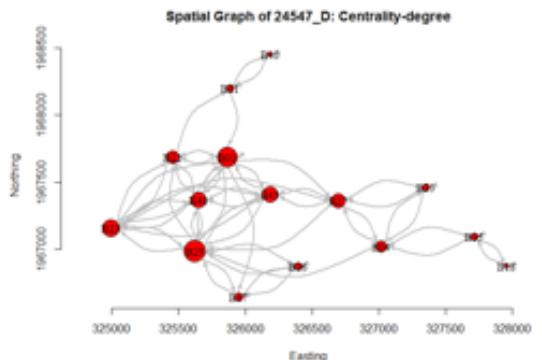
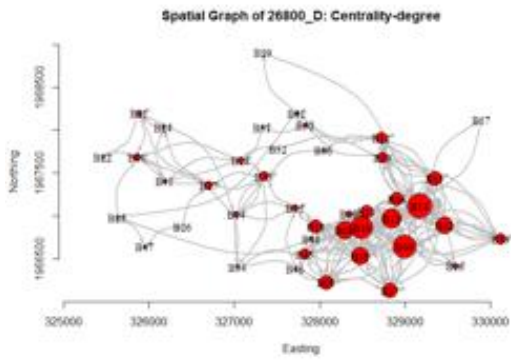
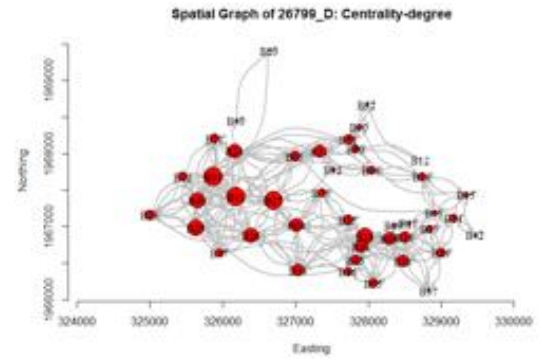
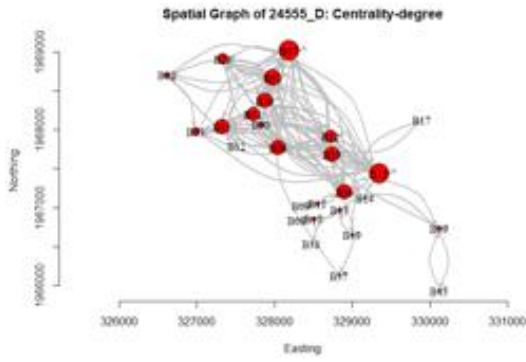


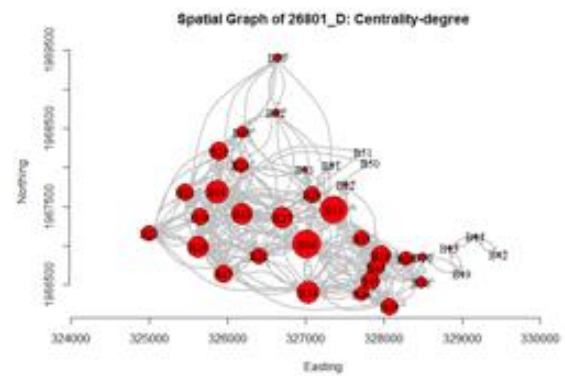
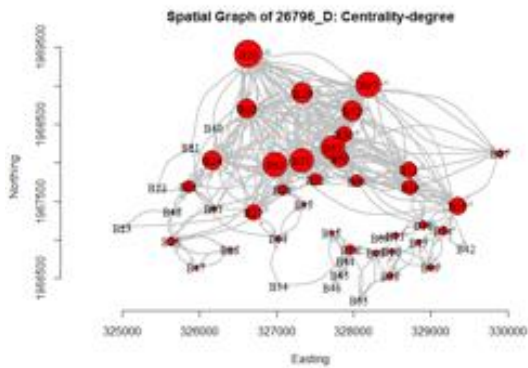
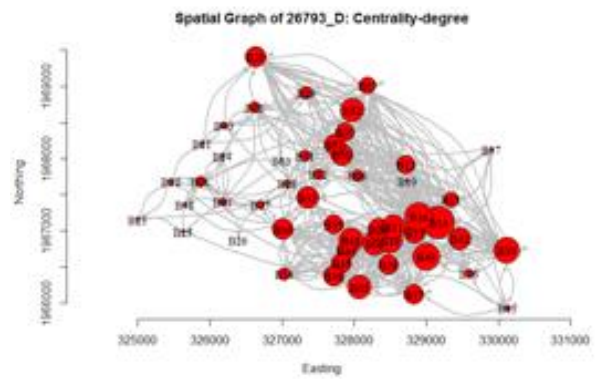
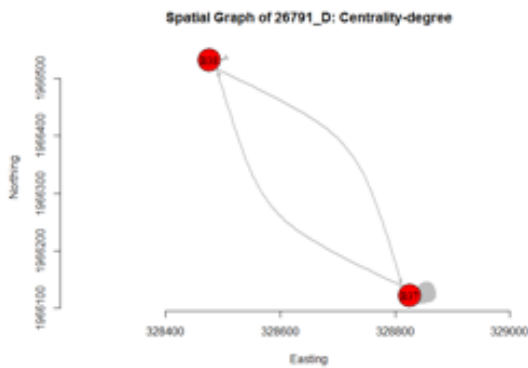
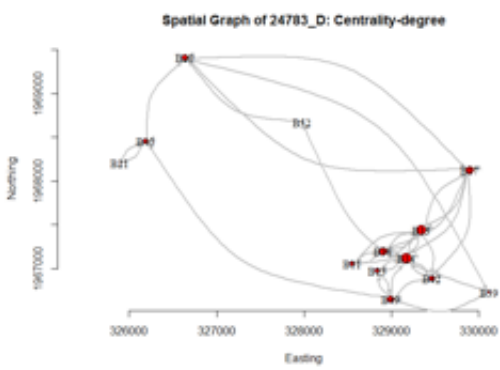
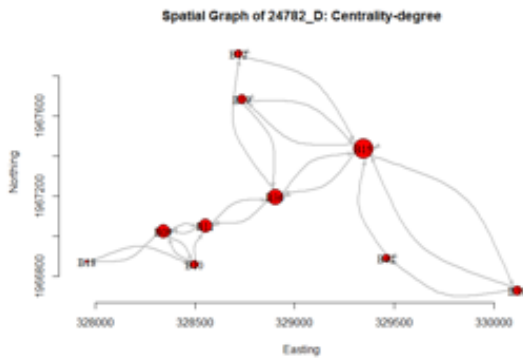
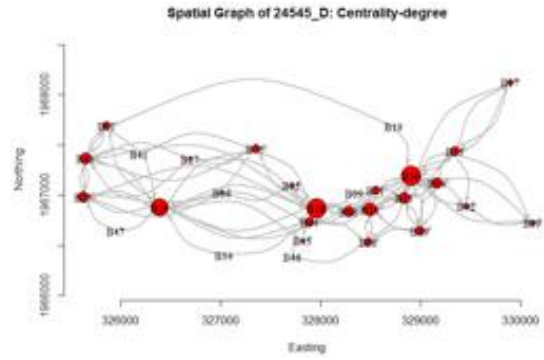
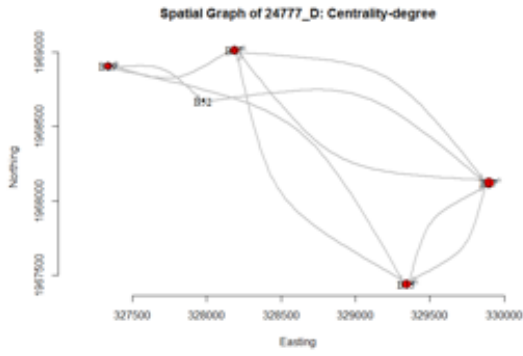
APPENDIX C

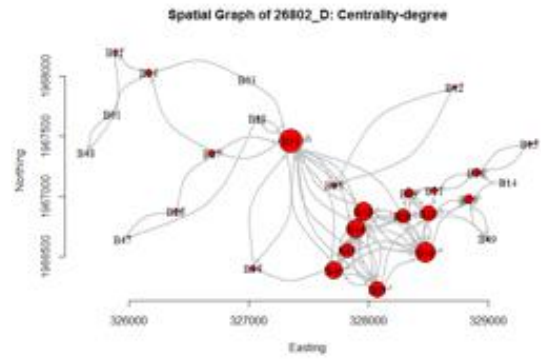
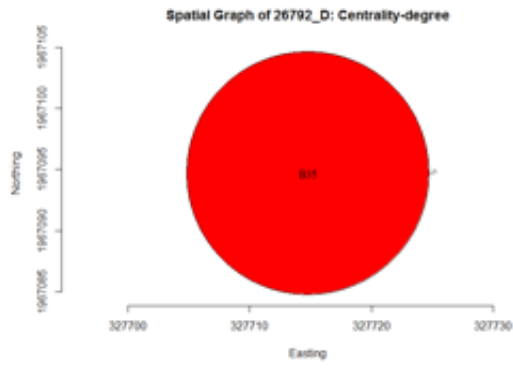
SUPPLEMENTAL FIGURES: NETWORK ANALYSIS CENTRALITY PLOTS



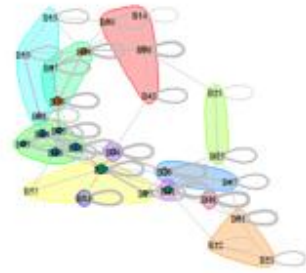




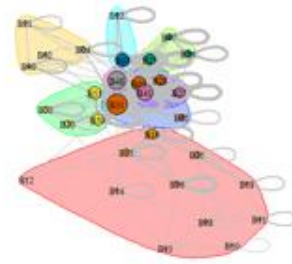




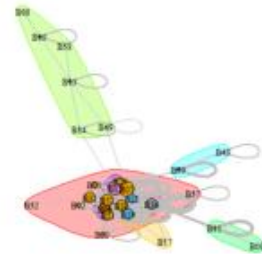
St. Croix Graph for 24551_D: Community Membership 'Fast Greedy'



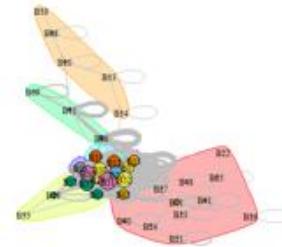
St. Croix Graph for 24554_D: Community Membership 'Fast Greedy'



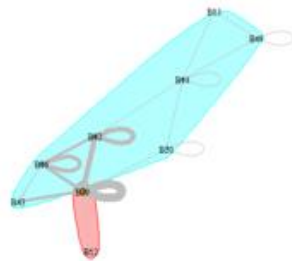
St. Croix Graph for 24555_D: Community Membership 'Fast Greedy'



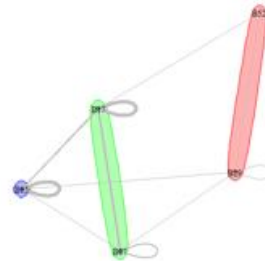
St. Croix Graph for 24556_D: Community Membership 'Fast Greedy'



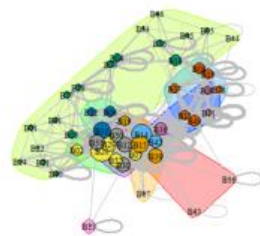
St. Croix Graph for 24776_D: Community Membership 'Fast Greedy'



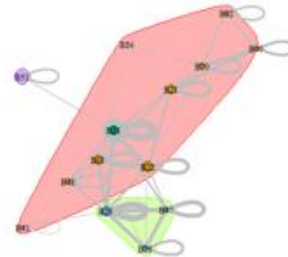
St. Croix Graph for 24777_D: Community Membership 'Fast Greedy'



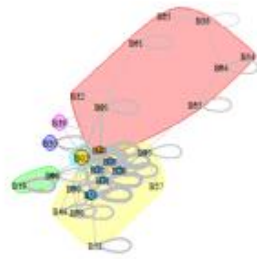
St. Croix Graph for 24778_D: Community Membership 'Fast Greedy'



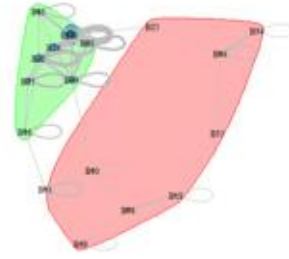
St. Croix Graph for 24779_D: Community Membership 'Fast Greedy'



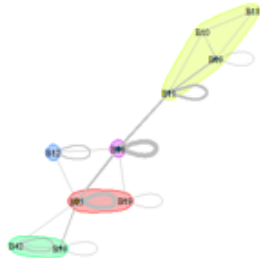
St. Croix Graph for 24780_D: Community Membership 'Fast Greedy'



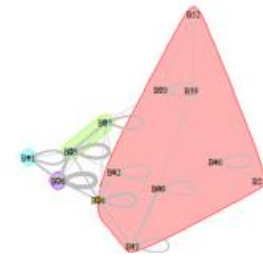
St. Croix Graph for 24781_D: Community Membership 'Fast Greedy'



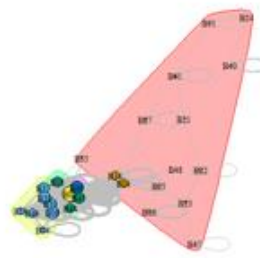
St. Croix Graph for 24782_D: Community Membership 'Fast Greedy'



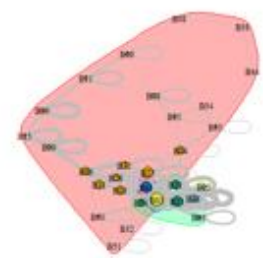
St. Croix Graph for 24783_D: Community Membership 'Fast Greedy'



St. Croix Graph for 24784_D: Community Membership 'Fast Greedy'



St. Croix Graph for 24785_D: Community Membership 'Fast Greedy'



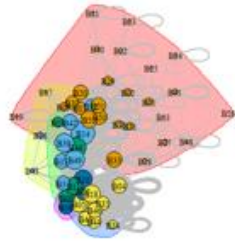
St. Croix Graph for 26791_D: Community Membership 'Fast Greedy'



St. Croix Graph for 26792_D: Community Membership 'Fast Greedy'



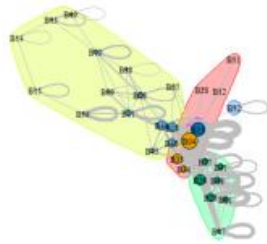
St. Croix Graph for 26793_D: Community Membership 'Fast Greedy'



St. Croix Graph for 26796_D: Community Membership 'Fast Greedy'



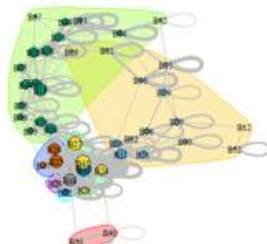
St. Croix Graph for 26797_D: Community Membership 'Fast Greedy'



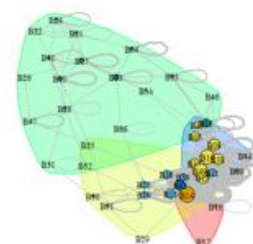
St. Croix Graph for 26798_D: Community Membership 'Fast Greedy'



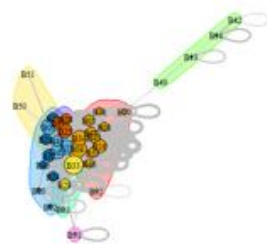
St. Croix Graph for 26799_D: Community Membership 'Fast Greedy'



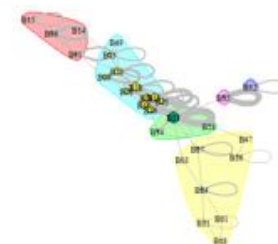
St. Croix Graph for 26800_D: Community Membership 'Fast Greedy'

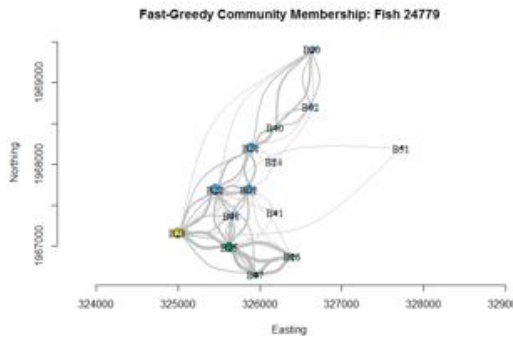
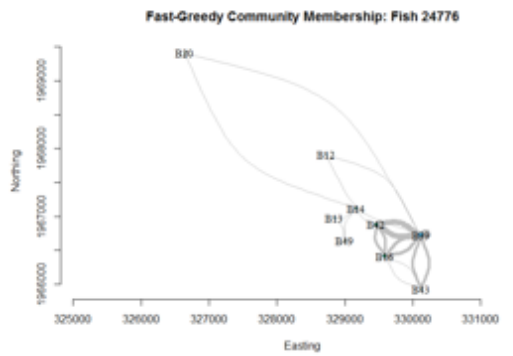
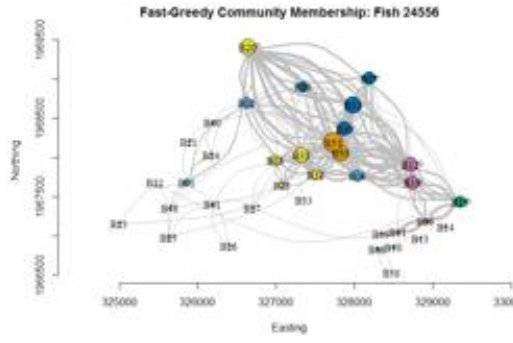
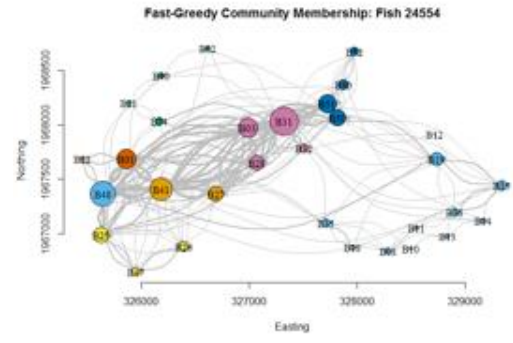
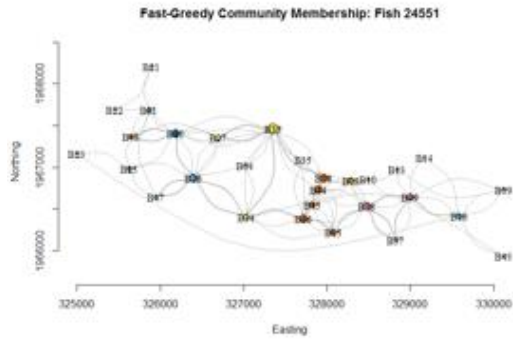


St. Croix Graph for 26801_D: Community Membership 'Fast Greedy'

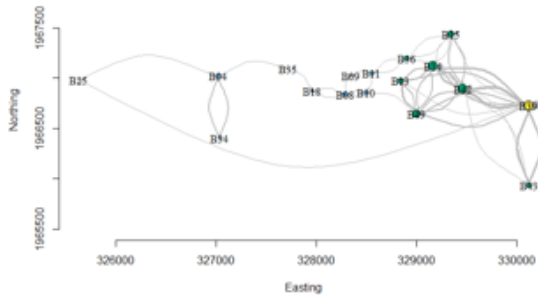


St. Croix Graph for 26802_D: Community Membership 'Fast Greedy'

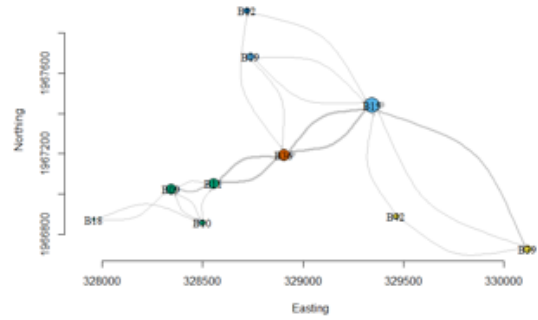




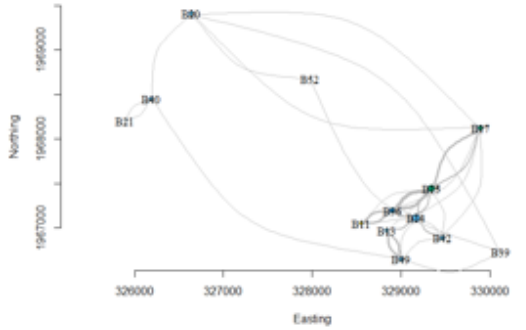
Fast-Greedy Community Membership: Fish 24781



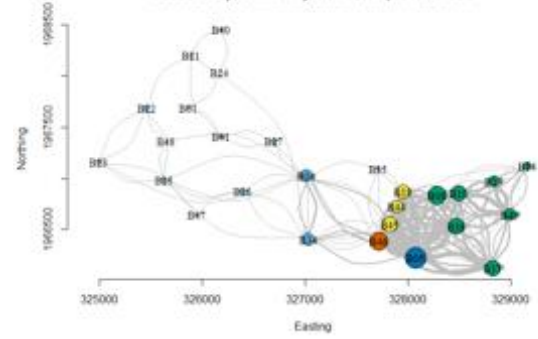
Fast-Greedy Community Membership: Fish 24782



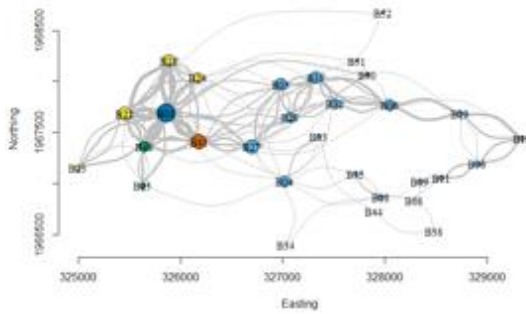
Fast-Greedy Community Membership: Fish 24783



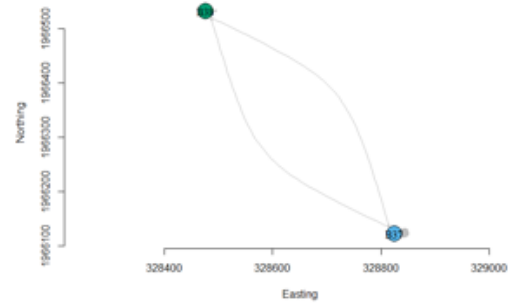
Fast-Greedy Community Membership: Fish 24784



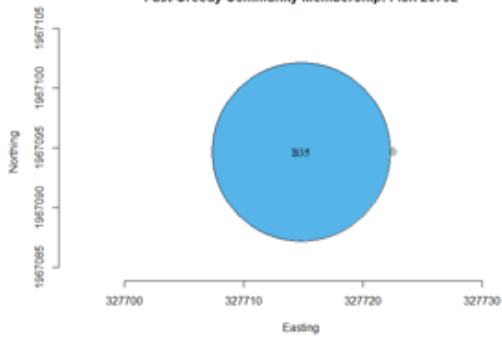
Fast-Greedy Community Membership: Fish 24785



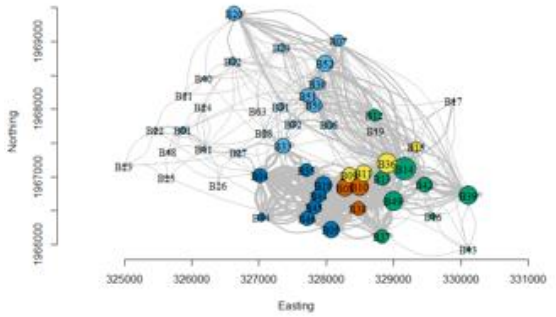
Fast-Greedy Community Membership: Fish 26791

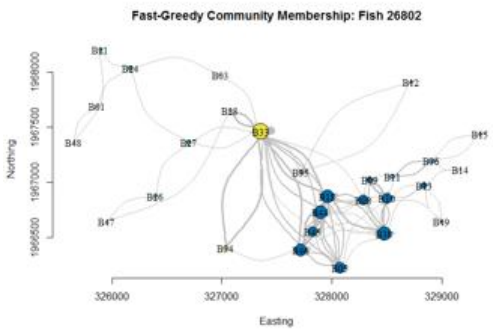
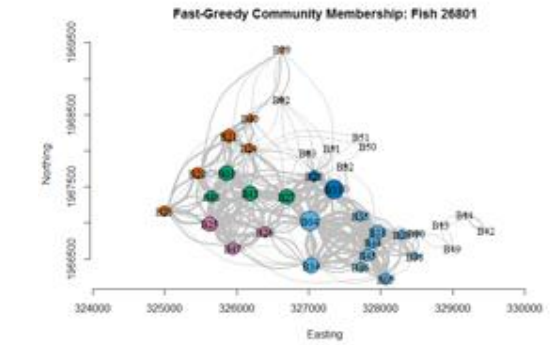
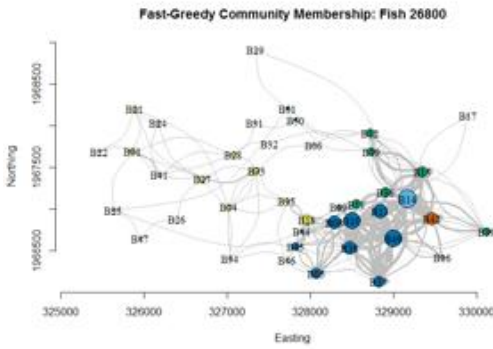
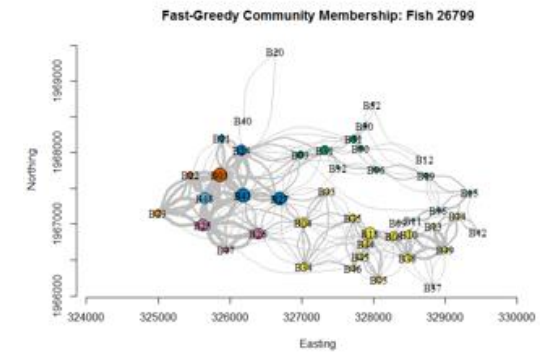
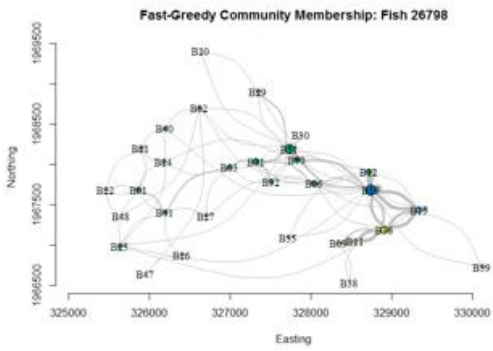
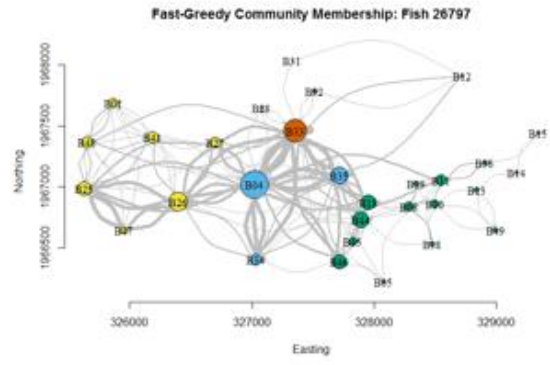
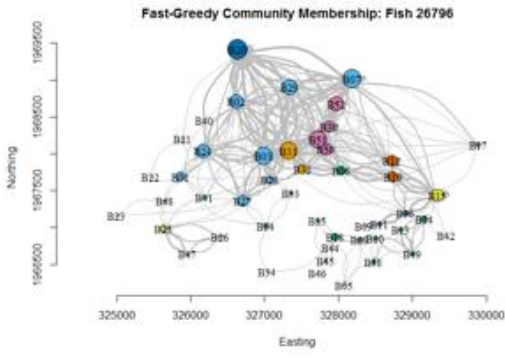


Fast-Greedy Community Membership: Fish 26792



Fast-Greedy Community Membership: Fish 26793

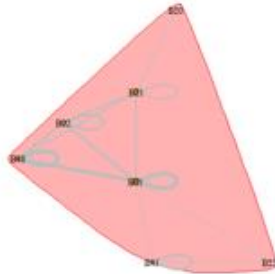




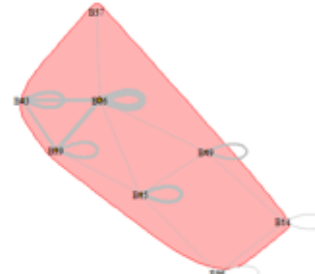
APPENDIX F

SUPPLEMENTAL FIGURES: WALKTRAP COMMUNITY MEMBERSHIP

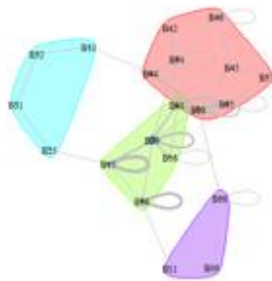
St. Croix Graph for 171_D: Community Membership 'Walktrap'



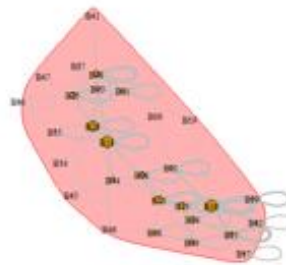
St. Croix Graph for 173_D: Community Membership 'Walktrap'



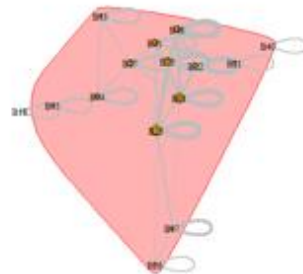
St. Croix Graph for 175_D: Community Membership 'Walktrap'



St. Croix Graph for 24545_D: Community Membership 'Walktrap'



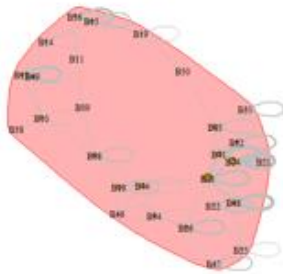
St. Croix Graph for 24547_D: Community Membership 'Walktrap'



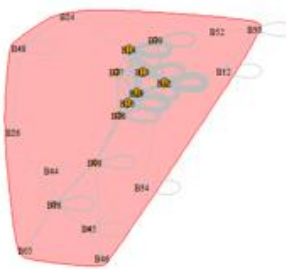
St. Croix Graph for 24548_D: Community Membership 'Walktrap'



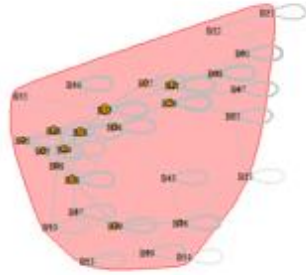
St. Croix Graph for 24549_D: Community Membership 'Walktrap'



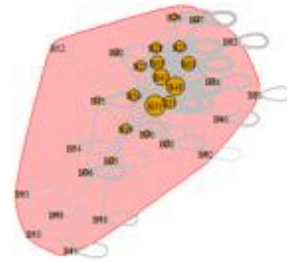
St. Croix Graph for 24550_D: Community Membership 'Walktrap'



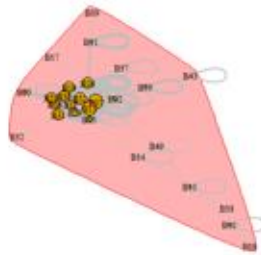
St. Croix Graph for 24551_D: Community Membership 'Walktrap'



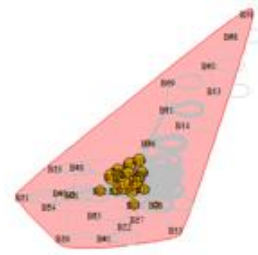
St. Croix Graph for 24554_D: Community Membership 'Walktrap'



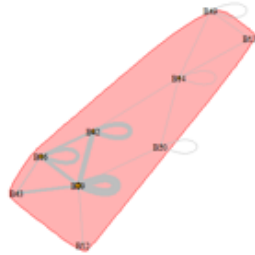
St. Croix Graph for 24555_D: Community Membership 'Walktrap'



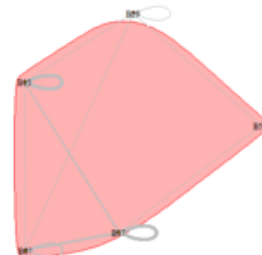
St. Croix Graph for 24556_D: Community Membership 'Walktrap'



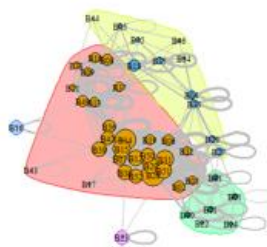
St. Croix Graph for 24776_D: Community Membership 'Walktrap'



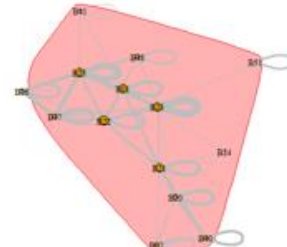
St. Croix Graph for 24777_D: Community Membership 'Walktrap'



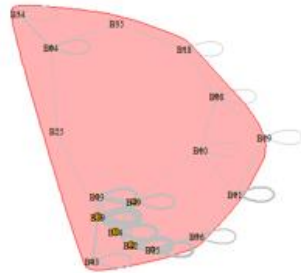
St. Croix Graph for 24778_D: Community Membership 'Walktrap'



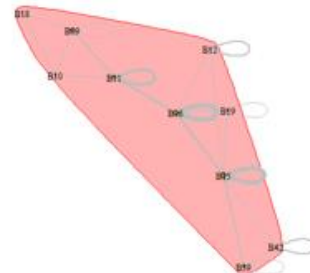
St. Croix Graph for 24779_D: Community Membership 'Walktrap'



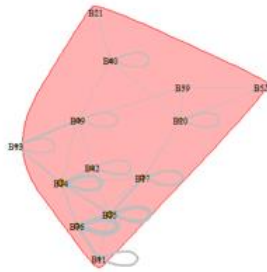
St. Croix Graph for 24781_D: Community Membership 'Walktrap'



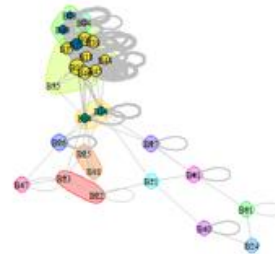
St. Croix Graph for 24782_D: Community Membership 'Walktrap'



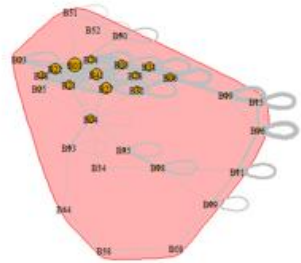
St. Croix Graph for 24783_D: Community Membership 'Walktrap'



St. Croix Graph for 24784_D: Community Membership 'Walktrap'



St. Croix Graph for 24785_D: Community Membership 'Walktrap'



St. Croix Graph for 26791_D: Community Membership 'Walktrap'



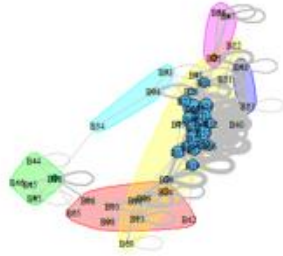
St. Croix Graph for 26792_D: Community Membership 'Walktrap'



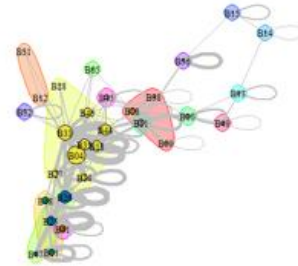
St. Croix Graph for 26793_D: Community Membership 'Walktrap'



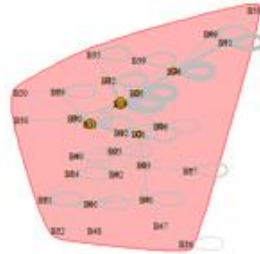
St. Croix Graph for 26796_D: Community Membership 'Walktrap'



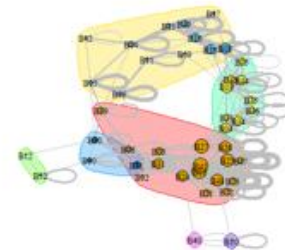
St. Croix Graph for 26797_D: Community Membership 'Walktrap'



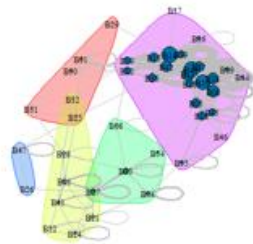
St. Croix Graph for 26798_D: Community Membership 'Walktrap'



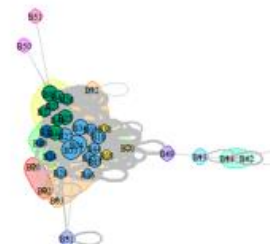
St. Croix Graph for 26799_D: Community Membership 'Walktrap'



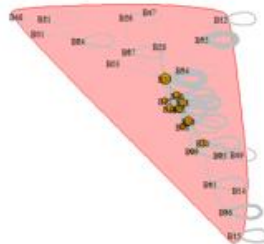
St. Croix Graph for 26800_D: Community Membership 'Walktrap'



St. Croix Graph for 26801_D: Community Membership 'Walktrap'



St. Croix Graph for 26802_D: Community Membership 'Walktrap'



APPENDIX G:
DATASET SUMMARY: CHAPTER 2

VEMCO ID	FL (cm)	All Detections	Detections>55	Observed /Expected	Days Heard
171	71.5	2212	762	0.289755875	106
173	84.5	19144	13572	5.160848734	117
175	99	380	229	0.087078865	112
24545	77	4535	3271	1.243820823	360
24547	66.5	10146	9713	3.693436763	322
24549	78	3300	1025	0.38976348	15
24550	97	27585	24433	9.290820595	364
24551	76	891	812	0.308768728	79
24554	61	15706	13282	5.050574188	364
24555	96	8587	7645	2.907065176	364
24556	85	51448	44037	16.74537988	364
24776	84.5	182495	152752	58.08502548	364
24777	95.5	896	251	0.095444520	30
24778	96	11388	10890	4.140999316	364
24779	92	31506	31106	11.82827591	348
24780	90.5	43067	39693	15.09354324	363
24781	92	17547	15625	5.941516465	247
24782	83.5	1232	1003	0.381397825	305
24783	79	1486	1477	0.561639668	360
24784	90.5	250055	224179	85.24564606	364
24785	79.5	191770	174354	66.29933835	364
26791	71.5	162528	113606	43.19948285	359
26792	108	54192	4262	1.620655563	251
26793	101.5	163087	73399	27.91048749	364
26796	63	39963	19178	7.292569777	364
26797	96	175140	77435	29.44520496	270
26798	89	102271	50343	19.14328086	361
26799	71	82509	51276	19.49806069	364
26800	97	221287	106074	40.33538672	364
26801	107	115956	57774	21.96897102	364
26802	103	152258	32225	12.25378356	332

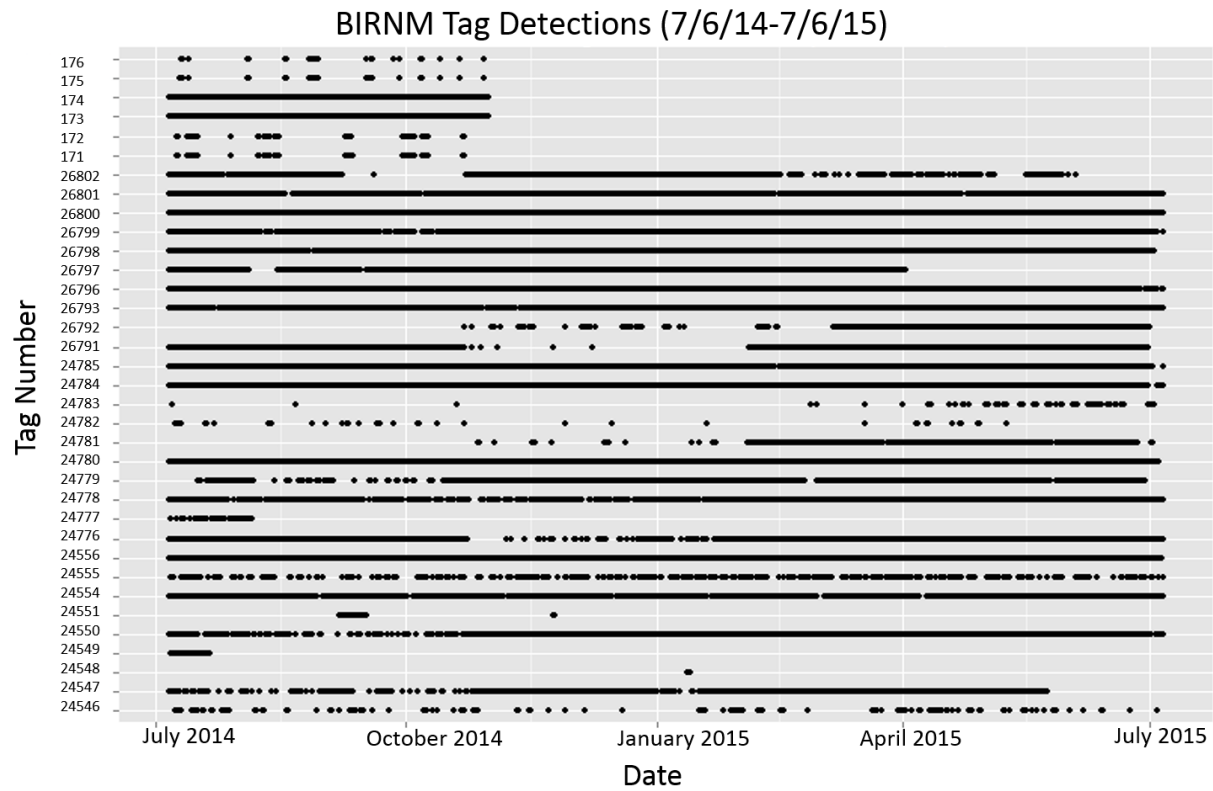
APPENDIX H

DATASET SUMMARY: CHAPTER 3

Tag	Observed /Expected	Days Out	Detections	Detections per week	Fork Length
173	5.160848734	117	13572	812	84.5
24550	9.290820595	364	24433	469.8653846	97
24554	5.050574188	364	13282	255.4230769	61
24556	16.74537988	364	44037	846.8653846	85
24776	58.08502548	364	152752	2937.538462	84.5
24779	11.82827591	348	31106	625.6954023	92
24780	15.09354324	363	39693	765.4297521	90.5
24784	85.24564606	364	224179	4311.134615	90.5
24785	66.29933835	364	174354	3352.961538	79.5
26793	27.91048749	364	73399	1411.519231	101.5
26796	7.292569777	364	19178	368.8076923	63
26797	29.44520496	270	77435	2007.574074	96
26798	19.14328086	361	50343	976.1800554	89
26799	19.49806069	364	51276	986.0769231	71
26800	40.33538672	364	106074	2039.884615	97
26801	21.96897102	364	57774	1111.038462	107
26802	12.25378356	332	32225	679.4427711	103

APPENDIX I

DATASET SUMMARY: RESIDENCY PLOT



APPENDIX J

ACTIVITY SPACE ESTIMATION RESULTS

Tag	CUR	GUR	KDE50	KDE95	DBBMM50	DBBMM95	BB_CUR
173	3	7	0.07	0.43	0.05	0.28	1
24550	5	17	0.12	0.92	0.08	0.83	1
24554	8	26	0.22	2.08	0.21	3.21	3
24556	8	28	0.37	2.32	0.27	2.05	3
24776	3	8	0.07	0.33	0.05	0.23	1
24779	5	12	0.09	0.78	0.06	0.83	1
24780	6	21	0.07	0.45	0.05	0.31	1
24784	7	22	0.08	0.59	0.06	0.46	1
24785	9	24	0.08	0.57	0.05	0.46	1
26793	12	33	0.50	2.52	0.41	2.42	7
26796	15	36	0.17	1.21	0.35	4.06	7
26797	9	25	0.17	1.21	0.11	0.88	2
26798	14	33	0.08	0.63	0.05	0.45	1
26799	10	28	0.21	1.84	0.16	1.70	3
26800	10	32	0.16	0.97	0.12	0.80	3
26801	9	21	0.52	3.15	0.39	2.82	7
26802	8	24	0.10	0.64	0.07	0.47	2
mean	8.29	23.35	0.18	1.21	0.15	1.31	2.65
median	8	24	0.12	0.92	0.08	0.83	2

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