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The Patterns of Occurrence, Management, and Behavioral Ecology of Fish Spawning Aggregations in Southeast Florida

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

THE PATTERNS OF OCCURRENCE, MANAGEMENT, AND BEHAVIORAL ECOLOGY OF FISH SPAWNING AGGREGATIONS IN SOUTHEAST FLORIDA

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Benjamin M. Binder

2022

To: Dean Michael R. Heithaus

College of Arts, Sciences and Education

This dissertation, written by Benjamin M Binder, and entitled The Patterns of Occurrence, Management, and Behavioral Ecology of Fish Spawning Aggregations in Southeast Florida, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

Yannis Papastamatiou

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Date of Defense: April 1, 2022

The Dissertation of Benjamin M. Binder is approved.

Dean Michael R. Heithaus

College of Arts, Sciences and Education

Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2022

Chapter I of this dissertation has been published in Frontiers of Marine Science and has been formatted according to their guidelines. Chapter IV is formatted to be submitted to “Fisheries Research” and a portion of Chapter V is soon to be prepared for submission to “Journal of Applied Ecology”.

CHAPTER I

Binder, B. M., Taylor, J. C., Gregg, K., and Boswell, K. M. (2021). Fish Spawning Aggregations in the Southeast Florida Coral Reef Ecosystem Conservation Area: A Case Study Synthesis of User Reports, Literature, and Field Validation Efforts. Front. *Mar. Sci.* 8. doi:10.3389/fmars.2021.671477.

DEDICATION

Had I written this section about five months ago, it would have been very different. But now, with my little boy on the way, there is nothing else I would rather do than dedicate this to you …… Apparently its bad luck to tell people your name before your born, so you get to be a series of dots for this one, even though all of our friends already know, whoops! I can’t wait to meet you and tell you about these last several years. They were tough, but this is for you and your momma, who made it all worth doing. Your mom is the most supportive person on the planet, and she has given me the space and assurance that I needed to get this done through long days and nights of analysis and writing. Thank you, my love. Naturally, mom and dad, you guys get a mention too! Where would I be without your motivation and work ethic? Thank you for pushing me to work harder and reach higher. I don’t know if I would have pushed this far along the path without your help. Lastly, my hams, Finn and Jack… You guys can’t read because you’re dogs, but everyone else will know how important you’ve been to me through this process.

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The list of people that deserve mentioning is long and I will certainly forget some of those that have been influential in my graduate school journey. I'll give it my best effort though, and begin where I began! I probably would not have gotten to this point if it had not been for Dr. Erin Burge, my research advisor at Coastal Carolina University, that forwarded a summer job opportunity one Friday morning in the spring of 2010. Thank you, Dr. Burge, for introducing me to the wide world of marine research, guiding me through my first conference experience, and kicking me out of CCU for a semester to work for FWC. That is one of the best decisions I've ever made. Which brings me to Dr. Alejandro Acosta. You must have seen potential I suppose, because you gave me the latitude to explore and learn while working at FWC. I developed too many skills to list while working with the fish team, and I believe that it made me the MacGyver field hand that I am today. It is because of the opportunities you gave me that I had the confidence to pursue graduate school. Jeff Simmonds, we miss you. I wish I could thank you for being such an awesome role model when I joined the fish team so many years ago. You and the fish team are the reason I have limitless confidence in the water. The good Dr. Taylor, Chris, you were there too. You are the reason I discovered FSA research and hydroacoustics (what a terrible word), and ultimately the reason I ended up here today I believe. Thank you for the comedy, professionalism, and guidance that you have provided along the way. I really hope there is more to come.

That gets us to FIU… still a long ways to go. I've been here a while, but there have been several people that have made it far more enjoyable and productive. Without a doubt, Dr. B, Kevin, Dr. Kevin Boswell (dad), has molded the way I think about science. Talk about opportunities. I’ve lived at the bottom of the sea, seen the sun for 3 weeks straight, seen whales from a zodiac, became a microgreens farmer, welder, mechanical and electrical engineer, been detained by customs in foreign countries, and held an authentic Tyrannosaurus Rex fossil while drinking excellent beer in Germany. This guy deserves a section to himself, but my time is coming to an end, so I’ll refer you to him directly for better stories. Thank you, Kevin, for everything above, and for providing spectacular guidance along the way. I made the right decision joining your lab and wouldn’t have it any other way.

What would this have been without friends and colleagues as well? Mark Barton, my roommate, hunting buddy (when I wasn’t boring), soon to be uncle to ……, my brother. Thank you for everything. You saw me through terrible hardship and the greatest of times. I have so many great memories through the years we’ve known each other, and it would have sucked without you there. Allison White and Nick Tucker, thank you both for your support in the field, friendship, brainstorming and editing help, and most importantly… Renaissance fair (and all other costume opportunities). Let’s be honest, we’d probably do that professionally if we could make a living! I hope the viking hoard rides again, and I am always at your disposal as you both finish your PhDs and beyond. Kirk Gastrich and Gina Clementi, thank you both for keeping the prop turning as we prepare for perm slammin in the Keys. That has truly been the greatest time I’ve ever had in the field, and I look forward to advancing our empire every year. Without your help it would not be possible to keep it going, and you both deserve many key lime pie bar’s on a stick for your service! To many others that have helped in the field, offered guidance, and been there, thank you all.

Lastly, the work contained in this dissertation and all my activities at FIU would not have been possible without funding provided by the Coral Reef Conservation Program, the Florida Department of Environmental Protection, Florida Fish and Wildlife Conservation Commission, the Marine Fisheries Initiative, Bonefish Tarpon Trust, and the FIU Dissertation Year Fellowship.

ABSTRACT OF THE DISSERTATION

THE PATTERNS OF OCCURRENCE, MANAGEMENT, AND BEHAVIORAL ECOLOGY OF FISH SPAWNING AGGREGATIONS IN SOUTHEAST FLORIDA

Benjamin M. Binder

Florida International University, 2022

Miami, Florida

Professor Kevin M. Boswell, Major Professor

The formation of fish spawning aggregations (FSAs) is an essential life history process for more than 150 species worldwide. Decades of research have provided a wealth of information to describe FSA dynamics, but there are many regions where their occurrence, behavior, and susceptibility to environmental variation remain uncharacterized. Even in regions that host an extensive research infrastructure such as South Florida, a standardized survey program to locate, validate, and monitor FSAs has not been established. This dissertation addresses those shortcomings in several ways. First, I present a comprehensive synthesis of available FSA literature from the region, which was combined with unpublished data sources, local reports from stakeholders, and field validation efforts to aid resource managers in identifying priority areas and species for future management activities. The successive chapters use goliath grouper (*Epinephelus itajara*, GG) as a model species to evaluate three topics in FSA research. First, I characterize the response of GG and local fish communities to intense storm activity and sustained periods of high

turbidity and demonstrate their capacity to adapt to rapidly changing conditions, with the understanding that climatic conditions and continued urbanization may eventually lead to disruption in ecosystem processes. In chapter four, I focus on the application of active acoustics to remotely assess FSAs at multiple spatiotemporal scales. I also evaluate changes in GG density as a factor of survey approach and provide recommendations for an optimized technique to monitor GG aggregations statewide. In chapter five, I integrate data from multiple remote-sensing platforms to take a closer look at fine-scale behaviors beyond the reach of active acoustics. Specifically, I test the capacity of acoustic telemetry to characterize behavioral changes in response to environmental variation and provide insight into analytically classified behaviors such as foraging and courtship. As GG spawning has remained historically elusive, these data contain unprecedented observations that could serve to improve our understanding of GG aggregation dynamics at previously undescribed scales. This dissertation is a culmination of research focused on improving regional FSA science, demonstrates the utility of remote sensing to monitor FSAs, and characterizes behaviors that were previously unobservable by traditional methodologies.

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CHAPTER I. INTRODUCTION

A wide range of marine fishes from around the world form transient spawning aggregations at recurring locations during well defined “spawning seasons” each year (Domeier and Colin 1997). These events are characterized by the arrival of 10’s – 1000’s of individuals that may have traveled 100’s of kilometers for the sole purpose of participating in group spawning events at distinct bathymetric or oceanographic features (e.g., high-relief promontories or areas of dynamic current activity) (Sadovy de Mitcheson and Colin 2012). There is uncertainty related to spawning frequency during a given year (for many species), but conservative estimates from well-studied species have indicated that each spawning event may represent 30-100% of an individual’s annual reproductive investment (Domeier and Colin 1997). As such, these events represent exceptionally important periods in the life history of aggregating species, and steer the trajectory of population growth or decline through time.

While we consider many FSAs to be relatively predictable in space and time, some species exhibit a high degree of variability in occurrence, especially in areas of contiguous reefs with poorly defined promontories (Farmer et al. 2017, Kobara et al. 2013). As a result, many aggregations remain understudied, with an estimated 50% of worldwide aggregations uncharacterized or unmanaged (Russell et al. 2016). This paucity of information does not exclusively originate from remote locations that present significant logistical challenges to researchers, but includes highly developed coastal regions with extensive marine research infrastructure, such as southeast Florida (Binder et al. 2021). The nature of this issue is complex, but due to environmentally driven variations in occurrence, habitat degradation that has seen aggregations scattered over broad regions, or years of intense fishing that has depleted aggregations, they remain unaccounted for in many regional resource management plans (Binder et al. 2021). Indeed, combined with their ephemeral nature and variability, traditional observational or extractive sampling methods have required enormous effort to demonstrate long-term success (Feeley et al. 2018, Farmer et al. 2017).

Remote sensing offers solutions to FSA detection and monitoring and has been applied successfully across a wide-range of aggregating species (Brownscombe et al. 2020, Keller et al. 2020, Feeley et al. 2018, Barbieri et al. 2018, and others). These techniques offer several advantages, but most importantly, they are generally non-invasive, and some techniques can provide near-continuous observations of animals or locations over a nearly unrestricted time series. For example, active acoustics (e.g., “sonar surveys”) have the capacity to efficiently sense the entire water column irrespective of depth, clarity, and light-levels, where visual based systems are limited. This facilitates the rapid non-invasive collection of spatially and temporally referenced data that can be used to estimate abundance, density, biomass, and in some cases taxonomic information (Simmonds and MacLennan 2005).

Acoustic telemetry has also become increasingly popular in the field of FSA research over the last 10-15 years. This approach has demonstrated the capacity to provide near-continuous data streams from free-ranging individuals at spawning sites and vast surrounding areas (e.g., 100’s-1000’s km^2), and has provided a comprehensive understanding of space use through time that was historically infeasible with traditional methods (Feeley et al. 2018, Koenig et al. 2017, Pittman et al. 2015, Ellis et al. 2013). Combined with supplemental information from environmental data loggers or periodic surveys by researchers, this technology can also be extended to evaluate discrete temporal variations in space use and behavior of organisms in response to myriad environmental conditions or interspecific relationships (Rooker et al. 2018, Adams et al. 2009). Indeed, indirect remote sensing systems, such as acoustic doppler current profilers, stationary water quality sensor packages, satellite-borne sensor packages, meteorological observatories, and buoy-borne local marine weather stations can provide environmental context to explain variations in aggregation dynamics with unparalleled temporal resolution.

The present dissertation is intended to identify and fill in regional knowledge gaps related to the occurrence of FSA's in Southeast Florida, where a paucity of information has left FSAs unaccounted for in regional management plans. Through the application of integrated remote sensing approaches, we also demonstrate how these techniques can be employed to develop a comprehensive understanding of FSA dynamics. In Chapter II, we provide a synthesis of available FSA literature from the region, which was combined with unpublished data sources, local reports from stakeholders, and field validation efforts to aid resource managers in identifying priority areas and species for future management activities. The successive chapters use goliath grouper (*Epinephelus itajara,* GG) as a model species to address three topics in FSA science. Specifically, Chapter III evaluates the response of GG and local fish communities to intense storm activity and sustained periods of high turbidity to characterize their capacity to adapt to rapidly changing environmental conditions using regional weather information, satellite data, and active acoustic surveys. Chapter IV focuses specifically on the application of active acoustics to remotely assess FSA's at multiple spatiotemporal scales, and evaluates the effect of survey timing on our ability to detect and monitor GG aggregations. In Chapter V, we integrate data from multiple remote-sensing platforms to take a closer look at fine-scale behaviors beyond the reach of active acoustics. Specifically, we test the capacity of acoustic telemetry to characterize behavioral changes in response to environmental variation, and provide insight into analytically classified behaviors such as foraging and courtship. Not only will these works improve our understanding of GG aggregation dynamics, but we hope that the findings and methods presented here lend themselves to advancing the field of integrative FSA research, and find wider application to improve our understanding of a broad range of species that are of significant conservation interest.

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CHAPTER II. FISH SPAWNING AGGREGATIONS IN THE SOUTHEAST FLORIDA CORAL REEF ECOSYSTEM CONSERVATION AREA: A CASE STUDY SYNTHESIS OF USER REPORTS, LITERATURE, AND FIELD VALIDATION EFFORTS

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ABSTRACT

The formation of fish spawning aggregations (FSAs) is an essential part of the life history of many economically important fish species; however, their status are often poorly described in the literature either due to their occurrence in remote locations, during seasons with unsafe ocean conditions, or because they move on space and time scales that are difficult to predict and validate. Even in areas that are relatively accessible and heavily fished, such as southeast Florida, regionally relevant information describing FSA dynamics is generally absent from the literature and unaccounted for in existing management plans. We propose that this can be attributed to the fact that information is often held by stakeholders or found in unpublished manuscripts and reports. These sources are not widely disseminated and are therefore difficult to locate and integrate into fisheries management decisions. In this paper, we present a case study demonstrating the value of regional data syntheses as a tool to improve management activities in southeast Florida. Specifically, we engaged with local stakeholders to collect reports of FSA occurrence, and used Web of Science queries to collate information describing the reproductive dynamics of locally occurring snapper and grouper species. Reports were combined with regional FSA literature and provided to managers as a support tool to anticipate FSA occurrence, and to guide policy development and future FSA research. Resource users identified 13 potential aggregations from five species, but Web of Science queries revealed a paucity of information. Echosounder, camera, and fisheries dependent surveys were then used to corroborate reportedly active cubera snapper (*Lutjanus cyanopterus*), hogfish

(*Lachnolaimus maximus*), and gag grouper (*Mycteroperca microlepis*) aggregations. Variability in the spatiotemporal aspects of FSA occurrence make them difficult to study, but this may also explain how certain species have avoided detrimental impacts from aggregation fishing. These data represent a first step towards describing FSAs that have historically occurred in the Southeast Florida Coral Reef Ecosystem Conservation Area and can be used by managers to prioritize future research efforts focused on species or hotspots of multispecies activity along the northern extent of the Florida Reef Tract.

INTRODUCTION

The formation of Fish Spawning Aggregations (FSAs) is a vital part of the life cycle of many fish species, with each spawning event representing 33-100% of the annual reproductive investment for transient aggregating species (Domeier & Colin 1997; Sadovy de Mitcheson et al. 2012). This reproductive strategy is shared by over 150 species world-wide (Claydon 2004), and sites are often used by multiple species, either simultaneously or across multiple seasons (Farmer et al. 2017; Johannes 1978; Kobara et al. 2013). Despite the documented occurrence of nearly 1000 aggregations across the globe, the status of approximately 50% of them are unknown due to the difficulty associated with locating FSAs and conducting field research that characterizes their biological and ecological dynamics (Russell et al. 2014).

Location is thought to be primarily dictated by the optimization of larval dispersal into environments where predation risk is minimized and food encounter rate in a heterogeneous landscape is maximized (Johannes, 1978; Karnauskas et al., 2011; Sadovy

De Mitcheson and Colin, 2012). However, fluctuations in oceanographic features (e.g. changes in flow direction and speed, temperature, etc.) are known to drive spatiotemporal patterns of occurrence (Heyman & Kjerfve 2008; Karnauskas et al. 2011). For instance, changes in tidal period or short-term upwelling events may disperse aggregated spawners over a period of a few hours, or shift their focal spawning area, making detection increasingly difficult. Beyond the environmental factors complicating FSA detection, aggregating species exhibit varying degrees of site fidelity and seasonality (Farmer et al. 2017). Certain species within the snapper-grouper complex, such as mutton snapper (Lutjanus analis) and goliath grouper (Epinephelus itajara), are known to maintain localized "home ranges" during discrete spawning periods (Koenig et al. 2017; Feeley et al. 2018), though other species such as gray snapper (L. griseus), yellowtail snapper (Ocyurus chrysurus), and hogfish (Lachnolaimus maximus) aggregate on a range of habitats, have relatively large spawning home-ranges and protracted spawning seasons (Muñoz et al. 2010; Farmer et al. 2017).

While hundreds to thousands of individuals have been documented traveling for weeks, over great distances (10-100s km) during specific times of the year for the sole purpose of spawning (Sadovy De Mitcheson and Colin, 2012), pinpointing their precise location in space and time is difficult without substantial effort and resources. Even in cases where high-resolution spatial and temporal information on aggregation occurrence have been provided in historical reports from resource users, documentation of FSA formation and spawning can take years, especially where heavy fishing pressure has depressed abundance (Burton et al. 2005; Feeley et al. 2018, Heyman and Kjerfve 2008). For example, a collaborative multi-agency effort to document the recovery of a mutton snapper aggregation near Dry Tortugas National Park, Florida required approximately ten years of consistent study before spawning was observed in 2009 (Feeley et al. 2018). Prior to the formation of the Tortugas South Ecological Reserve (TSER) in 2001, commercial fishing on Riley's Hump (the focal point of the TSER) had consistently occurred for over a decade (Burton et al. 2005). Following sharp declines in mutton snapper landings during the spawning season, concerned fishers approached the Florida Keys National Marine Sanctuary with reports of the decline and began assisting with the implementation of legislation that closed off the region surrounding Riley's Hump. With endorsement from the commercial fishing community, a comprehensive monitoring program was developed. Over the following ten year period, mutton snapper and numerous other aggregating species, including ocean triggerfish (*Canthidermis sufflamen*), cubera snapper (*L cyanopterus*), permit (*Trachinotus falcatus*), and horse-eye jacks (*Caranx latus*) were observed at the aggregation site (Feeley et al. 2018).

Similar to the successes seen in the Dry Tortugas, stakeholder involvement has led to the recovery of FSAs throughout the world (Russell et al. 2014). However, the dynamics of FSA occurrence are still poorly understood in many regions, even those that are easily accessible and widely discussed within the fishing community. The paucity of information can be attributed to biotic and abiotic factors that drive spatial and temporal variability as described, but a significant obstacle to successful FSA management and identification is the lack of peer-reviewed syntheses that combine stakeholder reports, relevant peer-reviewed sources, and gray literature sources to describe regionally specific FSA dynamics. Syntheses such as these may be generated as part of an agency report or technical review, but they are not widely disseminated in peer-reviewed journals due to their scope and are therefore difficult to locate and integrate into current and future FSA management activities. Large spatial-scale reviews are useful and represent a valuable tool to broadly describe the reproductive dynamics of selected species, but regionally specific reviews may provide the level of detail needed to make appropriate management decisions that address local resource needs.

In this paper, we present a case study in support of regional FSA syntheses. Using the FSA research guidelines presented by the Society for the Conservation of Reef fish Aggregations (Colin et al 2003), we gathered information from peer-reviewed literature, gray literature sources, and stakeholders to inform regional management decisions and develop an FSA validation field survey in the Southeast Florida Coral Reef Ecosystem Conservation Area (ECA). Specifically, we used multiple queries from Web of Science and engaged with local fishers and SCUBA divers to collect historical and current reports of FSA formation in the ECA. Reports from stakeholders were combined with information from regional FSA literature and provided to managers as a geospatial report of the occurrence of FSAs that could be used to guide conservation goals and future FSA research (https://ourfloridareefs.org/tool/). Field echosounder surveys, camera surveys, on-water fishing surveys, and trip-interviews were used to validate and assess reportedly active spawning aggregations, for which we had reports with meaningful spatial information. These data represent a first step toward describing FSAs that have historically occurred in the ECA and can be used by managers to prioritize future research and management efforts focused on individual species or hotspots of multispecies activity along the northern extent of the Florida Reef Tract.

The Southeast Florida Coral Reef Ecosystem Conservation Area – A Case Study

The Southeast Florida Coral Reef Initiative (SEFCRI) includes a collaborative advisory team and Technical Advisory Committee tasked with identifying and implementing priority actions needed to reduce key threats to coral reef resources off southeast Florida. The region extends along 150 km of coastline from the northern boundary of Biscayne National Park off Miami-Dade County, to the St. Lucie inlet in Martin County (Figure 1) (SEFCRI 2012). This portion of the Florida reef tract was designated as the Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) by the Florida Legislature in 2018. The SEFCRI team consists of governmental agencies, non-profit organizations, recreational and commercial fishing and diving stakeholders, and marine industry leaders, focused on providing recommendations to the Florida Department of Environmental Protection (FDEP) Coral Reef Conservation Program (CRCP) resource managers, related to priority projects consistent with their Charter. The SEFCRI Technical Advisory Committee is made up of subject matter experts who advise the SEFCRI Team on technical topics related to coral reef threats. Founded in 2004, the SEFCRI and FDEP CRCP have completed over 140 projects pertaining to awareness and appreciation (i.e., outreach and education), land-based sources of pollution, maritime industry and coastal construction, and fishing, diving and other uses. However, a state-adopted regional management plan has not been developed prior to the designation of the ECA, leaving the northern extent of the Florida Reef Tract largely under managed and under protected.

The Florida Reef Tract is comprised of nursery, spawning, and foraging habitats for a diverse assemblage of tropical and sub-tropical species (Arena et al. 2007).

Characterized by three distinct limestone reefs and nearshore ridge complex habitats that occur at increasing distances from shore, increasing in complexity seaward, the Florida Reef Tract is dominated by micro/macro-algae cover, interspersed with soft-coral colonies, sponges, and stony coral species, and bordered by expanses of sandy unconsolidated soft bottom (Walker & Gilliam 2013). State waters within the ECA also contain an extensive network of artificial reef complexes, both intentionally and unintentionally sunk (Walker et al. 2009) (Figure 2). These structures vary in spatial extent (i.e., footprint), vertical relief, overall complexity (rugosity) and age, but both natural and artificial reef habitats in the region are “hotspots” of fish aggregation, production and biodiversity in a heterogeneous (patchy) landscape of small and isolated islands (Arena et al. 2007; Walker et al. 2009).

Recognizing the importance of protecting sensitive living marine resources, SEFCRI launched the “Our Florida Reefs” campaign in 2013 to engage stakeholders, ocean users and the general public in a collaborative community planning effort that identified knowledge gaps and management priorities for the region (Reisewitz & Harper 2013). Among the gaps outlined by the team, delineating habitats used by fish (specifically recreationally and commercially important species) during spawning were specifically highlighted as a research priority for integration into the final management plan recommendation. Spawning habitats are already identified as a federal management priority with the provision of the Essential Fish Habitat amendment to the Magnuson Stevens Act in 2002 (Federal Register vol. 67, no. 12, 2002) and subsequent reauthorization in 2006, though information related to the spatial and temporal aspects of FSAs in the ECA are essentially absent from the scientific literature despite their ecological importance.

METHODOLOGY

Study Region and Target Species

Data collection and reports used for this synthesis were constrained to coastal state waters and adjacent federal waters (≤75 m depth) between the northern and southern boundaries of the ECA (Figure 1). Focal species were selected based on initial review of reports from users, government reports, theses and peer-reviewed publications from reports of spawning aggregation occurrence in the study region. Select taxa were within the Snapper-Grouper Complex managed by the US South Atlantic Fishery Management Council (Gould and Brawner, 1983): gray snapper, mutton snapper, cubera snapper, gag grouper (*M. microlepis*), and hogfish. Though hogfish are classified as a wrasse (Family: *Labridae*), they are a managed species of significant economic value within the snapper-grouper complex. Goliath grouper aggregations were not included in this synthesis, as their aggregations are well described in the literature, and they are currently protected from harvest.

Data Collection

Literature Review & User Reports

A keyword search was performed on Web of Science to compile available FSA literature pertaining to the ECA (Table 1). The search results were considered relevant and retained if they included species of interest occurring in the ECA. Those that pertained to the south Florida region and the species of interest were preserved, and location, time of aggregation occurrence, FSA size (geographic extent and relative abundance), and study dates were all recorded. Scientists in the region known to study snapper and grouper reproduction were also contacted to identify internal government reports and unpublished data sources that may contain relevant information pertaining to FSA spatiotemporal dynamics.

Anecdotal user reports were collected by means of direct interview and through the collection of second-hand reports from resource users in the region. Contacts were initially identified by established scientists working in the region, and additional contacts were generated through resource user interviews. Contacts included retired and active commercial fishers, charter guides, recreational anglers, and SCUBA diving shops. The information collected from users included species, location, time of aggregation occurrence, FSA magnitude, and age of the report.

Spawning Aggregation Validation

Validation efforts were performed using a combination of echosounder transects paired with 360° unbaited remote underwater video (URUV) surveys, drop cameras, fisheries observer surveys, and dockside interviews. All four methods were used to explore and confirm the occurrence of a gag grouper spawning aggregation that was reportedly active near Boynton Beach, Florida between January, and March of 2016. Paired echosounder and URUV/drop camera surveys were conducted near Jupiter, Florida on a reported gray snapper aggregation site, between July and September 2016. Observer surveys paired with dockside interviews were used to confirm the occurrence of cubera and mutton snapper aggregations offshore of Homestead, Florida between May and October of 2014 and 2015 (Figure 3).

Echosounder surveys consisted of parallel linear transects, spaced approximately 25 – 30 m apart, that bisected the reefs and surrounding habitat centered on the geographic position where aggregations were reported to occur (Figure 4). Survey extent and transect line lengths varied by site and were determined by precision of report. Echosounder data were collected with calibrated 38 and 120 kHz split-beam echosounders (SIMRAD EK60/EK80), operating at 0.256 µs pulse duration with a 10° and 7° beam-angle, respectively. The transducers were deployed from a pole mount, approximately 1 m below the surface. Echosounder surveys were primarily used as a tool to identify areas of increased fish biomass for camera (URUV and drop camera) surveys. Specifically, an adaptive sampling approach was implemented, where echosounder data were monitored for the presence of backscatter indicating fish aggregations, and cameras were immediately deployed when elevated backscatter was observed. The URUV system consisted of a weighted (10 kg of lead weights) aluminum tripod, with three GoPro Hero 3 action cameras (170° horizontal field of view). The cameras were mounted on a platform attached to the top of the tripod, that allowed for 360° viewing of the surrounding habitat. The overall height of the URUV was approximately one meter, to allow for unobstructed viewing over low lying visual obstructions (Supplementary Material). GoPro Hero 3 action cameras were also used for drop camera surveys. The three cameras were arranged on a weighted pipe to create a 360° video and deployed over the side with polypropylene rope. The pipe was deployed to the bottom, then recovered to suspend approximately 1-2 m over the substrate while the survey vessel held position over the site. Data collected during camera deployments were processed by a trained analyst proficient in reef fish identification, and the presence of aggregating target species was recorded along with additional reef fish species relative abundance (based on the maximum number of conspecifics seen in a single frame) (Ellis & DeMartini 1995).

Fisheries observer surveys consisted of on-water surveys aboard a charter fishing vessel. The observer recorded fishing pressure and landings at the reported aggregation, and reproductive state of fish that were harvested using standard gonad assessment protocols consistent with Lowerre-Barbieri et al. (2011). In addition to on-water surveys, participating charter fishers were interviewed upon returning from fishing activities and the reproductive state of harvested fish was assessed. Biweekly interviews were made during the aggregation period to confirm the occurrence of aggregation activity and consisted of general questions related to: 1) the targeted species, 2) locations and timing of any aggregations observed, 3) depth where aggregation fishing took place, 4) observations of milt or eggs flowing from captured fish, 5) size of aggregation(s), 6) age of report (i.e., when did they see an aggregation relative to when they were interviewed), 7) a general description of habitat where aggregations were observed (e.g., artificial reef or natural reef), 8) and observations of notable behaviors exhibited by aggregating fish (Supplementary Material).

RESULTS

Literature Review

Between the three Web of Science queries conducted, 178 articles were identified. Several of these articles were represented in multiple queries, reducing the total unique sources to 116 peer-reviewed journal articles (Table 2). Only 27 of these studies related to the target species, 24 of which were conducted outside of our current study region. The three remaining articles focused on mutton snapper age, growth, and mortality (Burton, 2002);

and the life history, movement and management of gray snapper (Faunce & Serafy 2007; Luo et al. 2009). No articles pertaining to the target species spawning in the ECA were identified, but eight articles related to spawning were identified from other regions in the coastal United States (i.e., Gulf of Mexico and South Atlantic). Nine additional Florida-centric references offer insight into the life history, management, movement, spawning, and general ecology of the study species and those grouper and snapper found in the ECA that are taxonomically similar (Table 3). Goliath grouper are not among the target species in this review, but they are known to spawn in the ECA. Seven studies characterizing aspects of goliath grouper life history, management, movement, spawning, and ecology were identified by our queries, four of which were conducted in the ECA. Black and red grouper were also excluded from our synthesis due to an absence of aggregation reports in the study region, but 11 studies characterizing their life history, management, movement, spawning and ecology were identified. Those studies were conducted near the West Florida Shelf, Dry Tortugas, Florida Keys, Puerto Rico, and US Virgin Islands.

Five articles describing hogfish life history, movement and habitat use in the eastern Gulf of Mexico, Eastern United States, and Florida Keys were identified outside of the Web of Science query, but information pertaining to spawning in the ECA is absent from the literature.

Unpublished Theses

Potential spawning locations for various snapper species along the east coast of Florida were identified by Tishler-Meadows (2012) who presented a survey that capitalized on fishers' ecological knowledge and identified 51 potential spawning locations for red snapper (*L. campechanus*) (27), gray snapper (19), mutton snapper (8), cubera snapper (6), and vermilion snapper (3). Nine of the reported aggregations were considered multi-species aggregations, four of which occurred just beyond the northern extent of the ECA. Species included in these aggregations were gray and mutton snapper (3), and gray, mutton and cubera snapper (1). Eight gray snapper aggregations, nineteen mutton snapper, and three cubera snapper aggregations were reported to occur within the northern extent of the ECA. Due to confidentiality agreements with fishers, the precise location of reported aggregations were not presented, thus it is uncertain whether all the reported aggregations lie within the ECA. Direct evidence of spawning (gametes released in water column) was only observed at two of the reported spawning sites (gray snapper), but advanced stage gonadal development was observed at 49 of the reported sites (all species). Reproductive seasonality varied for all species when compared to conspecific spawning periods in other regions throughout the Unites States and Greater Caribbean, but reports peaked between June and July, and ranged from April to September (Table 4).

Towne (2018) examined age and growth of hogfish in southeast Florida. The field effort was limited in scope, and focused on the expected peak of the spawning season between March and May (McBride and Richardson, 2007). Evidence of spawning in the ECA was presented, based on observations of courtship behavior by divers. Personal communication with the author (i.e., Towne) confirms that both male and female hogfish had fully developed gonads during the spring season, based on a macroscopic assessment of reproductive stage from harvested specimens. This interpretation is consistent with the observed spawning period identified in the Florida Keys, Puerto Rico, and eastern Gulf of Mexico(Colin 1982; McBride & Richardson 2007; Munoz et al. 2010; Collins & Mcbride

2015). Four additional reports related to hogfish were identified, including the most current Southeast Data, Assessment, and Review (SEDAR) hogfish stock assessment (SEDAR 37) (Cooper et al. 2012). An addendum to SEDAR 37 was released in 2018, though this pertained to the West Florida Shelf hogfish stock (Addis et al., 2018). Information related to spawning in the study area was absent from the identified reports.

User Reports

From 2014 through 2016, 13 potential aggregations were identified for the five different study species, between the southern extent of Miami-Dade County and the northern extent of Martin County (Table 5, Figure 3). Reports were collected from long-time professional fishers (>10 years of experience) and members of the South Atlantic Fisheries Management Council with connections to the fishing community. Reports were also provided by state and federal fisheries biologist that work primarily with the focal species. Goliath grouper spawning aggregations in Palm Beach County were identified by resource users as economically and ecologically important, and have been reported here, but were not a priority study species identified by the SEFCRI due to the harvest moratorium currently in place. One vermillion snapper (*Rhomboplites aurorubens)* aggregation was also reported to occur during the summer months, but precise information pertaining to timing and location could not be verified, and it was not prioritized as a study species.

Spawning Aggregation Validation

Only three aggregations out of the 13 identified were reported to be active with precise spatial information and selected for field validation. A gag grouper aggregation reported to occur near Boynton Beach, Florida was not observed despite multiple attempts to confirm their presence during the expected reproductive season in 2016. Echosounder surveys (*n*=8) were conducted over an approximately 60 km^2 region between January and March during full moon periods. URUV surveys (*n*=19) were conducted at high relief reef locations where small schools were detected, though gag grouper were not observed in URUV data. Video data consistently revealed a mixed reef fish assemblage and high-density schools of tomtates (*Haemulon aurolineatum*) (Figure 5). Bi-weekly interviews with a collaborating SCUBA diving shop during the 2016 and 2017 season (*n*=10) also indicated that gag grouper were never seen aggregated at the suspected aggregation site.

Paired echosounder and URUV surveys near Jupiter, Florida were also used to validate a reported gray snapper aggregation occurring over a discrete natural reef area (approx. 1.5 km^2), between July and September 2016 (*n*=6). No areas of concentrated backscatter were identified by echosounders, but URUV (*n*=5) and drop camera surveys (*n*=5) were performed near high-relief reef-sand interfaces (i.e., promontories), where gray snapper were expected to aggregate. Gray snapper were not observed in videos, and subsequent resource user interviews indicated that gray snapper in the study area are not often isolated to discrete regions as described by the original source.

A cubera and mutton snapper aggregation was reported to occur offshore of Homestead, Florida. The report indicated that the aggregations occurred annually from April-July (mutton snapper), and August-September (cubera snapper) during full moons. However, the mutton snapper aggregation had not been reported as active for several years, and both FSAs were heavily fished since the early 2000’s (no specific date could be provided). Researchers joined a recreational fishing charter on two occasions, in August

2014 and 2015, during full moon overnight fishing charters to confirm the occurrence of the cubera snapper FSA. Biweekly interviews were also conducted to assess the status of the cubera snapper aggregation. During field surveys, eight mature cubera snapper were captured (four each year), and four were harvested (two from each year). All eight fish were >80.0 cm total length, and the four harvested cubera snapper were spawning capable males with fully ripe gonads, qualified using the classification system developed by Domeier & Colin (1997). Surveys were not conducted in September of 2014 and 2015, or in the 2016 season, based on reports from the charter captain that the aggregations had not formed.

DISCUSSION

Information related to commercially and recreationally important snapper and grouper reproduction (specifically spawning aggregations) in the ECA is essentially absent from the peer-reviewed literature based on our Web of Science queries and a thorough review of additional primary and gray literature sources. No research specifically characterizing the spatial aspects of spawning aggregation formation (for the focal species), and their seasonality in the ECA was identified. However, numerous literature sources describing spawning seasonality in other regions were available and used to develop a calendar to forecast FSA seasonality, which showed a high degree of overlap with the reports of FSA occurrence provided by fishers. The information available in the literature was primarily limited to research describing life-history, movement, and seasonality of reproductive development. Thus, the paucity of data identified is likely an accurate reflection of the state of FSA science in the ECA.

When compared to the number of current and historical aggregations reported throughout the region by users, it is clear that a focused effort is required to confirm the presence of and characterize the state of regional FSAs that may still occur. Considering the high degree of spatiotemporal variability associated with FSA formation, it is not unreasonable to presume that aggregations were missed by our field and interview approach, which were dependent on up-to-date user reports distributed over a large geographical area for many species. While user reports do offer the highest spatial and temporal resolution, a lack of reports is not necessarily sufficient evidence to conclude that aggregations are not occurring in the reported region. This is exceptionally true in cases where users are not actively targeting the species of interest. For example, the gag grouper fishery is closed from January through April to protect their populations from exploitation during the reproductive season[1]. This precluded any targeted fishing by commercial and recreational anglers during the study period, which may have produced spawning reports useful to our field efforts had the fishery been open. Thus, in the case of the reported gag grouper aggregation near Boynton Beach, Florida, we were solely dependent on SCUBA diving charter reports and our own exploratory field surveys across a wide expanse of continuous reef. Had the commercial and recreational fishing community been targeting

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[1] https://safmc.net/regulations/regulations-by-species/gag-grouper/

the inshore gag grouper fishery at the time, it is possible that field survey efforts may have been more successful.

FSAs have also been historically reported to occur near natural and artificial promontories, which function as recurrent spawning sites for various species. Indeed, spawning aggregations have been found near promontories in the Florida Keys (Feeley et al., 2018a), northeast Florida (Koenig et al., 2000), and west Florida (Coleman et al., 1996), while in contrast, there are fewer promontories along the northern extent of the Florida Reef Tract, and fewer confirmed reports of spawning aggregation occurrence. This may explain why aggregations reported to occur in the study region are difficult to locate and exhibit lower site fidelity (i.e., they are not concentrated on discrete features). Furthermore, while high relief features do occur along the northern extent of the Florida Reef Tract, some features that may be ordinarily attractive to aggregating species occur beyond their typical spawning depths. For example, Tishler-Meadows (2012) reported gray snapper aggregations at depths between 15-60 m, but this is deeper than reported spawning depths in Florida Keys, Dry Tortugas, and Cuba (9-37 m) (Domeier & Colin 1997; Lindeman et al. 2000; Claro & Lindeman 2003).

In addition to abiotic considerations, species-specific reproductive behaviors and regional differences may further hinder our ability to detect aggregations. For instance, gray snapper aggregations are known to be less predictable in time and space, as they spawn repeatedly over protracted time periods and exhibit lower fidelity to discrete locations (Domeier & Colin 1997; Sadovy De Mitcheson et al. 2008; Farmer et al. 2017). They may form aggregations on large swaths of reef for short periods of time and inadvertently avoid exploitation because their occurrence is unpredictable, brief, and their movements are frequent. Even with respect to species that typically form predictable aggregations in discrete areas (i.e., mutton and cubera snapper), detection along continuous reefs has been historically difficult. For example, a black grouper aggregation was observed on one occasion by researchers near Key Largo, Florida (Eklund et al. 2000), but a subsequent study between 2008-2012 was only able to re-locate the aggregation on one occasion, despite repeated diver surveys paired with echosounder surveys over the four year period (*Taylor et al. Unpubl. data*).

Anthropogenic factors may also explain why FSAs have remained undetected and thus understudied in the ECA. Specifically, FSA identification (initial detection by managers and scientists), and subsequent investigation, has typically been tied to reports from resource users participating in targeted aggregation fishing activities that have occurred over extended periods. Drawing from examples found in the literature, aggregation fishing had occurred for extended periods, and only after decreases in catches became noticeable to resource users, did reports reach fisheries managers and scientists. At that point, most of the aggregations reported in the literature were overfished, extirpated, or were suffering substantial losses due to on-going fishing activities (Luckhurst 1998; 2010; Burton et al. 2005; Nemeth 2005). In the context of reports gathered during this study, only the cubera and mutton snapper aggregations identified near Homestead, Florida were reported by fishers as heavily fished, and had been for over a decade (*Binder personal comm.*). The user indicated that both cubera and mutton snapper abundance at the aggregation site had decreased steadily over a ten-year period and indicated that management intervention was needed to protect the two resources.

No users indicated that aggregating species in the ECA were consistently fished beyond the two reported cases. Indeed, despite the generally high pressure exerted on fishery resources in south Florida, specifically the snapper and grouper fisheries, very little evidence of on-going aggregation fishing was documented. A paucity of information in the media (i.e., newspapers and social media) also suggests that aggregating species are not exposed to aggregation fishing activity within the ECA. Conversely, media sources (newspaper, radio broadcast, and social media) and charter fishing services widely publicize and offer permit and mutton snapper aggregation fishing opportunities in the Florida Keys, which have resulted in heavy fishing pressure during spring and summer full moon periods at discrete FSA sites. Thus, it is plausible that the variability of aggregation occurrence, which is driven by ephemeral hydrodynamic events (i.e., current changes, upwelling, etc.) and the heterogeneous landscape (i.e., limited promontories and expanses of continuous reef interspersed with sandy substrate), mitigates aggregation fishing activity in the ECA.

Potentially the largest obstacle hindering effective FSA assessments and effective conservation has been the lack of real-time data streams in regions of concern (Kobara et al. 2013). Reports from resource users, that make their livelihoods using coastal resources, offer a wealth of real-time information collected over expansive geographical areas (Gerhardinger et al. 2006). Additionally, individuals from the local fishing community are capable of tracking fine-scale changes in environmental factors, using decades of experience (in some cases), to interpret environmental conditions that dictate where target fish schools may be on a given day. Indeed, numerous studies have successfully utilized local and traditional knowledge from fishers to achieve a baseline understanding of the spatial and temporal dynamics of aggregations (Johannes 1978; Lindeman et al. 2000; Sadovy De Mitcheson et al. 2008; Freitas et al. 2011), and invested resource users have contributed directly to the recovery of FSAs throughout the United States and Greater Caribbean (Lindeman et al. 2000; Burton et al. 2005; Nemeth et al. 2006; Feeley et al. 2018).

FSAs represent “hotspots” of fish production during ephemeral periods in time and space that often support multiple aggregating spawning species, and play a role in promoting overall ecosystem health through the stimulation of fish biomass and biodiversity (Schärer et al., 2010; Archer et al., 2015; Grüss et al., 2018). Unfortunately, FSAs also represent attractive targets to fishers, and there are many cases of decline and extirpation after extended periods of excessive fishing (Sadovy De Mitcheson et al. 2008). An erosion of trust between resource users and managers has resulted in challenges assimilating their knowledge into assessments and management process (Boonstra & Nhung 2012; Jagers et al. 2012). The SEFCRI was specifically created to bridge that gap between resource users and managers and develop effective long-term solutions to coastal and fisheries management issues. Cooperation between users and managers that result in actionable reports from users for field investigations are essential to the future of integrated fisheries management, especially with respect to protecting FSAs. The approach presented here is an important first step towards understanding the spatiotemporal dynamics of regional FSA occurrence, and represents a thorough synthesis of information describing the state of knowledge for recreational and commercially important aggregating species found in the ECA. These data can be used to inform future management plan development, and we hope that these data will be used as a framework for future studies focused on improving our understanding of FSA dynamics in south Florida.

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TABLES

Table 1 – A keyword search was performed in Web of Science (Clarivate Analytics, 2019) to identify primary literature relevant to spawning aggregation activity in the Southeast Florida Coral Reef Initiative Ecosystem Conservation Area. Duplicate entries returned in the second and third queries were removed from their respective tallies and included in the first query.

Keywords	**Citations**
Fish Spawning Aggregations + Florida	69
Spawning + Florida + Snapper	18
Spawning + Florida + Grouper	29

Table 2 – All web of science query results. Cross-reference numbers correspond to citations seen in table 3. **Bold citations** relate to spawning in the United States but not the Southeast Florida Coral Reef Initiative Ecosystem Conservation Area. Roman numerals within relevancy have been divided into five categories; I – irrelevant to study, II - out of study region, III – not related to target species, IV - multi-species spawning information, and V – related to target species. Subject codes correspond to E – Ecology, F – Fishing, LH – Life History, MG – Management, MV – Movement, and S – Spawning.

Query	**Cross-Reference**	**Citation**	**Relevancy**	**Subject**
FSA + Florida		Adams & Wolfe 2009. Mar Eco Prog Series. 389: 213-222	I	
		Aguilar-Perera 2004. Proc of the 55th GCFI. 543-556	I	
		Allee & David 2012. Seafloor Geomorphology as Benthic Habit. 435-448	**II & V**	**MG & S**
		Baumberger & Brown-Peterson 2010. Copeia. (1): 41-46	I	
		Bryan et al. 2015. Env Bio of Fishes. 98(11): 2263-2276	I	
		Bueno et al. 2016. J of Fish Bio. 89(1): 876-889	II & III	S
		Buitrago et al. 2006. Estuarine Coastal and Shelf Sci. 66(3-4): 634-642	I	
		Burton 2002. Fish Res. 59(1-2): 31-41	V	LH & MG
		Carson et al. 2011. Fishery Bul. 109(4): 416-428	II & V	MV & E
		Castro-Perez & Arias-Gonzalez 2018. Latin Amer J of Aquatic Res. 46(4): 717-726	II & IV & V	F
		Chiappone & Sluka 2000. Mar Eco Prog Series. 198: 261-272	II	MG
		Coleman & Scanlon 2011. Pro Geo. 63(4): 456-474	**II & IV**	**S & MG**

		D'Alessandro & Sponaugle 2010. Mar Eco Prog Series. 410: 159-175	II & V	LH
		Danylchuk et al. 2011. Mar Bio. 158(9): 1981-1999	I	
		Domeier 2004. Fish Oceanography. 13(5): 287-294	I	
		Donahue & Karnauskas 2015. Plos One. 10(6)	II & IV	LH & S
	6	Eklund & Mcclellan 2000. Bul of Mar Sci. 66(3): 721-728	III	S
	5	Farmer & Ault 2011. Mar Eco Prog Series. 433: 169-184	II & IV	MV
	4	Farmer & Ault 2018. Canadian J of Fish and Aquatic Sci. 75(3): 375-388	II & IV	MV
		Farmer et al. 2017. Plos One. 12(3)	II & V	S & MG
		Feeley et al. 2009. J of Fish Bio. 74(10): 2415-2421	I	
		Feeley et al. 2018. Fish Res. 204: 209-223	**II & V**	**S & MG & MV**
		Fitzhugh et al. 2005. Bul of Mar Sci. 77(3): 377-396	II & V	LH & MV
		Flaherty & Switzer 2014. Estuaries and Coasts. 37(1): 206-228	II & V	MV & E
		Frias-Torres 2013. Oryx. 47(1): 88-95	III	
	7	**Gleason & Kellison 2011. Pro Geo. 63(4): 443-455**	**II & IV**	**S**
		Gledhill & David 2004. Proc of the 55th GCFI. 614-625	II	MG
		Gruss & Biggs 2018. Scientific Reports. 8	II & IV	S & MG
		Hare & Walsh 2007. Canadian J of Fish and Aquatic Sci. 64(9): 1234-1247	I	

		Hernandez et al. 2013. Ices J of Mar Sci. 70(3): 628-635	I	
		Holt 2008. Trans of the Amer Fish Soc. 137(2): 551-561	I	
		Koenig & Coleman 2011. Bul of Mar Sci. 87(4): 891-911	III	MG & E
		Koenig et al. 2000. Bul of Mar Sci. 66(3): 593-616	**II**	**MG & S**
	8	Koenig et al. 2017. Bul of Mar Sci. 93(2): 391-406	III	S & E
		Leichter & Stokes 2008. Mar Eco Prog Series. 356: 123-138	I	
	2	Lindeman & Pugliese 2000. Bul of Mar Sci. 66(3): 929-956	IV	LH & MG & S
		Locascio & Mann 2011. Fishery Bul. 109(3): 327-338	I	
		Lowerre-Barbieri & Burnsed 2016. Eco App. 26(4): 979-995	I	
		Lowerre-Barbieri & Vose 2003. Trans of the Amer Fish Soc. 132(5): 940-952	I	
		Mann & Locascio 2016. Listening in the Ocean. 309-324	II	E
		Mcgovern et al. 2005. Bul of Mar Sci. 76(1): 47-59	III	MV
		Molloy & Reynolds 2009. Mar Eco Prog Series. 392(): 253-262	II	
		Munoz & Burton 2010. Bul of Mar Sci. 86(1): 93-116	**II & V**	**MV & MG & S & E**
		Murchie et al. 2012. Telemetry Techniques. 389-412	I	
		Nelson & Koenig 2011. Aquatic Bio. 12(2): 97-108	II & III	E

		Paris & Cowen 2005. Mar Eco Prog Series. 296: 93-106	I	
		Peebles & Hall 1996. Mar Eco Prog Series. 131(1-3): 61-73	I	
		Potts & Burton 2017. Peerj. 5	III	LH
		Provancha & Hall 1991. Env Bio of Fishes. 31(1): 41-54	I	
		Reed & Koenig 2007. Bul of Mar Sci. 81(3): 481-496	I	
		Reed et al. 2005. Cold-Water Corals and Ecosystems. 443-465	II	
		Rowell et al. 2012. Mar Eco Prog Series. 462: 241-250	I	
		Sadovy de Mitcheson et al. 2013. Fish and Fish. 14(2): 119-136	II & IV	MG
		Sanchez & Appeldoorn 2017. Fishery Bul. 115(2): 186-195	III	S & E
		Saucier & Baltz 1993. Env Bio of Fishes. 36(3): 257-272	I	
		Saul et al. 2013. Fish Res. 143: 12-20	II	
		Sedberry et al. 2001. American Fisheries Symposium. 25: 3-23	II	
		Shulzitski & Mccartney 2009. Fishery Bul. 107(4): 501-509	II & V	MV
		Switzer et al. 2015. N Amer J of Fish Mgmt. 35(6): 1132-1143	II & V	LH & E
		Taylor & Whittington 2001. N Amer J of Fish Mgmt. 21(1): 70-75	I	
		Todd & Morey 2014. J of Mar Res. 72(6): 445-475	I	
		Tupper 2002. Proc of the 53rd GCFI. 606-622	II	MG
		Tzadik et al. 2017. Estuaries and Coasts. 40(6): 1785-1794	III	LH

		Wall et al. 2014. J of Fish Bio. 85(5): 1470-1488	III	MV & E
		Walters & Lowerre-Barbieri 2009. Trans of the Amer Fish Soc. 138(1): 88-98	I	
		Walters et al. 2013. Mar Eco Prog Series. 479: 191-202	I	
		Woodson 2018. Annual Review of Mar Sci. 10: 421-441	I	
		Young & Yeiser 2014. Mar Eco Prog Series. 505: 227-240	I	
		Young et al. 2016. Trans of the Amer Fish Soc. 145(2): 400-415	I	
Spawning + Florida + Grouper		Barbour & Adams 2012. Mar Eco Prog Series. 457: 241-250	I	
		Bullock & Murphy 1994. Bul of Mar Sci. 55(1): 30-45	II & III	LH
		Crabtree & Bullock 1998. Fish Bul. 96(4): 735-753	III	LH & S
		Degidio et al. 2017. N Amer J of Aquaculture. 79(3): 205-215	I	
		Gilmore & Jones 1992. Bul of Mar Sci. 51(1): 83-103	II &V	E
		Gruss et al. 2017. Fish Res. 193: 129-142	II & III & IV	LH & MV
		Kadison et al. 2017. Plos One. 12(7)	II & III	MG
		Mann 2016. Effects of Noise on Aquatic Life. 875: 673-678	I	
		Marancik et al. 2012. Fish Bul. 110(1): 1-20	II & III	LH & MV

	3	Nelson et al. 2012. Mar Bio. 159(2): 365-372	I	
		Pichorim & Suzuki 2015. Oceans 2015 - Genova.	III	MG
		Porch & Eklund 2006. Fish Bul. 104(1): 89-101	III	MG
		Renan & Montero-Munoz 2016. Trans of the Amer Fish Soc. 145(6): 1252-1265	II & V	MG
		Shideler & Pierce 2016. Ocean & Coastal Mgmt. 129: 36-43	III	MG & F
		Strelcheck & Fitzhugh 2003. Fish Res. 60: 255-265	II & V	LH
		Wall & Donahue 2011. Mar Eco Prog Series. 431: 243-254	II & III	MV & S & E
		Weisberg & Zheng 2014. Continental Shelf Res. 88: 11-23	II & V	LH
		Ziskin & Harris 2011. Trans of the Amer Fish Soc. 140(2): 384-398	II & III	MG
Spawning + Florida + Snapper	1	Allman & Grimes 2002. Fish Bul. 100(3): 391-403	II & V	LH & MV
		Amezcua & Soto-Avila 2006. Fish Res. 77(3): 293-300	I	
		Ault & Bohnsack 1998. Fishery Bul. 96(3): 395-414	I	
		Bohnsack & Harper 1994. Bul of Mar Sci. 54(3): 982-1018	II	F
		Burton & Brennan 2005. Fishery Bul. 103(2): 404-410	**II & V**	**S**
		Collins et al. 2003. Proc of the 54th GCFI. 580-591	I	

	9	**Denit & Sponaugle 2004. Trans of the Amer Fish Soc. 133(6): 1339-1355**	**II & V**	**LH & S**
		Faunce & Serafy 2008. Estuarine Coastal and Shelf Sci. 79(1): 93-100	V	LH & E
		Garlock & Camp 2017. Fish Res. 186: 460-467	I	
		Hostetter & Munroe 1993. Fishery Bul. 91(1): 45-64	I	
		Johnson & Perry 2013. Trans of the Amer Fish Soc. 142(1): 50-58	I	
		Jue & Coleman 2014. Mar Bio. 161(8): 1905-1918	II & V	E
		Karnauskas et al. 2017. Mar and Coastal Fish. 9(1): 50-67	I	
		Le Port & Montgomery 2014. Mar Eco Prog Series. 515: 203-215	I	
		Lee et al. 1994. Bul of Mar Sci. 54(3): 621-646	II	LH
		Locascio & Burton 2016. Fishery Bul. 114(1): 103-116	II & III	S & E
		Luo et al. 2009. Mar Eco Prog Series. 380: 255-269	V	MV
		Manooch & Potts 1998. Fish Res. 38(1): 19-32	I	
		Mcgovern & Collins 2002. N Amer J of Fish Mgmt. 22(4): 1151-1163	I	
		Mcgovern et al. 1998. Fishery Bul. 96(4): 797-807	II & V	LH
		Nadon et al. 2015. Plos One. 10(8)	I	
		Pinkard & Shenker 2001. Amer Zoologist. 41(6): 1556-1557	I	
		Powell 2003. Fish Bul. 101(3): 704-711	I	
		Powell et al. 2004. Fishery Bul. 102(1): 142-155	I	

		Rotman et al. 2003. World Aquaculture Society	I	
		Saillant & Bradfield 2010. Ices J of Mar Sci. 67(6): 1240-1250	I	
		Turano & Davis 2000. J of the World Aquaculture Soc. 31(1): 59-68	I	
		Vaughan et al. 1998. Fishery Stock Assessment Models. 15: 121-136	I	
		White & Palmer 2004. Bul of Mar Sci. 75(3): 335-360	I	

Table 3 - Literature related to target and non-target (taxonomically similar) species found in Florida.. Mixed assemblages include species from the families *Lutjanidae*, *Serranidae, Haemulidae,* & *Balistidae*. Citations correspond to specific citations found in Table 2.

Subject	Region	Species	Citation
Fisheries	Florida Keys	Mixed Assemblage	1
Life History – Management – Spawning	Key West – Dry Tortugas	*Mycteroperca Spp.*	2
Management - Fisheries	Jupiter	*Epinephelus itajara*	3
Movement	Dry Tortugas	*Mycrteroperca bonaci*	4
		Lutjanus analis	5
Spawning	Florida Keys	*Mycteroperca bonaci*	6

		Mycteroperca bonaci – Lutjanus analis	7
Spawning – Ecology	Jupiter	*Epinephelus itajara*	8
	Dry Tortugas	*Mycteroperca bonaci- Epinephelus morio*	9

Table 4 – Spawning seasonality for study species found in the Southeast Florida Coral Reef Ecosystem Conservation Area. Regions in gray denote the reported spawning season, while black boxes indicate peak periods in spawning activity. *Black and goliath grouper were not focal species, but due to their occurrence in the study region, spawning seasons have been included. An example source has been provided, though others can be found in the literature.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Source
Grouper													
gag	▨	▨	▨	▨									Koenig et al. 2000
***black**	■	■	▨										Koenig et al. 2000
***goliath**							▨	■	■	▨			Koenig et al. 2017
Snapper													
cubera					▨	▨	▨	■	▨				Lindeman et al. 2000
gray						▨	■	■	▨				Lindeman et al. 2000
mutton				▨	■	■	▨						Lindeman et al. 2000
hogfish	▨	▨	■	■	▨	▨	▨						Towne 2018

Table 5 – Anecdotal reports of spawning aggregations in the Southeast Florida Coral Reef Ecosystem Conservation Area collected between 2014-2016. Aggregation descriptions are included.

Species	Location	Depth	Seasonality	Type	FSA Size	Age of report
Lutjanus analis	Homestead	60 m	April - July	Spawning	10's – 100's	1990's – present
	Discrete aggregation occurs over known artificial reef and has been heavily targeted for years. The report indicates that the duration and catchability of snapper has declined in recent years. This is also a multi-species aggregation site *Lutjanus cyanopterus*.					
L. cyanopterus	Homestead	60 m	Aug - Oct	Spawning	10's – 100's	1990's – present
	This is a multi-species aggregation site (*L. analis*; above). The aggregation has been heavily targeted for years, and a decline in catchability and the duration of aggregation occurrence has decreased.					
	Jupiter	5 m	June - Oct	Pre-spawning/ unknown	< 100	2010 – present
	A range of sizes are seen aggregating in Jupiter Inlet coincidently with common snook aggregations. Individuals are reported to average 75 cm total length.					
L. griseus	Miami	20 m	June – Sept	Spawning	100's – 1000's	2010 – present
	Aggregations are reported to form near natural limestone reefs southeast of Government Cut. Aggregations do not exhibit high site fidelity.					
	Fort Lauderdale	20 m	Aug – Sept	Spawning	100's – 1000's	2010 – present
	Aggregations occur near natural limestone reefs. Targeted by recreational charters at night. Information on site fidelity is unknown.					
	Jupiter	20 m	June – Sept	Spawning	100's – 1000's	2010 – present
	Aggregations are reported to form near natural limestone reefs. Aggregations do not exhibit high site fidelity.					

Lachnolaimus maximus	Fort Lauderdale	5 – 20 m	March – May	Spawning	< 20	2016 – present
	Small aggregations were observed on reef features across a wide range of depths. Reports indicate that individual length and aggregation size (abundance) increased with depth.					
Epinephelus itajara	West Palm Beach – Jupiter	15 – 45 m	July – October	Spawning	< 100	1980’s - present
	Well documented aggregations occur on natural and artificial reefs throughout Palm Beach and Martin County.					
Mycteroperca microlepis	Boynton Beach	10 – 20 m	Jan – April	Pre-spawning/ Spawning	≤ 100	1970’s – present
	Believed to be pre-spawning aggregations comprised of a range of sizes. Multiple aggregations have been reported on natural and artificial reefs at various depths. Their occurrence has declined in recent years, despite the annual harvest restrictions.					
Rhomboplites aurorubens	Fort Lauderdale	20 – 30 m	May – September	Unknown	100’s – 1000	2015
	Aggregation’s reportedly form on artificial reefs south of Port Everglades. Only one source available and has not been validated.					

FIGURES

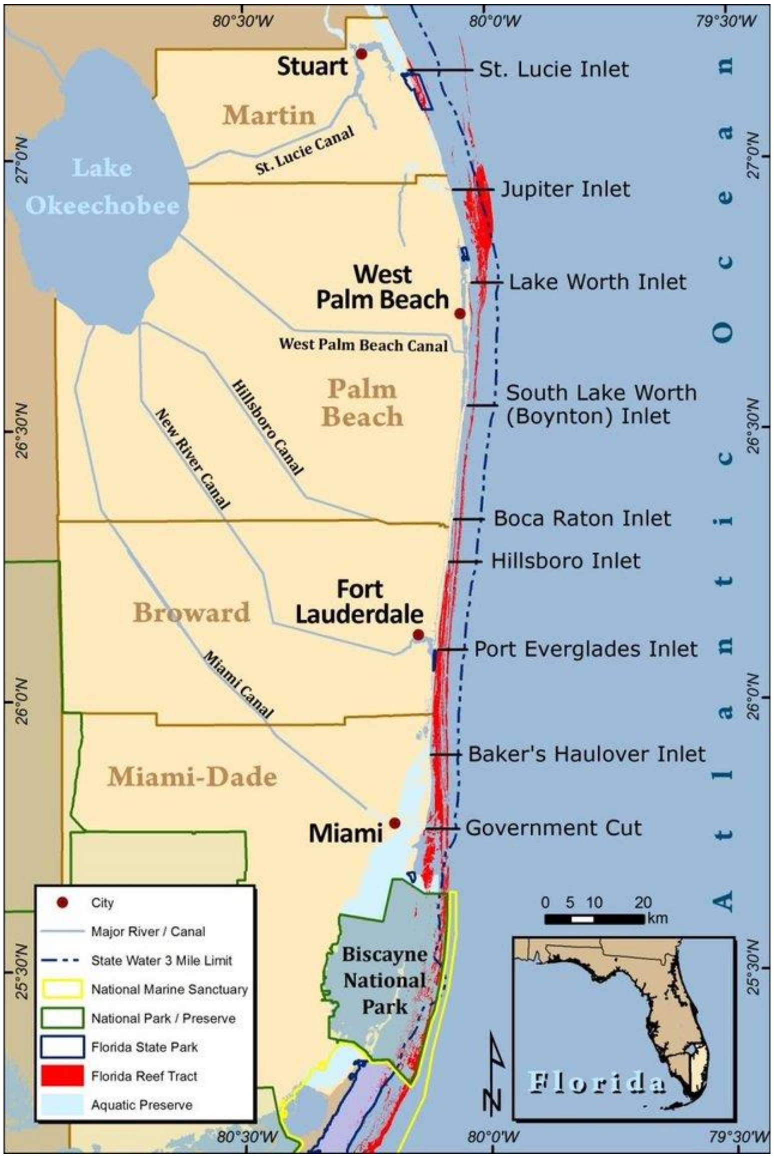

Figure 1 Counties included in the Southeast Florida Coral Reef Ecosystem Conservation Area, including major waterways, cities, and ocean inlets (Credit: Brian Walker 2013).

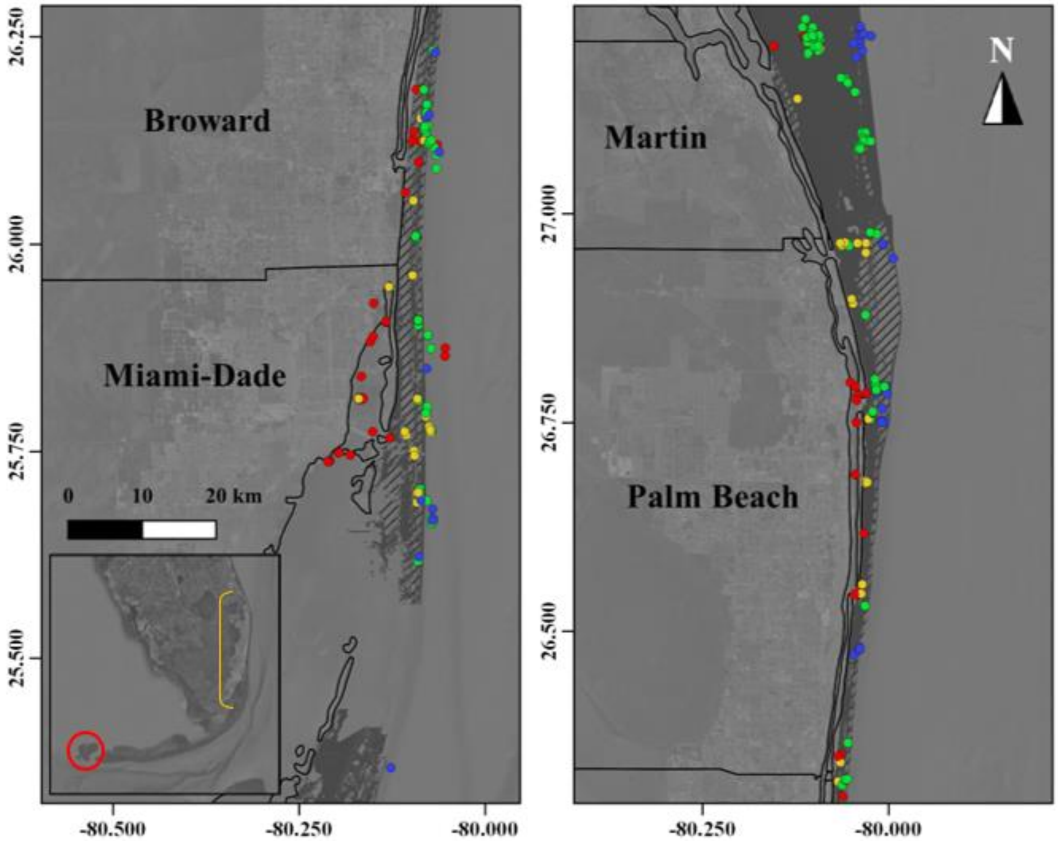

Figure 2 The Florida Reef Tract extends from the Dry Tortugas (Inset – red circle) to the northern extent of Martin County, Florida (north). Comprised of a range of habitats, harbottom limestone reefs (dashed gray polygons) are surrounded by unconsolidated sandy bottom (dark-gray polygons) in the Southeast Florida Coral Reef Ecosystem Conservation Area. Artificial reefs are distributed throughout the region at a range of depths. Colored circles represent reefs at depths between 1-25 m (red circles), 26-50 m (yellow circles), 51-75 m (green circles), and 75-100 m (blue circles). Ecosystem Conservation Area counties are labeled, and boundaries denoted by black lines.

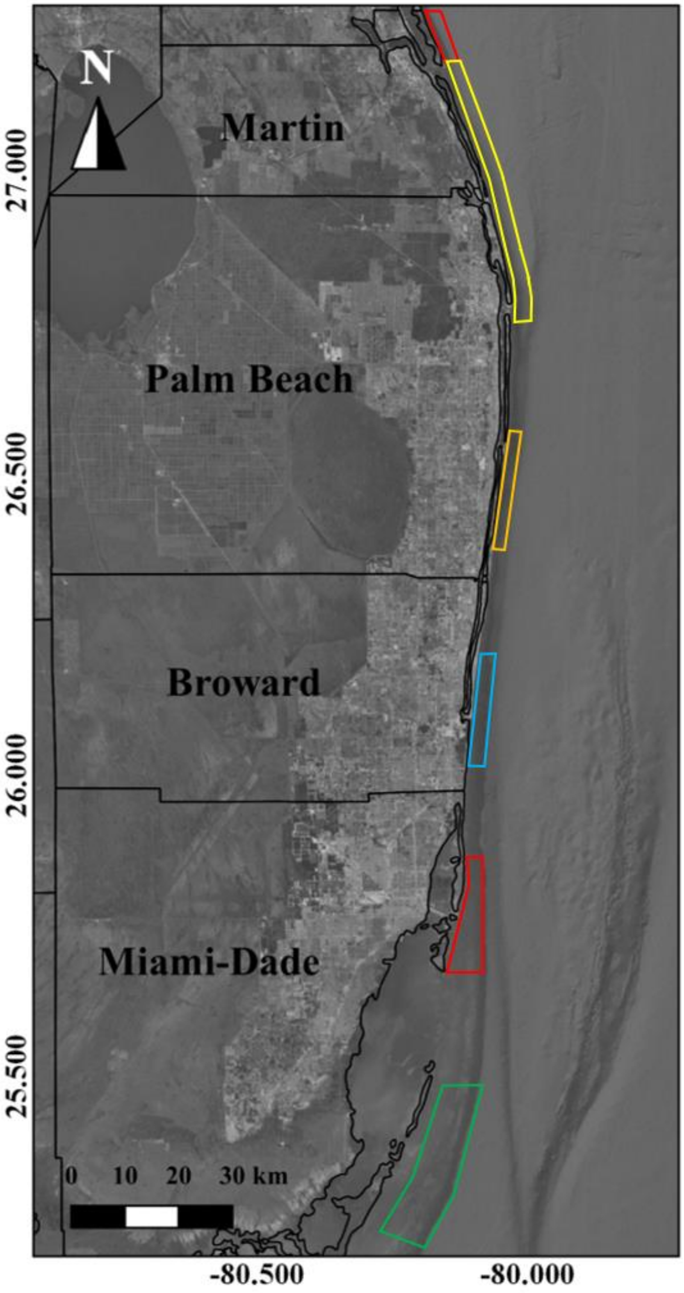

Figure 3 Extent of reports of FSAs for gray snapper (red), goliath grouper (yellow), gag and goliath grouper (orange), hogfish and vermillion snapper (blue polygon), and mutton snapper (green).

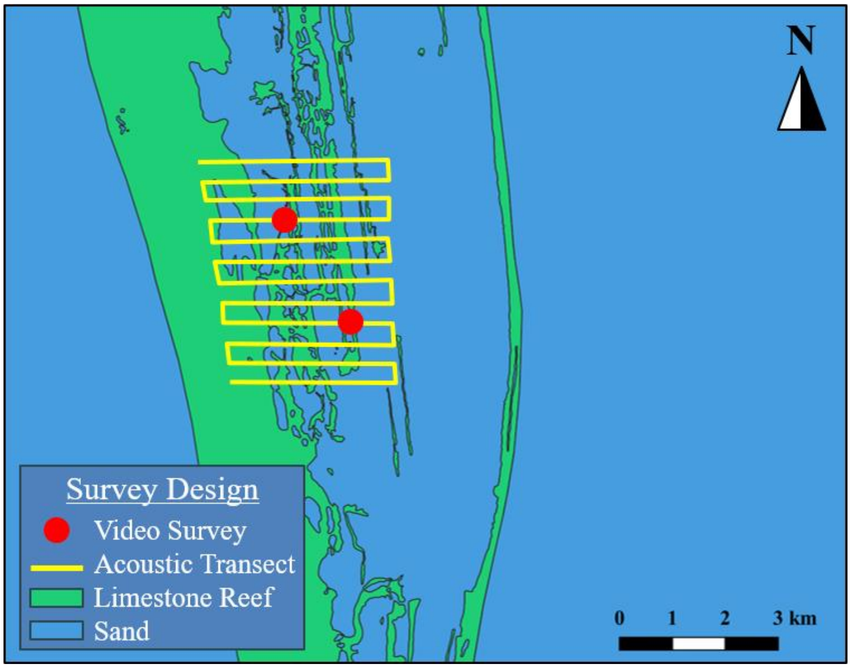

Figure 4 Example echosounder surveys (parallel line) paired with stationary video deployments (dots) along reef sand interface near promontories used to validate user reports.

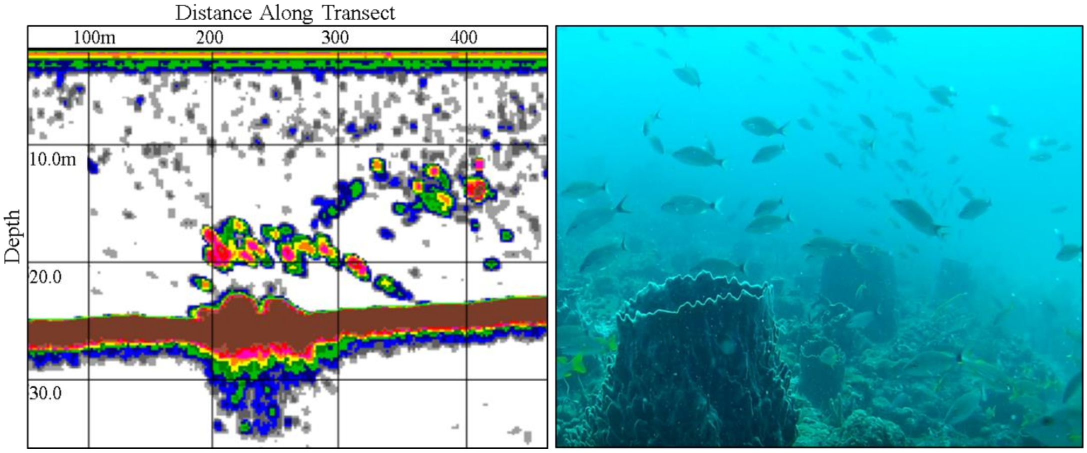

Figure 5 Echosounder surveys were conducted on a historically recognized gag grouper aggregation site east of Boynton Beach, Florida (left). Unbaited remote underwater video (URUV) tripods were deployed (right) where elevated backscatter was observed in echosounder surveys, to determine species identity and abundance, though no evidence of aggregating gag grouper was observed. Schools consisted of a mixed assemblage of reef fish, dominated by dense schools of tomtates (*Haemulon aurolineatum*).

CHAPTER III. HYDROACOUSTIC SURVEYS REVEAL COASTAL FISH COMMUNITY RESISTANCE TO AN ENVIRONMENTAL PERTURBATION IN SOUTH FLORIDA

ABSTRACT

Coastal fish communities are under increasing levels of stress associated with climate variation and anthropogenic activities. However, the high degree of behavioral plasticity of many species within these communities allow them to cope with altered environmental conditions to some extent. Here we combine meteorological information, data from hydroacoustic surveys, and recordings of goliath grouper sound production to examine the response of coastal fish communities to heavy rainfall events in South Florida, USA, that resulted in the release of excess storm water into surrounding estuaries and coastal waters. We observed a nearly 12,000% increase in water column acoustic backscatter following a heavy rainfall event of September 16th, 2015. Interestingly, estimates of school backscatter, a proxy for biomass, increased by 172% with the onset of the perturbation. Schooling fish density also increased by 182%, as did acoustically derived estimates of mean schooling fish length (21%). Following the perturbed period, school backscatter decreased by 406%, along with schooling density (272%), and mean schooling fish length (35%). Hydrophone and hydroacoustic data also revealed that goliath grouper (*Epinephelus itajara*) spawning aggregations were persistent in the region throughout the duration of the study and continued to exhibit courtship behavior during the perturbed period. Our observations demonstrate the high level of resistance common in coastal species but raises new questions regarding the threshold at which fish communities and reproductive activities are disrupted. As coastal land use continues to increase, and the effects of global climate change become more pronounced, more Before-After Control Impact (BACI) studies will provide

improved insight into the overall response of nearshore communities to future perturbations and the cumulative effect of repeated perturbations over extended periods.

INTRODUCTION

Coastal ecosystems are regularly exposed to various natural and anthropogenic stressors which can produce significant changes in community structure, behavior, and life history of coastal fish communities (Wilson et al. 2006, Walther 2010, Thom & Seidl 2016). In many areas, changes in perturbation regimes associated with increases in the severity or frequency of climate events over extended spatio-temporal scales are expected to have severe impacts on both aquatic and terrestrial ecosystems (Wilson et al. 2006, Paddack et al. 2009, Nicholls & Cazenave 2010, Knutson et al. 2010, Adam et al. 2014). In particular, the increased frequency of perturbations related to human activity and climate change have been identified as major drivers of increasing biotic and abiotic stress in coastal zones. Most notable of these stresses include the urbanization of coastlines, recreational activity, and episodic pulses of freshwater run-off into nearshore systems (Sime 2005, Mallin et al. 2009, Hoegh-Guldberg & Bruno 2010, Fabricius et al. 2014, Tilburg et al. 2015). Broadly, perturbations are well-known to play pivotal roles in ecosystem dynamics (Dornelas 2010), however it remains unclear how coastal fish communities will respond to anthropogenically-mediated events influenced by changing climatic norms that occur at varying spatiotemporal scales and intensities (Dale et al. 2000, Hoegh-Guldberg & Bruno 2010). The paucity of data currently available to describe the behavioral responses (e.g., habitat use, foraging patterns, reproduction, etc.) of coastal fishes to perturbations can, in part, be explained by the unpredictable nature of these events and the difficulty associated with carrying out well-timed observational field studies. Consequently, in situ studies conducted in coastal habitats are likely to lag behind events and fail to capture the full range of conditions throughout the perturbation and recovery period.

South Florida regularly experiences these periodic environmental perturbations, such as heavy seasonal rainfall events that offer a natural experimental setting to examine the community response to rapidly changing environmental conditions. Following heavy rainfall events in South Florida, coastal ecosystems are often inundated with runoff from local urbanized areas and are also susceptible to significant freshwater inputs from regional watersheds. During these periods of elevated storm activity, flood mitigation activities scheduled by the South Florida Water Management District (SFWMD) and Army Corps of Engineers are implemented to alleviate stress on the Herbert Hoover Dike that surrounds Lake Okeechobee (Figure 1), and to prevent wide-spread flooding in adjacent agricultural lands (Zheng et al. 2016). Recognizing the deleterious effects of untreated run-off into the estuary, the SFWMD uses Stormwater Treatment Areas (STA's) throughout the region to mitigate the amount of untreated terrestrial material entering the estuary. Unfortunately, the magnitude and frequency of rainfall events between September and November 2015 exceeded the storage capacity of the adjacent STA's and required the controlled release of 5.79×10^7 m^3 of freshwater into the St. Lucie River estuary (*personal communication from the SFWMD*, DBHYDRO [Dec. 10, 2018]). The influx drastically increased suspended sediment loads in coastal waters, and consequently diminished water clarity beyond 6 km from the shoreline for approximately one month (*Binder personal obs.*) This was also evidenced by satellite imagery from the time period that revealed increases in Chlorophyll-a concentrations in surface waters near the St. Lucie Estuary (Figure 2).

Coastal environments frequently experience shifts in environmental conditions that have the potential to modify local community composition and structure. Thus, the organisms that persist in coastal systems are generally adapted to variable conditions, such as seasonal changes in temperature, tidal effects, and rapid changes in turbidity. Recent research has also depicted fish schooling behavior as a highly dynamic and plastic process, such that individual fish are capable of altering their behavior (e.g., swimming faster and maintaining greater alignment with individuals in schools) in response to changes in local conditions to facilitate the transfer of information and favor survival (Rieucau et al. 2016). However, the ability to rapidly adjust to unexpected shifts in conditions may not extend to upper-trophic levels and has the potential to produce unpredictable changes in predator and prey dynamics (Rogers 1990, Syms & Jones 2000, Leahy et al. 2011, Ponge 2013), disrupt important life history processes such as aggregative spawning (Lewis 1998, Nemeth et al. 2012), alter social behavior (Berg & Northcote 1985), and decrease foraging success (Gregory & Northcote 1993). Among upper trophic level species of concern, the Atlantic goliath grouper (*Epinephelus itajara*) aggregates on South Florida reefs to spawn between August and November (Koenig et al. 2016) and may therefore be at particular risk. In this instance, the 2015 rainfall events occurred during the peak of their spawning season (Koenig et al. 2016), and though all life-history stages of goliath grouper spend a large portion of their time in nearshore habitats (e.g., Florida Everglades and Florida Bay), it is unclear if rapid changes in environmental conditions (e.g., increase in turbidity or the passage of storms) affect their spawning behavior. There are numerous studies that have demonstrated persistent spawning behavior in coastal species experiencing intense storm activity (Biggs et al. 2018, Locascio and Mann 2005), but others have shown obvious shifts in activity that indicate a significant disruption in “day-to-day” behavior (Bacheler et al. 2019). Further, even when temporary behavioral modifications are feasible, they are known to occur with poorly understood fitness trade-offs that may lead to a significant decrease in ecosystem function, loss of biodiversity, and ultimately fish production (Chabanet et al. 1995, Rooney & McCann 2012, Wong & Candolin 2015).

In the case study presented, we use regional meteorological data and hydroacoustic surveys to examine the relationship between rainfall events of September 2015 and the subsequent changes in suspended materials in the water column (Figure 3). Further, we investigate how this type of perturbation affects the morphological characteristics of fish schools (e.g., length, area, thickness, etc.), relative abundance, size distributions, schooling fish density. Recordings form seasonally deployed hydrophone arrays were also used to characterize changes in goliath grouper sound production after the storm events and through the perturbed period.

METHODOLOGY

Study region and data collection

Hydroacoustic surveys (n = 31) were conducted at five natural and artificial reef structures approximately 4 – 6 km East of Jupiter, Florida (N 26° 56.650, W 80° 04.370) at depths between 18 – 45 m (Figure 1). Sites were selected based on their use as goliath grouper spawning aggregation sites (Koenig et al. 2016) and surveyed from September – November 2015, near peak new and full moons, to capture the peak of goliath grouper activity. Hydroacoustic surveys were conducted at approximately 2.5 m s^{-1} and comprised of 8 – 12 600 m east-west linear transects at 25 – 30 m spacing that bisected the study reefs and surrounding habitat perpendicularly. Hydroacoustic data were collected with a calibrated Simrad EK60 120 kHz split-beam echosounder operating at 0.256 µs pulse duration with a 7° beam-angle. The transducer was deployed from a pole mount approximately 1 m below the surface. Standardized system calibration procedures were performed (Demer et al. 2015).

Passive acoustic recordings of goliath grouper sound production were made with calibrated DSG Acoustic Dataloggers (Loggerhead Instruments, Inc.) at two of the study sites, from September 20 through November 29, 2015 (immediately following the passage of the storm period). Acoustic data were recorded for 20 s every 5 min at 10 kHz sample rate. Sound pressure levels (SPL) for the 0-100 Hz frequency band were calculated for each .wav file as the mean SPL dB re: 1µ Pa.

A publicly available hydrological and meteorological dataset, DBHYDRO[2], was queried for precipitation (cm), flow rate (m^3s^{-1}), and freshwater release timing corresponding to the study period. Daily precipitation (cm) from eleven monitoring stations in the Okeechobee and St. Lucie watersheds were selected to quantify rainfall in the region, and the St. Lucie Lock and Dam provided daily flow (m^3s^{-1}) into the St. Lucie estuary along with the timing of dam openings (freshwater release events) (Figure 1).

Exploratory dives were conducted prior to, and during the perturbed period, to confirm the presence of goliath grouper and describe the fish communities. The increase in turbidity following the rainfall events precluded standardized visual assessments, but divers did make qualitative assessments of the species present. This included confirming that goliath grouper were present via direct observation and through the audible detection of their characteristic low-frequency vocalizations (aka ‘booming’). Hook-and-line sampling from the survey vessel was also used to identify the schooling species observed in the water column following hydroacoustic surveys.

Data processing

Echoview 8.0 (Sonar Data Pty. Ltd.) was used to process hydroacoustic data. An initial visual inspection of the raw data was conducted to identify and remove bad data and poor-quality data regions (i.e., spike noise, rapid speed changes, abrupt turns, etc.). A bottom

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[2] https://www.sfwmd.gov/science-data/dbhydro

detection algorithm was then used with a 0.5 m back-step to eliminate reverberation from the bottom, and a 2.0 m exclusion region was applied to the surface to eliminate the acoustic nearfield and artifacts from surface conditions (e.g., bubble ringdown). Fish schools and individual fish targets were then flagged and isolated for exporting. Fish schools were identified with an automated detection algorithm within Echoview (minimum school height and minimum length = 1.00 m, minimum candidate height and minimum length = 0.20 m, maximum linking distance vertical and horizontal = 1.00 m). Point targets with target strength (TS; dB) > -50.0 dB (equivalent to standard length (SL; cm) of > 4.9 cm) were identified and tracked in Echoview using an alpha-beta tracking algorithm (McCartney & Stubbs 1971, Blackman 1986). The schools and target tracks produced by the algorithms were manually evaluated for errors, and incorrectly classified regions were removed from the final output. Water column backscatter data, excluding school and fish targets, were echo integrated in 5 m horizontal by 5 m vertical bins to derive estimates of the Nautical Area Scattering Coefficient (NASC; m2 nmi^{-2}). NASC estimates were used as an index of scattering in the water column attributed to detritus, plankton and flocculent matter (Simmonds & MacLennan 2005a). Estimates of school NASC (i.e., NASC measurements constrained to the fish school region), which is proportional to "acoustic biomass" or energy density (Simmonds & MacLennan 2005a), were used to quantify changes in school biomass through the study period. The term "school NASC" is used hereafter as a proxy to describe changes in school biomass. Estimates of standard length (SL) were derived from point targets based on the relationship between TS and SL presented for a mixed assemblage of fish by McCartney & Stubbs (1971); where $TS = 24.50 \times log_{10}(SL) - 66.84$. Point targets that were associated with schools and within 2.0

m of the school periphery (referred to hereafter as, school adjacent fish targets) were used to estimate schooling fish length distributions (Kloser & Horne 2003), while additional point targets within 100.00 m of the study reefs were used to generate non-schooling fish length distributions. The complete point target sampling distribution was decomposed into two separate distributions, capturing those targets suspected to be goliath grouper (> -35 dB, *Binder et al., unpub. data*), and all other fish targets (>-50 dB and ≤ -35 dB). A visual inspection of those data was then performed to confirm the presence of goliath grouper during the three sampling periods. Estimations of schooling fish density (ρ, fish m^{-2}) were derived from the area backscattering coefficient (s_a; m^2 m^{-2}); where $\rho = s_a/10^{(\frac{TS}{10})}$ (MacLennan et al. 2002).

Passive acoustic data were recorded at field sites from September 20 through November 29th, 2015. A Fast Fourier Transformation of each 20 s .wav file was used to generate a power spectrum from which band sound pressure levels in 100Hz wide bins were produced. Passive acoustic data were analyzed with MATLAB R2009B software (Mathworks, Inc.). Nightly peaks in sound pressure levels in the 0-100Hz band were indicative of goliath grouper courtship behavior as described by Mann et al. (2009). Spectrograms of passive acoustic data were reviewed to confirm goliath grouper as the source of sounds in the 0-100Hz frequency band.

Data analysis

A Pearson product-moment correlation was performed to examine the relationship and the lag between rainfall and flow rate changes. A boot-strapped (1000 iterations) trimmed-mean (10%) one-way analysis of variance (ANOVA) for heteroscedasticity, followed by a “lincon” multiple comparisons test was used to characterize the variation in water column NASC (Wilcox 2011). The study period was then divided into three blocks (before, during, and after the perturbation). The metrics derived from the school detection and single target detection algorithms within Echoview (school area (m^2), school vertical distribution (m), school length (m), thickness (m), and school NASC), along with data pertaining to the acoustically derived mean length of schooling and non-schooling fish, were used to test for differences in school morphology (including schooling fish length), schooling fish density (fish m^{-2}), and non-schooling fish length.

School area and fish density were $\log_{10}$ transformed to meet the assumptions of normality and equal variance for a parametric ANOVA (Cox 2006). School length and school thickness did not conform to the assumptions of a parametric ANOVA and were analyzed with a Kruskal-Wallis one-way ANOVA followed by a Dunn’s post-hoc multiple comparison test. A k-sample Anderson-Darling Test performed on the remaining variables (school NASC, distance to seabed, school adjacent fish length, and individual fish length) found their distributions to differ significantly, and a boot-strapped (1000 iterations) trimmed-mean (10%) one-way ANOVA for heteroscedasticity, followed by a lincon multiple comparisons test was used to test for differences between the perturbed periods (Wilcox 2011). All analysis of hydroacoustic data, and presentation of DBHYDRO data were performed using R Statistical Software version 3.4.2 (R Core Team 2018).

RESULTS

Between September and November 2015, 5.79×10^7 m^3 of freshwater was released into the St. Lucie River estuary. Approximately 34% (1.95×10^7 m^3) of the total annual volume (1.8×10^9 m^3) was released during the week of September 13-19, 2015, following 19 cm of precipitation over a three-day period (Figure 4a). The peak flow of 98.97 m^3 s^{-1} occurred on September 18, 2015, and was approximately three times higher than the average flowrate associated with freshwater releases (Figure 4b). A positive correlation between rainfall and flow was found (Pearson's $r_{(74)} = 0.23$, $p < 0.05$) following a six-day lag. Field sampling intervals did not allow us to identify the lag between increased flow and changes in acoustic backscatter at the study sites (~ 25 km south); however, mean water column backscatter (NASC) representing particles or debris, with fish targets and schools removed, was significantly higher during the perturbation, compared to both before and after (lincon: $p < 0.001$) (Figure 4c).

School NASC, a proxy for biomass, was significantly different between all three periods (lincon: $p < 0.001$). Mean school NASC increased by 172% with the onset of the perturbation and decreased by 406% following the perturbation (Figure 5a). Schooling fish density was also significantly higher during the perturbation compared to both before and after (Tukey: $p < 0.005$), but density before and after were not significantly different from one another (Tukey: $p > 0.05$). Fish density increased by 182% with the onset of the perturbation and decreased by 272% following the perturbation (Figure 5b). Standard length (SL) estimates of peripheral fish targets derived from target strength data were determined to be significantly different among all three periods (lincon: $p < 0.001$), however estimates were variable and increased by only 21% during the perturbation, decreasing by 35% after the event (Figure 5c). Estimates of non-schooling fish length and school morphology (i.e., school length, thickness, area, and vertical distribution) did not significantly vary throughout the study period ($p > 0.05$).

Diel patterns of sound production at goliath grouper spawning sites revealed nightly peaks ranging from approximately 90 to 110 dB SPL (re 1µ Pa) through mid-October, a range consistent with goliath grouper courtship activity identified by Mann et al. (2009) (Figure 6). The absence of diel spikes in sound production after mid-October, also indicated that goliath grouper were likely present but not exhibiting courtship behavior, which was further validated in decomposed kernel density estimations of target strength distributions that revealed persistent peaks at approximately -33 dB (i.e., in the range assumed to be goliath grouper), though the study period. Also of note, kernel density plots reveal a bimodal distribution of fish targets ranging from -35 to -50 dB during the perturbed period. Peaks occurred at approximately -45 dB and -37 dB, characteristic of two dominant size classes of fish contributing to observed acoustic backscatter in the water column besides goliath grouper (Figure 7).

DISCUSSION

Our study demonstrates the direct relationship between terrestrial water management activities and the effects of large-scale water releases on coastal reefs in South Florida. Despite the occurrence of an significant increase in turbidity induced by heavy rainfall and the subsequent freshwater release from the St. Lucie estuary, the local fish community exhibited a high level of resistance to the perturbation. Contrary to our predictions, the data revealed that the morphology and habitat use of reef-associated fish schools remained unchanged, whereas school NASC, density, and the mean schooling fish length increased during the perturbed period. Data from the hydrophones also indicated that golaith grouper continued their courtship behavior (i.e., nightly chorusing) through the perturbed period, and we documented a natural cessation of vocalizations approaching the end of the spawning season. Notably, this is consistent with the observations of persistent spawning activity in various seatrout species documented by Biggs et al. (2018) and Locascio and Mann (2005).

In addition to the apparent ability to resist change during the perturbed period, we observed an increase in the abundance of pelagic species, including little tunny (*Euthynnus alletratus*; hereafter referred to as bonito), round scad (*Decapterus punctatus*), mackerel scad (*Decapterus macarellus*), and spanish sardines (*Sardinella aurita*), that closely preceded or coincided with the onset of turbid conditions. Their arrival to the study area could explain the observed increase in schooling fish length, school NASC, and fish density that was observed during the disturbed period. Their occurence was confirmed during the perturbed period with a combination of trolling hook-and-line surveys conducted simultaneously with hydroacoustic surveys, and during a limited number of exploratory dives made by researchers to qualitatively assess water conditions (i.e., estimated visibility for conducting visual surveys). In conjunction with the already present goliath grouper, the influx of bonito can explain the elevated estimates of school NASC, mean fish length, and school density.

Bonito, a mobile piscivorous species that forms large schools, were one of two numerically dominant fish species noted by divers compared to other common reef fish species present in the system before and during the perturbed period (author personal obs.). In addition to bonito, goliath grouper were present in high abundance at some sites (5-50 individuals per site) by early September 2015, and likely continued to increase in abundance approaching the peak new moon spawning period (Koenig et al. 2016). Sound production at the study sites also confirmed that goliath grouper were present and continued to exhibit courtship behavior through the perturbed period (September 26 – October 11), however it must be noted that the deployment of said hydrophones occurred three days after the passage of the storms. This limits our ability to make any definitive assessment of their response to the storm passage itself. The decrease in courtship associated sound production, following the new moon phase in mid-October, is consistent with the differential rates with which goliath grouper disperse at the end of the spawning season, and the persistence of small resident populations at the study sites throughout the year (Koenig et al. 2016). This was consistent with our observations of decreased school NASC and mean fish length after water column backscatter had decreased. Even at low abundance, goliath grouper are easily discernible as large single targets in hydroacoustic data when conspicuously present in the water column. As such, they have the potential to produce a significant positive shift in both metrics, due to their large swim-bladders and the associated acoustic response (Love 1971, Simmonds & MacLennan 2005b).

The combined influence of bonito and goliath grouper may explain the elevated school NASC and size estimates through the perturbed period, but their co-occurrence in the study area with several planktivorous fish species may also contribute to the observed changes. Round scad (*Decapterus punctatus*), mackerel scad (*Decapterus macarellus*), and spanish sardines (*Sardinella aurita*) are known to not only prey on goliath grouper eggs, but also use goliath grouper as a refuge from the piscivorous bonito (Macieira et al. 2010). The increase in planktivore abundance associated with the arrival of goliath grouper to the spawning sites, and possibly surplus food resources in the water column (e.g., organic suspended material), likely attracted and sustained the bonito population through the perturbed period. It is reasonable to assume that the planktivores followed the natural dispersion of the goliath grouper as the spawning season concluded in mid-October, and as suspended material in the water column decreased. Coincident with a decrease in prey biomass, the bonito naturally dispersed in search of more abundant prey beyond our study area.

The arrival and departure of pelagic species likely explains a large portion of the observed changes in schooling structure, though behavioral changes in resident reef fish species cannot be dismissed as a factor that potentially contributed to our observations. Indeed, we recorded a decrease in the number of schools and non-schooling fish targets during the disturbance. While these two metrics were not considered reliable indicators of change due to their susceptibility to biases associated with data collection and processing methods, they could help to explain the observed changes in school density and school NASC. The net reduction in both schools and individuals detected through the perturbed period could be attributed to a reduction in reef fish activity levels and/or a change in schooling structure that enabled them to avoid detection. Specifically, prey species (e.g., members of the *Haemulidae* family) are known to decrease activity levels and form denser groups in response to increased predation risk and decreased sensory perception (e.g., increased turbidity) (Leahy et al 2011). Denser schools have the benefit of improved transmission of predator-based information through the collective group (Rieucau et al. 2015). The formation of denser groups that occupy less space also reduces the overall surface area of schools, limiting the points of vulnerability experienced by all school members. It is therefore possible that the increase in school density and NASC was a product of reef fish consolidating into denser units that remained close to the reef (i.e., made fewer forays into open water). Our ability to justify this interpretation is potentially confounded by hydroacoustic data processing limitations, because schools swimming close to the reef can be difficult or impossible to detect due to occlusion by the acoustic deadzone (Ona and Mitson 1996). However, that in and of itself is consistent with the reduction in schools and individuals observed, as we expect a proportion of schools and individuals did occur in the acoustic deadzone. From the remaining schools preserved for analysis, inclusive of the pelagic schools, the increases could in fact be partially attributed to the proposed behavioral changes exhibited by reef fish.

Coastal environments are highly dynamic systems that experience frequent shifts in environmental conditions, and the organisms that inhabit these locations must be resilient to seasonal changes in temperature, tidal effects, and various episodic events. This is especially true for goliath grouper (not excluding other coastal species), that inhabit inshore systems that experience frequent and acute shifts in conditions (e.g., Florida Everglades, Florida Bay, etc.) throughout all life history stages, with no apparent consequences. If exposure to highly variable conditions was disadvantageous to their survival and performance, we would expect to see a shift in their distribution away from these habitats, though that is not the case. Indeed, elevated sound production associated with courtship through the perturbed period in our study provides evidence that the aggregations were present even after turbidity increased in response to the heavy rainfall event of September 16. However, despite their tolerance to turbid conditions, a direct correlation between sound production, courtship behavior, and active spawning has not been documented (Mann et al. 2009, Koenig et al. 2016). Previous studies have identified mixed response in overall activity, including spawning, with the onset of turbid conditions brought on by high-intensity storms, but the available information has focused on various smaller fish species (i.e., those at relatively higher risk of predation) (Leahy et al. 2011, Borner et al. 2015), or species that consistently occur in turbid environments (Bacheler et al. 2019, Biggs et al. 2018). Thus, it remains unclear whether the perturbation disrupted spawning during the peak of the spawning season, and further studies are needed to address this. However, considering their spawning season is central to the wet season, when estuarine food resources are most readily available to juvenile GG, it is possible that these high-flow perturbations confer an unquantified advantage to dispersed larva (Koenig et al. 2016).

Our observations of increased water column acoustic backscatter following the storm events of September 2015 highlight the sustained response of coastal waters to inland water management activities (i.e., the release of water from the water-control structure). The flow of water into the estuary and out the adjacent inlets is a natural, well-documented process that estuarine and coastal species experience regularly, but modifications to the natural drainage patterns from the watersheds through man-made canal systems introduces a level of variability that these organisms may not be able to cope with. In the absence of man-made canals and water-control structures, unregulated flow through the aquifer would be distributed naturally, mitigating large pulses of water from being injected directly into the estuaries and coastal waters. Together, the decrease in light penetration, increase in siltation, nutrients, and terrestrially derived toxicant load associated with high flow from the estuary can have negative impacts on important aspects of estuarine and coastal ecosystem function (Haunert 1988, Sime 2005). As coastal land utilization continues to increase, and unpredictable high intensity storms become more frequent with changing climatic norms, the potential for large-scale environmental perturbations to disrupt ecosystem function and affect community dynamics will only increase (Hoegh-Guldberg & Bruno 2010, Walther 2010). While our data suggests that the reef-associated and pelagic fish communities resisted possible detrimental effects produced by the perturbation, and remained present throughout the period, it is unclear whether the conditions elicited any negative indirect impacts through behavioral or physiological effects on goliath grouper reproductive performance or larval recruitment to nursery habitats.

Resource managers are not unfamiliar with the effects of runoff on estuarine and coastal systems, though the extent of their relationship is not often clear and may be underrepresented in ecosystem-based management strategies. Indeed, the event described here has implications for managers involved in agricultural land use (e.g., untreated fertilizer runoff), flood-mitigation, wetlands conservation, fisheries management, and myriad other issues across the State of Florida and analogous coastal areas. As we expect coastal land utilization to continue increasing into the future, along with a rise in storm intensity and frequency, a more comprehensive examination into the physiochemical processes that are associated with water column perturbations, and their effect on coastal fish communities is warranted. Lastly, more pre-emptive Before-After Control Impact studies in areas that experience semi-predictable perturbations will provide improved insight into the overall response of nearshore communities to future events, informing the development of more effective ecosystem-based management strategies that ensure the sustainable use of coastal resources.

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FIGURES

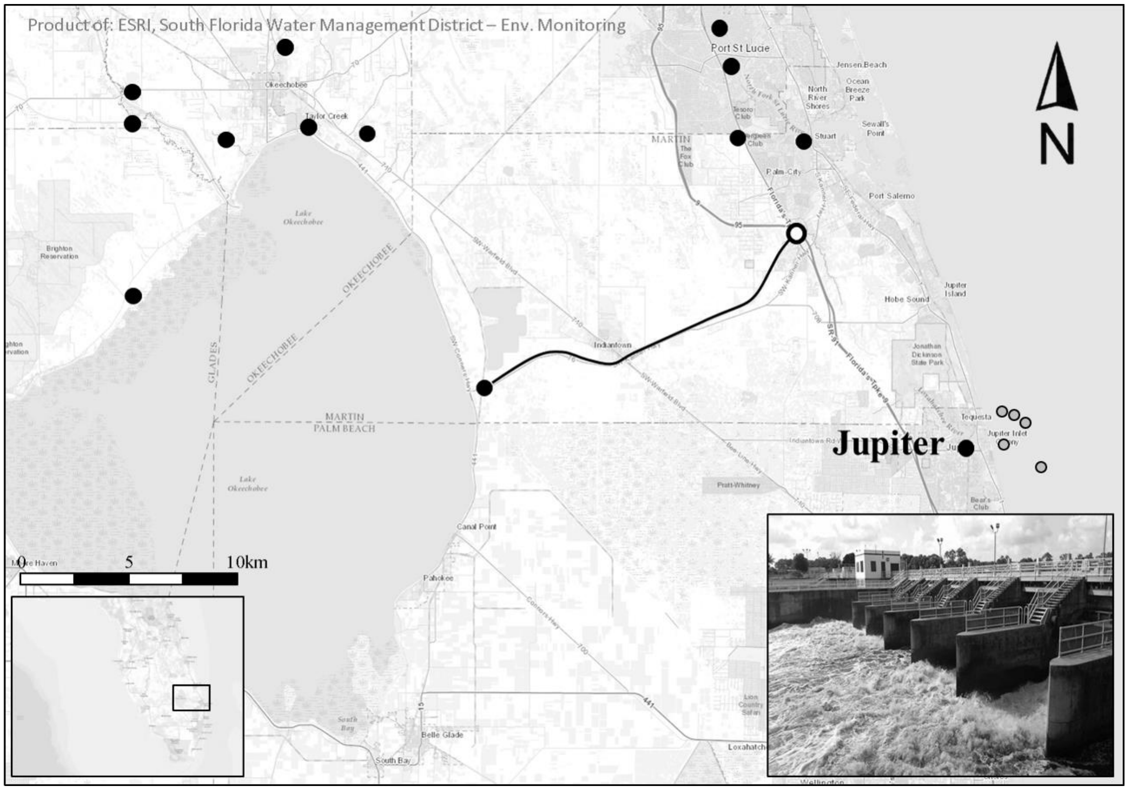

Figure 1 Study region. Closed black circles represent regional precipitation monitoring stations. The black line follows the St. Lucie Canal (C-44), the main waterway between Lake Okeechobee and the St. Lucie River Estuary. The white circle denotes the S-80 dam structure, the main drainage location for the St. Lucie and Okeechobee watersheds through the S-80 dam structure (inset picture; credit: WPTV). Black outlined gray circles denote goliath grouper spawning sites and hydroacoustic sampling locations east of Jupiter, FL.

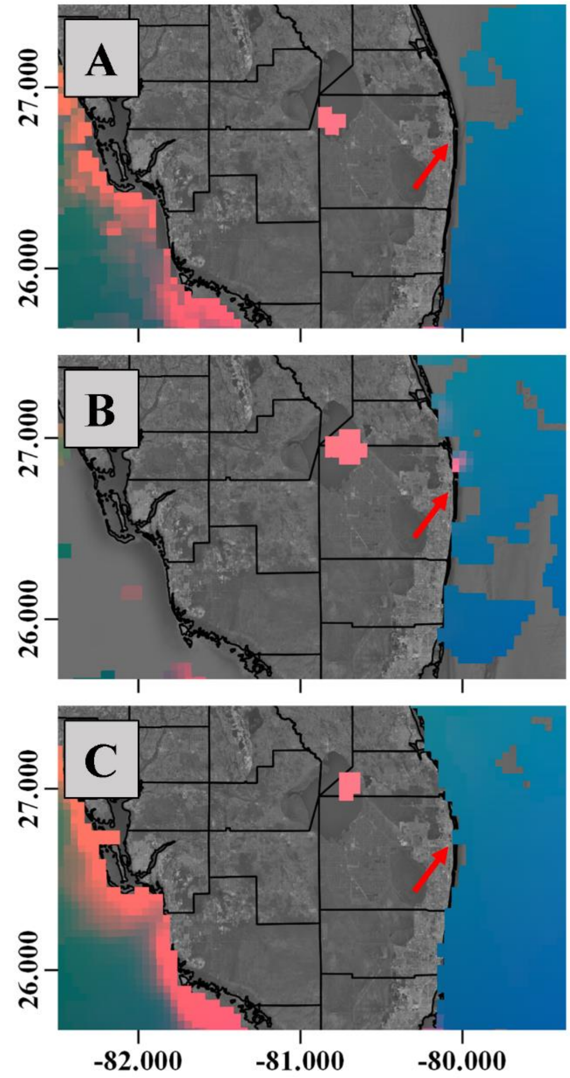

Figure 2 A) Weekly chlorophyll-a concentration composites derived from satellite Imagery corresponding to the pre-perturbation period (September 6th, 2015); B) the perturbed period (September 28th, 2015); and C) the period following the perturbation (November 1st, 2015). Note that warm colors correspond to areas of high productivity. The red arrow references the St. Lucie estuary inlet.

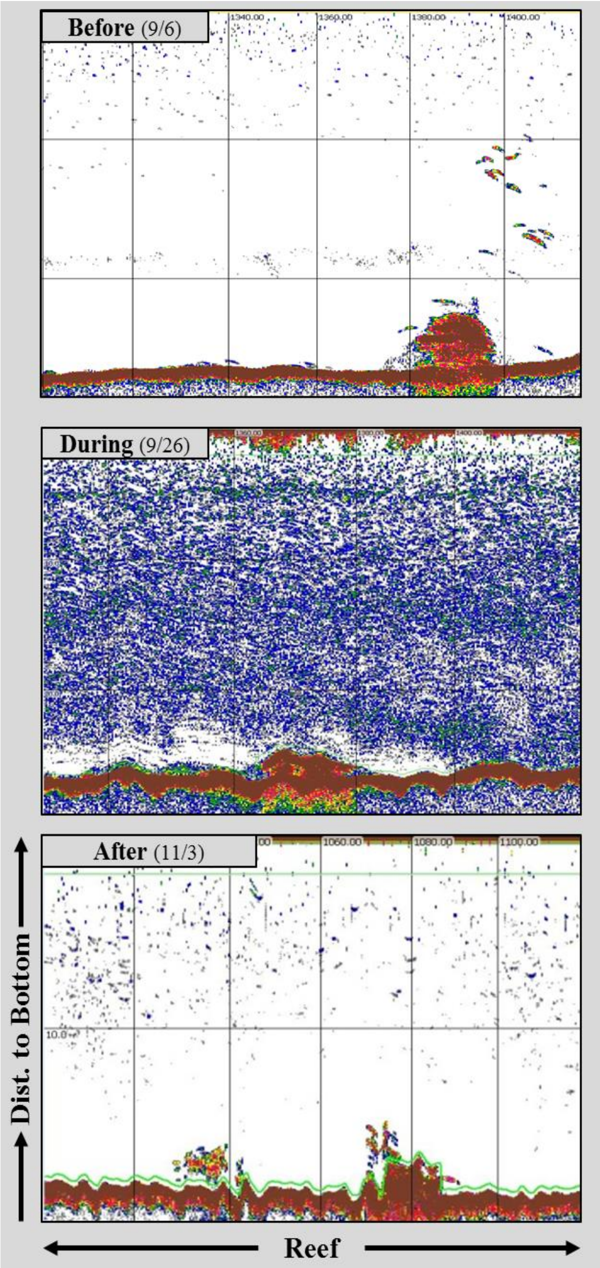

Figure 3 Example echograms from the three distinct sampling periods. Before) Prior to the storm activity, water column backscatter was negligible, and individual fish targets were clearly observed in acoustic data. During) Following the onset of storm activity and the subsequent freshwater releases, increased back scattering in the water column (blue pixilation in center panel) was observed. After) Approximately one month after the stormwater control structures were closed, and estuarine flushing had concluded, water column backscattering returned to a “pre-disturbance” state.

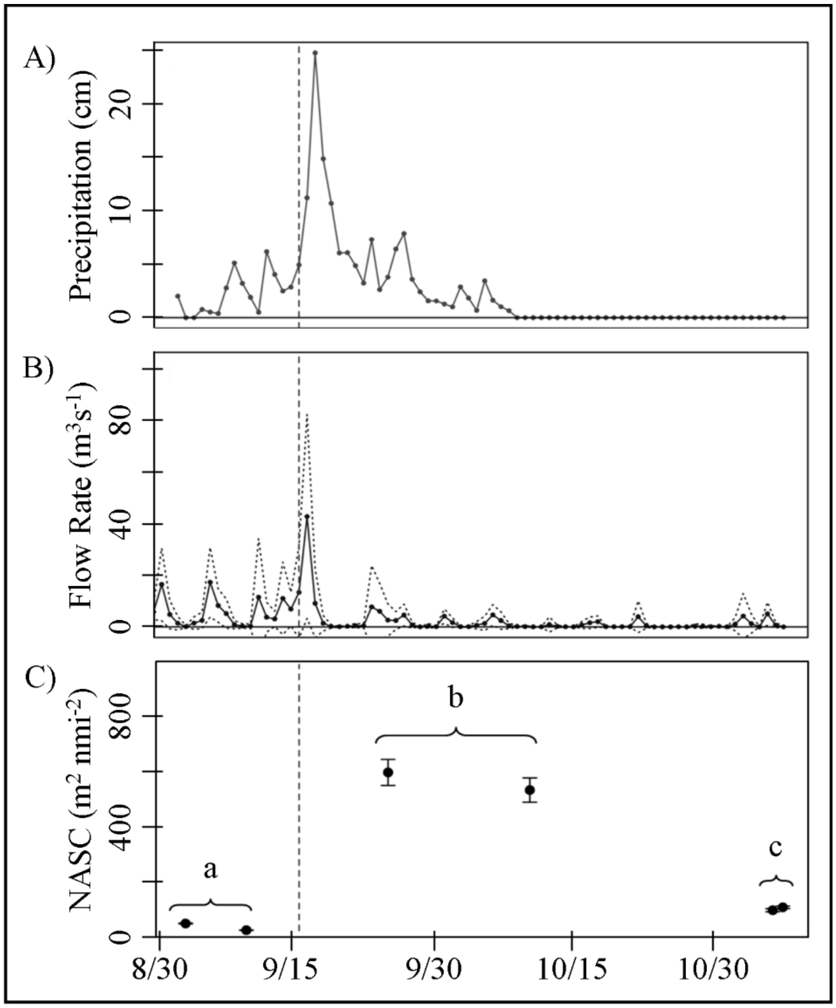

Figure 4 A) Solid line denotes daily rainfall average (cm) from the region adjacent to Lake Okeechobee and St. Lucie Estuary (seen in Figure 1). B) The solid line denotes daily average flow rate through the St. Lucie dam structure (S-80) (seen in Figure 1 inset). Dashed lines correspond to the standard deviation away from the mean associated with daily flow measurements. C) Circles represent total water column acoustic backscattering (NASC; m^2 nmi^{-2}), minus scattering attributed to fish targets, with their associated standard error. Brackets and corresponding letters denote statistical significance and categorization of sample periods a) before, b) during, and c) after the disturbance. The vertical lines represent the onset of the storm events beginning September 16th, 2015.

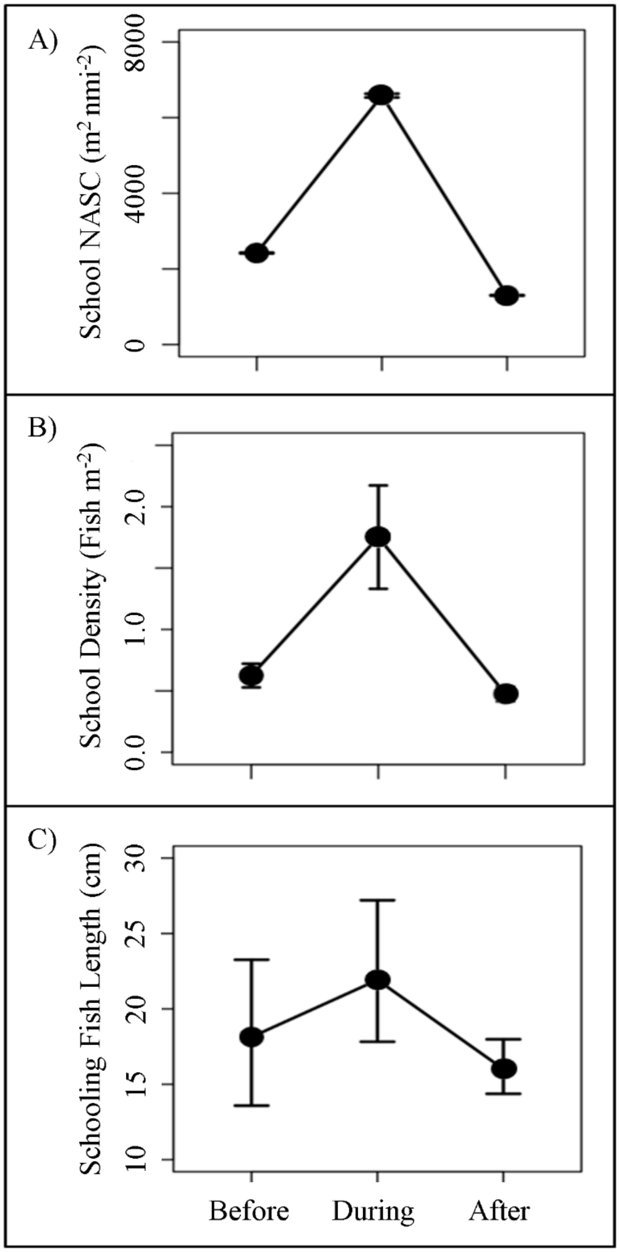

Figure 5 A) NASC (m^2 nmi^{-2}) estimates for fish schools from the three distinct study periods. B) Estimates of areal schooling fish density (ρ, fish m^{-2}) C) Estimates of schooling fish size (standard length; SL (cm)), derived from TS measurements. Note that sizes are estimated using the target strength (dB m^{-1}) to length equation: $SL = 10^{(\frac{TS+66.84}{24.5})}$. As such, small deviations in TS result in large changes in SL, partially explaining the high degree of error.

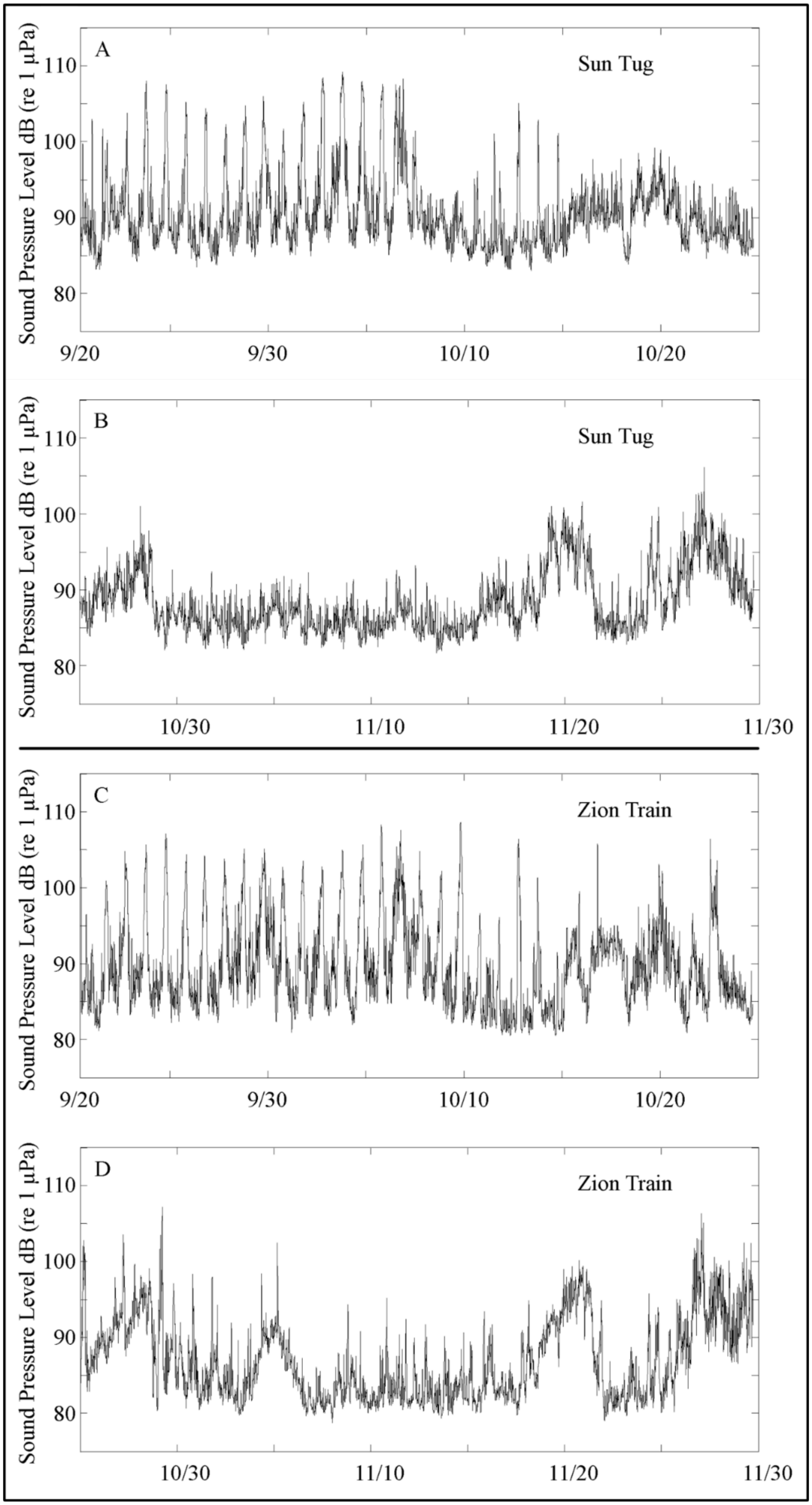
A
Sun Tug
B
Sun Tug
C
Zion Train
D
Zion Train
Sound Pressure Level dB (re 1 µPa)
80
90
100
110
9/20
9/30
10/10
10/20
10/30
11/10
11/20
11/30

Figure 6 Band sound pressure levels of the 0 – 100Hz frequency band recorded during September 20, through November 29th, 2015 at two Goliath grouper spawning aggregations sites near Jupiter, Florida; the Sun Tug (A and B) and the Zion Train (C and D). Nightly rises and falls in sound pressure levels associated with Goliath grouper courtship are evident between approximately 9/20 and 10/15. The new moon in October typically represents the end of the spawning season and this is reflected in the acoustic data.

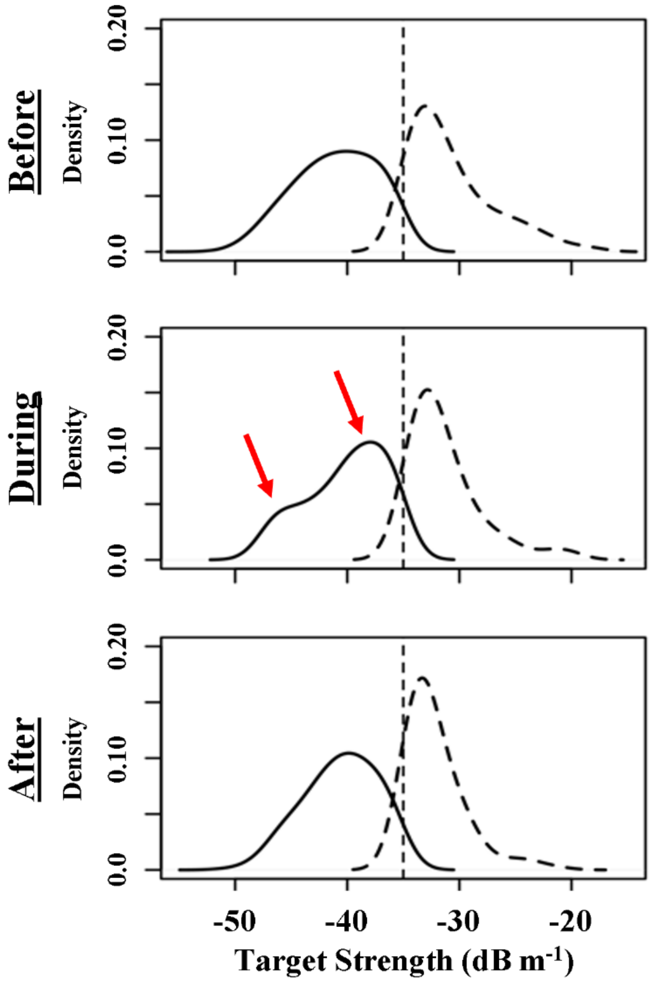

Figure 7 Decomposed target strength distributions for individually tracked fish targets based on kernel density estimation through the three periods. The complete sampling distribution was split at -35 dB, based on the assumption that targets > -35 dB were likely goliath grouper. TS estimates were aggregated into 1.5 dB bins. The vertical dotted line is used to simply denote the -35 dB division. Red arrows represent bimodal peaks suggestive of two distinct size classes observed during the disturbed period.

CHAPTER IV. ACOUSTIC SURVEYS REVEAL BROAD-SCALE SPATIOTEMPORAL PATTERNS OF GOLIATH GROUPER (*EPINEPHELUS ITAJARA*) OCCURRENCE AT SPAWNING AGGREGATIONS IN JUPITER, FLORIDA

ABSTRACT

A complete moratorium on the harvest of Atlantic goliath grouper *Epinephelus itajara* (GG) in the United States has been in effect for 32 years, following decades of heavy fishing and declines in abundance throughout their range. Notable recoveries have since been observed, primarily by way of diver visual surveys (DVS), though DVS have inherent limitations that preclude their use in certain settings. Alternative methods, such as active acoustic surveys (AAS), provide distinct advantages over DVS, and we present data here to demonstrate their utility as a supplemental tool to monitor GG. AAS were conducted between 2017-2020 at four aggregation sites in Jupiter, Florida (n=83). Our goal was to characterize diel, inter-lunar, seasonal, and inter-site variation in GG density, and to determine how the behavior of GG and local fish communities affected our estimates of density at those scales. The data revealed that daytime surveys provided the highest estimates of density, while surveys conducted after dark were often confounded by interference from planktivores in the water column and suspected nocturnal foraging behaviors of GG. Additionally, we identified a potential relationship between density and site composition that suggests GG preferentially select sites based on the availability of benthic habitat, that likely provides a surplus of food resources. Variation across the spawning season was negligible, indicating that there was no optimal survey period within the bounds of the spawning season (August-October), alleviating the logistical burden of executing specifically-timed surveys. Lastly, differences between years were also negligible, suggesting that aggregations have remained stable through the study period, a potentially valuable detail for future fisheries management activities. AAS are a useful tool to monitor GG aggregations, but rather than replace methodologies that have proven their

utility for decades, we strongly advocate for the integration of methods to reach a more complete understanding of GG aggregation dynamics.

INTRODUCTION

The Atlantic goliath grouper *Epinephelus itajara* (GG) is one of the largest fish in the world, reaching sizes of nearly 2.5 m in length and 3-400 kg (FAO 2005, Robins and Ray 1986). Combined with their generally placid nature in response to divers and seasonal participation in large predictable spawning aggregations, GG were an exceptionally easy and lucrative resource for fishers and spearfishers until 1990, when a complete moratorium on harvest was enacted in the United States (Collins et al. 2004, GMFMC 1990, SAFMC 1990). Prior to the closure, dating back to at least the 1920’s, goliath grouper were a common target of both recreational and commercial anglers (NMFS 2006, Mclenachan 2009). By the 1980’s, precipitous declines in their population had been observed throughout their range, largely due to overfishing, but also in response to the loss of juvenile and subadult habitats associated with coastal urbanization, and die-offs resulting from acute episodic disturbances (i.e., “cold snaps” and red tide) (Koenig et al. 2020).

The moratorium has produced a notable recovery in their abundance over the last three decades (NMFS 2006, Koenig and Coleman 2010, Koenig et al. 2020), prompting fisheries managers to re-evaluate the sustainability of a limited harvest in Florida. However, it is still unclear whether the presumed baseline “healthy population” data from the 1950’s, used in stock assessment to characterize the recovery, is actually representative of the healthy pre-exploitation population (Mclenachan 2009, Collins 2014, Bertonici et al. 2018). As such, efforts to monitor and assess the status of goliath grouper populations throughout Florida are ongoing, and a myriad of methodologies have been applied to characterize their populations.

Several diver visual survey programs gather abundance and distribution data annually (e.g., Great Goliath Grouper Count [Florida SeaGrant] and REEF visual survey program), and have been used for decades. Indeed, diver surveys represent the foundation of GG monitoring and have been used successfully throughout the recovery period, though they are largely limited by depth and water clarity, making them ineffective in some locations or in certain conditions. Alternative methods, such as active acoustics (i.e., "sonar surveys"), offer a few advantages over traditional methods that overcome these issues. Specifically, active acoustics has the capacity to efficiently sense the entire water column irrespective of depth, clarity, and light-levels. This facilitates the rapid non-invasive collection of spatially and temporally referenced data that can be used to estimate abundance, density, biomass, and in some cases taxonomic information (Simmonds and MacLennan 2005). Supplementary information (e.g., diver visual surveys or drop cameras) is necessary to ground-truth or aid in the interpretation of active acoustic data, but the large size of individual GG makes them conspicuous targets in active acoustic survey data. Measures can also be taken to improve survey efficacy, and great strides are being made in data processing and survey techniques to account for their limitations (White et al. 2022).

To demonstrate the utility of active acoustics to monitor GG, we conducted a series of active acoustic surveys at spawning aggregation sites near Jupiter, Florida to characterize variations in GG density at four temporal scales and between four well-known aggregation sites of various spatial extent and complexity. Surveys were conducted during both new and full moon periods, recognizing that GG aggregations are persistent through the spawning season (Koenig et al. 2017). However, behavioral variations associated with courtship activity may affect our ability to detect GG, and ultimately our estimates of density. Likewise, surveys were conducted midday and at night to determine if diel changes in GG behavior influence estimates of density. Seasonal differences were also evaluated to characterize trends in GG density over the four year study period. Lastly, acoustic backscatter (i.e., NASC m^2 nmi^{-2}), which is directly proportional to biomass (MacLennan et al. 2002), was used to determine how changes in overall fish biomass and their distribution on study reefs affect our ability to detect GG in active acoustic data. The decision to evaluate NASC was chosen based on the understanding that mixed-species schools in high abundance and/or density can detrimentally affect our ability to detect individual GG (Ona and Mitson 1996), which would result in an underestimation of density. Considering that GG are likely to be reinstated as a gamefish in the State of Florida[3], it is imperative that monitoring efforts are capable of identifying wide-scale and discrete changes in the population over coming years, and we propose that active acoustics represents an efficient tool to accomplish that goal.

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[3] https://myfwc.com/news/all-news/gag-comm-521/

METHODOLOGY

Site Selection

Data were collected at four artificial reefs of varying size and complexity (Esso Bonaire, Zion Train, MG111/Warriors Reef, and Sun Tug) approximately 4 – 6 km East of Jupiter, Florida (N 26 56.650, W 80 04.370) (Figure 1). The reefs were deployed between 1989-1997 in 18-25 m of water, and range in size from 30-60 m in length. The Esso Bonaire and Zion Train are separated by approximately 170 m. Both consist of high-relief artificial reefs (~5 m), but the Esso Bonaire is primarily surrounded by sand bottom. Conversely, the Zion Train is surrounded by metal debris and patches of low-relief hard-bottom limestone rock covered in various macroalgae species, offering it a substantial amount of additional habitat that supports a variety of benthic species. While smaller than the Esso Bonaire, they both offer abundant refuge within their internal structures (i.e., inside the hull, bilge, and hold of the wreck). The MG111 reef consists of a sunken barge covered in concrete columns and debris, that extends approximately 3-5 m into the water column. The reef itself is highly rugose and offers abundant three-dimensional structure to support a diverse assemblage of reef fish and marine organisms, including refuge opportunities for adult GG. Warrior Reef is immediately adjacent to MG111 (~25 m) and consists of ~3 m standing (and fallen) concrete columns (~1 m diameter) spaced at random intervals over a sandy expanse, roughly 100 m x 50 m in size. The columns themselves are effectively solid, but toppled columns offer some refuge to smaller fish and benthic organisms. MG111 and Warrior Reef are considered a “single reef complex” because goliath grouper are frequently observed moving between the two sites, as are the schools of fish frequently observed by divers. The Sun Tug reef is a relatively small artificial reef (a steel tugboat), approximately 20 m long, surrounded by sandy bottom. One notable artificial structure (a 10 m x 5 m rectangular barge) lies in close proximity to the Sun Tug reef, but neither extend more than 3-5 m into the water column. Sites were selected based on their consistent use as GG aggregation sites (Koenig et al. 2016).

Data Collection

Hydroacoustic surveys (n = 83) were conducted during peak new and full moon periods, mid-day (1100 – 1600hrs) and after dark (2000 – 0000hrs), between August – November, 2017 – 2020. Daytime surveys were paired with nighttime surveys based on anecdotal reports and previously collected hydrophone data that indicate GG become more active and ascend into the water column after sunset (Mann et al. 2009, Koenig et al. 2017). New and full moon surveys were contrasted to determine if there were measurable differences between lunar periods, on the basis that GG generally form persistent aggregations throughout the spawning season, rather than dispersing between reproductive events (Koenig et al. 2017). Survey start time varied based on the local tidal period and weather to ensure the safety of survey crew transiting through Jupiter Inlet, a significant navigation hazard under certain conditions.

Data were collected with a SIMRAD EK80 transceiver paired with an ES38-10 split-beam echosounder, operating at 0.256 µs pulse duration with 10^{o} beam-angle. The transducer was mounted to a custom towfish deployed to 1 – 1.5 m below the surface, 15 m behind the survey vessel, and towed at approximately 2.5 m s^{-1}. Surveys consisted of 15 – 20 300 m east-west parallel transects spaced approximately 20 m apart that bisected the study reefs and surrounding habitat perpendicularly. Standardized system calibration procedures were performed each season (Demer et al. 2015).

Data Processing

All acoustic data were reviewed and processed in Echoview 12.0 (Echoview Software Pty. Ltd.). An initial visual inspection of the raw data was conducted to identify and remove bad data and poor-quality data regions (i.e., spike noise, rapid speed changes, abrupt turns, etc.). A bottom detection algorithm was then used with a 0.5 m back-step to eliminate reverberation from the bottom, and a 5.0 m exclusion region was applied to the surface to eliminate the acoustic nearfield and artifacts from surface conditions (e.g., bubble ringdown). A -60 dB re. 1 m^{-1} threshold was applied to the volume back-scattering strength data (Sv; dB re 1 m^{-1}) to eliminate sources of backscatter that did not originate from fish, and a -40 dB re. 1 m^2 threshold was applied to the target strength data (TS; dB re. 1 m^2) to isolate large sources of backscatter representative of GG specifically. All exports from Echoview were organized in a 5 m horizontal by 5 m vertical grid of cells, referenced from GPS position along the transect and the water surface, respectively. Cells that were bisected by the bottom line by more than 90% (i.e., only 50 cm of the cell remained) were removed from the analysis based on the assumption that density estimates would be unrealistically inflated in these cases. Following quality control and pre-processing, backscatter estimates (i.e., NASC m^2 nmi^{-2}) for each 5 x 5 m cell were exported for analysis in R 4.1.2 (R Core Team 2021).

Echo-Counting (Fish-tracking)

Individual fish targets with a target strength > -40 dB re. 1 m^2, characteristic of GG (*Binder unpublished data*), were identified in Echoview using a single-target detection algorithm. The pulse length determination level was set to 6 dB and the minimum and maximum normalized pulse length were set at 0.70 and 1.50, respectively. A maximum beam compensation of 12 dB re. 1 m^2 and a maximum standard deviation of 0.6 degrees off the minor and major axis angles was used. Single targets were then passed through an alpha-beta tracking algorithm to identify individual fish tracks (or echo-traces) (Blackman 1986) meeting the criteria of at least 2 pings that were within 5 pings of one another. A manual review of the fish tracks was then used to identify additional tracks that were missed, and to remove those that were generated in error.

Fish density (fish m^{-3}) was then calculated by dividing the number of fish tracks identified by the beam volume sum in each 5 m x 5 m cell (Kieser and Mulligan 1984) along the transect. The beam volume of each cell was calculated using the beam geometry estimated from calibration data collected each season. Note that volumetric density estimates exceeding 1 fish m^{-3} were excluded from the analysis, as they were unrealistic relative to the size of GG. The 5 x 5 m gridded cell matrixes were then exported from Echoview to be processed and analyzed in R 4.1.2 (R Core Team 2021) (Figure 2B).

Data Analysis

Geostatistical Modeling

To account for bias associated with small differences in survey size, cell estimates used in analysis were restricted to those cells that fell within 100 m of the respective study reef. Exclusion of cells outside of the “analysis region” were identified by recursively referencing each georeferenced grid cell to the nearest node of a polygon representative of the study reefs. Polygons were generated manually from a review of composited echograms collected over the course of the study and covered the full extent of the study reefs. The exclusion distance was selected based on an evaluation of the raw data, which revealed that GG targets did not occur beyond 50m of the study reefs. Observations by divers confirmed that GG did not occur outside of that range, but the range was doubled as a conservative approach to ensure that GG were not excluded from analysis.

Adjacent cells along hydroacoustic transects are spatially autocorrelated to varying degrees, dependent on a number of factors ranging from study area to behavior of ensonified fish targets (Simmonds and MacLennan 2005). Thus, semivariograms were constructed with “gstat” in R to characterize the spatial autocorrelation observed in each survey. Multiple models were tested simultaneously, and the algorithm was allowed to select variogram parameters that achieved the best fit to the data. The autocorrelation structure identified in semivariograms was also assumed to account for any potential “double-counts” of GG on adjacent transects, down-weighting adjacent cells that indicated strong autocorrelation. GG are generally sedentary for long periods of time, and the spacing of the transects also eliminated the likelihood of covering the same area repeatedly (beam coverage was approximately 15-20% of sea bottom). The results from each semivariogram were then applied to an ordinary kriging function to generate spatially weighted estimates of mean fish density across the survey extent in evenly spaced gridded cells of approximately 5 m x 5m. This process was replicated for backscatter data, and the spatially weighted estimates of NASC were matched to the georeferenced fish density cell matrices for further comparison. Note that all statistical analysis was performed on the geostatistically predicted data, rather than the raw data, to account for spatial autocorrelation of the underlying distribution of fish.

Patterns of Fish Density

A generalized linear model (GLM) on the $\log_e$ transformed density data was used to identify parameters that contributed to differences in estimates of GG density. Stepwise model selection based on minimizing Akaike information criterion (AIC) was used to remove parameters and identify those that were most suitable for inclusion in the final reduced model (Table 1). Starting parameters for the full model included: *year, year day*, *site, time to sunset* (for diel comparison), *moon phase,* as well as interactions. *Site* and *moon phase* were treated as unordered factors. *Time to sunset* was included as a continuous variable (rather than day or night) to account for changes in survey start times, order of completion, and changes in sunset through the seasons. The mid-point of each survey was coded relative to local sunset, where negative values represented the hours before sunset, and positive values denoted surveys that occurred after sunset.

Factors that were identified as significant in the reduced GLM were investigated further using parametric and non-parametric tests (i.e., paired t-test and Kruskal-Wallis test), and post-hoc multiple comparisons (i.e., Dunn’s post-hoc tests) to identify significance between factor levels. A paired t-test on the $\log_e$ transformed density data was also used to assess differences with respect to surveys conducted during consecutive moon phases. Twenty-seven pairs were qualified for inclusion in the test, on the basis that the pairs were from the same site, the same time period (i.e., day or night), and from consecutive moon phases (i.e., within approximately 15 days of one another). Differences in GG density associated with "diel behavioral changes" were compared using a Wilcoxon Signed Rank Test. *Time to sunset* was simplified into day and night for the sake of this comparison. Thirty-seven pairs were qualified for inclusion in the test on the basis that the two surveys were conducted within 24 hrs of one another, at the same site.

Patterns of Backscatter (NASC m^2 nmi^{-2})

Acoustic backscatter (NASC m^2 nmi^{-2}) produced by all fish (including GG) was evaluated independently of density to aid in explaining trends in GG density, based on the understanding that density estimation could be confounded when non-target species (e.g., sardines or scad) occurred in high density and abundance, proximal to GG (Ona and Mitson 1996). Kruskal-Wallis and Dunn's post-hoc tests were used to compare between *sites*, and a Wilcoxon Signed Rank Test was used to make paired comparisons between both *day* and *night* surveys (simplified from *time to sunset*), and between new and full moon surveys that occurred across consecutive *moon phases*.

RESULTS

Patterns of Fish Density

The independent effects of *year day*, *site*, *time to sunset*, and *moon phase*, as well as the interaction between *year day* and *time to sunset* were retained in the reduced model, but they did not have a significant effect on GG density estimates ($P > 0.05$) (Table 2).

Conversely, a significant effect of *site* was identified ($F_{3,70}$ = 3.951, P = 0.01), and a post-hoc test revealed that this was driven by the difference between MG111 and the Sun Tug (Tukey: P = 0.01), and a difference between MG111 and the Esso Bonaire (Tukey: P = 0.04). Notably, MG111 is also the largest of the study sites with the inclusion of Warrior Reef, while Sun Tug is the smallest and least complex of the sites surveyed. Though inter-site differences were not significant between all sites, there is a clear decline in estimated density associated with decreasing site extent (Figure 2). An interaction between *time to sunset* and *moon phase* was also observed (t = 1.958, df = 76, P = 0.05). Density decreased slightly from day to night during new moons, though not significantly, while a decrease of approximately 66.7% was observed during full moon survey periods (Figure 3). A Wilcoxon signed rank test to compare consecutive *moon phases* (considered pairs) reaffirmed that no differences existed between new and full moon surveys when compared independently of *time to sunset* (W = 127, P = 0.14), however density estimates between paired day and night surveys were in fact significantly different (t = 3.05, df = 37, P = 0.004). This difference was represented by a 37% decrease from day to night survey periods (Figure 5).

Patterns of Backscatter (NASC m^2 nmi^{-2})

Contrary to density patterns of estimated density between sites, a Kruskal Wallis test did not indicate that there were significant differences in NASC, which represents the magnitude of total acoustic backscatter produced by all fish, between *sites* (P > 0.05). A paired comparison between day and night survey periods did reveal that NASC was consistently higher at night, exceeding daytime estimates by approximately 413% (W = 92; P < 0.001) (Figure 5A). This is interesting in that it contradicts trends in GG density, suggesting that overall backscatter, which is generated by all fish (meeting the -60 dB re 1 m^{-1} threshold), may have limited our ability to detect GG through the formation of high-density schools that were more evident at night (Figure 6). The magnitude of the difference is also significantly higher than the differences seen in density, which exclusively targeted GG, providing further evidence that additional species occurred in exceptionally high abundance in the water column after dark. Interestingly, NASC was also significantly higher during full moon surveys, exceeding new moon estimates by 310% (Figure 5B) (W = 1043; P < 0.01).

DISCUSSION

Inter-site patterns of density and backscatter

Goliath Grouper density was significantly different between sites and displayed a positive relationship with increased areal extent and habitat complexity. Specifically, density was consistently higher at the two larger reef complexes (MG111 and Zion Train) compared to the isolated artificial reefs (Esso Bonaire and Sun Tug). While the distinction between reefs and reef complexes was not explicitly considered as a factor in our analysis, the effect was captured within *site*. Indeed, the major distinction between the two groups is the field of columns extending north of MG111, and the patches of hard-bottom and scattered debris surrounding Zion Train. Both sites are provided a substantial amount of additional habitat with the inclusion of these benthic features, and the close proximity of the Esso Bonaire (i.e., ~150 m from the Zion Train fringing habitat) likely affords it additional benefits as well, explaining why density estimates approached those of Zion Train surveys. As such, the increase in resource availability afforded by additional benthic habitat may play an important role in attracting and maintaining GG aggregations.

This is consistent with long-standing knowledge that reef fish are generally drawn to more complex reefs of larger spatial area for foraging opportunities and shelter (Bejerano et al. 2013), and GG are typically associated with high relief, high volume reefs, even outside of the spawning season (Collins et al. 2014). MG111 in particular is surrounded by isolated concrete columns that are unsuitable as refuge (except from strong currents) but provides abundant internal refuge. The additional habitat also supports surplus food resources, which may explain why GG preferentially selected MG111. Indeed, GG aggregations represent a significant burden on local resources, and empirical evidence suggests that they largely subsist on benthic organisms (~63% crabs) (Koenig and Coleman 2010). Data characterizing the benthic community at aggregation sites is not available, but it is reasonable to suppose that the larger reef complexes, such as MG111 and Zion Train, support larger benthic communities, that in turn support larger GG aggregations.

Notably, the limited evidence of confirmed spawning (i.e., free-floating egg collections) was also obtained from the MG111 (and one ~ 45 m depth natural reef site several kilometers away) (Koenig et al. 2017), suggesting that our proposed relationship between density and site extent may be useful in identifying potential spawning sites where information is lacking. This is consistent with previous spawning aggregation research that has theorized that spawning may not occur until a critical density or abundance threshold is met (Sadovy de Mitcheson and Colin 2012). However, it is unclear how this applies to GG, as spawning has only been observed once in the history of GG research and aggregation sizes are highly variable (Koenig et al. 2017). Consequently, we cannot exclude the possibility that GG spawn, with some frequency, at all four sites surveyed during this study. It is also possible that the study area represents a larger network of interchangeable “staging areas” and spawning sites, a well-documented phenomenon for other species that form spawning aggregations (Brownscombe et al. 2020, Sadovy de Mitcheson and Colin 2012). Indeed, this concept has been suggested by previous research that demonstrated a level of interconnectedness between the study sites during the spawning season (Ellis et al. 2014), but again, spawning has yet to be observed at all but one of the study sites and alternative methods are still required to validate this hypothesis.

Diel and lunar patterns of density and acoustic backscatter

We expected to observe elevated GG density at night compared to daytime surveys, based on the assumption that GG ascend into the water column during the evening hours. This is consistent with previous research and anecdotal reports that documented increases in “call rates” (i.e., vocalizations associated with courtship) and a synchronized vertical shift in GG position during the late evening hours (Mann et al. 2009). As such, we would expect them to be easier to detect in active acoustic surveys when they are separated from benthic structures, that can confound our ability to detect individuals (e.g., in the “shadow” of the reef or in the “acoustic deadzone”) (Ona and Mitson 1996). However, our results suggest that we should reject this hypothesis, as we saw a decline in density at night during full moons in particular, as well as a slight decrease in density during new moon surveys after dark. Though surprising, there are two possible explanations that may drive the observed changes.

Aggregations are well known to attract a mixed assemblage of species, namely small planktivorous species (*Decapterus spp*, *Sardinella aurita*, and *Etrumeus teres*) that occur in high abundance and associate closely with GG during the spawning season (Koenig et al. 2017, Maciera et al. 2016). The nature of their relationship is not completely understood, though it is generally accepted that these planktivorous species opportunistically consume GG eggs during spawning events, while simultaneously using GG as shelter from piscivorous Scomberid’s and Carangid’s that also occupy the water column and occur during similar seasonal periods (Koenig et al. 2017). This association is the foundation for both hypotheses that explain why density estimates were lower at night, with one based around the limitations of active acoustic survey methodologies, and the second focused on foraging activity that may be most pronounced during brightly-lit full moon nights.

Firstly, the apparent decrease in GG density may be directly related to the occurrence of planktivorous species, and “single-target loss” associated with these tightly aggregated, mixed schools of GG and planktivores. Indeed, our ability to discern single-targets used in the fish-tracking algorithm is contingent on the echosounders ability to identify individual echoes produced by a single fish at a given range (Simmonds and MacLennan 2005). Where fish co-occur at similar depths, or in tightly aggregated mixed-species groups, single-targets are effectively lost by way of destructive interference produced by colliding echoes generated by multiple fish in close proximity to one another

(Simmonds and MacLennan 2005). If large schools of densely aggregated planktivorous fish move synchronously with GG as expected (i.e., into the water column at night), GG would have been effectively masked from the single-target detection algorithm. This would explain why density was lower at night, while backscatter was much higher compared to daytime estimates. Indeed, planktivores that remain close to GG and shelter during the day are most likely moving into the water column at night to feed by light of the full moon, obscuring GG targets that should be otherwise visible. Further, the restrictive threshold applied to echo-integration data did likely eliminate a large majority of non-aggregated "small" fish targets, but dense schools of fish (of any size), such as the planktivores attracted to GG, would meet the threshold requirements due to the additive effect of echo-integration (Simmonds and MacLennan 2005). If their behavior is in fact tied to an affinity for GG eggs and shelter, it is plausible that they would interfere with single-target detection at night, when GG are suspected to ascend into the water column.

While interference from schooling fish may explain why density decreased at night, it does not explain the difference in magnitude between new and full moons. However, this may be explained by the fact that Carangids are primarily visual predators (Ory et al. 2017), and lack the visual acuity to effectively capture GG eggs during moonless nights. Additionally, they may also avoid leaving the reef structure to reduce perceived risk associated with unseen predators (Wickham and Russell 1974). The data support this hypothesis, as we saw much higher backscatter at night during the full moon period, when light levels would be more conducive to hunting and avoiding predators. Therefore, we propose that our observations of comparable density during new moon periods may be rooted in the hypothesis that the adaptation to spawn during new moons is in fact an effective deterrent against egg predation, and planktivores are less likely to ascend into the water column when their ability to perceive eggs, and potentially predators, is diminished.

An additional or potentially supporting hypothesis to explain why density was so greatly diminished during full moons may be found in previously uncharacterized nocturnal foraging behaviors exhibited by GG, and may also be extended to the co-occurring planktivores. Specifically, well-lit full moon nights likely offer significant advantages in terms of foraging opportunities, not just for planktivores as mentioned above, but for GG as well. Adult GG are well understood to feed predominantly on crabs and other small crustaceans (Koenig and Coleman 2010), which display strong nocturnal tendencies (Cobb and Phillips 1980). Considering that GG are reported to spawn during new moons, it is possible that they also take advantage of the well-lit full moon nights to forage in between active spawning periods. Unfortunately, data from the off-peak lunar periods (i.e., waxing and waning) are not available to expand upon this theory, but a redistribution of GG around the site during foraging events could explain the decrease in density during full moon periods. Moreover, if courtship is in fact isolated to the new moon period, we would expect GG to remain consolidated over discrete areas as they prepare to spawn or participate in courtship activities, which is consistent with the observed stability in density during new moon surveys. Interestingly, this may represent additional indirect evidence to support the hypothesis that GG spawn during dark moonless nights to avoid egg predation.

Considerations for future acoustic survey implementation

Goliath grouper are generally sedentary, and considering the size of aggregations and study sites, a reduction in transect spacing may lead to better estimates of density, or more opportunities to detect GG where they are present (e.g., similar to a repeated measures sampling approach), that could be used to estimate abundance. Alternatively, a wider beam transducer would serve to sample a larger volume of water without increasing sampling effort. However, this approach comes with its own drawbacks. Specifically, a wider beam angle would produce a larger acoustic deadzone region close to the sea bottom and adjacent to high relief structures (Ona and Mitson 1996). This is an exceptionally important consideration for a species such as GG, that spends a great deal of their time in close proximity to three-dimensional structures.

A reduction in transect spacing and increase in both beam-angle would simultaneously increase the probability of detecting goliath grouper that were previously undetected due to their occurrence in between transects. In the current study, we assumed that goliath grouper were uniformly distributed over the reefs, and made forays away from the reef periodically, based on anecdotal reports from divers. Thus, our transect design covered a broad area around the core of the aggregation site (i.e., the artificial reef and the surrounding sand/hard bottom area) and covered 15-20% of the seabed within the bounds of the survey extent dependent on depth. Reducing the transect spacing to 20 m or using a wider beamed transducer could increase the total sampling volume to 15-35% total bottom coverage. Improvements may also include the implementation of a wide-band or multi-frequency survey approach that can better discriminate between species or groups of species based on their “acoustic fingerprint” (Boswell et al. 2020). Though applying this method effectively to coastal reef settings is still quite difficult, it has seen marked improvements in recent years.

Management Implications and Applications

A comparison among years revealed that there were no significant changes in density through the duration of the study. Though we lack the ground-truthing information to extend this to abundance, it is plausible to conclude that there were no notable increases or decreases in goliath grouper abundance at the studied spawning sites near Jupiter, Florida. Notably, this trend is corroborated by diver visuals survey estimates statewide, reported by the Reef Environmental Education Foundation (REEF: https://www.reef.org/goliath). These observations are especially interesting in the context of fisheries management, considering the ongoing management activity which recently saw the implementation of a limited harvest GG fishery in March 2022.

Considering that GG aggregations are known to draw individuals from a much larger region (>100 km) (Koenig et al. 2011), patterns of occurrence such as those described here (i.e., changes in abundance and density), provide insight into the status of the GG across a vast geographic area, well beyond the extent of the aggregation sites studied. Indeed, this concept of broader application of FSA data to explain regional stock status has been demonstrated for a range of species, and allows researchers to concentrate and optimize survey efficiency to extract the most value from field research efforts (Erisman et al. 2017, Heyman et al. 2014). While visual-based monitoring efforts are ongoing and have successfully captured the trend in GG recovery since the 1990 moratorium (Koenig et al. 2017), the limitations associated with diver surveys leave data gaps that could be well-addressed by a wide-scale active acoustic survey program. Active acoustic survey techniques have a well-established capacity to provide comparable results to visual-based surveys with clear advantages (Landero Figueroa et al. 2022, Zenone et al. 2017), and could be applied throughout the state of Florida to supplement ongoing visual-based population census programs. As it is a nearly unprecedented management action, to resume harvest after such an enduring closure (i.e., approximately 32 years), information such as this will be invaluable to monitoring efforts going forward.

Conclusions

Active acoustics is a useful tool to describe GG aggregations and co-occurring fish communities over broad spatiotemporal scales. Based on the data collected over the four year study period, estimates of GG density were generally highest during daytime surveys, and this was consistent between both new and full moons. Conversely, surveys conducted at night were dominated by fish backscatter in the water column, but apparently low GG density. As such, we propose that the most appropriate time to survey GG appears to center around new moons, during the day, when GG aggregations are more consolidated in preparation for courtship activities. We also identified a potential relationship between benthic habitat extent and GG aggregation site preference, that indicates GG are attracted to sites that offer abundant benthic resources. This is not surprising based on their preferred diet, but due to our limited understanding of the mechanisms that attract GG aggregations to certain locations, bears mentioning and requires further investigation. We hope that the data, methods, and discussion points presented here represent a basis to implement active acoustic surveys into future GG monitoring activities, and we strongly advocate for the integration of active acoustics with traditional methodologies to reach a more complete understanding of GG aggregation dynamics.

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TABLES

Table 1 – Full and reduced generalized linear models from backward model selection. Model was used to explain trends in fish density (fish m^{-3}) throughout the study. Each bold "F" indicates that the parameter was considered as a factor, rather than a continuous numerical variable.

Model Iteration	Model	AIC
1 (full)	Log_e (Fish Density_{ij}) = **F**(Year_{ij}) + Year Day_{ij} + **F**(Site_{ij}) + **F**(Moon Phase_{ij}) + Time to Sunset_{ij} + Year Day_{ij} x Time to Sunset_{ij}+ **F**(Moon Phase_{ij}) x Year Day_{ij}+ **F**(Moon Phase_{ij}) x Time to Sunset_{ij}	210.02
2	Log_e (Fish Density_{ij}) = Year Day_{ij} + **F**(Site_{ij}) + **F**(Moon Phase_{ij}) + Time to Sunset_{ij} + Year Day_{ij} x Time to Sunset_{ij}+ **F**(Moon Phase_{ij}) x Year Day_{ij}+ **F**(Moon Phase_{ij}) x Time to Sunset_{ij}	205.13
3 (reduced)	Log_e (Fish Density_{ij}) = Year Day_{ij} + **F**(Site_{ij}) + **F**(Moon Phase_{ij}) + Time to Sunset_{ij} + Year Day_{ij} x Time to Sunset_{ij}+ **F**(Moon Phase_{ij}) x Time to Sunset_{ij}	203.19

Table 2 - Estimated regression parameters, standard errors, t-values, and p-values for generalized linear model used to characterize changes in fish density. P- values represent significant differences relative to the reference level for factors.

Parameter	Estimate	Std. Error	t-value	P-value
Intercept	-8.842	1.263	-7.001	< 0.0001
Year Day	-0.002	0.005	-0.404	> 0.05
Esso Bonaire	Reference			
MG111	0.796	0.278	2.866	= 0.005
Sun Tug	-0.406	0.340	-1.194	> 0.05
Zion Train	0.513	0.286	1.792	> 0.05
Full Moon	Reference			
New Moon	0.205	0.252	0.815	>0.05
Time to Sunset	0.480	0.306	1.571	> 0.05
Year Day x Time to Sunset	-0.002	0.001	-1.974	> 0.05
Time to Sunset x Moon	0.146	0.055	2.669	= 0.009

FIGURES

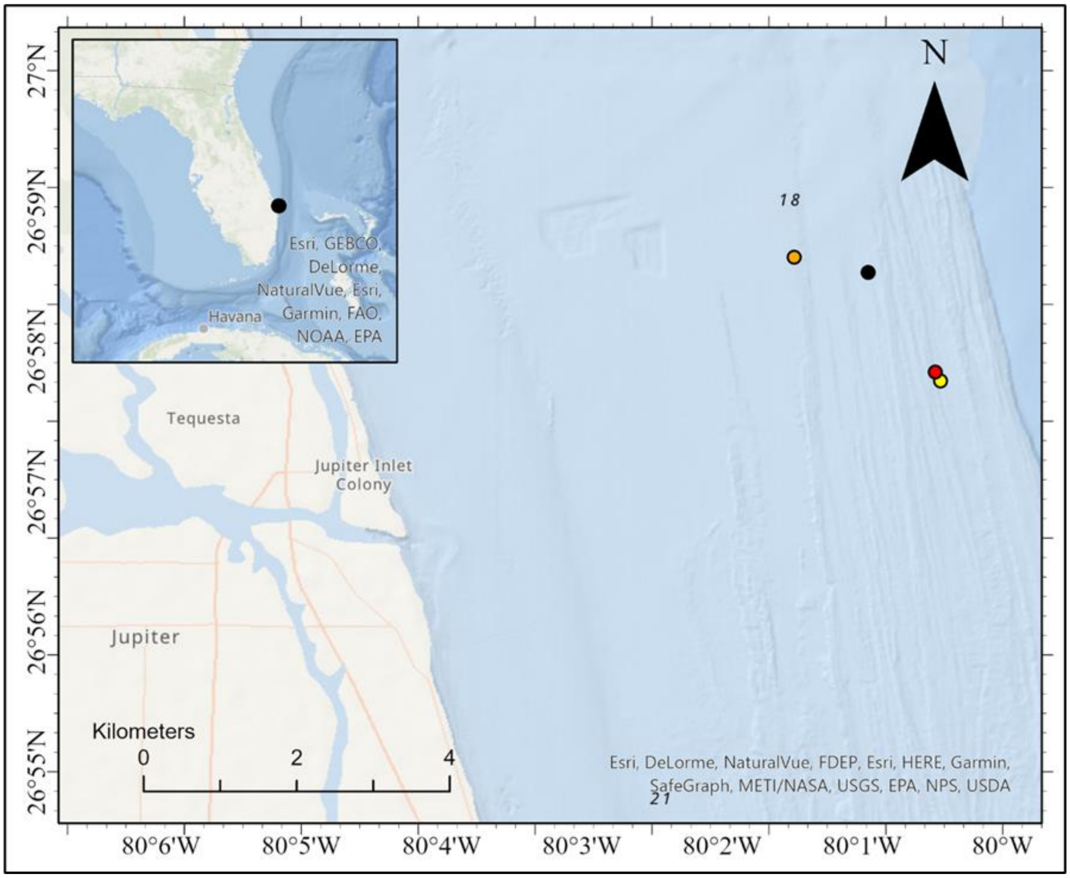

Figure 1 - Study sites are denoted by colored circles. Red and Yellow circles denote the location of Esso Bonaire and Zion Train. The black circle represents the Sun Tug, and the orange circle represents MG111. Inset provides a larger spatial context.

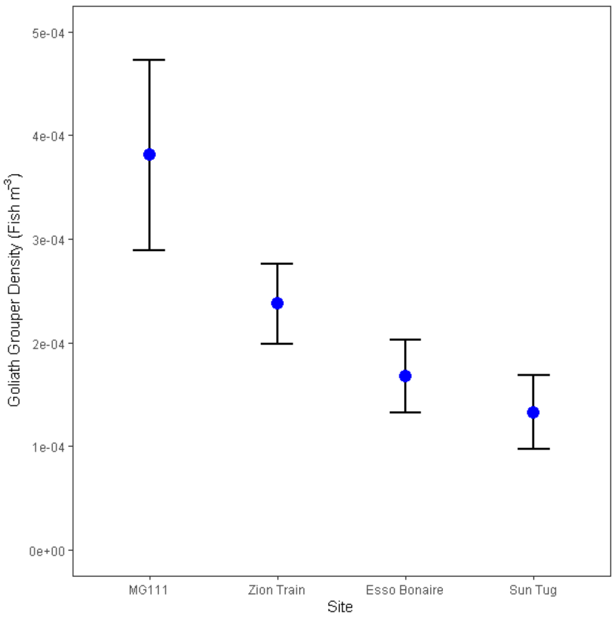

Figure 2 - Mean fish density (fish m^{-3}) by site. Error bars represent standard error. A decline in density is seen along a gradient corresponding to reef size in terms of spatial extent. Specifically, MG111 is the largest of the reef complexes followed by Zion Train. Esso Bonaire is an isolated reef, but possesses abundant three dimensional structure. Sun Tug is the smallest of the aggregation sites monitored in this study, and lacks surrounding habitat and any significant three dimensional refuge structure.

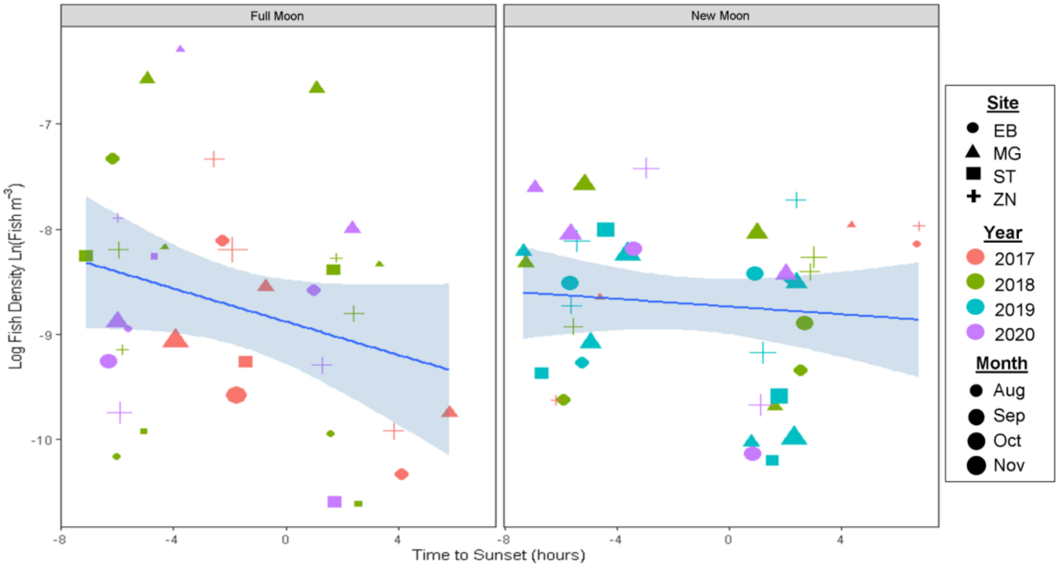

Figure 3 - Model fit for generalized linear model characterizing the relationship between fish density (fish m-3) and moon phase, time of day, study month, and study year. Blue

line represents fit for the respective panel and associated 95% confidence interval (shaded region). EB = Esso Bonaire, MG = MG111, ST = Sun Tug, and ZN = Zion Train.

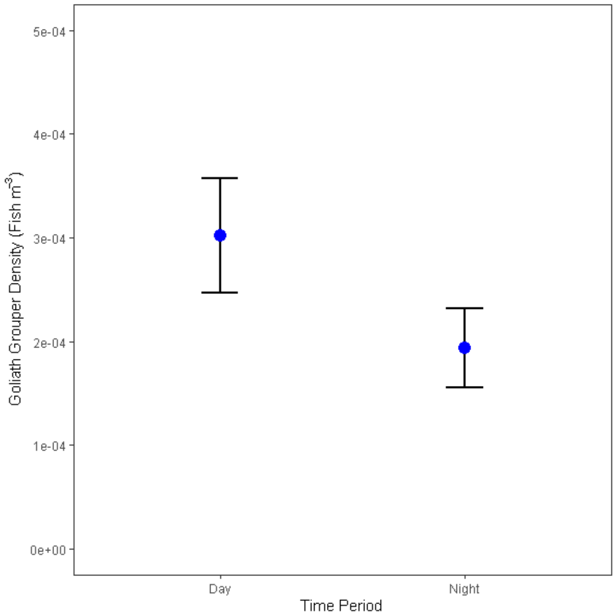

Figure 4 – Mean fish density (fish m^{-3}) during day and night survey periods. Error bars represent standard error. A decrease of approximately 67% was observed between day and night survey periods.

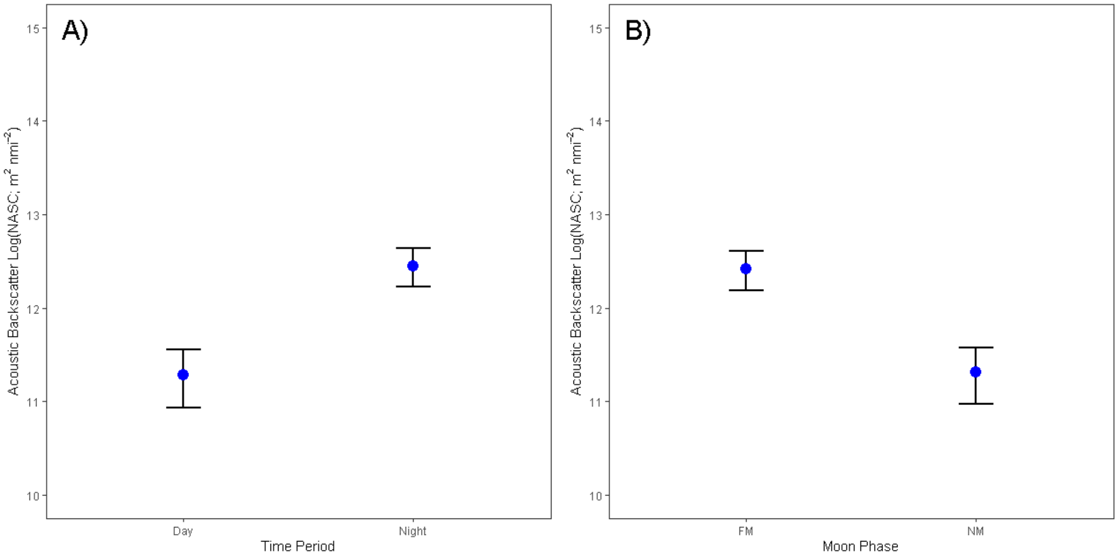

Figure 5 – Mean acoustic backscatter (NASC; m^2 nmi^{-2}) by A) survey time period, and B) moon phase. Error bars represent standard error. NASC estimates from surveys conducted at night exceeded day time estimates by 413% on average. Likewise, NASC estimates from surveys conducted during full moon periods exceeded new moons by 310%. Note that the y-axis is on a logarithmic scale, and does not start at zero.

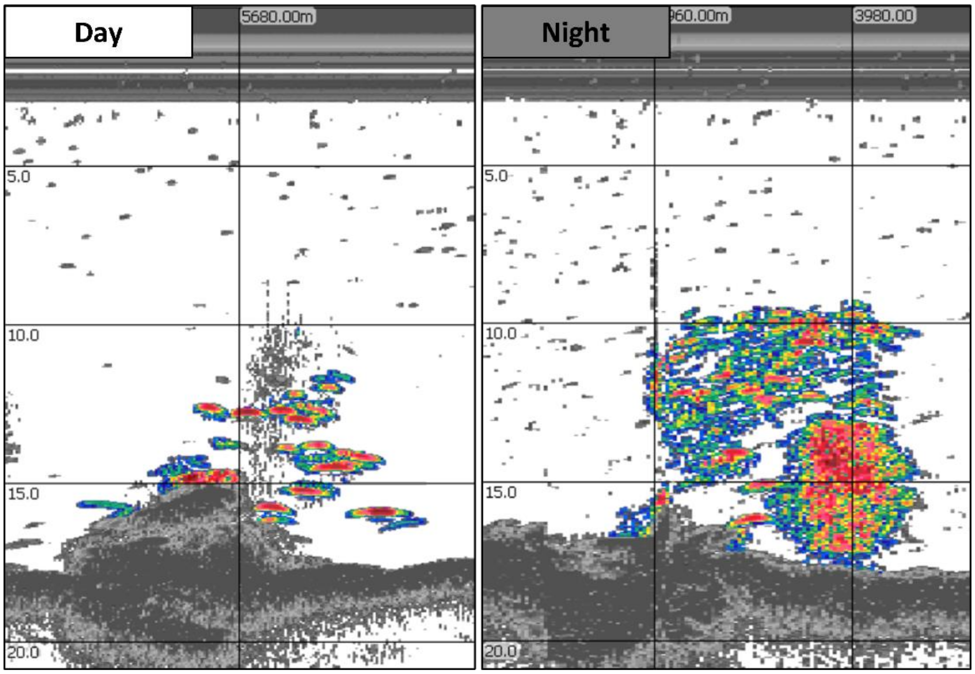

Figure 6 – Example echograms demonstrating the differences in schooling fish distribution around study reefs during the day and at night. The example of on the left (day survey) depicts several, clearly discernible goliath grouper around the study reef, compared to the right example (night) that reveals high density aggregation of small schools fish interspersed with faintly discernible goliath grouper targets. This phenomenon limits our ability to detect individuals, and ultimately affects density estimation.

CHAPTER V. APPLICATION OF ACOUSTIC TELEMETRY TO IDENTIFY SPAWNING AND AGGREGATION DYNAMICS OF A VULNERABLE MARINE PREDATOR

ABSTRACT

Traditional survey methodologies have provided a wealth of information about the biology and ecology of fish spawning aggregations, but they are limited in their ability to describe fine-scale and continuous behaviors over extended periods. Acoustic telemetry (AT) offers a solution, and has been used extensively to describe the spatiotemporal behaviors of many aggregating species. As the application of AT has expanded, so has the technology, with the integration of onboard sensors that offer new possibilities in terms of describing animal behavior. In this study we evaluated the capacity of accelerometer and depth sensing tags to characterize daily activity and distinguishable patterns of behavior, such as foraging and courtship activity in acoustically tagged goliath grouper (*Epinephelus itajara*, GG) (n = 8). A combination of supervised machine learning, generalized additive mixed models, and wavelet analysis (WA) were used to characterize the effects of a wide-array of environmental factors on activity levels, with the expectation that GG respond to periodic variation within their environment. Our results revealed that variability between individuals was high, but strong periodicity in diel movements during crepuscular periods were consistent, along with a response to increasing current velocity that saw GG seek shelter near the sea bottom. WA also revealed potential foraging and courtship activity on several occasions surrounding new and full moons through the spawning season. Specifically, three tagged GG made a sustained upward movement (5-7 m) into the water column that was characterized by increased variability in acceleration on the night of September 20, 2020, two days after the new moon. Though we cannot validate this hypothesis, all evidence suggests that these individuals participated in spawning activity. The data presented here highlight the complexity of GG behavior and demonstrate the

capability of these tags to detect and classify discrete ecologically significant behaviors in a myriad of species.

INTRODUCTION

Over 150 marine fish species form spawning aggregations globally (Claydon 2004). We know a great deal about what drives fish spawning aggregation (FSA) occurrence, and many are generally considered predictable in space and time, but FSA research has been historically difficult for a variety of reasons (Binder et al. 2021). Traditional research methodologies such as visual surveys, gonadal dissections, and otolith microchemistry from culled fish have revealed a wealth of information about the biology, ecology, and spatiotemporal dynamics of FSA's (Farmer et al. 2017, Kobara et al. 2013, Sadovy de Mitcheson and Colin 2012), but they are limited in their ability to capture high resolution temporal information related to behaviors that occur while fish are aggregated. This is not to say that they have not been successful (Waterhouse et al. 2020, Starr et al. 2018, Kadison et al. 2009, Nemeth 2005, and others), but visual based methods in particular are labor intensive and require well-timed execution to be effective. Indeed, researchers have spent upwards of 10 years attempting to observe spawning and validate the recovery of spawning aggregations at historically known sites (Heyman and Kjerfve 2008, Burton et al. 2005). As such, the daily behavioral patterns, frequency of spawning, and response of aggregated species to external stimuli, are generally uncharacterized for most aggregating species.

Remote sensing has the capacity to fill many of these knowledge gaps, and has seen extensive application in FSA research to answer a myriad of questions such as those identified. Indeed, the application of acoustic telemetry (AT) has become increasingly popular in the field of FSA research over the last 10-15 years, and has been widely successful at producing actionable data related to the seasonality of aggregating species, effectiveness of marine protected areas, and the potential effects of fishing on aggregations (Brownscombe et al. 2019, Feeley et al. 2017). Moreover, AT has demonstrated the capacity to provide near-continuous data from free-ranging individuals at spawning sites and vast surrounding areas (e.g., 100's-1000's km^2), to provide a comprehensive understanding of space use through time that was historically infeasible (Feeley et al. 2018, Koenig et al. 2017, Pittman et al. 2015, Ellis et al. 2013). Combined with supplemental information from environmental data loggers or periodic surveys by researchers, this technology can also be extended to evaluate discrete temporal variations in space use and behavior of organisms in response to myriad environmental conditions or interspecific relationships (Rooker et al. 2018, Adams et al. 2009).

Along with the broad application of AT, collaborative networks between universities, government agencies, and non-profit organizations (e.g., Florida Atlantic Coast Telemetry Network) have seen vastly improved data sharing potential, allowing individual researchers to leverage support from indirect collaborators, and effectively widen the geographic extent of their study area. Collaborations such as these and the realized utility of this technology has also driven researchers to apply AT techniques in novel ways over recent years (Lennox et al. 2017, Leos-Barajas et al. 2017, Papastamatiou et al. 2015), necessitating a response from industry, that has led to the integration of various sensors (e.g., temperature depth, acceleration, and others) into small form-factor acoustic tags. These sensor tags make it possible to hone in on the discrete behaviors that may occur on FSAs in response to uncharacterized biotic and abiotic forces. Moreover, addressing the question of individual spawning frequency may finally be attainable with the appropriate application of this technology. Where AT was historically limited to a "top-down" perspective to address spatiotemporal activities, integrated sensor tags can now simultaneously characterize behavior and activity with increased dimensionality, potentially providing a far more complete picture of FSA dynamics.

In this study we evaluate the capacity of accelerometer and depth integrated tags to capture day-to-day activity and distinguishable patterns of behavior, such as foraging and courtship activity in acoustically tagged goliath grouper (*Epinephelus itajara*). A combination of supervised machine learning (i.e., random forest regression) and wavelet analysis were used to characterize the effects of a wide-array of abiotic factors on activity levels, with the expectation that goliath grouper respond to periodic variation within their environment. Specifically, we expected to see reductions in activity associated with high-intensity storms and during periods of high flow, and changes in behavior associated with upwelling events that frequently push cold water into the study area. Considering that passive acoustic data have identified periods of high vocalization intensity at night during new moons (when they are expected to spawn) (Koenig et al. 2017, Mann et al. 2009), we also sought to isolate that signal in the accelerometry and pressure sensor data by proxy of modulated acceleration and depth, allowing us to indirectly infer spawning activity. With the continued expansion of AT nodes around Florida, combined with the ongoing advancements in tag technology, we anticipate that this novel approach to classifying behavior and detecting spawning activity will provide valuable insight into the day-to-day activity of goliath grouper.

METHODOLOGY

Species Profile

Atlantic goliath grouper (*Epinephelus itajara*; GG) form conspicuous spawning aggregations on natural and artificial reefs in the coastal waters surrounding Florida (Koenig et al. 2011), coastal areas around the Gulf of Mexico, Caribbean Sea, and along the northern coast of South America through part of Brazil (Bertoncini et al. 2018). Aggregations range in size from 10’s to 100 individuals, are understood to spawn during new moons after dark, and generally remain aggregated throughout the duration of their spawning season (Koenig et al. 2017, Ellis et al. 2013). Due to their high priority status to fisheries managers, the generally predictable nature of aggregation occurrence, and their charismatic behavior, they have been extensively studied throughout Florida. However, despite decades of research, their cryptic spawning behavior has rendered it effectively impossible to observe spawning, and researchers have been reliant on gonadal biopsy from live specimens (Koenig et al. 2017), and intense periods of vocalization (Mann et al. 2009) to infer that spawning is occurring at a given site. In this study we sought to identify additional means of validating spawning activity, based on characteristic behaviors exhibited by broadcast spawners (i.e., periods of agitation, movement away from the sea bottom, and “spawning rushes”) (Sadovy de Mitcheson and Colin 2012).

Study Site and Timeline

The study was conducted between August and November of 2020, during the annual GG spawning season (Koenig et al. 2017), at the MG111 and Warrior Reef artificial reef complex approximately 4 km East of Jupiter, Florida (N 26 56.650, W 80 04.370) (Figure

1). The site consists of one steel barge (~ 50 m x 10 m) covered in concrete debris, and a field of upright concrete columns (~ 1 m diameter) approximately 3-5 m in height, that extend to the north of the barge. Including the columns, the site is roughly 200 m x 50 m, running north to south in an expanse of unremarkable sandy bottom. The site was selected due to its use by GG as an aggregation site (Koenig et al. 2017), but also because it is less frequented by recreational divers, is shallower relative to other aggregation sites (~ 18 m; alleviating concerns of barotrauma in tagged fish), and sharks are less common (reducing concerns of predation following release).

Acoustic Tagging

Surgically implanted acoustic transmitters with acceleration and depth sensors (V-13AP, Vemco Inc, Halifax, NS, Canada) (Table 1) were used to document the behavior of GG at MG111 (n = 11) (Table 2). GG were captured for tagging using 15-20 m of 275 kg monofilament hand lines attached to 23.1 L (Polyform LD-2) buoys. Terminal tackle included a 1 m double-strand of monofilament (to accomodate chafing) secured to the hand line and 10/0 circle hooks (Mustad) with aluminum crimps. Bait consisted of cut and whole Carangids (e.g., “bonita”) acquired from local tackle shops. Buoys were used to ensure safety of angled goliath grouper and fisher. This system allows the fisher to “release” the angled goliath grouper if necessary, and recover the buoy when the situation is deemed safe.

Angled GG were recovered to the rear of the fishing vessel and transferred to a high-density polyethylene (HDPE) “slide” and operating table equipped with a non-recirculating saltwater gill irrigation system. HDPE was used to reduce the mechanical stress on goliath grouper as it is extremely slippery, making it easy to maneuver large fish along its surface. Seawater soaked towels were also placed over the fish's eyes to reduce stress induced by photo-sensitivity, and a 9.5 mm stainless steel trocar was used to vent gas trapped in the swim-bladder. Acoustic tags were then implanted intraperitoneally via a 3-4 cm incision anterior to the pectoral fins near the midline, that was closed using four dissolvable sutures (Ethicon coated VICRYL Sutures, reverse-cutting, size 10 half-circle). Fish were released over the study site and monitored by an in-water observer to ensure fish had regained equilibrium and could successfully swim down to the reef. Note that all capture and tagging procedures were conducted in accordance with approved Institutional Animal Care and Use Committee (IACUC) standards (protocol: IACUC-19-094) and under a Florida Marine Special Activities License (permit: SAL-19-1825A-SRP).

Tagged GG activity was documented by an array of six acoustic receivers (VR2W, Vemco Inc, Halifax, NS, Canada) that were deployed at the study location prior to tagging efforts. Four receivers were placed at intervals of approximately 50-100 m along the north to south expanse of the study reef, allowing for an overlap in detection ranges between receivers, in case of loss associated with tag collisions (i.e., when multiple tags transmit over the same period) and deflections by the reef structure. The two remaining receivers were deployed inshore and north of the study reef by ~ 100–150 m to capture any ranging GG and to cover a peripheral part of the study reef (Figure 1). Receivers were moored to the sea bottom using a 50 cm non-compressible closed-cell float attached to 3 m of 8 mm 3-strand polyethylene line anchored to a 1 m long “sand screw” (10 cm diameter blade). Receivers were hose clamped to the polyethylene line at approximately 2 m above the sea bottom.

Environmental Time-Series Data

Environmental data were collected using an Acoustic Wave and Current Profiler (AWAC; Nortek AWAC-1MHz) and publicly available data sources. The AWAC was deployed on a fixed aluminum stand approximately 10 m from the north end of the MG111 reef with a combination of sand-screws and stainless-steel stranded cable. The system was programmed to record data through the duration of the study period (approximately July - November, 2020) for five minutes at one-hour intervals. Current velocity (m s^{-1}) was recorded in vertically binned six meter intervals, beginning approximately 50 cm from the sea bottom (transducer face), ranging to the sea surface (~ 18.5 m). Bottom temperature (℃) and maximum wave height (m) were also recorded hourly. Daily estimates of sea surface temperature (℃) were extracted from AQUA MODIS satellite data (Level-3 AQUA MODIS, 11μ at 4 km resolution) to detect temperature gradients through the water column that may be associated with upwelling. High temporal resolution (6 min) measurements of atmospheric pressure (hpa) and wind speed (kts) were acquired from the National Data Buoy Center (NDBC station: LKWF1). Though the buoy is approximately 43 km south of the study site, it is the closest marine observatory available and we expect that the data provide a representative proxy for study-site conditions. Daily astronomical data consisting of moon phase and day length (hrs) were queried from the United States Naval Observatory (USNO) database.

Data Processing

Tracking data were downloaded from the acoustic receiver array in December of 2020. Approximately 160,000 detections were recorded between the six receivers, representative of activity from eight of eleven tagged GG. Two were only observed in the array for a day after tagging and another tag failed[4] halfway through the study period. After filtering the data and removing aberrant data points, the dataset was reduced to 33,022 paired detections that could be used for analysis (i.e., “matched” pairs of acceleration and depth recordings).

Filtering included the removal of detections collected within the first 24 hrs of deployment to avoid confounding effects associated with tagging. Near-simultaneous detections at multiple receivers (i.e., < 5 s apart) were then aggregated into a single record. Consecutive detections from the same transmitter that occurred more frequently than the minimum transmission interval (i.e., < 60 sec) were also removed. Filtered acceleration and depth data were then paired based on the understanding that the tags transmit depth and acceleration at alternating intervals. To accomplish this, the two data sets were merged and ordered by time of detection. An R script was then used to recursively inspect the detections one-by-one to confirm that the type (i.e., acceleration or depth) alternated, the tag serial numbers matched, and detections were recorded within the maximum transmission interval (i.e., < 180 s). If consecutive detections met those rules, they were considered pairs and appended to a new dataset with temporally matched environmental data (i.e., AWAC, satellite, buoy data, and UNSO). Those detections that did not match were excluded from analysis.

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[4] Failure was diagnosed and confirmed by the manufacturer.

Data Analysis

The tags used in this study have relatively long life spans, relative to the spawning season. However, this comes with the cost of being limited in their ability to detect and provide insightful evidence of short bursts of activity and rapid changes in depth that would likely be associated with “spawning rushes” commonly seen in aggregating broadcast spawners (Sadovy de Mitcheson and Colin 2012). Thus, the data were specifically analyzed with the intention of identifying periods of increased activity and sustained periods of depth change that could be associated with changes in local conditions, foraging, and most importantly, courtship behaviors.

As the changes in activity level, inferred from acceleration data, were expected to be discrete due to the temporal integration of data over the 57 second measurement period, and changes in depth could largely be attributed to environmental forcing, a supervised machine learning approach (random forest regression; Breiman 2001) was used to generate predictions based on an array of 13 predictor variables (Table 3). The data were first randomly sampled without replacement to generate a training data set consisting of 70% of the detections and corresponding environmental data. The remaining 30% of the data were “held-out” for model validation. Random forests were then generated with the training data using the R package ‘randomForest’ (RF; Liaw and Wiener 2002). Forests consisted of 500 trees, and samples were replaced after each draw, allowing the algorithm to redraw the same point more than once. The standard value for ‘mtry’, or the number of predictor variables randomly selected and tested at each tree junction, was also used (i.e., number of predictor variables / 3 = 4 rounded down). The bagged (i.e., averaged) predictions produced by the training model were evaluated based on the adjusted R^2 and Mean Square Error (MSE) (Breiman 2001). The held-out testing data were then passed through the model to estimate the variance that could be explained by the trained model and the Root Mean Square Error (RMSE) surrounding predictions.

A Generalized Additive Mixed Model (GAMM) with an assumed Gamma distribution was then fit with the three highest ranking predictor variables from RF's that consistently produced the greatest reduction in MSE and saw the highest node purity improvement (node purity improvement equates to a reduction in residual sum of squares error by including a given variable in successive RF's). This approach was used to determine how the variables identified in RF's contributed to predictions of depth. The RF used to characterize acceleration data was not analyzed with a GAMM due to poor RF performance. An autocorrelation structure (AR1) was also fit to the residuals to account for temporal autocorrelation between detections. Differences between individually tagged fish were evaluated by using transmitter identity (i.e., tag code) as an unordered random factor, and continuous variables were parameterized with thin-plate regression splines (Wood, 2021). Global smoothers for the predictor variables and the interaction between individual fish and predictor variables were all included in the model. Individual model terms were evaluated for significance using F-tests and the overall model performance was validated using a paired t-test between observed values and model predictions. All statistical analysis incorporating GAMM's were conducted using the 'mgcv' package (version 1.8-38; Wood 2021).

Continuous wavelet transformation was then used to identify discrete temporal patterns in GG activity (i.e., in terms of *depth*) using the ‘biwavelet” package (version 0.20.21; Gouhier et al. 2021). Cross wavelet analysis was also used to identify the relationship between depth modulation and variations in current velocity using the ‘WaveletComp’ package (version 1.1; Roesch and Schmidbauer 2018). *Mid-water current velocity* was selected due to its significance in RF’s and the GAMM, and *time of day* is captured in the time series data. Wavelet analysis allows for the decomposition of time-series data into the time-frequency domain to evaluate the dominant modes of variance over multiple scales within a time-series (Torrence and Compo 1998). Simply put, wavelet analysis allows for the visualization and characterization of complex patterns and associations that arise in time-series data that would be otherwise unobservable or difficult to characterize with traditional frequentist statistical techniques.

Due to the high residency exhibited by GG, there were only four hourly intervals across the duration of the study that had no detections. Thus, the data were binned by hour to accommodate the requirements of the wavelet decomposition algorithm, and the four missing data points were interpolated from adjacent values to generate a continuous time series (Boswell et al. 2019). Unfortunately, variation between individual GG could not be accounted for due to a lack of detections, relative to the study duration. A ‘Morlet’ basis function was used to improve scale detection and signal localization precision and wavelet power was corrected following the methods of Liu et al. (2007). Wavelet periods were assessed at 2 hour intervals to a maximum of 642 hrs (i.e., ~ 27 days), determined by the study duration and calculations in the “biwavelet’ R package. Wavelet transformations were used to generate scalograms (i.e., heatmaps) for visualization of the data, and the global wavelet power spectrum was estimated over the study duration (i.e., horizontal integration of pattern intensity at various hourly periods (2 – 642 hrs) through the study duration) to identify discrete periods of variation in *depth* (Torrence and Compo 1998). A red-noise test was used to identify significant periods of variation based on the correction presented by Liu et al. (2007). The scale averaged wavelet power was also calculated (i.e., the vertical integration of wavelet power) to identify large scale dominant periods across the time series (Torrence and Compo 1998).

A Cross Wavelet Analysis was then performed to determine if temporal patterns in *depth* variation could be explained by cyclical changes in *mid-water current velocity* (e.g., associated with tide or upwelling). This comparison was also used to disentangle current driven activity patterns from potential foraging and courtship associated behaviors. *Depth* and *acceleration* were then compared to identify periods of variation that may be associated with conspicuous behaviors such as foraging or courtship. Although *acceleration* was not included in the GAMM, we suspected that it may still be informative when combined with *depth* data. Specifically, inphase periods of high variability in depth and acceleration would be indicative of high frequency depth modulation and high frequency velocity modulation (i.e., changes in acceleration), consistent with courtship activity and potentially spawning. Conversely, anti-phase periods where depth modulation is low and acceleration is high, could indicate that GG are maintaining relatively consistent depth while modulating their acceleration. Such a pattern could be related to foraging or socialization, but most importantly, not behavior that is characteristic of broadcast spawner (i.e., upward rushes and periods of agitation) (Sadovy de Mitcheson and Colin 2012).

RESULTS

Environmental Data Synopsis

Sea surface temperature decreased from 31.7°C to 27.2°C between August 15th and October 21st, 2020, but no sharp drops were observed during the study period, indicating that cold upwelled water remained stratified beneath a layer of warm water at an unknown depth. (Figure 2). Unfortunately, discrete measurements of temperature throughout the water column were unavailable to determine where the stratification occurred, but a strong thermocline was observed by divers at 5-10 m off the sea bottom. There was one upwelling event, resulting in an 8.1°C drop in bottom water *temperature* over the course of a two-day period, that lasted approximately one day (Figure 2). The full evolution of the event lasted approximately four days, and the water column remained stratified during these periods, as evidenced by the stable *sea surface temperature*. *Upper*, *mid*, and *bottom water current velocity* varied from 0-1.2 m s^{-1}, and velocity was generally consistent between all three layers (Figure 2). Additionally, no major storm systems passed through the study area. As a result, *significant wave height* never exceeded 4.3 m, averaging 1.2 m +/- 0.01 m through the study, and atmospheric pressure never dropped below 1007.3 hpa (mean +/- se: 1014.0 +/- 0.04 hpa) (Figure 2).

Random Forest Regression

Random forest regression trees predicted GG depth with nearly 80% accuracy in both training and testing data sets (Figure 3), deviating by less than 0.70 m on average ($RMSE_{train}$: 0.684 m, $RMSE_{test}$: 0.692 m). Error reduction reached an asymptote at approximately 130 trees, where model performance ceased to improve (Figure 4). Of the

13 predictor variables included in the RF, only *transmitter ID*, *time of day*, and *mid-water current velocity* consistently produced significant improvements in error reduction and node purity (Figure 5). Notably, *Sea bottom temperature*, *atmospheric pressure*, and *max wave height* were not identified as significant predictors of GG depth, indicating that upwelling and storm activity (at least of the magnitude observed in 2020) did not influence GG activity. Conversely, *Transmitter ID* improved node purity by approximately 312% compared to the second most important variable (*mid-water current velocity*), suggesting that water column usage between individual GG is highly variable between individuals, rather than synchronized. *Time of day* was ranked highest in terms of error reduction in RF's, though it only exceeded *transmitter ID* by approximately 17.8%. Differences between predictors in terms of MSE reduction was consistently less significant through the ranking system compared to node purity, ranging from just 3.7 – 22.7%, suggesting that while many factors may not be independently influential, environmental factors likely play an interactive role in determining where goliath grouper position themselves in the water column.

Generalized additive mixed modeling

The GAMM explained 53.4% of the deviance seen in the data based on the three primary factors identified by RF's. A paired t-test did not find significant differences between fitted values and observed values ($t = 0.18$, $df = 33198$, $P = 0.852$), indicating that the RF-based model fit the data well. Further, the model revealed that all three variables likely play a significant role in determining where GG orient themselves in the water column. Both time of day ($F_{1,8.59} = 12.76$, $P < 0.0001$) and *mid-water current velocity* ($F_{1,9.48} = 6.50$, $P <$

0.0001) had an effect on predicting position in the water column. GG exhibited relatively low magnitude oscillations in water column usage over a 24 hr period, with rises at night and during crepuscular periods, potentially during foraging or social activities (Figure 6). The relationship between water column usage and current velocity was more directional, with a downward trend in depth (moving towards sea bottom) as current velocity increased, potentially associated with GG moving to the leeward side of reef structures near the sea bottom (Figure 6). The response of individual GG was also found to be significant ($F_{1,6.99} = 2452.74$, $P < 0.0001$), indicating a high degree of variability in their response to local conditions (refer to partial plot figures). Due to this individual variability, estimated mean depth differences between time periods (e.g., binned hourly means) and at different current velocities were not necessarily informative to identify patterns in GG behavior, which necessitated additional investigation (i.e., wavelet analysis). Four additional parameters used in RF's, that ranked in the top five (i.e., atmospheric pressure, max wave height, acceleration, and day length), were also tested to characterize their ability to further explain deviance, but model improvement tapered off at approximately 50% with the inclusion of the additional terms. To avoid over-parameterizing the model, the additional variables were excluded.

Wavelet Analysis

The wavelet analysis revealed one period of high variability, and three additional periods when GG spent extended periods further from the sea bottom (Figure 7). The pattern was also present in the decomposed continuous wavelet scalogram, but they were not obvious in the global power spectrum due to the low frequency of occurrence relative to the study duration (Figure 7). Most notably, each of those periods occurred within one week of peak new and full moons, when GG courtship activity is reportedly the highest, and saw GG move 4-7 m off the sea bottom. Distinct periods of high variability on diel (12 hr) scales through the duration of the study period were also observed, indicative of increased activity and a potential lack of synchronicity in movement between individuals (Figure 7). A second peak at 24 hrs was also noted, however it was determined to be representative of a harmonic peak associated with the diel activity occurring at 12 hr intervals. The global wavelet power spectrum, which integrates wavelet power throughout the duration of the study, also suggested that a significant biweekly increase in depth modulation occurred, which is consistent with the peaks that were also present in the scale averaged power spectrum (Figure 7) (Torrence and Compo 1998).

Cross-wavelet analysis revealed a 53.9% coherence between patterns of *mid-water current velocity* and *depth* with highly correlated periods on diel and daily scales (likely a harmonic pattern), similar to the depth specific wavelet decomposition described above. A high degree of coherence between responses was also detected at approximately three day intervals during two periods following the new moon (August 16 - 22 and October 17 - 30). Phase was variable through the study, but the dominant longer duration periods were consistently anti-phase (Figure 8).

Coherence between depth and acceleration was comparable at 66.9%. Peaks in coherence also occurred at similar diel and daily scales, and at the three day interval distributed though the study period (Figure 8). Three distinct periods were observed that displayed both in-phase and anti-phase behavior. Specifically, two periods of high variation in acceleration and decreased depth variation were observed at the beginning of the study and in late October. This period of anti-phase behavior indicates that GG were maintaining a relatively consistent position in the water column while modulating their velocity with increased frequency. Conversely, *depth* and *acceleration* were in phase close to the new moon period of September, indicating that they were both modulating their depth and acceleration simultaneously (Figure 8). This strong in phase period was produced by three of the eight individuals that participated in the upward shift in position described above. Several other short duration periods (3-5 days) of coherency were also observed between the three larger magnitude events, occurring both in phase and antiphase near full and new moons, respectively.

DISCUSSION

The random forest approach performed remarkably well with both training and testing data, explaining approximately 80% of the variability in *depth*. Combined with the GAMM, a high degree of variability between individuals was identified, but diel shifts upward into the water column during crepuscular periods were consistent, along with a response to increasing current velocity that saw GG seek shelter near the sea bottom and reef. The CWA confirmed these observations, identifying strong periodicity in diel activity and changes associated with current velocity. Beyond day-to-day activity levels, CWA also allowed us to identify and classify periods of potential foraging and courtship activity, which are unprecedented observations for this technology and GG research.

Evidence of courtship and foraging activity

A distinct period of in-phase variability occurred midway through the time series, peaking between September 19th and the 21st, when GG made a sustained shift from approximately 2 m off the sea bottom to 5-7 m off the sea bottom. Depth oscillated during this time but reached its peak at 1800 hrs on the 20th, and persisted until approximately 0500 hrs on the 21st. Coincidentally, this was also during the expected peak of the spawning season (mid-September), just two days after the new moon. Timing was also consistent with previous research that has documented sustained periods of high-intensity vocalizations associated with courtship, between midnight and 0300 hrs (Koneig et al. 2017, Mann et al. 2009). The binned hourly depth data alone reveal a distinct upward shift in depth during the period, and the wavelet analysis confirms that GG were mediating their depth and velocity with significant frequency during this period (Figure 8). This behavior is consistent with courtship activities displayed by many aggregating broadcast spawners (Sadovy de Mitcheson and Colin 2012), and reflects anecdotal reports of GG shifting into the water in the evening hours, presumably preparing to spawn. As this was not coincident with an upwelling event, or any other known environmental change, we can confidently exclude the possibility that this was in response to changes in local conditions. Moreover, this particular peak was produced by three of the eight tagged GG (size ranged from 141-199 cm total length), and though it is not possible to confirm that the three individuals were in fact participating in courtship activity, the timing and patterns of behavior provide compelling evidence that spawning likely occurred on that night.

Two periods of anti-phase activity were also observed at the beginning of the study and in late October, at the presumed end of the GG spawning season (Koenig et al. 2017). During these periods, variability in acceleration was high, but variability in depth was low. This relationship indicates that GG were making frequent changes in velocity while maintaining a relatively stable position in the water column, consistent with what we might expect during foraging events, social interactions, or while sheltering and maintaining their position in a strong current. During the first period (August 16-20) mean position in the water column oscillated between ~ 2 – 4.5 m off the sea bottom, and current velocity increased from < 0.25 to a sustained ~ 0.75 m s^{-1} (for approximately one week). Our hypothesis and results from the GAMM would predict a downward shift in position, however this was not the case. This observation further demonstrates the variability in behavior exhibited by individuals, but it must also be noted that this period of increasing current coincided with the approach of the late August new moon. Thus, it is possible that GG were preparing to spawn at this time, and their consideration for energy savings (through sheltering) was superseded by the drive to participate in courtship activities. Data do not exist to validate this hypothesis, however many species participate in reproductive behavior at the expense of their own overall health (Kuparinen et al. 2011), and there was a clear evolution of complex behavior during the period. Considering the complexity of this particular scenario, animal-borne cameras may be an effective solution to directly observe such behaviors. Moreover, data logging sensors with higher frequency collection periods or additional environmental sensor packages may provide additional insight to test our hypothesis.

Unlike the first anti-phase period, conditions in late October preclude us from drawing any definitive conclusions from the significant event identified in the depth and acceleration CWA. However, it is possible that this period represents foraging activity by the single remaining tagged GG at MG111, as all other tags had ceased functioning or left the array by approximately October 15th. The data indicate high modulation in velocity while holding a generally consistent depth (~ 2 m off the sea bottom). This period coincided with the late October full moon, when GG may benefit from well-lit crepuscular or nocturnal foraging opportunities. Indeed, stomach content analysis has demonstrated that GG feed primarily on crustaceans (~ 63%) (Koenig et al. 2011), which are generally considered cryptic nocturnal organisms (Cobb and Phillips 1980), and they have been observed consuming smaller fish in the surrounding water column during crepuscular periods. Similar short duration synchronous events were also observed during the early September and October full moons, and when considered with the diel shifts identified in the GAMM, these short in phase and antiphase periods may in fact be associated with crepuscular or nocturnal foraging events meant to sustain aggregated GG throughout the spawning season.

Response to upwelling and the passage of high intensity storms

While we initially expected upwelling to play a large role in dictating where GG orient themselves in the water column, the data suggest that current velocity was more influential, and drove GG towards the shelter of the reef. However, it must be noted that only one upwelling event was observed during the study, and though it produced an ~ 8 °C drop in temperature, only two tags had been deployed by that point in the study. Moreover, the authors have personally observed GG positioned above the thermocline in high current during previous site visitations, suggesting that temperature may play a larger role than identified in this study. With these caveats in mind, we propose that further investigation is warranted to better characterize the relationship between upwelling events, current velocity, and their effect on aggregating GG.

The 2020 season was also mild in terms of intense storm activity, and no major hurricanes or tropical storms passed over the study area. While there were six periods when wave height exceeded 3 m, reaching 4.3 m, the RF's and a review of the cross wavelet relationship between depth, acceleration, and wave height revealed that the storms experienced in 2020 were not of sufficient magnitude to elicit a response in GG. While the region was fortunate to not experience a major storm in 2020, it is inevitable that a high-intensity storm will pass over the coastal waters of South Florida at some point in the future. Given that storm intensity is likely to increase with shifting climatic conditions (Walsh et al. 2016, Ponge 2013), it is important to consider and understand the potential implications for GG spawning. Here we have demonstrated that GG are resistant to low magnitude events, and others have shown strong resistance to the passage of high intensity storms (Biggs et al. 2018, Locascio and Mann 2005), but previous research has seen a variety of marine fish species emigrate away from residency areas when storm intensity exceeds a certain threshold (Bacheler et al 2019, Bailey and Secor 2016). Should this hold true for GG, the potential to disrupt spawning is quite high, given that the spawning season coincides with the most active period of hurricane season. Therefore, a sustained effort to evaluate the effect of large storms on GG spawning is essential, and we propose that the methods described here may provide valuable insight into better understanding this relationship.

Limitations and Considerations

As is common with all experimental applications of technology, we discovered several obstacles that bear mentioning. The RF's performed poorly with acceleration data, only explaining approximately 20% of the variability in the dataset. Considering the logging specifications of the acceleration sensor onboard the tags, we did not have the resolution required for a finer evaluation. Specifically, the acceleration sensor used in the V13AP acoustic tag records data for a 57 s period after transmitting pressure (i.e., depth) information. The data are integrated over the "listening" period and provided as the root mean square of acceleration between all three axes (x,y,z). Ultimately, this method produces a smoothed signal that is incapable of detecting short duration bursts of activity that would be characteristic of broadcast spawning. The acceleration data were still useful in identifying sustained periods of activity that were characteristic of various behaviors, however observations of spawning are outside the reach of this particular sensor. Solutions do exist in the form of recoverable data loggers for instance, that may prove insightful, and tag technology is continuously moving forward to meet the demands of researchers.

Beyond this limitation, our greatest obstacle was capturing GG to implant tags early enough in the spawning season to maximize our chances of detecting courtship activity. Indeed, the small sample size available during the single upwelling event confounded our ability to draw strong conclusions from the data. This was more challenging because only a small resident population persists at MG111 throughout the year, and the tags being used only had a lifespan of 128 days (4.5 months). This is considerably longer than the expected spawning season (~ 3 months), but we were limited by our ability to catch GG early enough to produce meaningful data. Fortunately, this hurdle has since been remedied with the extension of the battery life in these tags, though we did not benefit from this upgrade.

Lastly, GG spawning has eluded researchers on all but one occasion, when a National Geographic photographer observed a female and presumably two males participate in a characteristic “spawning rush” (Koenig et al. 2017). Egg collection has also been exceptionally difficult to accomplish (Koenig et al. 2017), and this has forced us to rely heavily on multiple sources of indirect evidence, such as gonadal tissue biopsies (Malinowski et al. 2019) and vocalization intensity (Mann et al. 2009) at presumed spawning sites to validate their use and confirm that spawning has occurred. Here we have demonstrated a new method to infer spawning and characterize additional behaviors, but this still only represents indirect evidence that is consistent with historical literature that has described spawning behavior in analogous species. While the data overwhelmingly support our “observation” of courtship activity, the true utility of this technology will be realized when we can pair our data with ground-truthed observations, a common caveat that is ubiquitous with all fields of remote sensing (Nagai et al. 2020, Garrity 2009, McClatchie et al. 2000).

Conclusions

In this study we have demonstrated the capacity of acoustic telemetry to characterize discrete behaviors in GG that have been previously undescribed by traditional and remote sensing techniques alike. With a combination of depth and acceleration data collected from acoustically tagged GG, and multiple sources of environmental data, we were able to document day-to-day activity levels and the response of individuals to varying conditions; including changes in activity related to current velocity, diel shifts in space use, and potential foraging and spawning activity that occurred precisely when GG are reported to spawn. To date, GG spawning has only been directly observed on one occasion due to their cryptic, “darkest-moon” spawning behavior (Koenig et al. 2017). With the method described here, we move one step closer to indirectly validating spawning activity, and propose that our approach represents an effective method to not only detect spawning, but could be used to characterize individual spawning frequency, and monitor the response of GG to intense environmental disturbances (e.g., hurricanes or sustained upwelling periods). Considering that aggregations are relatively small (10’s-100 individuals), and the vast array of acoustic receivers distributed throughout Florida, depth and accelerometry enabled tags could be used statewide to further improve our understanding of regional GG spawning dynamics. Lastly, GG represent a test bed to demonstrate the capability of this technology, but the same methods have much greater applicability, and could be used to study spawning, general behavior, and the environmental tolerances of myriad species.

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TABLES

Table 1 - Tag specifications for accelerometer and pressure enabled acoustic tags used in study.

Tag Parameters (VEMCO V13AP)	**Spec**	**Unit**
Minimum / Maximum Transmit Interval	60-180	s
Pressure Sensor		
Accuracy	+/- 3.4	m
Resolution	0.3	m
Acceleration Sensor		
recording period	57	s
sample rate	12.5	Hz
detection range	+/- 4.9	m s^{-2}

Table 2 - List of goliath grouper tagged and corresponding information.

Tag ID	Fish	Tagging Date	Size (Total Length; cm)	Detections
1347000	1	8/15/2020	141	48000
1346999	2	8/15/2020	204	14500
1347005	3	9/5/2020	210	20650
1346996	4	9/5/2020	215	8700
1347001	5	9/5/2020	187	26800
1346995	6	9/5/2020	195	**LOST***
1347003	7	9/5/2020	210	**LOST***
1347002	8	9/5/2020	228	4250
1346998	9	9/19/2020	191	17200
1346997	10	9/19/2020	192	**FAILED****
1347014	11	9/19/2020	199	15160

* Detected for less than 24 hours after tagging.
** Failure identified for **tag 1346997** was confirmed by the manufacturer.

Table 3 - Variables used to generate random forest (RF) regression. RF's were used to predict depth and acceleration independently using 4 randomly selected variables at each "node" (branch in tree), until error had been minimized. Depth and acceleration are bold to indicate usage as a response variable in RF.

Random Forest Predictor Variables			
Tag Data	**General**	**Marine**	**Atmospheric**
Depth (m)	Time of Day	*Max Wave Height (m)	**Atmospheric Pressure (hpa)
Acceleration (m s^{-2})	Year Day	*Bottom Temperature (°C)	***Sea Surface Temperature (°C)

Unique Fish ID	****Day Length (hrs)	*Upper Water Current Velocity (6-0 m)	****Moon Phase
		*Mid Water Current Velocity (12 - 6 m)	
		*Bottom Water Current Velocity (18.5 - 12 m)	
Sources: * Nortek Acoustic Wave and Current Profiler ** National Data Buoy Center *** MODIS-AQUA Satellite **** United States Naval Observatory			

FIGURES

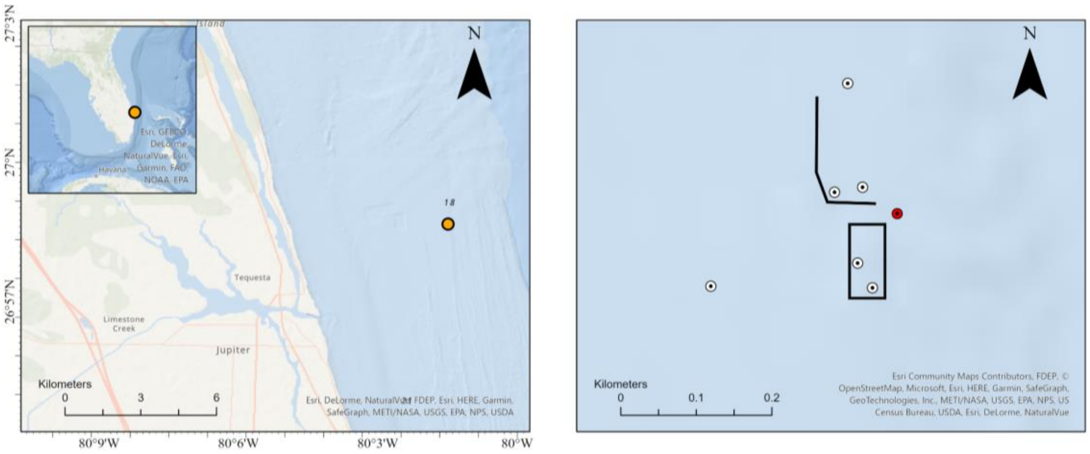

Figure 1 - The study was conducted at MG111 and Warriors Reef (orange circle), approximately four km east of Jupiter, Florida (Left). The panel on the right depicts the position of VEMCO VR2W receiver stations (white circles) relative to the MG111 (black rectangle) and Warriors Reef complex. Warriors reef columns are scattered between the northern extent of the MG111 and the northernmost receiver station, and their locations have been loosely approximated by the jointed black line. The Acoustic Wave and Current Profiler (NORTEK AWAC 1MHz) is denoted by the red circle.

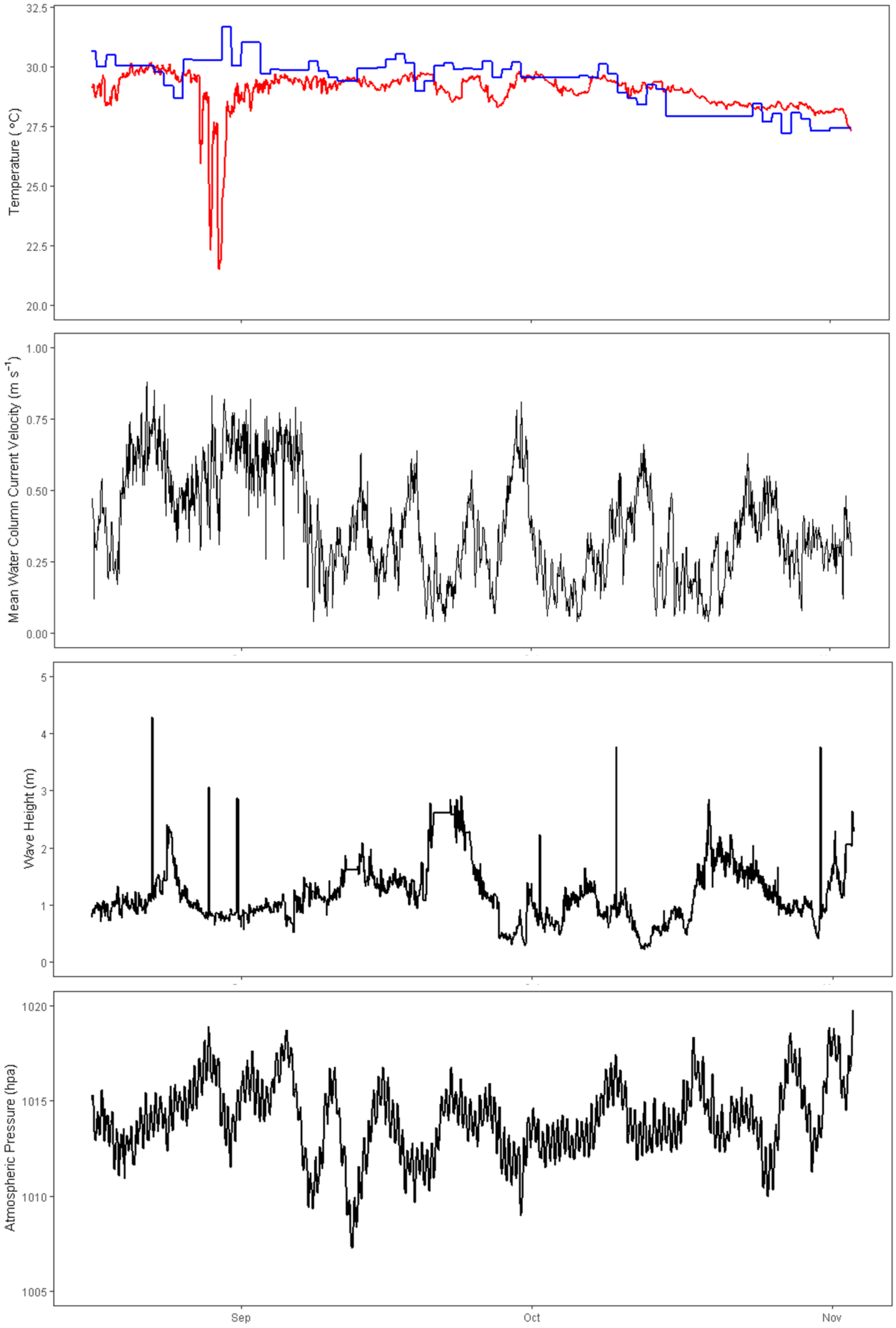

Figure 2 - Overview of environmental data time series through the study period.

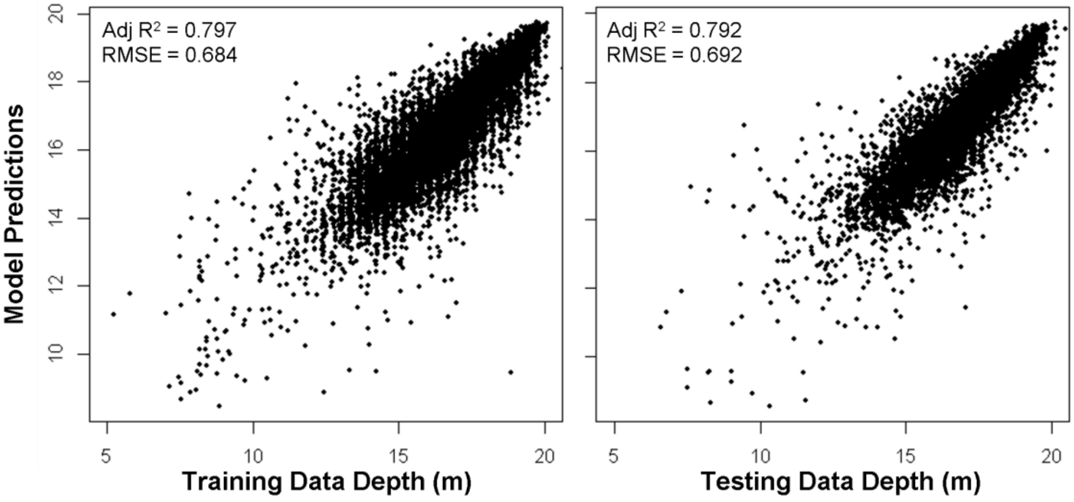

Figure 3 - Model predictions from training data (left) and testing data (right) used in random forest regression. Training data were generated by randomly sampling 70% of the samples from the full dataset (without replacement). The remaining 30% of the data were held-out for testing. Random forests consisted of 500 trees, and four predictors were randomly selected at each node from an array of 13 possible predictors. After training the model, held-out data were passed through the same 500 trees to generate new predictions. Striations along the x axis (left panel) are associated with tag accuracy limitations rather than an artifact of data processing and analysis.

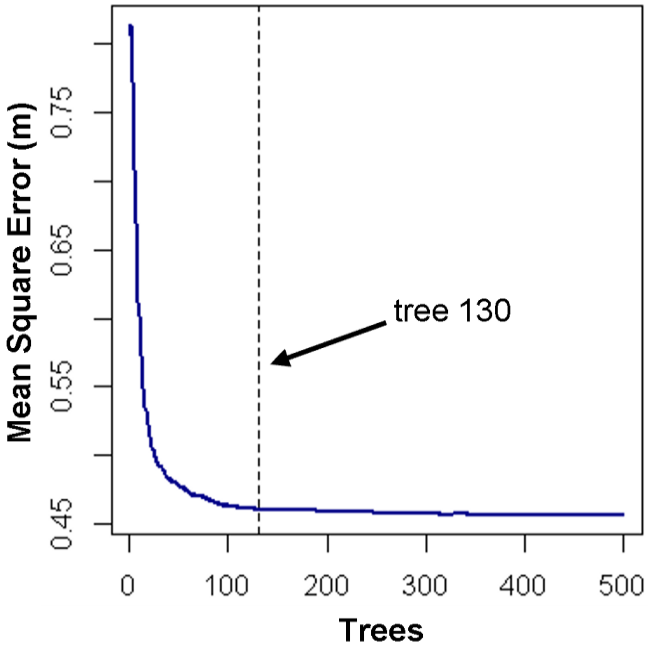

Figure 4 - Results from random forest regression indicate that mean square error reduction, a metric used to qualify overall model performance, reached an asymptote at approximately 130 trees. Beyond which no further improvements in the collective model were observed, however all 500 trees were used to evaluate model performance.

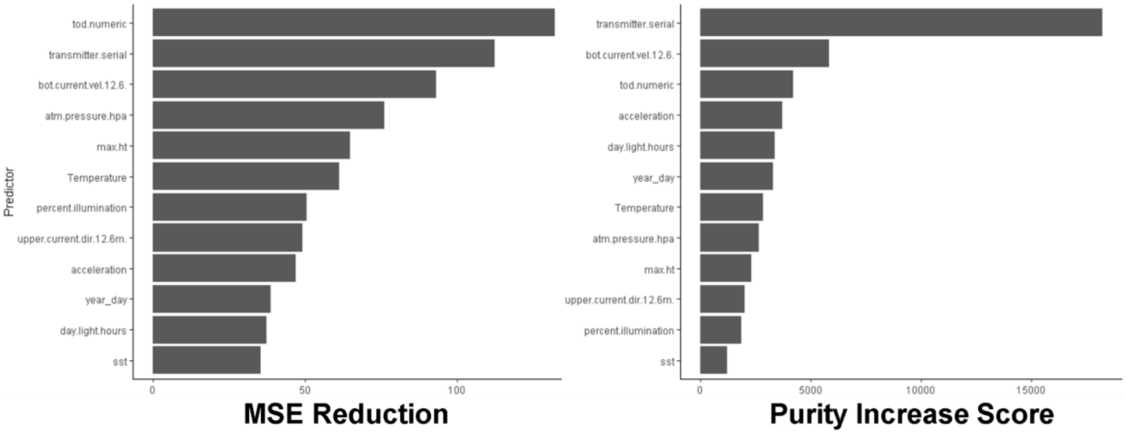

Figure 5 - Ranking of predictor variables used in random forest based on their contribution to mean square error reduction (left), and node purity increase (right). Purity corresponds to the total reduction in residual sum of squares after including a random variable in regression trees. Note that predictors rank differently with respect to error reduction and improvements in node purity, but the top three variables are consistent between both measures of variable importance.

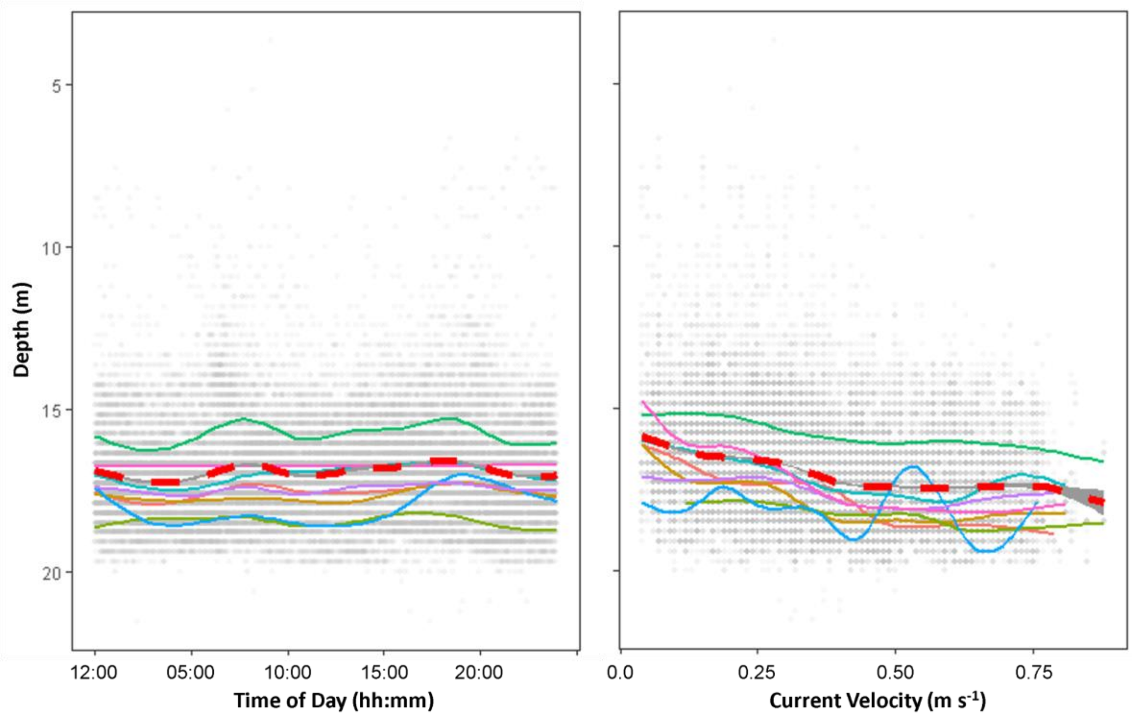

Figure 6 - Partial plots from GAMM representing the trend in goliath grouper position by time of day (left) and based on mid-water current velocity (right). Semi-transparent circles represent raw data, and are provided to illustrate variability in behavior. The level of transparency is relative to the number of data points at that given depth. Solid lines represent response of individual tagged GG, and the red dashed line denotes the mean GG position by time and with increasing current velocity. Oscillations over a 24 hr period were generally low magnitude and variable with peaks occurring late at night and during the crepuscular periods. Increased current velocity produced a downward trend in position towards the sea bottom, likely associated with GG moving into shelter in the lee of the current. Note the high degree of variability between individual GG.

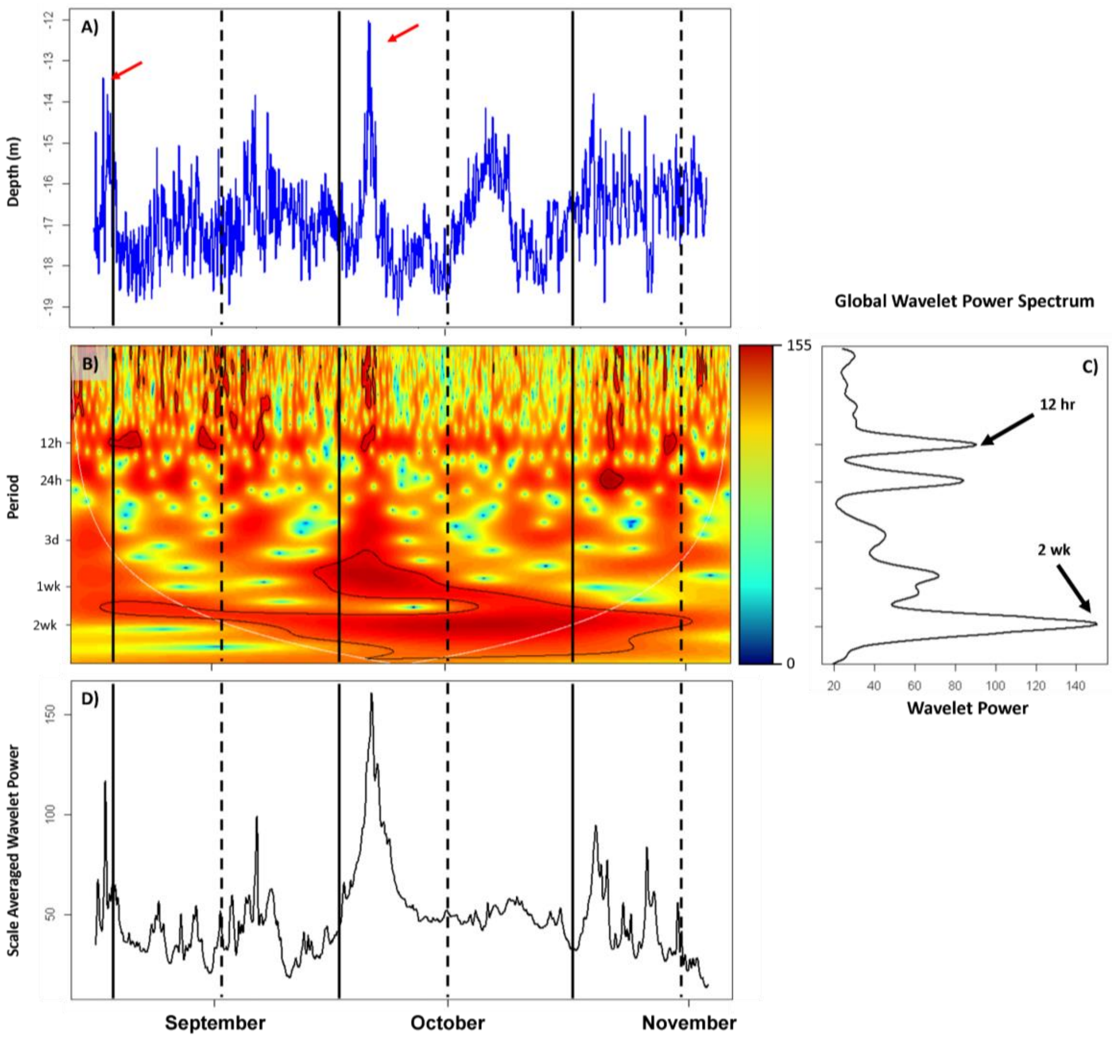

Figure 7 - A) The mean position of tagged goliath grouper in hourly bins through the duration of the study. Red arrows correspond to two potential spawning events occurring near the peak new moon. B) Continuous wavelet scalogram and the C) corresponding global wavelet power spectrum (horizontal integration of scalogram) reveal the presence of daily and diel peaks at 12 and 24 hr periods throughout the study, in addition to an event in mid-September (six days following the new moon). The thin black lines on the scalogram represent the 95% confidence boundary of a red-noise test, indicating that the period identified demonstrates significant signal above background "noise" (Torrence and Compo 1998). D) The scale averaged wavelet spectrum represents the vertically integrated power at each point through the time series, and illustrates the average power at each time step. Higher power indicates that variability is occurring at multiple discrete time scales (hours) at the corresponding point in the time series. Units of wavelet power are equivalent to variation in m^2 h^{-2}. Solid and dashed vertical black lines represent new and full moons, respectively. The white curved line in the scalogram denotes the "cone of influence", beyond which patterns become less reliable (Torrence and Compo 1998).

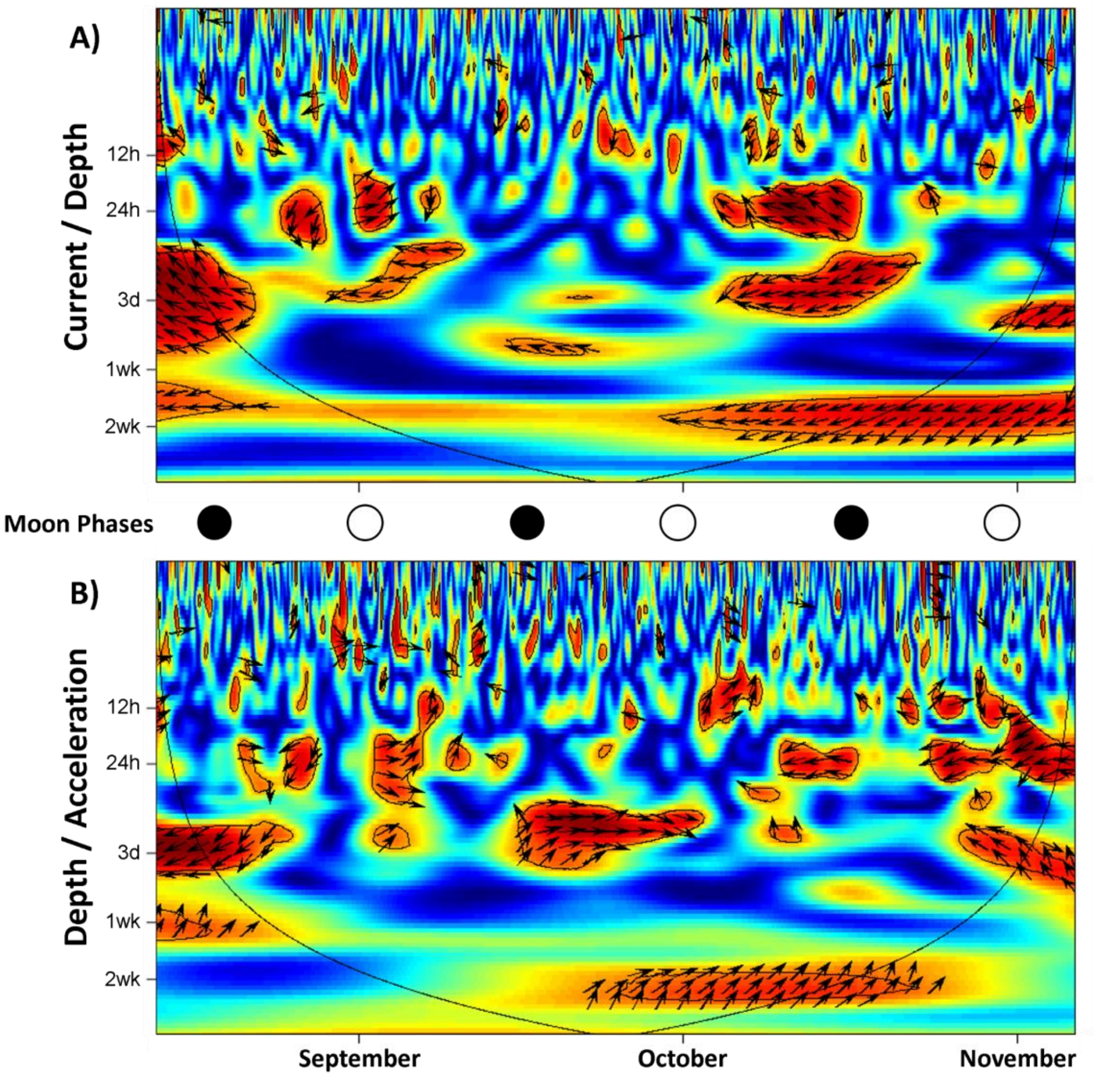

Figure 8 - Scalograms produced by cross-wavelet analysis illustrating the coherency between periods of variability in *current* and *depth* (A), and *depth* and *acceleration* (B). Warm colors indicate periods of stronger coherence. Thin black lines and arrows on scalograms denote areas of significance based on a red noise test and phase (i.e., the relationship) (Torrence and Compo 1998). Arrows pointing to the right indicate that patterns are in-phase, arrows pointing to the left indicate that variables are in anti-phase, those pointing upward indicate that changes in variable “2” precede changes in variable “1”, and arrows pointing downward indicate that changes in variable “1” precede changes in variable “2”. The cone of influence is denoted by a solid black curve in scalograms, beyond which patterns may be unreliable (Torrence and Compo 1998). Moon phases are denoted by open (full moon) and closed circles (new moon) positioned between panels. Note that the y axis is labeled by days, weeks and months rather than sequentially.

CHAPTER VI. CONCLUSIONS & FUTURE DIRECTIONS

CONCLUSIONS & FUTURE DIRECTIONS

Managing for spawning aggregations is difficult

Spawning habitats were identified as a federal management priority with the provision of the Essential Fish Habitat amendment to the Magnuson Stevens Act in 2002 (Federal Register vol. 67, no. 12, 2002) and subsequent reauthorization in 2006. As such, we might expect that fish spawning aggregations (FSAs) would become a foundational component of regional fisheries management plans, making research to locate, monitor, and protect FSAs ubiquitous with contemporary management activities. This is the case for a number of coastal regions, where information on spawning or population status is available from years of research, and aggregations are predictable in space or time. However, due to high degrees of variability in occurrence, socio political conflict, or unaligned priorities, many aggregations and species remain under protected or unaccounted for in regional management activities.

This was the case for Southeast Florida until recently, due in part to a lack of data describing the spatial and temporal dynamics of aggregating species in the region. Despite incredible research potential (i.e., numerous marine research groups in the region), regional literature describing the reproductive behaviors of commercially and recreationally important species were sparse. However, this is not to say that aggregations are absent from the region. Indeed, Chapter II clearly demonstrated that reports of aggregating species span the coast of Southeast Florida. Some of which have ceased to occur or declined to such a state that they are undetectable (i.e., gag grouper *Mycteroperca microlepis* and mutton snapper *Lutjanus analis*), and others remain intact but experience heavy fishing pressure with varying levels of protection and signs of decline (i.e., cubera snapper *L. cyanopterus*).

Unfortunately, the broad range in reports from various species across an expansive region may be partially responsible for the lack of management consideration. This is not to say the region is poorly managed but raises several important questions. Including conservation advocates (e.g., non-profit organizations, private citizens, or political lobbyists), that have the capacity to steer management priorities, researchers and managers have limited resources to apply to a finite number of issues. So, which species should be the focus of future research? Should depleted or extirpated FSAs be studied for signs of recovery? Are dollars best spent in FSA research, habitat restoration, water quality and infrastructure improvement, or elsewhere? There are no clear answers, as they are context dependent based on an extensive list of factors, but Chapter II represents a starting point to begin addressing these questions as they relate to FSAs, and hopefully will aid resource managers in identifying priority areas and species for future investigation.

Additionally, the value of local ecological knowledge from stakeholders, and their capacity to shoulder a great deal of the burden, cannot be overstated. With the explosion in media sharing potential over past years, we propose that citizen science collaborations could alleviate some of the difficulties associated with conducting wide-scale FSA monitoring programs. This approach has seen the protection of many FSAs world-wide and represents an opportunity to bring stakeholders into the management process. Not only will this provide access to untapped knowledge but may also serve to repair frayed relationships between managers and stakeholders that have worn through after years of perceived mismanagement of resources.

The power of remote sensing

This dissertation was originally conceived with the intention of focusing on regional FSA management through a combination of methods described in Chapter II. This was successful, but it became clear early on that there were uncharacterized areas in FSA research that may lend themselves to improving our overall understanding of FSA dynamics. Moreover, these topics have greater applicability than south Florida, and ultimately changed the trajectory of these combined works. Considering that resource allocation is a major concern in the realm of management and among fisheries researchers, it is logical that we might seek to apply methodologies that provide the most return on investment? Remote sensing, in its many forms, may be the answer to that question. It has become the backbone of many fisheries and FSA research programs around the world and has demonstrated its utility as a powerful research tool. Specifically, remote sensing techniques offer opportunities to describe FSA dynamics at a range of spatiotemporal scales, while simultaneously providing data to answer myriad other questions related to aggregating species, the surrounding environment, and other species captured in the scope of the applied technique.

Chapters III-V demonstrate this capacity to monitor FSAs at various scales, with a strong emphasis on the power of both active acoustics and acoustic telemetry. Both are powerful tools in the fisheries or FSA researcher’s toolkit, but the supporting data from acoustic doppler current profilers, stationary water quality sensor packages, satellite-borne sensor packages, meteorological observatories, and buoy-borne local marine weather stations can also provide environmental context to explain variations in aggregation dynamics with unparalleled temporal resolution. Moreover, many of these systems generate data at no cost to the researcher (i.e., the data are freely available), or their implementation only requires minimal resource investment associated with deployment and collection. This is where remote sensing excels and finds greater applicability in regional management applications; and ultimately, these data may be the key to explaining FSA dynamics and developing management strategies that afford them adequate protection. But what does FSA research tell us about the status of an entire stock, and how do we apply these data to stock assessment and management activities in a meaningful way?

Integrating FSA research into stock assessment and management activities

Stock assessment data are generally collected continuously (e.g., over a given year) and evaluated over time to characterize the status and trajectory of managed fish stocks over a broad geographic range within a "management unit", where a management unit is the geographic extent of a managed stock (e.g., Marine Recreational Intercept Program, MRIP). This is in juxtaposition to FSA research data, which are arguably, spatiotemporally discrete point counts within a larger management unit. This makes the integration of data from FSA research into traditional stock assessment challenging, as the findings may not be considered representative of a species throughout its managed region, and the metrics used to characterize FSAs are not easily translatable to fit within stock assessment models. However, FSAs are known to draw individuals from a much larger region (10's-100's of km), which has been discussed in this dissertation and demonstrated by countless acoustic telemetry and mark-recapture studies for a variety of species around the globe. This suggests that data describing patterns of FSA occurrence are informative of a much larger geographic area, well beyond the extent of the aggregation site(s) studied. As such, FSA data may in fact be valuable in stock assessment activities, and independently, as a tool to validate the predictions generated by stock assessment models. For example, an assessment that indicates a stock is stable could be validated by FSA monitoring efforts that identify stable aggregation sizes through time, at a range of sites within the management unit. Consider the broad application of an active acoustic survey program for GG aggregations as described in Chapter IV. Stable estimates of GG density or abundance over the coming years, at aggregations state-wide, would suggest that the opening of the limited-harvest fishery is sustainable and performing as expected by resource managers in the State of Florida. Alternatively, repeated observations of diminishing aggregation size over subsequent years could indicate that management practices for the species are not entirely appropriate, and more stringent protections may be required.

Beyond their application as a validation tool, the directed use of research dollars focused on FSAs has also been demonstrated to be an efficient approach to extend available resources and extract the most value per dollar out of survey efforts. Specifically, FSA research allows researchers to simultaneously capture a myriad of biological, demographic, and life-history characteristics that are all valuable in stock assessment model development. Behavioral data, such as the observations of courtship activity described in Chapter V could also be extended to fill in gaps related to the spawning frequency of individuals (helpful in estimating reproductive potential), sensitivity of aggregating species to environmental and anthropogenic stressors, and useful in identifying critical fish habitats that were previously unidentified and unmanaged (i.e., additional spawning aggregation sites). Indeed, these factors can all be accomplished far beyond the spatial and temporal scale described in this dissertation, by taking advantage of the ever-growing networks of telemetry arrays distributed throughout coastal areas and constantly improving sensor technology. Thus, even in cases where FSA research findings are not directly applicable to stock assessment modeling efforts specifically, the data collected therein have demonstratable value to fill in a range of data gaps and have invaluable potential to improve our understanding of regional fisheries management issues.

Concluding thoughts

Spawning aggregation research is difficult, and the management of these resources present many challenges. A range of factors are responsible for this, but there are many examples of successful FSA research and management that have been described in the literature. However, answers are not only contained within the literature and reports generated by FSA researchers but held by stakeholders that have passed on local ecological knowledge for decades. Integrating their perspective into the scientific and management process is the best way forward. Remote sensing also provides many opportunities to develop a comprehensive understanding of FSAs, while simultaneously describing regional ecosystem dynamics. Their utility has been demonstrated for a wide range of fisheries issues, and technological advancements will ensure that they continue to improve in their ability to answer novel questions at broad spatiotemporal scales. These works are intended to demonstrate these concepts, and we hope that the findings and methods presented here lend themselves to advancing the field of integrative FSA research, can be used to improve and validate fisheries management activities, and find wider application to improve our understanding of a broad range of topics that are of significant conservation interest.

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