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BUSINESS IN THE ESTUARY, PARTY IN THE SEA: MIGRATION PATTERNS OF STRIPED MULLET
(MUGIL CEPHALUS) WITHIN THE INDIAN RIVER LAGOON COMPLEX

by

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B.S. Georgia Institute of Technology, 2013

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Sciences
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Major Professor: Geoffrey S. Cook

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ABSTRACT

Commercial and recreational environmental enterprises in the Indian River Lagoon (IRL), Florida supply nearly 10,000 jobs and produce \$1.6 billion dollars a year in revenue. These waters contain iconic species of sportfish, including red drum, snook, and sea trout, as well as their lower trophic level prey such as snapper and mullet. Striped mullet (*Mugil cephalus*) are both commercially valuable as well as an indicator species for overall ecosystem health. From September to December, mullet in the IRL undergo an annual migration from their inshore foraging habitats to oceanic spawning sites. However, their actual migratory pathways remain unknown. To address this knowledge gap, I utilized passive acoustic telemetry to assess the migration patterns of *M. cephalus* within the IRL complex, particularly focusing on movement pathways from inshore aggregation sites to oceanic inlets to spawn. Coupling environmental metrics with movement data, I evaluated catalysts for migration as well as travel routes through the estuary. Network analyses identified potential conservation areas of interest and sites needing management intervention. Impoundments around the Merritt Island National Wildlife Refuge appear to serve as an important refuge area for striped mullet while the Banana and Indian Rivers act as corridors during their inshore migratory movements. The environmental metrics of depth, temperature, dissolved oxygen, pH, barometric pressure, and photoperiod were the best predictors for the number of detections and residency time produced by two case studies of striped mullet activity. An emphasis on spatial fisheries management along with vigilant environmental monitoring will ensure the status of this species, to the benefit of both natural and human systems in the Indian River Lagoon. The knowledge generated as a result of this project may also provide a framework for sustainably managing other migratory baitfish.

Dedicated to the glory of God and my parents, Geoffrey and Michele Myers.
We are part of each other.

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INTRODUCTION

Life history strategies incorporating mass movement can be found across many taxonomic groups (Gross et al., 1988; Wilcove and Wikelski, 2008; Milner-Gulland et al., 2011). From the arctic tern's annual 71,000-kilometer journey to the iconic herds of wildebeest and zebra traveling across the Serengeti, the phenomenon of migration is one of the most visually stunning displays of nature (Garrity, 2008; Wilcove and Wikelski, 2008; Inman, 2010). Unfortunately, due to various human influences, such as climate change and habitat degradation, many of these migrations have been altered and/or are in decline (Wilcove and Wikelski, 2008; Bowlin et al., 2010; Lohmann, 2018). Ecologically, this affects keystone species, such as the Australian grey-headed flying-fox (*Pteropus poliocephalus*), which plays a crucial role in the distribution of native plant species through seed dispersal and pollination (Jantos, 2014; Buechley et al., 2018). This also impacts economically important species, with the Chinook salmon (*Oncorhynchus tshawytscha*) fishery in Oregon and California experiencing a devastating closure in 2008 after habitat loss, water diversions, and dam construction blocked access to a large extent of spawning and rearing grounds (Tucker, 2008; Lindley et al., 2009; Willmes et al., 2018). The very mobility of these species often makes them extremely difficult to study in their natural environment, but the advent of new tracking technologies coupled with emerging methods to study social networks, has provided novel approaches to circumvent these challenges, and more rigorously analyze movement data. This particular study integrates passive acoustic telemetry and network analysis to evaluate the spatial and temporal components of striped mullet (*Mugil cephalus*) migration within the Indian River Lagoon in addition to assessing environmental variables that may be correlated with that mass movement. Focusing on the migratory movements of such a widespread and ecologically valuable species will allow this project to generate understanding that can inform the development of more effective management strategies for other migratory forage fish, many of which are crucial to preserving and maintaining biodiversity and ecosystem function in aquatic and marine environments.

CHAPTER I: PASSIVE ACOUSTIC TELEMETRY DEMONSTRATES DIFFERENT MOVEMENT STRATEGIES OF STRIPED MULLET (*MUGIL CEPHALUS*) WITHIN MERRITT ISLAND NATIONAL WILDLIFE REFUGE

Introduction

An estuary is defined as "a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of seawater and freshwater derived from land drainage" (Day, 1980). Species of fish and crustaceans found in high abundance in estuaries during some period of their life history are generally classified as estuarine-dependent (Lenanton and Potter, 1987). Diadromous fish spend some portion of their life cycles in both fresh and salt water. Included in this grouping are the subcategories of anadromous and catadromous fish, which are born in fresh or saltwater, respectively (U.S. Fish and Wildlife, 1997). These species then use estuaries as migratory routes to their antipodal spawning grounds (Lenanton and Potter, 1987). Estuarine dependent organisms are vital for both the ecosystems they inhabit as well as for human utilization, with an estimated 69% and 66% by weight of U.S. marine commercial fish and recreational catch being estuarine or estuarine dependent (Cooper, 2009). Unfortunately, these environments are facing degradation and destruction worldwide due to increasing fishing pressure and coastal development (Whitfield, 1994; Halpern et al., 2008; Barbier et al., 2011). Most coastal and estuarine fisheries are either entirely exploited or overexploited, leading to reduced abundance, altered age structure, and changes in both size and species composition (Blaber et al., 2000; Britten et al., 2016; FAO, 2018). In order to combat and eventually reverse these effects, there is the urgent need to develop more effective management strategies, both single-species and ecosystem-based, that conserve a sufficient amount of reproductive biomass to ensure long-term sustainability (Goodyear, 1980; Sadovy de Mitcheson and Erisman, 2011; Taylor et al., 2012).

The unpredictable presence or absence of animals at fishing grounds historically led to colloquially 'good' and 'bad' recruitment years in various worldwide fisheries. In the early 20th century, Johan Hjort originally hypothesized episodic dispersal from spawning grounds to nurseries could account for these annual fluctuations in year-class success (Hjort, 1914). Building upon this concept, Heape (1931) further defined spawning-related migration as the predictable movements between locations or habitats in which migrants are obligated to return to their natal sites. This migratory behavior is clearly distinct from both emigration and nomadism, defined as a unidirectional exodus with no return and indiscriminate roaming, respectively (Heape, 1931). Four different categories of migration have since been delineated; gametic, climatic, alimential, and osmoregulatory (Myers, 1949). Climatic, alimential, and osmoregulatory movements are generally initiated for self-preservation or physiological purposes, such as lack of resources or unsuitable habitat conditions (Heape, 1931). Gametic, or breeding migrations, are habitual, seasonal movements to breeding grounds beyond the scope of the species' normal non-reproductive range (Heape, 1931). Evolutionarily, each type of migration serves to maximize fitness over an organism's life cycle by allowing them to reach more suitable environments, thereby increasing their probability of survival or reproduction (Gross, 1987). In order for the behavior to be adaptive, the survival, energetic, and reproductive advantages must outweigh the corresponding risks and costs associated with the mass movement (Grubbs and Kraus, 2010).

While only approximately 2.5% of fish species migrate, those species (e.g. salmon, sturgeon, herring) are highly valuable, both ecologically and economically (Hinch et al., 2006; Binder et al., 2011; Cooke et al., 2011). As these fish travel, their routes and spawning sites are not always regulated, leaving them subject to pollution, habitat fragmentation due to anthropogenic devices such as dams, and fishing pressures. These corridors are vital to maintain the connectivity of habitat patches and to ensure the continuation of their life history strategy (Simberloff and Cox, 1987; Rouget et al., 2006; Gilbert-Norton et al., 2010). There are currently 888 spawning aggregations documented within the

Science and Conservation of Fish Aggregations (SCRFA) database, 91 of which occur in the United States (Russell et al., 2014). More than half of these aggregations are categorized as having an ‘unknown’ status (Russell et al., 2014). With this dearth of information, it is often difficult to determine what, where, and how often management actions need to be implemented. While not directly focusing on the management of aggregations, I hope to provide a foundation for this by examining the migration routes that lead to this behavior. I aim to address this knowledge gap locally by examining the essential migration routes of striped mullet (*Mugil cephalus*) within the Indian River Lagoon; a key mid-trophic level species that has been largely overlooked and relatively understudied to date. Focusing on the migratory movements of such a widespread and adaptable species will allow this project to generate understanding that can inform the development of more effective management strategies for other migratory forage fish.

Forage fish are vital species that serve as major conduits for energy transfer through the aquatic food web by converting zooplankton production into available forms for higher order predators (Bakun et al., 2010; Pikitch et al., 2014). Many higher trophic level species dependent on forage fish are listed as ‘Near Threatened’, are on the IUCN Red List, and/or are located in areas that are vulnerable to changes in forage fish abundance (Pikitch et al., 2014). Forage fish species also compose 30% of landed capture fisheries through human consumption, fishmeal, and fish oil (Alder and Pauly, 2006; Tacon and Metian, 2009). However, there is major evidence that these groups of fish are declining (Enticknap et al., 2011; Hall et al., 2012; Matthiessen, 2016). In 2015, Essington et al. examined 55 major forage fish stocks worldwide and concluded that 27 of those had experienced a collapse. Forage fish are often aggregating, migratory species as well, adding an additional dimension in which they may be exploited (Enticknap et al., 2011; The Pew Charitable Trusts, 2013; Bayard, 2015). By examining the movement of a key forage fish species within the Indian River Lagoon, the striped mullet, that knowledge may be extended to the management and fishing practices involving other such species in the future.

The striped mullet was selected as the model species for this study as it epitomizes the two most important functions of a forage fish; it facilitates energy transfer through the food web as a significant food source for many sportfish and other higher order predators and is targeted by both recreational and commercial fishing industries (Leard et al., 1995; Bester, 2014; NCDEQ, 2018). When they reach sexual maturity at around 3 years of age, these fish also conduct an annual migration from inshore waters to oceanic spawning locations, but little data exists concerning their exact migratory routes (Bacheler et al., 2005; Bester, 2014; Fowler et al., 2016). While striped mullet are relatively abundant, the lack of information on their migratory pathways still raises the possibility of the need for intervention or management (Bacheler et al., 2005; Fowler et al., 2016). This is common in many migratory species, due to the difficulty of direct observation created by their mobility (Kaimuddin, 2016; Crossin, 2017). This knowledge deficiency is also shared by other states, such as South Carolina, in which a Comprehensive Wildlife Conservation Strategy (CWCS) was performed for the striped mullet (McDonough, 2005). One of the resulting conservation recommendations of this report was to initiate a tagging study to evaluate the species' seasonal movement and distribution (McDonough, 2005). In the state's most recent State Wildlife Action Plan (the updated form of the CWCS), the striped mullet is still listed as a species of moderate conservation priority (SCDNR, 2015). Therefore, not only will utilizing this species contribute to the pool of knowledge regarding the populations of striped mullet within the Indian River Lagoon, but also to other locations that prioritize its status.

Objective: Identify and evaluate the spatial and temporal dynamics of migratory routes along which striped mullet disperse from known aggregation sites around Merritt Island National Wildlife Refuge to offshore spawning locations.

Question: Do striped mullet disperse from known staging sites around Merritt Island National Wildlife Refuge to offshore spawning locations?

Hypotheses:

H_0 : Striped mullet remain at their staging sites within Merritt Island National Wildlife Refuge.

H_{1A} : Striped mullet depart from their staging sites within Merritt Island National Wildlife Refuge and use the shortest routes through the estuary to reach their oceanic spawning grounds.

H_{2A} : Striped mullet depart from their staging sites within Merritt Island National Wildlife Refuge and use longer routes through the estuary to reach their oceanic spawning grounds.

Methods

Study Site

This study was conducted in the Indian River Lagoon Complex and within Merritt Island National Wildlife Refuge property. The Indian River Lagoon (IRL) Complex spans approximately 251 kilometers, nearly one-third of Florida's east coast, and is comprised of the Mosquito Lagoon, the Indian River, and the Banana River. Five primary inlets, Ponce de Leon, Sebastian, Ft. Pierce, St. Lucie, and Jupiter, connect this water system to the ocean (Figure 1). This area also includes the Merritt Island National Wildlife Refuge (MINWR), a 140,000-acre preserve on Kennedy Space Center property and one of the few relatively undeveloped barrier islands on the east coast of Florida (Adrian et al., 2008). The IRL, recognized as an "Estuary of National Significance," contains one of the highest levels of biological diversity in the United States, with 397 different fish species inhabiting its waters at some point of their

lifecycle (Gilmore, 1995). Commercial and recreational enterprises in the lagoon sustain nearly 10,000 jobs and directly generate over \$1.6 billion dollars per year (East Central Florida Regional Planning Council, 2016). The waters teem with economically important species, including the sport fish snook (*Centropomus undecimalis*), red drum (*Sciaenops ocellatus*), and sea trout (*Cynoscion nebulosus*) as well as key prey species such as pinfish (*Lagodon rhomboides*), Atlantic croaker (*Micropogonias undulatus*), and mullet (*Mugil spp.*) (Myers, 2013).

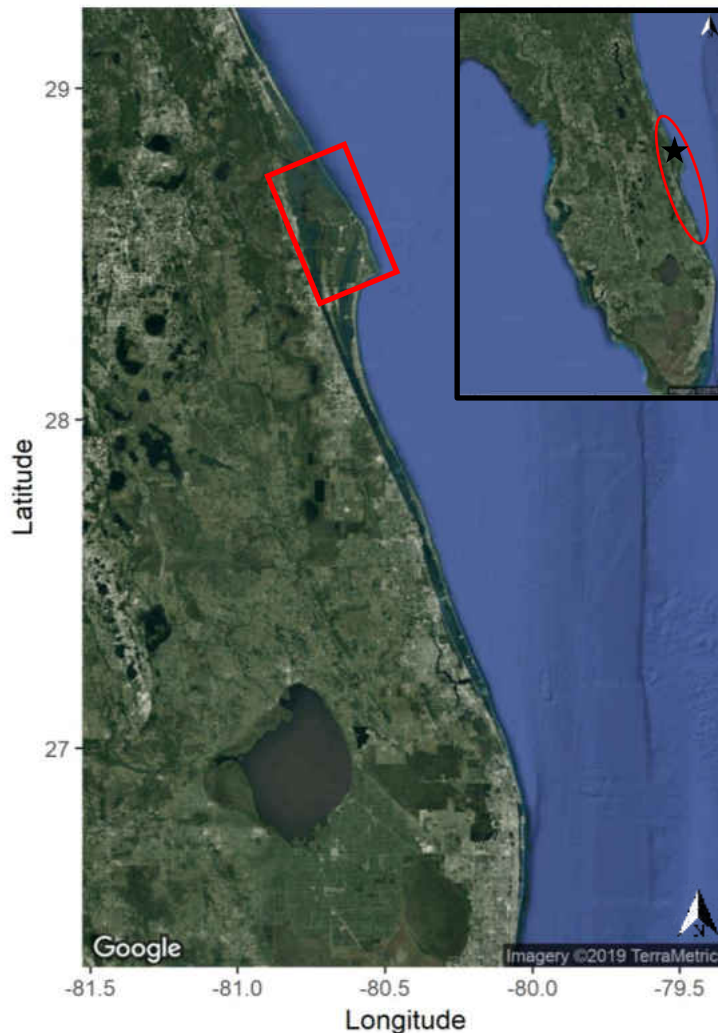


Figure 1: The Indian River Lagoon Complex (circled) and Merritt Island National Wildlife Refuge (star) as situated in the state of Florida (inset). Approximate boundaries of Merritt Island National Wildlife Refuge (red box).

Model Species

Mugil cephalus, also known as striped or black mullet, are globally distributed throughout tropic and temperate coastal waters, often moving into estuaries and other freshwater environs. In the western Atlantic, the species ranges from Nova Scotia to Brazil (Bester, 2014). Striped mullet are characterized by grey-olive or grey-brown color that fades to a silvery white towards the ventral side (Figure 2). They can grow to over 45 centimeters in length, weigh over 7 kilograms, and live from 4 to 16 years of age, reaching sexual maturity between 20-30 centimeters at approximately 3 years (McDonough, 2006; Bester, 2014). Migrating up to 50 miles offshore to spawn in large aggregations during fall and winter months, individual females can produce up to two million eggs (GSMFC, 1995; Bester, 2014). It is believed that decreasing water temperatures and barometric pressure may trigger their aggregation and spawning behavior (Mahmoudi, 2000). The mullet run, as local fishermen refer to their spawning migration, peaks during October and November in the Indian River Lagoon Complex.



Figure 2: A sexually mature striped mullet (VIMS, 2010).

Within Merritt Island National Wildlife Refuge and the IRL, mullet are often found in shallow water, near red mangroves and seagrass beds, and around manmade objects (Killer, 2012). This omnivorous species occupies a lower trophic level consuming zooplankton and detritus. As they are so

numerically abundant, the majority of higher order predators consume this fish. *Mugil cephalus* have a high individual productivity rate and are major contributors to secondary production; as such, *M. cephalus* is a critical link in the highly productive and diverse food web of the IRL (Whitfield et al., 2012). The striped mullet also serves as a proxy for overall ecosystem health, as they occupy a wide range of habitats and can be used to detect environmental stressors within those systems (McDonough, 2006; Whitfield et al., 2012).

Fisheries-Independent and Dependent Monitoring of *M. Cephalus*

Fisheries independent monitoring has been conducted in the Indian River Lagoon by the Florida Fish and Wildlife Conservation Commission (FWC); the FWC has monitored the Northern IRL since 1990, including waters of the Indian River Lagoon proper south to Vero Beach, and since 1997 they have monitored the Southern IRL, which runs from Vero Beach south to Jupiter Inlet (FWC-FWRI, 2015). In 2015, sampling in both regions collected 431,455 individuals in seines and otter trawls using a monthly stratified random sampling design. The vast majority of individuals (n=402,542) were collected from the Northern IRL with *M. cephalus* being among the top 10 numerically dominant taxa (n=7,248; FWC-FWRI, 2015). This number translates to a conservative density estimate of approximately 13 animals per 100 square meters (FWC-FWRI, 2015). Using these data, the FWC developed relative indices of abundance (IOAs) for young-of-the-year mullet (YOY; i.e. fish \leq 35 mm standard length [SL]), to estimate the size of each year class and to predict adult mullet abundances based on these recruitment estimates (FWC-FWRI, 2015). The IOAs in the IRL vary temporally from 1996-2014, with relatively high numbers of recruits in 2001, 2010, and 2015, and relatively low abundances in the remaining years (FWC-FWRI, 2015).

Indian River Lagoon counties (i.e. Brevard, Indian River, Martin, St. Lucie, and Volusia) contributed a combined 10 million pounds of commercial finfish in 2014, worth nearly \$17 million (ECFRC, 2016). The first documented commercial catch of mullet in Florida occurred in 1879, with 3.5 million pounds landed. This peaked at 50 million pounds during WWII before declining to roughly 30 million pounds for the next fifty years (Mahmoudi, 2014). Recreational estimates are less precise and much smaller, cresting at 5.5 million pounds in 1985 and composing only 18% of statewide total catch from 2004-2013 (Mahmoudi, 2014). In 2015, as one of Florida's top 20 fish species, mullet demanded \$0.70 per pound, resulting in a dockside value of \$6 million from the nearly 10 million pounds landed (Sleep, 2017). Commercial and recreational fisheries catch is largely dictated by oscillations in market demand, status of the environment, gear type, and instituted regulations (Mahmoudi, 2014).

Nearly 20 years ago, an entanglement net ban was instituted in Florida, including the Indian River Lagoon Complex. Proponents of the ban argued that commercial fishermen were devastating fish populations, including many species of mullet, an already restricted species (Mahmoudi, 2014). Since the ban was instituted, mullet catch in Florida decreased by 65%; from an average of 27 million pounds to 10 million pounds per year (Mahmoudi, 2014). Overall, fishing mortality rates have dramatically declined, allowing both total population and spawning stock biomass to increase (FWC-FWRI, 2015). It is now estimated that transitional spawning potential ratios have increased to 35%, suggesting the fishery is robust and is not being overfished (Mahmoudi, 2014). This is especially important for striped mullet in the IRL, as they are an integral species of the ecosystem and a vital baitfish utilized by sport fishermen. The lagoon itself also contains essential migration routes for the fish, but these pathways have been undocumented to date. This is of singular concern because it is believed that fishermen target gravid females during their migration (Ditty and Shaw, 1996). Cured mullet roe, known as bottarga, generally yields a higher profit than the fish itself, thereby increasing the demand for gravid females (Rutger, 2018). As this affects reproductive potential, this could also lead to negative impacts on the population

over time (Ditty and Shaw, 1996). The proportion of roe-season catch, or the proportion of gravid females, to total catch has increased since the net ban was instituted, with 76.8% of total landings occurring during spawning season (September-December) (Mahmoudi, 2014). This has been accompanied by an increase in the size of landed mullet in some regions. Considering the current status of the fishery, this particular project seeks to explore the migration patterns of *Mugil cephalus* within the Merritt Island National Wildlife Refuge and Indian River Lagoon Complex in order to provide fundamental knowledge necessary to adequately evaluate and potentially update management practices.

Acoustic Telemetry

Biotelemetry was developed over fifty years ago as a means to study organisms in their natural environment without the restrictions and biases of conventional sampling techniques (Hockersmith and Beeman, 2012; Kessel et al., 2014). Acoustic telemetry is unique in allowing for the continuous and simultaneous observation of animals in both space and time by attaching or implanting electronic devices that transmit a variety of data to programmed receivers (Cote et al., 1998; Heupel et al., 2006; Donaldson et al., 2014). The ever-evolving field of acoustic telemetry now enables scientists to address complex problems concerning behavioral, ecological, and physiological questions in the aquatic realm. Increasingly, this tool is being employed to quantify the fine scale, long-term movement patterns of marine animals in order to shed light on their life history, resource and habitat use, and ecological niches (Espinoza et al., 2011; Krueger et al., 2018). Passive acoustic monitoring is particularly useful when the goal is to determine the activity of an assemblage of individuals over large temporal and spatial scales (Espinoza et al., 2011; Donaldson et al., 2014). Networks of passive acoustic receivers have been deployed at strategic points in both inshore and offshore environments throughout the nation in

order to capture information about various marine species. These networks are composed of submerged, omnidirectional receivers strategically positioned to monitor the surroundings for unique transmitter signals and record the time, date, and identity of tagged individuals that enter the unit's range (Lacroix and Voegeli, 2000; Heupel et al., 2006). The collaborative [Florida Atlantic Coast Telemetry \(FACT\) Network](#), [Atlantic Cooperative Telemetry \(ACT\) Network](#), and [Integrated Track of Aquatic Animals in the Gulf of Mexico \(iTAG\)](#) arrays cover most of Florida's inshore waters, comprise nearly 2,000 receivers along the east coast of the United States, and currently track approximately 85 different species (FWCC, 2019).

*Acoustic Telemetry of *M. Cephalus**

This study spanned two spawning seasons, from 2017-2018 and 2018-2019. From October-December in 2017 and 2018, 32 sexually mature (individuals may vary, but generally, individuals measuring >30 cm SL are considered sexually mature; Greeley et al., 1987; McDonough, 2003; Bester, 2014) striped mullet were captured using a twelve-foot radius cast net and surgically implanted with a V9-2L acoustic transmitter (following methods in Reyier et al., 2011). Tagging activities occurred at two estuarine backwaters; the Banana River (comprised of the Upper Banana River and Integrate-Transfer-Launch (ITL) Impoundments) and Banana Creek, with 16 fish tagged in each region (Figure 3). These sites were selected due to the high density of acoustic receivers deployed in these areas (Figure 4), providing for more fine scale movement data, and because the locations capture the longest potential migratory routes striped mullet could take to reach their ocean spawning grounds. There is also a high abundance of sexually mature mullet in these areas, ensuring relative ease of capture and adequate sample size for statistical analyses (Reyier, Pers. Comm.).

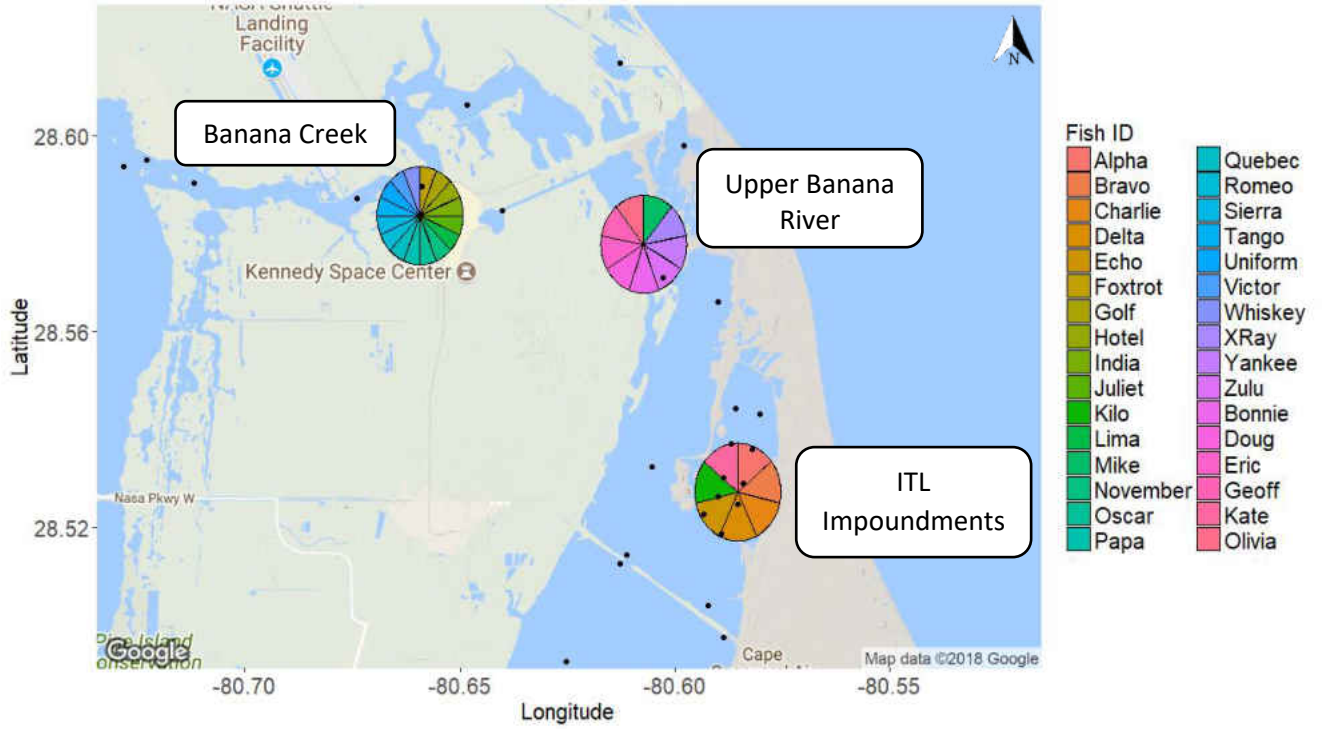


Figure 3: Pie charts represent the capture, tagging, and release locations of fish on Kennedy Space Center property, including the distribution of fish caught at each site. Nearby acoustic receivers are also marked with black dots.

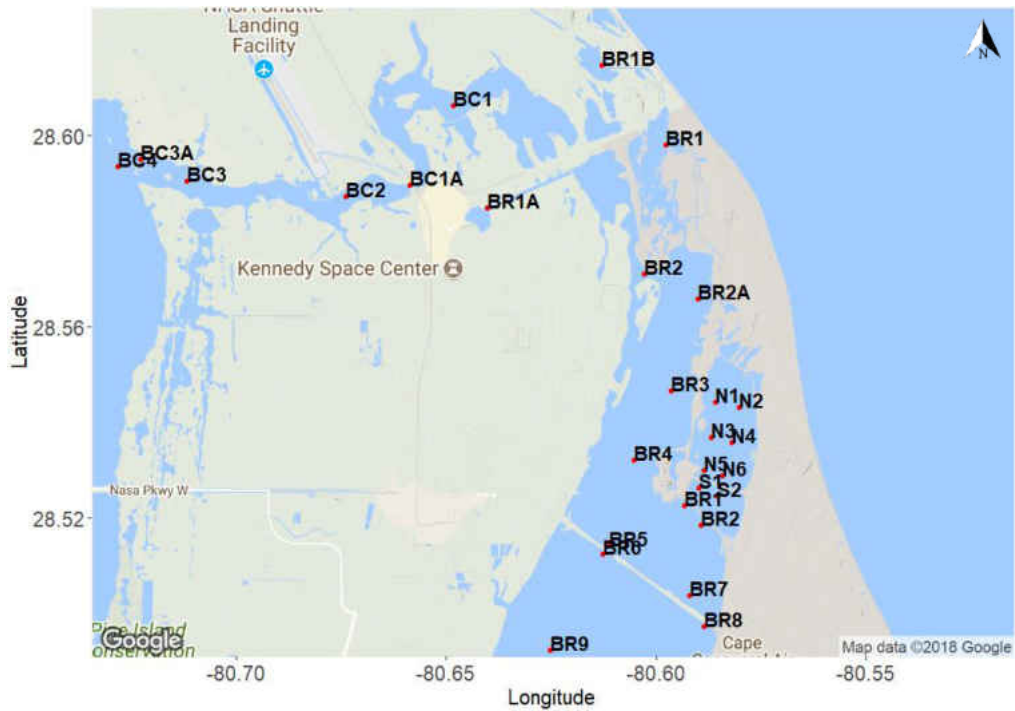


Figure 4: Acoustic receivers located on Kennedy Space Center property.

Mortality Event

On August 19, 2018, a massive fish mortality event occurred in the ITL impoundments due to a prolonged brown tide event, high temperatures, and resulting hypoxia. This event lasted approximately two weeks and caused dissolved oxygen levels to plummet to less than ~ 1.0 mg/L (Baker, Pers. Comm.). In order to prevent mortality-related tag loss, capture effort was concentrated outside of the ITL impoundments, with all but one fish caught in the Banana River region captured, tagged, and released in the Upper Banana River and adjacent locations.

Fish Measurement and Surgical Procedures

After each fish was captured, it was transferred to a 150-L tank and sedated using a 75 mg/L tricaine methanesulfonate water bath (MS-222, Western Chemical, Inc.; per American Fisheries Society [AFS] 2014). Once Stage IV anesthesia was reached (characterized by a total loss of equilibrium, slowed respiration, and a lack of response to stimuli), individuals were transferred to a wooden surgery board for acoustic tag implantation. Five to seven scales were removed and a 15-mm incision made parallel to the ventral midline, two to three centimeters anterior to the anus. A V9-2L acoustic transmitter (2.9 g weight in water, projected battery life of 685 days) was inserted into the peritoneal cavity and the incision closed with two to three absorbable sutures and Vetbond cyanoacrylate tissue adhesive (3M Corporation; VEMCO, 2019). The standard for internal tagging is for the device not to surpass 2% of the body weight of the fish, which was followed in all circumstances. In order to permanently identify fish and to potentially recover them if caught by fishermen, a dart tag was subcutaneously inserted near the base of the dorsal fin. Following internal and external tagging, fish were transferred into a recovery tank filled with fresh seawater to achieve equilibrium and normal swimming behavior (typically occurring in 10-15 minutes). Standardized biometric data, including fork length, standard length, total length, mass,

and weather conditions were also recorded before each individual was released near the capture location. Approximately 200 VEMCO VR-2W autonomous passive acoustic receivers, components of the FACT Network, have been deployed at strategic chokepoints throughout the Indian River Lagoon and nearshore waters (Figure 5). These receivers record the time and GPS coordinates of each fish as it enters receiver range, enabling the recreation of migratory tracks from staging sites in the estuaries to nearshore waters.

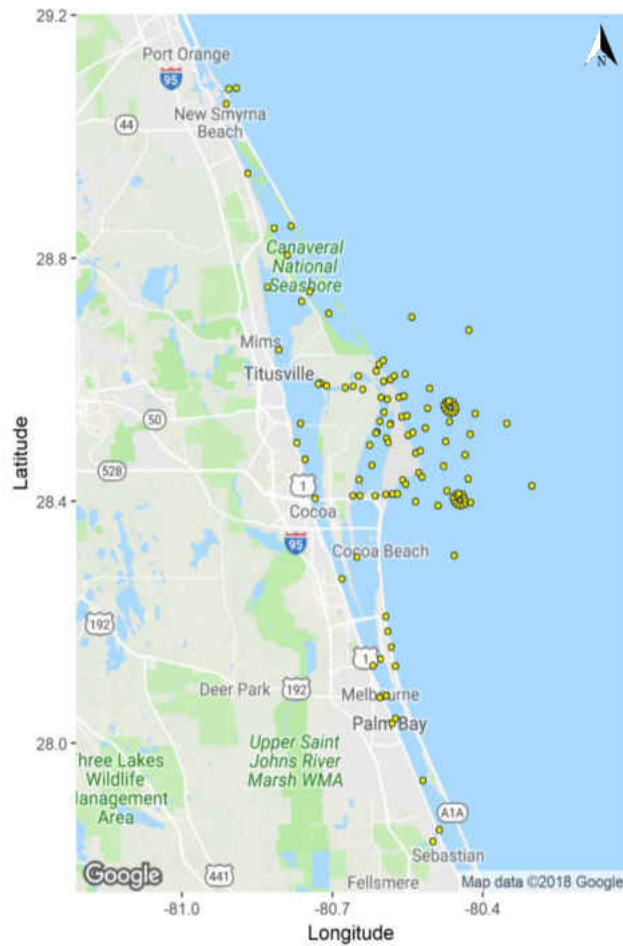


Figure 5: The KSC portion of the Florida Atlantic Coast Telemetry receiver array, with yellow dots signifying individual receivers.

Inherent Tagging Biases

Surgical procedures required for tag implantations can be stressful for any organism (Jepsen et al., 2002; Lee et al., 2013). If the health of the animal is negatively impacted by the procedure, its behavior may also be affected, leading to concerns regarding data veracity (Wagner and Cooke, 2005). This is especially problematic as acoustic telemetry studies are often operating under the assumption that the behavior of tagged individuals represent untagged members of the same species (Hondorp et al., 2015). However, years of experimentation have contributed to a now streamlined procedure that puts the least amount of stress possible on the tagging subject (Brown et al., 2011; Robillard et al., 2015). In addition, several studies report that internal tagging produced little to no adverse physical or behavioral responses in various species, for example, Chinook salmon (*Oncorhynchus tshawytscha*), Atlantic cod (*Gadus morhua*), and lake sturgeon (*Acipenser fulvescens*) (Adams et al., 1998; Cote et al., 1999; Hondorp et al., 2015). Nonetheless, in order to minimize any potential tagging effects on the fish's behavior, fish movement from release up to 48 hours after tagging were removed from all analyses.

Another constraint of passive acoustic telemetry is the detection range of the underwater receivers. The focus of this particular study is to evaluate migration patterns of a relatively small estuarine dependent fish. Fortuitously, the FACT Network strategically placed receivers at bottlenecks on Kennedy Space Center property and throughout the Indian River Lagoon. This approach, often referred to as acoustic curtains or gates, is designed to detect the passage of tagged animals as they enter or exit a moderately confined body of water, or as they progress in either direction along a coastline (Heupel and Heuter, 2001; Pincock and Johnston, 2012; Steckenreuter et al., 2016; Kraus et al., 2018). Based on the life history of the target species, individual mullet should pass through at least one of these gates on their migratory journey. This will allow for the assessment of their migratory routes (length, duration, etc.) from their staging sites, through the lagoon, and through inlets to the ocean to

spawn. Range tests were conducted in order to gauge the detection efficiency of the receivers, which is defined as, “the percentage of tagged fish that will be detected assuming a uniform distribution of position and depth of passage and taking into account all anticipated noise and signal propagation conditions” (Pincock and Johnston, 2012). In order to test this in a representative environment, six VEMCO® V16-4H acoustic tags were placed in ascending 100 m intervals away from receivers in the ITL impoundments. Receivers were able to detect the tags as far as 600 m. The tags used for this research (VEMCO V9-2L) have a smaller power output than the V16 (146 dB vs. 152 dB), so the detection radius will be respectively smaller, yielding a conservative detection range of approximately 200 m (Figure 6) (VEMCO, 2019).

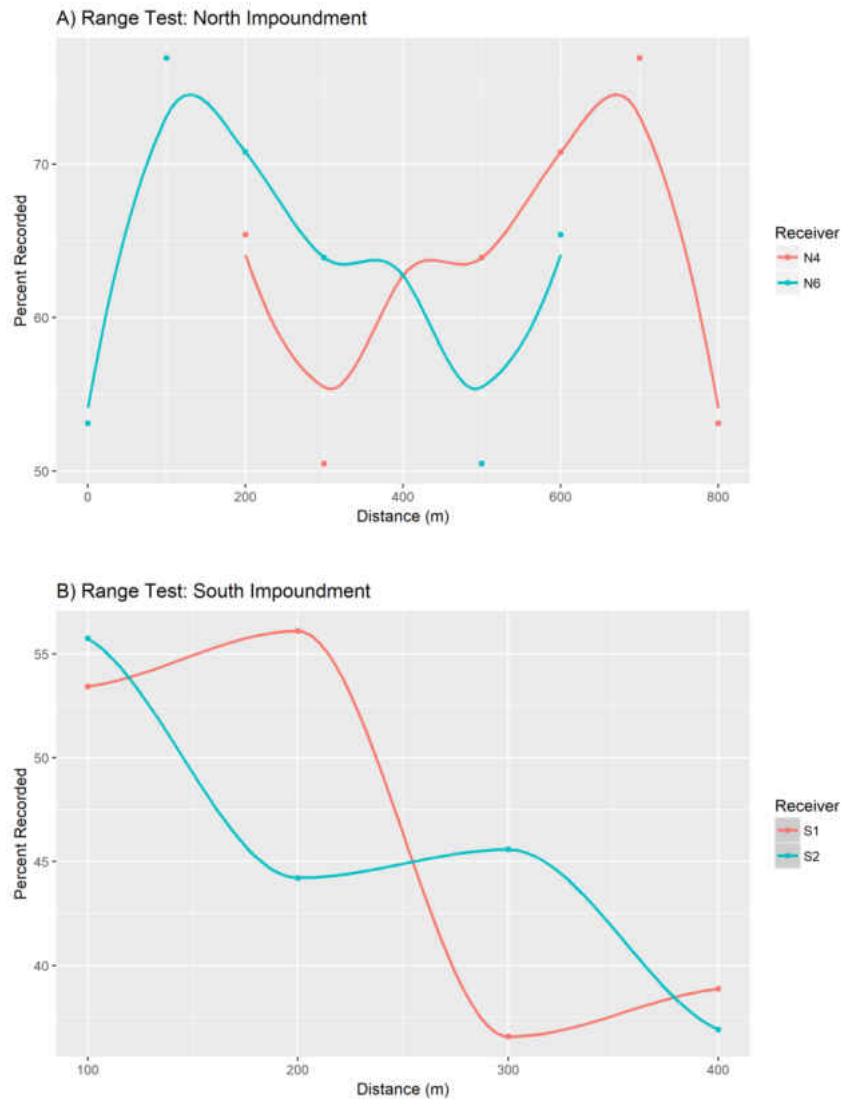


Figure 6: Range test results for the (A) ITL North Impoundment and (B) South Impoundment showing the percentage of detections registered at increasing 100-meter intervals.

Due to the arrangement of receivers within Kennedy Space Center, there were a number of receivers that were in close proximity to where the fish were captured. As such, when the fish were released after tagging, these receivers detected them almost immediately. This could lead to these particular locations being misconstrued as more important to the fishes' migratory movements than they truly are. This was managed in two ways. First, removing the forty-eight hours of fish movement immediately after capture from analyses, should eliminate any tagging effects that may cause the fish

deviate from normal behavior (e.g. not travelling in a normal manner). Second, residency time was evaluated at each receiver. It is important to distinguish this from overall detections because detections can be garnered from fish passing back and forth between receivers as well as from remaining near a single receiver for an extended period of time. This can be parsed using residency time, with longer residency time indicating the animal was spending a majority of its time in a particular area rather than just traveling through.

The fate of tagged fish is often one of the greatest uncertainties in acoustic telemetry studies (Thorstad et al., 2013; Halfyard et al., 2017). After tagged animals are released, they are subject to mortality by the surgical procedures necessary to implant the tag, predation due to tagging effects or through natural interactions, and other confounding scenarios. If or once these events occur, it can be difficult, at least for a time, to distinguish signals from live tagged fish as opposed to dead fish that are drifting with water flow, settled on the bottom during decomposition, or tags that are still communicating from inside a predator that consumed the original fish and its tag (Havn et al., 2017). In order to differentiate these occurrences, one can look at the rate of movement of the organism housing the tag. Striped mullet can travel anywhere from 0-9 km/day on average, with the rate varying seasonally (Bacheler et al., 2005). The mean cruising speed of mullet during migration is approximately seven body lengths per second (Peterson, 1976). Tags consistently detected (that is, detections corresponding with the minimum lag time of the tag) on the same receiver for an extended amount of time (>1 month) were considered to be a mortality event, whereas tags detected on multiple receivers in a rapid fashion were categorized as a predation event. Therefore it would be possible to eliminate the movement of these fish in each respective case, although none of the fish that exhibited movement beyond the 48-hour tagging effects filter met these mortality event filter criteria.

Movement Models and Simulations

Individual detections and path, detection events, and residency time were computed using the *glatos* package (Holbrook et al., 2018) in R (version 3.4.4). Detection events were only based on location changes, or when a fish move from one receiver to another, as this study is examining the possible broad-scale migratory patterns of striped mullet rather than the species' fine-scale habitat use.

Residency time was determined by combining the elapsed time in days (both individually and using the entire data set), produced by the *detection_events* function, for each fish at each receiver (Holbrook et al., 2018). These calculations were then input into the *pacter* and *VTrack* packages to visualize individual movement trends (Cagua, 2015; Campbell et al., 2012). More precise movements of tagged fish were calculated through the observation-weighted center of activity technique, which incorporates the mean of receiver locations weighted by the number of detections (Simpfendorfer et al., 2002; Farmer et al., 2013; Winton et al., 2018).

Location data were analyzed using the *BBMM*, *adehabitatHR*, and *adehabitatLT* packages in R to ultimately quantify movement trends for the entire data set (Calenge, 2006; Nielson et al., 2013).

Random walk, Brownian bridge, and biased random bridge movement models were attempted for the data set as a whole. Due to computing constraints, simulations ($n = 10$) of motion including random walk, Brownian bridge, and biased random bridge were compared to three case studies of empirical data to determine if the observed fish motion followed any of these patterns.

Random Walk Movement Model

The simplest random walk theory assumes the direction of movement is entirely independent of the previous directions moved; it is only affected by the location occupied during the immediately preceding interval (Codling, Plank, and Benhamou, 2008). This is most useful when there is little

information regarding the species' movement patterns (Horne et al., 2007). This model operates under the expectation that constant and continuous monitoring of an animal's path is not possible, but discrete points exist along that path (Horne et al., 2007). The subject's n discrete locations along its trajectory are assumed to be known and are used to approximate the animal's frequency of use of an area (Horne et al., 2007).

Brownian Bridge Movement Model

Brownian motion is the continuous counterpart to random walk (Kac, 1947; Horne et al., 2007). Contingent on the subject's starting and ending locations, Brownian bridge movement models are the stochastic process produced when Brownian motion is applied to a conditional random walk, allowing for the prediction of the trajectory between each sequential pair of locations (Horne et al., 2007). The Brownian bridge probability density associated with each pair of known consecutive coordinates along the mobile object's trajectory is an approximation of the time spent in an area during the time lag between those locations (Horne et al., 2007; Nielson et al., 2013). This method has the advantage of quantifying an animal's frequency of use based on a full trajectory as opposed to discrete positions, but still incorporates uniform movement (Kranstauber et al., 2012).

Biased Random Bridge Movement Model

Biased random bridge models combine the theoretical strength (constantly diffusive movements) of Brownian bridges with home range and habitat preferences that may affect space use patterns (Benhamou, 2011; Davis et al., 2017). Using pairs of consecutive locations along the animal's trajectory, the subject's position is interpolated between them through random walks. The activity time

between coordinates is then redistributed along the trajectory sections (Behamou and Riotte-Lambert, 2012; Vivancos and Closs, 2015). Due to the combination of its advective and diffusive properties, this method is particularly useful in evaluating habitat use during migration events, as increased advection produces more elongated, thinner bridges (Benhamou, 2011; Ferreira et al., 2019).

Kernel Density Estimation (KDEs)

Although normally used in the assessment of home range (Worton, 1989), kernel density estimations (KDEs) were performed on the Banana Creek and ITL impoundments data, as there is some evidence a number of fish remained near their capture site. Using the *adehabitatHR* package, the *ad hoc* method was used to estimate the bandwidth parameter (h) to generate both 50% and 95% KDEs for each region (specific h values are included in the results section). This method assumes a bivariate normal kernel and is referred to as a data-driven selector, as different smoothing parameters are produced based on the data input into the model (Calenge, 2006; Eidous et al., 2010). A 50% KDE represents the animals' core use area while a 95% KDE signifies overall home range (Kitts-Morgan et al., 2015; Spiegel and O'Farrell, 2019). The 95% KDEs were then compiled to construct maps overlaid with networks developed from detection data (discussed in more detail below), highlighting migration routes and conservation areas of interest, which can be employed in management strategies for this species (Shimazaki et al., 2004; Evans et al., 2016). In order to examine other dimensions such as seasonal or individual-based movements that may better inform management, the KDE method was visually compared to network analyses that incorporated corresponding fish case studies.

Network-Based Analyses

Due to the intricacy and broad area encompassed by these migratory routes, network-based analyses were performed on the detection data to assess movement patterns and route-specific connectivity elements. A subset of graph theory, network analysis works off the concept that intricate systems can be decomposed into relatively simple topological systems comprised of nodes and edges; represented by fixed, physical locations (i.e. nodes) and the frequency and directionality of connections between them (i.e. directed edges; Salanick, 1995; Rayfield et al., 2011; Jacoby et al., 2012). Node-based centrality metrics, ranging from relatively simple to complex, can be evaluated to determine the relative importance of individual locations or patches to the entire network structure and are dependent on the relative magnitude of interaction one node has with another (Lerman et al., 2010; Rayfield et al., 2011). Node degree can be enumerated as the number of edges connecting nodes while the frequency of individuals moving from one location to another produce weighted edges (Jacoby et al., 2012). This can be further partitioned into indegree and outdegree to identify where fish are entering and exiting specific sites as well as passages to/through areas of conservation interest. Eigenvector centrality measures the influence and accessibility of a location by comparing the centrality of a specific node to the centrality of its neighbors (Ghasemi et. al, 2014). Betweenness centrality focuses on the number of routes that pass through a specific node via the shortest path length. High betweenness centrality may suggest particular areas contain vital resources or refuge for migratory species, thereby encouraging aggregation (Jacoby et al., 2012). Special consideration will be taken when evaluating betweenness for receivers at chokepoint locations in order to prevent inflation of values. Not only is this method highly efficient at describing connectivity across broad spatial scales, but it also allows for the integration of species-specific biological characteristics, such as dispersal ability (Rayfield et al., 2011). The above dimensions are vital to assess the impact the landscape has on animal movements and were evaluated using the igraph, network, and sna packages in R (Csardi and Nepusz, 2006; Butts, 2015; Butts, 2016).

Network topology was visualized using the Fruchterman-Reingold (FR) algorithm (Fruchterman and Reingold, 1991). The FR algorithm used a force directed layout algorithm to generate a network, whereby connections between nodes (i.e. fish movement between acoustic receivers) are treated as springs, with the amount of tension on each spring related to the position of nodes (i.e. acoustic receivers) within the network (Fruchterman and Reingold, 1991). Receiver nodes are colored to indicate rough geographic region and the size of the nodes corresponds to the number of detections garnered at that location. In this network, edges are defined as fish movement among the receivers. In order to isolate specific paths, a simplified graph was produced; all edges with the same two endpoints are summed and combined to create a single, weighted edge. The edges are also directed, signified by arrows, showing the direction the fish is traveling. Additional FR networks were generated with the same general characteristics, but with a node size representing the degree and betweenness and eigenvector centrality of each node. Total degree (further partitioned into indegree and outdegree) as well as betweenness and eigenvector centrality were parsed for each receiver. Movement networks for fishes Delta, Kilo, and November, as each demonstrated a unique movement strategy, were then overlaid onto a map to provide geographic context.

Results

Acoustic Telemetry of *M. Cephalus*

Between November 2017 – November 2018, 32 fish were tagged, 16 each at Banana Creek and Banana River (Upper Banana River and ITL Impoundments) sites (Table 1). Downloads from 34 acoustic receivers have since produced approximately 65,000 detections from eighteen fish (Table 2). The first forty-eight hours of movement post-tagging was then removed, resulting in 58,643 detections. These detects were filtered for false detections using a time threshold of 3600 seconds, as based on a recommendation from the tag manufacturer (VEMCO), incorporating an average tag delay of 120

seconds (Pincock, 2012). Of these 58,643 detections, 402 (0.69%) were indicated to be potentially false and removed. This smaller subset (58,241) of detections was used for the entirety of data analysis. Total detections were pared down to 8,454 detection events, which details the time at which a fish was first and last detected at a particular receiver. The residency time, determined by combining detection event duration, was also assessed for each fish at each receiver.

Table 1: Biometric data, including standard (SL), fork (FL), and total length (TL), collected from all tagged fish.

Fish ID	SL (cm)	FL (cm)	TL (cm)	Region	Capture Date
Alpha	29	33.5	37	ITL Impoundments	12/3/2017
Bravo	29.5	34	37.5	ITL Impoundments	12/3/2017
Charlie	30	34.5	38.5	ITL Impoundments	12/3/2017
Delta	38.5	42	47	ITL Impoundments	12/3/2017
Echo	36	39.5	44	ITL Impoundments	12/3/2017
Foxtrot	30.5	35	38	Banana Creek	11/17/2017
Golf	33	37.5	41.5	Banana Creek	11/17/2017
Hotel	32	36	39	Banana Creek	11/17/2017
India	32	38	41.5	Banana Creek	11/17/2017
Juliet	30	33.5	36	Banana Creek	11/17/2017
Kilo	39	43	47.5	ITL Impoundments	12/3/2017
Lima	33	37.5	41	Banana Creek	12/3/2017
Mike	29.5	32.5	36	Banana River	12/3/2017
November	31	35.5	38.5	Banana Creek	12/3/2017
Oscar	30.5	36	39	Banana Creek	10/5/2018
Papa	30	34.5	37.5	Banana Creek	10/5/2018
Quebec	30	33.5	36.5	Banana Creek	10/5/2018
Romeo	31.5	36	40	Banana Creek	10/5/2018
Sierra	30	34	37.5	Banana Creek	10/5/2018
Tango	31	35	39	Banana Creek	10/12/2018
Uniform	30	32	36	Banana Creek	10/12/2018
Victor	29	31	35	Banana Creek	10/12/2018
Whiskey	40	43	48	Banana Creek	10/12/2018
XRay	29	32.5	34	Banana River	10/12/2018
Yankee	29	32.5	36	Banana River	10/27/2018
Zulu	29.5	32	34	Banana River	10/27/2018
Bonnie	29	32	36.5	Banana River	10/29/2018
Doug	29.5	33	36.5	Banana River	10/29/2018
Eric	30.5	33	36	Banana River	11/2/2018
Geoff	30	33.5	36	Banana River	11/2/2018
Kate	29.5	34	36.5	ITL Impoundments	11/2/2018
Olivia	29	31.5	35.5	Banana River	11/9/2018
Mean±SD	31.3±3.0	35.0±3.2	38.5±3.7		

Table 2: The total number of fish detections, total residency time of all fish at each receiver, and total number of fish detected per receiver.

Region	Station	Total Number of Detects	Residency Time (Days)	Number of Unique Fish Detected
Banana River	BR1	16	0.6	1
	BR1B	17316	105.1	2
	BR2	1	<0.1	1
	BR4	24	0.2	1
	BR5	4	<0.1	1
	BR6	2	<0.1	1
	BR7	8	0.2	1
	BR8	7	<0.1	1
	BR12	10	0.3	1
	Mean±S.D.	1932.0±5769.0	11.8±35.0	1.1±0.3
Total	17388	106.3	5	
Banana Creek	BC1	649	10.8	2
	BC1A	1712	9.0	3
	BC2	3041	317.8	7
	BC3	146	4.0	5
	BC3A	296	0.8	4
	BC4	166	8.8	3
	Mean±S.D.	1001.7±1159.0	58.2±127.1	4.0±1.8
Total	6010	351.1	8	
ITL Impoundments	ITL_N1	244	0.6	2
	ITL_N2	552	1.5	2
	ITL_N3	564	1.1	1
	ITL_N4	2368	99.8	2
	ITL_N5	1360	1.9	2
	ITL_N6	3627	37.0	2
	ITL_S1	17576	341.1	5
	ITL_S2	8260	28.4	5
	ITL_BR1	4	<0.1	1
	ITL_BR2	37	<0.1	1
	Mean±S.D.	3459.2±5565.6	51.1±106.6	2.3±1.5
Total	34592	511.3	6	
Indian River	IR4	6	0.5	1
	IR6	110	2.3	1
	IR9	22	1.9	1
	IR10	5	0.3	1
	IR13	12	<0.1	1
	IR14	412	21.5	1
	Mean±S.D.	94.5±160.6	4.4±8.4	1
Total	567	26.4	2	
Sebastian Inlet	SINJ	16	<0.1	1
	SISO	24	0.6	1
	SIWP	46	0.2	1
	Mean±S.D.	28.7±15.5	0.3±0.3	1
Total	86	0.80	1	

Detections and Residency Time

For the duration of this study, of the 32 fish that were tagged, 18 fish were detected on the acoustic array. Fish India and Lima were eliminated due to tagging effects (Figure 7). The mean (\pm s.d.) time that fish were detected within the array was $\sim 38 \pm 90$ days. Fish Kilo had the longest, most consistent time at liberty within the system at 444 days (Figure 7).

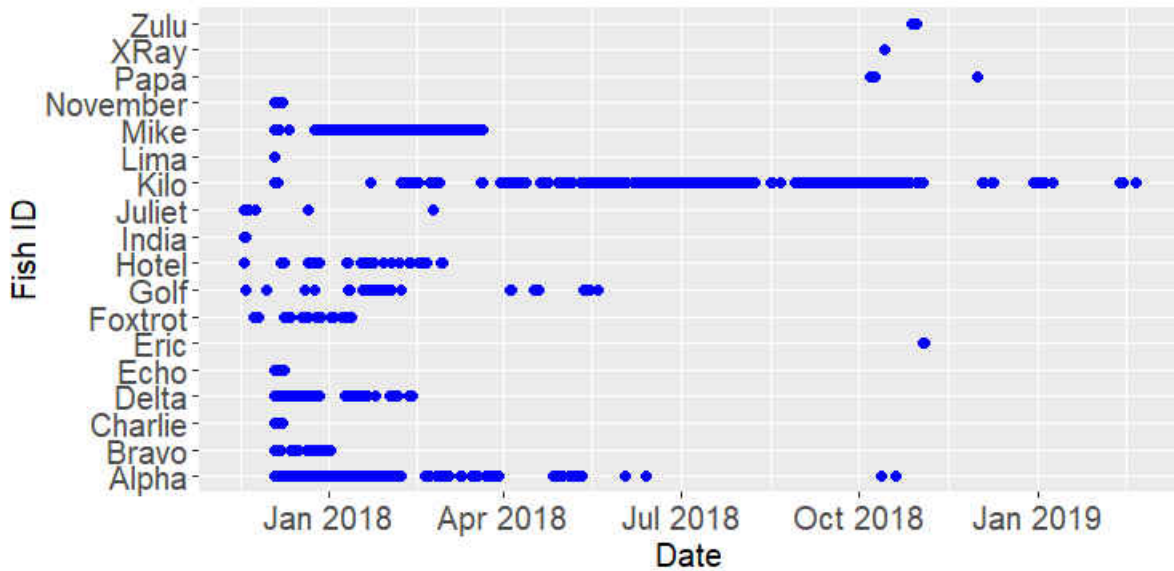


Figure 7: Individual fish time at liberty. Blue dots represent individual detections while gaps in between dots indicate that fish were not detected by a receiver during that period.

The number of detections and combined residency time of all fish per receiver are detailed in Table 2 and Figures 8 and 9. The ITL impoundments encompass a small area with relatively restricted entrance and egress points, within which is contained a fairly dense array of acoustic receivers; 10 receivers were placed at intervals of 183 m to support a concurrent red drum movement study. Due to these circumstances, this area accumulated nearly half of all total detections (25,836/53,380). The highest number of detections overall was seen at ITL_S1 with nearly 18,000 detections, also showing one of the highest combined residency times at 341 days. In comparison, ITL_S2 also had a large number of detections (8,260), but the combined residency time was only ~ 28 days. Both of these

receivers detected 5 unique fish. Outside of the ITL impoundments, BC2 had one of the highest numbers of detections at 3,000, with a combined residency time of 320 days. It also detected the highest number of unique fish (7; Table 2).

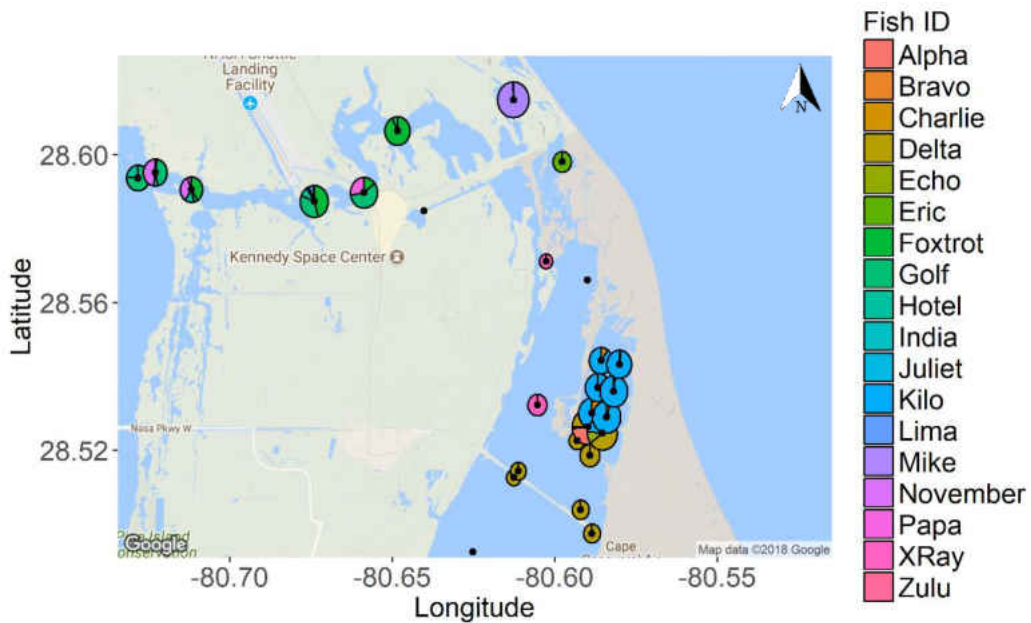


Figure 8: Number of detections of individual fish on Kennedy Space Center property. Pie chart color represents each unique fish ID and pie chart size is proportional to the overall number of detections at each receiver.

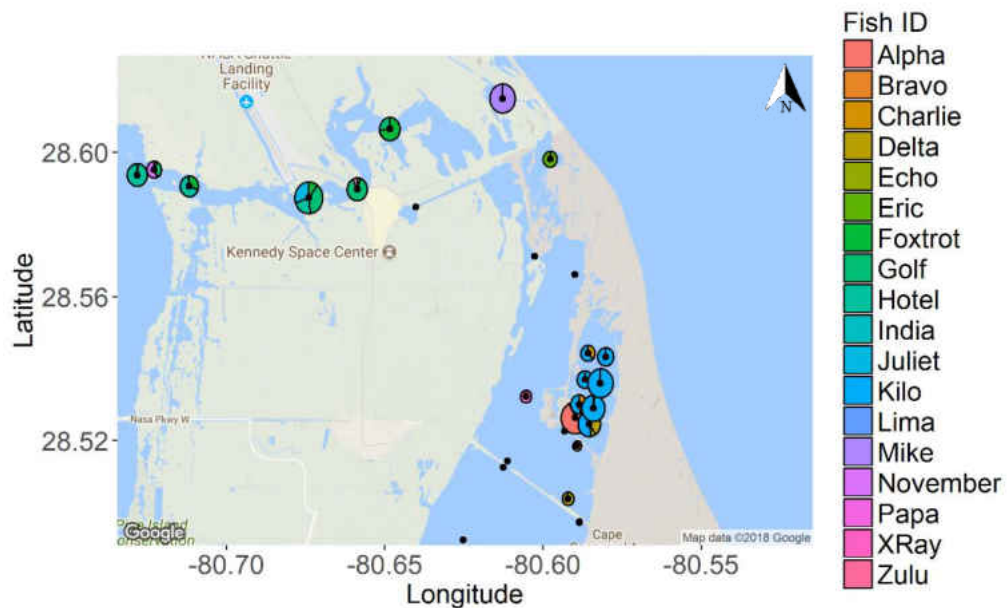


Figure 9: Residency time of individual fish on Kennedy Space Center property. Pie chart color represents each unique fish ID and pie chart size is proportional to the overall number of detections at each receiver.

Movement Trends

The paths of each individual fish were binned into thirty-minute intervals and linearly interpolated between receivers located within Kennedy Space Center as well as throughout the IRL (Figures 10 and 11). Three different categories of movement were exhibited by tagged fish, examples of which are illustrated below. One fish (Delta) showed possible migratory movement, from its capture site in the ITL impoundments to a location 80 kilometers south, exiting to the Atlantic Ocean through Sebastian Inlet. A second fish (November) also demonstrated potential migratory movement by exiting Banana Creek to the west and traveling south through the Indian River Lagoon. Finally, fish Kilo remained within the ITL Impoundments throughout the study period.

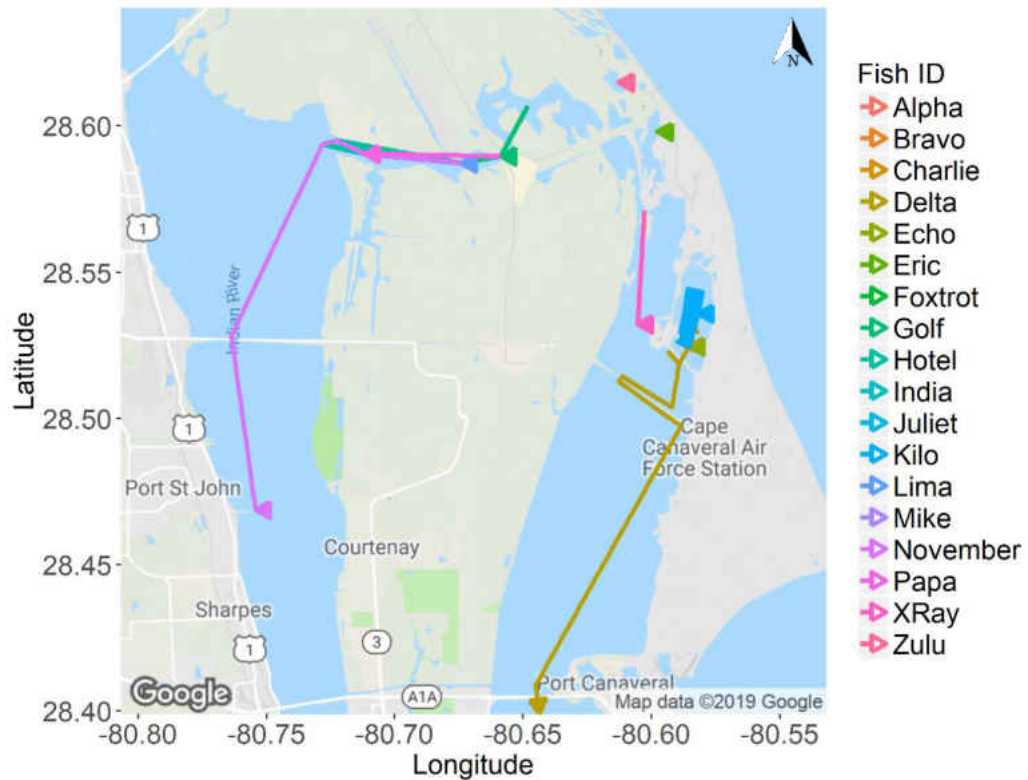


Figure 10: Individual fish path between receivers located on Kennedy Space Center property. Path color represents unique fish ID.

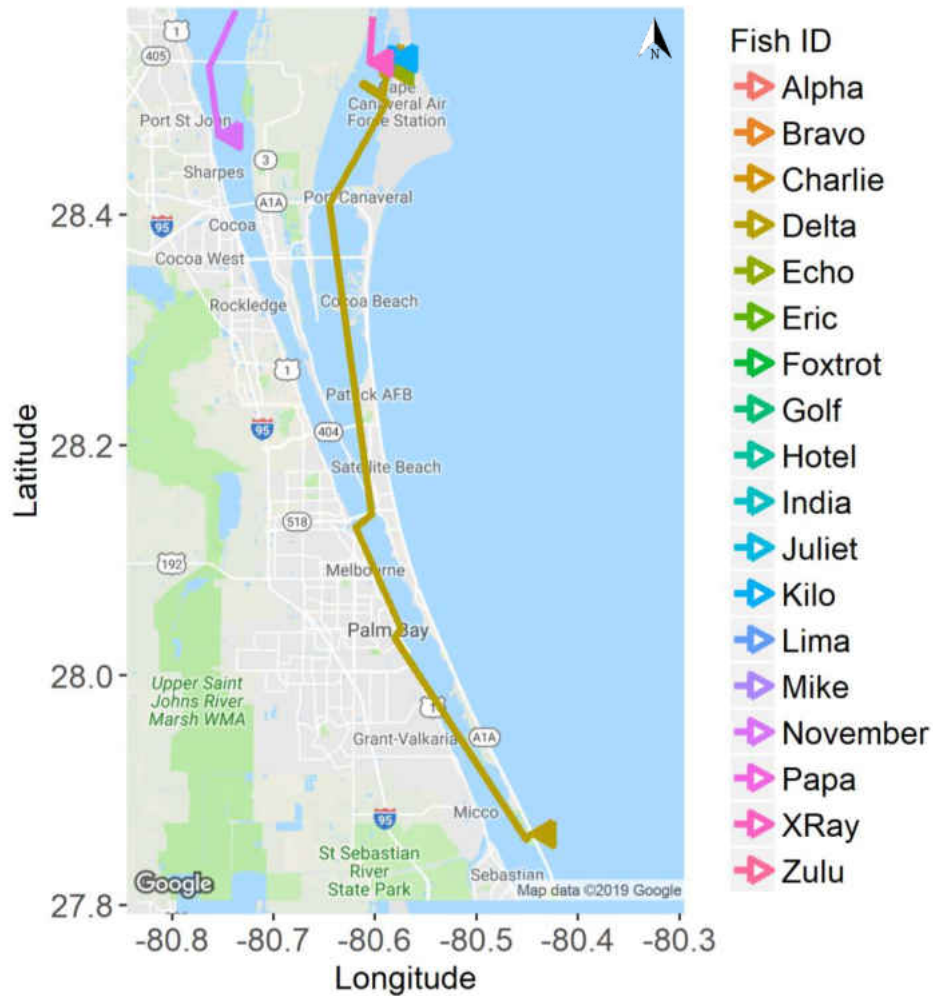


Figure 11: Individual fish path between receivers located on in the Indian River Lagoon. Path color represents unique fish ID.

Short term centers of activity were first evaluated for Kennedy Space Center and then scaled down to the ITL impoundments and Banana Creek areas. As the observation-weighted method was utilized, the centers of activity radiate outward from the receivers with the highest number of detections; ITL_S1, ITL_S2, and BC2 (Figure 12). With the ITL impoundments garnering more than half of the total detections, the centers of activity were then evaluated for each region separately to parse finer scale trends. At a finer scale in the ITL impoundments, higher concentrations can be seen in the southern impoundment (Figure 13). The centers of activity are more clearly defined in Banana Creek, although BC2 still has the highest concentration (Figure 14).

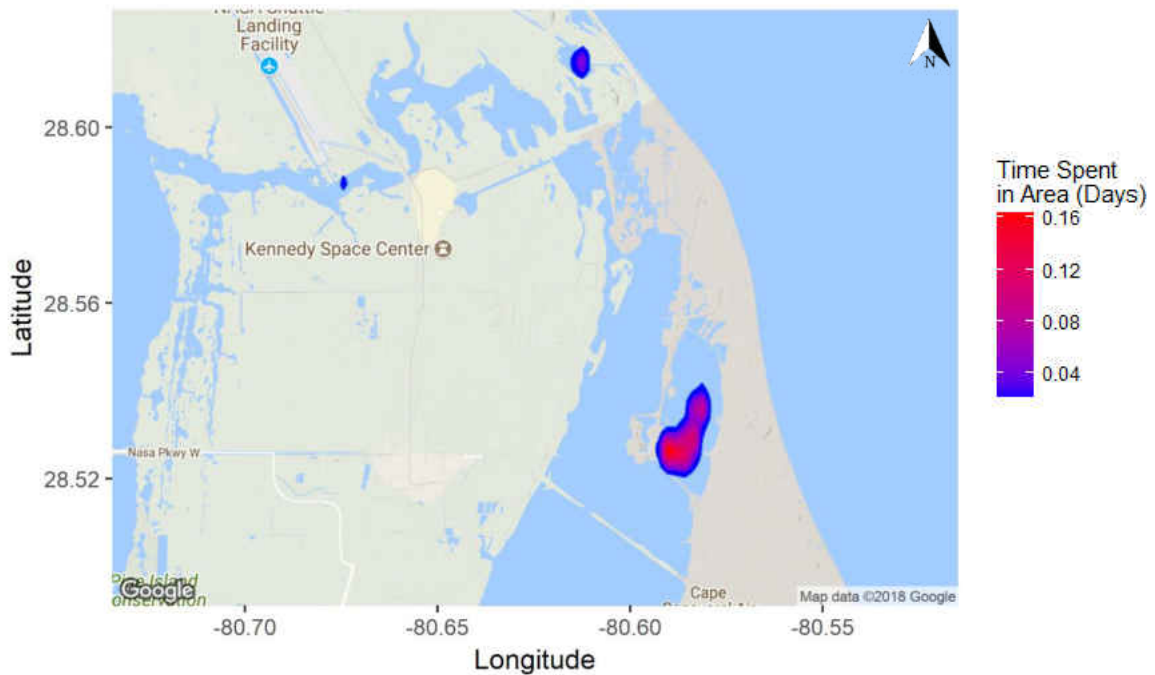


Figure 12: Estimated centers of fish activity within Kennedy Space Center property. The heat map indicates the estimated amount of time a fish spends in a location once it enters the area.

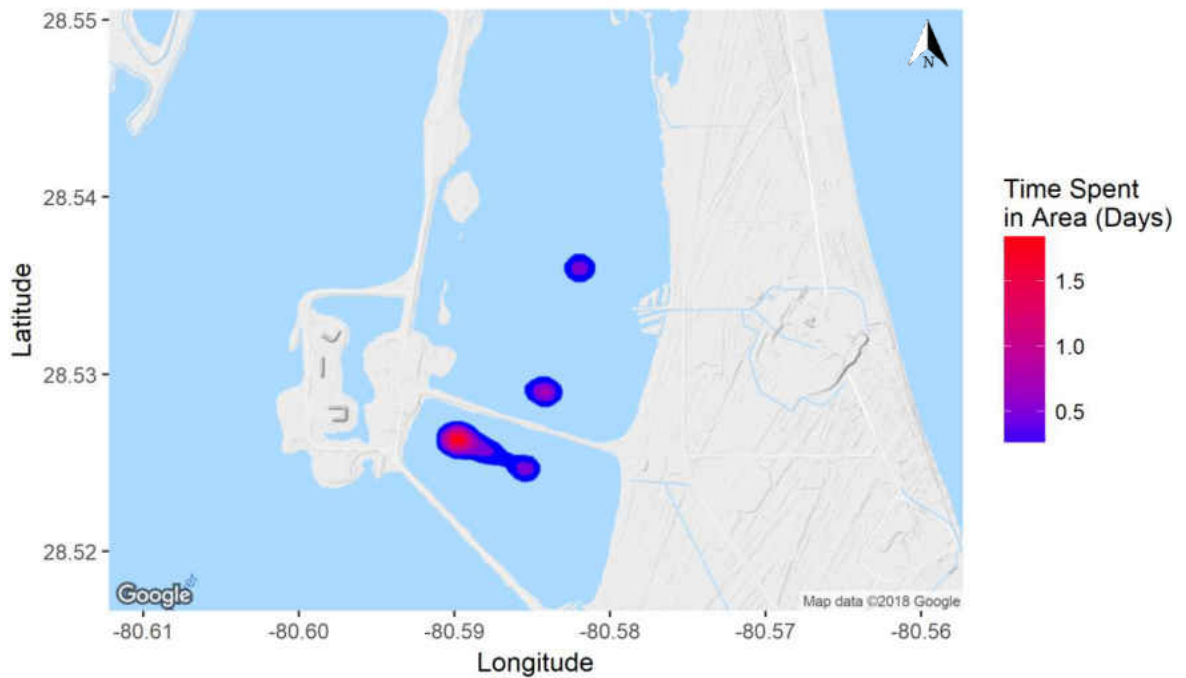


Figure 13: Estimated centers of fish activity within the ITL Impoundments. The heat map indicates the estimated amount of time a fish spends in a location once it enters the area.

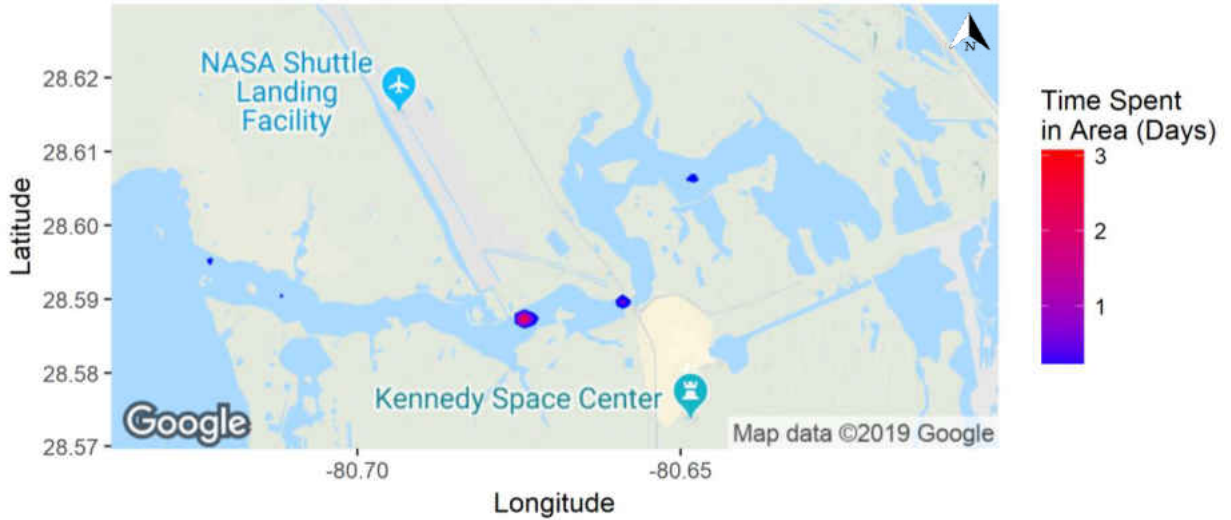


Figure 14: Estimated centers of fish activity within Banana Creek. The heat map indicates the estimated amount of time a fish spends in a location once it enters the area.

Movement Models and Simulations

Random walk, Brownian bridge, and biased random bridge movement models were attempted for the data set as a whole. When viewed across the entire study period, the probability of locating a fish in the areas produced by these models was very low and not ecologically relevant; probabilities of detection ranged from 10^{-8} to 10^{-6} (Table 3), therefore they are not graphically displayed here. The *ad hoc* method for the 50% and 95% kernel density estimations produced smoothing parameters of 504.4 and 101.5 for Banana Creek and the ITL Impoundments, respectively (Table 4). When taking scale into account, the KDE-predicted areas within the ITL impoundments were much larger than those in Banana Creek, showing a much larger home range in the ITL (Table 4, Figures 15 and 16).

Table 3: The probability of locating a fish in the given area generated by each respective model.

Method	Probability of Detection
Random Walk	4.72e-8
Brownian Bridge	6.34e-6
Biased Random Bridge	6.95e-6

Table 4: Smoothing parameters and total area for each region and corresponding %KDE.

Region	KDE	Smoothing Parameter	Total Area (hectares)
Banana Creek	50%	504.4	257.3
	95%	504.4	1670.6
ITL Impoundments	50%	101.5	18.9
	95%	101.5	109.38

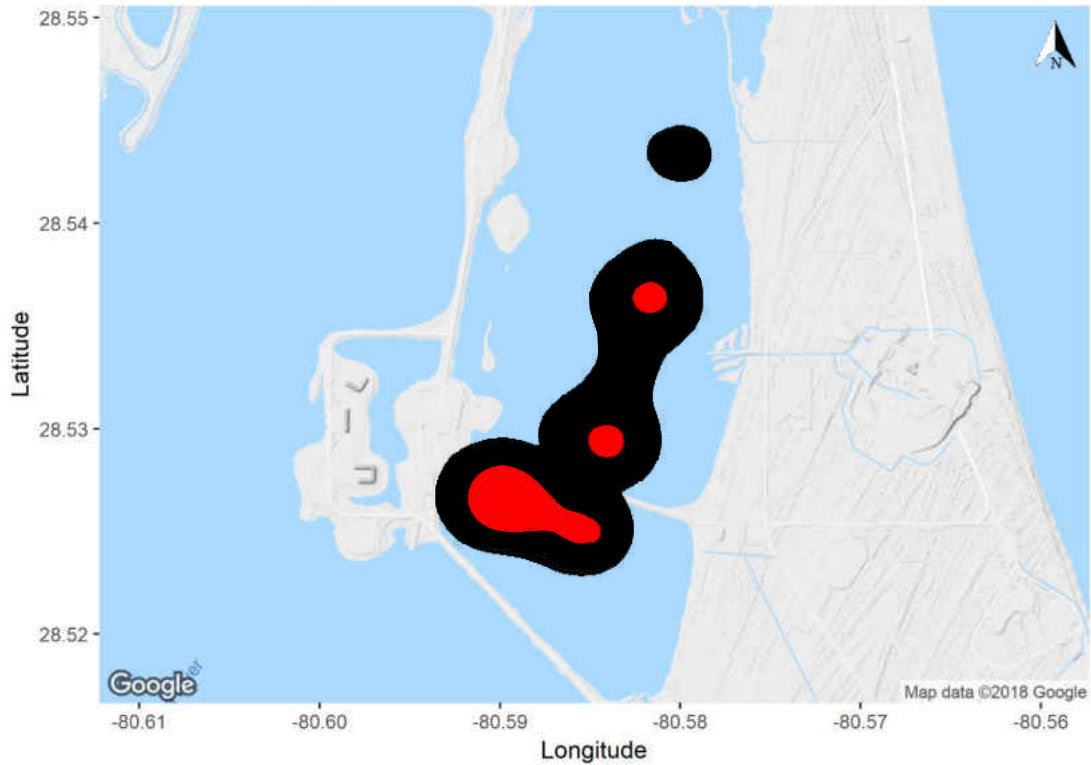


Figure 15: 95% (black) and 50% (red) kernel density estimation within the ITL impoundments.

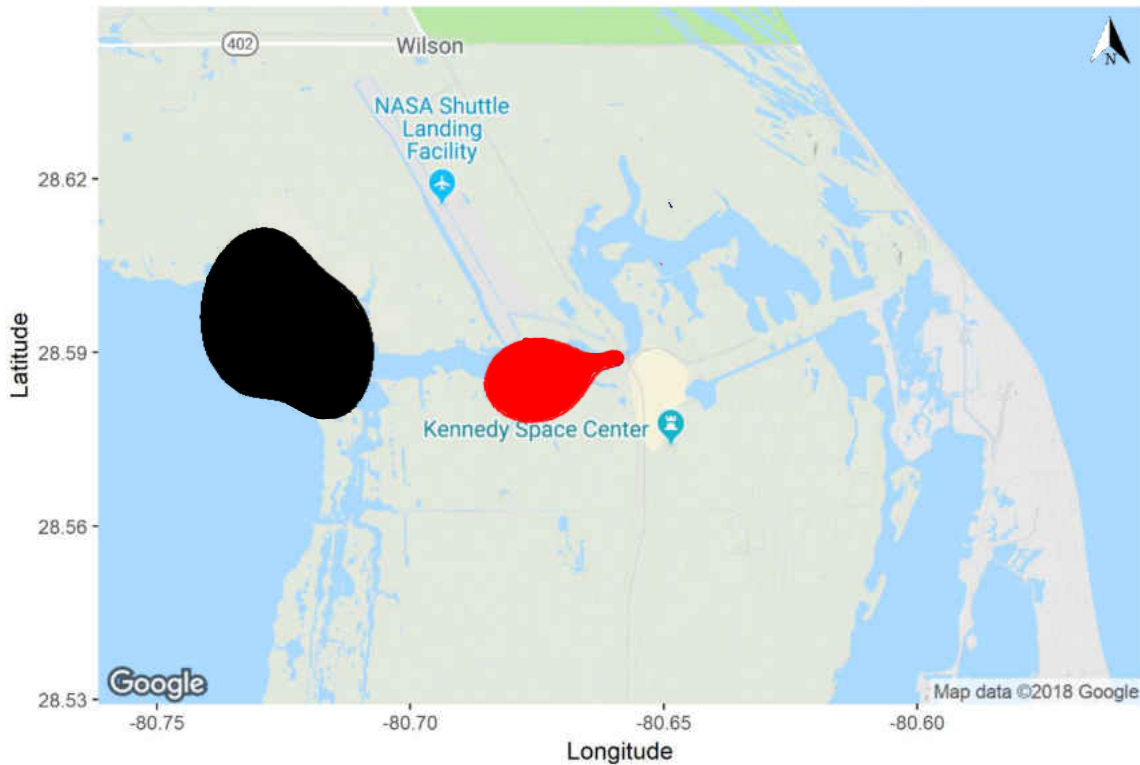


Figure 16: 95% (black) and 50% (red) kernel density estimation within the ITL impoundments.

Network-Based Analyses

A graph with a Fruchterman-Reingold (FR) layout was generated from the acoustic detection data, demonstrating that the ITL impoundments are connected to the Banana River and Indian River while Banana Creek feeds directly into Indian River. This is most likely due to the morphology of the lagoon, as fish are restricted to specific directions of movement. Paths were much more highly traveled within the ITL impoundments and Banana Creek and were accompanied by more detections at those nodes (Figures 17 and 18).

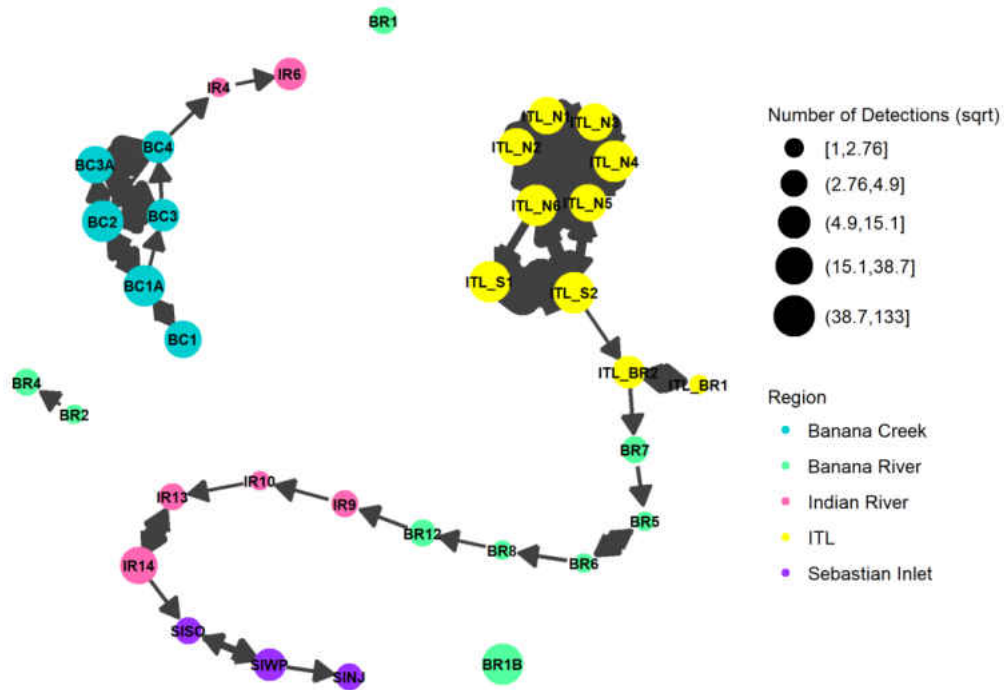


Figure 17: Fruchterman-Reingold network graph of receivers (nodes) and fish movement (edges) within the Indian River Lagoon. Node color indicates rough geographic region while node size represents the number of detections at each receiver. Edges are weighted by the number of times each path was used.

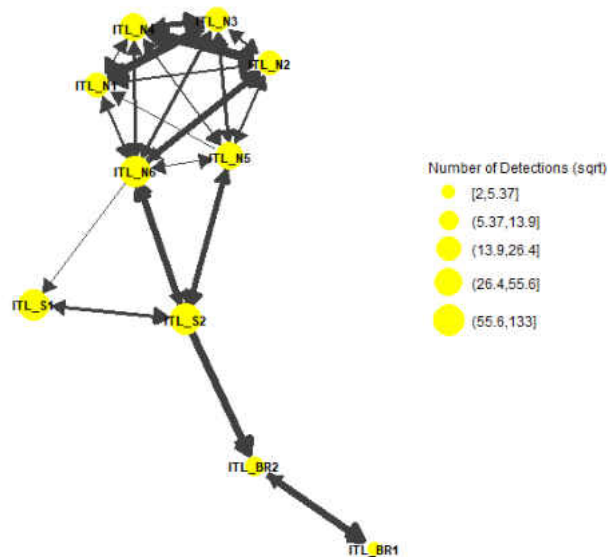


Figure 18: Fruchterman-Reingold network graph of receivers (nodes) and fish movement (edges) within the ITL Impoundments. Node size represents the number of detections at each receiver. Edges are weighted by the number of times each path was used.

Banana Creek

In Banana Creek, node degree ranged from 4-8. Receivers BC2 and BC3 had the highest total degree for the region at 8, with a value of 4 each for both indegree and outdegree (Appendix A, Table 5). Betweenness centrality ranged from 0.00-11.50, demonstrating a lack of connectedness to the other parts of the network. Receiver BC4, at the opening of Banana Creek to the Indian River, had the highest betweenness centrality for this area at 11.50 (Appendix A, Table 6). None of the receivers in Banana Creek had high eigenvector centrality values (0.00-5.86e-17), with the largest being 5.86e-17 at BC2, meaning that these locations are not influential within the network (Appendix A, Table 6).

Banana River

In Banana River, node degree ranged from 1-5. The highest total degree for the region was produced at receiver BR5, with values of 3 and 2 for indegree and outdegree, respectively (Appendix A, Table 5). Betweenness centrality ranged from 0.00 and 110.00. Receivers BR5 and BR7 are supported as valuable connections, as they each produced the highest betweenness centrality for this area at 110.00 (Appendix A, Table 6). The eigenvector centrality values were relatively low for this region, ranging from 7.54e-17 to 1.78e-2, with the largest being 1.78e-2 at BR7, again highlighting the lack of influence of this area (Appendix A, Table 6).

Indian River

In the Indian River, total degree ranged from 3-5. Both receivers IR13 and IR14 had the highest total degree at 5, but with differing values for indegree and outdegree (Appendix A, Table 5). Betweenness centrality ranged from 0.00-90.00 and eigenvector centrality ranged from 8.04e-17 to

4.97e-6. Receiver IR9 had both the highest betweenness and eigenvector centralities at 90.00 and 4.97e-6, respectively (Appendix A, Table 6). This shows that this particular receiver is influential in this region and is part of the shortest route through this body of water.

ITL Impoundments

In the ITL Impoundments, total node degree ranged from 2-15. Receiver ITL_N6 had the highest total degree for both the region and the network as a whole at 15, with values of 7 and 8 for indegree and outdegree, respectively (Appendix A, Table 5). Receiver ITL_BR2 had the highest betweenness centrality for both the area and the entire network at 116.00 while receiver ITL_N6 had the highest eigenvector centrality for the region and network at 1.00 (Appendix A, Table 6). All of these metrics illustrate that this is a highly trafficked area that plays an important role in striped mullet activity.

Sebastian Inlet

At Sebastian Inlet, total node degree ranged from 3-5. Receiver SIWP had the highest total degree at 5, with values of 2 and 3 for indegree and outdegree, respectively (Appendix A, Table 5). Betweenness centrality ranged from 0.00-38.00 and eigenvector centrality ranged from 3.51e-10 to 8.72e-9. Receiver SISO had both the highest betweenness centrality and eigenvector centrality for this area, at 38.00 and 8.72e-9, respectively (Appendix A, Table 6). This receiver resides in the area that provides the connection from the Indian River to the Atlantic Ocean.

Table 5: Total degree, indegree and outdegree of accessed receivers. Receivers with the highest total degree within each study sub-region are highlighted.

Region	Receiver	Total Degree	Indegree	Outdegree
Banana Creek	BC1	4	2	2
	BC1A	7	3	4
	BC2	8	4	4
	BC3	8	4	4
	BC3A	7	4	3
	BC4	7	3	4
Banana River	BR1	2	1	1
	BR1B	2	1	1
	BR2	1	0	1
	BR4	3	2	1
	BR5	5	3	2
	BR6	3	1	2
	BR7	4	2	2
	BR8	4	2	2
Indian River	BR12	4	2	2
	IR4	4	2	2
	IR6	3	2	1
	IR9	4	2	2
	IR10	4	2	2
	IR13	5	3	2
ITL Impoundments	IR14	5	2	3
	ITL_BR1	2	1	1
	ITL_BR2	6	3	3
	ITL_N1	11	6	5
	ITL_N2	12	6	6
	ITL_N3	12	6	6
	ITL_N4	12	6	6
	ITL_N5	13	6	7
	ITL_N6	15	7	8
	ITL_S1	5	3	2
Sebastian Inlet	ITL_S2	9	4	5
	SINJ	3	2	1
	SIWP	5	2	3
	SISO	4	2	2

Table 6: Betweenness and eigenvector centrality of accessed receivers. The highest betweenness and eigenvector centrality values for each sub-region are highlighted.

Region	Receiver	Betweenness	Eigenvector
Banana Creek	BC1	0.00	4.57e-17
	BC1A	10.00	4.45e-17
	BC2	7.50	5.86e-17
	BC3	10.00	0.00
	BC3A	2.00	2.33e-17
	BC4	11.50	0.00
Banana River	BR1	0.00	7.91e-17
	BR1B	0.00	8.98e-17
	BR2	0.00	1.32e-16
	BR4	0.00	7.54e-17
	BR5	110.00	3.69e-3
	BR6	108.00	6.16e-4
	BR7	110.00	1.78e-2
	BR8	104.00	1.24e-4
	BR12	98.00	2.48e-5
Indian River	IR4	6.00	6.72e-17
	IR6	0.00	8.04e-17
	IR9	90.00	4.97e-6
	IR10	80.00	9.97e-7
	IR13	68.00	2.08e-7
	IR14	54.00	4.18e-8
ITL Impoundments	ITL_BR1	0.00	1.48e-2
	ITL_BR2	116.00	8.87e-2
	ITL_N1	0.00	0.93
	ITL_N2	0.25	0.93
	ITL_N3	0.25	0.93
	ITL_N4	0.25	0.93
	ITL_N5	26.50	0.85
	ITL_N6	46.25	1.00
	ITL_S1	0.00	0.29
ITL_S2	104.50	0.43	
Sebastian Inlet	SINJ	0.00	3.51e-10
	SIWP	20.00	1.75e-9
	SISO	38.00	8.72e-9

The directed edges of the network for fish Delta demonstrate the fish entering and exiting each receiver it encountered in multiple ways (Figure 19). Fish November's network shows some directionality in Banana Creek, while travel through Indian River was more straightforward (Figure 20). The network for fish November reveals slightly more detections in the south and east, but many connections between all of the receivers in that region (Figure 21).

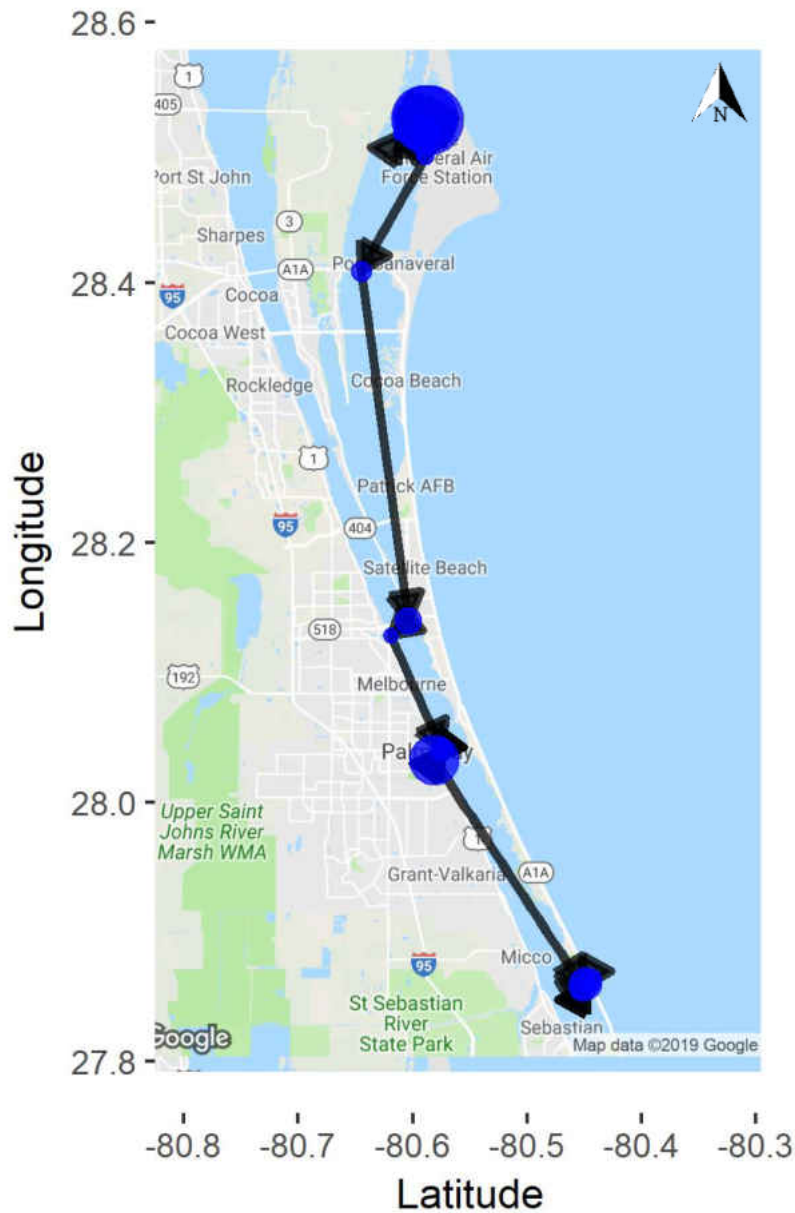


Figure 19: Fish Delta network overlaid onto a map of the Indian River Lagoon. Node size indicates the number of detections.

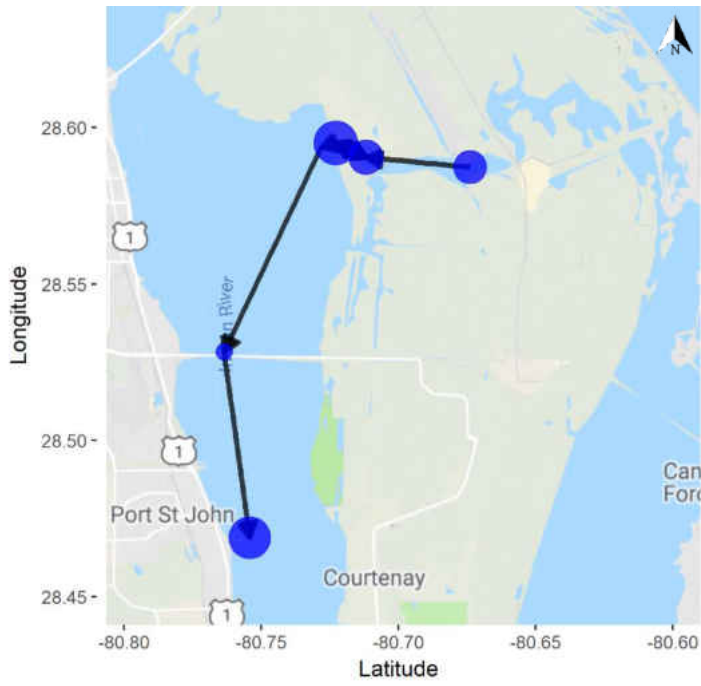


Figure 20: Fish November network overlaid onto a map of Banana Creek and Indian River. Node size indicates the number of detections.

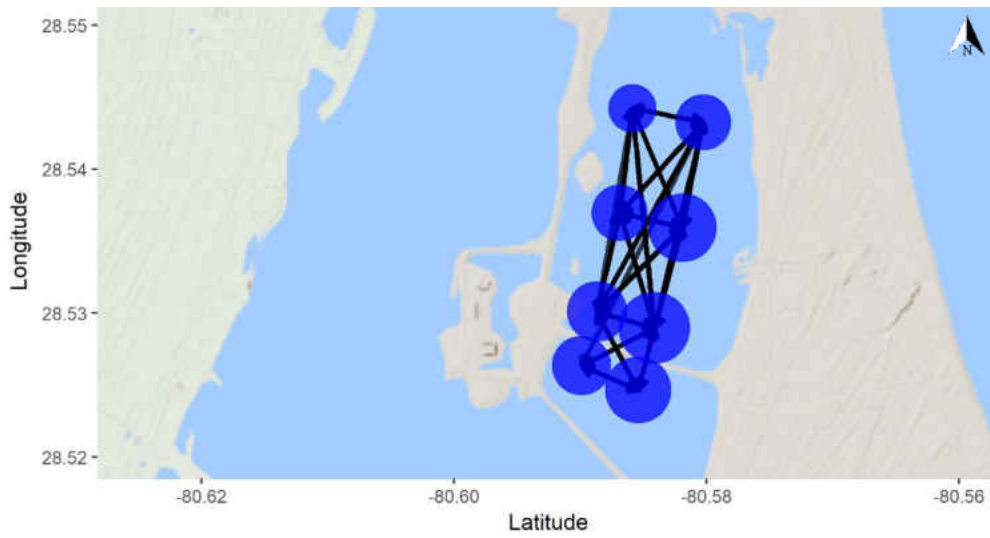


Figure 21: Fish Kilo network overlaid onto a map of the ITL impoundments. Node size indicates the number of detections.

The 95% KDE for Banana Creek matches the network for fish November fairly well (Figure 22). Through simple visual comparison, one can see the importance of the south impoundment emphasized by the 95% KDE while the network produced by fish Kilo also covers most of the north impoundment (Figure 23). The smoothing parameters for both regions are quite large (504.4 and 101.5 for Banana Creek and ITL Impoundments, respectively), leading to some concerns with overestimation. They also greatly differ, but this is most likely due to the marked difference in detections that took place within each region. When directly examining the detection data, a majority of Kilo's detections (3,006/3,841) took place in the north impoundment, but the KDE attributed more weight the south impoundment due to the large number of detections across all fish (primarily fishes Alpha and Delta) recorded there.

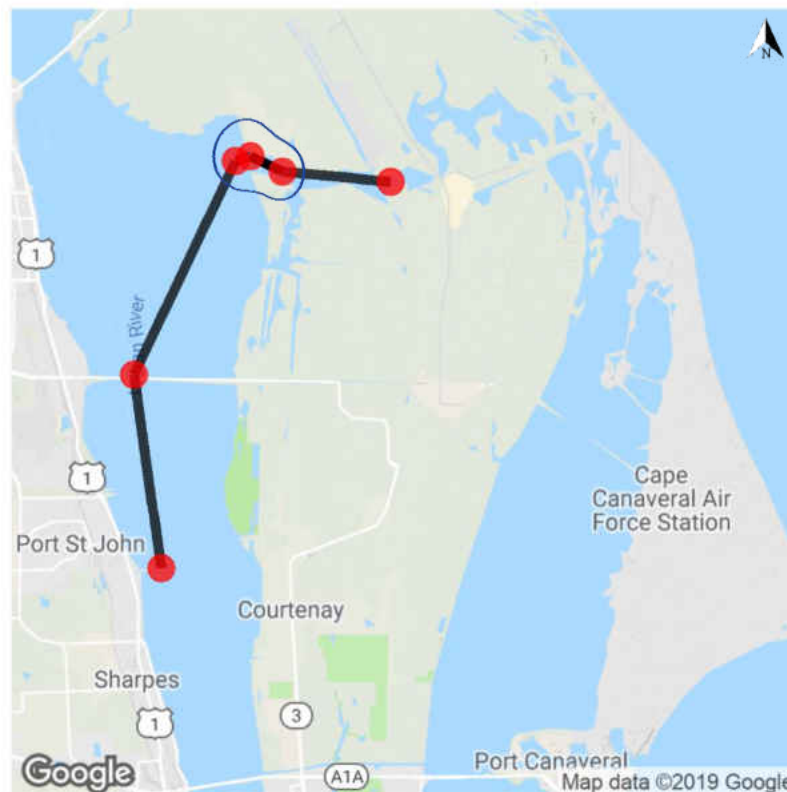


Figure 22: 95% KDE (blue line) for Banana Creek overlaid on the movement network of fish November. Within the network, red dots designate nodes (receivers) and black lines denote edges (fish paths).

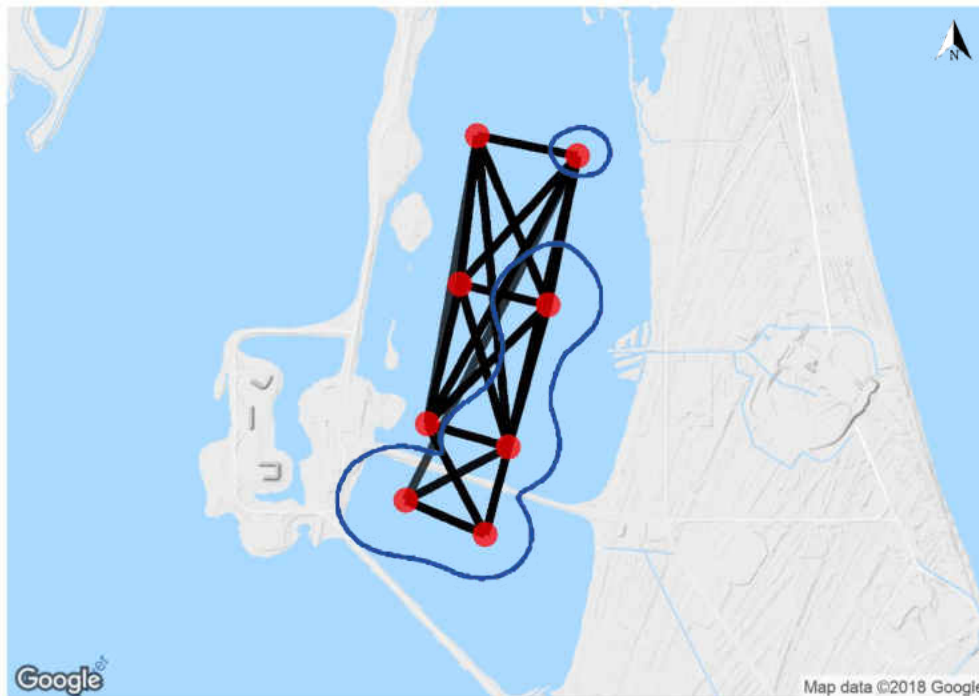


Figure 23: 95% KDE (blue line) for the ITL impoundments overlaid on the movement network of Fish Kilo. Within the network, red dots designate nodes (receivers) and black lines denote edges (fish paths).

Discussion

To date, this is the first study that has taken an in-depth view of the migration patterns of striped mullet (*Mugil cephalus*) in the Indian River Lagoon. Using passive acoustic telemetry, the detections and residency time data produced by these fish identified potential refuge areas and movement corridors. This study also distinguished specific locations in each region that are crucial in the daily activity of the animals. In addition, the data analysis parsed specific sites that may be in need of management in intervention. Lastly, this research obtained some of the first possible evidence to suggest that this population may undergo skipped spawning or partial migration. This new information may be used to update management practices for the striped mullet and support the future investigation of skipped spawning or partial migration in other migratory forage fish.

Acoustic Telemetry of *M. Cephalus*

Detections and Residency Time

ITL Impoundments

Most of the detections garnered in this study were from the ITL impoundments, due to the consistent activity from one fish (Kilo). However, parsing the data from each of the eight receivers in this area produces interesting patterns. The number of detections and residency time in the ITL impoundments show fish preference for the west half of the south impoundment and the southeast corner of the north impoundment, possibly for feeding or predator avoidance purposes. It should be noted that manatee exclusion bollards are located around four sets of drainage culverts, the only exit points out of the north impoundment. The western culverts are often silted in by sediment, frequently restricting fish movement to the eastern culverts within the north impoundment. This is where receivers ITL_N4 and ITL_N6 were located, potentially leading to the increase in numbers of detections and residency times, suggesting that this is a critical conduit linking the two waterbodies.

Banana River

Based on the relatively low number of detections and residency time in this area, Banana River appears to serve as a corridor for striped mullet on their journey to feeding or spawning grounds. In a similar case to the ITL impoundments, all detections and residency time at BR1B were generated solely from the activity of one fish. The area where this particular receiver is located is set somewhat apart from the main body of the Banana River and may also serve as a refuge area. Both of these waterways are main components of the Indian River Lagoon, thus the striped mullet are exposed to a variety of both aquatic and terrestrial predators as well as human activities (fishing, boating, etc.). Therefore, it may be advantageous for the fish to traverse these waters in an expeditious manner. However, fish

Delta spent an extended amount of time at IR14 (~21 days, Table 2), near Palm Bay, Florida, specifically within the freshwater tributary of Turkey Creek. This may have been for the purpose of gathering resources in a more sheltered area before traveling the remaining distance to the ocean to spawn. There is also evidence that fish Delta loitered in the Sebastian Inlet area, with more repeated movements between those receivers than those in the Banana or Indian Rivers.

Banana Creek

Banana Creek seems to contain refuge sites while also operating as a corridor for striped mullet, as it detected the greatest number of unique fish. Five out of the six receivers detected combined residency times of at least 4 days, with the exception of BC3A. Essentially, when combining the residency time of all of the fish registered by receivers in this area over the course of this study, fish were detected in this area for a time period amounting to four days. This is higher than all other study sub-regions with the exception of the ITL Impoundments. BC2, a central location within Banana Creek had the highest residency time, with detection events encompassing seven different fish. This demonstrates that multiple fish frequented this site for extended periods of time. Most of these receivers are also part of the security zone at Kennedy Space Center, allowing the fish to travel and forage in that area without much human exposure.

Movement Trends

The majority of fish presumably moved outside of the array or were lost to predation, preventing full analysis of their movement patterns. Striped mullet often move into peripheral habitats and marshy environments that cannot be effectively monitored, serving as a cautionary tale for other

acoustic telemetry studies involving forage fish species, as any type of movement study may underestimate their true range and/or habitat use. The fish that did provide a consistent amount of movement data exhibited two different movement trends. Two fish traveled southward from their capture locations, using two different bodies of water to reach the Indian River Lagoon proper. Two fish stayed in relatively close proximity to their capture locations and showed no signs of migratory movement over the course of this study.

There is some evidence that this species exhibits seasonal movement patterns (Thomson, 1955; McDonough, 2003; Fortunato et al., 2017). In North Carolina, Bachelor et al. (2005) found that the largest proportion of striped mullet in the study traveled southward during summer and fall months (August-October). This differs from the movement documented in this study, with the largest movements occurring in November and December, but this may also be due to the two populations differing in adaptations to their respective environments. The aforementioned study also demonstrated a mean daily distance comparable to fish November in this research (~3 km/day). In the Gulf of Mexico, when compared to white mullet (*Mugil curema*), the spawning migration of striped mullet occurred during the winter months (Ibanez and Benitez, 2004), which is also similar to the movement trends displayed by fishes November and Delta.

Fish Delta, caught in the ITL impoundments, moved south through the Banana River, crossed into the Indian River proper near Indian Harbour Beach, and continued south before exiting through Sebastian Inlet. This journey of approximately 80 km was made from mid-December to mid-February. fish November, captured in Banana Creek, moved westward into the Indian River and traveled southward for roughly 20 km. This movement occurred from December 4-8 of 2017, swimming 4 km the first day, 1 km the second day, and the greatest distance (14 km) covered during the third day. Both of these fishes' movements occurred in December and February, later than the historic peak in striped

mullet migration, October and November. This may be connected to environmental metrics, which will be discussed in more detail in the next chapter.

For both fish Delta and fish November, the nearest egresses to the ocean are Ponce de Leon Inlet via Haulover Canal (northward) and Port Canaveral (southward). The current acoustic data demonstrates that neither of these fish used these outlets to reach the Atlantic, mostly likely due to the restrictive nature of the canals and locks employed along those paths. Fish Delta exited the Indian River Lagoon through Sebastian Inlet, which is the next closest inlet to the south, lending credence to the hypothesis that fish utilize the shortest routes through the estuary to reach their spawning grounds. As more data are obtained, the exit strategy of fish November may bolster this finding.

Fish Kilo and fish Mike, caught in the ITL impoundments and Upper Banana River respectively, remained in those locations for the duration of this project. This may be an indication of skipped spawning, in which fish do not annually reproduce (Rideout and Tomkiewicz, 2011). Populations within other species have been documented exhibiting skipped spawning, such as snook (*Centropomus undecimalis*) and barramundi (*Lates calcarifer*) (Milton and Chenery, 2005; Trotter et al., 2012; Young et al., 2014). This strategy may be used in the case of poor health or as a density-dependent response to high population levels (Jorgensen et al., 2006; Rideout and Tomkiewicz, 2011; Skjæraasen et al., 2012). Another future avenue to explore is partial migration, in which only a proportion of a population migrates during a given season while others remain residents (Chapman et al., 2012; Shaw, 2016). This has recently been documented in striped mullet off the coast of Australia (Fowler et al., 2016). There are many different hypotheses as to what drives animals to conduct partial migration, from differences in physiology to competition to density dependence (Chapman et al., 2011; Shaw, 2016). Fish Mike was one of the smallest fish of the study and may have not yet reached true sexual maturity. However, fish Kilo was one of the largest fish of the study at 47.5 cm TL, and there was no indication of poor health at capture. The ITL impoundments are also unique in that they are located within the Kennedy Space

Center security zone, creating a de facto marine reserve. Thus, these sites may serve as refuges for fish that are experiencing skipped spawning or partial migration.

Based on their biometrics, all four of these fish were in the adult stage of their life cycle, so some unknown factor is influencing the decision to spawn each year. Regardless the ultimate cause, acoustic data suggest there are different patterns of spawning behavior in *M. cephalus*. Additional research focusing on more distinct size classes and/or incorporating a higher number of acoustic tags over a longer time periods would also aid in narrowing the scope of the above conclusions.

Movement Models and Simulations

Random walk, Brownian bridge, and biased random bridge movement models and simulations all produced extremely low probabilities for fish locations due to the irregular distance between relocations that was a consequence of working with such a large system and diffuse receiver array. Therefore, only the kernel density estimations (KDEs) will be interpreted here. As the KDEs were generated using the COAs which had in turn been created through the observation-weighted method, the home range estimation is related to the number of detections in each respective area. While this measure does have some value and provides baseline knowledge, it only represents activity in the form of detections, following the theory that the most detections will be recorded where the fish spends the most time (i.e. its home range). In addition, due to the linear arrangement of receivers within the FACT Network, movement on the North-South axis is recognized using the COA technique, but East-West movement is often overlooked. This method appears to generate appropriate results for Banana Creek and other areas where detections were evenly distributed, but seems to be skewed in the ITL impoundments. Fish could potentially favor that area due to plentiful resources or shelter from predators, as evidenced by the lopsided number of detections in the south impoundment. Kilo, being a

larger fish and possibly not undergoing spawning each year or at all, may mainly use the north impoundment for refuge purposes. This underscores the need to utilize multiple techniques to inform management strategies, as this area may not have been recognized without the combination of the KDE and network analysis.

Network-Based Analyses

Even being one of the simplest measures in network analysis, node degree is a useful metric as it can demonstrate fish dispersion across a region. For example, seven fish were caught and released in the ITL impoundments. The number of connections within the north impoundment are much higher than those in the south and decrease even further out into the Banana River, demonstrating the fish preference for the north impoundment. With Banana Creek, Banana River, and Indian River regions, it appears that fish dispersed somewhat evenly and had relatively equal preference for individual sites within each respective region, as the number of connections are fairly consistent across each receiver region. When node degree was parsed into indegree and outdegree centrality to better evaluate the frequency at which fish are moving in or out of a specific area, BC2 and most of the receivers in the north impoundment showed high indegree, demonstrating fish are remaining in that area, possibly due to increased resource availability, accessibility to shelter from predators, or generally favorable environmental conditions. ITL_N6 and BR6, with high outdegree, represent areas that fish are simply passing through, due to the location being a chokepoint, a lack of food, and/or increased predator presence. Locations with nodes of relatively high degrees are valuable to the fish in a myriad of ways and should be conserved for management purposes.

Most receivers in the Banana and Indian Rivers showed high betweenness centrality values (98-110 and 54-80, respectively), emphasizing their adjacent waters as corridors in this system. From the ITL

impoundments and Banana Creek to southern spawning grounds, these are some of the only routes available to these fish. The areas containing IR9-IR14 are especially crucial migratory corridors and should be priorities for conservation as fish have to migrate through this region to reach the ocean further south. In contrast, the betweenness centrality values associated with receivers in the ITL impoundments were on the lower end of the spectrum, ranging from 0-47, as once the fish is in that region, all of the adjacent habitat is easily accessible. The highest betweenness centrality value was produced at ITL_N6, suggesting this is one of the only pathways for fish to exit the north impoundment. In a similar vein, Banana Creek also showed low betweenness centrality, with the highest value located at the access point to the Indian River.

Eigenvector centrality, quantifying node influence, is one of the more abstract network analysis metrics as it's ecological interpretation can be incredibly diverse depending on the study system. In this study, receivers with the highest eigenvector value (~1 on a scale of 0-1) are connected by edges (i.e. moving fish) that in turn are connected to important receivers. The receivers in the ITL impoundments have the highest eigenvector centrality, as each of those nodes have high numbers and frequency of connections. Once again, this stresses the importance of this area, although it should also be considered in the context of the entire network. Receivers BR5-BR7 also had detectible eigenvector centrality, most likely due to their position between the ITL impoundments, which were very active, and the Banana River, which was exploited as a corridor to the south.

Management Recommendations

This study suggests that some sites that are crucial to mullet movement are currently in need of management intervention. First, the ITL impoundments have shown to be a vital refuge area for this species. However, of the four sets of culverts that connect the north and south impoundments, at least

two are often obstructed by sediment, confining fish passage through the eastern two culverts. This has already proved to be an issue, with a massive fish kill in the area linked to low levels of dissolved oxygen. Due to the restricted egress points, fish may have been unable to escape the area when dissolved oxygen reached critical levels. Therefore, it is recommended that a maintenance schedule be implemented for the removal of sedimentation. Second, more generally, the management plans for the main portions of the IRL (i.e. Banana River and Indian River) should be reviewed and incorporate actions based on the connectivity that it provides to the striped mullet. Not only will this benefit this particular species, but also produce a ripple effect through the food web that will positively impact the multitude of natural and human elements within the Indian River Lagoon that rely on this species for survival, recreation, and industry.

Conclusions

With notable exceptions (e.g. salmonids), the direct management of spawning-related migrations is rare in species that form relatively dense spawning aggregations (e.g. snapper and grouper spp.), despite the widespread decline of these spawning species (Sadovy de Mitcheson and Erisman, 2011). Only approximately 35% of aggregations are currently managed worldwide, through either marine protected areas (MPAs) or seasonal fishing closures. This management is riddled with inadequate spatial scaling, often not incorporating vital migratory routes (Russell et al., 2014; Sadovy de Mitcheson, 2016). Not surprisingly, if known migratory pathways and these large spawning aggregations are targeted by fishing efforts over a few spawning seasons, the corresponding reproductive stocks can plummet with both biological and economic consequences (Sadovy de Mitcheson and Erisman, 2011). Therefore, two main questions need to be addressed regarding the management of species with defined migratory pathways and spawning aggregations. First, do spawning aggregations and pathways need to

be expressly managed rather than relying on quotas or bans on certain gear types? Second, can threatened aggregating species recover once management has been implemented, and, if so, what is the timeline for their recovery? (Sadovy de Mitcheson and Erisman, 2011). The only way these uncertainties can be resolved is by exploring the migratory patterns of spawning fish, determining the impacts of fishing on those migrations, and using this understanding to inform the development of management strategies that optimize recreational and commercial fisheries. To build a foundation for answering the first question, here I have performed the first assessment and quantification of the migratory patterns of striped mullet in Merritt Island National Wildlife Refuge and adjacent waters of the Indian River Lagoon. While not currently at-risk, utilizing such a widespread and relatively common species will ultimately deepen our understanding of migration-related movement patterns that can be used to develop best available management practices for other migratory species.

CHAPTER II: ENVIRONMENTAL METRICS ASSOCIATED WITH STRIPED MULLET (*MUGIL CEPHALUS*) ACTIVITY AND MOVEMENT

Introduction

Migration is a vital process within the life history of many organisms, allowing them to reach more favorable conditions for breeding, feeding, and survival. Numerous cues, such as Earth's magnetic field, an innate, inherited sense, or changes in prey activity or abundance, can guide animals at all life stages to appropriate locations (nearby or at some distance) and times (daily, seasonally, or other) to engage in various behaviors (Sutherland, 1998; Newton, 2008; Milner-Gulland et al., 2011). Migratory movement may be triggered by an amalgamation of factors, including ontogenetic transitions, unpredictable environmental changes, and/or seasonal cues. Within vertebrates, migrations that occur due to ontogenetic or developmental triggers are generally distinct from adult migrations as they only occur once, while adult migrations take place multiple times over the subject's lifetime, often at some yearly interval (Ramenofsky and Wingfield, 2007). This is clearly demonstrated in diadromous fish such as salmonids which hatch and develop into parr in freshwater, metamorphize into smolt, and then migrate to saltwater where they sexually mature (Ramenofsky and Wingfield, 2007). Apart from natural influences, human activity can also impact fish movement (Evans and Johnston, 1980; Larinier, 2001; Reist et al., 2006; Farrell, 2009). For example, Williams et al. (2008) found that the construction of dams within the Snake River, Oregon led to a later migration of salmon fry. In addition to local-scale anthropogenic impacts, broad-scale changes to climate caused by human activities may permanently alter the global environment, resulting in sudden or erratic alterations in weather, climate, and physical surroundings (Wilcove and Wikelski, 2008; Milner-Gulland et al., 2011; Moore, 2011). Many species of fish migrate seasonally, relying on the signals of water temperature change, which may be affected by climate change (Jordan and Wortley, 1985; Jepsen and Berg, 2002; Binder et al., 2011; Milner-Gulland et al., 2011). Still others, such as the Pacific lamprey (*Entosphenus tridentatus*), rely on photoperiod to

synchronize their migratory activity (Andrews et al., 2010; Binder et al., 2011). The progression of all types of migration includes initial accumulation of resources, transit and energy reacquisition substages, and finally concluding at the terminus location. Each of these states involves strictly controlled physiologies and behaviors that must adjust according to local environmental conditions (Ramenofsky and Wingfield, 2007).

Consequently, many species have evolved physical characteristics and age-specific strategies that allow them to survive, utilize, and rely upon certain environmental cues (Jones and Petreman, 2015). For example, salmonids have thrived in their riverine environments by adapting their spawning and egg incubation to their local flow regime (Taylor, 1991). Theoretically, natural selection resulted in these responses because migration provides a net gain to fitness (Davidsen, 2010). Therefore, movement triggered by environmental factors, should be triggered by the combination of those that dictate the most beneficial timing, route, and duration of migration. Unfortunately, migration and any end goal activity may be delayed or missed entirely if environmental conditions are not suitable or if environmental triggers do not accurately communicate relevant information to the animals, underscoring the need to understand and maintain the environmental signals that are important to individual migratory species (Forsythe et al., 2012; Jones and Petreman, 2015).

In fish, season is the decisive trigger for many migratory movements and is most likely indicated to the fish by the length of day (Eriksson et al., 1982; Jonsson, 1991; Sandlund et al., 2014). However, annual variation in the timing and intensity of migration and movement are influenced by the environmental variables of water flow, water temperature, and photoperiod (Northcote, 1984; Jonsson, 1991; Sandlund et al., 2017), in addition to abiotic factors such as salinity, dissolved oxygen, and barometric pressure (Leggett, 1977; Sackett et al., 2008; Hays et al., 2016). Downstream migrations often take place during darkness, with progressively waxing moonlight actively reducing movement distance and speed (Mason, 1975; Jonsson, 1991). Even in laboratory-controlled experiments with a

complete lack of light and other variables constant, fish demonstrated innate activity rhythms that directly correlated with the lunar cycle (Boetus, 1967; Edel, 1976). While the cover of darkness is believed to assist in predator avoidance, daytime migrations have also been observed in other fish, such as brook sticklebacks (MacLean and Gee, 1971). Other abiotic factors such as water flow also influence the direction of migration, with the route of Atlantic salmon (*Salmo salar*) fluctuating with the current when moving seaward (Fried et al., 1978). Increased water discharge can also speed migration by allowing fish to travel downstream without expending energy to actively swim (Jonsson, 1991; Allen et al., 2018). A high water influx can also provide protection from visual predators due to increased turbidity and surface undulations (Hvidsten and Hansen, 1989).

As most fish are poikilothermic, their activity levels can be correlated to water temperature; relatively low activity occurs at low temperatures, whereas higher activity correlates with elevated temperatures, requiring greater energy expenditures (Jonsson, 1991; Lucas et al., 2001; Wootton and Smith, 2015). While water temperatures may stimulate migratory behavior, research suggests there is no specific threshold temperature to predict fish migration across multiple species (Jonsson, 1991). For example, while a 3-4° C difference between river and seawater temperature correlated with European silver elver movement, while brown trout exhibited movement over a wide range of temperatures (Gandolfi et al., 1984; Davies and Sloane, 1987). In most systems and species, there appears to be a suite of environmental and physiological factors that can play a role in initiating migration, and if one environmental catalyst does not occur, then another factor may initiate migration (Jonsson, 1991; Yoshioka and Yaegashi, 2018). This potential hierarchy of drivers can affect the timing of migratory movements, as phenological factors may arise at different points of a given migratory season. As well, different mechanisms may stimulate migration in disparate environments based on adaptations to local abiotic factors, ensuring that migratory movements begin when it is most advantageous to the species (Jonsson, 1991; Allen et al., 2018).

This study serves to assess the environmental metrics associated with striped mullet activity and movement. Abiotic factors that have historically been shown to trigger migratory movements, such as water temperature and photoperiod, as well as environmental variables that may affect other types of daily or seasonal movements, such as turbidity and dissolved oxygen, were both sampled and analyzed in association with fish activity and movement. By first evaluating the various trends in these metrics, differences in spatial and temporal scales may emerge and identify areas that are subject to fluctuations. The associations of specific variables with fish activity then provide insight into what environmental factors may need to be closely monitored in order to maintain fish behavior that supports both the focus ecosystem as well as any human dimensions that depend on it.

Objective: Assess environmental metrics associated with striped activity and movement.

Question: Do key environmental variables correlate with striped mullet movement and activity?

Hypotheses:

H₀: No specific environmental variables correlate with striped mullet movement and activity.

H_{A1}: The environmental variable of water temperature is most correlated with striped mullet movement and activity.

H_{A2}: The environmental variable of barometric pressure is most correlated with striped mullet movement and activity.

H_{A3}: The environmental variable of photoperiod is most correlated with striped mullet movement and activity.

H_{A4}: The additive or interactive effects of water temperature, barometric pressure, and photoperiod are most correlated with striped mullet movement and activity.

Methods

Study Site

The study location is identical to that described in Chapter I of this thesis (please see the Methods section, Chapter I above). Briefly, the Indian River Lagoon (IRL) Complex spans approximately 251 kilometers and is comprised of the Mosquito Lagoon, the Indian River, and the Banana River. This area also includes the Merritt Island National Wildlife Refuge (MINWR), a 140,000-acre preserve on Kennedy Space Center property (Adrian et al., 2008).

Abiotic Sampling

Abiotic factors, including water temperature, dissolved oxygen, turbidity (measured with an infrared light source in FNU, or formazin nephelometric unit, and equivalent to NTU, or nephelometric turbidity unit, which is measured with a white light; USGS, 2017), pH, salinity, depth, photoperiod, and barometric pressure were recorded, either *in situ* (this study using Onset® HOBO® loggers or a YSI-multi-parameter probe) or remotely from available online resources (St. Johns River Water Management District [SJRWMD]). These factors were evaluated in relation to the movement data (number of detections and residency time as separate response variables) to assess if certain abiotic conditions best predict different types of movement. Environmental variables were collected on three different spatial scales, lagoon, sub-regional, and site, and over two spawning seasons, from November 2017-February 2019.

To assess lagoon-wide environmental variability, five SJRWMD water quality monitoring stations surrounding and located within MINWR were selected and split into north, mid, and south regions (Figure 24). Environmental metrics were then averaged on a monthly basis. One-way ANOVAs were performed in order to determine if there was a significant difference in each environmental metric by

lagoon regions across spatial and temporal scales. Continuous Onset® HOBO® loggers were deployed at the rough geographic center of fish capture regions in order to evaluate any sub-regional differences in light penetration and water temperature (Figure 25). Finally, when detection data were downloaded each month, environmental metrics were also taken at each receiver (Please see Figure 4, Chapter 1). Due to their relatively close positions, the receivers in the ITL impoundments were grouped into North, South, and Banana River (BR), with the mean environmental metrics calculated for each region. The rest of the receivers were tested independently. One-way ANOVAs were performed in order to determine if there was a significant difference in each environmental metric by site across spatial and temporal scales. Posthoc Tukey HSD tests were conducted on all significant ANOVA results to assess sources of significant differences among locations.

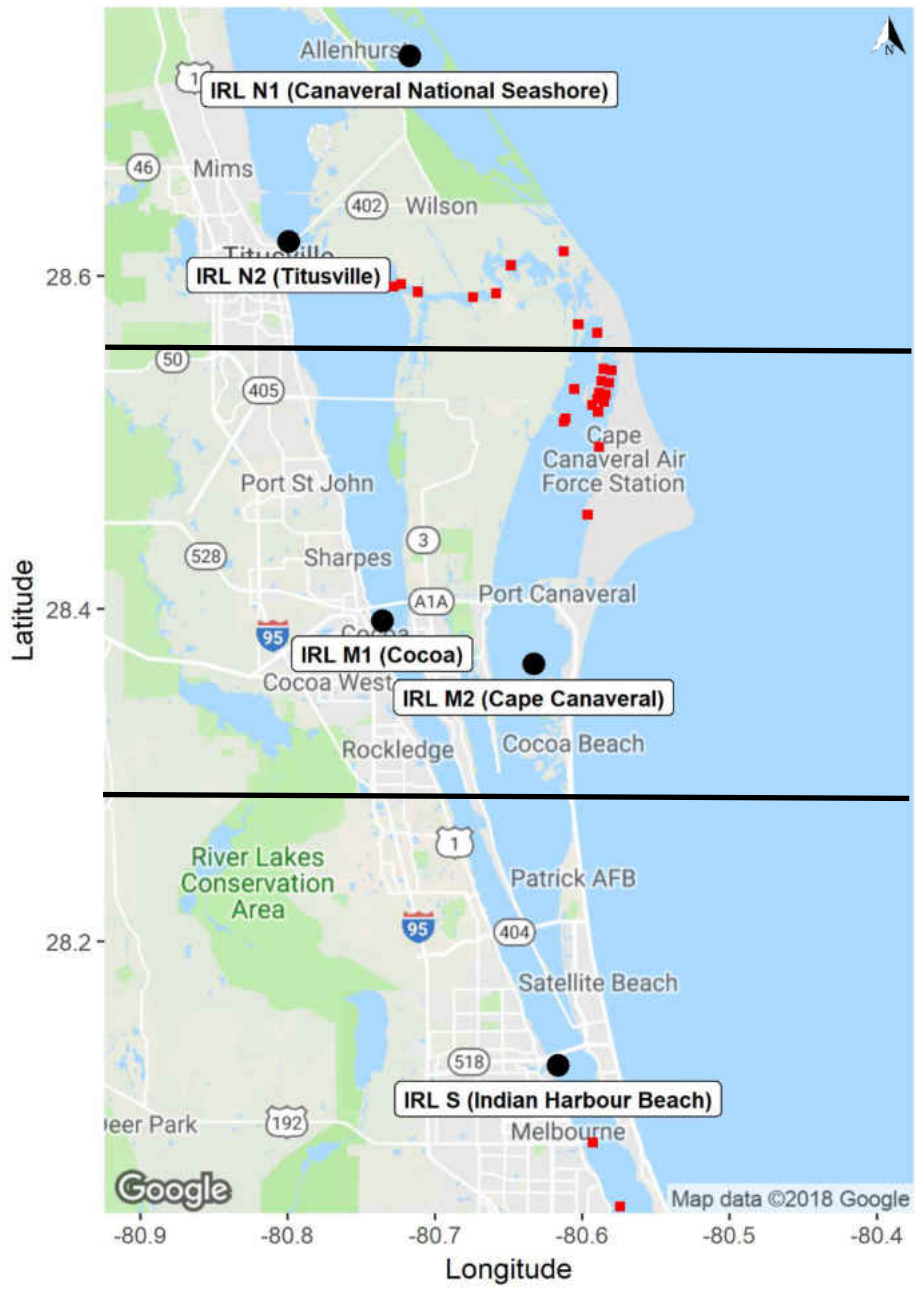


Figure 24: Acoustic receivers (red) within Kennedy Space Center property in relation to SJRWMD Continuous Monitoring Stations (black).

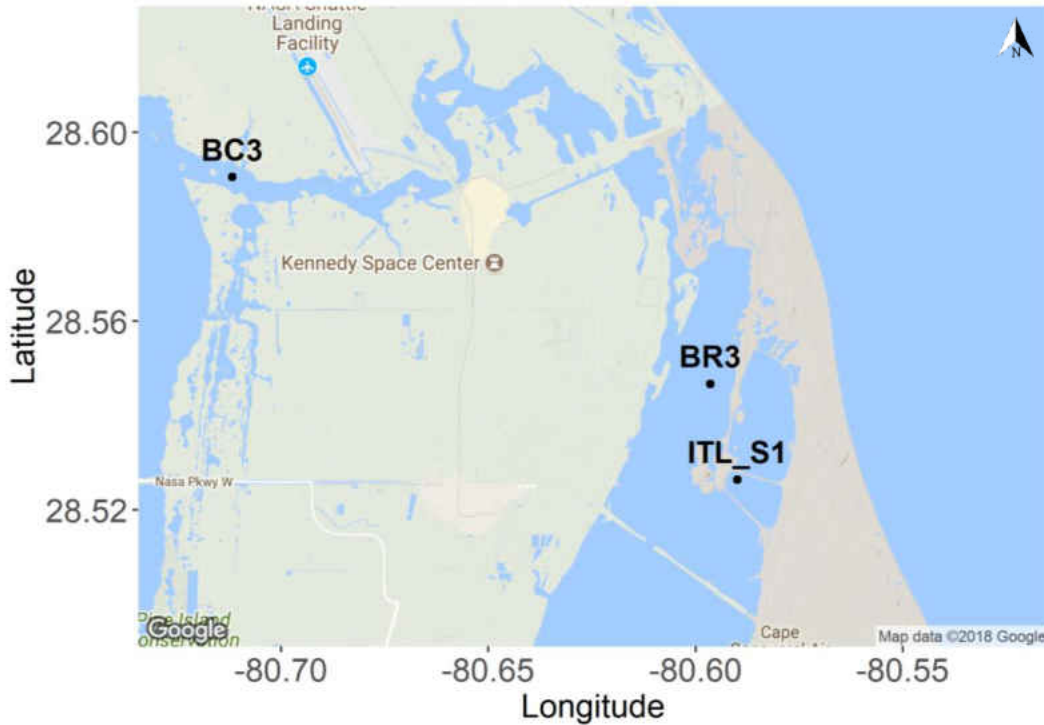


Figure 25: Locations of Continuous Onset HOBO loggers on Kennedy Space Center property

Variables and Linear Mixed Model Selection

Using the glmmADMB package (Skaug et al., 2016) in R, regression models of explanatory environmental variables were evaluated using the Akaike Information Criterion (AIC) in order to assess which environmental conditions are most associated with *M. cephalus* behavior, using two of the three fish case studies highlighted throughout this thesis (fishes Kilo and November). Fish Delta did not have adequate abiotic data in conjunction with movement data to develop models; hence it was not included in subsequent analyses. AIC is a statistical tool used to compare different models by producing a score based on how each model best fits the generated data. The model with the lowest AIC score is then judged to be the best fitting model and null hypothesis testing is employed to more explicitly interpret the relationship between included variables and the resulting outcome (Snipes and Taylor, 2014).

Linear mixed models were performed using temperature, dissolved oxygen, turbidity, pH, salinity, depth, barometric pressure, and photoperiod values from both site-specific locations (fish Kilo)

as well as SJRWMD Continuous Monitoring Stations (fish November). These metrics were assessed independently as well as in combination in order to explain the number of detections and residency time generated by each fish at each receiver. The first models were each selected to assess the effect that each variable individually may have on the number of detections. Month and receiver were included as random effects. Before any groupings were attempted, the variance inflation factor was calculated to identify any variables that may be collinear. Models included up to three abiotic factors, assessing all possible variables with both additive and interactive models. The best fitting models from each category were compared to determine the best fitting model overall (see Appendix B for full list of models tested). Lastly, the best fitting models were plotted with each response variable and both marginal and conditional coefficients of determination (R^2) evaluated. Marginal R^2 values represent the variance explained by the fixed effects while conditional R^2 values denote the variance described by the entire model, including both fixed and random effects (Nakagawa and Schielzeth, 2013).

Caveats

Determining which set of environmental data to include in the model selection process for fish Kilo produced a dilemma. The environmental monitoring conducted by the SJRWMD was much more robust and complete, with hourly samples over nearly the entire time scale of the study. However, the closest SJRWMD station was nearly 20 km distance from the ITL Impoundments, where the activity from fish Kilo was recorded. The abiotic sampling that was performed by the personnel in this study was only performed on a monthly basis, and therefore was not nearly as consistent, but was conducted in very close proximity to where the fish was located. Correlations were performed between the nearest SJRWMD station and monthly environmental data collected in the ITL Impoundments and produced poor results, meaning the data from the SJRWMD would not be reflective of the environmental conditions within the ITL Impoundments. Therefore, the monthly sampling would need to be used, even

though these were point data sources and not necessarily representative of longer-term temporal changes within the ITL Impoundments. In order to analyze fish activity and movement with these constraints, three days of activity that was known to have occurred at and around the time of the monthly personnel abiotic sampling were isolated and used in the model selection process.

Assessment of Movement Coupled with Abiotic Environment

One-way ANOVAs were conducted to evaluate differences in number of detections and residency time across environmental bins for each fish, using data from specific sites or the nearest SJRWMD continuous monitoring stations. Posthoc Tukey HSD tests were conducted on all significant ANOVA results to assess sources of significant differences among environmental variables. The location data were analyzed using the VTrack package in R to pinpoint the time and date of relatively large-scale movements. Environmental metrics that were found to be the best predictors for activity by both fish were isolated at each date interval and compared to those particular points of interest.

Results

Abiotic Sampling

Lagoon Scale

Water temperatures ranged from 8.4-33.2° C, following a seasonal trend (Figure 26). There were highly significant differences in temperature among the three broad regions and months (Region one-way ANOVA $F_{2,3} = 544.3$, $p < 0.001$; Month one-way ANOVA $F_{2,12} = 1025.6$, $p < 0.001$). The northern region had significantly lower temperatures throughout the year, followed by the mid and southern regions (all Tukey HSD p values < 0.001).

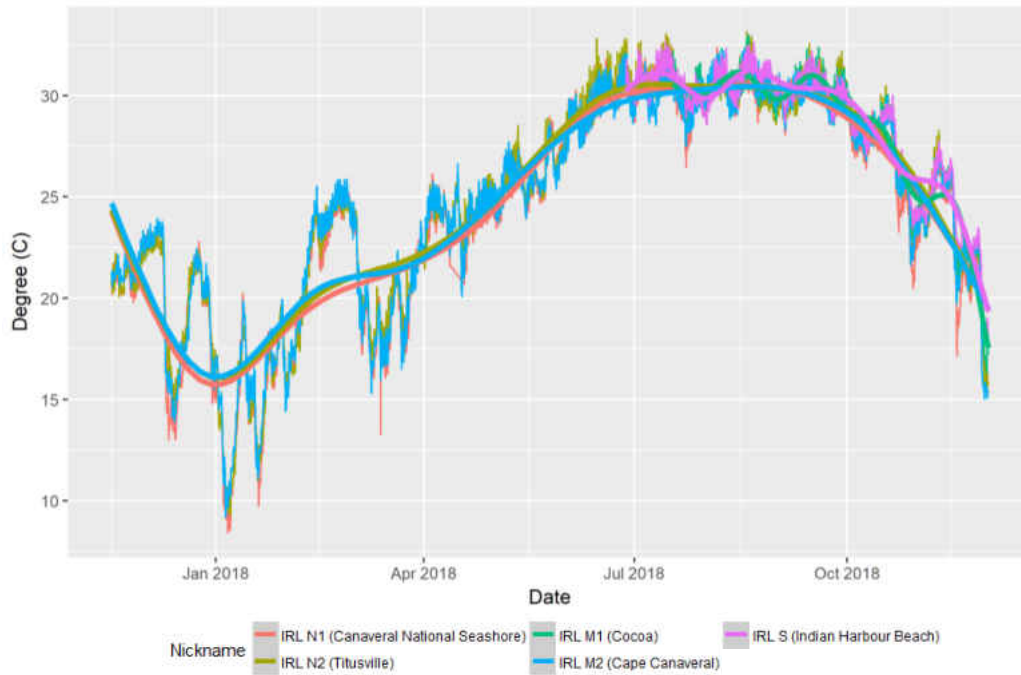


Figure 26: Temperature (°C) at SJRWMD Continuous Monitoring Stations over time.

Although much noisier, dissolved oxygen inversely followed the same trend, ranging from 0.03-16.4 mg/L (Figure 27). There was no significant difference among regions and a highly significant difference between months (Month one-way ANOVA $F_{2,12} = 19.88$, $p < 0.001$). Generally, months within the same season did not have significantly different levels of dissolved oxygen, but summer months had significantly lower levels of dissolved oxygen than winter months (all Tukey HSD p values < 0.05).

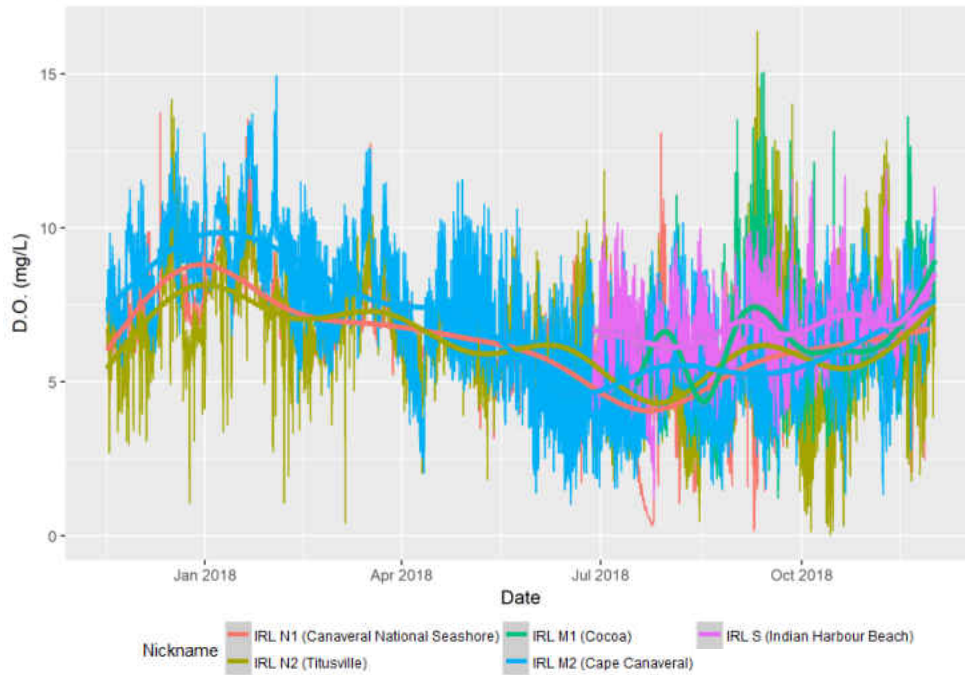


Figure 27: Dissolved oxygen (mg/L) at SJRWMD Continuous Monitoring Stations over time.

Turbidity showed a much wider range, from 0-493.2 FNU (Figure 28). There was a slight significant difference among regions and no significant difference between months (Region one-way ANOVA $F_{2,3} = 4.92$, $p < 0.05$). The southern region had significantly less turbidity than the northern region (Tukey HSD p value < 0.001).

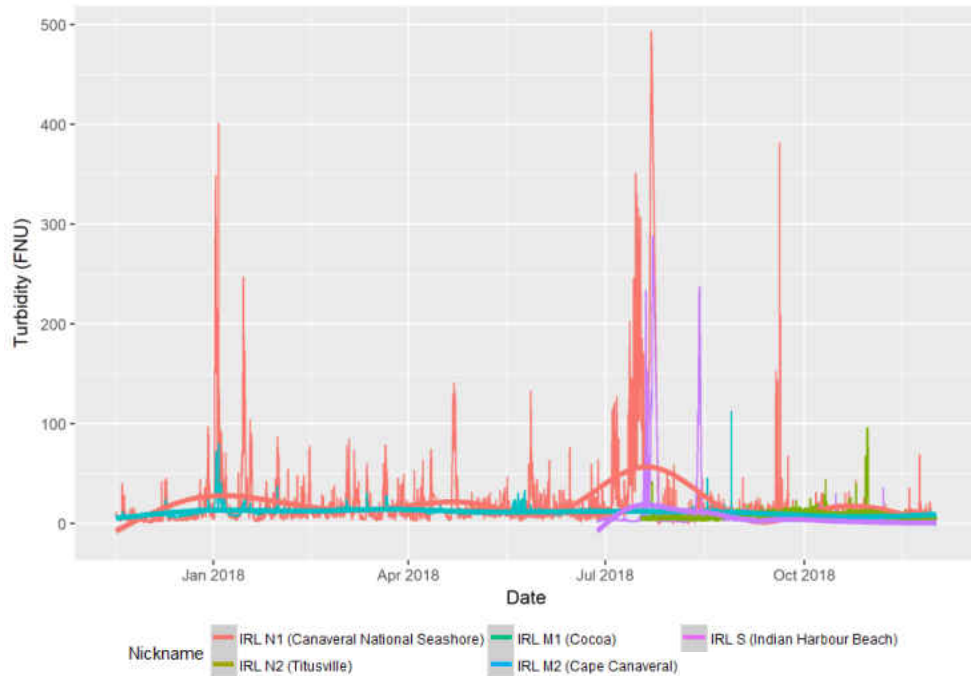


Figure 28: Turbidity (FNU) at SJRWMD Continuous Monitoring Stations over time.

Over the course of this study, pH ranged from 7.3-9.4 (Figure 29). There was a highly significant difference in pH across regions and no significant difference across months (Region one-way ANOVA $F_{2,3} = 15.55$, $p < 0.001$). The northern and southern regions had significantly lower pH than the mid region (Tukey HSD p values < 0.001).

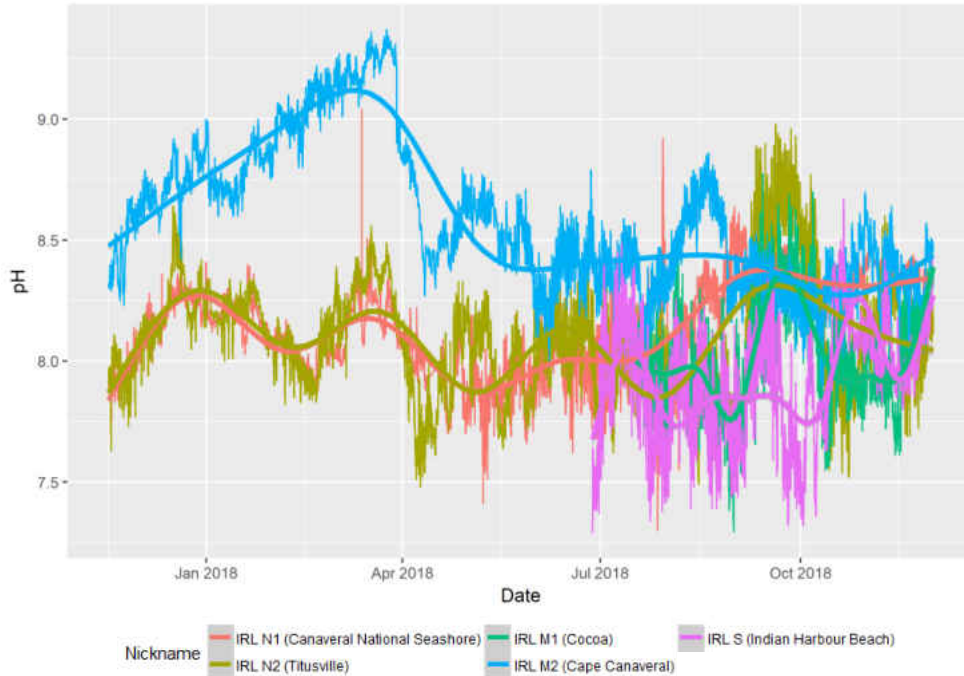


Figure 29: pH at SJRWMD Continuous Monitoring Stations over time.

While salinity was susceptible to short-term and somewhat erratic fluctuations in instrument readings, average salinity levels ranged from 16-36 ppt (Figure 30), with a highly significant difference across both region and month (Region one-way ANOVA $F_{2,3} = 42.09$, $p < 0.001$; Month one-way ANOVA $F_{2,12} = 4.29$, $p < 0.05$). The northern region had significantly higher salinity than the mid and southern regions (Tukey HSD p value < 0.05). The month of August had significantly higher salinity than the months of April and May (all Tukey HSD p values < 0.05).

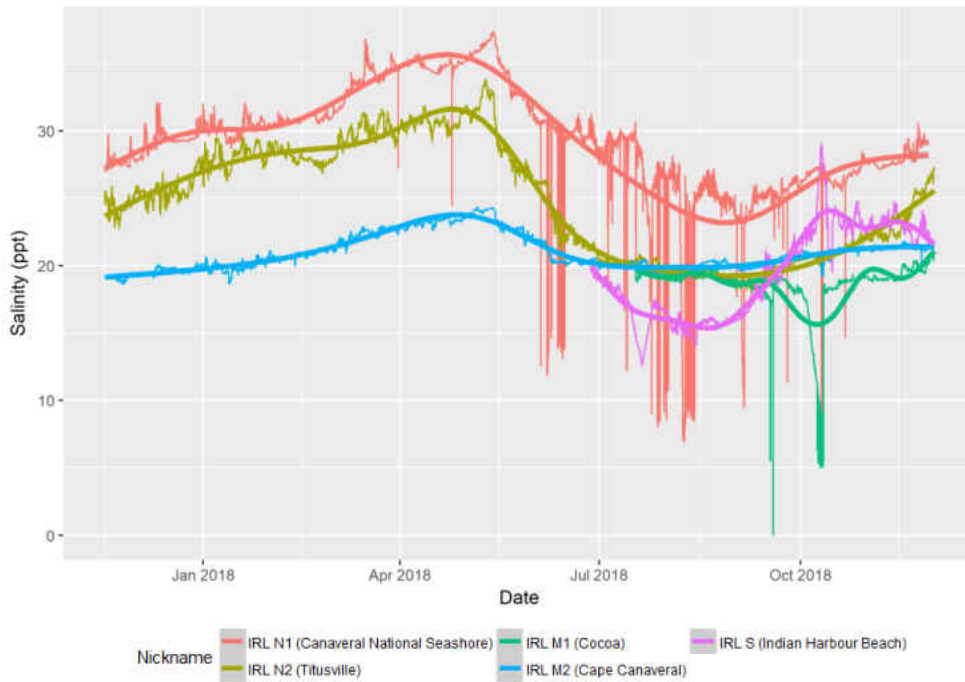


Figure 30: Salinity (ppt) at SJRWMD Continuous Monitoring Stations over time.

Sub-Regional Scale

Unfortunately, due to unit corrosion, data from the HOBO continuous logger at BC3 from May 2018 to present could not be retrieved. This produced an inconsistent amount of regional data that were not robust enough to accurately evaluate for significant differences. Therefore, only general trends for three sub-regions (Banana Creek, Banana River, and the ITL Impoundments) are described and displayed graphically. Over the course of this study, water temperature ranged from 10-30 C°, with an expected slow increase as the season transitioned from winter to summer (Figure 31). Light intensity was quickly overwhelmed by encrusting barnacles in the ITL impoundments (Myers Pers. Obs.), but remained fairly high in the Banana River, with little evidence of biofouling. After an initial peak in Banana Creek, light intensity ultimately decreased to roughly ITL levels (Figure 32).

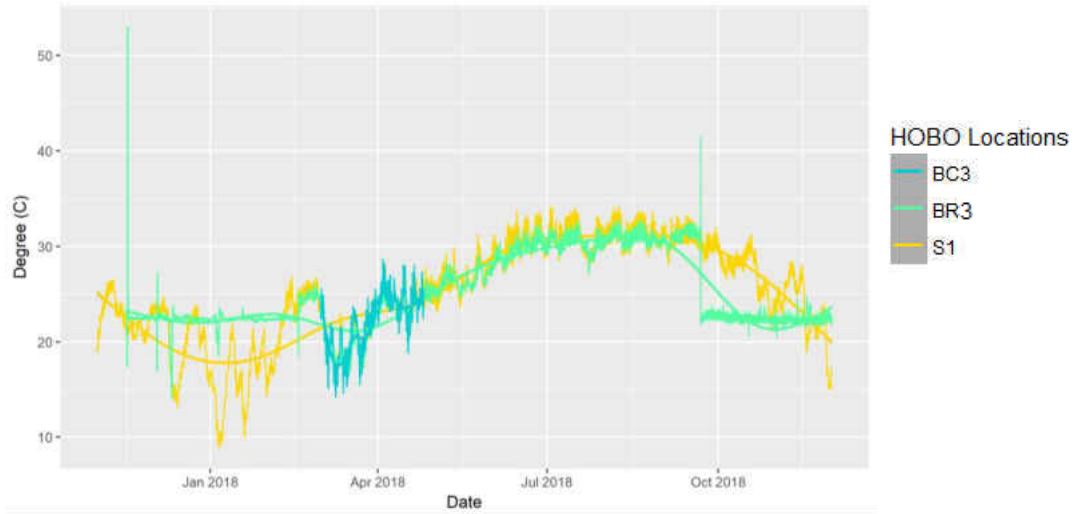


Figure 31: Water temperature (°C) across months and HOBO regions. Colors indicate receiver locations; Banana Creek in turquoise, Banana River in seagreen, and the ITL Impoundments in yellow.

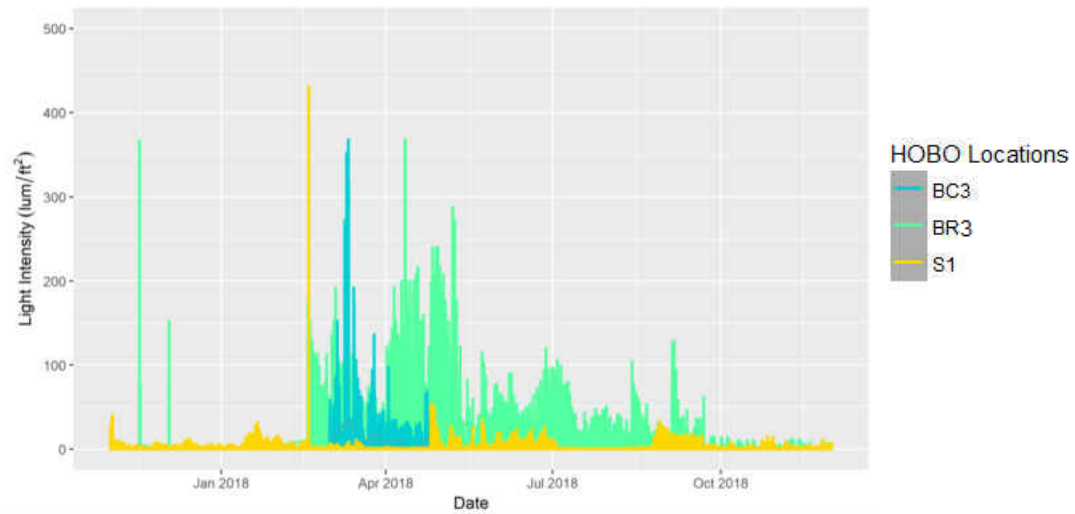


Figure 32: Light intensity (lum/ft²) across months and HOBO regions. Colors indicate receiver locations; Banana Creek in turquoise, Banana River in seagreen, and the ITL Impoundments in yellow.

Site Scale

Temperature, turbidity, and salinity samples taken at individual receivers were significantly different from each other by both site and month. While some sub-regional trends do emerge, such as turbidity levels in the ITL Impoundments, there is much more variation at an individual level, revealing specific outliers. For example, water temperatures at two receivers within the Banana River were significantly colder than the water temperatures at the other receivers in the system (all Tukey HSD p values < 0.001). Dissolved oxygen and depth samples deviated from this trend, showing significant differences by only month and site, respectively (Oxygen Month one-way ANOVA $F_{2,11} = 4.36$, $p < 0.001$; Depth Site one-way ANOVA $F_{2,12} = 26.38$, $p < 0.001$). Differences in all sampled environmental variables over months were generally dictated by seasonality.

There was a significant difference in water temperature by both site and month (Site one-way ANOVA $F_{2,12} = 24.34$, $p < 0.001$; Month one-way ANOVA $F_{2,11} = 155.65$, $p < 0.001$). Water temperatures at receivers BR5 and BR6 were significantly colder than the other receivers in the Banana River as well as receivers in the Banana Creek and the ITL Impoundments (Tukey HSD p values < 0.001). Monthly water temperatures ranged from 14.9° C to 30.6° C and followed a similar seasonal trend to the lagoon wide and regional water temperature data. Turbidity also showed significant differences by both site and month (Site one-way ANOVA $F_{2,12} = 3.59$, $p < 0.05$; Month one-way ANOVA $F_{2,11} = 3.14$, $p < 0.05$). Turbidity at receivers in the southern impoundment was significantly higher than the receivers in the Banana River adjacent to the ITL Impoundments (ITL_BR) (Tukey HSD p value < 0.05). The months of October and November had significantly lower turbidity levels than May (Tukey HSD p values < 0.05). Finally, there was a significant difference in salinity by both site and month (Site one-way ANOVA $F_{2,12} = 3.75$, $p < 0.05$; Month one-way ANOVA $F_{2,11} = 5.95$, $p < 0.001$). Water at receivers in the ITL Impoundments was significantly less saline than near Receiver BC4, and water at receivers BC4 and BC3A was significantly more saline than near BC2 (Tukey HSD p values < 0.05). From a temporal standpoint, water in August

was significantly less saline than water sampled in February, March and April; October water samples were significantly more saline than those from June, July, and August (Tukey HSD p values <0.05).

There was a significant difference in dissolved oxygen by month, but not by site (Month one-way ANOVA $F_{2,11} = 4.36$, $p < 0.001$). The month of September had significantly lower levels of dissolved oxygen than the months of February, April and May (all Tukey HSD p values < 0.05). Lastly, there was a significant difference in depth by site, but not by month (Site one-way ANOVA $F_{2,12} = 26.38$, $p < 0.001$). In general, Banana River was significantly deeper than both Banana Creek and the ITL Impoundments (Tukey HSD p values <0.05).

Variables and Linear Mixed Model Selection

The variance inflation factor found temperature and dissolved oxygen to be negatively collinear. Therefore, no models included both of these factors. Depth was the best singular environmental metric to predict both the residency time for fish Kilo and number of detections for fish November. Barometric pressure and temperature were the best single environmental variables to predict the number of detections for fish Kilo and residency time for fish November, respectively. Therefore, these metrics were used as base models and other environmental variables were added based on increasing AIC values. For example, as temperature had the next lowest AIC value after barometric pressure (fish Kilo, number of detections model), the subsequent model is constructed using two abiotic factors, the additive effect of barometric pressure and temperature on number of detections. Model development continued up to three abiotic factors, assessing all possible variables with both additive and interactive models (See all possible models in Appendix B). The number of detections produced by fish Kilo had four models with the same AIC scores, therefore the most parsimonious model (i.e. model with fewest parameters) was chosen; the additive effect of barometric pressure and temperature. The residency time generated by fish Kilo was best described by the interactive model of depth, pH, and photoperiod.

The number of detections produced by fish November was best explained by the interactive effect of depth and pH along with the additive effect of dissolved oxygen. The residency time generated by fish November was best described by the additive effect of temperature and depth along with the interactive effect of pH. The number of detections model for fish Kilo produced marginal and conditional R^2 values of ~ 0.63 (Figure 33). The residency time model of fish Kilo yielded marginal and conditional R^2 values of ~ 0.04 (Figure 34). The marginal and conditional R^2 values for the number of detections model for fish November were both ~ 0.99 (Figure 35). For the residency time model of fish November, the marginal R^2 value was ~ 0.56 with the conditional R^2 value at ~ 0.65 (Figure 36).

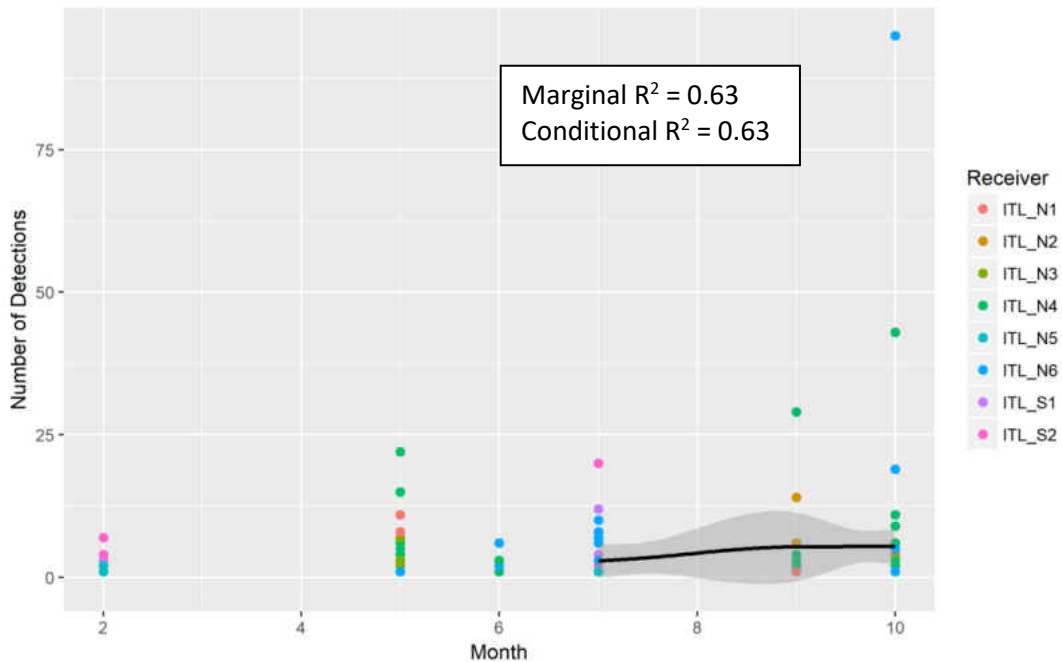


Figure 33: The best fitting model (Barometric pressure + temperature + 1|Month + 1|Station) plotted against the number of detections generated by fish Kilo over time.

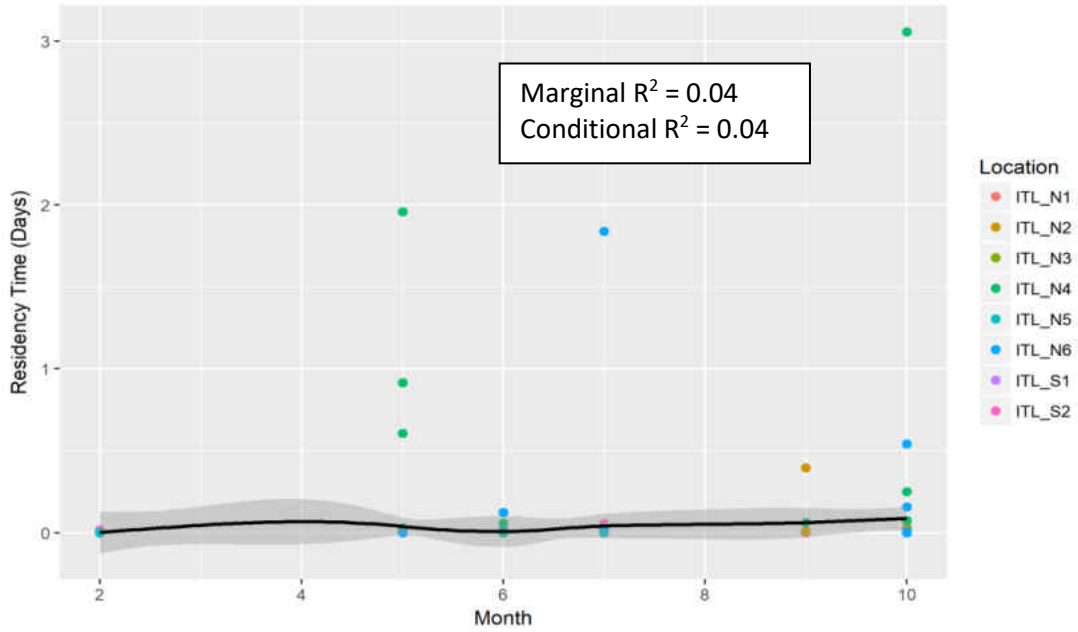


Figure 34: The best fitting model (Depth * pH * photoperiod + 1 | Month + 1 | Station) plotted against the residency time (days) of fish Kilo over time.

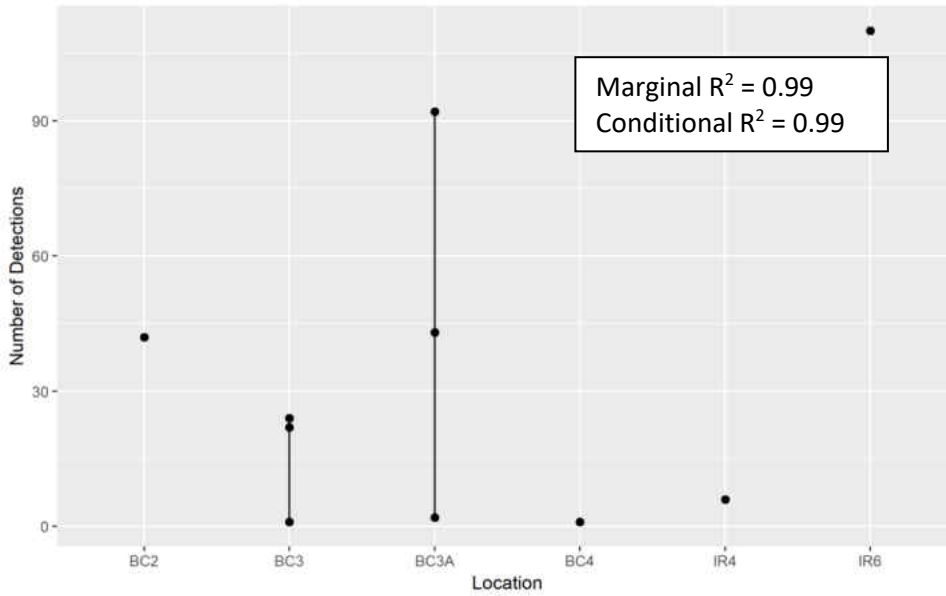


Figure 35: The best fitting model (Depth * pH + dissolved oxygen + 1 | Month + 1 | Station) plotted against the number of detections generated by fish November over time.

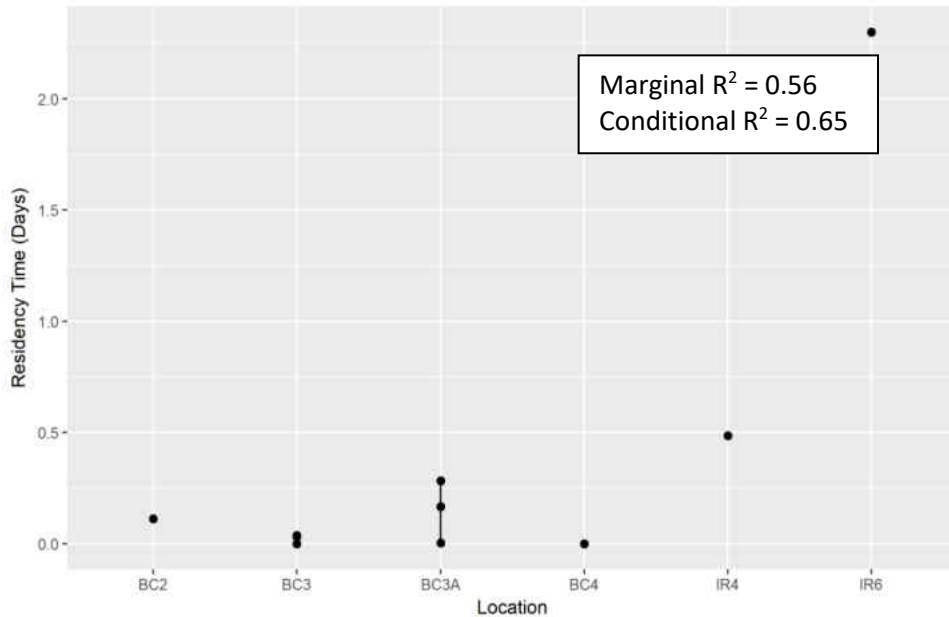


Figure 36: The best fitting model (Temperature + depth * pH + 1 | Month + 1 | Station) plotted against the residency time (days) of fish November over time.

Assessment of Movement Coupled with Abiotic Environment

Most detections and longer residency times for fish Kilo occurred between 27° and 30° C. All detections and residency times for fish November occurred between 22° and 23° C, with more detections at 22° C and slightly higher residency times at 23° C. Neither number of detections nor residency time were significantly different for either fish Kilo or fish November across temperature bins.

The majority of detections and longer residency times for fish Kilo were associated with saturated dissolved oxygen levels (~90-100%). There was a highly significant difference in the number of detections across dissolved oxygen bins for fish Kilo (Detection one-way ANOVA $F_{2,23} = 2.36$, $p < 0.001$; Figure 37). Super saturated dissolved oxygen levels (> 120%) were associated with significantly fewer detections (all Tukey HSD p values < 0.05). Most detections and residency time for fish November were associated with dissolved oxygen levels of approximately 6 mg/L, with ~7 mg/L being the highest

recorded. There were not a significant differences in the number of detections or residency time across dissolved oxygen bins for fish November.

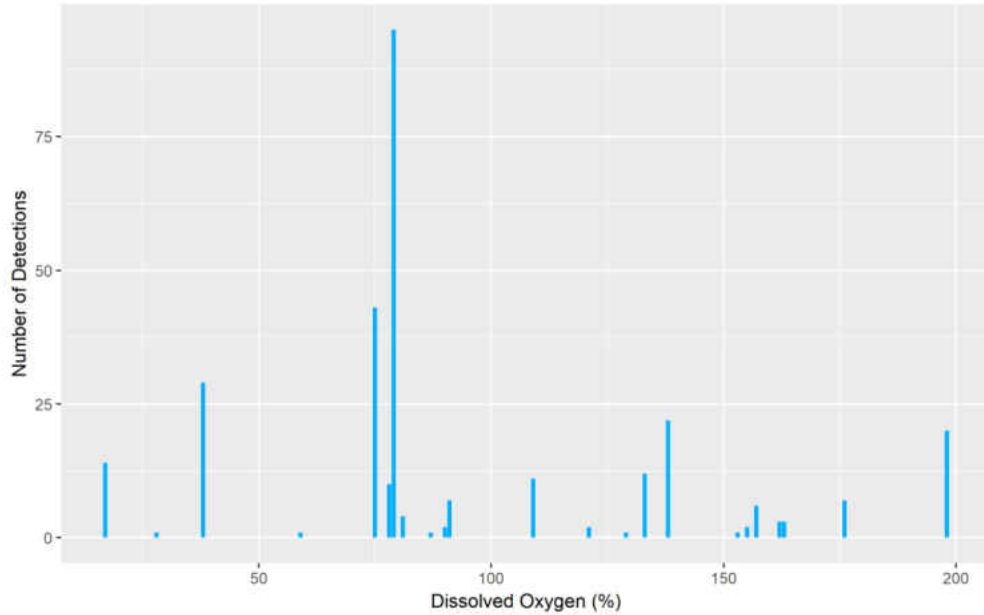


Figure 37: Number of detections generated by fish Kilo vs. dissolved oxygen (%) bins.

Detections and longer residency times largely occurred at lower levels of turbidity (<10 NTU) for fish Kilo, although there also were instances of higher residency times between 30-40 NTU. There was a significant difference in number of detections across turbidity bins for fish Kilo (Detection one-way ANOVA $F_{2,22} = 2.36$, $p < 0.05$; Figure 38). Significantly less detections occurred at turbidity levels greater than ~7 NTU (all Tukey HSD p values < 0.05). There were no data available to determine significant differences across turbidity bins for fish November.

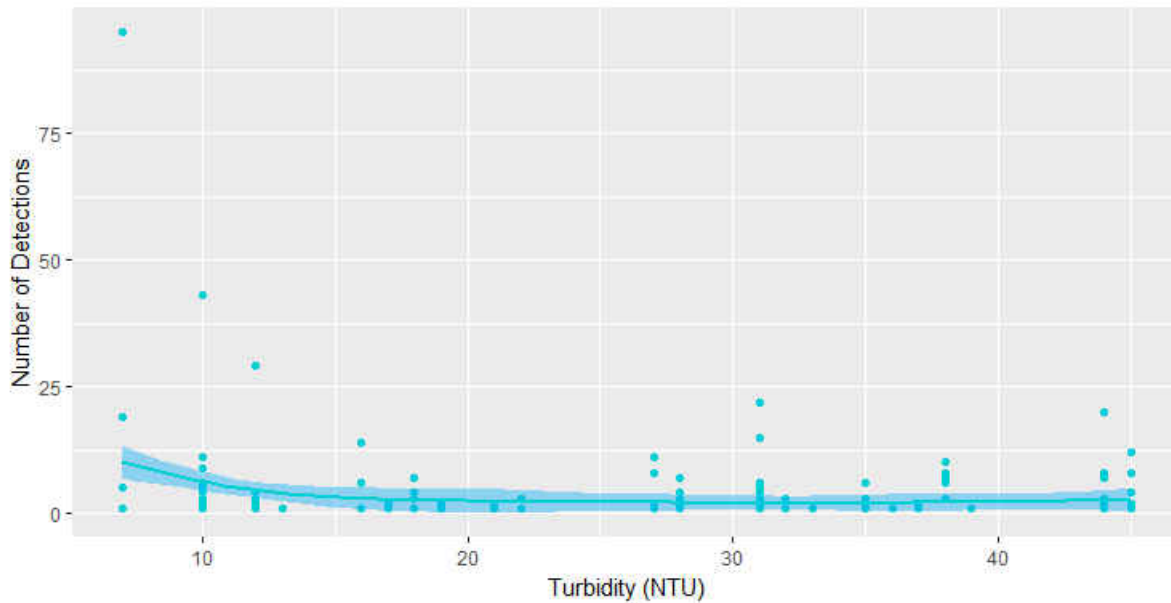


Figure 38: Number of detections generated by fish Kilo vs. turbidity (NTU) bins.

Most activity from fish Kilo transpired between pH levels of 8.0 and 8.2. There was a highly significant difference in the number of detections across pH bins for fish Kilo (Detection one-way ANOVA $F_{2,10} = 5.48$, $p < 0.001$; Figure 39). Significantly greater numbers of detections occurred at a pH of 8.0 than at all pH levels greater than 8.1 (all Tukey HSD p values < 0.05). All activity by fish November took place between pH levels of 8.0 and 8.2. There was a significant difference in residency time across pH bins for fish November (Time one-way ANOVA $F_{2,3} = 5.48$, $p < 0.001$; Figure 39). Residency time was significantly higher in waters with a pH of 8.1 than a pH of either 8.0 or 8.2 (all Tukey HSD p values < 0.05). No data are shown for pH 8.0 because the number of detections that occurred during that bin did not produce a measurable residency time (Figure 40).

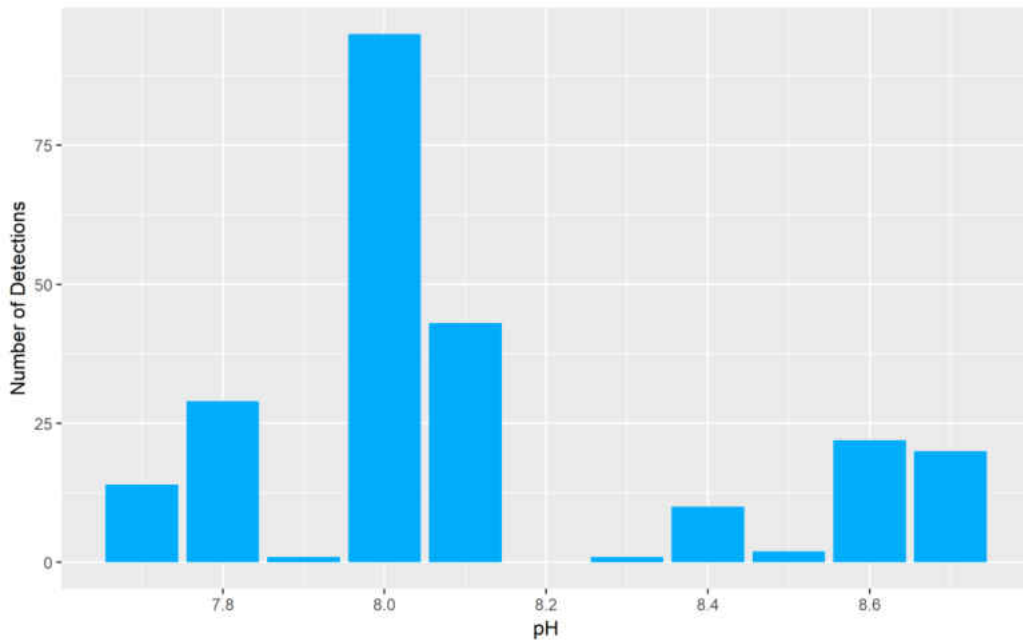


Figure 39: Number of detections generated by fish Kilo vs. pH bins.

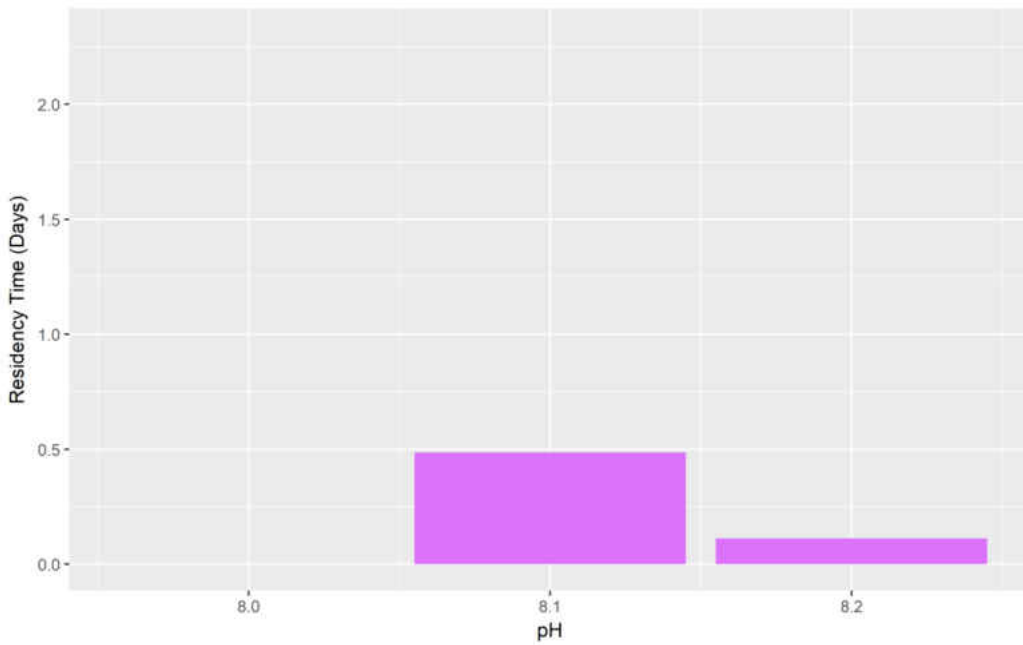


Figure 40: Residency time generated by fish November vs. pH bins.

Most detections by fish Kilo took place between salinity levels of 16 and 26 ppt, with higher residency times occurring between 19 and 26 ppt. There was a highly significant difference in number of

detections across salinity bins for fish Kilo (Detection one-way ANOVA $F_{2,11} = 4.33$, $p < 0.001$, Figure 41). Significantly more detections occurred at a salinity level of 25 ppt (all Tukey HSD p values < 0.05). All movement by fish November occurred when waters had salinity levels between 24 and 27 ppt, with 26 and 25 ppt producing a greater number of detections and residency time, respectively. There was no significant difference in the number of detections or residency time across salinity bins for fish November.

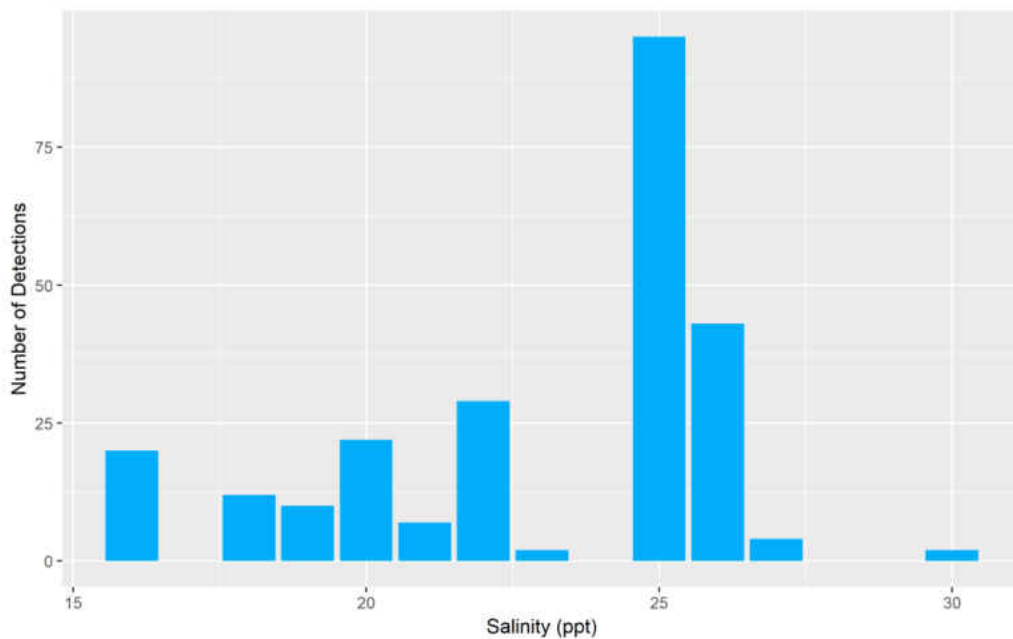


Figure 41: Number of detections generated by fish Kilo vs. salinity (ppt) bins.

Most detections and residency time for fish Kilo occurred at relatively greater depths, with higher activity between 1.2 and 1.4 m. However, there were no significant differences between number of detections or residency time across depth bins for fish Kilo. For fish November, all activity occurred at a depth of approximately 1.7 m, therefore significant differences between number of detections or residency time across depth bins could not be evaluated.

Fish Kilo demonstrated higher activity levels during photoperiods of 0.50, or 12 hours of daylight. There was not a significant difference in number of detections or residency time across photoperiod bins for fish Kilo. For fish November, all activity occurred at photoperiods of 0.40 (9.6 hours of daylight), therefore significant differences between number of detections or residency time across photoperiod bins could not be evaluated.

Lastly, activity generated by fish Kilo occurred during periods of barometric pressure ranging from 760.2 and 766.6, with most movement generally occurring during periods of relatively higher pressure. Neither number of detections nor residency time were significantly different across barometric pressure bins for fish Kilo. There were no data available to determine significant differences across barometric pressure bins for fish November.

The movement of the two fish case studies that have been described throughout this chapter were compared with averages of the best fitting explanatory environmental variables shared by both fish (depth, temperature, and pH). Fish November traveled from Banana Creek into the Indian River in early December, with depth remaining fairly stable. Temperature and pH both exhibited small fluctuations throughout. Data for December 8, as the fish moved farther south in the Indian River, were unavailable. Seasonal trends could not be determined due to the small window of movement produced (Figure 42). In terms of scale, fish Kilo did not disperse as great a distance as fish November, but had the most consistent activity as it remained within the ITL. The highest rate of activity corresponded with a decrease in depth, a slight decrease in temperature after a seasonal peak, and a slight decrease in pH (Figure 43).

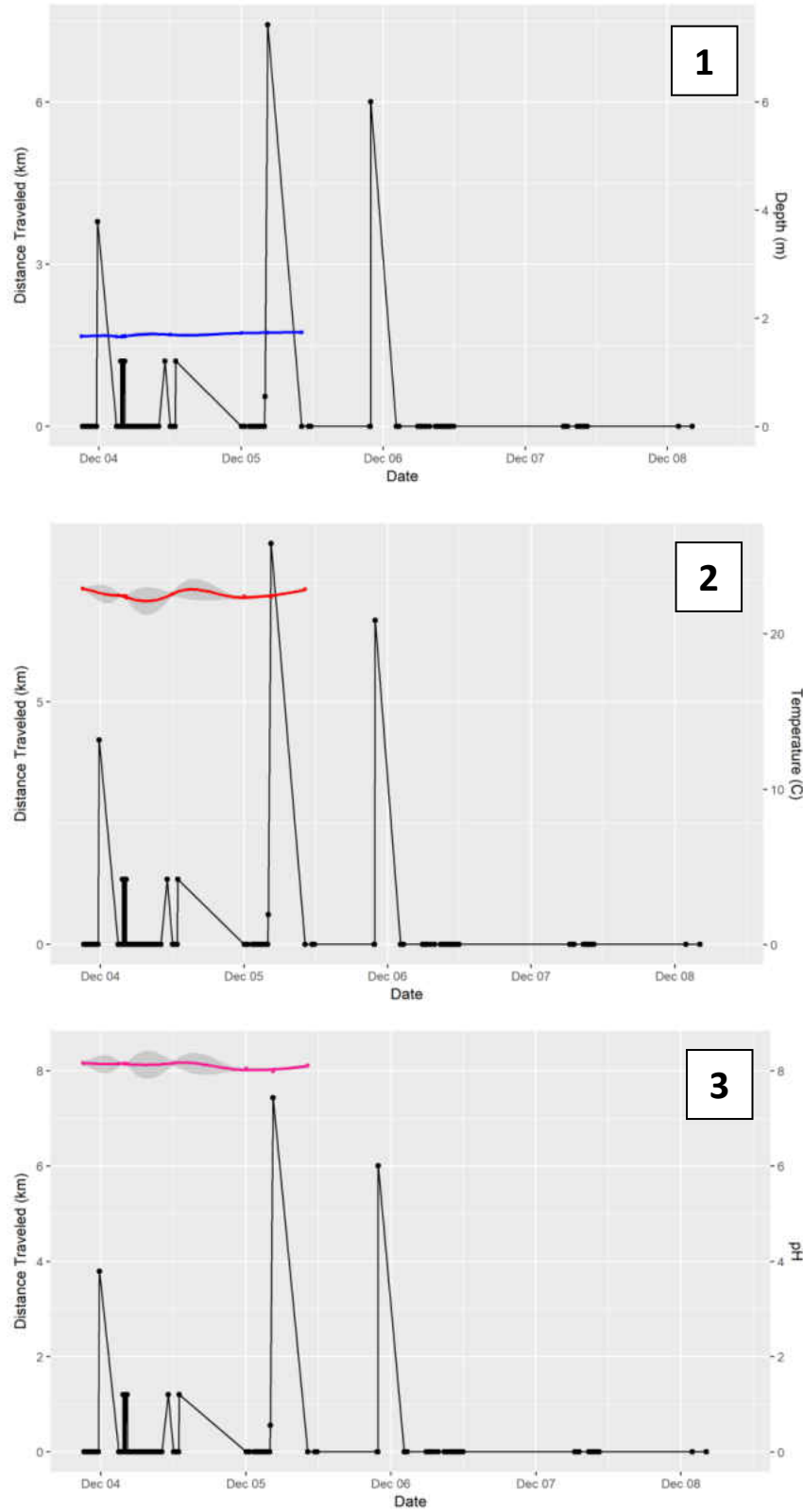


Figure 42: Distance traveled by fish November (black lines) compared to average hourly explanatory environmental variables 1) Depth (blue line), 2) Temperature (red line), 3) pH (pink line).

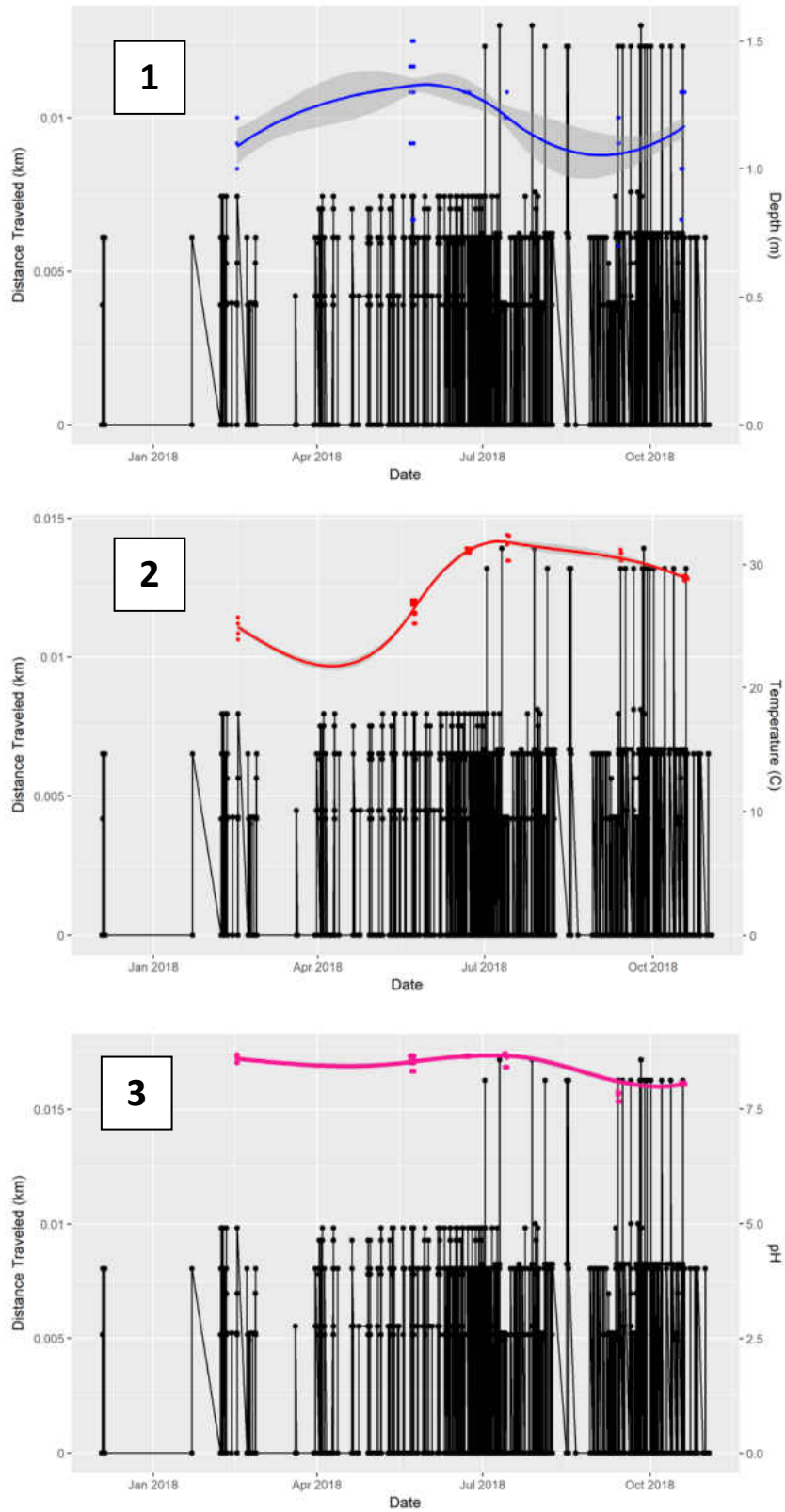


Figure 43: Distance traveled by fish Kilo (black lines) compared to monthly samples of explanatory environmental variables 1) Depth (blue line), 2) Temperature (red line), 3) pH (pink line).

Discussion

In this study, environmental factors were examined relative to fish movement and activity. Seasonal fluctuations in environmental metrics were observed at both broad and fine scales. Moving from lagoon scale to site specific sampling, much more individual variation was revealed, both spatially and temporally. The appropriate environmental data was assessed in relation to fish movement from two case studies and the data suggest that a multitude of abiotic factors should be considered when predicting the movement and activity of striped mullet, with each metric potentially affecting these fish in different ways. However, the model selection process demonstrated that the prediction value of most of the best fitting models relied heavily on random effects (e.g. month, site), rather than fixed effects (e.g. depth, pH). This should be taken into account when considering the prediction value of these models and their corresponding variables.

Abiotic Sampling

Lagoon Scale

On this large of a scale, geographic effects can be observed, with water temperature lower at higher latitudes. Interestingly, dissolved oxygen does not significantly follow the same trend, only corresponding to seasonal changes. Turbidity and pH are much more likely to be affected by region, with their levels impacted by surrounding land usage that determine the amount of sediment and particulate runoff into the water. Turbidity is also greatly impacted by wind and tides. Salinity can also be tied to a latitudinal gradient, with higher evaporation rates caused by increased temperatures. Regional characteristics coupled with seasonal fluctuations will dictate general striped mullet distribution and annual movement trends.

Sub-Regional Scale

Banana River exhibited higher amounts of light intensity than Banana Creek and the ITL Impoundments. This may contribute to the fishes' relatively fast movement through the area as increased amounts of light can leave them vulnerable to visual predators. The ITL Impoundments were most reflective of a seasonal pattern in temperature, most likely due to its shallow depths, allowing heat or cold to penetrate more quickly into the water column. However, this does pose a risk, as temperature can drive levels of dissolved oxygen dangerously low, leading to fish kills that have been observed in the study area.

Site Scale

By site, there was much more variation in all environmental metrics, with the exception of dissolved oxygen. This demonstrates that although these receivers are all in relatively close proximity in their respective geographic regions, site specific differences do occur. Favorable environmental conditions combined with explanatory factors such as an abundance of prey or refugia from predators may lead to fish favoring one particular site within a region; while habitat quality was not quantified in this study, this could be a potential reason why there were relatively higher detections near receivers BC2 or ITL_S1. The comparison is also somewhat skewed towards the metrics taken in the ITL Impoundments. Due to restrictions on project personnel and weather conditions, the Banana Creek and Banana River regions could not be sampled on a strict monthly basis.

Variables and Linear Mixed Model Selection

For both number of detections and residency time for both fish, the AIC scores for many of the models had relatively similar values, intimating that these factors are closely intertwined and all have an important role in predicting both of the response variables. For models concerning fish Kilo, the marginal and conditional R^2 values for number of detections were relatively high (~ 0.63), showing that the model fits the data well. However, as both values were the same, adding fixed effects did not improve the prediction ability of the model. Therefore, the random effects of month and site explained much of the variance while the fixed effects of abiotics (temperature and barometric pressure) did not account for any additional variance. For residency time, both the marginal and conditional R^2 values were quite low and also the same (~ 0.04), most likely due to the higher number of outliers throughout the residency time data set. Again, month and site, random effects, described most of the variance in residency time rather than the fixed effects of environmental metrics. For models concerning fish November, the marginal and conditional R^2 values for the number of detections were equally high (~ 0.99), demonstrating that this model fits the data extremely well. However, adding in abiotic variables (fixed effects) did not increase the prediction ability of the model, with the metrics of month and site describing most of the variance in fish November's number of detections. For residency time, the marginal and conditional R^2 values were relatively high (~ 0.56 and ~ 0.65 , respectively). This demonstrates that the random effects of month and site predict residency time values well, but including the environmental metrics (fixed effects) of temperature, depth, and pH will increase that ability. Although a myriad of environmental metrics influence fish behavior and movement, only the variables that were shown to be significant through this study's model selection (depth, temperature, dissolved oxygen, pH, barometric pressure, and photoperiod) are discussed below.

Previous research has shown that striped mullet may segregate by depth based on size, with larger fish preferring deeper water, especially during winter months (McDonough, 2006). As this study

contained only adult mullet, it can be deduced that most of the activity should have occurred at greater depths. The ITL impoundments are a shallow water habitat, never reaching more than 2.5 m in depth. As such, movement and residency time were restricted to these depths. However, portions of putative migratory pathways through the Indian River Lagoon, including the Banana and Indian Rivers are capable of reaching greater depths. The majority of movement and residency time in these deeper regions occurred at 6 m or greater. Striped mullet also primarily consume detritus and macroalgae, obtaining much of their prey from the benthos (Whitfield et al., 2012). Therefore, most of their foraging time will be spent near the bottom of the water column. Based on the size of the individual (as a proxy for age), depth may be used as a predictor variable of fish presence as it affects both short term and longer term activities.

It should also be noted that the detection range of these acoustic receivers is greatly affected by depth (Lacroix and Voegeli, 2000; Simpfendorfer et al., 2008; Mathies et al., 2014). Water depth and detection range are positively correlated; as water depth increases, so does the range of detection. Therefore, receivers in deeper waters (Banana and Indian Rivers, in this study) have the potential to record detections that would not necessarily be recorded at shallower receivers in Banana Creek and the ITL Impoundments. As number of detections was included as a response variable in the above models, including depth in the best fitting model may be a function of receiver location rather than a true indicator of striped mullet activity and movement. As such, the predictive value of this metric should be viewed with some caution.

On a broad scale, temperature is a vital metric that can dictate a species' physiology, behavior, and distribution (Magnuson et al., 1979; Harmon and Barton, 2013; Abram et al., 2017). By controlling the body temperature of an organism, this factor also regulates its metabolic rate and corresponding bodily functions (Kieffer et al., 1998). As such, organisms seek to occupy space that exhibit temperatures most ideal for performing crucial tasks, such as feeding and reproducing. If the temperature deviates

from optimal levels, organisms partake in thermoregulatory strategies to maintain appropriate physiological operations (Thorpe, 1994). Adult fish in particular are susceptible to thermal changes, having both a smaller range of thermal tolerance as well as exhibiting greater magnitudes of negative effects due to increased temperatures than juveniles (Rodnick et al., 2004; Portner and Farrell, 2008). On a species-specific level, temperature is well documented as regulating the rate of vitellogenesis in the striped mullet (Kuo et al., 1974; Kelley, 1990). In this study, fish activity generally occurred at temperatures less than 30° C, suggesting that water temperatures can be utilized to predict striped mullet movement based on their need to perform regulatory measures at higher temperatures or reproductive processes at seasonal low temperatures.

A major limiting factor for all aquatic organisms is oxygen, as there is both decreased availability of this resource in water and increased costs of its uptake (Kramer, 1983). Following the optimality theory in behavioral ecology, organisms will maximize resource extraction while concurrently minimizing its cost (Kramer, 1987). As oxygen uptake is critical for survival, fish will often forgo other resources in order to obtain this one vital element. For example, when fish are required to relocate to different areas for higher levels of dissolved oxygen, their predation risk and access to other resources (shelter, food, etc.) may be negatively affected. In addition, as more energy is required for oxygen extraction, less energy will be dedicated towards large movements, growth, and reproduction (Kramer, 1987). Although oxygen tolerance does vary somewhat by species, there is some evidence that the family *Mugilidae* is one of the most sensitive in this regard (Sylvester et. al, 1975; Wannamaker and Rice, 2000; Maes et al., 2007). This is supported by the results of this study, with most striped mullet activity occurring in waters with higher concentrations of dissolved oxygen (within their respective regions). While chronic decreased dissolved oxygen levels may have some long-term effects on reproduction and growth, acute changes due to temperature or phytoplankton blooms are more likely to influence the short-term activity of fish.

Sudden changes in pH can induce stress or death in aquatic organisms, even when the alterations occur within their typical range of tolerance (Zahangir, et al., 2015). Physiologically, when exposed to rapid fluctuations in pH, fish are unable to regulate their acid-base and ion levels and have difficulty maintaining proper ammonia excretion (Das et al., 2006). In addition, Jones et al. (1985) demonstrated that low pH led to both decreased activity and feeding, with fish actively avoiding the stressor when possible. In some fish species, low pH has also been linked to a decrease in oogenesis, egg fertility, and fry growth (Craig and Baksi, 1977; Ruby et al., 1977). Most fish activity took place in waters with a pH range of 7.7-8.2, suggesting that these levels are optimal for the fish. Due to the mainly physiological effect that pH has on fish, this metric is more likely to predict short-term activity, although seasonal mass movements and reproductive success may also be affected in the future through anthropogenic climate change.

Within the aquatic realm, fluctuations in barometric pressure are most associated with incoming weather fronts and storms. Prior studies have demonstrated that marine organisms will vacate areas in a storm's path, most likely due to a combination of signals from falling barometric pressure and other interrelated environmental metrics, such as wind speed (Heupel et al., 2003; Henderson et al., 2014). This is supported by the striped mullet movement in this study, as most activity took place during periods of higher pressure, which is often an indication of fair weather (UCAR, 2019). As well, some migratory species such as salmonids have also used barometric pressure as a cue to commence spawning migrations (Jonsson, 1991; Dedual and Jowett, 1999). Although there is not yet a definitive consensus, with other studies finding that barometric pressure has no effect on the movement of certain species (Warden and Lordio, 1975; Paukert et al., 2004), movement seems to be more closely tied to changes in barometric pressure rather than a specific barometric pressure value. (Rogers, 1998; Heupel et al., 2003; Henderson et al., 2014). In the future, research should incorporate differences in barometric pressure as a response variable to assess this metric's effect on fish activity and movement.

Photoperiod can impact both the behavioral habits and physiological characteristics of fish. In response to diurnal fluctuations in light regimes, many fish species exhibit cyclic movements amidst foraging and refuge habitats, known as diel vertical migration (Bentley et al., 2014). This behavior is performed as a dual feeding and predator avoidance strategy, with fish capitalizing on environmental conditions (i.e. darkness to obscure or limit predator vision) to minimize the risk of normally hazardous foraging grounds. Photoperiod duration is also recognized as playing a large role in regulating the seasonal reproductive cycle, mainly responsible for stimulating ovarian development in striped mullet (Kelley et al., 1991; McDonough et al., 2005). Multiple sources have observed the genesis of accelerated gonadal development and migratory behavior as natural photoperiod decreases to less than 12 hours (Dindo et al., 1978; Yelghi et al., 2011). The highest number of detections and residency time both occurred when percent daylight was less than 50%, suggesting that more fish movement transpired during these times. Thus, photoperiod may be used to assess fish movement based on their daily activity as well as a serve as possible indication for imminent migratory movement.

Assessment of Movement Coupled with Abiotic Environment

Of the two case studies assessed in this study, fish Kilo appeared to be more affected by environmental fluctuations. Dissolved oxygen, turbidity, pH, and salinity all had some effect on the movement (as a function of detections). The ITL impoundments, where all the movement from fish Kilo occurred, are a relatively small, enclosed area. As such, the fish may be more sensitive to changes in their environment, as certain environmental variables (e.g. dissolved oxygen) can reach tipping points that may cause conditions to deteriorate quite rapidly. By detecting these tipping points, fish may gain time to vacate the area before levels reach a critical status. Of all the abiotic measurements taken in association with the movement of fish November, only pH had a significant impact on residency time.

This may be due to the relatively small amount of movement data available to be analyzed in conjunction with complementary environmental data, as the environmental metrics associated with fish movement (DO, turbidity, pH and salinity) are unlikely to exhibit broad seasonal trends that could potentially trigger mass movements. More data is needed to be able to evaluate movement in the broader scale of the Indian River Lagoon, particularly in the Banana and Indian Rivers.

Although some environmental variables were able to accurately predict both the number of detections and the residency time of the fish at various locations, there did not seem to be an obvious catalyst to any of the movement documented in this study. In addition, only three distinct movement strategies were demonstrated, with a maximum of two fish employing each. More fish exhibiting each type of behavior are needed to provide additional support. Of those strategies, the movement that was displayed by fish November took place over a short amount of time and distance, only allowing for the analysis of a small fraction of environmental metrics experienced by the fish. Fish Kilo and Mike remained near their capture location, which does provide new information regarding skipped spawning, but does not serve to pinpoint specific catalysts for migratory movements. Future research should consider distance as a response variable to evaluate if any other metrics may be able to trigger large/mass movements.

Management Recommendations

Of the environmental variables shown to influence the movement of striped mullet in this study, pH and temperature are often greatly impacted through global-scale anthropogenic activities. Currently, fish can effectively respond to carbon dioxide induced acid-base fluctuations, but ocean acidification is beginning to impact a wide range of physiological functions in aquatic organisms (Munday et al., 2012; Heuer and Grosell, 2014). It is suggested that in the absence of rapid adaptation, increased carbon

dioxide levels may require an overall higher, more constant amount of ion exchange to maintain normal pH and ion balances within the fish (Heuer and Grosell, 2016). In turn, this would increase the cost of basic survival processes, which may cause negative trade-offs in other aspects of the species' life history, such as reproduction (Portner et al., 2004). With temperatures increasing relatively rapidly, many fish species are physically shifting their distributions northward (Goldfarb, 2017). Shifts in distribution are often accompanied by a host of issues, including altering available prey species, the amount of suitable habitat, and competition with other drifting species. Warming temperatures are also leading to a cruel paradox; higher temperatures result in higher metabolic rates while decreasing levels of dissolved oxygen in the ocean (Goldfarb, 2017; Breitburg et al., 2018). As large-scale fish kills have been witnessed in the study area, particularly the ITL Impoundments, this is an especially pertinent issue. On both coasts of Florida, red tide events in particular have been responsible for many recent fish kills that impacted thousands of mullet (Harpster, 2018; Munoz, 2018; Waymer, 2018). All of these factors may serve to limit fish activity and movement, particularly those involved with reproduction. Global-scale changes may impact striped mullet in several ways, from adjusting their prey base to shifting energy input from reproduction to survival. In order to address this, vigilant environmental monitoring as well as a sense of urgency regarding anthropogenic climate change need to be employed.

Conclusions

The future of the striped mullet will only be secured through the effective management of dispersal corridors. This mobile species relies heavily on secure dispersal pathways from inshore waters to offshore spawning grounds and only by effectively managing those dispersal corridors will this species reach and maintain sustainable levels. Striped mullet within the Indian River Lagoon face this very issue with nearly two dozen artificial structures dividing the waters of the Indian River Lagoon, interrupting historic flow and potentially affecting latitudinal movement of these fish (Gilmore, 1981; Larson, 1995;

Osborn, 2012). In this study, the metrics of network analysis identified areas that serve vital refuge and corridor functions. The environmental conditions associated with fish movement and activity were also evaluated on both spatial and temporal scales. By marrying the innate ecological and behavioral strategies of the species with the fluctuations and long-term trends of their natural environment, truly informed management actions can be implemented and produce positive results. This approach can also be applied to other migratory baitfish, as management begins to incorporate the more complex interactions that can often impact the movement and aggregation of these species. Fogarty and Botsford (2007) summarize this in a succinct manner, "In assessing actual management situations, the principal challenge is to go beyond simple model structures to provide more realistic representations of dispersal and connectivity linked to oceanographic conditions and to the behavior and life history characteristics of managed species."

APPENDIX A: CHAPTER I SUPPLEMENTAL GRAPHS

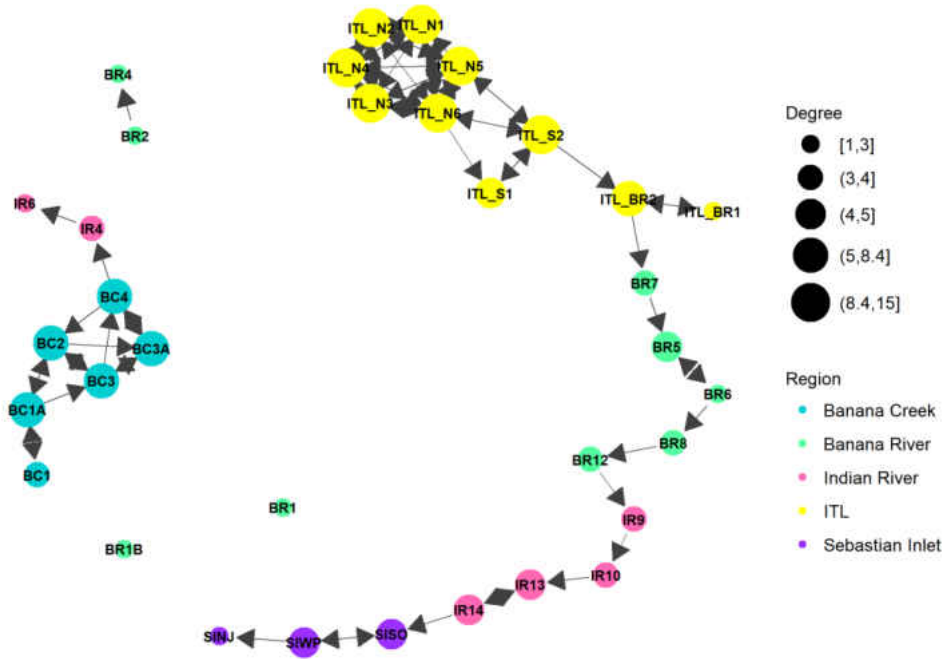


Figure 44: Fruchterman-Reingold network graph of receivers (nodes) and fish movement (edges) within the Indian River Lagoon. Node color indicates rough geographic region while node size represents degree centrality of each node.

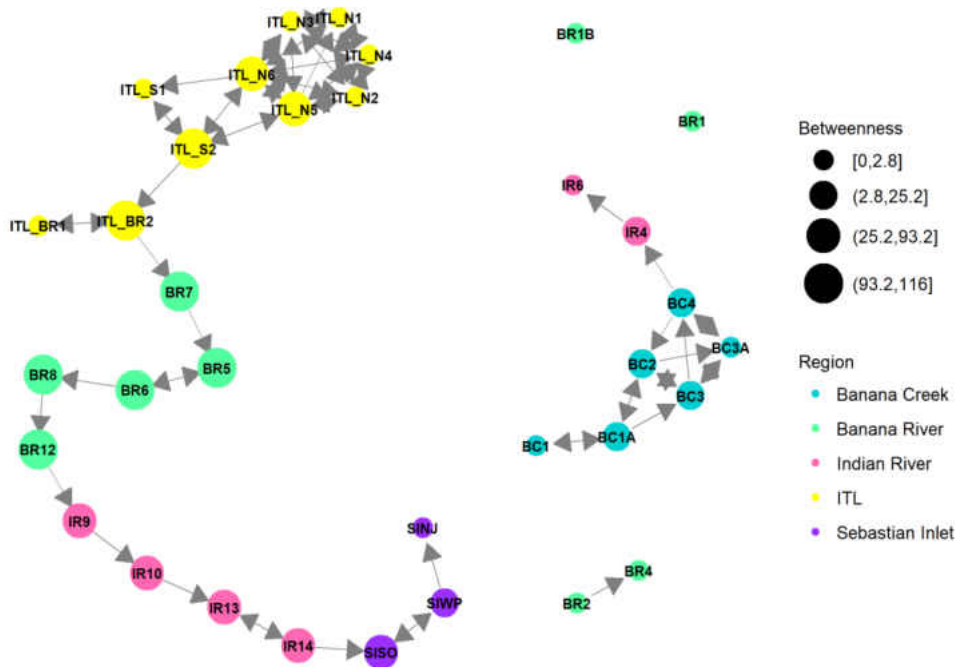


Figure 45: Fruchterman-Reingold network graph of receivers (nodes) and fish movement (edges) within the Indian River Lagoon. Node color indicates rough geographic region while node size represents betweenness centrality of each node.

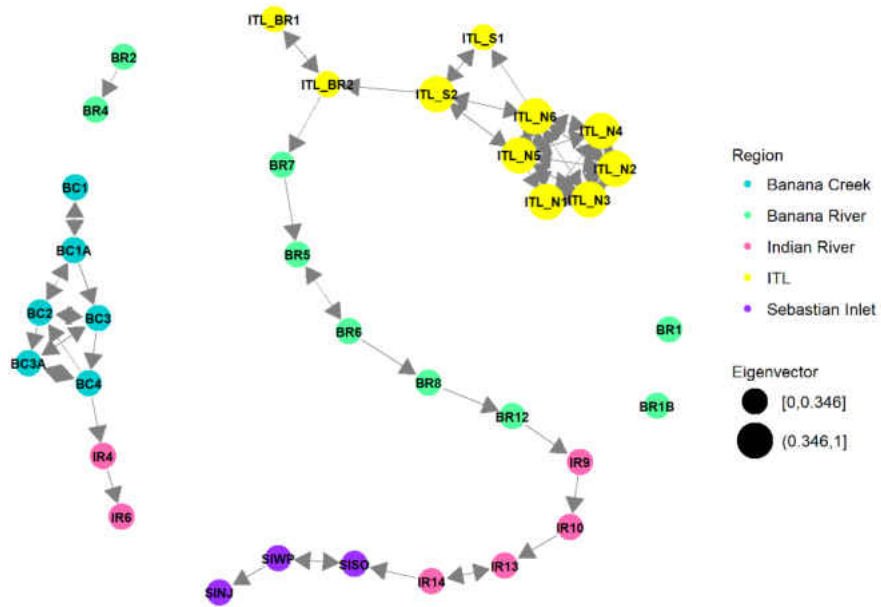


Figure 46: Fruchterman-Reingold network graph of receivers (nodes) and fish movement (edges) within the Indian River Lagoon. Node color indicates rough geographic region while node size represents eigenvector centrality of each node.

APPENDIX B: CHAPTER II SUPPLEMENTAL TABLES

Table 7: Mixed effect models used to explain number of detections for fish Kilo. The best fitting model in each group is bolded. The best fitting model overall is highlighted in yellow.

Fish Kilo: Detections			
One Environmental Variable			
Model	Model Variables	AIC Score	Weight
M1	Temp + (1 Month) + (1 Site)	1473.4	<0.001
M2	D.O. + (1 Month) + (1 Site)	1637.9	<0.001
M3	Turbidity + (1 Month) + (1 Site)	1597.6	<0.001
M4	Salinity + (1 Month) + (1 Site)	1603.3	<0.001
M5	pH + (1 Month) + (1 Site)	1635.3	<0.001
M6	Depth + (1 Month) + (1 Site)	1643.2	<0.001
M7	BP + (1 Month) + (1 Site)	989.8	1
M8	Day + (1 Month) + (1 Site)	1620.8	<0.001
Two Environmental Variables			
M9	BP + Temp + (1 Month) + (1 Site)	919.6	0.5
M10	BP + D.O. + (1 Month) + (1 Site)	991.9	<0.001
M11	BP + Turbidity + (1 Month) + (1 Site)	1006.4	<0.001
M12	BP + Salinity + (1 Month) + (1 Site)	988.6	<0.001
M13	BP + pH + (1 Month) + (1 Site)	997.8	<0.001
M14	BP + Depth + (1 Month) + (1 Site)	993.6	<0.001
M15	BP + Day + (1 Month) + (1 Site)	976.8	<0.001
M16	BP * Temp + (1 Month) + (1 Site)	919.6	0.5
M17	BP * D.O. + (1 Month) + (1 Site)	2864.2	<0.001
M18	BP * Turbidity + (1 Month) + (1 Site)	2707.0	<0.001
M19	BP * Salinity + (1 Month) + (1 Site)	3009.2	<0.001
M20	BP * pH + (1 Month) + (1 Site)	3116.9	<0.001
M21	BP * Depth + (1 Month) + (1 Site)	992.8	<0.001
M22	BP * Day + (1 Month) + (1 Site)	976.8	<0.001
Three Environmental Variables			
M23	BP + Temp + Turbidity + (1 Month) + (1 Site)	919.6	0.05
M24	BP + Temp + Salinity + (1 Month) + (1 Site)	919.6	0.05
M25	BP + Temp + pH + (1 Month) + (1 Site)	919.6	0.05
M26	BP + Temp + Depth + (1 Month) + (1 Site)	919.6	0.05

M27	BP + Temp + Day + (1 Month) + (1 Site)	919.6	0.05
M28	BP * Temp + Turbidity + (1 Month) + (1 Site)	919.6	0.05
M29	BP * Temp + Salinity + (1 Month) + (1 Site)	919.6	0.05
M30	BP * Temp + pH + (1 Month) + (1 Site)	919.6	0.05
M31	BP * Temp + Depth + (1 Month) + (1 Site)	919.6	0.05
M32	BP * Temp + Day + (1 Month) + (1 Site)	919.6	0.05
M33	BP * Temp * Turbidity + (1 Month) + (1 Site)	919.6	0.05
M34	BP * Temp * Salinity + (1 Month) + (1 Site)	919.6	0.05
M35	BP * Temp * pH + (1 Month) + (1 Site)	919.6	0.05
M36	BP * Temp * Depth + (1 Month) + (1 Site)	919.6	0.05
M37	BP * Temp * Day + (1 Month) + (1 Site)	919.6	0.05
M38	BP + Temp * Turbidity + (1 Month) + (1 Site)	919.6	0.05
M39	BP + Temp * Salinity + (1 Month) + (1 Site)	919.6	0.05
M40	BP + Temp * pH + (1 Month) + (1 Site)	919.6	0.05
M41	BP + Temp * Depth + (1 Month) + (1 Site)	919.6	0.05
M42	BP + Temp * Day + (1 Month) + (1 Site)	919.6	0.05
All Environmental Variables			
M43	Temp + Turbidity + Salinity + pH + Depth + BP + Day + (1 Month) + (1 Site)	919.6	0.5
M44	Temp + Turbidity + Salinity + pH + Depth + BP + Day + (1 Month) + (1 Site)	919.6	0.5
Best Fitting Models			
M7	BP + (1 Month) + (1 Site)	989.8	<0.001
M9	BP + Temp + (1 Month) + (1 Site)	919.6	0.25
M16	BP * Temp + (1 Month) + (1 Site)	919.6	0.25

M43	Temp + Turbidity + Salinity + pH + Depth + BP + Day + (1 Month) + (1 Site)	919.6	0.25
M44	Temp * Turbidity * Salinity * pH * Depth * BP * Day + (1 Month) + (1 Site)	919.6	0.25

Table 8: Mixed effect models used to explain residency time exhibited by fish Kilo. The best fitting model in each group is bolded. The best fitting model overall is highlighted in yellow.

Fish Kilo: Residency Time			
One Environmental Variable			
Model	Model Variables	AIC Score	Weight
M1	Temp + (1 Month) + (1 Site)	96.2	<0.001
M2	D.O. + (1 Month) + (1 Site)	66.0	0.0031
M3	Turbidity + (1 Month) + (1 Site)	64.2	0.0075
M4	Salinity + (1 Month) + (1 Site)	61.7	0.0255
M5	pH + (1 Month) + (1 Site)	56.1	0.4290
M6	Depth + (1 Month) + (1 Site)	55.7	0.5350
M7	BP + (1 Month) + (1 Site)	98.0	<0.001
M8	Day + (1 Month) + (1 Site)	74.3	<0.001
Two Environmental Variables			
M9	Depth + Temp + (1 Month) + (1 Site)	96.9	<0.001
M10	Depth + D.O. + (1 Month) + (1 Site)	68.0	0.0016
M11	Depth + Turbidity + (1 Month) + (1 Site)	65.6	0.0053
M12	Depth + Salinity + (1 Month) + (1 Site)	63.3	0.0167
M13	Depth + pH + (1 Month) + (1 Site)	56.9	0.4069
M14	Depth + BP + (1 Month) + (1 Site)	87.6	<0.001
M15	Depth + Day + (1 Month) + (1 Site)	74.7	<0.001
M16	Depth * Temp + (1 Month) + (1 Site)	86.1	<0.001
M17	Depth * D.O. + (1 Month) + (1 Site)	77.8	<0.001
M18	Depth * Turbidity + (1 Month) + (1 Site)	70.9	<0.001
M19	Depth * Salinity + (1 Month) + (1 Site)	66.3	0.0038
M20	Depth * pH + (1 Month) + (1 Site)	56.3	0.5648
M21	Depth * BP + (1 Month) + (1 Site)	90.1	<0.001
M22	Depth * Day + (1 Month) + (1 Site)	70.6	<0.001
Three Environmental Variables			
M23	Depth + pH + Temp + (1 Month) + (1 Site)	98.9	<0.001

M24	Depth + pH + D.O. + (1 Month) + (1 Site)	69.6	<0.001
M25	Depth + pH + Turbidity + (1 Month) + (1 Site)	67.0	<0.001
M26	Depth + pH + Salinity + (1 Month) + (1 Site)	64.7	<0.001
M27	Depth + pH + BP + (1 Month) + (1 Site)	88.0	<0.001
M28	Depth + pH + Day + (1 Month) + (1 Site)	55.9	<0.001
M29	Depth * pH + Temp + (1 Month) + (1 Site)	94.6	<0.001
M30	Depth * pH + D.O. + (1 Month) + (1 Site)	68.9	<0.001
M31	Depth * pH + Turbidity + (1 Month) + (1 Site)	66.2	<0.001
M32	Depth * pH + Salinity + (1 Month) + (1 Site)	63.9	<0.001
M33	Depth * pH + BP + (1 Month) + (1 Site)	84.7	<0.001
M34	Depth * pH + Day + (1 Month) + (1 Site)	55.1	<0.001
M35	Depth * pH * Temp + (1 Month) + (1 Site)	82.8	<0.001
M36	Depth * pH * D.O. + (1 Month) + (1 Site)	93.0	<0.001
M37	Depth * pH * Turbidity + (1 Month) + (1 Site)	78.4	<0.001
M38	Depth * pH * Salinity + (1 Month) + (1 Site)	71.2	<0.001
M40	Depth * pH * BP + (1 Month) + (1 Site)	81.1	<0.001
M41	Depth * pH * Day + (1 Month) + (1 Site)	33.7	1
M42	Depth + pH * Temp + (1 Month) + (1 Site)	86.0	<0.001
M43	Depth + pH * D.O. + (1 Month) + (1 Site)	80.0	<0.001
M44	Depth + pH * Turbidity + (1 Month) + (1 Site)	74.7	<0.001
M45	Depth + pH * Salinity + (1 Month) + (1 Site)	70.0	<0.001
M46	Depth + pH * BP + (1 Month) + (1 Site)	88.4	<0.001
M47	Depth + pH * Day + (1 Month) + (1 Site)	52.2	<0.001
All Environmental Variables			

M48	Temp + Turbidity + Salinity + pH + Depth + BP + Day + (1 Month) + (1 Site)	919.6	0.5
M49	Temp * Turbidity * Salinity * pH * Depth * BP * Day + (1 Month) + (1 Site)	919.6	0.5
Best Fitting Models			
M6	Depth + (1 Month) + (1 Site)	56.1	<0.001
M20	Depth + pH + (1 Month) + (1 Site)	56.3	<0.001
M41	Depth * pH * Day + (1 Month) + (1 Site)	33.7	1
M48	Temp + Turbidity + Salinity + pH + Depth + BP + Day + (1 Month) + (1 Site)	919.6	<0.001

Table 9: Mixed effect models used to explain the number of detections for fish November. The best fitting model in each group is bolded. The best fitting model overall is highlighted in yellow.

Fish November: Detections			
One Environmental Variable			
Model	Model Variables	AIC Score	Weight
M1	Temp + (1 Site)	321.3	0.48
M2	D.O. + (1 Site)	347.0	<0.001
M3	Salinity + (1 Site)	346.6	<0.001
M4	pH + (1 Site)	346.3	<0.001
M5	Depth + (1 Site)	321.2	0.52
Two Environmental Variables			
M6	Depth + Temp + (1 Site)	260.8	<0.001
M7	Depth + D.O. + (1 Site)	291.8	<0.001
M8	Depth + Salinity + (1 Site)	249.5	<0.001
M9	Depth + pH + (1 Site)	293.7	<0.001
M10	Depth * Temp + (1 Site)	214.2	<0.001
M11	Depth * D.O. + (1 Site)	158.1	<0.001
M12	Depth * Salinity + (1 Site)	249.4	<0.001
M13	Depth * pH + (1 Site)	123.4	1
Three Environmental Variables			
M14	Depth + pH + Temp + (1 Site)	176.4	<0.001
M15	Depth + pH + D.O. + (1 Site)	147.2	<0.001
M16	Depth + pH + Salinity + (1 Site)	155.5	<0.001
M17	Depth * pH + D.O. + (1 Site)	98.0	1
M18	Depth * pH + Salinity + (1 Site)	120.9	<0.001
All Environmental Variables			
M19	Temp + Salinity + pH + Depth + (1 Site)	121.3	1
Best Fitting Models			
M5	Depth + (1 Site)	321.2	<0.001
M13	Depth * pH + (1 Site)	123.4	<0.001
M17	Depth * pH + D.O. + (1 Site)	98.0	1
M19	Temp + Salinity + pH + Depth + (1 Site)	121.3	<0.001

Table 10: Mixed effect models used to explain residency time for fish November. The best fitting model in each group is bolded. The best fitting model overall is highlighted in yellow.

Fish November: Residency Time			
One Environmental Variable			
Model	Model Variables	AIC Score	Weight
M1	Temp + (1 Site)	-12.5	1
M2	D.O. + (1 Site)	109.3	<0.001
M3	Salinity + (1 Site)	107.1	<0.001
M4	pH + (1 Site)	103.8	<0.001
M5	Depth + (1 Site)	102.9	<0.001
Two Environmental Variables			
M6	Temp + Salinity + (1 Site)	-15.1	0.0018
M7	Temp + pH + (1 Site)	-14.7	0.0014
M8	Temp + Depth + (1 Site)	-17.5	0.0058
M9	Temp * Salinity + (1 Site)	-19.0	0.0123
M11	Temp * pH + (1 Site)	-25.3	0.2887
M12	Temp * Depth + (1 Site)	-27.0	0.6901
Three Environmental Variables			
M14	Temp + Depth + Salinity + (1 Site)	-19.7	<0.001
M15	Temp + Depth + pH + (1 Site)	-22.5	<0.001
M16	Temp * Depth + Salinity + (1 Site)	-27.4	<0.001
M17	Temp * Depth + pH + (1 Site)	-30.1	<0.001
M18	Temp + Depth * Salinity + (1 Site)	-27.6	<0.001
M19	Temp + Depth * pH + (1 Site)	-72.5	1
All Environmental Variables			
M20	Temp + Salinity + pH + Depth + (1 Site)	-25.1	1
Best Fitting Models			
M5	Temp + (1 Site)	-12.5	<0.001
M13	Temp * Depth + (1 Site)	-27.0	<0.001
M17	Temp + Depth * pH + (1 Site)	-72.5	1
M19	Temp + Salinity + pH + Depth + (1 Site)	-25.1	<0.001

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